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ORIGINAL PAPER

Prospects for improved off-crop habitat management for pollen beetle control in oilseed rape

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Abstract

There is an urgent need to develop sustainable and environmentally benign integrated pest management (IPM) strategies for arable crops. The enhancement and manipulation of naturally occurring populations of the natural enemies of crop pests through habitat management for 'conservation biological control', as well as habitat management to manipulate populations of the pests themselves, have the potential to become major components of successful IPM strategies. We review the studies that have contributed to our current understanding of how the crop margin, local landscape, and regional landscape can influence pollen beetle *Brassicogethes aeneus* (syn. *Meligethes aeneus*) (Coleoptera: Nitidulidae) abundance and damage to oilseed rape crops (*Brassica napus*), and the efficacy of their natural enemies. We also discuss how habitat management across these multiple scales may improve pollen beetle control, reducing the need for insecticide use and contributing towards sustainable production of this important crop which is grown on increasing areas for both food and fuel.

Keywords *Brassica napus* · *Brassicogethes aeneus* · Conservation biocontrol · Field margin · Habitat management · Trap crop · *Meligethes* · Sustainable agriculture

Introduction

Throughout Europe, the pollen beetle *Brassicogethes aeneus* F. (syn. *Meligethes aeneus*) (Coleoptera: Nitidulidae) is a major pest of oilseed rape *Brassica napus* L. (Brassicaceae) (OSR) (Williams 2010). The crop is an increasingly important source of vegetable oil and biofuel feedstock, with EU production rising from 19.0 M tonnes in 2008 to 21.7 M tonnes in 2015 (Eurostat 2016). Seed yield losses caused by pollen beetles can be significant, particularly in spring-sown crops (Hansen 2004) although widespread losses to winter-sown crops have been reported (Free and Williams 1978a; Zlof 2008). The adult beetles emerge in early spring from their overwintering habitats in wood- and grassland (Rusch et al. 2012a), and feed on pollen from a range of spring flowers, before seeking brassicaceous plants for feeding and oviposition (Free and Williams 1978b). Feeding damage of adults, and in some cases larvae, to flower buds can lead to abscission and subsequent podless stalks (Nilsson 1988). Both visual and olfactory cues are used for host plant location (Williams and Cook 2010), and the beetles colonise OSR crops at or around the green bud stage (Cook et al. 2006; Williams 2010). After eggs are laid in the buds, the developing larvae feed for around 2 weeks before pupation within the soil. New generation adults emerge in summer and again feed on pollen from plants of various families before overwintering (Williams and Free 1978; Ouvrard et al. 2016).

Over the last 40 years, heavy use of pyrethroid insecticides, often applied prophylactically, has led to the increasing occurrence of insecticide resistant pollen beetle populations (Thieme et al. 2010; Zimmer et al. 2014), and hence there is an urgent need to reduce insecticide use and develop more sustainable integrated pest management (IPM) practices for this pest. IPM is defined as the 'careful consideration of all available plant protection methods and subsequent integration of appropriate measures that discourage the development of populations of harmful organisms and keep the use of plant protection products and other forms of intervention to levels that are economically and ecologically

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justified and reduce or minimise risks to human health and the environment. IPM emphasises the growth of a healthy crop with the least possible disruption to agroecosystems and encourages natural pest control mechanisms' [European Union Framework Directive on the Sustainable Use of Pesticides (Directive 2009/128/EC)]. Several tactics for IPM strategies of pollen beetles in OSR are under development. These include efforts to reduce prophylactic insecticide applications through improved pollen beetle forecasting (Johnen and von Richthofen 2013; Ferguson et al. 2016), and monitoring (Cook et al. 2013; Skellern et al. 2017), and determination of more accurate control thresholds (AHDB-HGCA 2012; Ellis and Berry 2012; Ramsden et al. 2017). Other strategies aim to reduce pest numbers to below economic threshold levels; these include the use of plant- or insect-derived semiochemicals or 'signal chemicals', enabling behavioural manipulation of pests or their natural enemies (Cook et al. 2007a; Mauchline et al. 2008, 2013; Pavela 2011; reviewed by Mauchline et al. in press), botanical insecticides or other natural products such as silicate dusts as alternatives to synthetic insecticides (Pavela 2011; Daniel et al. 2013; Dorn et al. 2014), modification of crop management practices (Valantin-Morison et al. 2007; Veromann et al. 2009, 2013; reviewed by Skellern and Cook in press), breeding for OSR resistance to the pest (reviewed by Hervé and Cortesero 2016; Hervé 2017), and inundative biological control via the application or release of natural enemies such as entomopathogenic fungi (e.g. Hokkanen 1993; Husberg and Hokkanen 2001; reviewed by Hokkanen and Menzler-Hokkanen 2017) or nematodes (Menzler-Hokkanen and Hokkanen 2005).

Research into the use of generalist predators and specialist parasitoids of the immature stages of pollen beetles (see Table 1) in IPM strategies has focussed on conservation biological control (CBC), rather than the release of imported exotic or mass-reared natural enemies for biocontrol (Williams 2010). CBC involves the manipulation of the environment (i.e. the habitat) of natural enemies to enhance their survival and/or physiological performance resulting in enhanced effectiveness (Barbosa 1998). It is 'based on the premise that countering habitat loss and environmental disturbance associated with intensive crop production will conserve natural enemies, thus contributing to pest suppression' (Begg et al. 2017). CBC practices are therefore central to delivering pest management ecosystem services within IPM strategies.

Management of the crop itself can contribute to CBC of OSR crop pests, including pollen beetles (reviewed by Rusch et al. 2010; Skellern and Cook in press). However, the crop margin (crop scale), local landscape [the field surroundings up to a range of a few thousand metres; at the scale of the farm unit or several adjacent farm units suitable to the dispersal abilities of the pest (e.g. Juhel et al. 2017)], and regional landscape (large land tracts of indefinite extent, but over scales of tens or hundreds of kilometres, that are sufficiently homogeneous in physical geography or ecology to be viewed as an entity distinct from other adjacent regions) are also known to affect OSR pest abundance and damage, as well as natural enemy efficacy (e.g. Thies and Tscharntke 1999; Buchi 2002; Cook et al. 2004; Rusch et al. 2010, 2011, 2013b). Therefore, better informed management of habitats over these multiple scales has great potential for improving pollen beetle control while diminishing the need for insecticide use. We review the studies that have contributed to our current understanding of how habitat management in non-cropped areas ('off-crop') may improve pollen beetle control. We first consider management of the crop margin, in terms of the development of trap cropping strategies, where plant stands are grown to attract pest insects to protect target crops from attack (Hokkanen 1991), and in terms of the potential of flower-rich field margins to enhance natural pest control. We then consider larger-scale landscape effects on pollen beetles and their natural enemies, and their implications for habitat management strategies. These are summarised in Table 2.

Habitat management of the crop margin

Trap cropping to reduce pollen beetle infestation of oilseed rape

Trap crops are 'plant stands that are, per se or via manipulation, deployed to attract, divert, intercept, and/or retain targeted insects or the pathogens they vector in order to reduce damage to the main crop' (Shelton and Badenes-Perez 2006). Pollen beetles show clear host plant preferences that can be exploited in trap cropping strategies (Cook et al. 2006), which aim to concentrate the pest on attractive trap crop plants while detracting it from the target OSR at its damage-susceptible stage (Hokkanen 1991); i.e. at the green-yellow bud stage (Williams 2010). Trap cropping has potential for management of pollen beetles in OSR, especially as the 'pull' element in push–pull strategies which combine a trap crop or other attractant or arrestant stimulus outside the crop and a deterrent or repellent near or within the crop, to divert pests, reducing their populations on the target crop (Cook et al. 2007b; Eigenbrode et al. 2016).

Several species of the Brassicaceae appear more attractive to pollen beetles than spring-sown OSR, including turnip rape *Brassica rapa* (Hokkanen 1989, Hokkanen et al. 1986; Buchi 1990; Cook et al. 2004, 2006, 2007c), yellow mustard *Brassica juncea* (Kaasik et al. 2014b), black mustard *Brassica nigra* (Veromann et al. 2012; Kaasik et al. 2014a), and white mustard *Sinapis alba* (Kaasik et al. 2014b). However, few studies have tested the possibility that trap crops can

Table 1 Main natural enemies of pollen beetles present in Europe pertinent to conservation biological control via habitat management

Order	Family	Species or genera noted as pollen beetle predators or associated with OSR crops	Mode of attack	References
Hymenoptera	Ichneumonidae subfamily Tersilochinae		Univoltine, koinobiont endoparasitoids:	
		Phradis interstitialis	Parasitise eggs and L1 larvae in buds	Jourdheuil (1960); Osbourne (1960); Wyrostkiewicz and Blazejewska (1985); Nilsson and Andreasson (1987); Klingenberg and Ulber (1994); Buchi (2002); Kraus and Kromp (2002); Nilsson (2003); Ulber et al. (2010)
		Phradis morionellus	Parasitise L1 larvae in buds; most common in spring OSR	Jourdheuil (1960); Osbourne (1960); Nilsson and Andreasson (1987); Hokkanen (1989); Billqvist and Ekbom (2001b); Nilsson (2003); Veromann et al. (2006); Jönsson and Anderson (2007); Ulber et al. (2010)
		Tersilochus heterocerus	Parasitise mainly L2 larvae in flowers	Jourdheuil (1960); Osbourne (1960); Wyrostkiewicz and Blazejewska (1985); Nilsson and Andreasson (1987); Klingenberg and Ulber (1994); Buchi (2002); Kraus and Kromp (2002); Nilsson (2003); Ulber et al. (2010)
	Braconidae, superfamily Helconinae		Multivoltine koinobiont endoparasitoids:	
		Blacus nigricornis	Parasitise L1 and L2 larvae in buds and flowers. Most common in spring OSR	Nilsson and Andreasson (1987); Nilsson (2003); Ulber et al. (2010)
		Diospilus capito		Nilsson and Andreasson (1987); Billqvist and Ekbom (2001a); Veromann et al. (2006); Hokkanen 2008; Nilsson (2003); Ulber et al. (2010)
	Proctotrupidae	*Brachyserphus parvulus*	Multivoltine koinobiont endoparasitoids; more common in spring OSR	Nilsson and Andreasson (1987); Nilsson (2003); Ulber et al. (2010)
Coleoptera	Carabidae	*Amara similata*[a]	Surface active larval predators (plant-climbing, may prey on larvae from flowers[a]; burrowing species, may prey on pupating larvae[b])	Williams et al. (2010)
		Anchomenus dorsalis		Schlein et al. (2006)
		Bembidion lampros		Williams et al. (2010)
		Clivina fossor[b]		Williams et al. (2010)
		Harpalus affinis		Schernéý (1959); Schernéý (1961); Luka et al. (1998); Warner (2001)
		Harpalus rufipes		Williams et al. (2010)
		Loricera pilicornis		Williams et al. (2010)
		Nebria brevicollis		Piper and Williams (2004); Warner et al. (2008)
		Poecilus cupreus		Schlein et al. (2006)
		Pterostichus madidus		Piper and Williams (2004); Schlein et al. (2006)
		Pterostichus melanarius		Williams et al. (2010)
		Trechus quadristriatus		Williams et al. (2010)
	Coccinellidae	*Coccinella septum punctata*	Adults and larvae may predate on larvae in flowers	Friederichs (1920); Nilsson and Andreasson (1987)
	Melyridae	Malachius spp.	Predate on larvae in flowers	Friederichs (1920); Nilsson and Andreasson (1987)

Table 1 (continued)

Order	Family	Species or genera noted as pollen beetle predators or associated with OSR crops	Mode of attack	References
	Staphylinidae	*Anotylus* spp. *Lathrobium* spp. *Lesteva* spp. *Mycetoporus* spp. *Omalium* spp. *Philonthus* spp. *Proteinus* spp. *Tachyporus* spp. *Xantholinus* spp.	Surface/canopy active predators	Nilsson and Andreasson (1987); Krooß (1996) Büchs and Alford (2003)
Araneae	Lycosidae	*Pardosa* spp.	Surface active predators	Harenberg (1997); Frank et al. (2010)
	Linyphiidae	*Bathyphantes* spp. *Erigone* spp. *Lepthyphantes* spp. *Oedothorax* spp.	Surface/canopy active predators	Nilsson and Andreasson (1987); Harenberg (1997); Büchs (2003)
	Tetragnathidae	*Pachygnatha degeeri*	Surface/canopy active predators	Harenberg (1997); Büchs (2003)
	Theridiidae	*Theridion impressum*	Canopy active predator	Harenberg (1997); Büchs (2003)
	Salticidae	*Salticus scenicus*	Surface active predator	Harenberg (1997); Büchs (2003)

reduce populations in OSR crops in practice. Hokkanen et al. (1986) and Hokkanen (1989) tested turnip rape trap crops comprising 1–15% of the main crop, placed in the middle or surrounding spring OSR fields. Areas of 10–15% reduced pollen beetle populations in the OSR crop and reduced the need for insecticide applications by 50–85%. Simulations using a spatially explicit individual-based model indicate that a perimeter trap crop would be the most appropriate arrangement (Potting et al. 2005). Cook et al. (2004) showed that spring OSR plots with a perimeter trap crop comprising c. 10% of the crop area had significantly reduced pollen beetle populations compared with control plots; populations were maintained below threshold levels and bud damage was significantly reduced. The turnip rape developed more quickly than the OSR and flowered c. 2 weeks before OSR; early flowering was also mentioned as essential to function by Hokkanen et al. (1986) and growth stage shown to be a critical mechanism of the success of turnip rape as a trap crop in later studies (Cook et al. 2007c). Buchi (1990) attributed the attraction of pollen beetles to turnip rape to the yellow-green colour of the leaves which may be more attractive than the blue-green colour of OSR. Studies on the colour responses of pollen beetles support this theory (Döring et al. 2012). Host plant odour has also been studied and the increased amounts of phenylacetaldehyde and indole in turnip rape also play a role in its success (Cook et al. 2007c).

While early studies focussed on spring OSR crops, later research investigated transfer to winter-sown systems, using a forage rape × forage turnip hybrid 'Pasja' (Cook et al. 2013) or a forage turnip × Chinese cabbage hybrid 'Perko' (Čuljak et al. 2016). Both studies tested the strategy on a field scale, showing that trap crop plants were significantly more infested by pollen beetles than OSR plants in the borders of control fields (Cook et al. 2013) or in field centres (Čuljak et al. 2016). While Čuljak et al. (2016) showed that trap crop strips, representing 15–25% of the total crop area, were able to maintain within-crop pollen beetle infestation at below threshold levels for 97.5% of the crop area, Cook et al. (2013) found the effect of the trap crop inconsistent between sites and years. However, in replicates/years where the trap crop was ineffective, flowering of the trap crop and OSR occurred only c. 1 week apart, and brassicas flowering 2–3 weeks earlier than the main crop are needed for the strategy to be reliable (Cook et al. 2013). Spraying the trap crop had no significant impact on populations in the main crop (Cook et al. 2013). For a conventionally managed crop, a cost:benefit analysis indicated that trap cropping is not cost effective, with a return of c. £400/ha compared with c. £450 if the crop needs to be sprayed and c. £480/ha if the crop receives no insecticide. Currently the strategy is only likely to be economically useful to organic growers who can gain a significant premium on seed grown in this way (Cook

Table 2 Summary of effects of habitat management on pollen beetles and their natural enemies in oilseed rape (OSR)

Scale	Management practice	Effect of management practice on pollen beetle pest	Effect of management practice on parasitoids of pollen beetle	Effect of management practice on generalist predators of pollen beetle
Crop scale (off-crop at interface between crop edge and field boundary)	Trap cropping to prevent infestation of pollen beetles into main crop, e.g. using turnip rape *Brassica rapa* types	Pollen beetle populations reduced in the main crop: SOSR (Hokkanen et al. 1986; Hokkanen 1989; Cook et al. 2004; Buchi 1990); WOSR (Cook et al. 2013; Čuljak et al. 2016)	Parasitoids attracted earlier to main crop (Defra 2010); modelled effects suggest improved biocontrol Vinatier et al. (2012)	No reports of effects
	Trap cropping to prevent beetles migrating out of crops; dead-end trap cropping using e.g. fodder radish *Raphanus sativus*	Pollen beetle populations reduced in the main crop and larval development poor in trap crop (Veromann et al. 2012, 2014)	Parasitism rates on *Raphanus sativus* reported to be lower than on *B. napus* (Kaasik et al. 2014a); in other studies *R. sativus* found to facilitate high parasitoid production (Defra 2013)	No reports of effects
	Flower-rich field margins	Could support pollen beetle populations by provision of pollen and nectar resources	Flowering margins benefit parasitoid populations (Rusch et al. 2013a; Mansion-Vaquié et al. 2017; Hatt et al. in press) and provision of flowering resources increases parasitism (Thies and Tscharntke 1999; Buchi 2002)	Proximity to flower strips reduced pollen beetle larval abundance due to predation (Buchi 2002); flower strips increased species richness (of carabid beetles and spiders) in OSR crops (Frank and Nentwig 1995; Frank 1997). Flower strips could exacerbate other pest problems, e.g. slugs (Frank 1998)
	Flower-rich field margins including or comprising plant species of the Brassicaceae	Will support pollen beetle populations by provision of pollen and nectar resources and reproduction sites, but this can be offset if plants benefit populations of natural enemies more than the pest	*Brassica* margins can support large numbers of parasitoids of oilseed rape pests (PURE 2013) *B. nigra* is particularly well utilised by the parasitoid *Tersilochus heterocerus* (Kaasik et al. 2014a)	Brassica margins support *Amara ovata*, a carabid species typical of communities associated with OSR (which also include *Poecilus cupreus* and *Amara similata*) (Brooks et al. 2008; PURE 2013)
		Egg production and larval survival/development reduced on *Sinapis alba* (Ekbom 1997; Hopkins and Ekbom 1999; Ekbom and Popov 2004)	*Sinapis alba* supports increased parasitism by *Diospilus capito* and *Phradis morionellus* (Billqvist and Ekbom 2001a, b); wildflower margins with high *S. alba* abundance hosted more parasitoids and suffered reduced herbivory (Scheid et al. 2011) Forage rape cv Hobson (*B. napus*) supports high parasitoid production (Defra 2013)	

Table 2 (continued)

Scale	Management practice	Effect of management practice on pollen beetle pest	Effect of management practice on parasitoids of pollen beetle	Effect of management practice on generalist predators of pollen beetle
Local scale (the field surroundings up to a range of a few thousand metres; at the scale of the farm unit or several adjacent farm units)	Landscape complexity (proportions of semi-natural habitats or non-crop area)	Increased pollen beetle density and/or pollen beetle-associated damage with increased landscape complexity (Zaller et al. 2008b; Rusch et al. 2012b, 2013b)	Increased landscape complexity has positive effects on pollen beetle parasitism (Thies and Tscharntke 1999; Thies et al. 2003; Scheid et al. 2011; Rusch et al. 2012b; Beduschi et al. 2015)	
		Reduced pollen beetle density and/or reduced pollen beetle-associated damage with increased landscape complexity (Thies and Tscharntke 1999; Thies et al. 2003; Gladbach et al. 2011; Beduschi et al. 2015)	Negative relationship (Schneider et al. 2015) No relationship (but was conducted post-flowering; Gladbach et al. 2011)	
	Woodlands	Increasing proportions of woodland associated with higher pollen beetle density and damage (Valantin-Morison et al. 2007; Zaller et al. 2008b, 2009; Rusch et al. 2012b, 2013b)	Increasing proportions of woody habitats associated with higher parasitism rates in OSR (Zaller et al. 2009; Rusch et al. 2011, 2012b)	Spider species richness positively related to increasing proportions of woody and non-crop areas (Drapela et al. 2008)
	Grasslands	Increased grassland area may have both negative (Thies and Tscharntke 1999) and positive (Rusch et al. 2013b) effects on pollen beetle density and damage	Area of grassland has positive effects on parasitism rates in OSR (Thies and Tscharntke 1999; Zaller et al. 2009; Rusch et al. 2011, 2012b) either via improved floral resource provision and/or via density dependence with pollen beetle hosts	Nutritional condition of male *Poecilus cupreus* and *Amara similata* carabid beetles related to distance from the nearest fallow (Haschek et al. 2012); Oocyte numbers in female *A. similata* negatively related to distance from the nearest fallow (Haschek et al. 2012) Greater grass strip length and shorter distance to the nearest fallow most influenced activity–density of *Pardosa* predatory spiders (Drapela et al. 2011)

Table 2 (continued)

Scale	Management practice	Effect of management practice on pollen beetle pest	Effect of management practice on parasitoids of pollen beetle	Effect of management practice on generalist predators of pollen beetle
	OSR area (in the current season)	No influence on density and damage (Thies and Tscharntke 1999; Thies et al. 2003, 2008; Gladbach et al. 2011; Scheid et al. 2011; Rusch et al. 2013b; Skellern et al. 2017) Negative relationship [attributed to dilution effects; (Zaller et al. 2008a, b; Moser et al. 2009; Schneider et al. 2015)] Positive relationship (Valantin-Morison et al. 2007) Effect changes with time, from negative during flowering to positive after flowering (Beduschi et al. 2015)	No effect on parasitism (Thies and Tscharntke 1999; Thies et al. 2003, 2008; Beduschi et al. 2015) Increasing OSR in area has negative effect on parasitism (Hokkanen et al. 1988; Schneider et al. 2015)	Nutritional condition of male *Poecilus cupreus* and *A. similata* related to percentage of surrounding OSR crop area (Haschek et al. 2012)
	OSR area in the previous year	No influence on herbivory (Thies et al. 2008) Increase in area over previous year leads to reduced abundance and herbivory (through dilution; Schneider et al. 2015) ; negative effect on abundance seen 1 or 2 years later (Beduschi et al. 2015) Positive influence of the previous season's OSR proportion on trap catch (Skellern et al. 2017)	Positive effect of OSR in the previous year on parasitism (Beduschi et al. 2015) Proximity of OSR crops to those in OSR the previous year and the proportion of previous year's OSR fields under reduced post-harvest tillage regimes positively affect parasitism (Rusch et al. 2011, 2012b)	
Regional landscape scale (large land tracts of indefinite extent, but over scales of tens or hundreds of kilometres, that are sufficiently homogeneous in physical geography or ecology to be viewed as an entity distinct from other adjacent regions)	OSR area	To exploit the dilution effects that occur with increasing OSR proportions, a co-ordinated regional landscape-scale management scheme would increase annually the OSR cover within a region, maintaining the benefits of dilution effects for several years. A year with low crop cover (Schneider et al. 2015), or a year when OSR cultivation ceases (Beduschi et al. 2015) would then be used to 'reset' the rotation	The positive effects of pest dilution due to annually increasing OSR area may be offset by parasitoid dilution and lowered biological control (Schneider et al. 2015)	

Table 2 (continued)

Scale	Management practice	Effect of management practice on pollen beetle pest	Effect of management practice on parasitoids of pollen beetle	Effect of management practice on generalist predators of pollen beetle
	OSR area in the previous year	In complex landscapes (with ample breeding and overwintering sites necessitating only limited migration) beetle abundance is likely to reflect surrounding OSR area in the previous year, particularly where parasitism rates are low. In simple landscapes where long-distance migration is necessary, relationships between beetle abundance and the previous season's OSR area are unlikely to be found, particularly at relatively fine (e.g. 1000 m) sampling scales		
	Landscape complexity	If beetles migrate from regions with a paucity of overwintering sites to more structurally complex regions where overwintering sites are more abundant, the effect of high parasitism rates in these areas may be reduced by inward migration (Rusch et al. 2013b). Thus, efforts to promote biocontrol through parasitism are better applied within simple landscapes rather than in complex ones where parasitism rates are already high		

et al. 2013). Food-grade cultivars of turnip rape seeds can be harvested for oil as with OSR; however, it is lower-yielding, and tends to ripen faster, and thus requires harvesting earlier than OSR drilled at the same time if seed losses are to be avoided. If early flowering cultivars of OSR could be developed with the same attractive properties as turnip rape, then the strategy may be more cost effective (Cook et al. 2013).

The possibility of using trap crops to trap out pollen beetles as they move from winter to spring-sown OSR crops or other flowering resources before hibernation has been suggested (Veromann et al. 2012). Fodder Radish, *Raphanus sativus*, was more attractive than OSR in the flowering stages and was acceptable for oviposition but larval development on the plant has shown to be poor, leading to the suggestion that it may also have potential as a 'dead-end' trap crop (Shelton and Nault 2004) for pollen beetles (Veromann et al. 2012, 2014).

The effects of trap crops on general predators have not, to our knowledge, been reported and effects on parasitoids and parasitism of pollen beetle larvae in OSR have been little studied. There is some evidence of earlier parasitoid attraction to OSR crops when trap crops are present than in their absence (Defra 2010) and Vinatier et al. (2012) produced models suggesting that trap crops improved biocontrol of pollen beetles in OSR. As well as being planted as borders/strips to the crop, the trap plants could form part of field margin mixtures as part of conservation biocontrol measures for the parasitoids of pollen beetles and this is reviewed below.

The potential of flower-rich field margins to enhance natural pest control in oilseed rape

Field margins and other semi-natural habitats represent environments of relative stability compared with cropped areas, and can provide natural enemies with a source of alternative hosts and prey, overwintering habitat, refuges from biotic and abiotic conditions including tillage as well as floral resources (e.g. Sotherton 1984; Pickett and Bugg 1998; Thomas et al. 1991; Denys and Tscharntke 2002; reviewed by Gillespie et al. 2016). Provision of floral resources can promote the development and activity of populations of predators (e.g. Robinson et al. 2008; Tschumi et al. 2016; Hatt et al. 2017) and parasitoids (e.g. Baggen and Gurr 1998; Rebek et al. 2006). Access to nutrition provided by pollen and nectar has been shown to benefit natural enemies, improving their efficacy through increasing longevity and fecundity (reviewed by Lu et al. 2014; Gillespie et al. 2016).

There are at least nine species of hymenopteran parasitoids which attack pollen beetle (Nilsson 2003; Ulber et al. 2010), with six being of importance for biocontrol purposes (Table 1) exerting parasitism levels in the range of 25–50% (reviewed by Ulber et al. 2010). For these parasitoids, as their hosts specialise on plants of the Brassicaceae for reproduction, brassicaceous plants represent important breeding sites (Nilsson 2003; Ulber et al. 2010). Field margin mixtures designed with conservation biocontrol of OSR pests in mind are likely to perform well if they contain appropriate brassica species which could support pollen beetle parasitoids by acting as natural 'banker plants' (see Frank 2010), i.e. by providing natural infestations of host larvae for reproduction (Skellern et al. submitted; Defra 2013). As the univoltine parasitoids of pollen beetles overwinter in the soil in which the OSR crop was grown, emerging the following spring into the following crop in the rotation (often wheat), individuals developing on these plants and pupating in field margin soil would be protected from the insecticide- and tillage-related mortality experienced within-field (Nilsson 2010). Inclusion of these plants in field margins, as well as performing a trap cropping function, may also help to sustain parasitoid populations throughout the arable rotation, particularly when OSR is absent. This may be particularly relevant in landscapes where the spatial separation of large blocks of OSR fields forces the parasitoids, which have weaker dispersal abilities than their hosts (Thies and Tscharntke 2010) to migrate large distances from their emergence sites. Brassicas under consideration for field margin inclusion, however, should be carefully chosen to favour production of the parasitoids, and not that of their injurious hosts (see Gurr et al. 2004).

Studies assessing the influence of field margins on the biological control of pollen beetles in adjacent OSR crops have shown positive effects. Thies and Tscharntke (1999) observed that old field margin strips alongside winter OSR increased larval mortality through parasitism, and that larger, old fallows showed a more pronounced effect. Buchi (2002) showed that pollen beetle larval parasitism rates were significantly higher in OSR fields next to flower-rich margins than in those next to extensively managed meadows. Hatt et al. (in press) showed that the density of pollen beetle parasitoids caught in yellow traps within wildflower strips were related to floral traits not host abundance, but the relationship with adults, not the larval hosts was tested and parasitism was not assessed. In both studies where parasitism was assessed, better provision (quality and/or quantity) of floral resources from the field margins may have enhanced parasitoid activity in the crop. Indeed, Rusch et al. (2013a) showed that the parasitoid *Tersilochus heterocerus* (Hymenoptera: Ichneumonidae) had already consumed high amounts of sugar by the time they appeared in OSR fields, indicating their acquisition of non-OSR floral resources, and Jönsson and Anderson (2007) showed that starved *Phradis morionellus* (Hymenoptera: Ichneumonidae) parasitoids were less responsive than fed individuals to host-infested OSR racemes, perhaps because the starved individuals were in food-seeking rather than host-seeking mode.

Several studies have examined pollen beetle host plant preferences, performance, and parasitism rates on a range of species of the Brassicaceae, providing information that is relevant to a consideration of the utility of these as field margin banker plants. Brassicaceous plants vary in their acceptability for pollen beetle oviposition and feeding. While the beetles are a particular pest of OSR and turnip rape (Bromand 1990), other species accepted for oviposition and feeding include the mustards *B. juncea* and *B. nigra* and Abyssinian cabbage *B. carinata* (Ekbom and Borg 1996). White mustard, *S. alba*, and crambe, *Crambe abyssinica*, are accepted for feeding but have low acceptability for oviposition (Ekbom and Borg 1996). Winter cress *Barbarea vulgaris* and land cress *B. verna* have low acceptability for both oviposition and feeding (Borjesdotter 2000), and pollen beetle has been shown not to feed on candytuft, *Iberis amara* (Bartlet et al. 2004). Rocket, *Eruca sativa*, is relatively unattractive to the beetle (Ekbom 1998) and shows low acceptability for oviposition (Kaasik et al. 2014a).

Of the brassicaceous plants exploited by pollen beetles, *Brassica nigra* has been proposed as a potential 'banker plant' (Kaasik et al. 2014a) as it was particularly well utilised by *T. heterocerus*. Other studies, however, suggest that members of the brassicaceae which are lower quality host plants for the pest may also hold potential. Pollen beetles exhibit reduced egg production (Hopkins and Ekbom 1999) and egg size (Ekbom and Popov 2004) on less acceptable host plants (*S. alba*) vs. those of high quality (*B. napus*). Larvae reared on *S. alba* exhibit slow development, display increased mortality, and develop into smaller adults than those reared on high-quality host plants. In turn, the resultant smaller females also lay fewer eggs (Ekbom 1997). Furthermore, larvae developing on *S. alba* have been shown to have a significantly higher likelihood of being parasitised by both *Diospilus capito* (Hymenoptera: Braconidae) (Billqvist and Ekbom 2001a) and *P. morionellus* (Billqvist and Ekbom 2001b) than those developing on *B. napus*; the increased mobility of larvae on these plants may lead them to greater parasitoid exposure. Neither survival nor size of *D. capito* individuals appears to differ between those developing on *S. alba* and *B. napus* (Billqvist and Ekbom 2001a), suggesting that *S. alba* favours the production and survival of pollen beetle parasitoids over that of the pest. Indeed, Scheid et al. (2011) found that undisturbed sown wildflower fields with high *S. alba* densities hosted more pollen beetle parasitoids and suffered less from herbivory than fields with low *S. alba* densities. The authors concluded that undisturbed flower fields containing *S. alba* provide a suitable habitat for the build-up and maintenance of pollen beetle parasitoid populations, aside from OSR crops—in other words, *S. alba* appears to be a promising banker plant for inclusion in field margin mixtures.

Raphanus sativus is another poor-quality pollen beetle host plant with potential for use as a banker plant. Even though pollen beetle larval mortality on the plant is high (Veromann et al. 2012, 2014), emergence trap experiments showed that *R. sativus* facilitated high pollen beetle parasitoid production (Defra 2013; Skellern et al. submitted). However, there was also strong evidence that the plant could assist proliferation of seed weevil (*Ceutorhynchus obstrictus*) (Coleoptera: Curculionidae), as larval parasitism rates on *R. sativus* were extremely low. Forage rape cv. 'Hobson' exhibited similarly high pollen beetle parasitoid production characteristics to *R. sativus*, but there was no evidence that this brassica would exacerbate problems with other pests, indicating that it may be a favourable option as a banker plant in winter-sown mixtures (Defra 2013; Skellern et al. submitted).

The commercial field margin mixtures used in European agri-environment schemes so far have tended to be designed for conservation purposes of specific groups such as farmland birds (e.g. Vickery et al. 2009) or pollinators (e.g. Carvell et al. 2006), and few contain species in the Brassicaceae. However, these often have value for supporting predator species in agroecosystems (reviewed by e.g. Gurr et al. 2000; Haaland et al. 2011). Although predators are probably less important than parasitoids in biocontrol of pollen beetle (Nilsson and Andreasson 1987; Hokkanen et al. 1988), several species in groups including carabid beetles, rove beetles, and spiders may predate on pollen beetle larvae, either in the flowers or as they drop to the ground to pupate (Büchs and Alford 2003; Warner et al. 2008; Table 1). Data on predation rates and effects on populations of pollen beetles are scarce but predation has been estimated to cause around 20% of total pollen beetle mortality (Buchi 2002; reviewed by Büchs 2003). These groups are known to be supported by field margins due to provision of food and refuge sites, and in particular overwintering sites. Carabid beetles (e.g. Rouabah et al. 2015; reviewed by Haaland et al. 2011), ladybirds, in particular *Coccinella septempunctata* (e.g. Meek et al. 2002; Burgio et al. 2006; Tschumi et al. 2016) and Staphylinid beetles (e.g. Burgio et al. 2006) as well as some spiders (e.g. Meek et al. 2002) often show a greater diversity in flowering field margins than other margins or habitats, although vegetation structure species composition, age, and management are also important (Rouabah et al. 2015; reviewed by Haaland et al. 2011). Field margins have been shown to have positive effects on the abundance of these predators in adjacent crops including OSR; Frank and Nentwig (1995) and Frank (1997) showed species richness of carabid beetles and spiders in OSR was positively influenced by adjacent flowering 'weed' strips but the number of species and individuals was reduced with distance in-crop from the margin (see also Büchs 2003). A better understanding of the movement of predators between field margins and the crop (and vice versa) is required in order to optimise the potential of field margins to underpin conservation biocontrol by generalist predators in OSR (see Begg et al. 2017). The negative effects of these interventions on other pests must also be understood and minimised; wildflower strips sown next to OSR have been shown to lead to slug damage (Frank 1998).

In recent years, the focus has now turned towards development of 'multi-functional' margins that provide a wider range of ecosystem services to crops throughout entire arable rotations (Baverstock et al. 2014; Hatt et al. in press). Field margin mixtures containing at least a cereal, legume, and a member of the Brassicaceae have been shown to support populations of the natural enemies of crop pests of the main arable rotation, and careful selection of plant composition and timing of sowing can improve margin value by increasing floral resource availability early and late into the season (Baverstock et al. 2015; Defra 2016). In particular, margins containing flowering brassicas can support large numbers of parasitoids (Mansion-Vaquié et al. 2017), many of them brassica specialist (PURE 2013), and for generalists, there is some evidence that these margins may also support carabid species typical of communities associated with OSR (PURE 2013). Spatial positioning of margins also needs to be considered. There is potential to improve biocontrol by spatially separating margins with variation in flowering phenology; there is some evidence that spatial separation of margins providing early and late season floral resources may encourage aphid parasitoid movement into wheat crops (Defra 2016), but the potential of this method to encourage movement of the natural enemies of brassica specialist pests into OSR has not yet been investigated. Clearly more work is needed to optimise margin mixtures for biocontrol of pollen beetle, show yield effects in the crop, and elucidate minimum margin areas needed for maximal effect.

Local and regional landscape influences on pollen beetles and their natural enemies

Pollen beetle density and herbivory

Investigations into the impact of local landscape complexity (frequently measured as proportions of semi-natural habitats or non-crop area) on pollen beetle density and herbivory have had contrasting conclusions. Some studies found reduced densities or plant damage associated with more complex landscapes (Thies et al. 2003; Thies and Tscharntke 1999; Gladbach et al. 2011; Beduschi et al. 2015), while others have shown a positive relationship (Zaller et al. 2008b; Rusch et al. 2012b, 2013b). Differences in methodologies makes comparisons difficult, and for the studies showing negative relationships, assessments were sometimes made on potted spring OSR plants (Thies et al. 2003) or 'phytometer'

Sinapis arvensis plants (Gladbach et al. 2011) used towards the end of winter OSR flowering, rather than during initial crop colonisation from overwintering sites. Beetles dispersing from OSR crops at the end of flowering are likely to be less specific (to the Brassicaceae) in their requirements than those primarily interested in finding breeding sites early in the season, and may simply move on to other (non-brassicaceous) flowering plants to feed (Free and Williams 1978b; Williams and Free 1978; Ouvrard et al. 2016). The greater availability of these plants in more complex landscapes may have led to a dilution effect on beetle numbers found on the Brassicaceae sampled at that time of year.

When resolution of habitat types is increased and wooded areas are considered separately, the results have been more consistent across studies. Increasing proportions of woodland in the landscape are generally associated with higher pollen beetle densities and damage (Valantin-Morison et al. 2007; Zaller et al. 2008b, 2009; Rusch et al. 2012b, 2013b). Grasslands have shown inconsistent results, with both negative (Thies and Tscharntke 1999) and positive (Rusch et al. 2013b) relationships found between grassland proportions and pollen beetle infestation or herbivory. These results are most probably due to the role of such habitats, particularly woodlands, as overwintering sites which later become the springtime source of emerging beetles (Juhel et al. 2017). While Rusch et al. (2012a) showed that pollen beetles can overwinter in both woodland and grassland habitats, emerging beetles were more associated with local habitat characteristics such as low soil moisture and a thick litter layer than with habitat type per se. These characteristics may frequently be associated with woodlands, but less often with grasslands where the factors influencing litter thickness, such as habitat age and grazing intensity are likely to be more variable.

Oilseed rape area and spatial arrangement

Many studies that have investigated local landscape-scale effects of OSR area on pollen beetle density or damage in the same season have shown no influence (Thies and Tscharntke 1999; Thies et al. 2003, 2008; Gladbach et al. 2011; Scheid et al. 2011; Rusch et al. 2013b; Skellern et al. 2017), suggesting that proximity to overwintering and early spring feeding sites may be a more important determinant of infestation and damage than OSR area. Others, however, have shown negative relationships, often attributed to dilution effects (Zaller et al. 2008a, b; Moser et al. 2009; Schneider et al. 2015) or a positive relationship (Valantin-Morison et al. 2007). Interestingly, Schneider et al. (2015) found that a dilution of pollen beetle abundance associated with spatially increasing OSR landscape proportions led to higher OSR yields. Discrepancies among studies could result from unknown differences among study regions (Rusch et al. 2013b) or sampling methodology differences, particularly in relation to scale, or to the temporal dynamics of the relationship between the beetles and the OSR crop. Indeed, Beduschi et al. (2015) found that the effect of surrounding OSR area on beetle abundance changed with time, from negative during flowering to positive after flowering, probably reflecting dilution and crowding effects, respectively.

Few studies have investigated possible local landscape-scale effects of OSR area in the year previous to sampling, on pollen beetle infestation or damage. Schneider et al. (2015) showed that between-year increases in OSR proportions led to beetle dilution effects, and Beduschi et al. (2015) found that increasing landscape proportions of OSR negatively influenced beetle abundance 1 or 2 years later, though this effect was considered to be mediated through parasitism. Thies et al. (2008) observed no influence of this variable on pollen beetle herbivory, while a field-scale model of the influence of landscape and weather variables on trap catches of pollen beetles immigrating into OSR crops showed a positive influence of the previous season's OSR proportions on trap catch (Skellern et al. 2017). Factors including the extent to which regional-scale landscape structure necessitates long-distance migration (Rusch et al. 2013b), and differences in parasitism rates, may explain these differences. For example, in landscapes with ample breeding and overwintering sites where only limited migration is necessary, it might be expected that beetle abundance would reflect surrounding OSR area in the previous year, particularly where parasitism rates are low. By contrast, in landscapes where long-distance migration is necessary because they are more compartmentalised at the regional scale (i.e. some areas with large open fields and other distinct areas with more complex landscapes), relationships between beetle abundance and the previous season's OSR area are unlikely to be found, particularly at relatively fine (e.g. 1000 m) sampling scales.

Parasitism

Local landscape complexity effects on pollen beetle parasitism appear generally more consistent across studies than those acting on the beetles themselves, and positive relationships have usually been reported (Thies et al. 2003; Thies and Tscharntke 1999; Scheid et al. 2011; Rusch et al. 2012b; Beduschi et al. 2015), with the exception of two studies, one conducted post-OSR flowering, which found no relationship (Gladbach et al. 2011), and one which found a negative relationship (Schneider et al. 2015). Increasing proportions of woodland, and particularly of grassland within the landscape, are consistently associated with higher parasitism rates in OSR (Thies and Tscharntke 1999; Zaller et al. 2009; Rusch et al. 2011, 2012b). Flowering plants within grasslands and woodlands are likely to provide parasitoids with supplementary nectar resources, and sugar-feeding is known to increase parasitoid fecundity and longevity (e.g. Wäckers et al. 2005; Gillespie et al. 2016), the latter being a factor which could be particularly important during dispersal from emergence sites into OSR crops (Vinatier et al. 2013). In addition to effects over distances of 1500–2000 m, Rusch et al. (2011) noted strong positive smaller-scale (250 m) influences of woodland and grassland area on parasitism rates. This, coupled with the fact that pollen beetle parasitoids sometimes unexpectedly emigrate from OSR patches to the surrounding environment (Williams et al. 2007), suggests that they may supplement their OSR-nectar diets with nectar from the surrounding environment to optimise fitness. Aside from these energetic considerations, grasslands and woodlands may also enhance parasitoid populations through provision of alternative hosts or host plants (Gillespie et al. 2016). Wild Brassicaceae may be important in sustaining parasitoid populations in grassland environments (Hokkanen et al. 1988; Billqvist and Ekbom 2001a, b; Scheid et al. 2011). In woodlands, however, members of the Brassicaceae do not frequently occur, but several *Meligethes* species, feeding on herbs such as *Lamium* spp. and members of the Rosaceae which are commonly present, are also hosts of pollen beetle parasitoids (Horstmann 1981). The importance of alternative hosts in terms of parasitoid production, however, has yet to be ascertained. The positive relationship between parasitism rates and woodland or grassland proportions within the landscape could also be driven by host density dependence, with increased beetle infestation levels leading to enhanced parasitism rates; several studies have reported a density-dependence effect on pollen beetle parasitism (Zaller et al. 2009; Gladbach et al. 2011; Scheid et al. 2011; Schneider et al. 2015).

The reported influence of the current season's OSR proportions within the local landscape on parasitism rates has been mixed, with several studies finding no effect (Thies et al. 2003, 2008; Thies and Tscharntke 1999; Beduschi et al. 2015). However, Hokkanen et al. (1988) found that parasitism rates were lowest in areas where OSR cultivation occurred over the largest area. Similarly, Schneider et al. (2015) observed that parasitism rates decreased with spatially increasing OSR in the landscape and attributed this to dilution effects, and Thies et al. (2008) showed that inter-annual changes in OSR area resulted in concentration and dilution effects on parasitism (i.e. parasitism increased as OSR area decreased between years, and vice versa). Gladbach et al. (2011) found that parasitism rates on *S. alba* at the end of OSR flowering increased more strongly with larval density if the surrounding OSR crop area was high, possibly due to post-OSR flowering concentration effects.

The impact of OSR areas in the previous year has been more consistent. Beduschi et al. (2015) observed a strong positive effect of OSR in the previous year on parasitism rates in the next season, and this resulted in a carry-over effect to the following year, affecting the abundance of overwintered beetles. The proximity of OSR crops to those in OSR the previous year (Rusch et al. 2011) and the proportion of previous year's OSR fields under reduced post-harvest tillage regimes (Rusch et al. 2011, 2012b) have shown positive effects on parasitism rates. Models developed by Vinatier et al. (2012, 2013) indicated that parasitism rates were negatively influenced by longer crop rotations (which reflected a lower proportion of OSR in the landscape) because decreased connectivity between the previous and current season's OSR crops affected the parasitoid to a greater extent than the more dispersive pollen beetles. In general, the greater influence of the previous season's vs. the sampled season's OSR crop area on parasitism rates is not surprising since the parasitoids overwinter in the soil of former OSR fields and emerge from these sites in the following spring, and reduced tillage techniques used to establish crops following OSR minimise tillage-related mortality (Nilsson 2010).

Generalist predators

A handful of studies have investigated the influence of landscape factors on the fecundity, nutritional condition, activity–density, and species richness of generalist predators (spiders and carabids) within OSR crops. Haschek et al. (2012) found that *Amara similata* oocyte numbers were negatively related to distance from the nearest fallow, and that models best explaining the nutritional condition of male *Poecilus cupreus* and male *A. similata* contained parameters relating to percentage of surrounding crop area and distance from the nearest fallow, respectively. As grassy fallows and other non-crop areas represent important refuges for carabid beetles (Collins et al. 2002; Rouabah et al. 2015), the poorer condition of individuals needing to search further afield from these habitats may be related to scarcity of food resources. Indeed, pest abundance (a measure of prey availability) proved to be the most important factor explaining these measures of carabid fecundity and fitness, suggesting that knock-on effects of landscape factors on pest abundance are probably a more important influence on these characteristics in carabids than direct landscape effects.

In a study investigating landscape effects on *Pardosa* spp. wolf spiders, Drapela et al. (2011) showed that activity–density was highest when roadside grass strip length within the surrounding landscape was greatest, and the distance to the nearest fallow was shortest. There was also evidence to suggest that networks of grassy strips were more effective in facilitating colonisation of arable fields by *Pardosa* spp. than more patchily distributed fallow, as roadside strips showed higher explanatory power at large scales than fallow did at finer scales. Spider species richness has also been shown to positively respond to landscape factors, with increasing proportions of woody and non-crop areas (Drapela et al. 2008).

Land management implications and conclusions

The reviewed studies indicate that habitat management at the scales of the crop margin, the local landscape, and the regional landscape, particularly if conducted in a co-ordinated manner across these scales, has great potential for improving pollen beetle control and could reduce reliance on insecticides. However, the landscape factors affecting the abundance of pollen beetles on OSR and the efficacy of their natural enemies are complex, and the observations of different researchers in this area are often seemingly confounding. The apparent ambivalent effect of complex—especially woodland-rich—landscapes is particularly interesting as these characteristics promote high parasitism rates yet are also often associated with high beetle infestation and damage levels. However, this could be explained by regional-scale migration of pollen beetles just prior to overwintering (Rusch et al. 2013b; Mauchline et al. 2017); if beetles migrate from regions with a paucity of overwintering sites to more structurally complex regions where overwintering sites are more abundant, the effect of high parasitism rates in these areas may be reduced by inward migration. Thus, the major management implication of this regional-scale migration of beetles is that efforts to promote biological regulation should be concentrated within simple landscapes rather than in complex ones where parasitism rates are already high (see Tscharntke et al. 2005). Increased parasitism in structurally simple areas is likely then to have knock-on effects, lowering pollen beetle pressure in the more complex-landscaped areas.

The tendency of spatially and temporally (inter-annual) increasing OSR proportions within the landscape to result in dilution effects for pollen beetle abundance (Zaller et al. 2008a, b; Moser et al. 2009; Schneider et al. 2015) is important, particularly as pest dilution effects have now been shown to concurrently increase yields, despite the fact that dilution may also affect parasitism rates (Schneider et al. 2015). These findings have led to the proposal of a co-ordinated regional landscape-scale management scheme where OSR cover within a large area would be increased annually, maintaining the benefits of dilution effects for several years. A year with low crop cover (Schneider et al. 2015) or even a year when OSR cultivation ceases (Beduschi et al. 2015) would then be used to 'reset' the rotation. Again, however, such schemes are likely to be more successful in structurally simple regions, where dilution effects would not be counteracted by inward migration of beetles in search of overwintering sites, as in more complex landscapes. Also, practical implementation of such schemes, involving many individual land managers, may prove challenging.

Although landscape or regional-scale schemes hold great potential for improving pollen beetle control, fundamentally these must be underpinned by appropriate management at the within-field or crop margin scale, particularly within simple landscapes. The positive effects of pest dilution due to annually increasing OSR area may be offset by parasitoid dilution and lowered biological control (Schneider et al. 2015). Measures to bolster natural pest control are also therefore required, and could include encouraging farmers to use reduced tillage techniques or to leave fallow strips post-OSR in order to reduce tillage-related parasitoid mortality. In particular, however, the establishment of appropriate flower-rich field margin networks, containing appropriate brassicas acting as banker or trap crop plants, would continue to support parasitoid populations by providing nectar resources, encouraging parasitoid production, and aiding their dispersal through improving connectivity between current and previous year's OSR crops.

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