ANNUAL REVIEWS

Annual Review of Environment and Resources

The State of the World's Insects

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Annu. Rev. Environ. Resour. 2020. 45:61–82

First published as a Review in Advance on May 26, 2020

The *Annual Review of Environment and Resources* is online at environ.annualreviews.org

https://doi.org/10.1146/annurev-environ-012420-050035

Keywords

insects, agricultural intensification, climate change, pesticides, pollution

Abstract

This article reviews the present state of insects, describing their taxonomic position, cost, and value as well as the threats to their well-being. Insects are an important source of both ecosystem services and ecosystem disservices. Recent studies have indicated a worrying decline in insect species, especially in flying insects in the northern temperate region, and this has spawned much media attention. Some decline has occurred, it is clear, due to agricultural intensification, urbanization, overuse of pesticides, and global climate change. A decline would seriously affect the ecosystem services that insects provide. However, there is too little data to warrant the belief that all insects are declining everywhere. There is a pressing need for more basic research on insect diversity in the context of a changing world.

Contents

1. INTRODUCTION

Insects appear to be everywhere, and they seem eternal. They are a normal part of routine life: whether it is ants raiding your pantry, bees pollinating your apple tree, moths eating your clothes, or wasps spoiling a summer picnic. Insects have been thought to be an unchanging part of our world, and so it is with extreme urgency that recent reports have raised the alarm that everywhere insects may be in decline. This is alongside a fear that we are approaching a planetary tipping point, after which biological systems will inevitably decline (1, 2). This concern is not just scientific, as it is not only based on solid evidence, it is also emerging within the public consciousness—a general feeling that things are not what they used to be is seeping into that general view, at least in the developed world. This is probably best shown by the "windshield (or "windscreen") phenomenon," the sense that the number of insects crashing into windscreens has declined steeply over the past few years or decades (3, 4):

> Because insects are legion, inconspicuous and hard to meaningfully track, the fear that there might be far fewer than before was more felt than documented. People noticed it by canals or in backyards or under streetlights at night—familiar places that had become unfamiliarly empty. The feeling was so common that entomologists developed a shorthand for it, named for the way many people first began to notice that they weren't seeing as many bugs. They called it the windshield phenomenon. (5)

However, good quantitative data are scanty and the evidence is predominantly anecdotal (**https://ecologyisnotadirtyword.com/2019/07/07/the-windscreen-phenomenon-anecdata-is-not-scientific-evidence/**). In this review, I describe the diversity and role of insects and the recent flurry of concern about their possible fate, as well as place this into a broader scientific context of both time and place. Are insects really in decline globally? How good is the evidence? And what are the consequences if it is true?

Insects are relatively small animals (i.e., of the kingdom Metazoa), ranging in length from under 1 mm to some 20 cm. Within the animals, they are classified within the phylum Arthropoda (the arthropods), with an external hard skeleton, constructed of the polysaccharide, chitin, and they have jointed legs. They are in the arthropods along with the following subphyla: Crustacea (crabs, prawns, shrimp, etc.), Chelicerata (spiders, mites, scorpions, etc.), and Myriapoda (centipedes, millipedes, etc.) (6). They themselves are placed in another subphylum, the Hexapoda, along with a few other wingless groups [such as Collembola (springtails)]. They are considered to be " crustaceans that are mostly terrestrial," with their sister group being the obscure marine crustacean group, the Remipedia (7). This implies that Crustacea is not a natural group (monophyletic), so a new name was coined for the clade (Hexapoda + Crustacea), the Pancrustacea or Tetraconta (8). Insects appeared first in the Ordovician, approximately 480 million years ago, at approximately the same time as the first land plants evolved (9).

Insects were the first animals to evolve flight and have dispersed and diversified across most continents and into most niches from plant chewers to mammal parasites (10). They have a general ground plan of a segmented body made up of head, thorax, and abdomen. They have antennae, eyes, and feeding parts on the head; they have two pairs of wings (with the exception of Diptera and Strepsiptera, who have one pair of wings, and some wingless insects, both primarily and secondarily) and three pairs of legs attached to the thorax. They breathe, passively, through a system of thin tubes on the surface of their bodies that are open to the atmosphere (tracheoles), and they have reproductive parts on their abdomens (11). Within this general plan there is a large amount of variation (12). They are, inter alia, predators, herbivores, decomposers, and parasites, representing a wider range of life histories than the vertebrates. Their evolution of a plant feeding habit may have led to their massive diversification, as they had to diversify to deal with multiple plant defenses (13). They are defined as a class (Insecta) and split into some 29 orders. These orders can be split into three groups based on their development pattern: Some are holometabolous, with complete metamorphosis (i.e., larva, pupa, adult); others are hemimetabolous, with incomplete metamorphosis (i.e., nymphs with wing buds, which appear, otherwise, as adults and have no pupal stage); and there are some wingless insects that are ametabolous (i.e., no distinction between larvae and adult, no nymphs, with secondarily wingless insects not ametabolous). The largest of these orders are all holometabolous: Lepidoptera (butterflies and moths), Coleoptera (beetles), Hymenoptera (bees, ants, and wasps), and Diptera (true flies) (**Table 1**). They are extremely large groups, each one thought to have more than a million species, although many of them are not yet described. Coleoptera have the largest number of described species (14). They are within the largest group of arthropods, which, in turn, is the largest group of animals, and finally the animals have the most species of any kingdom across all the world's biota (**Figure 1**). Insects leave every other group seeming relatively small. Given that they account for such a large proportion of global diversity, it is no surprise that humanity is concerned about their possible loss.

Diptera: two-winged flies, with the hindwings modified into balancing organs—halteres; associated especially with decaying organic matter

Lepidoptera: moth and butterflies, with scaly wings; almost all herbivores as caterpillars (larvae) and nectar feeders as adults

Coleoptera: predators, herbivores, detritivores, fungus feeders, wood feeders, parasites, etc., with hardened forewings; adults and larvae often have different feeding habits and habitat preferences

Hymenoptera: ants, bees and wasps; most species are parasitoids, but some are predators and nectar feeders; include several groups that are eusocial insects

There is an old fable, recounted in a footnote of one of the most famous of all ecology papers (15, p. 146):

> There is a story, possibly apocryphal, of the distinguished British biologist, J.B.S. Haldane, who found himself in the company of a group of theologians. On being asked what one could conclude as to the nature of the Creator from a study of his creation, Haldane is said to have answered, "An inordinate fondness for beetles."

Although this anecdote has no basis in real evidence, and is neither admitted by Haldane or by the almighty, it emphasizes as well as anything that has been written the diversity of insects, especially beetles. There are more than a million described insect species, and the present estimate is that the total number of living species of insects is 5.5 million (16). Insects are the most taxonomically intractable of animal classes, and there are many undescribed species (17). This problem is influenced by the highest species richness of insects being in the tropics, especially in tropical rain forests, where they are often described as hyperdiverse (18). There have been many hypotheses suggested for this latitudinal gradient, with more species at lower latitudes (19, 20), but the general

Table 1 Estimated numbers of described species across the largest orders of insects (>1,000 species), as of 2019[a]

Order	Common name	Feeding habit	Numbers of described species
Blattodea*[,b]	Cockroaches/termites	Detritivores	5,710
Coleoptera	Beetles	Various	392,415
Dermaptera	Earwigs	Detritivores	1,982
Diptera	True flies	Various	160,591
Ephemeroptera	Mayflies	Aquatic predators	3,281
Hemiptera	Bugs	Herbivores/predators	104,165
Hymenoptera	Bees, ants, wasps	Predators/herbivores	152,677
Lepidoptera	Butterflies, moths	Herbivores	158,570
Mantodea*	Mantises	Predators[c]	2,447
Neuroptera	Net-winged insects	Predators	5,937
Odonata	Dragonflies, damselflies	(Aquatic) predators	6,650
Orthoptera	Grasshoppers, crickets	Herbivores	24,481
Phasmida*	Stick insects	Herbivores	3,270
Plecoptera	Stoneflies	Aquatic herbivores	3,930
Psocodea	Booklice, true lice	Parasites/detritivores	10,746
Siphonaptera	Fleas	Parasites	2,086
Thysanoptera	Thrips	Herbivores	6,157
Trichoptera	Caddisflies	Aquatic predators	15,233

[a]Orders Archaeognatha, Mecoptera, Megaloptera, Grylloblattodea, Mantophasmatodea, Raphidioptera, Zoraptera, and Zygentoma all have fewer than 1,000 described species each.

[b]Although most orders have more species in the tropics, orders with a clearly tropical bias are indicated with an asterisk.

[c]Many Hymenoptera are parasitoids; they develop inside other animals and kill them when they emerge as adults.

pattern is probably best explained by a mixture of some or all of the following: geographic area (that the tropics are larger than the temperate region), productivity (that tropical areas have higher energy, and hence this causes higher speciation rates), ambient energy (that tropical areas are more climatically stable), evolutionary speed (that heat causes organisms to speciate more rapidly at low latitudes), higher pathogen and predator pressure (encouraging more biotic filtering and speciation), and geometric constraints (that species' ranges tend to overlap more in the tropics, as this is in the middle of the globe, and so more species' ranges will overlap simply by chance). However, the actual diversity of tropical areas is made uncertain by an absence of information [with some exceptions (21–23)]. The main problem is distinguishing alpha diversity (the total number of species in a limited area) from beta diversity (the species compositional difference between areas—both nestedness and turnover) (24). Together they form gamma diversity (the number of species in a larger area, which is often the figure we are aiming to find, as it often includes a number of habitats). It is not assisted by the incomplete sampling that is made at any one place, thus inflating the level of beta diversity [i.e., pseudoturnover (25, 26)]. We cannot be sure of the baseline of insect diversity in the tropics and so we cannot yet calculate with any confidence the rate of change there (27). In the tropics, we do not know who the species are, what they do, or where they are found. Predicting their future rate of extinction is therefore likely to be wildly inaccurate.

The biomass of all insects across the globe is estimated to be approximately 200 Mt (million tonnes) of carbon (**Figure 2**). This is not particularly massive in global terms—compared with, say, plants, which are estimated to have one thousand times as much biomass (28)—but is approximately three times the weight of all humans, twice the weight of animal livestock, and more than twenty times the weight of other terrestrial vertebrates. Of this some 120 Mt is made up of

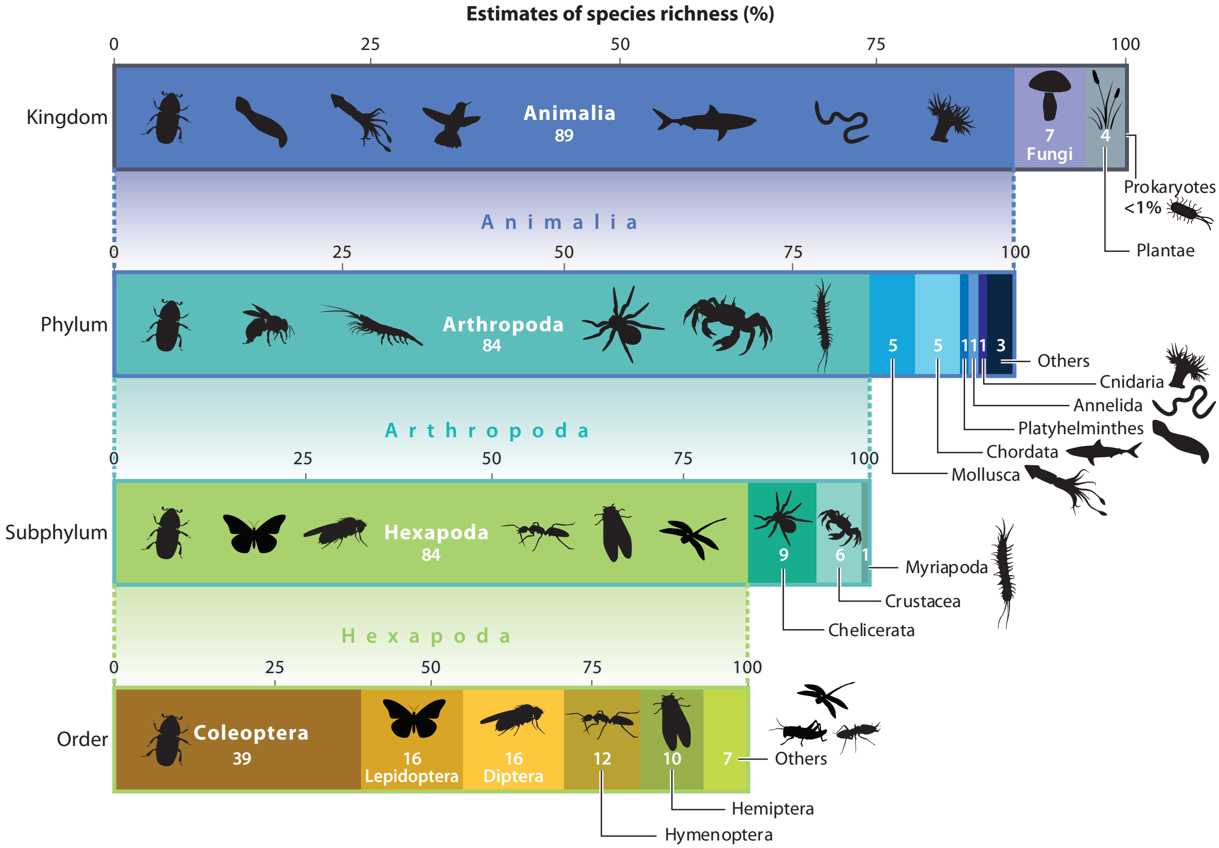

Figure 1

Present estimates of global biotic species richness for groups, expressed as percentage of higher taxonomic groups, at kingdom, phylum, subphylum, and order level. This is based on 2019 species estimates data (14) cited in the main text.

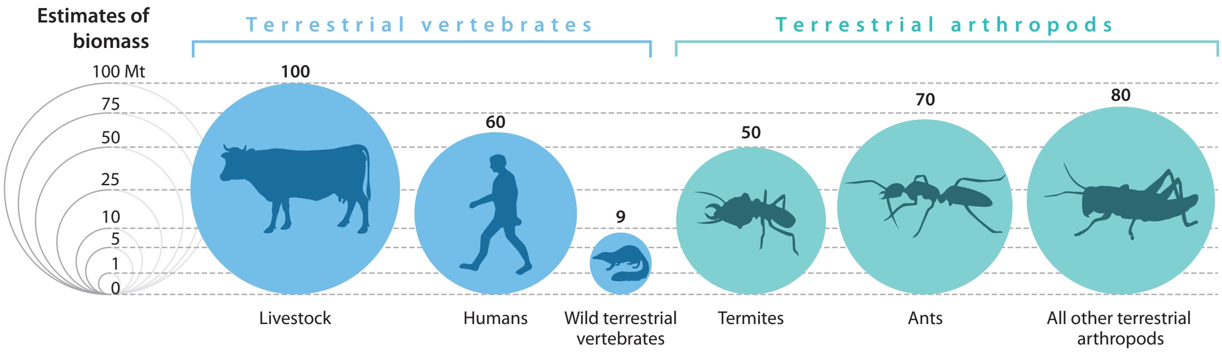

Figure 2

Estimates of biomass for groups of animals, contrasting vertebrate and insect biomass and emphasizing the important contributions of ants and termites. The single largest contribution is from livestock, emphasizing how important agriculture has become. Data from Reference 29, with permission from Wiley.

ants and termites (29). Given that these insects have only approximately 20,000–30,000 species between them (30, 31), this means they are disproportionately represented in the insect biota. If there are maybe 3–4 million species of insects, then the ants and termites make up approximately 1% of insect species but more than 50% of the biomass. The kings of the jungle are not the lion or the tiger, but the scurrying and tunneling hordes of social insects.

Ecosystem disservices: the direct and indirect contributions of ecosystems to human problems

Ecosystem services: the direct and indirect contributions of ecosystems to human well-being

2. INSECTS AND HUMANS

Insects influence human cultures in many ways. Most obviously, and perhaps the most persistent, are the many ecosystem disservices that insects have always provided, particularly to agricultural crops (32), timber (33, 34), and stored products (34). They are vectors of diseases (35), most famously as carriers of malaria; threats to hygiene, e.g., flies and cockroaches infecting food with bacteria (36); and general nuisances, particularly swarming flies (37). Insects were referred to in the earliest texts (38) and not always unfavorably. For example, dung beetles (scarabs) were sacred to the Ancient Egyptians (39). In the Medieval Era insects were often referred to symbolically (40), as markers of death and decay (41), or as examples of hard work and persistence (42). "Go to the ant thy sluggard, consider her ways and be wise" is from the King James version of the Old Testament (Prov. 6:6–8) and attests to ancient knowledge of insect diligence.

Up until recently, few insects were valued (i.e., for their ecosystem services). This was usually because they either provided food (43), pollination (e.g., honey bees) (44), and pest control (45) or were considered attractive or symbolic (46). However, in the past few decades, it has been realized that insects provide many useful ecosystem and cultural services: Many insects pollinate crops (47). These include bees, both social and solitary, moths and butterflies, wasps, and flies. Bees are thought to be the most important, with honey bees estimated to contribute more [estimated at $4,205 million in Europe in 2002 (48)] than other eusocial bees (49) and solitary bees (50). However, non-bee insects still contribute significantly (51), particularly in tropical regions [e.g., cocoa production relies on pollination by ceratopogonid flies (52)]. Hymenopteran and coleopteran predators and parasitoids can help in pest control (53), by feeding on pest species, such as caterpillars or Hemiptera. Soil insects (especially dung beetles and termites) assist soil fertility, by their transformation of soil (54), by soil bioturbation (55), by the way that they aid plant decomposition (56) and by assisting nutrient cycling (57) (**Table 2**). Termites in the tropics have a role somewhat analogous to temperate earthworms (58) and have a similarly high biomass, especially on wet acid

Table 2 Some examples of ecosystem services provided by insects[a]

Order	Ecosystem service	Feeding guild	Examples
Hymenoptera	Biological control	Predators	Formicidae (ants), Vespidae (wasps)
Hymenoptera	Biological control	Parasitoids	Ichnemonidae, Braconidae, Chalcidoidea
Hymenoptera	Pollination	Herbivores	Mostly Apidae (bees)
Hymenoptera	Seed dispersal	Scavengers	Formicidae (ants)
Hymenoptera	Bioturbation	Scavengers	Formicidae (ants)
Coleoptera	Biological control	Predators	Carabidae (ground beetles), Coccinellidae (ladybugs)
Lepidoptera	Pollination	Herbivores	Moths, mostly nocturnal
Diptera	Animal decomposition	Scavengers	Many families
Blattodea	Plant decomposition	Decomposers	Termites, dung beetles, weevils
Many	Human food	Many	Termites, locusts, beetle larvae
Blattodea	Bioturbation	Decomposers	Termite constructions

[a]This list is not exhaustive.

soils. Their contribution to ecosystem services has been valued at $47 billion a year (59). E.O. Wilson has referred to invertebrates generally, and with some justification, as the "little things that run the world" (60).

3. THE HISTORICAL RECORD

It is hard to examine the past, when we did things so differently then. Insects may well have been in decline in developed economies since before the Industrial Revolution (61, 62). The evidence for this is mostly from Lepidoptera (butterflies and moths), as they have been collected and studied for several hundred years in Europe (63) and other insects have been studied in detail only more recently. The causes of this decline are almost all hypothesized to be anthropogenic. They include urbanization and a shift from natural systems to agricultural ones. Perhaps the only good news for humans is that improved sanitation has reduced the number of disease-spreading insects, particularly in urban areas, and may well have contributed to the pre-antibiotic drop in human mortality in the nineteenth century (64).

It is hard to estimate the historical decline of insects in areas that were colonized by humans several centuries or millennia ago. Britain, for example, has been intermittently occupied by humans for more than 700,000 years (65). During most of that time, human environmental pressure must have been minimal, with populations of a few hundred thousand hunter-gatherers and no or little agriculture, but that has increased rapidly, in three phases. The first was from approximately 10,000 years ago, the Neolithic Revolution (toward the end of the Neolithic Period), when farming was first introduced to Britain and populations rose to more than a million: This also marks the beginning of systematic deforestation, as forests were cleared for agriculture (66), which must have had a major effect on insect communities, by removing and degrading vital insect habitats. Following that, although several thousand years later, there was another (the second) agricultural revolution, another period of agricultural intensification that raised the population from 5.5 million to 8 million during the eighteenth century. The third was the Industrial Revolution, which tripled the population to more than 32 million during 1801–1900. This was true of other developing societies in Europe and North America, but the growth was earlier and most evident in Britain. This means that Britain was the first to accelerate negative pressure on insects due to both agricultural intensification and urbanization. The effect that this had on insect populations is uncertain, as there are no records of insect numbers at that time; however, from what we know of the causes of recent insect decline, we can conclude that these human population rises were detrimental to insects, for the reasons discussed below. Britain may provide a conservative estimate of historical insect declines, as biodiversity started from a lower baseline, given that its biota was greatly reduced during the Last Glacial Maximum, so human effects may have been dampened by the general resilience of recolonizing faunas (67).

It seems that this background historical level of insect reductions was mostly not commented on (or just not noticed by scientists) in the literature before approximately 1980. This is partially due to a very different attitude to the natural world before then (68) and due to a lack of understanding of the many beneficial roles of insects. Insect conservation has been practiced for only approximately the past 100 years (69), and it is only recently that scientists and the general public have begun to be concerned about possible declines.

4. CATASTROPHIC DECLINE?

In the past few decades, there have been numerous scientific papers that have observed a sudden decline in the number of insects (70–74; see also **Table 3**). This interest has been stimulated in

Table 3 Number and proportion of papers with "insect decline" as a search term in Google, compared with the number with "insect" as a search term[a]

Decade	Decline papers	Total papers	Proportion
1950	0	20,400	0.0000%
1960	0	64,600	0.0000%
1970	3	182,000	0.0016%
1980	7	3,590,000	0.0002%
1990	5	950,000	0.0005%
2000	16	1,444,000	0.0011%
2010	163	840,000	0.0194%

[a]The proportional number has increased greatly over the past decade.

only the past decade. Before that, there was a minority interest in insect conservation, but it rarely saw insects as in critical decline (**Table 3** shows the sudden increase in the number of academic papers concerned with insect declines in the past decade). I present a critique of the evidence for this here. Is the decline really speeding up, or is it moving at the same rate but we are just finally becoming aware of it? This matters because an "insect Armageddon" (75) will require us to act quickly, while perhaps forgiving ourselves, at least temporarily, for the damage that we have already done. There is no doubt that human acts have caused a decline in insects; what is at question is whether there has been a sudden change in the rate of decline—whether we have reached a tipping point, the limits of resilience, where the world has lost many species and many ecological services permanently (76, 77).

The sudden eruption of wider concern was mostly triggered by one paper published in 2017 (72). This was a study based on Malaise trap (78) samples (a static net-like structure, which collects flying insects). The study was conducted for 27 years in 63 protected areas in Germany and showed that there was an overall decline of 76% in flying insect biomass over the sampling period, and a mid-summer decline of 82%. These were startling numbers, and the paper led to extensive media coverage (e.g., 79) and criticisms of its methods and approach (80). Overall, critics have pointed to two important factors. First, is that the studies generally only studied biomass, whereas the number of species lost would be more informative. The second is that it is hard to predict the trend in data from a few data points collected unevenly through time; it is not statistically valid to apply simple linear models and use those to predict where biomass will fall to zero. The general conclusion, however, was partially supported by numerous studies that showed a similar decline (74, 81, 82), all dealing with long-term longitudinal data, from agricultural and natural habitats. The last of these draws data from a 120-year study of urban Rome.

Studies of tropical insects are scanty but there is at least one relevant recent paper from Puerto Rico (83) that examined statistically comparable surveys between 1976 and 2012. They found that arthropod biomass decreased by 4–30 times and that this was related to temperature increases, which they suggested meant the collapse of food web structure in that system. However, the study has been heavily criticized for using only temperature as a possible cause of this decline and ignoring the effect of human disturbance and Hurricane Hugo. The critique also questioned the use of data. There was also concern that the data were not adjusted for differences in sampling effort, combining studies that are not strictly compatible, particularly within the temperature record. In the critique's reanalysis they found no evidence for a decline with temperature or for a collapsing food web (84).

A recent, but controversial, systematic review of insect declines reviews 73 studies of insect declines (70). Nearly all of these are from the United States or Europe. A great majority of them are studies of flying insects. They identified the larger orders as the most at risk (Lepidoptera, Hymenoptera, and Coleoptera), as well as several ecologically important aquatic orders (Odonata, Ephemeroptera, Plecoptera, and Trichoptera). All of these groups showed a greater than 40% decline. The overall conclusion was that 41% of insects were declining, and 31% were threatened (70). However, except for the Lepidoptera, the taxonomic coverage was poor in the orders. In Hymenoptera, it was heavily biased toward pollinator taxa (bumble bees and honeybees) and in Coleoptera toward dung beetles. This is not in itself necessarily a shortcoming of the review, but simply identifies that groups that provide useful ecosystem services to humans have been studied more carefully. However, there have been complaints about this paper (e.g., 85), emphasizing the limited geographical range and flawed study design, particularly their search strategy of examining only drivers that were associated with studies where there was a decline [i.e., potentially missing studies that showed no decline or an increase, thus increasing the chances of a type-one (false positive) statistical error].

Aquatic insects: insects that always have an aquatic larval stage (naiads). Some are aquatic as larvae and adults

An even more recent review examines changes in the distribution of more than 5,000 UK invertebrates over 45 years (86) and finds a complex set of different responses. They found that only terrestrial noninsect invertebrates showed an overall decline, and that terrestrial insects on average showed a range extension or remained static. There were many species that declined, for example many Gelechid moths (Lepidoptera), leaf seed beetles (Chrysomelidae), and soldier flies (Diptera: Stratiomyidae), and 10% of the species declined by 2.1% per year. Aquatic insects generally increased in distribution over time, after a drop before 1994—especially mayflies (Ephemeroptera)—probably as aquatic environments in the United Kingdom have since the mid-1990s had improved environmental policies and concerted management efforts. The study does not preclude the possibility that distributions are expanding or static in most cases, but individual species may be declining in abundance. However, there is likely to be a strong correlation between distribution extent and abundance.

The most recent nonreview quantitative paper on insect declines is, like the initial trigger paper, from Germany (71). This paper is more detailed with estimates of species loss, as well as abundance and biomass. It is based on sweep netting for 150 grassland sites and flight interception traps (which sample insects that fall when they hit a barrier) for 140 forest sites from 2008 to 2017. Their conclusion is that in annually surveyed grasslands, biomass, abundance and number of species declined over the study period by 67%, 78%, and 34%, respectively. In 30 forest sites, the annual inventories of biomass and species number—but not abundance—decreased by 41% and 36%, respectively. Rare species were affected most strongly, but abundant species did decline significantly. Sites found in areas with extensive agricultural land were also more affected. Although, again, it mostly dealt with flying insects, it seems to be the most convincing data yet showing broader geographical declines, even though it is still from a relatively limited area (Germany).

5. CAUSES

There is little doubt that the declines in insects are human-caused. There are no other major environmental changes that are not anthropogenic. The main threat to insects appears to be land use change, pesticides, and pollution, although climate change may become an increasing threat factor in time (62). The land use changes are multiple, but the most obvious are conversion of natural habitats to intensive agricultural (87, 88) and urban ones (89), the tendency for humans to tidy up seminatural and peri-urban ecosystems that they manage (90), overuse of pesticides (91), pollution (92), and global climate change (93). There is also an increased concern about the level of light pollution. These topics are discussed below.

5.1. Agriculture

The rate and intensity of agricultural intensification have accelerated in the past few centuries [globally, they expanded 466% in area from 1700 to 1980 (94)]. They have caused many changes in the composition of insect communities (81). There are several factors that are important, particularly in the temperate north. There is generally an absence of data from other areas.

First, artificial drainage has led to a reduction in wetlands, which are a specialized habitat, especially for aquatic insects (95), which are often poorly represented elsewhere. For example, in Britain between 1840 and 1890, 12 million acres (4.8 million hectares) of land was drained for agriculture (**https://www.trenchers.co.uk/products/agricultural-drainage-trenchers/a-brief-history-of-agricultural-drainage/**).

Second, the removal of trees, hedges, dry stone walls, woodland and scrub in agricultural landscapes are important microhabitats for insects (96–98). This is often associated with a reduction in size of field margins, vital for the insects and the birds that feed within them. There have been several studies on this, showing the importance of field margins for insect diversity for soil inhabiting, ground dwelling, and flying insects, especially staphylinid beetles, although this benefit was seen only in the margins and not in the field itself (99–102). It also emphasized the value to insects of hedgerows (99). This is of concern as the median size of fields is increasing worldwide, so that the proportional amount of field margin is reduced.

Third, there has been a general change from haymaking to silage making, for the winter feeding of livestock. Silage is compacted vegetable matter that is not dried and generally kept in a silo, and it is more intensive to make than hay and leads to a reduction in grassland habitats. This may lead to insect declines (103).

Fourth, the use of more inorganic fertilizers has led to the increased eutrophication of run-off water and of the habitats into which they feed. This has heavily influenced marine and freshwater systems. This particularly affects aquatic insects, for example, mayflies (Ephemeroptera) (103), which are highly sensitive to low oxygen levels. This is combined with increased stocking densities that have caused overgrazing and an increase in inputs due to supplementary feeding (104). This leads to both habitat degradation and eutrophication.

Fifth, there has been an increased use of pesticides in intensive agriculture. This is thought to have a major detrimental effect on pollinating insects, particularly bees (see below for a more detailed review). In addition, unless powerful insecticides are used there may be an increase in invasive pest insects (105).

5.2. Urbanization

Urbanization is increasing across the globe. It is estimated that the global urban area increased by 58,000 m^2 between 1970 and 2000 (106). It affects insects by leading to the fragmentation of habitats into small areas (107), and to both a simplification of communities (108) and their homogenization (108, 109), although such effects can be complex. For example, in tropical West Africa urbanization caused a decline in beetles and wasps but not in bees, but showed throughout a change in the relative proportions of species abundance (108). The effect may be influenced by the scales that are investigated, with Orthoptera in Paris being more negatively affected at greater spatial scales, as dispersive species were more greatly affected than sedentary ones (110). However, there may be some positive effects, especially in the increase in the number of urban pollinators (111).

5.3. Management Intensity

Natural, seminatural, or peri-urban systems are often managed intensively [particularly in nature reserves and national parks (112)], including regular mowing, weeding, and the clearing away of fallen vegetation. This has led to a reduction in insects due to a drop in the numbers of plant species (113) and a reduction in the amount of dead wood on the ground (114). This tidying up has included extensive salvage logging of timber, which has been shown to have detrimental effects on decomposer insects, especially saproxylic beetles (115). In recent years, it has become clear that the "tidying up" of urban, peri-urban, and rural environments, such as roadside verges and hedgerows, can cause a reduction in plant and insect diversity (116).

5.4. Pesticides

Pesticide use is implicated strongly in the loss of flying insects, particularly pollinators (117, 118). This is well established for older pesticides, such as DDT (119), but less so for more recent pesticides. However, there has been much criticism in the past ten years of the use of neonicotinoid pesticides (120), such as Imidacloprid and Thiacloprid (121). These pesticides, along with fipronil (a member of the phenylpyrazole family of pesticides) are probably the most widely used in the world in crop protection and veterinary medicine, because of their perceived low toxicity. However, the evidence for the effect of these pesticides especially on pollinating insects is growing (122), with rare species of wild bees and hoverflies more strikingly affected than common ones (123, 124), and there is no evidence that bees avoid neonicotinoid pesticides—they may even have a preference for them (125). The suspect pesticides all bioaccumulate in insects' bodies and therefore can be deleterious at low doses, with various effects, such as affecting bee navigation (126). This is perhaps where the insect decline, particularly in developed countries, is most concerning. The low dose effect on behavior means that ecosystem service changes may be long term and subtle.

5.5. Pollution

Pollution, although it is somewhat reduced now in many developed areas (127), is a global threat to insect well-being. Industrial pollution has long been known to reduce insect viability (128), and car exhaust fumes have been shown to still have this effect, particularly due to elevated levels of NOx (129). The most important forms of industrial pollution are heavy metals in soils and waterways (130), air pollution (131), aquatic pollution (132), and light pollution (133). The last cause is an emerging topic and requires more detailed discussion.

5.5.1. Light pollution. The excessive human use of lights has been recognized recently as a key driver of insect declines. Insects naturally use the light of the moon and stars in order to navigate (134) and are attracted to artificial lights (135, 136). This disrupts their mating, navigation, and migration behavior. UV light has especially been implicated, as it is particularly attractive to flying insects (137). Even black cars have been shown to be a problem (133, 138), as the matt surfaces polarize light, which causes insects to treat them as water surfaces. This is more of a problem in the Northern Hemisphere than the Southern Hemisphere, where there are far fewer urban and peri-urban areas (139). Light pollution is predicted, however, to increase with greater populations and more economic development.

5.6. Habitat Loss

The loss of habitats is, and has been, a major driver of insect loss. It may well be the single largest contributor to that loss. Although there have been few direct studies of insect declines due to this driver, it is well established that the hot spots of biodiversity are increasingly under threat

(140). It is estimated that some 22% of natural land has been converted to human use, with the greatest loss occurring in tropical forests, temperate woodland, Mediterranean forest, and scrub—with only boreal and tundra habitats being relatively unaffected (141). Although there have been many studies of the local effects of land degradation on insects (e.g., 142), there are few studies that examine the broader gamma diversity of an area. This is predominantly because insects are relatively intractable taxonomically, with many undescribed species, and so larger-scale studies have problems of repeatability and comparability.

5.7. Global Climate Change

The direct and indirect effects of climate change (predominantly global warming caused by atmospheric pollution, mostly from fossil fuel burning) on insect species are thought to be more complex than can be modeled, as they often have been, with simple linear effects with rising temperatures (143). They include phenological changes, such as earlier flight periods, enhanced winter survival, and changes in the tempos of development. Insects and hosts may lose their phenological synchronicity, although further genetic adaptation may well restore this. In some cases, warming may change the barriers that limit the ranges of species. Invasive alien species may colonize and spread in new areas. These are discussed in more detail below.

5.7.1. Phenology. Insects are expected to be highly responsive to climate change, because they have short life cycles that are strongly influenced by temperature. This has led to shifts in phenology, but not necessarily in predictable ways (144). Such shifts, associated with rising temperatures, have been found in butterflies, moths, and aphids (145). It was found that all three groups had had earlier adult emergence times but this was not buffered by more complex habitats (i.e., woodland versus open ground), as they showed the same pattern in a variety of habitats.

5.7.2. Range shifts. Another expected negative effect of global warming is the changes in the ranges of species and the possibility that many species will shift their ranges into regions beyond their present thermal tolerances. This range shift has been seen in British Odonata [dragonflies and damselflies (146)], where 35 out of 37 nonmigratory species showed northward range extension. The same pattern is found in butterflies (61).

A lot of research has examined environmental tolerances and how they may be challenged by rising temperatures (138). These studies have emphasized that different life stages have different tolerances (147). Niche width modeling (148) suggests many insects will be beyond their normal temperature tolerances as climate shifts. Consequences for the global biota are uncertain (149) but there is some evidence that tropical animals have narrower temperature tolerances (as they generally live in more climatically buffered environments, particularly those that live in rain forests) (150) and may be more affected than temperate ones in a warming world. Montane insects may be particularly impacted, as they shift their altitudinal ranges and many species may reach the limits of their range (151).

5.7.3. Invasive species. As the ranges of species change, coupled with the increased movement of human commerce, the impact of invasive species will inevitably increase. The consequences of climate change are thus numerous and include changes in methods of transfer and introduction of invasive species, the establishment of new invasive species, a change in the effects and distribution of existing invasive species, and changes in the effectiveness of control measures (152). Invasive species clearly may have negative effects on agriculture (as invasive pest species), but they may also cause the simplification and homogenization of existing insect communities. For example,

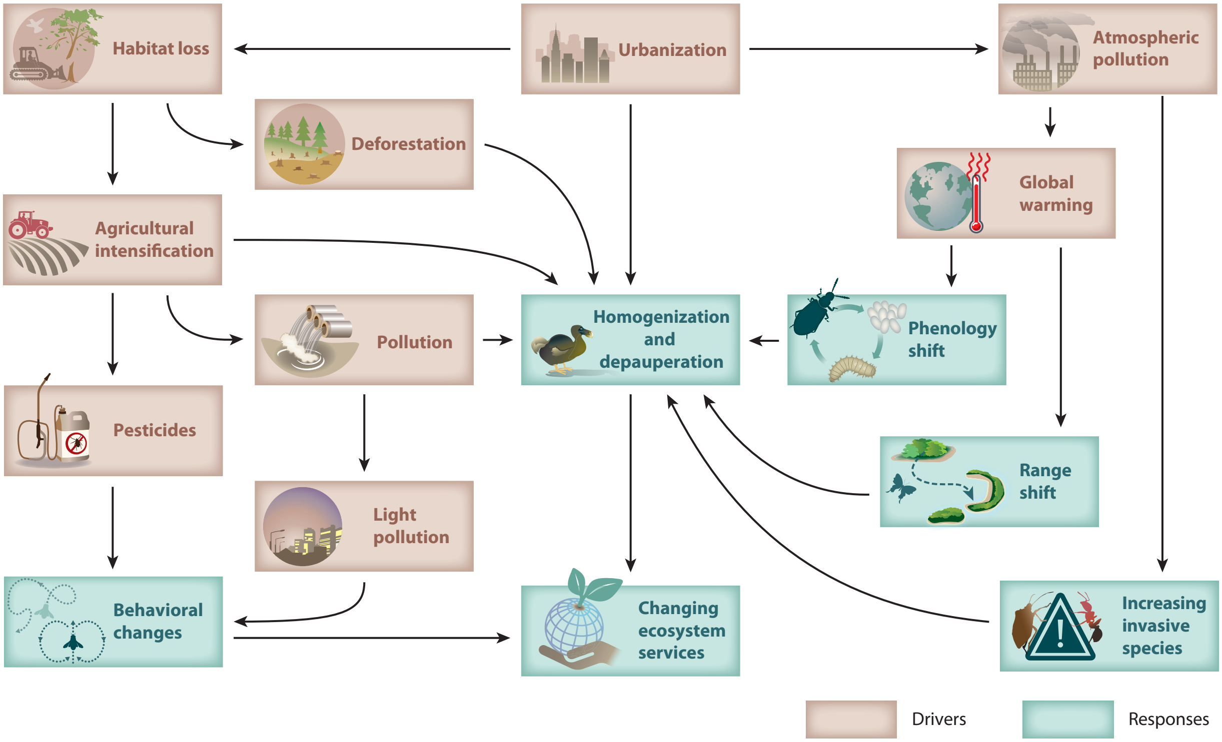

Figure 3

The network of interactions driving insect species richness and biomass. The brown boxes contain the drivers and the green boxes the range of responses. Depauperation is generally a loss of species, homogenization is when all the species in different areas become more similar.

the invasive little fire ant, *Wasmannia auropunctata*, has reduced the diversity of native ants across the Pacific islands that it has colonized (153).

6. CAVEATS

The most recent research suggests that some key factors are causing insect declines (**Figure 3**). This not only caused a reduction in insect diversity, but many factors also lead to ecological homogenization, as the species that survive (due to greater resilience, wider thermal tolerances, human introductions, etc.) spread like weeds across the world. These conclusions must be considered provisional, however. There are methodological problems with many of the studies (70), but the overarching problem is the limited nature of all the studies, in both time and space. Most research, including the most recent UK review, deals with one or a few decades of surveys and is from, at the most, a few European countries (86). Local extinctions are not global extinctions, and we should not be fooled into thinking that because a bad thing is happening here that it is happening everywhere. There may always be refugia from which species can recolonize areas, and apparently extinct species may well reappear. It is impossible to calculate extinction rates from the existing data, however. We still do not know how serious the problem really is for human well-being and the health of the planet generally. We can say that almost everywhere we examine it there is a decline, but we have only examined a small part of the potential problem. There remains

Ecological homogenization: all areas and habitats alter to have the same set of species (beta diversity declines) an imbalance in the funding of biology (154), with entomological research massively underfunded compared with vertebrates, given the relative levels of insect and vertebrate diversity.

The reality is that the depth of our ignorance of insects is staggering. We have described no more than some 20% of the species that are thought to exist (16), so we cannot easily identify which species it is important to conserve. We do not know whether we need many species to ensure that ecosystems function healthily, but the increasing consensus is that fewer species means poorer ecological services and a drop in human well-being (155). There is a pressing need to quantify more fully the contribution of insects to vital ecosystem services.

Insects are not in fact taxonomically tractable, even in the temperate north. The United Kingdom has some 27,000 insect species, and not all of them are described (e.g., parasitic wasps). This amounts to 300 years of work for many hundreds of taxonomists already. Perhaps insects are just too diverse, regardless of where you search for them, for generalizations to be possible (156). One additional major problem is that the taxonomy of immature forms is much less developed than that of adults, with many species having undescribed larvae. For example, the first Royal Entomological Society handbook [for species of adult longhorn beetles (Cerambycidae)] was published in 1952, whereas their only guide for larval beetles was published in 2019, and that only deals with higher taxonomic groups (**https://en.wikipedia.org/wiki/Royal_Entomological_Society_Handbooks**). This means that the decline of immature insects cannot even be guessed at. This also only complicates the problem that global warming will affect life stages of insects differentially.

This taxonomic impediment may be a purely academic point if insects disappear in great numbers. Then the problem of tractability will disappear along with the natural habitats. We are heading for a world that is a lot less various. Although there may be some uncertainty about his most famous quote, Haldane definitely said that the creator had a "particular fondness for beetles and stars" (157). We risk it being true only of stars, and within a generation. The truth is we cannot really say, and the data are contradictory, but it is reasonable for the global community to be alarmed.

Our lack of data from the tropics is unhelpful, particularly from tropical rain forests. Conversion of tropical forest to agricultural land reduces insect diversity and biomass (158), especially with the growing popularity of oil palm as a plantation crop and the direct conversion of rain forest to oil palm plantations. Although the response may differ from group to group, for most insect groups it is highly negative. For example, bats and bees generally increase in abundance but decline in species density in oil palm plantations (159), whereas most other groups decline in both species density and abundance. This may be the start of a process that has gone on for thousands of years in northern, more economically developed areas, and may lead to disproportional loss from tropical areas, which are more diverse to start with.

The decline in insects, whether it is local or global, will have serious consequences for ecosystems and, inevitably, the humans that depend on them. There are projected to be large changes in ecosystem services (160). This could include declines in pollination, soil fertility, and nutrient cycling, as well as an increase in the number of crop pests. The consequences of a decline in diversity, in itself, are uncertain and controversial, but high diversity is increasingly seen as a property adding to habitat resilience (161).

The effect may be greater in lower latitudes then higher ones, especially in the northern higher latitudes. The northern regions are still recovering from the Last Glacial Maximum, where insect species declined in the affected north. Some areas of tropics have had rain forest for 50 million continuous years (162). This, combined with the potentially greater effect on tropical insects of climate change, may mean that tropical regions will be more strongly affected (163). Given that we do not know the rate of even local insect extinctions in the tropics, this may mean that many species are lost before they are described (164). This emphasizes the need for more studies documenting insect diversity in tropical areas.

Strictly speaking, the question of the state of the world's insects has not been solved. It is a wicked problem in the terminology of the social sciences (165). It has the following relevant factors: (*a*) The question is not clearly stated; (*b*) there is no clear single answer to the problem; (*c*) we will never stop gaining data to answer the question; (*d*) every solution to the problem, however flawed, is in some way useful; (*e*) the solutions to the problem are inevitably incredibly varied as they deal with the responses of millions of species; (*f*) one or a few solutions cannot circumscribe the problem (e.g., the problem is unique, in the sense that there is only one world); and (*g*) whatever solution that we come up with will be wrong in some way. We have a lot to find out, and potentially little time in which to learn it.

SUMMARY POINTS

1. There has undoubtedly been a drop in local insect abundance, biomass, and species density, associated with anthropogenic activities. This is a general point and probably has been true for several centuries in developed areas.
2. Most of the decline so far described is for flying insects, especially pollinators, in the northern temperate region. However, these findings suffer from positive selection errors, in that declines are expected and so concentrated upon. This produces a statistical bias.
3. This decline may cause a local drop in insect-mediated ecosystem services: in pollination, soil fertility, nutrient recycling, predation, and herbivory. It may also cause an increase in ecosystem disservices due to greater numbers of invasive species.
4. There is some evidence that rare species are most affected and common species the least. There is also some risk of ecological homogenization as the more common species move into areas where the rare species have left.
5. It is somewhat precipitous to claim that there has been a sudden rate change in the global decline ("insect Armageddon"), as we have no global longitudinal studies. The most in-depth studies are limited in geographic scope or statistically or conceptually biased. These types of broad studies are essential if we are to calculate believable extinction rates. We also have very little information from the tropics or for nonflying insects. What has been found can also only be applied to limited areas. It is plausible that insects are in decline in all biotas but it is not proven.
6. The main drivers of this decline are human disturbance, conversion of natural ecosystems to agricultural ones, agricultural intensification, increased use of pesticides, and urbanization. The role of climate change is becoming more evident with species showing range shifts and phenological changes that are likely to make some species go locally extinct.
7. The largest drop is probably due to tropical deforestation as that is where most insect diversity is, although this is hard to calculate accurately as that biome is highly diverse and that diversity is poorly studied.
8. It is probable that many species went extinct in the tropics before they were scientifically described.

FUTURE ISSUES

1. Proper insect-friendly conservation management is needed, accounting for the specific needs of insects including encouraging plant diversity and ensuring a supply of dead wood for saproxylic insects.
2. Research is needed to help the insect taxonomic bottleneck, by finding ways of describing species at a faster rate, especially by incorporating DNA techniques into insect taxonomy using DNA barcoding and metabarcoding.
3. There needs to be a reduction and review of pesticide use throughout farming, particularly relating to neonicotinoid insecticides.
4. Improved land management is needed, with less tidying up of agricultural edges, verges, and reduction of so-called "weeds."
5. Further research into the effect of climate change on insects is needed, based on realistic models of projected climate change, combined with better data on insect species ranges and how they change over time.
6. Longitudinal studies of nonflying or rarely flying insects in natural or seminatural ecosystems are required, as these are less likely to be affected by pesticides or pollution.
7. More detailed global-level studies of insect declines and insect extinctions are needed.
8. A more measured approach to media coverage of insect declines would be helpful, including more science communication by entomologists.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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