The Extent and Future of Global Insect Diversity

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1 Introduction

The world is changing at an astonishing pace. Not since the emergence of life in the oceans has the Earth been modified so greatly and so quickly by one species – *Homo sapiens*.[1,2] Humans harvest a large fraction of global primary productivity;[3,4] we domesticate other species and grow them over vast areas in monoculture;[5] we release pollutants into the atmosphere that were stored underground millions of years ago;[6,7] and we knowingly and unknowingly spread exotic organisms around the globe.[8,9] Each of these changes has the potential to affect the global species pool, change local populations and cause extinctions. The impacts of anthropogenic change could be positive or negative for each affected species, but one thing is for certain – society ought to know what the consequences of such dramatic changes will be. If we do not understand the consequences of anthropogenic forces in the environment, we cannot take any steps to reduce or mitigate the negative effects of humanity on nature.

What do human-caused environmental changes mean for the species that inhabit this planet? To answer this question, we must know several essential pieces of information about biodiversity: where does it occur (*i.e.* what are the major biogeographic patterns on Earth?); how does it respond to global changes (*i.e.* what characteristics make particular taxa responsive or non-responsive to changes in the environment?); and what types of change is it experiencing (*i.e.* what are the major threats that species face and how do those threats interact?). Clearly, providing even superficial answers to these questions is a daunting task, and entire careers of researchers are devoted to addressing only parts of these questions. Nevertheless, from time to time scientists must ask themselves where they stand on these big questions – how much have we learned and what do we still need to know? Such surveys of scientific knowledge

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can form the basis of future research agendas and can motivate renewed effort to address questions that have long evaded quantification. In this chapter, we attempt such a survey for the most diverse and most abundant eukaryotic organisms on the planet – the insects.

New insect species, even entire orders of insects, are being discovered all the time.[10] It is impossible to predict accurately how many remain to be discovered, and whole regions of the planet have been incompletely surveyed for insect diversity and ecology. Individual ecologists do not typically have the funds or personnel to perform some of the legwork that is necessary to discover new species, uncover global patterns and thoroughly catalogue ecological threats. Nor are there many multi-person, organised projects to do so worldwide.[11]

It is shocking and, in many ways, depressing that science has sent astronauts to the moon and has extended the human lifespan by decades, but we lack a simple understanding of the number and type of organisms with which we share this planet. As will become evident, we cannot solve that shortcoming in this review. Instead, we synthesise what is known about the diversity and function of several insect groups. In pointing out the gaps in our knowledge about the causes and consequences of insect diversity for the functioning of ecosystems, we provide a guide for future research. Specifically, we focus on terrestrial species and on population size and species extinction. This reduces our task but ignores the abundant insect fauna in aquatic ecosystems and the myriad genetic and other non-extinction effects caused by global change. These are, of course, no less important, but we leave those factors for others to consider.

2 A Diversity of Species and Functions

Insects are small-bodied arthropods that inhabit terrestrial and freshwater ecosystems. (They rarely occur in marine systems with the exception of some intertidal and coastal regions.) Flight is a key ancestral trait, enabling their colonisation and use of a wide range of habitats. As ectothermic animals, insects are generally sensitive to environmental conditions, thus serving as useful indicators for many forms of environmental change. Below we briefly examine the broad range of ecological characteristics in insects to demonstrate their dominance on Earth and their potential significance to life processes worldwide.

First, insects have a high reproductive output and short generation times relative to other animals. These traits typically confer large population sizes and relatively rapid evolution and adaptation. Parthenogenesis (asexual reproduction) also can play an important role in rapidly increasing population size, and it occurs in many species.[12] This population potential makes insects tractable in ecological research.

One of the most notable features of insects is their large surface area to volume ratio. This high ratio puts them at risk of desiccation, thereby driving patterns of increased species richness in moist environments.[12] Yet, insects inhabit a wide range of moisture gradients and temperatures from the dry heat of deserts ($>50°C$) to dry, freezing temperatures below $30°C$,[13,14] and many disperse widely among different environments. To withstand environmental extremes, insects either tolerate the conditions or avoid the precise times and locations where extremes occur, and they achieve this using morphological, physiological or behavioural adaptations. Such adaptations include morphologies for minimising convective heat loss or gain, supercooling at temperatures below freezing and living underground. Numerous species also enter periods of quiescence or diapause as a strategy to avoid unfavourable conditions. Long-distance dispersal sometimes is accomplished with the aid of wind or non-powered flight.

Key to understanding the astonishing adaptations of insects is an appreciation of their long evolutionary history.[15] This history also has allowed, in part, their divergence into varied ecological roles and lifestyles. For example, some insects scavenge on dead organic matter, some feed on green plants and some are predatory or parasitic. Their mouth-parts include structures adapted for chewing, piercing, gnawing and sucking.

Nearly half of all insects are phytophagous, or plant-eating, and insects in the six largest orders derive much or most of their food from plants. Phytophagy has evolved repeatedly in the insect clade, probably from scavenging.[12] From the plant's perspective, this relationship is either negative or positive – causing reduced plant biomass or enabling pollination and seed dispersal. The sophisticated interaction between insects and plants has played a role in the diversification of plants and the evolution of insect structures.[13] In contrast to phytophagy, insects with a predatory lifestyle appear to be less diverse. In a thorough study of the insects of the British Isles, for example, less than 4% of insect species were predatory.[16,17] More diverse than predatory but less diverse than herbivorous, approximately 35% of the British Isles insect fauna is parasitic on animals. In poorly sampled areas, it is possible that the proportion of parasitic species could be higher, but we know about the biology, diversity and natural history of only a few important parasitic taxa (*e.g.* mosquitoes). Both predators and parasites have participated in complex co-evolutionary associations with host species and pathogens.[18]

This diversity of ecological roles among the insects makes summarising their response to global change difficult, but a consistently high level of specialization,[11] small body size and ectothermic nature enable some generality. We focus on these broad-brush traits to explore the risk of global change to insects generally. Although some species may flourish as humans modify the environment (*e.g.* red imported fire ants, cockroaches, *etc.*), others probably will become extinct, and the loss of species diversity will have broad consequences for the function of ecosystems and the services they provide to humanity.

3 Services Provided by Insects

The potential consequences of insect species loss stem, in part, from the abundant ecosystem services that insects provide, including pollination, food for higher trophic levels, including humans, control of weeds and insect pests, soil improvement, decomposition, seed dispersal and beneficial gene sequences and/or genetically based products. Insects also have the power to defoliate large swaths of forest or cropland, thereby affecting ecosystem processes such as nutrient cycling and fire frequency.[19] Though some insects are pests or transmit pathogens, many are beneficial – either directly or indirectly. For example, insects contribute more to agricultural value than they remove or degrade,[12] and insects pollinate at least 177 crops worldwide.[20] In the USA, ants also disperse the seeds of >50% of plant species in eastern deciduous forests.[21] A few authors have attempted to quantify the economic value of such insect functions to human society. Calculations by Losey and Vaughan,[22] for example, suggest that native dung beetles contribute $57 billion to the US economy simply from the burial of cattle dung! They also estimate that native, wild insects contribute $3 billion in US pollination services annually,[23] $4.5 billion for pest control of native herbivores and $50 billion in support of recreational activities such as fishing and wildlife-watching. Though this view of the importance of insects is highly human-centric, this rationale alone argues for careful stewardship of insect diversity.

Most ecological services are provided by insects that are either dominant (abundant) or that play a unique ecological role. Rare or endangered insects probably contribute to ecosystem function in a minor way, but we typically know little about their ecological roles.[22] Further, the abundance and role of insects – including those that provide ecological services – vary in space and time. For example, an insect can be a pest in one portion of its range but regulated or even rare in another place and time.[24,25] There also is some preliminary indication that species providing important functions are particularly sensitive to changes in the environment, including the transformational changes to ecological systems that we discuss below.[26,27]

The complexity of life histories and range of functions in insects has led some to argue for a process-based perspective on insect conservation and an eye to preserving diverse habitats and species interactions.[28] This perspective argues for conservation at large spatial scales – areas large enough to support insect activities but small enough to apply management techniques and tools.[28] A fine-scale approach to conservation may be appropriate in the preservation of individual, endangered species but is unlikely to capture the range of conditions necessary to maintain insect diversity. With a functional perspective in mind, maximising diversity is probably a wise conservation goal. From an ethical and aesthetic perspective, it also is easy to argue that a springtail or a locust is just as important as charismatic megafauna such as rhinos or lions.[29]

4 Global Patterns of Insect Diversity

The sheer abundance and diversity of insects, the product of 400 million years of evolution, is amazing. For example, locust swarms can consist of millions of individuals per hectare, and a single ant colony can contain millions or billions of workers.[30] In one square metre of pastureland, over 100 000 springtails have been collected.[31]

Of all described species, insects comprise somewhere between 80 and 95% of diversity, approximately two million named species.[32] Obtaining an estimate of the actual number of insect species has proven difficult, however. Erwin's[33] initial estimates of global diversity based on real empirical data (and some whopping assumptions) elicited a flurry of other attempts and refutations.[34] Erwin suggested that there could be up to 30 million insect species, but others say that the number is probably closer to 10 million.[35,36] Regardless of whether the total number of insect species is 2 million or 100 million, it means that we still have many species to describe. The principal factor limiting accurate estimates of species diversity is a lack of basic information on the taxonomy, distribution and biology of insects. There are concerted efforts to catalogue insect diversity, but not necessarily to tackle the Herculean taxonomic tasks of describing and naming all species.[37] Our view is that describing new insect species and providing precise taxonomic certainty are no longer necessary or sufficient for the conservation of insect diversity. Instead, knowing where that diversity occurs and how it varies spatially seems to be a much more efficient use of limited resources.

So where do insects live? The short answer is: in every terrestrial habitat on Earth, from near the North Pole to the South Pole, from Death Valley to extreme elevations in the Himalayas; in caves, salt lakes and pools of petroleum; from tens of metres deep in the soil to the very tops of the world's largest trees. Insects are indeed everywhere, but they are not equally everywhere. That is, both richness and abundance vary spatially and temporally.

Like most taxa, insects are more diverse in the tropics than in temperate regions, insect diversity varies along elevational gradients and there are more insect species in larger areas than in smaller areas.[34,38,40] The most striking pattern, the latitudinal gradient, has intrigued biologists since the days of Darwin, Wallace and Bates. But only relatively recently have there been quantitative assessments of the latitudinal gradient in diversity.[41,42]

Though the latitudinal gradient has intrigued some of the best minds in ecology (there are $\sim$2000 primary studies on diversity gradients in a variety of taxa), we still lack a fundamental understanding of why there are more species in the tropics than in temperate systems. Moreover, there are nearly as many hypotheses to explain the pattern as there are ecologists working on the pattern. Of the dozens of hypotheses to explain the latitudinal gradient in diversity, the following three are commonly cited. (1) It could be that the amount of available energy decreases with increasing latitude.[43] In the tropics, more energy, in the form of photosynthate, could lead to more individuals and more species. To most ecologists, this is likely to be seen as a leading cause of diversity gradients.[44] (2) Some authors have suggested that the latitudinal gradient arises because plant diversity is higher in the tropics. It has long been known that insect diversity is often correlated with plant diversity.[45] Thus, plant diversity may beget insect diversity by providing greater opportunities for specialisation. Another possibility is that the number of species per host plant is higher in the tropics.[36] However, global analyses of the number of insect species associated with plant species have found little evidence that the number of insects per plant could drive the latitudinal gradient.[46] Furthermore, disentangling the myriad ways in which plant diversity could drive insect diversity probably will require phylogenetically comparable plant communities in temperate and tropical sites.[11] (3) Some authors propose macroecological or metabolic explanations of the latitudinal gradient. These explanations posit that temperature might affect the speciation rate[47] or that body size–abundance relationships might create diversity gradients. These theories have received considerable theoretical, but little empirical, attention.[48,49]

Insect diversity also varies with elevation. Until recently, the general perception was that diversity declined monotonically with altitude.[39] But the patterns along elevational gradients vary among insect taxa, with nearly equal numbers of studies showing that diversity peaks at mid-elevations and that diversity declines with elevation.[50] Now that ecologists and biogeographers have at least begun to document the patterns in elevational diversity, the next critical step is to determine the underlying mechanisms that shape elevational diversity gradients. Many of the same mechanisms that shape latitudinal gradients in insect diversity probably also shape elevational gradients in diversity,[51,52] but that need not necessarily be the case. In fact, the mechanisms that shape diversity gradients, be they along elevational or latitudinal gradients, depend on the spatial and temporal scale that one considers.[50,53]

How close are we to knowing "the" mechanism that shapes insect diversity gradients? Our view is that as more data become available, from intensive surveys as well as climate data from increasingly sophisticated satellite imagery, our understanding of interacting mechanisms will be increased. There is no reason to think that a single factor drives all diversity gradients of the millions of insect species. Additionally, there are insect taxa for which the opposite trend – higher diversity in temperate zones than in the tropics – is observed (*e.g.* aphids, parasitic wasps).[16]

5 Threats to Insects Worldwide

If there are so many insect species, how can they possibly be threatened by human processes? And, of all of the organisms on Earth, why should we be concerned about the loss of the small-bodied and generally numerous insects? As we discuss above, insects provide essential functions in nature. As a group they are abundant, but as individual and specialised taxa, many of them are affected strongly by the environment and therefore may risk local or global extinction. This extinction risk arises from a number of factors including specialisation, small or widely fluctuating population sizes, sensitivity to thermal and chemical conditions in the environment and dependence on other species for basic life functions (see Table 1).

Table 1 Characteristics of insects likely to be high *vs*. low risk from global change, including land-use change, climate change and invasive species.

High risk	*Lower risk*
Small population size	Large population size
Narrow geographic range	Large geographic range
Widely fluctuating population size (exogenous population dynamics)	Regulated or stable population size (endogenous population dynamics)
Resource/habitat specialisation	Resource/habitat generalist
Narrow environmental tolerances (*e.g.* thermal tolerance)	Broad environmental tolerances and adaptive strategies for avoiding harsh conditions
High trophic position (*e.g.* parasitoid)	Basal tropic position (*e.g.* scavenger or plant-feeder)
Limited dispersal ability (*e.g.* wingless or small body size with limited flight distance)	High dispersal ability (*e.g.* winged with large flight muscles)
Involved in mutualism	Not dependent on mutualistic association with other organisms
Example: a small-bodied, specialised parasitoid with a small geographic distribution	Example: strong-flying butterfly that feeds on a number of abundant host plants and inhabits an entire continent

A number of studies indicate the role of early humans in influencing insect populations, through changes in the hydrological regime[54,55] and agricultural clearing,[28,56] for example. These changes were negative for some species, driving regional species losses, but were positive for other species. For example, agricultural clearing was largely considered beneficial for many species of Lepidoptera in Europe as they favour open conditions to closed forest in temperate regions.[57] As the various factors of global change interact and the extent of human modification of the environment grows, however, species losses may compound, further reducing global diversity.

Is there evidence of an emerging extinction crisis among the insect taxa? As with the debate over total insect diversity (above), there is little consensus about the rate of species loss within the insect clade.[29] Confirming a species loss also is dubious in insects because they are relatively hard to sample, many have small population sizes and many blink on-and-off in distinct habitat patches across a landscape.[28] Nonetheless, some authors suspect that 11 200 species have become extinct since 1600 AD and that perhaps at least 57 000 will become extinct in the next fifty years.[29,58] This rate of change, though uncertain, demands explanation and understanding so that future losses can be curbed or slowed by informed conservation management.

A variety of human-driven changes in the environment affect insects. Here we discuss three profound, and global, forms of environmental change: land use change, climate change and invasive species. In each case, we discuss potential vulnerabilities in insects and known responses.

6 Land-use Change

For those insects dependent on a particular habitat type, habitat loss due to land conversion means reduced availability of necessary resources. With reduced resources, we expect reduced population size and concordant species richness declines with incremental losses in habitat area. The principal drivers of habitat loss are agricultural conversion, land degradation from unsustainable agriculture, logging, urbanisation and human population growth. Habitat fragmentation, in contrast, is a by-product of habitat destruction. Some patches of habitat remain after a landscape has been modified, and these patches exist in a matrix of human-dominated ecosystems. When native patches are isolated from one another, each patch is vulnerable to penetration from organisms that persist in the matrix. Many of these organisms prey upon or compete with species that live in the patch.[59] With reductions in patch size and isolation from other patches, insects also move among patches less frequently.[60,61] For species that use a larger landscape to ensure regional persistence, this inability to disperse can cause decline or extinction.[62] We also expect isolated patches to have reduced species diversity relative to patches that are close together due to this process of dispersal limitation.

Using the traits in Table 1, we would expect species with specific habitat requirements and limited dispersal ability to be the most vulnerable to habitat loss and fragmentation.[63] The former implies harm from habitat degradation and an inability to persist in novel habitats; the latter implies an inability to escape affected areas by colonising other, suitable habitats. Some species, however, benefit from fragmentation by thriving in the matrix or in the secondary habitat occurring at the edge of the native-non-native border.[64] With greater intensification of land-use change over larger and larger areas, we would expect the negative effects of land use change to steadily reduce diversity, leaving behind a community composed of species with low-risk traits (Table 1).

Habitat loss and fragmentation take place in a wide variety of ecosystems, all of which contain insects. Many grassland and forest ecosystems, for example, have been converted to agriculture, forests have been lost to intensive logging and human settlement, and streams have been diverted or fragmented from hydrological projects. Habitat loss and fragmentation in the tropics, however, deserves special consideration as the diversity of insects occurring there is particularly large.[33,65] To make a rough, back-of-the-envelope calculation of species affected by tropical deforestation, we use a well-documented relationship in ecology called the species–area relationship. (This exercise was performed previously by Pimm[66] using estimates of deforestation that have since been updated.) The species–area relationship predicts the number of species occurring in a region using the surface area of that region and two empirically estimated parameters. For insect species living in continental areas, one of these two parameters – the one describing incremental losses in species richness with incremental losses in habitat area – falls in the range of 0.4 to 1.2, with an average of 0.7.[67] Plugging in the annual area lost to deforestation of 5.8 million ha year^{-1} in the 1990s[68] and using the average parameter value above, we predict extinction or severe declines in 4 million tropical forest species per year. Assuming that half of these are insects (probably a conservative value for the tropics) and that most tropical species are associated primarily with forest, we predict that 2 million insect species are impacted by tropical deforestation on an annual basis. (See also Ney-Nifle and Mangel[69] for a more sophisticated but similar approach to estimate species losses following deforestation.)

It is not clear if or how quickly these insect species will become extinct, however. Some may be doomed to extinction but hang on for some period of time due to high initial population sizes.[70,71] Others may persist elsewhere in the tropics if they have a large geographic range – that is, until a wider and wider region of tropical forest is logged and fragmented. At a constant rate of 5.8 million hectares deforested per year and a stock of 1150×10^6 hectares in 1990,[68] virgin or near-virgin tropical forest will be completely destroyed within 200 years and with it many of the insects species that reside there.

A number of studies support our back-of-the-envelope calculation that insect populations and species decline sharply in response to deforestation. Studies involving butterflies and termites, for example, indicate declines in species richness following the removal of tropical forest.[65,72,73,74,75] Still other studies suggest, however, that the quality of remaining patches is critical as is the dispersal distance of the individual affected species and historical land use in the area (*e.g*. Europe has long been converted to managed grassland, so the effects of modern habitat loss may be different or less than original loss).[76] The role of these mediating factors must be elucidated with further research, but a recent review of 20 experimental studies suggested that insects are consistent with theoretical expectations of land-use change.[77] The small body-size and short generation times of arthropods probably are the cause for the congruence of theory and empirical results.

As discussed above, a majority of insect species depends on plants for food resources, and we expect pronounced and direct changes in phytophagous species following land-use change. This expectation follows from the simple observation that the direct and immediate consequence of land use change is a shift in the plant community. Studies by Koricheva *et al.*,[78] for example, suggest that sessile species and specialists were strongly affected by changes in plant diversity in Europe, and plant species composition was the strongest factor in determining insect species change following land-use change. Such results suggest that much conservation of insect diversity can be accomplished by maximising the conservation of plant diversity.[28] This generalisation may even apply to species that indirectly consume plant material (*e.g*. scavengers) as leaf quality and the diversity of leaf species present in the leaf litter may maximise the diversity of the decomposing community.[79]

7 Climate Change

Increases in emissions of greenhouse gases from fossil fuel combustion and land-use conversion are changing regional patterns of temperature and precipitation.[6,7] In general, the climate is expected to become warmer and wetter, but the intensity of warming and precipitation will vary strongly by geographic location such that some areas actually will become dryer or cooler. Climate change is truly transformational – every organism will experience climate change – and many systems are responding to climatic modifications already.[80,81] The challenge for ecologists is understanding what features put populations and species at risk of extinction, what ecological processes might be disrupted and what conservation steps can be taken to mitigate negative impacts of climate change. As with land-use change above, potentially severe consequences of climate change argue for policies that slow or reverse carbon emissions, thereby preventing irreversible ecological damage. Using the traits in Table 1, we expect species with limited environmental tolerances (particularly thermal tolerances), resource specialists and species with specialised nutrient requirements to be the most vulnerable to climate change.[82–84] By vulnerable, we mean those most likely to experience population declines – declines that could lead to local extinctions, geographic range shifts or contractions, or even species losses.

The geographic ranges of several insect species have shifted in recent times, while others have contracted due to local population losses.[85,86] A range shift occurs when the equatorial edge of a geographic distribution becomes unsuitable while the poleward edge increases due to a shifting mean climate. That is, conditions systematically change across all of the habitats occupied by a species, pushing it to higher latitudes. Range contractions occur if populations decline at the equatorial and poleward range edges, and holes can appear within a species' range if centrally located populations are severely perturbed by climate change.

Changes in the distribution of functionally important species, endangered species, disease vectors and pest species all have potential ramifications for society. A recent study indicated that 13–85% of butterflies and other invertebrates could be threatened with extinction under climate change within 50 years, assuming a low-to-moderate amount of change and limited dispersal in the affected organisms.[87] This projection is based on the known geographic ranges of insects in Central America, South Africa and Australia; it estimates the distribution of these species pre- and post-climate change and uses the difference in occupied area in calculations with the species–area relationship. For all species on average, the authors predict that 22–37% of taxa will become extinct from climate change, suggesting that insects might be particularly vulnerable by comparison with other species. As with the rough calculation of extinction risk for land-use change above, these extrapolations are preliminary, but they are based on a well-documented empirical relationship. The sheer magnitude of these values suggests that much work needs to be done to understand the processes driving such dramatic change.

The view of climate change as a driving force of extinction, however, should be contrasted with its potential to cause increases in some species. Increases are likely to occur in species that tolerate changing conditions and exploit new niches as they come available. These species may have traits like those listed in the second column of Table 1. Unfortunately, some of the species that humanity fears the most – those with economic or human health consequences – might possess these very traits.[88] For example, evidence is accumulating that forest pest species are benefiting from climate change in regions where they did not previously occur and are causing extensive economic damage. The mountain pine beetle (*Dendroctonus ponderosae*) is a species that causes mortality of western pines in the USA. Potential hosts for this species extend into the Yukon and Northwest Territories, Canada, but outbreaks of the beetle have been restricted to southern British Columbia, Canada. Historically, winter temperatures in more northerly climates are thought to be too low for population persistence of the beetle, and extreme low temperatures are thought to end periods of outbreak in the historical beetle distribution.[89,90] Global warming may release this limitation on northward range expansion, however, enabling geographic spread of beetles and lengthening their outbreaks.[86] Recent records support this conclusion as pine beetle populations in British Columbia are steadily growing and damage has accumulated to record levels.[91] The outbreak probably will end with the depletion of suitable hosts.

Large-scale processes such as range shifts, range contractions, and altered pest–host relationships emerge because of localised processes playing out in many specific locations. A number of local factors can be important, but principle among them are the direct effects of changing climate on insects themselves. For example, the growth rate of individual insects varies linearly with temperature over a range of non-lethal values.[92] The slope and range of this linear function varies adaptively among species and potentially varies among populations within a species[93,94] The linear relationship leads to the expectation that warmer temperatures will increase individual performance and insect population size,[95,96] at least for temperatures up to the lethal limit. Extreme heat – those temperatures near the lethal maximum – also is predicted, either if the climate warms on average or if it becomes more variable.[6] High heat causes the denaturation of insect proteins, decreasing insect performance, and ultimately death.[97] Some insects have adaptive traits for physiologically moderating such conditions or behavioural mechanisms for avoiding them. To a degree, therefore, behavioural or developmental plasticity may reduce the direct effects of extreme temperature.

Temperature also has an effect on insect activity,[98] potentially affecting the ecological functions that insects perform. Individual insects are able to move about in the environment when temperature conditions fall within a narrow range.[99] Some species – including honeybees – extend the lower limit of this range with muscular shivering, but the body temperature of most insects is a simple function of ambient temperature. At the upper end of tolerable temperatures, for example, desert ants are active in the morning and evening so that the hottest hours of the day are spent in underground colonies.[100] Increased daytime temperature, therefore, could shift or modify available foraging times, affecting the dispersal of seeds. The activity of day-flying insects that pollinate plants also could be altered if temperatures shift outside the temperature range enabling flight. Figure 1, for example, shows the relationship

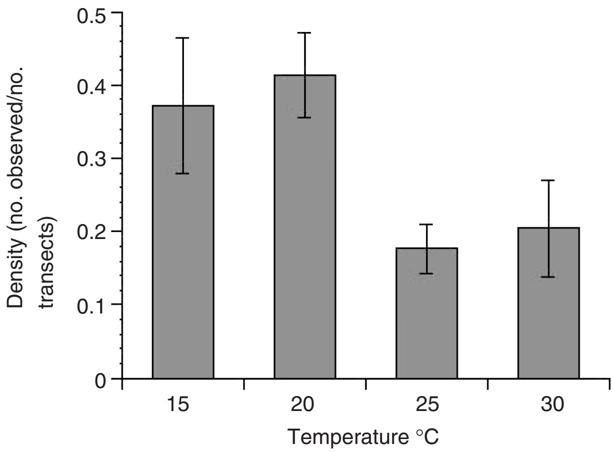

Figure 1 Relationship between the density of butterflies (*Eyrnnis propertius*) observed in flight and the ambient temperature recorded near the ground.[101] Bars are standard error. Data were recorded over three years at six locales on Vancouver Island, British Columbia, near the edge of the species range. Researchers counted flying butterflies along survey transects during sunny conditions. The number of 30 m transects surveyed in each site was standardised by habitat area so that density comparisons could be made among sites. A non-parametric statistical test equivalent to ANOVA (Kruskal–Wallis) indicates that butterfly density varies with temperature ($p = 0.02$) such that fewer butterflies are active at high temperatures. Survey date also describes some of the variation in butterfly density with fewer butterflies observed later in the season as temperatures increase and the end of the butterfly flight season approaches (regression analysis of density versus date: $R^2 = 0.08$, $n = 97$, $p = 0.005$).

between ambient temperature and the density of butterflies (*Erynnis propertius*) observed in flight during three years of surveys.[101] Observations were made only when conditions were warm enough to sustain flight, but extremely high temperatures correlated with diminished flight. If diminished flight occurs across many species, pollination and other functions may decline, affecting plant fitness and ecosystem productivity. If flight is diminished at the poleward edge of a species range, this process could limit colonisation and range shifts in flying insect species.

Reductions in insect population size also diminish activity-based ecosystem functions. A simple survey of the density of native, seed-harvesting ants in Eastern North America, for example, indicates declining population sizes at low elevations, presumably in response to increasing temperatures (Figure 2). If such species become locally extinct, the consequences, in terms of seed dispersal and nutrient cycling, could cascade across trophic levels.

The indirect effects of climate change on insects could be as or more pronounced than the direct effects. Indirect effects are those changes modified by other species with which an insect interacts. For example, the timing of plant

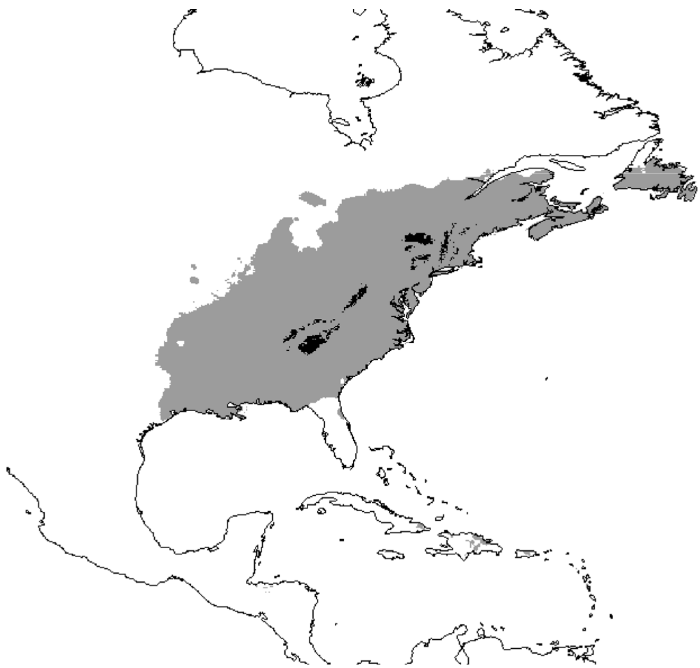

Figure 2 Range shifts of the forest ant *Aphaenogaster rudis* based on MaxEnt models[133] incorporating 78 occurrence points and climate variables considered to be important to determine distributions of ants at large spatial scales, including: mean annual precipitation, mean annual temperature, maximum temperature of the warmest month, minimum temperature of the coldest month and precipitation of the wettest/driest months. Future conditions represent the predicted mean conditions from the Canadian Climate Center GCM (CCM3) in the year 2100 under an assumption of doubling of CO_2 concentrations downscaled to *c.* 1 km resolution from *c.* 50 km using spatial interpolation. Grey area shows the predicted current distribution, and black area shows the predicted future distribution in 2100.

development may change at a different rate under climate change than insect development. Assuming historical adaptation of insects to the timing of their host plants, particularly in temperate regions, asynchrony with plants could reduce the developmental success of some herbivores.[95] As half of the world's insect fauna consume plants, this type of indirect effect could profoundly alter insect diversity in seasonal environments.

Changes in the atmospheric concentration of greenhouse gases, notably carbon dioxide, also may indirectly affect insect herbivores. Increases in atmospheric carbon enhance plant growth by increasing the availability of an essential element in photosynthesis. Most studies have found changes in the carbon-to-nitrogen ratio in leaf tissue under elevated CO_2, suggesting that herbivores will need to eat more plant biomass to acquire a constant amount of nitrogen.[102] Limitations on available foraging time, therefore, could reduce insect performance.[103] Research is mixed on the effect of CO_2 to change the concentration of chemical defences and other plant compounds that affect plant quality.[104] Further study in this area is needed so that general results of CO_2 effects on plant-feeding insects can be predicted and managed.

8 Invasive Species

Though some authors suggest that the threats posed by invasive species may be small in comparison to other forms of global change,[105,106] invasive species are known to threaten terrestrial, freshwater and marine ecosystems worldwide.[8] Thirteen of the one hundred world's worst invasive species are insects; of those thirteen, five are ants.[107] Such a high number of invasive insects is potentially consequential because invasive insects can affect other species with which they compete or prey upon. For example, the invasive fire ant reduced native ant biodiversity by 70% and non-ant arthropods by 30% in Texas.[108] Similarly, the invasive Argentine ant reduced native ant diversity by at least 65% in California.[109]

Other well-known invasive insects cause declines in native diversity,[110] inflict economic damages in terms of crops and forest products[111] and demand economic resources by households and governments to mitigate their effects or attempt their control. For example, billions of dollars have been spent in the USA to control the red imported fire ant, to no avail.[111] The prominent conservationist and myrmecologist E. O. Wilson has quipped that the failed attempts to control the fire ant are "the Vietnam of entomology".[112] A study using a well-known empirical relationship in ecology called the species accumulation curve, together with the relationship between the number of introduced insects and the amount of US imports, calculated that the number of species introduced to the US will grow over time.[113] Fitting historical data on invasive insects, this study suggests that at least 115 new insect species are likely to be introduced to the USA by 2020.

Reducing the flow of insect invaders will be difficult as their small size, ability to persist in a range of materials and diapause strategies facilitate their transport by people and industry. Regulatory agencies in the USA, for example, such as USDA APHIS are charged with protecting US agriculture from insect invaders, but their methods of permitting and sporadic inspection are probably insufficient given the potential pathways of introduction and the inconspicuous nature of many insects. Other voluntary, international agreements such as the International Plant Protection Convention impose policies such as fumigation treatment of wood pallets used in international shipping (Internal Standard for Phytosanitary Measure #15). These treatments aim to reduce the international transport of bark beetles with the potential to harm logging industries. The rate of bark beetle introduction by this method is estimated at one species year^{-1}, and a total of 25 bark beetle species have been introduced within the last 21 years.[114] Unlike the bark beetle, potential invaders with little or no economic value are generally unregulated.[115]

Invasive species that affect the structure of plant communities probably have the largest effect on native insect species by fundamentally changing the habitat itself, and such a transformation already is under way as 23% of plant species in the USA are non-native.[111] Local extinction of native plants used by specialist insect species also is a potential consequence of plant invasion.[116]

The invasions of insects and plants often are linked. For example, many insects were introduced as biological control agents to limit the spread or impact of invasive plant species. These attempts have met with limited success,[117] and some have even had detrimental non-target effects on native plant species.[118]

9 Where Do We Go from Here?

Insect diversity is everywhere, and much of humanity relies on insects to perform critical ecosystem functions. Insects are vulnerable to extinction, particularly in response to the transformational changes of habitat loss, climate change and invasive species. What is the best, most efficient path forward to document and understand the causes and consequences of insect biodiversity and its disappearance? We suggest that the following steps are needed to better understand insect diversity and its endangerment. We acknowledge that meeting these goals may be difficult, but science has conquered many difficult goals before. It's time to set high goals and achieve them in ecology also.

9.1 A New Taxonomy

Organismal biology is slowly losing taxonomic specialists who can perform identifications, and several authors have called for a new taxonomy specifically directed toward the study of risk assessment.[119–121] This new taxonomy would be more strategic – focusing on hyper-diverse or little explored areas. Moreover, rather than cataloguing new species in expensive and little-read journals, taxonomy and systematic surveys should be made freely available online to the conservation and ecological community.[122] This new taxonomy also should attempt to generalise from some groups to others – to derive general principles[123] – and it should provide morphological keys that are accessible to untrained practitioners on the ground. New technologies such as those involving portable, digital databases that can be taken into the field or devices that perform genetic-based identification on the fly are examples of new tools that someone performing an insect diversity survey might implement.

9.2 Systematic Sampling

Intensive sampling and local inventories of little-studied regions of the world, including sub-Saharan Africa, much of tropical Indonesia and the extreme forest canopies of old growth forests is much needed. Most ecologists and taxonomists live in developed countries and study patterns of diversity at relatively high latitudes. This new systematic sampling also could employ local peoples and establish a network of parataxonomists throughout the world. Technology transfer or funds for international collaboration between developed and developing countries is desperately needed to quantify diversity in hotspots of biodiversity. Quantitative tools for measuring and comparing diversity only now are emerging from their infancy and need further development[124] so that we can assess the extent to which particular locations have been undersampled and can more accurately compare diversity between and among locations.

9.3 Synthesis of Biodiversity Inventories

Because of limited funds, inherent interests and a fondness for particular locations, ecologists and entomologists often focus their research efforts on a particular taxon or on a particular region. The work gets published in peer-reviewed journals, but such data are infrequently combined and synthesised across locations. Such a combined database could be useful in initially assessing global patterns of biodiversity (at least until better surveys are available as described above).[121] Such a synthesis has been done for birds[125] – an interesting and well-studied group but one that is not as diverse as insects. We propose accomplishing the same task with particular insect taxa that are relatively well known and well studied. For example, a global database on butterfly diversity, compiled from field guides, ecological studies and collecting trips would be invaluable. To our knowledge, no such database exists except where compiled for individual regions of interest. Similarly, detailed faunistic surveys of particular places, such as the All Taxa Biodiversity Inventory in the Great Smoky Mountains National Park, USA, could be initiated at other locations.

9.4 Multi-factor Research

Because the various forms of global change act in concert, it will not be sufficient to measure and investigate each effect in isolation. A growing body of research shows that each of these factors can affect biodiversity in a synergistic way that may outweigh their independent effects.[126] Few experiments, however, manipulate multiple factors of global change in a factorial design. Such studies are needed to identify non-linearities and thresholds in species' responses. For example, studies that investigate multiple, interacting effects such as carbon and nitrogen fertilisation have been initiated, including studies that assess their impacts on herbivorous insects.[127–129] These studies also could be further integrated, for example, with the effect of resource availability due to habitat loss or invasive species.

9.5 Generating a Trait-based Understanding of Global Change

A particularly productive avenue for future research would be to identify the ecological traits – rather than the individual species – that make insects susceptible to habitat loss, climate change and invasive species. For example, species may vary in their ability to shift their geographic ranges under climate change in a way that can be predicted by their ecological traits and evolutionary history.[94] Invasion biologists also have been searching for traits associated with invasive species[130] and, to a lesser degree, susceptibility to invasive competitors and predators.[113] Complicating and confounding factors will mask the relationship between traits and functions, and these factors also must be understood. For example, particular ecological traits have been associated with some invasive species, but other taxa with these same characteristics have failed to take hold when introduced. Though potentially confounded with other factors and conditions, such trait-based studies offer the best opportunity for generalising among species and crafting management tools. Studies on the process of invasion itself, including interdisciplinary research on the pathways of human spread and the changes that globalisation and climate change will bring to these pathways, also are much needed. If general principles apply here, the flow of invasives might be slowed regardless of the species – and their traits – that compose that flow.

10 Conclusions

In this review, we have focused on transformative and global processes of environmental modification by humans. We have not considered factors such as local pollution (*e.g.* pesticide application) or natural disturbances such as fires. This is not to imply that these factors are not potentially important potential drivers of insect population losses and local declines in the functions and services that insects provide. Aquatic insects, for example, are known to be strongly affected by water pollution in regions near intensive agriculture and urbanisation.[131,132] Local factors, however, potentially have local solutions, and the negative effects of pollution and other anthropogenic disturbance agents could be mediated with local conservation attention.

The economic and demographic changes caused by global environmental change, in contrast, are vexing on the largest of scales. Society must ask itself: What kind of world do we want? What risks are we willing to impose on natural systems? Are we willing to accept the consequences of biomanipulation where some species benefit while others decline? Presently, *c.*10% of the terrestrial world is set aside for conservation. Does that 10% capture the diversity and ecosystem function of insects that need to be conserved? Until we address shortcomings in our understanding of insect species diversity and the consequences of extinctions, we cannot appreciate the full scope of global change. Until we re-evaluate and re-invent our society, we must live with the biological consequences – whether they are fully understood or not.

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