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1 **Moth biomass increases and decreases over 50 years in Britain**

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20 *Nature Ecology & Evolution Brief Communication*

21 **Abstract**

22

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

33

34

35 **Main text**

36 Reports of declining insect biomass¹⁻³ give credence to the notion that insects are at
37 the forefront of a ‘sixth mass extinction’⁴⁻⁶. However, some reports have received
38 criticisms for poorly justified conclusions, potential biases and extrapolating beyond
39 the data⁷⁻⁹. Regional abundance and distribution declines have taken place in many
40 individual species, but populations of other species are stable or increasing¹⁰⁻¹³,
41 leaving uncertainty over the consequences for biomass change and associated
42 ecosystem processes. Nearly all existing estimates of biomass change lack
43 continuous, systematically-controlled monitoring or sufficient survey sites. Hence,
44 analyses of continuously-collected data¹⁴ from multiple sites and environments are

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 $40782.8 \pm \text{SE } 2665.6$ mg for 2008-17, a 2.2-fold increase from
65 $18653.4 \pm \text{SE } 1639.9$ 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 \pm 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 insecticides⁶) and light pollution¹⁶; 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 periods¹⁸⁻²⁰ showed the same
106 trends (Extended Data 5). Previous reports of insect biomass decline in Europe¹
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 2015²¹ may have
119 increased total moth biomass at a national scale.

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, $n = 1238$; $R^2 = 0.36$, $\chi^2 = 222.0$, 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 climate²². 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 species²³, 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 1992/93²³). 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 quality²⁴, or plant quality changes
150 associated with CO₂ 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 systems²⁹. 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 Williams³⁰, 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 dawn³¹. 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 samples¹⁵, 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 LCM2007²⁰) 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: LCM1990¹⁹ and
250 the Land Utilization Survey of Britain 1931¹⁸ (data from the latter was digitized using
251 HistMapR³², 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 UK³³. 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 Engine³⁴, 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 3.6.1³⁵, using the package
268 ggplot2³⁶ to construct figures. Other packages used for specific tasks are described
269 below.

270

271 We constructed generalized linear and segmented models describing biomass
272 versus year (1967–2017) at the 34 trap sites, with a Gaussian error distribution and a
273 log-transformation applied to biomass estimates (we took this approach to reduce
274 the influence of extreme values of biomass). In addition to the full dataset, we
275 analysed subsets of data: (i) separating data for the three most abundant families of
276 moths (Erebidae, Geometridae, and Noctuidae), which collectively comprised 93.3 %
277 of total biomass in our dataset; (ii) separating data for traps in separate land-use
278 classes, (iii) separating data for both family and land-use simultaneously, (iv)
279 separating data for each of the 34 traps independently, and (v) using only data from
280 traps assigned to the same land-use classes in 1990-2007 and in 1931-2007
281 respectively. In each case, we fitted a generalized linear model using package
282 MASS³⁷, with the total biomass sampled per year at each trap location as the
283 dependent variable and year as the independent variable; testing significance of its
284 slope using an F-test. We then fitted a segmented model to the same data, using the
285 package segmented³⁸, and used a Likelihood Ratio Test to test the significance of its
286 goodness of fit compared to the linear model. We also compared the fit of the two
287 models using their respective Bayesian Information Criteria (BIC³⁹); BIC penalises
288 models more harshly for inclusion of additional parameters than does the related
289 Akaike's Information Criterion (AIC), and therefore presents a more rigorous test of
290 the improvement of the fit provided by segmentation. In eight out of ten comparisons,
291 the BIC and the Likelihood Ratio Test were in agreement that the segmented model
292 was the better fit; in the remaining two, the Likelihood Ratio Test favoured the
293 segmented model, but the BIC was marginally lower for the linear model
294 (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

320 BaSAR⁴⁰. 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

345 **Data availability**

346 Derived annual biomass data per site analysed in this study are included as
347 Supplementary Data 1. Raw data on species-by-night trap catch abundances are
348 retained by Rothamsted Insect Survey, and may be obtained by request from the
349 same source (<https://www.rothamsted.ac.uk/insect-survey>).

350

351 **Code availability**

352 All R scripts, from initial processing of datasets to final analyses, are archived online
353 at Zenodo (doi: [10.5281/zenodo.3356841](https://doi.org/10.5281/zenodo.3356841)).

354

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365

366 **Author information**

367 **Contributions**

368 CJM & CDT conceived the study, CJM & JHW carried out analyses, JRB provided
369 RIS data and expertise, CDT and CJM drafted the manuscript, and all authors

370 commented on it.

371

372 **Competing interests**

373 The authors declare no competing interests.

374

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437 **Figure legends**

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

446

447 **Figure 2 | Annual proportional changes in biomass, related to climate,**
448 **demography and land use.** The annual proportional change in biomass for each site
449 (since the previous year) is shown: **a** over time (grey lines are individual sites; black
450 zig-zag is geometric means of traps operating in each year), and compared to **b**
451 biomass in the previous year (i.e. density dependence), **c** mean monthly temperature,
452 and **d** annual rainfall (i.e. climate). Points in **b-d** indicate changes in biomass at
453 individual sites between successive years. Panels **e-j** show pairwise comparisons
454 between land-use types between the mean (across all sites within a land-use type) of
455 annual proportional change in biomass. Lines are plotted (blue) where relationships
456 were statistically significant ($P < 0.05$).

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