INSECT POPULATIONS

Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances

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Recent case studies showing substantial declines of insect abundances have raised alarm, but how widespread such patterns are remains unclear. We compiled data from 166 long-term surveys of insect assemblages across 1676 sites to investigate trends in insect abundances over time. Overall, we found considerable variation in trends even among adjacent sites but an average decline of terrestrial insect abundance by ~9% per decade and an increase of freshwater insect abundance by ~11% per decade. Both patterns were largely driven by strong trends in North America and some European regions. We found some associations with potential drivers (e.g., land-use drivers), and trends in protected areas tended to be weaker. Our findings provide a more nuanced view of spatiotemporal patterns of insect abundance trends than previously suggested.

Insects are the most ubiquitous and diverse animals on the planet (*1–3*), providing multiple critical ecosystem services (e.g., pollination and decomposition) and disservices (e.g., damaging crops and spreading disease) (*4*). Although population declines of many species have been previously documented (*5–7*), recent case studies showing drastic declines in the total biomass or abundance of entire insect assemblages (*8–11*) have caused a surge of interest in the plight of insects (*12*, *13*). Despite the attention from the media, policy-makers, and scientists, it remains unclear whether such declines are widespread across realms and among geographic regions. Here, we compiled as many openly available long-term (10+ years) standardized monitoring surveys of assemblages of insects and arachnids (for brevity, hereafter collectively referred to as "insects") as we could find (*14*). We used the amassed data to evaluate changes in total insect abundance and biomass, as well as the geographic distribution of such changes. Our dataset included 1676 sites from 166 studies spread over 41 countries (Fig. 1; see table S1 for a list of studies). Among these, 130 datasets reported only changes in insect abundances (i.e., number of individuals) in an assemblage, 13 datasets reported only the biomass of all insects in an assemblage, and 23 datasets reported both metrics. The data spanned from 1925 to 2018, with a median start year of 1986 and a median time span of 20 years. Because our main focus was on the temporal trend of changes within assemblages (i.e., time series of total biomass or abundance), we could combine data with different sampling methods, spatial scales, and metrics into one analysis.

Across all studies, there was great variation in trends even among geographically adjacent sites (Fig. 1). We analyzed the data using a hierarchical Bayesian model accounting for variation at the study, study area, and site level (*14*). From this, we inferred strong evidence for a mean trend when the posterior probability of the estimate was larger or smaller than zero with at least 95% certainty. Likewise, we inferred moderate or weak evidence for a mean trend when the posterior probability differed from zero with 90 or 80% certainty, respectively, and interpreted no evidence for a directional trend for probabilities <80%. Overall, we found strong evidence for a decline of terrestrial insects, which we estimated to be 0.92% per year (Fig. 2A and table S2), amounting to –8.81% per decade. By contrast, we found a 1.08% annual increase for freshwater insects, equaling +11.33% per decade (Fig. 2A). The mean trend estimates of insect abundance and biomass were similar (Fig. 2A) but differed in strength of evidence because of the lower data availability for biomass (table S2). The positive trends in the freshwater realm may partially counter the negative terrestrial trends, because a model combining both realms showed no evidence for a directional trend (Fig. 2A). However, because fresh water represents only 2.4% of the earth's terrestrial surface (*15*, *16*), such a combined model is likely to be a poor representation of trends in total insect numbers at any spatial scale.

The strongest evidence for declines in terrestrial insect assemblages was found in North America (Fig. 2B), but also in some European regions (fig. S1). The exclusion of all North American data thus tempered the overall decline (mean trend without North America: –0.49% per year), but there was still weak evidence for a negative mean trend. When estimating the trends in different climatic zones, we found strong evidence for directional trends in both realms in the temperate zone, as well as in Mediterranean and desert climates (drylands; Fig. 2C and table S2). We found no evidence for directional trends in other continents or climatic zones, where the data were much sparser (Fig. 2, B and C, and table S2). The increasing trend for the freshwater insects, particularly in the temperate zone, is consistent with recent analyses from these regions (*17–19*) and may at least partially reflect recovery from past degradation [e.g., the Clean Water Act and similar legislation (*20–23*)]. Other causes of this increase may have been climatic warming (*24*) and an enhanced productivity caused by nutrient inputs (*25*, *26*).

We tested whether these temporal trends changed over time by running the same model for progressively shorter timespans: since 1960, 1970, 1980, 1990, 2000, and 2005 (Fig. 3). No consistent temporal changes in trends were visible at the global level. However, in Europe, the mean slope estimate for the terrestrial insects became more negative over time and was steepest since 2005. By contrast, the overall negative trends for terrestrial insects in North America have tempered and were no longer negative since 2000. For freshwater insects, the trends became more positive in Europe and North America, as well as in Asia, where the overall increase was steepest since 1990, coinciding with the collapse of the Soviet Union and its heavy industries (*27*, *28*). Trends in the other continents seem relatively unchanged over time.

We evaluated associations of the observed trends in insect abundances with commonly hypothesized anthropogenic drivers, including land-use change and climate change (*10*, *11*, *29*). First, we found that the trends in protected areas were weaker than those in unprotected areas (Fig. 4), although there was still a moderate negative trend in terrestrial protected areas. This difference suggests a possible association between insect trends and land-use change. To evaluate this further, we used Geographic Information System (GIS) layers to extract urban and cropland cover surrounding the sampling sites at local (only available since 1992) and landscape (full period) scales (*14*). We found moderate evidence for a negative relationship between terrestrial insect abundance trends and landscape-scale urbanization (figs. S3 and S4a), potentially explained by habitat loss and light and/or chemical pollution associated with urbanization (*30*). By contrast, insect abundance trends were positively associated with crop cover at the local (but not landscape) scale in both realms (fig. S3). Specifically, in the terrestrial realm, temporal trends became less negative with increasing crop cover (fig. S4f),

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consistent with a high-profile case study (*10*). One explanation for this could be that areas with high crop cover tended to remain relatively stable over the study period (only 0.5% of the sites were converted into cropland) relative to land cover change in noncrop areas (3.8% of sites experienced other land-use change). In the freshwater realm, the trends became more positive with increasing crop cover (fig. S4), which could be because agricultural practices have become less detrimental to water quality than they were in the past. Finally, we calculated the relative change in temperature and precipitation over the sampling period at local and regional scales for each site (*14*) to test for a potential role of climate change, but found no evidence for any associations at either scale (figs. S3 and S5).

Although our data compilation has a large geographic and taxonomic scope, there are clear limitations to our analysis, so we remain cautious about generalizing these patterns. First, the trends were highly variable locally but also varied across regions, climatic zones, and time periods. Second, the strong trends in North America had a strong influence on the mean trend estimates. Finally, the manual exclusion of 14 datasets qualified as outliers [for more details, see (*14*)] provided strongly tempered trend estimates (terrestrial: −0.66%; freshwater: +0.34% per year), although there was still strong evidence for a decline for the terrestrial fauna. As with most data compilations of this kind, our data sources were not representatively spread across the world. Most data originated from temperate North America and Europe, but even here there was an underrepresentation of intensively modified sites (high urban or crop cover) compared with their global distribution (fig. S6). Likewise, protected areas were overrepresented in our dataset (34% of the sites) relative to the percentage of the terrestrial surface currently under protection (15%) (*31*). This means that locations where human land use is most intensive, and thus where the strongest effects on insect trends might be expected, were underrepresented. To infer broader patterns across the ecosystems of the world and for more comprehensive tests of human pressures, more data are needed from these underrepresented regions experiencing both low and high environmental change.

Our estimate of a 0.92% decline per year for terrestrial insects is 6-fold smaller than those

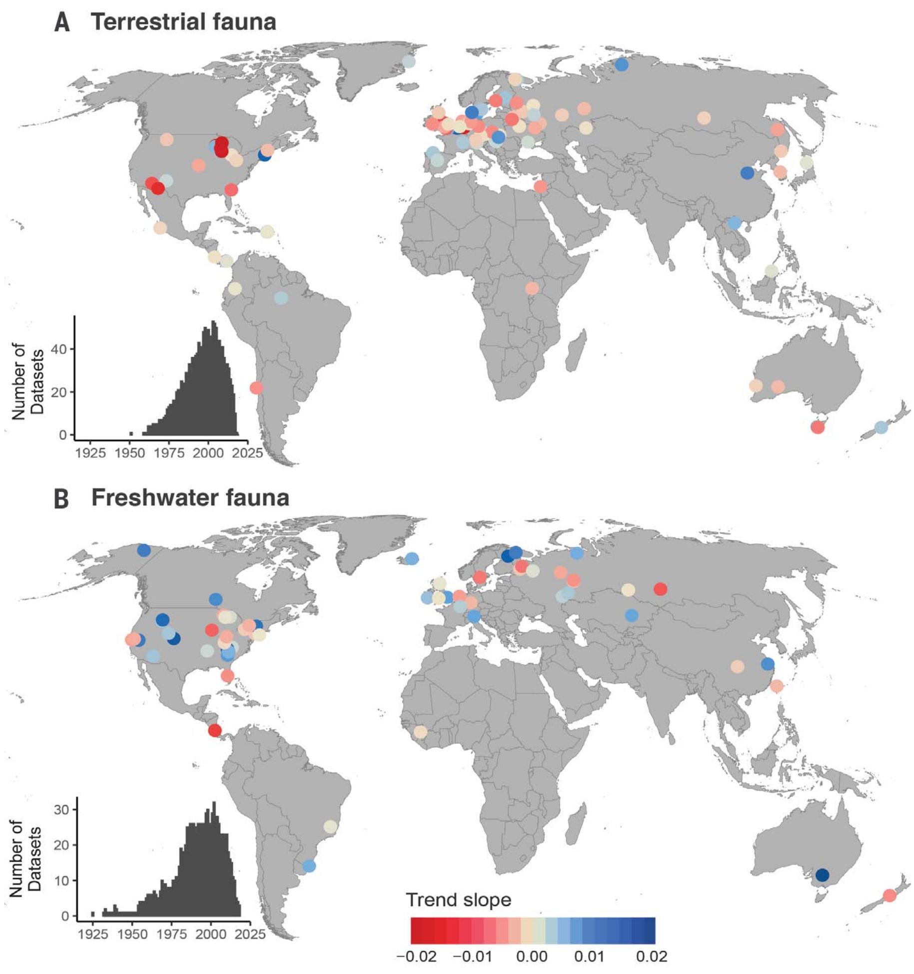

Fig. 1. Trend estimates of long-term changes in insect assemblage size, measured as insect abundance or biomass, of the 166 studies. Shown are trend estimates for terrestrial (**A**) and freshwater (**B**) fauna. The trend estimates of the individual studies were derived from the random effects of the hierarchical Bayesian model with only year as an explanatory variable. The insets show histograms of the number of datasets with at least one data point for each year.

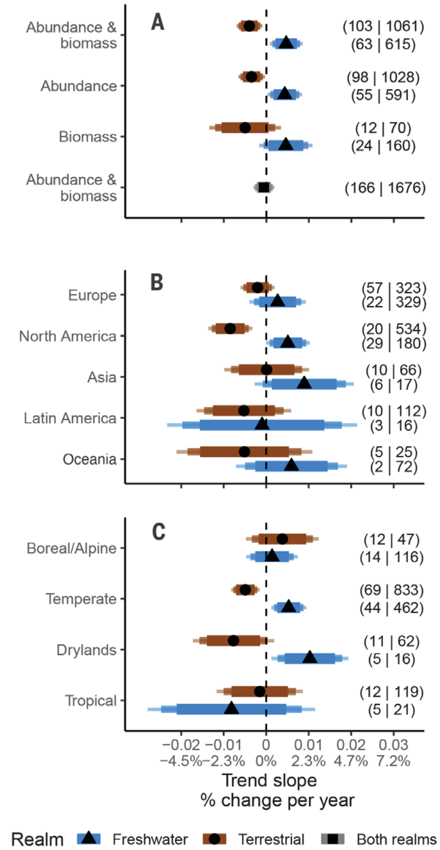

Fig. 2. Trend estimates (±80, 90, and 95% credible intervals). Shown are the trend estimates in insect abundance and biomass (**A**) at different continents (**B**) and climatic zones (**C**). Mean estimates are represented by symbols, with the error bars representing the three levels of credible intervals. The percentages below the *x*-axis indicate the annual change in insect abundance corresponding with the estimated slope. The bracketed numbers indicate the number of studies and the number of sites underlying each estimate, respectively. The continents are ordered by data availability, but Africa was omitted because of the wide credible intervals of its two studies (terrestrial: −8.93 to +18.34%; freshwater: −16.56 to +10.12% per year). Ecoregions are ordered from north to south from the Northern Hemisphere perspective.

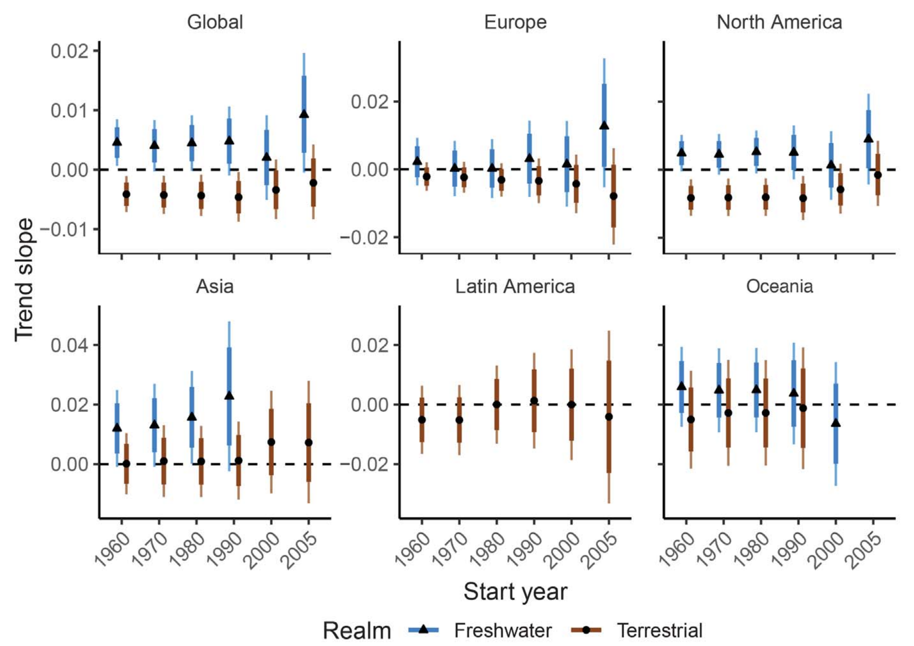

Fig. 3. Trend estimates (±80 and 95% credible intervals) for progressively shorter time periods since 1960. Each time slice included data until the last sampling date but excluded any sites spanning <9 years within the time slice. Only estimates with at least four datasets or 20 sites are shown. The continents are ordered by data availability. Annotation is as in Fig. 2.

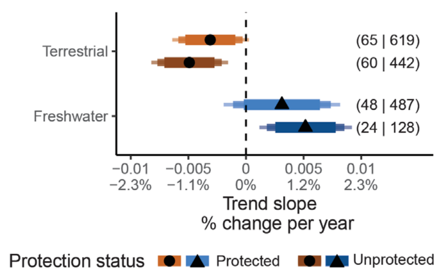

Fig. 4. Trend estimates (±80, 90, and 95% credible intervals) for terrestrial and freshwater insects inside and outside of protected areas. Bracketed numbers indicate the number of studies and number of sites underlying each estimate. Annotation is as in Fig. 2.

of recent high-profile case studies [e.g., 3 to 6% loss per year (*10*, *11*), which were included in our analysis]. Nevertheless, our more synthetic estimate translates to an average loss of 8.81% per decade in terrestrial ecosystems. Such a decline is concerning given the critical role that insects play in food webs and ecosystem services and may contribute to other changes such as the declines observed for some insectivorous bird populations (*32*–*34*). At the same time, we found an average increase in freshwater insect abundances that might, at least partially, reflect improvements in water quality. This, in combination with our finding that trends were weaker in protected areas, suggests that appropriate habitat protection and restoration may be effective strategies for mitigating changes in insect assemblages.

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SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/368/6489/417/suppl/DC1
Materials and Methods
Figs. S1 to S7
Tables S1 to S3
External Data S1 and S2
References (*37*–*206*)

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Local drivers of decline matter

Recent studies have reported alarming declines in insect populations, but questions persist about the breadth and pattern of such declines. van Klink *et al.* compiled data from 166 long-term surveys across 1676 globally distributed sites and confirmed declines in terrestrial insects, albeit at lower rates than some other studies have reported (see the Perspective by Dornelas and Daskalova). However, they found that freshwater insect populations have increased overall, perhaps owing to clean water efforts and climate change. Patterns of variation suggest that local-scale drivers are likely responsible for many changes in population trends, providing hope for directed conservation actions.

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