

Insect decline in the Anthropocene: Death by a thousand cuts

David L. Wagner^{a,1}, Eliza M. Grames^a, Matthew L. Forister^b, May R. Berenbaum^c, and David Stopak^d

Nature is under siege. In the last 10,000 y the human population has grown from 1 million to 7.8 billion. Much of Earth's arable lands are already in agriculture (1), millions of acres of tropical forest are cleared each year (2, 3), atmospheric CO₂ levels are at their highest concentrations in more than 3 million y (4), and climates are erratically and steadily changing from pole to pole, triggering unprecedented droughts, fires, and floods across continents. Indeed, most biologists agree that the world has entered its sixth mass extinction event, the first since the end of the Cretaceous Period 66 million y ago, when more than 80% of all species, including the nonavian dinosaurs, perished.

Ongoing losses have been clearly demonstrated for better-studied groups of organisms. Terrestrial vertebrate population sizes and ranges have contracted by one-third, and many mammals have experienced range declines of at least 80% over the last century (5). A 2019 assessment suggests that half of all amphibians are imperiled (2.5% of which have recently gone extinct) (6). Bird numbers across North America have fallen by 2.9 billion since 1970 (7). Prospects for the world's coral reefs, beyond the middle of this century, could scarcely be more dire (8). A 2020 United Nations report estimated that more than a million species are in danger of extinction over the next few decades (9), but also see the more bridled assessments in refs. 10 and 11.

Although a flurry of reports has drawn attention to declines in insect abundance, biomass, species richness, and range sizes (e.g., refs. 12–18; for reviews see refs. 19 and 20), whether the rates of declines for insects are on par with or exceed those for other groups remains unknown. There are still too little data to know how the steep insect declines reported for western Europe and California's Central Valley—areas of high human density and activity—compare to population trends in sparsely populated regions and wildlands. Long-term species-level demographic data are meager from the tropics, where considerably more than half of the world's insect species occur (21, 22). To consider the state of knowledge about the global

status of insects, the Entomological Society of America hosted a symposium at their Annual Meeting in St. Louis, Missouri, in November 2019. The Society was motivated to do so by the many inquiries about the validity of claims of rapid insect decline that had been received in the months preceding the annual meeting and by the many discussions taking place among members. The entomological community was in need of a thorough review and the annual meeting provided a timely opportunity for sharing information.

The goal of the symposium was to assemble world experts on insect biodiversity and conservation and ask them to report on the state of knowledge of insect population trends. Speakers were asked to identify major data gaps, call attention to limitations of existing data, and evaluate principal stressors underlying declines, with one goal being to catalyze activities aimed at mitigating well-substantiated declines. All 11 talks were recorded and are available on the Entomological Society of America's website, <https://www.entsoc.org/insect-decline-anthropocene>. Although this special PNAS volume is anchored to the St. Louis presentations, that effort is extended here to include new data, ideas, expanded literature reviews, and many additional coauthors.

What's in This Special Issue?

The 11 papers in this collection examine insect decline from geographic, ecological, sociological, and taxonomic perspectives; evaluate principal threats; delve into how the general public perceives news of insect declines; and offer opinions on actions that can be taken to protect insects. Insect declines have been the focus of a range of popular media, with widely varying levels of accuracy. Consequently, a core intention of this special issue is to provide a scientifically grounded assessment of insect population trends; contributors were urged to provide critical evaluations of raw data, published studies, and reviews, given that a few of the more highly publicized reports of insect decline suffered from unjustified assumptions, analytic issues, or

^aEcology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269; ^bDepartment of Biology, Program in Ecology, Evolution and Conservation Biology, University of Nevada, Reno, NV 89557; ^cDepartment of Entomology, University of Illinois at Urbana–Champaign, Champaign, IL 61801; and ^dNational Academy of Sciences, Washington, DC 20002

Author contributions: D.L.W., E.M.G., M.L.F., M.R.B., and D.S. wrote the paper.

The authors declare no competing interest.

Published under the [PNAS license](#).

¹To whom correspondence may be addressed. Email: david.wagner@uconn.edu.

Published January 11, 2021.

overextrapolation. For example, Willig et al. (23) and Schowalter et al. (24) provide data that insect numbers have not generally declined in Puerto Rico's Luquillo Experimental Forest, directly contradicting Lister and García's (25) claims of catastrophic collapse of the insect fauna, with linked effects to the forest's amphibian, reptile, and bird fauna. Hallmann et al. (26) model relationships among insect biomass, abundance, and diversity of hover flies, and explore how these measures interrelate in empirical and theoretical contexts. Many of the 11 contributions end with prospective elements that draw attention to data gaps, make methodological recommendations, and point to specific actions that may help insect populations and species survive (27–29).

Loss of Abundant Species. Although conservation efforts have historically focused attention on protecting rare, charismatic, and endangered species, the “insect apocalypse” presents a different challenge. In addition to the loss of rare taxa, many reports mention sweeping declines of formerly abundant insects [e.g., Warren et al. (29)], raising concerns about ecosystem function.

Insects comprise much of the animal biomass linking primary producers and consumers, as well as higher-level consumers in freshwater and terrestrial food webs. Situated at the nexus of many trophic links, many numerically abundant insects provide ecosystem services upon which humans depend: the pollination of fruits, vegetables, and nuts; the biological control of weeds, agricultural pests, disease vectors, and other organisms that compete with humans or threaten their quality of life; and the macrodecomposition of leaves and wood and removal of dung and carrion, which contribute to nutrient cycling, soil formation, and water purification. Clearly, severe insect declines can potentially have global ecological and economic consequences.

While there is much variation—across time, space, and taxonomic lineage—reported rates of annual decline in abundance frequently fall around 1 to 2% (e.g., refs. 12, 13, 17, 18, 30, and 31). Because these rates, based on abundance, are likely reflective of those for insect biomass [see Hallmann et al. (26)], there is ample cause for concern (i.e., that some terrestrial regions are experiencing faunal subtractions of 10% or more of their insects per decade). To what extent such declines translate into shifts or losses of ecosystem function has yet to be assessed.

Not all insects are declining. Four papers in this special issue note instances of insect lineages that have not changed or have increased in abundance (24, 29, 32, 33). Many moth species in Great Britain have demonstrably expanded in range or population size (34–36). Numerous temperate insects, presumably limited by winter temperatures, have increased in abundance and range, in response to warmer global temperatures (29, 32, 35; but see ref. 37). Anthropophilic and human-assisted taxa, which include many pollinators, such as the western honey bee (*Apis mellifera*) in North America, may well thrive due to their associations with humans. Increasing abundances of freshwater insects have been attributed to clean water legislation, in both Europe and North America (17, 18). In some places, native herbivores have flourished by utilizing nonnative plants as adult nectar sources or larval foodplants (38), and there are even instances where introduced plants have rescued imperiled species (39).

The Stressors. Abundant evidence demonstrates that the principal stressors—land-use change (especially deforestation), climate change, agriculture, introduced species, nitrification, and pollution—underlying insect declines are those also affecting other organisms. Locally and regionally, insects are challenged by

additional stressors, such as insecticides, herbicides, urbanization, and light pollution. In areas of high human activity, where insect declines are most conspicuous, multiple stressors occur simultaneously. Considerable uncertainty remains about the relative importance of these stressors, their interactions, and the temporal and spatial variations in their intensity. Hallmann et al. (13), in their review of the dramatic losses of flying insects from the Krefeld region, noted that no simple cause had emerged and that “weather, land use, and [changed] habitat characteristics cannot explain this overall decline...” When asked about his group's early findings of downward population trends in insects (12), Dirzo summed up his thinking by stating that the falling numbers were likely due to a “multiplicity of factors, most likely with habitat destruction, deforestation, fragmentation, urbanization, and agricultural conversion being among the leading factors” (40). His assessment seems to capture the essence of the problem: Insects are suffering from “death by a thousand cuts” (Fig. 1). Taking the domesticated honey bee as an example, its declines in the United States have been linked to (introduced) mites, viral infections, microsporidian parasites, poisoning by neonicotinoid and other pesticides, habitat loss, overuse of artificial foods to maintain hives, and inbreeding; and yet, after 14+ y of research it is still unclear which of these, a combination thereof, or as yet unidentified factors are most detrimental to bee health.

More than half of the contributions in this collection directly or indirectly advance knowledge of particular stressors. Climate change, habitat loss and degradation (especially of tropical forests), and agriculture emerged as the three most important stressors considered by our authors, with the first of these receiving the greatest attention in the symposium. Halsch et al. (41) review studies implicating climate effects as drivers of insect population changes and discuss the complexities of responses of species to climatic stress in montane habitats. Janzen and Hallwachs (27) point to a warming and increasingly erratic climate as the most probable stressor underlying the region-wide losses of moths and other insects that they are monitoring across a large and multiccosystem area of northwestern Costa Rica. Høye et al. (32) assess faunal changes in Greenland, far removed from direct human impacts, and report only a modest signal of climate impacts to the arthropod fauna there, with many lineages increasing in abundance. Schowalter et al. (24) present new data suggesting that insect responses to temperatures within Puerto Rico's Luquillo Experimental Forest, a hurricane-mediated ecosystem, are driven principally by frequent storms and poststorm successional history rather than by global climate warming. Three contributions from north temperate and Arctic locations point to range expansions or local population increases concomitant with warming temperatures (29, 32, 33), with the last of these noting examples of range extensions accompanied by declines in local abundance.

Many of the butterfly declines in Europe appear to be directly linked to changes in agricultural practices, with the rate of losses accelerating after World War II, when family farms began to amalgamate into larger commercial operations, modern tractors and mechanized equipment were employed to accelerate industrialization of agriculture, insecticides became widely available, and synthetic fertilizers could be manufactured and applied in prodigious volume (1, 16, 23, 42). Since the 1990s, the computerization of farming has dramatically changed the nature of agriculture (e.g., software-driven machinery can yield numerous efficiencies in planting, chemical applications, and harvest), further disadvantaging small-scale operations and practices. Much modern agriculture has become incompatible with nature, with its

Climate change is affecting ranges globally. Here ants are invading and consuming wildlife in cloud forest never before exposed to these marauders.

Global warming elevates fire risk. Fires in Australia, Amazonia, and California burned an unprecedented >5 million hectares of forest in 2019.

Arctic sea ice is declining precipitously, arctic-alpine and other cold-adapted communities are contracting, while sea-level rise threatens coastal ecosystems.

Climate changes bring stronger, more frequent storms and hurricanes; more fire-igniting lightening; and damaging flooding.

Periods with diminished precipitation are becoming longer, more frequent, and warmer, with grave consequences for all life.

Fertilizer and products of fossil fuels combustion are nitrifying the planet, challenging the biotas adapted to low-nutrient conditions.

Chemical, light, and sound pollution of water, air, and soil are impacting plant and animal life worldwide.

Our global population of 7.8 billion, spread planet-wide, comes at great cost to biodiversity and wildlands. Already, over 500 vertebrates have been driven to extinction.

Global trade is accelerating the movement of pernicious plants, animals, and pathogens to new regions—often with devastating consequences.

Industrialized agriculture, with its attendant increases in scale, monoculturalization, nutrient input, and pesticide use, is becoming increasingly nature unfriendly.

The tropics lost 11.9 million hectares of forest in 2019, mostly to agriculture.

Modern, industrialized agriculture, with its increasing reliance on chemical insecticides, has led to chronic contamination of wildlands and impacts to non-target insects.

effects in the tropics especially worrisome. There deforestation, principally for agricultural expansion, is progressing at alarming rates, with its effects on insects and other arthropods essentially unmeasured (1).

Wagner et al.
Insect decline in the Anthropocene: Death by a thousand cuts

(34, 42–44). Similarly, there is mounting evidence that light pollution is driving local declines in suburban and urban locations (45, 46). Although not an emphasis of the 11 articles, urbanization is increasingly recognized as an important stressor (47, 48).

Assessing Insect Population Trends is Difficult and the Details are Important. Essential time-series data on the rates, geographic scope, ecological aspects, and taxonomic nature of insect population trends are scant, relative to those for vertebrates. Most insect taxa are far more species-rich than vertebrate taxa; there are more than a million described species of insects and even the most modest estimates calculate that another 4.5 to 7 million remain unnamed (21, 22). Species-level taxonomy for many lineages is challenging and often effectively nonexistent, especially for tropical faunas (which represent the majority of insect diversity); identifying tiny species can involve microscopic study, genitalic dissection, and DNA analysis, requiring equipment and expertise far beyond that needed for the censusing of vertebrates or plants. As a consequence, essentially all historical datasets that could be used to study insect decline have been biased toward agriculturally important and showy, well-known, extratropical taxa with long histories of public interest. Even for butterflies, historical demographic data are limited, deriving primarily from a few historically wealthy countries with a relatively deep record of natural history study.

An especially challenging aspect of interpreting insect demographic data are their episodic generation-to-generation swings. Documenting a 1 to 2% rate of annual decline against a background of flux that may swing through two to three orders of magnitude in as many years often requires decades of census data, the collection of which can be labor-intensive and expensive. Additionally, because many insects are ecologically specialized and their home ranges minuscule, even small-scale spatial variation in environmental conditions (e.g., soil attributes or vegetation height) can add heterogeneity to census data (49, 50).

One way that researchers have dealt with the complexity of population-level stochasticity in insects is to aggregate data at higher taxonomic levels: For example, using total insect biomass as a proxy for biodiversity, or aggregating data across different sites. Studies that generalize across datasets, higher taxonomic categories, or ecological groups (e.g., refs. 17, 18, 51, and 52) provide much-needed perspectives relevant to ecological function as, for example, the amount of insect food available to nestlings (53) and other insectivores or the general health of a region's pollinators. Although data aggregation and meta-analyses are required approaches for understanding global phenomena, by their nature, they often overlook species-level trends.

To make predictions about what lineages will be most threatened and to inform policymaking and other conservation actions, it is essential to pay attention to the details and assumptions that underlie aggregated, multitaxon, and multiregion analyses. Much resolution is lost when data for insects with different demographic features or ecological needs are combined, such as, for example, when counts for crop-infesting aphids are analyzed with those for rare, habitat-restricted tiger beetles. Insect biomass is not interchangeable across food webs or among major taxa any more than hummingbirds and jaguars can be summed: An abundance of leafhoppers would be of little value to a nesting pair of warblers, relative to an abundance of caterpillars. Much can be learned by disambiguating the demographic data harvested from cities and intensively managed croplands from those derived from fragile communities: For example, cloud forests, rain forests, Arctic-

alpine systems, low-nutrient communities, island biotas, and others (Fig. 2). A common finding across many reports of insect decline is that the rates of decline for ecological specialists are much steeper than those for more generalized taxa (e.g., refs. 29, 33, 42, 54, and 55). Based on first principles, taxa representing higher trophic levels (e.g., insect parasitoids, and in turn their parasites) would be expected to be suffering some of the highest rates of decline, a matter where data are especially scant (but see refs. 27 and 56). Studies of divergent taxa or heterogeneous locations need to employ appropriate hierarchical analyses and exercise caution in accepting hypotheses of change or stasis, especially when statistical power is low.

History of Insect Decline Reports

An early high-profile data-driven study garnering global attention for the status of butterflies in Europe was the 2004 report by Thomas et al. in *Science* (57), which documented that the rate of butterfly decline in Great Britain was comparable with or exceeded those known for birds and plants. Colony collapse disorder and the honey bee's struggles with the ectoparasitic varroa mite and viral infections were among the first cases to draw global attention to insect decline. In 2007, the National Research Council of the National Academy of Sciences (58) released a high-profile report on the status of pollinators in North America, warning of long-term downward population trends in commercial honey bees that brought attention to the plights of several bumble bees, the monarch butterfly, and other pollinators, especially in Europe, that appeared to be in decline [see Althaus et al. (59)].

Dirzo et al.'s (12) "Defaunation in the Anthropocene" was the first metaanalysis to report global cross-lineage insect losses for beetles, dragonflies, grasshoppers, and butterflies. Across 16 studies, insect populations had declined by 45% in the last four decades. In spring 2017, Vogel (60) published early findings from Germany's Krefeld Entomological Society (Entomologischer Verein Krefeld), documenting steep, unexplained reductions of flying insects, across more than 60 sites in northwest Germany (all within preserves). Later that year, the first peer-reviewed report in English from the Krefeld data appeared (13): Flying insect biomass had dropped by 76% in 27 y, a finding that made global headlines.

In publishing her article, "The Insect Apocalypse is Here," in the *New York Times* in December 2018, science writer Brooke Jarvis brought much public attention to insect declines (61), inspiring national media attention in newspapers, journals, and radio programming. Another wave of media attention accompanied Sánchez-Bayo and Wyckhuys (19), a review of global insect declines with the claim that 40% of insect species might be at risk for extinction in coming decades, an assertion that was met by no fewer than six rebuttals and multiple blog posts detailing shortcomings of their review and conclusions. The past 2 y have seen a sea change in the number of peer-reviewed studies focused on insect population trends [see Althaus et al. (59)]: Most of these paint a far more complex and heterogeneous picture of the global status of insects than some of the initial reports.

In 2020, three large metaanalyses appeared, two of which focused on insects. The first, van Klink et al. (17, 18), examined 166 studies with demographic data spanning 9 to 80 y. Their assessment, driven largely by European and North American datasets, suggested terrestrial insects were declining at a rate close to 1% per year, while aquatic insects appeared to be increasing in abundance, again by about 1% per year. Pilotto et al. (52) analyzed the abundance, richness, diversity, and faunal turnover for 161 long-term biological time series (15 to 91 y) for more than 6,000

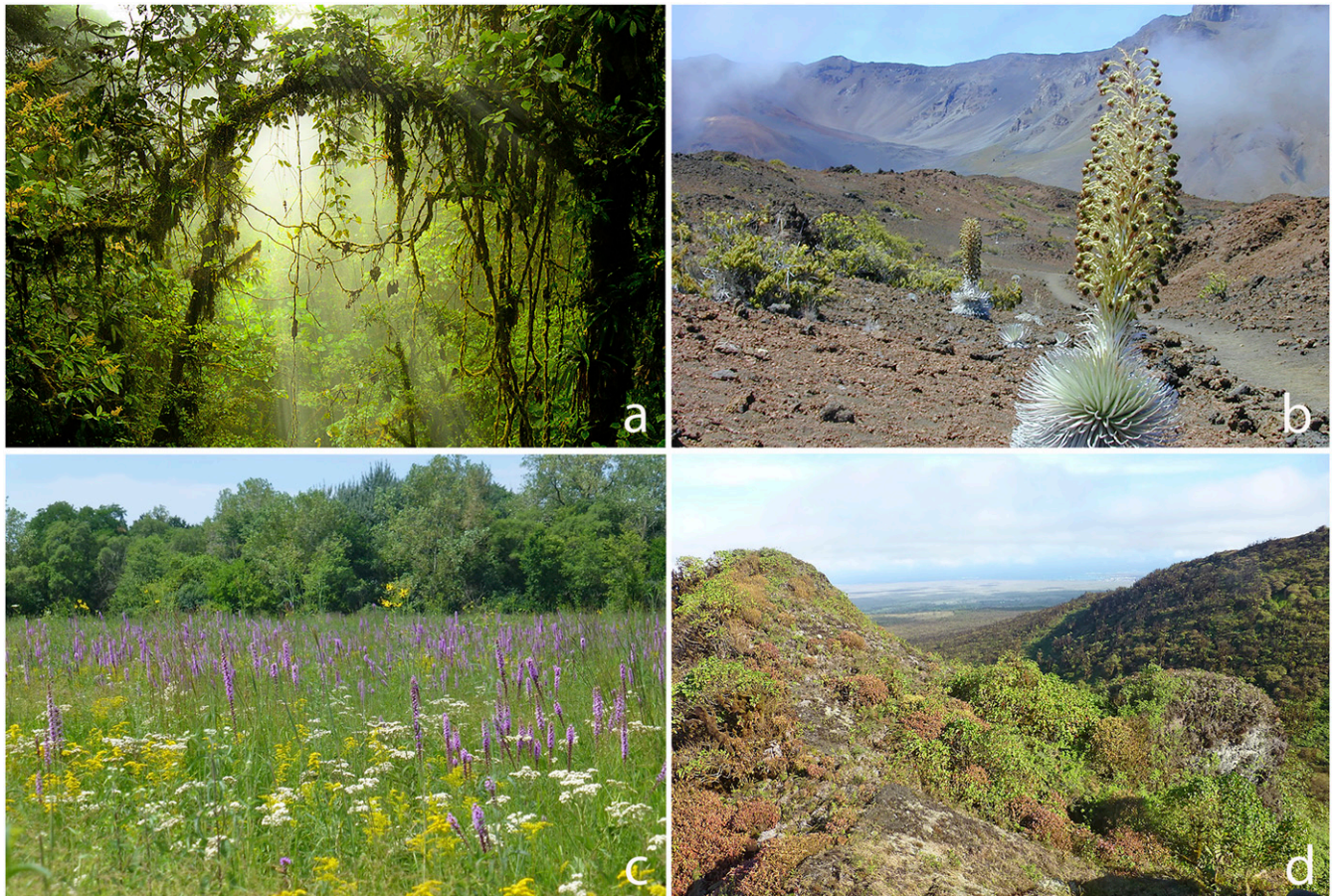


Fig. 2. Fragile communities challenged by global change. (A) Cloud forest, Monteverde, Costa Rica: Threatened by rising global temperatures that lead to greater numbers of cloud-free days and extended droughts. Image credit: Janet Ellis (photographer). (B) Silversword (*Argyroxiphium sandwicense* subsp. *macrocephalum*) grove, Haleakala National Park, Hawaii: Threatened by diminished water availability and related climate changes. Image credit: Flickr/Forest and Kim Starr, licensed under [CC BY 3.0](https://creativecommons.org/licenses/by/3.0/). (C) Tallgrass prairie, Markham, Illinois: Threatened by agriculture and insularization. Image credit: Abbie Schrottenboer (Trinity Christian College, Palos Heights, IL). (D) Community composed of endemic *Miconia robinsoniana* (sienna-colored shrubs), ferns, and sedges, Santa Cruz Island, Galápagos Islands, Ecuador: Threatened by many exotic plants; the yellow-green shrub is red quinine tree (*Cinchona pubescens*), an invasive on many Pacific islands. Image credit: Heinke Jäger (Charles Darwin Foundation, Galápagos, Ecuador).

European marine, freshwater, and terrestrial animal and plant taxa; 53 of their datasets were for insects. They found that freshwater insects had increased in diversity (but not abundance). In contrast, abundances of European terrestrial insects showed the strongest signal of decline across the taxa included in the study. Crossley et al.'s (51) metaanalysis of insect demographic data (spanning 4 to 36 y) for 15 long-term ecological research sites across the United States, reported no evidence of a continent-wide decline of insect abundance. The entomological community is still evaluating the accuracy of these recent findings [see Welti et al. (62) and *Assessing Insect Population Trends Is Difficult and the Details are Important*, above].

An important limitation of assessments based on long-term monitoring data are that they come from locations that have remained largely intact for the duration of the study and do not directly reflect population losses caused by the degradation or elimination of a specific monitoring site (although effects can be measured in a metapopulation context if the number of years sampled is sufficient in remaining sites). For example, butterfly censusing sites that have been lost to agriculture, urban development, or exotic plant invasions would not meet inclusion criteria

for a study aimed at calculating long-term rates of decline. Surely, the greatest threat of the Anthropocene is exactly this: the incremental loss of populations due to human activities. Such subtractions commonly go uncounted in multidecadal studies (5).

Where Are We Now? Although mainstream media in the United States has paid little attention to the plight of pollinators (59), some policymakers at the federal level have taken note and made millions of dollars available for pollinator research and habitat improvement (63, 64) since the National Research Council's (58) status report on pollinators, and the 2014 petition to list the monarch butterfly as a threatened species (65). The Agriculture Improvement Act of 2018 (66) is annually providing many millions of dollars for pollinator research and conservation across the United States.

Funding to support insect conservation research is growing. In June 2018, the European Union endorsed an initiative to protect pollinators across member states (67). Germany's federal government pledged \$118,500,000 for insect conservation, monitoring, and research in September 2019 (68). The Swedish government plans to spend \$25 million on pollinator protection

initiatives over the next 3 y (69). In the spring of 2020, the government of Costa Rica endorsed a \$100 million-effort to inventory and sequence the DNA barcode region of every multicellular creature in the country over a decade, with funding to come from international sources. Much of the country's biodiversity will be insects, with most of these to be captured by Malaise traps, as part of Costa Rica's BioAlfa initiative (27).

The European Union and several other countries have passed legislation to restrict use of some pesticides. Several neonicotinoids, insecticides that are commonly applied to seed coats and then taken up by the growing tissues, have been banned from use on field crops because even a treated plant's nectar and pollen can be toxic to nontarget insects that visit its flowers (70, 71). In January 2020, the Environmental Protection Agency released an interim decision on the use of neonicotinoids in the United States aimed at protecting pollinators (72). Another downside to the neonicotinoid class of systemic insecticides is their environmental persistence: Their half-lives can be up to 1,000 d in soils and more than a year in woody plants, and their water-solubility allows the pesticide to move into and accumulate in soil and lakes, creeks, and other water bodies (73).

Although recent positive actions have been taken by governments in Costa Rica, the European Union, Germany, Sweden, and the United States, changes in national leadership can easily reverse environmental initiatives. Under the Trump administration in the United States, multiple federal policy changes were made that are inimical to conserving biodiversity: mention of climate change was pulled from government websites; an Executive Order reduced the size of Grand Staircase-Escalante National Monument in Utah by a half-million acres; and the administration finalized plans to permit oil drilling in the Arctic National Wildlife Refuge.

The Xerces Society, the largest global group in the United States promoting insect conservation, has enjoyed considerable growth over the past two decades: from a staff of 4 in 2000 to 54 full-time employees in 2020. Their major priorities, while still rooted to the protection of rare and endangered species and fostering a greater appreciation for insects and other invertebrates, now include focused efforts to protect pollinators, make agriculture more diversity-friendly, reduce pesticide use and impacts, and take a more active role in developing policy for the protection of invertebrates. Their current mailings reach about 100,000 individuals, partners, and policymakers across the globe.

There are growing numbers of community (citizen) science and education initiatives to survey, conserve, and raise awareness of insects and their importance as pollinators, prey, nutrient recyclers, and focal organisms in science and technology, as well as art, literature, and other aspects of culture (28). Monarch Watch has 55,000 Canadian, Mexican, and US followers, many of whom are educators. The United Kingdom's Big Butterfly Count enjoyed the participation of more than 111,600 community scientists in 2020 (74). Costa Rica's BioAlfa is a tropical version (27), focused on having the entire country be appreciative of the socioeconomic opportunities offered by wild biodiversity. Such actions could play important roles in changing public attitudes toward insects and motivate efforts to protect them.

Social media groups with a focus on insects are flourishing. Facebook groups dedicated to insects are propagating worldwide, parsed by taxon, geographic region, and even life stage. Husbandry and pet keeping anchored to insects and other arthropods have become popular. The Caterpillar Identification of North America Facebook group presently has more than 13,100 members. Page views on the United States' Moth Photographer

Group's website have gone from 1.8 million in 2010 to more than 14.7 million in 2019. iNaturalist, an online resource for taxonomical identification, currently boasts more than 13,600,000 insect posts since 2010, with verifiable records from almost every country in the world (Fig. 3).

Where from Here?

There remains an urgent need for time-series data so that temporal and spatial population trends can be assessed. Such data can be used to identify stressors, rates of insect population changes, and lineages and ecological guilds that are changing in abundance. As has been noted by others, there are considerable biases in the global distribution of insect demographic studies with the vast majority of long-term data coming from Europe and the United States, areas that collectively support less than 20% of global insect species diversity (21). Future emphasis must be placed on acquiring trend data from the tropical regions of the Americas, Africa, and Asia.

Over the past 2 y, there have been many calls for a step-change in governmental funding to expand insect-monitoring programs and conservation initiatives, especially across European countries. Monitoring efforts that span gradients of anthropogenic stressors will be especially informative. The task of monitoring insects globally will require careful planning (e.g., subsampling) and the adoption of new technologies and methods. Efforts are being made to standardize collection methods, establish data-collections norms, and improve data storage and accessibility (75, 76). Insect traps with automated counting capacities are under development, some of which employ image- or sound-recognition technology to provide species-level data [e.g., Høye et al. (77)]. At present, such automated monitoring can be used only for areas of modest insect diversity, where the insect fauna is relatively well known. For comprehensive species-level data from hyperdiverse biotas, molecular methods will need to be implemented: For example, by tying identifications to COI sequence data (barcodes) and the automated assignment of index codes (=Barcode Index Numbers, BINs, ~species) (78, 79; see also ref. 27).

While such newly initiated efforts will provide future data for making informed decisions, they may take a decade or longer before they yield data useful for identifying the most severe insect declines and the stressors (59). But we need to make many decisions and act now: It is particularly urgent to know to what degree

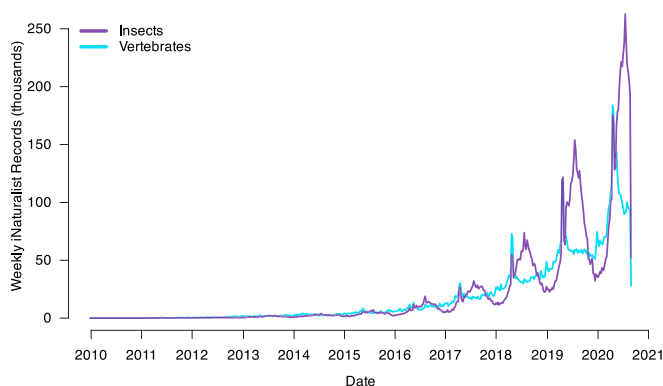


Fig. 3. iNaturalist popularity: Growth of insect (purple) and vertebrate (teal) records from iNaturalist from its inception in 2010 to present. Each record includes a photograph, occurrence data, and a wild observation. Data from Ken-ichi Ueda (iNaturalist).

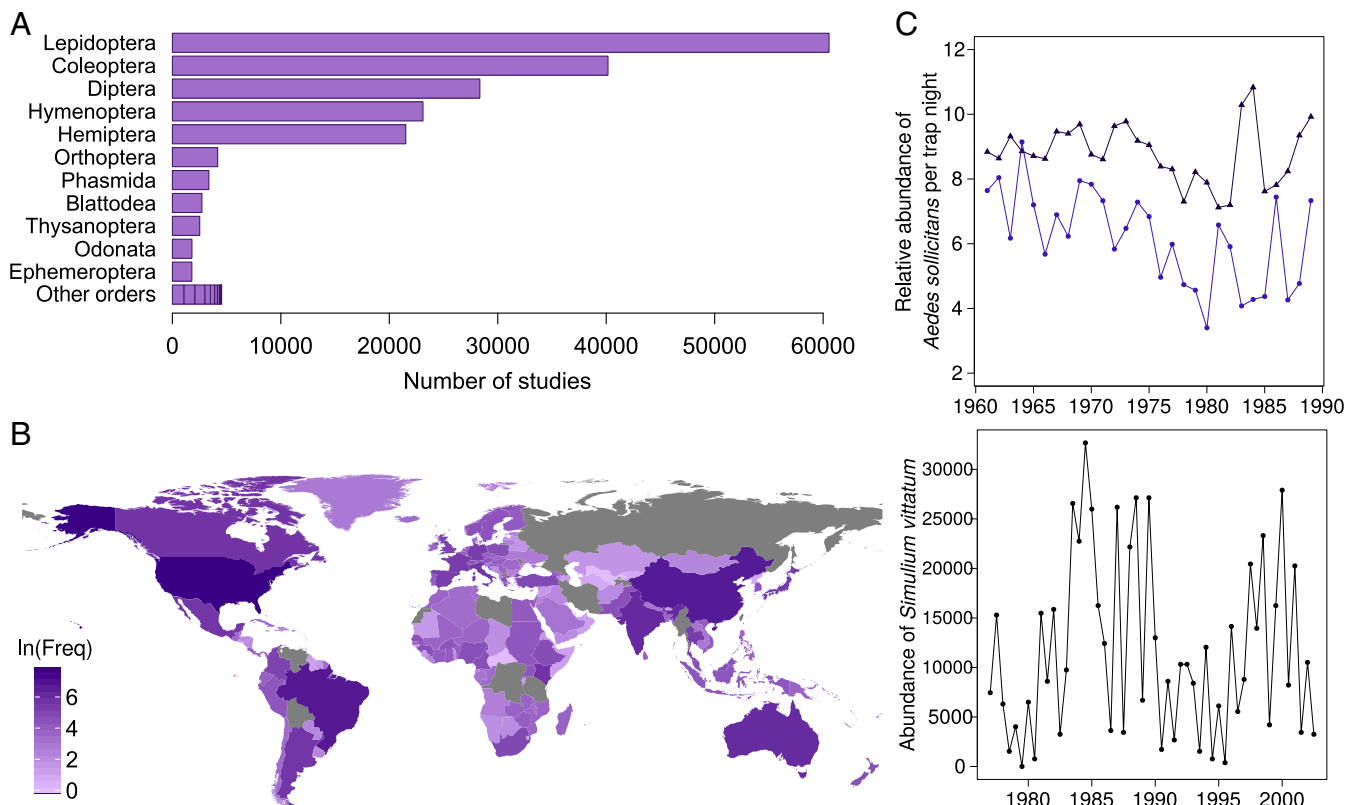


Fig. 4. Initial systematic search results from EntoGEM (<https://entogem.github.io/>): (A) Retrieved studies by order. (B) Locations of retrieved dipteran studies illustrating broad geographic scope, especially in tropical areas, which have been underrepresented in prior syntheses of insect decline. (C) Example dipteran data sets identified in initial screening. (Upper) Mosquitoes, trapped at two sites, Maryland, United States (83); (Lower) black flies, Iceland (53).

climate change is driving losses in the tropics, in mountains, and other wildlands away from pronounced anthropogenic activity.

Despite the urgent need for data to inform evidence-based plans for mitigating or reversing decline, there exist many datasets that remain unanalyzed (80). The United States Long-Term Ecological Research data recently assessed by Crossley et al. (51) is just one example of a publicly available dataset that had not been previously evaluated. At least two different research teams are currently working through the North American Butterfly Association's 4th of July butterfly count data, which include 497 sites with over 10 y of species-level demographic data. Other examples include the insects-as-food data of vertebrate biologists, annual survey data for medically important species, and many monitoring efforts in agricultural settings. Relatively little effort has been spent on assessing non-English literature, which may be rich in some Asian countries. EntoGEM (<https://entogem.github.io/>), a community-driven project to screen literature and other demographic data sources for insects, aims to retrieve and make available time-series data that could be used to document insect population trends (81). Already, EntoGEM and its aggregating software have identified more than a hundred 10+-y datasets that have not been referenced in any reviews, commentaries, or metaanalyses of insect decline (82) (Fig. 4).

The paucity of population trend data for insects, especially from the tropics and elsewhere in the Southern Hemisphere, is not for lack of want or methodology, but instead traces to small or nonexistent budgets, combined with the hyperdiversity, small size, and inchoate taxonomy of insects, which, together, make the processing and identification of most tropical insect species

impossible for all but the most familiar large-bodied lineages. Janzen et al. (84) recovered more than 14,520 "species" (=barcode haplotype clusters) of insects from a single Malaise trap in Costa Rica over 2 consecutive years, probably no more than 2 to 3% of which have been described by systematists. Armies of taxonomists would be needed to sort, name, and curate large trap catches from the tropics, and even larger numbers of lifetimes and resources to describe the world's tropical insect species. It is likely that many will be driven to extinction by anthropogenic stressors before they can be studied or, worse, their value realized.

In the future, many of the richest sources of occurrence data for insects will derive from community science efforts. If the growth of iNaturalist continues at its present rate, the amount of species-level occurrence data for visually identifiable insects may surpass that of any other single source. Already observational (~community science) data for insects in the Global Biodiversity Information Facility ($n > 76,613,000$ records) is twice that for specimen data ($n > 37,350,000$ records) (<https://www.gbif.org/>). Of particular value will be the community data deriving from methodologically standardized and annually repeated surveys such as the United Kingdom's Big Butterfly Count and North American Butterfly Association's 4th of July counts.

Even without much-needed monitoring and demographic data, enough is already known, based on first principles and records for amphibians, birds, flowering plants, mammals, reptiles, insects, and other taxa, to understand that a biodiversity crisis is accelerating as the planet's human population grows, increasingly exacerbated by unprecedented recent climate changes and other anthropogenic stressors. Time is not on our side, and urgent

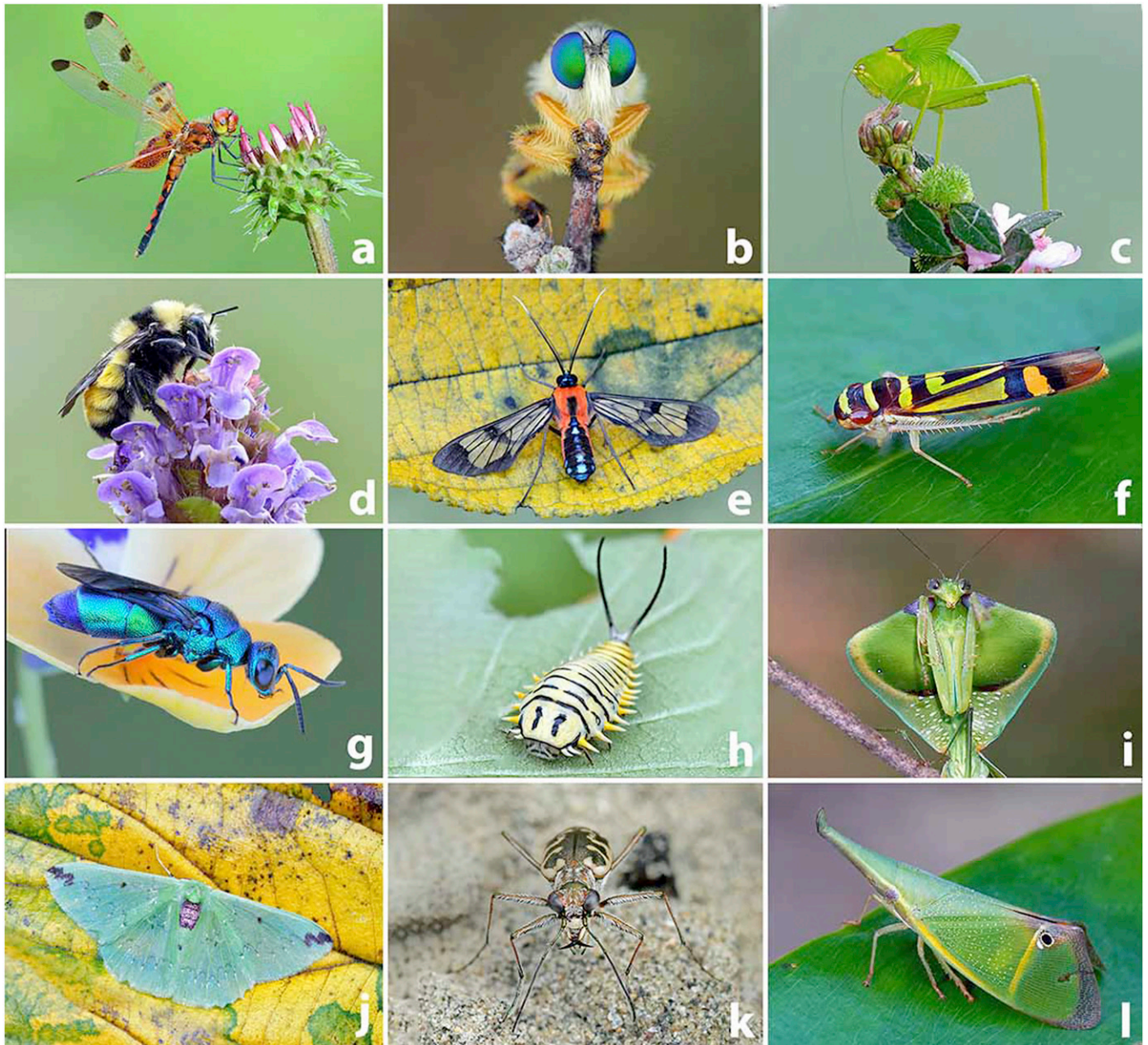


Fig. 5. Insect diversity. (A) Pennants (Libellulidae): Dragonflies are among the most familiar and popular insects, renowned for their appetite for mosquitoes. (B) Robber flies (Asilidae): These sit-and-wait predators often perch on twigs that allow them to ambush passing prey; accordingly they have enormous eyes. (C) Katydids (Tettigoniidae): This individual is one molt away from having wings long enough to fly (that also will be used to produce its mating song). (D) Bumble bees (Apidae): Important pollinators in temperate, montane, and subpolar regions especially of heaths (including blueberries and cranberries). (E) Wasp moths (Erebidae): Compelling mimics that are hyperdiverse in tropical forests; many are toxic and unpalatable to vertebrates. (F) Leafhoppers (Cicadellidae): A diverse family with 20,000 species, some of which are important plant pests; many communicate with each other by vibrating their messages through a shared substrate. (G) Cuckoo wasps (Chrysididae): Striking armored wasps that enter nests of other bees—virtually impermeable to stings—to lay their eggs in brood cells of a host bee. (H) Tortoise beetles (Chrysomelidae): Mostly tropical plant feeders; this larva is advertising its unpalatability with bold yellow, black, and cream colors. (I) Mantises (Mantidae): These voracious sit-and-wait predators have acute eyesight and rapid predatory strikes; prey are instantly impaled and held in place by the sharp foreleg spines. (J) Emerald moths (Geometridae): Diverse family of primarily forest insects; their caterpillars include the familiar inchworms. (K) Tiger beetles (Cicindelidae): “Tigers” use acute vision and long legs to run down their prey, which are dispatched with their huge jaws. (L) Planthoppers (Fulgoridae): Tropical family of splendid insects, whose snouts are curiously varied and, in a few lineages, account for half the body mass. Images credit: Michael Thomas (photographer).

action is needed on behalf of nature. Actions taken as individuals, groups, nations, and members of a global community are needed to address issues relating to insect diversity across multiple fronts (14, 85). Individuals can adopt behaviors that mitigate drivers of insect and biodiversity declines (28), vote for nature-friendly legislators and legislation, and promote local and global

environmental policies. Immediately and across all nations, people must find solutions to slow climate change (1, 41) and lessen the impacts of global agriculture, especially by slowing its expansion in the tropics (1, 29). Shared goals should be to change societal attitudes about insects, dispel misperceptions, and convey to others that insects are crucial components of functioning

ecosystems that also provide a diversity of cultural services, including aesthetic (Fig. 5), recreational, and health benefits. Scientists must educate a wider population about the ecological, economic, and scientific value of arthropods and find ways to integrate insects and other arthropods into the fabric of daily human life (27, 28).

Acknowledgments

The Entomological Society of America helped with the planning and supported the travel of international contributors. Virginia Wagner contributed the artwork

in Fig. 1; Kennedy Marshall assisted with graphic design and figure preparation. Mike Thomas supplied the images for Fig. 5. iNaturalist's creator and co-Director, Ken-ichi Ueda provided the data for Fig. 3. Steve Nanz shared data for Moth Photographer's Group website visitations; and Larry Gall provided the Global Biodiversity Information Facility metrics. Scott Black, David Cappaert, Richard Fox, Caspar Hallmann, Winnie Hallwachs, Dan Janzen, Akito Kawahara, Tanner Matson, Graham Montgomery, Peter Raven, Lawrence Reeves, Nick Rodenhouse, Tim Schowalter, Mike Thomas, Virginia Wagner, and Michael Willig made helpful suggestions on earlier drafts of this essay. This work was partially funded by an award from the Richard P. Garmany Foundation to D.L.W.

- 1 P. H. Raven, D. L. Wagner, Agricultural intensification and climate change are rapidly decreasing insect biodiversity. *Proc. Natl. Acad. Sci. U.S.A.*, 10.1073/pnas.2002548117 (2021).
- 2 P. G. Curtis, C. M. Slay, N. L. Harris, A. Tyukavina, M. C. Hansen, Classifying drivers of global forest loss. *Science* **361**, 1108–1111 (2018).
- 3 E. Stokstad, New global study reveals the 'staggering' loss of forests caused by industrial agriculture. *Science*, 10.1126/science.aav4177 (2018).
- 4 World Meteorological Organization, *WMO Statement on the State of the Global Climate in 2017*. WMO-No. 1212. (WMO, Geneva Switzerland, 2018).
- 5 G. Ceballos, P. R. Ehrlich, R. Dirzo, Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proc. Natl. Acad. Sci. U.S.A.* **114**, E6089–E6096 (2017).
- 6 P. González-Del-Piiego et al., Phylogenetic and trait-based prediction of extinction risk for data-deficient amphibians. *Curr. Biol.* **29**, 1557–1563.e3 (2019).
- 7 K. V. Rosenberg et al., Decline of the North American avifauna. *Science* **366**, 120–124 (2019).
- 8 IUCN, Issues Brief—Coral Reefs and Climate Change, (International Union for the Conservation of Nature, 2017).
- 9 United Nations Report, Nature's Dangerous Decline 'Unprecedented'; Species Extinction Rates 'Accelerating' (2019). <https://www.un.org/sustainabledevelopment/blog/2019/05/nature-decline-unprecedented-report/>. Accessed 15 November 2020.
- 10 G. N. Daskalova, I. H. Myers-Smith, J. L. Godlee, Rare and common vertebrates span a wide spectrum of population trends. *Nat. Commun.* **11**, 4394 (2020).
- 11 B. Leung et al., Clustered versus catastrophic global vertebrate declines. *Nature* **588**, 267–271 (2020).
- 12 R. Dirzo et al., Defaunation in the Anthropocene. *Science* **345**, 401–406 (2014).
- 13 C. A. Hallmann et al., More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One* **12**, e0185809 (2017).
- 14 M. L. Forister, E. M. Pelton, S. H. Black, Declines in insect abundance and diversity: We know enough to act now. *Conserv. Sci. Pract.* **1**, e80 (2019).
- 15 D. H. Janzen, W. Hallwachs, Perspective: Where might be many tropical insects? *Biol. Conserv.* **233**, 102–108 (2019).
- 16 S. Seibold et al., Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature* **574**, 671–674 (2019).
- 17 R. van Klink et al., Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science* **368**, 417–420 (2020a).
- 18 R. van Klink et al., Erratum for the report "Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances." *Science* **370**, eabf1915 (2020).
- 19 F. Sánchez-Bayo, K. A. G. Wyckhuys, Worldwide decline of the entomofauna: A review of its drivers. *Biol. Conserv.* **232**, 8–27 (2019).
- 20 D. L. Wagner, Insect declines in the Anthropocene. *Annu. Rev. Entomol.* **65**, 457–480 (2020).
- 21 N. E. Stork, How many species of insects and other terrestrial arthropods are there on Earth? *Annu. Rev. Entomol.* **63**, 31–45 (2018).
- 22 C. García-Robledo et al., The Erwin equation of biodiversity: From little steps to quantum leaps in the discovery of tropical diversity. *Biotropica* **52**, 590–597 (2020).
- 23 M. R. Willig et al., Populations are not declining and food webs are not collapsing at the Luquillo Experimental Forest. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 12143–12144 (2019).
- 24 T. D. Schowalter, M. Pandey, S. J. Presley, M. R. Willig, J. K. Zimmerman, Arthropods are not declining but are responsive to disturbance in the Luquillo Experimental Forest, Puerto Rico. *Proc. Natl. Acad. Sci. U.S.A.*, 10.1073/pnas.2002556117 (2021).
- 25 B. C. Lister, A. Garcia, Climate-driven declines in arthropod abundance restructure a rainforest food web. *Proc. Natl. Acad. Sci. U.S.A.* **115**, E10397–E10406 (2018).
- 26 C. A. Hallmann, A. Ssymank, M. Sorg, H. de Kroon, E. Jongejans, Insect biomass decline scaled to species diversity: General patterns derived from a hoverfly community. *Proc. Natl. Acad. Sci. U.S.A.*, 10.1073/pnas.2002554117 (2021).
- 27 D. H. Janzen, W. Hallwachs, To us insectometers, it is clear that insect decline in our Costa Rican tropics is real, so let's be kind to the survivors. *Proc. Natl. Acad. Sci. U.S.A.*, 10.1073/pnas.2002546117 (2021).
- 28 A. Y. Kawahara, L. E. Reeves, J. R. Barber, S. H. Black, Eight simple actions that individuals can take to save insects from global declines. *Proc. Natl. Acad. Sci. U.S.A.*, 10.1073/pnas.2002547117 (2021).
- 29 M. S. Warren et al., The decline of butterflies in Europe: Problems, significance, and possible solutions. *Proc. Natl. Acad. Sci. U.S.A.*, 10.1073/pnas.2002551117 (2021).
- 30 K. F. Conrad, M. S. Warren, R. Fox, M. S. Parsons, I. P. Woiwod, Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biol. Conserv.* **132**, 279–291 (2006).
- 31 T. Wepprich, J. R. Adron, L. Ries, J. Wiedmann, N. M. Haddad, Butterfly abundance declines over 20 years of systematic monitoring in Ohio, USA. *PLoS One* **14**, e0216270 (2019).
- 32 T. T. Høye et al., Nonlinear trends in abundance and diversity and complex responses to climate change in Arctic arthropods. *Proc. Natl. Acad. Sci. U.S.A.*, 10.1073/pnas.2002557117 (2021).
- 33 D. L. Wagner, R. Fox, D. M. Salcido, L. A. Dyer, A window to the world of global insect declines: Moth biodiversity trends are complex and heterogeneous. *Proc. Natl. Acad. Sci. U.S.A.*, 10.1073/pnas.2002549117 (2021).
- 34 R. Fox et al., Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. *J. Appl. Ecol.* **51**, 949–957 (2014).
- 35 Z. Randle et al., *Atlas of Britain and Ireland's Larger Moths* (Pisces Publications, Newbury, UK, 2019).
- 36 D. H. Boyes, R. Fox, C. R. Shortall, R. Whittaker, Bucking the trend: The diversity of Anthropocene 'winners' among British moths. *Front. Biogeogr.*, 10.21425/F5FBG43862 (2019).
- 37 J. E. Harris, N. L. Rodenhouse, R. T. Holmes, Decline in beetle abundance and diversity in an intact temperate forest linked to climate warming. *Biol. Conserv.* **240**, 108219 (2019).
- 38 S. D. Graves, A. M. Shapiro, Exotics as host plants of the California butterfly fauna. *Biol. Conserv.* **110**, 413–433 (2003).
- 39 M. V. Herlihy, R. G. Van Driesche, D. L. Wagner, Persistence in Massachusetts of the veined white butterfly due to use of the invasive form of cuckoo flower. *Biol. Invas.* **16**, 2713–2724 (2014).
- 40 C. Schwägerl, What's causing the sharp decline in insects, and why it matters. YaleEnvironment360, 6 July 2016, https://e360.yale.edu/features/insect_numbers_declining_why_it_matters. Accessed 29 November 2020.
- 41 C. A. Halsch et al., Insects and recent climate change. *Proc. Natl. Acad. Sci. U.S.A.*, 10.1073/pnas.2002543117 (2021).

- 42 J. C. Habel et al., Agricultural intensification drives butterfly decline. *Insect Conserv. Divers.* **12**, 289–295 (2019).
- 43 M. Gross, We need to talk about nitrogen. *Curr. Biol.* **22**, R1–R4 (2012).
- 44 J. Pöyry et al., The effects of soil eutrophication propagate to higher trophic levels: Effects of soil eutrophication on herbivores. *Glob. Ecol. Biogeogr.* **26**, 18–30 (2017).
- 45 D. H. Boyes, D. M. Evans, R. Fox, M. S. Parsons, M. J. O. Pocock, Is light pollution driving moth population declines? A review of causal mechanisms across the life cycle. *Insect Conserv. Divers.*, 10.1111/icad.12447 (2020).
- 46 R. H. A. van Grunsven et al., Experimental light at night has a negative long-term impact on macro-moth populations. *Curr. Biol.* **30**, R694–R695 (2020).
- 47 M. S. Fenoglio, M. R. Rossetti, M. Videla, Negative effects of urbanisation on terrestrial arthropod communities: A meta-analysis. *Glob. Ecol. Biogeogr.* **29**, 1412–1429 (2020).
- 48 E. Piano et al., Urbanization drives cross-taxon declines in abundance and diversity at multiple spatial scales. *Glob. Change Biol.* **26**, 1196–1211 (2020).
- 49 J. G. Harrison et al., Species with more volatile population dynamics are differentially impacted by weather. *Biol. Lett.* **11**, 20140792 (2015).
- 50 C. C. Nice et al., Extreme heterogeneity of population response to climatic variation and the limits of prediction. *Glob. Change Biol.* **25**, 2127–2136 (2019).
- 51 M. S. Crossley et al., No net insect abundance and diversity declines across US long term ecological research sites. *Nat. Ecol. Evol.* **4**, 1368–1376 (2020).
- 52 F. Pilotto et al., Meta-analysis of multidecadal biodiversity trends in Europe. *Nat. Commun.* **11**, 3486 (2020).
- 53 A. Gardarsson, A. Einarsson, Relationships among food, reproductive success and density of harlequin ducks on the River Laxá at Myvatn, Iceland (1975–2002). *Waterbirds* **31**, 84–91 (2008).
- 54 J. S. Kotiaho, V. Kaitala, A. Komonen, J. Päävinen, Predicting the risk of extinction from shared ecological characteristics. *Proc. Natl. Acad. Sci. U.S.A.* **102**, 1963–1967 (2005).
- 55 N. Mattila, V. Kaitala, A. Komonen, J. S. Kotiaho, J. Päävinen, Ecological determinants of distribution decline and risk of extinction in moths. *Conserv. Biol.* **20**, 1161–1168 (2006).
- 56 D. M. Salcido, M. L. Forister, H. Garcia Lopez, L. A. Dyer, Loss of dominant caterpillar genera in a protected tropical forest. *Sci. Rep.* **10**, 422 (2020).
- 57 J. A. Thomas et al., Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science* **303**, 1879–1881 (2004).
- 58 National Research Council, *Status of Pollinators in North America* (The National Academies Press, Washington, DC, 2007).
- 59 S. L. Althaus, M. R. Berenbaum, J. Jordan, D. A. Shalmon, No buzz for bees: Media coverage of pollinator decline. *Proc. Natl. Acad. Sci. U.S.A.*, 10.1073/pnas.2002552117 (2021).
- 60 G. Vogel, Where have all the insects gone? *Science* **356**, 576–579 (2017).
- 61 B. Jarvis, The insect apocalypse is here. *New York Times Magazine*, 27 November 2018. <https://www.nytimes.com/2018/11/27/magazine/insect-apocalypse.html>. Accessed 28 November 2020.
- 62 E. A. R. Welti et al., Meta-analyses of insect temporal trends must account for the complex sampling histories inherent to many long-term monitoring efforts. *EcoEvoRxiv*. <https://ecoevorxiv.org/v3sr2>. Accessed 15 November 2020.
- 63 National Fish and Wildlife Fund, Monarch Butterfly and Pollinators Conservation Fund (2018–2020). <https://www.nfwf.org/programs/monarch-butterfly-and-pollinators-conservation-fund>. Accessed 6 November 2020.
- 64 US Fish and Wildlife Service, Wildlife and Sport Fish Restoration Program. Pollinators. 2018–2020. <https://www.fws.gov/pollinators/programs/assistance.html>. Accessed 6 November 2020.
- 65 Center for Biological Diversity, Center for Food Safety, The Xerces Society; L. Brower, Petition to protect the Monarch Butterfly (*Danaus plexippus plexippus*) under the Endangered Species Act (2014). https://www.biologicaldiversity.org/species/invertebrates/pdfs/Monarch_ESA_Petition.pdf. Accessed 6 November 2020.
- 66 Agriculture Improvement Act of 2018 (Farm Bill), <https://www.govtrack.us/congress/bills/115/hr2>. Accessed 6 November 2020 (see also <https://www.ers.usda.gov/agriculture-improvement-act-of-2018-highlights-and-implications/>).
- 67 European Commission, Communication from the Commission to the European Parliament, The Council, the European Economic and Social Committee and the Committee of the Regions: EU Pollinators Initiative (2018). https://ec.europa.eu/environment/nature/conservation/species/pollinators/documents/EU_pollinators_initiative.pdf. Accessed 6 November 2020.
- 68 G. Vogel, €100 million German insect protection plan will protect habitats, restrict weed killers, and boost research. *Science* (2019). <https://www.sciencemag.org/news/2019/09/100-million-german-insect-protection-plan-will-protect-habitats-restrict-weed-killers>. Accessed 6 November 2020.
- 69 Government Office of Sweden, SEK 70 million to benefit pollinating insects. (2020). <https://www.government.se/press-releases/2019/09/sek-70-million-to-benefit-pollinating-insects/>. Accessed 6 November 2020.
- 70 E. Stokstad, European Union expands ban of three neonicotinoid pesticides. *Science*, <https://www.sciencemag.org/news/2018/04/european-union-expands-ban-three-neonicotinoid-pesticides> (2018). Accessed 6 November 2020.
- 71 M. Farmer, Entire European Union bans a Bayer insecticide. *Modern Farmer* (2020). <https://modernfarmer.com/2020/01/entire-european-union-bans-a-bayer-insecticide/>. Accessed 6 November 2020.
- 72 Environmental Protection Agency, Proposed Interim Decision on Neonicotinoids, (2020). <https://www.epa.gov/pollinator-protection/epa-actions-protect-pollinators>. Accessed 6 November 2020.
- 73 J.-M. Bonmatin et al., Environmental fate and exposure; neonicotinoids and fipronil. *Environ. Sci. Pollut. Res. Int.* **22**, 35–67 (2015).
- 74 Butterfly Conservation, Big Butterfly Count 2020: The results Butterfly Conservation (UK), <https://butterfly-conservation.org/news-and-blog/big-butterfly-count-2020-the-results>. Accessed 3 November 2020.
- 75 G. A. Montgomery et al., Is the insect apocalypse upon us? How to find out. *Biol. Conserv.* **241**, 108327 (2019).
- 76 G. A. Montgomery, M. W. Belitz, R. P. Guralnick, M. W. Tingley, Standards and best practices for monitoring and benchmarking insects. *Front. Ecol. Evol.* **8**, 579193 (2020).
- 77 T. T. Høye et al., Deep learning and computer vision will transform entomology. *Proc. Natl. Acad. Sci. U.S.A.*, 10.1073/pnas.2002545117 (2021).
- 78 S. Ratnasingham, P. D. Hebert, BOLD: The Barcode of Life Data System (<http://www.barcodinglife.org>). *Mol. Ecol. Resour.* **7**, 355–364 (2007).
- 79 S. Ratnasingham, P. D. Hebert, A DNA-based registry for all animal species: the barcode index number (BIN) system. *PLoS One* **8**, e66213 (2013).
- 80 A. McDermott, To understand the plight of insects, entomologists look to the past. *Proc. Natl. Acad. Sci. U.S.A.*, 10.1073/pnas.2018499117 (2020).
- 81 E. M. Grameš, et al, Trends in global insect abundance and biodiversity: A community-driven systematic map protocol, <https://osf.io/q63uy>. Accessed 6 November 2020.
- 82 E. M. Grameš, T. Amano, D. Wagner, C. S. Elphick, Global syntheses of biodiversity are hampered by biases introduced by information retrieval methods. *Science e-Letter*, <https://science.sciencemag.org/content/368/6489/417/tab-e-letters>. Accessed 6 November 2020.
- 83 S. M. Shone, F. C. Curriero, C. R. Lesser, G. E. Glass, Characterizing population dynamics of *Aedes sollicitans* (Diptera: Culicidae) using meteorological data. *J. Med. Entomol.* **43**, 393–402 (2006).
- 84 D. H. Janzen et al., Using DNA-barcoded Malaise trap samples to measure impact of a geothermal energy project on the biodiversity of a Costa Rican old-growth rain forest. *Genome* **63**, 407–436 (2020).
- 85 J. A. Harvey et al., International scientists formulate a roadmap for insect conservation and recovery. *Nat. Ecol. Evol.* **4**, 174–176 (2020).