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Studies of insect temporal trends must account for the complex sampling histories inherent to many long-term monitoring efforts

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arising from M. S. Crossley et al. *Nature Ecology & Evolution* <https://doi.org/10.1038/s41559-020-1269-4>(2020).

Crossley et al.¹ examine patterns of change in insect abundance and diversity across US Long-Term Ecological Research (LTER) sites, concluding a "lack of overall increase or decline". This is notable if true, given mixed conclusions in the literature regarding the nature and ubiquity of insect declines across regions and insect taxonomic groups2–6 . The data analysed, downloaded from and collected by US LTER sites, represent unique time series of arthropod abundances. These long-term datasets often provide critical insights, capturing both steady changes and responses to sudden unpredictable events. However, a number of the included datasets are not suitable for estimating long-term observational trends because they come from experiments or have methodological inconsistencies. Additionally, long-term ecological datasets are rarely uniform in sampling effort across their full duration as a result of the changing goals and abilities of a research site to collect data7 . We suggest that Crossley et al.'s results rely on a key, but flawed, assumption that sampling was collected "in a consistent way over time within each dataset". We document problems with data use prior to statistical analyses from eight LTER sites due to datasets not being suitable for long-term trend estimation and not accounting for sampling variation, using the Konza Prairie (KNZ) grasshopper dataset (CGR022) as an example.

Unsuitable datasets to estimate long-term observational trends

Several of the LTER datasets included in Crossley et al. document experiments that either have confounding treatment effects or are too variable in sampling methods to allow for comparison of samples across time. Additionally, in one case, lepidopteran outbreak dynamics with long intervals (10–13 years) at Hubbard Brook limit the power to detect meaningful trends without extremely long-term data8 . Datasets from Cedar Creek include arthropods collected in plots with nitrogen addition, herbivore exclosures and manipulated plant diversity. All three of the datasets from Harvard Forest included in Crossley at al.'s analysis have large methodological inconsistencies over time and one dataset documents ants collected in a canopy manipulation experiment, including one treatment where trees were girdled to simulate hemlock woolly adelgid (*Adelges tsugae*) infestation of the hemlock trees years prior to the arrival of the invasive insect to the area. One dataset from North Temperate Lakes documents the responses of two crayfish species in a lake where one species was being experimentally removed. With a few exceptions for partial components of these datasets (for example, control plots in the arce153 Cedar Creek dataset), these data are inappropriate for estimation of long-term observational species trends.

Not accounting for sampling variation and Konza grasshoppers as a case in point

The KNZ CGR022 dataset documents grasshopper species abundances on 15 KNZ watersheds and spans 1982 to present (up to 2015 included in Crossley et al.). Crossley et al. analyse time series of individual species from each dataset (the number of 'time trends' in their Table 1). However, regardless of variant sampling effort, they regularly sum all individuals within LTER datasets to yield a single value of abundance for a given species and year. This is the case for KNZ grasshoppers and most other included datasets (number of 'sites' in their Table 1). Importantly, sampling effort at KNZ and other LTER sites was not constant. At KNZ, variation occurred in the number of samples per watershed and the number of watersheds in which grasshoppers were collected per year (Fig. 1). Most notably, six bison-grazed watersheds were added to KNZ sampling in 2002. Changes in sample numbers over time are documented in the online metadata ([http://lter.konza.ksu.edu/content/cgr02-swe](http://lter.konza.ksu.edu/content/cgr02-sweep-sampling-grasshoppers-konza-prairie-lter-watersheds) [ep-sampling-grasshoppers-konza-prairie-lter-watersheds](http://lter.konza.ksu.edu/content/cgr02-sweep-sampling-grasshoppers-konza-prairie-lter-watersheds)).

Not accounting for sampling effort and data structure causes errors in trend estimates (see also Supplementary Information and Supplementary Fig. 1). At KNZ, bison-grazed watersheds support higher grasshopper abundances and species richness^{9,10}. In a recent analysis using the CGR022 dataset, to account for this change in sampling effort, only data collected in the same years from watersheds were combined (for example, by splitting samples from grazed watersheds into a separate time series) and abundances within each watershed and year were divided by the number of samples. Analysis of the data structured in this way showed a>2% annual decline in grasshopper abundance, with only one common species increasing¹¹. Crossley et al., in contrast, report that most grasshopper species increased in abundance from 1982 to 2015. Crossley et al.

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Fig. 1 | The complex history of sampling of the KNZ grasshopper dataset. The KNZ grasshopper dataset (CGR022) exhibits high variance both in number of watersheds sampled per year (number of bars per year) and number of samples collected within each watershed each year (depicted in colour). Other complexities include the tragic loss of four years (1992–1995) of sampling due to a freezer crash, changes in sampling month, changes in watershed burn frequencies and the reintroduction of bison in the 1990s to six of the later-sampled watersheds.

note the discrepancy with both this study $^{\text{11}}$ and another³, and suggest it is "driven by falling numbers of just two once-dominant species…whereas many other formerly rare species have become more abundant and both evenness and species richness have increased". However, we believe the discrepancy arises because Crossley et al. did not account for variable sampling effort, including KNZ's incorporation of additional, more diverse grazed habitats midway in the time series. Similar errors, where data structure was not accounted for, are evident in 17 of the 19 datasets that we examined and were included in Crossley et al.'s results.

Conclusion

We have thus far been able to confirm issues with data from 8 of the 13 LTER sites (comprising 60% of Table 1's 'time trends') included in Crossley et al. We note that this is not a comprehensive assessment, as we have included errors only from datasets for which either we ourselves are the principal investigators or we have been able to confirm with the corresponding LTER principal investigators and information managers. The eight sites are: Baltimore, Cedar Creek, Central Arizona–Phoenix, Harvard Forest, Hubbard Brook, Konza Prairie, North Temperate Lakes and Sevilleta. We provide details on dataset unsuitability, mistakes in not accounting for sampling effort and several coding errors in the Supplementary Information.

Given these mistakes, we urge scepticism regarding Crossley et al.'s general conclusion of no net decline in insect abundances at US LTER sites in recent decades. Although their goal is laudable, both the use of unsuitable datasets and not taking sampling effort into account generate erroneous estimates of population change. Recently, a study reporting widespread collapse of rainforest insect populations at the LTER Luquillo site necessitated a similar correction⁵. We echo those authors, when they suggest that scientists can avoid errors by reading corresponding metadata. Contacting the data providers/field biologists in advance

(or even including them as authors) is an additional good practice that ensures appropriate use of the data. Like the ecology they document, it is important to take into account that long-term monitoring efforts by LTERs and similar institutions are themselves complex and full of history.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

KNZ grasshopper abundance data are available from the Long-Term Ecological Research Data Portal ([https://doi.org/10.6073/pasta/7](https://doi.org/10.6073/pasta/7b2259dcb0e499447e0e11dfb562dc2f) [b2259dcb0e499447e0e11dfb562dc2f\)](https://doi.org/10.6073/pasta/7b2259dcb0e499447e0e11dfb562dc2f). Citations for the additionally described LTER datasets are provided in the Supplementary Information.

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E.A.R.W., S.R., A.J. and M.K. conceived the idea for the paper. E.A.R.W. wrote the first draft. A.M.E., D.C.L., S.R., N.R. and E.H.S. identified further errors in the Crossley et al. online data. All authors significantly contributed to revisions.

Competing interests

The authors declare no competing interests.

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Methods

M. S. Crossley et al. reply

Michael S. Crossley ^{●1⊠}, William E. Snyder¹ and Matthew D. Moran^{●2}

replying to E. A. R. Welti et al. *Nature Ecology & Evolution* <https://doi.org/10.1038/s41559-021-01424-0> (2021) replying to M. Desquilbet et al. *Nature Ecology & Evolution* <https://doi.org/10.1038/s41559-021-01427-x>(2021)

Our recent study showing no broad-scale declines in arthropods at Long Term Ecological Research (LTER) sites across the USA has garnered critiques from peers. Welti et al.¹ note that the LTER sites have complex management histories, and describe instances where we failed to correct for changes in sampling intensity through time. Using their critique as a guide, we re-curated the LTER metadata to maintain per-sample (for example, per sweep, pitfall trap and so on) arthropod numbers. We then repeated the analyses of abundance and biodiversity trends for the arthropod taxa and sites described in Crossley et al.^{[2](#page-9-1)}, using several different approaches to generate trends for each taxon and site. Results were generally similar to our original findings, with broad variation in abundance and biodiversity trends among taxa and sites, but no clear overall pattern of abundance or biodiversity changes, supporting our original conclusion that LTER data do not show evidence of an "insect apocalypse". Desquilbet et al.^{[3](#page-9-2)} raise additional concerns that pertain to two aspects of our original study: selection criteria for studies included; and analysis. We find that the criticism of time series included is unwarranted, because the data from the Midwest Suction Trap Network are curated by an LTER and our inclusion of non-insect arthropods was intentional and clearly stated in the manuscript. The criticisms of our analysis are more substantial, but mostly represent ongoing debate on how to analyse time series data and what criteria should be utilized to include a time series. We note that within our publication, we address this uncertainty in several places and point out that changing criteria for time series inclusion has little effect on our results. We find that the criticisms of Desquilbet et al. 3 raise some important questions, but mostly reflect differences in opinion and not substantial flaws in our analysis and interpretation.

Welti et al. $¹$ $¹$ $¹$ begin their critique by noting that sampling intensity</sup> varied at several LTERs through time, and that Crossley et al.^{[2](#page-9-1)} failed to account for these changes when summing to generate taxon abundance trends. They also noted one instance (crayfish in North Temperate Lakes) where a coding error removed several time trends from analysis. We re-curated the metadata to correct these errors. Then, we repeated abundance and biodiversity trend analyses after collapsing abundances into a single trend per taxon (Methods). We found broad variability among taxa and sites in whether arthropods were decreasing or increasing through time (Fig. [1a\)](#page-7-0), yielding a net trend whose distribution overlapped with zero (Fig. [1b](#page-7-0)). Likewise, sites varied in whether the various biodiversity metrics were showing gains or declines, yielding no net directional trend across sites (Fig. [2a](#page-7-1)). These results are generally consistent with the findings of Crossley et al.^{[2](#page-9-1)}.

Second, Welti et al.^{[1](#page-9-0)} note that a simple summing across subplots at each LTER site may have masked important plot-specific differences in abundance trends that, had they been considered, would

have revealed general arthropod declines. To address this possibility, we calculated separate abundance trends for each species, at each subsite, before averaging these values to arrive at the single species-specific abundance trend per site. The revised dataset contained many more subsites within each main site, such that the overall number of abundance trends considered in the meta-analysis increased ~80%. We also separately calculated biodiversity trends for each subsite. Here again, results were broadly consistent with those in Crossley et al.², with broad variability in trends by species and site but no clear overall directional trend (Figs. [1c,d](#page-7-0) and [2b\)](#page-7-1).

Third, Welti et al.¹ suggest that three datasets are not appropriate for estimation of long-term arthropod trends because they involve observations made in experimentally manipulated plots (Cedar Creek arthropod sweep datasets acre153 and aage120) or physical removal of the focal taxon (North Temperate Lakes crayfish dataset knb-lter-ntl.217.9). While we consider these instances to be a special case where drivers of arthropod abundance change are potentially well known and not grounds to exclude trend data from our meta-analysis, a reanalysis of abundance trends after excluding these data did not change overall results (Extended Data Fig. 1).

Finally, since our paper was published, Didham et al.⁴ have suggested that time series that include at least 10 points may provide the most reliable measure of arthropod abundance change through time. Thus, we again repeated our analyses using only those subsites that included 10 or more data points. This process removed one LTER site (Baltimore) altogether, and several subdatasets at particular sites (Fig. [1e\)](#page-7-0). However, the general patterns were similar to those generated with other data treatments, with variability in abundance (Fig. [1f\)](#page-7-0) and biodiversity (Extended Data Fig. 2) trends but no clear overall directional change across sites. Despite a consistent finding of broad variability in trends, we note that a proportion of abundance trends changed sign after standardizing taxa counts by sampling intensity and accounting for subsite structure (Fig. [3](#page-8-0)). However, a roughly equal proportion of changing trends switched from positive to negative and vice versa, suggesting no upward bias in abundance trend estimates in our original analysis (for example, 19% and 17% changed to decreasing or increasing, respectively, after accounting for sampling effort).

A key challenge when searching for evidence of recent declines in many animal and plant groups is that it often is necessary to rely on data collected for other purposes. We acknowledge that there may be longer-term periodicity in arthropod trends, as elegantly described at several of the LTER sites^{[5](#page-9-4)[,6](#page-9-5)}, that make it difficult to isolate any recent arthropod declines. However, autoregressive models are capable of detecting general declines embedded within data that show periodicity^{[7](#page-9-6)}. Last, we found that net abundance trends across our many different analysis approaches were consistently weakly

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Fig. 1 | Time trends in arthropod abundance among LTERs. a, Violin plots showing the distribution of abundance trends per taxon, where abundances were standardized by sampling effort before trend estimation. **b**, Average trend in abundance and 95% confidence intervals from **a** when trends are averaged among LTERs (d.f. =12). Mean time trends were not significantly different from zero ($P = 0.55$). **c**, Violin plots showing the distribution of abundance trends per taxon averaged among subsites, where abundances were standardized by sampling effort and separated by subsite before trend estimation. **d**, Average trend in abundance and 95% confidence intervals from **c** when trends are averaged among LTERs (d.f. = 12). Mean time trends were not significantly different from zero ($P = 0.11$). **e**, Violin plots showing the distribution of abundance trends per taxon, averaged across subsites, where abundances were standardized by sampling effort before trend estimation, and time series with <10 data points were excluded. **f**, Average trend in abundance and 95% confidence intervals for **e** when trends are averaged among LTERs (d.f. = 11). Mean time trends were not significantly different from zero (*P*= 0.28). In **a**, **c** and **e**, the black diamonds within boxplots depict medians. The first and last years of LTER studies as well as the number of taxa time series are included below the violin plots. Blue shading and font indicate LTER sites reporting aquatic taxa. Orange shading and font indicate LTER sites in urban or agricultural landscapes. Unfilled violin plots and black font indicate LTER sites reporting terrestrial taxa in relatively less human-disturbed habitats.

Fig. 2 | Time trends in arthropod diversity among LTERs. a–**c**, Diversity trends estimated using the dataset where arthropod abundances were standardized by sampling effort, and time series with <4 data points were excluded. **d**–**f**, Diversity trends estimated using the dataset where arthropod abundances were standardized by sampling effort and separated by subsite, and time series with <4 data points were excluded. **a**,**d**, Trends in taxon richness (rarefied). **b**,**e**, Trends in taxon evenness (Pielou's index). **c**,**f**, Trends in *β* diversity (1 − Jaccard similarity index). Boxplots depict trends among insects as medians (thick line), 25th and 75th percentiles (box edges), 95th percentiles (whiskers) and outliers (circles). The right panels depict average change in diversity metrics and 95% confidence intervals among datasets (d.f. = 11). Time trends were not significantly different from zero at α = 5%. See the caption of Fig. [1](#page-7-0) for a description of the coloured text.

negative (although statistically non-significant), suggesting that there may be some underlying general decline trend at LTER sites, but that the data are too few, and too variable, to clearly reveal it on their own. Interestingly, richness, evenness and *β* diversity patterns showed no evidence of any overall trend (positive or negative), providing little evidence of widespread biodiversity loss over time.

Desquilbet et al.^{[3](#page-9-2)} begin their critique by proposing four modi-fications to the analysis of Crossley et al.^{[2](#page-9-1)}. First, Desquilbet et al.³ suggest a minimum time series length criterion of 16 years, citing White^{[8](#page-9-7)}. However, White⁸ prescribes no single threshold, emphasizing that "More importantly, however, there is wide distribution of estimated minimum times. Therefore, it is not wise to use a simple threshold number of years in monitoring design". In addition, White^{[8](#page-9-7)} states that "Approximately, 72% of the [822] populations required at least 10 years of monitoring.", which is in line with recent recommendations for analysing insect population trends^{[4](#page-9-3)}, and

Fig. 3 | Comparison of abundance trends per taxon between original and updated datasets. a, Comparison of abundance trends per taxon, where abundances were standardized by sampling effort before trend estimation. **b**, Comparison of abundance trends per taxon averaged among subsites, where abundances were standardized by sampling effort and separated by subsite before trend estimation. **c**, Comparison of abundance trends per taxon averaged among subsites, where abundances were standardized by sampling effort and separated by subsite before trend estimation, and time series with <10 data points were excluded. Pink lines divide plots into quadrants, and grey lines depict 1:1 relationships.

which, through our reanalysis conducted in response to Welti et al.^{[1](#page-9-0)}, we demonstrated did not alter the conclusions of Crossley et al.². We also mention in the paper that restricting the analysis to only those time series that are more than 4, 8 or 15 years has relatively little effect on the results and their interpretation. Second, Desquilbet et al.^{[3](#page-9-2)} recommend using zero-inflated models over linear regression of log-transformed counts for estimating trends. While we appreciate this suggestion, we emphasize that there are genuine differences of opinion about how zero counts are handled in ecological data, and that log transformation is still widely accepted^{9,[10](#page-9-9)}. Third, Desquilbet et al.³ recommend accounting for imperfect detection in ecological count data, illustrating their point with a large apparent increase observed for the aphid *Aphis asclepiadis* in a site where the first years of the time series reported zeros. These cases were uncommon (occurring in 195 of the 5,375 trends), and were similarly likely to contribute to large apparent declines (occurring in 109 of the 5,375 trends), among time series in Crossley et al.^{[2](#page-9-1)}, and enforcing of stricter criteria for inclusion of time series, as done in Crossley et al.^{[2](#page-9-1)} and in response to Welti et al.^{[1](#page-9-0)}, suggests that these cases did not alter the original conclusions of Crossley et al.^{[2](#page-9-1)}. Fourth, Desquilbet et al.^{[3](#page-9-2)} caution that summarizing many abundance trends drawn from different populations using violin plots, medians or means is statistically inappropriate. While we generally agree that summarizing a wealth of informative trends using a few summary statistics is not ideal, there is an understandable desire to summarize overall trends in insect abundance time series to allow some degree of comparability among studies. We stand by our original visual summary of abundance trends using violin plots, and note that this does not meaningfully diverge from other meta-analyses 11 . Last, Desquilbet et al.³ note that analyses of diversity trends shared the same issues as analyses of abundance trends. Again, in response to Welti et al.¹ we show that reanalysis using stricter criteria does not change the original conclusions of Crossley et al.².

Next, Desquilbet et al.^{[3](#page-9-2)} raise three concerns with the inclusion of certain arthropod time series in our analysis. First, they note that a large portion of arthropod abundance trends were derived from aphid species documented by the Midwest Suction Trap Network. While this is clearly acknowledged by Crossley et al.², the implication that these data primarily represent pests that benefit from intensive agriculture is unfounded on two counts. First, the majority of aphid species (52 out of 96) documented by the Midwest Suction Trap Network do not feed on crops. Second, aphids do not benefit

from intensive agriculture, which, to the contrary, includes in its definition the extensive use of insecticides often applied specifically to kill aphids. Rather than bias our analysis toward detection of more increasing abundance trends, inclusion of data from the Midwest Suction Trap Network introduced a substantial proportion of decreasing abundance trends, as the aphid populations monitored by the suction trap network in the Midwest appear to have been largely in decline since the early 2000s. Desquilbet et al.³ also state that the Midwest Suction Trap Network is not an LTER. However, the data from these monitoring programmes have been included in Kellogg Biological Station's LTER datasets that are publicly available.

Desquilbet et al.³ conclude their critique by noting that 9% of the time series were of non-insect arthropods or included both insects and other arthropods, and that they therefore should have been excluded. While we understand this sentiment, we emphasize that we clearly state throughout Crossley et al.² that we intentionally included all arthropods that met our sampling criteria, not just insects. This was in part to obtain data on aquatic arthropods, which often include large numbers of crustaceans.

As an aside, Desquilbet et al.³ note that they had to re-program the R script provided in Crossley et al.² to make it run. In Crossley et al.², we state in the Code availability statement that the R code used to curate and analyse data is available at the Dryad Data Repository [\(https://doi.org/10.5061/dryad.cc2fqz645\)](https://doi.org/10.5061/dryad.cc2fqz645). We made this R code publicly available so that interested researchers could see how we handled the arthropod count data used in Crossley et al.². We note that part of the issue in repeatability probably stems from unavoidable differences in how original data were compiled from online repositories, and that we have provided updated R code in response to Welti et al.¹ that we are able to run.

In conclusion, we disagree with Desquilbet et al. 3 that the issues raised about data selection and analysis invalidate the original conclusion of Crossley et al.² that the available data reveal no evidence of consistent, general abundance and biodiversity decline that might be expected were a dramatic "insect apocalypse" impacting the LTER sites.

Methods

Abundance trends. Using the critique provided by Welti et al.^{[1](#page-9-0)} as a guide, we re-curated all taxa abundance time series using four diferent approaches, standardizing arthropod abundances by sampling effort (definition varies among datasets) in all four. A detailed description of curation changes for each

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dataset and responses to critiques provided in the Supplementary Information of Welti et al.¹ is provided in Supplementary Table 1, and R code used for curation and analysis is provided on GitHub ([https://github.com/mcrossley3/](https://github.com/mcrossley3/reWelti) [insectLTER](https://github.com/mcrossley3/reWelti)). In the frst approach, we summed arthropod abundances per taxon per year, standardizing abundances by associated sampling effort (for example, arthropods per sweep, aphids per day). As in the original analysis of Crossley et al.², we excluded time series with <4 data points. In the second approach, we further separated efort-standardized arthropod abundances by subsite (for example, watershed in Konza Prairie, experimental plot in Cedar Creek), again excluding any time series with <4 data points. In the third approach, we again separated efort-standardized arthropod abundances by subsite and excluded any time series with <4 data points, but we further removed data from subsites that were identifed as inappropriate for estimation of long-term arthropod abundance trends because they involved experimental manipulation of plots (Cedar Creek arthropod sweep datasets acre153 and aage120) or physical removal of the focal taxon (North Temperate Lakes crayfsh dataset knb-lter-ntl.217.9). For the Cedar Creek arthropod sweep datasets, we retained for analysis only observations from "control" plots (no exclosures, unfertilized, unburned, no experimental plant seeding). For the North Temperate Lakes crayfsh dataset involving removal of rusty crayfsh (*Orconectes rusticus*), we retained only data for *O. virilis*. In the fourth approach, we again separated efort-standardized arthropod abundances by subsite, but this time excluded any time series with <10 data points, following the minimum time series length recommended by Didham et al.^{[4](#page-9-3)} for arthropod time series analysis. For the two analyses that separated abundance time series by subsite, counts in the Konza Prairie grasshopper dataset were curated in a similar fashion to Welti et al.^{[5](#page-9-4)}. Specifcally, counts pre-1996 were excluded, and mean abundance trends per species were separated by grazed and ungrazed treatment.

Diversity trends. Using the re-curated dataset where arthropod counts were standardized by sampling effort and/or time series were separated by subsite, we recalculated diversity metrics (rarefied richness, evenness, *β* diversity) and estimated time trends using the same approach as in Crossley et al.^{[2](#page-9-1)}. Richness was rarefied using a minimum sample that was calculated on the basis of the 0.1 quantile per dataset (or the 0.2 quantile when the 0.1 quantile was substantially smaller than the number of species reported in a dataset). As effort-standardized arthropod counts were «1 for three datasets (Midwest aphids, Central Arizona–Phoenix sweep and pitfall2), precluding richness rarefaction, standardized abundances were multiplied by a constant (20, 20 and 10, respectively). Effort-standardized abundances for these datasets could thus be interpreted as aphids per 20 days, arthropods per 20 sweeps and arthropods per 10 traps, respectively.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

All curated data used for analyses in this study are available on GitHub ([https://](https://github.com/mcrossley3/insectLTER) github.com/mcrossley3/insectLTER).

Code availability

R code used to curate and analyse data in this study is available on GitHub [\(https://](https://github.com/mcrossley3/insectLTER) github.com/mcrossley3/insectLTER).

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Author contributions

M.S.C., W.E.S. and M.D.M. conceived of the idea of this study. M.S.C. conducted formal analysis. All authors contributed to the writing of the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at <https://doi.org/10.1038/s41559-021-01429-9>.

Supplementary information The online version contains supplementary material available at [https://doi.org/10.1038/s41559-021-01429-9.](https://doi.org/10.1038/s41559-021-01429-9)

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extended Data Fig. 1 | See next page for caption.

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extended Data Fig. 1 | Effort-standardized time trends in arthropod abundance among LTER subsites. a, Violin plots showing the distribution of abundance trends per taxon averaged among subsites, where abundances were standardized by sampling effort and separated by subsite prior to trend estimation, and trends with < 4 data points were excluded. This analysis differs from that depicted in Fig. [1c,d](#page-7-0) in that trends associated with experimental treatments in the Cedar Creek sweep nets and North Temperate Lakes crayfish datasets were excluded from analysis. **b**, Average trend in abundance and 95% confidence intervals from **a** when trends are averaged among LTERs (d.f. = 12). Mean time trends were not significantly different from zero ($p = 0.10$). **c**, Violin plots showing the distribution of abundance trends per taxon averaged among subsites, where abundances were standardized by sampling effort and separated by subsite prior to trend estimation, and trends with < 10 data points were excluded. This analysis differs from that depicted in Fig. [1e,f](#page-7-0) in that trends associated with experimental treatments in the Cedar Creek sweep nets and North Temperate Lakes crayfish datasets were excluded from analysis. **d**, Average trend in abundance and 95% confidence intervals from **c** when trends are averaged among LTERs (d.f. = 11). Mean time trends were not significantly different from zero ($p = 0.27$).

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extended Data Fig. 2 | See next page for caption.

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extended Data Fig. 2 | Effort-standardized time trends in arthropod diversity among LTER subsites. Time trends in arthropod diversity among LTERs, using the dataset where abundances were standardized by sampling effort and separated by subsite, and time series with < 10 data points were excluded. **a**, Trends in taxon richness (rarefied). **b**, Trends in taxon evenness (Pielou's Index). **c**, Trends in *β* diversity (1-Jaccard Similarity Index). Boxplots depict trends among insects as medians (thick line), 25th and 75th percentiles (box edges), 95th percentiles (whiskers), and outliers (circles). Right panels depict average change in diversity metrics and 95% confidence intervals among datasets (d.f.=7). Time trends were not significantly different from zero at α=5%. Please refer to Fig. [1](#page-7-0) legend for description of colored text.

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