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Moth biomass increases and decreases over 50 years in Britain

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Abstract

Steep insect biomass declines (or 'insectageddon') have been widely reported, despite a lack of continuously-collected biomass data from replicated long-term monitoring sites. Such severe declines are not supported by the world's longest-running insect population database: annual moth biomass estimates from British fixed monitoring sites revealed increasing biomass between 1967 and 1982, followed by gradual decline from 1982 to 2017, with a 2.2-fold net gain in mean biomass between the first (1967-76) and last decades (2008-17) of monitoring. High between-year variability and multi-year periodicity in biomass emphasise the need for long-term data to detect trends and identify their causes robustly.

Main text

Reports of declining insect biomass[1–3] give credence to the notion that insects are at the forefront of a 'sixth mass extinction'[4–6]. However, some reports have received criticisms for poorly justified conclusions, potential biases and extrapolating beyond the data[7–9]. Regional abundance and distribution declines have taken place in many individual species, but populations of other species are stable or increasing[10–13], leaving uncertainty over the consequences for biomass change and associated ecosystem processes. Nearly all existing estimates of biomass change lack continuous, systematically-controlled monitoring or sufficient survey sites. Hence, analyses of continuously-collected data[14] from multiple sites and environments are

2

45 necessary to establish the robustness of the conclusion that insect biomass is

46 declining.

47

48 Here, we report robust estimates of the changing biomass of adult moths, and find

49 many unexpected results. Moths represent the second most diverse group of insect

50 herbivores (after Coleoptera); they are important pollinators, support

51 predatory/parasitoid insect populations, and provide food for birds and bats. We use

52 continuous nightly samples from Rothamsted Insect Survey (RIS, fixed moth-trap)

53 locations in Great Britain where traps had run for at least 30 years (Extended Data

54 1), giving 34 sample sites: 9 were in woodland, 8 in grassland, 7 in arable and 10 in

55 urban environments (including gardens). We converted the abundances of species

56 of larger moths (all macro-moths, plus micro-moths from the families Crambidae and

57 Pyralidae) at each site into dry mass (using species-specific estimates of dry mass

58 per individual, from Kinsella et al.[15]), providing biomass totals per site-year from

59 1967 to 2017. These data provide the continuity, replication and duration of fixed-

60 location sampling that has been lacking.

61

62 Contrary to previous reports of insect biomass change, moth biomass increased

63 before it declined, and remains higher than in the late 1960s (Figure 1). Mean annual

64 biomass per trap was 40782.8 ± SE 2665.6 mg for 2008-17, a 2.2-fold increase from

65 18653.4 ± SE 1639.9 mg in 1967-76 (Welch's t-test, $n = 20$; t = -7.03, d.f. = 17.90, P

66 < 0.001), and the linear trend of biomass between 1967 and 2017 across all traps

67 was significantly positive (Supplementary Table 1). However, segmented regression

68 models (i.e., with a change in slope) outperformed linear regressions, indicating

69 biomass peaked around 1982; mean annual biomass per trap for 1978-87 was

70   46790.1 ± SE 3670.4 mg, significantly higher than in the first decade (Welch's t-test,

71   *n* = 20; t = -7.49, d.f. = 17.75, *P* < 0.001) but not the most recent (Welch's t-test, *n* =

72   20; t = -1.16, d.f. = 17.36, *P* = 0.264). Slope values for mixed-effect models in the

73   periods 1967-82 and 1983-2017 were extremely similar to those from segmented

74   regressions (Supplementary Table 1), indicating that our conclusions are robust to

75   the addition and removal of specific traps over time.

76

77   Segmented regression also fitted different subsets of the data, split by taxonomy

78   (different families of moths) and land-use type (woodland, grassland, arable, urban;

79   Figure 1; Supplementary Table 1). The general pattern of increase, followed by post-

80   1982 decline was consistent across land uses for Noctuidae, but other families

81   showed different patterns in different land uses (Extended Data 2). When biomass

82   patterns were assessed independently for each trap, six out of eight traps (75 %)

83   which ran for >12 years prior to 1982 were best-described by a segmented model

84   that increased initially, but then declined (Extended Data 3). The inflection took place

85   at approximately the same time (Extended Data 4) regardless of the exact pattern of

86   biomass change (e.g., increase to ~1982 and stable thereafter, or post-1982

87   decline). This suggests that some general phenomenon is operating.

88

89   Two popular hypotheses to explain insect biomass decline are land-use

90   intensification (encompassing effects of novel insecticides[6]) and light pollution[16]; and

91   these factors do affect some species[12,17]. Therefore, we separately considered

92   biomass trajectories for traps which operated in woodland (the least intensively

93   managed land use), grassland, arable land (which receives the highest chemical

94   inputs) and urban areas (where light pollution is greatest), splitting the data into

95   1967-82 and 1983-2017 periods, given the inflection point for the full model

96   (Extended Data 4). This reveals that the greatest pre-1982 increase took place in

97   woodland and on arable land, followed by grassland, while the greatest post-1982

98   declines also took place in woodland and grassland (Figure 1, Supplementary Table

99   1), with no decline on arable land (Supplementary Table 2). Neither agricultural

100   intensification nor urban light pollution (or other urban changes) have been the most

101   important drivers of site-level biomass change in Britain, perhaps because species

102   contributing most to biomass in arable and urban landscapes half a century ago

103   were already relatively robust to human interventions. Land-use change cannot

104   explain these patterns either, because the subset of sites that had consistent land

105   use across land cover datasets from different time periods[18–20] showed the same

106   trends (Extended Data 5). Previous reports of insect biomass decline in Europe[1]

107   were also from the later period, and in protected areas (i.e., not arable or urban,

108   although land use in the surrounding landscape may also influence insect biomass

109   trends). However, our continuous sampling data at fixed sites revealed lower rates of

110   decline (3.45 % increase to 18.00 % decline per decade, depending on land-use;

111   Supplementary Table 2) than Hallmann et al.[1]. These post-1982 declines are lower

112   than the 145.14 % to 290.00 % per decade increases observed in 1967-82, and

113   hence there was a net gain over the entire monitoring period.

114

115   Overall biomass levels were, nonetheless, typically lowest in urban and arable sites,

116   and nearly twice as high in woodland as any other habitat (Figure 1d; all pairwise

117   comparisons between land-use classes were significant, Supplementary Table 3).

118   Thus, the 3.6 % increase in woodland cover in Britain from 2006 to 2015[21] may have

119   increased total moth biomass at a national scale.

5

120

121   Between-year *changes* in biomass confirm that there were several high-growth years

122   in the mid- to late-1970s, and two periods of consistent negative change in the 1990s

123   (Figure 2a). A similar pattern of annual change operated in all land uses (Figure 2e-j;

124   Supplementary Table 4): this implies external forcing. Increases in biomass typically

125   followed low biomass years, although declines following high biomass years were

126   less evident (Likelihood Ratio Test, n = 1238; R^2 = 0.36, χ^2 = 222.0, d.f. = 1, P <

127   0.001; Figure 2b). Bayesian spectrum analysis found that approximately 3-5 years

128   elapsed between successive peaks in biomass change (highest peaks of the

129   posterior distribution function were at: 2.95, 3.40, 3.80 and 4.88 years; mean of

130   posterior distribution: 3.51 years, 95% CI: 2.07 – 11.26 years; Extended Data 6),

131   suggesting some pattern in the dynamics of measured biomass, but not the cause.

132

133   Biomass change was not correlated with precipitation, temperature, or primary

134   productivity (measured using normalized difference vegetation indices (NDVI) over

135   the shorter time period of 1982–2016) in the 'current year', nor in the 'previous year'

136   (Supplementary Table 5). Nonetheless, climate seems a plausible explanation for

137   the synchronisation of biomass dynamics among ecosystem types (Figure 2), given

138   that large-scale insect dynamics can be linked to the climate[22]. Climate variability

139   (specific events rather than averages) could perturb biomass, and thus engender

140   ecosystem-level feedbacks, perhaps via lagged responses of vegetation or natural

141   enemies. Given that the relatively dry year of 1975 generated extreme population

142   growth in 9 % of lepidopteran species, but the even-drier 1976 caused crashes in

143   >25 % of species[23], we hypothesise that the perturbation generated by these two

144   years, followed by subsequent recovery and internal ecosystem feedbacks,

145 underpins the rapid but short-term biomass growth seen in the late 1970s. Similarly,

146 much of the post-1982 decline is accounted for by declines in the 1990s (Figure 2a;

147 >10 % of lepidopteran species 'crashed' in 1992/93[23]). However, the duration of the

148 post-1982 reverse trajectories in woodland and grassland may indicate that other

149 drivers are operating (e.g., management, air quality[24], or plant quality changes

150 associated with CO_2 levels and N inputs). These warrant further investigation lest

151 they are symptomatic of persistent future declines.

152

153 Simplistic descriptions of decline do not apply to moth biomass change in Britain,

154 highlighting the importance of long-term standardised datasets. The population

155 densities of many insect species show considerable variation over short periods of

156 time[25–27] and we find the same is true for insect biomass. Mean annual biomass

157 (across traps) varied six-fold over the entire study period, and approximately two-fold

158 (range 1.42 – 3.81) within each decade. At individual traps, annual biomass varied

159 up to 50-fold across the study period (range 3.29 – 49.26), and up to 28-fold (range

160 1.04 – 27.69) within each decade (Figure 1a).

161

162 The spatiotemporal variability of biomass means that (i) short durations of data

163 provide unreliable estimates of longer-term biomass change (Extended Data 7a,c),

164 (ii) individual sites are associated with much greater levels of biomass variation

165 (Extended Data 7b,d), and (iii) interval sampling (comparing first and last year of a

166 sequence) incorrectly estimates the *sign of* regression-based 20-year trends 24 % of

167 the time (Extended Data 7e,f). Equally, the start (baseline) date is critical; the slopes

168 of 20-year trends depended on when a time series commenced, relative to the 1982

169 peak (Extended Data 8; the 1960s RIS 'baseline' should not be taken to represent

170   some long-term 'norm'). Infrequent sampling at inadequate numbers of sample sites,

171   over too short a duration, with arbitrary start and end dates, commonly generates

172   unreliable estimates of long-term biomass change.

173

174   In conclusion, we showed that post-1982 decline in the biomass of British moths was

175   preceded by a larger increase. However, it is unclear whether this represents true

176   long-term trends or simply the consequences of unusual climate-ecosystem

177   perturbations and feedbacks in the 1970s and 1990s. The decline in the post-1982

178   period is, nonetheless, qualitatively consistent with recent abundance and biomass

179   declines reported by previous studies[1,3,13,28], most of which were initiated after this

180   date (or shortly before). This consistency implies that prior increases might also

181   apply to other groups and regions, but there is a need for long-term replicated

182   datasets equivalent to the RIS to be gathered at a global scale, especially in tropical

183   systems[29]. The existence and scale of declines varied between taxa and land use

184   types; further work is warranted to identify drivers of such variability in declines. In

185   particular, two-thirds of individual moth species in Britain have declined[11,12], but

186   others have increased; the drivers of these changes in community composition and

187   their effects on biomass are uncertain. However, the increasingly widespread view

188   that insect biomass is collapsing finds little support in what is perhaps the best insect

189   population database available anywhere in the world.

190

191   **Methods**

192   *Data selection*

193   We used data obtained by the Rothamsted Insect Survey (RIS) Light-Trap Network

194   to investigate change in moth biomass over time at fixed sampling locations. Night-

195   flying and crepuscular moths are attracted to a 200 W tungsten bulb that has a wide

196   wavelength spectrum (400-700 nm), which is installed within a standard light-trap.

197   The design, components, and protocols for operation of RIS light-traps have

198   remained unchanged in design since Williams[30], throughout the entire duration of the

199   RIS. Set at a standard height of 1.2 m across the network and fixed *in situ* for the

200   period of operation, light traps are controlled by astronomical timers that operate

201   every night of the year between dusk and dawn[31]. Sampled moths are collected daily

202   or every few days, and the abundance of each species recorded. Thereby,

203   abundance data is generated for a fixed site, with a temporal resolution of one week

204   or better, over a period of many years.

205

206   To generate the most robust estimates possible, we restricted analysis to those traps

207   which had been continuously recorded for 30 years or more. In some instances,

208   trapping ceased at a given location for one or several years, but subsequently

209   recommenced at the same location. We included these traps in our dataset only

210   when the recording 'gap' was less than 10 years long, and also shorter than both the

211   number of continuous years trapped before the break, and the number of continuous

212   years trapped afterwards. After applying these criteria, our final dataset contained

213   annual moth abundance data for 34 fixed sampling locations, 30 monitored for 30–49

214   years and four for over 50 years (Supplementary Table 6). Traps did not always

215   operate fully in either the first or final year of recording. Therefore, we excluded data

216   from the first and last years of each recording period (including the years on either

217   side of any internal break in recording) from our final analyses, except traps were still

218   operative and data was up-to-date to 2017.

219

220   *Biomass estimation*

221   Kinsella et al.[15] provide dry body mass estimates of all British macro-moth species

222   (plus micro-moths of the families Crambidae and Pyralidae), based on modelling the

223   relationship between forewing length and dry body mass of a subset of species. We

224   used these to convert annual abundances of each species into total annual biomass

225   for each RIS trap. This procedure generated 91.5% accuracy when estimating

226   directly weighed *nightly* biomass samples[15], with much higher (likely >99%) accuracy

227   expected in comparisons of *annual* samples among sites, given that estimated and

228   measured nightly biomass samples fall on the 1:1 line.

229

230   Traps did not always operate every night (recorded as 'inopps' in the RIS database).

231   We excluded traps (for a given year) that were inoperative for more than 121 nights

232   (i.e. over 1/3 of the year). If a trap was inoperative for 1–121 days, we adjusted its

233   biomass estimate in proportion to the number of trap nights operated (i.e. a trap that

234   was inoperative for 10 nights in a non-leap year would have its estimated biomass

235   increased by 365/355). Overall, the majority of traps were inoperative for < 1 % of

236   days per year (median: 0.55 %) and there was no major seasonal bias in the timing

237   of inoperative days (Extended Data 9).

238

239   *Land-use, climate and primary production data*

240   The predominant land-use class for each of the 34 trap locations was deemed to be

241   the modal land-use class (derived from LCM2007[20]) from all 25 x 25 m grid cells

242   whose centroids fell within a 100 m radius of the trap location. Raw LCM2007 land-

243   use classes were grouped into four categories for this purpose: "arable" (LCM2007

244   aggregate class "arable" only); "grassland" (LCM2007 aggregate classes "improved

245 grassland" and "semi-natural grassland"); "woodland" (LCM2007 aggregate classes

246 "broadleaved woodland" and "coniferous woodland"); and "urban" (LCM2007

247 aggregate class "built-up areas and gardens" only). Changes to land-use at or near

248 individual trap locations might affect biomass; to assess this, land-use classes were

249 assigned as above using two additional, older land cover datasets: LCM1990[19] and

250 the Land Utilization Survey of Britain 1931[18] (data from the latter was digitized using

251 HistMapR[32], covering England and Wales only). For both 1931-2007 and 1990-2007,

252 we categorized traps according to whether they had the same land-use class in both

253 years.

254

255 Climate data were derived from the UKCP09 gridded climate observations for the

256 UK[33]. We extracted mean daily temperature and total annual rainfall for each year

257 from the 5 x 5 km grid cell in which each trap was located.

258

259 Primary productivity data were derived as Normalized Difference Vegetation Indices

260 (NDVI) from Landsat datasets 4–8 (courtesy of the U.S. Geological Survey) using

261 Google Earth Engine[34], and covered the years 1982–2016 only. We extracted the

262 median NDVI for each year from the 240 x 240 m grid cell (comprising an 8 x 8 grid

263 of 30 x 30 m observations) in which each trap was located.

264

265 *Statistical analysis*

266 *Linear and segmented regressions*

267 All statistical analyses were conducted in R version 3.6.1[35], using the package

268 ggplot2[36] to construct figures. Other packages used for specific tasks are described

269 below.

270

We constructed generalized linear and segmented models describing biomass

versus year (1967–2017) at the 34 trap sites, with a Gaussian error distribution and a

log-transformation applied to biomass estimates (we took this approach to reduce

the influence of extreme values of biomass). In addition to the full dataset, we

analysed subsets of data: (i) separating data for the three most abundant families of

moths (Erebidae, Geometridae, and Noctuidae), which collectively comprised 93.3 %

of total biomass in our dataset; (ii) separating data for traps in separate land-use

classes, (iii) separating data for both family and land-use simultaneously, (iv)

separating data for each of the 34 traps independently, and (v) using only data from

traps assigned to the same land-use classes in 1990-2007 and in 1931-2007

respectively. In each case, we fitted a generalized linear model using package

MASS[37], with the total biomass sampled per year at each trap location as the

dependent variable and year as the independent variable; testing significance of its

slope using an F-test. We then fitted a segmented model to the same data, using the

package segmented[38], and used a Likelihood Ratio Test to test the significance of its

goodness of fit compared to the linear model. We also compared the fit of the two

models using their respective Bayesian Information Criteria (BIC[39]); BIC penalises

models more harshly for inclusion of additional parameters than does the related

Akaike's Information Criterion (AIC), and therefore presents a more rigorous test of

the improvement of the fit provided by segmentation. In eight out of ten comparisons,

the BIC and the Likelihood Ratio Test were in agreement that the segmented model

was the better fit; in the remaining two, the Likelihood Ratio Test favoured the

segmented model, but the BIC was marginally lower for the linear model

(Supplementary Table 1).

295

296   Finally, to confirm the significance of biomass trends (both overall, and in each land-

297   use class) before and after the universal inflection point (estimated at 1982;

298   Supplementary Table 1), we split the dataset into "early" (1967–1982) and "late"

299   (1983–2017) periods. We then fitted a land-use factor variable and tested this within

300   generalized linear mixed-effects models (as above, with trap location included as a

301   random-intercepts factor, to control for turnover of traps in operation over time) for

302   both periods, using the overall dataset and each land-use class.

303

304   *Annual change in biomass*

305   To assess factors influencing annual fluctuations in biomass, we first calculated the

306   annual proportional change in biomass between each pair of consecutive years, both

307   for each individual trap location and on average across all trap locations. We

308   constructed generalized linear mixed-effects models with annual proportional

309   biomass change for individual traps as the response, and trap location as a random

310   effect. We tested the following fixed effects: (i) year (temporal effect); (ii) biomass in

311   the previous year (density-dependent effect); (iii) mean daily temperature (°C) in the

312   focal year and (iv) in the previous year; (v) total annual rainfall (mm) in the focal year

313   and (vi) in the previous year. We tested for significance using a Likelihood Ratio

314   Test. We also tested the relationships between mean annual changes across traps

315   in each land-use type.

316

317   To assess the possible periodic nature of annual change in biomass, we constructed

318   a time series of the mean values for proportional biomass change across all traps in

319   each year, and conducted a Bayesian Spectrum Analysis using the package

13

320   BaSAR[40]. We set the prior probability distribution for the frequency of cycles as 2–20

321   years and analysed 10,000 replicates. We calculated the 95 % confidence intervals

322   of the mean of the posterior distribution function (Extended Data 7), and recorded

323   the position of the highest peaks, to predict the most likely candidates for frequency

324   of cycles.

325

326   *Influence of data structure on estimated biomass change*

327   To assess the influence of sampling (continuous sampling versus comparison of two

328   dates) on estimated changes in biomass, we extracted all possible subsets of data of

329   at least five years' continuous duration from our dataset, both overall and at the level

330   of each individual trap. For every data subset, we estimated the annual rate of

331   biomass change using two approaches: (i) a two-sample approach, whereby the rate

332   of biomass change was directly calculated based on observed biomass in the first

333   and last years; and (ii) a linear-modelling approach, whereby a generalized linear

334   model was fitted to the data from all included years (as above) and the rate of

335   biomass change calculated from the slope of this model. We assessed the extent to

336   which the estimated trends depended on sampling duration for both approaches, and

337   evaluated whether the direction of change estimated by the two approaches (i.e.,

338   biomass increase or decline) was consistent for each data subset. Analyses were

339   conducted for the overall data and for the individual traps. Finally, among the data

340   subsets that were of exactly 20 years' duration, we assessed how the direction and

341   magnitude of estimated biomass change varied across time (i.e., with different start

342   dates).

343

344

14

Data availability

Derived annual biomass data per site analysed in this study are included as

Supplementary Data 1. Raw data on species-by-night trap catch abundances are

retained by Rothamsted Insect Survey, and may be obtained by request from the

same source (https://www.rothamsted.ac.uk/insect-survey).

Code availability

All R scripts, from initial processing of datasets to final analyses, are archived online

at Zenodo (doi: 10.5281/zenodo.3356841).

Author information

Contributions

CJM & CDT conceived the study, CJM & JHW carried out analyses, JRB provided

RIS data and expertise, CDT and CJM drafted the manuscript, and all authors

15

370   commented on it.

371

372   **Competing interests**

373   The authors declare no competing interests.

374

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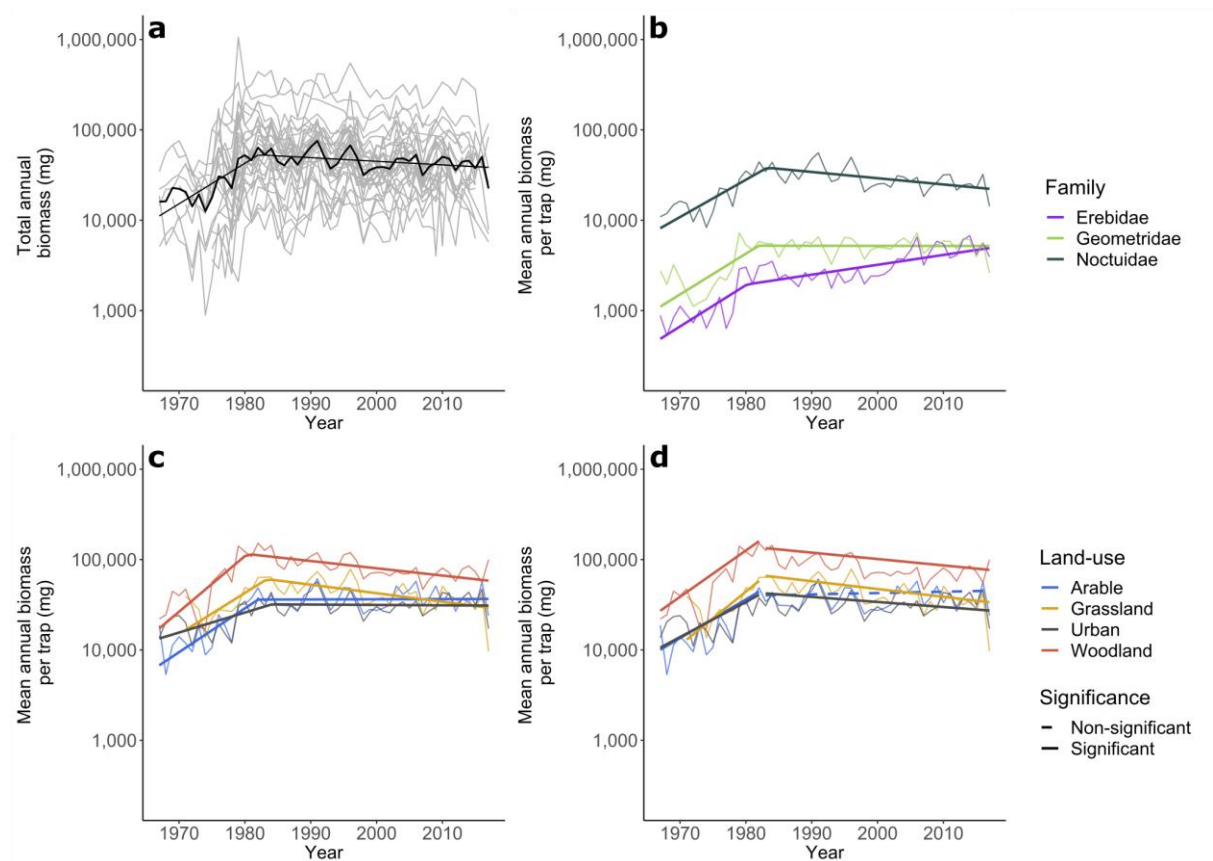424   32. Auffret, A. G. *et al. Methods Ecol. Evol.* **8**, 1453–1457 (2017).

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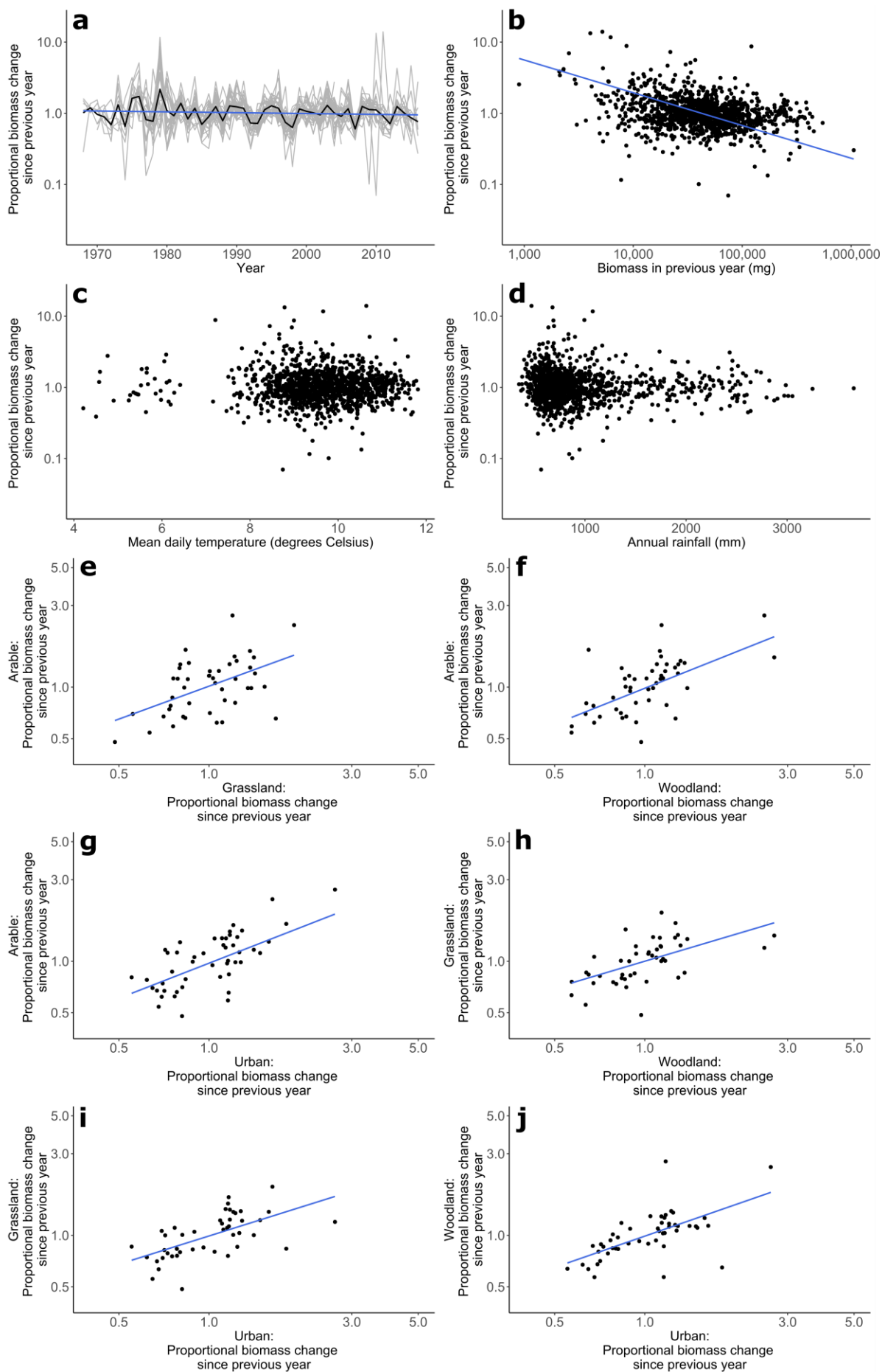434   40. Granqvist, E., Hartley, M. & Morris, R. J. *Biosystems.* **110**, 60–63 (2012).

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Figures

Figure 1 | Change in biomass of moths over time. Change over time in **a** total annual biomass is shown for the full dataset (individual trap sites in grey, and geometric mean as black zig-zag). Change over time in mean annual biomass per trap shown for: **b** the three moth families that comprise >90% of total biomass; **c,d**, the four major land-use types in the dataset (zig-zags indicate geometric means of traps operating in each year). In panels **a-c**, lines depict the trend fitted by a segmented regression; in panel **d**, lines depict the trends fitted by separate linear mixed-effects models for the period up to 1982 and the period from 1983 onwards.

448 **Figure 2 | Annual proportional changes in biomass, related to climate,**

449 **demography and land use.** The annual proportional change in biomass for each site

450 (since the previous year) is shown: **a** over time (grey lines are individual sites; black

451 zig-zag is geometric means of traps operating in each year), and compared to **b**

452 biomass in the previous year (i.e. density dependence), **c** mean monthly temperature,

453 and **d** annual rainfall (i.e. climate). Points in **b-d** indicate changes in biomass at

454 individual sites between successive years. Panels **e-j** show pairwise comparisons

455 between land-use types between the mean (across all sites within a land-use type) of

456 annual proportional change in biomass. Lines are plotted (blue) where relationships

457 were statistically significant ($P < 0.05$).

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