● SPECIAL FEATURE: PERSPECTIVE

A window to the world of global insect declines: Moth biodiversity trends are complex and heterogeneous

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Moths are the most taxonomically and ecologically diverse insect taxon for which there exist considerable time-series abundance data. There is an alarming record of decreases in moth abundance and diversity from across Europe, with rates varying markedly among and within regions. Recent reports from Costa Rica reveal steep cross-lineage declines of caterpillars, while other sites (Ecuador and Arizona, reported here) show no or only modest long-term decreases over the past two decades. Rates of decline for dietary and ecological specialists are steeper than those for ecologically generalized taxa. Additional traits commonly associated with elevated risks include large wingspans, small geographic ranges, low dispersal ability, and univoltinism; taxa associated with grasslands, aridlands, and nutrient-poor habitats also appear to be at higher risk. In temperate areas, many moth taxa limited historically by abiotic factors are increasing in abundance and range. We regard the most important continental-scale stressors to include reductions in habitat quality and quantity resulting from land-use change and climate change and, to a lesser extent, atmospheric nitrification and introduced species. Site-specific stressors include pesticide use and light pollution. Our assessment of global macrolepidopteran population trends includes numerous cases of both region-wide and local losses and studies that report no declines. Spatial variation of reported losses suggests that multiple stressors are in play. With the exception of recent reports from Costa Rica, the most severe examples of moth declines are from Northern Hemisphere regions of high human-population density and intensive agriculture.

Lepidoptera | insect decline | parasitoids | insectivores

While butterflies provide the deepest historical lens to examine the phenomenon of global insect decline, macrolepidopteran moths arguably supply the next largest set of historical records. In Europe, moths have been the focus of collecting efforts for over 200 y and systematic monitoring for many decades. Moths offer additional advantages over butterflies for assessing insect biodiversity change. They are much more ecologically diversified and at least 15 times more taxonomically diverse than butterflies (1). Their ranks include a wide spectrum of herbivores, including tree, shrub, forb, grass, fungus, lichen, and alga feeders, as well as detritivores (2). Moths include rich assemblages tied to all terrestrial plant communities from

subpolar regions to the equator. Their species taxonomy is less problematic than that of most insect lineages, and, for some countries, there have been reliable identification guides for more than a century. The immature stages of Lepidoptera are among the best known of any insect order, and knowledge of their host associations and other life-history traits can contribute considerably to efforts to understand and predict demographic declines and implications for ecosystem functioning. It is estimated that 90% have specialized host associations as larvae (3) and, thus, can serve as a fine-meshed filter for assessing changes across virtually all terrestrial plant communities. Moths represent a substantial component of the insect

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biomass available to insectivorous vertebrates, both as caterpillars and adults, and are an important dietary source for many animals, most notably bats and songbirds (4, 5). They are the very fabric underlying the species-rich radiations of parasitoids in the Chalcidoidea, Ichneumonoidea, and Tachinidae, which collectively make up much of the planet's metazoan species diversity (6), and moths likely play a much-underestimated role as pollinators of angiosperms (7). Depletions of moths will have effects that will cascade, upward and downward, triggering further losses of interactions and species. Thus, there is ample reason to regard macrolepidopterans as a worthy focal group to study global biodiversity change, and one which has much to offer as a proxy for other insect lineages with more nascent taxonomy, poorly known ecologies, and sparser long-term biomonitoring data. Because butterflies represent a polyphyletic group of diurnal moths, we include them loosely in our treatment (8).

Recent global attention on insect declines has focused on a handful of alarming reports of population collapses and seemingly remains anchored to these studies, even when some methods, results, interpretations, and universality are called into question (9, 10). Much remains unknown. To date, there have been only modest efforts to evaluate the spatial, temporal, and taxonomic aspects of insect declines, which has limited the capacity to identify the primary causal factors. Similarly, the extent to which rates of declines are commensurate with sympatric losses of vertebrates, plants, and other noninsect taxa has received only limited consideration. Empirical estimates in well-studied regions suggest that proportions of threatened species and rates of decline in insects are similar to or exceed those of vertebrates (11, 12).

Chronology of Moth Declines

Human-catalyzed changes to moth biodiversity commenced in prehistoric times, when people started diverting water and clearing forests for consumption, agriculture, and fuel (13). Museum collections provide a window to examine historical losses of macrolepidopterans, even though data may be sparse in cases, and especially so for nonlepidopterans. Habel et al. (14) reported that butterfly diversity in southwest Germany began to diminish more than a century ago and that rates of declines remained relatively constant until the industrialization of agriculture in the 1950s. The losses of butterflies from Belgium and Netherlands were already evident by the middle of the 20th century (15, 16).

Multidecadal time-series data on insect populations have the potential to reveal when declines began and how rates are varying. They also provide some power to suggest what stressors are the most relevant causal factors at a given site and over what time frames they function. For moths, the most comprehensive time-series data come from decades of standardized sampling carried out in the United Kingdom through the Rothamsted Insect Survey (17, 18). C. B. Williams initiated monitoring using light traps at Rothamsted, Hertfordshire, from 1933 to 1936 and 1946–49. Monitoring recommenced in 1960 and has continued ever since, now as part of a UK-wide network. This long time series at Rothamsted revealed a 71% reduction in average numbers of macrolepidopterans when comparing the pre-1950 data with catches between 1960 and 1979, which is attributed to land-use change and agricultural intensification (19). Subsequent analysis across the network revealed a significant decrease in macromoth abundance (31% decrease 1969–2016) for Great Britain (GB) (18). Moth biomass values derived from the Rothamsted Insect Survey increased rapidly from 1967 to 1982, but then declined from 1983 onward at an average rate of loss of 1.1% per year (20). Other multidecadal declines in moth faunas have been reported from Europe (e.g., refs. 21–24).

There are numerous historical time-series datasets of Lepidoptera and other insect populations that have yet to be analyzed in the context of current insect decline, including agricultural pest-monitoring data and studies of food availability for insectivorous birds. EntoGEM, a systematic mapping project to identify and collate insect population time-series studies (25), has uncovered many promising data sources that have the potential to further understand the scope and nature of global insect-population trends, resolve effect sizes, and identify knowledge gaps in the decline literature.

Moth Biodiversity Changes Are Spatially and Taxonomically Heterogeneous

Great heterogeneity in moth trends exists geographically and taxonomically, yielding a complex picture that cautions against ambitious extrapolation and generalization. There are also methodological and statistical issues that affect the reliability of trend estimates for moths and other insects (10).

Spatially, moth trends vary at continental, regional, and even local scales, which suggests that different stressors are in play. While patterns of moth decline are prevalent across western, central, and northern European countries (17, 21–24, 26), typically, there is considerable within-country heterogeneity. Conrad et al. (17) found that total abundance of macrolepidopterans decreased significantly (by 44%) in the southern half of GB over the period 1968–2002, but showed no overall change in the northern half. The median species trend at southern monitoring stations was a decrease three times greater than that at northern sites.

Regional assessments in the New World also provide evidence of spatial heterogeneity in trends. In the Missouri Ozarks, United States, a region with only modest human impacts, caterpillar numbers on oaks have fluctuated markedly over the past 20 y, but there is no signal of overall decline (27). Likewise, caterpillar collections from southeastern Arizona, United States, show great interannual fluctuation, but little evidence of decreasing abundances (data presented below). In the tropics, time-series data on moths are scarce, but two recent assessments from Central America reported greatly diminished macrolepidopteran diversity and abundance in Costa Rica (28, 29). Our data below for cloud forest caterpillars in Ecuador show no change.

Even in studies showing clear overall declines, some fraction of the moth fauna is increasing (e.g., refs. 17 and 21 and GB case study below). We are unaware of an instance where all lineages are in collapse, a signal that would implicate stressor(s) acting uniformly across families of Lepidoptera.

The assemblage-level signals described above are blind to taxonomy, lumping stenotopic species with generalists, and do not account for the colonizations of new taxa in response to land use and climate changes. Steep declines in the autochthonous fauna of a defined area could be masked by population increases of recent arrivals; for example, boreal communities undergoing long-term climate warming could be particularly susceptible to such processes.

The different metrics used to measure change can contribute additional complexity to our understanding of moth biodiversity trends. A long-term study in Hungary found significant reductions in alpha and beta diversity (indicating biotic homogenization of moth communities), but no decline in total abundance (22). In GB, imputed biomass of macrolepidopterans increased, whereas abundance decreased (18, 20). Of course, temporal changes in

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metrics used to assess changes in biotic communities, such as species richness, biomass, and trends in abundance and occupancy, can differ for many reasons. These could be spurious, stemming from differences in measurement, scale, or time lags, or they could reflect real discrepancies driven by differential responses of individual species, with the identities of winners and losers being due to different traits, demographics, and spatial distributions, generating conflicting signals at the assemblage level (30).

Case Studies

Below, we share data from a recent assessment of GB moth distributions, Costa Rican caterpillars, and two unpublished datasets on caterpillar abundance in Arizona and Ecuador. Methodological details for each study are included in *SI Appendix* and the legends for Figs. 1 and 2.

Distribution Trends Vary Among Macrolepidopterans in GB.
GB is one of the few places globally with spatially and temporally extensive surveillance of moth populations. In addition to multi-decadal analyses showing significant decreases in moth abundance in the standardized nightly sampling of the Rothamsted Insect Survey (17, 18, 31, 32), long-term distribution change of GB moths has also been assessed from nonsystematic observations made by citizen scientists.

An assessment of GB distribution records for 673 moth species for 1970–2010 found that 39% of species had decreased

Fig. 1. Summary of species-occupancy trends (log(trend + 100)) measured as the percentage change in modeled occupancy of 1-km × 1-km squares derived from citizen-science occurrence data for GB moth species for 1970–2016 (390 species) and 2000–2016 (559 species) (33), indicating the percentage of species belonging to each of four trend categories. The dashed horizontal line represents zero change; green points indicate species with positive trends and blue those with negative trends. Statistically significant changes (sig.) were assigned based on an alpha = 0.05. Recording intensity was lower in the early decades, so fewer species have sufficient data to enable the production of robust trends in the long-term assessment. Note that percent values do not necessarily sum to 100 due to rounding.

significantly in frequency of occurrence compared with 24% of species that had significant positive trends (26). Northerly distributed species decreased on average, consistent with a negative response to climate change, but widespread species decreased overall only in the southern half of GB, as had been found for moth abundance (17), suggesting that land-use change and urbanization may be driving these trends (26).

However, more recent studies (e.g., refs. 33 and 34) of the GB moth distribution data utilized in Fox et al. (26), using longer time periods and different analysis methods, show more mixed results—again revealing the complexity and heterogeneity in evidence of moth biodiversity change. Using 24 million moth-occurrence records, an occupancy-modeling approach generated robust longer-term (1970–2016) and short-term (2000–2016) trends in fine-scale (1 km × 1 km) spatial distribution for 390 and 559 species, respectively (33). The results (Fig. 1) show similar proportions of winners and losers, rather than a clear picture of overwhelming decline. Since 1970, for example, 121 species (31%) had decreased significantly, while 148 (38%) had increased significantly. Species that have increased in distribution are ecologically and taxonomically diverse and include long-term resident species as well as recent colonists (35).

Another assessment of the same GB moth data, using a Bayesian occupancy-modeling approach, recorded an overall increase (of 8.7%) in mean occupancy by moths (714 species) over the period 1970–2015 (34). The apparent decoupling of abundance and distribution trends in GB moths demonstrates the difficulty of assessing biodiversity change and its implications for ecological interactions, even where considerable data are available. The same pattern has also been reported for moths in Finland (24), where significant increases in species richness in a 20-y study, likely caused by climate-driven poleward range expansions, contrasted with simultaneous abundance decreases.

Caterpillar Abundance in Arizona, Ecuador, and Costa Rica.
We also examined a subset of sites from a long-term rearing program focused on cataloging caterpillar–parasitoid interaction diversity across the Americas (36). Annual trends in caterpillar abundances (from plot-based collecting) across an elevational gradient (1,200 to 2,800 m above sea level [a.s.l.]) in Arizona from 2004 to 2019 showed subtle to no declines for annual monthly means of abundances (Fig. 2A) (refer to *SI Appendix* for methods) and reflect the great temporal variation that is common to desert ecosystems. Although there were no strong trends over this 16-y period, some superfamilies were slightly increasing (e.g., Gelechioidea), while others were slightly decreasing (e.g., Zygaenoidea and Papilionoidea).

Similarly, for one well-sampled site in an Ecuadorian cloud forest (2000 m a.s.l.), there were no overall trends in caterpillar abundances from 2001 to 2019; again, there were subtle increases for a few superfamilies (e.g., Choreutoidea) and modest decreases for others (e.g., Zygaenoidea) (Fig. 2C). In contrast, caterpillar abundances in Costa Rica were characterized by substantive declines across all superfamilies and for two distinct sampling methods (Fig. 2C), with a 99% probability of decline for all families. Results from these three studies again highlight the spatially and taxonomically heterogeneous nature of moth declines. Differences in larval densities or abundance are similar for the two methodological approaches (Fig. 2), which is also true when patterns of abundance are corrected for sampling effort (*SI Appendix*, Fig. S2).
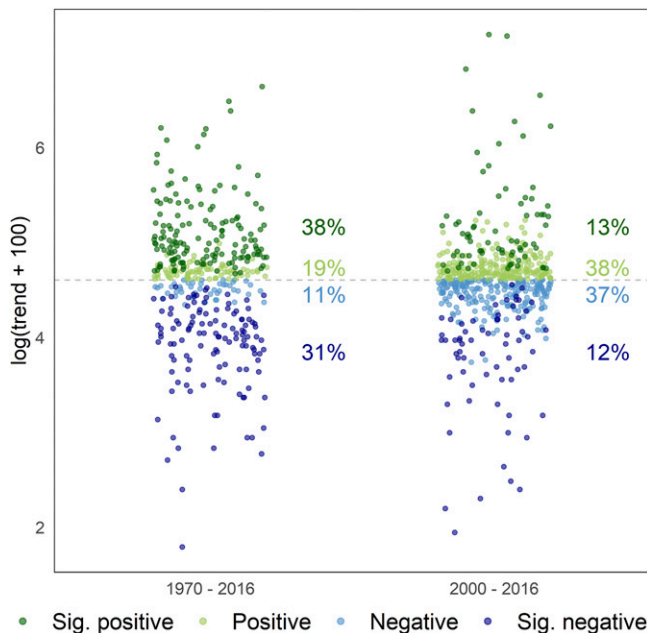
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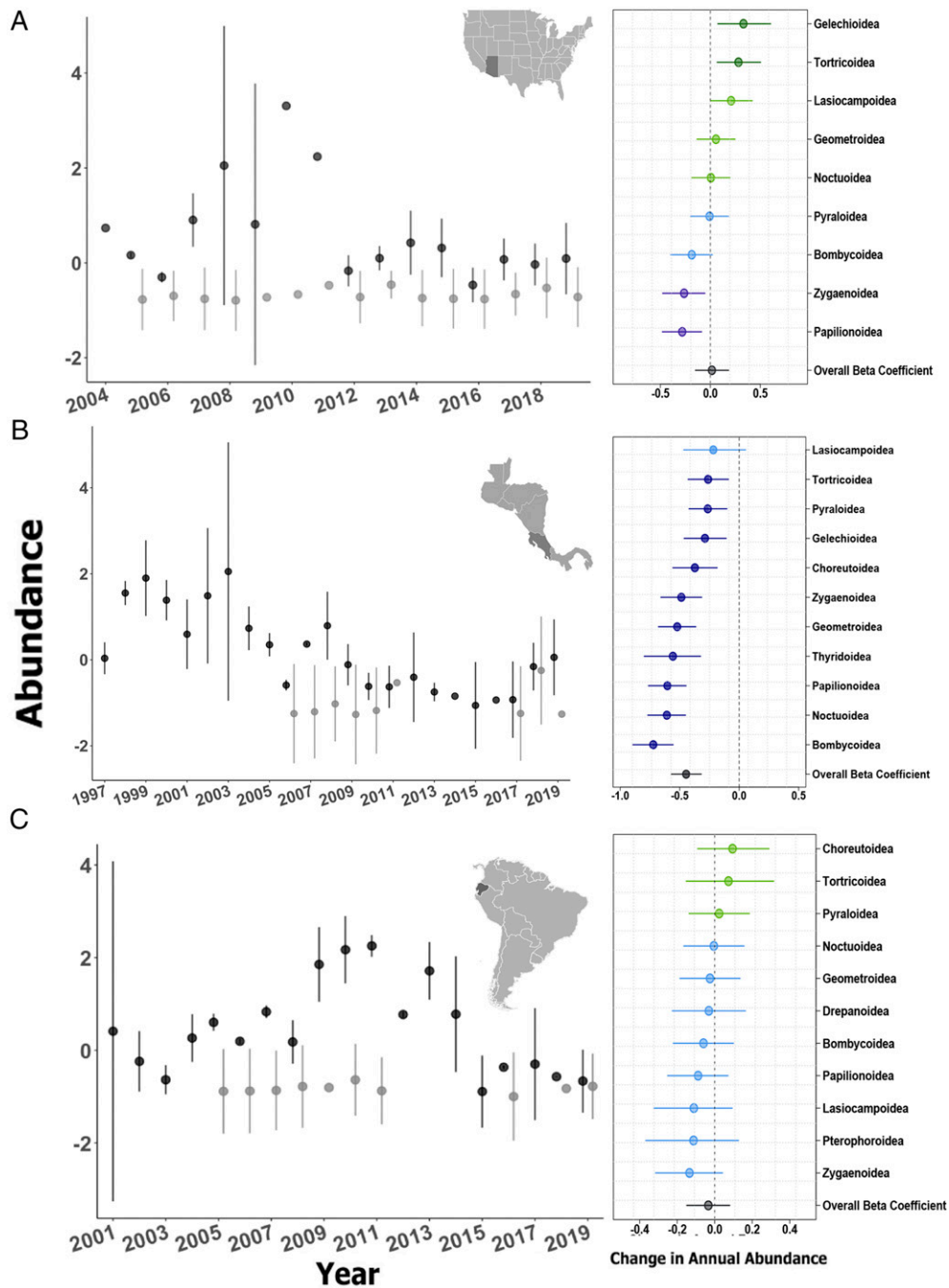
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Fig. 2. Trends for yearly caterpillar abundances for three New World sites: Arizona (*A*), Costa Rica (*B*), and Ecuador (*C*) (see *SI Appendix* for details). For all sites, externally feeding caterpillars and their insect parasitoids were collected via opportunistic and standardized plot-level methods and reared. Plots in *Left* show annual means and SEs of monthly abundance estimates (opportunistic collection: dark gray) and densities (standardized plot level: light gray). Plots in *Right* illustrate trends over time for each superfamily, measured as annual changes in abundances, summarized as β coefficients with 80% credible intervals estimated from hierarchical Bayesian linear regressions. Year coefficients (and intercepts) were estimated for each superfamily separately (as the lower level in the hierarchy) and simultaneously across all superfamilies ("overall beta coefficient"). Response variables were modeled as normal distributions with uninformative priors. As a complementary measure of confidence, we calculated the fraction of the posterior distribution less or greater than zero and colored accordingly. Colors can be interpreted as the probability that a superfamily has been observed decreasing (blue) or increasing (green) in frequency, where darker hues indicate superfamilies with over 95% of the distribution either above (dark green) or below (dark blue) zero. The estimate at the highest level of the hierarchy for which all superfamilies are nested is indicated by black and denoted as the overall beta coefficient. Abundance trends for different superfamilies varied the most for the Arizona site, with some superfamilies slightly increasing and others slightly decreasing. Using Bayesian hierarchical linear models, we estimated superfamily abundances across years and provide evidence for no change in abundances and densities of moth caterpillars (Arizona), overall decreases (Costa Rica), and slight decreases (Ecuador). Results are similar when correcting for sampling effort and examining abundances or densities per person-days (*SI Appendix*, Fig. S2). Expanded methodology and all β estimates are provided in *SI Appendix*.

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Stressors

One of the more salient aspects of reported insect declines is that multiple drivers are implicated. Drivers may interact additively, synergistically, or antagonistically and operate at different locations and over different time periods (12, 23). The principal causes of moth declines include many of the factors associated with biodiversity losses across the tree of life: habitat destruction and degradation, agricultural intensification, climate change, urbanization, pollution, and introduced species (31, 37). Below, we briefly summarize evidence for principal stressors in relation to population-level and diversity losses of moths.

Land-use changes comprise the primary drivers of historical declines in European butterflies dating to the 1800s and 1900s (14). Land-use change includes many stressors known to affect biodiversity: deforestation, agricultural intensification, commercial forestry practices, and urbanization. In this broad sense, land-use change surely has the greatest impact on the status of moths in Europe (23, 31, 38, 39) and on insects and other wildlife globally.

Faunal turnover associated with farmland abandonment and forest succession is an underappreciated factor affecting moth diversity. Much of Europe has been an agrarian and pastoral landscape for centuries, but since World War II, traditional farms have been converted to larger-scale, high-input, high-yield agriculture or abandoned and let go to reforest. Afforestation can result in sweeping faunal changes (40–42), as open, early successional habitats give way to closed-canopy forests—while both moth abundance and richness typically increase as a result, early seral taxa, which often include many threatened species in forested regions, can disappear over the course of a single decade or two.

Climate change is exerting substantial effects on biodiversity globally, including Lepidoptera (e.g., refs. 43 and 44). It has been linked to increasing rates of poleward expansion of macrolepidopterans in GB (45), some examples of range contractions (e.g., ref. 46), and overall declines in macromoth abundance (47). The impacts of extreme climatic events are increasingly considered important in driving changes in moth faunas. These include severe drought (48, 49) and the resultant increased frequency of wildfires (50), winter warmth (51), and flooding events (29). Years with extreme climatic conditions are associated with major population changes among moths (52) and may play a role in determining long-term trends in moth abundance and biomass (20, 21). The effects of increased climate variability, even in the absence of extreme events, is expected to impact many taxa.

Nitrification due to fertilizer use and combustion of fossil fuels, with the latter being especially problematic because of its ubiquity, is increasingly identified as an important driver of macrolepidopteran community changes (23, 26, 53, 54). Nitrogen input triggers complex changes to plant communities, including shifts in plant assemblages (55) that may lead to losses of specialized herbivores that are dependent on plants adapted to nutrient-limited soils (53). Enhanced plant growth, resulting from elevated levels of nitrogen, can be disadvantageous to thermophilic taxa, by shading out bare ground areas needed for growth and development (56). As a result of nitrification, moth taxa associated with nutrient-poor (and especially nitrogen-limited) habitats—bogs, oligotropic grasslands, barrens, sandplains, and dunes—are expected to be disproportionately impacted.

Myriad other stressors, individually and collectively, have been linked to the decline of moths and other insects at both local and regional scales. Pesticides are directly and indirectly—via contamination of nectar sources and larval host plants—implicated in the declines of Lepidoptera and other insects in Europe (57). Systematic insecticides, especially imidacloprids and related neonicotinoids, are receiving increasing scrutiny, given their wide use, broad toxicity, mobility in ground and surface water, and capacity to persist in soils for months (58, 59). Several studies have implicated exotic plants and introduced biological control agents as threats to moths (60, 61). While it is thought that artificial light at night is contributing to moth declines (62), it is difficult to separate impacts of light pollution from the manifold impacts of urbanization. The proportion of moth declines due to other aspects of urbanization is difficult to estimate, but a number of studies have documented that urbanization has large negative effects on moth diversity and abundance (e.g., ref. 63) and favors thermophilic and generalist species (64). Other stressors mentioned here may be intensified in urban areas; thus, species that are already at risk are more likely to decline in urban areas (65).

Common Traits Among Moth Taxa that Are Declining

Trait-based assessments can reveal patterns in the heterogeneity of diversity trends and help make predictions of risk. The most frequently reported trait correlated with declining moth taxa is larval diet breadth (66–69). Many of the moths that are increasing in northwestern Europe are generalized taxa and migrants (26, 35); their gains can mask declines in specialized taxa if species-level data are not considered.

In two studies, body size (forewing length) was the single best predictor of declining populations (70, 71). Reports from the northeast United States also draw attention to the decline of larger moths (72, 73). Other traits shared by declining moths include univoltinism, short flight seasons, low dispersal ability, and overwintering in the egg stage (21, 67, 68, 70, 71, 74). Moths with canalized phenotypes are declining faster than those that are polytypic (69, 75).

Consequences to Food Webs and Ecosystem Function

Moths are significant components of food webs in all terrestrial ecosystems, contributing substantially to network complexity, interaction diversity, and associated ecosystem stability (76). While adults are important as pollinators (7, 77), the best-resolved networks focus on trophic interactions, with moths providing a large proportion of the consumer nodes connected to plants, as well as the prey or host nodes connected to predators and parasitoids. Losses of moth species will deplete interaction diversity and catalyze further losses of species and interactions, contributing to ecological erosion (78) and reduced ecosystem functioning (29).

Population studies are the most effective means to understand how specific pollinators, herbivores, or prey items will impact associated organisms (79). They can also provide insight into how different species may be responding to stressors, be used to parameterize population models and extrapolate community responses, and guide experimental approaches to studying mechanistic hypotheses about declines. On the other hand, diversity metrics or network parameters are better suited for quantifying losses of ecosystem function and for understanding how food webs are changing.

At the largest scales—biogeographic regions—there is little doubt that moth diversity has decreased, but the details and consequences of those declines are best studied at smaller scales (80) that are sensitive to the idiosyncrasies of different ecosystems and assemblages. For example, plant–caterpillar–enemy webs or plant–pollinator webs in many tropical ecosystems are likely to be more specialized than those in temperate ecosystems (3), so

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declines of moths from these webs will have greater impacts on interaction diversity and ecosystem function (76).

For generalized insectivores, the consequences of declining lepidopteran numbers might be evaluated from summary measurements of moth abundance or biomass, as opposed to assessing the population dynamics of any focal species or declines in interaction diversity. This could be the case for many vertebrates dependent on lepidopteran prey, including most bats and many insectivorous birds, such as caprimulgids, cuckoos, gnatcatchers, warblers, vireos, and kinglets. Even birds commonly considered to be granivores, such as finches and sparrows, switch to diets largely consisting of caterpillars and other soft-bodied arthropods over the breeding season. Virtually all temperate-zone forest bats are moth specialists, with scarab beetles being of secondary importance. One special case is that of the grizzly bear (*Ursa arctos horribilis*) population of Yellowstone National Park, where as much as one-third of the annual calorific requirement may derive from the consumption of a single moth species, i.e., aestivating adults of *Euxoa axilliaris* (81).

Reports of vertebrate insectivore declines are mixed with regard to severity and the likely causal factors (82), and there are few cases that convincingly attribute these declines to reductions in Lepidoptera populations. In a recent assessment of the declines in North American birds, insectivores as a group were not faring well, but there was no obvious signal of elevated decline rates for insect-feeding taxa, relative to other feeding guilds (83).

For specialized interactions, both population-level and community-level declines can be highly consequential. Declines or losses of an individual pollinator species might cause population declines or local extinctions of plants they pollinate, which affects other mutualists, parasites, and competitors of that plant (84). The fates of specialist invertebrate predators, parasitoids, and hyperparasitoids are tied to the population fluctuations of their hosts. Most insect parasitoids are often specialized to a single life stage or even instar of their host (85), which, no doubt, has contributed to their evolutionary radiation, estimated to be well over 400,000 species (6). Long-term decreases in both the absolute numbers and frequency of parasitism in macrolepidopteran caterpillars have been reported in Costa Rica, concomitant with moth-population declines (28, 29).

Concluding Remarks

Global reports of moth demographic trends include cases of increasing, apparently unaffected, and declining faunas. Long-term datasets from western, central, and northern European countries confirm that moth decline is widespread across the continent, but demographic data from outside of Europe are sparse. While our data for caterpillar abundances in Arizona, Costa Rica, and Ecuador contribute to an understanding of population and community dynamics of Lepidoptera outside of Europe, there remains an urgent need for more data to make robust conclusions about the scope and nature of global insect declines. Time-series demographic data are especially needed from the tropics, where the majority of insect-species diversity resides. Both within Europe and elsewhere, the details of moth-biodiversity change reveal great heterogeneity, even within single regions, a pattern that underscores the importance of local stressors. Where species-level data are available for reported declines, essentially all reports convey that some species and lineages are increasing, while a great many are declining, with stenopic, dietarily specialized, and larger species among the biggest losers.

Our understanding of global moth declines suggests that deforestation, agricultural intensification, and climate change, particularly with regard to extreme weather events, are the principal stressors driving long-term losses of moth diversity, with pesticide use, urbanization, invasive alien species, and others likely contributing to declines at more local scales. We see growing evidence that extreme climate events are driving some regional losses and regard droughts, upward shifts in cloudbanks, and other causes of water stress to be especially potent drivers of present and future insect (and plant) declines. Other effects of climate change, such the reduction of winter snow cover and increased fire risk, are also likely to be important. Wet and dry deposition of nitrogen represent a cumulative threat to moths with specialized associations with larval hostplants adapted to low-nutrient conditions. Given the complexity of results from well-studied faunas, such as those of GB, it seems likely that multiple stressors are acting synergistically in any given region, making it difficult to determine causality in cases of moth decline.

If the reported cases of moth-biodiversity change tell us anything, it is that we do not yet know enough. Current knowledge is insufficient to dissect the impacts of numerous potential drivers or to generalize trends across communities, countries, and biomes. Recognizing this point, however, should be a spur to action, rather than a cause of despair. Researchers should focus efforts on synthesizing historical data—where troves of long-term insect data currently exist in museum collections, pest-management and agricultural records, and ecological surveys cataloguing diet or host records. Gathering more high-quality data, especially from the tropics and Southern Hemisphere temperate zone, will be particularly important (9). Meanwhile, actions must be taken now, by individuals, land managers, and governments, to mitigate stressors and address moth-population declines (86–89) to safeguard nature's vast, essential, and wondrous insect biodiversity.

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