

Accounting for year effects and sampling error in temporal analyses of population and biodiversity change

Response to Seibold et al. 2019 "Arthropod decline in grasslands and forests is associated with landscape-level drivers". Nature, 574(7780), 671-674.

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This comment was submitted in December 2019 and was under review at Nature for nine months before a decision was made to not publish the exchange. We now share the comment and response from Seibold et al. 2019 as preprints to further the discussion of how best to model and interpret population and biodiversity change.

Summary

An accumulating number of studies are reporting severe biomass, abundance and/or species richness declines of insects (Hallmann et al., 2017; Lister & Garcia, 2018; Seibold et al., 2019; Sánchez-Bayo & Wyckhuys, 2019). Collectively these studies aim to quantify the net change in invertebrate populations and/or community composition over time and to establish whether such changes can be attributed to anthropogenic drivers (Macgregor, Williams, Bell, & Thomas, 2019; Saunders, Janes, & O'Hanlon, 2019; Thomas, Jones, & Hartley, 2019; Montgomery et al., 2020; van Klink et al., 2020). Seibold *et al.* 2019 analysed a dataset of arthropod biomass, abundance and species richness from forest and grassland plots in a region of Germany and report significant declines of up to 78% over the time period of 2008 to 2018 (Seibold et al., 2019). However, their analysis did not account for the confounding effects of temporal pseudoreplication of observations from the same years. We show that simply by including a year random effect in the statistical models and thereby accounting for the common conditions experienced by observations from proximal sites in the same years, four of the five reported declines become non-significant out of six tests overall. To place their estimated effect sizes and those of other recent studies of insect declines in a broader geographic context, we analysed invertebrate biomass, abundance and species richness over time from 640 time series from 1167 sites around the world. We found that the average trend across the terrestrial and freshwater realms was not significantly distinguishable from no net change. Shorter time series that are likely to be most affected by sampling error variance – such as those reported in Seibold *et al.* 2019 – yielded the most extreme estimates of decline or increase. We suggest that the uncritical media uptake of extreme negative trends from short time series may be serving to exaggerate the speed of "insect Armageddon" and could eventually undermine public confidence in biodiversity research. We advocate that future research include all available data and use model structures that account for uncertainties to build a more robust understanding of biodiversity change during the Anthropocene and its variation among regions and taxa (Kunin, 2019; Saunders et al., 2019; Thomas et al., 2019; Didham et al., 2020; Dornelas & Daskalova, 2020).

Appropriate spatial and temporal structure in time series analysis

Field studies that yield multiple observations per year from sites within a region are likely to be influenced by many shared uncontrolled variables, creating a ‘year effect’ because observations from the same year will often be more similar (Werner, Stuble, Groves, & Young, 2020). If this year pseudoreplication is ignored, our confidence in trends estimated across years and type I errors can be greatly inflated (Knape, 2016). A simple remedy for year effects is to include a year intercept random term in statistical models (Knape, 2016; Werner et al., 2020). Seibold *et al.* 2019 presented an analysis of arthropod diversity trends across 140 (30 in some analyses) forest plots and 150 grassland plots over a 10-year period (a nine-year period in some cases). Their statistical analysis considered the spatial structure of the data in relation to consistent differences among plots and included plot ID as a random intercept nested within region. While Seibold *et al.* 2019 noted that there were “high numbers of arthropods in 2008”, and among year heterogeneity is clearly visible in their Figure 1, their analyses did not include a year random intercept term. Instead, they assessed the sensitivity of their findings to exclusion of different years, which revealed that the significance of their evidence for a decline was dependent on inclusion of data from 2008 (Seibold *et al.* 2019 Extended Data Figure 2). They also include multiple environmental correlates, which suggest that they were concerned about year effects. However, even well-chosen covariates are unable to capture all aspects of the environment that affect diversity in a year and year effects are likely to remain and inflate type I errors.

Here, we show that four of the five arthropod declines reported in Seibold *et al.* 2019 that are ‘statistically significant’ without a year random term became non-significant with the inclusion of a year random term in both a simplified version of their models as well as in models including the environmental variables they tested (Figure 1, Extended Data Tables 1-2). With a year random effect included, we estimated the among-year variances across metrics to be substantial and highly significant even when environmental covariates were included (Extended Data Tables 1-2). We recognise that a more robust model in this case would also incorporate autocorrelation among sites and among years, because year and site effects tend to be more similar between neighbouring samples, but for the sake of isolating the influence of the year effect, we have excluded autocorrelation terms here. Not accounting for year pseudoreplication in time series analyses in ecology is far from an issue specific to Seibold *et al.* 2019 (e.g., see Møller, 2019). As we work towards a more comprehensive understanding of change over time across invertebrate taxa (Saunders et al., 2019; Thomas et al., 2019), scientists need to use statistical methods that incorporate the pronounced spatial and temporal structure of population and biodiversity data.

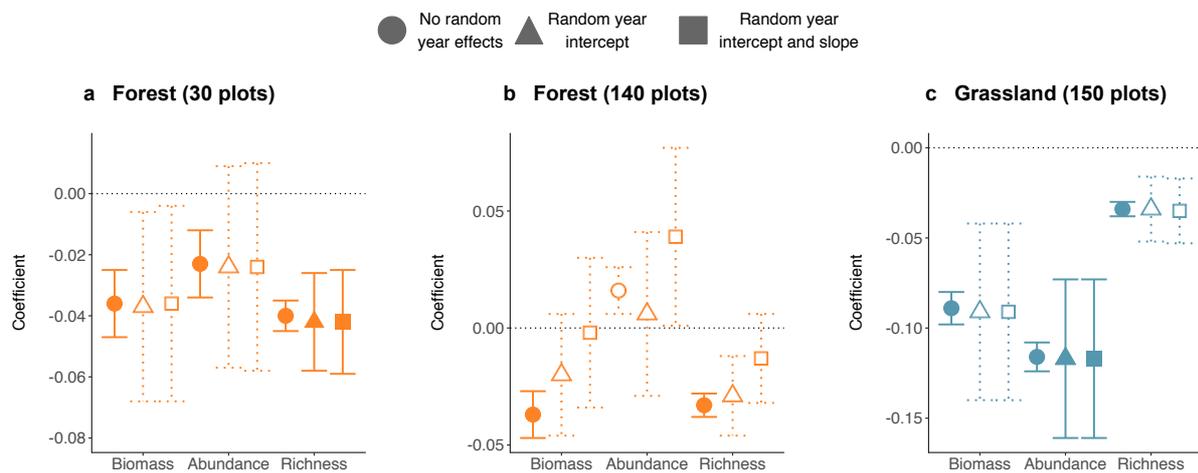


Figure 1. Accounting for temporal pseudoreplication shifts four of the five detected declines out of six tests in Seibold *et al.* 2019 from significant to non-significant declines. The six Seibold *et al.* 2019 tests refer to their six models of biomass, abundance and richness over time in forests and grasslands (three metrics, two habitats). Points represent the model coefficient for the trend over time and error bars show standard error, as derived from the three different model structures (see legend). We focused on the key results in Seibold *et al.* 2019 (a, c) and did not include separate models for different trophic groups, but we anticipate that the significance of other findings reported in this study would be similarly affected by inclusion of a year random effect. Our reanalysis differed slightly from Seibold *et al.* (see methods for details) and thus we found a statistically significant relationship for abundance in the forest habitat without inclusion of a year random effect (a). We also analysed the three-year in addition to annual interval data from the forest plots (b) and found no net declines once random effects are included for the full dataset (b). See Supplementary Information for methods, Extended Data Figure 1 for model prediction fits, Extended Data Table 1 for full model outputs and Extended Data Table 2 for summary of analyses including environmental covariates.

Incorporating baselines and year to year variance in time series analyses

Climate research has recognised for some time (Stocker *et al.*, 2013), and biodiversity researchers more recently (Mihoub *et al.*, 2017; Fournier, White, & Heard, 2019; Didham *et al.*, 2020), that where there is substantial year to year variance in a metric, the start and end date of a time series can have a strong effect on the estimated effect size and significance. For this reason, it is valuable to consider the baseline conditions before monitoring began in the interpretation of the significance of trends found within data (Mihoub *et al.*, 2017). A visual inspection of Figure 1 in Seibold *et al.* 2019 indicates that the biomass, abundance and richness were higher than average in 2008, the first year of the time series. With the start point of their analyses being 2008, the observations in subsequent years were generally lower in comparison. When 2008 is removed from the analysis, the trends between 2009 and 2017 do not exhibit large directional changes (as is also evident in Seibold *et al.* 2019 Extended Data Figure 2). By accounting for the fluctuations in biomass, abundance and species richness among years, our reanalysis returned estimates with much greater uncertainty and the variance in year effects was

estimated to be substantial and highly significant for all metrics (Extended Data Tables 1-2).

Monitored populations viewed as a sample of trends across sites globally

Concern about insect declines, as well as a general shortage of insect data, has led to a reliance on short time series, with Siebold *et al.* 2019 an example of this. To examine how Siebold *et al.*'s findings fit within a global sample of insect biodiversity trends we combined them with recent temporal studies of the biomass, abundance and richness of invertebrate species as compiled by the global-extent BioTIME database¹⁹ and data from the recent meta-analysis by van Klink *et al.* 2020⁹ (but note that both data compilations include geographic gaps). The two compilations of time series data represent a variety of habitats and environmental conditions and were collected using different survey techniques, but the methods were always consistent within time series (for further details see original papers^{9,19}). Our analysis of 283 BioTIME freshwater and terrestrial time series from 95 sites around the world indicated a decline in freshwater invertebrate biomass (slope = -0.02, CI = -0.04 to -0.01) and no net change in terrestrial invertebrate biomass (slope = 0.02, CI = -0.06 to 0.11, with units of log(biomass) per year, measured in grams), no net change in abundance (freshwater slope = 0.01, CI = -0.08 to 0.09, terrestrial slope = -0.01, CI = -0.04 to 0.02, with units of log(abundance) per year, measured in number of individuals) and no net change in richness (freshwater slope = -0.01, CI = -0.04 to 0.02, terrestrial slope = 0.01, CI = -0.01 to 0.02, with units of log(species) per year). Within these on average non-directional trends, we detected substantial variation including both declines and increases (figure 2). For example, for freshwater abundance the model estimates suggest that 25% of time series (i.e., 18/72 time series) may have a decline of 5% or more per year. In our analysis of 357 time series from the van Klink *et al.* 2020⁹ data compilation, insect abundance increased in the freshwater realm but declined in the terrestrial realm (see Extended Data Table 3 for effect sizes and credible intervals).

In statistics, there is a general expectation that the contribution of sampling error to effect size estimation increases as sample size and precision decline, and this effect is often visualised as a funnel plot (Egger, Smith, Schneider, & Minder, 1997; Gurevitch, Koricheva, Nakagawa, & Stewart, 2018). We found clear evidence of this effect as the most extreme biodiversity trends were for the shortest time series (Figure 2). An increase in the severity of declines toward the present time would see the most recent - and therefore shortest - time series being the most negative. However, this differs from the pattern we observed, where short time series returned the most extreme positive and negative trends (Figure 2), as expected if the effect was due to sampling variance. Additionally, longer-term studies, which should better capture the mean trend, did not present the dramatic declines reported in shorter term studies (Figure 2, and similar to the effects found in other longer-term studies like Macgregor *et al.*, 2019; Saunders *et al.*, 2019). Overall, we detected considerable variation across realms and among sites, with some individual locations exhibiting both substantial increases and decreases (Extended Data Table 3, Extended Data Figure 1).

Our reanalysis of Seibold *et al.* 2019 returned very similar effect sizes to those reported in the original study, with estimated declines remaining substantial, yet with much higher uncertainty. When we considered the estimates from Seibold *et al.* 2019 in the broader geographic and taxonomic context of results from other temporal analyses, their effect sizes represented the negative end of the distribution but were not extreme in comparison to other time series of similarly short duration. It is striking that some of the prominent studies in the insect decline literature have been of short duration, potentially revealing a bias toward high impact journals publishing more extreme and “surprising” results and/or their subsequent amplification by the media (Figure 2).

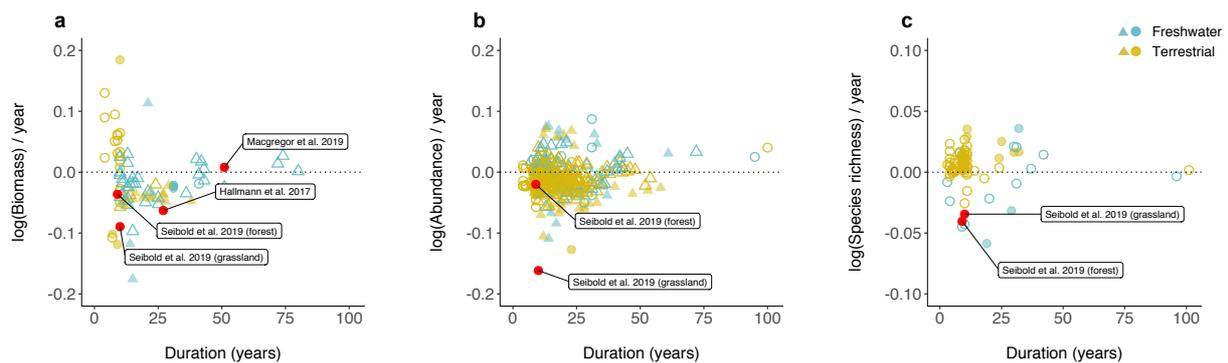


Figure 2. Invertebrate trends over time span a spectrum of decreases, increases and no net change in biomass (a), abundance (b) and species richness (c). Points show effect sizes from time series from terrestrial and freshwater taxa, as well as effect sizes from published studies (Hallmann *et al.*, 2017; Macgregor *et al.*, 2019; Seibold *et al.*, 2019; red points, statistical significance of the literature-reported effect sizes not presented). Circles show time series from the BioTIME database (Dornelas *et al.*, 2018) and triangles show time series from the compilation of van Klink *et al.*, 2020. Note that for visualisation purposes, we did not include the effect size (slope = -0.86) for abundance change in arthropods in a hurricane-dominated system from (Lister & Garcia, 2018), because this slope value was an extreme outlier in the distribution of trends (Blowes *et al.*, 2019). See Supplementary Information for methods and Extended Data Table 3 for full model outputs.

Conclusion

Our analysis of 640 time series from the BioTIME and van Klink *et al.* 2020 databases demonstrated no evidence for invertebrate declines on average. However, steep declines could potentially be occurring in certain parts of the world and/or for specific taxa (Macgregor *et al.*, 2019; Didham *et al.*, 2020; van Klink *et al.*, 2020). Moreover, based on the lower 95% confidence intervals, we cannot reject the possibility that the average trend may be of a shallow decline (1 - 6% per year) for the various biodiversity metrics and ecosystems for which data are available, which would still be very severe. Therefore, we suggest that on the balance of evidence to date, the scientific community should prioritise data collection to monitor local and global trends in invertebrate numbers. Against this backdrop, we suggest that alarmist media attention that overstates the problem runs the risk of later undermining wider public confidence in biodiversity research.

Acknowledgements

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Competing interests

The authors declare no competing interests.

Author contributions

GND, ABP and IHMS conceptualised the reply. ABP reanalysed the Seibold *et al.* 2019 data with input from IHMS and GND. GND analysed time series data from the BioTIME database with input from IHMS and ABP. GND visualised results. All authors contributed to writing and editing of the comment.

Supplementary Information for response to Seibold *et al.* 2019

“Arthropod decline in grasslands and forests is associated with landscape-level drivers”

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Supplementary Methods

Data sources

We used the data published in Seibold *et al.* 2019 to test the influence of temporal pseudoreplication and model structure. We used 640 time series of biomass, abundance and species richness from the publicly available data from BioTIME and van Klink *et al.* 2020 to demonstrate the larger distribution of the varying trends of invertebrate biodiversity over time as well as our concerns about model structure (Extended Data Figure 2). The time series had a duration of at least five years and together represented 1169 locations. The BioTIME data were rarefied based on sample size and study area as per (Blowes *et al.*, 2019). The van Klink *et al.* 2020 data were used in their original form.

Statistical methods to reanalyse the data in Seibold et al. 2019

We reanalysed the data provided by Seibold *et al.* 2019 by applying three alternative model structures to data on biomass (log transformed), abundance and species richness (both using Poisson link) separately for forest and grassland plots. Model 1 was intended to be similar to the structure used by the authors, and included year as a continuous predictor, region as a fixed effect (rather than random term, as there are only three levels) and plot within region as a random term. Model 2 included year as a factor as an additional term and model 3 included a random year slope term across sites. The motivation for including model 3 was to estimate whether diversity trends vary across sites. To account for overdispersion, when modelling count data using a Poisson error structure, abundance and richness models also included a random intercept for a PlotIDYear variable (concatenation to specify each plot in each year) for Models 2 and 3.

We replicated the model structure used in Seibold *et al.* 2019 which included environmental covariates and compared the detected temporal trends among models with and without a year random effect. We included the same environmental covariates as Seibold *et al.* 2019 – mean winter temperature, precipitation over the growing season, their interaction, land-use intensity, grassland cover, arable land cover and the interactions between year and land-use intensity, grassland cover and arable land cover. We advocate that the random effect model structure should be determined *a priori* rather *post hoc* based on retaining only terms that are statistically significant. Models were fitted using the same lme4 package as the authors, via the lmer and glmer functions (Bates, Mächler, Bolker, & Walker, 2014). Significance of the temporal trends was estimated using lmer via the lmerTest package (Kuznetsova, Brockhoff, & Christensen, 2017). We inferred the significance of the year random intercept term via a likelihood ratio test comparing model 1 to model 2. For the forest plots, we ran two sets of analyses, one

restricted to the 30 plots with annual data and a second analysis using all 140 plots. We found less pronounced diversity declines for the second analysis.

Statistical methods to demonstrate the wider distribution of invertebrate trends

We used a Bayesian modelling framework through the package MCMCglmm (Hadfield, 2010) to fit a model with a Gaussian error to analyse invertebrate biomass (logged) as a function of year (centred with a median of zero) and a random intercept term for year of observation, as well as year of observation grouped by ecoregion, and random slopes for the relationship between biomass and year at each plot. We allowed for covariation between the random intercepts and slopes across plots. The models we used for invertebrate abundance and richness followed a similar structure except they assumed a Poisson error distribution, since those data represent count integer data. We extracted the random slope values for each time series from the BioTIME and van Klink *et al.* 2020 data. We presented the effect sizes, together with the effect sizes of published papers, in Figure 2.

Supplementary methods references

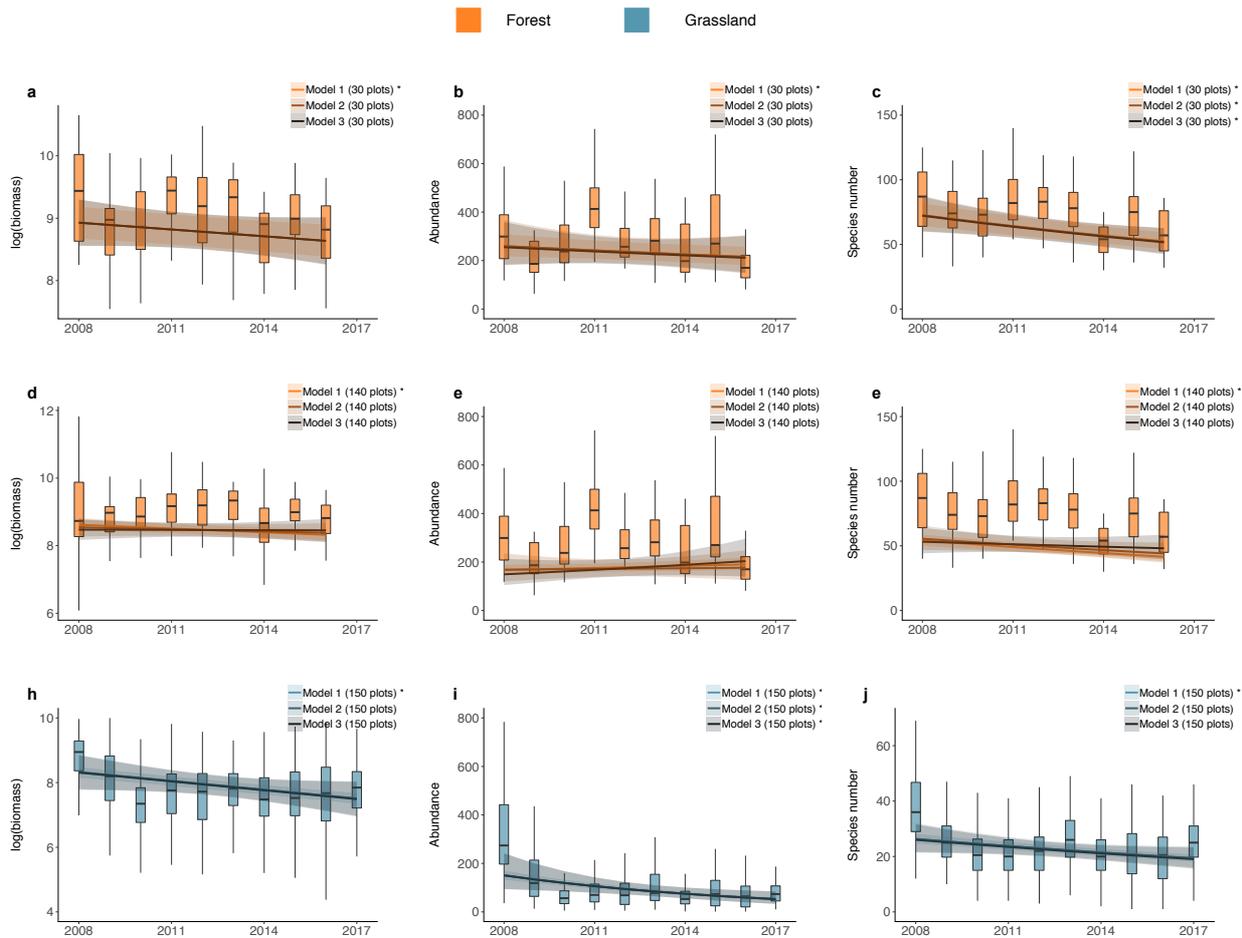
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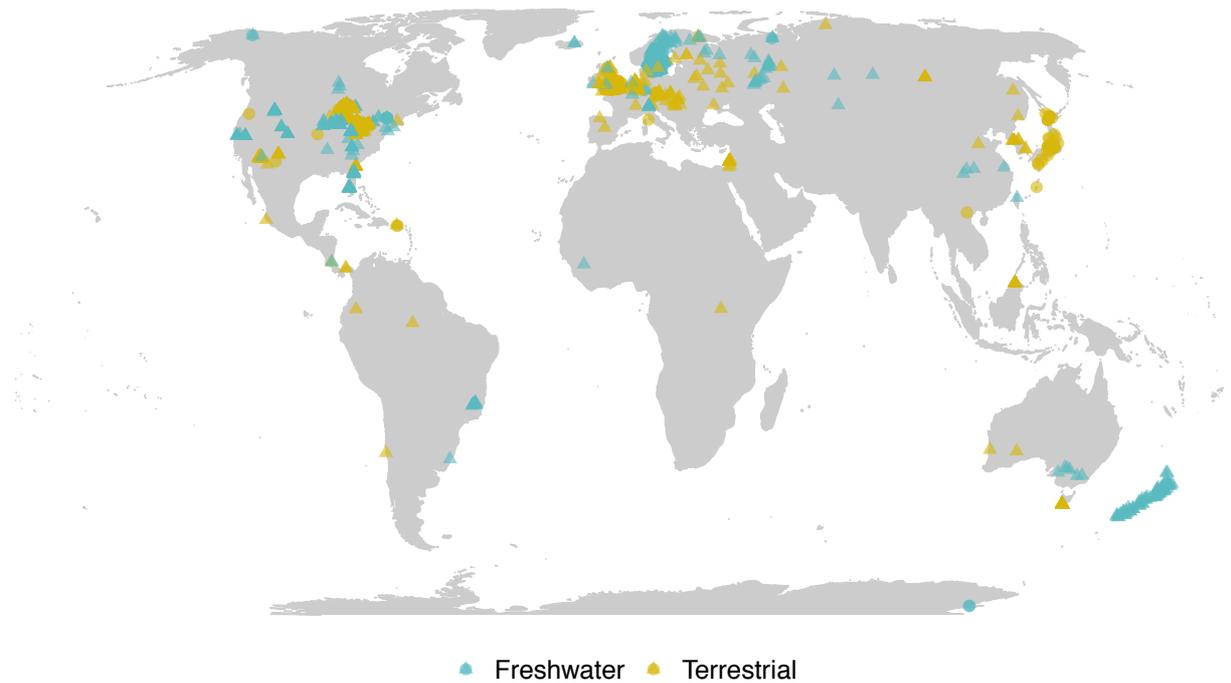
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Code and data availability

The data from Seibold *et al.* 2019 are available from the original paper. The raw BioTIME time-series data are available from <http://biotime.st-andrews.ac.uk/>. The rarefied version of the BioTIME time series is available from the authors upon request. All code for statistical analyses is available from the following GitHub repository https://github.com/gndaskalova/Seibold_et_al_Reply.



Extended Data Figure 1. Accounting for temporal pseudoreplication shifts four of the five detected declines in Seibold *et al.* 2019 from significant to non-significant declines. Model structure was as follows: plots as random intercept (Model 1), plots and years as random intercepts (Model 2), random slopes and intercepts for year across plots (Model 3). Boxplots show the distribution of the raw data. Note that, like in Seibold *et al.* 2019, for visualisation purposes some of the boxplots do not include outliers. Lines and error bands show model fit and 95% confidence intervals, respectively. Models with significant trends are marked with an asterisk. Although the magnitude of the effect sizes for change over time were similar across the three types of models that we ran, adding a year random term (models 2 and 3) demonstrated no net changes in arthropod metrics over time, with two exceptions. First, grassland abundance declined on average in all three models. The second exception was grassland species richness, where we also documented a net decline, but that was only when we used the smaller dataset of 30 plots monitored annually. When using the full dataset (140 plots), we found no net change in species richness. See Supplementary Information for methods and Extended Data Table 1 for full model outputs.



Extended Data Figure 2. Geographical distribution of time series from freshwater and terrestrial invertebrate taxa part of the BioTIME database¹⁹. Circles show time series from the BioTIME database¹⁹ and triangles show time series from the compilation of van Klink *et al.* 2020⁹. These locations represented the following numbers of BioTIME time series – freshwater biomass (5), terrestrial biomass (21), freshwater abundance (72), terrestrial abundance (90), freshwater richness (15), terrestrial richness (80), of a total of 283 time series. The sample sizes for the van Klink *et al.* 2020 time series were as follows – freshwater biomass (39), terrestrial biomass (18) freshwater abundance (79) and terrestrial abundance (221), resulting in 357 time series. Sampling methods varied among time series, but were always consistent within time series.

Extended Data Table 1. Summary table of outputs for the reanalysis of Seibold *et al.* 2019 for models with plots as random intercept (Model structure 1), plots and years as random intercepts (Model structure 2), random slopes and intercepts for year across plots (Model structure 3). For model structure 3, we found plot-level variation in trends, with biomass, abundance and richness increasing in some plots, while other plots showed decreases or no net change. To account for overdispersion, often the case when modelling count data using a Poisson error structure, abundance and richness models also included a random intercept for a PlotIDYear variable (concatenation to mark each plot in each year) for model structures 2 and 3.

Habitat	Response	N. plots	Model structure	Year slope coefficient +/- s.e	Proportional change per year	Year slope P value	Year (RE) variance	Year slope variance	LR for model 1 v 2 or 2 v 3	P value from LR test of model 1 v 2 or 2 v 3
forest	biomass	30	1	-0.036 +/- 0.011	0.964	0.001	-	-	-	-
forest	biomass	30	2	-0.037 +/- 0.031	0.964	0.269	0.05	-	34.082	<0.001
forest	biomass	30	3	-0.036 +/- 0.032	0.964	0.29	0.051	0.003	10.2319	0.006
forest	biomass	140	1	-0.037 +/- 0.01	0.963	0	-	-	-	-
forest	biomass	140	2	-0.02 +/- 0.026	0.98	0.46	0.032	-	25.6603	<0.001
forest	biomass	140	3	-0.002 +/- 0.032	0.998	0.939	0.043	0.02	50.5905	<0.001
grassland	biomass	150	1	-0.089 +/- 0.009	0.914	0	-	-	-	-
grassland	biomass	150	2	-0.091 +/- 0.049	0.913	0.1	0.192	-	212.6024	<0.001
grassland	biomass	150	3	-0.091 +/- 0.049	0.913	0.101	0.194	0.003	9.9108	0.007
forest	abundance	30	1	-0.023 +/- 0.011	0.977	0.036	-	-	-	-
forest	abundance	30	2	-0.024 +/- 0.033	0.977	0.48	0.062	-	70.186	<0.001
forest	abundance	30	3	-0.024 +/- 0.034	0.977	0.488	0.063	0.001	3.7243	0.1553
forest	abundance	140	1	0.016 +/- 0.01	1.016	0.112	-	-	-	-
forest	abundance	140	2	0.006 +/- 0.035	1.006	0.867	0.065	-	121.1933	<0.001
forest	abundance	140	3	0.039 +/- 0.038	1.04	0.31	0.071	0.019	66.1134	<0.001
grassland	abundance	150	1	-0.116 +/- 0.008	0.891	0	-	-	-	-
grassland	abundance	150	2	-0.117 +/- 0.044	0.89	0.008	0.156	-	329.8063	<0.001
grassland	abundance	150	3	-0.117 +/- 0.044	0.89	0.008	0.156	0.002	7.8177	0.0201
forest	richness	30	1	-0.04 +/- 0.005	0.96	0	-	-	-	-
forest	richness	30	2	-0.042 +/- 0.016	0.959	0.009	0.014	-	71.7612	<0.001

forest	species richness	30	3	-0.042 +/- 0.017	0.959	0.012	0.015	0	8.8626	0.0119
forest	species richness	140	1	-0.033 +/- 0.005	0.967	0	-	-	-	-
forest	species richness	140	2	-0.029 +/- 0.017	0.972	0.088	0.015	-	129.7137	<0.001
forest	species richness	140	3	-0.013 +/- 0.019	0.988	0.511	0.018	0.003	37.4154	<0.001
grassland	species richness	150	1	-0.034 +/- 0.004	0.966	0	-	-	-	-
grassland	species richness	150	2	-0.034 +/- 0.018	0.967	0.058	0.025	-	225.8448	<0.001
grassland	species richness	150	3	-0.035 +/- 0.018	0.966	0.053	0.025	0.001	25.9936	<0.001

Extended Data Table 2. Summary table of outputs for the reanalysis of Seibold *et al.* 2019 including environmental covariates for models with plots as random intercept (Model structure 1), plots and years as random intercepts (Model structure 2). We included the same environmental covariates as Seibold *et al.* 2019 – mean winter temperature, precipitation over the growing season, their interaction, land-use intensity, grassland cover, arable land cover and the interactions between year and land use intensity, grassland cover and arable land cover. The year (random effect) variance remained substantial in the models with a year random term and environment variables (i.e., when compared to models with the random term but without the environmental variables, Extended data Table 2). For further details, see analysis scripts at https://github.com/gndaskalova/Seibold_et_al_Reply.

Response variable	Year trend (no year random term)	Year trend (with year random term)	Year (RE) variance in models with year random term and environmental variables
forest biomass (30)	1	0	0.07
forest biomass (140)	1	0	0.18
grassland biomass	1	0	0.27
forest abundance (30)	1	0	0.24
forest abundance (140)	1 (increase)	0	0.40
grassland abundance	1	0	0.31
forest species (30)	1	1	0.02
forest species (140)	1	0	0.40
grassland species	1	0	0.04

Extended Data Table 3. Summary table of outputs for the analysis of the BioTIME¹⁹ and van Klink *et al.* 2020⁹ time series for models of biomass, abundance and richness change in invertebrate taxa over time. Each model included year as a continuous fixed effect and a random intercept term for year of observation, as well as year of observation grouped by ecoregion, and random slopes for the relationship between diversity metric (biomass, abundance or richness) and time for each time series. Models did not include a plot or PlotIDYear random intercept as data did not consistently have a nested plot within site structure.

Model	Variable	Post. mean	Lower 95% CI	Upper 95% CI	Eff. sample	pMCMC	Effect
Biomass (freshwater, BioTIME, n = 5)	(Intercept)	1.413	-0.342	3.204	7,605.473	0.083	fixed
	year	-0.023	-0.038	-0.007	9,000	0.011	fixed
	year (random)	0.069	0	0.157	190.091		random
	BIOME_MAP:year	0.060	0	0.151	156.001		random
	(Intercept):(Intercept).timeseries_id	4.263	0.210	13.385	98.580		random
	year:(Intercept).timeseries_id	-0.003	-0.029	0.019	9,000		random
	(Intercept):year.timeseries_id	-0.003	-0.029	0.019	9,000		random
	year:year.timeseries_id	0.0001	0	0.0003	3,152.831		random
	residual	3.381	3.344	3.422	9,000		residual
Biomass (terrestrial, BioTIME, n = 21)	(Intercept)	3.406	2.783	3.993	9,000	0.0001	fixed
	year	0.023	-0.059	0.106	8,891.493	0.543	fixed
	year (random)	0.073	0	0.222	856.275		random
	BIOME_MAP:year	0.069	0	0.208	642.891		random
	(Intercept):(Intercept).timeseries_id	1.669	0.768	2.892	814.857		random
	year:(Intercept).timeseries_id	0.040	-0.019	0.112	9,388.619		random
	(Intercept):year.timeseries_id	0.040	-0.019	0.112	9,388.619		random
	year:year.timeseries_id	0.009	0.003	0.016	4,591.964		random
	residual	5.407	5.328	5.483	8,256.110		residual
Abundance (freshwater, BioTIME, n = 72)	(Intercept)	-35.552	-38.277	-32.656	17.361	0.0001	fixed
	year	0.008	-0.076	0.090	1,028.219	0.870	fixed
	year (random)	0.249	0	0.867	333.450		random
	BIOME_MAP:year	0.264	0	0.882	465.401		random
	(Intercept):(Intercept).timeseries_id	4.173	0.461	10.428	355.982		random
	year:(Intercept).timeseries_id	0.039	-0.119	0.235	1,949.763		random
	(Intercept):year.timeseries_id	0.039	-0.119	0.235	1,949.763		random
	year:year.timeseries_id	0.008	0.00000	0.026	479.210		random
	residual	161.640	141.372	185.506	9.507		residual
Abundance (terrestrial, BioTIME, n = 90)	(Intercept)	-7.198	-7.929	-6.533	576.513	0.0001	fixed
	year	-0.010	-0.041	0.020	691.455	0.506	fixed
	year (random)	0.020	0	0.064	184.098		random
	BIOME_MAP:year	0.291	0.199	0.396	509.243		random

	(Intercept):(Intercept).timeseries_id	5.020	2.963	7.461	243.295		random
	year:(Intercept).timeseries_id	0.025	-0.022	0.077	761.867		random
	(Intercept):year.timeseries_id	0.025	-0.022	0.077	761.867		random
	year:year.timeseries_id	0.003	0.001	0.005	331.897		random
	residual	4.175	4.080	4.272	200.122		residual
Richness (freshwater, BioTIME, n = 15)	(Intercept)	1.757	1.027	2.426	7,208.066	0.0002	fixed
	year	-0.009	-0.036	0.018	5,559.542	0.486	fixed
	year (random)	0.008	0	0.026	4,003.809		random
	BIOME_MAP:year	0.008	0	0.025	3,603.565		random
	(Intercept):(Intercept).timeseries_id	1.790	0.596	3.387	660.368		random
	year:(Intercept).timeseries_id	-0.024	-0.067	0.013	5,776.470		random
	(Intercept):year.timeseries_id	-0.024	-0.067	0.013	5,776.470		random
	year:year.timeseries_id	0.002	0.0002	0.004	1,515.561		random
	residual	0.072	0.036	0.112	2,169.687		residual
	Richness (terrestrial, BioTIME, n = 80)	(Intercept)	2.908	2.669	3.123	7,866.785	0.0001
year		0.008	-0.001	0.018	2,168.926	0.082	fixed
year (random)		0.005	0	0.016	147.846		random
BIOME_MAP:year		0.024	0.012	0.038	411.633		random
(Intercept):(Intercept).timeseries_id		0.880	0.596	1.222	3,726.325		random
year:(Intercept).timeseries_id		-0.001	-0.009	0.005	702.989		random
(Intercept):year.timeseries_id		-0.001	-0.009	0.005	702.989		random
year:year.timeseries_id		0.0003	0.00003	0.001	62.303		random
residual		0.002	0.0002	0.005	150.395		residual
Biomass (freshwater, van Klink <i>et al.</i> , n = 39)		(Intercept)	2.697	1.678	3.720	9,000	0.0001
	year	-0.024	-0.053	0.006	9,000	0.102	fixed
	year (random)	0.012	0	0.043	7,110.446		random
	WWFecoRegion:Year	0.360	0.228	0.500	8,523.191		random
	(Intercept):(Intercept).Timeseries_id	10.262	5.813	15.677	1,401.594		random
	year:(Intercept).Timeseries_id	0.083	-0.013	0.185	8,629.515		random
	(Intercept):year.Timeseries_id	0.083	-0.013	0.185	8,629.515		random
	year:year.Timeseries_id	0.005	0.002	0.009	4,509.669		random
	residual	2.676	2.540	2.823	9,000		residual
	Biomass (terrestrial, van Klink <i>et al.</i> , n = 18)	(Intercept)	2.585	0.638	4.578	9,000	0.013
year		-0.041	-0.062	-0.022	6,912.661	0.0004	fixed
year (random)		0.071	0.00000	0.136	4,538.983		random
WWFecoRegion:Year		0.022	0	0.075	3,905.155		random
(Intercept):(Intercept).Timeseries_id		17.272	7.219	31.697	673.187		random
year:(Intercept).Timeseries_id		-0.019	-0.121	0.058	1,710.907		random
(Intercept):year.Timeseries_id		-0.019	-0.121	0.058	1,710.907		random
year:year.Timeseries_id		0.0005	0	0.001	3,755.425		random
residual		0.862	0.796	0.928	8,782.746		residual

Abundance (freshwater, van Klink <i>et al.</i> , n = 79)	(Intercept)	5.837	5.329	6.386	9,000	0.0001	fixed
	year	0.001	-0.014	0.017	8,704.744	0.845	fixed
	year (random)	0.006	0	0.021	4,628.452		random
	WWFecoRegion:Year	0.103	0.067	0.141	8,409.004		random
	(Intercept):(Intercept).Timeseries_id	5.313	3.531	7.221	2,155.026		random
	year:(Intercept).Timeseries_id	0.013	-0.022	0.050	7,383.029		random
	(Intercept):year.Timeseries_id	0.013	-0.022	0.050	7,383.029		random
	year:year.Timeseries_id	0.002	0.001	0.004	3,465.915		random
	residual	1.608	1.552	1.664	6,042.458		residual
Abundance (terrestrial, van Klink <i>et al.</i> , n = 221)	(Intercept)	4.511	4.111	4.893	9,000	0.0001	fixed
	year	-0.014	-0.021	-0.006	4,679.015	0.0001	fixed
	year (random)	0.003	0	0.009	2,901.541		random
	WWFecoRegion:Year	0.036	0.021	0.051	3,663.796		random
	(Intercept):(Intercept).Timeseries_id	8.731	7.106	10.400	4,209.539		random
	year:(Intercept).Timeseries_id	0.003	-0.018	0.025	1,510.321		random
	(Intercept):year.Timeseries_id	0.003	-0.018	0.025	1,510.321		random
	year:year.Timeseries_id	0.001	0.001	0.002	1,687.778		random
	residual	1.528	1.498	1.558	2,078.304		residual