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Investigating the Mechanisms Behind Moth Declines: Plants, Land-use and Climate

Dan Blumgart

August 2020

A thesis submitted to Lancaster University in fulfilment of the requirements for the degree of Doctor of Philosophy

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Declaration and funding statement

I declare that the work presented in this thesis is my own and has not been submitted elsewhere for the award of a degree of Doctor of Philosophy. The illustrations at the beginning of each chapter are also my own work.

This work was funded by the Natural Environment Research Council (NERC) through the Envision Doctoral Training Program awarded to Lancaster University and Rothamsted Research.

Dan Blumgart

22nd August 2020

Acknowledgements

Thanks go firstly to James Bell, Rosa Menendez and Marc Botham, my three supervisors. Thanks to James, for his encouragement and enthusiasm, and all the hours spent with me going through my work. Thank to Rosa for being so quick and thorough with corrections and feedback, and thanks to Marc for pushing me to think more deeply about the ways of moths. Thanks to everyone in the Rothamsted Insect Survey team, especially to Chris Shortall for answering my endless questions about the database and to Mike Hall for all the woodwork he did for me, as well as all the advice on everything DIY-related. Thanks to Butterfly Conservation for support and to the Centre for Ecology and Hydrology for hosting me several times and arranging my stay at Hillesden Farm. Also, thanks to the Ecological Community Trust for funding the purchase of the grass and wildflower seed used in my field trials. Thanks to Paul Compton for his help with designing and making 25 LED battery-powered moth-traps. I don't know what I would've done without his electronics knowledge. Thanks to Todd Jenkins and Alex Dye for their loyal assistance with the night-time fieldwork. There aren't many people who would enjoy, or even tolerate, wandering along the edges of fields catching moths deep into the night. Despite the fatigue, I enjoyed our deep chats and the excitement of finding something that wasn't yet another *Agriphilla straminella*! Thanks also to my temporary field assistants Dion, Kelly, Meg, Sarah, Cait and Mum. Thanks especially to Mum – I have never seen anyone so excited about catching a moth in a net. Thanks to the farm team, especially Chris Mackay, for sowing and maintaining my field margins. Thanks to Jamie Orpwood who let me camp out at Hillesden Farm during fieldwork in my first field season.

Thanks to Suzanne Clark for all the statistics consultations and for helping me design the randomised blocked field trial. Thanks also to Kirsty Hassall for help with my idiosyncratic stats problems. Thanks to Donna Fellowes for her flawless running of the postgrad system at Rothamsted. Thanks to Colin Harrower for teaching me how to up my game in R and saving me countless hours of labour by showing me how to write loops. Thank you to all the volunteers of the RIS light-trap network, with special thanks to Paul Verrier for maintaining the database. Without all of you, my project could never have existed. Thanks to Colin Plant for teaching me how to dissect moths and mount their genitals. Also thank you to my housemates, Matt and Cassie, for tolerating my constant occupation of the kitchen table

while I dissected my endless quantities of moth genitals. Thanks again to Mum for her proofreading services. Thanks to my friend, colleague, and PhD predecessor Aislinn Pearson for her bountiful advice about everything PhD-related. If it weren’t for her, I’d still be using R and Word like an amateur. Finally, thanks to my family: Mum, Dad, Julie, and Cait, for supporting me in my decision to become a doctor of moths.

Abstract

Moth populations have declined across large areas of north-western Europe since the mid-20th century, mirroring similar declines in other insect groups. The mechanisms behind these declines are likely manifold, but it is believed that agricultural intensification is a key factor. There were two aims of this thesis: (1) to elucidate the mechanisms behind moth decline in the UK, and (2) to determine ways in which farmland habitats could be improved for moths. Counter to expectations, between 1968 and 2016, the declines in total moth abundance were least severe in the most agriculturally intensive areas and were most severe in semi-natural habitats, as well as in urban environments. Species richness, while remaining stable at the national level, declined in only one habitat type: broadleaf woodland. No evidence was found to support the hypotheses that habitat loss, shading of the understory by canopy-closure, or overgrazing by deer had driven these declines within broadleaf woodland. Evidence was found that warm winters negatively impacted moth abundance, but this effect was consistent across all habitats. Although declines were least severe in improved grassland and arable land, the declines in total abundance were significant and ongoing, despite widespread and increasing adoption of agri-environment schemes (AES) since the early 1990s. In this thesis, the role of nectar resources and larval hostplants were explored within AES field margins on arable land, with the aim of determining how these small areas of habitat could be best managed to enhance moth abundance and diversity. It was found that the diversity of moths was greatly increased, and abundance moderately so, when margins were sown with a wide range of wildflowers and grasses, in comparison to only grasses. The evidence suggested that this was due primarily to the provision of larval hostplants, with nectar resources playing a secondary role. Overall, this thesis demonstrates that, in order to improve the environment for moths, AES wildflower margins should be encouraged over and above plain grass margins. This thesis also demonstrates that while agricultural intensification is likely responsible for some of the observed declines in moths, there are other mechanisms, as yet unknown, at work in both semi-natural habitats and urban areas.

Contents

List of acronyms used

AES – Agri-environment Scheme

AICc – Akaike Information Criterion (corrected for small sample size)

ALAN – Artificial Light at Night

CC – Cross Compliance

CEH – Centre for Ecology and Hydrology

CI – Confidence interval

CMR – Capture-mark-recapture

DEFRA – Department for Environment, Food and Rural Affairs

DF – Degrees of freedom

ELM – Environmental Land Management

ELS – Entry Level Stewardship

GAI – Generalised Abundance Index

GAMM – Generalized Additive Mixed Model

GAM – Generalized Additive Model

GLMM – Generalised Linear Mixed Model

HLS – Higher Level Stewardship

IUCN – International Union for Conservation of Nature

JNCC – Joint Nature Conservation Committee

LCM – Land Cover Map

LED – Light emitting diode

LM – Linear Model

LMM – Linear Mixed Model

LRT – Likelihood Ratio Test

MGLM – Multivariate Generalized Linear Model

ML – Maximum likelihood

MV – Mercury vapour

NA – Not applicable

NMRS – National Moth Recording Scheme

NMDS – Non-metric Multidimensional Scaling

REML – Restricted maximum likelihood

RIS – Rothamsted Insect Survey

SE – Standard Error

UK – United Kingdom

UKBMS – United Kingdom Butterfly Recording Scheme

UV – Ultraviolet

W - Watts

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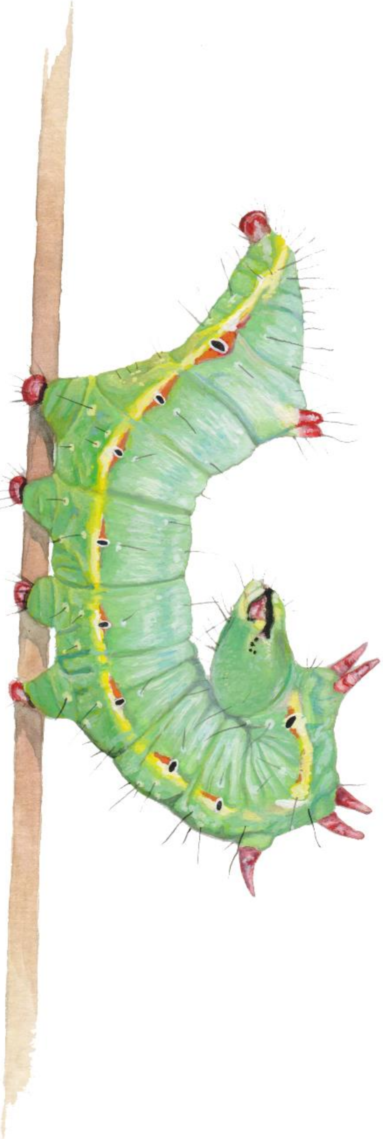
Chapter 1



Introduction and literature review

Chapter 1. Introduction and literature review

In the UK, the total abundance of moths has been in decline since the 1960s (Conrad et al., 2004, Conrad et al., 2006, Fox et al., 2013) and levels of species occupancy have also been retracting (Fox et al., 2014). Before this time, standardised longitudinal sampling of moth populations are known to be rare, but the few data that do exist suggest that moth populations were already much reduced when compared to the 1930s and 40s (Taylor, 1973, Woiwod and Gould, 2008). Although the overall moth trend is one of decline in the UK, there is regional variation, with the strongest declines occurring in the south and especially the south-east (Conrad et al., 2004). The trends of individual species vary widely, with some remaining stable over time and a minority increasing rapidly (Boyes et al., 2019) (section 1.2.1). These declines mirror similar moth trends reported in other north-western European countries (Franzén and Johannesson, 2007, Groenendijk and Ellis, 2011, Mattila et al., 2006, Mattila et al., 2008) and are part of a wider decline in insect abundance and diversity that has been recorded in Europe over the last half-century (Powney et al., 2019, Thomas et al., 2004, Wenzel et al., 2006).

The Lepidoptera, of which moths constitute the overwhelming majority, are one of the most species-rich groups of insects with roughly 2500 species recorded in the UK (Waring and Townsend, 2017). Moths have essential ecosystem roles as primary consumers, prey-items and pollinators. As prey, the decline in moth populations is projected to affect higher trophic levels such as birds and bats (Visser et al., 2006) whilst as pollinators moth declines are expected to affect the reproductive capability of primary producers (Pettersson, 1991, Young, 2002).

In this chapter, the evidence for moth declines both within the UK (section 1.2.1) and in other countries in north-west Europe (section 1.2.2) is reviewed and understood in the context of insect declines globally over the same period (section 1.1). Importantly, the mechanisms driving these declines are also assessed (section 1.3) alongside potential practical mitigation strategies (section 1.4).

1.1 Overview of insect declines

The abundance and diversity of insects globally has been in decline since long before standardised monitoring programs began (Leather, 2017). However, the evidence for declines prior to the mid-20th century is mostly anecdotal or logically assumed due to the habitat loss that has accompanied agricultural expansion around the globe. The concept of an 'insect Armageddon' made headlines recently after the release of an influential yet methodologically flawed review paper on global insect declines (Sánchez-Bayo and Wyckhuys, 2019) which claimed that 40% of the world's insect species are 'threatened with extinction' over the next few decades. Although the scientific community was highly critical of this paper due to its poor methodology and alarmist language (Komonen et al., 2019, Mupepele et al., 2019, Simmons et al., 2019, Thomas et al., 2019, Wagner, 2019), the consensus was that whilst global insect declines are undeniably real we do not have sufficient data to make estimates about the scale of the declines globally. Notably, long-term, continuous records of insect abundance and distribution are very rare in much of the world and are essentially absent in the tropics where the majority of insect diversity is found. In this section, the evidence for insect decline across the world is reviewed and then later a focus on moths in particular is presented (section 1.2).

1.1.1 Insect declines in the UK

The UK is fortunate in having a high density of entomologists with a long history of collection and recording of insects. Although species extinctions at the local and national level have been recorded since well before the Second World War (Ollerton et al., 2014, Thomas and Morris, 1994), it was not until the 1960s and 70s that standardised monitoring programs began which allowed for the creation of annual abundance indices and hence estimates of changes in abundance. Notable examples include the Rothamsted Insect Survey (RIS), the UK Butterfly Monitoring Scheme (UKBMS) and latterly the Environmental Change Network (ECN), Anglers' Riverfly Monitoring Initiative (ARMI), Bumblebee Conservation Trust's BeeWalks and the UK Pollinator Monitoring Scheme (PoMS).

Declines in butterflies in the post-war period in the UK are well-documented (Brereton et al., 2011) and declines in butterflies are shown to be more severe than for comparable trends in birds and vascular plants (Thomas et al., 2004). Of 33 butterfly species studied between 1976 and 2014, 61% decreased in abundance and 70% of species decreased in range (Fox et al., 2015). These changes in distribution and abundance were also noted by Warren et al. (2001) who provided clear evidence that sedentary specialist species had declined the most while mobile generalist species had tended to remain stable or increase.

Other insect groups have also experienced decline in recent decades. Over a 15-year period, three-quarters of carabid species declined in abundance (Brooks et al., 2012) and comparison of pre- and post-1980 records of bees and hoverflies in the UK found a decline in bees, although there was no clear trend in hoverflies (Biesmeijer et al., 2006). Another study on bees and hoverflies for years 1980 – 2013 found declines in 33% of species with no clear differences between bees and hoverflies (Powney et al., 2019). Declines in arthropod abundance were also reported from a cereal farm in Sussex surveyed from 1970 – 2011 (Ewald et al., 2015). Analysis of aerial insect biomass from four suction-trap sites in southern England between 1973 to 2002 showed a significant decline at only one site, Hereford, with no overall trend at the other three sites (Shortall et al., 2009). More detailed analysis of the Hereford site revealed that the bulk of this decline was driven by a single species of large-bodied fly (*Dilophus febrilis).* The reasons for the decline of this fly in this location are unclear.

1.1.2 Global insect declines

Insect declines are likely a proxy for moth declines and the majority of long-term records of insect abundance and distribution are to be found in western Europe and to a lesser extent in North America. The development of agriculture in post-war North America shares a similar timeline to that of western Europe, so changes in insect populations since this time are likely to share similar drivers. Butterflies are the most extensively recorded insect taxa and declines in butterfly populations have been demonstrated in the United States (Forister et al., 2010, Swengel et al., 2011, Wepprich et al., 2019), the Mediterranean (Melero et al., 2016), Germany (Wenzel et al., 2006), Belgium (Maes and Van Dyck, 2001), the Netherlands (Van Dyck et al., 2009), Finland (Kotiaho et al., 2005) and Sweden (Franzén and Johannesson, 2007). A review of European butterflies found that 31% of Europe’s 576 species are in significant decline and 9% of these are threatened according to IUCN terminology (Van Swaay et al., 2010). Declines in less well-recorded insect taxa are also prevalent across Europe and North America, such as in carabid beetles (Desender and Turin, 1989), ladybirds

(Coccinellidae) (Harmon et al., 2006), dung beetles (Carpaneto et al., 2007, Lobo, 2001), saproxylic beetles (Nieto and Alexander, 2010), dragonflies (Kalkman, 2010) and grasshoppers, crickets and bush-crickets (Hochkirch et al., 2016). Insect declines have also been recorded in the Arctic (Loboda et al., 2018), demonstrating that the phenomenon is not limited to agricultural or human-dominated landscapes.

Bees are also known to be in decline in western Europe (Potts et al., 2010). Of the 407 species of bees recorded in the European Red List (Nieto et al., 2014), 150 of those had declining populations while only 13 were found to be increasing. Indeed, a large review of bumblebees and cuckoo bees in western and central Europe found widespread declines over the twentieth century with 80% of the 60 known taxa threatened in at least one of the countries studied (Kosior et al., 2007). Independent bee diversity and abundance analyses in the Netherlands (Biesmeijer et al., 2006), Sweden and Denmark (Dupont et al., 2011), Canada (Colla and Packer, 2008) and the United States (Gardner and Spivak, 2014, Koh et al., 2016) support this.

As well as declines in specific taxa, general declines in insect numbers and biomass have been reported across Europe. In Denmark, the number of insects killed on a car windscreen declined by 80% and 97% along two transects regularly sampled between 1997 and 2017, and these finding were corroborated by the trends of insects caught in sweep nets and sticky-traps and in the abundance of insectivorous birds at the same location (Møller, 2019). A study from Germany found a 75% decline in biomass over 27 years across 63 nature reserves in Germany (Hallmann et al., 2017). Although most of these sites were sampled only once, with a maximum time series of four years, the sites that were sampled multiple times showed trends consistent with the overall decline.

Tropical ecosystems contain the highest levels of insect abundance and diversity worldwide, but long-term monitoring of their populations is largely absent. However, studies that do exist, combined with anecdotal and indirect evidence, suggest that insect declines are also occurring in these regions (Janzen and Hallwachs, 2019). For example, Nemésio (2013) found that the abundance of forest-dependant orchid bees had declined by 50% when sites were re-sampled after a 12 year gap in a forest in Brazil. In Costa Rica, the abundance and species richness of bees declined in a forest from 1972 - 2004 (Frankie et al., 2009). A study that took place in a protected forest in Puerto Rico, reported declines in insect biomass of 75 – 98% (depending on the taxa and the methods used) between the years of 1976/77 - 2012/13, with parallel declines in insectivorous lizards of around 50% (Lister and Garcia, 2018). Although it should be noted that no insect biomass measurements were taken between the two end points of this study, making trend estimates unreliable (Didham et al., 2020, MacGregor et al., 2019b).

1.2 Evidence for moth population decline

1.2.1 UK trends

The most spatio-temporally extensive standardised moth monitoring project in the world is the UK's Rothamsted Insect Survey (RIS) light-trap network which has operated light-traps across the country every night since 1964 (Woiwod and Gould, 2008). Analysis of RIS data (Conrad et al., 2004, Conrad et al., 2006) showed that the overall abundance of macro-moths had declined by 31% between the years 1968 – 2002. Analysis of the trends of 337 common species by Conrad et al. (2004) showed that 54% of species had declined significantly with at least 10% decline per decade, and less than half as many species had significantly increased (22%). However, these trends were not uniform across the country. Declines in the south were more severe (overall decline of 44%) whereas overall moth abundance in the north was stable (non-significant increase of 5%). When the country was further subdivided into north, south-west and south-east, Conrad et al. (2004) demonstrated that the declines were more concentrated in the south-east. Trends were calculated for a subset of moths that were both abundant and widespread (219 species) and the proportion of moths found to be increasing was highest in the north (23% north, 9% south-west, 13% south-east); conversely the proportion with decreasing trends was highest in the south-east (33% north, 47% south-west, 65% south-east). Although the north had stable overall abundance trends, the proportion of species with significantly declining abundance trends was still greater than species that were shown to be increasing (i.e. 35% decreasing, 39% stable, 26% increasing). Subsequent analysis of this dataset has shown that the overall abundance of moths has continued to decline up to 2016 (Bell et al., 2020, Fox et al., 2013). A recent analysis of RIS moth data in Scotland showed that although abundance trends were stable up until 2002, recent declines have meant that the overall moth abundance fell by 20% over the years 1975–2014 (Dennis et al., 2019). Curiously, although the actual abundance of species had fallen, the data showed that the occupancy rate of moth species was growing larger over the same period. This implies that although the abundance of individual moths has declined, the geographical area which species occupy has increased, inferring some redistribution and range expansion. On a species-by-species basis, the trends in abundance and in occupancy were significantly positively correlated, but only very weakly so, suggesting that occupancy trends are not a strong predictor of changes in abundance

Similar trends in British moth occupancy rates were demonstrated by Fox et al. (2014) using a different dataset. In this study, occupancy data for 673 species of macro-moth were extracted from the National Moth Recording Scheme (NMRS) for the years 1970-2010. The NMRS dataset consists of records submitted by volunteers including county moth recorders, amateur entomologists and members of the public. The overall trends in moth occupancy were also very similar; for example, in the NMRS study 62% of species were found to have negative occupancy trends (compared to 66% in the RIS study) and 38% had positive trends (compared to 34% in the RIS study). In the NMRS study, 39% of species showed significant declines and 24% significantly increased - the equivalent figures in the RIS study are 54% increase and 22% decrease. However, a reanalysis in Randle (2019) of moth distribution in the UK showed that occupancy trends were stable overall. Whether this is due to an amelioration of the situation, or differences in analytical methods is unknown (Randle, 2019). MacGregor et al. (2019b) showed that, despite declines in abundance, moth biomass had increased from 1968 – 2017. This surprising result implies that although moths have become less abundant, their community composition has become more dominated by larger-bodied moths. The reasons behind this trend and its implications for ecosystem functioning require further investigation.

1.2.2 European trends

An overall decline in moth abundance and occupancy in agricultural landscapes in the 20th century has been recorded across several countries in north-western Europe: Finland (Mattila et al., 2006, Mattila et al., 2008), Sweden (Franzén and Johannesson, 2007), Germany (Habel et al., 2019b) and the Netherlands (Groenendijk and Ellis, 2011). The UK trends reported by Conrad et al. (2004, 2006) and Fox et al. (2014) are mirrored by a similar study in the Netherlands. Groenendijk and Ellis (2011) found that distributions of 733 species of macro-moth had declined by 37% between the years of 1980 and 2009. The authors used data from the online database Noctua, which is similar in structure to the NMRS. Overall declines in the Netherlands were calculated as 37%, compared to 31% in the RIS study by Conrad et al. (2006). In the Netherlands, 71% of moths had negative population trends compared to 66% in the RIS study, and, 29% had positive trends, compared to 34% in the RIS study. In the Netherlands, 6% of species were found to be strongly declining and 2% were strongly increasing. While not absolutely comparable due to difference in methods used, the proportion of strongly increasing to strongly decreasing species in Great Britain is similar; 1.8% of species are strongly increasing (i.e. >50% increase per 5 years) and 4.5% strongly decreasing (i.e. >50% decrease per 10 years). There were also similarities with regard to trait predictors of decline: those species that overwintered as eggs (69 species) declined most severely whereas those overwintering as adults (8 species) tended to be stable or increasing.

Studies by Mattila et al. (2006) and Mattila et al. (2008) in Finland showed significant overall declines in distribution for 590 species of noctuid and geometrid moths. These results were obtained using the Atlas of Finnish Macrolepidoptera (Huldén et al., 2000) by comparing records of the presence of species within 10 x 10 km grid squares between two time periods: pre-1988 compared to the period 1988-1997. Mattila et al. (2006,2008) found that species that were listed as threatened or near-threatened by IUCN categories had declined in distribution more than those non-threatened species. Specifically, threatened and near-threatened moths had decreased in distribution by 45.7% and 41.3% respectively, whereas non-threatened moths had decreased by 18.5% and 18.1%. For geometrids the tendency for decline was significantly predicted by traits related to larval specificity, overwintering stage and length of flight period. Geometrids most likely to decline were those with monophagous larvae, those that overwintered as larvae or pupae, and those with shorter flight-periods. For noctuids, the only significant predictor was overwintering stage; again, with those overwintering as larvae or pupae declining most.

Presence/absence data is a problematic way to estimate population change as it cannot fully account for the abundance of individuals or for sampling effort, which are often concentrated around centres of human population (Dennis et al., 1999). However, it is unlikely that the declines measured by Mattila et al. are an artefact of the methods used for two reasons: firstly, there were more records from the later period than the earlier (i.e, sampling effort increased); secondly, in 1993 a nation-wide monitoring scheme was started, consisting of almost 100 light traps distributed evenly across Finland (Väisänen, 1993). Records between 1988 and 1997 were therefore more numerous and possibly more widely distributed than records pre-1988, so one would expect a risk of falsely measuring increases in species distributions. This suggests that the declines measured are representative of an actual phenomenon rather than an artefact of the methods used and are potentially a conservative estimate of declines.

A study at Kullaberg Nature Reserve in southern Sweden revealed that 27% (159 out of 597) of macro-lepidopteran species present in the 1950s were no longer present in 2004, compared to 22 species which had colonised the area (Franzén and Johannesson, 2007). During this period, the Kullaberg reserve had lost traditional meadows to improved grassland and golf courses, wetland areas had been colonised by forest and arable fields had undergone typical intensification. Species traits associated with disappearance were very similar to those outlined by Mattila et al. (2006,2008): high larval specificity, short flight-period and those that are categorised as threatened by the IUCN. Additionally, species associated with non-forest habitats were found to be more at risk of extinction at Kullaberg. By using distribution change data obtained from the Atlas of Finnish Macrolepidoptera (Huldén et al., 2000), the authors showed that: i) those species extinct from Kullaberg had also declined in Finland, ii) those that had colonised Kullaberg had increased in Finland and, iii) those still present in Kullaberg were more likely to be stable in Finland.

Not all moth trends in Europe are negative. A study from remote northern Finland found that more species had increased than had decreased (Hunter et al., 2014). This region has had little direct human influence over the time period, lending evidence to the hypothesis that declines are due to direct human habitat modification and destruction. Furthermore, moth species richness increased in Finland over a twenty-year period, especially in the north (Antão et al., 2020), although overall abundance declined over this period.

1.3 Drivers of moth population change

The possible reasons behind these population changes are reviewed in Fox (2013) where they are grouped into five broad categories: habitat loss, chemical pollution, light pollution, climate change and invasive species. A sixth category, over-collection of specimens, is implicated in a few cases in some very rare and localised species but the effect in general is considered to be negligible. Other potential regulators of moth populations such as changes in predation and pathogen pressure are not assessed in this review. Fox points mainly to habitat loss as the key driver of decline, including loss of habitat due to agricultural intensification (e.g., hedge removal and change in field boundaries, conversion of flower-rich hay meadows to improved grassland and wetland drainage), habitat loss through urban development, and habitat loss resulting from changes in land management practises, for example, the loss of young regrowth habitats in woodlands due to the cessation of coppicing. In this section, the potential drivers of decline, mostly following the categorisation structure of Fox (2013), are discussed and current evidence related to each driver is presented.

1.3.1 Habitat loss

Habitat loss is widely recognised as a major driver of biodiversity loss worldwide (Dirzo and Raven, 2003). Currently, the majority of habitat loss is occurring in the tropical eco-regions where species-rich habitats are undergoing conversion to agriculture (Chaudhary et al., 2016, Newbold et al., 2014) or are subject to wildfires caused by longer periods of drought (Bush et al., 2008, Taufik et al., 2017). Current habitat loss in Europe is qualitatively different to that of the tropics as much of the European landscape was converted to low intensity agriculture during the late Holocene (Ellis et al., 2013) and the UK has been a mostly sustainable agricultural landscape for at least the last 1000 years (Fyfe et al., 2015). In the UK, habitat loss in the post-war period was characterised by an increase in agricultural intensity that saw the loss of semi-natural habitats to widescale mechanisation and changes in woodland management to more commercial forestry.

1.3.1.1 Habitat fragmentation

In addition to habitat loss, the fragmentation of habitats detrimentally affects species abundance and diversity because of isolation and edge effects (Fahrig, 2003). Species with low dispersal ability and high habitat specificity are more vulnerable to isolation and intermittent local extinction that in turn leads to population decline (Saccheri et al., 1998a).

It has been demonstrated that smaller, more isolated habitat patches tend to have lower species richness of moths (Fuentes-Montemayor et al., 2012, Merckx et al., 2012a, Usher and Keiller, 1998) and tend to be dominated by highly mobile generalist species (Öckinger et al., 2010). The effect of habitat isolation at a small scale has been demonstrated for the November moth (*Epirrita dilutata*) where populations from two woodlands separated by 1400m were found to be genetically distinct (Wynne et al., 2003). In contrast, populations from three woodlands in close proximity (separated by maximum 620m) that were linked by hedgerows were found to be genetically indistinct and thus more closely related.

Although habitat fragmentation may lead to reduced species richness at small scales, there is no direct evidence that fragmentation is linked to the decline in moths over the last half-century. A larger wingspan is typically associated with higher dispersal ability (Nieminen et al., 1999, Slade et al., 2013) and this trait is considered a valid proxy for dispersal ability in Lepidoptera (Sekar, 2012). If habitat fragmentation were a key driver of decline, we would expect to see declines disproportionately affecting moths with low dispersal ability and hence small wingspans, but the evidence for this is inconclusive. MacGregor et al. (2019b) found that moth biomass in the UK had increased over the same period in which moth abundance had declined (1969 – 2017). As biomass was estimated as a function of wingspan (Kinsella et al., 2019), this suggests that average wingspan has increased over this time. In contrast, Coulthard et al. (2019) found that large wingspan was the best predictor of moth population decline at the species level in the UK, although this finding may be highly influenced by a subset of small moths with strong population increases. In Finland and Sweden, no statistical relationship between wingspan and moth declines or extinction was found (Franzén and Johannesson, 2007, Mattila et al., 2006). Although mobility and dispersive behaviour is not well-known for most moth species, a series of capture-mark-recapture studies suggests that moths in general are relatively mobile at the farm-scale (Merckx et al., 2009a, Merckx et al., 2010b, Merckx et al., 2010a, Slade et al., 2013). Indeed, a study on a small rocky island off of Sweden captured 51 species that would have had to travel 8 km to reach that island from the nearest suitable habitat (Betzholtz and Franzén, 2011), demonstrating high mobility in at least a subset of moths. Merckx et al. (2019) found that most landscape-level species richness was driven by the amount of habitat within a landscape rather than the isolation or size of individual habitat patches per se. In practice, habitat loss and habitat fragmentation often occur together, and this lack of independence creates difficulties when attempting to attribute these potential drivers of decline separately. Overall, the studies suggest that habitat fragmentation may be an exacerbating factor in addition to habitat loss, but evidence for fragmentation as a driver of decline in its own right is weak.

1.3.1.2 Agricultural intensification

In 20th century UK agriculture, intensification has impacted both physically (e.g., loss of natural vegetation and plant species diversity) and chemically (e.g., increased use of pesticides, herbicides and artificial fertilisers) on the landscape (Robinson and Sutherland, 2002), but their individual effects are confounded (Chamberlain et al., 2000). For example, an increase in artificial fertilisers typically leads to a reduction in plant diversity (Plantureux et al., 2005). Although it is generally not possible to disentangle the relative impacts of environmental changes in retrospect, we can look at how manipulating the farmland environment affects moth populations either over time (a before-and-after study) or over space (treatments compared to a control), or a combination of the two, and infer the effect of various landscape changes from these studies. However, it must be acknowledged that standardised ecological monitoring schemes pre-1960s are very rare (Woiwod and Gould, 2008) and therefore the opportunity for longitudinal analyses are somewhat limited. For clarity, evidence derived from experiments manipulating the physical and chemical environment over time and/or space is presented in section 1.4 (Conservation measures). In the current section (1.3), all other relevant evidence examining the link between agricultural intensification and moth decline is presented.

Agricultural intensification has been identified as a key driver of decline in butterflies (Asher et al., 2001, Habel et al., 2019c, Maes and Van Dyck, 2001, Nilsson et al., 2013) and other insects (Seibold et al., 2019), and it is likely to have influenced moth populations (Fox, 2006). A study in south-west Germany found that the relative abundance of butterfly and burnet moth species had been in decline since records began in 1750, but the most severe decline only happened after the mid-1950s, when agricultural intensification began (Habel et al., 2019b). The effects of agricultural expansion on moths can be traced back before the Green Revolution of the 1950s and 60s. For example, the draining of wetlands for agriculture during the mid-19th century was demonstrably responsible for the extinction of a number of wetland specialist moths in the UK such as the Reed Tussock (*Laelia coenosa*) and the Many-lined Moth (*Costaconvexa polygrammata*) (Ford, 1955). The near total loss of unimproved grasslands between the 1930s and 1980s (Ridding et al., 2015) is almost certainly cause of local extinctions of habitat specialist moths such as the Straw Belle (*Aspitates gilvaria*) and the Black-veined Moth (*Siona lineata*) (Fox et al., 2010).

If agricultural intensification was the main cause of moth decline, it would be expected that moth populations in non-agricultural environments should be stable or potentially increasing due to a warming climate which allows for range expansions of moths and additional generations within one season (Macgregor et al., 2019a). Indeed, there have been several studies showing this. Trends in moth populations between 1978 and 2009 at a site in Finnish Lapland (250km north of the Arctic Circle) showed that 90% of species were either stable (57%) or increasing (33%), over which time the annual average temperature rose by 1.96˚C (Hunter et al., 2014). There were 11 traps at this site and the habitat consisted largely of mixed forest with no human-induced habitat alteration over this time. Similarly, a RIS site in a Scottish ancient broadleaf woodland reported significant increases in abundance (62% increase) and diversity (Fisher's α, increase of 19%) between the years of 1968 and 2003 (Salama et al., 2007), although the cause might actually be due to colonisation by moths moving northward that were tracking a climate envelope.

A long-term study of moth populations in Hungary showed that moth abundance remained stable at 7 woodland sites that experienced little or no human-induced habitat alteration between 1962 and 2009 (Valtonen et al., 2017), although species richness did fall. Stable or increasing moth trends within woodland habitats is not universal. Woiwod and Gould (2008) showed that overall moth abundance in a mature woodland in southern England declined by 49% on a log-linear scale between the 1960s and the early 2000s, mirroring changes in the wider UK moth population. However, as this woodland was only 1.7 ha in size and surrounded by intensive farmland and suburban development, it is possible that the changes in the surrounding land are responsible for the measured drop in abundance.

Analysis of RIS data by Conrad et al. (2006, 2006) revealed that moths species found mainly in pasture, arable and downland habitats were more likely to decline than those that specialised in woodland habitats. It must be also acknowledged that moths specific to coastal, heathland and upland habitats were just as likely to decline as agricultural specialists.

Furthermore, when population trends were assessed by larval food preference, it was shown that species feeding on shrubs (n = 38 species), grasses (n = 20) and low-growing plants (n = 71) declined the most compared to those that fed on deciduous trees (n = 68) which were largely stable, or conifers (n = 10) or lichen (n = 13) which tended to increase. Merckx et al. (2012b) found that the proportion of arable land within an 800m radius of the sample site had a significant negative effect on the abundance of nationally declining moth species (150 species) but had a non-significant slight positive effect on species that are nationally increasing (76 species). These findings support the idea that most species of moth that are declining are doing so because of intensification of agricultural land; the species that are nationally increasing are more resilient or have adapted to intensification.

Increased levels of grazing through increases in livestock density represents another aspect of agricultural intensification. The abundance and diversity of invertebrate taxa typically declines under intensive grazing (Dennis et al., 2008, Kruess and Tscharntke, 2002), but the effects vary widely between taxa, with some species preferring an intermediate sward or a highly specific grazing regime – e.g., the Large Blue butterfly (*Phengaris arion*) (Thomas et al., 2009). Experiments regarding the effects of grazing regimes on moths are examined in section 1.4.3.

A decrease in nectar resources in the wider landscape has been suggested as an additional driver of decline for nectivorous species (Baude et al., 2016) and a link has been demonstrated between butterfly declines and declines in key nectar plants in The Netherlands (Wallisdevries et al., 2012). Many species of moth feed on nectar during their adult life, as well as other sugar sources such as over-ripe fruit and honeydew (Waring and Townsend, 2017), but no connection has been made between loss of nectar resources and moth decline to date.

1.3.1.3 Urban development

Development of the built environment is often seen as having a negative impact on wildlife, particularly when planning intent includes changes to semi-natural habitats, greenbelt or even brownfield sites, such as the Thames Gateway and West Thurrock Marshes. Development often removes and/or fragments existing habitat and, typically, replaces it with impervious surfaces that support only simple communities. Urbanisation has been associated with moth declines (Taylor et al., 1978) and it has been responsible for the local extinctions of highly-localised species such as the Sandhill Rustic at a site in Lancashire (Ford, 1955). As well as habitat destruction, urban development often brings increased light pollution to an area, the effects of which are discussed in section 1.3.3, and road traffic which may also negatively affect insect populations through direct mortality (Baxter-Gilbert et al., 2015, Muñoz et al., 2015). Merckx et al. (2018) found that the body size of moths was larger in more urbanised areas, both at the species and community level. The authors suggest that fragmentation of habitat within urban areas has selected for larger, more mobile moths and that the slightly warmer average temperatures that occur in urban areas allows for larger bodied moths as they need less time for pre-flight thorax warm-up. How this relates to MacGregor et al. (2019b), who found that larger-bodied moth species were likely becoming more common across the UK, is unknown but would make an interesting line of enquiry.

As well as uninhabitable surfaces, urban development often also contains gardens, parks, street trees and other areas of vegetation that act as valuable habitat for insects (Helden and Leather, 2004, Helden et al., 2012). A study from 12 urban centres across the UK found that bee species richness was actually higher in urban sites than in nearby farmland, although abundance of hoverflies was reduced in urban centres (Baldock et al., 2015). Urbanisation has not been linked to moth declines at a national or landscape level, and despite rapid urbanisation in the UK over the last century, urban and suburban land (including parks and gardens) accounts for only 5.9% of the land cover (Morton et al., 2011).

1.3.1.4 Changes to woodland

Broadleaf woodland is one of the few habitats that has increased in the UK in recent decades, and together with coniferous plantations, woodland coverage in the UK is at its highest point in 600 years (DEFRA, 2013). Despite the growing area of woodland, indicators in key taxa are pointing to a decline in woodland biodiversity in recent decades such as birds (Fuller et al., 2005b) and butterflies (Fox et al., 2015). The growth in conifer plantations since World War I is likely the reason that conifer-feeding moth species have experienced large population increases since 1968 (Conrad et al., 2004). Although coniferous afforestation in Breckland heath is probably to blame for the extinction of habitat specialists such as the Spotted Sulphur (*Emmelia trabealis*) (Majerus, 2002).

British woodlands have become much less managed in the post-war period, mainly due to the cessation of coppicing and other wood-harvesting activities (Kirby et al., 2017). As a result, they have lost much of their early-successional habitat (Clarke et al., 2011) and have become more shaded, which typically leads to a reduction in plant species diversity (Sparks et al., 1996). The change in habitat management to a largely closed canopy has had negative effects on many species of woodland butterflies (Fartmann et al., 2013, Robertson et al., 1995) and negative effects of shading have been found in other insect taxa (Greatorex-Davies et al., 1994). Most butterflies prefer to fly in sunlight as it is metabolically advantageous, so it is not surprising that an increase in shade will make the habitat less suitable. Moths may be less affected by shade as most species are nocturnal so cannot use sunlight to enhance their metabolic activity at night, although sunlight may still be advantageous for the larvae of some species (Bryant et al., 2000).

Moth community composition within coppice woodlands is affected by the age of the coppice regrowth. Broome et al. (2011) found that young stands of sweet chestnut coppice were dominated by moths with a preference for open habitats, and 60% of species captured in these plots feed on herbaceous plants. Older stands were dominated by moths associated with woodlands including a third of species that feed on lichens, fungi and decaying material. Moth abundance and species richness was slightly higher in the older plots, but this was not tested statistically. Merckx et al. (2012a) found similar results, with more sheltered, shady and mature forests containing a higher abundance and species richness of moths than early-successional coppice. Moths found in coppice tended to be more associated with more open habitats. The results suggest that moth diversity could be maximised at the woodland and landscape scale by providing a mixture of mature woodland and early- to mid-successional coppice to maximise the amount of micro-climatic niches and foodplant diversity.

The size and location of a woodland partly determines the type of moth community, with larger woodlands that are close to other woodlands having a higher abundance and species richness of moths than smaller, more isolated ones (Fuentes-Montemayor et al., 2012, Merckx et al., 2012a, Usher and Keiller, 1998). There is evidence to suggest that woodland grazing has a negative effect on the abundance and species richness of moths (Fuentes-Montemayor et al., 2012). Grazing by deer in woodland can have both negative and positive effects on butterflies (Feber et al., 2001) and other invertebrates (Stewart, 2001), but the effect on moths remains largely unstudied. A high diversity of tree species, especially native broadleaf trees (as opposed to conifers) is associated with higher abundance and richness of moths (Fuentes-Montemayor et al., 2012, Kirkpatrick et al., 2017, Thorn et al., 2015), which is unsurprising considering the relatively small number of species which feed on coniferous trees (Waring and Townsend, 2017).

The importance of structural diversity in woodlands was demonstrated by a long-term monitoring program in Hungary that sampled moths at seven woodland sites across the country over the years 1962 – 2009 (Valtonen et al., 2017). There was a significant reduction in species richness across the network and community composition across the sites became more homogenous. Species most likely to disappear from woodlands in the Hungarian network are those which specialise in dry grassland and open rocky areas. Hungarian woodlands have undergone similar changes to UK woodlands with an increase in mature, closed canopy forest. The amount of forested land in Hungary has significantly increased and the amount of grassland significantly decreased over the study period. These factors may explain the trend for homogenisation and overall species loss across these seven woodland sites.

1.3.2 Direct and indirect effects of agrochemicals

The most extensive form of chemical pollution that might affect moths in the UK is likely to be spray drift and leaching by insecticides (e.g. pyrethroids and neonicotinoids), herbicides (e.g. glyphosate) and fertilisers (e.g. nitrogen-phosphorus-potassium) used in agriculture. Although these are generally applied directly onto the crop, the habitats adjacent to the crop may be subject to chemical drift (Longley et al., 1997). A small proportion of farms in the UK are certified as organic and do not use any of the synthetically-derived chemicals that are applied in conventional agriculture. Comparisons of moth abundance and community composition on organic and conventional farms is presented in section 1.4.2. There is a very large body of evidence demonstrating the negative effects of sub-lethal doses of various insecticides on the survival rate of Lepidoptera in the lab (Çilgi and Jepson, 1995, Davis et al., 1991, Sinha et al., 1990). While this is unsurprising, as insecticides are specifically designed to kill insects, the important issue is the effect of insecticides on insects outside of the treated area; how far-reaching these effects are and for how long they persist. In a field experiment by Hahn et al. (2015), a hay meadow was divided into 8 x 8m plots and treated with combinations of fertiliser (granular nitrate, phosphorus and potassium plus calcium carbonate and ammonium nitrate), herbicide (Atlantis WG, a sulfonylurea) and pesticide (Karate Zeon, a pyrethroid) in quantities that are typical for the first 1 m of a field margin adjacent to a winter wheat crop. The abundance of caterpillars in insecticide-treated plots was extremely low compared to other plots. Herbicides had no effect on caterpillar abundance and the addition of fertiliser resulted in a slightly higher abundance. In the same study, the abundance of caterpillars caught in sweep net samples in field margins adjacent to winter wheat was found to be 35-60% lower compared to the abundance in a nearby meadow.

As moths and butterflies have similar life histories and are closely related, the effects of insecticides on the two groups are likely to be similar. A review on the effect of insecticides on butterflies (Braak et al., 2018) stresses that insecticides, especially systemic insecticides such as neonicotinoids, can come into contact with butterflies via a range of indirect routes; for example, through the ingestion of the nectar of treated plants or by feeding on plants that have absorbed neonicotinoid-contaminated water (Goulson, 2013). The review presents strong evidence that insecticides have contributed to observed declines in butterflies in agricultural landscapes worldwide and that low doses of insecticide results in a wide range of sub-lethal effects for butterflies, implying that the same is likely true for moths.

Over-zealous application of fertilisers causes agricultural run-off and eutrophication, known to reduce plant diversity and result in the dominance of nitrogen-loving plants (Payne et al., 2017). There is evidence that butterflies that feed on nitrogen-loving plants are more likely to have stable or increasing populations (Öckinger et al., 2006) and increased nitrogen levels have been linked to declines in butterfly abundance and diversity (De Vries and Van Swaay, 2013, Hodgson et al., 2014). In moths, increases in occupancy have been linked to a preference for nitrogen-loving and light-loving plants (Betzholtz et al., 2013, Fox et al., 2014). There seems to be either a neutral or a positive effect of increased nutrient deposition on the abundance and biomass of moths and other insects (Hahn et al., 2015, Lind et al., 2017). Ingestion of herbicides by Lepidopteran larvae may also result in deleterious sub-lethal effects (Hahn et al., 2014), but again, evidence for effects at the landscape-scale have not been published.

Air pollution has been greatly reduced in the UK over the last half-century, particularly after the clean air acts in 1956 and thereafter, and it is thought that the drop in sulphur dioxide pollution has led to a recovery of lichens across the country (Gilbert, 1992). This is likely to be the reason that lichen-feeding moths are one of the few groups that have experienced large increases over this time period (Conrad et al., 2004, Pescott et al., 2015).

1.3.3 Light pollution

The majority of nocturnal moths, as well as many other nocturnal insects, are attracted to light, but the reason for this physiological response remains largely unknown (Frank et al., 2006, Shimoda and Honda, 2013). Moths tend to show greater attraction to the bluer end of the light spectrum and are especially sensitive to ultra-violet radiation that is invisible to the human eye (Cowan and Gries, 2009, Huemer et al., 2010, Somers-Yeates et al., 2013), although this varies among species (Eguchi et al., 1982). Experiments have shown that moths do not exhibit a simple positive phototaxis when in close proximity to a light source, but rather exhibit behaviour that suggests disorientation (Gaydecki, 2018). Artificial light at night (ALAN) can have negative effects on moths through mechanisms such as increased exposure to predators (Minnaar et al., 2015), reduced larval growth rates (Grenis and Murphy, 2019), disruption to mating behaviour (Frank et al., 2006, Van Geffen et al., 2015b, Van Geffen et al., 2015a), and dispersal (Degen et al., 2016). Direct mortality can occur as a result of collision, heat, exhaustion or becoming trapped in the light housing (Eisenbeis, 2006). ALAN has also been shown to affect flower-visitation in moths and reduce pollination success in insect-pollinated plants (Macgregor et al., 2015, Macgregor et al., 2017, Knop et al., 2017).

Evidence that ALAN has been responsible for a decline in moth populations is scarce due to a lack of light pollution data, the difficulty in isolating the potential effects of ALAN from other factors such as urbanisation and the difficulty of sampling moths without the use of light. Conrad et al. (2006) compared moth population trends at two sets of sites in the UK: one set which had experienced an increase in ALAN between 1992 – 2000 (81 sites) and one set that was dark and had remained dark (or become darker) over that period (35 sites). They found no differences in the trends of moths between the two groups and no differences in general abundance either. However, the shortness of the time period by which sites were classified means that ALAN cannot be excluded as a potential driver of decline. Wilson et al. (2018)

found that moth abundance was lower in more brightly-lit areas, but the authors were unable to exclude competition from background illumination and other lights as a mechanism for the lower counts. Van Langevelde et al. (2018) found that Dutch moths were more likely to have declined since 1985 if they were nocturnal and more attracted to light; diurnal species and nocturnal species that are not attracted to light were found to be largely stable. ALAN may be an overlooked key driver of moth decline (Owens et al., 2019) and it has been suggested that street lighting should be used only when necessary and should consist of dimmed, warm coloured lights to reduce the impact on moths and other insects (Longcore et al., 2015, Poiani et al., 2015).

1.3.4 Climate change

The effects of climate are highly variable and some moths are evidently benefitting from the increasingly warm weather, taking the opportunity to expand their range northwards (Battisti et al., 2005, Mason et al., 2015) and complete additional generations within one year (Altermatt, 2009, Fletcher, 2006, Macgregor et al., 2019a). For other moths, the warmer, wetter winters may be detrimental (Conrad et al., 2002, Conrad et al., 2003). Several studies have found a link between moth decline and overwintering stage, with species that overwinter in an immature form (especially as an egg) more likely to decline than the few species that overwinter as adults (Conrad et al., 2004, Groenendijk and Ellis, 2011). It is known that winter temperatures can affect the abundance of insects later in the year (Bell et al., 2015), and warm winter temperatures have been linked to higher winter mortality in butterflies (Klockmann and Fischer, 2019, Stuhldreher et al., 2014, WallisDeVries et al., 2011). For montane and northerly species, the warming climate is likely to shrink the extent of their ecological niche which is cited as the cause of their decline in recent decades (Conrad et al., 2004, Fox et al., 2014, Morecroft et al., 2009). In the case of the Wall butterfly (*Lasiommata megera*), the warming climate appears to be responsible for their decline because of disruption to their phenology (Van Dyck et al., 2015). Changes in the phenology of insects in relation to climate change has been demonstrated (Bell et al., 2019, Thackeray et al., 2016) and it is hypothesised that phenological mismatches between taxa could have negative impacts on insect populations (Donnelly et al., 2011). The negative effect of phenological asynchrony has been demonstrated in the Winter Moth (*Operophtera brumata*) (Visser and

Holleman, 2001) but effects are likely to vary widely between species (Forrest, 2016). Watt and Woiwod (1999) found no evidence for phenological asynchrony in British moths as year-to-year variation in moth abundance was no different for those species whose larvae emerge around bud-bust and those who emerge at other times of year. Although the effects of phenological asynchrony are demonstrably real in some taxa, it remains unclear as to what extent phenological asynchrony is a permanently changing feature of the natural world rather than a result of climate change in recent decades (Singer and Parmesan, 2010).

1.3.5 Non-native species

Invasive species are a key driver of biodiversity loss worldwide and their negative effects on ecosystems in the UK are well-known. For moths, the proliferation of non-native woody plants in woodlands can reduce foodplant availability for Lepidopteran larvae and result in a reduction in moth abundance and species richness (Kadlec et al., 2018). Overgrazing by both native and non-native deer can reduce foodplant availability within woodlands, although the evidence for this as a driver of decline is sparse (Fuentes-Montemayor et al., 2012). For spatially restricted habitat specialists, the effects of invasive plant species can be large, such as for the Slender Scotch Burnet (*Zygaena loti*) where its habitat has been colonised by invasive *Cotoneaster* shrubs (Fox, 2013). Invasive predators such as the Harlequin ladybird (*Harmonia axyridis*) also have the potential to impact moth populations through predation, but this has not been demonstrated.

In contrast to this, the spread of novel plants into the UK has allowed several species of moth to exist here which otherwise would not. For example, the cypress-feeding moths Blair's Shoulder-Knot (*Lithophane leautieri*), Cypress Carpet (*Thera cupressata*) and Cypress Pug (*Eupithecia phoeniceata)* all feed on the apparently benign cypress trees that are planted ornamentally in parks and gardens.

1.4 Conservation measures

While the preservation of large areas of natural habitat is the ideal for the conservation of most species, the reality in the UK is that over 70% of land area is under some form of agriculture (DEFRA, 2018). Effective conservation of moths and other taxa in the UK must therefore include agricultural land within its strategy. Conservation measures in agriculturally productive land can often be divided into two categories: land sharing and land sparing (Phalan et al., 2011). A land sharing strategy involves low intensity wildlife-friendly agriculture where the two objectives of conservation and production both occur on the same piece of land. A land sparing strategy involves dividing land into one category or the other, where some land is used intensively and is largely hostile to wildlife, and some land is left as natural habitat. However, the dichotomy between the two strategies is often not clear-cut (Herzog and Schüepp, 2013, Kremen, 2015). For example, conservation measures on farmland do not always come at a production cost and often have the potential to enhance production through ecosystem services such as pollination, pest control and soil conservation (Evans, 2006, Pywell et al., 2015, Tschumi et al., 2016). Agri-environment schemes (AES) are widely used in Europe as a way of mitigating against biodiversity loss in the agricultural landscape while at the same time providing the ecosystem services mentioned. These schemes offer financial rewards to farmers for carrying out practices that benefit wildlife and the environment. Measures can include, among other things, the creation and sympathetic management of hedgerows, the reduction of fertiliser inputs into grassland or, as is the subject of Chapter 4 of this thesis, the creation of sown buffer strips of grasses or wildflowers in field margins. AES came into effect in arable land in England 2002 and underwent an expansion in 2005 (Grice et al., 2006). The effects of these schemes on groups such as birds, pollinating insects and predators of pests are relatively well-studied, with results that are generally positive but often with some variation (Kleijn and Sutherland, 2003, Kleijn et al., 2006, Marshall et al., 2006). The effects of AES on moth populations remain relatively understudied, but research so far suggests positive results (Alison et al., 2016, Merckx et al., 2012b).

1.4.1 Field margin creation

A field margin is typically defined as the vegetation occurring between the edge of a crop and the boundary of the field. For the purposes of this thesis, a field margin refers only to the low-growing vegetation and excludes any boundary feature such as hedges or walls. Field margins and hedges are a key feature of the British landscape, and in intensively farmed areas they often represent the only semi-natural habitat. They are thus a vitally important resource for wildlife (Marshall and Moonen, 2002) and serve important ecosystem services by providing nesting sites and alternative food sources for pollinators and predators of agricultural pests (Wratten et al., 2012). In the post-war period, many field margins were destroyed or degraded due to agricultural intensification (Robinson and Sutherland, 2002). For example, many kilometres of hedgerows and their associated field margins have been removed in order to increase the size of fields. Changes in farm machinery have meant that crops can be sown right up to the edge of the fields, further reducing the width of the field margins. Furthermore, insecticides, herbicides and fertilisers applied to the crop can drift into the field margins, reducing floral diversity (Kleijn and Verbeek, 2000) and negatively affecting invertebrate communities (Braak et al., 2018, Hahn et al., 2015).

Agri-environment schemes aim to restore the biodiversity value of field margins while at the same time providing ecosystem services to the farm. In England, current AES guidelines (under Countryside Stewardship) allow for several types of field margin including simple grass mixes, pollen and nectar mixes and various types of wildflower mix (DEFRA, 2019). A large body of research comparing species richness and abundance of insects in different types of field margin is available (Haaland et al., 2011). While the abundance and diversity of many invertebrate groups are enhanced by the more florally diverse margins, this is not always the case. For example, Ramsay et al. (2007) found that planthoppers (Fulgoromorpha) were more abundant in plain grass plots compared to two types of florally enhanced plots. Although certain taxa may favour certain types of field margin, field margins typically support a much higher abundance and diversity of insects than does the crop which the margin replaces (Haaland et al., 2011), with the exception of certain groups such as carabid beetles which are sometimes more abundant (or more active) in the crop (Birkhofer et al., 2014). The value of field margin habitats for nocturnal moths remains understudied in comparison to other invertebrate groups, and studies comparing the relative value of different types of field margin are yet to be carried out.

A study by Merckx et al. (2009a) tested the effect of 6 m tussocky grass margins and hedgerow trees on the abundance of nine species of common moth. They found that abundance was 40% higher in field margins with 6 m grassy strips in comparison to standard 1 m strips, with the presence of a hedgerow tree having no effect. Merckx et al. (2009a) found that the effect of the extended field margins carried over into field centres with 58% more individuals captured in the centre of fields with extended margins compared to the control. The positive effects of extended field margins were found to be greater for species with lower mobility (i.e., those found to fly shorter distances in a capture-mark-recapture aspect of the same study). This study was the first in a series of similar studies by the same authors and although the subsequent studies also find generally positive effects of extended field margins, the effects are less clear.

The second study in the series (Merckx et al., 2009b) found that extended field margins significantly increased moth species diversity but not abundance. Hedgerow trees had a greater effect on species diversity than margins but neither intervention affected abundance. A later study by Merckx et al. (2012b) re-evaluated these findings with more experimental data. They found that 6 m wide grass margins around arable fields significantly increased moth species richness but did not affect overall moth abundance; this was true both when considering all species of moth or only those that feed on grasses and forbs. The presence of 6 m grass margins also resulted in a higher species richness of shrub/tree-feeding moths. The authors suggest this may be due to the presence of nectar resources in the margins and/or the effect of buffering the hedgerows against chemical applications. The presence of hedgerow trees also increased richness but not abundance, but this effect was much stronger when considering a subset of species which fed only on trees and shrubs.

The final study by Merckx et al. (2010a) investigated the same two habitat features but focussed on 23 species of common macro-moth across 5 arable fields on one farm over one year. Again, they found that abundance was not affected by the 6 m grassy margins compared to control margins (both when considering all moths and grass/forb-feeding species only); although a significant positive effect was detected for hedgerow trees on shrub/tree-feeding species.

Apart from the first study in this series, extended 6 m margins did not significantly influence the abundance of moths captured; although there were generally positive trends. Species richness and diversity was higher in AES margins in the larger two studies where this variable was measured. The presence of hedgerow trees had a consistently greater positive effect on moth abundance and diversity compared to the 6 m margins; this corroborates with studies by (Kühne et al., 2015) and (Woiwod and Gould, 2008) who found that amount of woody vegetation around a trap had a much larger influence on moth abundance and diversity than did amount of grassland.

Alison et al. (2016) showed that moths with grassland habitat preference (24 species) were 42% more abundant in 6 m grassy margins compared to control margins, although there was no significant difference in abundance of other types of moth (141 species). Abundance of these 24 species of grassland moths in extended field margins was at the same level recorded in nearby chalk grasslands; although the abundance of chalk grassland specialist moths (15 species) was much reduced in grassy margins compared to the chalk grasslands. Counter-intuitively, the abundance of non-grassland moths was significantly higher in the chalk grasslands compared to field margins.

A study in Scotland took 18 pairs of farms with/without AES interventions and compared moth abundance and richness at various habitat types (Fuentes-Montemayor et al., 2011). They detected a significantly higher abundance and richness of micro-moths in the AES margins compared to control margins, although no significant effects were detected for macro-moths. In this study, they also looked at AES water-margins which leave a 3 m buffer strip between crop/grazing land and a water body. For this habitat, the abundance of both macro- and micro-moths was higher in the AES treatment than the control, but species richness was not affected. Fuentes-Montemayor et al., (2011) also investigated the effect of land-use at various radii surrounding the traps and found that the most important predictor was the amount of semi-natural habitat with 250 m of the trap. Here, rough grassland and scrub had a significant positive effect on species richness and abundance on micro-moths. However, macro-moths did not show the same trend; benefitting in species richness, but not abundance when rough grassland and scrub were in close proximity. Fuentes-Montemayor et al., (2011) also compared species-rich AES grassland to conventional grassland and found that micro-moth abundance and richness was significantly higher in AES grassland; as was macro-moth species richness, but again abundance did not show a positive effect.

Overall, these studies suggest that the species richness and abundance of moths have the tendency to be higher in AES margins in comparison to control margins, but the differences are often small, non-significant or unclear. In the studies mentioned above, AES field margins had a significant effect on macro-moth species richness/diversity in two out of the three studies in which richness/diversity was measured. For macro-moth abundance, a positive effect of AES margins was detected in only two out of six studies.

1.4.2 Reduction in chemical input

A key component of organic agriculture is the prohibition of the use of synthetically-derived chemicals. Under most organic certification schemes, the use of certain plant-derived or non-synthetic substances such as copper sulphate are allowed, but are typically used in moderation (Trewavas, 2001). Organic agriculture is often promoted as an environmentally-friendly method of food production, and it is hoped that the reduction of both synthetically- and non-synthetically derived insecticides will allow for larger populations of non-pest insects to exist within farmland (Reganold and Wachter, 2016). While the benefits of organic farming has been demonstrated for a range of insect fauna (Feber et al., 1997, Holzschuh et al., 2007, Taylor and Morecroft, 2009) the effects of organic agriculture at the farm scale are often unclear (Fuller et al., 2005a, Hole et al., 2005). There have been several studies comparing moth populations on organic farms to conventional farms, with mixed results. A study in southern Canada (Boutin et al., 2011) compared eight organic and eight conventional arable farms and found no difference in the abundance of moths in hedgerows. Neither was there was a difference in moth abundance or species richness in the field centres across farm types. The only significant difference reported was an increase in the species richness in the family Notodontidae at hedgerows in organic farms compared to conventional, but as the authors made no adjustments in the model for multiple comparisons, it is likely that this result is a chance occurrence. A study in the UK sampled moths in 42 paired cereal fields (21 organic and 21 conventional) and found no overall differences in moth abundance except for the Geometridae family which was significantly more abundant on conventional farms (Pocock and Jennings, 2008).

In contrast, Wickramasinghe et al. (2004) compared the abundance of moths across 24 pairs of organic and conventional farms that consisted of both arable and pastoral habitat. They found that the abundance of noctuid, geometrid and arctiid moths was higher on organic farms, but only in the pastoral habitat; no such effect was detectable in arable habitat. Jonason et al. (2013) found a transient peak in moth diversity on farms after conversion to organic, with peak diversity occurring on farms that had been organic for less than six years.

Farms that had been organic for over 15 years were equivalent in moth diversity to conventional farms. A study by Taylor and Morecroft (2009) tracked the abundance and richness of several taxa on a farm transitioning from a conventionally managed farm to an organic farm with AES habitats from 1994 to 2006, following conversion to organic farming in 2002. They found significant increases in abundance and species richness of moths and butterflies. However, as well as the cessation of chemical inputs, there were major changes to habitats including a conversion of arable land to high-diversity grassland, so the increases in biodiversity cannot be attributed to its organic status alone.

From the studies reviewed above, there is very little evidence to support the hypothesis that reductions in synthetic agri-chemical applications result in a higher abundance and diversity of moths. Although organic farming has the potential to increase biodiversity at the local scale, it can be argued that in organic systems larger areas of land would need to be brought under cultivation to produce the same amount of yield; resulting in a net loss of biodiversity when compared to a strategy of combining conventional agriculture with some land set aside for habitat (Gabriel et al., 2013, Hodgson et al., 2010).

1.4.3 Reduction in grazing intensity

As stated in section1.3.1, grazing intensity affects different species in different ways and moderate levels of grazing are advantageous to many species, but generally, intensive grazing is deleterious for biodiversity. This was demonstrated by (Littlewood, 2008) in a Scottish upland estate. They found that moth abundance was increased by 50% and species richness increased by 20% when grazing intensity was reduced from the standard commercial stocking density. Rickert et al. (2012) found similar results but also noted that the effects of low stocking density were no different to that of abandonment, which again suggests a tipping point in terms of grazing intensity.

1.4.4 Hedgerow management

Hedgerows are a vitally important part of the British countryside and often represent the only permanent woody vegetation within intensively farmed areas. As well as providing breeding sites for moths, they act as corridors between other habitat patches (Coulthard et al., 2016).

While it is very clear that moth abundance and diversity is enhanced by the presence of hedgerows (Boutin et al., 2011), the way in which hedgerows are managed also determines their value to moths. Froidevaux et al. (2019) found that the abundance and species richness of tree/shrub-feeding moths increased with the time since the last cutting. Similar results were found by Staley et al. (2016) who also noted the advantage of cutting hedges later in the year (in winter rather than autumn). These studies show that the effects of hedgerow cutting regime on moths tend to be quite subtle and limited to the species that feed on the hedgerow plants. A study by Facey et al. (2014) found mixed results of cutting regime on moth larvae, with no effect on free-living larvae, but a greater abundance of concealed larvae (e.g., leaf-miners) on more infrequently cut hedges. Fuentes-Montemayor et al. (2011) found no effect of AES subscriptions to hedgerows on moths. Overall, it appears that moth abundance and richness can be enhanced by reducing the cutting rate of hedges and cutting them in winter rather than autumn, although the effects of these practices on moths are likely to be small.

1.5 Research objectives and thesis structure

The decline in moths that has occurred in the UK and other north-western European nations is likely to have negative consequences for ecosystem functioning, such as reduced food availability for birds, small mammals and other invertebrates (Visser et al., 2006) and the pollination success of wild flowering plants (Pettersson, 1991, Young, 2002). Agricultural intensification is often cited as the key driver behind these losses, but studies directly supporting this hypothesis are lacking (Fox, 2013). In order to address the decline in moths, it is important to know which of the hypothesised drivers are the most influential and what measures, such as agri-environment schemes, can be taken to reduce their negative effects on moths as well as other insects. The main aims of this thesis fall into two parts. 1) To determine whether the decline in moth populations is primarily due to agricultural intensification (Chapter 2), and 2) To determine whether field margin agri-environment schemes are an effective tool for conserving moths in farmland (Chapters 3 and 4). The experimental portion of this thesis is split into 3 chapters; the aims and objectives of which are presented here.

1.5.1 Chapter 2 – The effect of land-use and species traits on the long-term trends of abundance and diversity of moths in the UK

Background: Moth populations in the UK have declined since 1968 with the strongest declines in the south and south-east (Conrad et al., 2004, Conrad et al., 2006, Fox et al., 2013). Declines in moths, butterflies and other insects have been linked to agricultural intensification in other north-western European countries (Habel et al., 2019b, Seibold et al., 2019) and agricultural intensification is widely postulated as the key driver of moth decline in the UK (Fox, 2013). This hypothesis is supported by the fact that the south and south-east of the UK is primarily arable, which has arguably undergone more severe intensification than other land-use types since the 1960s. This chapter uses historical moth data collected by the Rothamsted Insect Survey to test the hypothesis that moth declines have been the most severe in the most agricultural intensified parts of the country since 1968 and have been least severe in more semi-natural areas such as broadleaf woodlands. The interaction between species traits and habitats is also examined.

Aim 1: Assess whether overall population trends in moths have been more severe in intensive agricultural areas and less severe in semi-natural areas.

Aim 2: Test whether individual species traits such as feeding guild and wingspan influence their population trends in different habitats.

1.5.2 Chapter 3 – Design and testing of a low-cost UV LED moth-trap

Background: Ecological experiments on moths typically use a 6 W Actinic Heath trap for sampling (Fuentes-Montemayor et al., 2011, Merckx et al., 2012b). These traps have been shown to have a small attractive radius (< 30 m), making them appropriate for sampling very specific areas (Merckx and Slade, 2014, Van Grunsven et al., 2014). As these are niche products, they are expensive, so a lower-cost equivalent would be preferable for studies using many of these traps. Furthermore, it is not known what proportion of captured moths escape during the night, resulting in underestimates and noise in the data. An improvement to the design could prevent the moths from escaping. In this chapter, a design for an ultra-violet

(UV) LED moth-trap is presented. Comparisons are made between three prototypes of UV LED trap: a standard design, an automatically closing trap and a kill-trap. The attractive radius and the abundance and community composition of moths attracted to a UV LED trap are compared to more widely used traps. This chapter acts as a foundation for the main fieldwork section of this thesis (Chapter 4), as the UV LED traps are used throughout.

Aim 1: To compare the attractive radius and community composition of moths captured in a UV LED trap to more frequently used moth traps

Aim 2: To determine the percentage of moths that escape a trap during the night and to modify the trap to prevent escapes

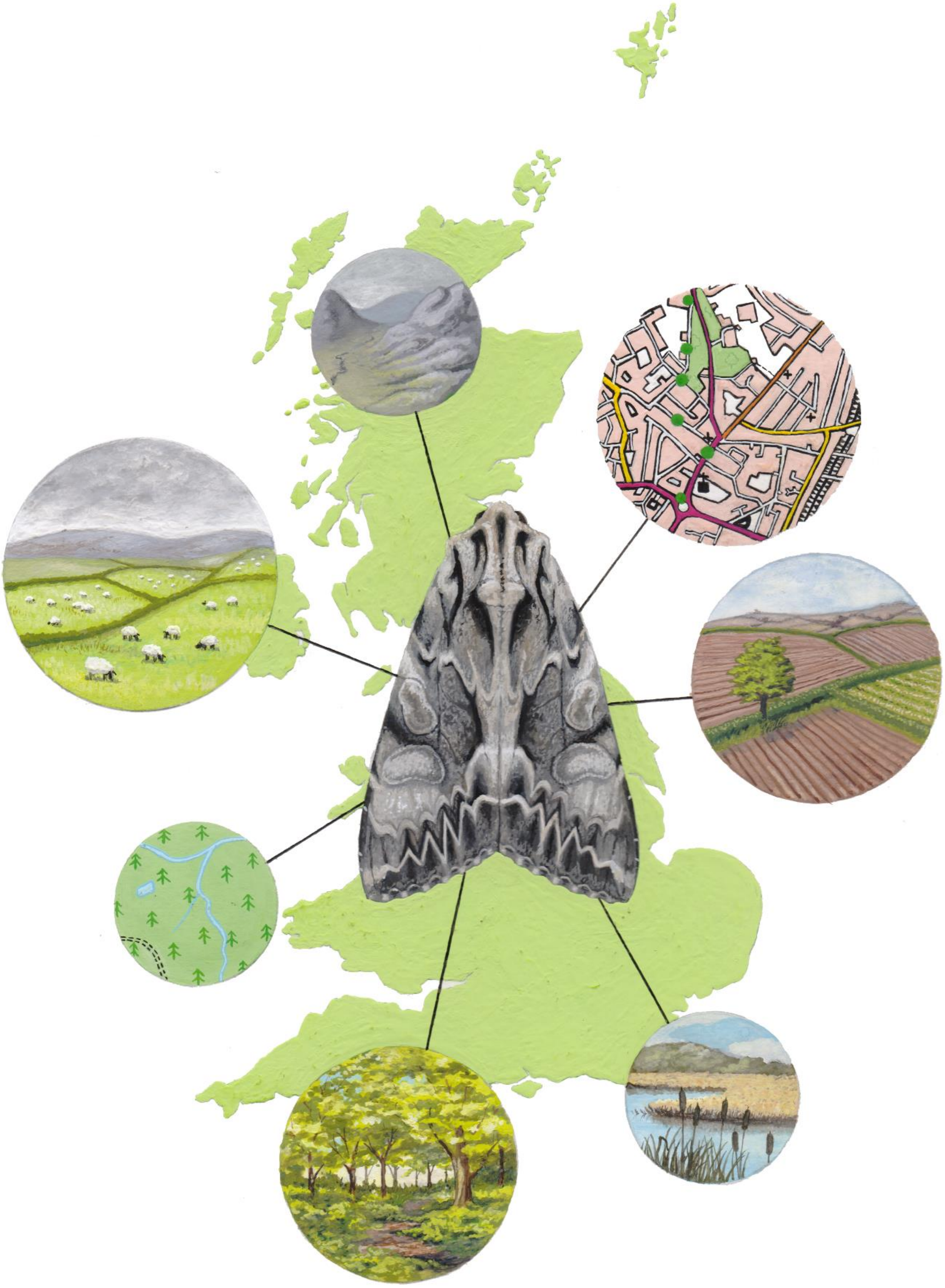
1.5.3 Chapter 4 – The effect of florally enhanced field margin strips on moth abundance and diversity

Background: While it is known that field margins can enhance the abundance and diversity of moths at the field or farm scale (Alison et al., 2016, Merckx et al., 2012b), the mechanisms behind this enhancement are unknown. For instance, the field margins may be providing larval food plants, roosting sites or nectar resources and may be acting as a buffer between hedges and the crop, reducing the chemical drift and disturbance to moths in the hedge. Moths may also be mainly using field margins and hedges as dispersal corridors (Coulthard et al., 2016) rather than a resource in their own right. Moth abundance and diversity across different types of field margin has not before been studied. As space for field margin vegetation in arable farms is limited, it is important to know how to provide the most effective and resource-rich habitat on the land available. In this chapter, the abundance and community composition of moths in differing field margin types is assessed using two techniques: trapping and nocturnal transects. The effect of the field margin type is considered within the context of the surrounding landscape. The utilisation of nectar resources by moths is also quantified and the density of larvae in different field margin types is estimated.

Aim: Assess whether the provision of nectar resources and hostplant diversity enhances the value of field margins for moths.

> Objective 1: Compare the abundance of moths in adult and larval stages across three field margin treatment types: grass only, grass enhanced with moth-pollinated flowers, and a diverse wildflower mix.
>
> Objective 2: Determine whether moths are encouraged to utilise nectar-rich grass margins over nectar-poor grass margins by comparing rates of ovipositing and mating behaviour across margin types.
>
> Objective 3: Record the frequency of nectar-feeding in moths through observations during transects. Determine the preference of moths for different types of wildflower and assess whether sown flowers are utilised more or less than self-seeded flowers.
>
> Objective 4: Determine whether the abundance and community composition estimates using the two techniques (traps and transects) are in agreement and assess whether the techniques are influenced differently by different factors, e.g., surrounding land-use.

Chapter 2



The effect of land-use and species traits on the long-term trends of abundance and diversity of moths in the UK

Chapter 2. The effect of land-use and species traits on the long-term trends of abundance and diversity of moths in the UK

2.1 Abstract

The total abundance of moths in the UK has declined since standardised recording began in the late 1960s, but significant variation in trends exist among species and between regions and habitat types. Previous work has shown that species with certain life history traits are more likely to decline than others, and that negative trends are more severe in the south of the country. Recent studies have also suggested that declines are less severe in agriculturally intensive areas. There has been little research into the interaction effects between species traits, habitat and region. Furthermore, the long-term trends in species richness and diversity are largely unknown. Here, the interaction effects of species traits, habitat and region (north vs south) are investigated, and the effect of habitat and region on the long-term trends of species richness and diversity are modelled. Total UK moth abundance declined by -36% from 1968 – 2016. Of the seven habitat types analysed, declines were least severe in the most agriculturally intensive areas (-18% in arable land and -34% in improved grasslands). In contrast, abundance declined by -44% in broadleaf woodland and by -45% in 'other semi-natural' habitats. Species richness and diversity declined significantly in broadleaf woodland (by -12.5% and -9.7% respectively) in contrast to all other habitat types in which richness and diversity were either stable or increasing. Trends in abundance, richness and diversity tended to be more positive in the north, with overall species richness significantly increasing in this region. Interaction effects between species traits and habitat were mainly non-significant, although species that feed on grasses and low-growing plants fared better in uplands compared to other habitats. Shading and over-grazing by deer were investigated as drivers of decline in woodland, but there was no evidence that species that feed on low-growing and shade-intolerant plants declined more in woodlands than in other habitats. Climate was also investigated as an interaction effect but this was also largely non-significant. A significant negative effect of warm winters was detected, suggesting that climate change should be further investigated as a potential driver of moth decline.

2.2 Introduction

The decline of insect abundance in the UK and elsewhere in Europe has been attributed primarily to habitat loss through agricultural intensification (Fox et al., 2013, Groenendijk and Ellis, 2011, Habel et al., 2019a). In the second half of the 20th century in the UK, many miles of hedgerows and their associated field margins were removed, insecticide and herbicide applications increased and fallow land became scarcer (Boatman et al., 2007, Robinson and Sutherland, 2002). Furthermore, the loss of important habitats such as hay-meadows had an undeniable negative effect on insect populations, including moths (Fox, 2013). The sudden changes that occurred in the 1950s are demonstrated by the first Rothamsted Insect Survey (RIS) moth trap: a light-trap run in the 1930s and 40s that was decommissioned during the entire 1950s. When it started up again in the 1960s, it was found that the annual catch had dropped by -71% (Woiwod and Gould, 2008). Unfortunately, the evidence provided by one trap does not allow for generalisations across the whole country. However, since the mid-1960s, the RIS has run a standardised network of traps that have produced highly robust trends of moth abundance and have found that the decline noted in the early 1960s has continued to the present day (Bell et al., 2020, Conrad et al., 2006, Harrower et al., 2019).

Two recent studies have challenged the assumption that agricultural intensification is the main driver behind the post-1960s moth decline. MacGregor et al. (2019b) found that, contrary to abundance trends, the total biomass of moths increased rapidly between 1967 and 1982, and declined from 1982 to 2017, but remains higher than its 1967 level. Furthermore, when the sites were split into four habitats: urban, woodland, grassland and arable, it was shown that the post-1982 decline did not occur in arable land, but rather, biomass remained stable. Likewise, Bell et al. (2020) found that moth abundance in farmland showed no significant directional trend, while it did decline in woodland, urban and coastal sites.

While it is surprising that moth abundance has not declined in arable sites, it is perhaps more surprising that moths have declined so severely in woodland sites. This decline is unexpected as previous studies suggest that species with a preference for woodland habitat and those that feed on broadleaf trees were less likely to decline than other species, both in the UK (Conrad et al., 2004) and elsewhere in Europe (Franzén and Johannesson, 2007, Potocký et al., 2018, Valtonen et al., 2017). The area of broadleaf woodland in the UK has increased since the 1960s (DEFRA, 2013) so habitat loss in a broad sense is unlikely to be the cause. However, woodland structure has undergone substantial changes since the 1960s. The cessation of coppicing and the increase in deer grazing pressure has led to a sparser and more shaded understory with a larger proportion of mature canopy trees and fewer low-growing plants and shrubs (Fuller et al., 2007). Invasive species such as *Rhododendron ponticum* and the planting of exotic conifers for timber may also have influenced the moth trend that we observe. In line with these structural changes, the previous studies mentioned above (Conrad et al., 2004, Franzén and Johannesson, 2007) found that species that feed on grasses and forbs were more likely to have declined than those that feed on woody vegetation.

Several species traits are associated with decline in moths, some of which are shared by butterflies (see Table S2.1 for an overview). Decline is associated with species that feed on shrubs, grasses and forbs, those that prefer non-woodland habitat, overwinter in an immature stage (Conrad et al., 2004) and have a larger wingspan (Coulthard et al., 2019). Additionally, species that feed on nitrophobic or photophilic plants, or both, are more likely to have declined in distribution (Fox et al., 2014). It is not known whether these traits that predict decline act equally across all habitat types or are habitat-specific. The interaction between species traits and habitat is an important knowledge-gap in understanding the mechanisms behind moth decline.

The effect of climate on moth population change is not well studied. While warm and wet winters have been linked to declines in butterflies (Klockmann and Fischer, 2019, Stuhldreher et al., 2014, WallisDeVries et al., 2011), the decline of the Garden Tiger moth, *Arctia caja* (Conrad et al., 2003) and a reduction in moth species richness (Turner et al., 1987), no equivalent studies exist for UK moth abundance as a whole. Hunter et al. (2014) found that moth per capita growth rates were negatively associated with weather variables associated with climate change (i.e., increased temperature and precipitation) in northern Finland. However, moth populations had remained mainly stable or increased, suggesting that the drivers of change, in this case, were factors other than the direct effects of climate. Likely, the stage in which the moth overwinters interacts with climate variables (Conrad et al., 2004) but this has not been tested for moths. To better understand the drivers of moth decline, it is necessary to model population trends in as many habitats as possible and to understand how species traits interact with these habitats and with climate. Furthermore, it is necessary to address the knowledge-gap regarding species richness and diversity in the UK. While it is known that the total number of species inhabiting the UK has increased since the 1960s (Fox et al., 2013), likely due to the warming climate, it is not known whether site-specific richness and diversity have also increased. In this chapter, the interactions between key habitats and species traits are modelled so that inferences may be drawn. The effect of climate and its interaction with habitat is also modelled. Finally, changes in species richness and diversity are, for the first time, modelled to produce both national and habitat-specific indices of change.

Hypothesis

A composite hypothesis is tested, that i) Species abundance and diversity trends differ in direction and magnitude across habitats, and ii) Change in species abundance trends are associated with certain moth traits, climate and region. A description and breakdown of the hypotheses to be tested are presented in Table 2.1.

Table 2.1. A description of the composite hypothesis to be tested in Chapter 2.

Hypothesis	Explanation
1a. Moth abundance and diversity has changed over time (1968 – 2016). 1b. Changes in moth abundance and diversity vary by habitat and by latitude.	Trends in abundance and diversity respond to land-use change and climate change. These changes have affected different habitats and latitudes differently.
2a. Species that specialise on grasses, forbs and shrubs have declined more in broadleaf woodlands than in other habitats. 2b. Species that specialise on photophilic hostplants have declined more in broadleaf woodlands than in other habitats.	Broadleaf woodlands have become more shaded and more browsed by deer since the 1960s, resulting in an understory more devoid in low-growing plants – especially photophilic plants.
3. Species that specialise on nitrophobic hostplants have declined more in arable and improved grassland sites than in other habitats and vice versa for nitrophilic hostplants.	Application of nitrogen fertiliser to farmland has resulted in a plant species composition shift towards more nitrophilous plants.
4. Moths with higher habitat specificity and hostplant specificity have declined more than generalist species, especially in rarer, more isolated habitats.	Generalist species are generally better able to adapt and thrive in changing environments. Species with specialist habitat requirements are more likely to decline under environmental change.
5. Moths with smaller wingspans have declined more in discrete habitat patches (broadleaf woodlands and 'other semi-natural' habitats than in more widespread habitat (arable and improved grassland)	Habitat fragmentation has adverse effects on species with low dispersal ability, i.e., small wingspans.
6. Climate variables (temperature and rainfall) affect annual moth abundance. Warm, wet winters have adverse effects on moths, and this varies according to overwintering stage.	Warm and wet winters are known to negatively affect the survival rate some Lepidoptera – possibly due to increased vulnerability to fungal pathogens. Some overwintering stages may be more vulnerable than others

2.3 Methods

2.3.1 Moth data

Moth records from 1968 - 2016 were extracted from the RIS database for every site in the UK including the Isle of Man but excluding the Channel Isles. Sites from the Republic of Ireland were excluded due to sparseness of sites and lack of comparable land-use data. The RIS network consists of standardised light-traps that operate every night of the year. The traps use a 200 W incandescent tungsten bulb situated at 1.2 m above the ground and have a roof that prevents light from shining upwards to avoid attracting moths passing overhead. The design, described in Williams (1948) has remained unchanged since the inception of the network, making catches directly comparable throughout the time-series. Moths are captured every night and are either identified daily or are combined into multi-day catches, depending on trap operator. As the sites are run voluntarily, sites vary in length from 3 to 48 years, resulting in 349 sites used from which all macro-moths recorded were included in the analysis.

2.3.2 Land use data and habitat allocation

Land use data (25 m raster data) was extracted from the Land Cover Map 2015 (LCM2015) for Great Britain (Rowland et al., 2017a) and Northern Ireland (Rowland et al., 2017b). Using ArcMap version 10.4 (Esri, 2018), buffers were drawn around each site using 500 m radii. The intersections of the land cover and each buffer were calculated and tabulated. Sites were first divided into upland and lowland using 300 m in altitude as a cut-off (JNCC, 2015). As very few sites (n = 15) were at 300 m or higher, no further habitat subdivisions could be made for this group, so all 15 sites were categorised as ‘upland’. Of the remaining (lowland) sites, six habitat categories were allocated based on the modal (i.e., dominant) land cover type (excluding marine systems) within the 500 m radius: (1) arable, (2) conifer plantation, (3) broadleaf woodland, (4) improved grassland, (5) other semi-natural and (6) urban (Fig. 2.1). Table 2.2 shows how the habitat types were allocated based on the modal LCM 2015 land cover type. The habitat category ‘other semi-natural’, although it includes a disparate range of habitats, are all open, typically low-nutrient environments that serve as a contrast against the other habitats. To avoid ambiguity, this habitat type is always written in inverted commas when referred to in the text. To look at the effect of latitude, the UK was then split into two ‘regions’: north and south at the 4500 N gridline on the British National Grid (roughly 53.9° in latitude), following Conrad et al. (2006). Table 2.3 shows the distribution of sites across the seven habitat types and two regions.

***Table 2.2. Habitat classification according to the LCM 2015**. The seven habitat types used for analysis in this chapter (Habitat allocation). For each site, the modal land cover type within a 500 m radius according to the LCM 2015 was extracted. The table shows how many sites of each LCM 2015 land cover type are allocated to each of the seven habitat types.*

Altitude class	LCM 2015	Number of sites	Habitat allocation
Upland (300 m or higher)	Acid grassland	6	Upland
	Bog	2	
	Coniferous woodland	2	
	Improved grassland	5	
Lowland (lower than 300 m)	Arable and horticulture	70	Arable
	Coniferous woodland	12	Conifer plantation
	Broadleaved woodland	48	Broadleaf woodland
	Improved grassland	115	Improved grassland
	Acid grassland	2	Other semi-natural
	Calcareous grassland	1	
	Heather	2	
	Heather grassland	4	
	Littoral sediment	1	
	Neutral grassland	1	
	Saltmarsh	3	
	Supra-littoral rock	1	
	Supra-littoral sediment	1	
	Urban	8	Urban
	Suburban	65	

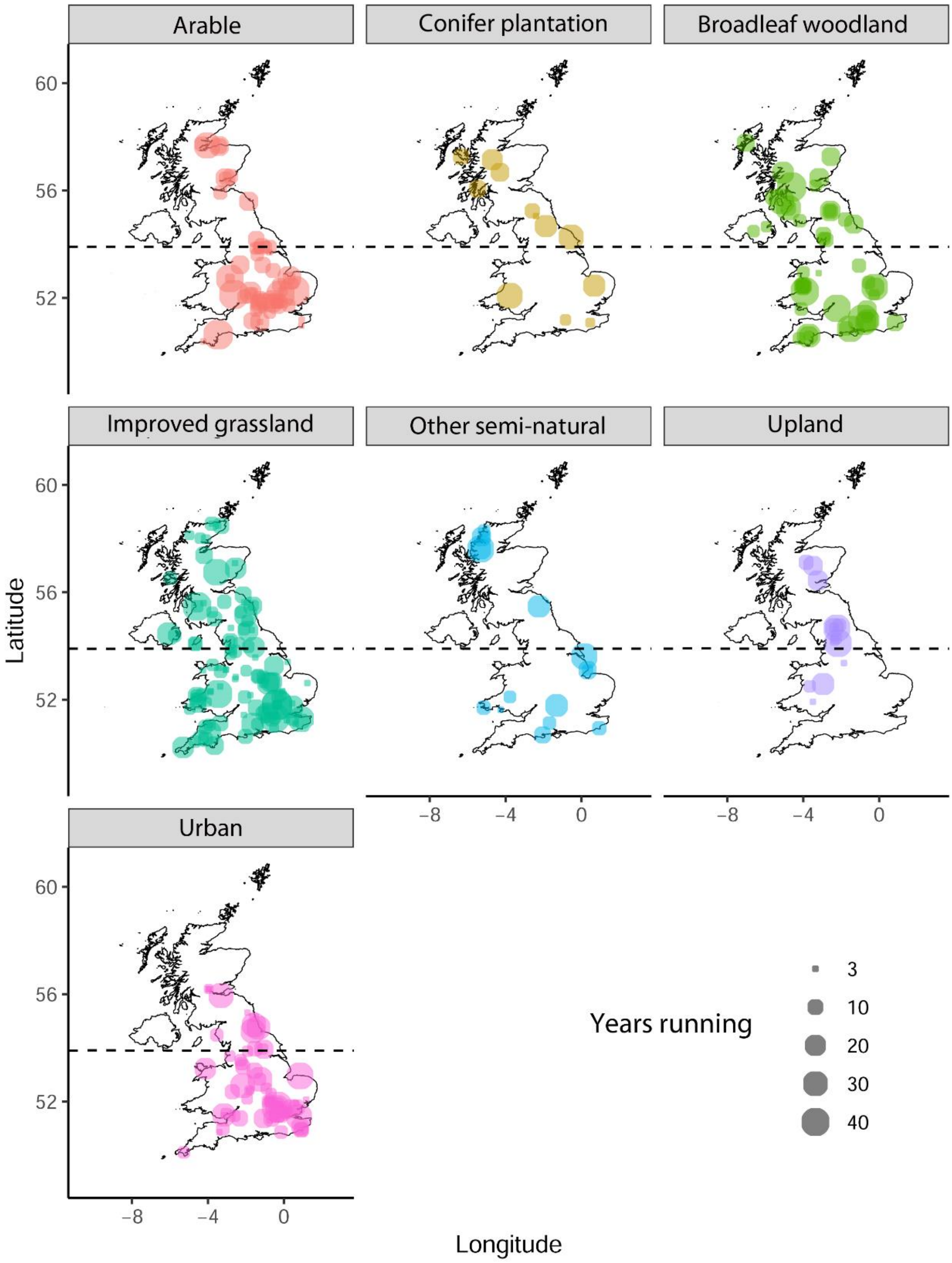


Fig. 2.1. Location of the 349 RIS moth-trap sites within the UK used in this study across seven habitat types. *The size of the point is proportional to the number of years the trap ran for between 1968 and 2016. The dashed line shows the 4500 Northings gridline that was used to divide the country into north and south.*

Table 2.3. The number of sites allocated to each habitat type within each region (north or south) in the UK.

Habitat	North	South	Total
Arable	10	60	70
Conifer plantation	8	4	12
Broadleaf woodland	21	27	48
Improved grassland	38	77	115
Other semi-natural	6	10	16
Upland	10	5	15
Urban	13	60	73
Total	106	243	349

2.3.3 Species traits data

The following species traits were extracted from Waring and Townsend (2017) and supplemented by information form Sterling and Henwood (2020): (1) Feeding guild, (2) Feeding specificity, (3) Habitat specificity, (4) Overwintering stage, (5) Host plant Ellenberg value for nitrogen, (6) Host plant Ellenberg value for light, (7) Forewing length. The association of the host plants with nitrogen and light were quantified using Ellenberg numbers extracted from Hill et al. (1999). Ellenberg values were only used for moth species with three or fewer host plants. When species had between 2-3 host plants, the mean Ellenberg number of the host plants was used. Only species that had at least 20 individuals caught across the entire time series were included in traits models as there is insufficient data to model scarce species and their contribution to the overall trends are negligible. Table 2.4 describes the levels of each trait, including a description of which plant species were defined as ‘trees’ or ‘shrubs’. Table S2.2 presents a list of each moth species with its associated traits.

Table 2.4. Moth species traits used in this study with descriptions of the levels within each trait.

Trait	Level of trait	Notes
Feeding guild	Conifers	Feeds exclusively on coniferous trees and shrubs
	Broadleaf shrubs	Feeds exclusively on broadleaf shrubs. In this case, a ‘shrub’ is a woody plant that does not exceed 15 m in maximum height and is typically not a canopy-forming plant in mature woodland. E.g., hawthorn, blackthorn, hazel, elder, privet, rowan, rose, bramble, currant, spindle, heather, gorse, broom, grey willow. This category also includes species that feed exclusively, or preferentially, on low regrowth or small trees – e.g., Puss Moth (*Cerura vinula*) on low re-growth of poplars, willows and aspen.
	Broadleaf trees	Feeds exclusively on broadleaf trees. In this case, a ‘tree’ is a woody plant that exceeds 15 m in maximum growth and is often canopy-forming when growing in mature woodland. E.g., ash, beech, oak, lime, elm, hornbeam, birch, poplar, field maple, alder, white willow.
	Broadleaf polyphagous	Polyphagous on both broadleaf trees and shrubs.
	Woody polyphagous	Polyphagous on both broadleaf and coniferous trees and shrubs.
	Forbs	Feeds exclusively on herbaceous plants, excluding grasses.
	Grasses	Feeds exclusively on grasses, including reeds and sedges.
	Herbaceous polyphagous	Polyphagous on both grasses and forbs. Foodplants can include bramble, honeysuckle and heathers, but hostplants must be primarily herbaceous.
	Highly polyphagous	Feeds on a range of both woody and herbaceous plants.
	Lichens	
	Mosses	
	Other	E.g., stored foodstuffs, fungi, wool, bird’s nests.
	Unknown	

Trait	Level of trait	Notes
Feeding specificity	Monophagous	Feeds on strictly one species of hostplant.
	Oligophagous	Host plants are all within the same plant family. E.g., feeds on willows and poplars, or, feeds on *Gallium sp*., etc. Also includes species that are usually monophagous but are known to use other hostplants.
	Polyphagous	Feeds on multiple plant families, but always either woody or non-woody plants, never both.
	Highly polyphagous	Feeds on a range of both woody and non-woody plants. This includes species that feed on woody plants during one larval stage and herbaceous plants during another – e.g., the Sallow (*Cirrhia icteritia)* which feeds on sallows/poplars and later on herbaceous plants. Although this larval strategy may be more limiting than being oligophagous, it is placed in the 'highly polyphagous' category for consistency.
Habitat specificity	An integer from 1 – 8	The value equates to the total number of the following habitat types in which a species is known to occur: (1) woodland, (2) farmland, (3) coastal, (4) wetland, (5) unimproved grassland, (6) heathland, (7) upland and (8) gardens/parks.
Overwintering stage	Adult	
	Pupa	
	Larva	
	Egg	
Host plant Ellenberg value for nitrogen	1 – 9	Only for species that feed on three or fewer host plants: where there are more than one, the mean average value is used.
Host plant Ellenberg value for light	1 - 9	
Forewing length		Continuous variable (mm)

2.3.4 Climate data

Climate data was acquired from the UKCP09, a Met Office dataset containing historical daily precipitation and temperature records in the UK at a 5 km resolution (Met Office, 2017). The following six climate variables were calculated for each year in each site: (1) summer temperature, (2) summer rainfall, (3) temperature of previous winter, (4) rainfall of previous winter, (5) temperature of previous summer and (6) temperature of previous winter. All values were expressed as a mean average daily reading of °C for temperature and mm for rainfall. 'Summer' was defined as April – September and 'winter' was defined as October – March. As moth activity peaks in mid/late July, this definition ensured that the 'summer' months included the flight periods of almost all species.

2.3.5 Analysis

All statistical analysis was carried out in R (version 4.0.1).

2.3.5.1 Estimating site-year completeness

In order to maximise the amount of data available, incomplete site-years were used, and missing counts were estimated using species flight periods. The data processing was as follows:

Step 1. 'Derived' nightly counts were calculated by dividing the total number caught by the number of nights sampled. E.g., if one moth were caught over a three-night period, each night would be recorded as having caught 0.33 moths.

Step 2. Each calendar year was divided into 52 weeks. Within each week, a maximum 'derived' nightly count was extracted for each species at each site.

Step 3. Flight periods for each species in each year in each region (north/south) were calculated using Generalised Additive Models (GAMs). The maximum 'derived' nightly count was modelled as a function of calendar week. Flight periods were scaled so that the area under each curve summed to 1. Each calendar week for each species-year-region combination now has a value equivalent to the proportion of the flight period that occurred in that week.

Step 4. For each species-site-year combination (‘species-site-year’ from here), the calendar weeks in which the trap was running were extracted. As the dataset only included positive counts, true zero counts had to be inferred. For each night (or multi-night period) with a positive count for any species, all other species that were not caught that night were recorded as zero. Weeks for which no records existed were classified as inoperative. For a week to be classed as operative, at least one count, of any species, had to occur.

Step 5. For each species-site-year, each calendar week was matched to the appropriate flight season for that species in that year in that region (north/south). The total proportion of the flight period sampled for that species-site-year was then estimated as follows. Each week within each species-site-year has already been allocated as either operative or inoperative (Step 4). Each operative week for each species-site-year was compared against the regional flight period for that species-year-region combination. For all operative weeks, the proportion of the flight period that occurred within each week was extracted (Step 3) and summed. The resulting figure is referred to from here on as ‘site-year completeness’ and takes a value from 0 to 1. Where a site was operative throughout the entire flight period for a species-site-year, the site-year completeness was equal to 1.

Step 6. ‘Site indices’ were calculated for each species-site-year by dividing the raw sum (total number of individuals of that species caught in that site-year) divided by the site-year completeness for that species. For example, if 100 individuals were caught, and site-year completeness was 0.8, then the resulting ‘site index’ would be equal to 125 This is the estimated number of individuals that would have been caught had the trap been continually running. Where site-year completeness is 1 (i.e., complete), then the site index is equal to the raw sum. Site indices are used as the response variable in all models involving abundance in this thesis.

Note that a site-year can have different site-year completeness scores for different species within the same year. For example, if a trap is running throughout summer but is inoperative in autumn, species with summer flight periods will have site-year completeness score of 1, whereas species with flight periods overlapping autumn will have a site-year completeness score of less than 1.

As well as species-specific annual abundances, total abundance of macro-moths per site-year was also estimated in the same way, but with the following adjustments. Rather than counts of individual species, the summed total of all moths captured per night was used. The first and final two weeks of the year (Julian weeks 1, 2, 51 and 52) were ‘anchored’, i.e., dummy zeros were imputed to improve the stability of the flight period estimation. This method is commonly used in modelling butterfly abundance trends (Rothery and Roy, 2001). This technique is used to prevent the GAM from extrapolating early and late season counts into the middle of winter where there were no records, which would result in spuriously large estimations of the proportion of the flight season occurring in winter. This technique reduces the influence of moths with substantial proportions of their flight periods in late December and early January from models involving total moth abundance. However, as there are only four species in this study for which this is the case: *Conistra vaccinia* (Chestnut), *Conistra ligula* (Dark Chestnut), *Operophtera fagata* (Northern Winter Moth) and *Operophtera brumata* (Winter Moth). The total number of individuals caught of these four species accounted for only 2.1% of the total number of moths recorded in the dataset (239,964 out of 11,298,188) so the effect of this artefact is assumed to be negligible. Furthermore, three out of these four species have the majority of their flight periods outside of December and January (Randle, 2019) and are therefore less affected by the flight period anchoring. It is only the Winter Moth that peaks in December, and this species accounted for only 0.89% of all individuals recorded.

In all models, to prevent spurious estimations, any species-site-year combination which had a completeness of less than 0.5 was omitted.

2.3.5.2 Species richness and diversity

Species richness and diversity were estimated using (individual-based abundance) rarefaction in the iNEXT package (Hsieh et al., 2016). These measures are based on the Hill numbers (see section 4.3.6.2 and Chao et al. (2014)). Species richness (H = 0) is the estimated number of species present at each site. Species diversity (H = 1) is based on the Shannon diversity index and is expressed as the number of ‘effective common species’ (section 4.3.6.2), but will be referred to as ‘diversity’ from here on. Both linear and non-linear changes in diversity according to habitat type and region were modelled using linear mixed models (LMM) and additive mixed models (GAMM), respectively. The LMMs were used to test whether the change in species richness/diversity was significant and whether there was a significant interaction between year and habitat and/or region. The percentage change was calculated using the predicted species richness/diversity in the first and last year of the time series. GAMMs were run primarily for visualisation and to supplement the information provided by the linear models. The GAMMs were also used to test whether the baseline species richness/diversity differed significantly between habitat/region while ignoring the time factor. Data exploration revealed that the estimated species richness and diversity was positively related to the estimated completeness of the site-year (Fig. S2.1) so site-year completeness was included as an explanatory variable in all models to account for this.

Effect of habitat

To estimate linear changes in species richness and diversity, two linear mixed effects models were run: one for species richness and one for diversity. Models were run using the lmer() function in the lme4 package (Bates et al., 2015). Number of species (or ‘effective common species’ - see above) per year was modelled as a function of the interaction between year and habitat plus site-year completeness, with random intercepts for each site and each year. A Gaussian error distribution was assumed. To test if the year:habitat interaction was significant, the model was refitted with ML instead of REML and a nested model without the interaction was compared against the full model with the interaction using a likelihood ratio test. If a significant interaction was detected through model difference ($p < 0.05$), then a post hoc test was run using the emmeans package (Lenth, 2019) to determine which slopes differed significantly from zero. The emtrends() function was used to extract the estimated year coefficient for each habitat along with the 95% confidence intervals. The slope was considered as statistically significant when the 95% CIs did not overlap zero.

Non-linear changes in species richness and diversity were modelled with a GAMM using the gam() function in the mgcv package (Wood, 2017). Species per year was modelled as the function of the interaction between year and habitat, using the ‘by’ argument, as in s(year , by = habitat), plus a parametric effect of habitat, plus a smooth term for site-year completeness. Thin-plate regression splines were used. Random effects for site and year were included using simple random effect structures with the bs = “re” argument within gam().

Effect of region

Both LMMs and GAMMs were run as above but with region (north/south) replacing habitat as the factor with which year interacts. There were not enough sites for most habitats to include a region:habitat interaction, but there were at least 20 sites for both broadleaf woodland and improved grassland, so these habitats were investigated separately. The dataset was split into two subsets: one containing only broadleaf woodland sites and one containing only improved grassland sites. The same models were then run on these two subsets.

Overall changes in species richness and diversity

To determine how species richness and diversity has changed across the country as a whole, a final series of LMMs and GAMMs were run, whilst putting habitat and region aside due to lack of model power. The model structures were the same as above but without any interaction effects.

2.3.5.3 Total abundance trends

The R package poptrend (Knape, 2016) was used to fit Generalised Additive Mixed Models (GAMM) to model change in abundance over time. This package uses the underlying mgcv package and offers advantages over other abundance trend models such as Generalised Abundance Index (GAI) or Generalised Additive Models (GAM) by including a random year effect that absorbs year-to-year 'noise' and detects the true 'signal' of the trend (Knape, 2016). Simulations have shown that this technique reduces the likelihood of detecting a false trend. The model returns a single value for percentage change in abundance. A further benefit of this package is that the significance of short-term trends within the long-term trend is tested. When plotted, significant short-term declines are displayed in orange and significant increases in green. This allows important periods of change to be located within the time series.

Effect of habitat

Eight models were run: one including all sites and one for each of the seven habitat types separately. A tensor product smooth for latitude and longitude, and altitude were included in all models apart from sparsely populated habitat models (i.e. conifer plantation, 'other semi-natural' and upland habitats) where the smaller sample sizes did not allow for these covariates. In all models, an additional random effect for site was added using the bs = “re” term within the mgcv package. A starting k value of 16 was used for the year effect, following Fewster et al. (2000) who recommends that non-linear degrees of freedom should be one third the length of the time-series. Generalised cross-validation within the mgcv package was used to reduce the degrees of freedom down to the optimum value. A negative binomial error structure was used, and 95% confidence intervals were calculated using bootstrapping with n = 5000 unless one of the intervals was very close to zero in which case n = 100,000 was used.

The poptrend package only models relative change rather than absolute change in abundance, which, whilst providing a robust comparative model approach, does not indicate the true magnitude of the absolute abundance. Yearly abundance in some habitats is likely higher than in others, but this information is not reported when using poptrend. Thus, to understand the effect of habitat and time on absolute abundance as well as the relative changes, a single GAMM was fit using the mgcv package to model yearly abundance as a function of the interaction between year and habitat with an additional parametric coefficient for habitat. Random effects were included for both year and site to account for repeated measures using the bs = “re” argument. The model predictions were plotted with their 95% confidence intervals, the raw data, and the global geometric mean annual catch to visualise the change in absolute abundance across habitat types.

Effect of region

To understand the differences in abundance change depending on latitude, the UK was split into north and south, and a poptrend analysis was run for the two regions separately. For most habitat types, there were not enough sites in both regions to allow for a region:habitat interaction analysis. However, the improved grassland and broadleaf woodland habitats both had over 20 sites in each region, so a further four models were run: one for each of the two regions in these two habitat types.

2.3.5.4 Species-specific trends

For each species, the change in estimated yearly abundance was modelled using the poptrend package as above, but excluding the latitude, longitude and altitude effects to maximise the number of species that could be modelled. Eight models were run for each species: one for all habitats combined and one model for each of the seven habitat types. In addition to only including site-years with a completeness of at least 0.5 and only using sites with at least three years of data, the following quality-control measures were implemented. For each species-habitat combination, trends were only modelled if (1) the species was recorded in at least six sites, (2) the number of site-years in the model was greater than 100, (3) the number of individuals recorded in the time series was at least 200 and (4) the time series included both the first (1968) and final (2016) year. Despite these checks, the poptrend model occasionally failed to converge on some species-habitat combinations due to insufficient degrees of freedom. These models were also excluded. The estimated percentage change for each species-habitat combination was stored along with the 95% confidence intervals. These estimated percentage changes were used as the response variable in the next stage of modelling.

The effect of habitat on species-specific trends was modelled with LMMs. The trends of each species in each of the seven habitats were used as the response variable. The trends were log(trend + 100) transformed following Dennis et al. (2019) so that the distribution of trends approximated a normal distribution. Trend was modelled as a function of habitat with a random intercept for each species. Each species-habitat observation was weighted according to its log-transformed total sample size using the ‘weights =’ argument. As the uncertainty of the trend was greater for trends with smaller sample sizes, this ensured that more weight was given to trends with more certainty. To test whether the interaction was significant, the model was refitted using ML instead of REML, and a reduced model with the interaction term omitted was compared against the full model with a likelihood ratio test. If significant ($p < 0.05$), a post hoc test was carried out using the emmeans package. The contrasts between the estimated marginal mean trend between habitat types were calculated using the emmeans() function with the Tukey method for multiple comparisons.

2.3.5.5 Habitat-trait interactions

All habitat-trait interaction models followed the same basic structure and procedure. The categorical trait variables were implemented as follows:

1. Feeding guild. Moths were grouped into 13 feeding guilds as described in Table 2.4 but the feeding guilds of ‘mosses’, ‘other’ and ‘unknown’ were excluded as they contained too few species, leaving a total of 10 feeding guilds.
2. Feeding specificity. Moths were grouped into four feeding specificities, ranging from ‘monophagous’ to ‘highly polyphagous’.
3. Habitat specificity. Moths were given an integer value from 1 – 8 based on how many habitats they are associated with.
4. Overwintering stage. Moths were grouped into four overwintering stage groups. Immigrant species that do not overwinter in the UK were excluded as they were too few to model.

The continuous trait variables were implemented as follows:

5. Mean of Ellenberg nitrogen value of host plant. Only species classed as monophagous or near-monophagous were used in this model.
6. Mean of Ellenberg light value of host plant. Only species classed as monophagous or near-monophagous were used in this model.
7. Forewing length.

A separate model was run for each of the seven traits. Modelling procedure was as described above (section 2.3.5.4), but the trends were modelled as a function of the interaction between habitat and species trait. For categorical variables, the significance of the difference in mean abundance trend between habitats within each feeding guild was tested using the joint_tests() function. The contrasts between the estimated marginal mean abundance trend between habitat types were calculated for each feeding guild, using the emmeans() function with the Tukey method for multiple comparisons.

For continuous trait variables, post hoc tests using the emtrends() function in the emmeans package were used to determine which slopes differed from each other, using the Tukey method for multiple comparisons. The 95% CIs of the estimated marginal means of the slopes were also extracted using this function, and they were considered to be significant if the CIs did not overlap zero.

Where there was no significant trait-habitat interaction, the habitat term was removed from the model, and the overall abundance trends for each species was used as a response variable. In these cases, a simple linear model was run, again, using log(sample size) as a weighting factor for each species. The significance of the species trait in predicting abundance trend was tested by running a reduced model against the full model and comparing the two models with an F test, as before.

In addition to these models, a model was run with an interaction between habitat specificity, feeding specificity and habitat. This interaction model was run to account for the possibility that the two ‘specificity’ traits interact in determining a species’ risk of decline. For example, it may be the case that monophagous species are more likely to decline, but only if they are also habitat specialists. The significance of each model term was tested as described above. If there was no significant interaction with habitat, the term was removed from the model.

2.3.5.6 Climate variables

The annual abundance of moths cannot be simply modelled against climate variables such as average temperature as both of these variables may be correlated with time, leading to spurious conclusions (Iler et al., 2017). To address this, climate variables and annual moth abundance were detrended using the following procedure. Seven separate linear regression models were run: one for each of the six climate variables and one for log-transformed annual (site index) moth abundance. The response variable in each case was modelled as a function of the interaction between year (continuous) and site. A Gaussian error structure was assumed for all models. The residuals from each model were extracted, and response variables were scaled by subtracting the mean and dividing by the standard error. These residuals became the detrended climate data. The detrended variables retain information about relative annual temperature and precipitation but do not retain any information about long-term changes. See Iler et al. (2017) for more information.

Climate-habitat interaction

An LMM was run in which moth abundance residuals were modelled as a function of the interaction between habitat and each of the six climate variables. A random slope for each variable at each site was also included. The initial model structure was as follows:

```
lmer(Moth_abundance_resids ~ Summer_temp_resids*Habitat  +
Summer_rain_resids*Habitat + Prev_summer_temp_resids*Habitat +
Prev_summer_rain_resids*Habitat  + Winter_temp_resids*Habitat  +
Winter_rain_resids*Habitat  + (Summer_temp_resids|Site) + (Summer_rain_resids| Site) +
(Prev_summer_temp_resids| Site)+ (Prev_summer_rain_resids| Site) +
(Winter_temp_resids| Site) + (Winter_rain_resids| Site))
```

The model was then simplified using the backwards stepwise approach. Each interaction was removed in turn from the model and was refit in ML instead of REML, and a likelihood ratio test was used to compare the reduced model against the full one. If the interaction was not significant ($p \geq 0.05$) the interaction was dropped, and the process repeated for all other interactions and main effects. Model simplification stopped once all the terms in the model were significant at the 0.05 level. For significant interactions between climate and habitat, post hoc tests were carried out using the emtrend() function to determine which slopes differed from zero.

Climate-region interaction

To investigate the interaction between climate and region (north vs south) in determining abundance trends, the same model was run as above but with the 'habitat' factor replaced with 'region'. Model simplification and interpretation were then carried out as before. To include the effect of habitat, the full dataset was split into two subsets: broadleaf woodland sites and improved grassland sites. The same modelling process was then applied to these two data sets separately.

Climate-overwintering stage interaction

The process described in this section was repeated, with the following adjustments. Moth abundance per site-year was summed for moths in each of the four overwintering stages (egg, larva, pupa, adult). The site index was calculated as before, by dividing the total by the site-year completeness, and the resulting site-indices were log(x + 1)-transformed as the variables contained zeros. Transformed abundance was modelled against year as before and the residuals extracted. The model structure, as described above, was then rerun but with ‘overwintering stage’ as the interacting factor rather than habitat or latitude. Model simplification and interpretation then continued as before.

2.4 Results

A total of 11,298,188 macro-moths belonging to 756 species within thirteen families were caught across 349 sites between the years of 1968 and 2016. The maximum number of years sampled at any site was 49, and any site with fewer than three sample years was excluded. The mean years sampled per trap was 11.5.

2.4.1 Species richness and diversity

2.4.1.1 Overall trends

Linear trend

There was no significant effect of year on species richness (LRT, X2 = 1.63, p = 0.20) but there was a significant effect of year on diversity (LRT, X2 = 5.88, p = 0.015, 9.1%) which increased over time (Fig. 2.2).

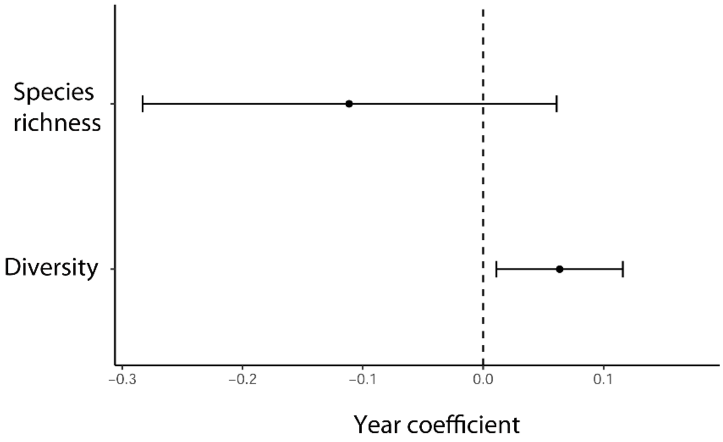


Fig. 2.2. Overall changes in species richness and diversity 1968 - 2016. *Year coefficients with 95% CIs from two GLMMs modelling species richness/diversity as a function of year. Each model included all 349 sites. Dashed line shows zero effect.*

Non-linear trend

There was a significant non-linear trend for both species richness (p = 0.0003) and diversity (p = 0.006) (Table S2.3). Species richness showed a hump-shaped trend with a peak around 1990 (Fig. 2.4 a).

2.4.1.2 Effect of habitat

Linear trend

There was a significant year:habitat interaction for species richness (X^2 = 26.84, p = 0.0002) and diversity (X^2 = 37.07, p < 0.0001). Post hoc tests showed that changes in richness/diversity did not change significantly in most habitats, although broadleaf woodland showed significant declines in both measures (Fig. 2.3). The largest significant percentage decrease was for broadleaf woodland, which showed a decline in species richness of -12.5% (Table 2.5). The largest increase was for arable habitat, which showed an increase in diversity of 24.1%. Overall, there were more increases in species richness and diversity than there were decreases.

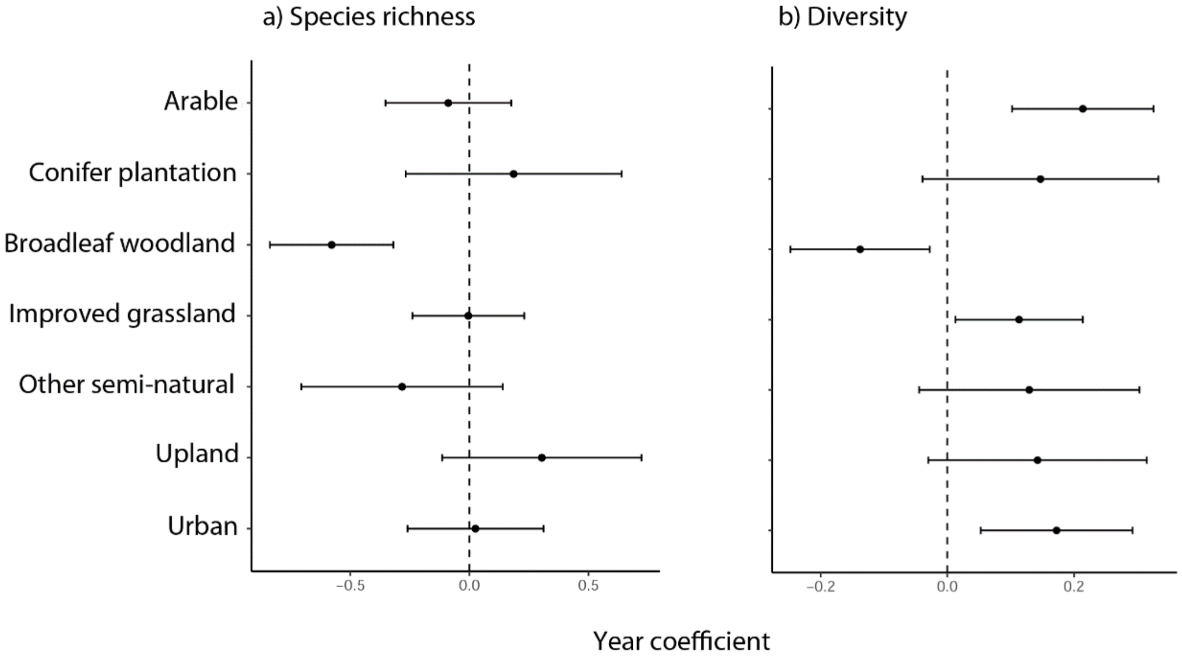


Fig. 2.3. Overall changes in species richness and diversity 1968 – 2016, split by habitat. *The estimated marginal mean year coefficients with associated 95% CIs for each habitat type from two GLMMs with response variables (a) species richness, and (b) diversity (effective common species).*

Table 2.5. Post hoc analysis of changes in species richness and diversity 1968 – 2016, split by habitat. *The marginal mean year coefficients and associated standard errors (SE) and 95% CIs from two GLMMs. The predicted percentage change in species richness of diversity (effective common species) between 1968 – 2016 is shown. Habitat-specific year coefficients are considered significant if the 95% CIs do not overlap zero - these are highlighted in bold. Analysis was done in the emmeans package in R.*

Response	Habitat	Year coef.	SE	CI lower	CI upper	Perc. change
Species richness	Arable	-0.089	0.135	-0.352	0.175	-2.3%
	Conifer plantation	0.186	0.231	-0.268	0.639	4.6%
	Broadleaf woodland	**-0.578**	**0.132**	**-0.837**	**-0.319**	**-12.5%**
	Improved grassland	-0.005	0.120	-0.239	0.230	-0.12%
	Other semi-natural	-0.283	0.216	-0.705	0.140	-7.3%
	Upland	0.304	0.213	-0.114	0.722	10.7%
	Urban	0.025	0.146	-0.260	0.311	0.75%
Diversity (effective common species)	**Arable**	**0.214**	**0.057**	**0.1024**	**0.325**	**24.1%**
	Conifer plantation	0.147	0.095	-0.039	0.333	11.7%
	Broadleaf woodland	**-0.138**	**0.056**	**-0.247**	**-0.028**	**-9.7%**
	Improved grassland	**0.113**	**0.051**	**0.0130**	**0.214**	**10.7%**
	Other semi-natural	0.129	0.089	-0.045	0.303	14.6%
	Upland	0.142	0.088	-0.030	0.315	19.4%
	Urban	**0.173**	**0.061**	**0.0528**	**0.292**	**17.2%**

Non-linear trend

There were significant non-linear changes in species richness and diversity both overall (Fig. 2.4) and over several habitat types (Table S2.4, Fig. 2.5 and Fig. 2.6) with results mostly matching the linear trends. Broadleaf woodland showed a significant decline in both richness and diversity, whereas arable habitats showed an increase in diversity.

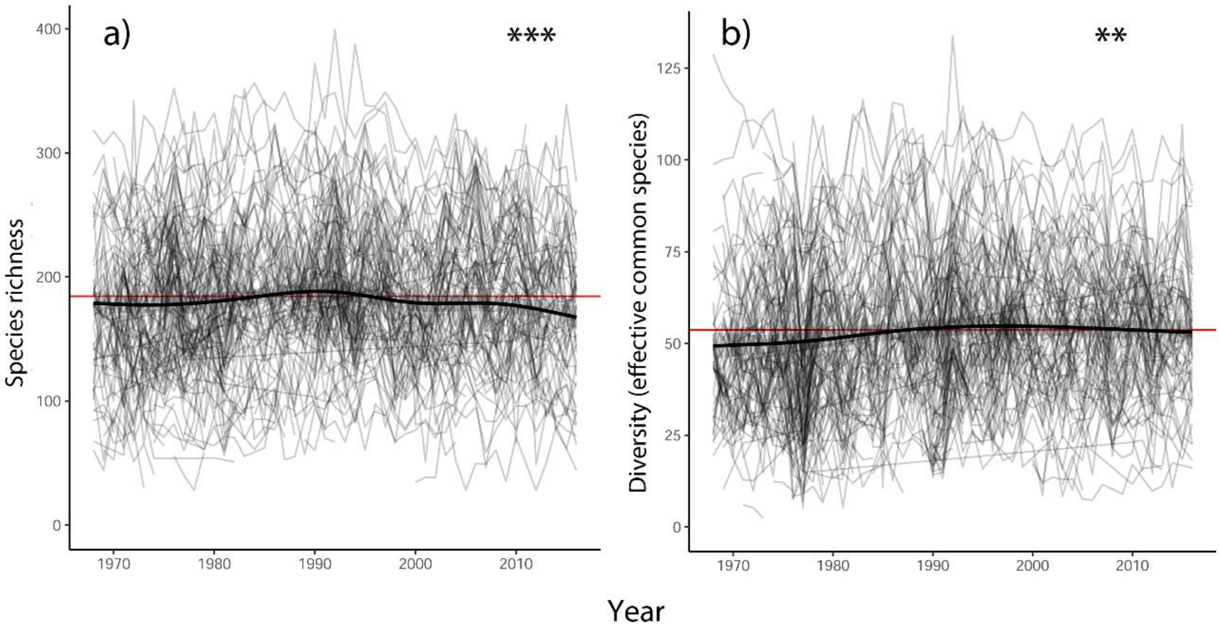


Fig. 2.4. Non-linear trends of species richness and diversity 1968 – 2016. *Model predictions from two GAMMs with response variables: (a) species richness, and (b) diversity (effective common species). Solid black line and grey ribbon show model predicted means and 95% CIs. Grey lines show the raw data. Red line shows global geometric mean average. Asterisks denote the significance of the fixed effect smooth term for year ($p < 0.05$ '*', < 0.01 '**', < 0.001 '***')*

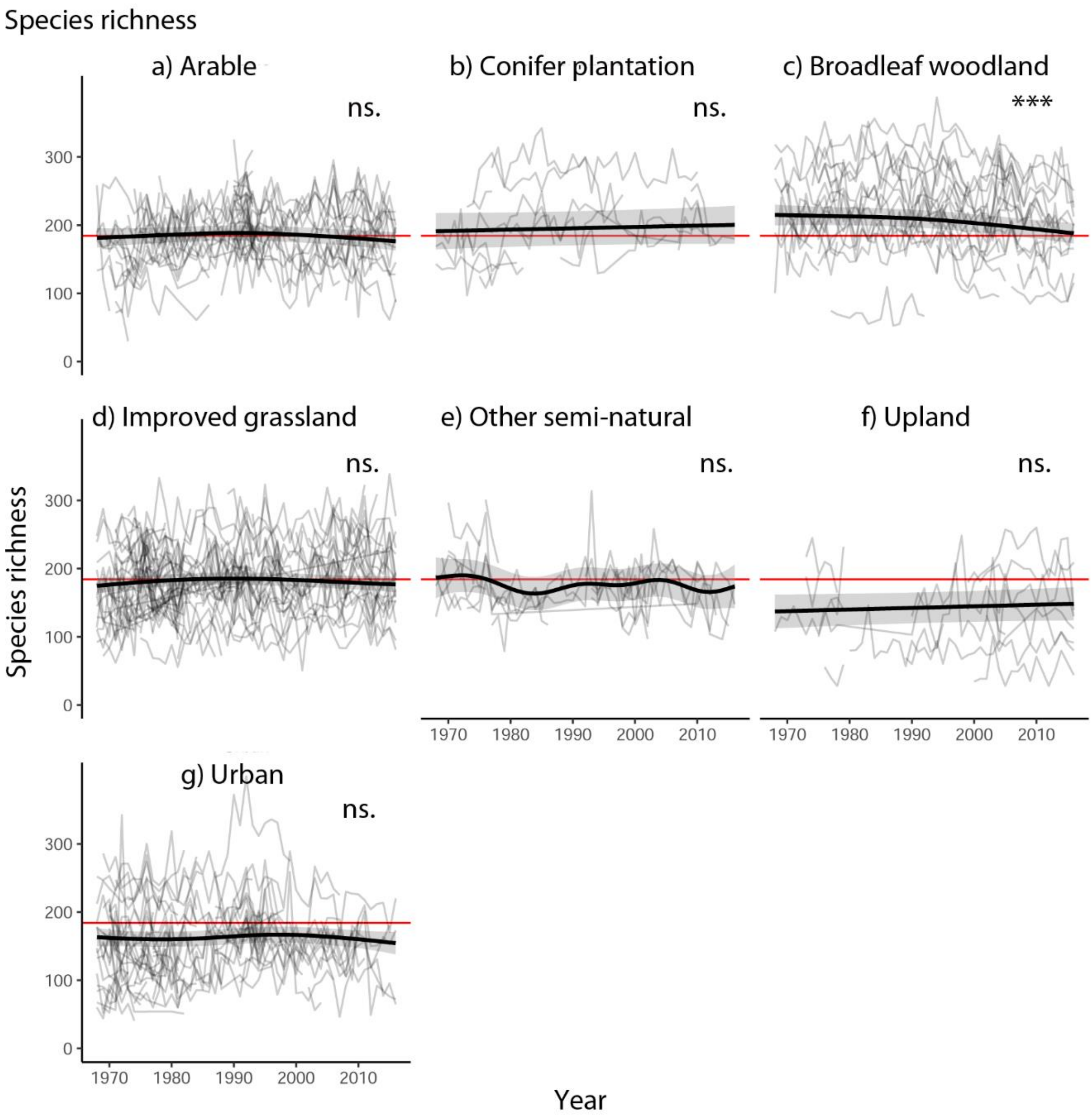


Fig. 2.5. Non-linear trends of species richness 1968 – 2016, split by habitat. *Model predictions from a GAMM that modelled species richness as a function of the interaction between year and habitat. Solid black line and grey ribbon show model predicted means and 95% CIs. Grey lines show the raw data. Red line shows global geometric mean average. Asterisks denote the significance of the fixed effect smooth term for year ($p < 0.05$ '*', < 0.01 '**', < 0.001 '***')*

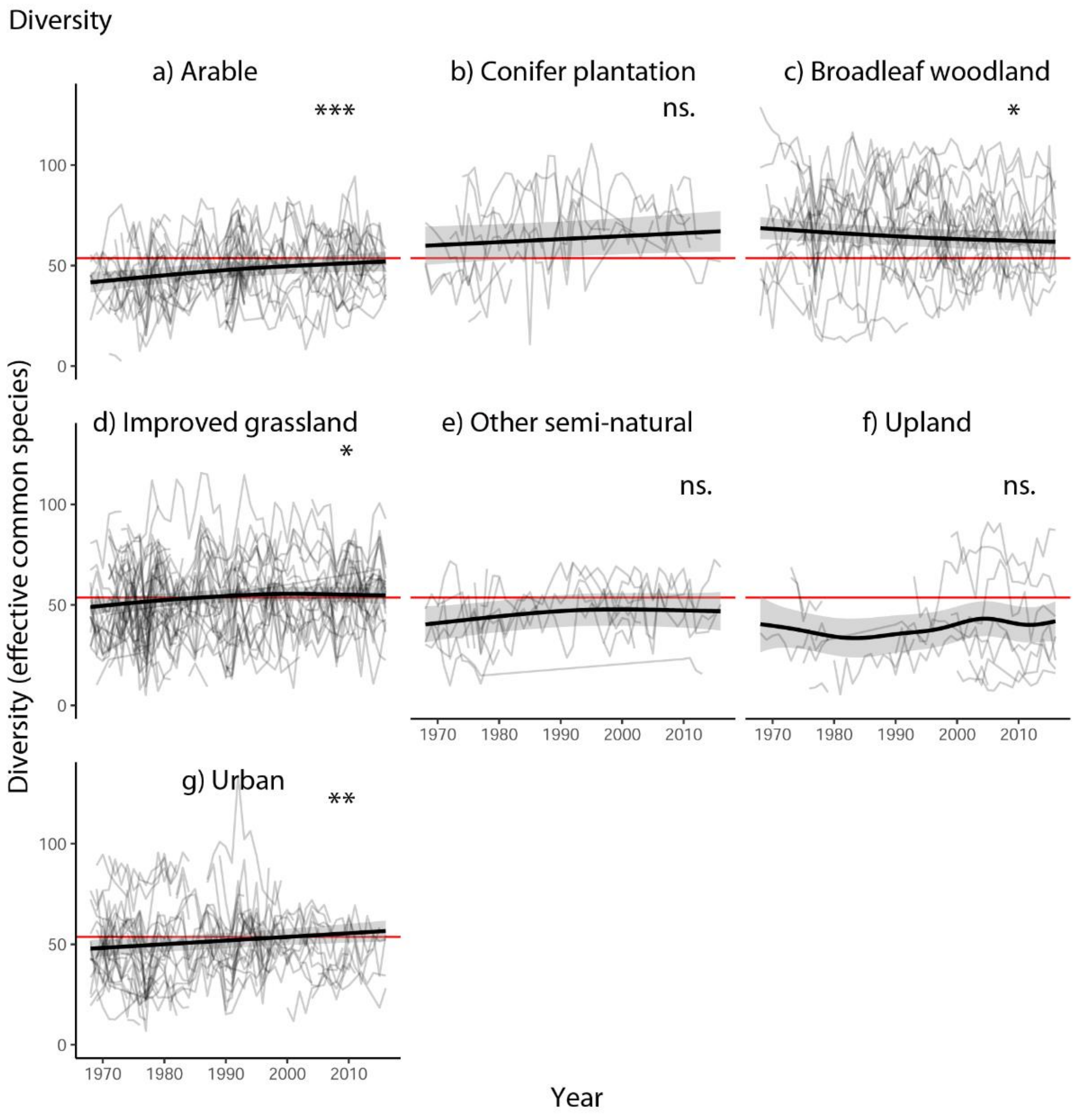


Fig. 2.6. ***Non-linear trends of species diversity 1968 – 2016, split by habitat.*** *Model predictions from a GAMM that modelled species diversity (effective common species) as a function of the interaction between year and habitat. Solid black line and grey ribbon show model predicted means and 95% CIs. Grey lines show the raw data. Red line shows global geometric mean average. Asterisks denote the significance of the fixed effect smooth term for year (p < 0.05 '*', < 0.01 '**', < 0.001 '***')*

2.4.1.3 Effect of region

Linear trend

There was a significant year:region interaction effect for species richness (LRT, $X^2 = 21.39$, $p < 0.0001$) but not for diversity (LRT, $X^2 = 2.68$, $p = 0.102$, Fig. 2.7). Within broadleaf woodland habitat, there was no significant year:region effect for species richness (LRT, $X^2 = 1.97$, $p = 0.160$) but there was a significant effect for diversity (LRT, $X^2 = 6.35$, $p = 0.012$). Within Improved grassland habitat, there was a significant year:region interaction effect for species richness (LRT, $X^2 = 20.7$, $p < 0.0001$) but no significant effect for diversity (LRT, $X^2 = 0.62$, $p = 0.432$). In all cases where the effect of region was significant, the trends of northern sites were positive and the trends of southern sites were negative. Post hoc tests showed that in several cases, the trend of richness/diversity was significantly positive in the north and significantly negative in the south (Table 2.6).

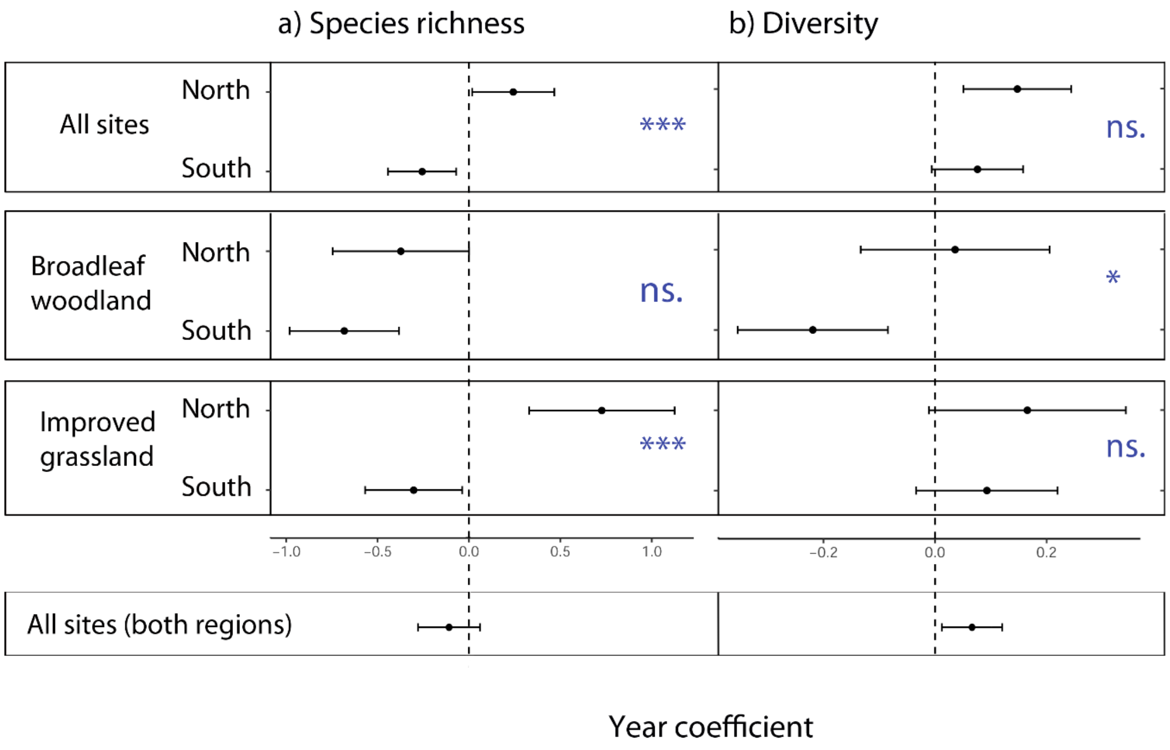


Fig. 2.7. Linear trends of species richness and diversity 1968 – 2016, split by region and habitat. *The estimated marginal mean year coefficients and 95% CIs extracted from six LMMs where (a) species richness, and (b) diversity (effective common species) were modelled as the function of the interaction between year and region (north/south). The top panel includes all sites, the second panel includes only broadleaf woodland sites and the third panel included only improved grassland sites. The bottom panel includes all sites for comparison. Dashed lines show zero effect. Asterisks denote the significance of the year:region interaction effect ($p < 0.05$ '*', < 0.01 '**', < 0.001 '***'). Analysis was done in the emmeans package in R.*

Table 2.6. Post hoc analysis of linear trends of species richness and diversity 1968 – 2016, split by habitat and region. The estimated marginal mean year coefficients with associated standard errors and 95% CIs extracted from three separate LMMs where species richness and diversity (effective common species) were modelled as the function of the interaction between year and region (north/south). Predicted percentage change in species richness/diversity across the whole time series (1968 – 2016) are shown. Year coefficients are considered significant if the 95% CIs do not overlap zero and are highlighted in bold. Post hoc tests were only performed on models for which the year:region interaction was significant at the $p < 0.05$ level (Fig. 2.7). Analysis was done in the emmeans package in R.

Response	Habitat	Region	Year coef.	SE	CI lower	CI upper	Perc. change
Species richness	All sites	**North**	**0.242**	**0.115**	**0.017**	**0.467**	**7.58%**
		South	**-0.256**	**0.095**	**-0.443**	**-0.070**	**-6.26%**
	Improved grassland	**North**	**0.726**	**0.202**	**0.329**	**1.124**	**23.9%**
		South	**-0.303**	**0.135**	**-0.569**	**-0.037**	**-7.29%**
Diversity (effective common species)	Broadleaf woodland	North	0.036	0.086	-0.133	0.205	3.28%
		South	**-0.219**	**0.068**	**-0.354**	**-0.084**	**-13.5%**

Non-linear trend

GAMMs showed that both the baseline species richness and diversity were typically lower in the north but tended to increase over time while richness and diversity were higher in the south but tended to decrease over time (Fig. S2.2, Fig. S2.3 and Table S2.5). A notable exception is that species richness in broadleaf woodland in the north shows a hump-shaped trend with a peak around 1990.

2.4.2 Total abundance

2.4.2.1 Overall trend and effect of habitat

Between 1968 and 2016, total moth abundance in the UK significantly declined by -36% (Fig. 2.8). Abundance significantly declined in all habitat types; arable: -18%, conifer plantation: -30%, broadleaf woodland: -44%, improved grassland: -34%, other semi-natural: -45%, upland:

-47% and urban: -47%. Several habitats showed non-linear trends: in broadleaf woodlands total moth abundance had a period of stability after which it declined, whereas upland and ‘other semi-natural’ sites showed the opposite pattern with the period of decline in the earlier part of the time-series, after which it stabilised. The significance of the smooth terms in the GAMM generally agreed with the poptrend models for all habitat types (Fig. 2.9, Table S2.6), apart from arable, for which the trend was significant in the poptrend model but marginally non-significant in the GAMM ($p = 0.063$). In comparison to arable sites as a reference level, the baseline abundance was significantly higher in conifer plantation ($z = 1.973$, $p= 0.049$) and broadleaf woodland sites ($z = 2.334$, $p = 0.020$) and significantly lower in urban sites ($z = -6.948$, $p < 0.0001$, Table S2.6).

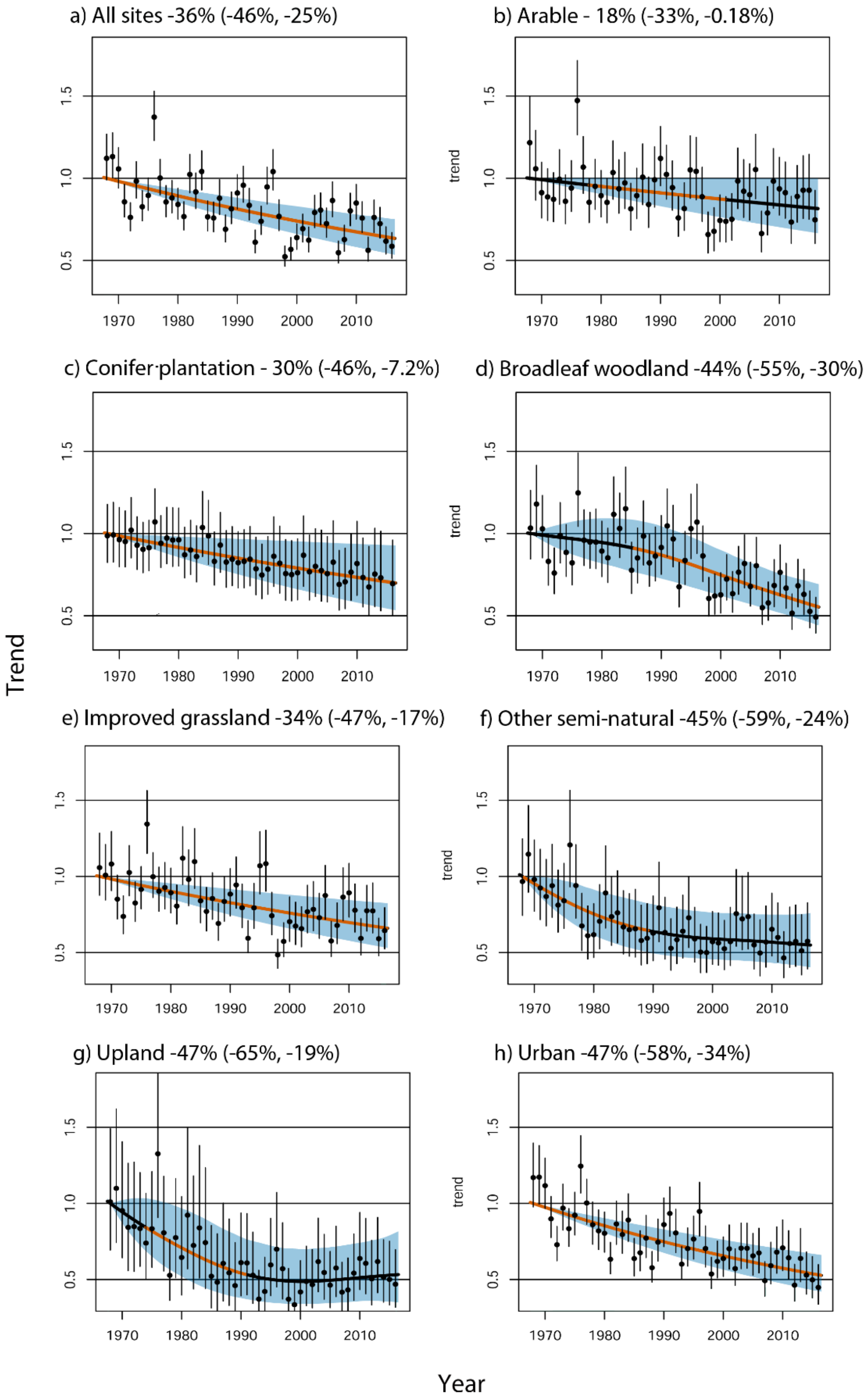


Fig. 2.8. ***Poptrend models of total abundance 1968 – 2016, split by habitat.*** *Trends of total moth abundance across (a) all sites and (b – h) seven habitat types. The black line shows the long-term trend and significant periods of decline are indicated with an orange line. The 95% confidence intervals are shown in blue. The percentage change for each habitat (± 95 % CI) is shown in text above each plot. Points and whiskers represent year random effects. All trends are relative and scaled to the starting year (1968) at 1. Models shown here were run in the 'poptrend' package in R.*

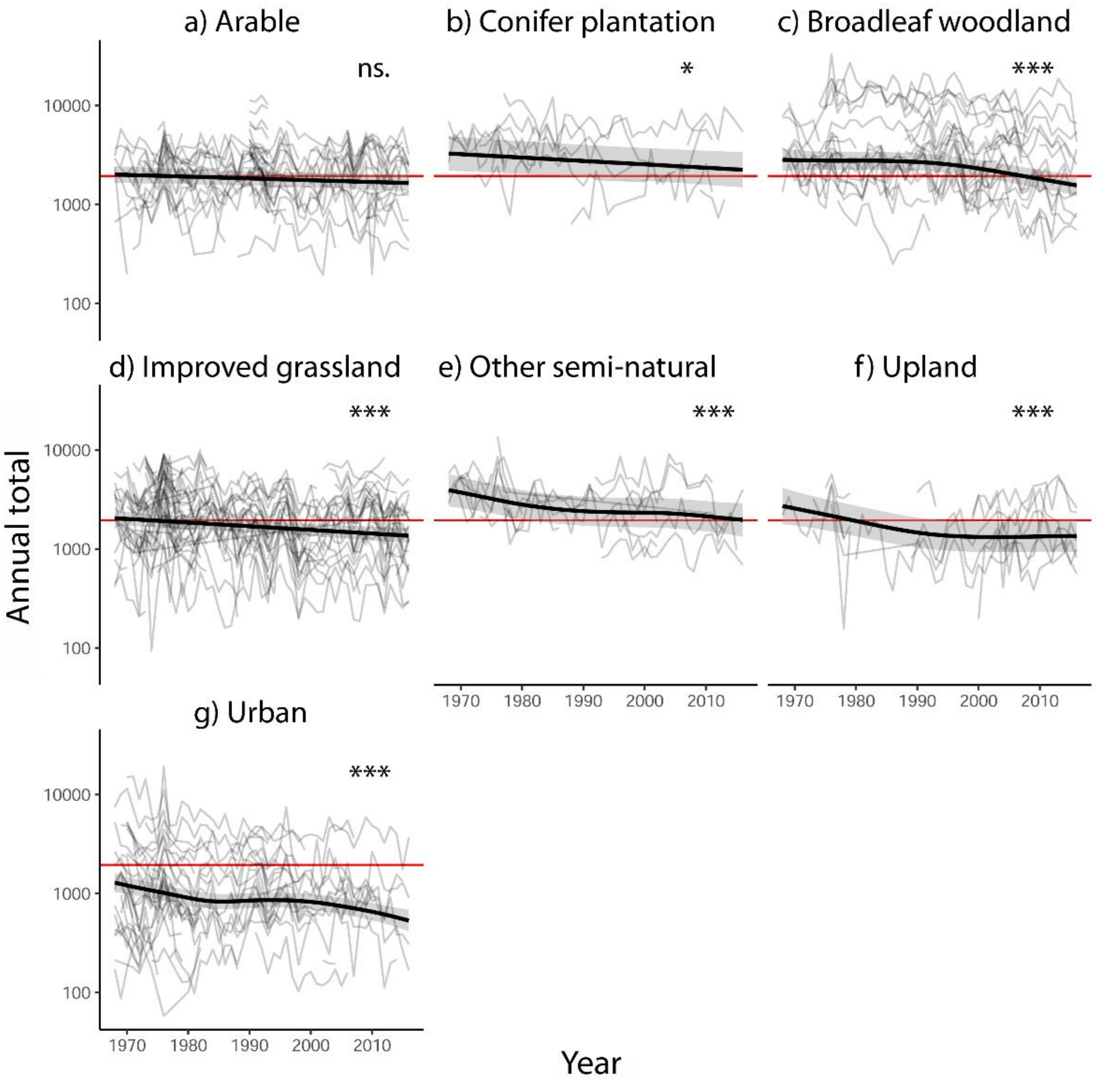


__Fig. 2.9. Non-linear trends of total abundance 1968 – 2016, split by habitat__. Model predictions from a GAMM that modelled annual abundance as a function of the interaction between year and habitat. Solid black line and grey ribbon show model predicted means and 95% CIs. Grey lines show the raw data. Red line shows global geometric mean average. Note the log-scale on the y-axis. Asterisks denote the significance of the fixed effect smooth term for year ($p < 0.05$ ‘’, < 0.01 ‘**’, < 0.001 ‘***’)*

2.4.2.2 Effect of region

Moth abundance declined significantly in both the north and the south by -25% and -41%, respectively (Fig. 2.10). When two habitat types, broadleaf woodland and improved grassland, were analysed separately, there was no significant overall change in the northern sites in either habitat, but abundance declined significantly in the south by -51% in broadleaf woodland and by -39% in improved grasslands. The abundance trend of moths in northern broadleaf woodland had a period of significant increase during the 1970s and a period of significant decline during the 1990s and 2000s. The abundance trend in southern improved grasslands was stable until the early 1980s whereafter it declined until the year 2000 and then stabilised.

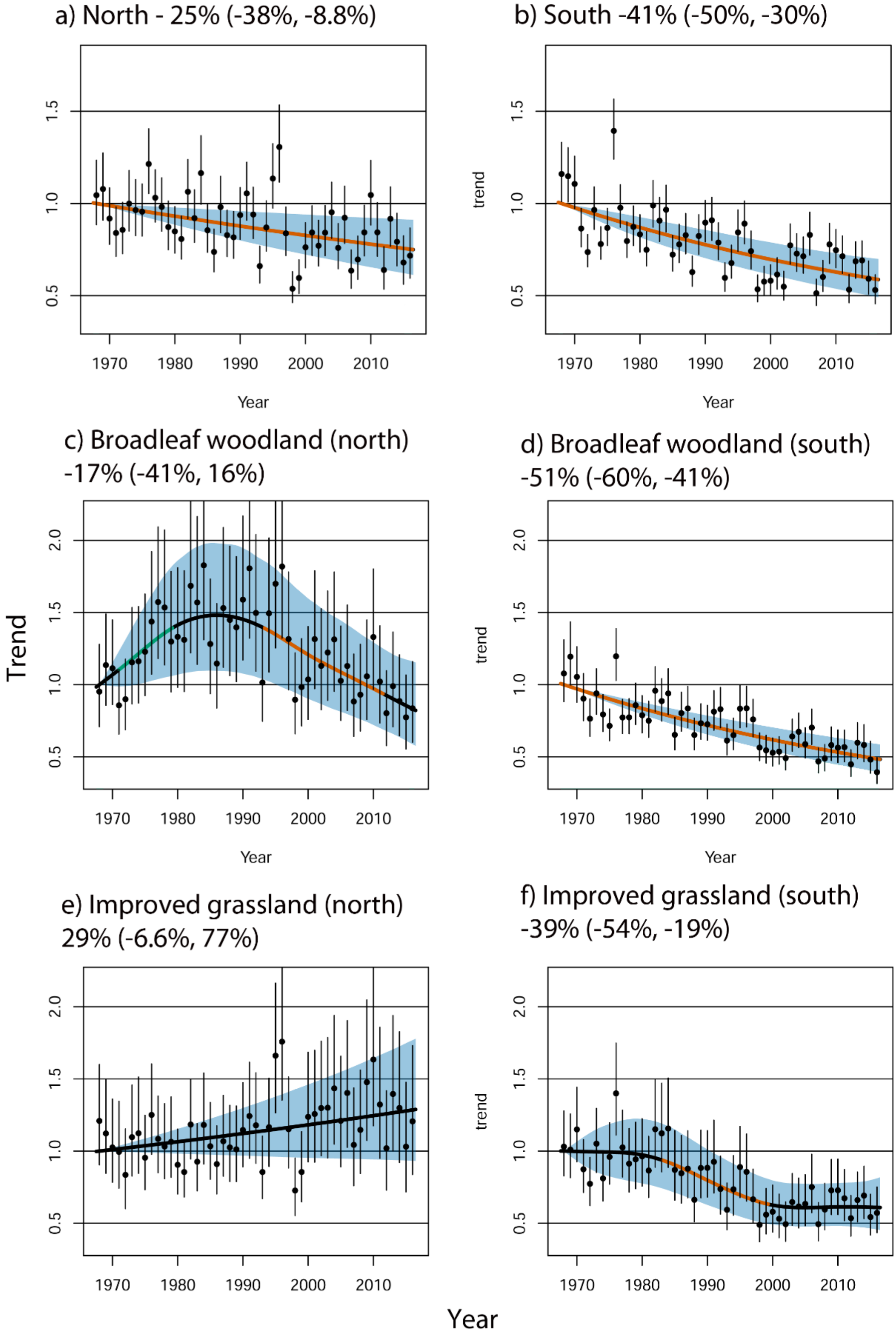


__Fig. 2.10. Poptrend models of total abundance 1968 – 2016, split by habitat and region.__ Trends of total moth abundance with sites split by (a – b) region and (c – f) both region and habitat type. The black line represents the trend. Significant periods of decline are indicated with an orange line and significant periods of increase with a green line. The 95% confidence intervals are shown in blue. Points and whiskers represent year random effects. All trends are relative and scaled to the starting year (1968) at 1. Models shown here were run in the 'poptrend' package in R.

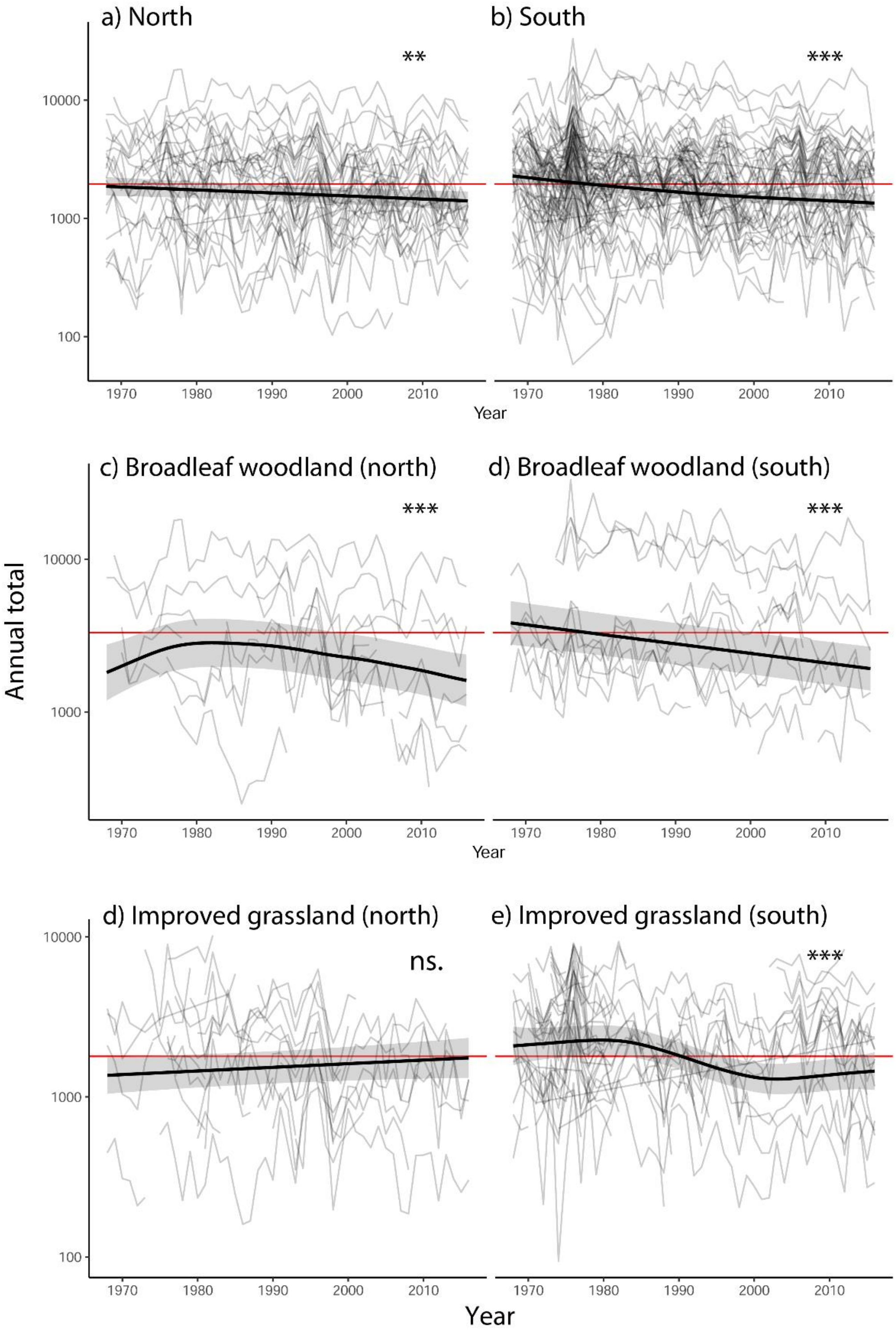


Fig. 2.11.Non-linear trends of total abundance 1968 – 2016, split by habitat and region**. Model predictions from three GAMMs that modelled annual abundance as a function of the interaction between year and region. In (a) and (b), all sites were included, in (c) and (d) only broadleaf woodland sites were included and (d) and (e) only improved grassland sites. Solid black line and grey ribbon show model predicted means and 95% CIs. Grey lines represent the raw data adjusted for missing counts. Red line shows global geometric mean average. Note the log-scale on the y-axis. Asterisks denote the significance of the fixed effect smooth term for year (p < 0.05 ‘*’, < 0.01 ‘**’, < 0.001 ‘’)*

2.4.3 Species-specific trends and habitat

A total of 376 species had enough data to be modelled for at least one habitat type. There was a significant effect of habitat on abundance trends (LRT, X^2 = 109.4, $p < 0.0001$, Fig. 2.12 and Fig. S2.4). A post hoc test showed that the majority of significant pairwise comparisons were between the arable habitat and uplands, in which species were stable on average, and the other habitats in which species were generally declining (Table S2.8). In addition, average species trends in urban sites were found to be declining more than in improved grassland sites.

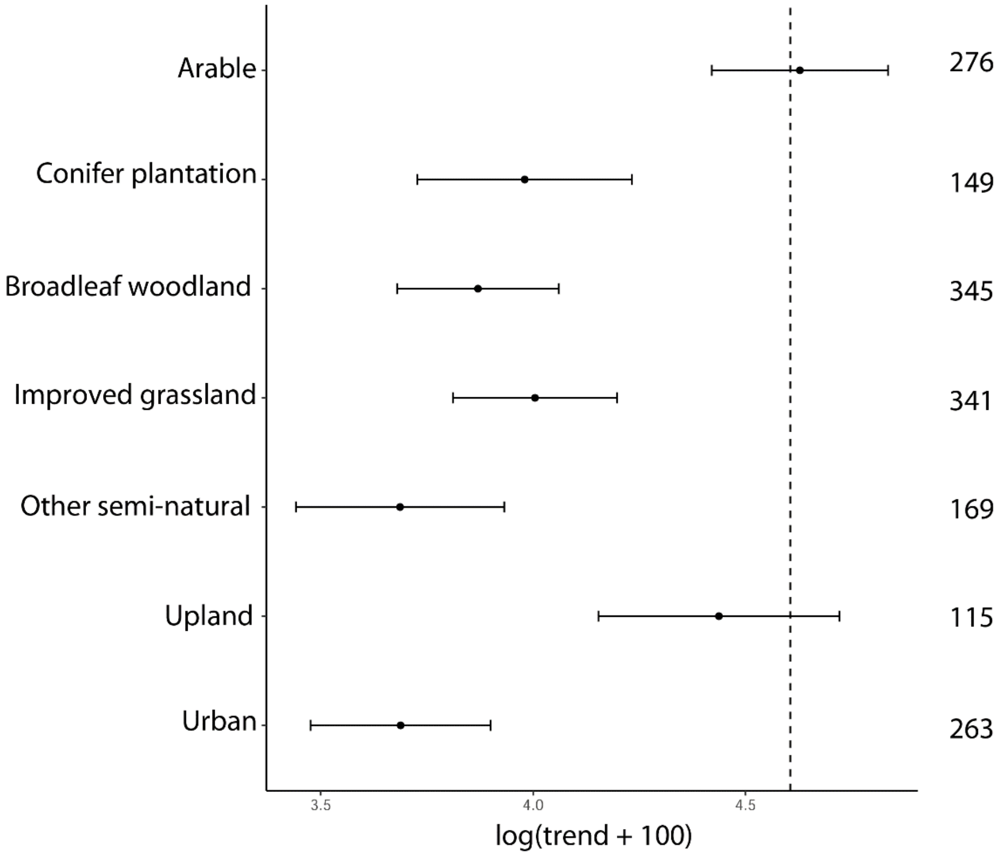


Fig. 2.12. Mean species-specific abundance trends 1968 – 2016, split by habitat. *Estimated marginal mean abundance trends (± 95% CIs) of moths across seven habitat types. The response variable is the percentage change in abundance for each species, log(x + 100)-transformed. Figures on the right show the number of species modelled in each habitat. Dashed line shows zero trend. The same plot with raw data included can be seen in Fig. S2.4.*

2.4.4 Habitat-trait interactions

2.4.4.1 Feeding guild

Overall, there was a significant effect of feeding guild on abundance trend ($F_{9,383}$ = 5.04, p = < 0.0001, Fig. 2.13). A post hoc test showed that this effect was driven almost entirely by lichen-feeders which had more positive abundance trends than most groups (Table S2.9).

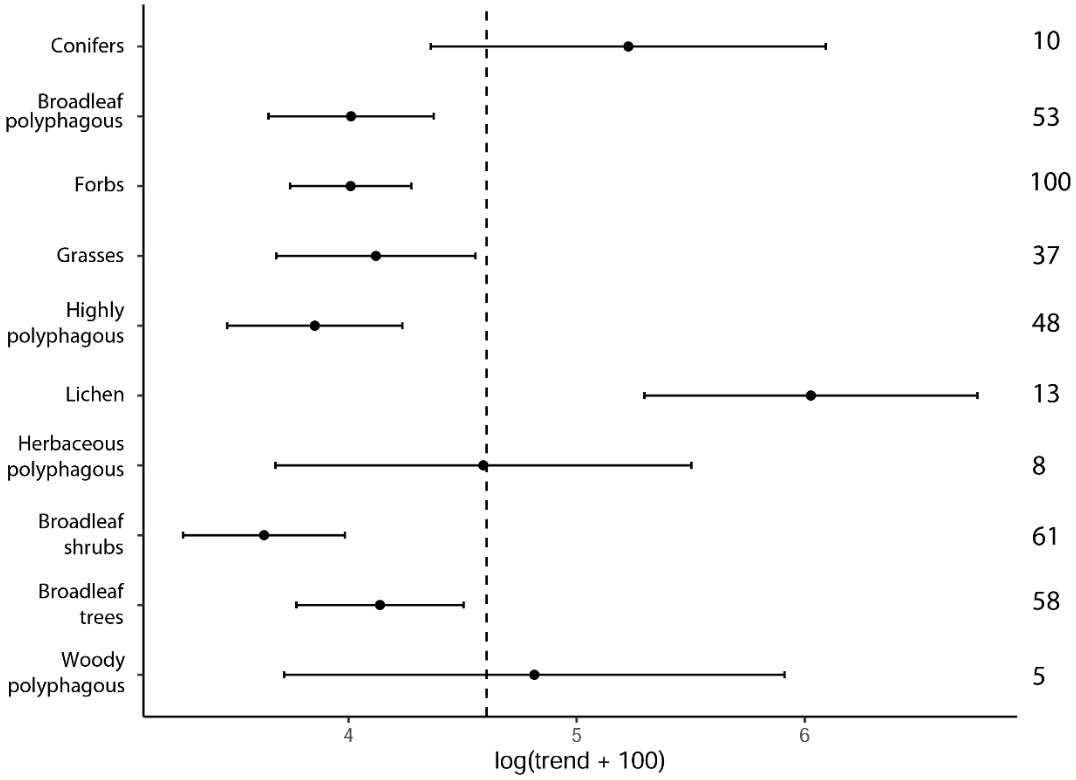


Fig. 2.13. Mean species-specific abundance trends of moths in 10 feeding guilds 1968 – 2016. *Estimated marginal mean abundance trends (± 95% CIs) of moth species belonging to 10 feeding guilds. The response variable is the percentage change in abundance for each species from 1968 – 2016, log(x + 100)-transformed. Figures on the right show the number of species in each group. Dashed line shows zero trend.*

There was a significant interaction between habitat and feeding guild (LRT, X^2 = 94.031, p = 0.0006). A post hoc test showed that moth trends significantly differed between habitats in seven out of the 10 feeding guilds (Fig. 2.14 and Table S2.10). Of the 210 possible pairwise comparisons, 25 of these were found to be statistically significant at the p < 0.05 level (Table S2.11). The feeding guild-specific species trends across habitats tended to match the overall pattern across habitats (compare Fig. 2.13 with Fig. 2.14) with species in arable and upland sites faring best and those in urban and 'other semi-natural' sites faring worst. Some exceptions to this included lichen-feeders in urban habitats whose trends were relatively positive compared to urban as a whole, and broadleaf-, broadleaf shrub- and woody plant-feeders in 'other semi-natural' habitats whose trends were also relatively positive.

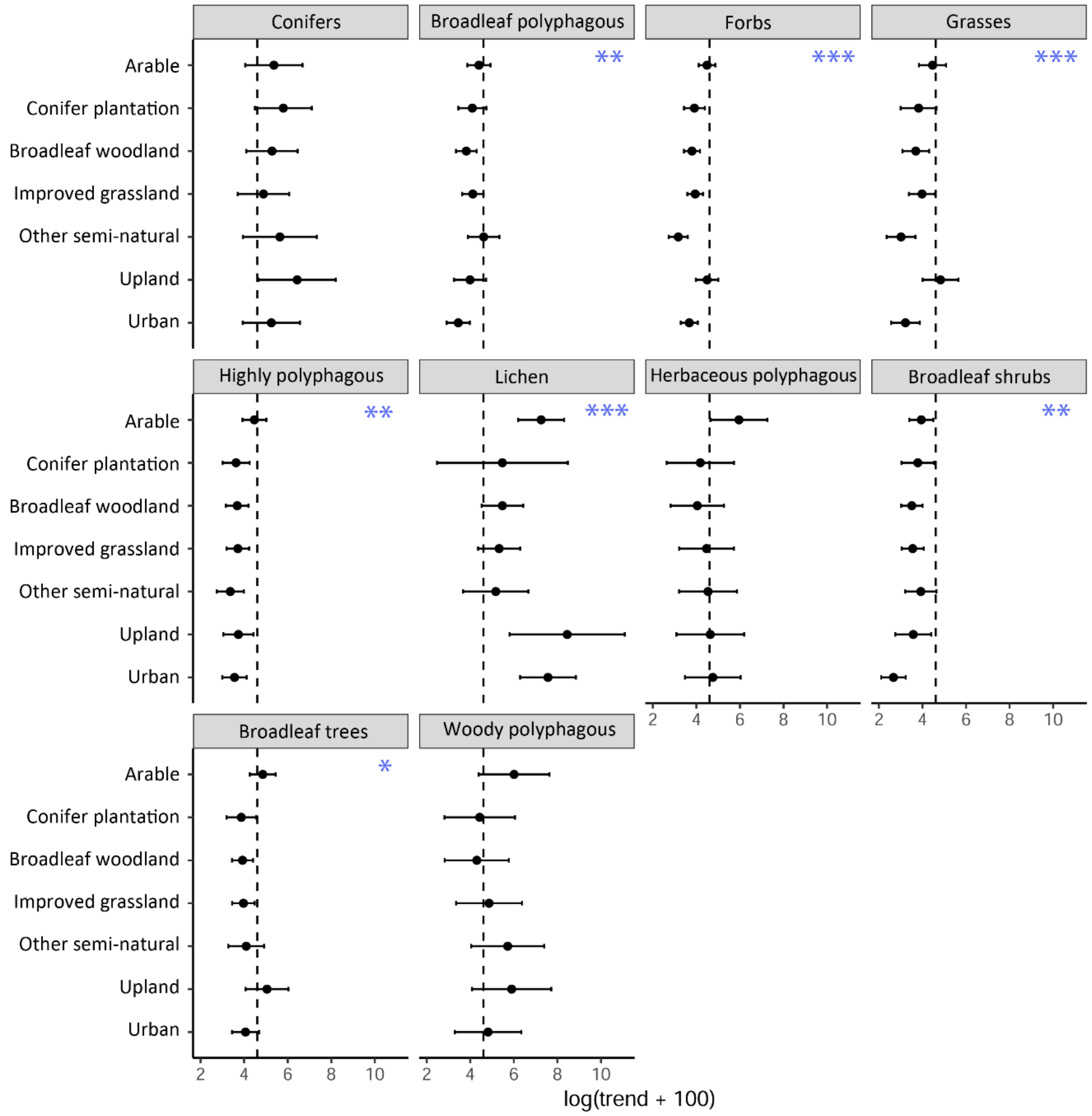


Fig. 2.14. ***Mean species-specific abundance trends of moths in 10 feeding guilds 1968 – 2016, split by habitat****. Estimated marginal mean abundance trends (± 95% CIs) of moths in 10 feeding guilds in seven habitat types. The response variable is the percentage change in abundance for each species from 1968 – 2016, log(x + 100)-transformed. Dashed line shows zero trend. Asterisks denote the significance of a post hoc test that determines whether the trends differ significantly among habitats within each feeding guild (p < 0.05 '*', < 0.01 '**', < 0.001 '***').*

2.4.4.2 Feeding and habitat specificity

The was no significant interaction between feeding specificity, habitat specificity and habitat (LRT, X^2 = 92.5 p = 0.30). When this three-way interaction was removed, there was no significant interaction between habitat and feeding specificity (LRT, X^2 = 26.4, p = 0.09) and no significant interaction between habitat and habitat specificity (LRT, X^2 = 48.4, p = 0.081). When habitat was dropped from the model, there was no interaction between habitat specificity and feeding specificity ($F_{16,366}$ = 0.57, p = 0.91). When the 'habitat specificity:feeding specifity' interaction was dropped from the model, there was no significant effect of habitat specificity ($F_{6,382}$ = 0.35, p = 0.91) or feeding specificity ($F_{3,382}$ = 0.70, p = 0.55).

To confirm that there was no effect of habitat specificity on moth abundance trends, the whole modelling procedure described above was repeated but with habitat specificity treated as a continuous variable (with values 1 – 8) rather than a categorical variable. This gave the models more power to detect subtle linear effects of habitat specificity as it used fewer degrees of freedom. Again, there was no significant three-way interaction effect (LRT, X^2 = 23.7, p = 0.16) and there was no significant interaction between habitat and habitat specificity (LRT, X^2 = 3.17, p = 0.79). When the effect of habitat was removed, there was no interaction between habitat specificity and feeding specificity ($F_{3,384}$ = 0.29, p = 0.83). When all interactions were removed, there was no effect of habitat specificity ($F_{1,387}$ = 1.06, p = 0.30).

2.4.4.3 Overwintering stages

Overall (disregarding habitat type), there was a significant effect of overwintering stage on mean abundance trend ($F_{3,387}$ = 6.74, p = 0.0002, Fig. 2.15). A post hoc test showed the effect was driven primarily by differences in trends between those that overwinter as eggs and those that overwinter as larvae or adults (Table S2.12). Those overwintering as eggs had declined most whereas those that overwinter as adults tended to remain stable. There was a significant interaction between habitat and overwintering stage (LRT, X^2 = 31.27, p = 0.027). A post hoc test showed that the moth trends significantly differed between habitats in three out of the four overwintering stages with no significant effect of habitat in moths that overwinter as adults (Fig. 2.16, Table S2.13). Of the 84 possible pairwise comparisons, 15 of these were found to be statistically significant at the $p < 0.05$ level (Table S2.14). Despite the significant habitat:overwintering stage interaction, the effect of habitat seemed consistent across the three major overwintering stages (egg, larva and pupa) with species faring best in arable and upland habitats and worst in urban and 'other semi-natural' habitats (compare Fig. 2.15 with Fig. 2.16). The interaction effect seems to be driven by moths that overwinter as adults as the overall trend is partly reversed here: with those in urban and 'other semi-natural' habitats faring best and those in uplands faring worst. Especially notable is the significant positive trend of species that overwinter as adults in urban habitat compared to the strong negative trends of the other three groups in this habitat.

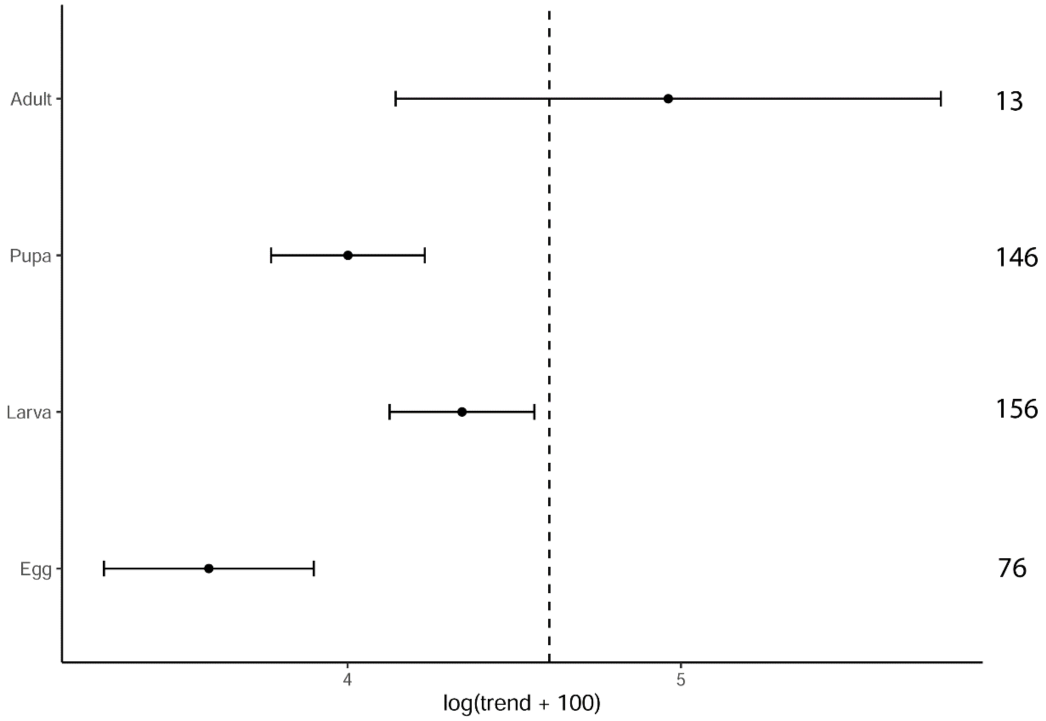


Fig. 2.15. Mean species-specific abundance trends of moths in four overwintering groups 1968 – 2016. *Estimated marginal mean abundance trends (± 95% Cis) of moths belonging to four overwintering stage groups. The response variable is the percentage change in abundance for each species from 1968 – 2016, log(x + 100)-transformed. Figures on the right show the number of species in each group. Dashed line shows zero trend.*

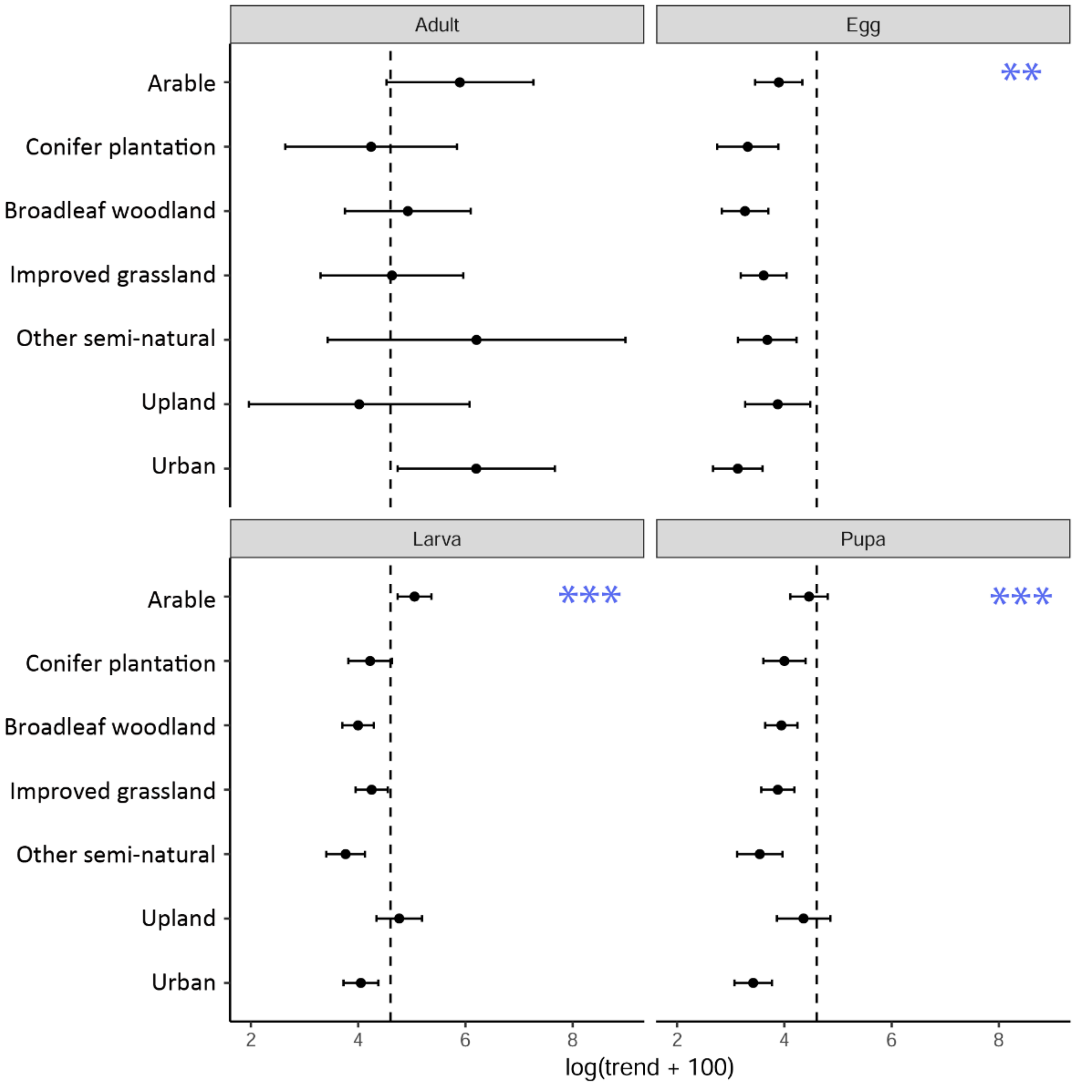


Fig. 2.16. Mean species-specific abundance trends of moths in four overwintering groups 1968 – 2016, split by habitat. *Estimated marginal mean abundance trends in each habitat, split by the overwintering stage of the species. The response variable is the percentage change in abundance for each species from 1968 – 2016, log(x + 100)-transformed. Asterisks denote the significance of a post hoc test that determines whether the trends differ significantly among habitats within each feeding guild (p < 0.05 '*', < 0.01 '**', < 0.001 '***').*

2.4.4.4 Ellenberg values

There was no interaction effect between Ellenberg value for nitrogen and habitat (LRT, X^2 = 6.16, p = 0.41, Fig. 2.17 a). Nor was there a significant interaction between Ellenberg value for light and habitat (LRT, X^2 = 10.9, p = 0.092, Fig. 2.17 b). When the interaction with habitat was removed from the models, there was no effect of Ellenberg value for nitrogen ($F_{3,73}$ = 1.57, p = 0.21) or light ($F_{3,73}$ = 0.20, p = 0.66).

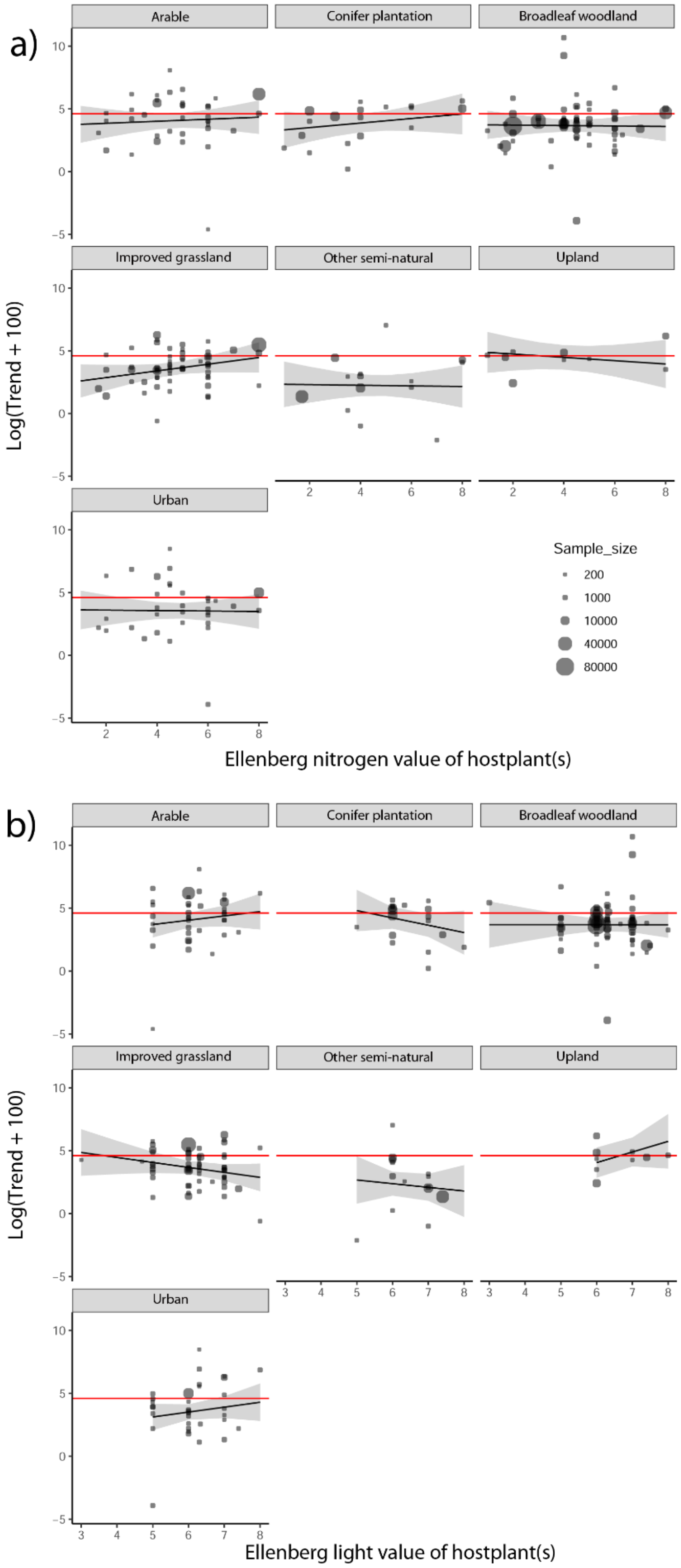


Fig. 2.17. Species-specific abundance trends according to nitrogen- and light-affinity of hostplants. *The effect of Ellenberg (a) nitrogen and (b) light values of host plants on moth abundance trends. The response variable is the percentage change in abundance for each species from 1968 – 2016, log(x + 100)-transformed. Model predictions from LMMs are shown with black lines and 95% Cis by grey ribbons. CIs are for fixed effects only. The raw data is represented in points with the size proportional to the log of the sample size. Red lines show zero trend.*

2.4.4.5 Forewing length

There was no interaction effect between log-transformed forewing length and habitat (LRT, X^2 = 3.094, p = 0.797). When the habitat interaction was removed from the model, there was a significant negative effect of forewing length on abundance trend, with large species decreasing and small species increasing ($F_{1,393}$ = 12.8, p = 0.0004, Fig. 2.18).

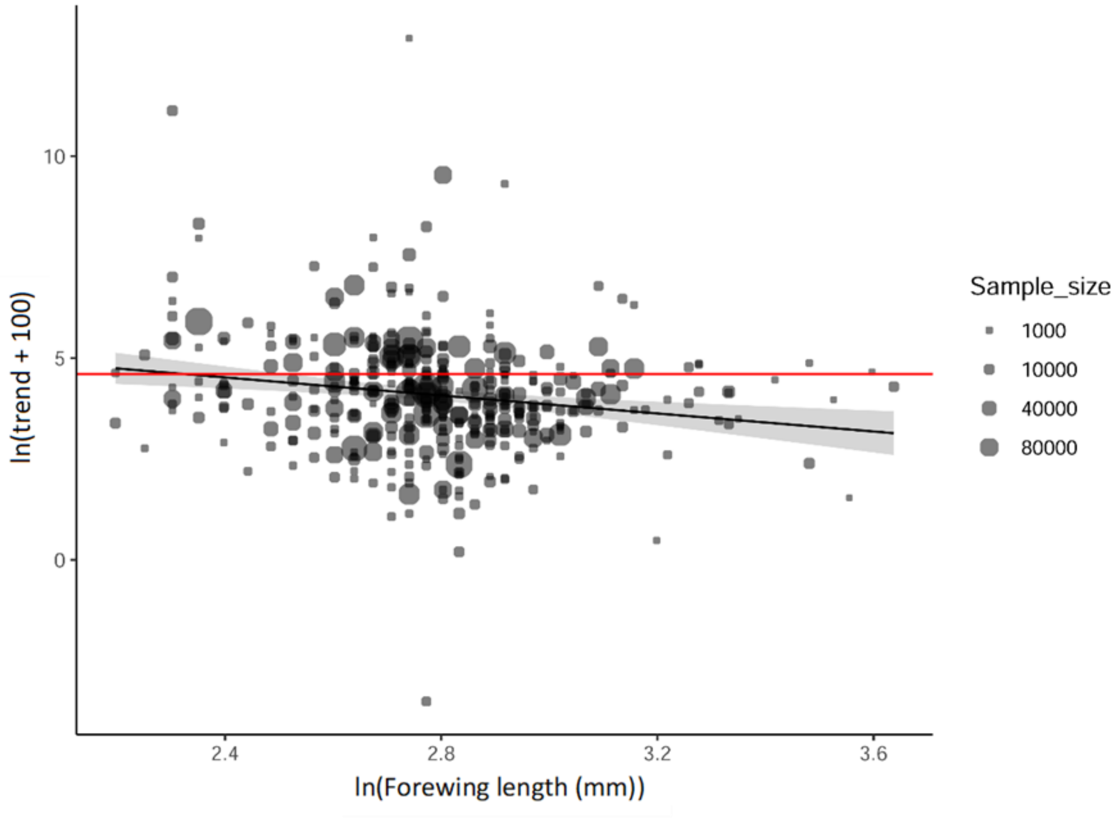


***Fig. 2.18. Species-specific abundance trends according to forewing length**. The response variable is the percentage change in abundance for each species from 1968 – 2016, ln(x + 100)-transformed. Black line with grey ribbon shows model predictions with 95% CIs. Red line shows zero trend. Each point represents one species, with the point size relative to the log of the sample size.*

2.4.5 Climate variables

2.4.5.1 Climate-habitat interaction

Moth abundance declined with increasing summer rainfall in all habitats apart from conifer plantations and uplands (LRT, X^2 = 16.88, p = 0.001, Fig. 2.19, Table S2.15 and Table S2.16). Four other climate variables had a consistent effect across all habitat types: previous summer temperature had a positive effect (effect size = 0.012; LRT, X^2 = 4.03, p = 0.045, Fig. 2.20 a), as did current summer temperature (effect size = 0.060, LRT; $X^2 = 90.27$, $p < 0.0001$, Fig. 2.20 c). Previous summer rainfall had a negative effect (effect size = -0.054, LRT; $X^2 = 76.18$, $p < 0.0001$, Fig. 2.20 b), as did winter temperature (-0.070, LRT; $X^2 = 133.70$, $p < 0.0001$, Fig. 2.20 d). There was no effect of winter rainfall (LRT; $X^2 = 3.16$, $p < 0.076$).

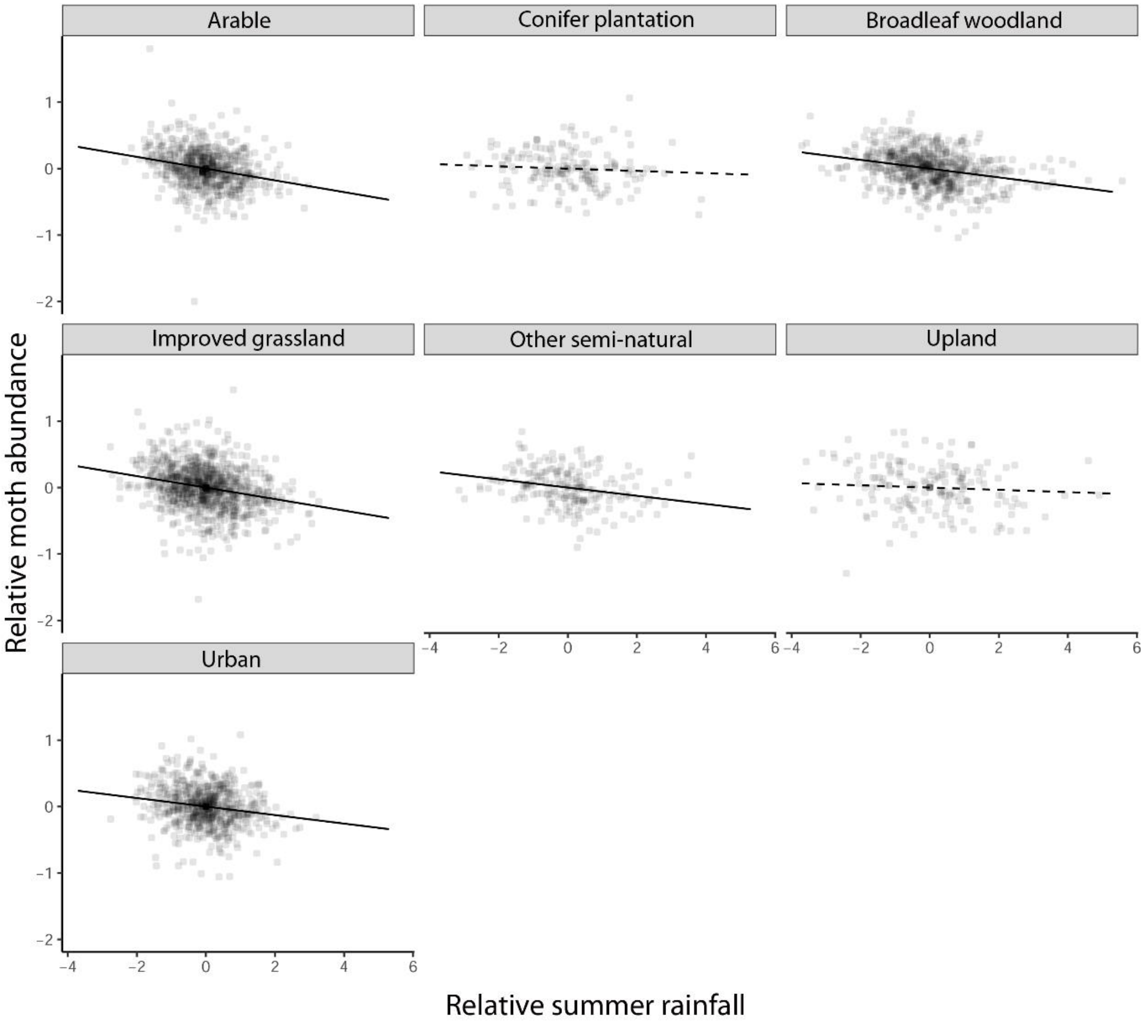


Fig. 2.19. The effect of annual summer rainfall on annual moth abundance in seven habitat types. Summer is defined as April to September. Both variables are detrended and scaled. Lines show model predictions from an LMM with solid lines denoting trends that differ significantly from zero according to a post hoc test, and dashed lines denoting those with no significant trend. Points show raw data.

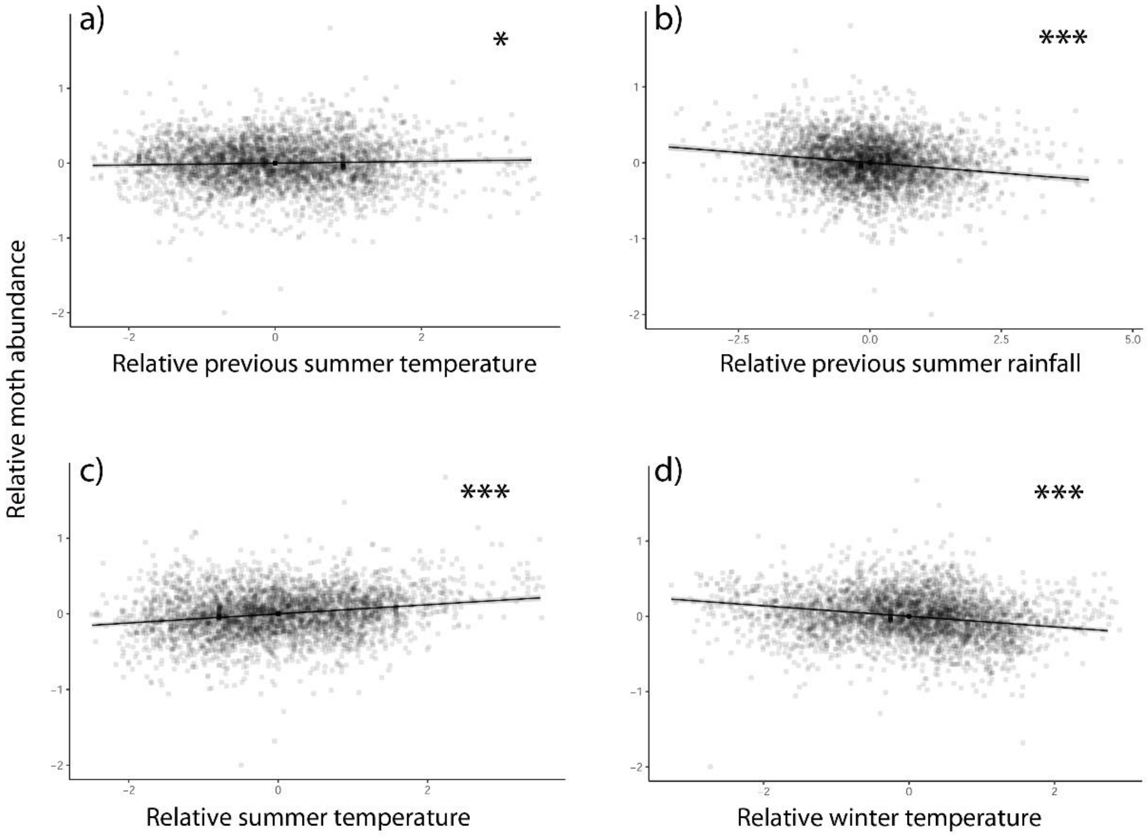


Fig. 2.20. The effect of four climate variables on annual moth abundance**. All variables are detrended and scaled. Lines with grey ribbons show model predicted means (± 95 % CIs) from an LMM. Points show raw data. Asterisks denote the significance of the effect (p < 0.05 '*', < 0.01 '**', < 0.001 '').*

2.4.5.2 Climate-region interaction

Overall, only one climate-region interaction was significant which, again, was summer rainfall (LRT, X^2 = 11.03, p = 0.0008, Fig. 2.21). Abundance was negatively associated with high summer rainfall, but the relationship was more strongly negative in the north (Table 2.7).

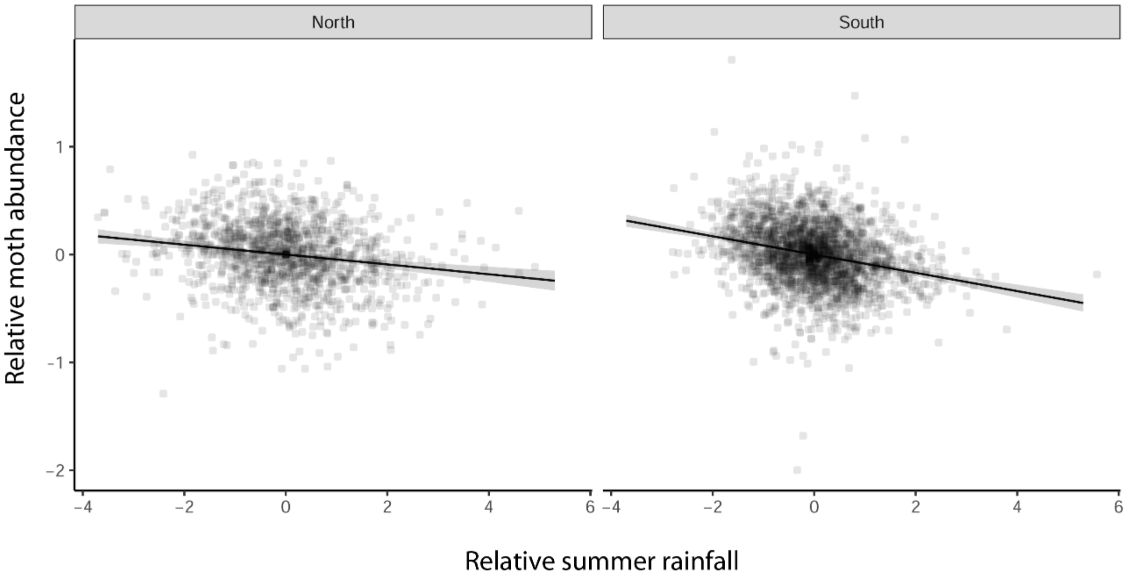


Fig. 2.21. The effect of annual summer rainfall on annual moth abundance, split by region. *Summer is defined as April to September. All variables are detrended and scaled. Lines with grey ribbons show model predicted means (± 95 % CIs from an LMM. Points show raw data.*

Table 2.7. Post hoc analysis to determine whether summer rainfall significantly affects total moth abundance in both regions. *The estimated marginal mean effect of summer rainfall on moth abundance in the north and the south, showing associated standard errors ad 95% CIs. The effect of rainfall is considered significant at the $p < 0.05$ level if the 95% CIs do not overlap zero. Significant effects highlight in bold. Analysis was done in the emmeans package in R.*

Region	Effect of summer rainfall	SE	Df	Lower 95% CI	Upper 95% CI
North	**-0.046**	**0.009**	**Inf**	**-0.063**	**-0.029**
South	**-0.085**	**0.008**	**Inf**	**-0.100**	**-0.070**

Within broadleaf woodland habitat, there were no significant climate-region interactions. Within improved grasslands there was one significant climate-region interaction: the rainfall of the previous summer (LRT, $X^2 = 4.29$, $p < 0.038$). Both slopes were significantly negative, but the effect of previous summer rainfall in the north had a more severe negative effect on abundance than in the south (Fig. 2.22, Table 2.8).

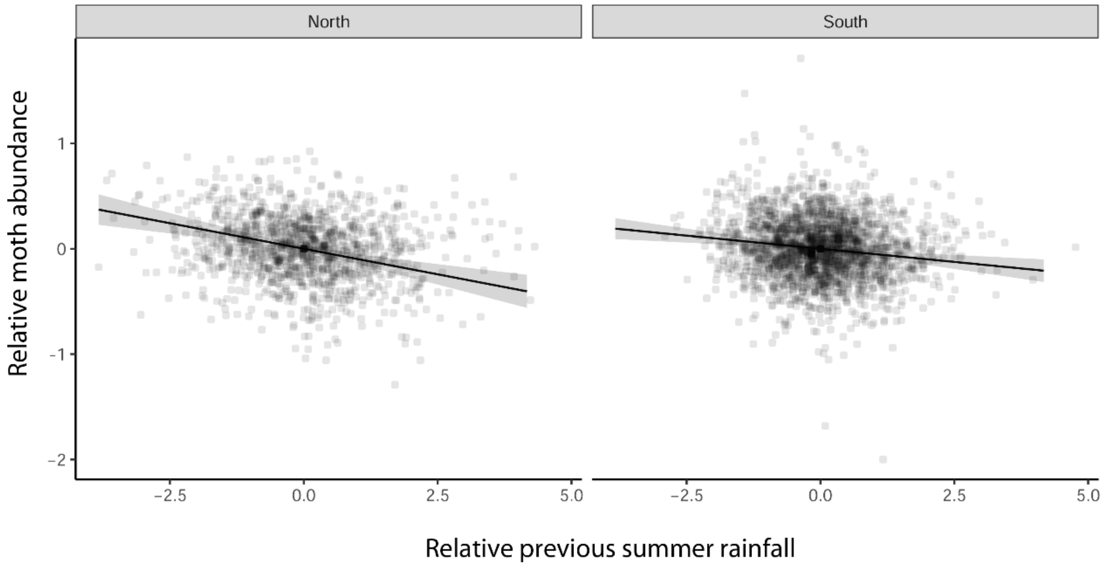


Fig. 2.22. The effect of the previous summer's rainfall on annual moth abundance in improved grassland*. Lines with grey ribbons show model predicted means (± 95 % CIs) from an LMM. Points show raw data.*

Table 2.8. Post hoc analysis to determine whether the previous summer's rainfall significantly affects total moth abundance in improved grassland in both regions. *The estimated marginal mean effect of the previous summer's rainfall on moth abundance in the north and the south (within improved grassland sites only), showing associated standard errors ad 95% CIs. The effect of rainfall is considered significant at the p < 0.05 level if the CIs do not overlap zero. Significant effects highlight in bold. Analysis was done in the emmeans package in R.*

Region	Effect of previous summer rainfall	SE	Df	Lower 95% CI	Upper 95% CI
North	**-0.097**	**0.019**	**37.1**	**-0.136**	**-0.058**
South	**-0.050**	**0.013**	**42.9**	**-0.077**	**-0.023**

2.4.5.3 Climate-overwintering stage interaction

There was a significant interaction between overwintering stage and five out of the six climate variables tested. The only non-significant interaction was for the rainfall of the previous summer (LRT, X^2 = 2.82, p = 420). The interaction between overwintering stage and winter rainfall was weakly significant (LRT, X^2 = 14.2, p = 0.027) and all other interactions were highly significant (p < 0.0001, Fig. 2.23). In the final model, all variance inflation factors for the main effects were below 3, indicating that collinearity in the explanatory variables did not destabilise the model. A post hoc test showed that the interaction effect was driven by different contrasts between overwintering stage depending on the climate variable (Table

S2.17). Typically, those that overwinter as eggs were more negatively affected by warm winters and rainy summers, whereas those overwintering as pupae responded less negatively to these variables. Warm summers were especially beneficial to species that had overwintered as pupae, but this appeared to have a negative impact on the following year's abundance of those same species (Fig. 2.23).

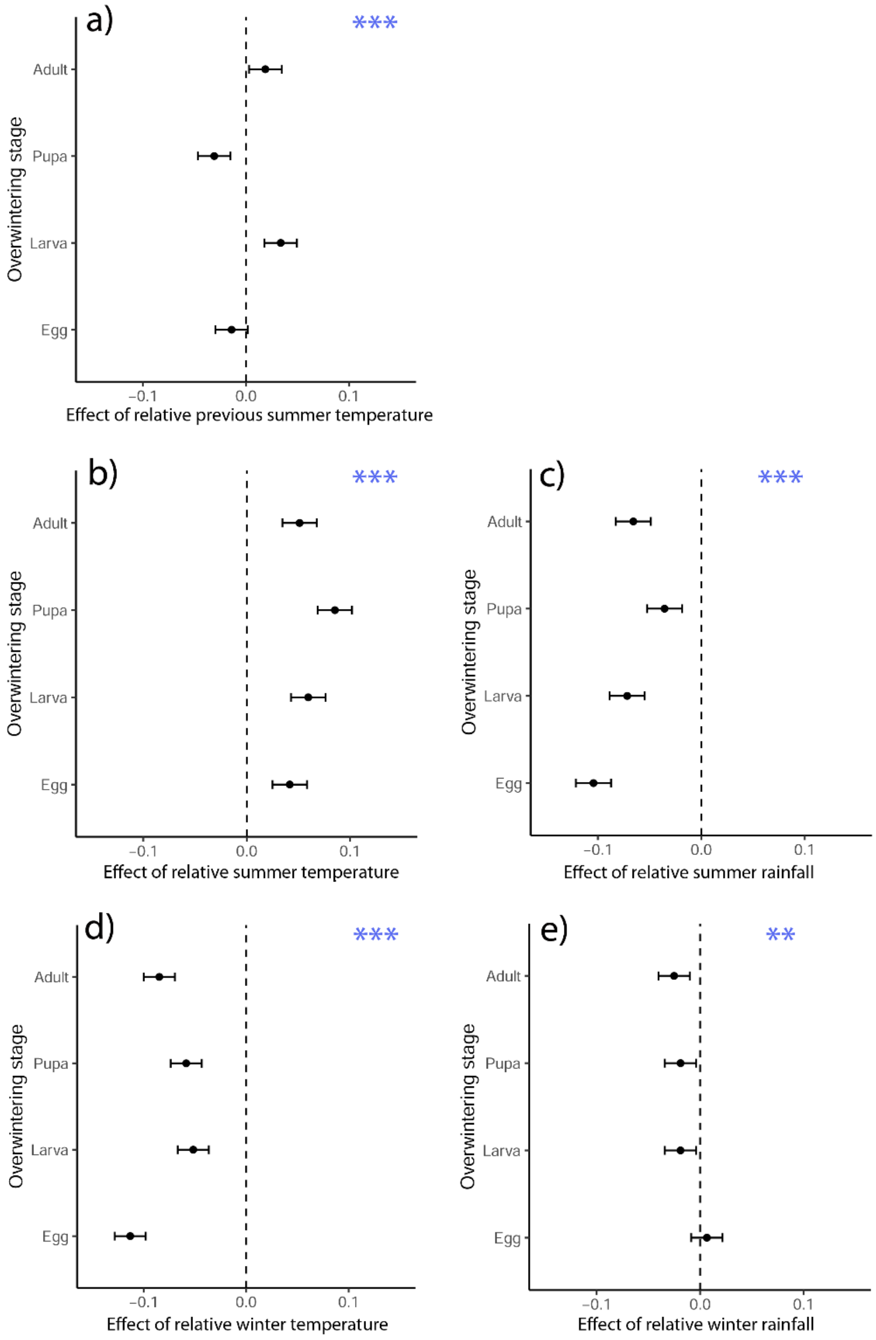


Fig. 2.23. The interaction between climate and overwintering stage in determining annual total abundance. *The estimated marginal mean effects (± 95 % CIs) of five climate variables across species within four overwintering stage groups. Dashed lines show zero effect. Asterisks denote the significance of a post-hoc test that determines whether the climate effect differs significantly among overwintering stages ($p < 0.05$ '*', < 0.01 '**', < 0.001 '***').*

2.5 Discussion

The decline in UK moth abundance since 1968 has occurred in all habitats, but the declines have been the least severe in the most agriculturally intensive areas (Fig. 2.8). Despite declines in abundance, species richness has remained stable, and diversity increased at the national scale (Fig. 2.2). Species richness and diversity have either remained stable or increased across all habitat types apart from broadleaf woodland in which they have fallen (Fig. 2.3). The mechanisms behind the declines in abundance are complex and involve interactions between habitat, climate and species traits. However, the primary cause of decline is still unclear. The estimated total decline in abundance of -36% shown here is more severe than the previous estimation of -31% based on similar data (Bell et al., 2020). The explanation for this discrepancy is twofold: firstly, the subsets of data used in the two studies differed - in this thesis only sites with at least three years of data were included, whereas in Bell et al. (2020) only sites with at least nine years of data were included. Secondly, in this thesis, missing counts were estimated and imputed – a process that was not applied in previous analyses. The data show that there were more incomplete site-years earlier in the time series (Fig. S2.5) which has the effect of artificially lowering the abundance early in the time series and thus, where missing counts are not estimated and imputed, reducing the apparent rate of decline. It, therefore, follows that previous analyses of the RIS moth data (Bell et al., 2020, Conrad et al., 2004, Conrad et al., 2006, Fox et al., 2013) may have slightly underestimated the rates of decline.

Each of the six hypotheses posited in Table 2.1 is discussed.

2.5.1 Hypothesis 1: Total abundance change

a) Moth abundance and diversity has changed over time (1968 – 2016). b) Changes in moth abundance and diversity vary by habitat and by latitude.

Almost every subset of sites studied showed significant declines in overall moth abundance. The only exception to these were northern broadleaf woodland and improved grassland sites, which both remained stable overall (Fig. 2.10). Northern broadleaf woodlands showed a significant increase followed by a significant decrease with a peak abundance in the late 1980s. Abundance in northern improved grasslands increased throughout the time-series, although with a large amount of uncertainty, meaning the trend was not significant. The hump-shaped abundance trend in the north was also found by Dennis et al. (2019) in Scotland, although they found that abundance peaked a little later in the mid-1990s.

Declines in the south were found to be more severe than those in the north (-25% vs -41% respectively, Fig. 2.10). Conrad et al. (2006) found that between 1968 and 2002, total abundance in the north was stable (non-significant 5% increase) while abundance in the south had declined by -44%. With the updated abundance trends, it seems that decline in the south may have ameliorated slightly between the years 2002 and 2016, but strong recent declines in the north have counteracted this. This phenomenon was also found by Dennis et al. (2019) who showed that total moth abundance in Scotland was stable between 1975 and 2002 but had declined by -20.4% by 2014.

The habitats with the most severe overall abundance declines were urban and uplands (Fig. 2.8). While the severe declines in urban areas are unsurprising given the continuing expansion of urban sprawl, the declines in upland habitats are less easy to explain. The overall abundance trend in upland sites superficially contradicts the species-specific abundance trends. Despite the sizeable overall decline in upland sites, the mean abundance trend of the 115 species common enough to model did not differ significantly from zero in this habitat (Fig. 2.12 and Fig. S2.4), and the trend of species richness and diversity is positive, although not significant. This discrepancy suggests that in upland sites, a small number of highly abundant species have declined rapidly, while a larger number of less numerous species have increased, including new species joining the species pool. This is discussed further in section 2.5.7.6.

Perhaps the most surprising finding regarding habitats is the fact that declines have been the least severe in arable land (-18%) and are nearly non-significant. While the decline found in improved grasslands was significant (-34 %), this decline was less severe than any other habitat type apart from conifer plantations at -30%. This finding is at odds with many studies implicating agricultural intensification as the primary cause of decline in insects in western and northern Europe in the latter half of the twentieth century to the present day (Fox, 2013, Habel et al., 2019c, Nilsson et al., 2013, Seibold et al., 2019). Before absolving agriculture, it is important to note that the Green Revolution of the 1950s and 1960s demonstrably had severe negative consequences for insects and wider biodiversity in the UK (Robinson and

Sutherland, 2002) so it is likely that the RIS time-series began only after the most severe declines had occurred. The findings regarding farmland are discussed further in sections 2.5.7.1 and 2.5.7.4.

2.5.2 Hypothesis 2: Shading and grazing in woodland

a) Species that specialise on grasses, forbs and shrubs have declined more in broadleaf woodlands than in other habitats. b) Species that specialise on photophilic hostplants have declined more in broadleaf woodlands than in other habitats.

A key hypothesis proposed to explain the decline of moths in broadleaf woodlands is an increase of shading, due to lack of management, and overgrazing of the understory by deer (Fox, 2013). If this were true, it would follow that moths that feed on low-growing plants such as forbs, grasses and shrubs, especially light-loving plants, would be faring especially badly in broadleaf woodland habitats compared to other habitats. In contrast, those that feed on large trees would be relatively stable in broadleaf woodlands. However, the evidence presented here does not support this. Moths that feed on grasses, forbs, low-growing plants and shrubs did not decline more severely in broadleaf woodlands than they did in most other habitats (Fig. 2.14 and Table S2.11). Furthermore, the trends of moths that feed on broadleaf trees or woody plants were no more positive in broadleaf woodlands than in most other habitats. There was also no evidence that moths that feed on light-loving plants have declined in woodlands any more than those that feed on shade-loving plants (Fig. 2.17 b). The same holds for sites classified as conifer plantations.

It should be noted that the split between ‘broadleaf woodland’ and ‘conifer plantation’ in this study is not strict, but rather depends on which forest type was more common within 500 m of the trap site in 2015. The categorisation does not account for mixed woodlands or woodlands that have undergone a conversion from broadleaf to conifer plantation or vice versa. From the data presented here, it does not appear that either broadleaf woodlands or conifer plantation sites within the network have become any more dominated by conifers since the beginning of the time series, as species that feed on conifers in these habitats have not increased any more than in any other habitat (Fig. 2.14). Although, there is evidence that the planting of conifers in upland sites could have influenced moth communities, as conifer-feeders have significantly increased in this habitat type (Fig. 2.14). The trends of moths in conifer plantations and broadleaf woodlands are discussed further in sections 2.5.7.2 and 2.5.7.3, respectively.

2.5.3 Hypothesis 3: Eutrophication

Species that specialise on nitrophobic hostplants have declined more in arable and improved grassland sites than in other habitats and vice versa for nitrophilic hostplants.

There was no significant relationship between moth abundance trends and the nitrogen-affinity of their hostplants, although there appears to be a weak non-significant relationship in improved grassland (Fig. 2.17 a). This finding was unexpected as the link between nitrogen-enrichment and changes to butterfly community composition is well-known (Betzholtz et al., 2013, Öckinger et al., 2006) and moths are associated with nitrophilous hostplants have increased in distribution (Fox et al., 2014). The effect of nitrogen enrichment on insect communities in farmland is discussed further in sections 2.5.7.1 and 2.5.7.4.

2.5.4 Hypothesis 4: Hostplant and habitat specificity

Moths with higher habitat specificity and hostplant specificity have declined more than generalist species, especially in rarer, more isolated habitats.

Moths with high habitat and feeding specificity did not decline any more than generalist species, and this was true across all habitats (section 2.4.4.2). This finding was surprising as the link between the degree of specialisation and decline in butterflies is a well-known phenomenon (Eskildsen et al., 2015, Fox et al., 2015, Kotiaho et al., 2005, Table S2.1 b).

2.5.5 Hypothesis 5: Forewing length

Moths with smaller wingspans have declined more in discrete habitat patches (broadleaf woodlands and ‘other semi-natural’ habitats than in more widespread habitat (arable and improved grassland).

Moths with larger wingspans were more likely to decline than those with small wingspans. This finding is in agreement with a previous analysis of the RIS data (Coulthard et al., 2019).

There was no interaction between wingspan and habitat, suggesting that the factors driving this trend are consistent across habitats. The relationship between wingspan and abundance trend is counter to that of butterflies where it is well-documented that smaller, more sedentary species are more vulnerable to decline than larger, more mobile species (Eskildsen et al., 2015, Maes and Van Dyck, 2001, Pöyry et al., 2017, Warren et al., 2001, Wenzel et al., 2006). It is generally believed that this is due to the effects of habitat fragmentation as more sedentary species are more vulnerable to both inbreeding depression and local extinction (Nieminen et al., 2001, Saccheri et al., 1998b). If this is the case for butterflies, it is unclear why this should not be the case for moths, as larger-bodied moths are, like butterflies, better able to disperse (Jones, 2014, Nieminen et al., 1999). It is argued by Slade et al. (2013) that for woodland-specialist moths, large body size is a disadvantage due to larger habitat requirements and smaller population size. While the mechanism selecting for smaller-bodies moths is unknown, it is surprising that the relationship was consistent across all habitats. Merckx et al. (2018) found that moth communities in urban environments were more dominated by larger-bodied species, but there was no evidence in this thesis that larger-bodied moths declined less in urban habitats than in other habitats. Although habitat fragmentation is likely to be a problem for some Lepidoptera (Öckinger et al., 2010), the findings in this thesis show that decline is associated with larger moths and is consistent across habitats. This finding suggests that habitat fragmentation is unlikely to be a key driver of widespread moth decline in the UK.

2.5.6 Hypothesis 6: Climate change

Climate variables (temperature and rainfall) affect annual moth abundance. Warm, wet winters have an adverse effect on moths, especially species that overwinter in immature stages.

Annual moth abundance was negatively affected by high summer rainfall and warmer temperatures in the previous winter. Warm winters negatively affected moths of all four overwintering stages but were most detrimental to species that overwinter as eggs and as adults (Fig. 2.23 d). The link between warm winters and low abundance in the following spring/summer has been demonstrated in the Garden Tiger moth (Conrad et al., 2003) and is also known in butterflies (WallisDeVries et al., 2011). This effect is thought to be due to an increased mortality rate in diapausing insects during winter (Klockmann and Fischer, 2019, Stuhldreher et al., 2014). The effects of warming winters on insect diapause are complex and include both positive and negative effects depending on species (Bale et al., 2002, Bale and Hayward, 2010). Warm winters may leave moths more vulnerable to predators (Bale and Hayward, 2010) and fungal pathogens (Klockmann and Fischer, 2019). Furthermore, moths overwintering in the adult stage may suffer from unnecessary energy expenditure that cannot be replenished through nectar (WallisDeVries et al., 2011). Counterintuitively, reduced snow cover due to warmer winters can result in increased mortality to species diapausing below the soil through exposure to low temperatures (Bale and Hayward, 2010). Snow cover acts as a buffer during winter which keeps soil temperature both higher and more stable than the air temperature (Bale, 1991, Edwards and Cresser, 1992). It has been demonstrated that removal of the insulating snow layer during winter results in higher mortality rates in some arthropod groups due to exposure to temperatures below freezing-point (Sulkava and Huhta, 2003, Templer et al., 2012).

The link between overwintering stage and rate of decline in the UK has was demonstrated by Conrad et al. (2004) and corroborated in this thesis (Fig. 2.15). Those overwintering as eggs were most likely to decline, whereas those overwintering as adults are most likely to have remained stable. Warm winters may explain the high rates of decline among those that overwinter as eggs. Still, they cannot explain why those that overwinter as adults have remained stable despite being more sensitive to warm winters than those that overwinter as larvae or pupae. Those overwintering as adults were positively affected by high summer temperatures of the previous year whereas those that overwinter as eggs were negatively affected (Fig. 2.23) so the positive effect of warming summers may counteract the negative effects of warming winters for those that overwinter as adults. At present, this is purely speculative and elucidating the climate-related drivers of moth decline is beyond the scope of this these. However, the findings demonstrate that climate change is likely an important factor driving moth abundance decline, and further research in this field is necessary to fully understand the mechanisms behind moth decline in the UK.

2.5.7 Discussion of habitat-specific trends

2.5.7.1 Arable

Moth abundance declined significantly in arable habitat by -18%, but these declines were the least severe of any habitat type (Fig. 2.8) and bordered on statistical non-significance. While this result was not entirely unexpected due to recent studies with similar findings (Bell et al., 2020, MacGregor et al., 2019b) they are contrary to many papers that point to agricultural intensification as a key driver of insect decline over the last six decades (Habel et al., 2019c, Groenendijk and Ellis, 2011, Maes and Van Dyck, 2001, Nilsson et al., 2013). The reasons for a decline in moth abundance in farmland since 1968 are manifold and are explored in section 1.3.1.2. The interesting point of discussion here is not why moths have declined in arable habitat, but rather: why have they declined less in arable habitat than in all other habitats? Furthermore, why has species diversity increased? There are several potential explanations for the observed patterns:

Arable habitat was already so degraded by 1968 that abundance was near its minimum, so could not decline much further.

It is almost certain that moth abundance in arable farmland was substantially higher before the intensification that took place post-World War II. As a point of evidence, the average number of moths caught in a light-trap at Rothamsted Research – a typical, mainly arable, farm in the south-east of England – dropped from roughly 4000 in the 1930/40s to 1100 in the 1960/70s (Woiwod and Gould, 2008). Unfortunately, the trap was not run during the 1950s, but the rate of decline during this period was evidently severe at a rate of -71% in little over a decade. The national -36% decline that continued over the following five decades seems moderate in comparison. Comparison of maps of the trap site, known as Barnfield, show that between 1933 and 1972, there was some replacement of permanent grassland with arable land, a loss of hedgerows adjacent to the trap and an increase in buildings and paved roads. Due to the multiple changes that occurred at this site over this period and the lack of temporal resolution of these changes, it is not possible to disentangle the relative impact. However, the changes that occurred are typical of land-use change across much of the UK during this time, so it is not unreasonable to assume that the scale of loss across the country would have been similar. Indeed, despite the regeneration of a large hedgerow adjacent to the trap and the conversion of an adjacent arable field to a hay-meadow, the annual abundance, although increasing, is still less than half of the geometric mean average in the 1930/40s (Fig. S2.6).

If abundance in arable land were already so low in 1968 that it could not decline much further, we would expect that baseline annual abundance was lower in arable than in other habitats. However, Fig. 2.9 shows that the model-predicted abundance in 1968 was in line with the geometric mean abundance of all habitats in all years. Furthermore, predicted abundance in 1968 was equivalent to that of improved grassland and was higher than that of urban habitat. It is therefore unlikely that the lack of severe decline in arable land is due to an already depleted population.

Disturbance-sensitive species were already absent by 1968, and current populations consist of disturbance-tolerant species that were not heavily impacted by further intensification.

If moth populations in arable habitats were dominated by a small community of disturbance-tolerant moths, we would expect to see that species richness and diversity were lower in arable habitat than in other habitats. However, model-predicted species richness in 1968 was as high or higher than all other habitat types apart from broadleaf woodland (Fig. 2.5). Similarly, species diversity was no lower than in any other habitat type apart from conifer plantations and broadleaf woodlands (Fig. 2.6). While the community of moths found in arable habitat may be composed of more disturbance-tolerant species (this was not investigated here), it is clear that moth abundance and diversity were no lower in arable habitats than in most other habitats. Hence, dominance by a small number of moths adapted to frequent anthropogenic disturbance is not a valid explanation for the lack of severe decline in this habitat.

Agri-environment schemes and regulations implemented in recent decades have ameliorated the effects of intensification

Agri-environment schemes (AES) were first introduced to England in 1987 (Ovenden et al., 1998) and rapidly expanded in scope. The number of hectares under higher-level or targeted AES rose from half a million to over 3 million between 1992 and 2018 (JNCC, 2019). If the application of AES at the national scale were the reason behind the relatively mild declines in arable land, we might expect to see a decline in abundance from 1968 to the early 1990s with agricultural intensification and then a recovery from the 1990s to the present day as AESs are adopted. The data presented here does not offer strong evidence for this hypothesis. Fig. 2.8 b shows a linear decline across the entire time series with no pattern of decline and recovery. The model, however, determined that the rate of decline was only significant between the late 1970s and the early 2000s, with rates of change either side classed as non-significant. This pattern means that although abundance continued to decline from 2000 onwards, it did so at a non-significant rate, indicating that there may have been some amelioration of the drivers of decline, albeit subtle. Furthermore, the decline in improved grassland (discussed in section 2.5.7.4), which have also been subject to AES, showed no sign of slowing (Fig. 2.8).

Nitrogen-enrichment has led to more prolific growth in wild plants, resulting in more hostplant resources.

Nitrogen enrichment can lead to enhanced growth rates of crop-adjacent plants (Schmitz et al., 2014) and nitrogen enrichment of plants can enhance their nutritional value to Lepidoptera (Myers and Post, 1981, Pöyry et al., 2017), especially for species that specialise on nitrophilous hostplants (Kurze et al., 2017). Wild plants growing on land adjacent to arable fields may have become more voluminous over time due to nutrient enrichment of the soil which, in turn, led to an increase in hostplant availability, offsetting the other negative effects of agricultural intensification. However, if this were the case, we would expect moths that feed on nitrophilous plants to have fared better than those that feed on nitrophobic plants. Section 2.4.4.4 shows that this is not the case as there was no interaction between nitrogen-affinity and habitat. Nitrogen enrichment is also associated with a decrease in plant diversity (Payne et al., 2017). It is therefore surprising that moth species diversity increased in arable land (section 2.4.1.2). This finding matches the pattern for the country as a whole (Fig. 2.2) so it likely that the driver behind this increase in diversity, likely climate-related, is typical across most habitats and not specific to arable land.

2.5.7.2 Conifer plantation

The division of woodlands in conifer plantations and broadleaf woodlands is imperfect (see section 2.5.8.1), and the sample size of conifer plantation sites is only small (12 sites) so these results should be interpreted with caution. The decline in abundance found here (-30%) is less severe than all other habitat types apart from arable. The most obvious explanation for a decline in abundance is an intensification of productivity within the plantations – as broadleaf woodlands were still being replaced by conifer plantations up until the 1980s (Rackham, 2003). The data, however, do not support this hypothesis as there was no significant increase in conifer feeders in this habitat (Fig. 2.14). Significant declines in forb and broadleaf shrub feeders indicate a loss of hostplants at the field and shrub layer, but declines in these groups were present across most habitat types so do not offer specific information regarding the decline of moths in conifer plantations.

2.5.7.3 Broadleaf woodland

The findings in broadleaf woodland are troubling, as this was the only habitat type in which species richness and diversity declined as well as abundance (section 2.4.1.2). Hypotheses regarding shading and overgrazing by deer as drivers of decline are not supported by the data (section 2.5.2). The cessation of coppicing and other forms of active management might be invoked to explain the decline in species richness and diversity, as plant diversity tends to decrease after cessation of coppicing (Müllerová et al., 2015). However, this is not true for moth communities which are typically both more abundant and diverse in mature, shaded woodlands than in more open woodlands, including coppice and woodland edges (Broome et al., 2011, Merckx et al., 2012a, Sebek et al., 2015).

The drivers behind abundance decline in woodland are also unclear. The key driver of habitat loss that applies to many semi-natural habitats in the UK is not relevant here, as the area of broadleaf woodland has increased since 1968 (DEFRA, 2013, Hopkins and Kirby, 2007). To further complicate the matter, it was found that the decline in abundance was concentrated in the southern broadleaf woodlands with a decline of -51% compared to a non-significant, non-linear decline of -17% in the north. The trend in northern broadleaf woodland shows a significant increase up until the late 1980s where it peaks at 150% of its 1968 level, before declining significantly to its present level (Fig. 2.10). Additionally, there was a significant difference in the change in diversity between northern and southern woodlands, with a decline in the south and stability in the north (Fig. 2.7 b). This regional trend also occurred in improved grasslands and across the country as a whole, with diversity and abundance declining more in the south.

Changes in hostplant abundance within woodlands did not explain the trends observed. Amar et al. (2010) found that the percentage canopy cover of oak in woodlands across Great Britain had significantly decreased between the 1980s and 2003/4 while the percentage cover of ash had increased. While there are not enough monophagous moth species for robust analysis, a cursory look at the data shows that oak-feeders in broadleaf woodland have indeed tended to decline, but so have both of the species that specialise on ash (Fig. S2.8). Two oak-feeding species have undergone severe declines in broadleaf woodland: *Ennomos fuscantaria* (Dusky Thorn) and *Cymatophorina diluta* (Oak Lutestring) at -95% and -100% respectively. Similarly, although Amar et al. (2010) reported significant increases in the cover of honeysuckle at the shrub layer, the only honeysuckle-specialist moth was found to have declined by -34% in broadleaf woodland, although not significantly so (95% CI: -60%, 7%). Furthermore, despite evidence that deer grazing in woodlands may favour the growth of grasses over forbs (Dolman et al., 2010), moths that feed on grasses declined at a similar rate to those that feed on forbs in broadleaf woodland habitat (Fig. 2.14). Similarly, domination by bracken is also associated with over-grazing by deer (Putman et al., 1989) yet the three species that specialise on bracken have all declined, although non-significantly, in broadleaf woodland; *Petrophora chlorosata* (Brown Silver-lines): -36% (95% CI: -58%, 1.4%), *Phymatopus hecta* (Gold Swift): -40% (-80%, 108%) and *Euplexia lucipara* (Small Angle Shades): -41% (-65%, 3.9%).

None of the hypotheses posited to explain the decline in abundance and diversity of moths in broadleaf woodland are supported by the data in this thesis. The mechanisms behind moth decline in woodland is of key importance to halting the decline in moths, and suggestions for further research are discussed in section 5.4.1.

2.5.7.4 Improved grassland

Grassland was severely impacted by agricultural intensification in the post-war period (Boatman et al., 2007). Like arable habitats, grassland was subject to hedgerow removal and increased chemical inputs, but also experienced changes that did not apply to arable land: not least, the ‘improvement’ that gives this land-use type, improved grassland, its name. Improvement in this context refers to the replacement of a diverse sward with a monoculture of productive grass (e.g., *Lolium perenne*) and enhancement with nutrient inputs (Laidlaw and Frame, 2013). The disastrous consequences of these changes for insect diversity in grasslands are well-known (Asher et al., 2001, Robinson and Sutherland, 2002), but the effect on the abundance and diversity of moths is not well-studied. The majority of improvement to grassland occurred before 1968 (Fuller, 1987), so this time series did not capture most of the resulting effect on moths. However, these changes continued more slowly into the 1980s, and the extent of semi-natural (unimproved) grassland in England and Wales is now 3% of its 1930 level. Similar figures are expected in lowland Scotland (Bullock et al., 2011). It is therefore surprising that moth species richness remained stable over this time, and diversity significantly increased (Fig. 2.3). When improved grasslands were split by north and south, it was found that while species richness declined significantly in the south, species richness increased significantly in the north (Fig. 2.7). Similarly, the decline in abundance in this habitat was restricted to the south – abundance increased non-significantly in the north. This regional difference suggests that climate may play a role. Still, only one climate variable was found to interact with region in determining abundance: high rainfall in the previous summer had a more negative effect on moth abundance in northern improved grassland compared to southern improved grassland (Fig. 2.22).

The increase in grazing intensity over the time-period may explain the observed decline in moth abundance as high levels of grazing by livestock are associated with low moth abundance (Littlewood, 2008). Both forb and grass feeders declined in improved grassland habitat (Fig. 2.14) which is consistent with this hypothesis, although species polyphagous on low-growing plants remained stable. Grazing intensity by sheep has increased more in England than in Scotland and Wales (Fuller and Gough, 1999), which may partly explain why the abundance and diversity have declined in the south but not in the north.

2.5.7.5 Other semi-natural

This habitat category contains several habitat types (see section 2.3.2) that have different land-use histories and pressures, so generalisations about potential drivers of change are not possible. The dominant land-use types in this category are open, low-fertility environments such as calcareous grassland and coastal vegetation (Table 2.2). This category was designated mainly as a further contrast against agriculturally intensive habitat (arable and improved grassland) and closed habitats (broadleaf woodland and conifer plantation) to test hypotheses regarding agricultural intensification and woodland management. Total moth abundance was relatively severe at -45%, and all the significant decline occurred before 1990, after which abundance stabilised (Fig. 2.8 f). Trends of individual species were more negative than in most other habitats (Fig. 2.12), but species richness and diversity showed no significant change (Fig. 2.3). Species that feed on forbs and grasses fared especially badly in this habitat with both groups declining more in this habitat than in any other (Fig. 2.14). Species that feed on broadleaf trees, broadleaf shrubs, or both, all remained stable, in contrast to the national situation in which these species declined significantly (Fig. 2.13). The loss of species that feed on low-growing plants and the stability of woody plant feeders points to factors scrub-encroachment as drivers of decline (Balmer and Erhardt, 2000). While the small sample size of highly disparate sites in this habitat category makes speculatio, the results demonstrate that moth declines have occurred in all habitats and, since 1968, appear to have been more severe in presumably less agriculturally intensive areas than in arable and improved grassland habitat.

2.5.7.6 Upland

The decline in total moth abundance in uplands was more severe than in any other habitat type apart from urban – with both habitats showing a decline of -47%. The decline in total abundance was countered by the average abundance trend of individual common species (Fig. 2.12), which were stable on average. This implies that a small number of highly abundant species have delined, and these make up the bulk of the total decline. When the data were examined in more detail, it was found that three species were notably dominant in the upland sites: *Xanthorhoe montanata* (Silver-ground Carpet), *Orthosia gothica* (Hebrew Character) and *Cerapteryx graminis* (Antler Moth) (Fig. S2.7). Together, these three species accounted for 20.5% of all individuals recorded in the upland sites. The most abundant of these, *C. graminis*, showed a non-significant increase in abundance of 118% whereas *X. montanata* and *O. gothica* showed significant declines of -61% and -63%, respectively. These large declines in two of the most abundant species partly explain why overall abundance in uplands has declined whereas the average species trend is stable. The reasons for decline in these two species are not clear: both are very common and widespread species found in most habitats. Both these species declined significantly at the national level (*O. gothica*: -31%, *X. montanata*: -61%), meaning that the drivers of their declines are not limited to upland habitats.

Although it is well-known that climate change has led to declines in cold-adapted species at high altitudes (Wiens, 2016), it appears that this is not the reason for the decline in total abundance in uplands. There were no cold-adapted species common enough in the RIS database for which to produce meaningful trends. While it is likely that such species have indeed declined in upland sites, they do not contribute enough to influence the overall trend, suggesting that the drivers of decline in uplands are due to other factors such as habitat change. Grazing intensity has increased in the uplands since 1968 (Fuller and Gough, 1999) and, as with lowlands, overgrazing results in reduced moth abundance through the loss of hostplants (Littlewood, 2008). However, species that feed on grasses or forbs both remained stable in upland habitats (Fig. 2.14), so a loss of forbs and grasses through grazing is not likely. The largest declines in uplands occurred in species that feed on broadleaf shrubs. It is known that overgrazing by sheep reduces the cover of shrubs in upland habitat (Hulme et al., 1999, Mardon, 2003) and this may partly explain the decline in shrub-feeding species.

2.5.7.7 Urban

Despite rapid urban development in the 20th century, less than 6% of the UK consists of continuous and discontinuous urban fabric (Rae, 2017), although this figure is higher in England at 9%. Within discontinuous urban fabric (suburbs), a large proportion of land – up to 50% – consists of green space including parks, gardens and recreational ground (Rae, 2017). While it is not possible to quantify the precise amount of urban development that has occurred around the RIS network sites, by comparing the 1990 and 2015 Land Cover Maps, it is clear that by far the most urban development has occurred in sites classified as ‘urban’ (Fig. S2.9). Due to the differing methodologies of the 1990 and 2015 maps, the two cannot be directly compared. Indeed, this is clearly the case, as many sites in the network apparently become substantially less urban during the 25-year period (Fig. S2.9). This reduction in urban land cover is a highly unlikely situation and is almost certainly due to errors in classification in the earlier map. However, in all six habitat categories apart from urban, the median change in urban land cover was ~ 0% whereas in urban sites, the median was 12.8%. This means that the ‘urban’ habitat category includes both historically urban sites and sites that have become more urban during the time series. For this reason, the habitat category should be considered as ‘urban and urbanising’. While this is not ideal, until high-resolution, accurate, historical land-use data is available, this is a necessary compromise.

Considering that urban habitat has undergone urbanisation in the post-1968 period, it is not surprising that this habitat type has suffered a severe loss in total moth abundance at -47%. Trends of individual species have also been severe (Fig. 2.12). Investigation of feeding guilds shows that species feeding on broadleaf shrubs have fared especially badly while those that feed on lichens are doing relatively well (Fig. 2.14). The success of lichen-feeders is presumably due to the increased air quality and subsequent proliferation of lichens (Gilbert, 1992). It is likely that in urban areas, air pollution was more prevalent than in the surrounding countryside, so the lichens and lichen-feeders had more to gain when air pollution was ameliorated. Also notable, is the significant increase in of species that overwinter as adults in urban habitat compared to the other three overwintering stage groups in this habitat (Fig. 2.16). It could be argued that the warmer micro-climate of urban environments makes overwintering survival easier for adult moths, but this contradicts findings that warm winters have an especially negative effect on species that overwinter as adults (Fig. 2.23). An alternative explanation is that the urban environment provides an abundance of dry and sheltered places in which to overwinter, with reduced pressure from fungal pathogens and potentially reduced predation rates. However, this is speculative and would require further research in overwintering mortality of adult moths in contrasting situations to elucidate.

With urban spread, the abundance and diversity of a variety of taxa are typically, but not always, reduced, depending on the taxa in question and the habitat type that the urban development is replacing (Kowarik, 2011, McKinney, 2008). Urban development replaces pre-existing vegetation with non-porous surfaces. This land-use change is self-evidently detrimental to moth species that feed on the plants that have been removed. However, the parks, gardens, roadside verges and increased structural diversity that accompanies urban development are beneficial to some species, and this may help explain why species diversity, but not richness, significantly increased in this habitat type. The role of artificial light at night (ALAN) may have also played a role in the decline of moths in this habitat. There are several deleterious effects of ALAN on moths (Van Langevelde et al., 2018) and increased ALAN has been linked to abundance decline (Wilson et al., 2018). ALAN has increased since 1968 (Bennie et al., 2014), so it is likely that, along with habitat loss, ALAN has partly driven the sharp decline in moth abundance that we see in urban habitat.

2.5.8 Limitations of the study

2.5.8.1 Spatial and temporal limitation of the network

Despite being the most spatially and temporally extensive insect monitoring network in the world, the RIS still suffers from limitations and biases. Although the trap sites are well distributed throughout the UK (Fig. 2.1), there is a clear southern bias: of the 349 sites included in this study, 243 were in the south, and 106 were in the north. Furthermore, due to the nature of the trapping system, site locations need to be located where there is access to mains electricity and frequent human maintenance; effectively excluding large areas of remote, especially upland, habitat. As discussed in section 2.5.8.1, the spatial extent of the survey allows for very robust estimates of moth abundance trends at the national scale, but when only a small subset of sites are taken to represent a single habitat, the individual situation of each site becomes more important. The observed trends may not accurately represent the situation at the national level. For this reason, findings regarding under-sampled habitats (conifer plantations, uplands and 'other semi-natural' habitats) should be interpreted with caution.

While the overall decline in moth numbers caught in RIS moth traps across the UK had undoubtedly declined since 1968, the claims made here about habitat-specific trends must be interpreted with caution. The network of traps used here consisted of 349 traps, which allows for very robust estimates of national abundance trends. However, once the sites are split into habitat categories, the idiosyncrasies of individual sites become more important, especially for the conifer plantation, 'other semi-natural' and upland categories which consisted of 12, 16 and 15 sites each, respectively. Furthermore, the categorisation of sites into discrete habitats is somewhat artificial as each site is, in reality, a mixture of several habitats. Using the modal habitat within a certain radius has certain problems. For example, if a site were 40% woodland, 30% arable land and 30% improved grassland, it would be classed as woodland. But if a site were 40% woodland and 60% arable, it would be classed as arable, despite having the same amount of woodland as the first site. Alternatives to this approach include using all habitat types as continuous variables, but this results in extremely high variance inflation factors due to the perfect collinearity of areas within a circle. The use of Principal Components Analysis to give each site a set of uncorrelated continuous habitat-spectrum variables is also possible, but the difficulty of interpreting the results tends to make things less clear rather than more so. Simplifying the habitat types down to a binary variable such as farmland/not farmland is another option, but the value in doing so is questionable. The habitat selection technique used here, although not free of limitations, is probably the best method available.

2.5.8.2 Reduction in trap efficacy due to light pollution

There is potential that the efficacy of the light traps themselves may have been reduced due to light pollution. There are two ways in which this could have happened. 1) It is well-known that light pollution has increased since the 1960s which has resulted in a higher level of background light and skyglow at night (Bennie et al., 2014). It is possible that the reduced contrast between the light-trap and the surrounding environment has made the traps less attractive or has reduced their attractive radius. It is known that background illumination by moonlight reduces the attractiveness of light-traps to moths (Bowden, 1982), but it is not known to what extent illumination caused by artificial light at night has the same effect. Conrad et al. (2006) addressed this issue by comparing time-series of 8 years at 116 RIS sites that had/had not increased in light pollution (quantified using satellite data) and showed the abundance trends did not differ between the two groups. Although this analysis was quite coarse, it does demonstrate that if background illumination is having an effect, it is likely to be small. 2) Moths in areas of high light pollution may have a reduced flight-to-light response due to evolution through natural selection. Altermatt and Ebert (2016) tested a single moth species and found that individuals collected in areas with high light pollution engaged in flight-to-light behaviour 30% less than those collected in dark areas. While this phenomenon is unlikely to affect moths in the countryside, abundance trends of moths in urban areas may be at least partly influenced by this artefact. Further research into the effect of background illumination on light-trap attractiveness would be needed to resolve this issue. Additionally, repeating the experiment by Altermatt and Ebert (2016) on other moth species is necessary to determine whether this is a potential problem for light-trap networks.

2.5.8.3 Artefacts due to changes in woodland structure

As discussed in section 2.4.7.3, woodlands in the UK have become sparser at the field and shrub layer (<2 m in height) and denser at the sub-canopy layer. The Rothamsted light trap is specifically designed to prevent attracting moths flying overhead. The light is situated 1.2 m above the ground, and it has a black opaque lid that directs the light downwards (Williams, 1948). A potential artefact of the canopy becoming denser, at the expense of the field and shrub layer, are changes to vertical stratification of moth communities. Insect abundance and activity varies across a vertical gradient within woodlands (Ulyshen, 2011) and it is known that moth activity-density decays with vertical height (De Smedt et al., 2019, Taylor and French, 1974). With more of the foliage in the canopy layer, it follows that moth activity may also be concentrated higher up in the woodland canopy and further away from the light trap, reducing the likelihood of being attracted and caught. Whether or not this concern is realistic is entirely unknown. Vertical stratification of moths in temperate broadleaf woodland is not well studied (De Smedt et al., 2019). Consequently, nothing is known about the relationship between the stratification of plants and moths within woodlands. Addressing this knowledge gap is necessary to fully understand how changes in woodland structure have affected both the real and perceived changes in moth abundance.

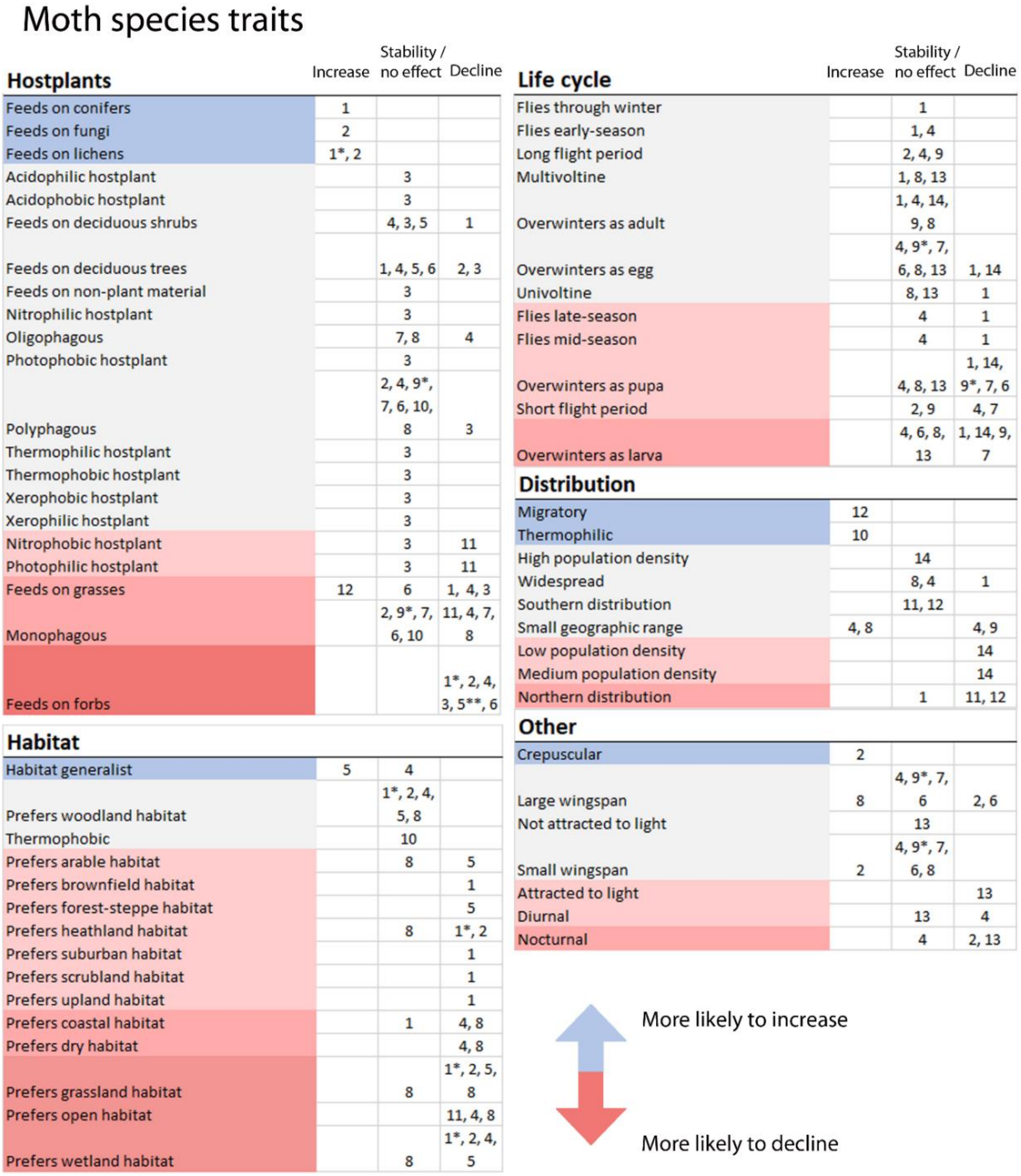
2.6 Conclusions

The decline of moths in broadleaf woodlands is especially concerning as we do not know what is driving these changes. Climate may have a role, but this appears to be mostly consistent across habitats, so cannot explain the decline in woodlands. It could be that moth communities in farmlands underwent their major decline during the Green Revolution of the 1950s and the communities of broadleaf woodlands are experiencing the effects of agricultural intensification and habitat fragmentation more slowly. However, there is no evidence presented here to support this. Moth abundance declined across all habitat types in the UK from 1968 to 2016, and the declines were especially severe in urban habitats, uplands, broadleaf woodland and ‘other semi-natural’ habitats and least severe in farmland. Species life-history traits including feeding guild, overwintering stage and wingspan influenced their likelihood of decline, and there was some interaction between habitat and feeding guild. There was no evidence that a reduction in hostplant abundance due to shading and deer browsing is the mechanism behind moth decline in broadleaf woodlands as declines were independent of feeding guilds. Warm winters were associated with low moth abundance the following year and species in all four overwintering stage groups were adversely affected by warm winters, especially those that overwinter as eggs and adults. It is likely that climate change has played a role in the decline of moths in the UK, but these have been at least partially mitigated by increased species richness in the north of the UK due to expanding climatic envelopes, as well as warmer summers which are associated with higher abundance.

2.7 Supporting information

Table S2.1. Species traits associated with changes in a) moth and b) butterfly abundance and distribution. *Papers are grouped into those that associate each trait with increase, decline or stability/no effect. Each trait is coloured either blue for increase, red for decrease, or grey for no effect. The strength of the colour represents the relative weight of the evidence. Weight it calculated by number of papers reporting increase, minus number reporting decrease with each report that finds stability/no effect pulling the weight half a unit towards zero. Papers that have the same findings based on the same data are shown with an asterisk and only the first one is used in the weighting. References are shown at the bottom.*

Table S2.1 a)



Moth species traits

Hostplants	Increase	Stability / no effect	Decline
Feeds on conifers	1		
Feeds on fungi	2		
Feeds on lichens	1*, 2		
Acidophilic hostplant		3	
Acidophobic hostplant		3	
Feeds on deciduous shrubs		4, 3, 5	1
Feeds on deciduous trees		1, 4, 5, 6	2, 3
Feeds on non-plant material		3	
Nitrophilic hostplant		3	
Oligophagous		7, 8	4
Photophobic hostplant		3	
Polyphagous		2, 4, 9*, 7, 6, 10, 8	3
Thermophilic hostplant		3	
Thermophobic hostplant		3	
Xerophobic hostplant		3	
Xerophilic hostplant		3	
Nitrophobic hostplant		3	11
Photophilic hostplant		3	11
Feeds on grasses	12	6	1, 4, 3
Monophagous		2, 9*, 7, 6, 10	11, 4, 7, 8
Feeds on forbs			1*, 2, 4, 3, 5**, 6

Habitat	Increase	Stability / no effect	Decline
Habitat generalist	5	4	
Prefers woodland habitat		1*, 2, 4, 5, 8	
Thermophobic		10	
Prefers arable habitat		8	5
Prefers brownfield habitat			1
Prefers forest-steppe habitat			5
Prefers heathland habitat		8	1*, 2
Prefers suburban habitat			1
Prefers scrubland habitat			1
Prefers upland habitat			1
Prefers coastal habitat		1	4, 8
Prefers dry habitat			4, 8
Prefers grassland habitat		8	1*, 2, 5, 8
Prefers open habitat			11, 4, 8
Prefers wetland habitat		8	1*, 2, 4, 5

Life cycle	Increase	Stability / no effect	Decline
Flies through winter		1	
Flies early-season		1, 4	
Long flight period		2, 4, 9	
Multivoltine		1, 8, 13	
Overwinters as adult		1, 4, 14, 9, 8	
Overwinters as egg		4, 9*, 7, 6, 8, 13	1, 14
Univoltine		8, 13	1
Flies late-season		4	1
Flies mid-season		4	1
Overwinters as pupa		4, 8, 13	1, 14, 9*, 7, 6
Short flight period		2, 9	4, 7
Overwinters as larva		4, 6, 8, 13	1, 14, 9, 7

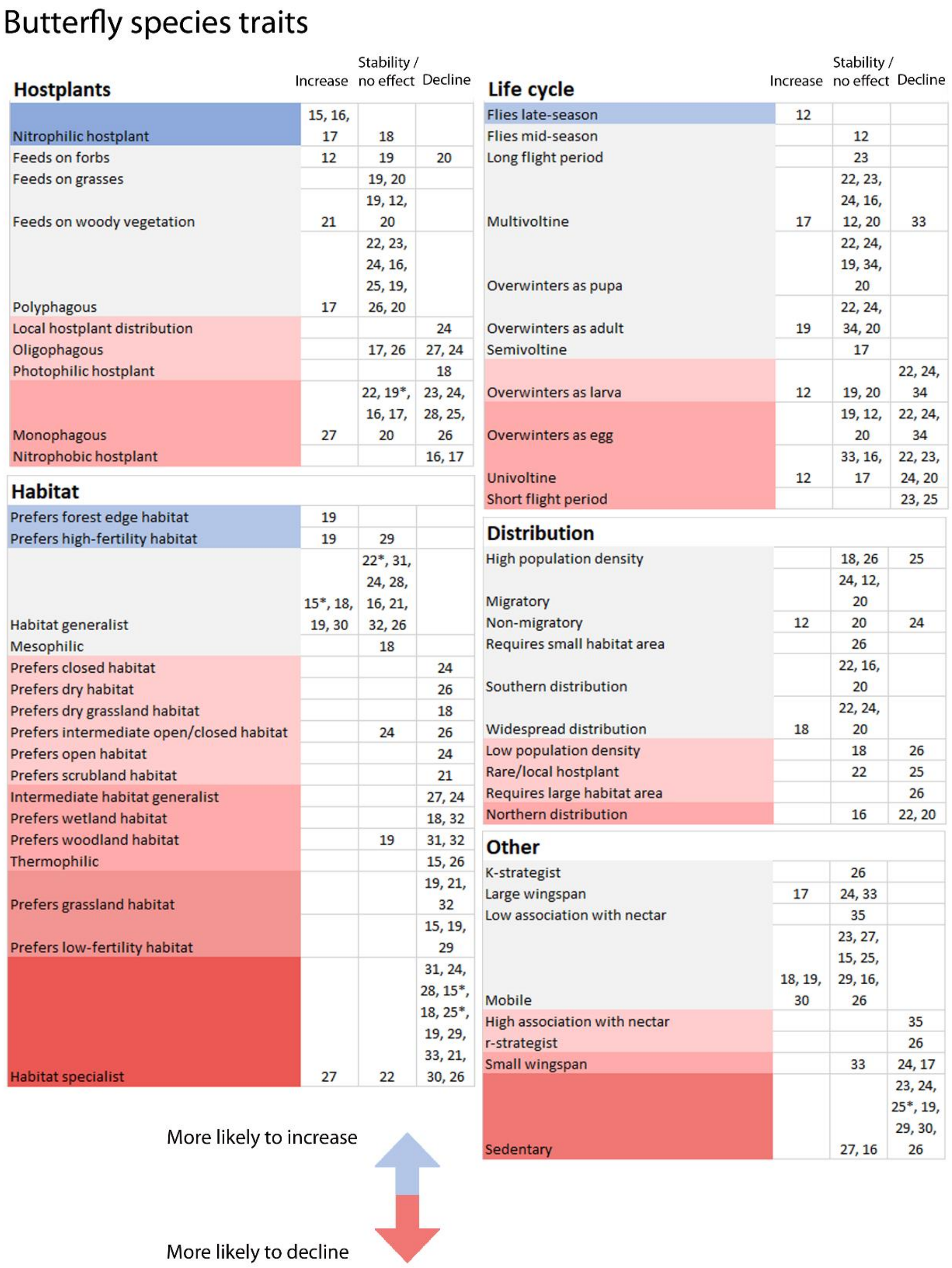
Distribution	Increase	Stability / no effect	Decline
Migratory	12		
Thermophilic	10		
High population density		14	
Widespread		8, 4	1
Southern distribution		11, 12	
Small geographic range	4, 8		4, 9
Low population density			14
Medium population density			14
Northern distribution		1	11, 12

Other	Increase	Stability / no effect	Decline
Crepuscular	2		
Large wingspan	8	4, 9*, 7, 6	2, 6
Not attracted to light		13	
Small wingspan	2	4, 9*, 7, 6, 8	
Attracted to light			13
Diurnal		13	4
Nocturnal		4	2, 13

More likely to increase

More likely to decline

Table S2.1 b)



Butterfly species traits

Hostplants	Increase	Stability / no effect	Decline
Nitrophilic hostplant	15, 16, 17	18	
Feeds on forbs	12	19	20
Feeds on grasses		19, 20	
Feeds on woody vegetation	21	19, 12, 20	
Polyphagous	17	22, 23, 24, 16, 25, 19, 26, 20	
Local hostplant distribution			24
Oligophagous		17, 26	27, 24
Photophilic hostplant			18
Monophagous	27	22, 19*, 16, 17, 20	23, 24, 28, 25, 26
Nitrophobic hostplant			16, 17

Habitat	Increase	Stability / no effect	Decline
Prefers forest edge habitat	19		
Prefers high-fertility habitat	19	29	
Habitat generalist	15*, 18, 19, 30	22*, 31, 24, 28, 16, 21, 32, 26	
Mesophilic		18	
Prefers closed habitat			24
Prefers dry habitat			26
Prefers dry grassland habitat			18
Prefers intermediate open/closed habitat		24	26
Prefers open habitat			24
Prefers scrubland habitat			21
Intermediate habitat generalist			27, 24
Prefers wetland habitat			18, 32
Prefers woodland habitat		19	31, 32
Thermophilic			15, 26
Prefers grassland habitat			19, 21, 32
Prefers low-fertility habitat			15, 19, 29
Habitat specialist	27	22	31, 24, 28, 15*, 18, 25*, 19, 29, 33, 21, 30, 26

Life cycle	Increase	Stability / no effect	Decline
Flies late-season	12		
Flies mid-season		12	
Long flight period		23	
Multivoltine	17	22, 23, 24, 16, 12, 20	33
Overwinters as pupa		22, 24, 19, 34, 20	
Overwinters as adult	19	22, 24, 34, 20	
Semivoltine		17	
Overwinters as larva	12	19, 20	22, 24, 34
Overwinters as egg		19, 12, 20	22, 24, 34
Univoltine	12	33, 16, 17	22, 23, 24, 20
Short flight period			23, 25

Distribution	Increase	Stability / no effect	Decline
High population density		18, 26	25
Migratory		24, 12, 20	
Non-migratory	12	20	24
Requires small habitat area		26	
Southern distribution		22, 16, 20	
Widespread distribution	18	22, 24, 20	
Low population density		18	26
Rare/local hostplant		22	25
Requires large habitat area			26
Northern distribution		16	22, 20

Other	Increase	Stability / no effect	Decline
K-strategist		26	
Large wingspan	17	24, 33	
Low association with nectar		35	
Mobile	18, 19, 30	23, 27, 15, 25, 29, 16, 26	
High association with nectar			35
r-strategist			26
Small wingspan		33	24, 17
Sedentary		27, 16	23, 24, 25*, 19, 29, 30, 26

More likely to increase

More likely to decline

1 (Conrad et al., 2004), 2 (Coulthard et al., 2019), 3 (Hallmann et al., 2020), 4 (Franzén and Johannesson, 2007), 5 (Kadlec et al., 2018), 6 (Mattila et al., 2009), 7 (Mattila et al., 2008), 8 (Valtonen et al., 2017), 9 (Mattila et al., 2006), 10 (Thomsen et al., 2016), 11 (Fox et al., 2014), 12 (Morecroft et al., 2009), 13 (Van Langevelde et al., 2018), 14 (Groenendijk and Ellis, 2011), 15 (Habel et al., 2016), 17 (Pöyry et al., 2017), 18 (Habel et al., 2019b), 19 (Kuussaari et al., 2007), 20 (Wepprich et al., 2019), 21 (Stefanescu et al., 2011), 22 (Breed et al., 2013), 23 (Carnicer et al., 2013), 24 (Eskildsen et al., 2015), 25 (Kotiaho et al., 2005), 26 (Wenzel et al., 2006), 27 (Dapporto and Dennis, 2013), 28 (Fox et al., 2015), 29 (Maes and Van Dyck, 2001), 30 (Warren et al., 2001), 31 (Brereton et al., 2011), 32 (Van Swaay et al., 2006), 33 (Melero et al., 2016), 34 (Wallisdevries and Van Swaay, 2006), 35 (Wallisdevries et al., 2012)

Table S2.2. Moth traits for each species used in species-specific long-term abundance trend models.

Agassiz code	Binomial	Common name	Total caught	Feeding guild	Feeding specificity	Ellenberg N mean	Ellenberg light mean	Overwinter stage	Forewing length	Habitat specificity
3.001	*Triodia sylvina*	Orange Swift	22834	Herbaceous polyphagous	Polyphagous	NA	NA	Larva	19	8
3.002	*Hepialus lupulinus*	Common Swift	41966	Herbaceous polyphagous	Polyphagous	NA	NA	Larva	15.5	8
3.003	*Pharmacis fusconebulosa*	Map-winged Swift	21430	Herbaceous polyphagous	Polyphagous	NA	NA	Larva	20	3
3.004	*Phymatopus hecta*	Gold Swift	1400	Forbs	Oligophagous	3	6	Larva	14	2
3.005	*Hepialus humuli*	Ghost Swift	3859	Herbaceous polyphagous	Polyphagous	NA	NA	Larva	28	2
50.002	*Zeuzera pyrina*	Leopard Moth	43	Broadleaf polyphagous	Polyphagous	NA	NA	Larva	27.5	2
53.001	*Apoda limacodes*	Festoon	111	Broadleaf polyphagous	Oligophagous	4.75	4.65	Larva	11.5	1
54.001	*Jordanita globulariae*	Scarce Forester	92	Forbs	Oligophagous	4	7.5	Larva	12.5	1
65.001	*Falcaria lacertinaria*	Scalloped Hook-tip	7797	Broadleaf shrubs	Oligophagous	4	7	Pupa	16	3
65.002	*Watsonalla binaria*	Oak Hook-tip	3536	Broadleaf trees	Oligophagous	4.5	6.3	Pupa	15.5	1
65.003	*Watsonalla cultraria*	Barred Hook-tip	316	Broadleaf trees	Monophagous	5	3	Pupa	14.5	1
65.005	*Drepana falcataria*	Pebble Hook-tip	6985	Broadleaf trees	Oligophagous	5	6	Pupa	19	3

65.007	*Cilix glaucata*	Chinese Character	21801	Broadleaf shrubs	Polyphagous	NA	NA	Pupa	11.5	3
65.008	*Thyatira batis*	Peach Blossom	7619	Broadleaf shrubs	Oligophagous	6	6	Pupa	17.5	2
65.009	*Habrosyne pyritoides*	Buff Arches	9099	Broadleaf shrubs	Oligophagous	6	6	Pupa	18.5	1
65.010	*Tethea ocularis octogesima*	Figure of Eighty	692	Broadleaf trees	Oligophagous	6.3	6	Pupa	18	4
65.011	*Tethea or*	Poplar Lutestring	267	Broadleaf trees	Oligophagous	6.3	6	Pupa	17.5	1
65.012	*Tetheella fluctuosa*	Satin Lutestring	1955	Broadleaf trees	Oligophagous	4	7	Pupa	19	1
65.013	*Ochropacha duplaris*	Common Lutestring	9876	Broadleaf trees	Oligophagous	4	7	Pupa	16	2
65.014	*Cymatophorina diluta hartwiegi*	Oak Lutestring	6671	Broadleaf trees	Oligophagous	4.5	6.3	Egg	16	1
65.015	*Polyploca ridens*	Frosted Green	1167	Broadleaf trees	Oligophagous	4.5	6.3	Pupa	16	1
65.016	*Achlya flavicornis*	Yellow-horned	21717	Broadleaf trees	Oligophagous	4	7	Pupa	18.5	2
66.001	*Poecilocampa populi*	December Moth	74365	Broadleaf polyphagous	Polyphagous	NA	NA	Egg	18.5	3
66.002	*Trichiura crataegi*	Pale Eggar	5313	Broadleaf polyphagous	Polyphagous	NA	NA	Egg	15.5	5
66.003	*Malacosoma neustria*	The Lackey	18795	Broadleaf polyphagous	Polyphagous	NA	NA	Egg	17	3
66.006	*Lasiocampa trifolii*	Grass Eggar	25	Herbaceous polyphagous	Polyphagous	NA	NA	Egg	25.5	1

66.007	*Lasiocampa quercus*	Oak Eggar	816	Broadleaf shrubs	Polyphagous	NA	NA	Larva	32.5	5
66.008	*Macrothylacia rubi*	Fox Moth	1660	Highly polyphagous	Highly polyphagous	NA	NA	Larva	26.5	8
66.010	*Euthrix potatoria*	The Drinker	25758	Grasses	Oligophagous	NA	NA	Larva	28	3
66.012	*Gastropacha quercifolia*	The Lappet	251	Broadleaf shrubs	Polyphagous	NA	NA	Larva	35	2
68.001	*Saturnia pavonia*	Emperor Moth	285	Highly polyphagous	Highly polyphagous	NA	NA	Pupa	34	8
69.001	*Mimas tiliae*	Lime Hawk-moth	176	Broadleaf trees	Polyphagous	NA	NA	Pupa	31	2
69.002	*Smerinthus ocellata*	Eyed Hawk-moth	127	Broadleaf polyphagous	Oligophagous	NA	NA	Pupa	40	3
69.003	*Laothoe populi*	Poplar Hawk-moth	11342	Broadleaf trees	Oligophagous	NA	NA	Pupa	38	8
69.006	*Sphinx ligustri*	Privet Hawk-moth	165	Broadleaf shrubs	Polyphagous	NA	NA	Pupa	48	8
69.007	*Hyloicus pinastri*	Pine Hawk-moth	59	Coniferous	Oligophagous	NA	NA	Pupa	38	1
69.016	*Deilephila elpenor*	Elephant Hawk-moth	582	Forbs	Oligophagous	NA	NA	Pupa	30.5	7
69.017	*Deilephila porcellus*	Small Elephant Hawk-moth	163	Forbs	Oligophagous	NA	NA	Pupa	28	4
70.004	*Idaea rusticata*	Least Carpet	13826	Highly polyphagous	Highly polyphagous	NA	NA	Larva	10	3
70.006	*Idaea fuscovenosa*	Dwarf Cream Wave	13735	Forbs	Polyphagous	NA	NA	Larva	10	3

70.008	*Idaea seriata*	Small Dusty Wave	28586	Forbs	Polyphagous	NA	NA	Larva	10	2
70.009	*Idaea subsericeata*	Satin Wave	6660	Forbs	Polyphagous	NA	NA	Larva	11	3
70.010	*Idaea sylvestraria*	Dotted Border Wave	454	Unknown	Unknown	NA	NA	Larva	10.5	1
70.011	*Idaea dimidiata*	Single-dotted Wave	80815	Forbs	Polyphagous	NA	NA	Larva	10	4
70.012	*Idaea trigeminata*	Treble Brown Spot	20393	Forbs	Polyphagous	NA	NA	Larva	10.5	1
70.013	*Idaea biselata*	Small Fanfooted Wave	272571	Forbs	Unknown	NA	NA	Larva	10.5	3
70.015	*Idaea emarginata*	Small Scallop	10931	Forbs	Oligophagous	NA	NA	Larva	12	3
70.016	Idaea aversata	Riband Wave	209937	Forbs	Polyphagous	NA	NA	Larva	15	8
70.017	*Idaea degeneraria*	Portland Riband Wave	55	Unknown	Unknown	NA	NA	Larva	14	1
70.018	*Idaea straminata*	Plain Wave	1451	Forbs	Polyphagous	NA	NA	Larva	14	4
70.022	*Scopula rubiginata*	Tawny Wave	53	Forbs	Unknown	NA	NA	Larva	10	2
70.023	*Scopula marginepunctata*	Mullein Wave	2903	Forbs	Polyphagous	NA	NA	Larva	13.5	1
70.024	*Scopula imitaria*	Small Blood-vein	17367	Broadleaf shrubs	Oligophagous	NA	NA	Larva	14	7
70.025	*Scopula immutata*	Lesser Cream Wave	1829	Forbs	Oligophagous	5	6.5	Larva	12.5	3

70.026	*Scopula ternata*	Smoky Wave	3367	Broadleaf shrubs	Polyphagous	2	6.5	Larva	13.5	2
70.027	*Scopula floslactata*	Cream Wave	19578	Forbs	Oligophagous	NA	NA	Larva	14.5	3
70.028	*Scopula emutaria*	Rosy Wave	495	Unknown	Unknown	NA	NA	Larva	12	3
70.029	*Timandra comae*	Blood-vein	35333	Forbs	Polyphagous	NA	NA	Larva	16.5	3
70.030	*Cyclophora pendularia*	Dingy Mocha	32	Broadleaf trees	Oligophagous	NA	NA	Pupa	13	2
70.031	*Cyclophora annularia*	The Mocha	141	Broadleaf trees	Monophagous	6	5	Pupa	12.5	2
70.032	*Cyclophora albipunctata*	Birch Mocha	1158	Broadleaf trees	Oligophagous	4	7	Pupa	13	2
70.035	*Cyclophora porata*	False Mocha	167	Broadleaf trees	Oligophagous	4.5	6.3	Pupa	13	2
70.036	*Cyclophora punctaria*	Maiden's Blush	3323	Broadleaf trees	Oligophagous	4.5	6.3	Pupa	14.5	1
70.037	*Cyclophora linearia*	Clay Triple-lines	2469	Broadleaf trees	Monophagous	5	3	Pupa	15	1
70.038	*Rhodometra sacraria*	The Vestal	1112	Forbs	Polyphagous	NA	NA	Immigrant	13	8
70.039	*Phibalapteryx virgata*	Obliqued Striped	463	Forbs	Monophagous	2	7	Pupa	11	3
70.040	*Scotopteryx mucronata*	Lead Belle	2529	Broadleaf shrubs	Oligophagous	3.15	7.65	Larva	17	2
70.041	*Scotopteryx luridata*	July Belle	2762	Broadleaf shrubs	Oligophagous	3	8	Larva	17	8

70.043	*Scotopteryx bipunctaria*	Chalk Carpet	32	Forbs	Oligophagous	NA	NA	Larva	16.5	2
70.045	*Scotopteryx chenopodiata*	Shaded Broad-bar	25301	Forbs	Oligophagous	NA	NA	Larva	17.5	8
70.046	*Orthonama vittata*	Oblique Carpet	4526	Forbs	Oligophagous	NA	NA	Larva	12.5	3
70.047	*Orthonama obstipata*	The Gem	655	Forbs	Polyphagous	NA	NA	Immigrant	13	8
70.048	*Xanthorhoe decoloraria*	Red Carpet	11655	Forbs	Oligophagous	NA	NA	Larva	13.5	1
70.049	*Xanthorhoe fluctuata*	Garden Carpet	97005	Forbs	Oligophagous	NA	NA	Pupa	14.5	8
70.050	*Xanthorhoe biriviata*	Balsam Carpet	331	Forbs	Oligophagous	NA	NA	Pupa	13	3
70.051	*Xanthorhoe spadicearia*	Red Twin-spot Carpet	75838	Forbs	Polyphagous	NA	NA	Pupa	12.5	8
70.052	*Xanthorhoe ferrugata*	Dark-barred Twin-spot Carpet	98311	Forbs	Polyphagous	NA	NA	Pupa	12.5	8
70.053	*Xanthorhoe designata*	Flame Carpet	49157	Forbs	Oligophagous	NA	NA	Pupa	12.5	8
70.054	*Xanthorhoe montanata*	Silver-ground Carpet	248904	Forbs	Polyphagous	NA	NA	Larva	15.5	7
70.055	*Xanthorhoe quadrifasciata*	Large Twin-spot Carpet	5014	Forbs	Polyphagous	NA	NA	Larva	15	3
70.056	*Catarhoe cuculata*	Royal Mantle	108	Forbs	Oligophagous	3	7	Pupa	13	2
70.057	*Catarhoe rubidata*	Ruddy Carpet	786	Forbs	Oligophagous	3	7	Pupa	14	3

70.059	*Camptogramma bilineata*	Yellow Shell	7311	Forbs	Polyphagous	NA	NA	Larva	14	8
70.060	*Epirrhoe tristata*	Small Argent & Sable	182	Forbs	Monophagous	3	6	Pupa	12	1
70.061	*Epirrhoe alternata*	Common Carpet	85205	Forbs	Oligophagous	NA	NA	Pupa	13.5	8
70.062	*Epirrhoe rivata*	Wood Carpet	3611	Forbs	Oligophagous	3	7	Pupa	15	3
70.063	*Epirrhoe galiata*	Galium Carpet	1630	Forbs	Oligophagous	3	6.666667	Pupa	14	3
70.064	*Euphyia biangulata*	Cloaked Carpet	591	Forbs	Oligophagous	NA	NA	Pupa	15.5	1
70.065	*Euphyia unangulata*	Sharp-angled Carpet	5002	Forbs	Unknown	NA	NA	Pupa	14.5	1
70.066	*Anticlea badiata*	Shoulder Stripe	15458	Broadleaf shrubs	Oligophagous	NA	NA	Larva	16	2
70.067	*Anticlea derivata*	The Streamer	16273	Broadleaf shrubs	Oligophagous	NA	NA	Larva	15	3
70.068	*Mesoleuca albicillata*	Beautiful Carpet	1367	Broadleaf shrubs	Oligophagous	NA	NA	Pupa	16.5	1
70.069	*Pelurga comitata*	Dark Spinach	3412	Forbs	Oligophagous	NA	NA	Pupa	17	2
70.070	*Larentia clavaria*	The Mallow	2740	Forbs	Oligophagous	5	7.333333	Egg	20.5	3
70.071	*Entephria flavicinctata*	Yellow-ringed Carpet	83	Forbs	Oligophagous	NA	NA	Larva	17.5	2
70.072	*Entephria caesiata*	Grey Mountain Carpet	10216	Broadleaf shrubs	Oligophagous	2	6.5	Larva	17.5	1
70.073	*Spargania luctuata*	White-banded Carpet	544	Forbs	Monophagous	5	6	Pupa	14.5	1

70.074	*Hydriomena furcata*	July Highflyer	234270	Woody polyphagous	Polyphagous	NA	NA	Egg	16	4
70.075	*Hydriomena impluviata*	May Highflyer	4192	Broadleaf trees	Monophagous	6	5	Pupa	14.5	2
70.076	*Hydriomena ruberata*	Ruddy Highflyer	745	Broadleaf shrubs	Oligophagous	NA	NA	Pupa	15.5	4
70.077	*Thera firmata*	Pine Carpet	7982	Coniferous	Oligophagous	2	7	Egg	14.5	1
70.078	*Thera cognata*	Chestnut-coloured Carpet	185	Coniferous	Monophagous	3	8	Larva	12.5	3
70.079	*Thera britannica*	Spruce Carpet	14511	Coniferous	Oligophagous	NA	NA	Larva	15	2
70.081	*Thera obeliscata*	Grey Pine Carpet	35793	Coniferous	Oligophagous	NA	NA	Larva	15	2
70.082	*Thera juniperata*	Juniper Carpet	2146	Coniferous	Oligophagous	3	8	Egg	12.5	3
70.082	*Thera cupressata*	Cypress Carpet	270	Coniferous	Oligophagous	NA	NA	Larva	13.5	1
70.084	*Plemyria rubiginata*	Blue-bordered Carpet	2163	Broadleaf shrubs	Polyphagous	NA	NA	Egg	13.5	2
70.085	*Cidaria fulvata*	Barred Yellow	18191	Broadleaf shrubs	Oligophagous	NA	NA	Egg	13	3
70.086	*Electrophaes corylata*	Broken-barred Carpet	7057	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	15	2
70.087	*Cosmorhoe ocellata*	Purple Bar	37405	Forbs	Oligophagous	NA	NA	Larva	14	7
70.089	*Eulithis prunata*	The Phoenix	4444	Broadleaf shrubs	Oligophagous	6	5	Egg	18	2
70.090	*Eulithis testata*	The Chevron	42221	Broadleaf shrubs	Polyphagous	NA	NA	Egg	16	2

70.091	*Eulithis populata*	Northern Spinach	120413	Broadleaf shrubs	Monophagous	2	6	Egg	15.5	2
70.092	*Eulithis mellinata*	The Spinach	2058	Broadleaf shrubs	Oligophagous	6	5	Egg	17	2
70.093	*Eulithis pyraliata*	Barred Straw	115477	Forbs	Oligophagous	NA	NA	Egg	16.5	3
70.094	*Ecliptopera silaceata*	Small Phoenix	55367	Forbs	Oligophagous	NA	NA	Pupa	15	7
70.095	*Chloroclysta siterata*	Red-green Carpet	30531	Broadleaf polyphagous	Polyphagous	NA	NA	Adult	15.5	3
70.096	*Chloroclysta miata*	Autumn Green Carpet	17720	Broadleaf polyphagous	Polyphagous	NA	NA	Adult	16	3
70.097	*Chloroclysta concinnata*	Arran Carpet	51	Broadleaf shrubs	Oligophagous	2	6.5	Larva	16.5	2
70.097	*Chloroclysta truncata*	Common Marbled Carpet	129279	Highly polyphagous	Highly polyphagous	NA	NA	Larva	16.5	8
70.098	*Chloroclysta citrata*	Dark Marbled Carpet	115068	Broadleaf shrubs	Polyphagous	NA	NA	Egg	16.5	5
70.099	*Colostygia olivata*	Beech-green Carpet	2206	Forbs	Oligophagous	3	6.666667	Larva	14	2
70.100	*Colostygia pectinataria*	Green Carpet	86961	Forbs	Oligophagous	NA	NA	Larva	13.5	8
70.101	*Colostygia multistrigaria*	Mottled Grey	48715	Forbs	Oligophagous	NA	NA	Pupa	15	4
70.102	*Coenotephria salicata*	Striped Twin-spot Carpet	6273	Forbs	Oligophagous	NA	NA	Pupa	13.5	1
70.103	*Lampropteryx suffumata*	Water Carpet	26683	Forbs	Oligophagous	NA	NA	Pupa	15.5	4

70.104	*Lampropteryx otregiata*	Devon Carpet	8329	Forbs	Oligophagous	4	7	Pupa	13	1
70.105	*Operophtera fagata*	Northern Winter Moth	24350	Broadleaf polyphagous	Polyphagous	NA	NA	Egg	16	3
70.106	*Operophtera brumata*	Winter Moth	120826	Broadleaf polyphagous	Polyphagous	NA	NA	Egg	14.5	3
70.107	*Epirrita dilutata*	November Moth	228675	Broadleaf polyphagous	Polyphagous	NA	NA	Egg	17.5	3
70.108	*Epirrita christyi*	Pale November Moth	53754	Broadleaf polyphagous	Polyphagous	NA	NA	Egg	17.5	1
70.109	*Epirrita autumnata*	Autumnal Moth	47328	Broadleaf polyphagous	Polyphagous	NA	NA	Egg	18	1
70.110	*Epirrita filigrammaria*	Small Autumnal Moth	24649	Broadleaf shrubs	Polyphagous	NA	NA	Egg	16	1
70.111	*Asthena albulata*	Small White Wave	4192	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	10	1
70.112	*Euchoeca nebulata*	Dingy Shell	1645	Broadleaf trees	Monophagous	6	5	Pupa	10.5	2
70.113	*Hydrelia sylvata*	Waved Carpet	1223	Broadleaf trees	Polyphagous	NA	NA	Pupa	12	3
70.114	*Hydrelia flammeolaria*	Small Yellow Wave	770	Broadleaf trees	Polyphagous	6	4.666667	Pupa	10	3
70.115	*Venusia cambrica*	Welsh Wave	7572	Broadleaf trees	Polyphagous	NA	NA	Pupa	14	2
70.116	*Discoloxia blomeri*	Blomer's Rivulet	116	Broadleaf trees	Monophagous	NA	NA	Pupa	11.5	1
70.117	*Minoa murinata*	Drab Looper	31	Forbs	Monophagous	6	4	Pupa	10	1
70.118	*Philereme vetulata*	Brown Scallop	361	Broadleaf shrubs	Monophagous	6	7	Egg	14.5	2

70.119	*Philereme transversata britannica*	Dark Umber	2370	Broadleaf shrubs	Oligophagous	5.5	6.5	Egg	18.5	2
70.121	*Rheumaptera undulata*	Scallop Shell	2199	Broadleaf shrubs	Polyphagous	NA	NA	Pupa	17.5	2
70.122	*Rheumaptera cervinalis*	Scarce Tissue	350	Broadleaf shrubs	Monophagous	NA	NA	Pupa	20.5	2
70.123	*Triphosa dubitata*	The Tissue	405	Broadleaf shrubs	Oligophagous	5.5	6.5	Adult	20.5	4
70.125	*Coenocalpe lapidata*	Slender-striped Rufous	725	Forbs	Oligophagous	NA	NA	Egg	14.5	2
70.126	*Horisme vitalbata*	Small Waved Umber	3109	Broadleaf shrubs	Monophagous	5	6	Pupa	15.5	2
70.127	*Horisme tersata*	The Fern	3296	Broadleaf shrubs	Monophagous	5	6	Pupa	16	4
70.128	*Melanthia procellata*	Pretty Chalk Carpet	3247	Broadleaf shrubs	Monophagous	5	6	Pupa	17	2
70.130	*Odezia atrata*	Chimney-sweeper	172	Forbs	Oligophagous	5	6	Egg	13.5	3
70.131	*Perizoma didymata*	Twin-spot Carpet	29441	Highly polyphagous	Highly polyphagous	NA	NA	Egg	13	3
70.132	*Perizoma affinitata*	The Rivulet	20855	Forbs	Monophagous	7	5	Pupa	13.5	3
70.133	*Perizoma alchemillata*	Small Rivulet	68804	Forbs	Oligophagous	7	6.5	Pupa	10	7
70.134	*Perizoma bifaciata*	Barred Rivulet	744	Forbs	Monophagous	5	7	Pupa	10	5
70.136	*Perizoma blandiata*	Pretty Pinion	674	Forbs	Monophagous	3	8	Pupa	10	8

70.137	*Perizoma albulata*	Grass Rivulet	4427	Forbs	Monophagous	4	7	Pupa	11	2
70.138	*Perizoma flavofasciata*	Sandy Carpet	17259	Forbs	Oligophagous	6	6.333333	Pupa	12.5	4
70.139	*Perizoma taeniata*	Barred Carpet	224	Moss	Unknown	NA	NA	Larva	11.5	1
70.141	*Gymnoscelis rufifasciata*	Double-striped Pug	51718	Highly polyphagous	Highly polyphagous	NA	NA	Pupa	9	8
70.142	*Chloroclystis v-ata*	V-Pug	3850	Highly polyphagous	Highly polyphagous	NA	NA	Pupa	9	3
70.143	*Pasiphila chloerata*	Sloe Pug	150	Broadleaf shrubs	Monophagous	6	6	Egg	9.5	1
70.144	*Pasiphila rectangulata*	Green Pug	15744	Broadleaf shrubs	Oligophagous	NA	NA	Egg	9.5	7
70.145	*Pasiphila debiliata*	Bilberry Pug	5732	Broadleaf shrubs	Monophagous	5	6	Egg	10	3
70.146	*Eupithecia haworthiata*	Haworth's Pug	1920	Broadleaf shrubs	Oligophagous	5	6	Pupa	8.5	3
70.147	*Eupithecia tenuiata*	Slender Pug	1395	Broadleaf trees	Oligophagous	NA	NA	Egg	9	2
70.148	*Eupithecia inturbata*	Maple Pug	1623	Broadleaf trees	Monophagous	6	5	Egg	9	2
70.149	*Eupithecia abietaria*	Cloaked Pug	56	Coniferous	Oligophagous	NA	NA	Pupa	13	1
70.150	*Eupithecia linariata*	Toadflax Pug	1501	Forbs	Monophagous	6	7	Pupa	9.5	1
70.151	*Eupithecia pulchellata*	Foxglove Pug	7985	Forbs	Monophagous	5	6	Pupa	11	8

70.153	*Eupithecia plumbeolata*	Lead-coloured Pug	3473	Forbs	Monophagous	3	5	Pupa	9.5	2
70.154	*Eupithecia pygmaeata*	Marsh Pug	29	Forbs	Oligophagous	NA	NA	Pupa	8.5	2
70.155	*Eupithecia venosata*	Netted Pug	532	Forbs	Oligophagous	4.5	7.5	Pupa	12	3
70.156	*Eupithecia abbreviata*	Brindled Pug	42794	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	11	1
70.157	*Eupithecia dodoneata*	Oak-tree Pug	2430	Broadleaf polyphagous	Polyphagous	5	5.9	Pupa	9.5	2
70.158	*Eupithecia pusillata*	Juniper Pug	8614	Coniferous	Oligophagous	3	8	Egg	10	2
70.159	*Eupithecia phoeniceata*	Cypress Pug	644	Coniferous	Oligophagous	NA	NA	Larva	10.5	2
70.160	*Eupithecia tripunctaria*	White-spotted Pug	3157	Highly polyphagous	Highly polyphagous	NA	NA	Pupa	11	3
70.161	*Eupithecia virgaureata*	Golden-rod Pug	5347	Forbs	Oligophagous	3.5	6	Pupa	10.5	7
70.162	*Eupithecia tantillaria*	Dwarf Pug	1516	Coniferous	Oligophagous	NA	NA	Pupa	10	1
70.163	*Eupithecia lariciata*	Larch Pug	2712	Coniferous	Monophagous	3	7	Pupa	11	2
70.165	*Eupithecia pimpinellata*	Pimpinel Pug	69	Forbs	Monophagous	3	7	Pupa	11.5	2
70.166	*Eupithecia simpliciata*	Plain Pug	455	Forbs	Oligophagous	NA	NA	Pupa	12	2
70.168	*Eupithecia nanata angusta*	Narrow-winged Pug	16741	Forbs	Oligophagous	2	7	Pupa	10.5	2

70.169	*Eupithecia fraxinata*	Ash Pug	832	Broadleaf trees	Monophagous	6	5	Pupa	11	4
70.169	*Eupithecia innotata*	Angle-barred Pug	159	Broadleaf shrubs	Polyphagous	NA	NA	Pupa	11	1
70.170	*Eupithecia irriguata*	Marbled Pug	103	Broadleaf trees	Monophagous	4.5	6.3	Pupa	10	1
70.171	*Eupithecia indigata*	Ochreous Pug	947	Coniferous	Oligophagous	NA	NA	Pupa	9	1
70.172	*Eupithecia distinctaria constrictata*	Thyme Pug	390	Forbs	Monophagous	2	8	Pupa	9	2
70.173	*Eupithecia centaureata*	Lime-speck Pug	9018	Forbs	Polyphagous	NA	NA	Pupa	11	7
70.174	*Eupithecia insigniata*	Pinion-spotted Pug	43	Broadleaf shrubs	Oligophagous	NA	NA	Pupa	11	1
70.175	*Eupithecia trisignaria*	Triple-spotted Pug	280	Forbs	Oligophagous	6	7	Pupa	10.5	2
70.176	*Eupithecia intricata*	Edinburgh Pug	4665	Coniferous	Oligophagous	NA	NA	Pupa	12.5	2
70.177	*Eupithecia satyrata*	Satyr Pug	2359	Forbs	Polyphagous	NA	NA	Pupa	11	1
70.178	*Eupithecia extensaria occidua*	Scarce Pug	1159	Broadleaf shrubs	Monophagous	NA	NA	Pupa	12	1
70.179	*Eupithecia goossensiata*	Ling Pug	276	Broadleaf shrubs	Oligophagous	1.7	7.4	Pupa	11.5	2
70.179	*Eupithecia absinthiata*	Wormwood Pug	12003	Forbs	Oligophagous	NA	NA	Pupa	11.5	8

70.180	*Eupithecia expallidata*	Bleached Pug	128	Forbs	Monophagous	3	5	Pupa	12.5	1
70.181	*Eupithecia valerianata*	Valerian Pug	208	Forbs	Monophagous	5	6	Pupa	9	2
70.182	*Eupithecia assimilata*	Currant Pug	4537	Broadleaf shrubs	Polyphagous	6.666667	5.333333	Pupa	11	3
70.183	*Eupithecia vulgata*	Common Pug	85785	Highly polyphagous	Highly polyphagous	NA	NA	Pupa	11	7
70.184	*Eupithecia exiguata*	Mottled Pug	17325	Broadleaf shrubs	Polyphagous	NA	NA	Pupa	11.5	3
70.185	*Eupithecia denotata*	Campanula Pug	34	Forbs	Oligophagous	NA	NA	Pupa	12	3
70.186	*Eupithecia millefoliata*	Yarrow Pug	123	Forbs	Monophagous	4	7	Pupa	12.5	1
70.187	*Eupithecia icterata*	Tawny-speckled Pug	8139	Forbs	Oligophagous	3.5	7	Pupa	12	8
70.188	*Eupithecia succenturiata*	Bordered Pug	2538	Forbs	Oligophagous	NA	NA	Pupa	12.5	2
70.189	*Eupithecia subumbrata*	Shaded Pug	722	Forbs	Polyphagous	NA	NA	Pupa	11	4
70.190	*Eupithecia subfuscata*	Grey Pug	12193	Highly polyphagous	Highly polyphagous	NA	NA	Pupa	11	7
70.191	*Carsia sororiata anglica*	Manchester Treble-bar	174	Broadleaf shrubs	Oligophagous	NA	NA	Egg	13	3
70.192	*Aplocera plagiata*	Treble-bar	2107	Forbs	Oligophagous	NA	NA	Larva	20.5	8
70.193	*Aplocera efformata*	Lesser Treble-bar	594	Forbs	Oligophagous	NA	NA	Larva	17.5	8

70.195	*Chesias legatella*	The Streak	17747	Broadleaf shrubs	Oligophagous	NA	NA	Egg	18	5
70.196	*Chesias rufata*	Broom-tip	2960	Broadleaf shrubs	Monophagous	4	8	Pupa	15	4
70.197	*Lithostege griseata*	Grey Carpet	48	Forbs	Monophagous	6	8	Pupa	15	2
70.198	*Lobophora halterata*	The Seraphim	447	Broadleaf trees	Oligophagous	6.3	6	Pupa	13.5	1
70.199	*Pterapherapteryx sexalata*	Small Seraphim	1487	Broadleaf trees	Oligophagous	NA	NA	Pupa	10.5	2
70.200	*Acasis viretata*	Yellow-barred Brindle	3976	Broadleaf shrubs	Polyphagous	NA	NA	Pupa	12	2
70.201	*Trichopteryx polycommata*	Barred Tooth-striped	97	Broadleaf trees	Polyphagous	5.5	5.5	Pupa	15.5	2
70.202	*Trichopteryx carpinata*	Early Tooth-striped	21915	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	15.5	3
70.205	*Abraxas grossulariata*	The Magpie	61126	Broadleaf shrubs	Polyphagous	NA	NA	Larva	21.5	3
70.206	*Abraxas sylvata*	Clouded Magpie	1235	Broadleaf trees	Oligophagous	NA	NA	Pupa	20	1
70.207	*Lomaspilis marginata*	Clouded Border	99665	Broadleaf trees	Polyphagous	NA	NA	Pupa	12.5	3
70.208	*Ligdia adustata*	Scorched Carpet	5433	Broadleaf shrubs	Monophagous	5	5	Pupa	13	1
70.211	*Macaria notata*	Peacock Moth	2589	Broadleaf trees	Oligophagous	4	7	Pupa	15	2
70.212	*Macaria alternata*	Sharp-angled Peacock	7491	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	14	3

70.214	*Macaria liturata*	Tawny-barred Angle	7141	Coniferous	Polyphagous	NA	NA	Pupa	15.5	1
70.215	*Macaria wauaria*	The V-moth	2350	Broadleaf shrubs	Oligophagous	6	5	Egg	15.5	1
70.217	*Itame brunneata*	Rannoch Looper	75	Broadleaf shrubs	Oligophagous	2	6	Egg	12	1
70.218	*Chiasmia clathrata*	Latticed Heath	11102	Forbs	Oligophagous	NA	NA	Pupa	13	8
70.221	*Cepphis advenaria*	Little Thorn	176	Broadleaf shrubs	Oligophagous	NA	NA	Pupa	15.5	1
70.222	*Petrophora chlorosata*	Brown Silver-line	84038	Forbs	Monophagous	3	6	Pupa	16.5	3
70.223	*Plagodis pulveraria*	Barred Umber	8363	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	18	1
70.224	*Plagodis dolabraria*	Scorched Wing	9985	Broadleaf trees	Polyphagous	NA	NA	Pupa	17.5	1
70.225	*Pachycnemia hippocastanaria*	Horse Chestnut	6424	Broadleaf shrubs	Oligophagous	1.5	7.5	Pupa	15	1
70.226	*Opisthograptis luteolata*	Brimstone Moth	127098	Broadleaf shrubs	Polyphagous	NA	NA	Larva	17.5	5
70.227	*Epione repandaria*	Bordered Beauty	8357	Broadleaf trees	Polyphagous	NA	NA	Egg	14.5	2
70.229	*Pseudopanthera macularia*	Speckled Yellow	35	Forbs	Oligophagous	3	6	Pupa	14	2
70.230	*Angerona prunaria*	Orange Moth	749	Broadleaf shrubs	Polyphagous	NA	NA	Larva	25	1
70.231	*Apeira syringaria*	Lilac Beauty	6233	Broadleaf shrubs	Polyphagous	NA	NA	Larva	20.5	1

70.232	*Ennomos autumnaria*	Large Thorn	607	Broadleaf polyphagous	Polyphagous	NA	NA	Egg	24.5	2
70.233	*Ennomos quercinaria*	August Thorn	6529	Broadleaf polyphagous	Polyphagous	NA	NA	Egg	20	1
70.234	*Ennomos alniaria*	Canary-shouldered Thorn	24301	Broadleaf trees	Polyphagous	NA	NA	Egg	18	2
70.235	*Ennomos fuscantaria*	Dusky Thorn	6207	Broadleaf trees	Oligophagous	6	5	Egg	19	3
70.236	*Ennomos erosaria*	September Thorn	6172	Broadleaf trees	Polyphagous	NA	NA	Egg	19	2
70.237	*Selenia dentaria*	Early Thorn	103412	Broadleaf shrubs	Polyphagous	NA	NA	Pupa	18.5	3
70.238	*Selenia lunularia*	Lunar Thorn	6337	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	19	1
70.239	*Selenia tetralunaria*	Purple Thorn	12100	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	20	3
70.240	*Odontopera bidentata*	Scalloped Hazel	47430	Woody polyphagous	Polyphagous	NA	NA	Pupa	22	3
70.241	*Crocallis elinguaria*	Scalloped Oak	42169	Broadleaf polyphagous	Polyphagous	NA	NA	Egg	20	3
70.243	*Ourapteryx sambucaria*	Swallow-tail Moth	8708	Broadleaf shrubs	Polyphagous	NA	NA	Larva	26	3
70.244	*Colotois pennaria*	Feathered Thorn	56187	Broadleaf polyphagous	Polyphagous	NA	NA	Egg	21	1
70.245	*Alsophila aescularia*	March Moth	40723	Broadleaf polyphagous	Polyphagous	NA	NA	Larva	17.5	3
70.246	*Apocheima hispidaria*	Small Brindled Beauty	4224	Broadleaf trees	Oligophagous	NA	NA	Pupa	16	1

70.247	*Apocheima pilosaria*	Pale Brindled Beauty	22519	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	21.5	1
70.248	*Lycia hirtaria*	Brindled Beauty	16075	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	21	3
70.251	*Biston strataria*	Oak Beauty	8925	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	22	1
70.252	*Biston betularia*	Peppered Moth	5490	Highly polyphagous	Highly polyphagous	NA	NA	Pupa	25	3
70.253	*Agriopis leucophaearia*	Spring Usher	10799	Broadleaf trees	Oligophagous	4.5	6.3	Pupa	15.5	1
70.254	*Agriopis aurantiaria*	Scarce Umber	35219	Broadleaf polyphagous	Polyphagous	NA	NA	Egg	19	2
70.255	*Agriopis marginaria*	Dotted Border	32928	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	18	5
70.256	*Erannis defoliaria*	Mottled Umber	116215	Broadleaf polyphagous	Polyphagous	NA	NA	Egg	21.5	1
70.257	*Menophra abruptaria*	Waved Umber	2425	Broadleaf shrubs	Oligophagous	NA	NA	Pupa	19.5	3
70.258	*Peribatodes rhomboidaria*	Willow Beauty	33316	Woody polyphagous	Polyphagous	NA	NA	Larva	20.5	3
70.262	*Selidosema brunnearia*	Bordered Grey	27	Forbs	Oligophagous	NA	NA	Larva	19	1
70.263	*Cleora cinctaria*	Ringed Carpet	360	Broadleaf shrubs	Polyphagous	NA	NA	Pupa	18	2
70.264	*Deileptenia ribeata*	Satin Beauty	7255	Coniferous	Oligophagous	NA	NA	Larva	22	1
70.265	*Alcis repandata*	Mottled Beauty	81517	Highly polyphagous	Highly polyphagous	NA	NA	Larva	22.5	8
70.266	*Alcis jubata*	Dotted Carpet	20724	Lichen	Oligophagous	NA	NA	Larva	14.5	1

70.267	*Hypomecis roboraria*	Great Oak Beauty	1266	Broadleaf trees	Monophagous	4	7	Larva	27.5	1
70.268	*Hypomecis punctinalis*	Pale Oak Beauty	4265	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	24	1
70.270	*Ectropis bistortata*	The Engrailed	75741	Woody polyphagous	Polyphagous	NA	NA	Pupa	18.5	3
70.272	*Paradarisa consonaria*	Square Spot	647	Woody polyphagous	Polyphagous	NA	NA	Pupa	19	1
70.273	*Parectropis similaria*	Brindled White-spot	3084	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	18.5	1
70.274	*Aethalura punctulata*	Grey Birch	3140	Broadleaf trees	Oligophagous	4	7	Pupa	14.5	1
70.275	*Ematurga atomaria*	Common Heath	61	Forbs	Polyphagous	NA	NA	Pupa	13.5	3
70.276	*Bupalus piniaria*	Bordered White	1829	Coniferous	Oligophagous	NA	NA	Pupa	18	1
70.277	*Cabera pusaria*	Common White Wave	95346	Broadleaf trees	Polyphagous	NA	NA	Pupa	16	1
70.278	*Cabera exanthemata*	Common Wave	70837	Broadleaf trees	Oligophagous	NA	NA	Pupa	15	2
70.279	*Lomographa bimaculata*	White-pinion Spotted	6135	Broadleaf shrubs	Polyphagous	NA	NA	Pupa	13.5	3
70.280	*Lomographa temerata*	Clouded Silver	14253	Broadleaf shrubs	Polyphagous	NA	NA	Pupa	14	3
70.281	*Aleucis distinctata*	Sloe Carpet	488	Broadleaf shrubs	Monophagous	6	6	Pupa	13.5	1
70.282	*Theria primaria*	Early Moth	5350	Broadleaf shrubs	Oligophagous	5.75	5.75	Pupa	15.5	2

70.283	*Campaea margaritata*	Light Emerald	97916	Broadleaf polyphagous	Polyphagous	NA	NA	Larva	22	3
70.284	*Hylaea fasciaria*	Barred Red	21289	Coniferous	Oligophagous	NA	NA	Larva	19	1
70.285	*Gnophos obfuscata*	Scotch Annulet	213	Broadleaf shrubs	Oligophagous	NA	NA	Larva	19	1
70.287	*Charissa obscurata*	The Annulet	87	Forbs	Polyphagous	NA	NA	Larva	16.5	4
70.288	*Cleorodes lichenaria*	Brussels Lace	3314	Lichen	Oligophagous	NA	NA	Larva	16	2
70.292	*Dyscia fagaria*	Grey Scalloped Bar	1691	Broadleaf shrubs	Oligophagous	1.7	7.4	Larva	18	3
70.294	*Semiaspilates ochrearia*	Yellow Belle	1940	Forbs	Polyphagous	NA	NA	Larva	14	7
70.295	*Perconia strigillaria*	Grass Wave	972	Broadleaf shrubs	Oligophagous	NA	NA	Larva	17.5	2
70.297	*Pseudoterpna pruinata atropunctari*	Grass Emerald	2213	Broadleaf shrubs	Oligophagous	2.766667	7.766667	Larva	16.5	4
70.299	*Geometra papilionaria*	Large Emerald	8890	Broadleaf trees	Polyphagous	NA	NA	Larva	26.5	4
70.300	*Comibaena bajularia*	Blotched Emerald	3821	Broadleaf trees	Oligophagous	4.5	6.3	Larva	15.5	1
70.302	*Hemistola chrysoprasaria*	Small Emerald	1756	Broadleaf shrubs	Monophagous	5	6	Larva	18.5	3
70.303	*Jodis lactearia*	Little Emerald	8690	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	12.5	5
70.304	*Thalera fimbrialis*	Sussex Emerald	40	Forbs	Monophagous	3	8	Larva	15.5	1

70.305	*Hemithea aestivaria*	Common Emerald	39130	Highly polyphagous	Highly polyphagous	NA	NA	Larva	15.5	5
70.306	*Chlorissa viridata*	Small Grass Emerald	52	Broadleaf shrubs	Polyphagous	NA	NA	Pupa	12	1
71.001	*Thaumetopoea processionea*	Oak Processionary Moth	29	Broadleaf trees	Oligophagous	4.5	6.3	Egg	15.5	2
71.003	*Cerura vinula*	Puss Moth	110	Broadleaf shrubs	Oligophagous	NA	NA	Pupa	34.5	5
71.005	*Furcula furcula*	Sallow Kitten	293	Broadleaf shrubs	Oligophagous	NA	NA	Pupa	16	4
71.007	*Furcula bifida*	Poplar Kitten	56	Broadleaf trees	Oligophagous	NA	NA	Pupa	19	1
71.009	*Stauropus fagi*	Lobster Moth	560	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	28.5	1
71.010	*Drymonia dodonaea*	Marbled Brown	5561	Broadleaf trees	Oligophagous	4.5	6.3	Pupa	18.5	1
71.011	*Drymonia ruficornis*	Lunar Marbled Brown	1762	Broadleaf trees	Oligophagous	4.5	6.3	Pupa	18	2
71.012	*Notodonta dromedarius*	Iron Prominent	1576	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	21	3
71.013	*Notodonta ziczac*	Pebble Prominent	4047	Broadleaf trees	Oligophagous	NA	NA	Pupa	21.5	3
71.016	*Peridea anceps*	Great Prominent	4346	Broadleaf trees	Oligophagous	4.5	6.3	Pupa	27.5	1
71.017	*Pheosia tremula*	Swallow Prominent	1860	Broadleaf trees	Oligophagous	NA	NA	Pupa	25	3
71.018	*Pheosia gnoma*	Lesser Swallow Prominent	13745	Broadleaf trees	Oligophagous	4	7	Pupa	23	4

71.020	*Pterostoma palpina*	Pale Prominent	9740	Broadleaf trees	Oligophagous	NA	NA	Pupa	21.5	8
71.021	*Ptilodon capucina*	Coxcomb Prominent	18962	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	19.5	1
71.022	*Ptilodon cucullina*	Maple Prominent	273	Broadleaf trees	Oligophagous	6	5	Pupa	17.5	2
71.023	*Odontosia carmelita*	Scarce Prominent	749	Broadleaf trees	Oligophagous	4	7	Pupa	19.5	1
71.024	*Ptilophora plumigera*	Plumed Prominent	44	Broadleaf trees	Oligophagous	6	5	Egg	17.5	2
71.025	*Phalera bucephala*	Buff-tip	8365	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	28	3
71.027	*Clostera curtula*	Chocolate-tip	1020	Broadleaf trees	Oligophagous	NA	NA	Pupa	15.5	4
71.028	*Clostera pigra*	Small Chocolate-tip	55	Broadleaf shrubs	Oligophagous	NA	NA	Pupa	12.5	3
72.001	*Scoliopteryx libatrix*	The Herald	521	Broadleaf trees	Oligophagous	NA	NA	Adult	21	5
72.002	*Rivula sericealis*	Straw Dot	127277	Grasses	Oligophagous	NA	NA	Larva	14	4
72.003	*Hypena proboscidalis*	The Snout	161014	Forbs	Monophagous	8	6	Larva	17	4
72.004	*Hypena rostralis*	Buttoned Snout	84	Broadleaf shrubs	Monophagous	8	6	Adult	14	1
72.007	*Hypena crassalis*	Beautiful Snout	6949	Broadleaf shrubs	Oligophagous	2	6	Pupa	15	3
72.009	*Leucoma salicis*	White Satin Moth	473	Broadleaf trees	Oligophagous	NA	NA	Larva	22.5	3
72.010	*Lymantria monacha*	Black Arches	7745	Woody polyphagous	Polyphagous	NA	NA	Egg	23	1

72.011	*Lymantria dispar*	Gypsy Moth	42	Broadleaf polyphagous	Polyphagous	NA	NA	Egg	27.5	1
72.012	*Euproctis chrysorrhoea*	Brown-tail	4245	Broadleaf shrubs	Polyphagous	NA	NA	Larva	18	3
72.013	*Euproctis similis*	Yellow-tail	45261	Broadleaf polyphagous	Polyphagous	NA	NA	Larva	19.5	3
72.015	*Calliteara pudibunda*	Pale Tussock	8632	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	26	8
72.016	*Dicallomera fascelina*	Dark Tussock	331	Broadleaf shrubs	Polyphagous	NA	NA	Larva	23	2
72.017	*Orgyia antiqua*	The Vapourer	444	Broadleaf polyphagous	Polyphagous	NA	NA	Egg	14.5	8
72.019	*Spilosoma luteum*	Buff Ermine	106278	Highly polyphagous	Highly polyphagous	NA	NA	Pupa	19.5	8
72.020	*Spilosoma lubricipeda*	White Ermine	163620	Forbs	Polyphagous	NA	NA	Pupa	20.5	8
72.021	*Spilosoma urticae*	Water Ermine	647	Forbs	Oligophagous	NA	NA	Pupa	19.5	2
72.022	*Diaphora mendica*	Muslin Moth	15858	Forbs	Polyphagous	NA	NA	Pupa	16.5	8
72.023	*Diacrisia sannio*	Clouded Buff	1009	Forbs	Polyphagous	NA	NA	Larva	20.5	2
72.024	*Phragmatobia fuliginosa*	Ruby Tiger	10089	Forbs	Polyphagous	NA	NA	Larva	16.5	8
72.026	*Arctia caja*	Garden Tiger	14512	Forbs	Polyphagous	NA	NA	Larva	32.5	8
72.027	*Arctia villica britannica*	Cream-spot Tiger	137	Forbs	Polyphagous	NA	NA	Larva	28.5	5
72.029	*Callimorpha dominula*	Scarlet Tiger	144	Forbs	Polyphagous	NA	NA	Larva	25	2

72.030	*Euplagia quadripunctaria*	Jersey Tiger	75	Forbs	Polyphagous	NA	NA	Larva	30.5	2
72.031	*Tyria jacobaeae*	Cinnabar	41053	Forbs	Oligophagous	4	7	Pupa	20	5
72.032	*Coscinia cribraria*	Speckled Footman	34	Herbaceous polyphagous	Oligophagous	NA	NA	Larva	16.5	1
72.035	*Miltochrista miniata*	Rosy Footman	15535	Lichen	Oligophagous	NA	NA	Larva	13.5	2
72.036	*Nudaria mundana*	Muslin Footman	21210	Lichen	Oligophagous	NA	NA	Larva	11	2
72.037	*Thumatha senex*	Round-winged Muslin	2894	Lichen	Oligophagous	NA	NA	Larva	10.5	4
72.038	*Cybosia mesomella*	Four-dotted Footman	22989	Lichen	Oligophagous	NA	NA	Larva	14.5	4
72.041	*Lithosia quadra*	Four-spotted Footman	360	Lichen	Oligophagous	NA	NA	Larva	22	1
72.042	*Atolmis rubricollis*	Red-necked Footman	469	Lichen	Oligophagous	NA	NA	Pupa	16.5	1
72.043	*Eilema depressa*	Buff Footman	13129	Lichen	Oligophagous	NA	NA	Larva	16	4
72.044	*Eilema griseola*	Dingy Footman	83354	Lichen	Oligophagous	NA	NA	Larva	16.5	1
72.045	*Eilema lurideola*	Common Footman	287204	Lichen	Oligophagous	NA	NA	Larva	15.5	7
72.046	*Eilema complana*	Scarce Footman	12606	Lichen	Oligophagous	NA	NA	Larva	16.5	8
72.047	*Eilema caniola*	Hoary Footman	507	Lichen	Oligophagous	NA	NA	Larva	16	1
72.048	*Eilema pygmaeola*	Pygmy Footman	156	Lichen	Oligophagous	NA	NA	Larva	12.5	1
72.049	*Eilema sororcula*	Orange Footman	1933	Lichen	Oligophagous	NA	NA	Pupa	14.5	1

72.051	*Paracolax tristalis*	Clay Fan-foot	129	Broadleaf trees	Oligophagous	4.5	6.3	Larva	15	1
72.052	*Macrochilo cribrumalis*	Dotted Fan-foot	79	Grasses	Oligophagous	3.333333	5.333333	Larva	13.5	1
72.053	*Zanclognatha tarsipennalis*	The Fan-foot	29000	Broadleaf trees	Oligophagous	NA	NA	Larva	14.5	3
72.054	*Herminia tarsicrinalis*	Shaded Fan-foot	169	Unknown	Unknown	NA	NA	Larva	13	1
72.055	*Herminia grisealis*	Small Fan-foot	35815	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	12	3
72.056	*Pechipogo strigilata*	Common Fan-foot	283	Broadleaf trees	Oligophagous	NA	NA	Larva	15	1
72.060	*Hypenodes humidalis*	Marsh Oblique-barred	2167	Unknown	Unknown	NA	NA	Larva	10	2
72.061	*Schrankia costaestrigalis*	Pinion-streaked Snout	2759	Unknown	Unknown	NA	NA	NA	10	4
72.062	*Schrankia taenialis*	White-line Snout	279	Unknown	Unknown	NA	NA	Larva	10	2
72.063	*Lygephila pastinum*	The Blackneck	655	Forbs	Oligophagous	5	7	Larva	19.5	4
72.066	*Parascotia fuliginaria*	Waved Black	3774	Other	Oligophagous	NA	NA	Larva	12.5	2
72.067	*Phytometra viridaria*	Small Purple-barred	236	Forbs	Oligophagous	2.5	8	Pupa	10	3
72.069	*Laspeyria flexula*	Beautiful Hook-tip	4046	Lichen	Oligophagous	NA	NA	Larva	14	2
72.078	*Catocala nupta*	Red Underwing	378	Broadleaf trees	Oligophagous	NA	NA	Egg	36.5	3

73.001	*Abrostola tripartita*	The Spectacle	12137	Forbs	Monophagous	8	6	Pupa	16	2
73.002	*Abrostola triplasia*	Dark Spectacle	1100	Forbs	Oligophagous	8	6	Pupa	16	8
73.011	*Diachrysia chryson*	Scarce Burnished Brass	34	Forbs	Monophagous	7	7	Larva	22	3
73.012	*Diachrysia chrysitis*	Burnished Brass	20654	Forbs	Oligophagous	8	6	Larva	17.5	4
73.014	*Polychrysia moneta*	Golden Plusia	206	Forbs	Oligophagous	NA	NA	Larva	18.5	1
73.015	*Autographa gamma*	Silver Y	82055	Forbs	Polyphagous	NA	NA	Immigrant	17	8
73.016	*Autographa pulchrina*	Beautiful Golden Y	16957	Forbs	Polyphagous	NA	NA	Larva	18.5	8
73.017	*Autographa jota*	Plain Golden Y	4448	Forbs	Polyphagous	NA	NA	Larva	19	8
73.018	*Autographa bractea*	Gold Spangle	2621	Forbs	Polyphagous	NA	NA	Larva	19.5	4
73.021	*Syngrapha interrogationis*	Scarce Silver Y	494	Broadleaf shrubs	Oligophagous	2	6.5	Larva	16.5	1
73.022	*Plusia festucae*	Gold Spot	2210	Herbaceous polyphagous	Oligophagous	NA	NA	Larva	16.5	8
73.023	*Plusia putnami gracilis*	Lempke's Gold Spot	519	Grasses	Oligophagous	NA	NA	Larva	14.5	2
73.024	*Protodeltote pygarga*	Marbled White-spot	12842	Grasses	Oligophagous	NA	NA	Pupa	11.5	3
73.026	*Deltote uncula*	Silver Hook	266	Grasses	Oligophagous	NA	NA	Pupa	11.5	2
73.031	*Tyta luctuosa*	Four-spotted	36	Forbs	Monophagous	6	7	Pupa	12.5	1

73.032	*Colocasia coryli*	Nut-tree Tussock	14203	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	15.5	1
73.033	*Diloba caeruleocephala*	Figure of Eight	10935	Broadleaf shrubs	Polyphagous	NA	NA	Egg	17	3
73.034	*Moma alpium*	Scarce Merveille du Jour	58	Broadleaf trees	Oligophagous	4.5	6.3	Pupa	18.5	1
73.036	*Acronicta alni*	Alder Moth	156	Broadleaf trees	Polyphagous	NA	NA	Pupa	17.5	1
73.037	*Acronicta tridens*	Dark Dagger	310	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	18.5	8
73.038	*Acronicta psi*	Grey Dagger	1373	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	18.5	8
73.039	*Acronicta aceris*	The Sycamore	64	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	20	2
73.040	*Acronicta leporina*	The Miller	159	Broadleaf trees	Polyphagous	NA	NA	Pupa	18.5	8
73.042	*Acronicta menyanthidis*	Light Knot Grass	1678	Broadleaf shrubs	Oligophagous	NA	NA	Pupa	18	2
73.045	*Acronicta rumicis*	Knot Grass	3254	Highly polyphagous	Highly polyphagous	NA	NA	Pupa	18	8
73.046	*Acronicta megacephala*	Poplar Grey	706	Broadleaf trees	Oligophagous	6.3	6	Pupa	18.5	3
73.047	*Craniophora ligustri*	The Coronet	925	Broadleaf polyphagous	Oligophagous	6.25	5.75	Pupa	18	3
73.052	*Cucullia umbratica*	The Shark	419	Forbs	Oligophagous	NA	NA	Pupa	24	4
73.053	*Cucullia chamomillae*	Chamomile Shark	142	Forbs	Oligophagous	NA	NA	Pupa	21	3
73.055	*Cucullia asteris*	Star-wort	50	Forbs	Oligophagous	NA	NA	Pupa	21	2

73.058	*Shargacucullia verbasci*	The Mullein	77	Forbs	Oligophagous	NA	NA	Pupa	21.5	4
73.061	*Stilbia anomala*	The Anomalous	3512	Grasses	Oligophagous	3.5	6	Larva	15	2
73.062	*Amphipyra pyramidea*	Copper Underwing	1322	Broadleaf shrubs	Polyphagous	NA	NA	Egg	23.5	3
73.063	*Amphipyra berbera svenssoni*	Svenssons Copper Underwing	1468	Broadleaf trees	Oligophagous	NA	NA	Egg	23.5	3
73.064	*Amphipyra tragopoginis*	Mouse Moth	13377	Highly polyphagous	Highly polyphagous	NA	NA	Egg	17	8
73.065	*Asteroscopus sphinx*	The Sprawler	18534	Broadleaf polyphagous	Polyphagous	NA	NA	Egg	19.5	1
73.066	*Brachionycha nubeculosa*	Rannoch Sprawler	55	Broadleaf trees	Oligophagous	4	7	Pupa	22	1
73.068	*Allophyes oxyacanthae*	Green-brindled Crescent	29900	Broadleaf shrubs	Polyphagous	NA	NA	Egg	18.5	3
73.069	*Xylocampa areola*	Early Grey	7079	Broadleaf shrubs	Oligophagous	5	5	Pupa	16.5	3
73.070	*Pyrrhia umbra*	Bordered Sallow	107	Highly polyphagous	Oligophagous	NA	NA	Pupa	17.5	2
73.072	*Heliothis viriplaca*	Marbled Clover	25	Forbs	Polyphagous	NA	NA	Pupa	14	4
73.074	*Heliothis peltigera*	Bordered Straw	102	Forbs	Polyphagous	NA	NA	Immigrant	17.5	1
73.076	*Helicoverpa armigera*	Scarce Bordered Straw	49	Forbs	Polyphagous	NA	NA	Immigrant	17.5	1
73.082	*Cryphia algae*	Tree-lichen Beauty	28	Lichen	Oligophagous	NA	NA	Larva	11.5	2

73.084	*Cryphia domestica*	Marbled Beauty	8160	Lichen	Oligophagous	NA	NA	Larva	13	8
73.085	*Cryphia muralis*	Marbled Green	212	Lichen	Oligophagous	NA	NA	Larva	13	1
73.087	*Spodoptera exigua*	Small Mottled Willow	216	Forbs	Polyphagous	NA	NA	Immigrant	13.5	1
73.091	*Elaphria venustula*	Rosy Marbled	190	Forbs	Polyphagous	NA	NA	Pupa	10.5	2
73.092	*Caradrina morpheus*	Mottled Rustic	56458	Forbs	Polyphagous	NA	NA	Larva	14.5	7
73.095	*Caradrina (Paradrina) clavipalpis*	Pale mottled willow	2147	Grasses	Polyphagous	NA	NA	Larva	13.5	3
73.096	*Hoplodrina alsines*	The Uncertain	69659	Forbs	Polyphagous	NA	NA	Larva	15	7
73.097	*Hoplodrina blanda*	The Rustic	26199	Forbs	Polyphagous	NA	NA	Larva	14.5	7
73.099	*Hoplodrina ambigua*	Vine's Rustic	9479	Forbs	Polyphagous	NA	NA	Larva	14.5	4
73.100	*Chilodes maritimus*	Silky Wainscot	135	Other	Oligophagous	NA	NA	Larva	14.5	1
73.101	*Charanyca trigrammica*	Treble Lines	9435	Forbs	Polyphagous	NA	NA	Larva	16	8
73.102	*Rusina ferruginea*	Brown Rustic	87669	Forbs	Polyphagous	NA	NA	Larva	17	8
73.103	*Athetis (Hydrillula) pallustris*	Marsh Moth	38	Forbs	Oligophagous	NA	NA	Larva	12.5	2
73.105	*Dypterygia scabriuscula*	Bird's Wing	367	Forbs	Oligophagous	NA	NA	Pupa	16	2

73.106	*Trachea atriplicis*	Orache Moth	106	Forbs	Oligophagous	NA	NA	Pupa	21	1
73.107	*Mormo maura*	Old Lady	196	Highly polyphagous	Highly polyphagous	NA	NA	Larva	33	4
73.109	*Thalpophila matura*	Straw Underwing	20605	Grasses	Oligophagous	NA	NA	Larva	18.5	8
73.110	*Hyppa rectilinea*	The Saxon	391	Broadleaf shrubs	Polyphagous	NA	NA	Larva	17.5	3
73.113	*Phlogophora meticulosa*	Angle Shades	17262	Highly polyphagous	Highly polyphagous	NA	NA	Larva	23	8
73.114	*Euplexia lucipara*	Small Angle Shades	8769	Highly polyphagous	Highly polyphagous	NA	NA	Pupa	16.5	3
73.118	*Celaena haworthii*	Haworth's Minor	3541	Grasses	Oligophagous	1	8	Egg	12	2
73.119	*Celaena leucostigma leucostigma*	The Crescent	4338	Herbaceous polyphagous	Oligophagous	5	7.5	Egg	15.5	2
73.120	*Eremobia ochroleuca*	Dusky Sallow	3007	Grasses	Oligophagous	NA	NA	Egg	15	2
73.121	*Gortyna flavago*	Frosted Orange	7382	Forbs	Polyphagous	NA	NA	Egg	17.5	4
73.123	*Hydraecia micacea*	Rosy Rustic	89517	Forbs	Polyphagous	NA	NA	Egg	17.5	3
73.126	*Amphipoea fucosa fucosa*	Saltern Ear	3160	Grasses	Oligophagous	NA	NA	Egg	15	3
73.127	*Amphipoea lucens*	Large Ear	12248	Grasses	Oligophagous	1.5	7.5	Egg	15.5	2
73.128	*Amphipoea oculea*	Ear Moth	5962	Grasses	Oligophagous	NA	NA	Egg	13.5	4

73.129	*Amphipoea crinanensis*	Crinan Ear	3716	Unknown	Unknown	NA	NA	Egg	14	2
73.131	*Luperina testacea*	Flounced Rustic	259208	Grasses	Oligophagous	NA	NA	Larva	16	4
73.134	*Rhizedra lutosa*	Large Wainscot	2688	Grasses	Monophagous	6	7	Egg	19.5	1
73.136	*Nonagria typhae*	Bulrush Wainscot	301	Grasses	Oligophagous	7	8	Egg	22	1
73.137	*Arenostola phragmitidis*	Fen Wainscot	809	Grasses	Monophagous	6	7	Egg	15	1
73.138	*Chortodes elymi*	Lyme Grass	1367	Grasses	Monophagous	6	9	Larva	16.5	1
73.139	*Archanara geminipuncta*	Twin-spotted Wainscot	137	Grasses	Monophagous	6	7	Egg	13.5	1
73.141	*Archanara dissoluta*	Brown-veined Wainscot	502	Grasses	Monophagous	6	7	Egg	13.5	2
73.142	*Coenobia rufa*	Small Rufous	1601	Grasses	Oligophagous	NA	NA	Larva	11	1
73.144	*Chortodes pygmina*	Small Wainscot	45374	Grasses	Oligophagous	NA	NA	Larva	12	3
73.145	*Chortodes fluxa*	Mere Wainscot	3112	Grasses	Monophagous	6	7	Larva	13.5	2
73.146	*Photedes captiuncula*	Least Minor	23	Grasses	Oligophagous	2	7	Larva	8	2
73.147	*Photedes minima*	Small Dotted Buff	53542	Grasses	Monophagous	4	6	Larva	12.5	3
73.149	*Chortodes extrema*	Concolorous	302	Grasses	Oligophagous	NA	NA	Larva	12	1
73.151	*Archanara sparganii*	Webb's Wainscot	172	Grasses	Oligophagous	NA	NA	Egg	16.5	1
73.154	*Apamea remissa*	Dusky Brocade	4847	Grasses	Oligophagous	NA	NA	Larva	18	4

73.155	*Apamea epomidion*	Clouded Brindle	420	Grasses	Oligophagous	NA	NA	Larva	18.5	1
73.156	*Apamea crenata*	Clouded-bordered Brindle	7779	Grasses	Oligophagous	NA	NA	Larva	20	4
73.157	*Apamea anceps*	Large Nutmeg	5085	Grasses	Oligophagous	NA	NA	Larva	18.5	1
73.158	*Apamea sordens*	Rustic Shoulder-knot	6944	Grasses	Oligophagous	NA	NA	Larva	17.5	4
73.159	*Apamea unanimis*	Small Clouded Brindle	740	Grasses	Oligophagous	NA	NA	Larva	16	1
73.160	*Apamea scolopacina*	Slender Brindle	4866	Grasses	Oligophagous	NA	NA	Larva	15.5	1
73.161	*Apamea oblonga*	Crescent Striped	238	Grasses	Oligophagous	NA	NA	Larva	19.5	2
73.162	*Apamea monoglypha*	Dark Arches	123561	Grasses	Oligophagous	NA	NA	Larva	22.5	8
73.163	*Apamea lithoxylaea*	Light Arches	6070	Grasses	Oligophagous	NA	NA	Larva	20.5	4
73.164	*Apamea sublustris*	Reddish Light Arches	610	Grasses	Oligophagous	NA	NA	Larva	19.5	2
73.165	*Apamea furva britannica*	The Confused	311	Grasses	Oligophagous	NA	NA	Larva	17.5	2
73.167	*Apamea zeta*	Northern Arches	54	Grasses	Oligophagous	NA	NA	Larva	18	1
73.168	*Apamea ophiogramma*	Double Lobed	624	Grasses	Oligophagous	7.5	7	Larva	14.5	1
73.169	*Mesapamea secalis GenitaliaChecked*	Common rustic moth	140	Grasses	Oligophagous	NA	NA	Larva	14	5

73.171	*Mesoligia literosa*	Rosy Minor	3718	Grasses	Oligophagous	NA	NA	Larva	11.5	4
73.172	*Mesoligia furuncula*	Cloaked Minor	29158	Grasses	Oligophagous	NA	NA	Larva	11	3
73.173	*Oligia strigilis*	Marbled Minor	19441	Grasses	Oligophagous	NA	NA	Larva	12	5
73.174	*Oligia latruncula*	Tawny Marbled Minor	13694	Grasses	Oligophagous	NA	NA	Larva	12.5	4
73.175	*Oligia versicolor*	Rufous Minor	9809	Grasses	Oligophagous	NA	NA	Larva	11.5	4
73.176	*Oligia fasciuncula*	Middle-barred Minor	63499	Grasses	Oligophagous	4	6	Larva	11	3
73.178	*Leucochlaena oditis*	Beautiful Gothic	270	Grasses	Oligophagous	NA	NA	Larva	15	2
73.179	*Xanthia citrago*	Orange Sallow	814	Broadleaf trees	Oligophagous	5.7	4.7	Egg	16	2
73.180	*Xanthia aurago*	Barred Sallow	4205	Broadleaf trees	Oligophagous	5.5	4	Egg	15	3
73.181	*Xanthia togata*	Pink-barred Sallow	19854	Highly polyphagous	Highly polyphagous	NA	NA	Egg	14.5	3
73.182	*Xanthia icteritia*	The Sallow	13546	Highly polyphagous	Highly polyphagous	NA	NA	Egg	15.5	4
73.183	*Xanthia gilvago*	Dusky-lemon Sallow	991	Broadleaf trees	Monophagous	NA	NA	Egg	16.5	1
73.184	*Xanthia ocellaris*	Pale-lemon Sallow	49	Broadleaf trees	Oligophagous	6.3	6	Egg	18.5	2
73.186	*Agrochola lychnidis*	Beaded Chestnut	86671	Highly polyphagous	Highly polyphagous	NA	NA	Egg	16.5	8
73.187	*Agrochola (Anchoscelis) litura*	Brown-spot Pinion	20326	Highly polyphagous	Highly polyphagous	NA	NA	Egg	15.5	4

73.188	*Agrochola (Anchoscelis) helvola*	Flounced Chestnut	3700	Broadleaf polyphagous	Polyphagous	NA	NA	Egg	17	3
73.189	*Agrochola (Leptologia) lota*	Red-line Quaker	14720	Broadleaf polyphagous	Oligophagous	NA	NA	Egg	16.5	5
73.190	*Agrochola (Leptologia) macilenta*	Yellow-line Quaker	61938	Broadleaf polyphagous	Polyphagous	NA	NA	Egg	15	5
73.192	*Agrochola (Sunira) circellaris*	The Brick	15239	Broadleaf polyphagous	Polyphagous	NA	NA	Egg	16.5	2
73.193	*Omphaloscelis lunosa*	Lunar Underwing	157534	Grasses	Oligophagous	NA	NA	Larva	15.5	3
73.194	*Conistra vaccinii*	The Chestnut	126237	Highly polyphagous	Highly polyphagous	NA	NA	Adult	14	2
73.195	*Conistra ligula*	Dark Chestnut	5402	Highly polyphagous	Highly polyphagous	NA	NA	Adult	14	2
73.197	*Conistra rubiginea*	Dotted Chestnut	399	Broadleaf shrubs	Oligophagous	NA	NA	Adult	16	2
73.200	*Lithophane semibrunnea*	Tawny Pinion	84	Broadleaf trees	Monophagous	6	5	Adult	18	3
73.201	*Lithophane hepatica*	Pale Pinion	442	Broadleaf polyphagous	Polyphagous	NA	NA	Adult	18.5	1
73.202	*Lithophane ornitopus lactipennis*	Grey Shoulder-knot	1300	Broadleaf trees	Oligophagous	4.5	6.3	Adult	18	1

73.206	*Lithophane leautieri hesperica*	Blair's Shoulder-knot	1618	Coniferous	Oligophagous	NA	NA	Egg	18.5	2
73.207	*Lithomoia solidaginis*	Golden-rod Brindle	438	Broadleaf shrubs	Oligophagous	NA	NA	Egg	19.5	3
73.208	*Xylena exsoleta*	Sword-grass	145	Forbs	Polyphagous	NA	NA	Adult	26.5	3
73.209	*Xylena vetusta*	Red Sword-grass	1676	Highly polyphagous	Highly polyphagous	NA	NA	Adult	26.5	3
73.210	*Eupsilia transversa*	The Satellite	15321	Broadleaf polyphagous	Polyphagous	NA	NA	Adult	18.5	3
73.211	*Enargia paleacea*	Angle-striped Sallow	166	Broadleaf trees	Oligophagous	5	6.5	Egg	18.5	2
73.212	*Ipimorpha retusa*	Double Kidney	591	Broadleaf trees	Oligophagous	NA	NA	Egg	14	2
73.213	*Ipimorpha subtusa*	The Olive	1237	Broadleaf trees	Oligophagous	6.3	6	Egg	15	3
73.214	*Cosmia diffinis*	White-spotted Pinion	162	Broadleaf trees	Oligophagous	NA	NA	Egg	15	1
73.215	*Cosmia affinis*	Lesser-spotted Pinion	1630	Broadleaf trees	Oligophagous	NA	NA	Egg	14	2
73.216	*Cosmia trapezina*	The Dun-bar	62076	Broadleaf polyphagous	Polyphagous	NA	NA	Egg	14.5	1
73.217	*Cosmia pyralina*	Lunar-spotted Pinion	3561	Broadleaf polyphagous	Oligophagous	NA	NA	Egg	14.5	2
73.219	*Atethmia centrago*	Centre-barred Sallow	6121	Broadleaf trees	Monophagous	6	5	Egg	16.5	1
73.220	*Brachylomia viminalis*	Minor Shoulder-knot	18204	Broadleaf trees	Oligophagous	NA	NA	Egg	14	3

73.221	*Parastichtis suspecta*	The Suspected	416	Broadleaf trees	Oligophagous	NA	NA	Egg	15	4
73.222	*Parastichtis ypsillon*	Dingy Shears	699	Broadleaf trees	Oligophagous	NA	NA	Egg	17	2
73.224	*Dichonia aprilina*	Merveille du Jour	2603	Broadleaf trees	Oligophagous	4.5	6.3	Egg	20.5	1
73.225	*Dryobotodes eremita*	Brindled Green	6940	Broadleaf trees	Oligophagous	4.5	6.3	Egg	16.5	1
73.228	*Antitype chi*	Grey Chi	1240	Highly polyphagous	Highly polyphagous	NA	NA	Egg	17	1
73.229	*Trigonophora flammea*	Flame Brocade	199	Highly polyphagous	Highly polyphagous	NA	NA	Larva	21.5	5
73.230	*Aporophyla australis pascuea*	Feathered Brindle	188	Herbaceous polyphagous	Polyphagous	NA	NA	Larva	15.5	2
73.231	*Aporophyla lutulenta*	Deep-brown Dart	3396	Highly polyphagous	Highly polyphagous	NA	NA	Larva	16.5	8
73.232	*Aporophyla lueneburgensis*	Northern Deep-brown Dart	420	Highly polyphagous	Highly polyphagous	NA	NA	Larva	16	2
73.233	*Aporophyla nigra*	Black Rustic	4941	Highly polyphagous	Highly polyphagous	NA	NA	Larva	19	3
73.234	*Dasypolia templi*	Brindled Ochre	2300	Forbs	Oligophagous	6	7	Adult	20.5	3
73.235	*Polymixis lichenea*	Feathered Ranunculus	13857	Forbs	Oligophagous	NA	NA	Larva	16.5	1
73.236	*Polymixis xanthomista statices*	Black-banded	38	Forbs	Oligophagous	NA	NA	Egg	17	1

73.237	*Polymixis flavicincta*	Large Ranunculus	826	Forbs	Polyphagous	NA	NA	Egg	19.5	2
73.238	*Mniotype adusta*	Dark Brocade	3687	Highly polyphagous	Highly polyphagous	NA	NA	Larva	19.5	4
73.241	*Panolis flammea*	Pine Beauty	2996	Coniferous	Oligophagous	NA	NA	Pupa	15.5	1
73.242	*Orthosia incerta*	Clouded Drab	33257	Broadleaf trees	Polyphagous	NA	NA	Pupa	18	1
73.243	*Orthosia miniosa*	Blossom Underwing	1265	Broadleaf polyphagous	Polyphagous	4.5	6.3	Pupa	16	1
73.244	*Orthosia cerasi*	Common Quaker	83139	Broadleaf trees	Polyphagous	NA	NA	Pupa	15	1
73.245	*Orthosia cruda*	Small Quaker	168912	Broadleaf trees	Polyphagous	NA	NA	Pupa	13.5	2
73.246	*Orthosia populeti*	Lead-coloured Drab	1336	Broadleaf trees	Oligophagous	6.3	6	Pupa	16	1
73.247	*Orthosia gracilis*	Powdered Quaker	7231	Highly polyphagous	Highly polyphagous	NA	NA	Pupa	17	1
73.248	*Orthosia opima*	Northern Drab	75	Highly polyphagous	Highly polyphagous	NA	NA	Pupa	16	7
73.249	*Orthosia gothica*	Hebrew Character	369468	Highly polyphagous	Highly polyphagous	NA	NA	Pupa	16	8
73.250	*Orthosia munda*	Twin-spotted Quaker	14000	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	18.5	1
73.252	*Tholera cespitis*	Hedge Rustic	3689	Grasses	Oligophagous	NA	NA	Egg	17	3
73.253	*Tholera decimalis*	Feathered Gothic	12634	Grasses	Oligophagous	NA	NA	Egg	19	3
73.254	*Cerapteryx graminis*	Antler Moth	110526	Grasses	Oligophagous	NA	NA	Egg	14.5	2

73.255	*Discestra trifolii*	The Nutmeg	7156	Forbs	Polyphagous	NA	NA	Pupa	16	8
73.257	*Anarta myrtilli*	Beautiful Yellow Underwing	228	Broadleaf shrubs	Oligophagous	2	7	Larva	11	2
73.259	*Polia bombycina*	Pale Shining Brown	375	Forbs	Unknown	NA	NA	Larva	21	1
73.260	*Polia trimaculosa*	Silvery Arches	55	Broadleaf shrubs	Polyphagous	NA	NA	Larva	24	3
73.261	*Polia nebulosa*	Grey Arches	1728	Highly polyphagous	Highly polyphagous	NA	NA	Larva	23.5	1
73.263	*Lacanobia w-latinum*	Light Brocade	233	Highly polyphagous	Highly polyphagous	NA	NA	Pupa	19.5	3
73.264	*Lacanobia thalassina*	Pale-shouldered Brocade	11317	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	18	3
73.265	*Lacanobia contigua*	Beautiful Brocade	226	Highly polyphagous	Highly polyphagous	NA	NA	Pupa	17.5	3
73.266	*Lacanobia suasa*	Dog's Tooth	1449	Forbs	Polyphagous	NA	NA	Pupa	17.5	5
73.267	*Lacanobia oleracea*	Bright-line Brown-eye	25927	Highly polyphagous	Highly polyphagous	NA	NA	Pupa	16.5	8
73.270	*Melanchra persicariae*	Dot Moth	5249	Highly polyphagous	Highly polyphagous	NA	NA	Pupa	18.5	3
73.271	*Melanchra pisi*	Broom Moth	17078	Highly polyphagous	Highly polyphagous	NA	NA	Pupa	18	8
73.272	*Papestra biren*	Glaucous Shears	1489	Highly polyphagous	Highly polyphagous	NA	NA	Pupa	16.5	1
73.273	*Hada plebeja*	The Shears	13144	Forbs	Oligophagous	NA	NA	Pupa	15.5	4
73.274	*Mamestra brassicae*	Cabbage Moth	8155	Highly polyphagous	Highly polyphagous	NA	NA	Pupa	18	1

73.275	*Sideridis albicolon*	White Colon	237	Forbs	Polyphagous	NA	NA	Pupa	18.5	1
73.276	*Hadena rivularis*	The Campion	1629	Forbs	Oligophagous	5.666667	6.666667	Pupa	15	4
73.277	*Heliophobus reticulata*	Bordered Gothic	141	Forbs	Oligophagous	NA	NA	Pupa	18	1
73.278	*Hadena luteago barrettii*	Barrett's Marbled Coronet	100	Forbs	Oligophagous	NA	NA	Pupa	17	1
73.279	*Hecatera bicolorata*	Broad-barred White	1575	Forbs	Oligophagous	NA	NA	Pupa	14	2
73.281	*Hadena bicruris*	The Lychnis	2655	Forbs	Oligophagous	6.5	6	Pupa	15.5	7
73.282	*Hadena compta*	Varied Coronet	114	Forbs	Oligophagous	NA	NA	Pupa	14	2
73.283	*Hadena confusa*	Marbled Coronet	1112	Forbs	Oligophagous	NA	NA	Pupa	15	2
73.284	*Hadena albimacula*	White Spot	21	Forbs	Monophagous	4	8	Pupa	16	2
73.286	*Hadena perplexa perplexa*	Tawny Shears	1062	Forbs	Oligophagous	NA	NA	Pupa	14	4
73.286	*Hadena perplexa capsophila*	Pod Lover	400	Forbs	Oligophagous	NA	NA	Pupa	14	2
73.288	*Mythimna turca*	Double line	5044	Grasses	Oligophagous	NA	NA	Larva	20.5	3
73.289	*Mythimna pudorina*	Striped Wainscot	4103	Grasses	Oligophagous	NA	NA	Larva	17.5	1
73.290	*Mythimna conigera*	Brown-line Bright-eye	10821	Grasses	Oligophagous	NA	NA	Larva	16	4
73.291	*Mythimna pallens*	Common Wainscot	133185	Grasses	Oligophagous	NA	NA	Larva	15.5	3

73.293	*Mythimna impura*	Smoky Wainscot	126618	Grasses	Oligophagous	NA	NA	Larva	16	8
73.294	*Mythimna straminea*	Southern Wainscot	267	Grasses	Oligophagous	NA	NA	Larva	16	1
73.295	*Mythimna vitellina*	The Delicate	74	Grasses	Oligophagous	NA	NA	Immigrant	13	1
73.296	*Mythimna (Pseudaletia) unipuncta*	White-speck	312	Grasses	Oligophagous	NA	NA	Immigrant	19.5	1
73.297	*Mythimna (Hyphilare) albipuncta*	White-point	1066	Grasses	Oligophagous	NA	NA	Larva	15.5	1
73.298	*Mythimna (Hyphilare) ferrago*	The Clay	23951	Grasses	Oligophagous	NA	NA	Larva	16.5	8
73.299	*Mythimna (Hyphilare) litoralis*	Shore Wainscot	356	Grasses	Monophagous	3	9	Larva	16.5	1
73.300	*Mythimna (Hyphilare) l-album*	L-album Wainscot	253	Grasses	Monophagous	3	9	Larva	16.5	1
73.301	*Mythimna comma*	Shoulder-striped Wainscot	5420	Grasses	Oligophagous	NA	NA	Larva	17.5	1
73.302	*Mythimna obsoleta*	Obscure Wainscot	71	Grasses	Monophagous	6	7	Larva	16.5	1
73.303	*Mythimna putrescens*	Devonshire Wainscot	168	Grasses	Oligophagous	NA	NA	Larva	15.5	2
73.305	*Senta flammea*	Flame Wainscot	35	Grasses	Monophagous	6	7	Pupa	16	1

73.307	*Peridroma saucia*	Pearly Underwing	362	Forbs	Polyphagous	NA	NA	Immigrant	21	1
73.308	*Actebia praecox*	Portland Moth	133	Forbs	Oligophagous	NA	NA	Larva	19	1
73.311	*Euxoa cursoria*	Coast Dart	127	Forbs	Oligophagous	NA	NA	Egg	16	1
73.312	*Euxoa obelisca grisea*	Square-spot Dart	39	Forbs	Oligophagous	NA	NA	Egg	16	1
73.313	*Euxoa tritici*	White-line Dart	2017	Forbs	Polyphagous	NA	NA	Egg	15	4
73.314	*Euxoa nigricans*	Garden Dart	2627	Forbs	Polyphagous	NA	NA	Egg	16.5	7
73.316	*Agrotis cinerea*	Light Feathered Rustic	305	Forbs	Oligophagous	2	8	Larva	15	2
73.317	*Agrotis exclamationis*	Heart & Dart	264889	Forbs	Polyphagous	NA	NA	Larva	17	8
73.319	*Agrotis segetum*	Turnip Moth	6611	Forbs	Polyphagous	NA	NA	Larva	18.5	4
73.320	*Agrotis clavis*	Heart & Club	4213	Forbs	Polyphagous	NA	NA	Larva	16	2
73.322	*Agrotis vestigialis*	Archer's Dart	1952	Forbs	Oligophagous	NA	NA	Larva	16	2
73.323	*Agrotis ripae*	Sand Dart	1169	Forbs	Polyphagous	NA	NA	Larva	16	1
73.324	*Agrotis trux lunigera*	Crescent Dart	162	Forbs	Oligophagous	NA	NA	Larva	17.5	1
73.325	*Agrotis puta*	Shuttle-shaped Dart	18573	Forbs	Polyphagous	NA	NA	Larva	14	5
73.327	*Agrotis ipsilon*	Dark Sword-grass	1677	Forbs	Polyphagous	NA	NA	Immigrant	20	1
73.328	*Axylia putris*	The Flame	24606	Forbs	Polyphagous	NA	NA	Pupa	15	8
73.329	*Ochropleura plecta*	Flame Shoulder	88879	Forbs	Polyphagous	NA	NA	Pupa	13.5	8
73.331	*Diarsia dahlii*	Barred Chestnut	21428	Highly polyphagous	Highly polyphagous	NA	NA	Larva	16.5	2

73.332	*Diarsia brunnea*	Purple Clay	46020	Highly polyphagous	Highly polyphagous	NA	NA	Larva	18	1
73.333	*Diarsia mendica*	Ingrailed Clay	126481	Highly polyphagous	Highly polyphagous	NA	NA	Larva	15	3
73.334	*Diarsia rubi*	Small Square-spot	235916	Forbs	Polyphagous	NA	NA	Larva	14	8
73.336	*Cerastis rubricosa*	Red Chestnut	31970	Highly polyphagous	Highly polyphagous	NA	NA	Pupa	16.5	3
73.337	*Cerastis leucographa*	White-marked	277	Unknown	Unknown	NA	NA	Pupa	15	1
73.338	*Lycophotia porphyrea*	True Lover's Knot	72920	Broadleaf shrubs	Oligophagous	1.7	7.4	Larva	13.5	2
73.339	*Rhyacia simulans*	Dotted Rustic	181	Unknown	Unknown	NA	NA	Larva	19	8
73.341	*Standfussiana lucernea*	Northern Rustic	64	Forbs	Oligophagous	NA	NA	Larva	19	1
73.342	*Noctua pronuba*	Large Yellow Underwing	120111	Herbaceous polyphagous	Polyphagous	NA	NA	Larva	23.5	8
73.343	*Noctua fimbriata*	Broad-bordered Yellow Underwing	1350	Highly polyphagous	Highly polyphagous	NA	NA	Larva	23.5	1
73.344	*Noctua orbona*	Lunar Yellow Underwing	76	Herbaceous polyphagous	Polyphagous	NA	NA	Larva	18.5	2
73.345	*Noctua comes*	Lesser Yellow Underwing	24178	Highly polyphagous	Highly polyphagous	NA	NA	Larva	18.5	8
73.346	*Noctua interjecta caliginosa*	Least Yellow Underwing	583	Highly polyphagous	Highly polyphagous	NA	NA	Larva	15.5	5

73.348	*Noctua janthe*	Lesser Broad-bordered Yellow Underwing	32754	Highly polyphagous	Highly polyphagous	NA	NA	Larva	18	8
73.349	*Spaelotis ravida*	Stout Dart	153	Forbs	Oligophagous	NA	NA	Egg	20	2
73.350	*Eurois occulta*	Great Brocade	309	Highly polyphagous	Highly polyphagous	NA	NA	Larva	25.5	3
73.351	*Graphiphora augur*	Double Dart	6604	Highly polyphagous	Highly polyphagous	NA	NA	Larva	19.5	4
73.352	*Anaplectoides prasina*	Green Arches	5495	Highly polyphagous	Highly polyphagous	NA	NA	Larva	22.5	2
73.353	*Xestia baja*	Dotted Clay	35268	Highly polyphagous	Highly polyphagous	NA	NA	Larva	19	4
73.354	*Xestia rhomboidea*	Square-spotted Clay	352	Forbs	Oligophagous	NA	NA	Larva	18.5	1
73.355	*Xestia castanea*	Neglected or Grey Rustic	1035	Broadleaf shrubs	Oligophagous	1.7	7.4	Larva	17	3
73.356	*Xestia agathina*	Heath Rustic	2696	Broadleaf shrubs	Oligophagous	2	7	Larva	15	2
73.357	*Xestia xanthographa*	Square-spot Rustic	201216	Herbaceous polyphagous	Polyphagous	NA	NA	Larva	15.5	4
73.358	*Xestia sexstrigata*	Six-striped Rustic	31392	Forbs	Polyphagous	NA	NA	Larva	16	2
73.359	*Xestia c-nigrum*	Setaceous Hebrew Character	141853	Forbs	Polyphagous	NA	NA	Larva	16.5	7
73.360	*Xestia ditrapezium*	Triple-spotted Clay	6288	Highly polyphagous	Highly polyphagous	NA	NA	Larva	18	2
73.361	*Xestia triangulum*	Double Square-spot	34532	Highly polyphagous	Highly polyphagous	NA	NA	Larva	18	3

73.363	*Xestia alpicola alpina*	Northern Dart	21	Broadleaf shrubs	Oligophagous	NA	NA	Larva	16	1
73.364	*Coenophila subrosea*	Rosy Marsh Moth	1099	Broadleaf shrubs	Oligophagous	NA	NA	Larva	19.5	1
73.365	*Eugnorisma glareosa*	Autumnal Rustic	8124	Highly polyphagous	Highly polyphagous	NA	NA	Larva	15.5	8
73.366	*Eugnorisma depuncta*	Plain Clay	1610	Forbs	Polyphagous	NA	NA	Larva	18	1
73.367	*Protolampra sobrina*	Cousin German	359	Broadleaf shrubs	Oligophagous	NA	NA	Larva	15.5	3
73.368	*Naenia typica*	The Gothic	1761	Highly polyphagous	Highly polyphagous	NA	NA	Larva	19.5	4
74.002	*Meganola albula*	Kent Black Arches	888	Broadleaf shrubs	Oligophagous	NA	NA	Larva	10.5	4
74.003	*Nola cucullatella*	Short-cloaked Moth	13275	Broadleaf shrubs	Oligophagous	NA	NA	Larva	9	3
74.004	*Nola confusalis*	Least Black Arches	10132	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	10	1
74.007	*Bena bicolorana*	Scarce Silver-lines	149	Broadleaf trees	Oligophagous	NA	NA	Larva	21	1
74.008	*Pseudoips prasinana britannica*	Green Silver-lines	1437	Broadleaf polyphagous	Polyphagous	NA	NA	Pupa	17.5	1
74.009	*Nycteola revayana*	Oak Nycteoline	835	Broadleaf trees	Oligophagous	4.5	6.3	Adult	12	1
74.011	*Earias clorana*	Cream-bordered Green Pea	207	Broadleaf trees	Oligophagous	NA	NA	Pupa	11	1
NA	*Eupithecia species*	Pug moths	101689	NA	NA	NA	NA	NA	NA	0

NA	*Unidentifiable macro spp*	Unidentifiable macros	56727	NA	NA	NA	NA	NA	NA	0
NA	*Amphipoea species*	Ear moths	8639	NA	NA	NA	NA	NA	NA	0
NA	*Epirrita species*	November moths	69650	Broadleaf polyphagous	Polyphagous	NA	NA	Egg	NA	1
NA	*Hoplodrina species*	Rustic moths	5031	Forbs	Polyphagous	NA	NA	Larva	14.5	8
NA	*Oligia species*	Minor moths	12259	Grasses	Oligophagous	NA	NA	Larva	12	8
NA	*Idaea species*	Wave moths	1048	NA	NA	NA	NA	NA	NA	0
NA	*Chloroclysta species*	Carpet moths	690	NA	NA	NA	NA	NA	NA	0
NA	*Acronicta species*	Dagger moths	486	NA	NA	NA	NA	NA	NA	0
NA	*Amphipyra species*	Copper Underwing moths	54	Broadleaf polyphagous	Polyphagous	NA	NA	Egg	23.5	1
NA	*Mesapamea didyma secalis*	Common Rustic agg	142011	Grasses	Oligophagous	NA	NA	Larva	13.5	5
NA	*Geometridae species*	Geometrid sp	40	NA	NA	NA	NA	NA	NA	0
NA	*Noctuidae species*	Noctuid sp	32	NA	NA	NA	NA	NA	NA	0
NA	*Sterrhinae species*	Sterrhinae sp	38	NA	NA	NA	NA	NA	NA	0

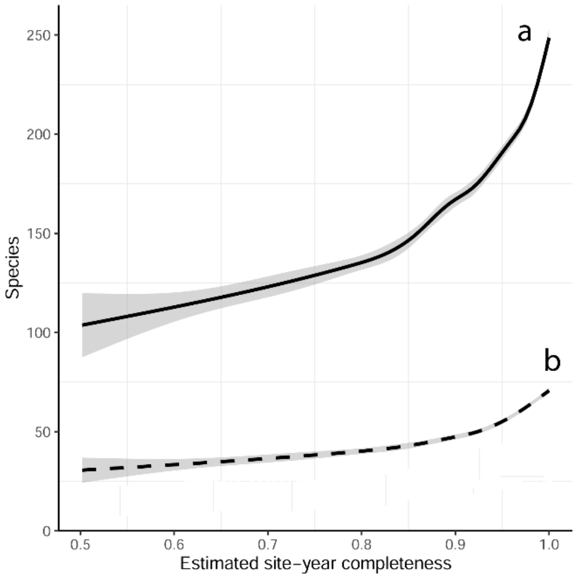


Fig. S2.1. Relationship between species richness/diversity and site-year completeness. *The estimated a) species richness, and b) diversity (measured as 'effective common species') as a function of estimated site-year completeness. Showing model predictions and 95% confidence intervals (grey ribbon) from two separate GAMs.*

2.7.1 Species richness and diversity

2.7.1.1 Overall changes in species richness and diversity

Table S2.3. Model output: overall non-linear changes in species richness and diversity 1968 – 2016. *Model coefficients for three GAMMs that modelled species richness/diversity as a function of year and site-year completeness.*

Response	*Parametric coefficients*	*Estimate*	*Std. Error*	*t-value*	*p-value*
Species richness	Intercept	181.5036	2.5938	69.9752	< 0.0001
	Smooth terms	*edf*	*Ref.df*	*F-value*	*p-value*
	Year	5.544	5.8198	4.2039	0.0003
	Site-year completeness	2.0318	2.5757	224.2836	< 0.0001
	Site random effect	330.6955	348	24.5786	< 0.0001
	Year random effect	33.5351	47	4.3761	< 0.0001

Response	*Parametric coefficients*	*Estimate*	*Std. Error*	*t-value*	*p-value*
Diversity (effective common species)	*Parametric coefficients*	*Estimate*	*Std. Error*	*t-value*	*p-value*
	Intercept	52.9054	0.9956	53.1402	< 0.0001
	Smooth terms	*edf*	*Ref.df*	*F-value*	*p-value*
	Year	3.3339	3.4776	3.8715	0.0062
	Site-year completeness	1.2367	1.4341	153.1123	< 0.0001
	Site random effect	326.4555	348	22.4755	< 0.0001
	Year random effect	38.3938	47	10.4976	< 0.0001

2.7.1.2 Effect of habitat

Table S2.4. Model output: overall non-linear changes in species richness and diversity 1968 – 2016, split by habitat. *Model summaries from three GAMMs that modelled annual moth species richness/diversity as function of year interacting with habitat (smooth terms) plus a parametric habitat effect.*

Response variable					
Species richness	*Parametric coefficients*	*Estimate*	*Std. Error*	*t-value*	*p-value*
	Intercept (Arable)	185.8877	5.354	34.7191	< 0.0001
	Conifer_plantation	10.8141	13.6812	0.7904	0.4293
	Broadleaf_woodland	21.7205	8.2212	2.642	0.0083
	Improved_grassland	-3.0098	6.7086	-0.4487	0.6537
	Other semi-natural	-8.2121	12.2125	-0.6724	0.5013
	Upland	-42.2195	12.5482	-3.3646	0.0008
	Urban	-22.4352	7.4557	-3.0091	0.0026
	Smooth terms	*edf*	*Ref.df*	*F-value*	*p-value*
	Year:Arable	2.1929	2.7167	2.3209	0.0721
	Year:Conifer_plantation	1.0001	1.0002	0.7159	0.3975
	Year:Broadleaf_woodland	1.9751	2.4426	9.7465	< 0.0001
	Year:Improved_grassland	2.5089	3.0726	2.2795	0.0748
	Year:Other_semi-natural	7.06	8.1117	1.9707	0.0519
	Year:Upland	1.0001	1.0001	1.2174	0.2699
	Year:Urban	3.1727	3.9352	1.6092	0.1819

	Site-Year completeness	2.0173	2.5569	210.2122	< 0.0001
	Site random effect	323.2073	342	22.4261	< 0.0001
	Year random effect	38.3697	47	7.237	< 0.0001
Diversity (effective common species)	*Parametric coefficients*	*Estimate*	*Std. Error*	*t-value*	*p-value*
	Intercept (Arable)	47.5747	1.9075	24.9409	< 0.0001
	Conifer_plantation	15.837	4.8061	3.2951	0.001
	Broadleaf_woodland	17.2541	2.889	5.9723	< 0.0001
	Improved_grassland	6.1432	2.3646	2.598	0.0094
	Other_semi-natural	-1.7537	4.2886	-0.4089	0.6826
	Upland	-9.544	4.4376	-2.1507	0.0316
	Urban	4.5561	2.6318	1.7312	0.0835
	Smooth terms	*edf*	*Ref.df*	*F-value*	*p-value*
	Year:Arable	1.6742	2.053	7.3987	0.0006
	Year:Conifer_plantation	1.0001	1.0001	2.4923	0.1145
	Year:Broadleaf_woodland	1.6254	1.993	3.4662	0.0293
	Year:Improved_grassland	2.41	2.975	3.12	0.0253
	Year:Other_semi-natural	1.8833	2.3539	1.9208	0.1328
	Year:Upland	5.093	6.1695	1.1683	0.2723
	Year:Urban	1	1.0001	9.2247	0.0024
	Site-Year completeness	1.412	1.718	126.2288	< 0.0001
	Site random effect	317.016	342	18.6615	< 0.0001
	Year random effect	40.3737	47	13.8262	< 0.0001

2.7.1.3 Effect of region

Non-linear trends

Table S2.5. Model output: overall non-linear changes in species richness and diversity 1968 – 2016, split by habitat and region. *Coefficients of nine separate GAMMs testing the effect of region (north/south) on the change in species richness/diversity over time.*

Response	Habitat	*Parametric coefficients*	*Estimate*	*Std. Error*	*t-value*	*p-value*
Species richness	All sites	Intercept (North)	158.93	4.5432	34.9823	< 0.0001
		South	31.72	5.2913	5.9943	< 0.0001
		Smooth terms	*Edf*	*Ref.df*	*F-value*	*p-value*
		Year:North	1	1	4.2556	0.0392
		Year:South	1.05	1.0796	7.7723	0.0064
		Site-year completeness	2.02	2.5584	221.7917	< 0.0001
		Site random effect	329.57	347	21.192	< 0.0001
		Year random effect	41.04	47	23.0844	< 0.0001
	Broadleaf woodland	*Parametric coefficients*	*Estimate*	*Std. Error*	*t-value*	*p-value*
		Intercept (North)	179.87	7.9611	22.5932	< 0.0001
		South	61.30	10.5821	5.7932	< 0.0001
		Smooth terms	*Edf*	*Ref.df*	*F-value*	*p-value*
		Year:North	5.75	6.7514	3.6177	0.0009
		Year:South	3.68	4.3921	7.2594	< 0.0001
		Site-year completeness	3.71	4.6007	19.7024	< 0.0001
		Site random effect	43.57	46	22.8206	< 0.0001
		Year random effect	17.98	47	0.7406	0.0008
	Improved grassland	*Parametric coefficients*	*Estimate*	*Std. Error*	*t-value*	*p-value*
		Intercept (North)	162.57	6.4326	25.2726	< 0.0001
		South	30.39	7.8303	3.8812	0.0001
		Smooth terms	*Edf*	*Ref.df*	*F-value*	*p-value*
		Year:North	2.12	2.5911	5.9209	0.0012
		Year:South	4.36	5.1442	5.8777	< 0.0001
		Site-year completeness	2.18	2.7478	86.3168	< 0.0001
		Site random effect	103.38	113	10.695	< 0.0001

Response	Habitat	*Parametric coefficients*	*Estimate*	*Std. Error*	*t-value*	*p-value*
		Year random effect	20.40	47	0.9333	0.001
Diversity (effective common species)	All sites	*Parametric coefficients*	*Estimate*	*Std. Error*	*t-value*	*p-value*
		Intercept (North)	48.23	1.58	30.59	< 0.0001
		South	6.92	1.77	3.91	0.0001
		Smooth terms	*Edf*	*Ref.df*	*F-value*	*p-value*
		Year:North	15	15	4.93	< 0.0001
		Year:South	2.00	2.08	2.98	0.0515
		Site-year completeness	1.67	2.09	106.64	< 0.0001
		Site random effect	321.27	347	20.83	< 0.0001
		Year random effect	41.62	47	14.27	< 0.0001
	Broadleaf woodland	*Parametric coefficients*	*Estimate*	*Std. Error*	*t-value*	*p-value*
		Intercept (North)	55.54	3.23	17.19	< 0.0001
		South	18.68	4.29	4.35	< 0.0001
		Smooth terms	*Edf*	*Ref.df*	*F-value*	*p-value*
		Year:North	1.77	2.14	0.78	0.5077
		Year:South	8.77	8.94	4.84	< 0.0001
		Site-year completeness	1	1	33.43	< 0.0001
		Site random effect	42.90	46	20.41	< 0.0001
		Year random effect	19.12	47	0.789	0.0012
	Improved grassland	*Parametric coefficients*	*Estimate*	*Std. Error*	*t-value*	*p-value*
		Intercept (North)	47.79	2.52	18.97	< 0.0001
		South	8.50	3.00	2.83	0.0047
		Smooth terms	*Edf*	*Ref.df*	*F-value*	*p-value*
		Year:North	7.60	8.39	2.13	0.0406
		Year:South	2.244	2.49	1.78	0.1742
		Site-year completeness	7.93	8.68	8.86	< 0.0001
		Site random effect	100.99	113	10.55	< 0.0001
		Year random effect	32.79	47	3.96	< 0.0001

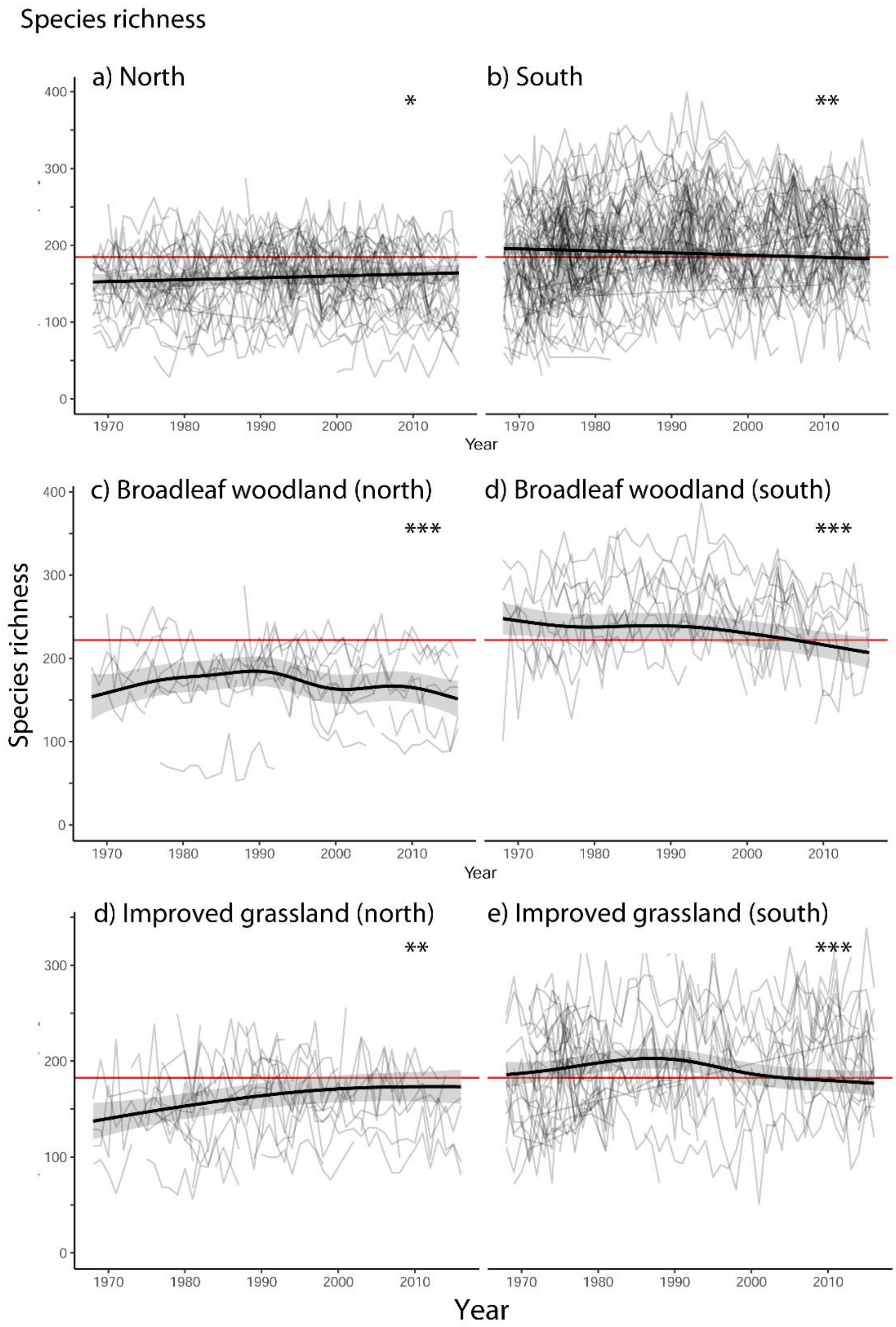


*Fig. S2.2. **Non-linear trends of species richness 1968 – 2016, split by habitat and region**. Model predictions from three GAMMs that modelled annual species richness as a function of the interaction between year and region. In (a) and (b), all sites were included, in (c) and (d) only broadleaf woodland sites were included and (d) and (e) only improved grassland sites. Solid black line and grey ribbon show model predicted means and 95% CIs. Grey lines represent the raw data. Red line shows global geometric mean average. Note the log-scale on the y-axis. Asterisks denote the significance of the fixed effect smooth term for year ($p < 0.05$ '*', < 0.01 '**', < 0.001 '***')*

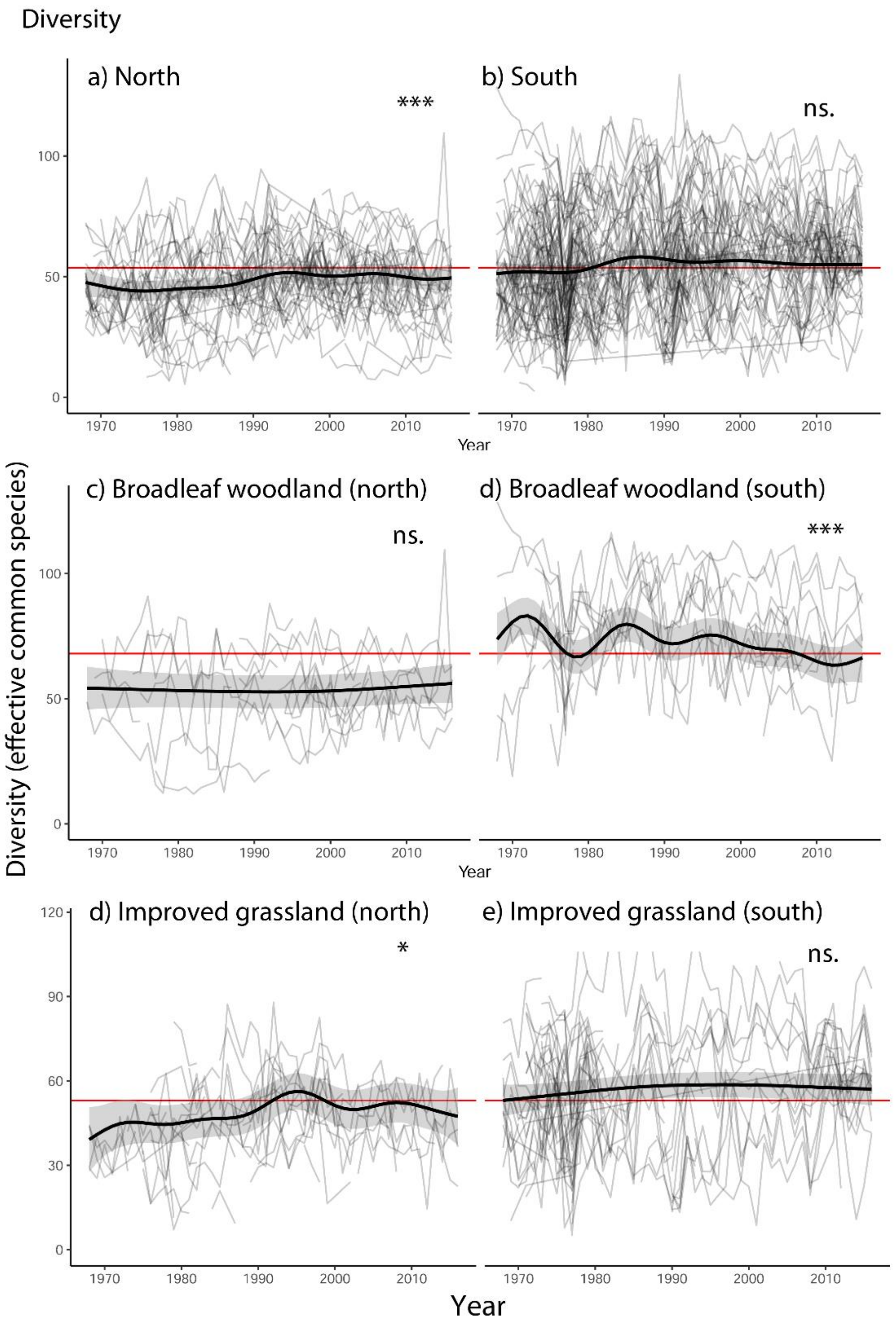


__Fig. S2.3. Non-linear trends of diversity 1968 – 2016, split by habitat and region__. Model predictions from three GAMMs that modelled annual species diversity (effective common species) as a function of the interaction between year and region. In (a) and (b), all sites were included, in (c) and (d) only broadleaf woodland sites were included and (d) and (e) only improved grassland sites. Solid black line and grey ribbon show model predicted means and 95% CIs. Grey lines represent the raw data. Red line shows global geometric mean average. Note the log-scale on the y-axis. Asterisks denote the significance of the fixed effect smooth term for year ($p < 0.05$ ‘’, < 0.01 ‘**’, < 0.001 ‘***’)*

2.7.2 Total abundance

2.7.2.1 Effect of habitat

***Table S2.6. Model output: non-linear trends of total abundance 1968 – 2016, split by habitat**. Model summary from a GAMM modelling annual moth abundance as a function of year interacting with habitat (smooth terms) plus a parametric habitat. Model assumes a negative binomial error structure. Estimates are on the predictor (log) scale. Edf = estimated degrees of freedom, Ref.df = reference degrees of freedom.*

Parametric coefficients	*Estimate*	*Std. Error*	*t-value*	*p-value*
Intercept (Arable)	7.7812	0.082	94.8369	< 0.0001
Conifer_plantation	0.4024	0.204	1.9725	0.0485
Broadleaf_woodland	0.2859	0.1225	2.3345	0.0196
Improved_grassland	-0.0811	0.0996	-0.8143	0.4154
Other_semi-natural	0.3414	0.1816	1.8802	0.0601
Upland	-0.1168	0.1867	-0.6256	0.5316
Urban	-0.7676	0.1105	-6.9479	< 0.0001
Smooth terms	*Edf*	*Ref.df*	*F-value*	*p-value*
Year:Arable	1.0093	1.0176	3.5032	0.0631
Year:Conifer_plantation	1.0104	1.0203	6.1975	0.0134
Year:Broadleaf_woodland	3.2641	4.1039	52.8515	< 0.0001
Year:Improved_grassland	1.0022	1.004	16.8707	< 0.0001
Year:Other_semi-natural	2.9953	3.7758	21.4623	0.0003
Year:Upland	2.7802	3.4609	27.7024	< 0.0001
Year:Urban	4.7573	5.845	50.8169	< 0.0001
Site random effect	329.726	342	18572.17	< 0.0001
Year random effect	44.8583	47	2388.05	< 0.0001

2.7.2.2 Effect of latitude

Table S2.7. Model output: non-linear trends of total abundance 1968 – 2016, split by habitat and region. *Model summaries from three GAMMs modelling annual moth abundance as a function of year interacting with region (smooth terms) plus a parametric region effect. Separate models were run for (1) all sites, (2) broadleaf woodland sites only and (3) improved grassland sites only. Models assume a negative binomial error structure. Estimates are on the predictor (log) scale. Edf = estimated degrees of freedom, Ref.df = reference degrees of freedom.*

Habitat					
All sites	*Parametric coefficients*	*Estimate*	*Std. Error*	*T-value*	*P-value*
	Intercept (north)	7.6373	0.0755	101.1081	< 0.0001
	South	0.0369	0.0861	0.4281	0.6685
	Smooth terms	*Edf*	*Ref.df*	*F-value*	*P-value*
	Year:north	1.0379	1.056	8.4939	0.0038
	Year:south	2.3084	2.8552	38.1025	< 0.0001
	Site random effect	337.2809	347	23817.35	< 0.0001
	Year random effect	44.7239	47	2397.096	< 0.0001
Broadleaf woodland	*Parametric coefficients*	*Estimate*	*Std. Error*	*T-value*	*P-value*
	Intercept (north)	7.9689	0.17	46.8632	< 0.0001
	South	0.1354	0.2247	0.6026	0.5468
	Smooth terms	*Edf*	*Ref.df*	*F-value*	*P-value*
	Year:north	4.5616	5.6501	41.9395	< 0.0001
	Year:south	1.0083	1.0113	45.4054	< 0.0001
	Site random effect	45.4564	46	8232.781	< 0.0001
	Year random effect	39.9362	47	496.3262	< 0.0001
Improved grassland	*Parametric coefficients*	*Estimate*	*Std. Error*	*T-value*	*P-value*
	Intercept (north)	7.6167	0.1011	75.326	< 0.0001
	South	0.1361	0.1194	1.1399	0.2543
	Smooth terms	*Edf*	*Ref.df*	*F-value*	*P-value*
	Year:north	1.0074	1.0111	2.7957	0.0963
	Year:south	4.4636	5.342	48.5042	< 0.0001
	Site random effect	106.188	113	3261.432	< 0.0001
	Year random effect	39.5483	47	459.8611	< 0.0001

2.7.3 Species-specific trends and habitat

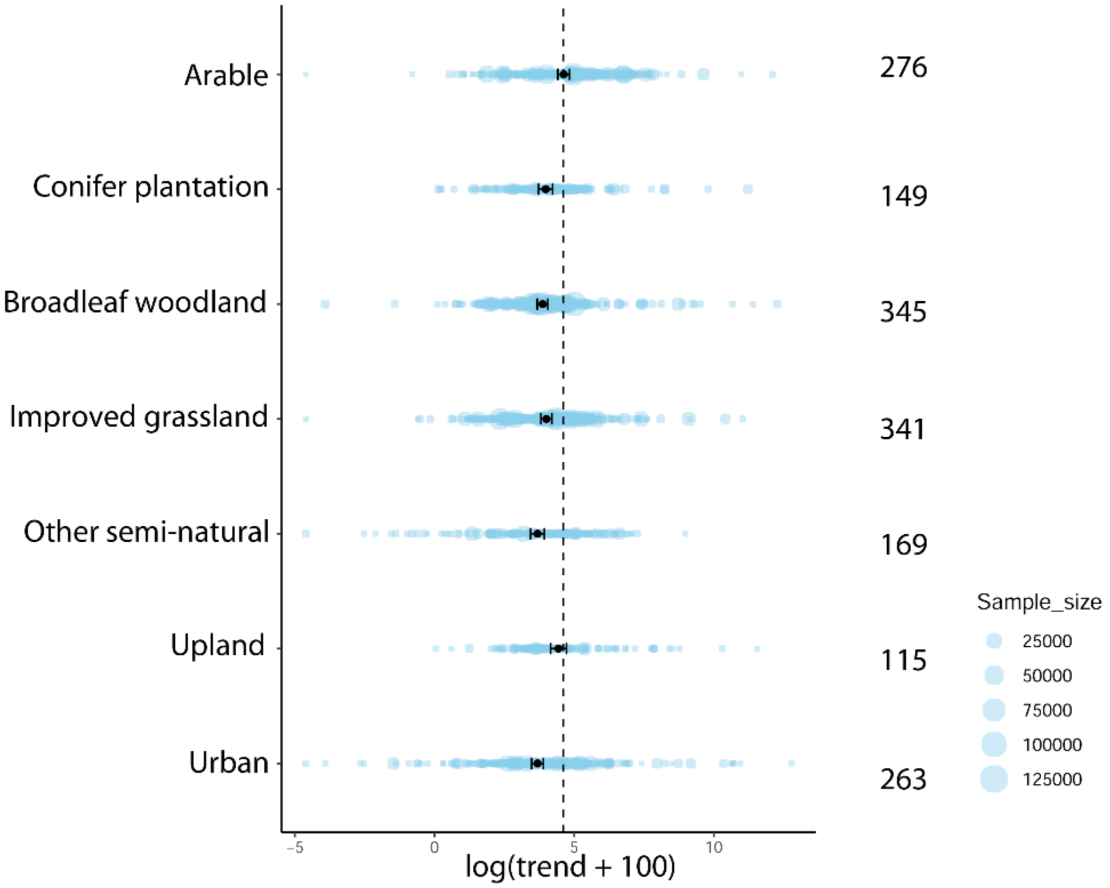


Fig. S2.4. Mean species-specific abundance trends 1968 – 2016, split by habitat. *Estimated marginal mean abundance trends (± 95% CIs) of moths across seven habitat types. The response variable is the percentage change in abundance for each species, log(x + 100)-transformed. Figures on the right show the number of species modelled in each habitat. Dashed line shows zero trend. Blue points represent the trend for each species, with the size of the point representing the sample size. The black points and whiskers are the estimated marginal mean trends with 95% confidence intervals.*

Table S2.8. Post hoc analysis of mean species-specific abundance trends between habitats. *Post hoc pair-wise contrasts of estimated marginal mean trends between habitat types. Estimates are the differences between the estimated marginal means. P-values are corrected for multiple comparisons with the Tukey method. Significant contrasts (p < 0.05) are highlighted in bold. Analysis was done in the emmeans package in R.*

Contrast	Estimate	Std. Error	df	t-ratio	p-value
Arable - Conifer_plantation	**0.648**	**0.128**	**78980.3**	**5.044**	**< 0.0001**
Arable - Broadleaf_woodland	**0.758**	**0.100**	**81071.1**	**7.571**	**< 0.0001**
Arable - Improved_grassland	**0.624**	**0.100**	**79220.5**	**6.227**	**< 0.0001**
Arable - Other_semi-natural	**0.941**	**0.124**	**75057.3**	**7.606**	**< 0.0001**
Arable - Upland	0.191	0.144	73033.1	1.322	0.842
Arable - Urban	**0.940**	**0.108**	**74600.6**	**8.734**	**< 0.0001**
Conifer_plantation - Broadleaf_woodland	0.110	0.123	83121.9	0.893	0.974
Conifer_plantation - Improved_grassland	-0.024	0.124	81368.7	-0.195	1.000
Conifer_plantation - Other_semi-natural	0.293	0.142	76072.8	2.061	0.376
Conifer_plantation - Upland	-0.457	0.157	73592.9	-2.915	0.055
Conifer_plantation - Urban	0.292	0.131	77255.2	2.238	0.275
Broadleaf_woodland - Improved_grassland	-0.134	0.093	83217.5	-1.448	0.776
Broadleaf_woodland - Other_semi-natural	0.183	0.119	77642.8	1.535	0.724
Broadleaf_woodland - Upland	-0.567	0.140	75278.3	-4.061	0.001
Broadleaf_woodland - Urban	0.182	0.103	78174.1	1.776	0.565
Improved_grassland - Other_semi-natural	0.318	0.120	76856.5	2.652	0.111
Improved_grassland - Upland	**-0.433**	**0.140**	**74444.3**	**-3.093**	**0.033**
Improved_grassland - Urban	**0.316**	**0.103**	**76377.6**	**3.080**	**0.034**
Other_semi-natural - Upland	**-0.751**	**0.156**	**71561.3**	**-4.798**	**< 0.0001**
Other_semi-natural - Urban	-0.001	0.126	73291.2	-0.010	1.000
Upland - Urban	**0.749**	**0.146**	**71709.8**	**5.128**	**< 0.0001**

2.7.3.1 Feeding guild

Table S2.9. Post hoc analysis of mean species-specific abundance trends between moth feeding guile. *Post hoc pair-wise contrasts of estimated marginal mean trends between feeding guild. Estimates are the differences between the estimated marginal means. P-values are corrected for multiple comparisons with the Tukey method. Significant contrasts ($p < 0.05$) are highlighted in bold. Analysis was done in the emmeans package in R.*

Contrast	Estimate	SE	Df	t.ratio	p.value
Coniferous - Broadleaf polyphagous	1.216	0.478	383	2.546	0.248
Coniferous - Forbs	1.217	0.461	383	2.642	0.202
Coniferous - Grasses	1.107	0.493	383	2.244	0.428
Coniferous - Highly_polyphagous	1.375	0.482	383	2.853	0.123
Coniferous - Lichen	-0.801	0.576	383	-1.390	0.930
Coniferous - Herbaceous_polyphagous	0.636	0.640	383	0.994	0.993
Coniferous - Broadleaf_shrubs	**1.597**	**0.476**	**383**	**3.356**	**0.029**
Coniferous - Broadleaf_trees	1.089	0.478	383	2.276	0.407
Coniferous - Woody polyphagous	0.412	0.711	383	0.580	1.000
Broadleaf polyphagous - Forbs	0.002	0.229	383	0.007	1.000
Broadleaf polyphagous - Grasses	-0.109	0.289	383	-0.377	1.000
Broadleaf polyphagous - Highly_polyphagous	0.159	0.269	383	0.592	1.000
Broadleaf polyphagous - Lichen	**-2.016**	**0.415**	**383**	**-4.863**	**< 0.0001**
Broadleaf polyphagous - Herbaceous_polyphagous	-0.580	0.499	383	-1.162	0.977
Broadleaf polyphagous - Broadleaf_shrubs	0.381	0.258	383	1.479	0.900
Broadleaf polyphagous - Broadleaf_trees	-0.127	0.262	383	-0.483	1.000
Broadleaf polyphagous - Woody polyphagous	-0.804	0.588	383	-1.367	0.936
Forbs - Grasses	-0.111	0.260	383	-0.426	1.000
Forbs - Highly_polyphagous	0.157	0.238	383	0.662	1.000
Forbs - Lichen	**-2.018**	**0.395**	**383**	**-5.107**	**< 0.0001**
Forbs - Herbaceous_polyphagous	-0.582	0.483	383	-1.204	0.971
Forbs - Broadleaf_shrubs	0.380	0.225	383	1.685	0.804
Forbs - Broadleaf_trees	-0.128	0.230	383	-0.557	1.000

Contrast	Estimate	SE	Df	t.ratio	p.value
Forbs - Woody polyphagous	-0.805	0.574	383	-1.403	0.926
Grasses - Highly_polyphagous	0.268	0.296	383	0.906	0.996
Grasses - Lichen	**-1.907**	**0.433**	**383**	**-4.409**	**0.0005**
Grasses - Herbaceous_polyphagous	-0.471	0.514	383	-0.917	0.996
Grasses - Broadleaf_shrubs	0.490	0.286	383	1.715	0.787
Grasses - Broadleaf_trees	-0.018	0.290	383	-0.062	1.000
Grasses - Woody polyphagous	-0.695	0.601	383	-1.157	0.978
Highly_polyphagous - Lichen	**-2.175**	**0.420**	**383**	**-5.185**	**< 0.0001**
Highly_polyphagous - Herbaceous_polyphagous	-0.739	0.503	383	-1.469	0.904
Highly_polyphagous - Broadleaf_shrubs	0.222	0.266	383	0.837	0.998
Highly_polyphagous - Broadleaf_trees	-0.286	0.270	383	-1.058	0.988
Highly_polyphagous - Woody polyphagous	-0.963	0.591	383	-1.628	0.834
Lichen - Herbaceous_polyphagous	1.436	0.594	383	2.417	0.319
Lichen - Broadleaf_shrubs	**2.398**	**0.413**	**383**	**5.809**	**< 0.0001**
Lichen - Broadleaf_trees	**1.889**	**0.416**	**383**	**4.546**	**0.0003**
Lichen - Woody polyphagous	1.213	0.670	383	1.809	0.729
Herbaceous_polyphagous - Broadleaf_shrubs	0.962	0.498	383	1.932	0.647
Herbaceous_polyphagous - Broadleaf_trees	0.453	0.500	383	0.907	0.996
Herbaceous_polyphagous - Woody polyphagous	-0.223	0.726	383	-0.308	1.000
Broadleaf_shrubs - Broadleaf_trees	-0.508	0.260	383	-1.958	0.629
Broadleaf_shrubs - Woody polyphagous	-1.185	0.586	383	-2.021	0.585
Broadleaf_trees - Woody polyphagous	-0.677	0.588	383	-1.150	0.979

Table S2.10. Post hoc analysis testing whether mean species-specific abundance trends differ between habitat types within feeding guilds. *Post-hoc tests produced using the joint_tests() function in the emmeans package. The tests determine whether the response variable (moth abundance trend) differs between habitats within each feeding guild. 'df' = degrees of freedom. P-values less than 0.05 shown in bold. Analysis was done in the emmeans package in R.*

Feeding guild	df-1	df-2	F-ratio	p-value
Conifers	6	50778.9	0.652	0.688779
Broadleaf shrubs	**6**	**65624.35**	**3.667**	**0.001211**
Broadleaf trees	6	58088.45	2.735	0.011726
Broadleaf polyphagous	**6**	**66837.1**	**2.97**	**0.006702**
Forbs	**6**	**76439.09**	**7.813**	**< 0.0001**
Grasses	**6**	**80717.11**	**5.938**	**< 0.0001**
Highly polyphagous	**6**	**70400.41**	**2.852**	**0.008876**
Lichen	**6**	**50383.53**	**5.152**	**< 0.0001**
Herbaceous polyphagous	6	82850.48	1.805	0.093788
Woody plants	6	84364.19	1.574	0.150161

Table S2.11. Post hoc analysis to test which habitats differed from each other in terms of species-specific abundance trends within each feeding guild. *Post hoc pairwise contrasts of estimated marginal mean abundance trends between habitat types within feeding guilds. Estimates are the differences between the estimated marginal means. P-values are corrected for multiple comparisons with the Tukey method. Significant contrasts (p < 0.05) are highlighted in bold. Analysis was done in the emmeans package in R.*

Feeding guild	Contrast	Estimate	Std. Error	df	t-ratio	p-value
Conifers	Arable - Conifer_plantation	-0.433	0.721	62925.5	-0.600	0.997
	Arable - Broadleaf_woodland	0.087	0.692	60565.1	0.126	1.000
	Arable - Improved_grassland	0.479	0.671	54743.1	0.714	0.992
	Arable - Other_semi-natural	-0.275	0.897	65251.0	-0.306	1.000
	Arable - Upland	-1.068	0.934	56038.3	-1.143	0.915
	Arable - Urban	0.116	0.711	50778.9	0.164	1.000
	Conifer_plantation - Broadleaf_woodland	0.520	0.660	79539.3	0.788	0.986
	Conifer_plantation - Improved_grassland	0.911	0.661	71225.4	1.378	0.814
	Conifer_plantation - Other_semi-natural	0.158	0.880	76262.5	0.180	1.000
	Conifer_plantation - Upland	-0.636	0.918	63933.4	-0.692	0.993

Feeding guild	Contrast	Estimate	Std. Error	df	t-ratio	p-value
	Conifer_plantation - Urban	0.549	0.720	63556.5	0.763	0.988
	Broadleaf_woodland - Improved_grassland	0.392	0.616	69212.9	0.636	0.996
	Broadleaf_woodland - Other_semi-natural	-0.362	0.857	76549.0	-0.422	1.000
	Broadleaf_woodland - Upland	-1.155	0.897	63683.4	-1.289	0.857
	Broadleaf_woodland - Urban	0.029	0.690	61317.4	0.043	1.000
	Improved_grassland - Other_semi-natural	-0.753	0.858	71614.6	-0.878	0.976
	Improved_grassland - Upland	-1.547	0.897	60098.5	-1.724	0.600
	Improved_grassland - Urban	-0.362	0.668	55664.0	-0.542	0.998
	Other_semi-natural - Upland	-0.794	1.029	62686.7	-0.772	0.988
	Other_semi-natural - Urban	0.391	0.894	66302.9	0.438	0.999
	Upland - Urban	1.185	0.931	56833.5	1.272	0.865
Broadleaf shrubs	Arable - Conifer_plantation	0.159	0.389	74695.9	0.409	1.000
	Arable - Broadleaf_woodland	0.434	0.275	71482.2	1.575	0.698
	Arable - Improved_grassland	0.394	0.276	70974.7	1.426	0.788
	Arable - Other_semi-natural	0.019	0.374	71896.8	0.051	1.000
	Arable - Upland	0.368	0.432	71706.8	0.851	0.979
	Arable - Urban	**1.276**	**0.299**	**65624.4**	**4.266**	**0.0004**
	Conifer_plantation - Broadleaf_woodland	0.275	0.374	78621.2	0.736	0.990
	Conifer_plantation - Improved_grassland	0.235	0.376	77794.4	0.625	0.996
	Conifer_plantation - Other_semi-natural	-0.140	0.443	74214.9	-0.315	1.000
	Conifer_plantation - Upland	0.209	0.484	75234.6	0.431	1.000
	Conifer_plantation - Urban	1.117	0.395	72926.1	2.830	0.070
	Broadleaf_woodland - Improved_grassland	-0.040	0.253	75087.1	-0.159	1.000

Feeding guild	Contrast	Estimate	Std. Error	df	t-ratio	p-value
	Broadleaf_woodland - Other_semi-natural	-0.415	0.360	74684.2	-1.153	0.912
	Broadleaf_woodland - Upland	-0.066	0.417	74344.4	-0.158	1.000
	Broadleaf_woodland - Urban	**0.842**	**0.282**	**69313.1**	**2.987**	**0.045**
	Improved_grassland - Other_semi-natural	-0.374	0.363	74522.6	-1.032	0.947
	Improved_grassland - Upland	-0.026	0.417	74453.5	-0.062	1.000
	Improved_grassland - Urban	**0.883**	**0.283**	**68735.5**	**3.114**	**0.030**
	Other_semi-natural - Upland	0.349	0.482	72492.2	0.723	0.991
	Other_semi-natural - Urban	**1.257**	**0.379**	**70255.0**	**3.317**	**0.016**
	Upland - Urban	0.908	0.438	70157.6	2.073	0.369
Broadleaf trees	Arable - Conifer_plantation	0.985	0.367	69007.1	2.688	0.101
	Arable - Broadleaf_woodland	**0.930**	**0.296**	**67769.9**	**3.146**	**0.028**
	Arable - Improved_grassland	0.886	0.306	63820.7	2.893	0.059
	Arable - Other_semi-natural	0.760	0.435	64820.4	1.748	0.583
	Arable - Upland	-0.195	0.517	58088.4	-0.377	1.000
	Arable - Urban	0.793	0.342	60938.5	2.315	0.236
	Conifer_plantation - Broadleaf_woodland	-0.056	0.334	78315.0	-0.166	1.000
	Conifer_plantation - Improved_grassland	-0.099	0.343	73473.8	-0.288	1.000
	Conifer_plantation - Other_semi-natural	-0.225	0.454	67911.1	-0.496	0.999
	Conifer_plantation - Upland	-1.180	0.529	60508.3	-2.231	0.278
	Conifer_plantation - Urban	-0.192	0.377	67987.9	-0.510	0.999
	Broadleaf_woodland - Improved_grassland	-0.043	0.255	71426.1	-0.170	1.000
	Broadleaf_woodland - Other_semi-natural	-0.169	0.410	68648.3	-0.414	1.000
	Broadleaf_woodland - Upland	-1.125	0.495	59740.0	-2.271	0.258

Feeding guild	Contrast	Estimate	Std. Error	df	t-ratio	p-value
	Broadleaf_woodland - Urban	-0.137	0.309	66249.2	-0.444	0.999
	Improved_grassland - Other_semi-natural	-0.126	0.416	66678.5	-0.303	1.000
	Improved_grassland - Upland	-1.081	0.501	58632.3	-2.160	0.318
	Improved_grassland - Urban	-0.094	0.318	62576.6	-0.294	1.000
	Other_semi-natural - Upland	-0.955	0.577	58349.3	-1.656	0.646
	Other_semi-natural - Urban	0.033	0.442	63609.7	0.074	1.000
	Upland - Urban	0.988	0.523	57485.8	1.888	0.488
Broadleaf polyphagous	Arable - Conifer_plantation	0.303	0.329	77125.5	0.921	0.969
	Arable - Broadleaf_woodland	0.580	0.251	84993.3	2.307	0.240
	Arable - Improved_grassland	0.279	0.258	78408.0	1.081	0.934
	Arable - Other_semi-natural	-0.219	0.368	71243.0	-0.594	0.997
	Arable - Upland	0.408	0.376	66837.1	1.085	0.933
	Arable - Urban	**0.949**	**0.275**	**74590.4**	**3.454**	**0.010**
	Conifer_plantation - Broadleaf_woodland	0.277	0.313	84109.1	0.885	0.975
	Conifer_plantation - Improved_grassland	-0.024	0.318	79792.4	-0.076	1.000
	Conifer_plantation - Other_semi-natural	-0.522	0.411	71729.4	-1.271	0.865
	Conifer_plantation - Upland	0.105	0.409	68314.3	0.255	1.000
	Conifer_plantation - Urban	0.646	0.332	76106.7	1.946	0.450
	Broadleaf_woodland - Improved_grassland	-0.301	0.232	88665.4	-1.296	0.854
	Broadleaf_woodland - Other_semi-natural	-0.799	0.356	74811.4	-2.247	0.270
	Broadleaf_woodland - Upland	-0.172	0.361	70034.8	-0.477	0.999
	Broadleaf_woodland - Urban	0.369	0.253	82746.5	1.460	0.769
	Improved_grassland - Other_semi-natural	-0.498	0.360	72401.8	-1.383	0.811

Feeding guild	Contrast	Estimate	Std. Error	df	t-ratio	p-value
	Improved_grassland - Upland	0.129	0.366	67798.4	0.352	1.000
	Improved_grassland - Urban	0.670	0.260	76369.8	2.572	0.135
	Other_semi-natural - Upland	0.627	0.447	64846.1	1.403	0.800
	Other_semi-natural - Urban	**1.168**	**0.371**	**70873.7**	**3.151**	**0.027**
	Upland - Urban	0.541	0.378	66232.9	1.431	0.785
Forbs	Arable - Conifer_plantation	0.578	0.243	84418.0	2.378	0.208
	Arable - Broadleaf_woodland	**0.690**	**0.191**	**83736.9**	**3.605**	**0.006**
	Arable - Improved_grassland	0.542	0.187	84284.7	2.890	0.059
	Arable - Other_semi-natural	1.319	0.220	76905.5	5.996	< 0.0001
	Arable - Upland	-0.005	0.263	76439.1	-0.019	1.000
	Arable - Urban	**0.812**	**0.199**	**78353.4**	**4.084**	**0.001**
	Conifer_plantation - Broadleaf_woodland	0.113	0.238	86163.2	0.474	0.999
	Conifer_plantation - Improved_grassland	-0.036	0.236	86334.2	-0.151	1.000
	Conifer_plantation - Other_semi-natural	0.741	0.260	78994.6	2.848	0.066
	Conifer_plantation - Upland	-0.582	0.291	77231.1	-2.004	0.412
	Conifer_plantation - Urban	0.235	0.246	81348.2	0.953	0.964
	Broadleaf_woodland - Improved_grassland	-0.148	0.180	84731.2	-0.822	0.983
	Broadleaf_woodland - Other_semi-natural	0.629	0.216	77949.2	2.905	0.057
	Broadleaf_woodland - Upland	-0.695	0.257	77394.0	-2.700	0.098
	Broadleaf_woodland - Urban	0.122	0.195	79175.0	0.626	0.996
	Improved_grassland - Other_semi-natural	**0.777**	**0.214**	**78536.0**	**3.637**	**0.005**
	Improved_grassland - Upland	-0.547	0.256	77663.9	-2.138	0.330
	Improved_grassland - Urban	0.271	0.191	79543.0	1.414	0.794

Feeding guild	Contrast	Estimate	Std. Error	df	t-ratio	p-value
	Other_semi-natural - Upland	**-1.324**	**0.280**	**73563.2**	**-4.723**	**< 0.0001**
	Other_semi-natural - Urban	-0.507	0.224	74073.3	-2.265	0.261
	Upland - Urban	**0.817**	**0.266**	**74079.5**	**3.070**	**0.035**
Grasses	Arable - Conifer_plantation	0.641	0.416	80717.1	1.539	0.721
	Arable - Broadleaf_woodland	0.771	0.309	83788.7	2.490	0.163
	Arable - Improved_grassland	0.485	0.299	88071.6	1.621	0.669
	Arable - Other_semi-natural	**1.448**	**0.327**	**81436.8**	**4.422**	**0.0002**
	Arable - Upland	-0.365	0.412	82246.8	-0.885	0.975
	Arable - Urban	**1.246**	**0.324**	**83272.6**	**3.846**	**0.002**
	Conifer_plantation - Broadleaf_woodland	0.130	0.410	80085.8	0.317	1.000
	Conifer_plantation - Improved_grassland	-0.155	0.409	81894.6	-0.380	1.000
	Conifer_plantation - Other_semi-natural	0.807	0.425	78009.1	1.900	0.480
	Conifer_plantation - Upland	-1.006	0.474	76766.7	-2.120	0.340
	Conifer_plantation - Urban	0.605	0.427	78673.8	1.418	0.792
	Broadleaf_woodland - Improved_grassland	-0.286	0.298	85653.9	-0.959	0.963
	Broadleaf_woodland - Other_semi-natural	0.677	0.326	78852.1	2.080	0.365
	Broadleaf_woodland - Upland	-1.136	0.408	81708.5	-2.785	0.079
	Broadleaf_woodland - Urban	0.475	0.326	81072.5	1.457	0.770
	Improved_grassland - Other_semi-natural	**0.963**	**0.320**	**82972.1**	**3.013**	**0.041**
	Improved_grassland - Upland	-0.850	0.406	83761.5	-2.094	0.356
	Improved_grassland - Urban	0.761	0.318	84790.5	2.395	0.200
	Other_semi-natural - Upland	**-1.813**	**0.423**	**79549.4**	**-4.288**	**0.0004**
	Other_semi-natural - Urban	-0.202	0.342	78682.8	-0.590	0.997
	Upland - Urban	**1.611**	**0.423**	**79945.3**	**3.811**	**0.003**

Feeding guild	Contrast	Estimate	Std. Error	df	t-ratio	p-value
	Arable - Conifer_plantation	0.840	0.318	74617.9	2.641	0.114
	Arable - Broadleaf_woodland	0.789	0.268	80433.7	2.949	0.050
	Arable - Improved_grassland	0.758	0.267	78665.5	2.839	0.068
	Arable - Other_semi-natural	**1.106**	**0.315**	**70625.6**	**3.508**	**0.008**
	Arable - Upland	0.733	0.353	70400.4	2.080	0.365
	Arable - Urban	**0.912**	**0.282**	**74132.2**	**3.231**	**0.021**
	Conifer_plantation - Broadleaf_woodland	-0.051	0.305	79450.8	-0.167	1.000
	Conifer_plantation - Improved_grassland	-0.082	0.306	77548.8	-0.267	1.000
	Conifer_plantation - Other_semi-natural	0.266	0.347	70607.4	0.766	0.988
	Conifer_plantation - Upland	-0.106	0.373	69336.8	-0.285	1.000
	Conifer_plantation - Urban	0.072	0.323	74179.6	0.223	1.000
	Broadleaf_woodland - Improved_grassland	-0.031	0.254	84489.9	-0.122	1.000
	Broadleaf_woodland - Other_semi-natural	0.317	0.305	74382.6	1.040	0.945
	Broadleaf_woodland - Upland	-0.056	0.342	73839.2	-0.163	1.000
	Broadleaf_woodland - Urban	0.123	0.273	79299.1	0.450	0.999
	Improved_grassland - Other_semi-natural	0.348	0.305	73208.5	1.140	0.916
	Improved_grassland - Upland	-0.025	0.341	72548.9	-0.072	1.000
	Improved_grassland - Urban	0.154	0.272	77791.4	0.565	0.998
	Other_semi-natural - Upland	-0.372	0.379	67922.2	-0.983	0.958
	Other_semi-natural - Urban	-0.194	0.320	69869.6	-0.606	0.997
	Upland - Urban	0.178	0.358	70235.7	0.499	0.999
Lichen	Arable - Conifer_plantation	1.779	1.529	50383.5	1.163	0.908
	Arable - Broadleaf_woodland	**1.776**	**0.509**	**80706.5**	**3.486**	**0.009**

Feeding guild	Contrast	Estimate	Std. Error	df	t-ratio	p-value
	Arable - Improved_grassland	**1.927**	**0.514**	**78036.2**	**3.752**	**0.003**
	Arable - Other_semi-natural	2.082	0.760	70977.8	2.738	0.089
	Arable - Upland	-1.197	1.347	83665.7	-0.888	0.974
	Arable - Urban	-0.314	0.650	71882.1	-0.484	0.999
	Conifer_plantation - Broadleaf_woodland	-0.003	1.519	50135.2	-0.002	1.000
	Conifer_plantation - Improved_grassland	0.148	1.521	50049.5	0.098	1.000
	Conifer_plantation - Other_semi-natural	0.303	1.645	51032.2	0.184	1.000
	Conifer_plantation - Upland	-2.975	1.801	58548.8	-1.652	0.648
	Conifer_plantation - Urban	-2.093	1.596	50303.7	-1.312	0.847
	Broadleaf_woodland - Improved_grassland	0.151	0.463	81979.5	0.327	1.000
	Broadleaf_woodland - Other_semi-natural	0.306	0.746	70239.6	0.411	1.000
	Broadleaf_woodland - Upland	-2.973	1.336	83877.7	-2.225	0.282
	Broadleaf_woodland - Urban	**-2.090**	**0.629**	**72894.5**	**-3.322**	**0.016**
	Improved_grassland - Other_semi-natural	0.155	0.745	70534.1	0.208	1.000
	Improved_grassland - Upland	-3.124	1.338	83518.4	-2.335	0.227
	Improved_grassland - Urban	**-2.242**	**0.631**	**72223.7**	**-3.553**	**0.007**
	Other_semi-natural - Upland	-3.279	1.477	77993.6	-2.220	0.285
	Other_semi-natural - Urban	-2.397	0.834	68376.8	-2.873	0.062
	Upland - Urban	0.882	1.423	79111.3	0.620	0.996
Herbaceous polyphagous	Arable - Conifer_plantation	1.772	0.770	85349.6	2.303	0.243
	Arable - Broadleaf_woodland	**1.912**	**0.630**	**93223.4**	**3.036**	**0.039**
	Arable - Improved_grassland	1.487	0.632	99869.7	2.355	0.218
	Arable - Other_semi-natural	1.419	0.676	93119.8	2.100	0.352
	Arable - Upland	1.315	0.775	82850.5	1.698	0.618

Feeding guild	Contrast	Estimate	Std. Error	df	t-ratio	p-value
	Arable - Urban	1.200	0.641	93545.6	1.870	0.500
	Conifer_plantation - Broadleaf_woodland	0.140	0.753	81386.7	0.186	1.000
	Conifer_plantation - Improved_grassland	-0.285	0.755	85002.4	-0.377	1.000
	Conifer_plantation - Other_semi-natural	-0.353	0.784	80915.7	-0.450	0.999
	Conifer_plantation - Upland	-0.456	0.859	73099.6	-0.532	0.998
	Conifer_plantation - Urban	-0.572	0.765	81193.5	-0.749	0.989
	Broadleaf_woodland - Improved_grassland	-0.425	0.603	89966.4	-0.705	0.992
	Broadleaf_woodland - Other_semi-natural	-0.493	0.641	86046.3	-0.769	0.988
	Broadleaf_woodland - Upland	-0.597	0.758	79044.3	-0.787	0.986
	Broadleaf_woodland - Urban	-0.713	0.614	84076.3	-1.161	0.909
	Improved_grassland - Other_semi-natural	-0.068	0.659	91771.9	-0.103	1.000
	Improved_grassland - Upland	-0.172	0.761	82460.3	-0.225	1.000
	Improved_grassland - Urban	-0.287	0.617	89333.3	-0.466	0.999
	Other_semi-natural - Upland	-0.104	0.789	78677.4	-0.132	1.000
	Other_semi-natural - Urban	-0.220	0.669	86671.5	-0.329	1.000
	Upland - Urban	-0.116	0.770	78920.5	-0.150	1.000
Woody polyphagous	Arable - Conifer_plantation	1.576	0.796	98725.1	1.979	0.428
	Arable - Broadleaf_woodland	1.710	0.742	112897.9	2.306	0.241
	Arable - Improved_grassland	1.147	0.758	103700.3	1.513	0.737
	Arable - Other_semi-natural	0.290	0.827	84364.2	0.351	1.000
	Arable - Upland	0.110	0.901	86051.8	0.122	1.000
	Arable - Urban	1.193	0.765	100054.1	1.559	0.708
	Conifer_plantation - Broadleaf_woodland	0.134	0.740	113768.3	0.180	1.000

Feeding guild	Contrast	Estimate	Std. Error	df	t-ratio	p-value
	Conifer_plantation - Improved_grassland	-0.429	0.757	104359.6	-0.567	0.998
	Conifer_plantation - Other_semi-natural	-1.286	0.826	84844.8	-1.558	0.709
	Conifer_plantation - Upland	-1.466	0.898	87190.0	-1.633	0.661
	Conifer_plantation - Urban	-0.383	0.764	100624.0	-0.502	0.999
	Broadleaf_woodland - Improved_grassland	-0.563	0.682	117159.0	-0.825	0.982
	Broadleaf_woodland - Other_semi-natural	-1.420	0.773	93948.0	-1.836	0.523
	Broadleaf_woodland - Upland	-1.600	0.851	94488.6	-1.880	0.493
	Broadleaf_woodland - Urban	-0.517	0.690	111503.2	-0.749	0.989
	Improved_grassland - Other_semi-natural	-0.857	0.789	87713.6	-1.086	0.932
	Improved_grassland - Upland	-1.037	0.866	89117.4	-1.198	0.895
	Improved_grassland - Urban	0.046	0.710	100061.6	0.065	1.000
	Other_semi-natural - Upland	-0.180	0.924	77854.5	-0.194	1.000
	Other_semi-natural - Urban	0.903	0.796	85129.8	1.135	0.918
	Upland - Urban	1.083	0.872	86718.6	1.241	0.878

2.7.3.2 Overwintering stages

Table S2.12. Post hoc analysis to determine whether species-specific abundance trends differed according to overwintering stage*. Post-hoc pairwise contrasts of estimated marginal mean abundance trends between species in four overwintering stage groups. Estimates are the differences between the estimated marginal means. P-values are corrected for multiple comparisons with the Tukey method. Significant contrasts (p < 0.05) are highlighted in bold. Analysis was done in the emmeans package in R.*

Contrast	Estimate	SE	DF	t.ratio	p.value
Adult - Egg	**1.378**	**0.445**	**387**	**3.093**	**0.011**
Adult - Larva	0.619	0.430	387	1.438	0.476
Adult - Pupa	0.961	0.431	387	2.224	0.119
Egg - Larva	**-0.759**	**0.194**	**387**	**-3.905**	**0.0006**
Egg - Pupa	-0.417	0.198	387	-2.104	0.154
Larva - Pupa	0.342	0.161	387	2.125	0.147

Table S2.13. Post hoc analysis testing whether mean species-specific abundance trends differ between habitat types within four overwintering groups. *Post-hoc tests produced using the joint_tests() function in the emmeans package. The tests determine whether the response variable (moth abundance trend) differs between habitats within each feeding guild. 'df' = degrees of freedom. P-values less than 0.05 shown in bold. Analysis was done in the emmeans package in R.*

Overwintering_stage	DF-1	DF-2	F-ratio	p-value
Adult	6	67225.24	1.595	0.144
Egg	**6**	**70664.64**	**2.875**	**0.008**
Larva	**6**	**75806.46**	**13.276**	**P < 0.0001**
Pupa	**6**	**66262.48**	**6.596**	**P < 0.0001**

Table S2.14. Post hoc analysis to determine whether species-specific abundance trends differed according to habitat, split by overwintering stage*. Post-hoc pairwise contrasts of estimated marginal mean abundance trends between species in 10 habitats, split by overwintering stage. Estimates are the differences between the estimated marginal means. P-values are corrected for multiple comparisons with the Tukey method. Significant contrasts ($p < 0.05$) are highlighted in bold. Analysis was done in the emmeans package in R.*

Overwintering stage	Contrast	Estimate	Std. Error	DF	t-ratio	p-value
Adult	Arable - Conifer_plantation	1.656	0.859	67225.24	1.928	0.461
	Arable - Broadleaf_woodland	0.971	0.672	74763.13	1.445	0.777
	Arable - Improved_grassland	1.267	0.725	76572.98	1.749	0.583
	Arable - Other_semi-natural	-0.309	1.421	75505.49	-0.218	1.000
	Arable - Upland	1.878	1.068	71645.54	1.758	0.577
	Arable - Urban	-0.305	0.765	69009.97	-0.398	1.000
	Conifer_plantation - Broadleaf_woodland	-0.686	0.794	68669.25	-0.864	0.978
	Conifer_plantation - Improved_grassland	-0.389	0.852	70017.34	-0.457	0.999
	Conifer_plantation - Other_semi-natural	-1.966	1.526	71722.05	-1.288	0.858
	Conifer_plantation - Upland	0.222	1.119	70777.73	0.198	1.000
	Conifer_plantation - Urban	-1.961	0.912	65482.36	-2.150	0.323
	Broadleaf_woodland - Improved_grassland	0.297	0.672	80012.16	0.441	0.999
	Broadleaf_woodland - Other_semi-natural	-1.280	1.398	76124.86	-0.916	0.970
	Broadleaf_woodland - Upland	0.907	1.031	73987.74	0.880	0.976
	Broadleaf_woodland - Urban	-1.275	0.722	71930.02	-1.765	0.572
	Improved_grassland - Other_semi-natural	-1.577	1.419	76478.95	-1.111	0.925
	Improved_grassland - Upland	0.611	1.060	74528.41	0.576	0.997
	Improved_grassland - Urban	-1.572	0.773	74378.14	-2.032	0.394
	Other_semi-natural - Upland	2.188	1.658	73481.44	1.319	0.843
	Other_semi-natural - Urban	0.005	1.436	75347.21	0.003	1.000

Overwintering stage	Contrast	Estimate	Std. Error	DF	t-ratio	p-value
	Upland - Urban	-2.183	1.124	69718.06	-1.942	0.452
Egg	Arable - Conifer_plantation	0.579	0.289	82438.93	2.008	0.410
	Arable - Broadleaf_woodland	0.631	0.220	82961.46	2.861	0.064
	Arable - Improved_grassland	0.283	0.216	77072.21	1.306	0.849
	Arable - Other_semi-natural	0.214	0.276	73027.67	0.777	0.987
	Arable - Upland	0.020	0.306	73975.85	0.064	1.000
	Arable - Urban	**0.765**	**0.233**	**70664.64**	**3.279**	**0.018**
	Conifer_plantation - Broadleaf_woodland	0.051	0.284	88928.32	0.180	1.000
	Conifer_plantation - Improved_grassland	-0.297	0.284	85838.44	-1.046	0.943
	Conifer_plantation - Other_semi-natural	-0.365	0.326	78040.73	-1.121	0.922
	Conifer_plantation - Upland	-0.560	0.343	77507.4	-1.632	0.662
	Conifer_plantation - Urban	0.185	0.296	78737.58	0.626	0.996
	Broadleaf_woodland - Improved_grassland	-0.348	0.213	87220.83	-1.634	0.660
	Broadleaf_woodland - Other_semi-natural	-0.416	0.272	78015.63	-1.531	0.726
	Broadleaf_woodland - Upland	-0.611	0.301	78803.21	-2.033	0.394
	Broadleaf_woodland - Urban	0.134	0.231	77790.65	0.581	0.997
	Improved_grassland - Other_semi-natural	-0.068	0.271	75505.01	-0.252	1.000
	Improved_grassland - Upland	-0.263	0.301	76342.69	-0.874	0.976
	Improved_grassland - Urban	0.482	0.227	73108.21	2.121	0.340
	Other_semi-natural - Upland	-0.195	0.342	72306.08	-0.569	0.998
	Other_semi-natural - Urban	0.550	0.285	70689.87	1.932	0.459
	Upland - Urban	0.745	0.313	71301.41	2.383	0.206
Larva	**Arable - Conifer_plantation**	**0.829**	**0.206**	**81803.45**	**4.021**	**0.001**
	Arable - Broadleaf_woodland	**1.054**	**0.153**	**84795.58**	**6.887**	**< 0.0001**

Overwintering stage	Contrast	Estimate	Std. Error	DF	t-ratio	p-value
	Arable - Improved_grassland	**0.801**	**0.153**	**85611.01**	**5.242**	**< 0.0001**
	Arable - Other_semi-natural	**1.287**	**0.180**	**79181.12**	**7.134**	**< 0.0001**
	Arable - Upland	0.286	0.215	75806.46	1.326	0.840
	Arable - Urban	**1.002**	**0.163**	**82147.32**	**6.161**	**< 0.0001**
	Conifer_plantation - Broadleaf_woodland	0.225	0.201	83450.26	1.123	0.921
	Conifer_plantation - Improved_grassland	-0.028	0.201	83393.3	-0.141	1.000
	Conifer_plantation - Other_semi-natural	0.457	0.221	78260.59	2.069	0.371
	Conifer_plantation - Upland	-0.544	0.244	74858.58	-2.224	0.282
	Conifer_plantation - Urban	0.173	0.210	81157.39	0.824	0.983
	Broadleaf_woodland - Improved_grassland	-0.254	0.145	86083.77	-1.754	0.579
	Broadleaf_woodland - Other_semi-natural	0.232	0.175	79392.27	1.323	0.841
	Broadleaf_woodland - Upland	**-0.769**	**0.210**	**76551.27**	**-3.662**	**0.005**
	Broadleaf_woodland - Urban	-0.052	0.158	83076.47	-0.332	1.000
	Improved_grassland - Other_semi-natural	0.486	0.175	80474.34	2.768	0.082
	Improved_grassland - Upland	-0.515	0.210	76937.01	-2.456	0.176
	Improved_grassland - Urban	0.201	0.157	84020.7	1.278	0.862
	Other_semi-natural - Upland	**-1.001**	**0.230**	**73664.03**	**-4.359**	**0.0003**
	Other_semi-natural - Urban	-0.284	0.184	77960.42	-1.546	0.717
	Upland - Urban	0.716	0.219	75170.39	3.275	0.018
Pupa	Arable - Conifer_plantation	0.459	0.209	72727.42	2.198	0.297
	Arable - Broadleaf_woodland	**0.515**	**0.172**	**74008.14**	**2.988**	**0.045**
	Arable - Improved_grassland	**0.582**	**0.174**	**71207.07**	**3.347**	**0.014**
	Arable - Other_semi-natural	**0.918**	**0.222**	**68528.24**	**4.146**	**0.001**
	Arable - Upland	0.102	0.261	66738.66	0.390	1.000

Overwintering stage	Contrast	Estimate	Std. Error	DF	t-ratio	p-value
	Arable - Urban	**1.041**	**0.188**	**66262.48**	**5.526**	**< 0.0001**
	Conifer_plantation - Broadleaf_woodland	0.057	0.194	79513.81	0.292	1.000
	Conifer_plantation - Improved_grassland	0.124	0.196	76218.42	0.633	0.996
	Conifer_plantation - Other_semi-natural	0.460	0.237	70683.66	1.942	0.452
	Conifer_plantation - Upland	-0.357	0.269	68135.45	-1.327	0.839
	Conifer_plantation - Urban	0.582	0.210	70992.55	2.780	0.080
	Broadleaf_woodland - Improved_grassland	0.067	0.152	77247.81	0.442	0.999
	Broadleaf_woodland - Other_semi-natural	0.403	0.210	72682.53	1.922	0.465
	Broadleaf_woodland - Upland	-0.414	0.249	69431.63	-1.659	0.644
	Broadleaf_woodland - Urban	**0.526**	**0.172**	**71375.15**	**3.051**	**0.037**
	Improved_grassland - Other_semi-natural	0.336	0.211	70909.35	1.592	0.687
	Improved_grassland - Upland	-0.481	0.250	68125.49	-1.920	0.467
	Improved_grassland - Urban	0.459	0.174	68110.85	2.634	0.116
	Other_semi-natural - Upland	-0.817	0.282	65723.43	-2.895	0.058
	Other_semi-natural - Urban	0.123	0.222	66786.71	0.551	0.998
	Upland - Urban	**0.939**	**0.262**	**65572.32**	**3.591**	**0.006**

2.7.4 Climate variables

2.7.4.1 Climate-habitat interaction

Table S2.15. Post hoc analysis to determine whether the effect of summer rain on annual moth abundance differed between habitats*. Post-hoc pairwise contrasts of estimated marginal mean effect of summer rainfall on moth abundance across seven habitat types. Estimates are the differences between the estimated marginal means. P-values are corrected for multiple comparisons with the Tukey method. Significant contrasts (p < 0.05) are highlighted in bold. Analysis was done in the emmeans package in R.*

Contrast	Estimate	SE	Df	z.ratio	p.value
Arable - Conifer_plantation	-0.071	0.026	Inf	-2.799	0.082
Arable - Broadleaf_woodland	-0.022	0.019	Inf	-1.185	0.900
Arable - Improved_grassland	-0.002	0.018	Inf	-0.109	1
Arable - Other_semi-natural	-0.027	0.026	Inf	-1.014	0.951
Arable - Upland	-0.072	0.025	Inf	-2.857	0.065
Arable - Urban	-0.024	0.021	Inf	-1.169	0.906
Conifer_plantation - Broadleaf_woodland	0.0485	0.024	Inf	2.001	0.414
Conifer_plantation - Improved_grassland	0.069	0.024	Inf	2.909	0.056
Conifer_plantation - Other_semi-natural	0.044	0.031	Inf	1.457	0.770
Conifer_plantation - Upland	-0.0003	0.029	Inf	-0.0114	1
Conifer_plantation - Urban	0.047	0.026	Inf	1.815	0.538
Broadleaf_woodland - Improved_grassland	0.020	0.016	Inf	1.260	0.870
Broadleaf_woodland - Other_semi-natural	-0.004	0.025	Inf	-0.172	1
Broadleaf_woodland - Upland	-0.049	0.024	Inf	-2.076	0.367
Broadleaf_woodland - Urban	-0.002	0.019	Inf	-0.097	1
Improved_grassland - Other_semi-natural	-0.025	0.025	Inf	-1.010	0.952
Improved_grassland - Upland	**-0.070**	**0.023**	**Inf**	**-3.017**	**0.041**
Improved_grassland - Urban	-0.022	0.018	Inf	-1.215	0.889
Other_semi-natural - Upland	-0.045	0.030	Inf	-1.496	0.748
Other_semi-natural - Urban	0.002	0.027	Inf	0.092	1
Upland - Urban	0.047	0.025	Inf	1.877	0.496

Table S2.16. Post hoc analysis to determine in which habitats summer rainfall significantly affects total moth abundance. *The estimated marginal mean effect of annual summer rainfall on moth abundance in each habitat, showing associated standard errors ad 95% CIs. The effect of rainfall is considered significant at the p < 0.05 level if the 95% CIs do not overlap zero. Significant effects highlight in bold. Analysis was done in the emmeans package in R.*

Habitat	Effect of summer rainfall	SE	df	Lower 95% CI	Upper 95% CI
Arable	**-0.088**	**0.015**	**Inf**	**-0.117**	**-0.060**
Conifer_plantation	-0.017	0.021	Inf	-0.059	0.024
Broadleaf_woodland	**-0.066**	**0.012**	**Inf**	**-0.090**	**-0.042**
Improved_grassland	**-0.086**	**0.011**	**Inf**	**-0.108**	**-0.065**
Other_semi-natural	**-0.062**	**0.022**	**Inf**	**-0.105**	**-0.019**
Upland	-0.0169	0.020	Inf	-0.057	0.023
Urban	**-0.06413**	**0.015**	**Inf**	**-0.093**	**-0.035**

2.7.4.2 Climate-overwintering stage interaction

Table S2.17. Post hoc analysis to determine whether climate variables affect moth abundance differently depending on species overwintering stage. *Post-hoc pairwise contrasts of estimated marginal mean effects of five climate variables on the annual abundance of species in four overwintering stages. Estimates are the differences between the estimated marginal means. P-values are corrected for multiple comparisons with the Tukey method. Significant contrasts (p < 0.05) are highlighted in bold. Analysis was done in the emmeans package in R.*

Climate variable	contrast	estimate	SE	Df	z-ratio	p-value
Summer temperature	Egg - Larva	-0.018	0.0097	Inf	-1.855	0.248
	Egg - Pupa	**-0.044**	**0.0097**	**Inf**	**-4.522**	**< 0.0001**
	Egg - Adult	-0.010	0.0097	Inf	-0.988	0.756
	Larva - Pupa	-0.026	0.0097	Inf	-2.666	0.038
	Larva - Adult	0.008	0.0097	Inf	0.867	0.822
	Pupa - Adult	**0.034**	**0.0097**	**Inf**	**3.534**	**0.002**
Summer rainfall	**Egg - Larva**	**-0.033**	**0.0094**	**Inf**	**-3.457**	**0.003**
	Egg - Pupa	**-0.069**	**0.0094**	**Inf**	**-7.283**	**< 0.0001**

Climate variable	contrast	estimate	SE	Df	z-ratio	p-value
	Egg - Adult	**-0.039**	**0.0094**	**Inf**	**-4.086**	**0.0002**
	Larva - Pupa	**-0.036**	**0.0094**	**Inf**	**-3.826**	**0.0008**
	Larva - Adult	-0.006	0.0094	Inf	-0.629	0.923
	Pupa - Adult	**0.030**	**0.0094**	**Inf**	**3.197**	**0.008**
Previous summer temperature	**Egg - Larva**	**-0.048**	**0.0093**	**Inf**	**-5.123**	**< 0.0001**
	Egg - Pupa	0.0169	0.0093	Inf	1.810	0.268
	Egg - Adult	**-0.033**	**0.0093**	**Inf**	**-3.521**	**0.002**
	Larva - Pupa	**0.065**	**0.0093**	**Inf**	**6.933**	**< 0.0001**
	Larva - Adult	0.015	0.0093	Inf	1.602	0.378
	Pupa - Adult	**-0.050**	**0.0093**	**Inf**	**-5.331**	**< 0.0001**
Winter temperature	**Egg - Larva**	**-0.061**	**0.0097**	**Inf**	**-6.308**	**< 0.0001**
	Egg - Pupa	**-0.055**	**0.0097**	**Inf**	**-5.605**	**< 0.0001**
	Egg - Adult	**-0.028**	**0.0097**	**Inf**	**-2.909**	**0.019**
	Larva - Pupa	0.007	0.0097	Inf	0.703	0.896
	Larva - Adult	**0.033**	**0.0097**	**Inf**	**3.399**	**0.004**
	Pupa - Adult	**0.026**	**0.0097**	**Inf**	**2.696**	**0.035**
Winter rainfall	**Egg - Larva**	**0.025**	**0.0092**	**Inf**	**2.779**	**0.028**
	Egg - Pupa	**0.025**	**0.0092**	**Inf**	**2.775**	**0.028**
	Egg - Adult	**0.032**	**0.0092**	**Inf**	**3.459**	**0.003**
	Larva - Pupa	0.000	0.0092	Inf	-0.003	1
	Larva - Adult	0.006	0.0092	Inf	0.680	0.905
	Pupa - Adult	0.006	0.0092	Inf	0.683	0.903

2.8 Discussion

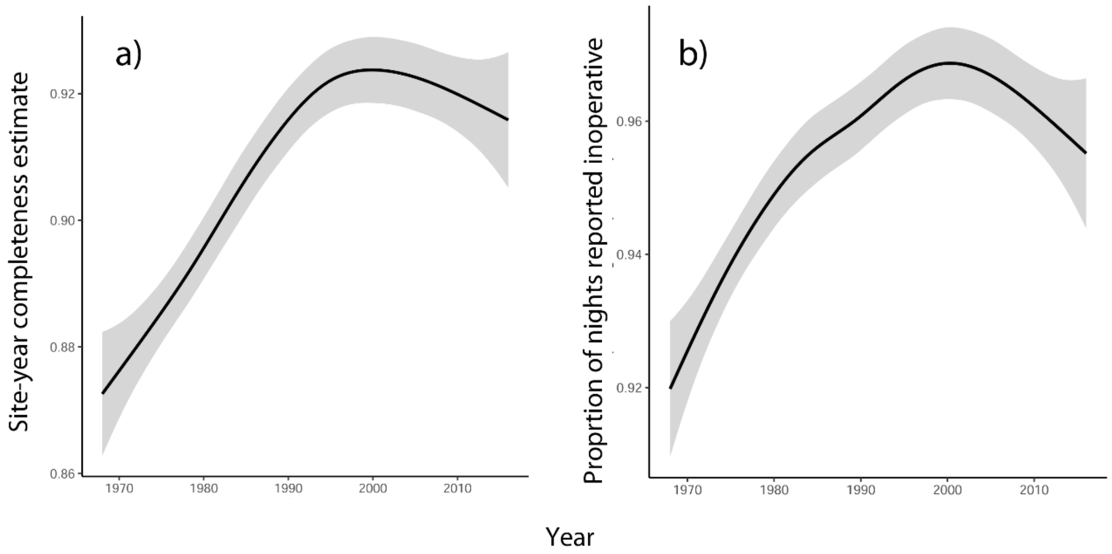


Fig. S2.5. Change in site-year completeness 1968 – 2016. *Model predictions from a GAM of a) estimated site-year completeness based on proportion of flight period sampled and b) estimated proportion of nights sampled based on reported inoperative nights in database. Showing model estimated mean and 95% CIs.*

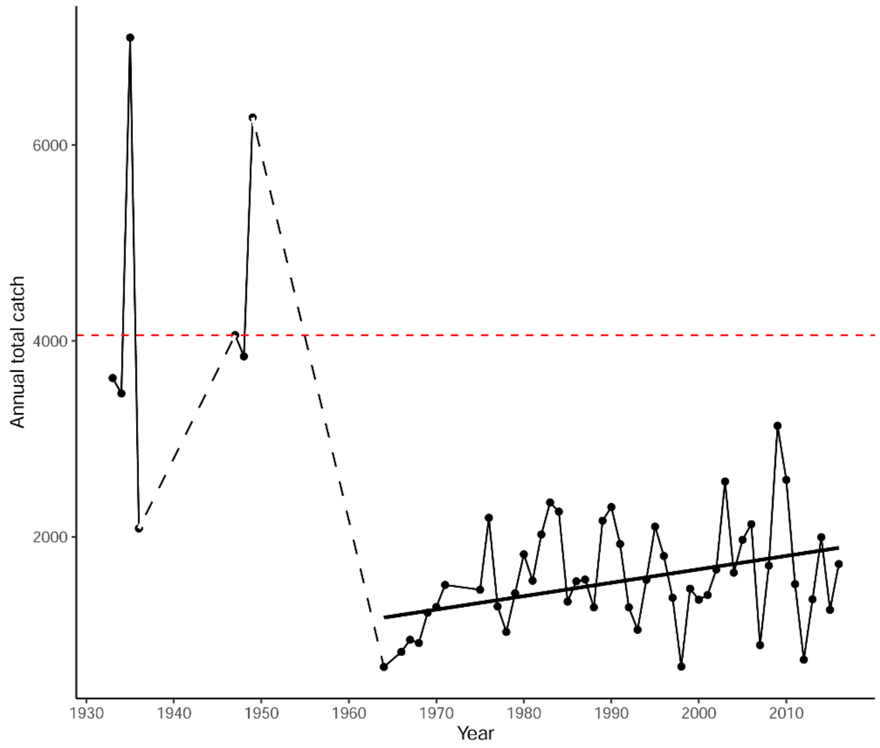


Fig. S2.6. Moth abundance at Barnfield 1933 – 2016. *Total annual moth abundance at Barnfield trap at Rothamsted Research between 1933 and 2016. Black dotted lines show when trap was inoperative. Red dotted line is the geometric mean average abundance for 1933 – 1949. Black regression line is for 1964 to 2016.*

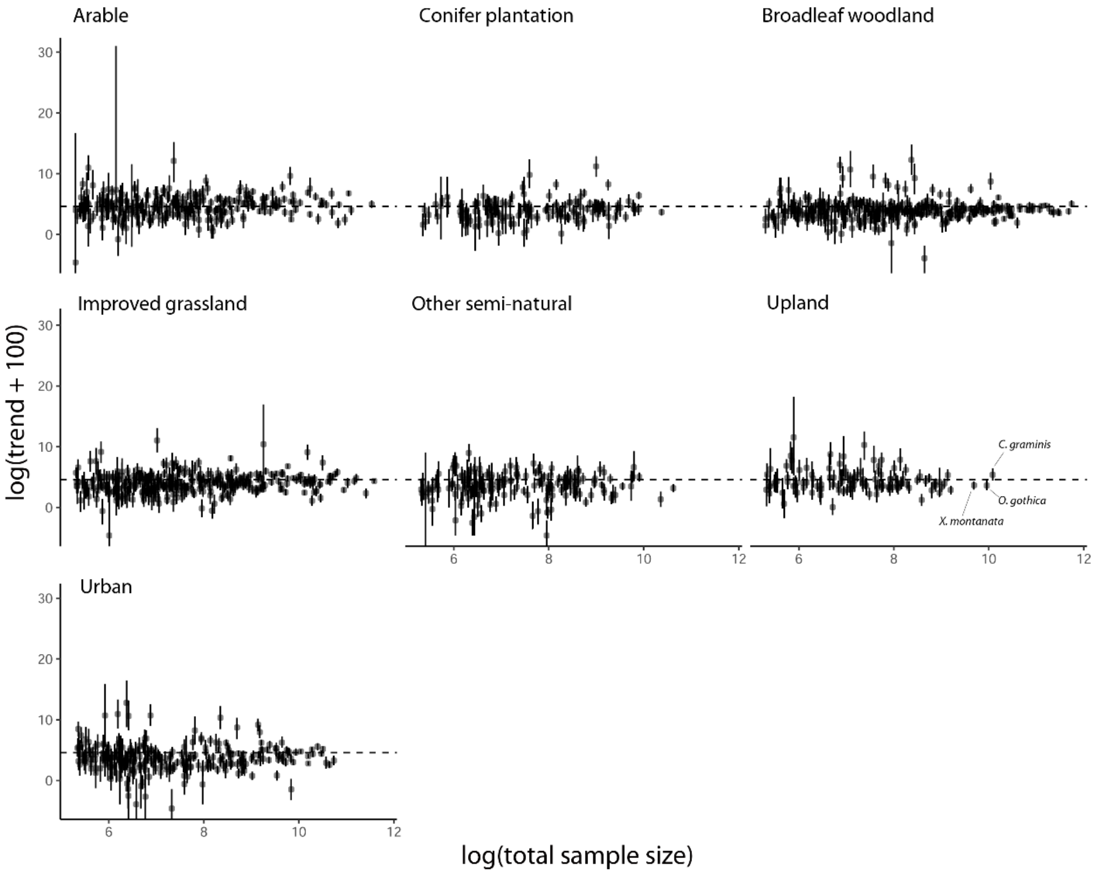


__Fig. S2.7. The relationship between moth abundance trends and sample size__. Abundance trends of individual moth species plotted against the total sample size split by habitat. Trends are on the scale of ln(x + 100), sample sizes are on the log-scale. Error-bars show 95% confidence intervals of trends. Dotted line is at trend = 0. Three notable species are labelled in the Upland category: Xanthorhoe montanata (Silver-ground Carpet), Orthosia gothica (Hebrew Character) and Cerapteryx graminis (Antler Moth).

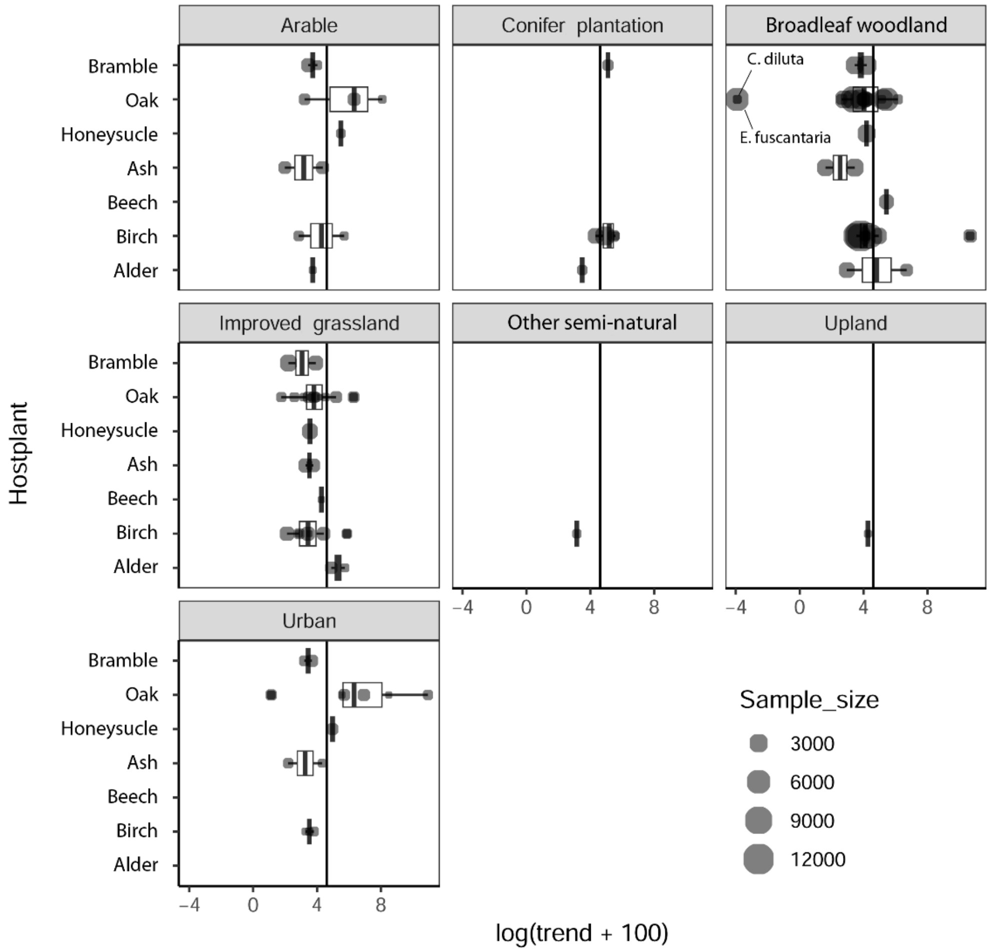


Fig. S2.8. Habitat-specific abundance trends of a selection of monophagous moth species plotted against hostplant. *Size of point is equal to total sample size of moths. Two notable species are labelled in the broadleaf woodland category: Ennomos fuscantaria (*Dusky Thorn*) and Cymatophorina diluta (*Oak Lutestring*).*

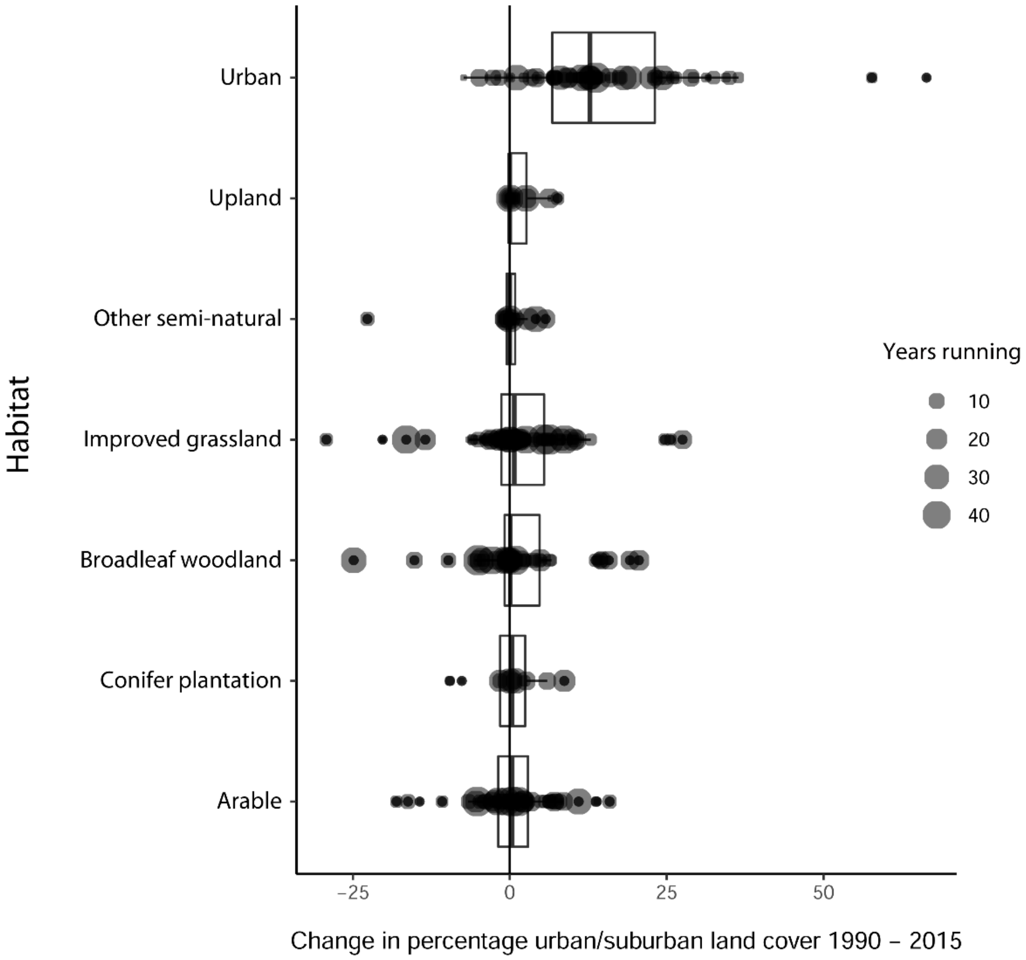


Fig. S2.9. Estimate of urbanisation in the network. *The change in percentage cover of urban and suburban land within 500 m of trap sites between 1990 and 2015 in seven different habitat types.*

Chapter 3

Design and testing of a low-cost UV LED moth-trap

Chapter 3. Design and testing of a low-cost UV LED moth-trap

3.1 Abstract

Light-traps are often used in ecological studies to assess the abundance and community composition of moths both spatially and temporally. Typically, moth-traps use light sources that are rich in UV radiation as moths are especially sensitive to this part of the electromagnetic spectrum. Currently, 6 W actinic fluorescent and 125 W mercury-vapour bulbs are most commonly used, but LED-based traps are becoming more popular due to their increasingly low cost and high energy efficiency. To compare findings between studies, it is important to know whether the attractiveness of LED-based light-traps differs to that of more conventionally used traps. Here, the attractive radius and catch-rate of a UV LED moth trap is compared to that of other more widely-used traps. Additionally, the rate at which moths escape a moth trap is estimated by comparing catch rates between a live-trap and a kill-trap. Here, it is shown that (1) a UV LED moth trap has a similar attractive radius to the more commonly used 6 W actinic trap at roughly 25 m, (2) the species richness attracted by a UV LED light is the same as that of a 200 W incandescent bulb that emits a full spectrum of light and is higher than that of a 'incandescent equivalent' LED light low in UV, and (3) an estimated 60 % of moths that enter a moth-trap escape before sunrise. The findings show that the attractive radius of a UV LED moth-trap is small and the range of species attracted is high despite the narrow spectral emittance, making it highly suitable for sampling the moth fauna of a specific location. Sample size can be increased by preventing escapes by using a kill-trap rather than a live-trap.

3.2 Introduction

Moth records represent an important data-source for monitoring biodiversity change in the UK (Fox et al., 2014, Hayhow et al., 2019). The number of moth records submitted by amateur recorders has grown greatly in recent years and the National Moth Recording Scheme (NMRS) has collated more than 25 million observational records for macro-moths alone (Fox et al., 2011). As most moth species are nocturnal and are attracted to light, light-traps are widely used for sampling moths, and they typically outperform other methods such as handsearching, pheromone lures and sugar-baiting, both in terms of the range of species captured and the economy of effort (Waring and Townsend, 2017). In addition to amateur records, light-traps are commonly employed in ecological studies to compare the abundance and richness of moth populations both spatially (Alison et al., 2016, Fuentes-Montemayor et al., 2012, Merckx et al., 2012b) and temporally (Conrad et al., 2006, Valtonen et al., 2017).

A light-trap is made of two parts: a light source and a trap body. In most cases, the body of a trap employs the lobster-pot principle, where it is easy for a moth to enter the trap but difficult to escape. The widely used Heath (Heath, 1965), Robinson (Robinson and Robinson, 1950) and Skinner traps all use a variation of this principle. The Rothamsted trap, which is used in the Rothamsted Insect Survey (RIS) light-trap network uses a killing-jar (Williams, 1948). Currently, the most commonly used light-sources are actinic fluorescent tubes, which are often used with Heath traps, 125 W mercury-vapour bulbs, typically used with Robinson traps, and 200W tungsten incandescent bulbs which are used in Rothamsted traps. The spectral sensitivity of moths is biased towards shorter (i.e., bluer) wavelengths and they are especially sensitive to ultra-violet (UV) radiation that is invisible to the human eye (Cowan and Gries, 2009, Johnsen et al., 2006), although the peak spectral sensitivity varies between species (Briscoe and Chittka, 2001). As a general rule, higher intensity lights of a shorter wavelength will attract more moths (Barghini and Souza de Medeiros, 2012, Bates et al., 2013, Bowden, 1982) but the relative attractiveness of various wavelengths of light is known to vary among families (Somers-Yeates et al., 2013).

Estimates of the attractive radius of a moth trap vary widely from over 500 m (Bowden and Morris, 1975) to 2 m (Baker and Sadovy, 1978) depending on the methods, the trap-type and the definition of attractive radius used. For a 6 W actinic Heath trap, the most commonly used trap in field studies, the attractive radius is likely to be less than 30 m, but this is known to vary between habitats and taxonomic group of moth (Merckx and Slade, 2014, Van Grunsven et al., 2014). Most moth researchers and amateur recorders use live-traps, while the RIS light-trap network uses kill-traps. A minority of studies use live-traps into which a killing-fluid is placed in the morning (e.g. Froidevaux et al., 2019). Although it is known anecdotally that moths escape moth-traps during the night, this has not before been quantified, and it is not known whether the likelihood of escape depends on the taxonomic group of the moth. The settling behaviour of moths at light traps has been shown to vary among families (Wölfling et al., 2016) and this may bias the species assemblage caught in live-traps towards those types of moths more likely to settle and thus less likely to escape.

Due to recent advances in LED technology, LED-based light-traps are now cheaper, more energy-efficient, more robust and more easily transported than 6 W actinic traps, and are likely to become more widely used in future (Brehm, 2017, Green et al., 2012, Palmer, 2017, White et al., 2016). As moths are highly attracted to UV radiation, several of these new traps use only UV LEDs that emit little or no visible light. As these UV LED traps are likely to become more widely used in ecological studies, it is important to know how they relate to more commonly used light-traps in terms of their attractive radius and the community composition of moths attracted. As the 200 W tungsten bulbs used in the RIS are no longer manufactured, a replacement light-source will be needed in future; ideally one with an attractiveness identical to a 200 W tungsten bulb. LED lights could perform this task, but better understanding is needed of how the distribution of spectral emissions affects the community of moths attracted. For instance, a 200 W tungsten bulb emits light across the whole visible spectrum (Fig. 3.1) in addition to UV radiation, but it is not known whether the same range of species attracted to a tungsten bulb is also attracted to an LED light emitting only UV.

As yet, there are few studies comparing UV LED traps to other traps, but studies that exist suggest that they are likely to perform similarly (Green et al., 2012, Infusino et al., 2017). In this thesis, UV LED moth traps are used throughout Chapter 4, with a series of prototypes developing over time: from a live-trap, to an automatically closing trap, and finally to a kill-trap. As the traps are used to sample a highly localised moth fauna, it is important to confirm that they have a small (< 30 m) attractive radius and that they are attracting a large range of the moth fauna rather than just a subset. In this chapter, the design for a UV LED Heath-style moth trap is presented. The attractive radius and catch-rate of this UV LED trap was estimated and compared to those of more commonly used moth traps, looking also at the community composition and species accumulation curves of moths captured. Catch rates between a live-trap and a kill-trap were compared to estimate the escape-rate of a Heath-style moth trap. The following hypotheses were tested: (1) the attractive radius of a new UV LED moth trap is similar to that of a 6 W actinic Heath trap at around 25 m, (2) the species accumulation rate of moths attracted to a UV LED is similar to that of a 200 W incandescent bulb and an ‘incandescent equivalent’ LED bulb, and (3) the catch-rate of a kill-trap is higher than that of a live-trap due to escapees, and the escape-rate varies according to family.

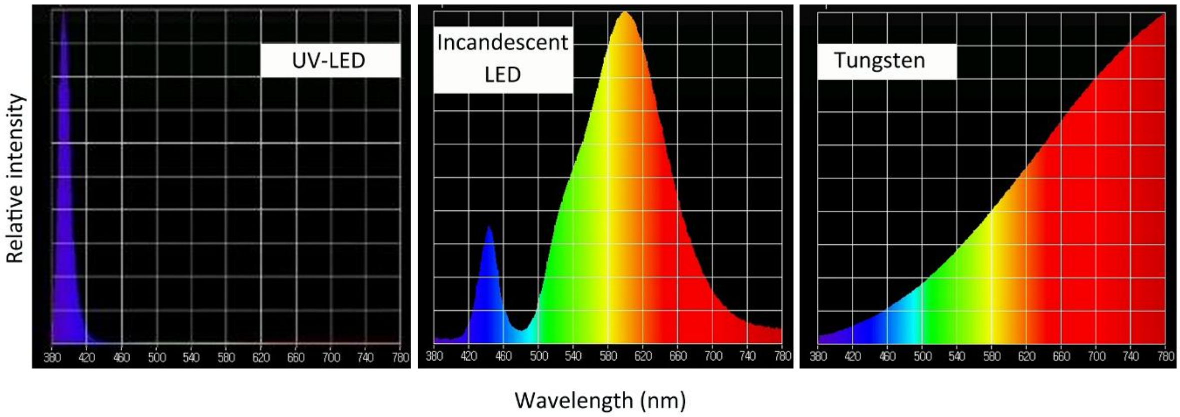


Fig. 3.1. The spectral distribution emitted by three bulb types. *Measurements taken using a UPRtek MK350S Handheld Spectrometer and presented on a scale of relative intensity.*

3.3 Methods and results

3.3.1 Design of UV LED trap

A new low-power light-trap is described based on a strip of 30 x 12 volt UV LEDs. As the prototype developed, the design improved from a live-trap to an automated system and finally to a kill-trap. This low-power light-trap design was used to test for attractive radius, catch rate and escape rate in three separate experiments described below.

3.3.1.1 LED bulbs and associated devices

The ‘light bulb’ unit was made from a strip of UV LEDs (x 30 LED units, chip type 3528 SMD, 12 volts) wrapped around a plastic cylinder inserted into a clear polystyrene 30 ml casing (Fig. 3.2). The bulb unit had an output power of less than 3 W and was powered by a lead-acid 12 volt battery. The LEDs had a narrow spectral emittance from 395 – 405 nm with a peak at 400 nm (Fig. 3.1), effectively on the edge of the UV and visible spectrum, and hence appearing to the human eye as violet. The light bulb was connected to an automatic clock timer enclosed in a waterproof plastic clip-lock box. The clock timer was programmed manually to switch on at sunset and off at sunrise.

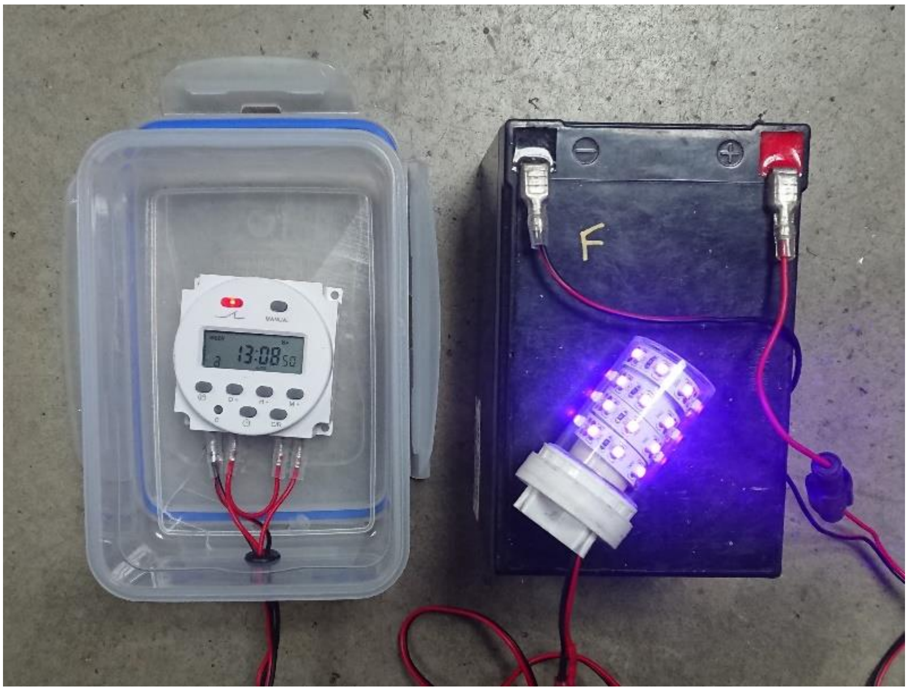


Fig. 3.2. The electronic clock, light and battery setup for the UV-LED moth-trap.

3.3.1.2 Housing and internal structure

The light source was suspended above a funnel (upper and lower diameter: 220 and 70 mm respectively) that channelled moths into a 15-litre container in which egg boxes were packed to provide overnight shelter. The baffles, rain guard and funnel were made from 0.75 mm clear PETG and the rain guard was layered in black duct tape so that the light was not visible from above (prototype v1.1, Fig. 3.3). This was then modified to include automated closure via an Arduino Nano microcontroller which drove a servomotor that secured the catch overnight (prototype v1.2). This design was then modified again to include a rain-resistant kill-jar: a 1-litre Kilner jar lined with plaster (gypsum) and infused each night with Tetrachloroethylene as is used by the Rothamsted Insect Survey (prototype v1.3).

Fig. 3.3. UV LED moth-trap (live-trap – prototype v.1.1).

3.3.2 Attractive radius of UV LED trap

3.3.2.1 Methods

Two experiments were run to understand possible differences in attractiveness: in Australian tropical forest and British temperate woodland.

Australian Tropical Forest

The study took place in a tree plantation bordering a tropical rainforest on the edge of Wooroonooran National Park in Queensland, Australia, (-17.44396, 145.72812). Capture-mark-recapture (CMR) experiments took place on 4 nights in December 2017. On the nights preceding the CMR experiments, a light trap was placed in the forest adjacent to the plantation to collect moths for the experiment. Moths were collected in the morning and put in a refrigerator at 5 °C for 3 hours. The cooled (and hence less mobile) moths were marked with a unique code using a fine Staedtler Lumocolor permanent marker pen (see Merckx and Slade, 2014 for details of methods) (Fig. 3.4). Only moths with a wingspan of 20 mm or greater were used as it was impractical to mark those that were smaller. The moths were then photographed, randomly assigned to a release distance and transferred to plastic containers corresponding to their release distance where they were kept in a shaded indoor location at ambient temperature until the evening. Moths were identified to family using Zborowski and Edwards (2007) and Common (1990). Individuals that could not be confidently identified to family level were categorised as 'other'.

At 1 hour after sunset (19:45), the plastic tubs containing the moths were placed on the ground at one of 5 release-points at 2, 5, 10, 20 or 40 m from the trap. Moths were allocated release points so that each family was evenly represented at all distances. The release-points were along a single south-west/north-east axis with the trap at the north-east end. A UV LED light-trap (prototype v1.1) was placed with the light source at 0.5 m above the ground. The view of the light was unobstructed at all distances. The lids were then all removed, and a stopwatch was started. Most of the moths flew as soon as the container was opened. All moths that returned to the trap within 15 minutes were recorded, and any moths still in their containers after this time (both dead and alive) were excluded from the analysis. The temperature remained at 24 ˚C throughout the experiment and there was no wind.

Fig. 3.4. An example of a geometrid moth that has been cooled and marked with fine permanent marker.

British Temperate Woodland

The study took place in a small woodland at Rothamsted Farm, UK (51.80647, -0.37417) on 28th August 2019. The previous night, a 125 W MV trap was placed on the edge of the woodland. All moths with a wingspan greater than 20 mm were collected and cooled to 5 ˚C in a refrigerator. The cooled moths were taken out and marked with a unique code using a fine permanent marker (Staedtler Lumocolor) as before. Moths were kept in separate pots, labelled with their unique code, at room temperature until the evening. A UV LED trap (v1.1) was placed with the light-source at 0.5 m above the ground, and release points were set up on the ground in four directions (north, south, east and west) at 5 distances: 1.5, 5, 10, 15 and 20 m, resulting in 20 release points, each with 6 or 7 moths in individually marked containers. In contrast to the tropical forest experiment, moths were released closer to the trap to better understand their response at close range. Moths were assigned release points in a way that ensured a range of release distances were tested in each family, apart from the Erebidae which only had 1 individual.

The pots were opened at 21:30 (1 h 30 mins after sunset). As the moths were less active here than in the tropical forest study, the experiment was run for longer to allow moths to warm up their flight muscles. Any moth that landed either on or in the trap was collected and the time of recapture was written on the pot. The moths at the release points were regularly checked to determine whether the moths had alighted or not. Any moths that were still in their pots at 23:00 were excluded from analysis. The temperature remained at 18 ˚C throughout the experiment and there was no wind.

3.3.2.2 Analysis

All analyses were run in R version 3.6.1 (R Core Team, 2020). As the data was binary (recaptured/not recaptured), generalized linear models (GLM) with a logit link function were fitted. In the tropical forest experiment, only the effect of distance on recapture rate was tested, and in the temperate woodland experiment, the effect of distance and direction were tested. To test whether distance affected the probability of a moth leaving its release point, another GLM was run with a binary response variable: left/did not leave release point. Moths that were found dead were excluded from this analysis. Wald tests were used to determine whether the model terms were significant. Models were tested to ensure there was no over-dispersion, residuals were plotted against explanatory variables to ensure there were no patterns, and additional model residual diagnostics were carried out using the DHARMa package (Hartig, 2019). Coefficients from the final models were used to estimate the distance at which return rate reached 5 % so that the estimated attractive radius could be compared to similar studies (Merckx and Slade, 2014).

3.3.2.3 Results

Australian tropical forest

149 individuals were captured and marked (Geometridae: 123, Noctuidae: 6, Anthelidae: 4, Pyralidae: 2, and 'other': 14). As so few individuals from families other than Geometridae were caught, all moths were analysed as one group. On one occasion, all moths ($n = 17$) at a release point were predated upon by a weta and so were removed from the analysis. Of the remaining moths, 13 % were found dead at the release point and 18 % had not alighted within 15 mins, leaving a total of 91 moths in the analysis. Data from all 4 release dates were combined as conditions were very similar on each night: windless with an average temperature of 24 ˚C. Distance from trap had a significant effect on the proportion of moths recaptured (Wald $X^2 = 11.3$, df = 1, $p < 0.001$, Fig. 3.5). The model predicted a recapture rate of 5 % at 24 m. The probability of a moth leaving its release point was not affected by distance (Wald $X^2 = 0.82$, df = 1, $p = 0.36$).

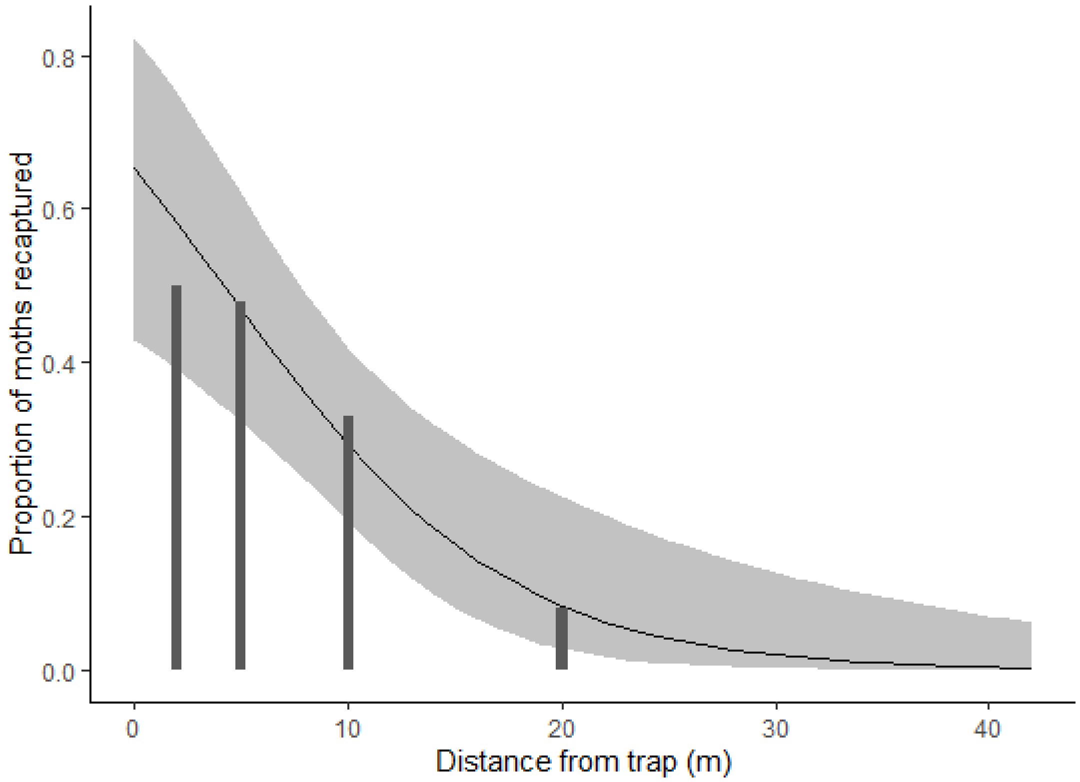


Fig. 3.5. The probability of recapture for moths released at increasing distance from a UV LED light (Australian tropical forest). *Vertical bars show the proportion of moths returned to the trap, smooth line and grey ribbon show model fit with 95 % confidence intervals. Note that no moths were recaptured at 40 m. N = 91 moths.*

British temperate woodland

123 individuals of 22 species in 4 families were captured and marked. None of the moths died during the experiment but 29 % of moths did not leave their positions by 23:00 and so were excluded from analysis, leaving 87 moths (Noctuidae: 72, Geometridae: 11, Hepialidae: 3, Erebidae: 1). As so few moths from families other than Noctuidae were included in the analysis, all moths were analysed as one group. All moths that flew to the trap did so within 5 minutes of leaving their release point. There was no significant difference in the recapture rate in different directions (Pearson's X^2 = 1.24, df = 3, p = 0.74), so all four directions were combined. The effect of distance on recapture rate was significant (Wald X^2 = 12.4, df = 1, p < 0.001, Fig. 3.6). The model predicted a recapture rate of 5 % at 27m, which was outside the bounds of the actual data. The probability of a moth leaving its release point was not affected by distance (Wald X^2 = 0.14, df = 1, p = 0.71).

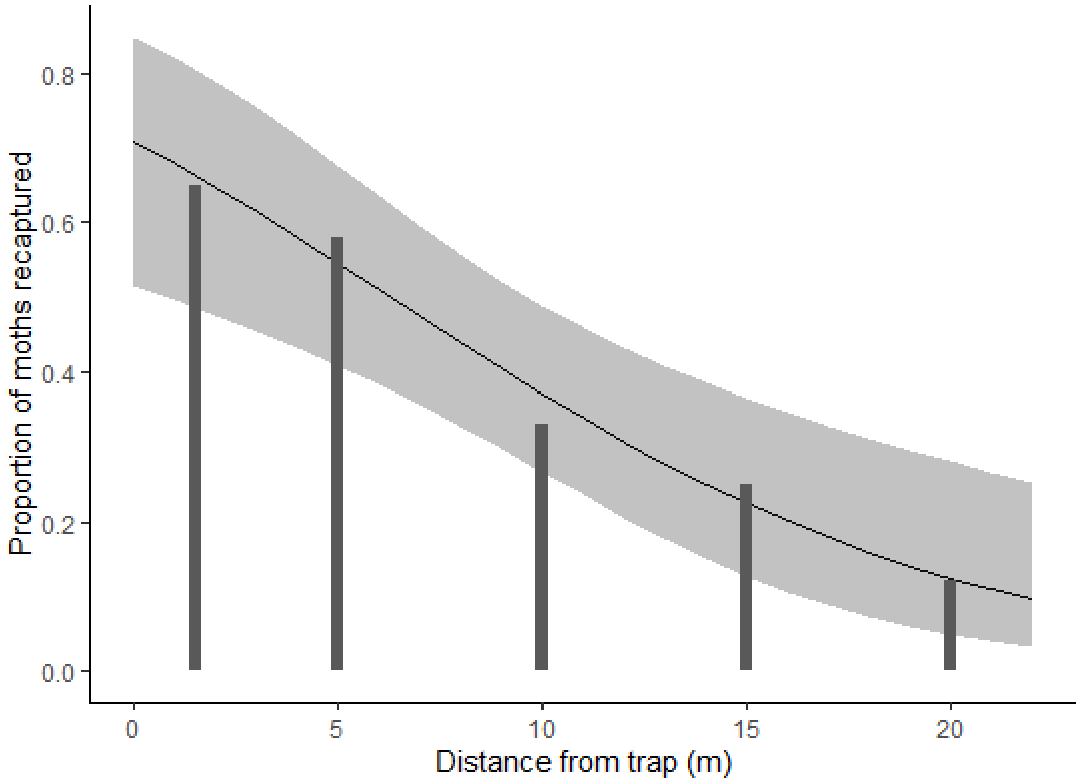


Fig. 3.6. The probability of recapture for moths released at increasing distance from a UV LED light (British broadleaf woodland). *Experiment took place in a British broadleaf woodland. Vertical bars show the proportion of moths returned to the trap, smooth line and grey ribbon show model fit with 95 % confidence intervals. N = 87 moths.*

3.3.3 Catch rate of UV LED compared to other light-sources

3.3.3.1 Methods

Experimental setup

Three Rothamsted moth-traps (Williams, 1948) were set up at Rothamsted Farm, UK (51.80647, -0.37417). A Rothamsted trap consists of a wooden frame, fixed into the ground, a glass pyramidal structure into which the moths fall, and an opaque lid that prevents light from shining upwards. The traps are mains-powered and typically use a 200 W tungsten incandescent bulb; although in this experiment other bulbs were used in addition. The traps were positioned at the corners of an equilateral triangle of side length 80 m. The line of sight between each trap was partially obscured by intervening shrubby vegetation. The surrounding habitat within a 200 m radius consisted of arable land, permanent grassland, short turf and small amounts of woody vegetation and artificial surfaces. Three lights were tested: (1) A UV LED bulb as is used in prototypes v1.1 - 1.3, (2) an 'incandescent LED' bulb which is an LED bulb designed to mimic the light of an incandescent bulb (23 W, colour: 2700 K, 2500 lumens, brand: LOHAS), and (3). A 200 W incandescent tungsten bulb as is used in the Rothamsted Insect Survey (1800 lumens). Fig. 3.1 shows the spectral distribution emitted by the three bulb types, measured using a handheld spectrometer (URPtek, model MK3505). Note that the incandescent LED emits very little UV radiation (< 400 nm) compared to the other two. Trapping took place over nine nights between 27th June and 25th July 2019. Each morning of the experiment, the moths were collected from the kill-jars and the bulbs were moved clockwise to a new position. The body of the traps remained in the same position throughout. All moths were counted and identified to species or genus level where possible.

Analysis

All Analyses were run in R version 3.6.1 (R Core Team, 2020). Differences in nightly catch-rate and Shannon's diversity index between the three bulbs were tested by using generalized linear mixed effects models (GLMM) with a negative binomial error structure for the catch-rate model and a Gaussian error structure for the Shannon's diversity model. To test for differences in catch-rate between moth families, the model also included family as a factor and bulb*family interaction term. Models were run in the lme4 package (Bates et al., 2015). Trap position, bulb type and family were included as fixed effects and the trapping night was included as a random effect. Models were tested to ensure there was no over-dispersion, residuals were plotted against explanatory variables to ensure there were no patterns, and additional model diagnostics were carried out using the DHARMa package (Hartig, 2019). Although there was no significant effect of trap position in the catch-rate model, the term was left in the final model as it was integral to the dependency structure of the data (i.e., samples from the same position are not independent) and the number of positions (3) was too small to be used as a random effect. Likelihood ratio tests were used to determine whether fixed effects parameters differed significantly from zero. Pairwise comparisons of mean average catch-rate and diversity between bulb types were tested using the emmeans package (Lenth, 2019) using a Tukey adjustment for multiple comparisons. Differences in community composition of moths between the bulb types were projected using non-metric multidimensional scaling (NMDS) and the significance of the differences were tested using the adonis function in the vegan package (Oksanen et al., 2019). Species rarefaction curves with bootstrapping-derived 95 % confidence intervals were produced using the iNEXT package (Chao et al., 2014) to determine if there were differences in the species richness of moths captured between bulb types. For community composition tests, all individuals that could not be identified to species or genus level were removed.

3.3.3.2 Results

A total of 3828 individuals across 199 taxa were captured. The position of the moth-trap had no effect on overall catch-rate (LRT X^2 = 3.3, df = 2, p = 0.19). There was a significant effect of bulb type on overall catch-rate (LRT X^2 = 109.5, df = 2, p < 0.001). Post-hoc tests revealed significant differences in overall catch rates between all three pairwise comparisons between bulb types (p < 0.01 for all comparisons, Fig. 3.7). When considering the catch-rate of different families, there was a significant interaction term between bulb type and family (LRT X^2 = 32.2, df = 8, p < 0.001) indicating that moth families react differently to the three bulb types. This appeared to be driven mainly by the Noctuidae which were captured in the UV LED trap in higher relative abundance to other families (Fig. 3.8). There was a significant effect of trap position on the Shannon's diversity index (LRT X^2 = 13.9, df = 2, p < 0.001) and a significant effect of bulb type (LRT X^2 = 8.5, df = 2, p = 0.014, Fig. 3.7). Post-hoc tests revealed a significant difference in diversity between the UV LED and the incandescent LED bulbs (z = 2.74, p = 0.02) and no significant difference between the tungsten and incandescent LED bulbs (z = 2.23, p = 0.06). The mean Shannon diversity index was lowest in the incandescent LED bulb. Moth community composition differed significantly between bulb types (adonis, R^2 = 0.16, p = 0.019). Visualisation through NMDS showed that the difference was driven primarily between differences in the tungsten and UV LED bulbs (Fig. 3.9). Rarefaction curves showed that the number of species recorded increased with sample size at the same rate for the UV LED and the tungsten bulbs, but the incandescent LED accumulated species at a lower rate (Fig. 3.10 The 95 % confidence intervals for the incandescent LED bulb and the other two bulbs did not overlap at any point.

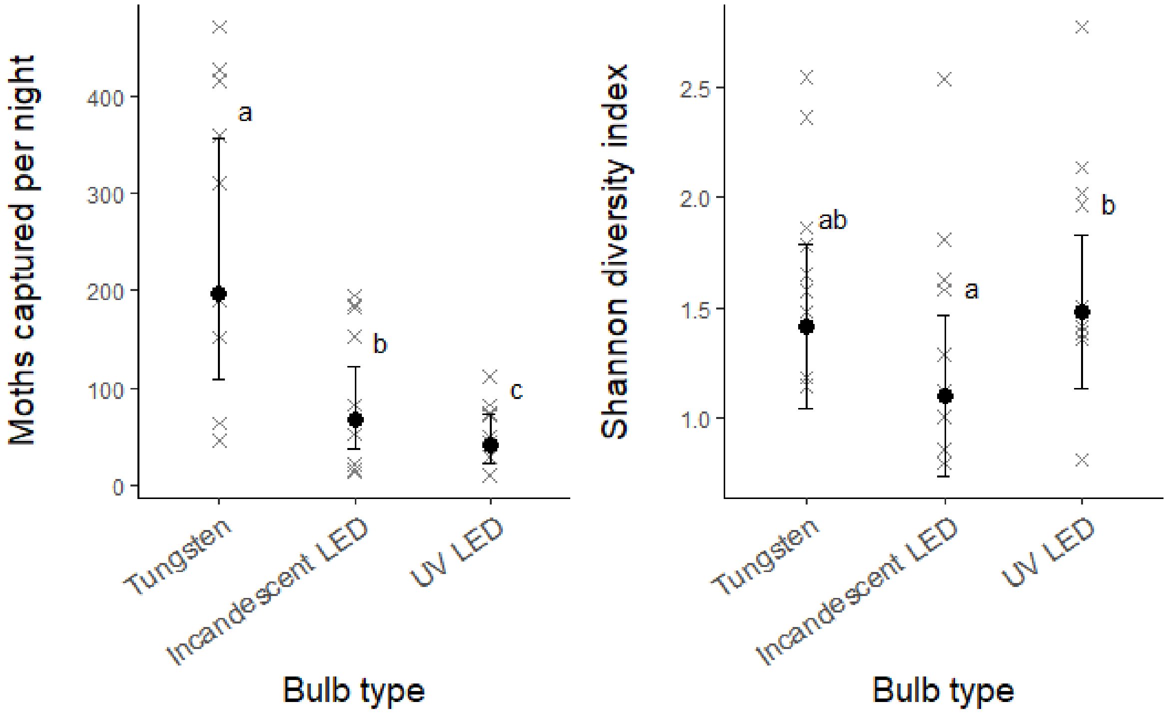


Fig. 3.7. The effect of bulb type on nightly catch rate and Shannon diversity index of moths. *Points and error bars show model predictions and 95 % confidence intervals with trap in position 1. Uncertainty estimates are for fixed effects only, with random effects set to zero. Different letters above the bars represent significant differences between bulb types as estimated in a post-hoc test with p = 0.05 accounting for multiple comparisons. Grey crosses show raw data.*

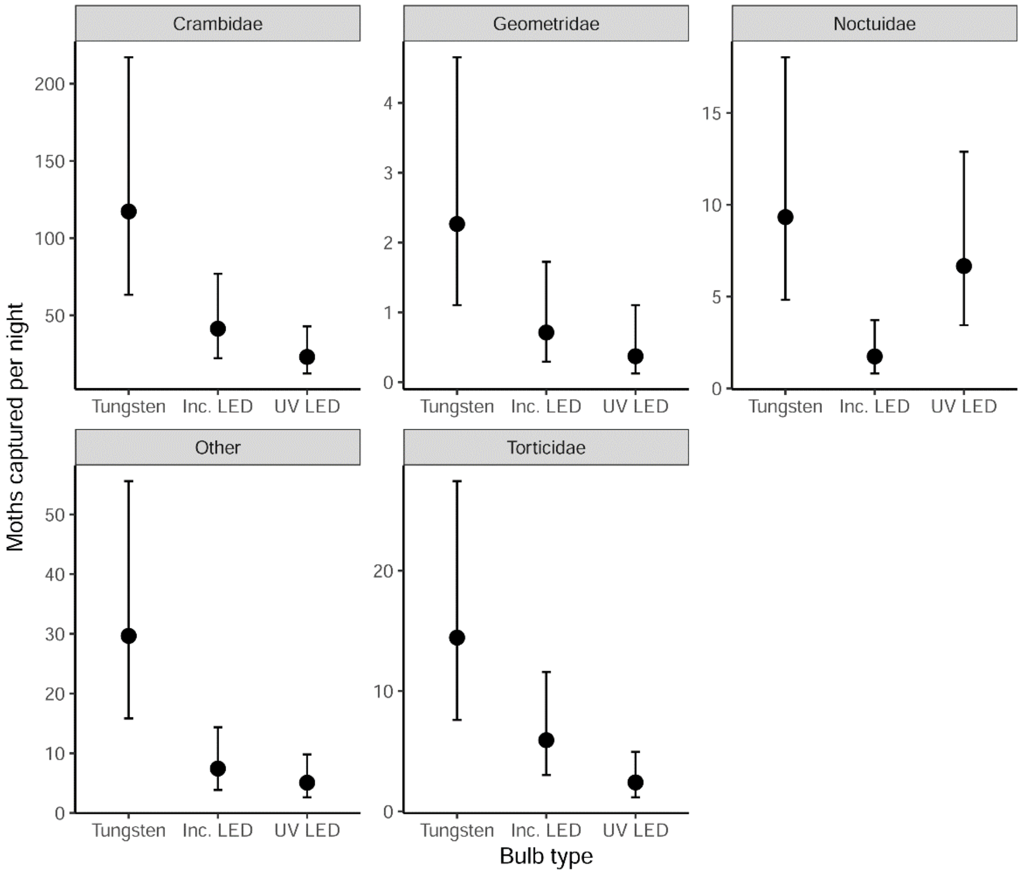


Fig. 3.8. Catch rates of three bulb types, split by moth family. *Number of moths captured per night using three bulb types across 4 families and 1 aggregate group. Points and error bars show model predictions with 95 % confidence intervals for a trap in position 1. Uncertainty estimates are for fixed effects only, with random effects set to zero. Note differing scales on the y-axes.*

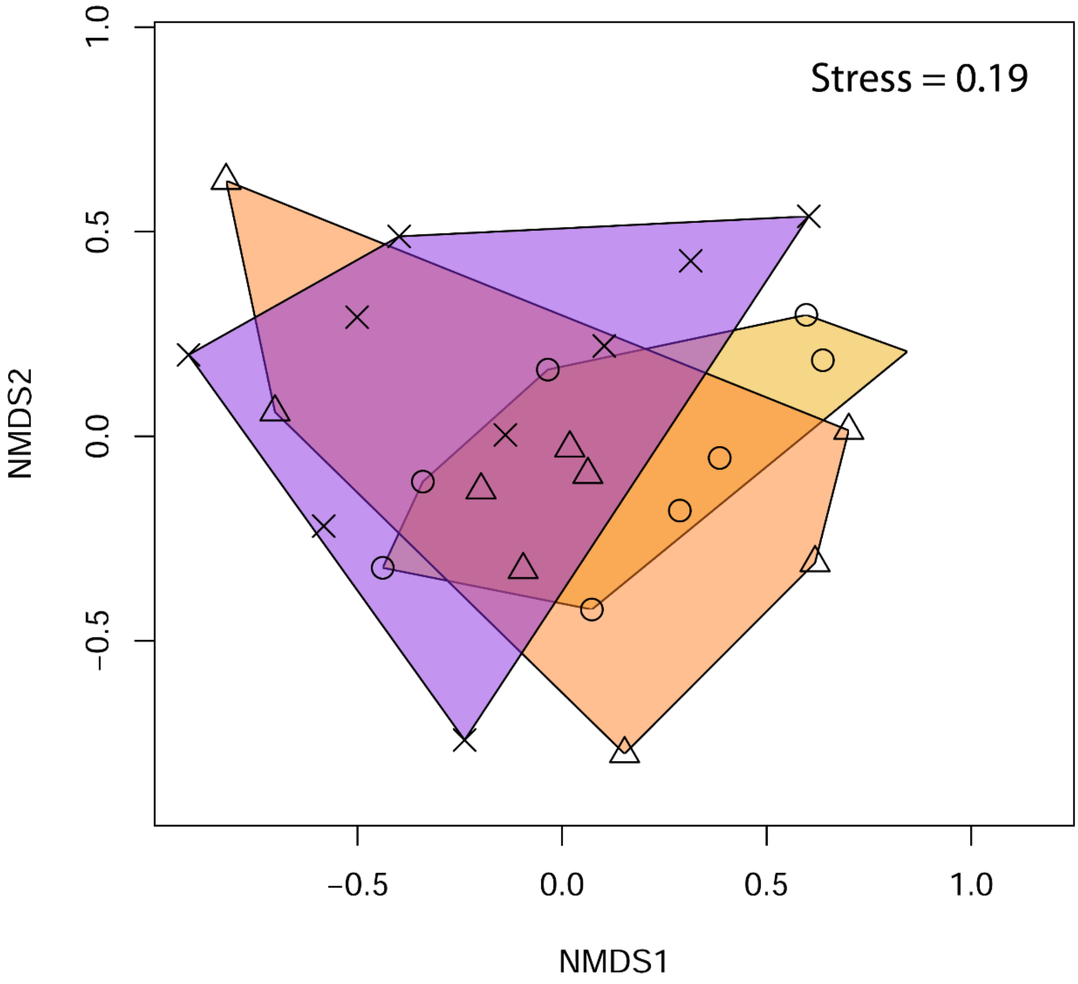


Fig. 3.9. Community composition of moths attracted by three bulb types. *Non-metric multidimensional scaling (NMDS) with convex hulls of each bulb type. Each point represents the community composition of moths caught in one trap in one night. Triangles with* orange *= incandescent LED, circles with* yellow *= tungsten, crosses with* purple *= UV LED.*

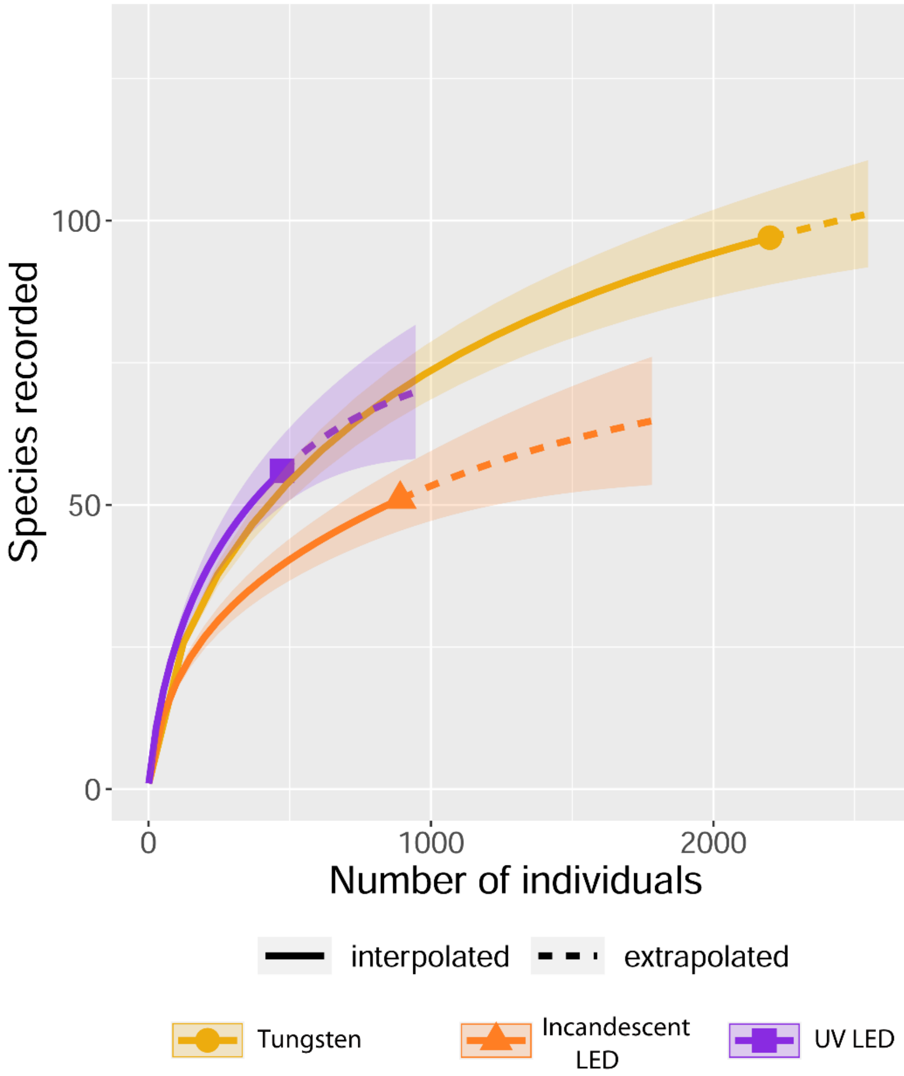


Fig. 3.10. Effect of bulb type on species richness recorded. *Sample-size-based rarefaction curves for three bulb types with 95 % confidence intervals.*

3.3.4 Escape-rate of UV LED trap

3.3.4.1 Methods

Experimental setup

Two UV LED moth-traps were run simultaneously over 57 nights between 10th August 2018 and 7th Sept 2019. These were prototypes v1.2 and v1.3 as described above. In trap prototype v1.2, hereafter referred to as the auto-trap, moths were kept alive and a device attached to the bottom of the funnel closed the trap automatically at sunrise. In prototype v1.3, hereafter referred to as the kill-trap, moths entered a kill-jar. The traps were alternated each night between two positions 25 m apart in a small patch of mixed woodland (Rothamsted Estate 51.80623, -0.37210). The lights were not directly visible to each other at night due to intervening vegetation. The traps were placed on top of poles so that the light was 1.5 m above the ground and a piece of Perspex 1.5 m square was suspended horizontally above each trap to prevent rain reaching them. On 27th June 2019 (sample night 40), a third type of trap was introduced into the setup, along with a third position which formed the third corner of a 25 m equilateral triangle. This trap was prototype v1.1 (hereafter referred to as the live-trap) and was collected at a varying time each morning, between 2 and 8 hours after sunrise. This trap was introduced to compare against the auto-trap to test if the catch-rate in the two traps was similar. Moths were identified to species or genus level where possible.

Analysis

All Analyses were run in R version 3.6.1 (R Core Team, 2020). The analysis was split into two parts: (1) to test whether the catch rate differed between the kill-trap and the auto-trap and whether this depended on family, and (2) to test whether there was a difference in catch rate between the auto- and live-trap. For part 1, a GLMM with a negative binomial error structure and log-link function was used. Nightly catch rate was modelled as the interaction between trap type and family, plus the effect of trap position, with night number as a random effect. The significance of individual parameters was tested using Likelihood Ratio Tests and non-significant terms ($p > 0.05$) were removed from the model, apart from trap position which was necessary for the dependency structure of the data. To test whether the species richness sampled by the auto- and kill-trap was the same, a rarefaction curve was calculated for both traps. For part 2, the dataset was restricted to night 40 and later, after which the live-trap was included; the kill-trap was not included in this part of the analysis. Nightly catch rate was modelled as before, but with only trap type and position as fixed effects and night number as a random effect. Interactions between family and trap type were not tested due to small sample size. All GLMMs were run in lme4 (Bates et al., 2015) and model diagnostics carried out in DHARMa (Hartig, 2019). Rarefaction curves were run in iNEXT (Chao et al., 2014).

3.3.4.2 Results

A total of 2766 individuals across 217 taxa were caught. The following number of individuals of each of the following families were caught: Blastobasidae: 393, Crambidae: 243, Erebidae: 78, Geometridae: 547, Noctuidae: 1060 and Tortricidae: 150. Moths belonging to families with low sample sizes (< 60 individuals) and those that could not be identified to family were excluded from analysis when testing for the effect of family. In part 1, when comparing the kill-trap to the auto-trap, there was no interaction between family and trap type (LRT, X^2 = 5.89, df = 5, p = 0.32) so the interaction term was removed from the model. As there was no interest in the effect of family alone, this term was also removed from the model. There was a significant effect of trap type on catch-rate (LRT, X^2 = 76.8, df = 1, p < 0.001, Fig. 3.11). The parameters of the model revealed that the catch-rate of the kill-trap was 2.62 times higher than that of the auto-trap. Rarefaction curves showed that the species accumulation rate was the same for the automatic and kill-traps (Fig. 3.12). In part 2, comparing the live-trap to the auto-trap, there was a significant effect of trap-type on catch rate (LRT, X^2 = 10.0, df = 1, p = 0.002, Fig. 3.11). Model parameters revealed that the catch-rate of the auto trap was 1.46 times higher than that of the live trap.

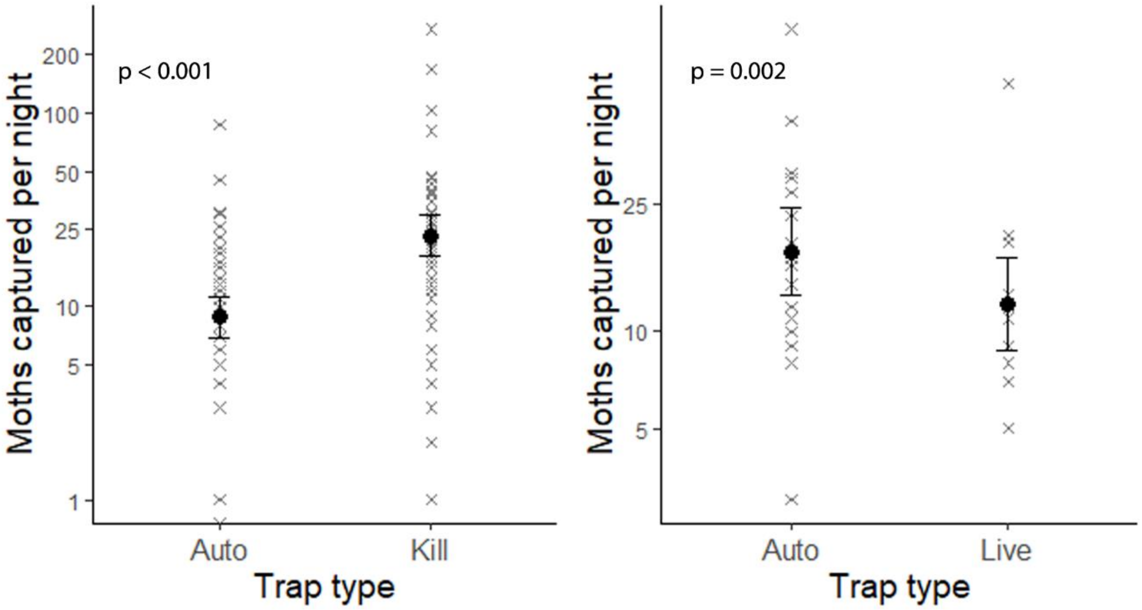


Fig. 3.11. Number of moths caught per night in live- vs kill-traps. *Comparing auto- vs kill-trap over 57 nights and auto- vs live-trap over 17 nights. Points and error bars represent model predictions and 95 % confidence intervals for traps in position 1. Uncertainty estimates are for fixed effects only, with random effects set to zero. Note differing scales on the y-axis. Grey crosses show raw data. P values represent the effect of trap type in the GLMM, modelled separately for each comparison.*

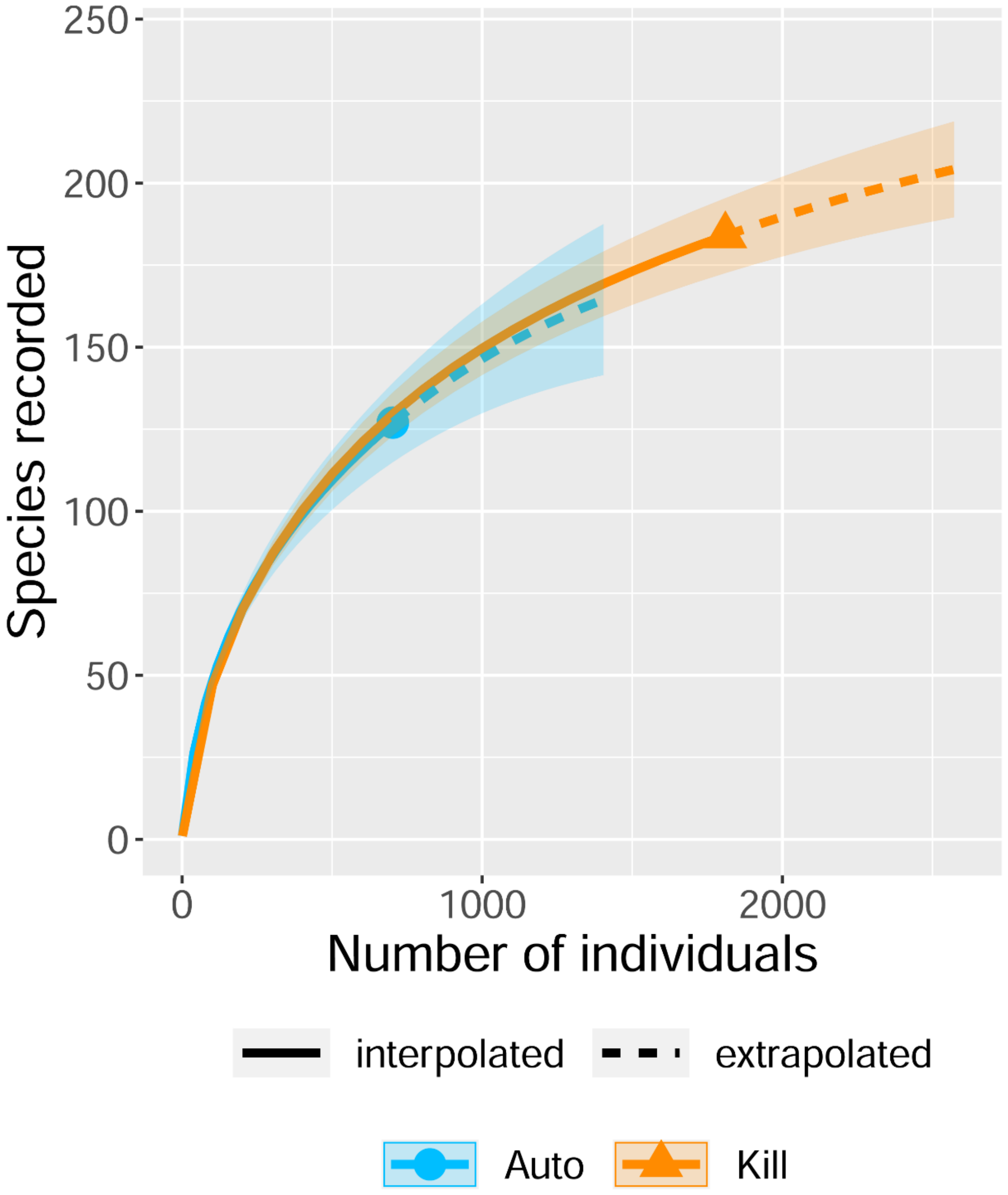


Fig. 3.12. Individual-based rarefaction curves for auto- and kill-traps with 95 % confidence intervals.

3.4 Discussion

3.4.1 Attractive radius of UV LED trap

It was demonstrated that the recapture rate of moths decreased at an increasing distance from a 3 W UV LED trap and that the likelihood of recapture approached zero at around 40 m. The definition of an 'attractive radius' of a moth-trap is not yet settled as the percentage of moths recaptured at a light source decreases smoothly over time, and does not reach 100 % even when released within 2 m (Van Grunsven et al., 2014). This was also found in the experiments presented here, where the recapture rate at 2 m was estimated to be 60 – 70 % (Fig. 3.5 and Fig. 3.6). Beck and Linsenmair (2006) defined the attractive radius as the distance at which 50 % of moths return, but this can lead to negative predictions when return-rate is low. A 5 % return rate has been suggested by Merckx and Slade (2014) and under this definition, the attractive radius of a 6 W actinic Heath trap is shown to be in the region of 10 – 50m depending on family (Merckx and Slade, 2014, Van Grunsven et al., 2014) with similar results found for a 15 W actinic Heath trap (Truxa and Fielder, 2012). Under this definition, the UV LED trap tested had an attractive radius 24 m in the Australian forest study and 27 m in the British woodland.

The differences in attraction between families is inconsistent in previous studies. Truxa and Fielder (2012) and Van Grunsven et al. (2014) both found that Geometridae were attracted from greater distances than Noctuidae while Merckx and Slade (2014) found the opposite. Sample sizes in the experiments presented here were not large enough to allow for comparisons between families. However, in the Australian tropical forest experiment, the samples were strongly dominated by Geometridae, comprising 83 % of moths tested. The attractive radius of the moth trap for this group was shown to be 23 m which matches precisely the estimates for Geometridae provided by Merckx and Slade (2014). In the British woodland experiment, 83 % of moths tested were Noctuidae, but the attractive radius of the trap for this group, 27 m, did not match the estimate for Noctuidae by Merckx and Slade (2014) of 10 m. The attractive radius studies cited vary both in methodology and results and are prone to numerous biases and sources of error. For example, the moths captured to take part in the study are not selected at random from the population as a light-trap is used to catch them, potentially biasing the sample towards more light-attracted individuals, which typically consists of more males than females (Altermatt et al., 2009). The disturbance from handling, cooling, marking and transportation of the moths may alter their behaviour (Qureshi et al., 2005). A further issue with CMR experiments is that they do not account for the random movement of moths. For example, if the true attractive radius of a moth trap was 3 m, one can show using simple geometry that a moth released at 30 m from the trap, flying in a random direction, has a greater than 5 % chance of entering the 3 m radius around the trap. The attractive radius is also known to vary according to habitat. Merckx and Slade (2014) tested an actinic Heath trap in both woodland and open field conditions and found that the recapture-rate in the open field was so low that it could not be meaningfully analysed. Whether this was due to wind, the effect of light pollution or the slightly lower temperature in the open field was unclear. As the UV LED trap was tested in woodland conditions, this implies that the attractive radius of the trap in open field conditions, as it is used in Chapter 4 of this thesis, is likely to be smaller.

Despite the flaws and variation inherent in the estimation of attractive radii, previous studies agree that the attractive radius of a variety of moth-traps is likely to be less than 50 m and probably considerably smaller (2 – 30 m), which match the figures estimated in this chapter for a UV LED moth trap. This means that, like other low-power moth-traps, the UV LED trap presented here is appropriate for sampling moth populations at a very local scale.

3.4.2 Catch rate of UV LED compared to other light-sources

The species accumulation curve of a 3 W UV LED moth trap was found to equal that of a 200 W tungsten bulb despite the large differences in spectral emissions. This demonstrates that the UV LED moth-trap catches a much smaller but still representative sample of the local moth fauna when compared to a bulb that emits radiation across the whole visible spectrum as well as the UV. This suggests that visible light is potentially unnecessary in a moth trap, especially if maximum energy-efficiency is a factor in design. Moths are especially attracted by UV radiation in comparison to other wavelengths (Cowan and Gries, 2009, Longcore et al., 2015, Van Langevelde et al., 2011) as is the case for many other insects (Barghini and Souza de Medeiros, 2012, Wakefield et al., 2016). Studies on the spectral sensitivity of Lepidoptera show that moths tend to be most sensitive to UV radiation and low in sensitivity towards to green and red part of the spectrum (Briscoe and Chittka, 2001, Eguchi et al., 1982), although some exceptions exist, e.g., the Wax Moth (*Galleria mellonella*) appears to be only sensitive to green light (Briscoe and Chittka, 2001). The effectiveness of UV at attracting moths was demonstrated by Fayle et al. (2007) who compared catches from a 125 W MV bulb to the same type of bulb coated in a substance that absorbs all visible light, leaving only UV radiation. Although the abundance of moths was significantly lower in the UV-only trap, the abundance to species richness ratio remained the same and the evenness at the family level increased in the UV-only trap. This suggests that removing visible light from a wide-spectrum bulb attracts a smaller but still representative sample of the local fauna.

The species richness estimated by a species accumulation curve was lower in the incandescent LED bulb than in the other two bulbs (Fig. 3.10) despite being the brightest of the three bulbs at 2500 lumens. The spectral distribution of the incandescent LED bulb was relatively lower in UV radiation than the UV LED and the tungsten bulb (Fig. 3.1). The lack of UV radiation may explain why the species richness of moths attracted was lower, as this bulb would be mainly attracting a subset of species which are more sensitive to the visible part of the spectrum (Briscoe and Chittka, 2001, Eguchi et al., 1982), whereas the other two bulbs would be attracting the much larger group of moths which are attracted to UV. This may also explain why the Shannon's diversity index of nightly catches tended to be lower at the incandescent LED bulb as a smaller range of species was attracted each night. It appears that the presence or absence of UV affected mainly the Noctuidae (Fig. 3.8) which were found in disproportionately high numbers in the UV LED trap. It is known that Noctuidae show a disproportionate attraction to UV in comparison to other families (Somers-Yeates et al., 2013). The community composition, while different between the UV LED and the tungsten bulb tended to be more stable on a night-to-night basis, as opposed to the incandescent LED whose community composition varied widely (Fig. 3.9). Overall, the data suggest that a UV LED light attracts as wide a range of species as a tungsten bulb despite having a very restricted spectral composition. However, as the community composition attracted by the UV LED and the tungsten bulb differed significantly, this means that neither a UV-only light source or an 'incandescent equivalent' LED would be an appropriate substitute for tungsten bulbs in the Rothamsted Insect Survey if continuity of data is to be preserved.

3.4.3 Escape-rate of UV LED trap

The nightly catch-rate in a lethal trap was 2.6 times higher than in a live (automatically closing) trap, suggesting that roughly 60 % of moths that enter a live-trap will escape during the night. While it is known anecdotally that many of the moths seen in and around a moth-trap during the night are no longer present when the trap is collected in the morning, this is the first time to my knowledge it has been quantified. The Rothamsted Insect Survey moth-trap network avoids this issue of escapees by using kill-jars - a method that has the added benefit of avoiding repeated counting of the same individuals. Although the killing of insects this way probably has negligible impacts on populations (Gezon et al., 2015) it is still better to avoid killing insects where possible for ethical reasons. Indeed, the vast majority of ecological studies on moths use non-destructive sampling (e.g., Alison et al., 2016, Merckx et al., 2019) although exceptions exist (Boutin et al., 2011, Froidevaux et al., 2019)..

There was a significant difference in catch-rate between the regular live-trap and the automatically closing trap (Fig. 3.11) with the auto-trap catching 1.5 times as many moths as the regular live-trap. From this study, it is not possible to determine whether this discrepancy arises from moths escaping between sunrise and late morning when the live-trap was collected, or whether the difference in design makes the auto-trap more effective at retaining moths. As the device that automatically closes the moth-trap is quite large and is situated inside the moth trap, it may block the moths from exiting. Either way, the study showed that the kill-trap was significantly more effective at catching moths than a live-trap. The rarefaction curves suggest that the species richness of moths sampled by kill-trap and the auto-trap were almost identical (Fig. 3.12), meaning that the expected number of species captured by the auto-trap is likely the same as that of the kill-trap given the same sample size. Contrary to expectations, there was no effect of family on the likelihood of moths escaping. This suggests that the moth community sampled by the kill-trap is not different to the live trap in terms of species composition, it simply provides a larger sample size. A potential flaw of this study was the small distance (25 m) that the traps were situated from each other, which could lead to interference: e.g., through one trap masking the light of another if moths were approaching from one direction, as has been demonstrated in windy conditions (McGeachie, 1987). However, as this study took place in a sheltered woodland environment, and as the traps were rotated nightly with the position accounted for in the model, it is unlikely that interference between traps affected the results.

The advantage to using destructive sampling is that it allows for the inclusion of species, mainly micro-moths, that can only be identified by dissection. Many micro-moth species are highly specialised and often have low dispersal ability, making them excellent indicators of local environmental conditions. However, most ecological studies on moths include only macro-moths, which can largely be identified in-field. The inclusion of micro-moths in field studies may reveal differences in community structure that analysis of macro-moths alone would overlook. It has been shown in this section that a kill-trap reduces the chances of moths escaping and thus increases the completeness of the sample which allows a greater diversity of moths to be identified to species level. Using a kill-trap thus provides data more suitable to answering the questions presented in Chapter 4 of this thesis.

3.5 Conclusions

The attractive radius of a 3 W UV LED moth trap was shown to be comparable to that of more widely used moth traps and thus appropriate for sampling moth communities within a 30 m radius as is done in Chapter 4 of this thesis. The species richness of moths attracted to a UV LED light was shown to be equivalent to that of a 200 W tungsten bulb despite having only a small fraction of the spectral output, demonstrating that using only UV and not visible light is effective at attracting a wide and representative range of moth species. The data provided by the traps was improved by using kill-jars and the sample size in these traps was found to be 2.6 times higher than in live-traps. Overall, this study shows that UV LED traps are an effective way of sampling moth populations at the field-scale.

3.6 Pilot-study: moth abundance and diversity at the farm scale

3.7 Pilot study: Summary

In order to test the novel moth trap design and the methods involved in analysing moth abundance and diversity at the farm scale, a pilot study was run at a farm with established agri-environment scheme (AES) field margins. The aim of the pilot study was twofold: 1) to determine whether moth abundance and diversity were higher in AES margins than in control margins, and 2) to reveal any methodological issues to resolve before undertaking the main field experiment. In this study, the proportion of AES vegetation within a 25 m radius of the trap had a significant effect on forb feeder abundance but not abundance as a whole. Diversity was also enhanced in areas with more AES habitat. Some major methodological flaws were also revealed; these were as follows:

- The sample size of moths caught per trap per night was very small (geometric mean average of 6.4 per night), making the statistical analyses weak. In the next experiment, kill-traps will be used instead of live-traps as this is expected, at minimum, to double the sample size (see section 3.3.4.2).
- The diversity of AES field margin types did not allow for statistical analysis of the different types due to low sample size. In the next experiment, three clearly defined treatment types will be designed and sampled equally.
- There was a problem with clustering of treatment types which made it difficult to separate the effect of treatment from the effect of location. In the next experiment, a blocked design will be used so that each location contains an entire replicate of treatment types.
- Of the 31 sites sampled, 26 were adjacent to a hedgerow, and five were not. In the analysis, it transpired that hedgerows were an important determining factor, but the small sample size of non-hedgerow sites weakened the analysis. In the next experiment, sites will be spread more equally between hedgerow and non-hedgerow sites.

3.8 Pilot study: Introduction

In 2005, a randomised block experiment was set up at Hillesden Farm to compare the effect of Higher Levels Stewardship (HLS) on various taxa in comparison to cross-compliance (CC) controls. A study on moths at this time found that AES treatments had a positive effect on the abundance (but not diversity) of micro-moths, but no effect on abundance or diversity was found for macro-moths (Heard et al., 2012). Furthermore, abundance of both micro- and macro-moths was lower in 2010 compared to the 2006 baseline. Although abundance and diversity of Section 41 Priority species increased over this time. This pre-existing experimental setup of AES on a commercial farm was utilised to test the methodologies used in Chapter 4.

3.8.1 Methods

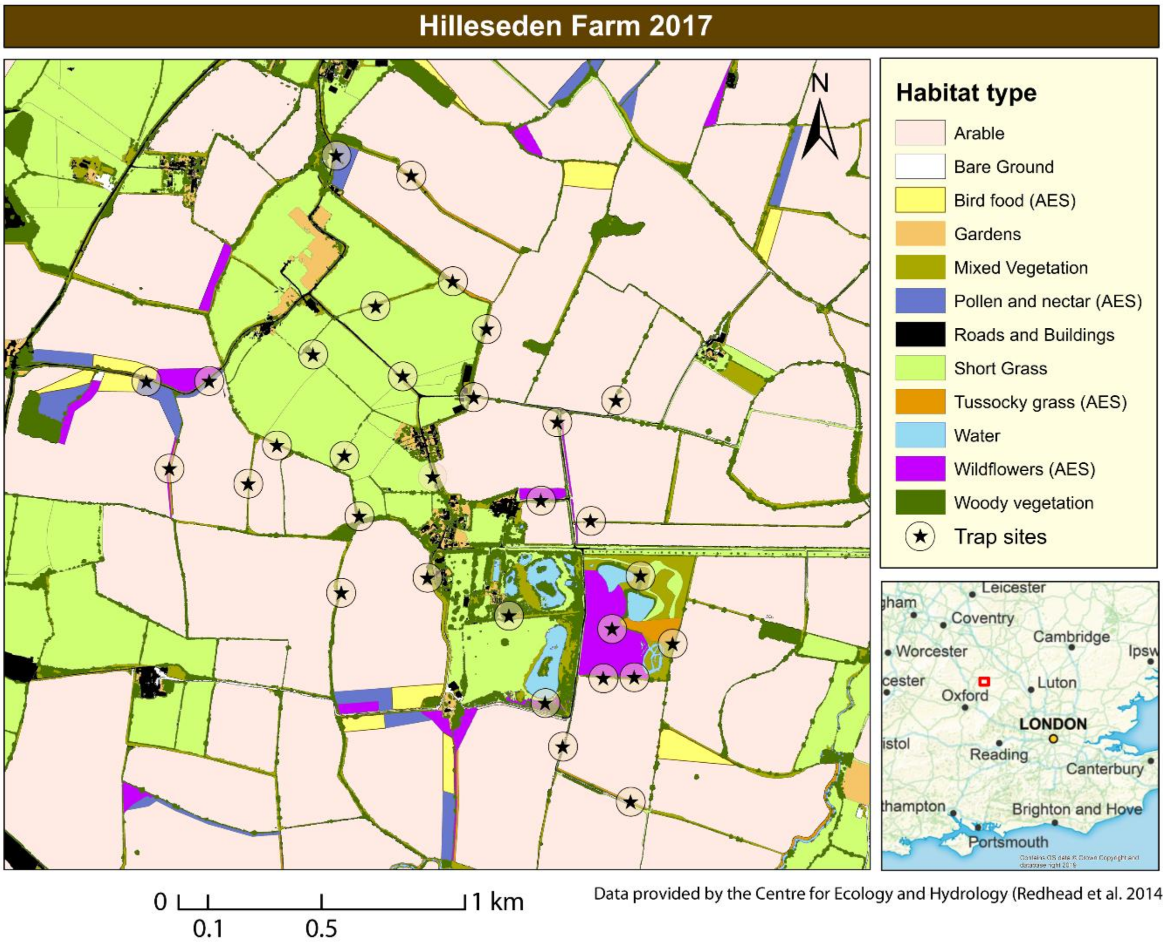
3.8.1.1 Hillesden Farm

Fieldwork took place at Hillesden Farm and adjacent Jubilee Farm in Buckinghamshire between May 16th and September 1st, 2017. Hillesden is a c. 1000 ha arable farm situated on lowland heavy clay soils (elevation 80 – 110m), producing winter wheat, oilseed rape, barley and field beans, containing semi-natural habitats including hedgerows, isolated trees and copses. There is also 4 ha of improved grassland on which deer are grazed, and 1.3 ha of improved grassland containing cattle. Since 2005, the farm has established a network of AES habitats across the farm according to the specifications of Entry-Level Stewardship (ELS) and Higher-Level Stewardship (HLS) (DEFRA 2005). Habitats created on arable land are tussocky grass margin (EE3), ELS bird food (EF2), HLS bird food (HF12), ELS pollen and nectar margin (EF4), pollen and nectar margin (HE10), resource protection buffer (EJ9) and wildflower margin (EF1). In addition, there is an area of 30 ha in the centre of the farm that, in the 1970s, was converted from arable land to a network of woodland, lakes, wetlands and high-diversity meadows on which cattle are grazed intermittently. Jubilee Farm is a c. 70 ha livestock farm consisting of improved grassland grazed by sheep with hedgerows, hedgerow trees and a small copse. Jubilee farm is bordered on all sides by Hillesden arable land. Surrounding these two farms, the landscape consists of arable (51%), improved grassland (31%), woody vegetation (8%) and urban (2%).

3.8.1.2 Sampling procedure

Sampling took place on alternate weeks with 2 – 4 sample nights per week between May 16th and September 1st, 2017, with a total of 22 trapping nights. Moths were sampled using custom-built traps with 30 ultra-violet LEDs powered by a 12v battery (prototype v.1.1, see section 3.3.1). On sample nights, one trap was put out at each site and was set to turn on automatically at sunset and turn off at sunrise. Traps were placed on the top of a wooden post so that the trap was 1 m from the ground. Thirty-one sites were chosen across the two farms at roughly equal spacing (Fig. 3.13), to include several replicates of the main habitat types. Trap sites were at least 100m from other traps but were generally over 200m from each other. Most of the trap sites (n = 26) were placed at 1 m from a standard hedge (2-4m tall and 2-4m wide, consisting mainly of blackthorn and hawthorn). A land-use map was adapted from Redhead et al. (2014) to match the AES schemes coverage as it was in 2017. Buffers were drawn around each site in using ArcMap version 10.4 at radii of 25, 50, 100, 200 and 400 m, and the proportion land-use, including species AES scheme, was extracted and tabulated.

A maximum of 16 sites was sampled per night. The area was divided into two sections; a north-west section (15 sites) and a south-east section (16 sites). On one night, either the NW or the SE section was sampled. At sunrise, traps were collected from their sample sites, and the bucket was sealed with a lid. All traps were taken back to a central location where the moths were identified and counted. Micro-moths and difficult macro-moth species were preserved for dissection later. All moths were identified using Waring and Townsend (2017) and Sterling and Parsons (2012). The larval feeding guild of each species was recorded: (1) grass feeders, (2) forb feeders and (3) woody feeders (including both broadleaved and coniferous woody plants) and (4) other (e.g., polyphagous species and lichen/moss feeders). This categorisation was used because it was expected that landscape features (i.e., woody vegetation and AES land) would affect species differently depending on their larval hostplants.



Data provided by the Centre for Ecology and Hydrology (Redhead et al. 2014)

Fig. 3.13. Hillesden Farm and surrounding area*. Showing habitat types, including AES vegetation, and moth-trap sites with 50 m radius buffers.*

3.8.1.3 Analysis

Abundance

Abundance was measured as the number of moths caught per trap per night. Four response variables were used: (1) total abundance (all species), (2) abundance of grass feeders, (3) abundance of forb feeders, and (4) abundance of woody feeders. Generalised Linear Mixed Models (GAMMs) were used as it was expected there would be non-linear spatial effects. The gam() function in the mgcv package was used (Wood, 2017). In each of the four models, abundance was modelled as a (parametric) function of the percentage AES vegetation within a certain radius (selection of radii will be explained) plus the percentage woody vegetation within a certain radius plus a two-level factor for hedgerow (yes/no). To account for spatial non-independence of the sites, a smooth tensor of latitude and longitude was included in the model. Finally, random intercepts (using the bs = “re” argument) were included for ‘site’ and for ‘night’ to account for temporal non-independence and repeated measures at the same site. A negative binomial error structure was assumed. To select the best spatial scale, the AICc of the model for each of the 25 possible combinations of 25, 50, 100, 200 and 400 m for both landscape variables (percentage AES and percentage woody) were calculated. The model with the spatial scale that produced the lowest AICc was selected for analysis. Wald tests, accessed via the summary() function within mgcv, were used to determine whether parameter coefficients differed significantly from zero. Parameters were considered statistically significant if $p > 0.05$.

Diversity

Due to a high frequency of very low counts, species diversity could not be measured on a nightly basis. For example, a catch of two individuals from two species cannot produce a meaningful diversity score. Instead, one species richness score and one diversity score was calculated for each site. A species-by-site matrix was produced with 31 rows (one for each site) and one column for each species. Cells were populated with the total number of each species caught in each trap across the entire season. Using the iNEXT package (Hsieh et al., 2016), species richness and diversity were estimated using rarefaction. Diversity, in this case, is based on the Shannon diversity index, but is expressed as ‘effective common species’ – see section 4.6.3.2 and Chao et al. (2014). Two of the sites were only run during the second half of the season. These were excluded from the models as they would have artificially low richness/diversity scores as they were not running during the flight periods of early-flying species. Two Linear Models (LMs) were run: one with species richness as the response variable and one with diversity. Normal error distributions were assumed. Wald tests were used to determine whether parameter coefficients differed significantly from zero. Parameters were considered statistically significant if $p > 0.05$.

3.8.2 Results

Abundance

The percentage of AES habitat with a 25 m radius of the trap site had a significant positive effect on forb feeder abundance ($p = 0.007$, Fig. 3.14 b), but AES did not affect overall abundance or the abundance of grass and woody feeders (Table 3.1). The percentage of woody vegetation surrounding the traps had significant positive effects on total abundance ($p = 0.0006$, Fig. 3.14 a) and the abundance of forb feeders ($p = 0.0002$) and woody feeders ($p = 0.0004$). The presence of a hedgerow had a significant positive effect on total abundance ($p = 0.04$) and forb feeder abundance (0.007).

Table 3.1. Model output: the effect of AES and two landscape variables on moth abundance. *Model coefficients from four GAMMs, showing only parametric terms. Significant terms ($p < 0.05$) are highlighted in bold ($p < 0.05$ '*', < 0.01 '**', < 0.001 '***').*

Response variable	Parameter	Estimate	Std. Error	z-value	p-value
Total abundance	**Woody (25 m)**	**0.0131**	**0.0039**	**3.412**	**0.0006*** **
	AES (25 m)	0.0032	0.0025	1.302	0.1928
	Hedgerow	**0.3208**	**0.1547**	**2.074**	**0.0381* **
Grass feeder abundance	Woody (25 m)	-0.0336	0.0381	-0.882	0.3780
	AES (200 m)	0.0594	0.0355	1.675	0.0940
	Hedgerow	0.1037	0.1914	0.542	0.5880
Forb feeder abundance	**Woody (100 m)**	**0.0271**	**0.0073**	**3.717**	**0.0002*** **
	AES (25 m)	**0.0087**	**0.0032**	**2.719**	**0.0066** **
	Hedgerow	**0.5466**	**0.2019**	**2.708**	**0.0068** **
Woody feeder abundance	**Woody (25 m)**	**0.0233**	**0.0066**	**3.511**	**0.0004*** **
	AES (25 m)	-0.0122	0.0112	-1.093	0.2742
	Hedgerow	0.6295	0.3250	1.937	0.0528

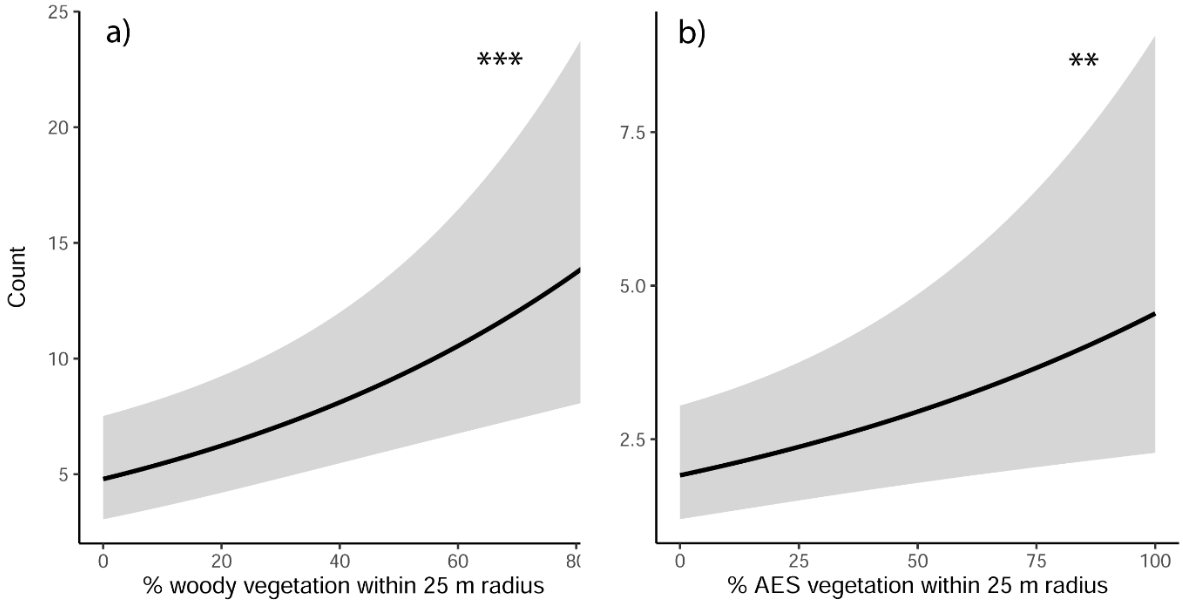


Fig. 3.14. Effect of AES and woody vegetation on moth abundance. *Estimated number of moths caught per site per night, showing (a) total abundance as a function of the percentage woody vegetation within a 25 m radius and (b) abundance of forb feeders as a function of the percentage AES vegetation within a 25 m radius. Plots shows model estimated means when other explanatory variables are held at their mean, with no hedgerow. Grey ribbons show 95% CIs (for fixed effects only). Note the differing scales on the y-axis. Asterisks denote the significance of the effect (p < 0.05 '*', < 0.01 '**', < 0.001 '***').*

Diversity

The percentage of AES habitat within a 400 m radius had a significant positive effect on diversity (p = 0.016, Fig. 3.15). No other significant effects were found for either diversity or species richness (Table 3.2).

Table 3.2. Model output: the effect of AES and two landscape variables on species richness and diversity*. Model coefficients are from two LMs. Significant terms (p < 0.05) are highlighted in bold.*

Response variable	Parameter	Estimate	Std. Error	t-value	p-value
Estimated species richness	Woody (50 m)	0.4704	0.4479	1.050	0.3037
	AES (400 m)	1.3682	0.7982	1.714	0.0989
	Hedgerow	7.9341	14.683	0.540	0.5937
Estimated diversity ('effective common species')	Woody (50 m)	0.3440	0.1920	1.791	0.0854
	AES (400 m)	**0.8862**	**0.3422**	**2.590**	**0.0158***
	Hedgerow	5.7314	6.2940	0.911	0.3712

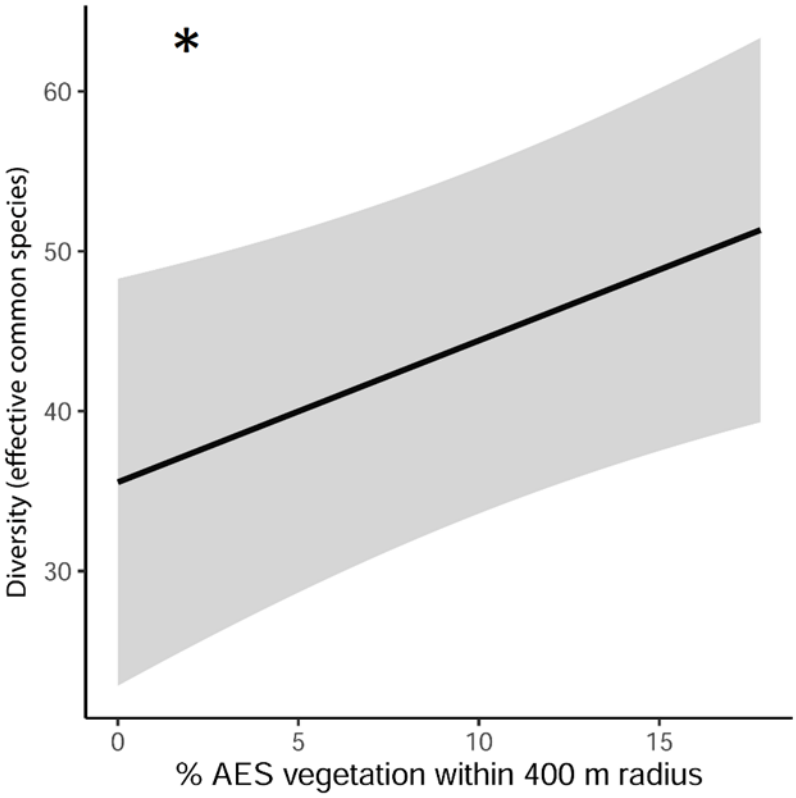


Fig. 3.15. The effect of AES on species diversity. *Estimated species diversity (expressed as 'effective common species) of moths caught across the entire sampling season, as a function of the percentage AES vegetation within a 400 m radius. Grey ribbon shows 95% CIs. The effect is statistically significant (p = 0.016).*

3.9 Pilot study: Discussion

The effect of AES vegetation on moth abundance was small in comparison to that of woody vegetation. However, AES proved effective at enhancing the abundance of moths that feed on forbs. An increase in AES vegetation at the 25 m radius scale from 0% to 100% resulted in a 2.4-fold increase in forb feeder abundance (Fig. 3.14 b). As most of the AES types at Hillesden farm were rich in forbs (Fig. 3.13), the forb feeders likely benefitted from the provision of larval hostplants. Other feeding guilds may have benefitted from the provision of nectar as an adult food source (Merckx et al., 2012b), but the data did not support this. AES vegetation also had a significant effect on species diversity, whereas neither woody vegetation nor the presence of a hedgerow achieved this. An increase in AES vegetation at the 400 m scale from 0% to 18% resulted in a 1.4-fold increase in species diversity (Fig. 3.15). This pilot study shows that AES schemes are effective at enhancing the abundance of specific feeding guilds of moths as well as species diversity at the farm scale. These findings are in line with similar studies that showed increased moth abundance and diversity in AES field margins compared to controls (Alison et al., 2016, Fuentes-Montemayor et al., 2011).

In line with (Heard et al., 2012), AES was not found to increase the total abundance of moths: it was only when the subset of forb feeders was investigated that an effect was revealed. The reasons for the lack of effect found by Heard et al. may include the coarseness of the response variable measured (i.e., total abundance/diversity of macro/micro moths) or the sampling method. In their experiment, 125W MV Robinson traps were used – which are known to be more attractive than more commonly used traps such as 6/15 W Heath Actinic traps (Bates et al., 2013). Thus, it may be that the traps were sampling too large an area and losing the spatial resolution needed to pick up an effect.

The purpose of this pilot study was to gain experience in the fieldwork required for Chapter 4 of this thesis. The pilot brought to light several issues and design flaws that will be improved upon in the next experiment. Each of these issues is discussed below. Plans for design improvement are discussed.

3.9.1 Non-standardisation of AES schemes

AES vegetation was classified as one vegetation type in this analysis, but in reality, it consisted of seven. These were: tussocky grass margin (EE3), ELS bird food (EF2), HLS bird food (HF12), ELS pollen and nectar margin (EF4), pollen and nectar margin (HE10), resource protection buffer (EJ9) and wildflower margin (EF1). The diversity of AES field margin types did not allow for statistical analysis of the different types due to low sample size. Moths will likely react differently to different treatment types: for example, forb feeders are unlikely to benefit from tussocky grass margins. In the next experiment, a small number of standardised treatments will be used.

3.9.2 Spatial non-independence

There was a problem with clustering of treatment types which made it difficult to separate the effect of treatment from the effect of location. For example, the map in Fig. 3.13 shows that most AES vegetation is in the north-west and south-east of the farm, with most of the non-AES sites in the middle. These means that nuisance variables such as wind direction or land-use history can potentially affect one are more than others, creating a false treatment effect. In the next experiment, a blocked design will be used so that each location contains an entire replicate of treatment types.

3.9.3 Small sample size

The sample size of moths caught per trap per night was very small (geometric mean average of 6.4 per night), making the statistical analyses weak. For example, the difference between the minimum and maximum predicted forb feeding abundance was less than three moths (Fig. 3.14 b). In a highly stochastic system, an effect size of three moths is easily lost in the noise. In the next experiment, kill-traps were used instead of live-traps as this was expected to, at minimum, double the sample size (see section 3.4.3).

3.9.4 Unequal experimental design

Of the 31 sites sampled, 26 were adjacent to a hedgerow and five were not. In the analysis, it transpired that hedgerows were an important determining factor (Table 3.1), but the small sample size of non-hedgerow sites weakened the analysis. In the next experiment, sites were spread more equally between hedgerow and non-hedgerow sites.

3.10 Pilot study: Conclusions

This small pilot study provides evidence that AES field margins enhance species diversity and enhance the abundance of forb feeding moths. The data suggest the provision of larval hostplants rather than other factors, such as nectar sources, is responsible for this effect. An experimental design whereby nectar resources and hostplant resources are decoupled (as far as that is possible) will be needed to disentangle the two effects. Hedgerows and other woody vegetation had a stronger overall effect than AES vegetation, and this will have to be accounted for in the following experiment through a blocked design and an equal weighting of hedgerow and non-hedgerow sites.

Chapter 4

The effect of florally-enhanced field margin strips on moth abundance and diversity

Chapter 4. The effect of florally enhanced field margin strips on moth abundance and diversity

4.1 Abstract

Moth populations are known to have declined across large areas of north-western Europe since the mid-20th century. It is believed that the intensification of agriculture that occurred over this time period is at least partly responsible for these declines. Agri-environment schemes (AES) are widely implemented across Europe as a means of protecting biodiversity in agricultural landscapes. Sown field margins are a popular AES option and the benefit of these schemes to numerous insect taxa has been widely demonstrated. However, the efficacy of AES field margins as a conservation tool for moths remains largely unstudied. Here, the relative importance of two field margin features are investigated: the provision of larval hostplants and the provision of nectar for adult moths. Three treatments were compared: (1) a plain grass mix, (2) a grass mix enhanced with two species of moth-pollinated flowers, and (3) a grass and wildflower mix. Depending on year and sampling method used, the difference in total abundance between the plain grass treatment and wildflower treatment ranged from no effect to 1.4 times higher in wildflower treatment. Difference in species Shannon diversity ranged from no effect to 3.3 times higher in the wildflower treatment. Traits-based analysis showed that the increased abundance was due primarily to the provision of larval hostplants: species that specialise on forbs sown in the wildflower margins were between 3.1 and 24.7 more abundant in the wildflower treatment than in the grass treatment, while there was no difference in the abundance of species that specialise on woody plants and a mainly negative effect of floral resources on species that specialise on grasses. The effect of nectar provision was inconsistent and the difference in the abundance and diversity of moths between the plain grass and nectar-enhanced treatments varied according to species traits and sampling method. Results suggest that the diversity of moths was enhanced in wildflower margins compared to the other two treatments, but abundance was only moderately enhanced. It is concluded that larval hostplants were the key driver of moth abundance and diversity in this experiment, with nectar resources playing only a small secondary role.

4.2 Introduction

Agricultural intensification is a major driver of biodiversity loss in western Europe (Donald et al., 2001, Robinson and Sutherland, 2002) and has been linked to the declines of numerous insect taxa including Lepidoptera (Habel et al., 2019b, Habel et al., 2019c, Maes and Van Dyck, 2001). Agri-environment schemes (AES) are widely implemented across Europe with the aim of conserving biodiversity and enhancing ecosystem services (Batáry et al., 2015, Kleijn et al., 2006). Field margin schemes are a popular AES option and have been widely adopted, mainly in central and northern Europe and especially in the UK and Switzerland (Haaland et al., 2011). These schemes typically apply to arable land and require that farmers remove the edges of their fields from production and sow them instead with grasses and/or forbs (DEFRA, 2019). The benefits of AES field margins include the enhancement of farmland biodiversity (Marshall et al., 2006, Vickery et al., 2002), the prevention of soil erosion and the protection of watercourses from agricultural runoff (Marshall and Moonen, 2002). Field margins are also important within the agricultural matrix functioning as dispersal corridors linking fragmented habitat patches (Delattre et al., 2013, Threadgill et al., 2020).

There is a large literature documenting the effect of field margins on agriculturally important insects such as pollinating insects (Carvell et al., 2007, Pywell et al., 2007) and predators of pests (Pfiffner and Wyss, 2004). A review by Haaland et al. (2011) found that wildflower strips are an effective conservation measure for many insect taxa in arable land and that these strips are generally an improvement upon plain grass margins. Many studies have shown that butterfly density and diversity is enhanced with the creation of field margins and in some cases is richer than in nearby meadow habitat (Haaland and Bersier, 2011). Despite the large declines in moths documented across Europe, the conservation potential of field margins for this group remains unclear. The effect of AES field margins on moth abundance and diversity has been investigated in several studies (Alison et al., 2016, Fuentes-Montemayor et al., 2011, Merckx et al., 2012b), with generally positive but often unclear results. In some cases, moth species richness, but not abundance, is enhanced in wildflower plots compared to plain grass controls (Alanen et al., 2011, Korpela et al., 2013). With the exception of Alanen et al. (2011) and Korpela et al. (2013), neither of which included nocturnal moths, previous studies on the effect of field margin types on moths have compared field boundaries with and without AES margins, but have not compared different types of treatments within field margins.

Specifically, the relative importance of plants as larval food sources and as sources of nectar for adults remains largely unknown in this context. Furthermore, previous studies have typically focussed on macro-moths or diurnal moths only, with the more species-rich micro-moths largely ignored.

It is known that in several Lepidopteran species, fecundity can be increased with the provision of sugar sources (Mevi-Schütz and Erhardt, 2005, Song et al., 2007) and some species will preferentially oviposit on plants that are in flower (Janz et al., 2005, Liu et al., 2010), are producing more nectar (Adjei-Maafo and Wilson, 1983) or are in more nectar-rich areas (Janz, 2005). It follows that it may be possible to enhance the value of field margin habitats for moths through the provision of nectar resources. To test this hypothesis, field margin plots with three seed mixes were sown: grass only, grass plus two moth-pollinated flowers (with nectar provision but low larval hostplant value) and grass plus a diverse mix of wildflowers (of both nectar and hostplant value). Two sampling strategies were used: light-traps and nocturnal transects, which allowed for the observation of individual behaviours (i.e. nectaring, mating, ovipositing). It was hypothesised that the provision of nectar in the grass mixes would enhance the attractiveness and reproductive value of the field margins to moths resulting in a higher local abundance and a higher density of larvae (due to preferential oviposition in more nectar-rich areas). By dividing moths into their feeding guilds, the two effects of larval hostplant and adult nectar source can be separated. Hence, the following hypotheses were tested; (1) the abundance of grass feeding moths, both in adult and larval form, will be higher in grass margins enhanced with nectar resources than in plain grass margins, (2) the occurrence of reproductive behaviours (mating and ovipositing) will be more frequent in margins containing nectar resources, (3) the abundance of adult moths will be higher in margins with nectar resources, and (4) the diversity of moths will be higher in wildflower margins.

4.3 Methods

4.3.1 Experimental setup

A randomised block experiment was set up on Rothamsted Farm, UK (51.80773, -0.37611) in April 2017. Fifteen field margin blocks measuring 210 x 3 m were sown at the edges of arable fields. The locations of the blocks were chosen so that the surrounding landscape features were as constant as possible along the length of the entire block. Each block was split into 3 plots of 70 x 3 m resulting in a total of 45 plots across the whole experiment. One of three seed mixes (treatments) was sown into each plot within each block in a randomised order (3.13) such that each of the 15 blocks contained a full replicate of the three treatments. All blocks bordered an arable field in which was grown either wheat, barley or oilseed rape. Twenty-one of the plots also bordered a woody boundary feature such as a hedge (n = 12), a dense stand of trees (n = 8) or the edge of a block of woodland (n = 1). The other 24 plots were bordered by a strip of grassy vegetation of varying width and species composition. The three treatments were as follows: (1) 'grass' (GR) contained four species of non-competitive grasses (*Agrostis capillaris*, *Cynosurus cristatus*, *Festuca rubra* and *Phleum bertolonii*), (2) 'bladder campion' (BC) contained the same four grass species plus two moth-pollinated plants: *Silene vulgaris* (bladder campion) and *Silene noctiflora* (night-flowering catchfly), and (3) 'wildflower' (WF) contained the same four grasses plus 13 species of perennial wildflower widely used in agri-environment scheme margins. See Fig. S4.1, Table S4.1 and Text S4. 1 for details on how the field margins were prepared and the species composition of the three mixes.

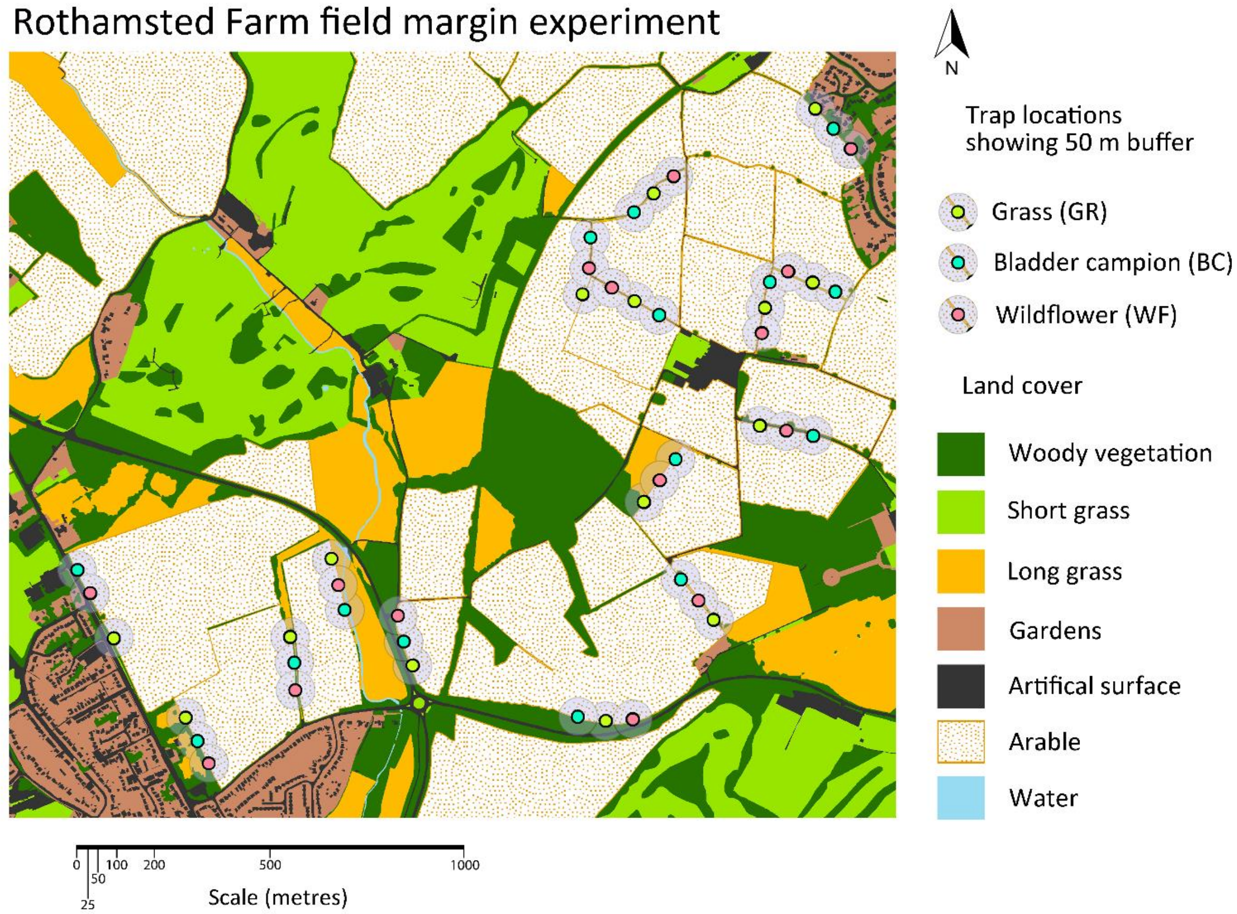


Fig. 4.1. Map of Rothamsted Farm, UK, showing the layout of the experimental field margins. *Each coloured point is at the centre of one treatment plot at which a moth-trap was placed. The plots are arranged into blocks of one of the three treatment types each. Scale shows 25, 50, 100 and 200 m as these radii were used in quantifying habitat surrounding trap sites. Map produced in ArcMap version 10.4.*

4.3.2 Sampling procedure

Sampling of adult moths ran over two field seasons: June – September 2018 and 2019. Additional sampling of larvae also took place in May 2018. Sampling of adult moths consisted of two techniques: trapping and transects. These two techniques are described separately.

4.3.2.1 Trapping

Moth trapping took place over eight alternate weeks starting in early June and ending in mid-September. This took place in 2018 and 2019 resulting in a total of 16 sample weeks. In each sample week, moths were trapped on four consecutive nights. Each night from Monday -

Wednesday, four blocks (i.e., 12 plots) were sampled. On the Thursday night the final three blocks were sampled, meaning that one full replicate of the experiment occurred each week. Nights in which strong winds or heavy rain was predicted were postponed to the following night. UV LED traps (section 3.3.1) were placed on platforms 1 m above the ground in the centre of each plot. Lethal-traps (prototype v1.3) were used in all but the first two weeks of 2018 where live-traps (prototype v1.1) were used. Traps were set automatically to switch on at sunset and off at sunrise. Over the course of the experiment there were six trap failures and these were entered as missing values. In one case, the trap failure occurred at the same plot two weeks running, so the whole sample night was repeated. Data from both sample nights were included in the dataset. In mid-July 2018, one of field margin blocks was burnt off in a fire. This margin was excluded from sampling for the rest of the year but regenerated well enough to be fully sampled in 2019.

4.3.2.2 Transects

Transects took place over six alternate weeks starting in mid-June and ending in early September. Transect weeks alternated with trap weeks so that in any given week only one sampling method was used. This took place in 2018 and 2019 resulting in a total of 12 sample weeks for transects. In each week, transects were carried out on four consecutive nights in the same sampling structure as above. Each night from Monday - Wednesday, four blocks (i.e., 12 plots) were sampled. On the Thursday night the final three blocks were sampled, meaning that one full replicate of the experiment occurred each week. Nights in which strong winds or heavy rain was predicted were postponed to the following night. The transects were carried out as follows. Two observers were each equipped with head torches (Black Diamond, Cosmo), butterfly nets and a bag of plastic sample pots and two empty bags. One observer also carried a notebook and a digital temperature meter (Preciva, part number HT154001). Head torches were used in their white light setting at the default level brightness. Although using red light mode would be less disruptive to moth behaviour, experience showed that this was impractical due to low visibility. We found that, despite the possibility of moths being attracted to the head torches, moths found engaging in behaviour such as nectaring or mating did not show any obvious signs of disturbance when illuminated and carried on engaging in these behaviours. Transects began each evening at 15 minutes after sunset. The observers began the transect at one end of the margin block, noting the time, the temperature (°C), percentage cloud cover and wind (calm, breezy or windy). The direction in which the block was sampled was alternated weekly. One observer was 1 m in from the crop edge, in the sown vegetation, the other observer was on the edge between the sown strip and the incidentally occurring vegetation on the side further from the crop. The observers walked at a very slow pace (35 m per minute) and scanned an area 1.5 m either side and in front of them, excluding anything 0.5 m above head height in a manner similar to a Pollard walk (Pollard and Yates, 1993). The surveyed area thus included the 3 m width of the sown strip, plus 0.5 m into the crop and 1.5 m into the incidentally growing vegetation on the side further from the crop.

When a moth (adult or larva) was encountered within the 1.5 m sample space, the individual was caught and placed in a sample pot. At this point, both observers would stop walking and the observer without the moth would turn off their head torch and cease to search for moths. If the moth could be identified in-field, its identity was recorded and the sample pot was placed into bag no. 1, if it could not be identified, or if it was a larva, a code was written both in the notebook and on the sample pot and it was put in bag no. 2. Any behaviours that were witnessed (nectaring, mating, ovipositing or emerging from pupa) were recorded. Moths found mating or ovipositing were recorded but not collected. At the half-way point of the transect, the number of flowers were counted within a 5 m stretch of the sown strip and 1.5 m either side. Where flowers were very abundant, their number was estimated to the nearest 10 or 100 as appropriate. A single flower was defined as a visually distinct unit; for example, an umbel inflorescence was considered as one flower. At the end of a block, all moths in bag no. 1 were released but moths in bag no. 2 were kept and the pots containing adults were put in a refrigerator overnight to be identified in the morning. Larvae were reared to adulthood indoors at ambient temperature and provided with the hostplant that they were found on.

On nights where moth abundance was low, the entire length of each 70 m of each plot was sampled. Where moth abundance was moderate to high, the plots were subsampled by only sampling the first 35 m of each plot. On several occasions in July and August 2019, the abundance was so high that subsampling of 17.5 m sections was required so that all plots could be sampled within the night. The discrepancies in distance covered was later accounted for statistically by using an offset so the response became moths per unit distance surveyed. Subsampling levels were always applied equally to every plot within a block. A sample night typically took 3 to 4 hours. Over the two field seasons, there was one sample night cancelled due to poor weather and one margin that was removed from sampling in July – September 2018 due to a fire, as described above.

In addition to the transects mentioned above, two full transect weeks were also conducted in May 2018. As there were almost no adult moths recorded in this time, these weeks were excluded from analysis of adult moths. However, many larvae were recorded during these weeks so these data were included in the analysis of larval abundance.

4.3.2.3 Sweep netting for larvae

Larvae were also sampled once in September 2019 using sweep netting during the final transect week. Sweep nets of diameter 400 mm were swept through the vegetation for a 35 m stretch of each plot, with 50 sweeps per plot. As the hostplants could not be determined from sweep net samples in the wildflower treatment, these larvae were identified to as specific a taxonomic group as possible using Sterling and Henwood (2020). Sweep netting was only done at the end of the experiment so as not to damage flowers during the flowering season.

4.3.3 Landscape variables

Around the centre of each plot, buffers of radii 25, 50, 100 and 200 m were drawn using ArcMap (version 10.4). The proportion of two habitat types (1) woody vegetation and (2) long grass habitat were calculated for each buffer size at each plot. These two habitats were chosen as they are known to be the most important determinants of moth abundance and diversity at the farm scale (Woiwod and Gould, 2008). Woody vegetation included hedgerows, woodlands and individual trees. Long grass habitat included rough grassland and any other semi-natural low-growing vegetation (see map, Fig. 4.1). In addition to the continuous variables, a two-level factor variable was also used to describe whether each plot was next to a linear woody boundary feature or not. This was included as moths are known to use linear woody boundary features as dispersion corridors (Coulthard et al., 2016).

4.3.4 Moth identification

All moths were identified to species level where possible and dissected if necessary. Several species groups were aggregated. These were groups that were either too difficult to identify even by dissection, were too numerous to dissect, or both. These eight aggregate groups are only a small proportion of the roughly 400 species recording during the experiment, so is unlikely to affect species diversity indices in a meaningful way. Species aggregates are shown in Table S4.2.

4.3.5 Species traits

Traits regarding larval feeding guild, nectar-affinity and national population trend were recorded for each species encountered. Larval feeding guilds were extracted from Waring and Townsend (2017) and Sterling and Parsons (2012). National populations trends were extracted from the latest trend analyses carried out by (Harrower et al., 2019). Trait descriptions are shown in Table 4.1 and a full list of species encountered with their corresponding traits can be found in Table S4.3.

Table 4.1. Species traits used in the analysis.

Trait	Levels of trait	Notes
Larval feeding guild	Woody feeder	Feeds on deciduous or coniferous trees and/or shrubs
	Grass feeder	Feeds exclusively on grasses
	Unsown forb feeder	Feeds exclusively on forbs but not on those sown in the treatments
	Sown forb feeder	Feeds either exclusively or mainly on forbs sown in the treatments
	Polyphagous	Feeds on both woody and herbaceous plants or feeds on both grasses and forbs
	Non-plant feeder	Feeds on non-plant material such as fungi and bird nests. This category also includes those that feed on lichen and mosses.
Adult nectar feeder	Yes	A species is considered a nectar feeder if it was encountered, in adult form, feeding on nectar at least once during the field experiment
	No	
Declining species	Yes	A species is considered declining if the 95% confidence interval of its population change from 1968 – 2016 does not include zero
	No	

4.3.6 Analysis

All statistical analyses were carried out in R 3.6.2 (R Core Team, 2020). The analyses were split into five different measures of response, with the first four relating to adult moths: (1) abundance, (2) diversity, (3) community composition, (4) behavioural events and (5) larval abundance. For all response measures, the aim was to determine the effect of treatment (seed mix) and the surrounding landscape on the abundance, diversity and community composition of moths and whether the effect of treatment depended on the sample year.

4.3.6.1 Abundance of adult moths

For trap data, abundance was defined as the number of moths caught per trap per night. For transect data, abundance was defined as the number of moths encountered in one 70 m transect per plot per night. Generalized Linear Mixed Effects models (GLMM) with a negative binomial error structure and a log-link function were fitted using the glmer.nb() function in the *lme4* package (Bates et al., 2015). Fixed explanatory variables were Treatment (factor, three levels), a Treatment:Year interaction (factor, six levels), Boundary (whether or not the site was bordered by woody vegetation; factor, two levels), Woody (the area of woody vegetation with a certain radius of the site; continuous, in metres squared) and Long_grass (the area of rough grassland habitat within a certain radius of the site; continuous, in metres squared). The continuous landscape variables were square root transformed and scaled (mean subtracted and divided by standard deviation) to account for them being on different spatial scales. For transect data the GLMMs, included an additional fixed effect, Temp (the air temperature at the start of the transect in each plot; continuous) was included to account for temperature-dependant moth activity within a given night and transect length was included as an offset using the 'offset =' argument within the glmer.nb() function. There were two partially crossed random effects: Night (the night on which the sampling took place) and Block (one of 15 margin blocks). The random effects accounted for the strong night-to-night variation in moth activity due to weather and also accounted for the non-independence of plots within the same Block.

Separate models were specified for each of the eight moth subsets (based on species traits – Table 4.1) and each of the sample methods (traps/transects), resulting in 16 models using abundance as the response variable. Model selection had two stages. (1) The best spatial scale for Long_grass and Woody were chosen by running separate models with all combinations of all spatial scales (25, 50, 100, 200 m) and selecting the model with the lowest AICc. The Boundary effect was also considered as a potential substitute for Woody but was not included in the same model with Woody due to collinearity. Only one of each of the spatial scales of Long_grass and Woody/Boundary were included in any one model. (2) Once the full model with the best spatial scale was selected, the significance of each parameter was tested using a Likelihood Ratio Test (LRT). If the Treatment:Year interaction was found to be non-significant at the p ≥0.05 level then it was removed. As there was no inherent interest in the

Year effect, this was removed as well. As each night of the study was included as a unique random effect, the problem of temporal pseudo-replication was avoided. All other variables were left in the model and reported, even if non-significant, as they are of inherent interest. Model assumptions were checked by plotting standardised residuals against the fitted values and against each explanatory variable to ensure there were no patterns (Zuur et al., 2009). Model fits were also checked using the *DHARMa* package (Hartig, 2019). Where a significant treatment effect was found ($p < 0.05$), pairwise post-hoc tests were carried out using the emmeans() function in the *emmeans* package (Lenth, 2019) to determine which treatments differed from each other.

4.3.6.2 Diversity of adult moths

Species diversity was measured using Hill numbers (Chao et al., 2014). This technique presents a standardised and intuitive way of understanding diversity measures. The Hill numbers are based on the following equation:

$$qD = \left(\sum_{i=1}^{S} p_i^q\right)^{1/(1-q)}$$

Where *D* = the measure of diversity of order *q*, *S* = the number of species in the assemblage and *p* = the proportion that species *i* represents in the assemblage. The Hill number is parameterised by *q* and can take any value, but typically takes the values 0, 1 and 2. Which correspond to the species richness, Shannon diversity and Simpson diversity respectively. Rather than calculating the raw diversity indices, the Hill number equation calculates the *effective* species diversity for $q = 1$ and 2, which makes interpretation more intuitive and makes comparison across studies easier. For example, for an assemblage of 50 species if $_1D$ (effective Shannon diversity) = 10, this means that the diversity of the sample is equal to an assemblage of 10 equally abundant species. As the parameter q increases the Hill number becomes less sensitive to rare species and gives more weight to common species in the assemblage. When $q = 0$, all species are given equal weight as *D* is simply species richness. When $q = 1$, this is known as the ‘effective number of common species’ as more weight is given to common species. When q = 2, this is known as the 'effective number of dominant species' as all but the most common, or dominant, species are disregarded.

The package iNEXT (Hsieh et al., 2016) was used to calculate the asymptotically estimated Hill numbers of orders q = 0, 1 and 2 using a rarefaction and extrapolation technique with individual-based data. This package exploits the mathematical properties of species richness and diversity data where species richness and diversity increase with a larger sample size asymptotically. Although the true species richness of a site is often not known from samples due to unobserved rare species, the rarefaction and extrapolation technique estimates the true number based on the relative abundance of species within the sample and quantifies uncertainty in the estimate through bootstrapping.

For both methods (traps/transects), all observations were combined for each treatment-year combination to give six assemblages for comparison per method. Nights in which a trap failure occurred (N = 7) were omitted so that the sample size remained the same across all treatments. Differences in richness/diversity between treatments were considered significant if their 95% confidence intervals did not overlap.

4.3.6.3 Community composition and species responses of adult moths

To test for the effect of treatment and surrounding landscape variables on the community composition of moths, multivariate generalized linear models (MGLM) with negative binomial error structures were fit using the manyglm() function in the *mvabund* package (Wang et al., 2012). This technique has been shown to outperform traditional distance-based techniques as it takes the mean-variance relationship into account, which allows for greater power to detect patterns when analysing all species simultaneously (Warton et al., 2012). Models were constructed separately for each method (traps/transects) within both years resulting in four models. All moth records were summed across all nights for each plot. Explanatory variables were Boundary, Long_grass at the 200 m radius and Block. The response variables were the total abundance of each moth species. These landscape variables were chosen as they were the spatial scales most often chosen as the best predictors in the abundance models. Block was included as a fixed effect as the manyglm function cannot handle random terms. Model assumptions were checked with in-built diagnostic plots within the *mvabund* package. The significance of the parameters was determined with a likelihood ratio test (LRT) and p-values were estimated using PIT-trap resampling with 999 iterations.

To understand which species were most affected by treatment, the parameter estimates of BC and WF treatments in relation to the baseline GR treatment for each species were investigated. Post-hoc pairwise tests with p-values adjusted for multiple comparisons were not appropriate in this case due to the large number of species being tested. Instead, the model coefficients were extracted from the *manyglm* models along with 95% confidence intervals. Any coefficient for which the 95% CIs did not overlap zero were considered significant. For species with very small sample sizes, it is not realistic to statistically test differences in abundance between treatments, however, as the standard error for such species will be very large, it is unlikely that the 95% will not include zero. Due to the large number of species being tested, there is a high chance of type I error. To account for this, species were only considered to be affected by treatment if the significant effect occurred either in more than one year or by using both sampling methods.

To visualise the differences in community composition, non-metric multidimensional scaling (NMDS) was carried out with the metaMDS() function in the *vegan* package. All moth records within one plot were summed and visualisations were carried out separately for each method within each year. A Bray-Curtis similarity matrix of square root transformed data was used and the number of dimensions used was increased until the stress value fell below 0.2, representing an acceptable fit (Clarke, 1993). Only the first two dimensions were plotted. Convex hulls displayed as polygons were plotted grouping the 45 points by variables of interest: Treatment, Boundary and Block. Note that no statistical inferences were made from these plots, they are purely for visualisation of the data. They operate on different assumptions to MGLM so are not directly comparable.

4.3.6.4 Behavioural events in adult moths

The occurrence of the four behavioural events (emerging from pupa, mating, nectaring and ovipositing) were summed up within each of the 45 plots across the two years. Only events occurring inside the sown strip were considered. GLMMs with negative binomial error structures were constructed for each of the four behaviours, with the total number of events observed per plot as the response variable. The glmer.nb() function in the *lme4* package was used, as before. Fixed effects were chosen in the same manner as for the abundance models. Treatment was always included and the best spatial scale for the Long_grass and Woody/Boundary variables were determined by running models with each of the 20 possible combinations and selecting the model with the lowest AICc. Block was included as a random intercept. The significance of the parameters was determined using LRTs as described above. All parameters were left in the final model even if not significant at the $p < 0.05$ level. Model assumptions were checked and post-hoc tests carried out as described above in 3.3.6.1.

To determine the relative visitation rates of flowers/fruits as a nectar/sugar source, all observations of nectaring events were summed up for each plant species across the entire experiment, including observations that occurred outside of the sown strips. A proxy for the total number of flowers observed was calculated by summing up all the flower/fruit units for each plant species counted in the central 5 m strips (see section 4.3.2.2) across the entire experiment. An index of relative visitation rate for each plant species was estimated by dividing the total number of visits by the total number of flowers/fruits counted, multiplied by 1000.

4.3.6.5 Larval abundance

All larval counts were summed up for each of the 45 plots across the two years. Only larvae found within the sown strips were considered. This was done separately for the two methods of counting larvae: transects and sweep-netting. For each method, a GLMM with a negative binomial error structure was constructed with the same modelling procedure as described in section 4.3.6.1.

4.4 Results

4.4.1 Abundance

4.4.1.1 Traps

A total of 14,769 individuals belonging to 371 taxa were caught across 711 light-trap samples (Table S4.3). 50% of the taxa and 65% of the individuals caught specialised on either forbs or grasses as larval hostplants (Table 4.2). While the abundance of grass feeders and forb feeders was roughly the same, forb feeders had a higher species richness and accounted for 37% of species caught, while grass feeders accounted for 13%. There was a significant effect of treatment on total moth abundance and on the abundance of most of the larval feeding guilds (apart from woody feeders and grass feeders), as well as on the abundance of moths with adults feeding on nectar and the abundance of declining macro-moth species (Table S4.4). In all cases where treatment effect was significant, post hoc tests revealed that moth abundance was significantly higher in the wildflower (WF) treatment than in the grass (GR) treatment and abundance in the bladder campion (BC) treatment was typically intermediate (Fig. 4.2, Table S4.5). For sown forb feeders, there was a significant treatment:year interaction ($p < 0.001$), showing that the effect of treatment became more pronounced in 2019. Model AICcs showed that the most influential spatial scale of the surrounding landscape varied widely between groups (Table S4.6) but the effect of surrounding landscape was non-significant for most subsets (Table S4.4). The total abundance was higher at sites with a woody boundary feature and the abundance of woody feeders was higher at sites with more woody vegetation at the 50 m radius scale (Table S4.7). The effect of the amount of long grass habitat around the site was not significant for any subset at any spatial scale.

Table 4.2. The number of individual moths and number of taxa caught in traps. *Showing figures for all moths combined, six feeding guilds and the subsets of nectar-feeding species and declining macro-moths.*

Subset	Number of individuals (% of total)	Number of taxa (% of total)
All moths	14,769	371
Larval hostplant type:		
Woody plant feeders	1,134 (7.7%)	122 (33%)
Grass feeders	4,834 (33%)	47 (13%)
Unsown forb feeders	3,711 (25%)	107 (29%)
Sown forb feeders	1,070 (7.2%)	30 (8.4%)
Polyphagous	1,555 (11%)	20 (5.6%)
Non-plant feeders	2,366 (16%)	39 (11%)
Other traits:		
Adult nectar feeders	6,933 (47%)	37 (10.2%)
Declining macro-moth species	1,580 (11%)	44 (12%)

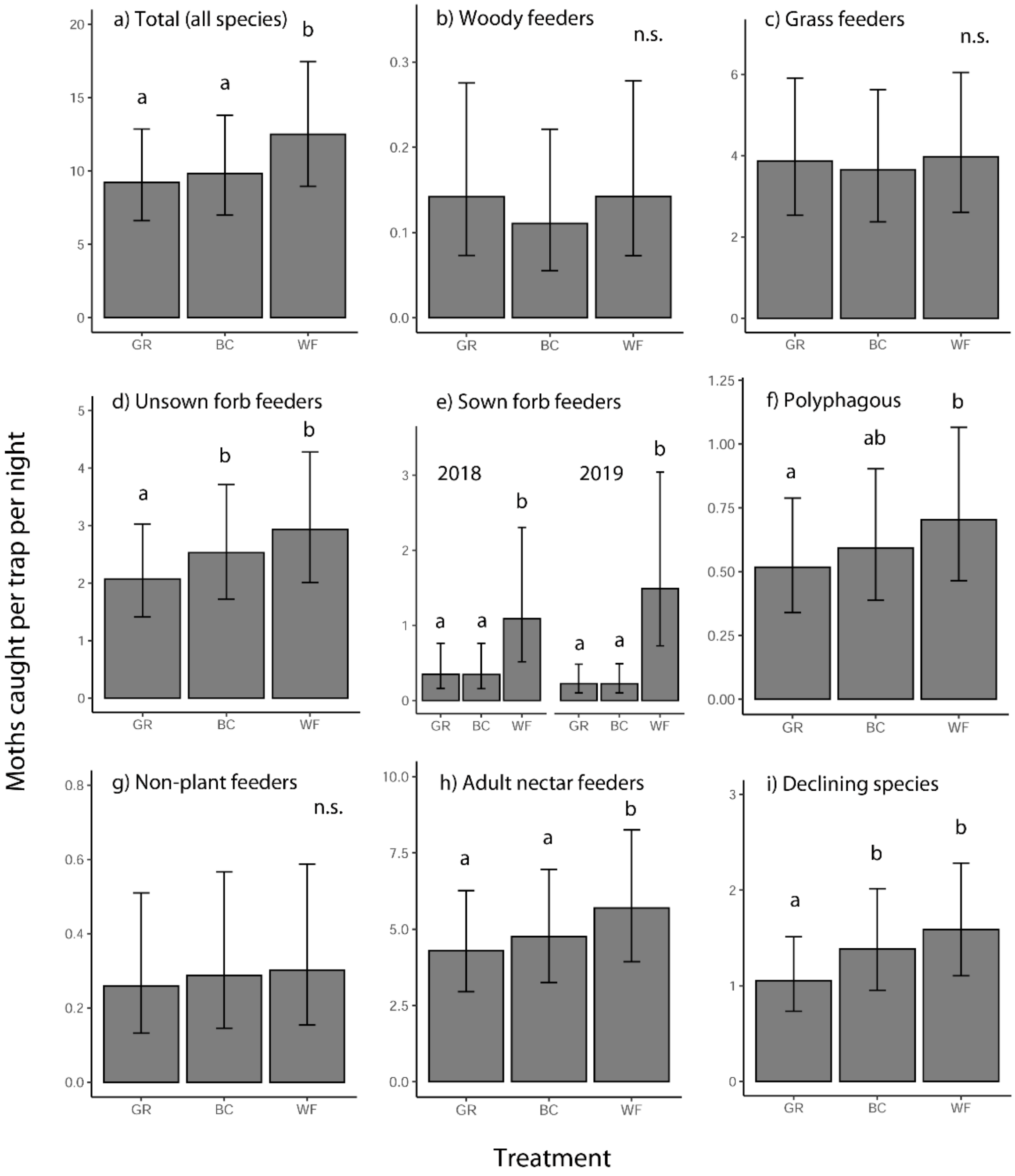


Fig. 4.2. The effect of field margin treatments on moth abundance in traps. *GLMM model predictions (response scale) of the expected number of moths (with 95% CIs) per trap night with surrounding landscape variables set to their minimum with no hedgerow. Showing results for all species (a), for species separate by larval feeding guilds: woody plant feeders (b), grass feeders (c), unsown forb feeders (d), sown forb feeders (e), polyphagous species (f), non-plant feeders (g); for species with adults found feeding on nectar (h) and for declining macro-moth species (i). Where there was a significant treatment:year interaction, the two years are plotted separately. The letters above the bars denote whether the expected counts differed between treatments according to Tukey post-hoc pairwise tests at the p < 0.05 level. No significant effect is denoted by 'ns'. GR = grass only, BC = grass plus moth-pollinated flowers, WF = grass and wildflower mix. Confidence intervals are for fixed effects only. Note that the scale on the y axes differ.*

4.4.1.2 Transects

A total of 5,297 adult moths belonging to 170 taxa were recorded across 516 transects (Table S4.3). 65% of taxa and 86% of individuals recorded specialised on forbs or grasses as larval hostplants (Table 4.3). While the abundance of grass feeders was over twice that of forb feeders, the species richness of forb feeders was 2.7 times as high as that of grass feeders. There was a significant treatment:year interaction for the total abundance of moths and for the abundance of some of the feeding guilds (grass feeders, sown forb feeders and non-plant feeders) as well as for species with adults found feeding on nectar (Table S4.4). In years where treatment effects were significant, post-hoc tests revealed that the effect of treatment depended on feeding guild (Fig. 4.3, Table S4.5). Unsown forb and sown forb feeders were most abundant in the WF treatment and this effect was more pronounced in 2019. Grass feeders were most abundant in GR treatment plots and this was also more pronounced in 2019. The effect of treatment on the abundance of species with adults feeding on nectar was inconsistent between year, being significantly higher in the WF than the GR treatment in 2018 and the opposite trend was found in 2019 (Fig. 4.3 h). Model AICcs showed that the most influential spatial scale of the surrounding landscape varied widely between groups (Table S4.8) and effects of surrounding landscape were mainly non-significant (Table S4.4). The total abundance of moths was significantly lower at sites with a larger amount of long grass within a 200 m radius (Table S4.7). The abundance of woody feeders was significantly higher at sites with a woody boundary. Finally, there was no significant effect of treatment or any other factors on the abundance of declining macro-moth species.

Table 4.3. The number of individual moths and number of taxa encountered during transects. *Showing figures for all moths combined, six feeding guilds and the subsets of nectar-feeding species and declining macro-moths.*

Subset	Number of individuals (% of total)	Number of taxa (% of total)
All moths	5,297	170
Larval hostplant type:		
Woody plant feeders	81 (1.5%)	27 (16%)
Grass feeders	2,857 (55%)	30 (18%)
Unsown forb feeders	725 (14%)	56 (33%)
Sown forb feeders	377 (7.1%)	24 (14%)
Polyphagous	676 (13%)	12 (7.1%)
Non-plant feeders	214 (4.0%)	20 (13.5%)
Other traits:		
Adult nectar feeders	2579 (49%)	31 (19%)
Declining macro-moth species	199 (3.8%)	24 (16%)

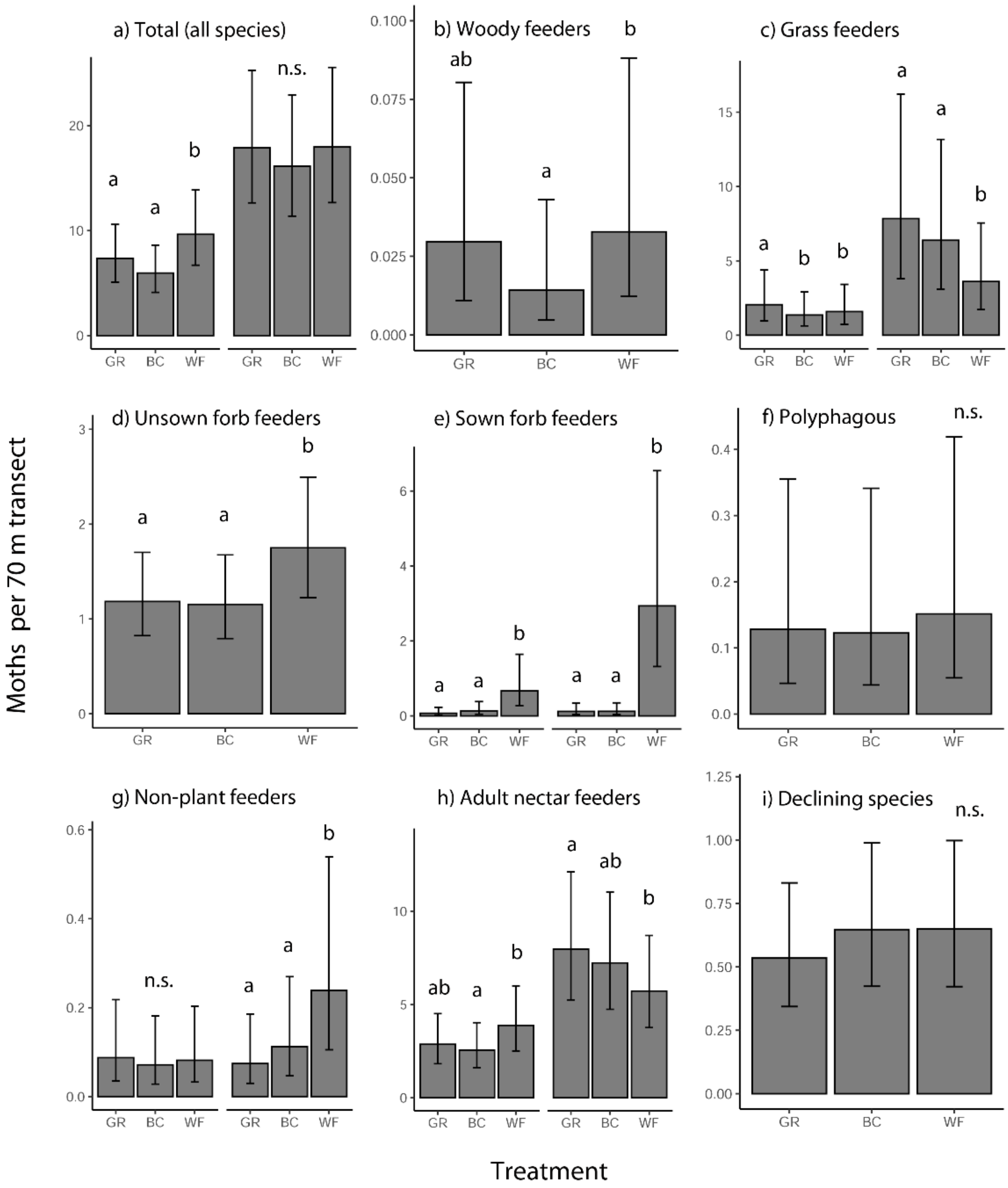


__Fig. 4.3. The effect of field margin treatments on moth abundance in transects.__ Model predictions (response scale) of the expected number of moths (with 95% CIs) for a 70 m transect on a typical night in a typical block with surrounding landscape variables set to their minimum with no hedgerow. Showing results for all species (a), for species separate by larval feeding guilds: woody plant feeders (b), grass feeders (c), unsown forb feeders (d), sown forb feeders (e), polyphagous species (f), non-plant feeders (g); for species with adults found feeding on nectar (h) and for declining macro-moth species (i). Where there was a significant treatment:year interaction, the two years are plotted separately. The letters above the bars denote whether the expected counts differed between treatments according to Tukey post-hoc pairwise tests at the p < 0.05 level. No significant effect is denoted by 'ns'. GR = grass only, BC = grass plus moth-pollinated flowers, WF = grass and wildflower mix. Confidence intervals are for fixed effects only. Note that the scale on the y axes differ.

4.4.2 Diversity

4.4.2.1 Traps

After omitting nights in which a trap failed to operate, there were 219 samples of each treatment. Estimated species richness (Hill number q = 0) did not significantly differ between treatments in either 2018 or 2019 (Fig. 4.4, Table S4.9). The effective number of common species (Hill number q = 1) was significantly higher in the WF compared with the GR treatment in 2018 and compared to both the BC and the GR treatments in 2019. The effective number of dominant species (Hill number q = 2) was significantly different in all three treatments in 2018 with WF highest and GR lowest. In 2019, WF again had the highest diversity but there was no difference between GR and BC.

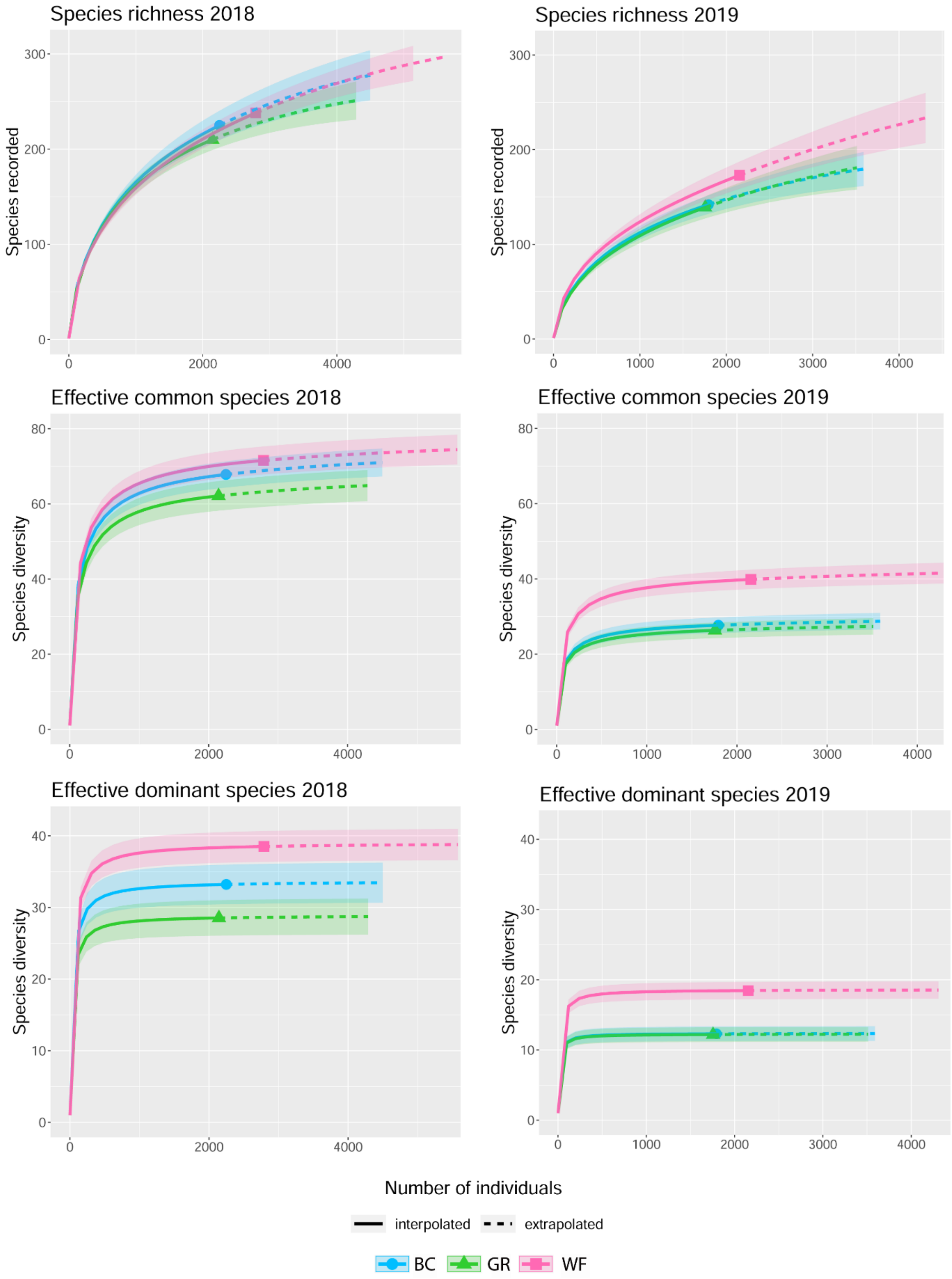


Fig. 4.4. Effect of field margin treatments on species richness and diversity in traps. *Individual-based rarefaction curves for three measures of species diversity in 2018 (a, c, d) and 2019 (b, d, f) of moths captured in traps in three treatment types: GR = grass only (triangle), BC = grass plus moth-pollinated flowers (circle), WF = grass and wildflower mix (square). Species richness (a, b) is equivalent to Hill number q = 0, effective common species (c, d) is equivalent to Hill number q = 1, and effect dominant species (e, f) is equivalent to Hill number q = 2.*

4.4.2.2 Transects

Estimated species richness (Hill number q = 0) did not significantly differ between treatment in 2018 but in 2019 WF had a higher species richness (Fig. 4.5, Table S4.9). The effective number of common species (Hill number q = 1) did not significantly differ between treatments in 2018 but all treatments were different in 2019 with WF highest and GR lowest. The effective number of dominant species (Hill number q = 2) did not differ between the three treatments in 2018, while in 2019 all three treatments were different with WF highest and GR lowest.

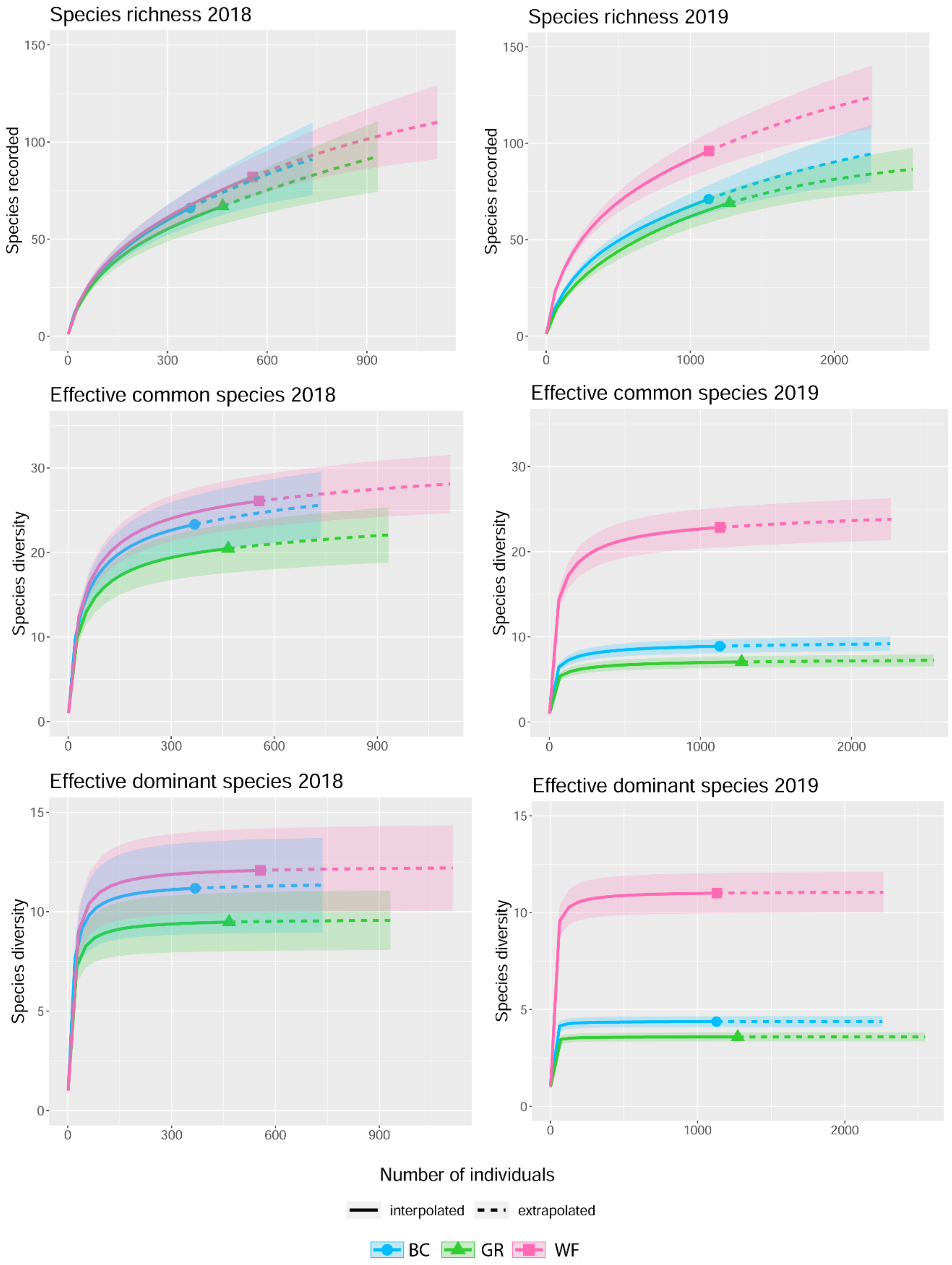


Fig. 4.5. Effect of field margin treatments on species richness and diversity in transects. *Individual-based rarefaction curves for three measures of species diversity in 2018 (a, c, d) and 2019 (b, d, f) of moths recorded in transects in three treatment types: GR = grass only (triangle), BC = grass plus moth-pollinated flowers (circle), WF = grass and wildflower mix (square). Species richness (a, b) is equivalent to Hill number q = 0, effective common species (c, d) is equivalent to Hill number q = 1, and effect dominant species (e, f) is equivalent to Hill number q = 2.*

4.4.3 Community composition

4.4.3.1 Traps

In 2018, the community composition of moths caught in traps was not significantly affected by treatment ($X^2 = 818$, $P = 0.08$), but was significantly affected by block ($X^2 = 5663$, $P < 0.0001$), woody boundary ($X^2 = 278$, $P < 0.0001$) and the amount of long grass habitat within 200 m of the site ($X^2 = 365$, $P = < 0.0001$). In 2019, the community composition of moths caught in traps was significantly affected by treatment ($X^2 = 656$, $P = 0.01$), block ($X^2 = 3742$, $P < 0.0001$), woody boundary feature ($X^2 = 161$, $P < 0.0001$) and the amount of long grass habitat within 200 m of the site ($X^2 = 271$, $P < 0.0001$). Visual inspection of community composition through NMDS supported these findings and suggested that the community composition of a site is strongly influenced by woody boundary and block, but less so by treatment type (Fig. 4.6). Analysis of species-specific responses showed that there were 12 species with significant responses to the BC treatment (8 positive and 4 negative) but none of these responses were consistent. There were 31 species with significant responses to WF treatment (24 positive, 7 negative). Fourteen of these species had consistent responses (Table S4.10).

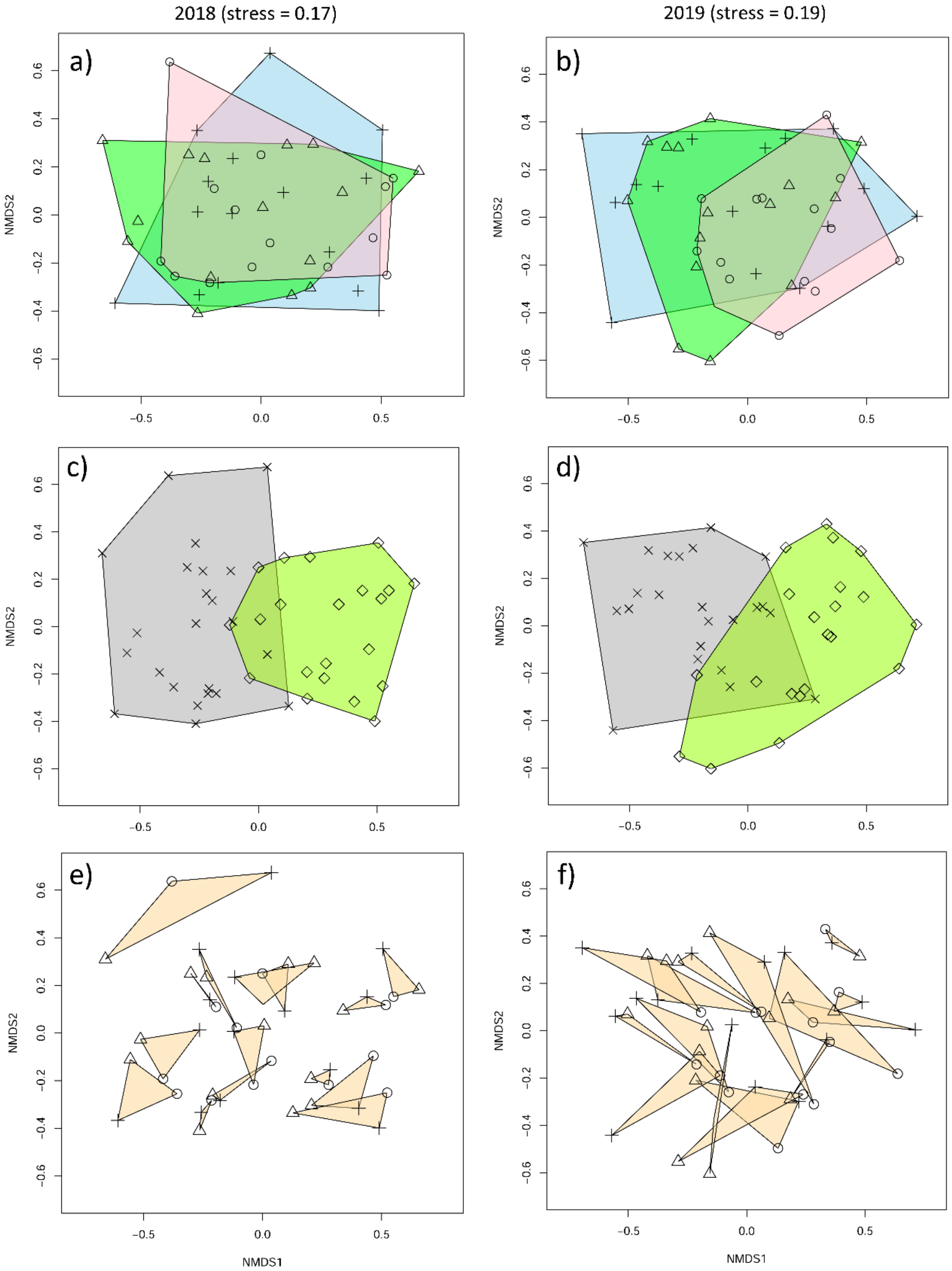


*Fig. 4.6. **Community composition of moths caught in traps, according to field margin treatment, woody boundary feature and location.** NMDS biplots of the community composition of moths caught in traps across 45 sites. Polygons show the convex hulls grouping the sites by; treatment (a, b), woody boundary (c, d) and block (e, f) for 2018 (left) and 2019 (right). In panels a and b, triangles and green polygons = GR (grass only), pluses and blue polygons = BC (bladder campion), circles and pink polygons = WF (wildflower). In panels c and d, diamonds and green polygons = with woody boundary, crosses and grey polygons = without woody boundary. In panels e and f, triangles = GR, pluses = BC, circles = WF. The stress value for each year is shown in parentheses.*

4.4.3.2 Transects

In 2018, the community composition of moths recorded in transects was significantly affected by treatment (X^2= 315.1, P = 0.012), block (X^2= 1573.8, P < 0.0001), woody boundary (X^2= 79.0, P < 0.0001) and the amount of long grass habitat within 200 m of the site (X^2= 95.2, P = 0.002). In 2019, the community composition of moths recorded in transects was significantly affected by treatment (X^2= 493.6, P < 0.0001), block (X^2= 262.8, P < 0.0001), woody boundary (X^2= 1538.9, P < 0.0001) and the amount of long grass habitat within 200 m of the site (X^2= 134.0, P < 0.0001). Visual inspection of community composition through NMDS supported these findings and suggested that the community composition according to treatment became more distinct in 2019 (Fig. 4.7). The points in 2018 are clustered relatively close together, suggesting that variation in community composition between sites was greater in 2019. Analysis of species-specific responses showed that there were 4 species with significant responses to the BC treatment (2 positive and 2 negative) with one species showing a consistent negative response. There were 11 species with significant responses to WF treatment (9 positive and 2 negative) with 8 of these showing a consistent response (Table S4.10).

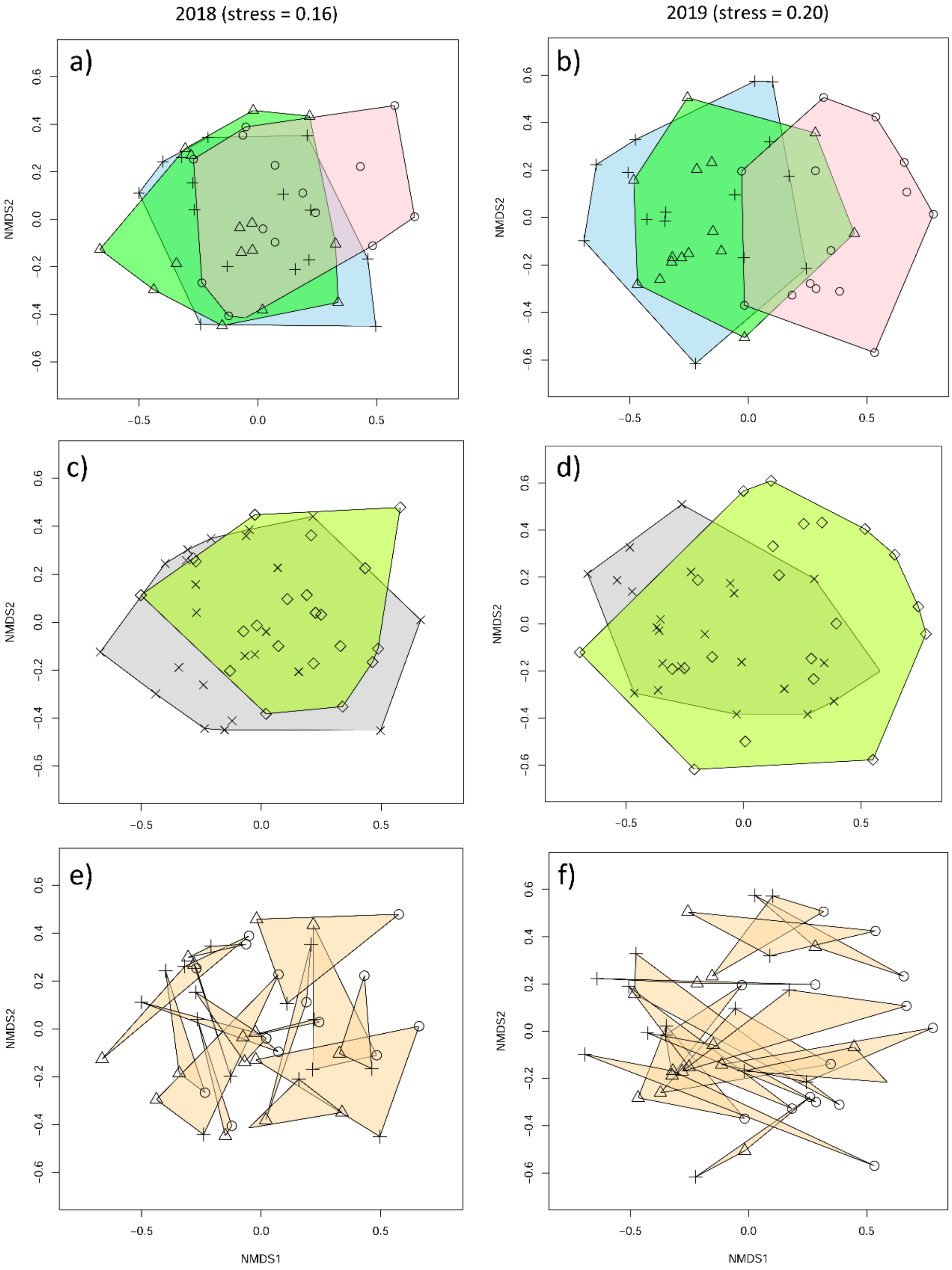


__Fig. 4.7. Community composition of moths encountered in transects, according to field margin treatment, woody boundary feature and location.__ NMDS biplots of the community composition of moths caught in transects across 45 sites. Polygons show the convex hulls grouping the sites by; treatment (a, b), woody boundary (c, d) and block (e, f) for 2018 (left) and 2019 (right). In panels a and b, triangles and green polygons = GR (grass only), pluses and blue polygons = BC (bladder campion), circles and pink polygons = WF (wildflower). In panels c and d, diamonds and green polygons = with woody boundary, crosses and grey polygons = without woody boundary. In panels e and f, triangles = GR, pluses = BC, circles = WF. The stress value for each year is shown in parentheses.

4.4.4 Behavioural events

4.4.4.1 Nectaring

Within the sown margins, a total of 62 nectaring events were observed involving 27 species of moth and 11 species of plants (Table S4.11). There was a significant effect of treatment on the number of nectaring events observed (X^2 = 12.99, p = 0.021) and a significant negative effect of the amount of long grass habitat within 50 m of the site (X^2 = 6.95, p = 0.019, Table S4.4 and Table S4.7). Post-hoc tests showed that there were equivalent numbers of nectaring events in the WF and BC treatments but less in the GR treatment (Fig. 4.8 a, Table S4.5). When including flowers and fruits growing outside of the sown strips, a total of 137 nectar events were observed. The visitation rates of flowers and blackberry fruits is shown in Fig. 4.9. The most frequently visited nectar sources tended to be wild rather than sown with the most frequently visited sugar source being blackberry fruits. Not shown in Fig. 4.9 are 29 nectaring events recorded at traveller's joy (*Clematis vitalba)*. This plant was not present in plots where flowers were counted (see section 4.3.1) so could not be quantified in a standard way. Also not shown is a single visit to cornflower (*Centaurea cyanus)* as this was also not present in the recorded plots.

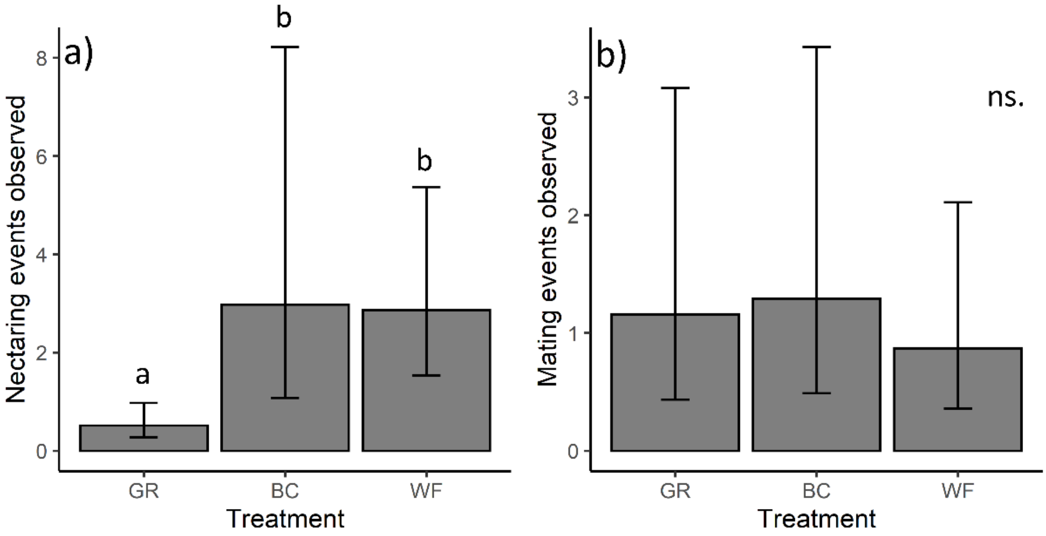


Fig. 4.8. Effect of field margin treatment on nectaring and mating. *Model predictions (response scale) of the total expected number of events for a single site (with 95% CIs) in a typical block with surrounding landscape variables set to their minimum with no hedgerow. Showing results for (a) nectaring events, and (b) mating events. Where there was a significant treatment effect, a post-hoc Tukey test was carried out on pairwise comparisons of treatment levels. The letters above the bars denote whether the expected counts differed between treatments. No significant effect is denoted by 'ns'. GR = grass only, BC = grass plus moth-pollinated flowers, WF = grass and wildflower mix. Confidence intervals are for fixed effects only.*

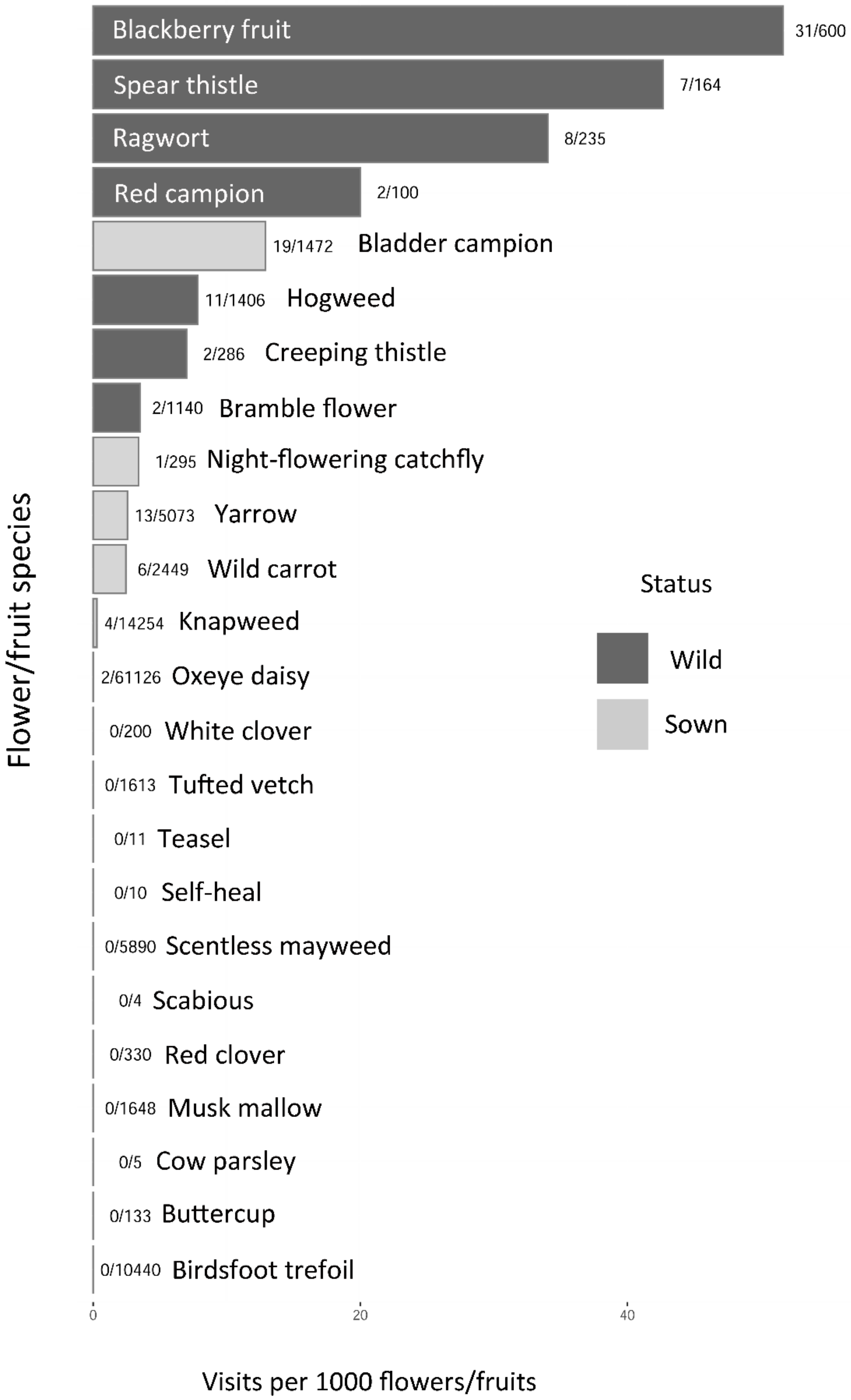


Fig. 4.9. The visitation rates of 23 species of flower plus blackberry fruits by moths over the 2-year survey period. *The rates are presented at the end of each bar as: number of nectaring events recorded / total number of flowers recorded of that species in the 5 x 3 m sampling plots. Not shown are 29 nectaring events at traveller's joy (Clematis vitalba) and one at cornflower (Centaurea cyanus).*

4.4.4.2 Mating and other observations

A total of 36 mating events (i.e. 72 moths) were recorded within the sown strips. 67% of these were *Xestia xanthographa* (Square-spot Rustic). The other species were two pairs of *Korscheltellus lupulina* (Common Swift), two pairs of *Triodia sylvina* (Orange Swift) and one pair each of *Agapeta hamana, A. zoegana*, *Eucosma cana*, *Hepialus humuli* (Ghost Moth), *Mesoligia furunculi* (Cloaked Minor)*, Mythimna impura* (Smoky Wainscot), *Pterophorus pentadactyla* (White Plume) and *Zygaena filipendulae* (Six-spot Burnet). There was no effect of treatment (X^2 = 0.504, P = 0.820) or any other landscape variable on the occurrence of mating events (Table S4.4). Oviposition was observed only twice, both in 2018. *Spilosoma lubricipeda* (White Ermine) was observed ovipositing on oxeye daisy in the WF treatment and *Sideridis rivularis* (The Campion) was observed ovipositing in night-flowering catchfly in the BC treatment. One *Apamea monoglypha* (Dark Arches) was also found freshly emerged from its pupa and expanding its wings in the GR treatment.

4.4.5 Larval abundance

A total of 98 larvae belonging to 11 identified species were recorded during transects in the sown strips. The observation of larvae was highest in May of 2018 where 77 were encountered. In proceeding transects, another 21 larvae were recorded over the entire two field seasons. 83% of larvae found were either known grass feeders or were found feeding on grass. Only 7 larvae were found that are known forb feeders or were found feeding on forbs. Of these, only two larvae (both *Noctua fimbriata,* Broad-bordered Yellow Underwing) were found feeding on a sown wildflower, this being wild carrot in both cases. In the sweep-net samples in September 2019, a total of 41 larvae belonging to at least four species were caught. In the transects, there was a significant effect of treatment on the number of larvae recorded (X^2 = 8.7286, P = 0.026, Fig. 4.10 a), with a post-hoc test showing that the BC treatment had higher larval abundance than the other two treatments (Table S4.5). In the sweep-net samples, there was also a significant effect of treatment (X^2 = 12.21, P = 0.010, Fig. 4.10 b), with a post-hoc tests showing that larval abundance was lower in the WF treatment than in the other two treatments (Table S4.5). Surrounding landscape at any spatial scale did not affect abundance (Table S4.4).

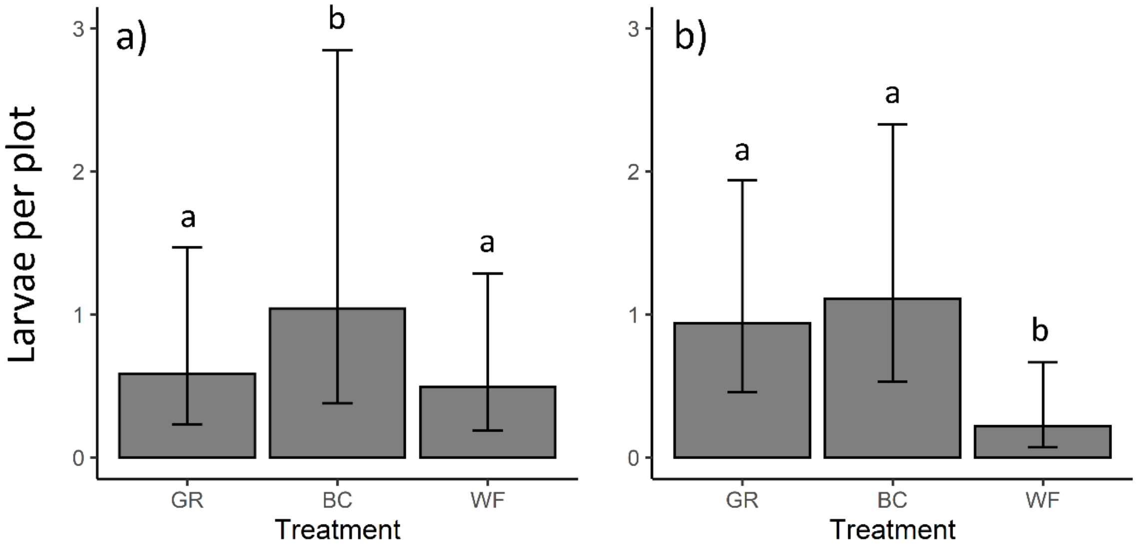


Fig. 4.10. Effect of field margin treatment on larval density. *Model predictions (response scale) of the total expected number of larvae per site (with 95% CIs) in a typical block with surrounding landscape variables set to their minimum with no hedgerow. Showing results for (a) larvae found during transects, and (b) larvae caught in sweep-netting. Where there was a significant treatment effect, a post-hoc Tukey test was carried out on pairwise comparisons of treatment levels. The letters above the bars denote whether the expected counts differed between treatments. GR = grass only, BC = grass plus moth-pollinated flowers, WF = grass and wildflower mix. Confidence intervals are for fixed effects only.*

4.5 Discussion

The diversity of adult moths was greatly enhanced and abundance moderately enhanced in the wildflower treatment (WF) compared to the other two treatments and this was driven primarily by larval hostplant availability. There was no evidence that including a moth-pollinated plant in a grass mix leads to an increased abundance of adult moths but there was weak evidence that larval density may be enhanced. Regarding the original hypotheses tested; (1) Contrary to expectations, the abundance of adult moths of species feeding on grasses as larva was not enhanced by nectar resources but there was weak evidence that grass feeding larvae were more abundant in the nectar-enhanced grass treatment (BC) than in the plain grass margin (GR). (2) The observation of mating events was not affected by treatment and oviposition was observed only twice so could not be analysed. (3) In the trap data, the abundance of adult moths was higher in WF than the other two treatments. The same result was found in the 2018 transect data but no treatment effect on abundance was found in 2019. No positive effect of the BC treatment was found in any guild in either method. (4) The effect of treatment on the diversity of moths was weak in the first year but very strong in the second year with WF showing a greatly enhanced diversity over the other two treatments. The diversity recorded in the BC treatment was also slightly higher compared to the GR treatment.

4.5.1 Effect of nectar resources on abundance

The results of this study suggest that the key determinant of the value of field margin habitat for moths is the provision of larval hostplants rather than the provision of nectar resources for adults. This finding agrees with Alanen et al. (2011) who found that larval hostplant was more important in determining the diversity of diurnal moths than nectar sources. When the moths that had been observed nectaring were analysed separately, the two sampling methods gave conflicting results regarding treatment effect. In the trap data, abundance of nectar feeders was higher in the WF treatment compared to the GR treatment, but abundance in BC was equivalent to both treatments (Fig. 4.2). In the transect data, abundance of nectar feeders in the first year was greater in the WF treatment compared to the BC treatment, but not to the GR treatment (Fig. 4.3). In the second year, abundance of nectar feeders was higher in GR than in WF but this is likely because of the dominance of the grass feeding moth *Chrysoteuchia culmella* which was highly abundant in the second year. There was therefore evidence that the provision of nectar enhanced the abundance of the subset of moths that were observed feeding on nectar, but the inconsistency of this effect across years and methods makes confidence in this finding weak.

These findings are consistent with previous work on butterflies which showed an increase in abundance and diversity in wildflower strips compared to grass or natural regeneration (Aviron et al., 2006, Feber et al., 1996, Pywell et al., 2007). In contrast to the findings in this chapter, several studies have shown that nectar is an important predictor of butterfly abundance (Curtis et al., 2015, Haaland and Bersier, 2011) and in some cases appears more important than the presence of larval hostplants (Clausen et al., 2001, Feber et al., 1996). It may be that moths, as a group, are less reliant on nectar than butterflies. In the field, nectaring events were rare: an average of only three nectaring events per 70 m wildflower block was recorded across the entire two-year experiment (Fig. 4.8). However, the apparent unimportance of nectar could also be due to inappropriate choices of wildflower in the seed mixes, as the large majority of nectaring events witnessed occurred on unsown flowering plants (Fig. 4.9, Table S4.11).

4.5.2 Effect of treatment on community composition

The relative importance of the variables affecting community composition can be seen in the NMDS ordination (Fig. 4.6 and Fig. 4.7). The treatment effect is more evident in transects than in traps, especially in the second year where a clustering of WF plots is observable (Fig. 4.7 b). However, differences in community composition, although revealed as statistically significant for transects (section 4.4.3.2), are obscured by the effects of hedgerow and margin. This is unsurprising, as the presence of hedgerows and other woody vegetation is known to be a stronger predictor of moth abundance and diversity than grassland (Woiwod and Gould, 2008). While several studies have found that AES margins benefit some groups of moths more than others – e.g., grassland specialists (Alison et al., 2016) or micro-moths (Fuentes-Montemayor et al., 2011), community composition, as measured by multidimensional scaling, appears unstudied.

Although differences in community composition between treatments were obscure, the results shed light on the biases of the two sampling methods: traps and transects. In the traps in the first year of the study, the community composition was driven primarily by the location of the margin block (Fig. 4.6 e) and secondarily by the presence of a woody boundary (Fig. 4.6 c). The polygons representing blocks in 2018 are almost non-overlapping, suggesting that the species mix was almost entirely determined by its surrounding habitat rather than treatment for which the polygons are largely overlapping. By contrast, in the transects data, there is more overlap among different blocks (Fig. 4.7 e and f) and a near-complete overlap between plots with/without a woody boundary feature, showing that these features are not as important in determining community sampled. These differences between the trap and transect data are also present in the abundance (Fig. 4.2 and Fig. 4.3) and diversity data (Fig. 4.4 and Fig. 4.5) where the distinctiveness of the different treatments is greater in transect data, especially in the second year. These results suggest that moth data from traps are more influenced by the wider environment than transect data which are more specific to the exact location. I.e., moths passing through and not directly utilising the field margins are more likely to be caught in a trap than encountered during a transect. Although transect data are more location-specific, the method is more time-consuming and the range of species sampled is much lower (compare Table 4.2 and Table 4.3).

The difference in the community composition sampled in traps and transects can be clearly seen in Fig. S4.2 where NMDS plots show there is no overlap in community composition across the two sampling methods in either year. Fig. S4.3 shows that the difference in community composition between years is small compared to the difference between sampling method. The discrepancies in relative abundance in the two methods can be seen in Table S4.3, which shows that when species are ordered by rank abundance, the ranking for each species differs widely between the two sampling methods for many species. It is clear that the species with the smallest wingspans are less likely to be sampled during transects (Fig. S4.4). There is a positive effect of forewing length on detectability in transects up to roughly 13mm after which the effect plateaus. This is likely due to smaller moths being more difficult to spot, especially those that are resting in vegetation rather than flying. In line with previous work (Birkinshaw and Thomas, 1999), the experiment showed that transects are an effective, and perhaps underused, way of sampling moth populations across a range of habitats. Results in this chapter show that transects are more sensitive to differences in community composition in adjacent habitat patches than are traps.

4.5.3 Effect of surrounding landscape on abundance

Contrary to the finding of Merckx et al. (2012b), the presence of hedgerows and trees did not appear to benefit any species group apart from those with tree/shrub feeding larvae. In the trap data, moth total abundance (all species) was higher in plots next to a woody boundary feature, but when modelling feeding guilds separately, this effect only held true for woody (tree/shrub) feeders, polyphagous species and non-plant feeders. Similarly, in the transect data there was no effect of surrounding woody vegetation on total abundance, but there was a positive effect on both woody feeders and non-plant feeders (Table S4.4 and Table S4.7). As the non-plant feeders included those that feed on lichens and leaf litter, their food sources are present in hedgerows and woodland. These findings suggests that, contrary to (Merckx et al., 2012b), the benefits of woody boundary features for moths derive only from their value as a larval food source, with no evidence of providing additional shelter benefits.

4.5.4 Species-specific responses to treatment

When comparing the BC to the GR treatment, only one species, *C. culmella*, showed a consistent response with fewer individuals in the BC treatment (Table S4.10). This is unexpected as *C. culmella* was recorded feeding on nectar (although not on species sown in the BC treatment) and was flying during the peak flowering of bladder campion and night-flowering catchfly (June). There were no moth species recorded nectaring on these two flowers that also showed a significant response to this treatment type. In contrast, there were several species with consistent response to the WF treatment. There were 10 species that were consistently found in higher numbers in the WF treatment, and of these, five are specialists of plants that were sown in the WF treatment (*Bucculatrix nigricomella;* oxeye daisy*, Cochylimorpha straminea;* knapweed*, Eucosma cana;* knapweed*, E. hohenwartiana;* knapweed *and Pexicopia malvella*; musk mallow), a further three are polyphagous on forbs or low-growing plants (*Caradrina morpheus*, *Idaea dimidiate* and *Xestia xanthographa*) and one is a specialist of grasses (*Mythimna pallens*). There were three species that were consistently found in lower numbers in the WF treatment, all of which were grass specialists (*Agriphila straminella, A. tristella* and *C. culmella).* These results further suggest the prime importance of hostplant availability over nectar availability. While adults of the three species C. *morpheus, I. dimidiate* and *X. xanthographa* were all observed feeding on nectar, the fact that they are all polyphagous on forbs means that their increased abundance could be due either to larval or adult food sources. The noctuid *M. pallens* perhaps represents the only species significantly affected by the nectar resources provided in the WF treatment as this species is a grass feeder and was observed nectaring at six plant species including wild carrot and yarrow. The lower abundances of the three grass-feeding moths is presumably due to the lower density of grass as a hostplant in the forb-rich WF treatment. The prime importance of hostplants, and secondary importance of nectar, for moths has been demonstrated previously for diurnal species (Alanen et al., 2011). Nectar resources have been suggested as a benefit of wildflower margins for moths (Alison et al., 2017, Merckx et al., 2012b) but a measurable effect is yet to be demonstrated in the field.

4.5.5 Field margins as breeding habitat

While it has been shown here that the abundance of adult moths is increased in diverse wildflower mixes compared to plain grass margins, there is a lack of information on other life stages. It has been suggested that annually ploughed nectar-rich field margins may act as a population sink, drawing in adult insects but inflicting high overwintering mortality (Ganser et al., 2019). However, the effectiveness of perennial field margins as overwintering sites has been demonstrated for numerous insect taxa (Ganser et al., 2019, Pfiffner and Luka, 2000, Schaffers et al., 2012), but comparable studies on Lepidoptera appear largely absent. Despite lack of direct evidence, the data here showed that treatment effects became more prominent in the second year of the study, suggesting that populations of moths specialising on the sown species had established. In line with previous studies, this trend is expected to continue in subsequent years as more species colonise the new habitat (Alanen et al., 2011, Korpela et al., 2013). The use of emergence traps would be useful in further studies to confirm that moths are indeed overwintering in perennial field margin habitats.

4.5.6 Effect of treatment on larval abundance

The low numbers of larvae encountered did not allow for rigorous analysis of this group, but the presence of larvae demonstrates that breeding is occurring. The two methods used (transects and sweep-netting) were biased towards sampling certain larvae; namely, large-bodied, conspicuous, externally feeding grass specialists which made up the large majority of larval counts. Experience in the field suggests that the simple linear form of grasses makes spotting larvae by eye easier than in the complex structures of the various wildflowers. Furthermore, smooth structure of grass is likely to make sweep-netting more effective in this habitat as the rim of the net can make contact with more of the plant. These two methods are also completely unsuited to sampling internally feeding larvae which were very common in the WF treatment (e.g., *E. hohenwartiana* and *C. straminea*) as well as subterranean larvae such as *Triodia sylvina* (Orange Swift). A more varied methodological approach is needed for a fuller picture of the larvae utilising the field margins. For example, emergence traps, soil coring and D-vac sampling have all been used successfully to sample the immature stages of Lepidoptera and this could be extended to use in field margin studies (Devotto et al., 2007, Dosdall, 1994, Doxon et al., 2011)

4.5.7 Limitations of study

The apparent lack of importance of nectar resources suggested by this study may be misleading for several reasons. Firstly, the most popular nectar/sugar sources recorded during observations were on naturally occurring rather than sown plant species (Fig. 4.9), suggesting that it is possible that the sources of nectar provided in the experiment were not the ones preferred by moths. Although two of the top nectar sources in this study, creeping thistle and spear thistle, are considered injurious weeds in the UK making them less than ideal species to cultivate in arable field margins. Secondly, the two moth-pollinated plants chosen to enhance nectar provision in grass margins (bladder campion and night-flowering catchfly) were in peak flower during June, with only minimal sporadic flowering for the rest of the sampling season (July and August). Night-flowering catchfly is also an annual plant and was almost entirely absent in the second year of the study. Thirdly, it seemed that the moths visiting the two moth-pollinated flowers were biased: 89% of visits to these flowers were noctuid moths compared to 60% in other flowers/fruits. A better way to test the importance of adult sugar provisioning may be to enhance grass margins with artificial sources such as sugar-water feeders so that the confounding effects of hostplants and seasonality could be avoided.

4.5.8 Conclusions

This experiment showed that local moth diversity was greatly enhanced by sowing diverse grass and wildflower field margins rather than plain grass margins in arable fields. Local abundance was also enhanced, but this effect was less clear: ranging from no effect, to a 1.4-fold increase when comparing wildflower margins to grass margins. The benefit of wildflower margins for moths was driven primarily by their role as a larval hostplant; their role as a source of nectar for adult moths appears of secondary importance. The value of wildflower field margins tends to increase with age (Alanen et al., 2011) as more species colonise the new habitat over time. In this experiment, the effects of the wildflower margins were more pronounced in the second year, highlighting the importance of maintaining long-term semi-natural habitats on farmland. This suggests that, for moths, perennial wildflower margins are of greater value than annually sown margins (Ganser et al., 2019). Sown field margin strips are an important tool in mitigating biodiversity loss in arable farmland (Marshall et al., 2006) and connecting existing areas of semi-natural grassland (Threadgill et al., 2020). Here it is shown that, for moths, the small amount of space allotted to sown field margins can be used more effectively to enhance local abundance and diversity by sowing a diverse range of wildflowers and grasses rather than plain grass. However, the gains in abundance are modest and it is likely that the preservation and creation of larger areas of habitat is needed to halt the decline in the abundance of moths.

4.6 Supporting information

4.6.1 Field margin setup

Fig. S4.1. Photos of field margin blocks at Rothamsted Farm, showing the three treatments. *Grass (GR): a, d, g, Bladder campion (BC): b, e, h, and Wildflower (WF): c, f, i. Photos taken in 2019 on June 20th (a – c), July 3rd (d – f) and July 5th (g – i). Traps on a 1 m platform are shown in a – f and only the platforms are shown in g – i.*

Text S4. 1. Timetable of the establishment and maintenance of the margin blocks.

Mid-April 2017: The 210 x 3 m margins were marked out and a herbicide (glyphosate) was applied to the plots to kill off any crops or pre-existing vegetation.

Late April 2017: The seeds were sown using a combination drill that cultivates in front of the drilling harrows. The drilling harrows lift right out of the ground so the seed is sprinkled on top, similar to being broadcast. Another set of harrows then followed behind the drilling harrows and lightly raked the soil, covering the seed. The soil was then rolled to consolidate the seed bed.

Late June 2017: Margins were cut close to ground level to suppress the annual weeds.

Mid-August 2017: Margins were cut again close to the ground to suppress annual weeds. Sown perennials now starting to establish.

May – September 2018: Field season 1. Some margins suffered lodging (vegetation falling over).

Late September 2018: Margins were cut and vegetation removed.

Mid-May 2019: The margins that suffered lodging last season (4 out of 15 margins) were cut to reduce the likelihood of lodging this year.

April – September 2019: Field season 2.

Table S4.1. The species composition, sowing rates and price per hectar of the three seed mixes (treatments) used in the experiment. *All seed mixes were sown at a rate of 10 kg/ha.*

Seed mix	Price (£/ha)	Common name	Scientific name	Percentage composition
Grass (GR)	£104	Common bent	*Agrostis capillaris*	10%
		Crested dogstail	*Cynosurus cristatus*	50%
		Slender-creeping red-fescue	*Festuca rubra*	35%
		Smaller cat's-tail	*Phleum bertolonii*	5%
Bladder campion (BC)	£191	Common bent	*Agrostis capillaris*	9%
		Crested dogstail	*Cynosurus cristatus*	46%

Seed mix	Price (£/ha)	Common name	Scientific name	Percentage composition
		Slender-creeping red-fescue	*Festuca rubra*	32%
		Smaller cat's-tail	*Phleum bertolonii*	5%
		Night-flowering catchfly	*Silene noctiflora*	6%
		Bladder campion	*Silene vulgaris*	2%
Wildflower (WF)	£360	Common bent	*Agrostis capillaris*	8%
		Crested dogstail	*Cynosurus cristatus*	40%
		Slender-creeping red-fescue	*Festuca rubra*	28%
		Smaller cat's-tail	*Phleum bertolonii*	4%
		Yarrow	*Achillea millefolium*	1.2%
		Common knapweed	*Centaurea nigra*	3%
		Wild carrot	*Daucus carota*	1%
		Field scabious	*Knautia arvensis*	0.6%
		Oxeye daisy	*Leucanthemum vulgare*	1.6%
		Birdsfoot trefoil	*Lotus corniculatus*	2%
		Musk mallow	*Malva moschata*	0.8%
		Cowslip	*Primula veris*	0.4%
		Selfheal	*Prunella vulgaris*	3%
		Meadow buttercup	*Ranunculus acris*	3.2%
		Red campion	*Silene dioica*	2%
		Wild red clover	*Trifolium pratense*	0.2%
		Tufted vetch	*Vicia cracca*	1%

4.6.2 Moth species information

Table S4.2. The nine groups of species that were combined into aggregate taxa for analysis purposes.

Aggregate name	Macro/micro moth	Species included in aggregate
Cnephasia agg.	Micro	All species in the *Cnephasia* genus excluding C. *longana*
Ectodemia sp.	Micro	All species in *Ectodemia* genus
Mesapamea agg.	Macro	*Mesapamea secalis* and *M. didyma*
Monopis agg.	Micro	*Monopis laevigella* and *M. weaverella*
Oegoconia sp.	Micro	All species in *Oegoconia* genus
Parornix sp.	Micro	All species in *Parornix* genus
Phyllonorycter sp.	Micro	All species in P*hyllonorycter* genus
Scoparia agg.	Micro	*Scoparia ambigulais* and *S. pyralella*
Stigmella sp.	Micro	All species in *Stigmella* genus

Table S4.3. The species traits for each of the 388 species and 9 aggregate taxa recorded in the experiment. *'Total abundance' is the number of individuals recorded across the entire two-year experiment, summed separately by sampling method (traps/transects).*

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
	Chrysoteuchia culmella	Micro	10.5	Crambidae	Grass feeder	Y		1527	1327	1	1
	Blastobasis adustella	Micro	7.5	Blastobasidae	Non-plant feeder	Y		1212	29	2	23
Diamondback	*Plutella xylostella*	Micro	7	Plutellidae	Unsown forb feeder			1139	81	3	7
Square-spot rustic	*Xestia xanthographa*	Macro	15.5	Noctuidae	Polyphagous	Y		968	599	4	3
	Agriphila straminella	Micro	9	Crambidae	Grass feeder			884	1130	5	2
Common wainscot	*Mythimna pallens*	Macro	15.5	Noctuidae	Grass feeder	Y	Y	856	66	6	8
Horse-chestnut leaf miner	*Cameraria ohridella*	Micro	4.5	Gracillariidae	Woody feeder			351	0	7	
	Celypha lacunana	Micro	7.5	Tortricidae	Polyphagous			337	52	8	12
Setaceous hebrew character	*Xestia c-nigrum*	Macro	16.5	Noctuidae	Unsown forb feeder	Y		293	9	9	43
	Agapeta hamana	Micro	10	Tortricidae	Unsown forb feeder			284	131	10	5
Common footman	*Eilema lurideola*	Macro	15.5	Erebidae	Non-plant feeder	Y		270	4	11	68
Smoky wainscot	*Mythimna impura*	Macro	16	Noctuidae	Grass feeder			243	11	12	38

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
	Celypha striana	Micro	9	Tortricidae	Unsown forb feeder			242	18	13	31
	Eucosma cana	Micro	9	Tortricidae	Sown forb feeder	Y		225	49	14	13
	Cochylimorpha straminea	Micro	8.5	Tortricidae	Sown forb feeder			206	152	15	4
	Crambus perlella	Micro	12.5	Crambidae	Grass feeder	Y		180	48	16	14
	Cnephasia agg.	Micro	9.5	Tortricidae	Sown forb feeder			166	2	17	93
Heart and dart	*Agrotis exclamationis*	Macro	17	Noctuidae	Unsown forb feeder	Y	Y	156	1	18	112
Common rustic agg.	*Mesapamea agg.*	Macro	14	Noctuidae	Grass feeder	Y		147	26	19	26
	Parornix sp.	Micro	5	Gracillariidae	Woody feeder			147	2	19	93
Dingy footman	*Collita griseola*	Macro	16.5	Erebidae	Non-plant feeder			145	6	21	55
	Elachista canapennella	Micro	4.5	Elachistidae	Grass feeder			132	0	22	
	Aspilapteryx tringipennella	Micro	6	Gracillariidae	Unsown forb feeder			120	0	23	
	Agriphila geniculea	Micro	11.5	Crambidae	Grass feeder	Y		114	27	24	24
	Scoparia agg.	Micro	9.5	Crambidae	Non-plant feeder			114	6	24	55
Mottled rustic	*Caradrina morpheus*	Macro	14.5	Noctuidae	Unsown forb feeder	Y	Y	112	4	26	68

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
	Eucosma hohenwartiana	Micro	9	Tortricidae	Sown forb feeder			107	45	27	16
Flounced rustic	*Luperina testacea*	Macro	16	Noctuidae	Grass feeder		Y	95	1	28	112
Large yellow underwing	*Noctua pronuba*	Macro	23.5	Noctuidae	Unsown forb feeder	Y		92	9	29	43
	Crambus lathoniellus	Micro	10.5	Crambidae	Grass feeder			88	10	30	40
Common plume	*Emmelina monodactyla*	Micro	11	Pterophoridae	Unsown forb feeder	Y		83	56	31	11
Single-dotted wave	*Idaea dimidiata*	Macro	10	Geometridae	Unsown forb feeder	Y		80	40	32	18
Cloaked minor	*Mesoligia furuncula*	Macro	11	Noctuidae	Grass feeder			79	39	33	19
Uncertain	*Hoplodrina octogenaria*	Macro	15	Noctuidae	Unsown forb feeder	Y		78	2	34	93
	Agriphila tristella	Micro	13	Crambidae	Grass feeder			77	62	35	9
Mother of pearl	*Patania ruralis*	Micro	16	Crambidae	Unsown forb feeder	Y		77	43	35	17
Vines rustic	*Hoplodrina ambigua*	Macro	14	Noctuidae	Unsown forb feeder	Y		73	6	37	55
	Aethes smeathmanniana	Micro	7.5	Tortricidae	Sown forb feeder			72	12	38	36
	Bryotropha terrella	Micro	7.5	Gelechiidae	Grass feeder			64	13	39	34
Lesser yellow underwing	*Noctua comes*	Macro	15.5	Noctuidae	Polyphagous	Y		62	1	40	112

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
	Blastobasis lacticolella	Micro	8.5	Blastobasidae	Non-plant feeder			60	21	41	29
Lesser broad-bordered yellow underwing	*Noctua janthe*	Macro	18	Noctuidae	Polyphagous			60	0	41	
Hollyhock seed moth	*Pexicopia malvella*	Micro	9.5	Gelechiidae	Sown forb feeder			58	4	43	68
	Helcystogramma rufescens	Micro	8	Gelechiidae	Grass feeder			56	0	44	
	Coleophora alcyonipennella	Micro	5.5	Coleophoridae	Unsown forb feeder			54	1	45	112
Water veneer	*Acentria ephemerella*	Micro	7	Crambidae	Non-plant feeder			53	0	46	
Brown rustic	*Rusina ferruginea*	Macro	16	Noctuidae	Unsown forb feeder		Y	52	0	47	
	Bucculatrix nigricomella	Micro	3.5	Bucculatricidae	Sown forb feeder			51	0	48	
	Eudonia mercurella	Micro	8	Crambidae	Non-plant feeder			51	2	48	93
Dusky sallow	*Eremobia ochroleuca*	Macro	15	Noctuidae	Grass feeder	Y		49	11	50	38
	Stigmella sp.	Micro	2.5	Nepticulidae	NA			49	0	50	
Least carpet	*Idaea rusticata*	Macro	9	Geometridae	Non-plant feeder	Y		48	13	52	34
	Paraswammerdamia nebulella	Micro	6.5	Yponomeutidae	Woody feeder			44	9	53	43

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
	Phyllonorycter sp.	Micro	4	Gracillariidae	Woody feeder			44	0	53	
	Crassa unitella	Micro	7	Oecophoridae	Non-plant feeder			42	2	55	93
Dwarf cream wave	*Idaea fuscovenosa*	Macro	10	Geometridae	Non-plant feeder			40	22	56	28
Riband wave	*Idaea aversata*	Macro	15	Geometridae	Unsown forb feeder	Y		39	8	57	50
Dark arches	*Apamea monoglypha*	Macro	22.5	Noctuidae	Grass feeder	Y	Y	37	32	58	21
Shaded broad-bar	*Scotopteryx chenopodiata*	Macro	17.5	Geometridae	Unsown forb feeder		Y	37	12	58	36
	Eudonia pallida	Micro	8.5	Crambidae	Non-plant feeder			36	1	60	112
Brown house moth	*Hofmannophila pseudospretella*	Micro	9	Oecophoridae	Non-plant feeder			36	6	60	55
Dun-bar	*Cosmia trapezina*	Macro	14.5	Noctuidae	Woody feeder			35	1	62	112
	Lobesia abscisana	Micro	5.5	Tortricidae	Unsown forb feeder			35	1	62	112
Blood-vein	*Timandra comae*	Macro	16.5	Geometridae	Unsown forb feeder		Y	35	25	62	27
	Cnephasia longana	Micro	9	Tortricidae	Sown forb feeder			34	0	65	
	Borkhausenia fuscescens	Micro	4	Oecophoridae	Non-plant feeder			33	0	66	

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
Straw underwing	*Thalpophila matura*	Macro	18.5	Noctuidae	Grass feeder			32	6	67	55
July high-flyer	*Hydriomena furcata*	Macro	16	Geometridae	Woody feeder			29	0	68	
Turnip moth	*Agrotis segetum*	Macro	18.5	Noctuidae	Unsown forb feeder		Y	28	1	69	112
Bee moth	*Aphomia sociella*	Micro	14.5	Pyralidae	Non-plant feeder			27	5	70	63
Common carpet	*Epirrhoe alternata*	Macro	13.5	Geometridae	Unsown forb feeder			26	3	71	83
	Oegoconia sp.	Micro	6.5	Autostichidae	Non-plant feeder			26	0	71	
Straw dot	*Rivula sericealis*	Macro	14	Noctuidae	Grass feeder			26	7	71	51
	Aproaerema anthyllidella	Micro	5.5	Gelechiidae	Sown forb feeder			25	0	74	
Treble lines	*Charanyca trigrammica*	Macro	16	Noctuidae	Unsown forb feeder			25	2	74	93
Double square-spot	*Xestia triangulum*	Macro	18	Noctuidae	Polyphagous			25	3	74	83
	Ypsolopha scabrella	Micro	9	Ypsolophidae	Woody feeder			25	1	74	112
	Monochroa palustrellus	Micro	8.5	Gelechiidae	Unsown forb feeder			24	0	78	
	Caryocolum fraternella	Micro	5.5	Gelechiidae	Unsown forb feeder			23	0	79	
Light brown apple moth	*Epiphyas postvittana*	Micro	9.5	Tortricidae	Non-plant feeder			23	33	79	20

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
	Endotricha flammealis	Micro	9	Pyralidae	Non-plant feeder	Y		22	27	81	24
Flame shoulder	*Ochropleura plecta*	Macro	13.5	Noctuidae	Unsown forb feeder			22	3	81	83
Silver y	*Autographa gamma*	Macro	17	Noctuidae	Unsown forb feeder	Y	Y	20	31	83	22
	Agapeta zoegana	Micro	10	Tortricidae	Sown forb feeder			19	10	84	40
Barred fruit-tree tortrix	*Pandemis cerasana*	Micro	9.5	Tortricidae	Polyphagous			19	4	84	68
Large nutmeg	*Apamea anceps*	Macro	18.5	Noctuidae	Grass feeder	Y	Y	18	5	86	63
Rustic shoulder-knot	*Apamea sordens*	Macro	17.5	Noctuidae	Grass feeder			18	0	86	
	Celypha rosaceana	Micro	8	Tortricidae	Unsown forb feeder			18	1	86	112
Plum tortrix	*Hedya pruniana*	Micro	8	Tortricidae	Woody feeder			18	3	86	83
	Paraswammerdamia albicapitella	Micro	5.5	Yponomeutidae	Woody feeder			18	4	86	68
Six-striped rustic	*Xestia sexstrigata*	Macro	16	Noctuidae	Unsown forb feeder			18	0	86	
	Batia lunaris	Micro	4.5	Oecophoridae	Non-plant feeder			17	0	92	
	Bucculatrix cristatella	Micro	3	Bucculatricidae	Sown forb feeder			17	0	92	
Ingrailed clay	*Diarsia mendica*	Macro	15	Noctuidae	Polyphagous	Y	Y	17	0	92	

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
Ruby tiger	*Phragmatobia fuliginosa*	Macro	16.5	Erebidae	Polyphagous			17	1	92	112
	Scrobipalpa atriplicella	Micro	6.5	Gelechiidae	Unsown forb feeder			17	1	92	112
Round-winged muslin	*Thumatha senex*	Macro	10.5	Erebidae	Non-plant feeder			17	4	92	68
Heart and club	*Agrotis clavis*	Macro	16	Noctuidae	Sown forb feeder			16	1	98	112
	Carcina quercana	Micro	9	Peleopodidae	Woody feeder			16	4	98	68
	Eudonia lacustrata	Micro	8.5	Crambidae	Non-plant feeder			16	1	98	112
Willow beauty	*Peribatodes rhomboidaria*	Macro	20.5	Geometridae	Woody feeder			16	1	98	112
Many-plumed moth	*Alucita hexadactyla*	Micro	8.5	Pterophoridae	Woody feeder			15	0	102	
	Cochylis atricapitana	Micro	7.5	Tortricidae	Unsown forb feeder			15	0	102	
	Homoeosoma sinuella	Micro	9.5	Pyralidae	Unsown forb feeder			15	0	102	
Rosy rustic	*Hydraecia micacea*	Macro	17.5	Noctuidae	Unsown forb feeder		Y	15	2	102	93
Middle-barred minor	*Oligia fasciuncula*	Macro	12	Noctuidae	Grass feeder	Y		15	0	102	
Brown plume	*Stenoptilia pterodactyla*	Micro	11.5	Pterophoridae	Unsown forb feeder			15	9	102	43

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
	Brachmia blandella	Micro	6	Gelechiidae	Woody feeder			14	0	108	
	Bryotropha senectella	Micro	5.5	Gelechiidae	Non-plant feeder			14	0	108	
	Coleophora striatipennella	Micro	6	Coleophoridae	Unsown forb feeder			14	0	108	
Scorched carpet	*Ligdia adustata*	Macro	13	Geometridae	Woody feeder			14	6	108	55
Brown-line bright-eye	*Mythimna conigera*	Macro	16	Noctuidae	Grass feeder	Y		14	0	108	
Short-cloaked moth	*Nola cucullatella*	Macro	9	Nolidae	Woody feeder		Y	14	1	108	112
Mouse moth	*Amphipyra tragopoginis*	Macro	17	Noctuidae	Polyphagous		Y	13	0	114	
	Argyresthia albistria	Micro	5	Argyresthiidae	Woody feeder			13	0	114	
	Mompha epilobiella	Micro	5.5	Momphidae	Unsown forb feeder			13	0	114	
Yarrow plume	*Platyptilia pallidactyla*	Micro	12	Pterophoridae	Sown forb feeder			13	57	114	10
	Coptotriche marginea	Micro	4	Tisheriidae	Woody feeder			12	0	118	
	Crambus pascuella	Micro	12	Crambidae	Grass feeder			12	9	118	43
Clay	*Mythimna ferrago*	Macro	16.5	Noctuidae	Grass feeder			12	2	118	93

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
	Phycitodes binaevella	Micro	11.5	Pyralidae	Unsown forb feeder			12	4	118	68
Shuttle-shaped dart	*Agrotis puta*	Macro	14	Noctuidae	Unsown forb feeder			11	0	122	
	Coleophora flavipennella	Micro	5.5	Coleophoridae	Woody feeder			11	0	122	
	Coleophora hemerobiella	Micro	6.5	Coleophoridae	Woody feeder			11	0	122	
	Coleophora saxicolella	Micro	7	Coleophoridae	Unsown forb feeder			11	0	122	
	Coleophora versurella	Micro	6	Coleophoridae	Unsown forb feeder			11	0	122	
Scalloped oak	*Crocallis elinguaria*	Macro	20	Geometridae	Woody feeder		Y	11	0	122	
	Lathronympha strigana	Micro	7	Tortricidae	Unsown forb feeder			11	0	122	
Bud moth	*Spilonota ocellana*	Micro	6.5	Tortricidae	Woody feeder			11	1	122	112
	Acrobasis advenella	Micro	9.5	Pyralidae	Woody feeder			10	1	130	112
Small magpie	*Anania hortulata*	Micro	14.5	Crambidae	Unsown forb feeder			10	7	130	51
Flame	*Axylia putris*	Macro	15	Noctuidae	Unsown forb feeder	Y		10	0	130	
Small rivulet	*Perizoma alchemillata*	Macro	10	Geometridae	Unsown forb feeder			10	0	130	

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
	Phycita roborella	Micro	12.5	Pyralidae	Woody feeder	Y		10	0	130	
	Scoparia subfusca	Micro	11.5	Crambidae	Unsown forb feeder			10	1	130	112
	Ancylis achatana	Micro	7.5	Tortricidae	Woody feeder			9	0	136	
	Ancylis badiana	Micro	6.5	Tortricidae	Sown forb feeder			9	1	136	112
Yellow shell	*Camptogramma bilineata*	Macro	14.4	Geometridae	Unsown forb feeder	Y		9	90	136	6
	Coleophora argentula	Micro	5.5	Coleophoridae	Sown forb feeder			9	0	136	
Barred straw	*Eulithis pyraliata*	Macro	16.5	Geometridae	Unsown forb feeder		Y	9	3	136	83
Lime-speck pug	*Eupithecia centaureata*	Macro	11	Geometridae	Unsown forb feeder	Y		9	6	136	55
Small scallop	*Idaea emarginata*	Macro	12	Geometridae	Unsown forb feeder			9	2	136	93
	Mompha subbistrigella	Micro	4.5	Momphidae	Unsown forb feeder			9	0	136	
Least yellow underwing	*Noctua interjecta*	Macro	15.5	Noctuidae	Polyphagous			9	0	136	
	Swammerdamia pyrella	Micro	6	Yponomeutidae	Woody feeder			9	0	136	
Orange swift	*Triodia sylvina*	Macro	19	Hepialidae	Unsown forb feeder			9	18	136	31

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
	Blastodacna hellerella	Micro	5	Elachistidae	Woody feeder			8	0	147	
Common wave	*Cabera exanthemata*	Macro	15	Geometridae	Woody feeder			8	0	147	
	Calybites phasianipennella	Micro	5	Gracillariidae	Unsown forb feeder			8	0	147	
	Coleophora peribenanderi	Micro	6.5	Coleophoridae	Unsown forb feeder			8	0	147	
Snout	*Hypena proboscidalis*	Macro	17	Noctuidae	Unsown forb feeder			8	10	147	40
	Metalampra italica	Micro	7	Oecophoridae	Woody feeder			8	0	147	
	Monopis agg.	Micro	7.5	Tineidae	NA			8	1	147	112
	Udea prunalis	Micro	12	Crambidae	Sown forb feeder			8	4	147	68
Strawberry tortrix	*Acleris comariana*	Micro	7	Tortricidae	Unsown forb feeder			7	0	155	
	Catoptria falsella	Micro	9.5	Crambidae	Non-plant feeder			7	0	155	
	Coleophora mayrella	Micro	5	Coleophoridae	Unsown forb feeder			7	0	155	
White-shouldered house moth	*Endrosis sarcitrella*	Micro	7.5	Oecophoridae	Non-plant feeder			7	0	155	
Double-striped pug	*Gymnoscelis rufifasciata*	Macro	9	Geometridae	Polyphagous			7	9	155	43

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
Gold triangle	*Hypsopygia costalis*	Micro	9	Pyralidae	Non-plant feeder			7	0	155	
	Metzneria metzneriella	Micro	8.5	Gelechiidae	Sown forb feeder			7	3	155	83
Bramble shoot moth	*Notocelia uddmanniana*	Micro	8.5	Tortricidae	Woody feeder			7	15	155	33
Garden carpet	*Xanthorhoe fluctuata*	Macro	14.5	Geometridae	Unsown forb feeder		Y	7	0	155	
Mottled beauty	*Alcis repandata*	Macro	22.5	Geometridae	Woody feeder			6	0	164	
Beautiful plume	*Amblyptilia acanthadactyla*	Micro	10	Pterophoridae	Unsown forb feeder			6	3	164	83
	Coleophora adspersella	Micro	7	Coleophoridae	Unsown forb feeder			6	1	164	112
	Coleophora therinella	Micro	7	Coleophoridae	Unsown forb feeder			6	1	164	112
	Depressaria pulcherrimella	Micro	9	Elachistidae	Sown forb feeder			6	0	164	
Scarce footman	*Eilema complana*	Macro	16.5	Erebidae	Non-plant feeder	Y		6	0	164	
	Elachista maculicerusella	Micro	5	Elachistidae	Grass feeder			6	0	164	
	Endothenia gentianaeana	Micro	7.5	Tortricidae	Unsown forb feeder			6	0	164	
	Eucosma obumbratana	Micro	8	Tortricidae	Unsown forb feeder			6	0	164	

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
	Gelechia scotinella	Micro	6	Gelechiidae	Woody feeder			6	0	164	
Marbled orchard tortrix	*Hedya nubiferana*	Micro	8.5	Tortricidae	Woody feeder			6	1	164	112
Treble brown spot	*Idaea trigeminata*	Macro	10.5	Geometridae	Non-plant feeder			6	21	164	29
Apple leaf miner	*Lyonetia clerkella*	Micro	4.5	Lyonetiidae	Woody feeder			6	0	164	
White point	*Mythimna albipuncta*	Macro	15.5	Noctuidae	Grass feeder			6	0	164	
	Scrobipalpa acuminatella	Micro	6	Gelechiidae	Unsown forb feeder			6	0	164	
Hawthorn moth	*Scythropia crataegella*	Micro	6.5	Yponomeutidae	Woody feeder			6	0	164	
	Tinea trinotella	Micro	7	Tineidae	Non-plant feeder			6	0	164	
Garden rose tortrix	*Acleris variegana*	Micro	7.5	Tortricidae	Woody feeder			5	0	181	
Light arches	*Apamea lithoxylaea*	Macro	20.5	Noctuidae	Grass feeder			5	7	181	51
	Coleophora trifolii	Micro	8.5	Coleophoridae	Unsown forb feeder			5	0	181	
Rustic	*Hoplodrina blanda*	Macro	14.5	Noctuidae	Unsown forb feeder		Y	5	0	181	
Common swift	*Korscheltellus lupulina*	Macro	15	Hepialidae	Grass feeder			5	0	181	
Oak nycteoline	*Nycteola revayana*	Macro	12	Noctuidae	Woody feeder			5	1	181	112

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
Pale mottled willow	*Paradrina clavipalpis*	Macro	13.5	Noctuidae	Grass feeder			5	0	181	
Angle shades	*Phlogophora meticulosa*	Macro	23	Noctuidae	Polyphagous			5	2	181	93
	Pseudopostega crepusculella	Micro	4.5	Opostegidae	Non-plant feeder			5	0	181	
	Recurvaria leucatella	Micro	6.5	Gelechiidae	Woody feeder			5	0	181	
	Scrobipalpa costella	Micro	6.5	Gelechiidae	Unsown forb feeder			5	0	181	
Cinnabar	*Tyria jacobaeae*	Macro	20	Erebidae	Unsown forb feeder			5	1	181	112
	Batrachedra praeangusta	Micro	7.5	Batrachedridae	Woody feeder			4	0	193	
	Bedellia somnulentella	Micro	4	Bedelliidae	Unsown forb feeder			4	0	193	
Common white wave	*Cabera pusaria*	Macro	16	Geometridae	Woody feeder			4	7	193	51
	Coleophora serratella	Micro	6	Coleophoridae	Woody feeder			4	0	193	
Nut-tree tussock	*Colocasia coryli*	Macro	15.5	Noctuidae	Woody feeder			4	0	193	
Old lady	*Mormo maura*	Macro	33	Noctuidae	Polyphagous			4	0	193	
	Nephopterix angustella	Micro	10	Pyralidae	Woody feeder			4	0	193	
	Notocelia trimaculana	Micro	8	Tortricidae	Woody feeder			4	0	193	

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
	Opostega salaciella	Micro	5.5	Opostegidae	Unsown forb feeder			4	0	193	
	Pediasia contaminella	Micro	12	Crambidae	Grass feeder			4	1	193	112
Holly tortrix	*Rhopobota naevana*	Micro	6.5	Tortricidae	Woody feeder			4	1	193	112
Early thorn	*Selenia dentaria*	Macro	18.5	Geometridae	Woody feeder		Y	4	0	193	
	Sitochroa verticalis	Micro	13.5	Crambidae	Unsown forb feeder			4	1	193	112
White ermine	*Spilosoma lubricipeda*	Macro	20.5	Erebidae	Unsown forb feeder		Y	4	0	193	
	Teleiodes vulgella	Micro	6	Gelechiidae	Woody feeder			4	0	193	
Silver-ground carpet	*Xanthorhoe montanata*	Macro	15.5	Geometridae	Unsown forb feeder		Y	4	2	193	93
Bird-cherry ermine	*Yponomeuta evonymella*	Micro	11	Yponomeutidae	Woody feeder			4	0	193	
	Ypsolopha dentella	Micro	10.5	Ypsolophidae	Woody feeder			4	0	193	
	Acleris forsskaleana	Micro	7	Tortricidae	Woody feeder			3	0	211	
	Acleris laterana	Micro	8	Tortricidae	Woody feeder			3	0	211	
Deep-brown dart	*Aporophyla lutulenta*	Macro	16.5	Noctuidae	Polyphagous		Y	3	0	211	
	Athrips mouffetella	Micro	8	Gelechiidae	Unsown forb feeder			3	0	211	

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
	Caloptilia semifascia	Micro	5.5	Gracillariidae	Woody feeder			3	0	211	
	Caloptilia stigmatella	Micro	6.5	Gracillariidae	Woody feeder			3	0	211	
	Clepsis consimilana	Micro	7.5	Tortricidae	Woody feeder			3	0	211	
	Coleophora coracipennella	Micro	4.5	Coleophoridae	Woody feeder			3	0	211	
	Ectodemia sp.	Micro	3	Nepticulidae	NA			3	0	211	
	Elachista sp.	Micro	5	Elachistidae	Grass feeder			3	0	211	
	Epermenia chaerophyllella	Micro	5.5	Epermeniidae	Sown forb feeder			3	0	211	
Common pug	*Eupithecia vulgata*	Macro	11	Geometridae	Polyphagous		Y	3	1	211	112
Small-waved umber	*Horisme vitalbata*	Macro	16.5	Geometridae	Woody feeder			3	0	211	
	Lozotaenia forsterana	Micro	12	Tortricidae	Non-plant feeder			3	1	211	112
Kent black arches	*Meganola albula*	Macro	10.5	Nolidae	Woody feeder			3	0	211	
	Metzneria lappella	Micro	9	Gelechiidae	Unsown forb feeder			3	0	211	
	Mompha ochraceella	Micro	6.5	Momphidae	Unsown forb feeder			3	0	211	
Tawny marbled minor	*Oligia latruncula*	Macro	12	Noctuidae	Grass feeder		Y	3	1	211	112

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
	Parectopa ononidis	Micro	4	Gracillariidae	Sown forb feeder			3	0	211	
White plume	*Pterophorus pentadactyla*	Micro	14	Pterophoridae	Unsown forb feeder			3	48	211	14
Large wainscot	*Rhizedra lutosa*	Macro	20.5	Noctuidae	Grass feeder			3	0	211	
Orchard ermine	*Yponomeuta padella*	Micro	10	Yponomeutidae	Woody feeder			3	0	211	
	Yponomeuta plumbella	Micro	9	Yponomeutidae	Woody feeder			3	0	211	
	Acrobasis suavella	Micro	11	Pyralidae	Woody feeder			2	0	234	
	Agonopterix heracliana	Micro	9.5	Tortricidae	Sown forb feeder			2	1	234	112
	Agonopterix kaekeritziana	Micro	11	Tortricidae	Sown forb feeder			2	0	234	
	Agriphila selasella	Micro	13	Crambidae	Grass feeder			2	0	234	
	Aleimma loeflingiana	Micro	8	Tortricidae	Woody feeder			2	0	234	
Dusky brocade	*Apamea remissa*	Macro	18	Noctuidae	Grass feeder		Y	2	1	234	112
	Argyresthia semifusca	Micro	6	Argyresthiidae	Woody feeder			2	0	234	
	Caloptilia rufipennella	Micro	5.5	Gracillariidae	Woody feeder			2	0	234	
Light emerald	*Campaea margaritata*	Macro	21	Geometridae	Woody feeder			2	0	234	
	Coleophora conspicuella	Micro	7	Coleophoridae	Sown forb feeder			2	1	234	112

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
	Coleophora deauratella	Micro	5	Coleophoridae	Sown forb feeder			2	1	234	112
Tree-lichen beauty	*Cryphia algae*	Macro	11.5	Noctuidae	Non-plant feeder			2	0	234	
Shark	*Cucullia umbratica*	Macro	24	Noctuidae	Unsown forb feeder			2	0	234	
Small square-spot	*Diarsia rubi*	Macro	14	Noctuidae	Unsown forb feeder		Y	2	0	234	
Red-barred tortrix	*Ditula angustiorana*	Micro	7	Tortricidae	Woody feeder			2	0	234	
	Endothenia marginana	Micro	6	Tortricidae	Unsown forb feeder			2	0	234	
	Endothenia oblongana	Micro	6	Tortricidae	Unsown forb feeder			2	0	234	
Yellow-tail	*Euproctis similis*	Macro	19	Lymantriidae	Woody feeder			2	0	234	
	Gelechia senticetella	Micro	7	Gelechiidae	Woody feeder			2	0	234	
	Gypsonoma dealbana	Micro	5.5	Tortricidae	Woody feeder			2	0	234	
	Haplotinea insectella	Micro	7	Tineidae	Non-plant feeder			2	0	234	
	Luquetia lobella	Micro	9	Elachistidae	Woody feeder			2	0	234	
Cork moth	*Nemapogon cloacella*	Micro	6.5	Tineidae	Woody feeder			2	0	234	

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
Broad-bordered yellow underwing	*Noctua fimbriata*	Macro	24.5	Noctuidae	Unsown forb feeder			2	0	234	
Lunar underwing	*Omphaloscelis lunosa*	Macro	15.5	Noctuidae	Grass feeder			2	0	234	
Brimstone moth	*Opisthograptis luteolata*	Macro	17.5	Geometridae	Woody feeder	Y		2	4	234	68
	Pyrausta purpuralis	Micro	9	Crambidae	Unsown forb feeder			2	0	234	
Buff ermine	*Spilarctia luteum*	Macro	19.5	Erebidae	Polyphagous		Y	2	0	234	
	Udea lutealis	Micro	11.5	Crambidae	Unsown forb feeder			2	1	234	112
	Udea olivalis	Micro	12.5	Crambidae	Sown forb feeder			2	1	234	112
	Zeiraphera isertana	Micro	8.5	Tortricidae	Woody feeder			2	0	234	
	Acleris aspersana	Micro	6.5	Tortricidae	Unsown forb feeder			1	0	265	
	Acleris ferrugana	Micro	7	Tortricidae	Woody feeder			1	0	265	
	Acleris hastiana	Micro	10	Tortricidae	Woody feeder			1	0	265	
	Acleris holmiana	Micro	6.5	Tortricidae	Woody feeder			1	0	265	
	Aethes beatricella	Micro	8	Tortricidae	Unsown forb feeder			1	0	265	

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
	Agonopterix arenella	Micro	10	Tortricidae	Sown forb feeder	Y		1	2	265	93
	Agonopterix purpurea	Micro	6.5	Tortricidae	Sown forb feeder			1	0	265	
	Altenia scriptella	Micro	6.5	Gelechiidae	Woody feeder			1	0	265	
Svenssons copper underwing	*Amphipyra berbera*	Macro	23.5	Noctuidae	Woody feeder			1	0	265	
	Anania coronata	Micro	12	Crambidae	Woody feeder			1	0	265	
	Ancylis unguicella	Micro	7.5	Tortricidae	Unsown forb feeder			1	0	265	
Double lobed	*Apamea ophiogramma*	Macro	14.5	Noctuidae	Grass feeder			1	1	265	112
Timothy tortrix	*Aphelia paleana*	Micro	10	Tortricidae	Grass feeder			1	3	265	83
	Argyresthia bonnetella	Micro	5.5	Argyresthiidae	Woody feeder			1	0	265	
	Argyresthia brockeella	Micro	5.5	Argyresthiidae	Woody feeder			1	0	265	
	Argyresthia goedartella	Micro	5.5	Argyresthiidae	Woody feeder			1	0	265	
	Argyrotaenia ljungiana	Micro	7	Tortricidae	Polyphagous			1	0	265	
	Aroga velocella	Micro	8	Gelechiidae	Unsown forb feeder			1	0	265	

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
Centre-barred sallow	*Atethmia centrago*	Macro	16.5	Noctuidae	Woody feeder			1	0	265	
	Bactra furfurana	Micro	7.5	Tortricidae	Grass feeder			1	0	265	
	Bryotropha affinis	Micro	5.5	Gelechiidae	Non-plant feeder			1	0	265	
	Bucculatrix bechsteinella	Micro	3.5	Bucculatricidae	Woody feeder			1	0	265	
	Caryocolum tricolorella	Micro	5.5	Gelechiidae	Unsown forb feeder			1	0	265	
	Cochylidia heydeniana	Micro	5	Tortricidae	Unsown forb feeder			1	0	265	
	Cochylis hybridella	Micro	7	Tortricidae	Unsown forb feeder			1	0	265	
	Coleophora caespititiella	Micro	4	Coleophoridae	Grass feeder			1	0	265	
	Coleophora glaucicolella	Micro	5	Coleophoridae	Grass feeder			1	1	265	112
	Coleophora lineolea	Micro	6	Coleophoridae	Unsown forb feeder			1	0	265	
	Coleophora milvipennis	Micro	6	Coleophoridae	Woody feeder			1	0	265	
	Coleophora spinella	Micro	5.5	Coleophoridae	Woody feeder			1	0	265	
Green carpet	*Colostygia pectinataria*	Macro	13.5	Geometridae	Unsown forb feeder			1	3	265	83
Chestnut	*Conistra vaccinii*	Macro	14.5	Noctuidae	Polyphagous			1	0	265	

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
Box tree moth	*Cydalima perspectalis*	Micro	18	Crambidae	Woody feeder	Y		1	0	265	
	Cydia splendana	Micro	8.5	Tortricidae	Woody feeder			1	0	265	
	Depressaria badiella	Micro	9	Elachistidae	Unsown forb feeder			1	0	265	
	Dichrorampha acuminatana	Micro	6	Tortricidae	Sown forb feeder			1	4	265	68
	Dichrorampha simpliciana	Micro	7	Tortricidae	Unsown forb feeder			1	0	265	
Barred hook-tip	*Drepana cultraria*	Macro	14.5	Drepanidae	Woody feeder			1	0	265	
Hoary footman	*Eilema caniola*	Macro	16	Erebidae	Non-plant feeder			1	0	265	
	Elachista argentella	Micro	5.5	Elachistidae	Grass feeder			1	0	265	
	Elachista stabilella	Micro	3.5	Elachistidae	Grass feeder			1	0	265	
Common heath	*Ematurga atomaria*	Macro	13.5	Geometridae	Unsown forb feeder			1	0	265	
	Ephestia woodiella	Micro	8	Pyralidae	Non-plant feeder			1	0	265	
	Epiblema foenella	Micro	10	Tortricidae	Unsown forb feeder			1	0	265	
	Epinotia tedella	Micro	5.5	Tortricidae	Woody feeder			1	0	265	

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
	Epinotia tenerana	Micro	6.5	Tortricidae	Woody feeder			1	0	265	
	Eulamprotes atrella	Micro	5.5	Gelechiidae	Woody feeder			1	0	265	
Phoenix	*Eulithis prunata*	Macro	18	Geometridae	Woody feeder			1	0	265	
Wormwood pug	*Eupithecia absinthiata*	Macro	12	Geometridae	Unsown forb feeder			1	1	265	112
Mottled pug	*Eupithecia exiguata*	Macro	11.5	Geometridae	Woody feeder			1	0	265	
Tawny speckled pug	*Eupithecia icterata*	Macro	12	Geometridae	Sown forb feeder		Y	1	1	265	112
Maple pug	*Eupithecia inturbata*	Macro	9	Geometridae	Woody feeder		Y	1	0	265	
Toadflax pug	*Eupithecia linariata*	Macro	9.5	Geometridae	Unsown forb feeder		Y	1	0	265	
Yarrow pug	*Eupithecia millefoliata*	Macro	12.5	Geometridae	Sown forb feeder			1	3	265	83
Slender pug	*Eupithecia tenuiata*	Macro	9	Geometridae	Woody feeder		Y	1	0	265	
Drinker	*Euthrix potatoria*	Macro	28	Lasiocampidae	Grass feeder			1	2	265	93
	Euzophera cinerosella	Micro	10.5	Pyralidae	Unsown forb feeder			1	0	265	
Garden pebble	*Evergestis forficalis*	Micro	14	Crambidae	Unsown forb feeder			1	2	265	93
Frosted orange	*Gortyna flavago*	Macro	17.5	Noctuidae	Unsown forb feeder			1	0	265	

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
	Gypsonoma oppressana	Micro	6.5	Tortricidae	Woody feeder			1	0	265	
Buff arches	*Habrosyne pyritoides*	Macro	18.5	Thyatiridae	Woody feeder		Y	1	0	265	
Lychnis	*Hadena bicruris*	Macro	15.5	Noctuidae	Unsown forb feeder		Y	1	1	265	112
Tawny shears	*Hadena perplexa*	Macro	14	Noctuidae	Unsown forb feeder			1	0	265	
Campion	*Hadena rivularis*	Macro	15	Noctuidae	Sown forb feeder			1	0	265	
Broad-barred white	*Hecatera bicolorata*	Macro	14	Noctuidae	Unsown forb feeder		Y	1	0	265	
	Hedya ochroleucana	Micro	8.5	Tortricidae	Woody feeder			1	0	265	
Ghost moth	*Hepialus humuli*	Macro	28	Hepialidae	Grass feeder			1	2	265	93
Fern	*Horisme tersata*	Macro	16	Geometridae	Woody feeder			1	0	265	
Small fan-footed wave	*Idaea biselata*	Macro	10.5	Geometridae	Non-plant feeder			1	0	265	
Small dusty wave	*Idaea seriata*	Macro	10	Geometridae	Non-plant feeder			1	1	265	112
Bright-line brown-eye	*Lacanobia oleracea*	Macro	16.5	Noctuidae	Polyphagous		Y	1	2	265	93
Poplar hawk moth	*Laothoe populi*	Macro	8	Sphingidae	Woody feeder			1	0	265	

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
Shoulder-striped wainscot	*Leucania comma*	Macro	17.5	Noctuidae	Grass feeder		Y	1	0	265	
Clouded border	*Lomaspilis marginata*	Macro	12.5	Geometridae	Woody feeder			1	0	265	
Dotted fan-foot	*Macrochilo cribrumalis*	Macro	13.5	Noctuidae	Grass feeder			1	4	265	68
	Monochroa hornigi	Micro	5	Gelechiidae	Unsown forb feeder			1	0	265	
Thistle ermine	*Myelois circumvoluta*	Micro	15	Pyralidae	Unsown forb feeder	Y		1	4	265	68
	Notocelia rosaecolana	Micro	8.5	Tortricidae	Woody feeder			1	0	265	
Pebble prominent	*Notodonta ziczac*	Macro	20.5	Notodontidae	Woody feeder		Y	1	0	265	
Scalloped hazel	*Odontopera bidentata*	Macro	22	Geometridae	Woody feeder			1	0	265	
Minor sp.	*Oligia sp.*	Macro	NA	Noctuidae	Grass feeder			1	1	265	112
Marbled minor	*Oligia strigilis*	Macro	12	Noctuidae	Grass feeder		Y	1	0	265	
	Orthotaenia undulana	Micro	8	Tortricidae	Polyphagous			1	0	265	
Swallow-tailed moth	*Ourapteryx sambucaria*	Macro	26	Geometridae	Woody feeder		Y	1	0	265	
	Pammene fasciana	Micro	6.5	Tortricidae	Woody feeder			1	0	265	
Waved black	*Parascotia fuliginaria*	Macro	12.5	Noctuidae	Non-plant feeder			1	0	265	

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
Buff-tip	*Phalera bucephala*	Macro	30	Notodontidae	Woody feeder		Y	1	0	265	
Dark umber	*Philereme transversata*	Macro	18.5	Geometridae	Woody feeder			1	0	265	
Brown scallop	*Philereme vetulata*	Macro	14.5	Geometridae	Woody feeder			1	0	265	
	Phtheochroa rugosana	Micro	7.5	Tortricidae	Woody feeder			1	0	265	
Olive	*Prays oleae*	Macro	15	Noctuidae	Woody feeder			1	0	265	
	Prays ruficeps	Micro	16	Praydidae	Woody feeder			1	0	265	
	Pseudoswammerdamia combinella	Micro	7.5	Yponomeutidae	Woody feeder			1	0	265	
Pale prominent	*Pterostoma palpina*	Macro	21.5	Notodontidae	Woody feeder		Y	1	0	265	
	Recurvaria nanella	Micro	5.5	Gelechiidae	Woody feeder			1	0	265	
Herald	*Scoliopteryx libatrix*	Macro	21	Noctuidae	Woody feeder			1	1	265	112
Small blood-vein	*Scopula imitaria*	Macro	14	Geometridae	Non-plant feeder		Y	1	2	265	93
	Sorhagenia janiszewskae	Micro	9	Cosmopterigidae	Woody feeder			1	0	265	
	Sorhagenia rhamniella	Micro	4.5	Cosmopterigidae	Woody feeder			1	0	265	
	Swammerdamia caesiella	Micro	5.5	Yponomeutidae	Woody feeder			1	0	265	

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
	Thiotricha subocellea	Micro	4.5	Gelechiidae	Unsown forb feeder			1	0	265	
	Tinea pellionella	Micro	6	Tineidae	Non-plant feeder			1	0	265	
Common clothes-moth	*Tineola bisselliella*	Micro	6	Tineidae	Non-plant feeder			1	0	265	
Green oak tortrix	*Tortrix viridana*	Micro	10.5	Tortricidae	Woody feeder			1	0	265	
	Triaxomasia caprimulgella	Micro	10	Tineidae	Non-plant feeder			1	0	265	
Dark-barred twin-spot carpet	*Xanthorhoe ferrugata*	Macro	12.5	Geometridae	Unsown forb feeder		Y	1	0	265	
Willow ermine	*Yponomeuta rorrella*	Micro	11	Yponomeutidae	Woody feeder			1	0	265	
	Ypsolopha parenthesella	Micro	8	Ypsolophidae	Woody feeder			1	0	265	
	Ypsolopha sequella	Micro	9	Ypsolophidae	Woody feeder			1	0	265	
Magpie moth	*Abraxas grossulariata*	Macro	21.5	Geometridae	Woody feeder			0	5		63
Spectacle	*Abrostola tripartita*	Macro	16	Noctuidae	Unsown forb feeder			0	1		112
	Anania pelucidalis	Micro	11	Crambidae	Unsown forb feeder			0	1		112
	Argyresthia pygmaeella	Micro	6	Argyresthiidae	Woody feeder			0	1		112

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
Toadflax brocade	*Calophasia lunula*	Macro	14.5	Noctuidae	Unsown forb feeder			0	1		112
	Catoptria pinella	Micro	11.5	Crambidae	Grass feeder			0	1		112
Chinese character	*Cilix glaucata*	Macro	11.5	Drepanidae	Woody feeder		Y	0	2		93
	Cochylis molliculana	Micro	7	Tortricidae	Unsown forb feeder			0	1		112
	Coleophora sternipennella	Micro	6	Coleophoridae	Unsown forb feeder			0	1		112
	Dichrorampha aeratana	Micro	7	Tortricidae	Sown forb feeder			0	5		63
	Dichrorampha alpinana	Micro	7	Tortricidae	Sown forb feeder			0	5		63
	Dichrorampha petiverella	Micro	6	Tortricidae	Sown forb feeder			0	4		68
	Dichrorampha vancouverana	Micro	6.5	Tortricidae	Sown forb feeder			0	9		43
Burnet companion	*Euclidia glyphica*	Macro	14	Noctuidae	Unsown forb feeder			0	1		112
	Eucosma sp.	Micro	8.5	Tortricidae	Unsown forb feeder			0	1		112
Grey pug	*Eupithecia subfuscata*	Macro	11	Geometridae	Polyphagous		Y	0	1		112
Small emerald	*Hemistola chrysoprasaria*	Macro	18.5	Geometridae	Woody feeder			0	1		112
Common emerald	*Hemithea aestivaria*	Macro	15.5	Geometridae	Woody feeder			0	4		68

								Total abundance		Rank abundance	
Common name	Scientific name	Size class	Forewing length	Family	Feeding guild	Found nectaring	Declining species	Trap	Transect	Trap	Transect
Small fan-foot	*Herminia grisealis*	Macro	12	Noctuidae	Woody feeder			0	1		112
Ash bud moth	*Prays fraxinella*	Micro	7.5	Pyralidae	Woody feeder			0	1		112
	Tischeria ekebladella	Micro	4.5	Tischeriidae	Woody feeder			0	1		112
Sallow	*Xanthia icteritia*	Macro	15.5	Noctuidae	Polyphagous		Y	0	1		112
Red twin-spot carpet	*Xanthorhoe spadicearia*	Macro	12.5	Geometridae	Unsown forb feeder			0	2		93
Six-spot burnet	*Zygaena filipendulae*	Macro	17	Zygaenidae	Unsown forb feeder			0	6		55

4.6.3 Model outputs and statistical tests

4.6.3.1 Abundance

Table S4.4. The effect of field margin treatment on the abundance of adult moths and larvae; and the frequency of behavioural events observed. *Significance of parameters of GLMMs according to Likelihood Ratio Tests with subsets of moth abundance as response variables, and Treatment (or Treatment:Year) plus two landscape variables as the explanatory variables. Significant parameters ($p < 0.05$) are highlighted in bold.*

Method	Response	Parameter	Likelihood ratio test statistic (x^2)	p-value
Traps	Total (all species)	**Treatment**	**44.6**	**< 0.0001*****
		Woody boundary	**7.62**	**0.006****
		Long grass 200 m	0.434	0.510
	Woody plant feeders	Treatment	4.76	0.093
		Woody 50 m	**16.4**	**< 0.0001*****
		Long grass 200 m	1.90	0.168
	Grass feeders	Treatment	1.55	0.461
		Woody 25 m	1.75	0.186
		Long grass 200 m	0.922	0.337
	Unsown forb feeders	**Treatment**	**22.0**	**< 0.0001*****
		Woody boundary	2.90	0.088
		Long grass 50 m	0.319	0.572
	Sown forb feeders	**Treatment:year**	**14.0**	**0.00092*****
		Woody 25 m	2.14	0.144
		Long grass 200 m	0.538	0.463
	Polyphagous	**Treatment**	**10.7**	**0.0048****
		Woody boundary	**15.3**	**< 0.0001*****
		Long grass 50 m	**9.71**	**0.002****
	Non-plant feeders	Treatment	2.00	0.368
		Woody boundary	**29.1**	**< 0.0001*****
		Long grass 100 m	0.749	0.387
	Nectar feeders	**Treatment**	**24.5**	**< 0.0001**
		Woody boundary	**3.87**	**0.049***
		Long grass 100 m	0.616	0.532
	Declining species	**Treatment**	**22.2**	**< 0.0001*****
		Woody boundary	**4.03**	**0.045***
		Long grass 200 m	1.37	0.241
Transects	Total (all species)	**Treatment:year**	**6.57**	**0.037***
		Woody 100 m	0.873	0.350
		Long grass 200 m	**5.86**	**0.016***
		Temperature	**8.58**	**0.003****

Method	Response	Parameter	Likelihood ratio test statistic (x^2)	p-value
	Woody plant feeders	**Treatment**	**8.91**	**0.012***
		Woody boundary	**13.8**	**0.0002*****
		Long grass 200 m	2.89	0.089
		Temperature	0.115	0.735
	Grass feeders	**Treatment:year**	**11.6**	**0.003****
		Woody 200 m	3.33	0.068
		Long grass 100 m	1.79	0.181
		Temperature	1.57	0.210
	Unsown forb feeders	**Treatment**	**13.8**	**0.001****
		Woody boundary	2.94	0.086
		Long grass 200 m	**9.06**	**0.003****
		Temperature	1.99	0.158
	Sown forb feeders	**Treatment:year**	**10.0**	**0.007****
		Woody 25 m	2.61	0.106
		Long grass 200 m	1.79	0.181
		Temperature	**6.96**	**0.008****
	Polyphagous	Treatment	1.69	0.429
		Woody boundary	2.10	0.147
		Long grass 25 m	**9.81**	**0.002****
		Temperature	2.09	0.148
	Non-plant feeders	Treatment:year	6.88	0.032
		Woody 100 m	**16.3**	**< 0.0001*****
		Long grass 200 m	2.54	0.111
		Temperature	**6.45**	**0.011***
	Nectar feeders	**Treatment:year**	**13.5**	**0.001****
		Woody 25 m	0.872	0.351
		Long grass 200 m	**4.81**	**0.028***
		Temperature	2.10	0.148
	Declining species	Treatment	1.29	0.526
		Woody 25 m	3.10	0.078
		Long grass 200 m	0.274	0.601
		Temperature	1.87	0.171
Larvae counts	Larval abundance	**Treatment**	**10.3**	**0.006****
		Woody 50 m	2.68	0.102
		Long grass 25 m	3.37	0.067
Sweep net samples sept 2019	Larval abundance	**Treatment**	**13.2**	**0.001****
		Woody boundary	1.82	0.177
		Long grass 200 m	0.667	0.414
Behavioural observations	Nectaring events	**Treatment**	**13.0**	**< 0.0001*****
		Woody boundary	2.45	0.118
		Long grass 50 m	**6.95**	**0.008****
	Mating events	Treatment	0.508	0.776
		Woody boundary	2.29	0.130

Method	Response	Parameter	Likelihood ratio test statistic (x^2)	p-value
		Long grass 100 m	0.194	0.659

Table S4.5. Post hoc analysis to determine whether field margin treatment affects moth abundance according to species feeding guild*. Post-hoc pairwise contrasts of estimated marginal mean abundance between treatments in nine species groups. Estimates are the differences between the estimated marginal means. P-values are corrected for multiple comparisons with the Tukey method. Significant contrasts (p < 0.05) are highlighted in bold. Analysis was done in the emmeans package in R. Treatment abbreviations: GR = Grass, BC = Bladder campion, WF = Wildflower.*

Method	Response	Treatment comparison	Contrast estimate	Std. Error	Z	p-value
Traps	Total (all species)	GR - BC	-0.0638	0.050	-1.29	0.403
		GR - WF	**-0.304**	**0.049**	**-6.28**	**< 0.0001*****
		BC - WF	**-0.241**	**0.049**	**-4.92**	**< 0.0001*****
	Unsown forb feeders	**GR - BC**	**-0.201**	**0.075**	**-2.68**	**0.0204***
		GR - WF	**-0.349**	**0.075**	**-4.70**	**< 0.0001*****
		BC - WF	-0.148	0.074	-2.00	0.112
	Sown forb feeders 2018	GR - BC	0.0129	0.178	0.0730	0.997
		GR - WF	**-1.14**	**0.161**	**- 7.05**	**< 0.0001*****
		BC - WF	**-1.15**	**0.163**	**-7.05**	**< 0.0001*****
	Sown forb feeders 2019	GR - BC	0.0020	0.229	0.01	1.00
		GR - WF	**- 1.90**	**0.189**	**-10.0**	**< 0.0001*****
		BC - WF	**-1.90**	**0.191**	**-9.96**	**< 0.0001*****
	Polyphagous	GR - BC	-0.135	0.097	-1.40	0.342
		GR - WF	**-0.307**	**0.097**	**-3.24**	**0.003****
		BC - WF	-0.172	0.093	-1.85	0.154
	Nectar feeders	GR - BC	-0.100	0.058	-1.72	0.194
		GR - WF	**-0.281**	**0.058**	**-4.87**	**< 0.0001*****
		BC - WF	**-0.180**	**0.058**	**-3.09**	**0.006****
	Declining species	**GR - BC**	**-0.275**	**0.091**	**-3.03**	**0.007****
		GR - WF	**-0.410**	**0.088**	**-4.64**	**< 0.0001*****
		BC - WF	-0.135	0.086	-1.58	0.254
Transects	Total (all species) 2018	GR - BC	0.211	0.117	1.81	0.168
		GR - WF	**-0.272**	**0.113**	**-2.42**	**0.042***
		BC - WF	**-0.483**	**0.115**	**-4.20**	**< 0.0001*****
	Woody plant feeders	GR - BC	0.732	0.315	2.33	0.052
		GR - WF	-0.101	0.252	-0.40	0.915
		BC - WF	**-0.834**	**0.307**	**-2.71**	**0.018***
	Grass feeders 2018	**GR - BC**	**0.413**	**0.173**	**2.38**	**0.046***
		GR - WF	0.252	0.168	1.50	0.292
		BC - WF	-0.160	0.176	-0.91	0.633
		GR - BC	0.207	0.129	1.60	0.246

Method	Response	Treatment comparison	Contrast estimate	Std. Error	Z	p-value
	Grass feeders 2019	**GR - WF**	**0.776**	**0.135**	**5.73**	**< 0.0001*******
		BC - WF	**0.569**	**0.138**	**4.13**	**0.0001*******
	Unsown forb feeders	GR - BC	0.0285	0.134	0.212	0.976
		GR - WF	**-0.3873**	**0.128**	**-3.03**	**0.007****
		BC - WF	**-0.4158**	**0.128**	**-3.24**	**0.003****
	Sown forb feeders 2018	GR - BC	-0.634	0.506	-1.25	0.421
		GR - WF	**-2.26**	**0.444**	**-5.10**	**< 0.0001*******
		BC - WF	**-1.62**	**0.374**	**-4.35**	**< 0.0001*******
	Sown forb feeders 2019	GR - BC	-0.0131	0.482	-0.03	0.998
		GR - WF	**-3.21**	**0.377**	**-8.50**	**< 0.0001*******
		BC - WF	**-3.19**	**0.369**	**-8.65**	**< 0.0001*******
	Non-plant feeders 2019	GR - BC	-0.413	0.351	-1.18	0.466
		GR - WF	**-1.17**	**0.321**	**-3.64**	**0.001*******
		BC - WF	**-0.753**	**0.286**	**-2.64**	**0.023***
	Nectar feeders 2018	GR - BC	0.117	0.158	0.74	0.738
		GR - WF	-0.302	0.153	-1.98	0.118
		BC - WF	**-0.419**	**0.155**	**-2.71**	**0.019***
	Nectar feeders 2019	GR - BC	0.0969	0.128	0.76	0.730
		GR - WF	**0.331**	**0.132**	**2.52**	**0.032***
		BC - WF	0.234	0.132	1.78	0.178
Larvae counts	Larval abundance	**GR - BC**	**-0.579**	**0.243**	**-2.38**	**0.046***
		GR - WF	0.169	0.291	0.58	0.829
		BC - WF	**0.748**	**0.262**	**2.86**	**0.012***
Sweep net samples. Sept 2019	Larval abundance	GR - BC	-0.169	0.329	-0.51	0.865
		GR - WF	**1.47**	**0.556**	**2.64**	**0.023***
		BC - WF	**1.64**	**0.549**	**2.98**	**0.008****
Behavioural observations	Nectaring events	**GR - BC**	**-1.75**	**0.493**	**-3.55**	**0.001****
		GR - WF	**-1.71**	**0.495**	**-3.46**	**0.002****
		BC - WF	0.0383	0.281	0.14	0.990

Table S4.6. Selection of best spatial scale for traps. *AICc values of GLMMs with moth abundance caught in traps as a function of treatment plus two landscape variables: one 'woody' and one 'grassy'. The woody variable can be either a continuous variable (percentage woody vegetation within a certain radius of the trap site) or a binary variable (trap site is/is not adjacent to a woody boundary feature). The grassy variable is the percentage of long grass and rough low vegetation within a certain radius of the trap site. The models are ordered by increasing AICc. The model with the lowest AICc was used.*

Moth subset	Woody variable	Grassy variable	AICc	ΔAICc
Total (all species)	Boundary	200 m	4804.826	0
	Boundary	50 m	4804.939	0.113
	Boundary	100 m	4805.022	0.196
	Boundary	25 m	4805.246	0.42
	200 m	200 m	4808.568	3.742
	200 m	100 m	4809.859	5.033
	200 m	25 m	4810.294	5.468
	50 m	200 m	4810.375	5.549
	50 m	25 m	4810.786	5.96
	50 m	100 m	4810.822	5.996
	100 m	200 m	4810.883	6.057
	100 m	25 m	4810.887	6.061
	100 m	100 m	4811.002	6.176
	25 m	25 m	4811.208	6.382
	25 m	100 m	4811.616	6.79
	50 m	50 m	4811.735	6.909
	25 m	200 m	4811.834	7.008
	200 m	50 m	4811.906	7.08
	100 m	50 m	4812.31	7.484
	25 m	50 m	4812.478	7.652
Woody plant feeders	50 m	200 m	1486.389	0
	50 m	100 m	1486.743	0.354
	Boundary	50 m	1487.167	0.778
	Boundary	100 m	1487.22	0.831
	50 m	25 m	1487.432	1.043
	50 m	50 m	1487.519	1.13
	Boundary	25 m	1488.029	1.64
	Boundary	200 m	1488.043	1.654
	25 m	50 m	1494.619	8.23
	25 m	25 m	1494.686	8.297
	25 m	100 m	1494.796	8.407
	100 m	25 m	1495.443	9.054
	25 m	200 m	1495.447	9.058
	100 m	100 m	1495.462	9.073
	100 m	50 m	1495.754	9.365
	100 m	200 m	1496.596	10.207
	200 m	25 m	1498.253	11.864

Moth subset	Woody variable	Grassy variable	AICc	ΔAICc
	200 m	50 m	1498.347	11.958
	200 m	100 m	1498.463	12.074
	200 m	200 m	1500.468	14.079
Grass feeders	25 m	200 m	3488.699	0
	Boundary	200 m	3489.302	0.603
	200 m	200 m	3489.398	0.699
	25 m	50 m	3489.421	0.722
	25 m	25 m	3489.493	0.794
	25 m	100 m	3489.56	0.861
	Boundary	50 m	3489.978	1.279
	100 m	200 m	3490.025	1.326
	Boundary	25 m	3490.105	1.406
	50 m	200 m	3490.191	1.492
	Boundary	100 m	3490.214	1.515
	50 m	50 m	3490.635	1.936
	50 m	25 m	3490.643	1.944
	200 m	50 m	3490.888	2.189
	50 m	100 m	3490.927	2.228
	200 m	25 m	3490.971	2.272
	100 m	25 m	3491.05	2.351
	100 m	50 m	3491.08	2.381
	100 m	100 m	3491.617	2.918
	200 m	100 m	3491.619	2.92
Unsown forb feeders	Boundary	50 m	3324.87	0
	Boundary	25 m	3325.079	0.209
	Boundary	100 m	3325.162	0.292
	Boundary	200 m	3325.162	0.292
	100 m	25 m	3326.203	1.333
	50 m	25 m	3326.405	1.535
	100 m	100 m	3326.49	1.62
	100 m	200 m	3326.511	1.641
	50 m	200 m	3326.601	1.731
	50 m	100 m	3326.626	1.756
	50 m	50 m	3326.628	1.758
	200 m	25 m	3326.772	1.902
	100 m	50 m	3326.782	1.912
	25 m	25 m	3326.83	1.96
	200 m	200 m	3327.188	2.318
	200 m	100 m	3327.206	2.336
	25 m	100 m	3327.436	2.566
	25 m	200 m	3327.447	2.577
	200 m	50 m	3327.606	2.736
	25 m	50 m	3327.704	2.834

Moth subset	Woody variable	Grassy variable	AICc	ΔAICc
Sown forb feeders	25 m	200 m	1688.274	0
	25 m	25 m	1688.281	0.007
	25 m	50 m	1688.47	0.196
	25 m	100 m	1688.53	0.256
	100 m	200 m	1689.721	1.447
	100 m	100 m	1689.725	1.451
	100 m	50 m	1689.727	1.453
	100 m	25 m	1689.742	1.468
	50 m	200 m	1689.794	1.52
	50 m	25 m	1689.808	1.534
	50 m	50 m	1689.871	1.597
	50 m	100 m	1689.874	1.6
	Boundary	50 m	1690.082	1.808
	Boundary	100 m	1690.169	1.895
	Boundary	25 m	1690.176	1.902
	Boundary	200 m	1690.18	1.906
	200 m	50 m	1690.206	1.932
	200 m	100 m	1690.234	1.96
	200 m	200 m	1690.252	1.978
	200 m	25 m	1690.266	1.992
Polyphagous	Boundary	50 m	2179.829	0
	Boundary	100 m	2179.904	0.075
	Boundary	200 m	2183.158	3.329
	Boundary	25 m	2184.055	4.226
	25 m	100 m	2184.541	4.712
	50 m	100 m	2185.753	5.924
	25 m	50 m	2185.976	6.147
	50 m	50 m	2186.034	6.205
	25 m	200 m	2187.515	7.686
	50 m	200 m	2188.924	9.095
	50 m	25 m	2189.389	9.56
	25 m	25 m	2189.58	9.751
	100 m	100 m	2190.153	10.324
	200 m	100 m	2190.677	10.848
	200 m	50 m	2191.115	11.286
	100 m	50 m	2191.253	11.424
	100 m	200 m	2192.162	12.333
	200 m	25 m	2192.279	12.45
	200 m	200 m	2192.368	12.539
	100 m	25 m	2193.309	13.48
Non-plant feeders	Boundary	100 m	1994.365	0
	Boundary	25 m	1994.741	0.376
	Boundary	50 m	1994.925	0.56

Moth subset	Woody variable	Grassy variable	AICc	ΔAICc
	Boundary	200 m	1995.016	0.651
	50 m	100 m	1998.903	4.538
	50 m	200 m	1999.384	5.019
	50 m	25 m	1999.53	5.165
	50 m	50 m	1999.789	5.424
	25 m	25 m	2001.897	7.532
	25 m	100 m	2001.969	7.604
	25 m	50 m	2002.275	7.91
	25 m	200 m	2002.341	7.976
	100 m	100 m	2006.154	11.789
	100 m	25 m	2007.079	12.714
	100 m	50 m	2007.958	13.593
	200 m	100 m	2008.051	13.686
	100 m	200 m	2008.78	14.415
	200 m	25 m	2009.786	15.421
	200 m	50 m	2011.09	16.725
	200 m	200 m	2011.415	17.05
Nectar feeders	Boundary	100 m	3917.751	0
	Boundary	200 m	3917.883	0.132
	Boundary	25 m	3918.065	0.314
	Boundary	50 m	3918.387	0.636
	50 m	200 m	3920.225	2.474
	50 m	100 m	3920.281	2.53
	50 m	25 m	3920.334	2.583
	25 m	25 m	3920.384	2.633
	25 m	100 m	3920.448	2.697
	100 m	25 m	3920.618	2.867
	200 m	25 m	3920.732	2.981
	100 m	100 m	3920.816	3.065
	25 m	200 m	3920.852	3.101
	200 m	100 m	3921.031	3.28
	100 m	200 m	3921.371	3.62
	25 m	50 m	3921.471	3.72
	50 m	50 m	3921.486	3.735
	200 m	200 m	3921.613	3.862
	100 m	50 m	3922.172	4.421
	200 m	50 m	3922.408	4.657
Declining species	Boundary	200 m	2509.361	0
	50 m	200 m	2509.813	0.452
	Boundary	50 m	2510.496	1.135
	Boundary	25 m	2510.631	1.27
	Boundary	100 m	2510.67	1.309
	25 m	200 m	2510.825	1.464

Moth subset	Woody variable	Grassy variable	AICc	ΔAICc
	100 m	200 m	2511.203	1.842
	50 m	50 m	2511.652	2.291
	50 m	100 m	2511.815	2.454
	25 m	50 m	2511.831	2.47
	50 m	25 m	2511.865	2.504
	25 m	100 m	2512.015	2.654
	25 m	25 m	2512.019	2.658
	100 m	100 m	2513.38	4.019
	200 m	200 m	2513.433	4.072
	100 m	25 m	2513.581	4.22
	100 m	50 m	2513.757	4.396
	200 m	25 m	2514.548	5.187
	200 m	100 m	2514.685	5.324
	200 m	50 m	2514.787	5.426

Table S4.7. Model output: the effect of field margin treatment type on moth abundance and behaviour. *Model coefficients from a GLMM.. All intercepts are for Treatment = GR, Boundary = n, and Woody and Grassy habitat set to their mean value. Values are on the predictor (log) scale. P-values shown here were not used to assess significance of parameters (this was done in Table S4.4) but are shown for completeness. For this reason, bold font and asterisks are not included here. Landscape variables are square root transformed and scaled (mean subtracted and divided by standard error).*

Method	Response	Parameter	Estimate	Std. Error	Z	p-value
Traps	Total (all species)	Intercept	2.18	0.159	13.7	< 0.0001
		BC	0.06	0.0500	1.29	0.198
		WF	0.30	0.049	6.28	< 0.0001
		Woody boundary	0.23	0.083	2.74	0.006
		Long grass 200 m	-0.04	0.058	-0.672	0.501
	Woody plant feeders	Intercept	-1.35	0.282	-4.80	< 0.0001
		BC	-0.25	0.131	-1.91	0.057
		WF	0.003	0.127	0.0200	0.984
		Woody 50 m	0.62	0.125	4.99	< 0.0001
		Long grass 200 m	-0.16	0.118	-1.39	0.165
	Grass feeders	Intercept	1.17	0.189	6.16	< 0.0001
		BC	-0.06	0.068	-0.84	0.401
		WF	0.03	0.067	0.39	0.697
		Woody 25 m	-0.09	0.073	-1.22	0.222
		Long grass 200 m	-0.08	0.085	-0.98	0.325
	Unsown forb feeders	Intercept	0.76	0.176	4.33	< 0.0001
		BC	0.20	0.075	2.68	0.008
		WF	0.35	0.075	4.67	< 0.0001
		Woody boundary	0.21	0.136	1.52	0.128

Method	Response	Parameter	Estimate	Std. Error	Z	p-value
		Long grass 50 m	0.04	0.075	0.55	0.583
	Wildflower feeders	Intercept	-1.30	0.360	-3.60	0.0003
		BC	-0.02	0.178	-0.07	0.942
		WF	1.14	0.161	7.05	< 0.0001
		Year 2019	-0.45	0.488	-0.91	0.362
		Woody 25 m	-0.13	0.089	-1.51	0.131
		Long grass 200 m	-0.09	0.119	-0.76	0.451
		BC : year 2019	0.01	0.288	0.04	0.970
		WF : year 2019	0.76	0.248	3.06	0.002
	Polyphagous	Intercept	-0.53	0.208	-2.54	0.011
		BC	0.14	0.097	1.40	0.162
		WF	0.31	0.095	3.24	0.001
		Woody boundary	0.37	0.091	4.01	< 0.0001
		Long grass 50 m	0.16	0.052	3.16	0.002
	Non-plant feeders	Intercept	-1.43	0.329	-4.35	<0.0001
		BC	0.01	0.108	0.94	0.347
		WF	0.15	0.108	1.39	0.166
		Woody boundary	0.94	0.172	5.49	< 0.0001
		Long grass 100 m	-0.10	0.112	-0.87	0.386
	Nectar feeders	Intercept	1.41	0.176	8.00	< 0.0001
		BC	0.10	0.058	1.73	0.084
		WF	0.28	0.058	4.87	< 0.0001
		Woody boundary	0.21	0.106	1.96	0.051
		Long grass 100 m	-0.07	0.080	-0.82	0.414
	Declining species	Intercept	-0.06	0.166	-0.28	0.778
		BC	0.28	0.091	3.03	0.002
		WF	0.41	0.088	4.64	< 0.0001
		Woody boundary	0.27	0.132	2.05	0.040
		Long grass 200 m	-0.10	0.084	-1.20	0.230
Transects	Total (All Species)	Intercept	1.50	0.163	9.24	< 0.0001
		BC	-0.21	0.117	-1.81	0.071
		WF	0.27	0.113	2.42	0.016
		Year 2019	0.89	0.218	4.08	< 0.0001
		Woody 100 m	0.05	0.051	0.94	0.349
		Long grass 200 m	0.14	0.057	2.40	0.016
		Temperature	0.18	0.062	2.96	0.003
		BC : year 2019	0.11	0.153	0.72	0.473
		WF : year 2019	-0.27	0.150	-1.78	0.075
	Woody plant feeders	Intercept	-3.90	0.448	-8.71	< 0.0001
		BC	-0.73	0.315	-2.32	0.020
		WF	0.10	0.253	0.40	0.688
		Woody boundary	2.01	0.414	4.86	< 0.0001
		Long grass 200 m	0.31	0.186	1.71	0.088

Method	Response	Parameter	Estimate	Std. Error	Z	p-value
		Temperature	0.06	0.184	0.34	0.735
	Grass feeders	Intercept	0.24	0.348	0.69	0.491
		BC	-0.41	0.173	-2.38	0.017
		WF	-0.25	0.168	-1.50	0.134
		Year 2019	1.34	0.471	2.85	0.004
		Woody 200 m	0.17	0.089	1.85	0.064
		Long grass 100 m	-0.14	0.100	-1.38	0.167
		Temperature	0.12	0.092	1.26	0.209
		BC : year 2019	0.21	0.216	0.95	0.341
		WF : year 2019	-0.52	0.215	-2.43	0.015
	Unsown forb feeders	Intercept	-0.27	0.174	-1.55	0.121
		BC	-0.03	0.134	-0.20	0.839
		WF	0.39	0.128	3.05	0.002
		Woody boundary	0.26	0.158	1.64	0.102
		Long grass 200 m	0.26	0.088	2.95	0.003
		Temperature	0.16	0.090	1.42	0.157
	Sown feeders	Intercept	-3.41	0.532	-6.40	< 0.0001
		BC	0.63	0.506	1.25	0.210
		WF	2.26	0.444	5.08	< 0.0001
		Year 2019	0.53	0.675	0.78	0.433
		Woody 25 m	-0.23	0.133	-1.73	0.084
		Long grass 200 m	0.22	0.173	2.62	0.206
		Temperature	0.42	0.161	2.22	0.009
		BC : year 2019	-0.62	0.699	-0.89	0.375
		WF : year 2019	0.95	0.580	1.63	0.102
	Polyphagous	Intercept	-2.29	0.469	-4.88	< 0.0001
		BC	-0.05	0.173	-0.27	0.785
		WF	0.17	0.171	0.96	0.335
		Woody boundary	0.37	0.256	1.43	0.152
		Long grass 25 m	0.53	0.173	3.02	0.003
		Temperature	-0.30	0.208	-1.46	0.145
	Non-plant feeders	Intercept	-2.01	0.362	-5.56	< 0.0001
		BC	-0.20	0.360	-0.57	0.570
		WF	-0.07	0.356	-0.20	0.840
		Year 2019	-0.17	0.481	-0.34	0.731
		Woody 100 m	0.62	0.148	4.16	< 0.0001
		Long grass 200 m	0.23	0.143	1.57	0.116
		Temperature	0.37	0.146	2.57	0.010
		BC : year 2019	0.62	0.501	1.23	0.217
		WF : year 2019	1.24	0.478	2.59	0.010
	Nectar feeders	Intercept	0.60	0.196	3.04	0.002
		BC	-0.12	0.158	-0.74	0.458
		WF	0.30	0.153	1.98	0.048

Method	Response	Parameter	Estimate	Std. Error	Z	p-value
		Year 2019	1.02	0.257	3.98	< 0.0001
		Woody 50 m	0.06	0.066	0.95	0.341
		Long grass 200 m	0.16	0.077	2.10	0.036
		Temperature	0.12	0.081	1.45	0.148
		BC : year 2019	0.02	0.203	0.10	0.920
		WF : year 2019	-0.63	0.201	-3.15	0.002
	Declining species	Intercept	-1.50	0.177	-8.47	< 0.0001
		BC	0.19	0.195	0.98	0.326
		WF	0.19	0.196	0.99	0.323
		Woody 100 m	-0.16	0.090	-1.75	0.081
		Long grass 200 m	0.05	0.096	0.53	0.599
		Temperature	-0.15	0.111	-1.37	0.170
Larvae counts	Overall larval	Intercept	0.22	0.298	0.73	0.463
		BC	0.58	0.243	2.38	0.017
		WF	-0.17	0.291	-0.58	0.560
		Woody 50 m	0.33	0.206	1.61	0.107
		Long grass 25 m	0.41	0.227	1.80	0.072
Sweep net samples	Overall larval	Intercept	-0.20	0.339	-0.59	0.552
		BC	0.17	0.329	0.51	0.608
		WF	-1.47	0.556	-2.64	0.008
		Woody boundary	0.53	0.378	1.39	0.165
		Long grass 100 m	-0.17	0.207	-0.81	0.419
Behaviour	Nectaring events	Intercept	-1.15	0.500	-2.30	0.022
		BC	1.75	0.493	3.55	0.0004
		WF	1.71	0.495	3.46	0.0005
		Woody boundary	-0.67	0.409	-1.63	0.104
		Long grass 50 m	-0.60	0.225	-2.65	0.008
	Mating events	Intercept	0.76	0.442	1.71	0.088
		BC	0.11	0.552	0.20	0.841
		WF	-0.29	0.570	-0.50	0.614
		Woody boundary	-0.74	0.485	-1.52	0.128
		Long grass 100 m	-0.10	0.232	-0.44	0.658

Table S4.8. Selection of the best spatial scale for transects. *AICc values of GLMMs with moth abundance observed per 70 m transect as a function of treatment plus two landscape variables: one 'woody' and one 'grassy'. The woody variable can be either a continuous variable (percentage woody vegetation within a certain radius of the trap site) or a binary variable (trap site is/is not adjacent to a woody boundary feature). The grassy variable is the percentage of long grass and rough low vegetation within a certain radius of the trap site. The models are ordered by increasing AICc. The model with the lowest AICc was used.*

Moth subset	Woody variable	Grassy variable	AICc	ΔAICc
All species (total abundance)	100 m	200 m	3277.588	0
	200 m	200 m	3277.77	0.182
	50 m	200 m	3278.007	0.419
	Boundary	200 m	3278.448	0.86
	25 m	200 m	3278.459	0.871
	200 m	25 m	3280.65	3.062
	200 m	100 m	3281.041	3.453
	200 m	50 m	3281.091	3.503
	100 m	25 m	3281.903	4.315
	100 m	100 m	3282.011	4.423
	100 m	50 m	3282.321	4.733
	50 m	100 m	3282.714	5.126
	50 m	25 m	3282.82	5.232
	25 m	100 m	3283.007	5.419
	Boundary	100 m	3283.03	5.442
	50 m	50 m	3283.17	5.582
	25 m	25 m	3283.439	5.851
	Boundary	25 m	3283.465	5.877
	25 m	50 m	3283.664	6.076
	Boundary	50 m	3283.694	6.106
Woody plant feeders	Boundary	200 m	417.0219	0
	Boundary	100 m	418.8613	1.8394
	Boundary	25 m	419.4172	2.3953
	Boundary	50 m	419.6654	2.6435
	25 m	200 m	422.6915	5.6696
	25 m	100 m	423.64	6.6181
	25 m	25 m	424.0625	7.0406
	25 m	50 m	424.3139	7.292
	50 m	200 m	426.3035	9.2816
	50 m	50 m	426.307	9.2851
	50 m	100 m	426.3162	9.2943
	50 m	25 m	426.4012	9.3793
	100 m	200 m	427.0033	9.9814
	200 m	50 m	427.1209	10.099
	100 m	100 m	427.1413	10.1194
	200 m	200 m	427.1487	10.1268

Moth subset	Woody variable	Grassy variable	AICc	ΔAICc
	200 m	25 m	427.1657	10.1438
	200 m	100 m	427.17	10.1481
	100 m	50 m	427.2212	10.1993
	100 m	25 m	427.2259	10.204
Grass feeders	200 m	100 m	2395.285	0
	200 m	50 m	2395.481	0.196
	50 m	200 m	2395.875	0.59
	100 m	200 m	2396.009	0.724
	100 m	50 m	2396.193	0.908
	100 m	100 m	2396.219	0.934
	200 m	25 m	2396.46	1.175
	100 m	25 m	2396.653	1.368
	200 m	200 m	2396.874	1.589
	50 m	50 m	2397.068	1.783
	50 m	100 m	2397.083	1.798
	50 m	25 m	2397.258	1.973
	Boundary	50 m	2397.328	2.043
	25 m	200 m	2397.532	2.247
	Boundary	200 m	2397.799	2.514
	Boundary	25 m	2397.837	2.552
	Boundary	100 m	2397.985	2.700
	25 m	50 m	2398.264	2.979
	25 m	100 m	2398.57	3.285
	25 m	25 m	2398.675	3.39
Unsown forb feeders	Boundary	200 m	1673.178	0
	50 m	200 m	1674.699	1.521
	100 m	200 m	1675.125	1.947
	200 m	200 m	1675.438	2.26
	25 m	200 m	1675.962	2.784
	Boundary	100 m	1676.922	3.744
	200 m	100 m	1678.039	4.861
	50 m	100 m	1678.166	4.988
	100 m	100 m	1678.581	5.403
	200 m	50 m	1679.499	6.321
	25 m	100 m	1679.562	6.384
	Boundary	50 m	1679.571	6.393
	200 m	25 m	1679.861	6.683
	50 m	50 m	1680.683	7.505
	Boundary	25 m	1680.818	7.640
	100 m	50 m	1680.852	7.674
	100 m	25 m	1681.623	8.445
	50 m	25 m	1681.85	8.672
	25 m	50 m	1682.446	9.268

Moth subset	Woody variable	Grassy variable	AICc	ΔAICc
	25 m	25 m	1683.366	10.19
Sown forbs	25 m	200 m	847.0959	0
	25 m	25 m	848.3352	1.239
	25 m	100 m	848.4843	1.388
	25 m	50 m	848.7372	1.641
	200 m	200 m	848.9871	1.891
	50 m	200 m	849.3248	2.229
	Boundary	200 m	849.3981	2.302
	100 m	200 m	849.6235	2.528
	Boundary	25 m	850.9007	3.805
	50 m	25 m	850.9466	3.851
	200 m	25 m	851.0691	3.973
	100 m	25 m	851.1582	4.062
	50 m	100 m	851.3526	4.257
	Boundary	100 m	851.4521	4.356
	50 m	50 m	851.5663	4.470
	Boundary	50 m	851.5703	4.474
	200 m	100 m	851.7002	4.604
	200 m	50 m	851.7882	4.692
	100 m	100 m	851.8596	4.764
	100 m	50 m	851.8694	4.774
Polyphagous	Boundary	25 m	1095.823	0
	25 m	25 m	1096.845	1.022
	Boundary	50 m	1097.523	1.700
	100 m	25 m	1097.92	2.097
	200 m	25 m	1097.999	2.176
	50 m	25 m	1098.04	2.217
	25 m	50 m	1098.605	2.782
	100 m	50 m	1098.744	2.921
	50 m	50 m	1099.071	3.248
	200 m	50 m	1099.12	3.297
	100 m	100 m	1100.861	5.038
	50 m	200 m	1101.044	5.221
	100 m	200 m	1101.082	5.259
	50 m	100 m	1101.126	5.303
	Boundary	100 m	1101.166	5.343
	Boundary	200 m	1101.423	5.600
	200 m	100 m	1101.696	5.873
	25 m	100 m	1101.762	5.939
	200 m	200 m	1101.822	5.999
	25 m	200 m	1101.948	6.125
Non-plant feeders	100 m	200 m	779.8543	0
	100 m	100 m	781.396	1.542

Moth subset	Woody variable	Grassy variable	AICc	ΔAICc
	50 m	200 m	781.5946	1.740
	100 m	50 m	781.9378	2.084
	100 m	25 m	782.0656	2.211
	50 m	100 m	782.5665	2.712
	Boundary	200 m	782.7066	2.852
	25 m	200 m	783.0936	3.239
	200 m	50 m	783.4043	3.550
	200 m	25 m	783.4282	3.574
	200 m	200 m	783.4531	3.599
	200 m	100 m	783.4695	3.615
	50 m	50 m	783.6151	3.761
	50 m	25 m	784.5006	4.646
	Boundary	100 m	784.6837	4.829
	25 m	100 m	785.6661	5.812
	Boundary	50 m	786.6154	6.761
	Boundary	25 m	787.3405	7.486
	25 m	50 m	788.1033	8.249
	25 m	25 m	788.7323	8.878
Nectar feeders	50 m	200 m	2579.152	0
	100 m	200 m	2579.505	0.353
	25 m	200 m	2579.743	0.591
	Boundary	200 m	2579.935	0.783
	200 m	200 m	2579.96	0.808
	100 m	25 m	2581.235	2.083
	200 m	25 m	2581.316	2.164
	50 m	50 m	2581.976	2.824
	25 m	25 m	2582	2.848
	Boundary	25 m	2582.251	3.099
	100 m	50 m	2582.27	3.118
	200 m	50 m	2582.287	3.135
	200 m	100 m	2582.795	3.643
	50 m	25 m	2582.803	3.651
	50 m	100 m	2582.803	3.651
	100 m	100 m	2582.857	3.705
	25 m	50 m	2583.017	3.865
	Boundary	50 m	2583.083	3.931
	Boundary	100 m	2583.355	4.203
	25 m	100 m	2583.504	4.352
Declining species	100 m	200 m	811.4559	0
	200 m	200 m	811.9398	0.484
	100 m	25 m	812.1134	0.658
	100 m	50 m	812.1236	0.668
	100 m	100 m	812.1406	0.685

Moth subset	Woody variable	Grassy variable	AICc	ΔAICc
	25 m	50 m	812.5914	1.136
	25 m	100 m	812.6645	1.209
	25 m	200 m	812.7088	1.253
	25 m	25 m	812.8523	1.396
	50 m	50 m	812.9415	1.486
	50 m	200 m	812.9595	1.504
	50 m	100 m	813.065	1.609
	50 m	25 m	813.1787	1.723
	200 m	25 m	813.4482	1.992
	200 m	100 m	813.5208	2.065
	200 m	50 m	813.5732	2.117
	Boundary	200 m	813.9226	2.467
	Boundary	50 m	813.9795	2.524
	Boundary	100 m	814.03	2.574
	Boundary	25 m	814.1649	2.709

4.6.3.2 Diversity

Table S4.9. The effect of field margin treatment on species richness and diversity. *Observed and asymptotically estimated species diversity measures for moths recorded in traps and transects in years 2018 and 2019 for Hill numbers q = 0, 1 and 2.*

Sample method	Year	Diversity measure (hill number)	Treatment	Observed	Estimated	Standard error of estimate	Lower 95%	Upper 95%
Traps	2018	q = 0	GR	210	276.0	21.9	245.1	334.3
			BC	225	317.1	28.0	276.5	390.0
			WF	238	344.2	31.1	298.5	424.4
		q = 1	GR	62.1	66.7	2.35	62.1	71.3
			BC	67.8	73.2	2.40	68.6	77.9
			WF	71.6	76.5	2.29	72.2	80.8
		q = 2	GR	28.5	28.9	1.10	28.5	31.1
			BC	33.2	33.7	1.21	33.2	36.1
			WF	38.5	39.0	1.22	38.5	41.4
	2019	q = 0	GR	139	223.1	30.4	181.3	306.1
			BC	142	211.4	25.6	176.5	281.8
			WF	173	333.4	54.2	257.1	478.7
		q = 1	GR	26.3	28.2	1.26	26.3	30.5
			BC	27.7	29.5	1.32	27.7	32.1
			WF	39.9	43.1	1.67	39.9	46.3
		q = 2	GR	12.2	12.3	0.52	12.2	13.3

			BC	12.3	12.4	0.52	12.3	13.4
			WF	18.5	18.6	0.72	18.5	20.0
Transects	2018	q = 0	GR	67	156.8	52.7	97.9	327.9
			BC	66	129.8	32.9	90.7	231.3
			WF	82	142.1	27.2	107.8	222.1
		q = 1	GR	20.5	23.8	2.00	20.5	27.7
			BC	23.3	27.8	2.35	23.3	32.4
			WF	26.1	29.8	2.12	26.1	34.0
		q = 2	GR	9.5	9.7	0.81	9.5	11.2
			BC	11.2	11.5	0.10	11.2	13.5
			WF	12.1	12.3	0.92	12.1	14.1
	2019	q = 0	GR	69	95.3	12.8	79.6	134.0
			BC	71	124.3	27.1	91.8	207.6
			WF	96	158.2	28.8	122.2	243.7
		q = 1	GR	7.1	7.4	0.35	7.1	8.0
			BC	8.9	9.4	0.55	8.9	10.5
			WF	22.8	24.6	1.23	22.8	27.0
		q = 2	GR	3.6	3.6	0.14	3.6	3.9
			BC	4.4	4.4	0.17	4.4	4.7
			WF	11.0	11.1	0.52	11.0	12.1

Table S4.10. Species-specific responses to field margin treatments. *Results of multivariate GLMs constructed to test the individual species response to treatment. Species-specific treatment effects for BC and WF treatments compared against the baseline GR treatment. Only species with significant treatment effects are shown (95% confidence intervals do not include zero). The 'estimate' refers to difference in annual total per block of individual moths expected in the BC or WF treatment in comparison to the GR treatment (on the log-scale). Species marked * have a significant treatment effect in either both years or in both sample methods and are considered to have a consistent treatment effect. Forb species marked † are those that were sown in the BC and WF treatments Species marked with ‡ have a negative response to the treatment being tested.*

Method	Year	Taxa	Treatment	Estimate (±SE)	95% confidence interval	Hostplant(s)	Observed feeding on nectar
Traps	2018	*Coleophora alcyonipennella*	BC	1.53 (±0.65)	0.27, 2.80	White clover	
		Celypha striana		1.00 (±0.35)	0.33, 1.68	Dandelion	
		Timandra comae (blood vein)		1.00 (±0.51)	0.00, 1.99	Polyphagous on forbs	
		Caradrina morpheus (mottled rustic)		0.85 (±0.35)	0.16, 1.54	Polyphagous on forbs	Wild carrot† and yarrow†
		Eilema griseola (dingy footman)		0.71 (±0.25)	0.22, 1.20	Lichens	
		Xestia xanthographa (square spot rustic)		0.49 (±0.14)	0.21, 0.77	Polyphagous on grasses and forbs	Blackberry fruit, ragwort and spear thistle
		Cameraria ohridella (horse chestnut leaf-miner)		-0.57 (±0.28)	-1.12, -0.01	Horse chestnut	
		Lobesia abscisana‡		-1.09 (±0.52)	-2.12, -0.07	Creeping thistle	
		Cnephasia longana‡		-2.78 (±1.18)	-5.09, -0.46	Oligophagous on forbs	
Traps	2018	*Bucculatrix nigricomella**	WF	3.59 (±1.27)	1.09, 6.08	Oxeye daisy†	

Method	Year	Taxa	Treatment	Estimate (±SE)	95% confidence interval	Hostplant(s)	Observed feeding on nectar
		*Cochylimorpha straminea**		3.50 (±0.59)	2.33, 4.66	Common knapweed†	
		Aspilapteryx tringipennella		2.57 (±1.08)	0.45, 4.69	Ribwort plantain	
		Charanyca trigrammica (treble lines)		2.50 (±1.09)	0.36, 4.64	Polyphagous on forbs	
		Pexicopia malvella (hollyhock seed moth)*		2.14 (±0.62)	0.92, 3.35	Marsh mallow and hollyhocks†	
		Eudonia pallida		1.85 (±0.73)	0.41, 3.29	Moss	
		Coleophora alcyonipennella		1.72 (±0.64)	0.47, 2.98	White clover	
		Aethes smeathmanniana		1.70 (±0.44)	0.85, 2.56	Yarrow†, common knapweed* and corn chamomile	
		Idaea dimidiata (single dotted wave)*		1.15 (±0.41)	0.35, 1.96	Polyphagous on forbs	Traveller's joy
Traps	2018	*Caradrina morpheus* (mottled rustic)*	WF	1.10 (±0.33)	0.44, 1.75	Polyphagous on forbs	Wild carrot† and yarrow†
		Agriphila geniculea		0.93 (±0.41)	0.12, 1.74	Grasses	Yarrow†
		Mesapamea secalis (common rustic agg.)		0.92 (±0.41)	0.11, 1.73	Grasses	Blackberry fruit and yarrow†
		Hoplodrina octogenaria (uncertain)		0.90 (±0.40)	0.12, 1.68	Polyphagous on forbs	Traveller's joy
		*Eucosma hohenwartiana**		0.83 (±0.40)	0.04, 1.62	Common knapweed†	

Method	Year	Taxa	Treatment	Estimate (±SE)	95% confidence interval	Hostplant(s)	Observed feeding on nectar
		Cnephasia sp		0.64 (±0.28)	0.10, 1.18	Several species feed on oxeye daisy† as well as other forbs	
		*Eucosma cana**		0.58 (±0.22)	0.14, 1.02	Knapweeds† and thistles	Yarrow†
		*Blastobasis adustella**		0.55 (±0.15)	0.25, 0.86	Polyphagous	Blackberry fruit and yarrow†
		Eilema griseola (dingy footman)		0.53 (±0.25)	0.05, 1.02	Lichens	
		Xestia xanthographa (square spot rustic)*		0.51 (±0.14)	0.24, 0.79	Polyphagous on grasses and forbs	Blackberry fruit, ragwort and spear thistle
		Mythimna pallens (common wainscot)*		0.40 (±0.17)	0.05, 0.74	Grasses	Blackberry fruit, ragwort, Traveller's joy, wild carrot† and yarrow†
		Cameraria ohridella (horse chestnut leaf-miner) ‡		-0.67 (±0.28)	-1.22, -0.12	Horse chestnut	
		Mesoligia furuncula (cloaked minor) ‡		-1.22 (±0.61)	-2.42, -0.03	Grasses	
		Cnephasia longana‡		-1.52 (±0.68)	-2.84, -0.19	polyphagous on forbs	
Traps	2019	*Mythimna impura* (smoky wainscot)	BC	1.40 (±0.53)	0.35, 2.44	Grasses	
		Agriphila straminella‡		-0.33 (±0.14)	-0.61, -0.05	Grasses	

Method	Year	Taxa	Treatment	Estimate (±SE)	95% confidence interval	Hostplant(s)	Observed feeding on nectar
		Agriphila tristella‡		-1.03 (±0.40)	-1.81, -0.26	Grasses	
Traps	2019	*Eucosma cana**	WF	3.00 (±0.57)	1.89, 4.12	Knapweeds† and thistles	Yarrow†
		*Eucosma hohenwartiana**		2.63 (±0.52)	1.60, 3.66	Common knapweed†	
		*Cochylimorpha straminea**		2.41 (±0.40)	1.63, 3.19	Common knapweed†	
		*Bucculatrix nigricomella**		2.32 (±1.16)	0.04, 4.60	Oxeye daisy†	
		Pexicopia malvella (hollyhock seed moth)*		2.27 (±0.82)	0.67, 3.88	Marsh mallow and hollyhocks†	
		Caradrina morpheus (mottled rustic)*		1.63 (±0.76)	0.13, 3.13	Polyphagous on forbs	Wild carrot† and yarrow†
		Mythimna impura (smoky wainscot)		1.15 (±0.57)	0.03, 2.26	Grasses	
		Celypha lacunana		0.81 (±0.23)	0.36, 1.26	Polyphagous on forbs	
		Xestia c-nigrum (setaceous hebrew character)		0.71 (±0.22)	0.29, 1.14	Polyphagous on forbs	Blackberry fruit and hogweed
		*Chrysoteuchia culmella**‡		-0.38 (±0.13)	-0.64, -0.13	Grasses	Hogweed, wild carrot† and yarrow†
		*Agriphila straminella**‡		-0.76 (±0.16)	-1.06, -0.45	Grasses	
		*Agriphila tristella**‡		-0.95 (±0.36)	-1.65, -0.25	Grasses	
		Blastobasis lacticolella		-2.41 (±1.05)	-4.46, -0.36	polyphagous	

Method	Year	Taxa	Treatment	Estimate (±SE)	95% confidence interval	Hostplant(s)	Observed feeding on nectar
Transect	2018	*Chrysoteuchia culmella**‡	BC	-0.63 (±0.22)	-1.05, -0.20	Grasses	Hogweed, wild carrot† and yarrow†
		Pterophorus pentadactyla (white plume) ‡		-2.90 (±1.04)	-4.93, -0.86	Bindweeds	
Transect	2018	*Eucosma cana**‡	WF	2.10 (±0.73)	0.68, 3.53	Knapweeds† and thistles	Yarrow†
		Emmelina monodactyla (common plume)		1.46 (±0.56)	0.36, 2.56	Bindweeds	Knapweed†, spear thistle and yarrow†
		Mythimna pallens (common wainscot)**		0.87 (±0.43)	0.03, 1.72	Grasses	Blackberry fruit, ragwort, Traveller's joy, wild carrot† and yarrow†
Transect	2018	*Xestia xanthographa* square spot rustic)*	WF	0.44 (±0.20)	0.04, 0.83	Polyphagous on grasses and forbs	Blackberry fruit, ragwort and spear thistle
		*Agriphila tristella**‡		-1.99 (±0.76)	-3.47, -0.50	Grasses	
Transect	2019	*Agriphila geniculea*	BC	1.97 (±0.98)	0.05, 3.88	Grasses	Yarrow†
		*Chrysoteuchia culmella**‡		-0.37 (±0.15)	-0.66, -0.08	Grasses	Hogweed, wild carrot and yarrow†
		Crambus perlella‡		-1.96 (±0.71)	-3.35, -0.57	grasses	Creeping thistle
Transect	2019	*Gillmeria pallidactyla* (yarrow plume)	WF	4.05 (±1.06)	1.97, 6.13	Yarrow†	
		*Cochylimorpha straminea**		3.42 (±0.61)	2.23, 4.62	Common knapweed†	

Method	Year	Taxa	Treatment	Estimate (±SE)	95% confidence interval	Hostplant(s)	Observed feeding on nectar
		Idaea dimidiata (single dotted wave)*		1.88 (±0.86)	0.20, 3.56	Polyphagous on forbs	
		*Blastobasis adustella**		1.88 (±0.78)	0.35, 3.40	Polyphagous	Blackberry fruit and yarrow†
		Camptogramma bilineata (yellow shell)		0.78 (±0.33)	0.13, 1.43	Polyphagous on forbs	Bramble flower and hogweed
		*Agriphila straminella**‡		-0.44 (±0.19)	-0.81, -0.08	Grasses	
		*Chrysoteuchia culmella**‡		-1.12 (±0.16)	-1.43, -0.81	Grasses	Hogweed, wild carrot† and yarrow†

4.6.3.3 Behavioural events and larvae

Table S4.11. Behavioural events. *All events observed during the experiment in both the sown part of the block and the incidentally growing vegetation within 1.5 m of the edge (Inc.).*

Year	Julian day	Time	Temp	Block	Part	Treatment	Moth species	Plant	Event	Total
2018	150	22:05	20	7	Sown	BC	*Autographa gamma* (Silver Y)	Bladder campion	Nectaring	1
		22:05	20	7	Sown	BC	*Autographa gamma* (Silver Y)	Bladder campion	Nectaring	1
	151	22:31	19	10	Sown	BC	*Autographa gamma* (Silver Y)	Bladder campion	Nectaring	1
		22:16	20	10	Sown	WF	*Autographa gamma* (Silver Y)	Red campion	Nectaring	1
		23:50	17	11	Sown	WF	*Eupithecia centaureata* (Lime-speck Pug)	Oxeye daisy	Nectaring	1
		23:42	17	11	Sown	WF	*Spilosoma lubricipeda* (White Ermine)	Oxeye daisy	Ovipositing	1
		23:14	18	12	Sown	WF	*Agnopterix arenella*	Oxeye daisy	Nectaring	1
		00:05	17	13	Sown	BC	*Korscheltellus lupulina* (Common Swift)	Grass	Mating	2
		00:23	17	13	Sown	WF	*Korscheltellus lupulina* (Common Swift)	Oxeye daisy	Mating	2
	152	23:11	19	12	Sown	BC	*Hadena rivularis* (The Campion)	Night flowering catchfly	Ovipositing	1

Year	Julian day	Time	Temp	Block	Part	Treatment	Moth species	Plant	Event	Total
		22:06	20	14	Sown	BC	*Autographa gamma* (Silver Y)	Bladder campion	Nectaring	1
		22:06	20	14	Sown	BC	*Autographa gamma* (Silver Y)	Bladder campion	Nectaring	1
		22:06	20	14	Sown	BC	*Autographa gamma* (Silver Y)	Night flowering catchfly	Nectaring	1
		22:06	20	14	Sown	BC	*Autographa gamma* (Silver Y)	Red campion	Nectaring	1
	162	22:20	18	1	Sown	BC	*Diachrysia chrysitis* (Burnished Brass)	Bladder campion	Nectaring	1
	164	23:50	17	10	Inc.		*Xestia c-nigrum* (Setaceaous Hebrew Character)	Hogweed	Nectaring	1
		23:28	15	11	Sown	GR	*Hepialus humuli* (Ghoast Moth)	Grass	Mating	2
		22:37	15	13	Inc.		*Axylia putris* (The Flame)	Hogweed	Nectaring	1
		22:50	15	13	Inc.		*Agrotis exclamationis* (Heart and Dart)	Hogweed	Nectaring	1
		22:50	15	13	Inc.		*Diarsia mendica* (Ingrailed Clay)	Hogweed	Nectaring	1
		22:45	15	13	Inc.		*Oligia fasciuncula* (Middle-barred Minor)	Hogweed	Nectaring	1
		22:50	15	13	Inc.		*Oligia fasciuncula* (Middle-barred Minor)	Hogweed	Nectaring	1
	165	22:51	13	14	Inc.		*Myelois circumvolute* (Thistle Ermine)	Hogweed	Nectaring	1

Year	Julian day	Time	Temp	Block	Part	Treatment	Moth species	Plant	Event	Total
	176	01:20	14	1	Sown	GR	*Agapeta hamana*	Creeping thistle	Mating	2
		22:22	18	4	Inc.		*Escaped*	Hogweed	Nectaring	1
	177	00:16	14	8	Sown	GR	*Pterophorus pentadactyla* (White Plume)	Grass	Mating	2
	179	23:17	16	14	Sown	WF	*Mythimna pallens* (Common Wainscot)	Yarrow	Nectaring	1
	190	23:12	18	3	Sown	BC	*Mythimna pallens* (Common Wainscot)	Ragwort	Nectaring	1
		23:12	18	3	Sown	WF	*Mythimna pallens* (Common Wainscot)	Wild carrot	Nectaring	1
	191	22:51	15	7	Sown	WF	*Eremobia ochroleuca* (Dusky Sallow)	Spear thistle	Nectaring	1
		22:51	15	7	Sown	WF	*Myelois circumvoluta* (Thistle Ermine)	Common knapweed	Nectaring	1
	194	22:29	19	11	Sown	WF	*Chysoteuchia culmella*	Wild carrot	Nectaring	1
	195	21:38	23	14	Sown	WF	*Dichrorampha petiverella*	Wild carrot	Nectaring	1
		21:38	23	14	Sown	WF	*Dichrorampha petiverella*	Wild carrot	Nectaring	1
		21:38	23	14	Sown	WF	*Caradrina Morpheus* (Mottled Rustic)	Wild carrot	Nectaring	1
		23:22	19	15	Sown	WF	*Dichrorampha petiverella*	Wild carrot	Nectaring	1
	204	22:22	21	1	Sown	BC	*Endotricha flammealis*	Spear thistle	Nectaring	1
		21:48	22	2	Sown	WF	*Patania ruralis* (Mother of Pearl)	Spear thistle	Nectaring	1
	205	21:42	21	8	Sown	GR	*Eremobia ochroleuca* (Dusky Sallow)	Spear thistle	Nectaring	1

Year	Julian day	Time	Temp	Block	Part	Treatment	Moth species	Plant	Event	Total
		22:53	20	9	Sown	GR	*Patania ruralis* (Mother of Pearl)	Spear thistle	Nectaring	1
	220	22:07	17	14	Sown	GR	*Hoplodrina ambigua* (Vine's Rustic)	Ragwort	Nectaring	1
	232	20:49	20	2	Inc.		*Noctuid sp.*	Blackberry fruit	Nectaring	1
	233	21:22	18	8	Inc.		*Mythimna pallens* (Common Wainscot)	Blackberry fruit	Nectaring	1
		21:22	18	8	Inc.		*Xestia xanthographa* (Square-spot Rustic)	Blackberry fruit	Nectaring	1
		22:05	18	9	Inc.		*Xestia xanthographa* (Square-spot Rustic)	Dock	Mating	2
		22:06	18	9	Inc.		*Xestia xanthographa* (Square-spot Rustic)	Dock	Mating	2
	234	21:11	19	13	Inc.		*Triodia sylvina* (Orange Swift)	Grass	Mating	2
	246	20:53	18	2	Inc.		*Xestia xanthographa* (Square-spot Rustic)	Blackberry fruit	Nectaring	1
		20:53	18	2	Inc.		*Xestia xanthographa* (Square-spot Rustic)	Blackberry fruit	Nectaring	1
		20:53	18	2	Inc.		*Hoplodrina ambigua* (Vine's Rustic)	Blackberry fruit	Nectaring	1
		21:02	18	2	Inc.		*Noctua comes* (Lesser Yellow Underwing)	Blackberry fruit	Nectaring	1
		21:02	18	2	Inc.		*Xestia xanthographa* (Square-spot Rustic)	Blackberry fruit	Nectaring	1
		21:02	18	2	Inc.		*Xestia xanthographa* (Square-spot Rustic)	Blackberry fruit	Nectaring	1

Year	Julian day	Time	Temp	Block	Part	Treatment	Moth species	Plant	Event	Total
		21:02	18	2	Inc.		*Xestia xanthographa* (Square-spot Rustic)	Blackberry fruit	Nectaring	1
	247	21:36	16	5	Inc.		*Xestia xanthographa* (Square-spot Rustic)	Nettle	Mating	2
		20:36	16	7	Sown	GR	*Xestia xanthographa* (Square-spot Rustic)	Dock	Mating	2
		20:15	15	8	Sown	GR	*Xestia xanthographa* (Square-spot Rustic)	Blackberry fruit	Nectaring	1
		21:06	16	9	Inc.		*Xestia xanthographa* (Square-spot Rustic)	Spear thistle	Nectaring	1
	248	20:58	17	10	Sown	BC	*Xestia xanthographa* (Square-spot Rustic)	Night flowering catchfly	Mating	2
		21:12	17	10	Sown	GR	*Xestia xanthographa* (Square-spot Rustic)	Grass	Mating	2
	260	20:25	18	3	Inc.		*Xestia xanthographa* (Square-spot Rustic)	Blackberry fruit	Nectaring	1
2019	175	23:17	19	2	Sown	WF	*Eucosma cana*	Common knapweed	Mating	2
	177	21:50	14	10	Sown	BC	*Noctuid sp.*	Bladder campion	Nectaring	1
		23:15	13	12	Sown	BC	*Apamea anceps* (Large Nutmeg)	Bladder campion	Nectaring	1
	178	21:58	15	14	Sown	BC	*Apamea monoglyphal (Dark Arches)*	Bladder campion	Nectaring	2
		22:38	15	14	Sown	BC	*Apamea monoglypha (Dark Arches)*	Bladder campion	Nectaring	1

Year	Julian day	Time	Temp	Block	Part	Treatment	Moth species	Plant	Event	Total
		22:38	15	14	Sown	BC	*Noctua pronuba* (Large Yellow Underwing)	Bladder campion	Nectaring	2
		22:09	15	14	Sown	BC	*Autographa gamma* (Silver Y)	Bladder campion	Nectaring	1
		22:14	15	14	Sown	WF	*Emmelina monodactyla* (Common Plume)	Common knapweed	Nectaring	1
		23:06	13	15	Sown	BC	*Apamea anceps* (Large Nutmeg)	Bladder campion	Nectaring	1
		23:10	13	15	Sown	BC	*Noctuid sp.*	Bladder campion	Nectaring	1
		23:03	13	15	Sown	GR	*Apamea monoglypha (Dark Arches)*	Grass	Emerged	1
	189	22:07	17	3	Inc.		*Camptogramma bilineata*	Bramble flower	Nectaring	1
		23:05	15	4	Sown	BC	*Apamea monoglypha (Dark Arches)*	Bladder campion	Nectaring	1
		23:05	15	4	Inc.		*Agrotis exclamationis* (Heart and Dart)	Hogweed	Nectaring	1
		23:15	15	4	Sown	WF	*Eucosma cana*	Yarrow	Nectaring	1
	190	22:39	17	5	Inc.		*Chrysoteuchia culmella*	Hogweed	Nectaring	1
		22:39	17	5	Inc.		*Camptogramma bilineata*	Hogweed	Nectaring	1
	193	23:17	18	14	Inc.		*Crambus perlella*	Creeping thistle	Nectaring	1
		23:00	18	14	Sown	WF	*Caradrina morpheus* (Mottled Rustic)	Yarrow	Nectaring	1
	203	23:10	19	1	Inc.		*Cydalima perspectalis* (Box Tree Moth)	Traveller's joy	Nectaring	1

Year	Julian day	Time	Temp	Block	Part	Treatment	Moth species	Plant	Event	Total
		23:10	19	1	Inc.		*Lacanobia oleracea* (Bright-line Brown-eye)	Traveller's joy	Nectaring	1
		23:10	19	1	Inc.		*Manulea lurideola* (Common Footman)	Traveller's joy	Nectaring	1
		23:10	19	1	Inc.		*Endotricha flammealis*	Traveller's joy	Nectaring	5
		23:10	19	1	Inc.		*Idaea rusticate* (Least Carpet)	Traveller's joy	Nectaring	6
		23:10	19	1	Inc.		*Eilema complana* (Scarce Footman)	Traveller's joy	Nectaring	1
		23:10	19	1	Inc.		*Hoplodrina octogenaria*	Traveller's joy	Nectaring	1
		23:30	19	1	Sown	WF	*Agapeta zoegana*	Common knapweed	Mating	2
		23:09	19	1	Sown	WF	*Micro sp.*	Common knapweed	Nectaring	1
		22:19	19	2	Sown	WF	*Endotricha flammealis*	Yarrow	Nectaring	1
		00:10	15	4	Sown	GR	*Mythimna impura*	Grass	Mating	2
	204	22:44	22	5	Sown	BC	*Endotricha flammealis*	Bladder campion	Nectaring	1
		22:26	24	5	Sown	WF	*Manulea lurideola*	Cornflower	Nectaring	1
		22:26	24	5	Sown	WF	*Endotricha flammealis*	Yarrow	Nectaring	1
		23:41	22	8	Inc.		*Chrysoteuchia culmella*	Grass	Mating	2
		23:41	22	8	Sown	WF	*Endotricha flammealis*	Yarrow	Nectaring	1
		23:41	22	8	Sown	WF	*Zygaena filipendulae*	Grass	Mating	2
	205	22:39	19	10	Inc.		*Endotricha flammealis*	Traveller's joy	Nectaring	2

Year	Julian day	Time	Temp	Block	Part	Treatment	Moth species	Plant	Event	Total
		22:39	19	10	Inc.		*Agrotis exclamationis* (Heart and Dart)	Traveller's joy	Nectaring	1
		22:39	19	10	Inc.		*Idaea rusticata* (Least Carpet)	Traveller's joy	Nectaring	3
		22:39	19	10	Inc.		*Noctua comes* (Lesser Yellow Underwing)	Traveller's joy	Nectaring	1
		22:39	19	10	Inc.		*Phycita roborella*	Traveller's joy	Nectaring	1
		22:39	19	10	Inc.		*Eilema complana* (Scarce Footman)	Traveller's joy	Nectaring	2
		22:39	19	10	Inc.		*Idaea dimidiata* (Single-dotted Wave)	Traveller's joy	Nectaring	1
		22:39	19	10	Inc.		*Hoplodrina octogenarian* (The Uncertain)	Traveller's joy	Nectaring	1
		22:28	19	10	Sown	WF	*Eremobia ochroleuca* (Dusky Sallow)	Common knapweed	Nectaring	1
		21:57	20	12	Inc.		*Mesoligia furunculi* (Cloaked Minor)	Dock	Mating	2
		22:39	19	13	Sown	WF	*Idaea aversata* (Riband Wave)	Yarrow	Nectaring	1
	206	00:26	23	14	Sown	WF	*Blastobasis adustella*	Yarrow	Nectaring	1
		22:29	24	15	Sown	BC	*Chrysoteuchia culmella*	Yarrow	Nectaring	1
		22:29	24	15	Sown	BC	*Endotricha flammealis*	Ragwort	Nectaring	3
		22:29	24	15	Sown	BC	*Idaea rusticata* (Least Carpet)	Ragwort	Nectaring	2
		22:29	24	15	Sown	BC	*Udea sp.*	Bladder campion	Nectaring	1

Year	Julian day	Time	Temp	Block	Part	Treatment	Moth species	Plant	Event	Total
		22:10	26	15	Sown	GR	*Mesoligia furuncula* (Cloaked Minor)	Grass	Mating	2
	217	22:57	19	2	Inc.		*Blastobasis adustella*	Blackberry fruit	Nectaring	1
		22:57	19	2	Inc.		*Mesapamea secalis agg.* (Common/Lesser Common Rustic)	Blackberry fruit	Nectaring	1
	218	23:01	16	5	Inc.		*Patania ruralis* (Mother of Pearl)	Creeping thistle	Nectaring	1
	219	22:42	16	10	Inc.		*Emmelina monodactyla* (Common Plume)	Spear thistle	Nectaring	1
	220	21:58	21	16	Sown	WF	*Mesapamea secalis agg.*	Yarrow	Nectaring	1
	232	23:04	13	8	Sown	WF	*Xestia xanthographa* (Square-spot Rustic)	Grass	Mating	2
	233	22:50	15	10	Inc.		*Xestia xanthographa* (Square-spot Rustic)	Grass	Mating	2
		22:13	15	11	Sown	BC	*Xestia xanthographa* (Square-spot Rustic)	Grass	Mating	2
		21:11	16	13	Sown	BC	*Xestia xanthographa* (Square-spot Rustic)	Grass	Mating	2
	234	22:18	17	14	Sown	BC	*Xestia xanthographa* (Square-spot Rustic)	Grass	Mating	2
		22:24	17	14	Sown	WF	*Emmelina monodactyla* (Common Plume)	Yarrow	Nectaring	1
		21:54	18	16	Sown	BC	*Triodia sylvina* (Orange Swift)	Grass	Mating	2
		21:07	18	16	Sown	WF	*Agriphila geniculea*	Yarrow	Nectaring	1
		20:59	18	16	Sown	WF	*Endotricha flammealis*	Yarrow	Nectaring	1

Year	Julian day	Time	Temp	Block	Part	Treatment	Moth species	Plant	Event	Total
	245	22:11	17	1	Inc.		*Mythimna pallens* (Common Wainscot)	Traveller's joy	Nectaring	1
		22:54	18	2	Inc.		*Mythimna pallens* (Common Wainscot)	Blackberry fruit	Nectaring	1
		22:54	18	2	Inc.		*Noctua pronuba* (Large Yellow Underwing)	Blackberry fruit	Nectaring	1
		23:00	18	2	Inc.		*Noctua pronuba* (Large Yellow Underwing)	Blackberry fruit	Nectaring	1
		22:54	18	2	Inc.		*Xestia xanthographa* (Square-spot Rustic)	Blackberry fruit	Nectaring	3
		22:54	18	2	Inc.		*Xestia xanthographa* (Square-spot Rustic)	Blackberry fruit	Nectaring	1
		22:46	18	2	Inc.		*Xestia c-nigrum* (Setaceous Hebrew Character)	Blackberry fruit	Nectaring	1
		22:46	18	2	Inc.		*Xestia xanthographa* (Square-spot Rustic)	Blackberry fruit	Nectaring	3
		21:18	18	4	Sown	BC	*Xestia xanthographa* (Square-spot Rustic)	Dock	Mating	2
		21:18	18	4	Sown	BC	*Xestia xanthographa* (Square-spot Rustic)	Dock	Mating	2
		21:18	18	4	Sown	BC	*Xestia xanthographa* (Square-spot Rustic)	Creeping thistle	Mating	2
	246	22:26	19	5	Inc.		*Opisthograptis luteolata* (Brimstone Moth)	Blackberry fruit	Nectaring	1
		22:26	19	5	Inc.		*Xestia c-nigrum* (Setaceous Hebrew Character)	Blackberry fruit	Nectaring	1

Year	Julian day	Time	Temp	Block	Part	Treatment	Moth species	Plant	Event	Total
		22:26	19	5	Inc.		*Xestia xanthographa* (Square-spot Rustic)	Blackberry fruit	Nectaring	4
		22:14	19	5	Sown	GR	*Xestia xanthographa* (Square-spot Rustic)	Grass	Mating	2
		21:39	18	7	Sown	GR	*Triodia sylvina* (Orange Swift)	Grass	Mating	2
		21:16	17	8	Sown	GR	*Xestia xanthographa* (Square-spot Rustic)	Grass	Mating	2
		21:04	17	8	Sown	WF	*Xestia xanthographa* (Square-spot Rustic)	Common knapweed	Mating	2
		20:12	18	9	Sown	BC	*Xestia xanthographa* (Square-spot Rustic)	Dock	Mating	2
		20:12	18	9	Sown	BC	*Xestia xanthographa* (Square-spot Rustic)	Grass	Mating	2
	247	21:57	15	10	Sown	BC	*Xestia xanthographa* (Square-spot Rustic)	Grass	Mating	2
		22:05	15	10	Sown	GR	*Xestia xanthographa* (Square-spot Rustic)	Grass	Mating	2
		22:00	15	10	Sown	WF	*Xestia xanthographa* (Square-spot Rustic)	Grass	Mating	2
		22:02	15	10	Sown	WF	*Xestia xanthographa* (Square-spot Rustic)	Grass	Mating	2
		22:02	15	10	Sown	WF	*Xestia xanthographa* (Square-spot Rustic)	Common knapweed	Mating	2
		21:34	15	11	Sown	BC	*Xestia xanthographa* (Square-spot Rustic)	Grass	Mating	2
		21:18	15	11	Sown	GR	*Xestia xanthographa* (Square-spot Rustic)	Grass	Mating	2

Year	Julian day	Time	Temp	Block	Part	Treatment	Moth species	Plant	Event	Total
		21:25	15	11	Sown	WF	*Xestia xanthographa* (Square-spot Rustic)	Grass	Mating	2
	248	20:48	14	14	Sown	BC	*Xestia xanthographa* (Square-spot Rustic)	Grass	Mating	2
		20:54	14	14	Sown	GR	*Xestia xanthographa* (Square-spot Rustic)	Ragwort	Nectaring	1

Table S4.12. Selection of the best spatial scale for larvae*. AICc values of GLMMs with four different response variables. Each response variable is number per 70 m transect. Response variables are function of treatment plus two landscape variables: one 'woody' and one 'grassy'. The woody variable can be either a continuous variable (percentage woody vegetation within a certain radius of the trap site) or a binary variable (trap site is/is not adjacent to a woody boundary feature). The grassy variable is the percentage of long grass and rough low vegetation within a certain radius of the trap site. The models are ordered by increasing AICc. The model with the lowest AICc was used.*

Response variable	Woody variable	Grassy variable	AICc	ΔAICc
Number of larvae found during transects	50 m	25 m	172.0536	0
	25 m	25 m	172.3229	0.269
	25 m	200 m	173.1794	1.126
	50 m	200 m	173.4264	1.373
	50 m	50 m	174.2554	2.202
	100 m	25 m	174.3167	2.263
	200 m	200 m	174.5554	2.504
	200 m	25 m	174.6705	2.617
	Boundary	25 m	174.671	2.617
	50 m	100 m	174.7416	2.688
	25 m	50 m	174.749	2.695
	100 m	200 m	175.0194	2.966
	25 m	100 m	175.0974	3.044
	Boundary	200 m	175.2093	3.156
	100 m	50 m	176.0731	4.020
	100 m	100 m	176.2191	4.166
	Boundary	50 m	176.5123	4.458
	200 m	50 m	176.5525	4.499
	200 m	100 m	176.5556	4.502
	Boundary	100 m	176.5711	4.518
Number of larvae caught during sweep netting	Boundary	100 m	119.9405	0
	200 m	100 m	119.9778	0.037
	100 m	100 m	120.2109	0.270
	Boundary	50 m	120.2525	0.312
	Boundary	25 m	120.3683	0.428
	Boundary	200 m	120.4609	0.520
	100 m	50 m	120.6677	0.727
	25 m	100 m	120.79	0.850
	200 m	50 m	120.8938	0.953
	25 m	50 m	121.0388	1.098
	100 m	25 m	121.0697	1.129
	25 m	25 m	121.2421	1.302
	100 m	200 m	121.3388	1.398
	50 m	100 m	121.3642	1.424
	200 m	200 m	121.4299	1.489
	200 m	25 m	121.4681	1.527

Response variable	Woody variable	Grassy variable	AICc	ΔAICc
	25 m	200 m	121.5054	1.565
	50 m	50 m	121.6709	1.730
	50 m	25 m	121.9194	1.979
	50 m	200 m	122.1087	2.168
Number of nectaring events observed	Boundary	50 m	139.317	0
	Boundary	25 m	140.2129	0.896
	25 m	50 m	140.8458	1.529
	25 m	25 m	141.2619	1.945
	200 m	50 m	141.4951	2.178
	100 m	50 m	141.614	2.297
	50 m	50 m	141.6469	2.330
	50 m	25 m	141.868	2.551
	200 m	25 m	141.8715	2.555
	100 m	25 m	141.8994	2.582
	Boundary	100 m	142.6077	3.291
	25 m	100 m	143.5485	4.232
	Boundary	200 m	143.6718	4.355
	50 m	100 m	143.6739	4.357
	200 m	100 m	143.7949	4.478
	100 m	100 m	143.874	4.557
	25 m	200 m	144.3968	5.080
	50 m	200 m	145.0081	5.691
	100 m	200 m	145.2094	5.892
	200 m	200 m	145.2101	5.893
Number of mating events observed	Boundary	100 m	168.0936	0
	Boundary	50 m	168.2223	0.129
	Boundary	25 m	168.2386	0.145
	Boundary	200 m	168.2865	0.193
	100 m	200 m	168.3922	0.299
	100 m	50 m	168.6065	0.513
	100 m	25 m	168.6514	0.558
	50 m	100 m	168.6545	0.561
	100 m	100 m	168.6936	0.6
	50 m	25 m	168.7135	0.620
	50 m	50 m	168.7336	0.64
	50 m	200 m	168.7403	0.647
	25 m	100 m	169.4802	1.387
	25 m	25 m	169.5798	1.486
	25 m	50 m	169.5942	1.501
	25 m	200 m	169.6116	1.518
	200 m	100 m	170.0796	1.986
	200 m	200 m	170.2243	2.131
	200 m	25 m	170.2582	2.165

Response variable	Woody variable	Grassy variable	AICc	ΔAICc
	200 m	50 m	170.2647	2.171

4.6.4 Contrasts between traps and transects as sampling methods

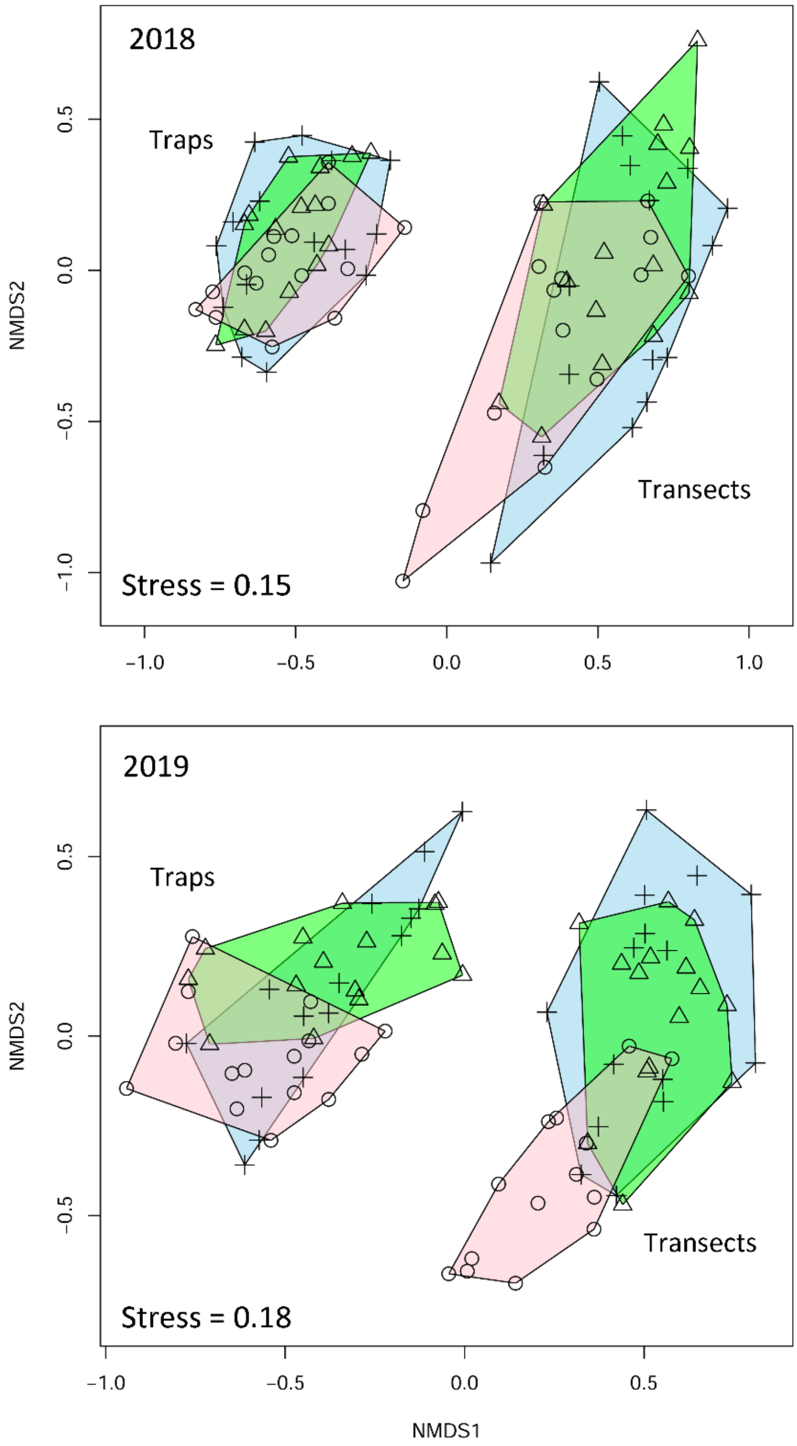


Fig. S4.2. Comparison of community composition recorded by traps vs transects in 2018 and 2019. *NMDS biplots of the community composition of moths caught in traps and transects across 45 sites over two years. Polygons show the convex hulls grouping the sites by treatment. Each point represents one site. Triangles and green polygons = GR (grass only), pluses and blue polygons = BC (bladder campion), circles and pink polygons = WF (wildflower).*

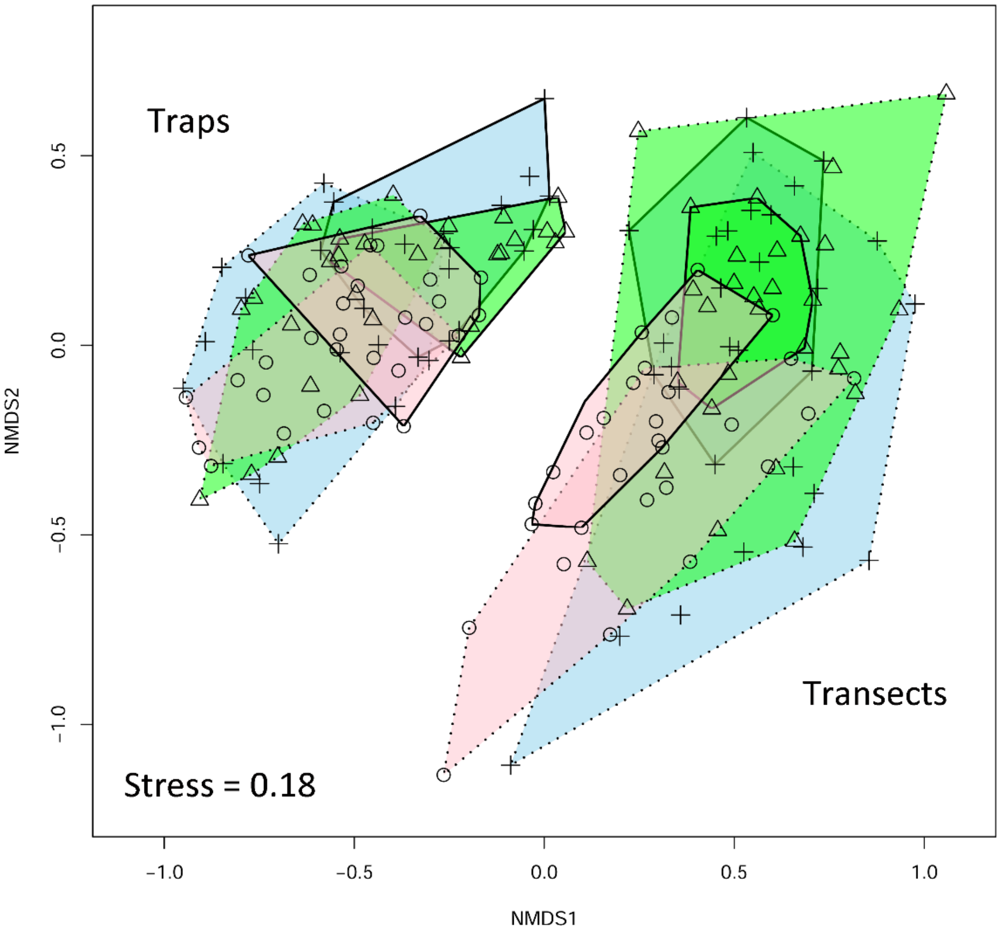


Fig. S4.3. Comparison of community composition recorded by traps vs transects, and 2018 vs 2019. *NMDS biplots of the community composition of moths caught in traps and transects across 45 sites over two years. Polygons show the convex hulls grouping the sites by treatment. Each point represents one site. Triangles and green polygons = GR (grass only), pluses and blue polygons = BC (bladder campion), circles and pink polygons = WF (wildflower). Dotted lines show polygons for 2018, solid lines for 2019.*

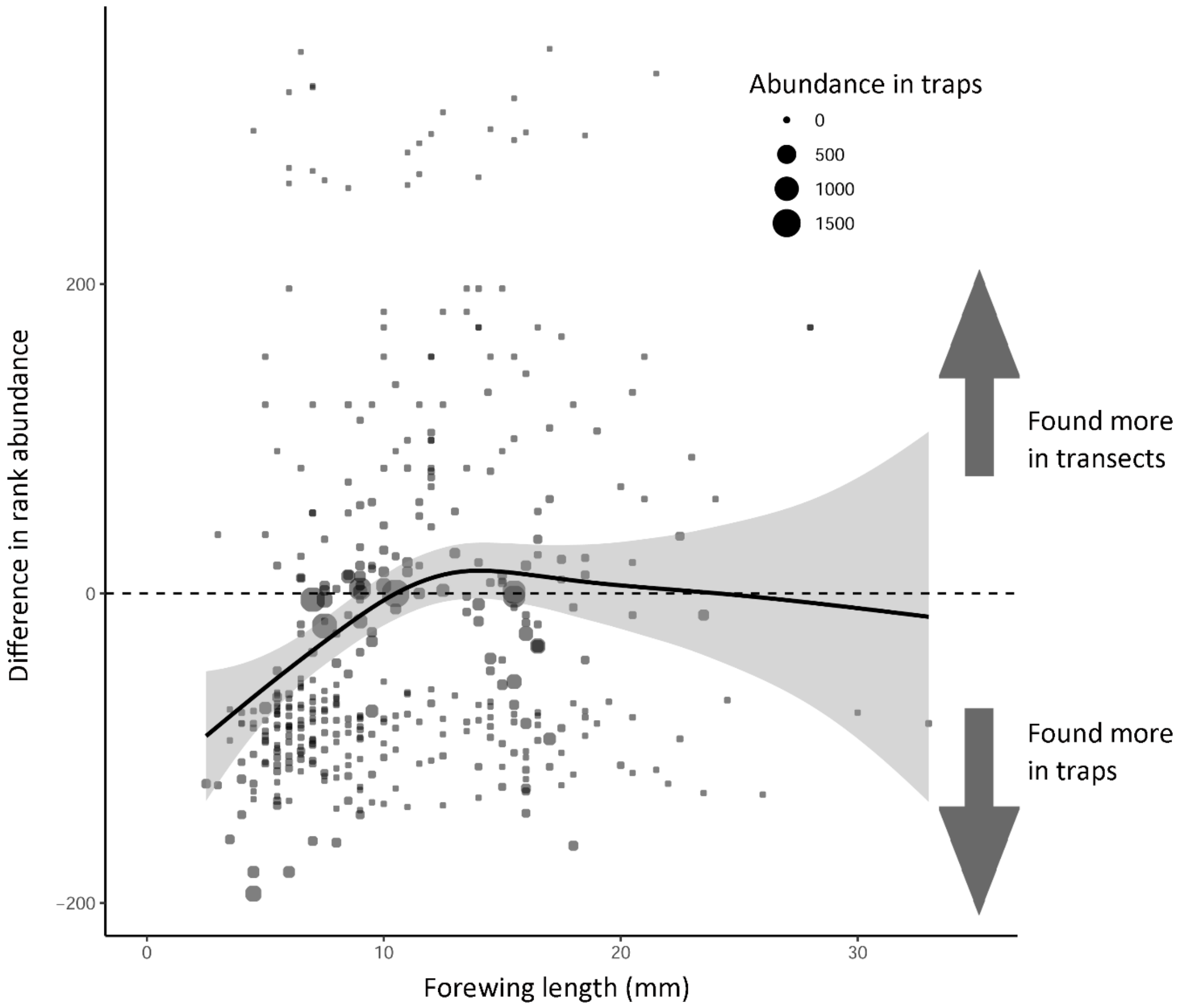


Fig. S4.4. The effect of forewing length on trap vs transect sampling bias. *The difference in rank abundance of each moth species in traps and transects as a function of forewing length. Difference calculated by subtracting the total abundance rank of each species in transects from that of traps. Species with a positive difference in rank abundance were relatively more abundant in transect samples and those with a negative difference were relatively more abundant in traps. Solid black line and grey ribbon shows model predictions from a GAM with 95% confidence intervals. Size of points represents the total abundance of moths caught in traps over the two-year experiment.*

Chapter 5

General discussion

Chapter 5. General discussion

The findings in this thesis provide clear evidence that moth abundance has declined significantly in the UK since 1968, which supports previous assessments (Bell et al., 2020, Conrad et al., 2004, Conrad et al., 2006). This thesis advances previous knowledge by demonstrating that, counterintuitively, the declines have been less severe in more intensively farmed landscapes. Between 1968 and 2016, moth abundance declined in arable and improved grassland habitats by -18% and -34%, respectively, while in broadleaf woodland and 'other semi-natural' habitats abundance declined by -44% and -45%. The worst declines occurred in upland and urban habitats: both of which showed a decline of -47%. Surprisingly, moth diversity increased, and species richness did not significantly change over this period. Declines in abundance were also more severe in the south: -25% in the north and -41% in the south, with a national decline of -36%. The reasons behind these declines are likely to be manifold, interacting and habitat-specific: these are discussed in section 2.5. Even more surprisingly, despite evidence of reduced insect diversity in intensified farmland (Albrecht et al., 2007, Diekötter et al., 2008), moth diversity increased in arable and improved grassland habitats while both richness and diversity declined in broadleaf woodland. There was also a clear regional effect to changes in abundance, richness and diversity. Species richness increased in the north of the UK and declined in the south.

It is also clear from this thesis that while the enrichment of arable field margins with sown forbs may greatly enhance species richness and diversity, and moderately enhance abundance, supporting previous evidence (Alison et al., 2016, Merckx et al., 2012b), these interventions, at present, only play a small role in halting the decline in moth abundance in farmland. For example, (Clothier and Pike, 2013) found that, as of 2012, 19% of arable farms in England had AES grass margins, whereas only 1% had AES wildflower margins. For wildflower margins to have a meaningful impact at the national scale, there would need to be a large increase in uptake of the schemes.

5.1 The mechanisms behind moth decline

The most likely drivers of decline in each habitat are discussed in sections 1.3 and 2.5.7, including agricultural intensification, overgrazing by deer, urbanisation, light pollution and, potentially, climate change. However, there was a lack of clear evidence that favours any one driver above the others. What has been made clear in this thesis is that the declines are not restricted to any one group of moths or any particular habitat, but are both taxonomically and geographically widespread, indicating a general environmental degradation on a national scale. The exception that proves the rule in this case is the group of species which feed on lichens: this group has increased rapidly both in abundance (Conrad et al., 2004 and section 2.4.4.1) and distribution (Randle, 2019). This phenomenal recovery may in part be due to the proliferation of lichens following the Clean Air Act of 1956 (Pescott et al., 2015). A similar startling trend can be seen in the occupancy rates of freshwater invertebrates in the UK, where a very strong decline occurred between 1970 and the early 1990s, until just after the European Urban Wastewater Treatment Directive came into effect in 1991, after which invertebrate occupancy increased rapidly and now exceeds its 1970 level (Outhwaite et al., 2020). These examples demonstrate that when a specific problem is identified and acted upon appropriately, ecological deterioration can be reversed. While there are still unresolved questions regarding moth decline, there is more than enough information on which we can act to halt the decline of insects (Forister et al., 2019). Samways et al. (2020) provides a thorough and wide-ranging overview of such solutions, some of which are expanded upon in this chapter. Section 5.2 discusses how the findings in this thesis apply to current agri-environment scheme (AES) field margins and section 5.3 discusses what changes are necessary at the national level to improve the environment for both moths and wider biodiversity.

5.2. Application of findings to agri-environment policy

5.2.1 The efficacy of field margins as conservation tools

Field margins are a commonly applied AES option across the UK (Batáry et al., 2015). Benefits include not only enhancement of biodiversity (Haaland et al., 2011) but also increased ecosystem services including predation of crop pests by natural enemies (Balmer et al., 2013, Mansion-Vaquié et al., 2017) and, for insect-pollinated crops, enhanced pollination (Blaauw and Isaacs, 2014). At present, farmers can choose from a range of field margin seed mixes, including both plain grass mixes, grass and wildflower mixes, and a selection of other mixes aimed at specific taxa, e.g., pollinators and birds (DEFRA, 2019). For many insect taxa, it has been shown that abundance and diversity is higher in wildflower-enriched grass margins (from here on referred to as 'wildflower margins') than in plain grass margins (Alanen et al., 2011, Dicks et al., 2014, Smith and Everett, 2010, Vickery et al., 2009). However, it was not known to what extent nocturnal moth abundance and diversity can be enhanced through the inclusion of wildflowers within grass mixes. The aim of Chapter 4 of this thesis was to find out (1) if moth abundance and diversity is higher in wildflower margins than in plain grass margins and (2) whether this discrepancy is due to the provision of hostplants, nectar resources, or both. The field experiment demonstrated that moth species richness/diversity and, to a lesser extent, abundance, were enhanced with the inclusion of wildflowers and that this was due, almost entirely, to the presence of suitable hostplant species rather than plants only providing nectar sources. Although AESs have been widespread in the UK since the early 1990s (JNCC, 2019), with field margin schemes becoming widespread from the mid-2000s, there is little evidence that declines have slowed in agricultural land over this period (section 2.5.7.1 and 2.5.7.4). Furthermore, although diversity has increased in arable land since 1968, most of this increase occurred prior to 1990 (Fig. 2.6), excluding AES as an explanation. This suggests that improvements to the current AESs, as well as an increased uptake among farmers, is needed if moth decline is to be reversed.

The relevance of these findings to policy are discussed below.

5.2.2 Field margin policy recommendations

Both abundance and diversity of moths were higher in wildflower margins than in plain grass margins (section 4.4). The first policy recommendation is therefore to encourage the sowing of wildflower margins rather than grass margins in arable land. This conclusion is in line with many other studies showing that insect abundance and diversity is higher in wildflower strips than in plain grass strips (see review by Haaland et al. (2011)). The inclusion of moth-pollinated plants – bladder campion (*Silene vulgaris*) and night-flowering catchfly (*Silene noctiflora)* – did not enhance either abundance or diversity, so these plants cannot be recommended as a tool for enhancing the value of field margins for moths. Furthermore, these flowers tended to be visited almost exclusively by a small number of Noctuid species, meaning that their benefit as a nectar source may be limited to only a small subset of species. Of the top three flowers most frequently visited by moths during the experiment, two of them are classed as 'injurious weeds' – ragwort (*Jacobaea vulgaris*) and spear thistle (*Cirsium vulgare*) – so are unlikely candidates to be included in a sown field margin mix (Fig. 4.9).. Wildflowers that were utilised both as hostplants and nectar sources were wild carrot (*Daucus carota*) and yarrow (*Achillea millefolium*), and wildflowers that were utilised as hostplants, but typically not as nectar sources were oxeye daisy (*Leucanthemum vulgare*), common knapweed (*Centaurea nigra*) and musk mallow (*Malva moschata*) (Table S4.10). Moth species that specialise on knapweed and yarrow were especially abundant in the wildflower margins in this study (Table S4.3), so the inclusion of these two plants can be recommended to enhance abundance. It should be noted, however, that these wildflower species, commonly sown in AES field margins, may not act as hostplants for as many moth species as other wild plants do. The Database of Insects and their Food Plants maintained by the Biological Records Centre report 42 species that feed on yarrow, 29 on wild carrot, 25 on common knapweed, 13 on oxeye daisy and none that feed on musk mallow (implying that the database is incomplete). In contrast, the database reports 63 moth species that feed on dandelion (*Taraxacum officinale*), 59 that feed on broad-leaved dock (*Rumex obtusifolius*) and 46 that feed on common nettle (*Urtica dioica*). While it is not reasonable to recommend the sowing of dandelion and dock, two very common and abundant farmland wild plants, it should be noted that such naturally-occurring plants should be allowed to flourish where it is appropriate to do so.

Regarding sources of sugar, the most frequently visited source in this experiment was blackberry fruit (bramble – *Rubus fruticosus*) (Fig. 4.9). In a similar study, Coulthard (2015) found that bramble flowers were the most frequently visited sugar source, which demonstrates the importance of bramble as a resource for moths during both is flowering and fruiting phase. These findings emphasise the vital importance of hedgerows in the landscape. They provide not only hostplants (Facey et al., 2014), shelter (Merckx et al., 2010a) and dispersal corridors (Coulthard et al., 2016) but also sugar resources.

5.3 The future of UK conservation

5.3.1 ELM and new Agriculture Bill

The current AES are often criticised for being too bureaucratically burdensome (DEFRA, 2020), too piecemeal (Emery and Franks, 2012) and ineffective at preserving biodiversity (Kleijn et al., 2001). It is also the case that schemes such as field margins tend to promote the conservation of widespread and common species but do little for rarer species in need of conservation action (Kleijn et al., 2006). The new generation of AES, the Environmental Land Management schemes (ELMs), a key part of the UK's new Agriculture Bill, seek to rectify these flaws and greatly expand on the concept of public money for public goods: paying farmers to protect not only biodiversity, but also for 'ecosystem services' such as flood mitigation, water filtration, soil preservation, carbon sequestration and public access to nature (DEFRA, 2020). There is also to be a larger emphasis placed on results rather than purely on compliance, which gives farmers more flexibility to employ management strategies appropriate for their land, while also allowing for greater creative participation in the schemes. Another key component of the ELMs is its focus on the cooperation of farms within a region to create joined-up areas of high biodiversity. Field margins are a prominent and important component of the ELMs, but, as has been made clear in this thesis, the capacity of field margins to enhance moth biodiversity is limited to small areas within a specific land-use type. If the decline in moths is to be halted, large changes will need to occur not just in arable farmland but in all habitat types across the entire country.

5.3.2 Conservation of moths on uplands

In this thesis, moth abundance in the uplands declined more than any other habitat apart from urban, with both habitats showing a -47% decline, and species richness and diversity, although not declining, are significantly lower than the national average (Fig. 2.5 and Fig. 2.6). The uplands of the UK are dominated largely by sheep farming, grouse moors, and, to a lesser extent, conifer plantations (Watson et al., 2011). In addition, the Scottish Highlands are used for deer-stalking and are severely overgrazed (Sansom, 1999). Much has been written about the low levels of biodiversity in the British uplands, especially compared to equivalent upland areas in most other countries in Europe (Macdonald, 2019, Monbiot, 2013a). It is in the uplands that large-scale ecosystem restoration, or 'rewilding' has the potential for enormous benefits to biodiversity (Sandom and Wynne-Jones, 2019). Several projects are already succeeding in the uplands – for example, Wild Ennerdale in Cumbria, and Dundreggan in the Scottish Highlands. Such projects typically involve the reduction or cessation of grazing and allow succession through natural regeneration to take place. Reintroductions of keystone species such as beaver are also becoming more common across the UK (Sandom and Wynne-Jones, 2019). Elsewhere in Europe, the reintroduction (or cessation of persecution) of apex predators such as wolf and lynx is also utilised to reduce grazing pressure (Navarro and Pereira, 2015). It is logically expected that such changes will benefit moth communities due to increased larval hostplants and shelter through the development of scrub (Merckx, 2015), and it has been demonstrated that moth abundance can be increased in upland habitats through reduced grazing (Littlewood, 2008). However, longitudinal studies, or comparisons between 'rewilded' sites and controls, appear lacking, as they are for most other taxa (Klink and WallisDeVries, 2018). The ecological restoration of Britain's uplands is an essential piece of the strategy to halt biodiversity loss. Grazing of sheep does not have to end in its entirety for this to happen, but the vast, treeless, overgrazed and burned landscapes need to be allowed, in part at least, to undergo natural succession and to regain the mosaic of grassland, scrub and woodlands that would offer vastly more habitat to wildlife, including moths (Macdonald, 2019). Indeed, there are tentative steps in this direction currently proposed in national park policy (Glover, 2019) but there is an ongoing and necessary debate regarding the conflict between the preservation of historic cultural landscapes and wildlife preservation (Jepson, 2016).

5.3.3 Conservation of moths on farmland

While rewilding is suitable for many areas, especially infertile uplands, the fact remains that farms still need to produce food at a reasonable price and turn a profit for the people who own them. There is a vast literature on improving farmland for wildlife, so this section will focus on what can be done specifically for moths – although these changes are very likely to benefit other taxa as well. The vast majority of moths are, in their larval stage, herbivorous, and are limited by hostplant availability. The simplest improvement that can be applied at the farm scale is to increase hostplant abundance and diversity through measures including wildflower field margins (Haaland et al., 2011) and establishment of hedgerows and hedgerow trees (Merckx et al., 2012b). Many species also benefit from sugar sources as adults. The findings of this thesis suggest that this is not efficiently achieved through the sowing of moth-pollinated flowers, as these only benefit a small number of moth species, but rather by allowing certain wild plants to grow: especially bramble, but also thistles and ragwort where appropriate (section 4.4.4.1). It is also highly beneficial to take parts of the farm out of production and allocate them as wildlife habitat: for example, wildflower meadows (Taylor and Morecroft, 2009). Flagship farms such as Hope Farm and Hillesden Farm (see section 3.6) have successfully integrated such habitats into productive agri-businesses (Aebischer et al., 2016, Heard et al., 2012, Morris et al., 2010). The amount of land to be taken out of production will depend on the characteristics of the farm, but as an example, Hillesden Farm took only 6% of its land out of production for AES and witnessed increased abundance and diversity of farmland birds (Hinsley et al., 2010), small mammals (Broughton et al., 2014) and bumblebees (Carvell et al., 2011) while increasing crop yields (Pywell et al., 2015). However, long-term effects on moths at Hillesden remain unclear, with large interannual fluctuations due to weather conditions (Heard et al., 2012). In addition to removing field margins from production, there are currently financial incentives offered by Countryside Stewardship (which will run until its replacement with ELM) for the creation of new woodland and lowland heath on current arable or improved grassland. For low-productivity farmland, these schemes may be especially beneficial both to farmers, through income via subsidies, and wildlife.

5.3.4 Conservation of moths in urban areas

Along with uplands, urban habitats also suffered the worse declines in overall abundance at -47% (Fig. 2.8). As explained in section 2.5.7.7, this habitat type also contained sites that had undergone urbanisation during the time series, so part of the loss in abundance can be attributed to the paving over of previously vegetated areas, or replacement of suitable habitat with amenity grassland. However, the decline is likely also due to less obvious effects such as light pollution (Owens et al., 2019) and the 'tidying up' of parks and gardens. Excluding densely urbanised city centres, land considered 'urban' contains a substantial amount of green space (Rae, 2017) and has the potential to offer high-quality habitat for moths. There is vast improvement that could be made regarding wildlife habitat in the built environment. For example, although exact figures do not exist, the majority of amenity trees and shrubs planted by councils are exotic rather than native (Monbiot, 2013b) and hence support fewer species (Helden et al., 2012). Moth species feeding on broadleaf shrubs experienced higher rates of decline in urban areas than in any other habitat (Fig. 2.14) so the widespread planting of native shrubs and small trees in urban areas is especially important. Many vegetated urban areas such as roadside verges and roundabouts are cut far more than necessary, removing both hostplants and nectar resources (Helden and Leather, 2004, O'Sullivan et al., 2017). Additionally, 'wildlife gardening' is now a mainstream idea and allowing a lawn to grow to seed and flower is not as taboo as it once was (Thompson, 2011). Green roofs have been shown to accommodate a large diversity of invertebrate life (MacIvor and Lundholm, 2011, Schindler et al., 2011) and these could be further encouraged. Finally, the cessation of unnecessary lighting, especially of short-wavelength radiation, is an obvious, easy and money-saving strategy that could improve urban habitat for moths very quickly (Owens et al., 2019, Van Langevelde et al., 2018). Section 3.3.3.2 demonstrates that even a small amount of UV radiation is highly attractive to moths, so the elimination of this part of the spectrum in street lighting is critical. The UK's new Environment Bill proposes a 'net gain' in biodiversity is required for every new development project (DEFRA 2019). This promising new legislation may allow the changes outlined above become a politically supported reality.

5.4 Future work

The findings of this thesis create a wide range of questions for future work, and clear avenues of research have opened as a result. Presented here are some of the potential avenues of research that would further enhance our understanding of moth decline.

5.4.1 Changes in broadleaf woodland

Of all the declines presented here, it is the severe decline recorded in broadleaf woodlands that is perhaps the most surprising, concerning and mysterious (section 2.5.7.3). In addition to the decline in abundance, both species richness and diversity has also significantly declined; this is in contrast to all other habitat types where richness and diversity have either increased or remained stable (section 2.4.1.2). While it is known that the cessation of coppicing and other forms of woodland management has had a negative effect on woodland butterflies (Asher et al., 2001, Fox et al., 2015), the research suggests that, for a single site within a woodland at least, an increasingly mature and shady woodland should favour a more abundant and diverse community of moths (Broome et al., 2011, Merckx et al., 2012a, Sebek et al., 2015), so it is unlikely that cessation of coppicing alone is the answer. In section 2.5.7.3, the potential of the over-grazing by deer of the field and shrub layer within the woodland is discussed. In the RIS network, there are not enough long-term broadleaf woodland sites, and not enough data regarding their management and structural history, to carry out a thorough test of this hypothesis. However, long-term experiments regarding deer inclusion and exclusion have shown that the effects on the community composition of both plants and animals can be stark (Dolman et al., 2010). Either starting new long-term studies of deer inclusion/exclusion with moths in mind or utilising exiting experiments would yield valuable information in this regard.

5.4.2 Land-use change

A major limitation of this thesis is that land-use was measured as a static entity fixed at 2015. This is because the best data available was from the Land Cover Map (LCM) 2015 (Rowland et al., 2017a) and directly comparable data from earlier years was not available. Land-use is not likely to have remained the same since 1968, with urbanisation and conversions of broadleaf woodland to conifer plantations as two highly relevant changes that have occurred. However, very recently, a LCM from 1990 has been released that uses the same methodologies as the 2015 map, making the two directly comparable and enabling a calculation of land-use change over time (Rowland et al., 2020). Future work will benefit from using this data to access the relationship between land-use change and moth decline and may offer greater insight into the drivers of moth population change.

5.4.3 Climate change

While the analysis regarding climate in this thesis was very coarse, there were two important findings. 1) There was very little broad-scale interaction between climate and habitat on moth abundance and 2) warm winters predict low total moth abundance in the following growing season (section 2.4.5). The detrimental effect of warm winters on individual species of Lepidoptera is well-known (Conrad et al., 2003, Klockmann and Fischer, 2019, Stuhldreher et al., 2014) but this thesis presents the first evidence that warm winters have a detrimental effect on moth abundance as a whole. Countering this effect, warm summers of both the present and previous year were shown to positively affect moth abundance. As both winters and summers have become warmer since the 1960s in the UK (Kendon et al., 2020), it is not obvious whether the positive effect of warmer summers has countered the negative effect of warmer winters. Quantifying and disentangling these effects were beyond the scope of this thesis, but it is clear that climate plays an important role in changes to moth abundance and requires further and more detailed research to help us understand moth declines.

5.4.4 Biotic homogenisation

Species diversity is often split into three categories: alpha, beta and gamma (Whittaker, 1960). Alpha refers to the diversity of a single site, gamma refers to the total diversity of a group of sites, and beta diversity refers to the community turnover between those sites. What constitutes a ‘site’ depends on the context of the system being studied. In this thesis, it was found that, overall, species richness remained stable and alpha diversity increased (section 2.4.1) but this varied depending on region and habitat. While it is known that richness across the UK as a whole has increased since the 1960s due to adventive species outnumbering extinct species (Fox et al., 2013) it is not known how beta diversity has changed. A reduction in beta diversity across the landscape equates to an increasing biotic homogenisation; i.e., species assemblages at each location tend to resemble each other more over time. This phenomenon has been found in butterfly and diurnal moth assemblages in a European agricultural landscape (Ekroos et al., 2010) and has also been demonstrated for moths in Hungarian woodlands (Valtonen et al., 2017). It has been shown that beta diversity in moths is lower in urban habitats compared to woodland habitats, with a dominance in generalist species (Merckx and Van Dyck, 2019), and similar results have been found for moths in intensive versus non-intensive grassland habitat (Mangels et al., 2017). It follows that biotic homogenisation over time is likely, given the increased urbanisation and agricultural intensification that occurred in the post-war era. The spatially and temporally extensive data provided by the RIS, as well as the National Moth Recording Scheme, could together be used to explore this in detail to further enhance our understanding of changes to moth communities in the UK.

5.4.5 Light traps

The RIS constitutes the longest-running, most spatially extensive, standardised insect monitoring schemes in the world (Woiwod and Harrington, 1994). Without it, the decline in moth abundance would be largely unknown, or at least unquantifiable, as the data has been used in every publication on moth abundance trends produced in the UK (Bell et al., 2020, Conrad et al., 2004, Dennis et al., 2019, Randle, 2019). The importance of the RIS is demonstrated in (Dennis et al., 2019) who showed that while moth occupancy in Scotland had increased (NMRS data), the per-site abundance had declined (RIS data), meaning that presence only biological records are not a substitute for standardised abundance counts. It is therefore troubling that the RIS faces an idiosyncratic threat: that of running out of bulbs. The trap design has remained unaltered since the 1930s (Williams, 1948), including the 200 W incandescent bulbs. The fact that the same bulb type has been used throughout the time-series is invaluable as it allows direct comparisons in catch-rates to be made. However, with increased environmental legislation worldwide, the manufacture of these bulbs has largely ceased, and the RIS is relying on a stockpile. It is therefore necessary, if the light-trap network is to continue, that a replacement bulb is found: one that has the exact same attractive properties to moths as the original. In Chapter 3, a potential candidate was tested: a commercially available LED bulb designed to mimic the brightness and colour of a 200 W incandescent bulb. It was clear from the results that this bulb attracted far fewer moths (Fig. 3.7), but it was not clear why. The LED bulb had a higher output in lumens, but may have had a slightly lower emission rate of UV radiation, which is known to be more attractive to moths than longer wavelengths (Van Langevelde et al., 2011). Many experiments regarding brightness, spectral emissions and attractive radii of different lighting sources have already been done (Bates et al., 2013, Johnsen et al., 2006, Merckx and Slade, 2014, Somers-Yeates et al., 2013), but studies specifically designed to find a replacement light source for the RIS are needed if the light-trap network is to continue in perpetuity.

5.5 Concluding remarks

The findings of this thesis are troubling: moth abundance has declined drastically in almost every habitat type in the UK and in many cases the decline shows little sign of slowing. However, with the new Environment Bill, the new Agriculture Bill, the ELMs and the growing interest in large-scale ecological restoration, there may be hope for moths yet. A British countryside with a vast network of restored hedgerows, working woodlands, new nature reserves and rewilded areas is possible. Farms with extensive wildflower margins and low chemical inputs could become the rule rather than the exception, and our pastures and hay meadows could be restored to their former glory. Cities and towns could invest in arteries of green space which could be managed with wildlife, rather than neatness, in mind, and intelligent decisions in nocturnal lighting could restore our dark skies. With public and political will, these changes are possible, and moth abundance may once again reach the heights of Barnfield in the 1930s and 40s, and may one day even exceed it.

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