

Insect declines in the Anthropocene

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Standfirst: Reports of stark invertebrate biomass declines prompted attention-grabbing news headlines about an ‘insect apocalypse’, fuelling public and scientific interest in the insect biodiversity crisis. However, substantial discussion ensues regarding the magnitude and generality of these losses. In this Viewpoint, five researchers offer their views on the insect decline debate.

MAIN TEXT

Within protected areas in Germany¹, insect biomass declined by approximately 75% between 1989 and 2016. Over a similar time period, arthropod (including insect) biomass in Luquillo rainforest in Puerto Rico declined by 4 to 60%, depending on the trapping method². These alarming results prompted a wave of additional research, some of which received robust criticism^{3,4} regarding flaws in sampling design. After calls for caution and recommendations for improved research practice were issued^{5,6}, subsequent meta-analyses ultimately painted a more complex picture with both positive and negative trends⁷.

What aspects of insect declines are still under debate versus generally resolved?

Charlotte Outhwaite: The evidence base for considerable insect declines is now substantial, which is no surprise given the magnitude and extent of human pressures on the environment and the declines seen in other forms of biodiversity⁸. However, the existing evidence is fragmented, with much of the data originating in well-studied regions such as the UK, Europe, and North America. So, although insects have been shown to be in decline in many parts of the world, the magnitude and extent of this issue is not fully understood across all geographical regions or for many of the less well-studied insect groups.

Lynn Dicks: Although everyone agrees that some insect taxa are declining in some locations, some high-profile publications have attempted to make global inferences based on what many would argue are insufficient data or flawed analyses. In one case, powerful rebuttals were rapidly published by at least seven teams of entomologists and insect conservation scientists, across seven different journals (for example, ref. 9). Unfortunately, the flawed original articles tend to become highly cited when subsequent researchers uncritically cite them as strong evidence for rapid or widespread declines.

Matthew Forister: Many papers on insect declines begin with the idea that substantial uncertainty remains regarding the status of insects; although a useful rhetorical device, it is naive to suggest that most insect species are stable, let alone increasing. Vertebrate populations around the world are known to be in severe decline⁸, and there is no reason why insects would not be declining at comparable rates given their often specialized ecological habits and small ranges. Much of the apparent debate about insect declines derives from a narrow focus on monitored populations which loses sight of the masses of un-monitored insects lost to development and other land use change¹⁰.

Eleanor Slade: There is no doubt that insects – like other animals and plants – are experiencing changes in their distributions and abundances, and in some cases going extinct before they are even described scientifically. However, the extent of these declines and the range of species affected remains unclear. The worrying declines of terrestrial insects in Germany¹ and Puerto Rico² are countered by more reassuring stable or even increasing trends, such as for aquatic invertebrates in Switzerland¹¹. Where I work, in the tropics, many species remain undescribed and their distributions and population sizes unknown, so it is impossible to know if they have declined or increased. One benefit of the insect decline ‘debate’ has been to bring insects out of the shadow of the vertebrates and into the spotlight for a while. The debate raised both public and political awareness of insects, their importance in the ecosystem and for humans, and the need to study and monitor insects globally.

Nico Blüthgen: A key open question is the cause of unexplained variation in trends across regions, ecosystems and species. Time series duration could be an important factor. Most time series are short, and where scarce long-term data do exist, they are poorly replicated. In some cases, ecosystems might have suffered severe losses in the past but stabilized at low levels; in

the absence of long time series, shifting baselines like these prevent researchers from accurately documenting declines.

What are the main drivers and mechanisms of insect declines?

Matthew Forister: Across broad spatial and taxonomic scales, the drivers of decline include climate change, habitat loss, and habitat degradation including light pollution, pesticides, and invasive species. The picture becomes more complex at finer spatial and taxonomic scales where there is less agreement on the relative importance of different factors in specific landscapes or for different species. There is a general consensus that the importance of climate change as a stressor will increase in coming years, but the importance of habitat loss and land protections should not be neglected. The butterfly populations we monitor in the western United States show surprising resilience in some of the most heavily modified areas. Such resilience serves as a reminder not to discount the value of any open lands, as there is still much to learn about which species will survive in the Anthropocene.

Eleanor Slade: In tropical regions, negative effects of climate change interact synergistically with land use change – particularly conversion of forest and savanna landscapes into pasture, monoculture crops, and urban environments. As ectotherms, insects are affected by the temperatures of the local environment and often have specific thermotolerances which can constrain their range and habitat. Many insects can no longer survive when forests are converted to plantations and the microclimate becomes drier and hotter. When forest patches become small and isolated, the edges can also become too hot; forest-dependent species cannot move out of the patches to cooler undisturbed areas as they cannot cross the hotter plantation matrix landscapes. Thus, connectivity of habitat patches is key to allow species to move across human-modified habitats, particularly as temperatures grow warmer.

Nico Blüthgen: Intensifying agriculture also entails a loss of hedges, verges or surrounding natural habitats; very few above-ground insect species (aside from known agricultural pests) survive and reproduce in arable fields. Beyond escalating insecticide use, herbicides also affect insects indirectly via their food plants or gut microbiome. Because insects are mobile, declines caused by agriculture extend well beyond the actual field margins into nearby grasslands or nature reserves¹². Drivers of declines within forests are generally much less understood¹³, but likely include climate change, particularly extreme events. Heat waves and drought can have direct physiological impacts (mortality and desiccation) and indirect effects through reduced food availability.

Lynn Dicks: Expert elicitation^{14,15} has been a powerful tool to show that entomologists generally agree the dominant threats to insects are land use change, agricultural intensification, climate change and pesticide and fertilizer pollution—in that order. The drivers related to agriculture, which invariably come out on top in these analyses, harm insects partly by simplifying landscapes and reducing the diversity of resources or refuge areas available for them, and partly by making the environment toxic to them. Fortunately, it seems possible to reverse insect declines by reducing these pressures.—For example, effective water quality policies such as the

European Water Framework Directive have reduced the impact of intensive agriculture and urbanization on water quality, which many argue has reversed the fortunes of freshwater invertebrates in western Europe⁷. Such pressures have not been effectively removed in terrestrial environments, except arguably in landscapes with a high proportion of organic farms, where insects tend to be more numerous.

Charlotte Outhwaite: Climate change is often presented as a growing pressure that will become more of a problem in the future, but there is already considerable evidence that climate change is impacting insect biodiversity now, in several ways. For example, warming is causing range shifts, changes in the timing of biological events such as emergence, as well as affecting individual development and survival. Additionally, climate change can interact with other pressures, such as land use change, leading to greater impacts on biodiversity than when these pressures act alone. For example, climate change can exacerbate the already hotter and drier conditions experienced in intensively managed farmland.

Are all insects likely to suffer from these anthropogenic effects, or are any more or less vulnerable?

Lynn Dicks: Not all insects are suffering on the increasingly human-dominated planet. Species found to do well – in terms of increasing abundance or range expansion – are often generalists, able to use a range of habitats or food sources. Some studies have found smaller bodied species, such as Dutch bees¹⁶, are more likely to have stable or increasing populations. ‘Winner’ species might also be pests, such as British aphids, whose numbers are relatively stable in agricultural land¹⁷, perhaps because they essentially eat the same things humans eat and are continually evolving to resist attempts to eradicate them.

Charlotte Outhwaite: Insects are a highly diverse group with considerable variation in life histories, habitat and dietary preferences, dispersal abilities and other characteristics. This variation makes it challenging to monitor and assess general patterns of change as any average trend obscures species-level variation. Some species will be able to adapt or are already well-suited to survival in human-dominated landscapes. Conversely, rare or specialist species often suffer the most under environmental change as they have more specific requirements than generalists. Rather than focusing on average trends, it is crucial to consider variation in responses within and between groups. For example, an observed increase in abundance will not always be a positive thing if it is being driven by an invasive or pest species.

Eleanor Slade: Vulnerability to global change is likely species- and habitat-specific. For example, each of three dung beetle species I study in Bornean Malaysia is vulnerable to a different threat. One is only found in pristine, undisturbed forests, and is thus threatened by deforestation. Another lives at the tops of the highest mountains in the area and must move higher upslope to escape rising temperatures. A third thrives in oil palm monocultures, but its reproduction might be harmed by exposure to anti-parasitic drugs that are given to the cattle grazing in the plantations.

Matthew Forister: As the planet warms, many cold-adapted species are expected to suffer as their preferred environmental conditions become more restricted in time and space¹⁸. Other general ecological traits (for example trophic level or habitat specialization) have been associated with variable rates of decline, but the amount of variance explained is often low. Further, complex interactions among traits are likely, yet poorly understood. For example, high dispersal ability and dietary flexibility could increase resilience to change, but those traits could also expose species to more stressors. Wide-ranging host plant generalists might be more likely than less dispersive host specialists to encounter pesticides on agricultural lands, and dispersive generalists are indeed among the declining butterfly species in some regions.

Nico Blüthgen: Consistent with expectations in other animals that species at the top of the 'food chain' are most vulnerable, predatory insects have been found to decline more than herbivores¹³. Habitat dependency is also a critical factor determining the risk of decline. Insects from rapidly changing habitats such as wetlands should be particularly vulnerable, although these groups are poorly studied. Species relying on grasslands, particularly those that are mown rather than grazed, are vulnerable to high mortality from modern machinery¹⁹.

What are the best approaches to studying insect declines?

Nico Blüthgen: Given that comparing trends across sites is challenging owing to incomparable methods, a particularly fruitful approach is to sample across replicate sites with standardized methods. One such initiative is the Biodiversity Exploratories project sampling across 300 sites in Germany^{12, 13}; this kind of replicated spatial comparison can fill knowledge gaps on limited temporal trends and the underlying drivers of declines¹⁹. More experiments are also needed to dissect the direct and indirect drivers of insect trends²⁰. A key question to explore with experiments is the scale dependency of declines, for example by testing whether metapopulation dynamics compensate site-specific losses.

Matthew Forister: Although experiments will always be an important complement to observational work, the monitoring of natural populations and communities has a central place in documenting insect declines and should be both maintained and expanded. Sampling the same locations year after year with standardized protocols is neither convenient nor inexpensive. However, many drivers (and interactions among them) happen at the scale of landscapes and large metapopulations, and change can only be detected through repeated sampling. Although long time series provide the richest insights, launching new monitoring programs is essential and allows early career scientists to generate hypotheses and introduce students to natural history in the field.

Charlotte Outhwaite: Additional long-term monitoring is urgently needed to better understand how insect populations are changing over time, but it will take many years to build up this kind of data. In the short-term, researchers can incorporate multiple existing datasets and approaches to assess the current state of insect biodiversity. One example is the GLObal Insect Threat-Response Synthesis (GLITRS) project, which is combining expert elicitation, meta-

analytical approaches and space-for-time assessments, to synthesize how different insect Orders respond to various anthropogenic pressures at the global scale.

Eleanor Slade: Combining traditional taxonomic and survey methods with emerging technologies such as next-generation sequencing, eDNA techniques, autonomous samplers, bioacoustics, AI and machine learning²¹ is key to documenting hyper-diverse and abundant insect communities. Crucially, there also needs to be a greater investment in entomology and taxonomy. This need is particularly pressing in many tropical countries, where I have met many young people who are keen to study insects but face a lack of funding and infrastructure. Thus, regional capacity building and equitable cross-boundary collaborations to enable resource sharing, knowledge exchange, and long-term monitoring amongst countries and organizations are key if we are to study insect declines on a global scale. Some examples of these initiatives include the [Status of Insects Research Coordination Network](#) and EntoGEM²².

Lynn Dicks: Beyond basic research, the scientific community needs to re-think conservation approaches to make them more applicable to insects. Biodiversity conservation typically works best when it is carefully targeted to individual species in locations where the pressures are well understood and conservation actions can be taken at manageable scales. This species-focused approach – used mainly in vertebrate conservation – is less tenable for insects because there are too many species and it is unlikely that the same management will work for every member of this hyperdiverse group. Indeed, changes over time in the abundance of common taxonomic groups of insects or spiders (orders or families) were found to correlate only weakly with changes in other groups at the same sites, indicating no overall group can be used as an indicator²³. Given these complexities, a trait-focused approach could be a more effective conservation strategy for insects. Such an approach would be guided by the common responses of insects with shared life histories, resource requirements, or morphologies, to environmental change. This focus will first require additional high quality, open access trait databases for insects and other arthropods.

What data gaps or knowledge gaps are important to fill in the next few years?

Eleanor Slade: Greater investment in insect taxonomy and ecology is needed to reduce geographic data gaps in the tropics²⁴. Alongside this capacity building, efforts should be made to increase awareness of insects' importance. Such education has made the importance of bees and butterfly pollinators well-known to the public, but it needs to be expanded to other insect groups. Conservation funding globally for each species of arthropod (which includes insects) is about 1000 times less than that of each species of mammal²⁵, and this discrepancy needs to change if we are to address these knowledge and data gaps. Insects must be brought into political and policy agendas so that they are included in conservation initiatives both regionally and globally.

Lynn Dicks: It seems astonishing that even in well-studied areas, the status of key ecosystem service providers such as wild bees (pollination), ground beetles (pest regulation), or dung beetles (nutrient cycling), remains poorly known. Monitoring these service providers is a high

priority but can be costly. Advances in eDNA and image-based or acoustic monitoring are promising and will hopefully enable more long-term datasets in the future. For now, volunteer efforts from citizen scientists have proved successful in the UK²⁶ and would be valuable in more regions.

Nico Blüthgen: Future insect monitoring should prioritize sites where restoration, natural regeneration and management efforts are ongoing, because these sites will reveal how declines can be mitigated. Nature restoration approaches, when accompanied by unmanaged control sites²⁷ can be fruitful large-scale experiments testing how insect populations respond to management or land use changes. Such insights into potential recovery could inform conservation strategies and optimize management to mitigate declines or even bend the curve upwards.

Charlotte Outhwaite: The highest priority now is to determine what can be done to slow and then reverse insect declines. Recovery is possible if appropriate actions are taken. For example, increasing abundance and occurrence of freshwater insects in some regions is potentially linked to improvements in water quality^{28,7}. Although these systems are still impacted by human pressures, the ability of policy interventions to mitigate declines is cause for hope for other environments. Another important knowledge gap is to understand the roles of microhabitats and microclimatic variation, as these much smaller scales are most relevant to insects. Large scale studies, limited by the coarse resolution of most global-scale environmental data, have not typically been able to consider microclimate variation. However, microclimate data from across large areas are becoming available and are likely to substantially improve the modeling of insect biodiversity change.

Matthew Forister: I am looking forward to advances in the collation, analysis, and visualization of data from rapidly expanding and widely distributed community science platforms such as iNaturalist. Access to these real-time data not only facilitates science by increasing geographic coverage, but also deepens engagement with the public. Further, the ongoing digitization of museum specimens provides an important historical baseline against which contemporary observations can be compared. Expanded temporal and geographic coverage of occurrence records is important for a number of pressing issues in insect ecology and conservation. One urgent need is to quantify extinction debt, which is the idea that observed species richness is out of equilibrium with current conditions and can be expected to decrease even if land use and other stressors are unchanging. Critically, more research is needed to understand the conditions under which population connectivity and insect movement are sufficient to maintain functioning metapopulations in modified landscapes.

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Competing interests

The authors declare no competing interests.

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<https://www.nytimes.com/2018/11/27/magazine/insect-apocalypse.html>

The Atlantic article on the insect decline debate:

<https://www.theatlantic.com/science/archive/2019/02/insect-apocalypse-really-upon-us/583018/>

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