Causes and consequences of insect decline in tropical forests

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Abstract

Insects are crucial for the functioning of ecosystems and might be facing declines globally, although data are biased away from the tropics where insect diversity and abundance are highest. In this Review, we assess the current status of insect populations in the tropics and discuss the prevailing threats to tropical insect biodiversity. Burgeoning human populations, increasing urbanisation and land-use changes are leading to habitat loss and fragmentation, as well as increased pollution, including both light and pesticides. Insects on tropical islands are particularly sensitive to invasive species, which have already led to the extinction of multiple unique endemic species. Climate change further threatens insect populations across the tropics and might be disrupting crucial weather cycles such as *El Niño* and *La Niña* that are important drivers of phenology and synchrony at these latitudes. Tropical insect declines might alter fundamental ecosystem processes such as nutrient cycling, carbon sequestration and herbivory. Disruption of food webs could lead to increased outbreaks of pests and of insect-vectored diseases in humans and livestock, affecting human health and reducing food security. Methodological advances including artificial intelligence and computer vision, remote sensing and meta-barcoding, are facilitating taxonomy, speeding up identification of diverse samples and improving the monitoring of tropical insect biodiversity and will aid and guide future conservation efforts.

Introduction

Insects are among the most abundant, diverse and functionally influential animals on Earth. They drive key ecosystem processes including pollination, nutrient cycling, seed dispersal, herbivory, frugivory, parasitoidism and as a food source for other organisms. Alarmingly, insects might be facing rapid declines of species, populations and biomass globally[1], which has generated intense speculation about the likely causes. Habitat loss and degradation, pesticides and climate change have all been implicated in insect declines and act synergistically[2,3]. Most worrying are the potential declines reported from relatively intact tropical sites[4], which are the global centres of insect biodiversity.

Tropical forests represent less than 5% of the Earth's surface but contain over 50% of all described species[5,6] and 80% of insect species[7]. Despite the importance of this habitat, long-term monitoring of insects in tropical forests is limited[8]. Existing time-series to detect insect declines are mostly present in relatively disturbed landscapes in the temperate northern hemisphere[9]. Tropical regions are frequently underrepresented in biodiversity assessments owing to historical research biases favouring North America and Europe[10]. This bias presents a worrying problem during an era of rapid global change, as biodiversity indices are highly sensitive to spatial and taxonomic coverage[11]. An understanding of how tropical biodiversity is changing is therefore crucial for understanding and monitoring global trends in the Anthropocene.

The insects are the most diverse and functionally influential group of animals on Earth[8] but their overwhelming diversity and abundance means that taxonomic characterization is slow, which has hampered understanding of insects. Notably, an estimated 85–95% of insect species in tropical forests remain undescribed[12]. Compounding this knowledge gap, very few long-term monitoring studies of insects are in tropical regions and the few that are tend to be geographically clustered in the Americas and biased towards well-studied groups such as butterflies[13]. The lack of long-term monitoring studies in the tropics results from the overwhelming abundance and diversity of tropical insects, most of which are taxonomically intractable owing to issues such as cryptic species and the challenges of maintaining initiatives beyond the 2–5 year duration of most funding cycles for biodiversity research[14]. For these reasons, as human impacts continue worldwide, understanding population trends of tropical insects has become a research priority in the ecology and biodiversity fields.

Insect biodiversity faces many threats, including climate-related stressors, habitat loss and degradation, pollution (for example, from light and pesticides), and invasive species[15,16]. Importantly, these threats may affect insect assemblages differently in tropical regions compared with in temperate zones because of their distinct evolutionary histories[17-20]. Moreover, temperature declines much more slowly with increasing latitude close to the equator than it does at temperate latitudes, so tropical insects will have to shift their ranges much further than temperate insects to track historical climate envelopes[21]. Land-use change is also expected to have greater impacts in tropical regions than temperate ones[22], owing to a higher proportion of species living close to their physiological tolerances[23], extreme changes in microclimates following disturbance[24], and that most habitat conversion occurred more recently in tropical regions[22].

Although the impacts of tropical biodiversity loss for carbon storage have been explored for vertebrates[25], declining insect abundance and diversity might also affect carbon stocks given their functional dominance in the tropics. The high diversity of tropical insects implies high redundancy and resilience[26], yet shifts in the abundance of insects in different feeding guilds is expected to have functional and cascading consequences across multiple scales of ecological organisation. Insects are the primary drivers of pollination, seed dispersal, nutrient cycling, regulation of plant communities, and provision of food for other organisms in tropical forests[27]. The staggering diversity of tropical plants is itself a product of millions of years of interactions with insects[28], one of the most important biological relationships on Earth[29]. The diversity and density of tropical vegetation enables forests to sequester more carbon than any other terrestrial biome[30], and the interaction between tropical trees and the atmosphere is responsible for regulating weather systems both locally and globally[31]. Assessing the causes and consequences of insect decline in a tropical context is therefore imperative for understanding biodiversity and anthropogenic change at a global scale.

In this Review, we examine the current evidence for insect biodiversity loss in tropical forests and discuss potential reasons for why existing data show conflicting and inconclusive trends. We review the major prevailing threats to insects in tropical forests, with a focus on climate change, habitat degradation and associated stressors such as agrochemical pollution and invasive species introduction. Based on current knowledge of how insects respond to environmental change, we synthesize the functional, physiological and behavioural traits that are likely to define the winners and losers (species expected to increase or decline) in a human dominated world, and the likely socio-ecological consequences of changing insect populations in the tropics. Finally, we discuss the current trends in insect biodiversity research, highlight questions, initiatives and methods for collecting data to improve understanding of tropical insect diversity, and outline future directions that will advance our understanding of this globally important topic.

The evidence base for tropical insect declines

Space-for-time models

Given the paucity of standardized time-series datasets, space-for-time models currently dominate the literature on the effects of global environmental change on tropical insects. Projecting Responses of Ecological Diversity In Changing Terrestrial Systems (PREDICTS) is one of the most comprehensive datasets that provides diversity information across different land uses[32]. Examination of insect responses globally to habitat degradation and climate change using PREDICTS revealed that tropical insect assemblages are particularly sensitive to historical warming and agricultural intensification[18]. The impacts of agricultural expansion are almost universally negative across taxa, regions and land-use types. In fact, land-use changes in the tropics might have even stronger negative effects on insects than those in temperate regions[18]. Given that 50% of tropical forest habitat has already been converted to agriculture[33], it is likely that substantial declines in species richness and abundance of tropical insects recorded locally for some taxa[34-37] are occurring across insect groups at a global scale.

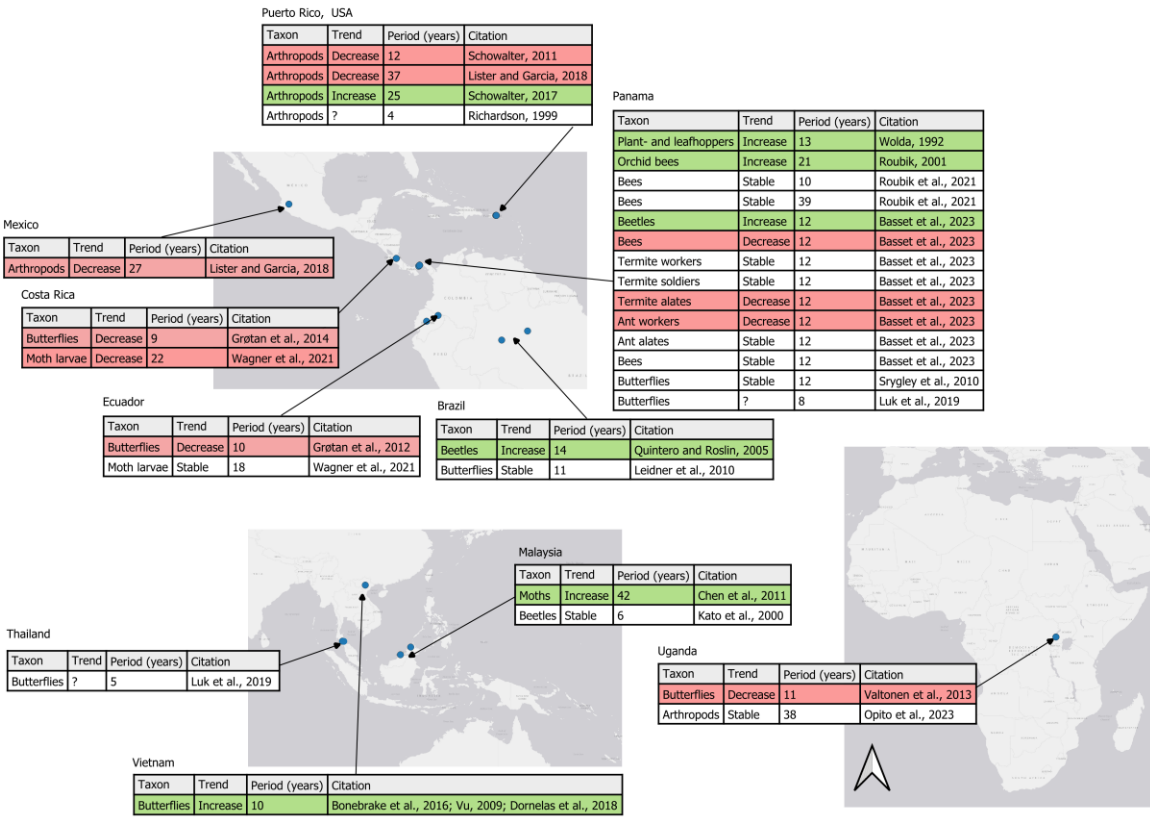

Fig. 1 | Geographic distribution of publicly accessible datasets for tracking tropical insect communities through time. The majority of datasets and reported trends are from a meta-analysis conducted in 2020 (ref. 1), to which we added a further 18 datasets from 5 sources that have been published since 2020 (Supplementary Table1; Supplementary Box1). In total, 31 publicly available datasets that track the trends of insect populations in the tropics are depicted. Where trends are depicted, the directions reported in the 2020 meta-analysis[1] or in the original studies are shown. Where trends are unknown, the data are from post-2021 studies that did not analyse long-term trends. Of 31 datasets, the majority (81%) are from the Americas, with half of those occurring in just one location, at the Smithsonian Tropical Research Institute on Barro Colorado Island, Panama. Across the tropics, 30% of studies focused on Lepidoptera. Substantial research gaps exist both taxonomically and spatially, particularly in the Australasian and Afro-tropical regions. References for all datasets and the articles from which we were able to directly access raw and unprocessed time-series datasets are available in Supplementary Table1.

Time series and long-term monitoring studies

Although there is evidence for insect declines where natural habitat has been lost, data on population trends from within the remaining tropical forests are scarcer. Monitoring insects in relatively undisturbed tropical forests where other threats are minimal is likely to provide unique insights into climate-related responses, yet individual studies report conflicting trends in the direction of population changes[38]. Moth caterpillars in protected forest in Costa Rica declined considerably in diversity and density between 1997 and 2019[4], whereas that of moth caterpillars in Ecuadorian cloud forests between 2001 and 2019 was unchanged[38]. The Smithsonian Tropical Research Institute (STRI) Arthropod Program monitored a range of insect taxa in protected forest in Panama[39] and showed that the abundance of beetles increased, that of termite workers and soldiers, army ant alates and orchid bees remained stable, and that of termite alates, litter ant workers, and nocturnal bees declined[40]. Another long-term study of arthropod biomass at the Luquillo Experimental Forest in Puerto Rico found that arthropods showed considerable short-term declines in response to disturbances, such as hurricanes, but were not declining overall[41]. A reanalysis[1] of some of these datasets revealed no consistent pattern for tropical forest sites, with overall declines for six sites and increasing trends for another six sites globally[13]. These disparate trends highlight the complex nature of insect dynamics and the pitfalls of generalising from a small sample of data sets of limited temporal and taxonomic scope[42].

Geographic biases

Of the few studies that have assessed temporal trends in tropical forest insect populations, twenty-three are from the Americas, two are from Africa, three are from tropical Asia and none are from Australia (**FIGURE 1**; **Supplementary table 1**). The tropics are not biologically uniform, with distinct assemblages of species occurring in different regions reflecting different biogeographic histories[43]. Threats also differ regionally[44] or even within single biogeographic zones. For example, southern Borneo faces considerable threats from forest fires, whereas such fires are much less frequent or severe in northern Borneo[45]. Such spatial differences in fires also occur across Amazonia[46]. As a result, insect responses to anthropogenic pressure across the tropics are unlikely to be uniform in space or time[6]. Despite this spatial heterogeneity, sampling of tropical biodiversity in general has historically been clustered in just a handful of places. Even in sub-regions such as Amazonia, biodiversity assessments are biased towards areas that are easily accessible or located close to research facilities[47].

Temporal biases

Temporal limitations also hinder the ability of researchers to make accurate predictions about the direction of population trends[48,49]. Analyses of the longest running standardized insect monitoring network in the world, the Rothamsted Insect Survey in the UK, indicate that moth biomass has fluctuated considerably between decline and recovery from the 1960s to the present, with no mean net decrease over that time[50]. These oscillations are probably due to periodic fluctuations in weather conditions[50]. In the tropics, no standardized insect monitoring studies are as long-running, yet tropical regions also undergo periodic climatic oscillations that have substantial effects on local ecological processes. For example, the sporadic mass flowering of Asian dipterocarp trees is linked to particularly strong *El Niño* events occurring once every 5–10 years[51], which drive booms and busts of some insect groups[52,53]. *El Niño* events also cause flushes of flowers and liana leaves in South America, leading to increases of bee and butterfly populations[39]. Many trees in Afro-tropical forests also exhibit supra-annual fruiting cycles[54], which are likely to have similar ecological effects on local invertebrate populations. Strong ecological effects of irregular climatic cycles in tropical forests create the appearance of directional trends in insect populations, dependent on where along a time-series the first sampling occurs, which is a particular issue for analyses occurring over relatively short periods or focussing on single taxonomic groups.

The taxonomic impediment

Perhaps the greatest impediment to the understanding of trends in biodiversity globally is the taxonomic bottleneck in identifying and describing tropical insect samples[8,55], which is compounded by the extreme diversity and abundance of insects in tropical forests. For example, more than 6000 species of invertebrates were recorded from a single 0.5-ha forest patch in Panama[56], a huge taxonomic effort that relied on the expertise of 102 specialists who invested a cumulative 24,354 days (or 67 years) of work[56]. Although low-cost, reliable methods for rapidly assessing tropical insect samples are improving[57,58], an estimated 85% of tropical insect species remain undescribed[7], with most expected to be on average smaller, rarer and more specialized than species already named[55,59]. Undescribed species are therefore less likely to feature in either space-for-time or long-term monitoring studies but, alarmingly, might be more sensitive to environmental disturbances[60]. Analyses examining trends in tropical insect assemblages are thus biased towards a subset of well-studied, less sensitive taxa such as ants, butterflies and some beetles, suggesting that rates of decline in tropical biodiversity could be underestimated[60].

Major threats to tropical insect biodiversity

Tropical insect biodiversity faces multiple major threats, including climate-related stressors (such as warming and extreme events), habitat loss and degradation, pollution (such as light and other pollutants), urbanization and the introduction of invasive species[15,16]. These threats might affect insect assemblages differently in tropical regions compared with in temperate zones, although studies are mostly based on single-locations and short-term sampling, meaning that key knowledge gaps remain. In the next sections, we discuss how climate change and rising temperatures might affect insect physiology and distribution, the consequences of habitat loss, degradation and pollution for insect diversity, behaviour and survival, and the effects of invasive species on ecological balance and insect species interactions in tropical regions.

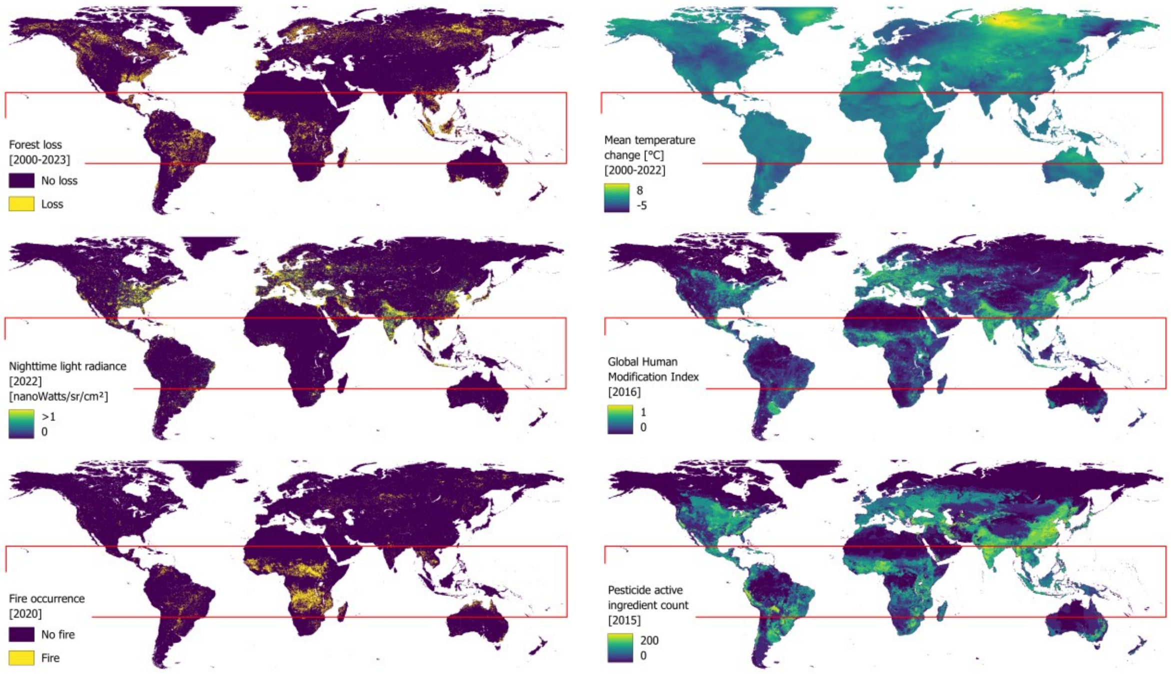

Fig. 2 | The global distribution of threats to tropical insects. Six major threats are identified and mapped with representative data: deforestation [282], mean temperature change[283], light pollution[284], urbanization (using the Global Human Modification Index[285]), wildfire occurrence[286] and pesticides[287]. All tropical regions (red rectangles) are exposed to multiple threats occurring simultaneously, although there are distinct prevailing threats in each biogeographic region. India is predominantly affected by urbanization, light pollution and human modification of the environment, northern Australia has been affected by large mean temperature increase, the greatest risk from wildfires is in central Africa, deforestation is the largest threat in South America and Southeast Asia, and the number of pesticides used is particularly high in central West Africa and South Asia.

Climate change

Climate change presents a major threat to tropical ecosystems (**FIGURE 2**) and insects[18], particularly from increases in mean temperature and the higher likelihood and intensity of extreme weather events[61]. Unlike insects in temperate regions, which experience seasonal variations in light and temperature, insects in the tropics have evolved with a range of relatively stable environmental conditions[62]. Consequently, temperature increases and variability are more likely to push insects in the tropics beyond their narrow physiological tolerances[23,63,64]. Although insect responses to warming might differ across geographical regions, ecosystems, taxonomic groups and trophic levels[65-69], the main impacts include shifts in distributions poleward or to higher elevations[70-72], disrupted phenology[19,73,74], and altered ecological interactions[75,76]. Even small, sub-lethal temperature increases are enough to restructure insect communities[77].

The paucity of long-term studies within tropical ecosystems[78], combined with taxonomic biases towards flora and vertebrates in long-term ecological experiments, mean that very little is known about tropical entomofauna evolution and responses to climate change. In the absence of long-term datasets, research on climatic gradients provides valuables insights into the likely responses of tropical insects to climate change. Species are tracking temperatures up elevation gradients in the tropics, even in protected areas[71], implying that climate change is already rewiring ecological systems where other threats are minimal. As temperatures continue to rise, insect assemblages in tropical forests are likely to change across the ground to canopy gradient. Trees buffer atmospheric conditions, with variation in temperature, humidity and radiation increasing dramatically into the canopy[79]. Such vertical gradients, combined with physiological mechanisms, might allow canopy species to track their abiotic niche downwards as conditions change[80]. Despite already being considerably hotter and drier than ground level, the rainforest canopy contains an extremely high diversity and abundance of insects[56], which might be able to provide ecological redundancy in a warmer future. Nevertheless, species that occupy the coolest microhabitats on the forest floor might have fewer options, and it is unclear which species will colonise vacant niches in the canopy. Similarly, not all insect species and life history stages will be able to move quickly from the canopy to the forest floor for thermoregulation; for example, queens, broods and nurses of canopy ants[81]. Furthermore, disturbed forests, in which microclimate shifts are analogous to decades of the most extreme climate change, retain substantial diversity and abundance of insects[82]. These patterns suggest that insect communities in forests with intact habitat structures should be moderately resilient to elevated mean temperatures in the future.

Aside from gradual changes to overall temperatures, climate change is also increasing the frequency and intensity of extreme weather events[83]. Predictions of insect outbreaks and collapses following extreme events are supported by empirical data from across the tropics[84]. For example, wet and dry extremes drive declines in tropical arthropods[85], providing evidence for the role of changes in rainfall regimes in altering insect communities and their interactions with plants and other organisms[86,87]. In Costa Rican forests, rainfall anomalies negatively affected parasitism rates[4], whereas extremely high temperatures have been associated with a 10-week lag in population density of the yellow fever mosquito (*Aedes aegypti*) in Thailand[88]. *El Ni*ño-associated extreme droughts have been followed by outbreaks of lepidopteran species in Panamanian forests[70] and a breakdown of dung beetle communities in Amazonian forests[61]. Extreme drought and rainfall events have also led to population declines in tropical freshwater insects[89,90]. Naturally occurring *El Niño* and *La Niña* cycles drive strong ecological responses across the tropics, creating seasonal conditions in otherwise unseasonal environments[91,92]. These sporadic events drive phenological shifts in Amazonian vegetation canopies[93] and stimulate the mass flowering and fruiting of tree species in Asia[51,94]. Alarmingly, the frequency and intensity of *El Niño*–Southern Oscillation (ENSO) cycles is becoming increasingly unpredictable with climate change[95-97], destabilising one of the most powerful regulating forces in tropical forest regions. Understanding how this destabilisation will affect tropical insect populations and their ecological functions is a research priority and will need coordinated long-term insect monitoring research across the tropics.

Habitat loss and degradation

In general, land-use changes in the tropics can either happen directly, through clearing large areas of native forests and savannas for agriculture expansion; or incrementally over time, beginning with gradual rounds of timber removal that target the largest trees from the most economically valuable species. These processes, and the associated fragmentation of habitat, affect insect species in various ways depending on their ecology and life-history characteristics. Changes in the abundance of some insect groups after logging are linked to their level of specialisation, such as how closely they rely on a specific host, prey or habitat type[98], as well as logging intensities and time since timber removal[99]. The effects of logging tend to emerge as shifts in the overall community composition of insects in logged compared with primary forests rather than absolute declines in diversity or abundance[100], including reductions of large-bodied predators and increases in herbivores and small-bodied generalists[26]. However, closed-canopy specialists[101] and species that feed on dead wood, such as termites and saproxylic beetles[93,94], are particularly sensitive to logging and show overall declines in diversity and abundance[100,102]. In some taxa, such as butterflies, the habitat heterogeneity resulting from forest disturbance can allow widespread, habitat-generalist taxa to colonise[103], balancing species losses or even enhancing local (alpha) diversity, but potentially leading to biotic homogenisation and reduced diversity at large spatial scales[104].

Aquatic insects are also negatively affected by habitat disturbance[105-107], with changes in insect communities often driven by declines in organic matter availability[108,109] and/or changes to riparian vegetation[110,111]. Human-modified forests are therefore functionally different entities to primary forest[34], but are still globally diverse, dynamic systems of considerable conservation value[112]. Multi-taxon analyses from Borneo suggest that, if protected, logged forests with less than 29% of tree biomass removed should fully recover their diversity and ecological functioning naturally[113], whereas heavily disturbed forests with over 60% of tree biomass removed are likely to require active restoration, such as tree planting and liana cutting.

In many regions, the economic value of tropical forest diminishes with recurrent fires and/or further rounds of logging, leading to conversion to agricultural lands, most often cattle pasture or coffee or soya cultivation in the Neo-tropics, and oil palm, rubber or acacia plantations in the Paleotropics. An estimated 50% of all tropical forest has been removed in this way and replaced by agriculture[6,33,114,115]. Unequivocally, habitat loss arising from the complete conversion of forest to agriculture is devastating for tropical insect diversity and function. Oil palm plantations in Malaysia contain only 50% of the insect species found in nearby primary and logged forests[116], with similar reductions in insect diversity observed with agricultural land use conversion in Amazonia[117,118]. Although species turnover might be low in large areas of lowland forest[119], the high historical conversion rates of forest to agriculture across the tropics means that it is likely that a large proportion of global insect diversity and abundance has already been lost to this process. Of particular concern is high levels of forest conversion in areas of high endemism, such as tropical montane areas and island groups. The 36 world biodiversity hotspots are estimated to have, on average, less than 15% remaining intact vegetation, although many have much less[120].

Mining, ranging from artisanal and small-scale to large-scale operations, is a widespread source of habitat loss and degradation in the tropics. Gold mining, in particular, severely impacts both aquatic and terrestrial insect biodiversity[121,122]. Artisanal gold mining in Costa Rica drives species richness declines and compositional changes in freshwater insect communities, which has been attributed to altered abiotic conditions in the aquatic ecosystems, including increased turbidity, sedimentation, and contamination by heavy metals (such as mercury)[123]. Furthermore, mayfly species turnover in streams in Amazonia is higher in non-mined areas than in mined areas[124]. Manganese and iron concentrations were higher in mining-affected ecosystems, and the researchers argued that greater environmental variation in disturbed streams is likely to disproportionately impact sensitive species and result in lower mayfly species turnover compared with in preserved streams[124]. This hypothesis is supported by a reduced richness of Ephemeroptera, Plectoptera and Trichoptera (EPT) specialists, as well as declines in the richness and abundance of generalist EPT species in mining-affected Amazonian streams[125]. Negative impacts go beyond taxonomic metrics and can persist over time. For example, changes in the taxonomic and functional composition of Ephemeroptera assemblages in gold-mined sites in French Guiana persisted for at least two years after the abandonment of the mining claims[126].

Agrochemicals and pollutants

Over half of the 2018 production of some pesticides banned in the EU went to developing countries in the tropics, which account for a quarter of global pesticide use[127]. This pesticide use raises many concerns for tropical insect biodiversity. First, agrochemicals can travel beyond their application sites, contaminating nearby ecosystems through drift and runoff, resulting in reduced tropical insect diversity and abundance, particularly for sensitive species and immature life-history stages[128-130]. For example, urbanization and large-scale soy and cattle farming in Amazonia have contributed to substantial runoff of pollutants into aquatic ecosystems in various regions[131,132]. Second, despite efforts to ban specific agrochemicals worldwide, some are still detected in tropical countries; for example, organochlorine pesticides in soil and/or air samples from South Asia[133], Mexico[134] and Brazil[135]. Third, environmental conditions in the tropics might accelerate the rates of pesticide volatility, degradation and dissipation[136,137], although this might vary across pollutants[138] and with soil types[139]. Finally, although some countries have introduced measures to reduce pesticide application, evidence from temperate regions raises concerns about the ongoing toxicity of previous applications for insects and aquatic invertebrates[140].

Although understudied in comparison with high latitude regions, the widespread use of agrochemicals in tropical regions has profound impacts for insects. For example, serious impacts of pesticides and other pollutants have been widely documented for bees[141], and for various insect species within temperate regions[15], but evidence from the tropics is much sparser and is based on single species or locations. Agrochemical pollutants induce behavioural, reproductive and morphological changes in insects[142,143]. The presence of heavy metals in water affects the growth, reproduction and lifespan of predatory insects, with cascading impacts on prey species[144]. Experimental work shows that pharmaceutical residues that remain biologically active in still and running water environments can affect membranes, cells and tissues, as well as mortality in the European non-biting midge (*Chironomus riparius*)[145]. Some pollution events have less subtle effects. For example, an oil spill in the Cururu stream in Central Amazonia[146], which was already impacted by domestic sewage, reduced the richness and abundance of aquatic insects to almost zero in the following year[146]. Domestic sewage pollution threatens aquatic insects in urban streams, driving declines in sensitive species while favouring a few disturbance-tolerant taxa[147]. Most studies assessing pollution in the tropics have focussed on aquatic insects. For example, only 1 of 154 studies considered in a review assessed the impact of metal pollution on tropical terrestrial invertebrates[148].

Urbanisation

The proportion of the world's population that lives in urban areas has risen from 39% in 1980 to 55% in 2018[149]. By 2018, more than 1.5 billion people lived in urban areas in the tropics[150]. If current population trends continue, then urban land cover might increase by 1.2 million km^2 by 2030, nearly tripling the estimate for 2000, with considerable habitat loss in biodiversity hotspots including the Eastern Afromontane, the Guinean Forests of West Africa, and the Western Ghats and Sri Lanka hotspots[150]. The consequences of urbanisation for insect communities in the tropics are likely to be at least as severe as in temperate regions, if not more so[151]. One of the major differences is linked to public and governmental perceptions of insects. In cities in non-tropical regions, town planning agendas have pivoted actively towards the conservation of insect diversity[152], whereas in many cities in the tropics, pesticides are applied daily to urban green spaces to reduce transmission of insect-vectored diseases[153].

Urban areas are typified by reduction in natural vegetation, which is replaced by large areas of hardened surfaces, simultaneously reducing available habitat and increasing local temperatures. Flood management moves water rapidly away from cities, severely impacting natural flows and freshwater insects. For terrestrial insects, abundance, diversity and community composition are lower in cities than in natural ecosystems, as demonstrated for geometrid moths in southern Ecuador[154]. By contrast, a few studies indicate a potential benefit of low urbanization densities for pollinators[155-157], and some tropical habitat remnants show strong potential for maintaining high levels of diversity[158]. Comprehensive studies of terrestrial and freshwater insects in urban areas in the tropics are lacking, making it difficult to identify broad patterns at community and population levels. This is a major knowledge gap typified by a lack of tropical urban ecology studies in general[151]. In cities in the tropics, such as Singapore, freshwater macroinvertebrate communities shifted from pollution-sensitive to pollution-tolerant through the loss of taxa such as mayflies, beetles and dragonflies[159]. In Amazonian Manaus, urbanisation is associated with declining richness of aquatic insect groups, due to changes in abiotic variables such as dissolved oxygen[160]. Further research with insect bioindicators might facilitate tackling of this knowledge gap, while revealing the influence of urban biotic and abiotic conditions on insect biodiversity within urban ecosystems in the tropics.

Light pollution

Urbanisation and electrification result in the establishment of massive contiguous light sources, disrupting night-active and light-attracted insects and altering their mating behaviour, orientation and foraging, leading to population declines for some groups of insects[161-163]. Tropical ecosystems are increasingly affected by exposure to artificial light[164], even within and around protected areas[165]. Light pollution is predicted to have greater negative effects on insects at lower latitudes than on those at higher latitudes, as their circadian rhythms have evolved in aseasonal environments[24,25]. Niche modelling with local ecological knowledge of the Chocó golden scarab (*Chrysina argenteola*) showed negative effects of light pollution and habitat loss and fragmentation[166]. Different wavelengths of artificial light might disproportionately impact some insect groups[167], with shorter wavelengths having negative impacts on insect biodiversity, probably due to the higher efficacy of these wavelengths in attracting some insect groups[168]. Reducing the blue wavelengths of light decreased impacts (for example, the number of attracted insects dropped by almost 60%) in Amazonia[169]. In Singapore, LED lamps, which emit a broader spectrum of wavelengths than sodium lamps, attracted fewer dipterans and more hemipterans and hymenopterans in comparison with high-pressure sodium sources[170]. The yucca moth (*Tegeticula maculata*), an obligate diurnal pollinator of the yucca plant (*Hesperoyucca whipplei*), exhibited increased 'day-time' activity owing to the presence of artificial light at night[171]. A key knowledge gap in understanding the impacts of light pollution on tropical insects is the absence of long-term studies[172], particularly in urban areas, which are expected to be especially vulnerable to light pollution[162].

Invasive species

Inter-regional travel, globalization and climate change facilitate the spread of non-native species, some of which become invasive and have environmental, economic and health impacts. Exotic insects negatively impact indigenous biodiversity, including native insect communities, both directly, by herbivory, predation and hybridization, and indirectly, through disease transmission and competition, leading to the displacement of indigenous species, which alters community structures, dynamics and interactions as well as ecological processes[173-175]. Invasive insects also interfere with the interactions of native and exotic herbivores with plants[176] and reduce the effectiveness of natural enemies[175]. Intensive farming of exotic insects for food, display or other purposes risks their accidental release and invasion, especially under climate change[177]. Given the narrow dietary specialization of some herbivorous insects, tropical insect communities might also be negatively impacted by the introduction of non-native plants and vertebrates that compete with and for their main food resources[178] (**Box 1**). These risks are not fully understood, particularly in the tropics.

Winners and losers

Given the evidence from time series and space-for-time substitutions, can we predict which tropical insect species are likely to be winners and losers in the future? Species traits provide a framework for linking community level responses of insects with environmental change and enable the effects of potential outcomes on ecological processes to be inferred. Discussing all traits thought to drive insect responses to anthropogenic threats is beyond the scope of this Review, but we highlight some of the major drivers (Table 1).

Species with a weaker dependence on cross-species interactions are likely to be at lower risk from ecosystem perturbations, whereas specialists are more likely to be lost from an ecosystem. Species with a restricted range are also likely to be at higher risk, as are species with a narrow environmental niche, for which smaller environmental changes are needed to exceed their niche thresholds. This increased risk is likely to be particularly true in tropical regions where niche spaces are assumed to be narrow owing to high diversity[179]. Insects with low physiological tolerances to increasing stressors will likely be at the highest risk from shifting environmental conditions driven by land-use change and climate change. Importantly, responses will be mediated by the microclimatic conditions experienced locally by organisms[180]. Although thermal tolerances might be useful predictors of insect declines, they are difficult to measure accurately because body temperature is a complex product of microhabitat occupancy, behaviour, colouration and morphology[181]. In general, organisms with lower electromagnetic reflectance are expected to decline with increasing temperature[182]. By contrast, organisms with lower reflectance have increased UV-B protection and experience decreased desiccation[183], enabling predictions of population changes to be made based on colour complex.

Logging, for example, results in increased solar radiation at the forest floor, decreased humidity and raised temperatures[184], increasing selection pressures on organisms to be both more reflective for lower operative body temperatures and less reflective to increase UV and desiccation tolerance. Such competing drivers might explain nonlinear colouration responses across a tropical forest disturbance gradient among dung beetles in Malaysia[185]. Species exhibiting high sexual selection often have bright colouration, which could affect thermal performance. Dragonflies[186] and dung beetles with high sexual ornamentation show positive responses to land-use and climate change, respectively[187], although the underlying mechanisms are unclear. Dispersal ability is crucial in shaping the response of species to multiple stressors, as it promotes metapopulation persistence[188] and allows species to track shifting climate envelopes[189] and avoid local extreme events[190]. Diapause capability might buffer some taxa from extreme thermal events[191], provided that environmental cues continue to trigger adaptive responses[192].

In terms of 'winning' taxa, we might expect species that occupy microhabitats that are buffered from extreme temperatures (for example, soil fauna, xylophages and some aquatic species) to fare best under climate change. Taxa at higher trophic levels have lower thermal limits (for example, odonates or parasites[193,194]) but, equally, they are highly mobile and behaviourally flexible, so might be able to shift their feeding patterns in ways that herbivores (such as immobile homopterans) cannot. Equally, taxa with more complex social systems might be buffered from extremes through altering nest architecture[195]. That said, species with more complex social systems tend to have longer life histories and therefore might have limited scope for short-term evolutionary rescue.

Ecological consequences of tropical insect decline

Herbivory

Tropical forest insect assemblages are dominated by herbivores[196], which can have major impacts on plant fitness[197]. Consequently, altered insect biodiversity will have 'top-down' impacts on plant communities. Few long-term studies exist on the impacts of insects on plants in tropical forests[198], but excluding insects can reduce diversity and alter the composition of plant communities[28,199]. In practice, loss of all insect herbivores is not a plausible scenario under global environmental change.

Instead, there will be 'winners' and 'losers', and insects that can exploit 'winning' resources such as plant species that are tolerant to climate-change or disturbance are expected to increase (**FIGURE 3**). Forest degradation and fragmentation is expected to favour insect species that are tolerant of hotter, high-light environments and trophic generalists, feeding on plant species with relatively weak anti-herbivore adaptations. The net outcome for herbivory is difficult to anticipate, with evidence of both increases and reductions in herbivory as habitat fragmentation increases[200].

Most studies of herbivory have focussed on folivores, yet other plant-feeding guilds such as seed predators[201] might have greater impacts on plants. These guilds are frequently more specialized than folivores, making them strong candidates for plant diversity-enhancing activity via the Janzen-Connell mechanism[202]. If the abundance and activity of these functionally important consumers change, then plant diversity and species composition will likely be affected[201].

Food webs

Insects are a major component of the diet of many vertebrates, including birds, reptiles, amphibians, bats and other mammals (Fig. 3). Although insect declines will have negative effects on these insectivores, the consequences of shifts in insect prey composition are more difficult to predict and will reflect the trophic specialisation of different consumers. Studies of food remains in the gut or in faeces, facilitated by DNA analysis, enable networks of feeding interactions and the degree of trophic specialisation to be resolved[203,204]. Most of these studies suggest that levels of trophic specialisation are relatively low, which will facilitate prey-switching and buffer insectivores from some of the negative impacts of insect declines, although not from the direct effects of climate change and forest degradation.

Invertebrate insectivores such as spiders, many ants and parasitoids are important regulators of their prey. As organisms at higher trophic levels typically have higher sensitivity to environmental change than those at lower trophic levels[194], reduced 'top-down' regulation under environmental change might lead to outbreaks of prey species, with consequences for human health and agriculture (**BOX 2**; **BOX 3**; **FIGURE 3**). Again, specificity of diets is all important, such that predator release effects are more plausible for the prey of more specialized consumers, such as many parasitoids[205].

Nutrient turnover

Insect-mediated nutrient turnover can have ecosystem-level impacts. For example, dung beetles shape plant diversity through seed dispersal[206] whereas bioturbation (mixing of soil or sediments by living organisms) and nutrient turnover by termites shape soil properties[206,207], with knock-on effects for seedling diversity, survival and, ultimately, ecosystem structure and function. Insect decomposers are essential for the breakdown of dead organic material, nutrient cycling and removal of carrion[208-210]. In the tropics, invertebrates, predominately termites, are responsible for more than half of deadwood decomposition[211], and tropical invertebrates decompose 1.4-fold more leaf litter than temperate invertebrates[212]. These ecosystem processes can also strongly fluctuate in response to changing abiotic factors. For example, during a drought, termite activity can double, resulting in higher decomposition rates, soil nutrient variability and seedling survival[207]. Freshwater-insect-mediated decomposition is also shifting in response to multiple human stressors[213], driven by the loss of freshwater macroinvertebrates [214,215]. As insect decomposers are sensitive to disturbance[216] and insect-mediated decomposition in the tropics is not yet included in earth system models, large uncertainties remain as to how insect-mediated nutrient turnover is shifting under global environmental change.

Insect-mediated carrion and dung removal are essential processes for breaking down organic material, reducing disease and shaping soil nutrient distribution. However, habitat disturbance disproportionally impacts major contributors to these processes, large dung beetles and ants[77,217,218], with knock-on effects such as the displacement of parasites[219]. In Brazil, carrion removal seems to be resilient to habitat fragmentation but the most efficient carrion-removing species are maintained in forests and lost from coffee plantations and pastures[220]. The responses of carrion and dung-removing insects to the combined effects of multiple human impacts in the tropics and the larger implications for ecosystem processing remain unclear.

Pollination

Tropical plant–insect pollinator interactions become simplified or decoupled under human disturbance, changing ecological functionality[221] and reducing food security[222]. Monoculture, climate change, pesticide use and land-use change are the largest threats to tropical pollination networks in natural and agro-ecosystems[222-225] (**Box 3**). Bees have received most attention and seem to be in decline globally[226]. Other insect groups, such as beetles, moths, flies, wasps and thrips, are also crucial for pollinating some crops[227,228] as well as native flowering plants[229-231], particularly in the tropics; however, few long-term data sets exist for these groups. The limited experimental and observational data demonstrate that land-use change can re-shape pollination networks[232]. The most specialized species interactions are likely to be the most vulnerable to human disturbance[233] but observed responses are variable for measures of network structure including nestedness (the extent to which more specialised interactions involve species that also interact with more generalised species) and connectance (a measure of the fraction of potential interactions between species that actually occur)[234]. Breakdown of pollination linkages has already been seen in simpler, subarctic ecosystems[235]; however, pollinator web data through time are rare for tropical systems and are needed to confirm whether breakdown is also occurring in the tropics. As networks are re-shaped, insect pollinators can experience higher rates of predation and parasitism[236]. Pollinator species often perform multiple ecological roles[237] across life-history stages. For example, herbivorous insect larvae can become pollinators as adults, adding more layers of complexity to responses to environmental change. Many insect pollinators are resilient to environmental change and are undergoing range expansions[238], although the impacts of these 'winners' on other pollinators, disease spread and crop yields in the tropics are poorly understood. Although there is increasing international focus on the loss of insect pollinators, partly owing to their direct role in provisioning services to humans, shifting tropical insect pollinators and their services remain a major knowledge gap.

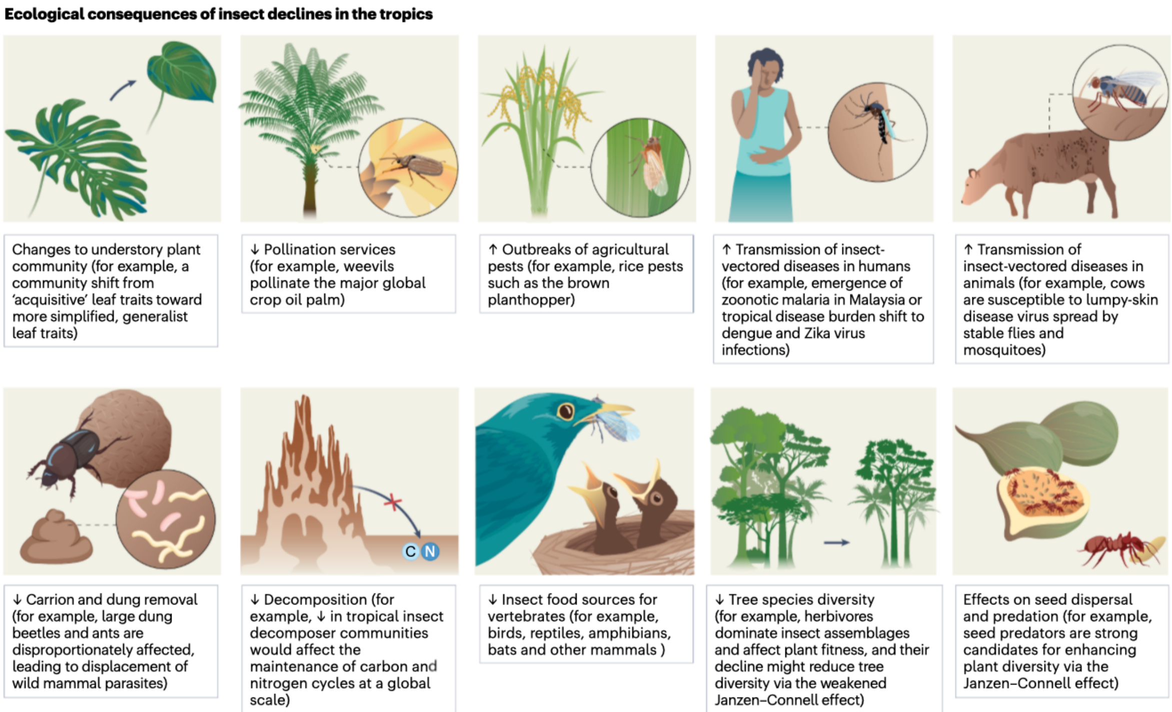

Fig. 3 | Ecological effects of declining insect diversity and abundance. In tropical forests, declining insect populations will have substantial effects on plant community dynamics, resulting in reduced biodiversity, alterations to functional community composition of plants and ultimately reduced nutrient cycling and carbon sequestration. Reductions in the abundance of insects will also have knock-on effects on insectivorous animals such as bats, birds and lizards. In forest-adjacent tropical communities, unequal patterns of decline across the trophic pyramid will result in a predator release effect on pest species, leading to reduced food security and increased outbreaks of insect-vectored disease in both humans and livestock. Increasing temperatures and changing rainfall patterns may affect pollinators, further exacerbating reductions in yields of locally and globally important crops. 'Acquisitive' leaf traits are those that maximize growth, such as high specific leaf area and leaf nitrogen content

Measuring insect biodiversity in tropical forests

Specific threats vary in kind and severity across tropical regions. Potentially, the largest, yet most poorly understood threats are the systemic decoupling of complex feedbacks between global climate and phenology that underpin the dynamics of tropical forests. In particular, increasingly unpredictable ENSO cycles are expected to become more important, especially within recently disturbed habitats that are already warmer and less stable than their undisturbed equivalents[184,239,240]. We expect that ecosystem services derived from predatory and parasitic insects will be amongst the most vulnerable to change[77,193,194]. These changes will have both ecological and societal consequences, with diminishing top-down control occurring in forests, and increasing outbreaks of agricultural pests and insect vectors of disease in adjacent settlements. Herbivory and decomposition show somewhat greater resilience[212] but are still likely to be affected if climate change, pesticide use and habitat disturbance continue unchecked[26]. In light of the range of threats to tropical insects and the consequences for ecosystem function, various approaches and technologies are available to address the priority challenge of tropical insect biodiversity loss[241].

Long-term monitoring

Improved understanding of the dynamics of tropical insects requires the establishment of current baselines of insect biodiversity and abundance across the tropics and subsequent regular monitoring using standardised methods. One approach is a trans-regional network of long-term monitoring sites[40], although the taxonomic impediment associated with the volume and diversity of tropical insect samples remains a challenge[7,8,55]. A viable solution for rapidly generating pan-tropical baselines is via the use of molecular techniques such as eDNA and metabarcoding, which in the past few years have improved markedly in terms of accessibility, scalability and price[242] for the assessment of bulk insect samples[58]. However, this approach still faces barriers to being a one-size-fits-all solution for monitoring tropical insect biodiversity[243,244], including the need to harmonize methods and databases globally[241], the obscuring of vital ecological information such as traits and abundances[245], limitations related to a lack of tropical bar-coding 'libraries'[246] and the overwhelming numbers of undescribed species[247]. However, modern approaches involving non-destructive methods[242,248,249] and the development of international standards for global arthropod monitoring using meta-barcoding[248,250] mean that generating baselines of insect diversity using these approaches are within reach for the first time[250].

Artificial intelligence and computer vision also hold promise for facilitating the monitoring of diverse insect samples[251]. Highly automated methodological pipelines incorporating automated robotic pipetting, mega-barcoding, and AI image recognition are being developed in Europe for this purpose[252,253].While these ambitious endeavours are admirable and should be developed for general use in the future, it is difficult to predict exactly how and when these approaches will become tractable at scale. Novel techniques should undergo a phase of 'innovation through simplification' so that they are applicable in the Global South, where biodiversity is highest and they are most needed[57]. Most AI applications rely on existing information and well-preserved, easy to recognize specimens for training. Accordingly, in the tropics, these applications will likely retain the current biases towards well-studied taxa such as butterflies, larger beetles, ants and odonates. To improve both molecular and AI-based identification methods in the tropics, the traditional taxonomic enterprise must be expanded, preferably by employing taxonomists within local institutions. Such a workforce would develop and calibrate AI tools for species naming and identification. Furthermore, here are large, undiscovered insect data sets across natural history museums and herbaria globally, which could be harnessed to help address the problem of unknown baselines across the tropics. However, there seems to be little appetite to fund such work, and its inevitable encyclopaedic nature attracts little respect among some elements of the scientific community. On the positive side, some initiatives, such as the Global Malaise Trap programme, have demonstrated that geographically ambitious sampling and processing of insect samples using meta-barcoding is possible[254], and the field should endeavour to establish a similar consortium focussed on, and based in, the tropics.

Remote sensing

Although lacking the resolution of traditional sampling approaches, remote sensing methods offer practical advantages for the analysis of broad-scale patterns of activity and abundance, not least because they do not rely on mass sampling[241] . In particular, advances in the collection, storage and analysis of passive acoustic data show much promise for monitoring the timing and intensity of insect activity[255]. Real-time acoustic information can be collected from tropical forests and analysed autonomously using machine-learning techniques[256]. Devices that run on solar power and upload data to the Cloud via mobile telephone networks can remain operational in tropical habitats for many weeks without human attendance[257]. Radar has also been employed to monitor the abundance of insects moving in the atmosphere in Europe[258,259], and increasingly used in the tropics[260,261]. At smaller scales, such as beneath forest canopies, light detection and ranging (LiDAR) can be used for tracking live insects moving in the understory[262-264].These techniques will be most powerful when coupled with hyper-spectral satellite-derived measurements of forest phenology and fine-scale climate data. Together, these approaches can address specific knowledge gaps, including long-term seasonality of insect activity and abundance and responses to changes in local and global climate cycles and forest phenology, which are highlighted here as a potential drivers of insect decline in undisturbed environments. For each of these remote sensing methods, carefully designed ground-truthing against traditional insect sampling at a few locations would increase confidence in their wider use.

Community science and Indigenous knowledge systems

In the absence of quantitative data, qualitative (or semi-quantitative) data from other sources are useful. Community science (also known as citizen science) has proved effective in detecting insect declines in temperate regions, including through the use of novel methods such as windscreen sampling[265,266]. Establishing similar collaborations with people living in tropical forest regions could lead to quantitative evidence of insect population trends, increased public engagement, and even stronger advocacy for policy change and scientific support[267].
Indigenous knowledge systems are generated by local and traditional people, including those in the tropics, who have a deep knowledge of the biological world around them[268]. In many parts of the world, especially the Neotropics, large territories of tropical forests are directly managed by indigenous communities themselves, such that effective incorporation of Indigenous knowledge systems and practices will be essential for insect conservation[268].

Summary and future directions

Tropical insects are likely to have already declined substantially, principally due to rapid agricultural expansion. The status of insects within the remaining forests is less clear, but there is evidence that community composition and ecological functions are changing, with anticipated losses of specialist predators and increases in generalist herbivores. However, assemblages of insects in disturbed (and therefore hotter and more extreme) tropical forest environments are still abundant and diverse. Protecting the remaining primary forests and extending this protection to adjacent degraded forests is the most urgent conservation solution. Moving forward, little progress will be made toward understanding long-term trends unless baselines of biodiversity from within tropical forests are recorded now, which requires the broad application of both traditional insect-monitoring protocols and new technologies including meta-barcoding. Methods need to be standardised and repeated through time via the collective enterprise of tropical scientists. The composition of insect assemblages is still likely to shift, even in these buffered habitats, as the climate changes but it is possible that essential functionality will be maintained. Should holistic declines across insect groups occur from within relatively intact forests, then we must infer a ‘slowing’ of the entire ecosystem and a collapse of phenological rhythms and species interactions, perhaps related to increasing instability and intensity of regulating climate cycles such as *El Niño* and La *Niña*. Such holistic declines will have catastrophic consequences for human well-being.

Acknowledgements

This work was supported by the RGC Collaborative Research Fund (C7048-22GF) and the NSFC National Excellent Young Scientist Fund (AR215206). F.M.F. and

K.D.d.S. are funded by the UKRI FLF (MR/X032949/1]) and CNPq (311550/2023-1, 443860/2024-6, 441257/2023-2 and 444350/2024-1). O.T.L. is funded by NERC NE/X000117/1. The authors thank P. Eggleton for comments on an early version of this manuscript and V. Amaral for assistance with Fig.3.

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Acknowledgements

This work was supported by the RGC Collaborative Research Fund (C7048-22GF) and the NSFC National Excellent Young Scientist Fund (AR215206). F.M.F. and K.D.S. are funded by the UKRI FLF (MR/X032949/1]) and CNPq (311550/2023-1, 443860/2024-6, 441257/2023-2, 444350/2024-1). O.L. is funded by NERC NE/X000117/1. The authors thank P. Eggleton for comments on an early version of this manuscript and V. Amaral for assistance with Figure 3.

Author contributions

M.J.W.B. and L.A.A. conceptualized and led the development of the manuscript. All authors contributed equally to the writing and editing.

Competing interests

The authors declare no competing interests.

Peer review information
Nature Reviews Biodiversity thanks G. Maharaj, D. Amorim and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.

Supplementary information
figure information is available for this paper at https://doi.org/10.1038/s415XX-XXX-XXXX-X

Display items

Tables

Table 1. Key research into trait-based insect responses to environmental change.

Trait	**Sensitivity**	**Potential consequences for temperate and tropical species**	**Refs**
Ecological specialisation	Specialist species are more at risk due to stronger biotic interactions and are more vulnerable to habitat loss and stochastic processes	Potentially greater consequences in the tropics where niche breadth is narrower Specialist mutualisms are more common in the tropics and might be particularly vulnerable, although some other interaction networks might be less specialised	[269,270,271]
Endemism and range size	Species with restricted ranges are more vulnerable to environmental change and their effective population sizes could already be low	Yes, as many biodiversity hotspots (with both high endemism and degree of threat) are tropical forests or islands	[272]
Body size	Decreased body size with increasing temperature Both small- and large-bodied insects decline with disturbance	Mixed evidence for Bergmann's rule[a] If tropical species are smaller, they may be better able to adapt to climate change	[273,274]
Physiological thermal limits	Species with low physiological thermal limits are more vulnerable to environmental change, although this is mediated by microhabitat	Tropical species might potentially be more vulnerable if they are closer to fundamental thermotolerance limits	[193,275,185]
Phenotypic plasticity	Phenotypic plasticity can buffer responses to environmental change	Tropical species with low plasticity could be more vulnerable	[276,277]
Microhabitat occupancy	Microclimates can buffer some impacts of climate change, if species can disperse into them	Species are more likely to benefit from microclimate buffering in the tropics, where buffering effects are the largest	[278]
Colouration	Lighter-coloured species have lower body temperatures, although there is a trade-off with	Depends on microclimate availability, and thermoregulatory, UV	[183,185,279]

	resistance to UV radiation and disease	radiation and disease resistance	
Sexual dimorphism	Higher sexual selection might increase resistance of sexually dimorphic species to environmental change	Potential for sexual selection to enhance adaptive responses in tropical species that are closer to their critical thermal limits	[187,186]
Dispersal ability	Species with a high dispersal ability are better able to track climatic envelopes or shift to a new habitat after disturbance	Tropical species could have generally lower dispersal abilities, limiting their ability to respond to environmental stress	[280,281]
Diapause	Diapause allows species to survive extreme events, although climate change is resulting in mismatches between phenological cues	Temperate species potentially vulnerable to phenological mismatches	[191]
Trophic level	Higher trophic levels are more vulnerable to increased temperatures and habitat loss	More studies are needed across latitudinal gradients Tropical species are potentially more robust owing to lower host plant specialisation	[193,194]
Social complexity	Nests of social insects might buffer them from extremes	Tropical colony size is smaller for ants but not for termites	[282,283,195]

[a]Animals in colder climates tend to be larger than those in warmer climates.

Figures

Figure 1. Geographic distribution of publicly accessible datasets for tracking tropical insect communities through time. The majority of datasets and reported trends are from a metanalysis conducted in 2020 (REF.[1]), to which we added a further 18 datasets from 5 sources that have been published since 2020 (**Supplementary table 1; Supplementary box 1**). In total, 31 publicly available datasets that track the trends of insect populations in the tropics are depicted. Where trends are depicted, the directions reported in the 2020 metanalysis[1] or in the original studies are shown. Unknown trends indicate post-2021 studies that did not analyse long-term trends. Of 31 datasets, the majority (81%) are from the Americas, with half of those occurring in just one location, at the Smithsonian Tropical Research Institute on Barro Colorado Island, Panama. Across the tropics, 30% of studies focussed on Lepidoptera. Substantial research gaps exist both

taxonomically and spatially, particularly in the Australasian and Afro-tropical regions. References for all datasets and the articles from which we were able to directly access raw and unprocessed time-series datasets are available in Supplementary table 1.

Figure 2. The global distribution of threats to tropical insects. Six major threats are identified and mapped with representative data, including deforestation[284], mean temperature change[285], light pollution[286], urbanisation (using the Global Human Modification Index[287]), wildfire occurrence[288] and pesticides[289]. All tropical regions (red rectangles) are exposed to multiple threats occurring simultaneously, although there are distinct prevailing threats in each biogeographic region. India is predominantly affected by urbanization, light pollution and human modification of the environment, Northern Australia has been affected by large mean temperature increase, the greatest risk from wildfires is in Central Africa, deforestation is largest threat in South America and Southeast Asia, and the number of pesticides used is particularly high in Central West Africa and South Asia. $nW.sr^{-1}.m^{-2}$, nanowatts per steradian per square metre.

Figure 3. Ecological effects of declining insect diversity and abundance. In tropical forests, declining insect populations will have substantial effects on plant community dynamics, resulting in reduced biodiversity, alterations to functional community composition of plants and ultimately reduced nutrient cycling and carbon sequestration. Reductions in the abundance of insects will also have knock-on impacts on insectivorous animals such as bats, birds and lizards. In forest-adjacent tropical communities, unequal patterns of decline across the trophic pyramid will result in a predator release effect on pest species, leading to reduced food security and increased outbreaks of insect vectored disease in both humans and livestock. Increasing temperatures and changing rainfall patterns may impact pollinators further exacerbating reductions in yields of locally and globally important crops.

Boxes

Box 1. Invasive species on tropical islands

Island biotas, of which insects are often a dominant part, are disproportionately vulnerable to anthropogenic change[311]. Forest degradation is the prevailing threat to insect biodiversity on tropical continental islands such as Borneo[312-314] and Madagascar[315-317], , although impacts reflect logging intensity[113]. Some reported threats have equivalent impacts on diversity in tropical oceanic islands. For example, urbanization and reduced vegetation density decrease invertebrate diversity and abundance on Indo-Pacific atolls[318]. Similarly, extinction of monophagous herbivorous insects globally on tropical islands has been linked to vegetation loss[316]. In addition, invasion by non-native species is a major threat to island insect biodiversity, especially on remote oceanic islands[319], where niche space is naturally unsaturated[320]. Invasive species are responsible for 90% of global extinctions on islands[321]. One example is Saint Helena in the mid-Atlantic, where species invasion is the largest current threat to insect diversity. At least 30 endemic species, including the St Helena earwig (the largest earwig species in the world), are believed to be extinct as a consequence of invasive species[322].

Non-native ants in particular threaten native insects, through higher competitive and predatory pressure[323-325], homogenizing ant assemblages globally[326]. For example, the big-headed ant (*Pheidole megacephala*) is an important insectivore that is spread widely by humans[327], and island infestation with this species is associated with reduced native diversity across multiple insect orders[328,329]. The Cape Verde-endemic ant *Monomorium boltoni* is presumed extinct through *P. megacephala* infestation[330].

Introduced rodents such as the brown rat (*Rattus norvegicus*) and black rat (*Rattus rattus*) prey heavily on tropical island insects[331,332]. The world's largest pseudoscorpion *Garypus titanius* was extirpated from Ascension Island directly through rat predation[333], as was the Lord Howe phasmid (*Dryococelus australis*), which survives only on the rat-free, offshore island Ball's Pyramid[334]. The Christmas Island flea (*Xenopsylla nesiotes*) disappeared with its island-endemic host *Rattus macleari*[335,336] owing to disease introduced with non-native rats. Both non-native rats[337] and ants[338] are targeted with local control efforts on islands, with success generally reduced in the tropics[337].

Box 2. Insects in tropical agricultural ecosystems

Tropical landscapes have been subjected to substantial land-use change including deforestation, mining, and the expansion of intensive agriculture, with diverse consequences for insects. How insects in these human-modified landscapes respond to climate change, particularly in tropical agricultural systems, remains a crucial question for both biodiversity and food security. The physiological consequences (especially at the metabolic and demographic levels) of increasing temperature driven by climate change are likely to have profound impacts on insect populations in tropical agriculture[23,290]. Although some modelling studies suggest that herbivory will decline in tropical agriculture following climate change[291], few consider the effect of species interactions. Thermal tolerances of invasive herbivorous pests are likely to be higher than the indigenous insect predators and parasitoids that control their populations[193,194]. Increasing temperatures might therefore lead to a predator-release effect, causing increased outbreaks of some pest species and reductions in local and global food security. Predator release is of particular concern for the cultivation of rice, which is a staple food for more than half of the world's population[292,293]. Pesticides are another important factor is the use of pesticides. Although agricultural pests have been controlled with chemicals, their harmful effects on non-target species have been widely demonstrated[294,295]. Chemicals also affect the physiological performance of insects in complicated ways[296,297]. How their use will lead to further imbalance in the thermal tolerances of insect pests and their natural enemies in tropical agricultural systems remains unknown. Aside from temperature, climate change is also altering rainfall patterns globally, and the consequences for populations of tropical insects is even less well understood[85]. Some economically important tropical crops such as oil palm are pollinated by a suite of insects[298]. Gradual reductions in pollination services in Indo-Malaysia have been attributed to increased rainfall seasonality, yet to date there have been no studies directly investigating the effects of climate change on oil palm pollination[298]. The retention of connected forest patches and riparian corridors both within and adjacent to agricultural areas in the tropics increases the abundance and diversity of functionally beneficial insects[299-301]. The tropics are experiencing the fastest human population growth globally, and much of the population still relies on small holdings and subsistence farming for income and food security. At the same time, large-scale tropical agriculture including soya, rice and palm oil produces crops that are economically important at a global scale. Understanding the effects of climate change on insects and their services in tropical agricultural systems should therefore be a research priority.

Box 3. Disease and tropical insect dynamics

Pathogens transmitted by biting arthropods are responsible for over 700,000 human deaths annually, overwhelmingly in tropical regions[302]. Over several decades, the incidence and distribution of many vector-borne diseases has shifted, emerging in new areas or re-emerging in areas from which they had previously been eradicated[303]. Infection results from complex interactions among vectors, hosts and pathogens, each responding non-linearly to biophysical conditions[304]. Environmental changes can have profound impacts on disease dynamics, with land-use a dominant driver of emergence. In Southeast Asia, agricultural exposure doubles the risk of infection with vector-borne diseases[305]. Forest loss is associated with the rapid emergence of zoonotic malaria in Malaysia[306]. Viral diseases transmitted by *Aedes* (*Stegomyia*) mosquitoes have increased dramatically following geographic expansion of the primary vectors[307]. Mechanistic models estimate that the thermal optimum for *Aedes*-vectored virus transmission is as high as 29°C, implying climate change might shift the tropical disease burden from cooler-adapted malaria to dengue and Zika virus disease[308]. Social factors are also crucial determinants of disease dynamics. In the Americas, the emergence of cutaneous leishmaniasis, which is transmitted by psychodid flies, has long been attributed to deforestation. However, the effect of deforestation on infection risk diminished considerably when accounting for socio-economic factors, revealing that socially excluded populations are at higher risk[309]. Insects are also responsible for a large disease burden in livestock in the tropics, increasing pressure on local food security and livelihoods[310]. A socio-ecological approach will be crucial for predicting how future land-use and climate change interact to impact vector-borne diseases.

ToC blurb

Insect biodiversity in tropical forests is poorly understood but is most likely facing declines, with serious consequences for ecosystem functions and services. This Review describes the major threats to insect biodiversity, which include impacts from a burgeoning human population and from climate change. The authors further highlight the urgent need for greater efforts to measure and monitor insect biodiversity in the tropics and discuss emerging approaches to facilitate these studies.