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Insect Declines in the Anthropocene

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Abstract

Insect declines are being reported worldwide for flying, ground, and aquatic lineages. Most reports come from western and northern Europe, where the insect fauna is well-studied and there are considerable demographic data for many taxonomically disparate lineages. Additional cases of faunal losses have been noted from Asia, North America, the Arctic, the Neotropics, and elsewhere. While this review addresses both species loss and population declines, its emphasis is on the latter. Declines of abundant species can be especially worrisome, given that they anchor trophic interactions and shoulder many of essential ecosystem services of their respective communities. A review of the factors believed to be responsible for observed collapses and those perceived to be especially threatening to insects form the core of this treatment. In addition to widely recognized threats to insect biodiversity, e.g., habitat destruction, agricultural intensification (including pesticide use), climate change, and invasive species, this assessment highlights a few less commonly considered factors such as atmospheric nitrification from the burning of fossil fuels and the effects of droughts and changing precipitation patterns. Because the geographic extent and magnitude of insect declines are largely unknown, there is an urgent need for monitoring efforts, especially across ecological gradients, which will help to identify important causal factors in declines. This review also considers the status of vertebrate insectivores, reporting bias, challenges inherent in collecting and interpreting insect demographic data, and cases of increasing insect abundance.



INTRODUCTION

The recent spate of high-profile reports of impoverished insect faunas from Europe and around the globe (68, 87, 88, 108, 109, 156, 186) have drawn the attentions of entomologists, vertebrate biologists, ecologists, conservation biologists, and other environmentalists, as well as the press, nongovernmental organizations, and policy makers. Adding to the worry are the countless anecdotal reports about fewer insects on windshields, diminishment of firefly displays, fewer moths seen at gas stations or flying around streetlights, and old-timers claiming that butterflies and other insect numbers have plummeted since the days of their youth. It is difficult to judge what is more disconcerting—the magnitude and rates of the reported losses or the inadequacy of credible demographic data for even the most familiar and abundant insects across many regions of the planet.

Rather than the loss of single species, the recent reports and heightened concerns are anchored in declines that extend broadly across arthropod lineages—collapses in number rather than kind—the types of losses that could cascade across trophic webs and result in the degradation of ecosystem services (28, 34, 54, 55, 156, 209). Foremost among these, and of immediate economic concern, are the pollination services of insects. More than 80% of the world's flowering plants are thought to be dependent on insects for pollination (135, 184). Approximately three-quarters of all crop species are dependent on insect pollination (94, 101, 184). Other insects are nutrient recyclers that serve important roles in macrodecomposition of wood (both standing and fallen), leaves, dung, and carrion (112, 212). Insects serve essential roles in the food webs of tropical and temperate terrestrial and freshwater ecosystems. The existence of most of the vertebrates on this planet is supported by insect life directly or indirectly, and the diminishment of insect numbers would greatly accelerate the sixth great planetary extinction (98, 204–206). Another key economic and food security benefit is the role of insects in controlling pest invertebrates, fungi, and weeds (10, 38, 112, 121, 133). Major losses of insect diversity and biomass, at rates already documented to be occurring in Europe, will have ramifications across the tree of life.

With some important exceptions, the phenomenon of insect decline is both poorly documented and poorly understood. Of critical importance will be identifying the spatial aspects of losses and gathering quantitative data that will reveal the magnitude and rates of decline, the timing of collapses, and what taxonomic and ecological functional groups are in greatest jeopardy. Frustratingly, even where losses have been documented, the suite of causal factors and, most importantly, their relative contributions remain in doubt. This treatment reviews major factors thought to be responsible for the observed collapses, especially those perceived to be the most threatening to insects as we move deeper into the Anthropocene. Emphasis is placed here on terrestrial groups; for a recent summary of declines across aquatic insect orders, I refer the reader to Reference 156.

THE NATURE OF THE DECLINES

Reports of insect decline have differing spatial, temporal, intensity, and taxonomic components that can help identify underlying causes. Most of the best-documented declines come from western and northern Europe (**Figure 1**), where collectors and dedicated naturalists have kept records on insect abundance for more than a century. Conclusions shared in the two meta-analyses (34, 156) of global insect declines were driven by data from the United Kingdom, Germany, the Netherlands, and other European countries. Reports from outside of Europe tend to be more anecdotal, local, taxonomically limited, or influenced by extreme weather events (e.g., 87, 109, 115). Data for North America are frustratingly sparse and tend to be significantly less extensive—spatially, taxonomically, and temporally—than those from Europe. Most derive from California (40–42, 90, 139) and the Midwestern and Northeastern United States (6, 116, 160, 161, 188, 199, 213). While next to nothing has been published for tropical regions, two recent accounts of decline, one in a

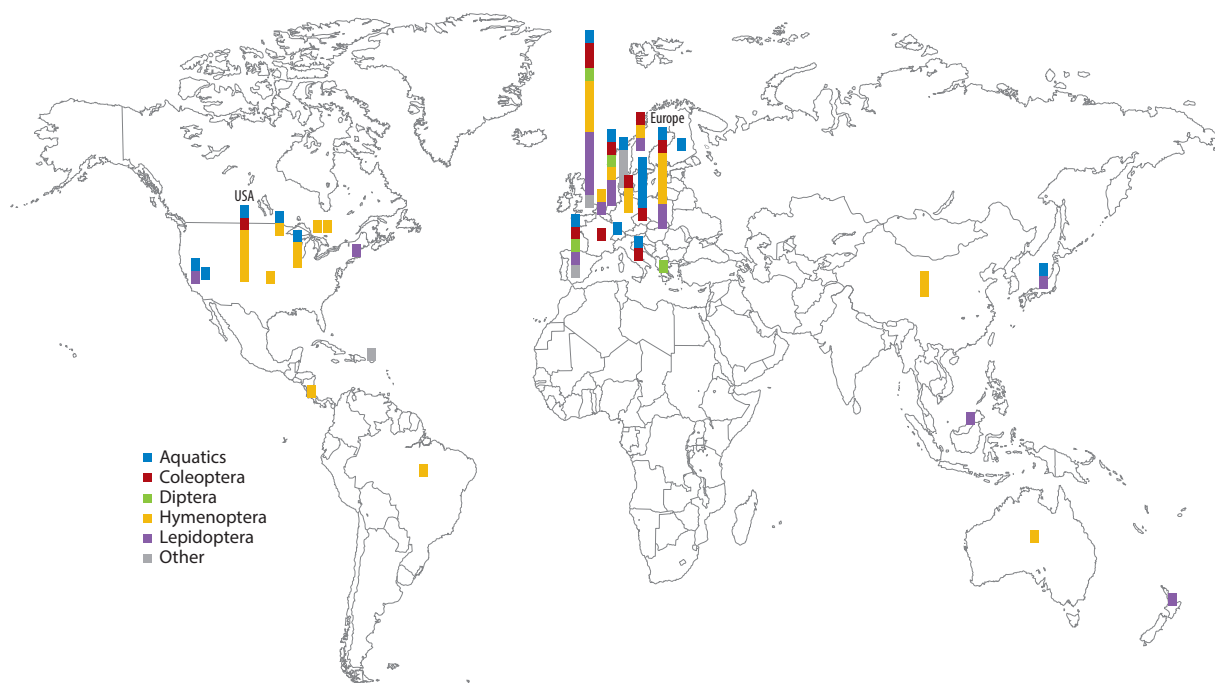


Figure 1

Location of 73 insect decline reports by taxon or group, adapted from Sánchez-Bayo & Wyckhuys (156). Each square represents a single study, with the base of each positioned over the country where a given study was conducted. Reports from China and Australia are based on managed honeybee colonies. Figure adapted with permission from Biological Conservation.

tropical forest in Puerto Rico (109; but see 203) and the other in northwestern Costa Rica (87), provide glimpses of the scope and magnitude of the phenomenon in the Neotropics. Reports of declines from the High Arctic (58, 79, 110) remind that different drivers appear to be operative over different parts of the globe.

In Northern Europe and New England, moth and butterfly declines differ in magnitude by region. The northern United Kingdom has fared markedly better than the more densely settled southern half of the country (28). Through southeastern Canada and New England and New Jersey in the United States, the extent of reported decline appears to vary, with some areas being little affected (160, 161, 188). One spatial aspect that warrants special mention is that many of the reported declines—in Costa Rica, the United Kingdom, Germany, the Netherlands, Puerto Rico, Sweden, and elsewhere—are occurring inside preserves and protected lands (51, 68, 87, 109, 148, 159).

Early reports of cross-taxon, country-wide insect declines began surfacing two decades ago (e.g., 2, 28, 29, 176). The data and conclusions in these initial reports, which have been supported by more recent studies, show that many of the declines began in the 1950s, at the beginning of the Anthropocene, and that losses have continued largely unabated for many taxa (**Figure 2**) (see 29, 34). Such patterns would argue for agricultural abandonment and afforestation, agricultural intensification, habitat destruction, and the collective impacts of human occupation as causal factors over more recent phenomena such as climate forcings, at least in Europe. By contrast, climate change is identified as the primary driver of changes occurring in Puerto Rico and Costa Rica (87, 109).

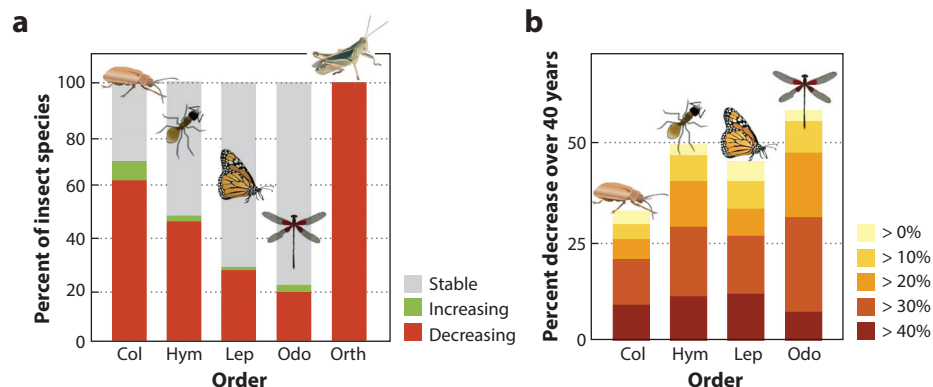


Figure 2

Population trends for insects tracked by the International Union for Conservation of Nature (IUCN) and UK insects from Dirzo et al. (34). (a) Trend data for IUCN-listed Coleoptera (Col), Hymenoptera (Hym), Lepidoptera (Lep), Odonata (Odo), and Orthoptera (Orth). (b) Insect trend data across the United Kingdom, the most well-studied entomofauna globally; over the four-decade period assessed by Dirzo et al., 30% to 60% of the species in each of four orders had negative population trends. Figure adapted with permission from Reference 34, copyright AAAS.

A global meta-analysis of insect abundances revealed a 45% decline in insect abundance across two-thirds of the taxa evaluated (34). The Krefeld Entomological Society's study of reserves across northwestern Germany—the most well-documented longitudinal study of insect biomass over a large region—suggests a >70% decline of flying insects over the past three decades (68, 163, 186). Catastrophic declines over a four-decade period are reported from Puerto Rico's Luquillo Forest Reserve (109): Insect biomass in sweep samples declined four- to eightfold, sticky trap catches 30- to 60-fold, and ground-trap catches 35-fold, but there are data that indicate that the reported findings are not representative of long-term population trends at Luquillo (203). A recent global assessment suggested that insect biomass was falling at a rate of 2.5% annually (156), but the projection appears to be an overreach of published data driven by western and northern European reports (99, 173, 190).

It is important to point out that some fraction of insect decline cases, both anecdotal and those in peer-reviewed literature, may be associated with local changes in land use, successional stage, or weather events (e.g., when observations are reflective of severe drought or storms). Examples of the former are discussed in the section titled Land-Use Change below.

TAXONOMIC PATTERNS

Reported faunal losses include aerial and ground-dwelling insects, freshwater and terrestrial species, and diurnal and nocturnal insects. Dirzo et al. (34) analyzed more than 90 million occurrence records for four orders of UK insects: Coleoptera, Hymenoptera, Lepidoptera, and Odonata. All four orders showed declines of 30–60% in occurrence frequencies over the most recent four decades. For UK and Swedish Lepidoptera, similar rates of loss have been documented for both butterflies and moths (28, 51). Dirzo et al. also found evidence of steep declines among orthopterans. Brooks et al. (14) concluded that three-quarters of UK carabids censused in their study had undergone population reductions of >30%. A similar rate of decline was documented for dung beetles in Italy (22). Numerous studies have focused on the losses of bumblebees (21, 92,

145, and references cited below). A global, taxon-by-taxon summary of 73 cases of insect decline concluded that 40% of insect taxa were in decline (156).

To understand key causal factors, especially regarding the spatial and temporal aspects of declines, it is judicious first to consider those taxa that are well studied and for which credible longitudinal population data exist. No group of insects is as well documented as butterflies. Moths, too, have long been a focus of collectors and long-term monitoring efforts. These two groups, as well as bees, are considered below.

Butterflies

Butterflies are generally considered to be the best-known lineage of insects, with the deepest historical record in the United Kingdom. Asher et al. (2) summarized occurrence data for more than 10 million observations dating back to the 1780s. Since that report, Butterfly Conservation and its partners have published two additional *State of UK Butterflies* reports in 2011 and 2015, based on an additional 6 and 3 million records, respectively (46, 47). In brief, the United Kingdom is documented to have lost five species of butterflies, 70% of the remaining species are declining in occurrence, and 57% are declining in abundance; 45% are formally recognized as being threatened (46, 47, 175, 176, 194). Franzén & Johannesson (51) report a disastrous decline of butterflies in Sweden—with 45% of the fauna experiencing negative population trends since 1950. Butterfly declines have been documented for most European countries. The most extreme case may be from the Flanders region of Belgium, where 19 of the 64 indigenous species have been lost, and half of the remainder are threatened (114).

Reported losses have important similarities: Declines have been particularly severe for habitat specialists and IUCN Red List species, declines often include formerly abundant and widespread species, the fractions of declining species are comparable across multiple European countries, dietary specialists and univoltine species are often at greater risk, and the declines are occurring even within protected lands (11, 46, 47, 51, 148, 174, 195, 199). Perhaps most importantly, there has been no obvious uptick in rates or magnitudes of declines over the past five decades (29, 34, 46), which takes away some force from claims that neonicotinoids, climate change, elevated atmospheric carbon dioxide levels, microwave exposure, or other recent stressors are the main drivers of butterfly declines in western and northern Europe.

One wonders to what extent the eastern North American monarch butterfly and its falling numbers might serve as a window into the plight of other insects. There is mounting evidence that the monarch has declined due to multiple stressors: chronic droughty conditions along and through breeding areas, nectar limitation, an increase in climatic fluctuation (especially elevated and freezing temperatures) at overwintering roosts attributable to local logging practices and climate change, Roundup Ready® crops, and the abandonment of small farms and other aspects of agricultural intensification across the monarch's summer breeding range (13, 15, 83, 115, 172).

Moths

Moths are the most taxonomically and ecologically diverse insect taxon for which there exist good longitudinal abundance data. Again, the best data come from the United Kingdom and elsewhere in northern Europe. Even if only macrolepidopteran moths are considered, the 14+ family-level taxa include tree-, forb-, and grass-feeders and represent an enormous range of ecologically diversified lineages. Much like butterflies, there is an alarming record of decreases in moth abundance and species diversity (28, 29, 32, 45, 48, 49, 115, 207). In the United Kingdom, two-thirds of the

country's macromoths have declined since 1970, with a quarter of these declines in abundance averaging approximately 10% per decade (28, 29, 48). Importantly, rates of decline vary by region, with southern UK sampling stations having twice the rate of loss as northern (less-populated) sites. A clear warning that arose from the work of Fox et al. (48) was that many widespread and common species across taxonomic lineages, representing a diverse spectrum of ecological niches, were showing signs of steep decline. These initial UK findings for moths (and butterflies) were an early warning sign of the multilineage insect declines now being reported across insect orders and guilds (34, 68, 156, 186).

Bees

Bees anchor the Earth's pollination services and are essential for food security and global economies (1, 61, 94, 101, 126, 135). Many papers in the past two decades have warned of pollinator decline, with most calling for more study and pointing out the need for population trend data (7, 61, 71, 126, 145, 184, 208). Agricultural intensification is recognized in many studies as a pervasive and increasing threat to bees and their ecosystem services (61, 103, 104, 164). Other commonly reported threats include pathogens, pesticides, and climate change (61, 69, 146, 184).

In Asia, Europe, and North America, several bumblebee species have already been lost to extinction or sit near its brink (20, 21, 60, 92, 100, 179, 202). Many others are experiencing declines in abundance and distribution. In the Western Hemisphere, some bumblebee subgenera are succumbing to *Nosema* and other pathogens (20, 122, 179), cold-adapted lineages appear to be losing ground to climate change across the Holarctic (92), and modern agricultural practices (and the scale of modern agriculture) are implicated in the declines of others (21, 26, 66, 164).

Most reports of bee decline are anchored to eusocial lineages. Comparatively few studies have evaluated the status of the world's >20,000 species of solitary bees. Bartomeus et al. (6) did not find a signal of widespread bee loss in their cross-taxon historical assessment of 187 bees in the Northeastern United States, except for three species of bumblebees in population collapse, purportedly from *Nosema* infections, and six solitary bees in *Andrena*, *Halictus*, and *Lasioglossum*. A more recent assessment of the apifauna of New Hampshire found evidence for declines of an additional eight species of solitary bees (116). Baude et al. (8) reported that both nectar availability and pollinator diversity dropped during the middle of the past century in the United Kingdom, but later stabilized and have even rebounded, evidently as a consequence of efforts to manage for pollinators and other biodiversity. A recent assessment of UK fauna reported declines for one-quarter and increases for approximately 10% of the 139 species studied (146). Two reports of bee decline from the Neotropics are associated with deforestation, agricultural expansion, and urbanization (50, 128). In contrast, at three intact forest sites in Panama, euglossine bee numbers and diversity have shown little change in abundances (153). Similarly mixed results were found in temperate areas: Across an area of intensive land use in Illinois, bee richness dropped by 50% over a 120-year period (19), whereas data from an undisturbed montane community collected over the past two decades showed no evidence of bee decline (76).

Reports of pollen limitation underscore the importance of maintaining pollinator diversity (3, 78, 95, 144, 210), but I am unaware of any reports of widespread pollinator limitation from intact natural communities.

THE THREATS

Insects are threatened by the same factors that affect other animal and plant life, e.g., habitat loss and degradation (from agriculture, development, logging, mining, damming, and others),

climate change, desertification, resource exploitation, environmental degradation, invasive species, and chemical pollution. Insects are affected by light pollution and agricultural intensification (including pesticides, anti-insect genetic engineering practices, and additional factors discussed below) to an arguably greater extent than vertebrates and plants. Some researchers have suggested that elevated atmospheric carbon dioxide levels could be playing a role in declines (see below). Wagner & Van Driesche (192) identified 17 threats implicated in the population declines of endangered and threatened insects in the United States. A new threat that must now be considered are the knock-on effects that will befall plant and animal populations in the Anthropocene: As lineages decline as a result of primary threats, there will be secondary consequences that propagate upward and downward through the world's communities and ecosystems (34, 54, 55, 86, 209). Because of space limitations, only some of these stressors and threats are discussed in this review.

Habitat Degradation

Deforestation, conversion of wildlands into agriculture and silviculture, residential and commercial development, and extractive land uses collectively make up the greatest current threat to global biodiversity (84, 107, 118, 201). Anthropogenic activities that affect local and regional geophysical processes, such as dune and river bank stabilization, can have far-reaching effects. Water consumption for agriculture, industry, mining, human welfare and recreation, and other purposes will be an increasing threat to insects and other biodiversity in arid regions. Deforestation and agriculture, taken together, account for the greatest annual losses of habitat and biodiversity—they are discussed separately below.

Deforestation

Tropical forests are home to much of the planet's terrestrial biodiversity, including the majority of insects (169). Clearing of tropical forests for crops, pasture, and wood fuel is proceeding at alarming rates in Central Africa, Central America, many parts of South America, and Southeast Asia. Between 2001 and 2015, an average of five million acres of tropical forest were lost annually to industrial-scale agriculture (168). In 2018, 12 million acres of tropical forest were cleared, one-third of which mapped as previously intact primary forest (198). Deforestation on larger scales has the potential to change local and regional weather and, in particular, alter rainfall patterns (39, 142, 171). Given that the great majority of insect species diversity is found in tropical ecosystems (169), deforestation for agriculture and other human uses surely ranks among the greatest threats to the world's entomofauna.

Tropical deforestation has been linked to population declines and extinctions of many plants and vertebrates (23, 80, 157). It seems likely that commensurate losses also have occurred among insects, although this is essentially undocumented. Lamentably, tropical insect faunas are especially poorly known, with the vast majority yet to be named and classified (169)—many species and perhaps lineages are likely to be lost before they can be studied. Still worse, given the limited taxonomic resources and training in most tropical countries, there is the additional concern that taxa will be lost before they can be collected and archived for future study.

With human populations increasing over much of the planet, it is certain that habitat destruction, and especially the conversion of forest into agriculture, will continue well into the foreseeable future. It will be imperative to identify ways to increase crop yields while at the same time adopting more sustainable practices that are more nature friendly, elevate diversity, and bolster the ecosystem services of insects (44, 102).

Agricultural Intensification

There is an ever-growing body of literature linking insect declines to agricultural intensification (4, 62, 64, 93, 103, 136, 156, 164, 174, 181; see also citations in discussion below). Many, if not most, of the recent reports of insect decline from western and northern Europe and the Central Valley of California are attributable to changes in agricultural practices, which have become increasingly unfriendly to nature. Modern farms and farming practices are often larger in extent, involve herbicide-tolerant crops that encourage herbicide use, are planted with genetically modified varieties that produce insect toxins, embrace monoculturing, have become increasingly dependent on pesticides and fertilizers, tile their fields to increase arable acreage, and place greater emphasis on hygiene and cosmetic practices (17, 24, 104, 181). Even if agriculture-linked deforestation and hydrological consequences of irrigation are ignored, the collective impacts of many modern farming practices are highly detrimental to biodiversity in general, and insects in particular.

All but one of the preserves in northwest Germany surveyed by the Krefeld Entomological Society (68) are proximate to agricultural fields. Agricultural intensification was identified as a likely cause of the insect collapses there. Essentially all of the studies evaluating the losses of butterflies and moths in the United Kingdom, Finland, the Netherlands, and Sweden identify agricultural intensification as a primary threat to Lepidoptera (28, 29, 45, 48, 51, 64, 117, 194). Likewise, those documenting butterfly declines in California's Central Valley (40) and others looking at the decline of the monarch (115, 166) implicate agricultural intensification as a primary or contributing cause. Among the studies ascribing cause to pollinator declines, agricultural intensification is the most commonly identified driver (e.g., 26, 66, 104, 164).

The avifaunas of farmlands, especially in Europe and North America, have been falling off in both species richness and abundance, with insectivorous birds among those showing the greatest population declines (9, 35, 56, 123, 130, 152).

Land-Use Change

Various European authors, especially those studying butterfly conservation, mention abandonment of small farms as a contributing factor in insect declines. For centuries, small farms with field margins, hedgerows, fallow fields, coppices, drainage ditches, and lightly grazed pastures provided relatively nature-friendly conditions for insects and wildflowers (2, 46, 47, 63, 64, 66, 131, 156, 174). In addition to butterflies, such seminatural grasslands support diverse faunas of bees, beetles, grasshoppers, hover flies, moths, and other early successional insects; even aquatic species such as dragonflies come to forage in these habitats while transitioning to reproductive maturity. However, as smaller family farms give way to commercial and residential development; are replaced by larger, more industrialized farms; or are simply abandoned and let go to forest, sweeping changes in plant diversity and insect faunas follow. Replacement of small traditional farms by development or larger, more industrialized farms yields outcomes that are obviously detrimental to wildlife. In cases of afforestation, the land remains undeveloped but is given over to a different entomofauna. Some of the accounts of insect decline across the globe, both anecdotal and from peer-reviewed journals, are rooted in the natural changes that follow from the abandonment and closure of once open, early successional communities or the gradual habitat (and faunal) losses that accompany residential development and other types of elevated human activity (22, 131, 165, 187, 189).

Insecticide Use

Numerous reports have explored the link between insecticides and insect declines, with much of the recent attention focused on neonicotinoids and fipronil, especially their threat to pollinators

(36, 57, 59, 72, 105, 106, 143, 156, 211). Many aspects of insecticide use are of concern: the recent emphasis on the development and application of systemics that have the potential to heighten exposure risks for nontarget insects; the unknown consequences of mixed applications; sublethal effects; the long half-lives of some pesticides in soil and water; and the movement of insecticides into preserves and other wildlands, including aquatic systems. Because trace amounts of insecticides are turning up in wildlands (72, 105, 211), there is great need to determine to what degree bees, butterflies, and other insects are stressed, disoriented, immunocompromised, or otherwise disadvantaged by nonlethal insecticide exposure.

Declines of butterflies in the United Kingdom and California's Central Valley have been linked to neonicotinoid use (40, 57). Neonicotinoids (e.g., imidacloprid) were identified as a potential causal factor in the decline of both insects and insectivorous birds in the Netherlands (68). However, many of the declines of butterflies and moths in the United Kingdom, New England, and elsewhere began before the introduction of neonicotinoids and other newly developed insecticides and have occurred in areas where there is little pesticide usage (2, 29, 47).

The movement of lethal and sublethal levels of pesticides from agricultural fields into wildlands is likely to be especially problematic in regions where a large fraction of the land area is used for agriculture. In Belgium, the United Kingdom, Germany, and the Netherlands, 40–70% of their respective land areas are used for agriculture—and as such, chances for drift of pesticides into preserves and adjacent lands and waters are greatly heightened. All but one of the 63 Krefeld sites that were the basis of the declines reported by Hallmann et al. (68) are adjacent to agricultural fields. In the Great Plains of North America, original and restored prairie remnants embedded in a matrix of agriculture would seem to be especially vulnerable to nontarget impacts.

Climate Change

As we move further into the Anthropocene, climate change may prove to be the greatest threat to biodiversity, rivaled only by habitat destruction in the tropical regions of the planet (12, 84, 85, 182, 196). The multifactorial threats of climate change have been treated in books, reviews, peer-viewed articles, Intergovernmental Panel on Climate Change reports, and white papers. There is only space in this review to touch on components that are especially relevant to insects and highlight a few of the studies that link insect declines to climate change.

Insects are poikilotherms that experience daily fluctuations in body temperatures—swings of 5°C to 15°C are not uncommon, with much larger fluctuations routine for temperate, desert, and montane species. Many researchers looking to explain insect declines or predict future effects of global warming have focused on temperature increases as a threat to insect biodiversity (27, 52, 109, 138, 155, 196). While temperature is sure to be a proximate driver of stress and decline, greater challenges of climate change to insects may stem from other aspects of climate change, e.g., more variable weather patterns (87), more extreme weather events (37, 75, 113), and reduced winter snow cover (72). Water stress, particularly droughts of increasing frequency, duration, and intensity, could prove to be an insurmountable stressor for many insects. Of special concern are areas where rising global temperatures are changing rainfall patterns and cloud cover, e.g., over volcanoes and mountains in the world's tropics (74). Forests that for millennia have been saturated with moisture are today facing unprecedented short- and long-term drying events. Insects have large surface-area-to-mass ratios that make them vulnerable to rapid desiccation, especially during flight—the physiological stresses of drying on insects and their habitats can scarcely be exaggerated, especially in those ecosystems that have not previously experienced appreciable moisture stress.

Water stress due to higher temperatures and/or droughts will have weighty indirect effects. Chronic drought can stress plants and make them more susceptible to attack by insect pests and diseases (97). Tree losses to bark beetles have been linked to drought stress, as well as to warmer winter temperatures that allow more individuals to overwinter successfully (25, 149). Fires become an increasing threat during periods of scarce rainfall and higher-than-normal temperatures. Nectar availability will drop off under conditions of elevated temperatures and or drought (140 and references therein).

Changes in northern Costa Rica draw focus to the problem of increased frequency and intensity of desiccating conditions (87). An example from the temperate zone illustrates the twofold affront of droughts accompanied by elevated temperatures. The greatest climate-associated population declines based on multidecadal butterfly monitoring sites in California were recorded at higher-elevation (mountain) sites, after periods of combined drought and higher-than-normal temperatures (41).

Changes in precipitation, both decreases and increases, will trigger changes in plant abundance and distributions. As plant communities across the planet wax, wane, turn over, adapt, and disappear, so will their dependent insect faunas. Changing floras will have cascading consequences for dietarily specialized herbivores, which may comprise a quarter of all metazoans on this planet (43, 147, 170). Of course, changes to ocean currents based on rising world temperatures would be expected to precipitate massive climatic and biotic changes.

Nitrification

The release of atmospheric nitrites from the burning of fossil fuels has the potential to change global ecology and ignite extinction cascades (141, 154). Nitrogen is often a limiting nutrient in terrestrial, freshwater, and marine systems. Many of the world's most speciose and specialized plant communities occur in nitrogen-poor soils (180). In a now-classic study, the generous addition of nitrogen to a pasture at the Rothamsted Experimental Station (in the United Kingdom) resulted in a 10-fold loss of plant richness over the course of the ensuing century (91).

The wet or dry deposition of atmospheric nitrogen to previously nitrogen-limited communities (e.g., bogs, heathlands, sand-based communities, pine barrens, oligotrophic grasslands, and many freshwater ecosystems) will change their fundamental ecology by altering edaphic conditions, nutrient cycling, species interactions and composition, and more. Butterfly declines in northern Europe have been linked to nitrogen deposition, particularly that associated with oligotrophic grasslands (64, 65, 134, 193).

Soil chemistry is a primary determinant of plant distributions—nitrogen deposition from fossil fuel consumption has the potential to trigger changes in plant communities worldwide. As plant abundance and species composition change, so will the associated entomofaunas. Approximately half of all described insects are plant feeders, and approximately 90% of these are thought to be dietarily specialized herbivores that depend upon just a small suite of closely related species (43, 147, 170). The potential consequences of atmospheric nitrogen deposition are grave and worthy of greater attention.

Invasive and Ornamental Species

Invasive and non-native species, be these pathogens, plants, or animals, pose an ever-increasing threat to biodiversity globally (192). Their effects are most severe on island biotas, where they frequently disrupt, and sometimes overrun, whole communities (192). In continental areas, invasive and ornamental plants pose a combined and growing threat, especially in areas or systems of high

human occupation and disturbance; exotic plants can diminish insect herbivore loads by more than 90%, which, in turn, negatively affects birds and other insectivores (18, 124, 125, 151, 158). The effects of purposely introduced biological control agents—and especially those that have generalized diets, such as lady beetles, lacewings, and egg parasitoids—on nontarget species have rarely been assessed. A special case, where there are ample data, is the competitive displacement of native lady beetles by exotic species introduced for biocontrol purposes (5, 16, 53, 70). While there are instances where exotic species (outside of a biocontrol effort) have served to rescue imperiled species, there is widespread agreement that invasives, as well as the profligate use of introduced plants in landscaping and forestry, remain one of the most important global threats to native floras and faunas (162, 185, 191, 192).

Light Pollution

The evidence for light pollution as a contributing factor in the decline of moths and other insects in Europe and elsewhere is mixed (see 28, 45, 51, 63, 137, 200, 207). The recent work of van Langevelde et al. (183) and Knop et al. (96) make convincing cases that light pollution has contributed to moth decline in the Netherlands and Switzerland. Based on first principles, it is hard to fathom how it would not be so, especially when one considers the sum total of predation around fixed-light sources by bats at night, birds and predatory wasps in the morning, and the myriad vertebrate and invertebrate ground-dwelling predators that devour night-flying insects that alight on the ground. To these can be added the losses that accrue to the insects that are drawn into headlights. It is surprising that less insect-attracting and more energy-saving lamp technologies have not been more widely adopted (outside of the European Union).

The specific contributions of light pollution to insect declines are difficult to measure because artificial lights are usually integral to areas of high human occupancy and activity, which come with the compounding effects of habitat destruction, invasive plants, nature-unfriendly landscaping, pesticide use, car strikes, and more. Some authors have noted that the magnitude and nature of the declines of diurnal species, be these butterflies, bees, or hover flies, across western and northern Europe are generally commensurate with those being reported for moths and other nocturnal lineages (e.g., 51), which would argue against light pollution being a major factor in region-wide declines, except in areas of dense human occupancy.

Elevated Atmospheric Carbon Dioxide Concentrations

Elevated concentrations of atmospheric carbon dioxide have the potential to alter nutritional properties of host plants for herbivorous insects. Plants grown under higher carbon dioxide concentrations commonly have lower available nitrogen and may augment their carbon-based plant defenses (30, 81, 214). Herbivores feeding on plant tissues with diminished concentrations of nitrogenous metabolites may consume more plant tissue and take longer to mature, thereby increasing their exposure to natural enemies (30). Other plant lineages may have lowered concentrations of secondary plant chemicals when grown under higher carbon dioxide concentrations. Monarch caterpillars fed *Asclepias curassavica* cultivated in chambers with elevated carbon dioxide concentrations had lower titers of cardenolides and as consequence had less tolerance to protozoan (*Ophryocystis elektroscirrha*) infections (31). Ziska et al. (214) reported a strong negative correlation between atmospheric carbon dioxide concentrations and the protein content of two goldenrod species. Given that all bees are nutritionally dependent on pollen, altered (lowered) nutritional quality would be expected to have important knock-on effects, such as lowered reproductive success and immunocompetence of affected individuals.

STATUS OF ENTOMOPHAGOUS ANIMALS

The status of an area's entomofauna can be indirectly assessed by examining the fates of local insectivorous vertebrates and, to a lesser extent, invertebrates. Demographic data for both birds and bats are often more widely available, more interpretable, and likely to extend further back in time than data for the same region's invertebrates. More importantly, resident insectivores forage across entire seasons and may live for years; thus, their status at any point in time provides a summation of past insect abundances.

Many insectivorous birds are experiencing population declines in Europe, Northeastern North America, and elsewhere. Aerial insectivores, including nightjars, swallows, and swifts, are among the most rapidly declining birds in both Europe and Northeastern North America (9, 127, 132). In Australia, some insect-feeding lineages of birds have declined faster than sympatric granivores (150, 197). Few studies have made a credible link between insectivorous bird declines and prey limitation; other factors, such as habitat destruction, agricultural intensification, land-use changes, and/or losses in the overwintering grounds may be involved in the observed declines. In the Netherlands, environmental levels of imidacloprid (and by extension diminished insect abundance) are correlated with rates of decline of 15 insectivorous passerines (67).

Downward trends in abundance for *Eleutherodactylus* frogs and three species of *Anolis* lizards in the Luquillo Forest Preserve in Puerto Rico have been reported (109); one *Anolis* disappeared from previously occupied sites, and mean body mass for the other two lizards dropped by more than one-third (but see 203).

If insect numbers, and especially those of moths, have declined globally at rates commensurate with those described in this review for parts of Europe (or Puerto Rico), then numbers of insectivorous bats should have plummeted in step (see 89), but there have been few such reports outside of areas where white-nosed syndrome has caused collapses. Population numbers for several European bat species have increased over the past 20 years (73). Between 10 and 20 million Brazilian free-tailed bats (*Tadarida brasiliensis*), whose diet consists of volant insects, roost in Bracken Cave in San Antonio, Texas through the warm season (120, 167). This single colony is thought to harvest more than 90,000 kilograms of flying insects in a single night (119)—even if this estimate is off by a factor of five or more, the colony represents an unrivaled barometer of regional insect health. Population numbers appear to have been relatively stable over the past two decades (167), although it is important to note that accurate census data are difficult to collect due to the tendency of free-tailed bats to move among roosting sites within and across seasons. To muddle the above results, the Carlsbad Caverns colony and other Brazilian free-tailed bat caves in the US Southwest and Mexico have declined over the past half century (119, 120).

Little peer-reviewed literature exists for the abundances and conservation status of entomophagous insect lineages, whether these be predators or parasitoids. Declines in carabids have been reported from western and northern European countries and New Zealand (14, 33, 34). Rates of declines from the United Kingdom are roughly similar to those of UK butterflies and other taxa discussed in this review (14).

REPORTING BIASES AND MEASURING FAUNAL LOSS

While there is an irrefutable signal of losses in insect richness and abundance across many countries and regions, the spatial scope of the declines is unknown. There is hope that many wildlands across the planet have insect faunas that are only modestly if at all diminished, and that few are suffering the rates of loss occurring across western and northern Europe. However, the opposite could well be true, i.e., that climate change is triggering even higher rates of extinction in some wildlands, e.g., across polar, arid, montane, and tropical regions. Deforestation and defaunation of

tropical forests are proceeding at alarming rates; surely insects are affected at rates commensurate with those documented for vertebrates and plants (for which there are less unambiguous data).

The recent set of studies that have raised global alarm could be biased toward those regions that are experiencing the greatest losses. Until now, few researchers and conservation biologists would have had incentive to report census data confirming no appreciable decline. However, we now find ourselves at the point where reporting results of little change or increasing abundance is relevant, timely, and necessary.

Frustratingly, verifying insect decline is a difficult problem. Many, if not most, insects are r-selected, and thus their numbers naturally fluctuate, sometimes by one or two orders of magnitude from generation to generation—a single census is uninterpretable without the context of multi-year, effort-standardized data. Moreover, declines can be subtle. Those for both butterflies and moths in the United Kingdom are on the order of 1–2% loss per year (28, 68). Similar rates were recently reported for German (148) and Ohio (199) butterflies. Such rates are slow enough that the decline over an average person's lifetime does not become obvious until decades have elapsed, but fast enough to be ecologically and evolutionarily calamitous.

NOT ALL SPECIES ARE DECLINING

While long-term data suggest that many entomofaunas are in danger, eco-evolutionary forcings yield winners and losers. Warmer global temperatures will benefit many species, especially in temperate regions where some fraction of the biota has been limited by winter lows (e.g., 77, 82). Fifteen of the United Kingdom's 60 butterflies are increasing in range, and most but not all of these are increasing in abundance (194). Of the 673 species of moths assessed by Fox et al. (48), 160 species are thought to be increasing in abundance, geographic range, or both. The transition of a woodland to a savanna or grassland due to climate change will benefit grass-feeding insects. There are numerous examples of increasing insect abundance and richness (156). However, such examples should be carefully considered—many of the reported increases involve ecologically generalized species, while stenotopic and otherwise specialized species are commonly reported to be losing ground (64, 129, 156).

Insect populations in areas remote from direct human impacts may be little affected [e.g., as reported by the two bee studies cited above (76, 153)]. Successful intervention and restoration efforts on behalf of imperiled species in Europe and the United States (e.g., 44, table 1) suggest that we are not dealing with ubiquitous and insurmountable problems, e.g., regionally omnipresent pesticide residues, carbon dioxide concentrations, or other unseen forces. Recent restorative efforts in the United Kingdom have reversed the long-term declines of the Duke of Burgundy, Pearl-bordered Fritillary, and Dingy Skipper butterflies (194).

CONCLUDING REMARKS

Rates of biotic losses in the Holocene are accelerating at an alarming rate. Extinction rates for metazoans are already believed to be 100 to 1,000 times that of the background rates for our planet. Where comparisons have been made, authors agree that rates of losses for insects are on par with (34, 176) or even greater than (156) those of plants and vertebrates. While the loss of species is both grievous and ethically unconscionable for those with a love for nature, it is not extinction but the population declines of abundant species that will have the most serious ecological consequences for planetary health and function: Abundant species tether food webs, account for much of the interaction diversity in a given community, and carry out the ecosystem services described above (Figure 3) (34, 54, 55, 177, 178, 189, 209).

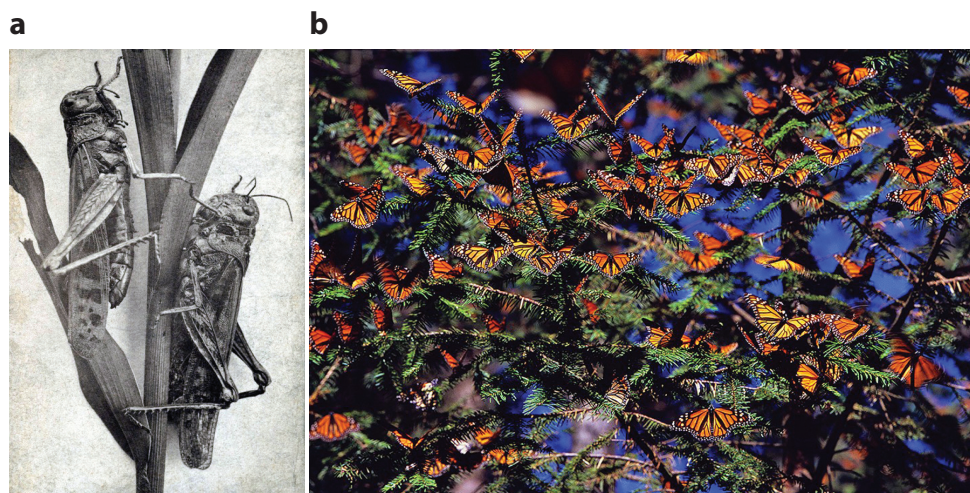


Figure 3

Reversal of fortunes. An important aspect of recent decline reports is evidence of steep population declines in formerly abundant species. (a) The Rocky Mountain locust (*Melanoplus spretus*)—regarded by many to have been among the planet's most abundant insects, with reported swarms comprised of billions if not trillions of individuals—was the first New World insect to go extinct (111). Figure adapted from Wikimedia (<https://commons.wikimedia.org/w/index.php?curid=18570553>)/CC-BY-SA 3.0; modified from an original image by Jacoby's Art Gallery (<http://www.mnopedia.org/multimedia/minnesota-locusts-1870s>). (b) The iconic migratory populations of the eastern North American monarch (*Danaus plexippus*)—among the world's most familiar and beloved insects—are in steep decline; its numbers have fallen steeply over the past two decades, so cataclysmically as to trigger a petition to have the insect protected under the United States Endangered Species Act. Photo by Michael Jeffords; reproduced with permission.

We do not yet know the geographic and taxonomic scope of the insect decline phenomenon, but presently, there is no evidence of a global, inexplicable driver of appreciable magnitude. However, rates of loss on the order of 1–2% per annum, as reported for multiple lineages and sites scattered across western and northern Europe (14, 28, 34, 48, 68, 148, 156) and the United States (199), are ecologically calamitous when summed across decades. Such rates are easily overlooked without decadal data, especially for taxa that naturally fluctuate, sometimes wildly, in number from year to year.

The best-documented and most interpretable insect declines come from areas of high human occupation, areas of intensive agriculture, and areas where wet forests are experiencing desiccating conditions due to climate change. Reported declines are roughly comparable for many terrestrial and aquatic insects, aerial and ground-dwelling insects, and nocturnal and diurnal insects. The Krefeld studies provide the best-documented longitudinal data for biomass: Across 63 sites in northwestern Germany, aerial insects have declined by 75% over the past three decades.

There is immediate need to disambiguate insect losses in areas of high human activity, where threats are generally understood, from those in wildlands. All but one of the 63 Krefeld sites is adjacent to or surrounded by agricultural fields. Equating losses of small European nations, with population densities of 200–400 people/km² and 40–70% of their land area used for agriculture, with conditions present in Australia, Brazil, Canada, and vast regions of the US West conflates and obscures. It is an overreach to extend findings from western and northern Europe to the globe, as was done in Reference 156.

Much uncertainty remains. The need for rigorous demographic data could scarcely be more urgent given the nature of the documented declines. The recent reports of declines in the High Arctic and Neotropics remind us of how little we know about insect health globally. Because many invertebrates routinely cycle through great fluctuations in abundance, getting credible population trend data may require efforts that extend over many years. As much as possible, sampling through entire field seasons is desirable, given the year-to-year vagaries of weather and insect phenologies. There is great need for the development of standardized sampling techniques, such as those employed by the Krefeld Entomological Society (68, 163). Data are needed from all continents, especially across ecological gradients, if we are to understand the most important causal factors. Collecting demographic data on vertebrate insectivores may provide valuable proxy data—and will have the advantage of being less volatile across years. Another important source of data will be efforts to repeat quantitative historical samples. While any single then-and-now comparison will be subject to stochastic factors, comparing data across independent studies will yield much-needed information.

While avian aerial insectivores, especially nightjars, swallows, and swifts, have declined in many areas (9, 127, 132), there is not yet an overwhelming signal that insectivorous birds have crashed globally to the extent that would be expected based on the more alarming reports (68, 109, 156) of insect declines. Nor is there appreciable evidence that insectivorous bat populations are collapsing in either North America or Europe due to food limitation.

Most attempts to identify the threats of insect decline have necessarily been ad hoc or correlative in nature. There is need for controlled experiments or otherwise carefully crafted studies that can clarify the relative importance of the various causal factors implicated in invertebrate (and insectivore) faunal losses. By way of example, the detrimental effects of pesticides and light pollution are difficult to disentangle from the collective effects of agricultural intensification and elevated human habitancy, respectively.

One unfortunate conclusion of this review is that many declines are occurring inside preserves (28, 68, 87, 109, 148, 159). Reserves, whether temperate or tropical, are often too small to buffer the effects of surrounding tracts of urbanization, nature-unfriendly agriculture, and other anthropogenic stressors. In the tropics, deforestation, agricultural intensification, and climate change are playing major (and synergistic) roles in diversity losses. The scale of current deforestation and agriculture is now so expansive in many tropical countries that they, separately or in combination, have the potential to change local and regional climates and further exacerbate the effects of climate change.

While many aspects of the insect decline phenomenon remain unquantified, especially its spatial extent, there is no uncertainty that climate change and its multifarious, knock-on effects pose a grievous and escalating global threat to insect diversity and ecosystem processes from the poles to the equator. Changes in precipitation will have enormous direct and indirect, immediate and time-lagged effects for insect (and plant) life. Where feasible, rewilding and establishment of biodiversity reserves and corridors, with special consideration given to preserves that include continuous elevational gradients, will be vital. Likewise, any efforts to make agricultural and silvacultural practices more sustainable and biodiversity friendly will have great dividends for insects and all the ecosystem processes that depend on them.

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