Integrating multiple evidence streams to understand insect biodiversity change

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Title: Integrating multiple evidence streams to understand insect biodiversity change

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Abstract

Insects dominate animal species diversity yet face many threats from anthropogenic drivers of change. Many features of insect ecology make them a challenging group, and the fragmented state of knowledge compromises our ability to make general statements about their status. Here, we discuss the challenges of assessing insect biodiversity change. We describe how multiple lines of evidence – time series, spatial comparisons, experiments, and expert opinion – can be integrated to provide a synthesis overview of how insect biodiversity responds to drivers. Applying this approach will generate testable predictions of insect biodiversity across space, time, and changing drivers. Given the urgency of accelerating human impacts across the environment, this approach could yield a much-needed rapid assessment of insect biodiversity change.

Introduction

Insects are an extraordinarily diverse and abundant group of animals (*1*, *2*), and are essential to terrestrial and freshwater ecosystem functioning (*3*, *4*) that is critical to human wellbeing (*5*). Most of the world's flowering plant species depend on animal pollinators to reproduce, with an estimated 82% of species pollinated exclusively by insects (*6*, *7*). Moreover, insects are a crucial trophic node linking primary production to higher trophic levels: insects comprise the bulk of food sources for many birds, bats, reptiles, freshwater fishes, and other vertebrates (*8*).

There is overwhelming evidence of changes in insect communities in recent decades. These changes include rapid local and regional declines in abundance, occupancy, biomass, and diversity, as well as the reorganization of communities (*9*–*17*). Concern over these changes has permeated across scientific, public and policy sectors (*11*, *15*–*18*). While some narratives have likely exaggerated the extent of insect declines (*22*, *23*), insects are clearly threatened by a combination of widespread anthropogenic drivers, including land-use change, climate change, agricultural intensification, pollution, and introduced species (*14*, *24*).

Despite the growing recognition of the ecological and economic importance of insects (*14*, *25*–*28*) research on insect biodiversity has been limited (*29*, *30*) and under-funded (*31*). As a result, the available evidence describing insect trends is spatially, temporally, and taxonomically unrepresentative (*32*, *33*), such that the overall magnitude of the problem remains unclear (*11*, *23*). Current evidence is biased towards human-dominated landscapes in Europe and North America (*13*, *34*, *35*). Taxonomic bias favors easily observed or identified groups, such as butterflies, bees, and dragonflies, while more taxonomically intractable or geographically isolated groups (e.g., parasitoid wasps, earwigs, or icebugs) have been neglected (*33*). Available time series are generally short, leading to extreme and potentially spurious inferences (*36*). The high interannual volatility of insect populations means that long-term trends and historical drivers of insect biodiversity change are particularly poorly captured by short time series (*37*). New approaches are required to understand and quantify changes in insect biodiversity and its drivers, to better support global policy recommendations and to target resources effectively to mitigate threats to insects. However, these challenges are exacerbated by the fact that insects are hyper-diverse, have complex lifecycles, and experience substantial population fluctuations.

For these reasons, a detailed global perspective of insect biodiversity change and its drivers remains elusive (*21*), making it challenging to develop specific measurable targets and goals for insects in large-scale biodiversity discussions and strategies (*38*). For example, Goal A of the Kunming-Montreal Global Biodiversity Framework refers to metrics such as population abundance and extinction risk, for which there are excellent data for vertebrates (*39*). In contrast, a mere ~1.2% of insect species (12,100 species out of ~1 million described insect species (*1*)) have undergone the International Union for Conservation of Nature (IUCN) Red List assessments necessary to calculate extinction risk, of which approximately a quarter (3,107 species) were evaluated as Data Deficient (*40*). An even smaller fraction has been assessed more than once, undermining any ability to understand changes in extinction risk (*40*).

These shortfalls underline the need for new approaches to deliver a more comprehensive, globally representative picture of the state of insects to inform scientific research, public understanding, and biodiversity policies. Sparked by reports of unexpectedly large insect declines (*9*), there has been a surge in the compilation and analysis of insect time-series data. While this effort has led to valuable insights, disagreement remains as to whether, where and why insects are declining. The 'why' question is particularly important because any attempts to reverse declines will need to address the drivers of change. Moreover, a synoptic overview of insect biodiversity change and its drivers is a prerequisite for making testable predictions about the effects of conservation or policy actions. For example, how much would insects benefit if we reduced global pesticide usage. Indeed, prediction is essential for demonstrating scientific understanding (*41*). A predictive understanding of insect biodiversity change would make it possible to project the potential future state of insect biodiversity and the consequences for ecosystems (e.g., the risk of reduced pollination services) and, thus, inform evidence-based policy recommendations and conservation action.

Here, we address the grand challenge of understanding insect biodiversity change from fragmentary data. Recent reviews on insect biodiversity have focused on the state of insects (*2*, *42*), the drivers of insect declines (*13*, *14*), and advocated priorities for data generation (*18*, *37*, *43*). In this paper we lay out the principles by which a more comprehensive understanding is possible via the integration of multiple imperfect lines of evidence that are already available.

We first outline the features of insect biology that make them challenging to study. We then explore the strengths and weaknesses of different evidence types for understanding how and why insect biodiversity is changing. Finally, we identify what is required to harness the breadth of currently available evidence to build a better understanding of the state of insect biodiversity. Our approach provides a basis for advances in understanding the drivers of insect biodiversity change that are not constrained by the limitations of only one evidence type. Our overall goal is to lay a roadmap toward a solid understanding of insect biodiversity change on which conservation policies can be built, without having to wait decades for comprehensive monitoring data.

The challenge of understanding insect biodiversity change

Insects are hyper-diverse, comprising up to 90% of all multicellular animal species, with the majority still undescribed (*1*, *2*). Beyond the numbers lie a staggering diversity of ecological adaptations and functional roles, from eusocial pollinators, to specialized parasitoids, to scavenging detritivores (*3*, *4*, *44*), in addition to highly complex lifecycles (*45*). Thus, we should expect insect biodiversity change to be extremely heterogeneous. Moreover, insect population sizes are more stochastic than for other taxonomic groups, so more datapoints are required to capture fluctuations than for vertebrates (*46*, *47*). Stochasticity is high both within and between years, with even small differences in the timing of annual monitoring resulting in dramatic differences in reported species abundance (*20*, *21*).

The complexity of insect biodiversity change is further compounded by a system of interacting drivers (*48*, *49*). At the local to landscape scale, there is strong evidence for land use, climate change, pesticides, disease, and invasive species as key drivers of insect biodiversity change (*2*, *14*, *50*, *51*). What is lacking is a quantitative assessment of the relative importance of the various drivers across scales, as well as knowledge on how these drivers interact to cause change. It is only by understanding these complex and dynamic driver-response relationships that it will be possible to identify when and where declines in insect biodiversity may be reversible (*52*) and deliver a synoptic view of insect biodiversity change and its consequences.

Ecology and Traits

The impact of direct drivers of change is mediated by insect ecology and evolution. Species traits have long been used to provide mechanistic insights into how biodiversity responds to drivers (*53*). Traits are likely to be especially valuable for understanding differential responses to drivers in insects, given the diversity of insect life histories and dearth of high-quality data. Indeed, as many insects undergo metamorphosis, their ecological niche changes dramatically during their lifecycle, such that environmental constraints on one life stage can be quite different to those on another (*54*). Thus, insect life histories are highly variable, encompassing inherent differences in life stages (e.g., larva vs adult), as well as in longevity, dormancy, synchronization (*55*), and reproductive strategies (sexual vs asexual; egg laying vs viviparity). Moreover, understanding how species with shared traits respond to drivers provides insights about the whole trait group, even when specific data are not available for all (which is often the case for insects). For example, whether forest-dwelling insects prefer open glades, closed understory, or forest canopy will influence how they respond to deforestation (*56*, *57*), and species preferences combined with rates of deforestation could be used to infer insect trends.

Species' ecology can also interact with characteristics of the surrounding landscape to increase susceptibility to decline (Fig. 1), with poorly dispersing or wingless species (*58*, *59*) or those unable to persist in certain habitat matrices (e.g. intensive agriculture) unable to survive (*60*). Better evidence on how insect traits and life stages mediate the impact of drivers is crucial to understanding their ongoing and future responses to global change (*61*).

Evolution and Plasticity

Global drivers subject insects to changing, and often strong, selection pressures, leading to evolutionary responses that also mediate the effects of drivers on insect diversity (*62*). Thus, understanding and predicting insect responses to environmental change is complicated by evolutionary dynamics and vice versa (*63*, *64*). For instance, dispersal, driven by land-use change, can shape the spatial pattern of insect genetics (*65*). Similarly, crop domestication has selected for some insects to become agricultural 'pests' (*66*, *67*).

Insects exhibit various examples of beneficial adaptive plasticity in response to environmental change, including diapause induction or suppression of reproductive output under harsh conditions (*68*). However, insects may also pursue maladaptive pathways (i.e., developmental traps). For example, climate change in the temperate zone is causing insects to complete their lifecycles more quickly, leading some to attempt additional generations (and often fail) before winter sets in (*69*). These short-term changes in turn impact insect population dynamics and can be translated into long-term adaptation. Temperature changes are a key driver of evolutionary adaptation in insects, and as suitable climates shift, insects are challenged with adapting to new conditions or tracking suitable ones (*72*). Conversely, pesticide resistance may actively select for certain species in agricultural settings, increasing their abundance while the majority are adversely affected (*73*). We must therefore consider adaptive capacity and plasticity in response to environmental drivers, since evolutionary rescue effects will be more apparent for insects than for longer-lived organisms (*76*, *77*).

Interaction networks

Insect populations are influenced by a range of antagonistic (e.g., predation or herbivory) and facilitative (e.g., pollination) interactions (Fig. 1). The consequences of environmental change for insects depend both on how they interact with other species and the structure of the whole network. Insect species often have specialized interactions, including as parasitoids, herbivores, or pollinators (*78*, *79*). For example, 27% of tropical herbivorous insects feed exclusively on a single host plant species, while 48% feed on plants within one genus and 60% within one family (*80*). Holometabolous insects (those with complete metamorphosis) experience shifting interactions throughout their lifecycles (e.g., many hoverflies change from predatory larvae to facultative pollinators as adults). This makes insects especially vulnerable to co-extinctions with their interaction partners (*81*, *82*). Furthermore, the loss of generalist insect species may have wide ranging consequences on network resilience and robustness through cascading extinctions (*63*), potentially resulting in coextinction of species with no direct interaction (*84*). These complexities mean that drivers that may superficially appear unimportant for certain species may still have consequences through indirect effects (*82*).

<FIGURE 1 HERE>

Emerging questions

These layers of complexity highlight the magnitude of the challenge in modeling insect biodiversity change from fragmentary data, but also suggest some emerging questions: which drivers are most important, for which insects, and what is the form and timing of the response? Can we extract sufficient signal to understand – broadly, if not precisely – the drivers of global change in insects, in models that are good enough to be useful for informing policy change or mitigation measures? Given the urgent need to address insect declines (*85*), we need to make better use of the data that is currently available.

Time series are not enough

Time series are comparable estimates of a biodiversity metric (e.g., population abundance, biomass) at a location at multiple points in time. Time series are therefore a direct form of evidence for biodiversity change, capturing the actual temporal dynamics of interest, and evidence from time series has formed a major part of current knowledge on insect change (*11*, *86*). Individual time series vary in their temporal, spatial, and taxonomic coverage, while time series are undertaken for diverse reasons, including monitoring associated with recovery following restoration, post pollution or weather events, or in habitats known to be under threat. Collectively, the portfolio of existing insect time series is neither spatially nor taxonomically representative (*35*). These issues hinder our ability to use time series to quantify how insect biodiversity is changing at global and regional scales, and limit how well we can identify the causes of change (*43*).

The temporal coverage of individual time series varies in terms of the *frequency* (number of sampling occasions) and the *span* (the length of time between the first and last samples) of the period assessed (Fig. 2). Ideally, the frequency of data collection would be sufficient to capture change from one generation to another, whilst accounting for within-season variation (e.g., as adults emerge and then die). Instead, most insect time series contain gaps (*35*, *37*), and many represent ‘snapshot’ resurveys of locations sampled once in the past (13% of studies analyzed in van Klink et al. (*11*); Fig. 2). Snapshot surveys are particularly problematic for insects, where year-to-year population variation can be much higher than for plants or vertebrates (*20*), creating substantial noise in the trend estimate and extreme sensitivity to the baseline conditions (*21*, *55*). This noise can introduce bias if there is any non-randomness in the circumstances of either the original or repeat survey (*87*). As a result, intermittently sampled (i.e., less frequent than annual sampling) time series spanning fewer than ten years are unlikely to provide reliable estimates of change in insect populations (*21*, *46*, *87*). But with little support for long-term monitoring (*20*), data are more typically collected over much shorter periods. Even for longer time series, the frequency and span of available time series (Fig. 2) means they often lack the statistical power to detect trends (*21*, *36*, *52*, *88*) or isolate associated drivers (*43*).

<FIGURE 2 HERE>

An essential quality for time-series data is that the sampling protocol should be consistent over time, so that comparable estimates of biodiversity are obtained (or that variation, e.g., due to surveyor identity, can be statistically accounted for). However, consistency is not sufficient for producing data that can inform the wider question of why insect biodiversity is changing. Collections of time-series data will only provide such information if they are representative of environmental gradients and the range of exposure to threats (*90*). Instead, site selection is often non-random, with many time series located at field stations or other areas likely to be buffered from ongoing threats (*35*, *87*) (e.g., 34% of plots in the meta-analysis by van Klink et al. (*11*) are located in protected areas). By contrast, other time series may have been initiated in response to an environmental perturbation, either natural (such as a weather event), catastrophic (e.g., pollution) or artificial (e.g., experimental, restoration or changing management). In the absence of matching controls, these data have the potential to skew our perception of how and why insect biodiversity is changing (*32*). Resource limitation typical to long-term sampling strategies may also mean that sampling effort is limited, raising questions as to the power to identify trends in some populations.

A further issue is that most time series lack scale-relevant information on external drivers and how they changed over time. Where this information is available, these drivers are often correlated and difficult to disentangle, which limits the ability of time-series data to attribute the causes of biodiversity change (*10*, *91*, *92*). Without quantification of how drivers affect insect diversity (e.g., driver decomposition; (*93*, *94*)) we cannot hope to predict how alternative policies and actions will affect future trends.

Sparked by the debate on insect biodiversity change, there have been calls to address the issues outlined above by greatly expanding the network of insect monitoring schemes (*18*, *37*, *52*). For instance, Didham et al. (*21*) suggested that intensive annual monitoring (e.g., (*95*)) could be complemented by extensive but infrequent occupancy surveys at large numbers of sites. A step-change in insect monitoring is indeed urgently required, and well-designed, long time series will ultimately provide the best quantification of biodiversity change (although attribution to drivers will remain difficult). However, the cost of ongoing inaction will be high, and we cannot wait decades to accumulate these data (*17*, *34*, *86*); there is enough evidence about insect declines in some regions to demand immediate remedial action (*85*). To target action where it is most needed, we require a rapid synthesis on the causes of insect biodiversity change using data from a broad range of evidence types, not from just time series.

Evidence beyond time series: developing threat-response models

Time series provide the best evidence that change has happened but struggle to tell us why that change occurred. Understanding why biodiversity has changed is critical if we are to reverse declines, prevent extinctions, and maintain ecosystem function into the future (*41*, *96*). To build a predictive understanding of insect biodiversity change we need to first model the relationships between biodiversity metrics and direct drivers. We refer to these relationships as threat-response models (TRMs; sensu (*97*), also known as pressure-impact relationships (*98*)). By quantifying the relationships between drivers and biodiversity metrics, it becomes possible to project the biodiversity response across spatial domains where the driver intensity is known. In this way, TRMs can be used to summarize the total impact of a driver within a given domain, and to make testable predictions for regions where no biodiversity data exists. Projecting TRMs in time makes it possible to re-evaluate historical baseline conditions (*99*) and compare biodiversity trends under a range of plausible futures of climate and socioeconomic change (*96*).

Well-established TRMs, such as those developed as part of the GLOBIO (*98*) and PREDICTS (*100*) projects, are parameterized largely using data from vertebrates. However, the ability of TRMs to simplify multidimensional responses using trait-based approaches makes them particularly valuable for insects (and other hyper-diverse groups). The notion of using models to link insect biodiversity with threat gradients has been gaining traction in recent years, with insights from studies at local (*101*), regional (*102*) and global (*48*) scales. More broadly, insect conservation biologists have argued that experimentation (*43*) or spatial comparisons (*52*) can be employed to build models and reveal the most important drivers of insect biodiversity change. Where rigorous data is lacking, models linking insect populations with threats can also be derived from eliciting the opinion of taxon experts, using techniques from the social sciences (*51*, *103*). Such approaches are particularly valuable for understudied taxa or geographic regions where structured expert opinion processes can provide key insights about population declines in the absence of quantitative data. These and other types of approaches all provide useful evidence, in the form of TRMs, to augment what can be learned from population time series.

The ideal dataset for building TRMs would measure change over a long period, have broad taxonomic and spatial coverage, and represent the full range of drivers. In reality, few biodiversity datasets come close to this ideal, although for well-studied groups such as birds and mammals they are sufficient for building useful TRMs. The evidence streams available for insects occupy different spaces along these three axes (Fig. 3): in other words, the available evidence types have complementary strengths and weaknesses.

<FIGURE 3 HERE>

To illustrate these complementarities, we evaluate each evidence type against six ‘ideal properties’ (Fig. 4) for understanding and predicting insect biodiversity change. These are 1) the ability to describe long-term trends, 2) the ability to capture transient dynamics, 3) whether the results of analyzes using the evidence type can be decomposed or aggregated across taxonomic and spatial scales, 4) whether the results of analyzes using the evidence type can be generalized and transferred, 5) whether corresponding driver information is available at the same scale as the evidence type, and 6) whether the evidence type can unpick mechanistic or causal threat-response relationships, including interacting (e.g., antagonistic, synergistic, additive) drivers.

<FIGURE 4 HERE>

Experiments

The strength of experiments lies in their ability to confirm causal links between drivers and biodiversity metrics (*43*). Experiments vary along a spectrum from lab-based, to plot or semi-field studies, up to more challenging landscape-scale manipulations (*104*). Whilst experiments deliver strong evidence, it is difficult to translate the outcomes to real world spatial and temporal scales (*91*). For instance, lab-based experiments are often targeted at individual species (minimal taxonomic breadth; Fig. 3) to characterize their response to a single factor e.g., thermal optima or agrochemical exposure (*49*, *105*), and are often short-term (*106*) (low temporal breadth; Fig. 3).

Whilst experiments provide an opportunity to identify casual relationships, the scope of environmental drivers manipulated is typically limited (i.e., low environmental breadth; Fig 3) and so may only partially capture causes of declines. Moreover, experiments often fail to capture how responses to drivers change when species are embedded in real interaction networks (Fig. 1) (although natural experiments are increasingly common (*107*)). Thus, simply scaling up the results of small-scale experiments may not be informative (*108*).

Ultimately, while experiments are common, there are few at a large enough spatial and temporal scale to fully capture real-world effects (*91*), reflecting practical and financial constraints (*109*). These limitations can be partially mitigated in distributed collaborative experiments (*99*) or transcended by synthesizing results across multiple experiments using meta-analysis. Combining multiple experiments provides a means to quantify generalized relationships between anthropogenic threats and insect diversity (*90*). Still, meta-analyses are subject to their own limitations, such as publication bias (*110*), inferential errors (*111*) and lack of data availability (*112*, *113*). Nevertheless, meta-analytic approaches have already been effective in assessing the average response of insects to drivers including urbanization (*114*), dams (*115*), and nutrient enrichment (*116*, *117*).

Spatial comparisons

Spatial comparisons – the comparison of biodiversity across sites – are often used to investigate insect biodiversity change (*48*, *118*, *119*). Their use assumes that patterns in space can shed light on patterns over time (*120*, *121*). For example, Hallmann *et al.* (*9*) synthesized data from 63 sites within protected areas in Germany – most visited only once – to infer a 27-year time series of flying insect biomass.

Spatial comparisons have high statistical power to identify relationships between drivers and biodiversity declines and quantify their potential impact (*52*). Indeed, comparisons across whole landscapes allow sites to be compared across multiple driver gradients, e.g. (*118*). In addition, larger-scale changes can be modeled by bringing such comparisons together. For example, the PREDICTS project has compiled a global database of hundreds of studies comparing sites differing in land use types and intensity (*122*). TRMs built with these data have estimated average responses of biodiversity metrics across land-use gradients, including for insects (*48*, *123*), and projected these responses in space and time (*100*).

Spatial comparisons have limitations for assessing changes in insect biodiversity (*91*, *124*). They are correlative, limiting causal inference, since correlation between drivers makes their effects hard to separate (although see (*125*)). By taking snapshots in time they risk being confounded by transient dynamics and legacies of site history, and they overlook gains or losses in the regional species pool (an aspect of ‘shifting baseline syndrome’ (*126*)). The advantage, however, lies in the relative simplicity of assembling the evidence base: they often sample more sites, can be undertaken in more locations (*91*) and, given the statistical power with which they link spatial variation in biodiversity and drivers, have so far been undervalued as evidence of insect biodiversity change (*52*). Perhaps most importantly, their collection can be achieved in very short time scales and can be reactive in terms of their focus, including under-represented regions, habitats, or taxonomic groups.

Expert elicitation

Information from experts (including scientists, indigenous people, and other non-scientist specialists) reflects their accumulated knowledge and experience. Expert elicitation around biodiversity trends, and the drivers thereof, is particularly valuable for poorly studied insect groups, in the absence of more direct forms of evidence. Expert elicitation may also provide insights into the impact of multiple interacting drivers on better-studied groups, which may be difficult to disentangle quantitatively but can be teased apart conceptually (*127*, *128*). A major limitation is the subjective nature of expert knowledge, which makes assessing the reliability and repeatability of results challenging, especially when very few experts are available (*14*, *30*). Similarly, the process of expert elicitation may introduce its own bias through survey design and choice of questions as well as interactions between participants in group meetings, although approaches such as the Delphi technique can be used to reduce some of these issues (*129*).

Given sufficient expertise, expert elicitation has the potential for high taxonomic and geographic coverage. It provides information that may be costly to gather in other ways (e.g. large-scale, long-term monitoring), although detailed species assessments (e.g., IUCN Red List assessments) can be time, data and cost intensive. At a broader scale, Miličić *et al.* (*51*) used a top-down expert elicitation process to gather information from 413 respondents on the most relevant threats to insect biodiversity in general, highlighting key differences between regions and taxa. This indirect evidence can be used to link the state of insect biodiversity with specific threats, especially where direct evidence is not available, or as a comparison to other types of evidence.

Harnessing the breadth of evidence

We have explored how TRMs based on experiments, spatial comparisons and expert elicitation provide alternative and complementary sources of evidence linking insect biodiversity change with drivers. Crucially, none of these evidence types alone can cover the full taxonomic, spatial, or temporal dimensions required for a synoptic and predictive understanding of insect biodiversity change (Figs. 3 and 4). Thus, there is an urgent need to harness this breadth of evidence, to synthesize the inferences from each evidence type in ways that maximize the complementarities and overcome the limitations of individual evidence types. To do this, we need to understand how to integrate diverse evidence streams and explore the limits to which we can combine TRMs and extend their inferences to different taxonomic, spatial, or temporal settings. Without attempts to generalize, the literature could become a descriptive ‘stamp collection’ of case studies (*90*).

One avenue for combining evidence is through model-based data integration, in which the relationship between data types is defined in terms of model parameters (*130*, *131*). Integrated modeling is particularly well developed in the context of species distribution models. For instance, Kotta *et al.* (*132*) combined experimentally defined tolerance levels with spatial data to model climate change effects on a macroalgal species and its herbivore. Domisch *et al.* (*133*) combined freshwater species occurrence information with expert range data leading to improved spatial predictions. Whilst integrated modeling is conceptually attractive, there are analytical challenges, particularly when combining data that differ in both quality and quantity (*134*) and where there are mismatches in spatial scale among data types (*135*). As a result, formal data integration may currently only be possible for well-studied regions and taxa where data availability is highest. This starting point, however, is fertile ground for new modelling tools to be developed (*136*).

A tractable alternative is to compare the predictions from different types of TRM against one another, by projecting the models across space (e.g., using spatial data layers) and taxa (e.g., using species traits). Regions of parameter space where the model projections agree about the direction and/or magnitude of biodiversity change indicate higher confidence in the state of insect biodiversity. Regions where they disagree highlight priority research gaps or model inadequacies. Regions where direct evidence of biodiversity change is available (i.e., time series) provide an opportunity for external validation (*90*, *137*) and a chance to demonstrate predictive understanding (*41*). This opens up a range of options for iterative model refinement to achieve the best fit to empirical data (known as a ‘digital twin’ (*138*)). For example, one could apply weights to each evidence type (*139*), then solve for the weights that optimize fit to the observed time-series trends, or test for lagged responses to increases in threat intensity (*140*). Similarly, when integrating TRMs for different threat types, one could compare models that assume additivity among threats with those in which the threats act synergistically or antagonistically.

Synthetic TRMs integrating evidence types and drivers would provide a starting point to answer some of the biggest questions about insect biodiversity change (Fig. 5). Projecting the model in space would make it possible to assess the magnitude of insect biodiversity change across large scales and to identify probable hotspots of decline. Projecting the model in time would make it possible to explore plausible future scenarios for insect biodiversity (*96*). Aggregating insects by functional traits (e.g., body size, diet, fecundity, etc.) (*141*) that underpin ecosystem processes would make it possible to explore the consequences of insect biodiversity change for higher trophic levels (especially insectivorous bats and birds) and on benefits that people derive from insects (including pollination, pest control and nutrient cycling, amongst others (*3*, *4*)). The modeling framework described here is also easily extensible to incorporate indirect drivers and the effects of mitigation strategies such as protected areas (*96*, *142*). Based on these principles, a broad-brush quasi-global model of insect responses to land-use is within reach (sensu (*48*, *100*)), as are regional models of multiple threats for well-studied Orders.

<FIGURE 5 HERE>

Whilst powerful, models have limitations. We see four major challenges for the development of large-scale and credible TRMs for insects. The first is around the technical aspects of model-fitting. There are well-known difficulties of modeling biodiversity using heterogenous data (*144*), especially where the scale of inference is different from the scale of the data (*135*) or where there is context-dependency (*111*). A second challenge is around scale: TRMs built to address global questions (e.g. about the net magnitude of change) will not be suitable for addressing local questions (e.g. about the effect of a given intervention). Thus, TRMs at different scales will be appropriate for addressing different questions, but identifying the appropriate level of detail for a particular application may not always be obvious. The third challenge is around communication: it will be important for models to capture and convey the many forms of uncertainty and validity (*90*, *145*). However, inferences around biodiversity change are often confounded by temporal, spatial and phylogenetic clustering within the data. Capturing all these uncertainties risks rendering the model uninformative for decision-making (*145*, *146*). Similarly, it will be important to avoid making unwarranted claims about generality (*90*), particularly when presenting models as being of global relevance (*147*). Formal analysis of the degree to which models can be validly extended (i.e., transferability) is useful to place limits on the potential inference and should become standard (*148*, *149*). Finally, there are ecological challenges that will be hard to overcome: certain aspects of insect ecology will be especially hard to model (as noted in Section 2). Early generations of insect biodiversity projection models will be unable to capture complex life histories or species interactions, but these and other processes could be added later (*143*). There are taxonomic groups and parts of the world where almost nothing is known about the insect fauna. Thus, one of the goals for the first generation of synthetic insect TRMs would be to highlight the remaining gaps (gaps not covered by data or by valid model inferences) where new data are urgently needed.

Outlook

Even with the caveats outlined above, there is sufficient evidence of changes in insect biodiversity to demand urgent action (*85*). This action needs to be informed and directed by a strong evidence base (i.e., sufficient extent, depth, and representativeness of evidence across time, space, and taxonomy, with levels of uncertainty that allow for clear decisions). Intergovernmental commitments to avert biodiversity loss will always be limited, so resources must be used effectively. Even when commitments are made, the historic track record of meeting such goals has been less than impressive (*150*). The recent Global Biodiversity Framework provides new impetus for action, with an ambitious target for the reduction of pressures on natural systems by 2030, and a goal (amongst others) to achieve healthy and resilient populations of wild species by 2050. There is an urgent need for the biodiversity modeling community to evaluate whether the scale of ambition defined in the targets is sufficient to put us on a pathway toward the 2050 goal, i.e. to 'bend the curve' (*96*). Due to the sheer number of insects, their vast ecological diversity and the paucity of available data, the challenge of understanding global insect biodiversity change is an immense task. To date, limited resources have been directed toward this task. We are not the first to point out that time series of insect populations alone are insufficient to address this problem (*43*, *52*). We have gone further in arguing that a broad suite of evidence types, brought into a common analytical framework, is required to evaluate the scale of the problem facing insect biodiversity, as well as providing a triage system to identify the highest priority taxa, places, and threats, and thus leverage points where mitigation can be most effective. Only through harnessing the full breadth of available evidence can we piece together the fragmentary data into a coherent picture. It is a small but important first step toward an insect-positive future.

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Figure Legends

Fig. 1. The complexity of insects in a changing world and the role of interactions. The center ring shows an example insect lifecycle, with curved arrows between life stages (here, larva, pupa, adult). Connected to the lifecycle are a simplified number of interacting species including a variety of taxonomic groups. The middle ring represents the landscape in which this lifecycle and the local interactions occur, often incorporating multiple habitat types and land uses. The outer ring shows some of the major drivers that act across the landscape and local scales, affecting the species found in those areas. These can act alone but can also interact.

Fig. 2. Frequency vs span of time series in a large insect time series database. The points represent the 1,657 sites (i.e., time series) included in the InsectChange database (*89*), which underpins a large-scale meta-analysis on insect trends (*11*). Note that only time series covering ~10 or more years were included in this database. The color underneath the points reflects the density of time series across the plot (red = highest density, white = lowest density). The lines represent approximately annual sampling (i.e., 10 sample events for a 10-year time series), ~seasonal sampling (i.e., 40 sample events for a 10-year time series), ~monthly sampling (i.e., 120 sample events for a 10-year time series), ~weekly sampling (i.e., 520 sample events for a 10-year time series).

Fig. 3. The power of attribution and breadth of coverage of different evidence types for insect biodiversity change across temporal, spatial/environmental, and taxonomic dimensions. Power of attribution refers to the potential for evidence types to identify causal links between insect biodiversity change and any external driver based on existing data. Experiments have high power because they are designed to quantify specific effects, whereas time series are typically set up without regard to the drivers present. Coverage captures the extent, depth, and representativeness of the evidence type in the three dimensions of time, space, and taxonomy. For example, taxonomic coverage reflects the number of insect Orders included (extent), the number of species within Orders (depth), and the representation of species across Orders (representativeness). Although inherently subjective, positioning of the shapes illustrates our interpretation of the strengths and weaknesses of the four evidence types; the size of each shape indicates the approximate variation in power of attribution and coverage within each evidence type. N.B. Evidence types are not mutually exclusive, e.g., some studies can be both experiments and time series, depending on how data were collected and analyzed.

Fig. 4. Properties of available data for understanding insect biodiversity change and underlying drivers. Grades and shading (A – greatest, dark to D – least, light) reflect the fulfilment of the ideal property for each evidence type. Each box contains our rationale for the assignment of grades to each property and evidence type.

Fig. 5. Establishing a synoptic overview of insect biodiversity change to inform policy and conservation action. Integrating multiple evidence types on the state of and changes in insect biodiversity with information on the drivers of this change can provide a synoptic overview of current patterns. This overview would underpin projections of insect biodiversity change across space and through time, as well as of the potential consequences of insect biodiversity change.