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MacGregor, Callum James orcid.org/0000-0001-8281-8284, Williams, Jonathan, Bell, James et al. (1 more author) (2019) Moth biomass increases and decreases over 50 years in Britain. Nature Ecology and Evolution. pp. 1-16. ISSN 2397-334X

https://doi.org/10.1038/s41559-019-1028-6

Moth biomass increases and decreases over 50 years in Britain

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Nature Ecology & Evolution Brief Communication

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 necessary to establish the robustness of the conclusion that insect biomass is declining.

Here, we report robust estimates of the changing biomass of adult moths, and find many unexpected results. Moths represent the second most diverse group of insect herbivores (after Coleoptera); they are important pollinators, support predatory/parasitoid insect populations, and provide food for birds and bats. We use continuous nightly samples from Rothamsted Insect Survey (RIS, fixed moth-trap) locations in Great Britain where traps had run for at least 30 years (Extended Data 1), giving 34 sample sites: 9 were in woodland, 8 in grassland, 7 in arable and 10 in urban environments (including gardens). We converted the abundances of species of larger moths (all macro-moths, plus micro-moths from the families Crambidae and Pyralidae) at each site into dry mass (using species-specific estimates of dry mass per individual, from Kinsella et al.[15]), providing biomass totals per site-year from 1967 to 2017. These data provide the continuity, replication and duration of fixed-location sampling that has been lacking.

Contrary to previous reports of insect biomass change, moth biomass increased before it declined, and remains higher than in the late 1960s (Figure 1). Mean annual biomass per trap was 40782.8 ± SE 2665.6 mg for 2008-17, a 2.2-fold increase from 18653.4 ± SE 1639.9 mg in 1967-76 (Welch's t-test, $n = 20$; $t = -7.03$, d.f. = 17.90, $P < 0.001$), and the linear trend of biomass between 1967 and 2017 across all traps was significantly positive (Supplementary Table 1). However, segmented regression models (i.e., with a change in slope) outperformed linear regressions, indicating biomass peaked around 1982; mean annual biomass per trap for 1978-87 was

46790.1 ± SE 3670.4 mg, significantly higher than in the first decade (Welch's t-test, $n = 20$; t = -7.49, d.f. = 17.75, $P < 0.001$) but not the most recent (Welch's t-test, $n = 20$; t = -1.16, d.f. = 17.36, $P = 0.264$). Slope values for mixed-effect models in the periods 1967-82 and 1983-2017 were extremely similar to those from segmented regressions (Supplementary Table 1), indicating that our conclusions are robust to the addition and removal of specific traps over time.

Segmented regression also fitted different subsets of the data, split by taxonomy (different families of moths) and land-use type (woodland, grassland, arable, urban; Figure 1; Supplementary Table 1). The general pattern of increase, followed by post-1982 decline was consistent across land uses for Noctuidae, but other families showed different patterns in different land uses (Extended Data 2). When biomass patterns were assessed independently for each trap, six out of eight traps (75 %) which ran for >12 years prior to 1982 were best-described by a segmented model that increased initially, but then declined (Extended Data 3). The inflection took place at approximately the same time (Extended Data 4) regardless of the exact pattern of biomass change (e.g., increase to ~1982 and stable thereafter, or post-1982 decline). This suggests that some general phenomenon is operating.

Two popular hypotheses to explain insect biomass decline are land-use intensification (encompassing effects of novel insecticides[6]) and light pollution[16]; and these factors do affect some species[12,17]. Therefore, we separately considered biomass trajectories for traps which operated in woodland (the least intensively managed land use), grassland, arable land (which receives the highest chemical inputs) and urban areas (where light pollution is greatest), splitting the data into

1967-82 and 1983-2017 periods, given the inflection point for the full model (Extended Data 4). This reveals that the greatest pre-1982 increase took place in woodland and on arable land, followed by grassland, while the greatest post-1982 declines also took place in woodland and grassland (Figure 1, Supplementary Table 1), with no decline on arable land (Supplementary Table 2). Neither agricultural intensification nor urban light pollution (or other urban changes) have been the most important drivers of site-level biomass change in Britain, perhaps because species contributing most to biomass in arable and urban landscapes half a century ago were already relatively robust to human interventions. Land-use change cannot explain these patterns either, because the subset of sites that had consistent land use across land cover datasets from different time periods[18–20] showed the same trends (Extended Data 5). Previous reports of insect biomass decline in Europe[1] were also from the later period, and in protected areas (i.e., not arable or urban, although land use in the surrounding landscape may also influence insect biomass trends). However, our continuous sampling data at fixed sites revealed lower rates of decline (3.45 % increase to 18.00 % decline per decade, depending on land-use; Supplementary Table 2) than Hallmann et al.[1]. These post-1982 declines are lower than the 145.14 % to 290.00 % per decade increases observed in 1967-82, and hence there was a net gain over the entire monitoring period.

Overall biomass levels were, nonetheless, typically lowest in urban and arable sites, and nearly twice as high in woodland as any other habitat (Figure 1d; all pairwise comparisons between land-use classes were significant, Supplementary Table 3). Thus, the 3.6 % increase in woodland cover in Britain from 2006 to 2015[21] may have increased total moth biomass at a national scale.

Between-year *changes* in biomass confirm that there were several high-growth years in the mid- to late-1970s, and two periods of consistent negative change in the 1990s (Figure 2a). A similar pattern of annual change operated in all land uses (Figure 2e-j; Supplementary Table 4): this implies external forcing. Increases in biomass typically followed low biomass years, although declines following high biomass years were less evident (Likelihood Ratio Test, $n = 1238$; $R^2 = 0.36$, $\chi^2 = 222.0$, d.f. = 1, $P < 0.001$; Figure 2b). Bayesian spectrum analysis found that approximately 3-5 years elapsed between successive peaks in biomass change (highest peaks of the posterior distribution function were at: 2.95, 3.40, 3.80 and 4.88 years; mean of posterior distribution: 3.51 years, 95% CI: 2.07 – 11.26 years; Extended Data 6), suggesting some pattern in the dynamics of measured biomass, but not the cause.

Biomass change was not correlated with precipitation, temperature, or primary productivity (measured using normalized difference vegetation indices (NDVI) over the shorter time period of 1982–2016) in the ‘current year’, nor in the ‘previous year’ (Supplementary Table 5). Nonetheless, climate seems a plausible explanation for the synchronisation of biomass dynamics among ecosystem types (Figure 2), given that large-scale insect dynamics can be linked to the climate[22]. Climate variability (specific events rather than averages) could perturb biomass, and thus engender ecosystem-level feedbacks, perhaps via lagged responses of vegetation or natural enemies. Given that the relatively dry year of 1975 generated extreme population growth in 9 % of lepidopteran species, but the even-drier 1976 caused crashes in >25 % of species[23], we hypothesise that the perturbation generated by these two years, followed by subsequent recovery and internal ecosystem feedbacks, underpins the rapid but short-term biomass growth seen in the late 1970s. Similarly, much of the post-1982 decline is accounted for by declines in the 1990s (Figure 2a; >10 % of lepidopteran species 'crashed' in 1992/93[23]). However, the duration of the post-1982 reverse trajectories in woodland and grassland may indicate that other drivers are operating (e.g., management, air quality[24], or plant quality changes associated with CO_2 levels and N inputs). These warrant further investigation lest they are symptomatic of persistent future declines.

Simplistic descriptions of decline do not apply to moth biomass change in Britain, highlighting the importance of long-term standardised datasets. The population densities of many insect species show considerable variation over short periods of time[25–27] and we find the same is true for insect biomass. Mean annual biomass (across traps) varied six-fold over the entire study period, and approximately two-fold (range 1.42 – 3.81) within each decade. At individual traps, annual biomass varied up to 50-fold across the study period (range 3.29 – 49.26), and up to 28-fold (range 1.04 – 27.69) within each decade (Figure 1a).

The spatiotemporal variability of biomass means that (i) short durations of data provide unreliable estimates of longer-term biomass change (Extended Data 7a,c), (ii) individual sites are associated with much greater levels of biomass variation (Extended Data 7b,d), and (iii) interval sampling (comparing first and last year of a sequence) incorrectly estimates the *sign of* regression-based 20-year trends 24 % of the time (Extended Data 7e,f). Equally, the start (baseline) date is critical; the slopes of 20-year trends depended on when a time series commenced, relative to the 1982 peak (Extended Data 8; the 1960s RIS 'baseline' should not be taken to represent some long-term ‘norm’). Infrequent sampling at inadequate numbers of sample sites, over too short a duration, with arbitrary start and end dates, commonly generates unreliable estimates of long-term biomass change.

In conclusion, we showed that post-1982 decline in the biomass of British moths was preceded by a larger increase. However, it is unclear whether this represents true long-term trends or simply the consequences of unusual climate-ecosystem perturbations and feedbacks in the 1970s and 1990s. The decline in the post-1982 period is, nonetheless, qualitatively consistent with recent abundance and biomass declines reported by previous studies[1,3,13,28], most of which were initiated after this date (or shortly before). This consistency implies that prior increases might also apply to other groups and regions, but there is a need for long-term replicated datasets equivalent to the RIS to be gathered at a global scale, especially in tropical systems[29]. The existence and scale of declines varied between taxa and land use types; further work is warranted to identify drivers of such variability in declines. In particular, two-thirds of individual moth species in Britain have declined[11,12], but others have increased; the drivers of these changes in community composition and their effects on biomass are uncertain. However, the increasingly widespread view that insect biomass is collapsing finds little support in what is perhaps the best insect population database available anywhere in the world.

Methods

Data selection

We used data obtained by the Rothamsted Insect Survey (RIS) Light-Trap Network to investigate change in moth biomass over time at fixed sampling locations. Nightflying and crepuscular moths are attracted to a 200 W tungsten bulb that has a wide wavelength spectrum (400-700 nm), which is installed within a standard light-trap. The design, components, and protocols for operation of RIS light-traps have remained unchanged in design since Williams[30], throughout the entire duration of the RIS. Set at a standard height of 1.2 m across the network and fixed *in situ* for the period of operation, light traps are controlled by astronomical timers that operate every night of the year between dusk and dawn[31]. Sampled moths are collected daily or every few days, and the abundance of each species recorded. Thereby, abundance data is generated for a fixed site, with a temporal resolution of one week or better, over a period of many years.

To generate the most robust estimates possible, we restricted analysis to those traps which had been continuously recorded for 30 years or more. In some instances, trapping ceased at a given location for one or several years, but subsequently recommenced at the same location. We included these traps in our dataset only when the recording ‘gap’ was less than 10 years long, and also shorter than both the number of continuous years trapped before the break, and the number of continuous years trapped afterwards. After applying these criteria, our final dataset contained annual moth abundance data for 34 fixed sampling locations, 30 monitored for 30–49 years and four for over 50 years (Supplementary Table 6). Traps did not always operate fully in either the first or final year of recording. Therefore, we excluded data from the first and last years of each recording period (including the years on either side of any internal break in recording) from our final analyses, except traps were still operative and data was up-to-date to 2017.

Biomass estimation

Kinsella et al.[15] provide dry body mass estimates of all British macro-moth species (plus micro-moths of the families Crambidae and Pyralidae), based on modelling the relationship between forewing length and dry body mass of a subset of species. We used these to convert annual abundances of each species into total annual biomass for each RIS trap. This procedure generated 91.5% accuracy when estimating directly weighed *nightly* biomass samples[15], with much higher (likely >99%) accuracy expected in comparisons of *annual* samples among sites, given that estimated and measured nightly biomass samples fall on the 1:1 line.

Traps did not always operate every night (recorded as 'inopps' in the RIS database). We excluded traps (for a given year) that were inoperative for more than 121 nights (i.e. over 1/3 of the year). If a trap was inoperative for 1–121 days, we adjusted its biomass estimate in proportion to the number of trap nights operated (i.e. a trap that was inoperative for 10 nights in a non-leap year would have its estimated biomass increased by 365/355). Overall, the majority of traps were inoperative for < 1 % of days per year (median: 0.55 %) and there was no major seasonal bias in the timing of inoperative days (Extended Data 9).

Land-use, climate and primary production data

The predominant land-use class for each of the 34 trap locations was deemed to be the modal land-use class (derived from LCM2007[20]) from all 25 x 25 m grid cells whose centroids fell within a 100 m radius of the trap location. Raw LCM2007 land-use classes were grouped into four categories for this purpose: "arable" (LCM2007 aggregate class "arable" only); "grassland" (LCM2007 aggregate classes "improved grassland" and "semi-natural grassland"); "woodland" (LCM2007 aggregate classes "broadleaved woodland" and "coniferous woodland"); and "urban" (LCM2007 aggregate class "built-up areas and gardens" only). Changes to land-use at or near individual trap locations might affect biomass; to assess this, land-use classes were assigned as above using two additional, older land cover datasets: LCM1990[19] and the Land Utilization Survey of Britain 1931[18] (data from the latter was digitized using HistMapR[32], covering England and Wales only). For both 1931-2007 and 1990-2007, we categorized traps according to whether they had the same land-use class in both years.

Climate data were derived from the UKCP09 gridded climate observations for the UK[33]. We extracted mean daily temperature and total annual rainfall for each year from the 5 x 5 km grid cell in which each trap was located.

Primary productivity data were derived as Normalized Difference Vegetation Indices (NDVI) from Landsat datasets 4–8 (courtesy of the U.S. Geological Survey) using Google Earth Engine[34], and covered the years 1982–2016 only. We extracted the median NDVI for each year from the 240 x 240 m grid cell (comprising an 8 x 8 grid of 30 x 30 m observations) in which each trap was located.

Statistical analysis

Linear and segmented regressions

All statistical analyses were conducted in R version 3.6.1[35], using the package ggplot2[36] to construct figures. Other packages used for specific tasks are described below.

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).

Finally, to confirm the significance of biomass trends (both overall, and in each land-use class) before and after the universal inflection point (estimated at 1982; Supplementary Table 1), we split the dataset into “early” (1967–1982) and “late” (1983–2017) periods. We then fitted a land-use factor variable and tested this within generalized linear mixed-effects models (as above, with trap location included as a random-intercepts factor, to control for turnover of traps in operation over time) for both periods, using the overall dataset and each land-use class.

Annual change in biomass

To assess factors influencing annual fluctuations in biomass, we first calculated the annual proportional change in biomass between each pair of consecutive years, both for each individual trap location and on average across all trap locations. We constructed generalized linear mixed-effects models with annual proportional biomass change for individual traps as the response, and trap location as a random effect. We tested the following fixed effects: (i) year (temporal effect); (ii) biomass in the previous year (density-dependent effect); (iii) mean daily temperature (°C) in the focal year and (iv) in the previous year; (v) total annual rainfall (mm) in the focal year and (vi) in the previous year. We tested for significance using a Likelihood Ratio Test. We also tested the relationships between mean annual changes across traps in each land-use type.

To assess the possible periodic nature of annual change in biomass, we constructed a time series of the mean values for proportional biomass change across all traps in each year, and conducted a Bayesian Spectrum Analysis using the package

BaSAR[40]. We set the prior probability distribution for the frequency of cycles as 2–20 years and analysed 10,000 replicates. We calculated the 95 % confidence intervals of the mean of the posterior distribution function (Extended Data 7), and recorded the position of the highest peaks, to predict the most likely candidates for frequency of cycles.

Influence of data structure on estimated biomass change

To assess the influence of sampling (continuous sampling versus comparison of two dates) on estimated changes in biomass, we extracted all possible subsets of data of at least five years' continuous duration from our dataset, both overall and at the level of each individual trap. For every data subset, we estimated the annual rate of biomass change using two approaches: (i) a two-sample approach, whereby the rate of biomass change was directly calculated based on observed biomass in the first and last years; and (ii) a linear-modelling approach, whereby a generalized linear model was fitted to the data from all included years (as above) and the rate of biomass change calculated from the slope of this model. We assessed the extent to which the estimated trends depended on sampling duration for both approaches, and evaluated whether the direction of change estimated by the two approaches (i.e., biomass increase or decline) was consistent for each data subset. Analyses were conducted for the overall data and for the individual traps. Finally, among the data subsets that were of exactly 20 years' duration, we assessed how the direction and magnitude of estimated biomass change varied across time (i.e., with different start dates).

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).

Acknowledgements

The Rothamsted Insect Survey, a UK National Capability, is funded by the Biotechnology and Biological Sciences Research Council (BBSRC) under the Core Capability Grant BBS/E/C/000J0200. JRB is also supported by Smart Crop Protection (SCP) strategic programme (BBS/OS/CP/000001) funded through BBSRC's Industrial Strategy Challenge Fund. We thank Paul Verrier and Chris Shortall for extracting the data and the RIS team and volunteer network for their unswerving contributions. CJM & CDT were supported by a grant from the Natural Environment Research Council (NERC; NE/N015797/1). We thank Rob Critchlow and Phil Platts for advice on data sources and statistics.

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 commented on it.

Competing interests

The authors declare no competing interests.

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Figure legends

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.

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