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Overview Article

Meta-synthesis reveals interconnections among apparent drivers of insect biodiversity loss

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Abstract

Scientific and public interest in the global status of insects has surged recently; however, understanding the relative importance of different stressors and their interconnections remains a crucial problem. We use a meta-synthetic approach to integrate recent hypotheses about insect stressors and responses into a network containing 3385 edges and 108 nodes. The network is highly interconnected, with agricultural intensification most often identified as a root cause. Habitat-related variables are highly connected and appear to be underdiscussed relative to other stressors. We also identify biases and gaps in the recent literature, especially those generated from a focus on economically important and other popular insects, especially pollinators, at the expense of non-pollinating and less charismatic insects. In addition to serving as a case study for how meta-synthesis can map a conceptual landscape, our results identify many important gaps where future meta-analyses will offer critical insights into understanding and mitigating insect biodiversity loss.

Keywords: Anthropocene, biodiversity loss, drivers of decline, insect conservation, systematic review

Rapidly accelerating environmental change over the previous century has resulted in biodiversity loss across the tree of life (Wilson 1992, Dirzo et al. 2014, Wagner et al. 2021b). This crisis is, in large part, a crisis of insects, because they represent the majority of terrestrial biodiversity (Stork 2018). Insects are crucial components of nearly all freshwater and terrestrial systems, contributing to vital ecosystem functions such as pollination, pest control, macro-decomposition, herbivory, food for higher trophic levels, and nutrient movement and cycling (Wilson 1987). Without question, widespread disruptions to insect communities will have considerable adverse effects across natural systems and society, many of which may be unforeseen (Vanbergen and Insect Pollinators Initiative 2013).

Although evidence of insect biodiversity loss extends as far back as the Industrial Revolution (Thomas et al. 2004, National Research Council 2007, Habel et al. 2016), there has been a recent and substantial shift in interest concerning the global status of insects (Althaus et al. 2021) following the publication of a landmark report in 2017 of large-scale reductions of flying insect biomass over several decades in protected areas near Krefeld, Germany (Hallmann et al. 2017). Recent years of research have added nuance to the concern over the threats facing insects (Saunders et al. 2020), with increasing numbers of studies highlighting the spatial, temporal, and taxonomic heterogeneity across reported declines (Wagner et al. 2021a). Although it is generally agreed that the major stressors acting on insect biodiversity are known, there remains a great need to untangle the relative importance of the diverse stressors and to determine how and to what extent the drivers are interconnected. Given the rapid increase in the number of publications, it becomes informative to examine the literature to understand what hypothesized drivers have been implicated, at which scales of biological organization, and for which taxa. Our goal in the present article is to provide an overview of the conceptual landscape within which researchers will work over the next decade.

Meta-synthesis to survey recent hypotheses of insect biodiversity loss

To understand and shape the discussion of insect biodiversity loss, we took a meta-synthesis approach, reviewing non-primary, peer-reviewed literature published since Hallman and colleagues (2017). We targeted synthesis papers because each summarizes a subset of the field, and collectively, they are an informative resource for efficiently sampling hypotheses about threats facing insects, identifying interconnections among them, and understanding gaps in current thinking. We performed a literature search of the ISI Web of Science Core Collection and SciELO using an inclusive set of search terms for insects (Haddaway et al. 2020) and terms related to insect decline (see the supplemental material for the specific search parameters). The search identified over 3500 studies published since 2017, including 175 reviews, meta-analyses, and perspectives from 661 authors that hypothesized or described how different drivers may affect insects.

We then applied a systematic and repeatable approach to review these syntheses (Grames and Elphick 2020), in which we extracted all proposed causal pathways (referred to in the present

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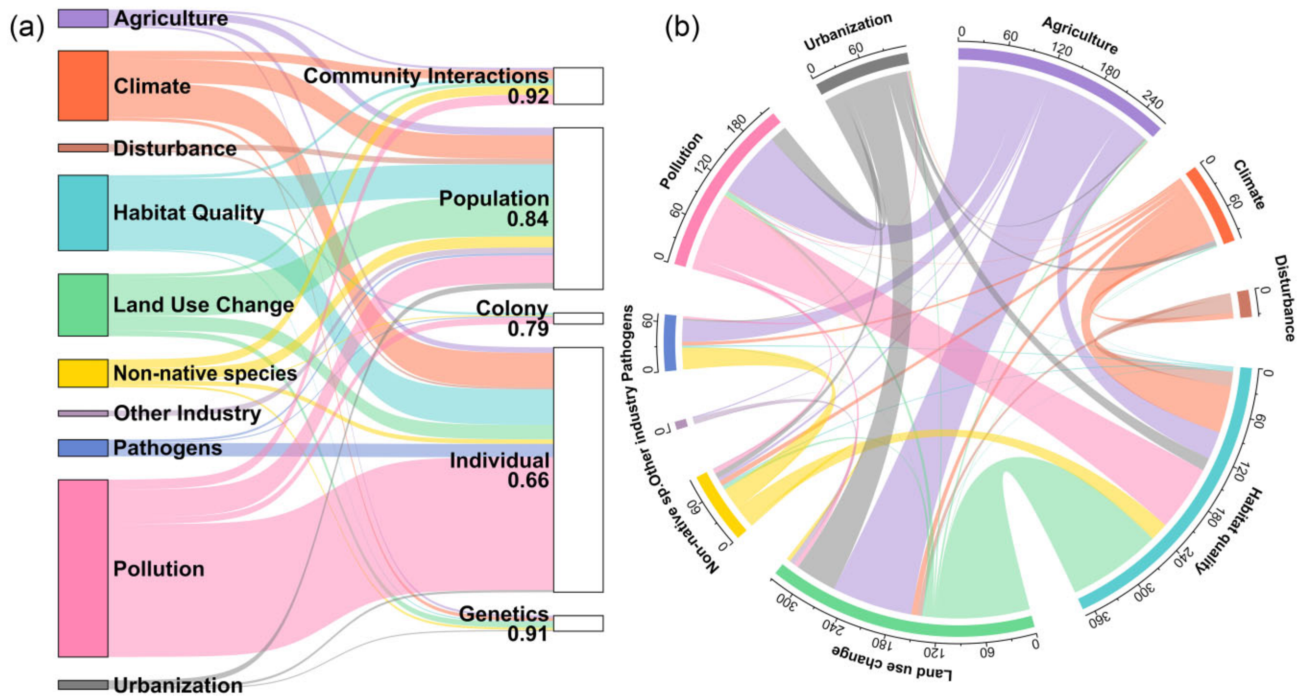

Figure 1. The frequency and interconnectivity of hypothesized drivers of insect decline at the broadest classification level. (a) The distribution of drivers (shown in color) and associated biological outcomes (shown by the white boxes). In both panels, the width of the link reflects the frequency with which the path is discussed in the literature. The number below each outcome label indicates the Pielou evenness for that variable (where 1 is the maximum evenness). (b) The interplay of different drivers of decline. Paths flow in the direction of hypothesized causality and are colored by the root drivers (e.g., pollution in the upper left primarily affects habitat quality in the lower right, whereas most of the incoming hypotheses about causes of pollution originate in agriculture). Overexploitation is not plotted because of low frequency.

article as *hypothesized drivers* or *hypotheses*) of how potential drivers relate to insect outcomes. Once the hypothesized causal pathways had been extracted from their source, they were incorporated into a network in which hypotheses form directed paths that link anthropogenic stressors with mediating variables and their effects on insects (Grames et al. 2022). The hypotheses were then nested at different resolutions with different degrees of specificity; for example, pollution was subdivided, at the second-highest resolution, into subcategories, including light pollution and pesticides, with the latter subdivided at the highest resolution into insecticides, fungicides, and herbicides. The resulting network of hypotheses consisted of 16 nodes at the lowest resolution and 108 nodes at the highest resolution (where *nodes* describes the proposed causes and outcomes), with 3385 edges (the connections between the nodes), summarizing 597 unique hypothesized causal pathways. The network is presented in the present article and as an interactive tool that readers can explore (see the supplemental material and online figshare respository).

Connections between frequently hypothesized drivers of decline

The hypothesized drivers of insect decline broadly fell into 11 categories when characterized at a coarse resolution, with pollution, climate change, habitat quality, and land-use change most frequently proposed as having direct links to insect outcomes (figure 1a). Further consideration of the connections between drivers revealed agriculture, climate change, and urbanization to be the most frequently proposed drivers that were almost exclusively root or upstream nodes, from which nearly all pathways leave and very few, if any, flow into (figure 1b). Among these coarse source drivers, agriculture, especially the effects associated with its intensification, was the most discussed. These impacts are widespread and are connected with land-use change through the destruction of natural habitats and the creation of monocultures (Kovács-Hostyánszki et al. 2017, Kline and Joshi 2020, Raven and Wagner 2021), connected to pollution through pesticides (Mupepele et al. 2019a, Tooker and Pearsons 2021, Toledo-Hernández et al. 2022), and connected to pathogens through the introduction of managed bees (Gisder and Genersch 2017, Owen 2017), many of which lead to downstream degradation of habitat quality through the loss and contamination of insect food resources (Durant and Otto 2019, Proesmans et al. 2021). Climate change and urbanization were also largely hypothesized as root drivers but were mentioned considerably less often than agriculture. Urbanization was primarily connected to land-use change through the densification and expansion of urban environments that begets habitat loss and fragmentation (Prendergast et al. 2022, Vaz et al. 2023). Climate change was the least connected of the other 10 broad categories of drivers of insect declines, largely linked with the degradation of habitat quality (Wilson and Fox 2021).

When categorized in greater detail, the number of stressors expanded to 77 (compared with the 11 lower-resolution categories). The three most frequently proposed specific drivers with direct links to insect outcomes were insecticides, the availability of critical plants (including host plants and floral resources), and habitat loss (figure 2). Discussions regarding the impacts of insecticides were particularly widespread because of studies of their lethal and sublethal effects on bees, representing 8.2% of all pathways across all syntheses. These most commonly proposed stressors were not necessarily regarded as root drivers. Among the high-resolution terms, general agriculture, unspecific climate, and unspecific urbanization were considered the most upstream, with

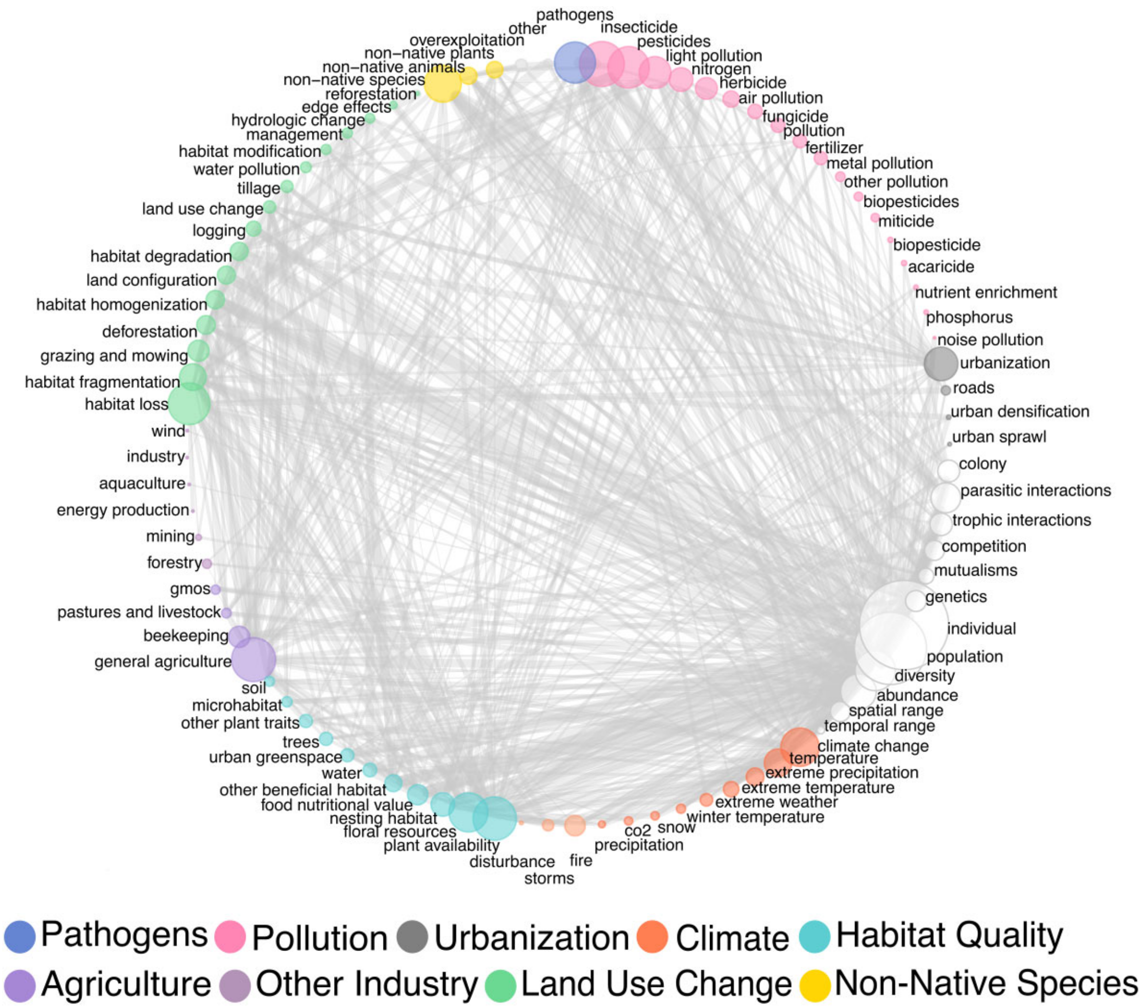

Figure 2. The interconnectivity of hypothesized drivers of insect decline at the most resolved level of classification (compared with the broader resolution of figure 1b). The width of an edge describes the frequency with which a particular connection is discussed in the literature, and the size of the symbol similarly indicates frequency. The colors indicate the broader categories shown in figure 1. A complete interactive diagram can be found in the supplemental materials.

95%, 99%, and 96% of the total pathways flowing outward, respectively. This highlights one issue with more detailed classifications: Some of the most numerous nodes could only be classified within a broad category. For instance, general agriculture, pesticides, and climate change were frequently suggested as drivers but are each multifaceted factors, and when proposed, the original text did not elaborate on the mechanisms.

Central ideas could be important foci for intervention

An advantage of the network synthesis approach is that additional metrics beyond frequency can be generated to assess the potential importance of an idea, such as the overall network connectivity and the centrality of each node. Although the frequency with which a hypothesis appears in the published literature indicates the dominant foci of a field (Anderson et al. 2021), this metric contains biases that are also potentially responsible for the commonness of a hypothesis and should not be treated as a direct index of biological importance (Gurevitch et al. 2018, Mupepele et al. 2019b). For instance, given the known geographic bias in insect decline studies (van Klink et al. 2020, Wagner 2020), it is likely that pathways more frequently considered in temperate regions are overrepresented in the literature, whereas stressors more relevant to the tropics are underrepresented (and remain in particular need of study). As an attempt to account for such biases, we assigned equal weights to each edge (removing the importance of frequency) and examined graph density (a measure of connectivity), clustering (a measure of modularity), and betweenness centrality (a measure of information flow).

First, we assessed the graph density, which measures how connected nodes are to each other across the entire network. When grouped using low-resolution terms, the network had a graph density of .4, indicating that the 16 driver and outcome nodes (figure 1a) were, on average, each connected to 6.4 other nodes. Agriculture, non-native species, and urbanization were the most connected and were all linked with a driver of a different category over 90% of the time. When grouped using more detailed terminology, the graph density drops to .07, where each node is connected to 7.5 of the 108 possible nodes. The nodes were most often directly linked to an outcome variable; however, a third of the edges were directed at other stressor variables. These mediating variables belonged to another driver category (i.e., pollution, urbanization, agriculture, climate, and other top-level categories from figure 1) 83% of the time, signifying that drivers are often hypothesized to act in combination.

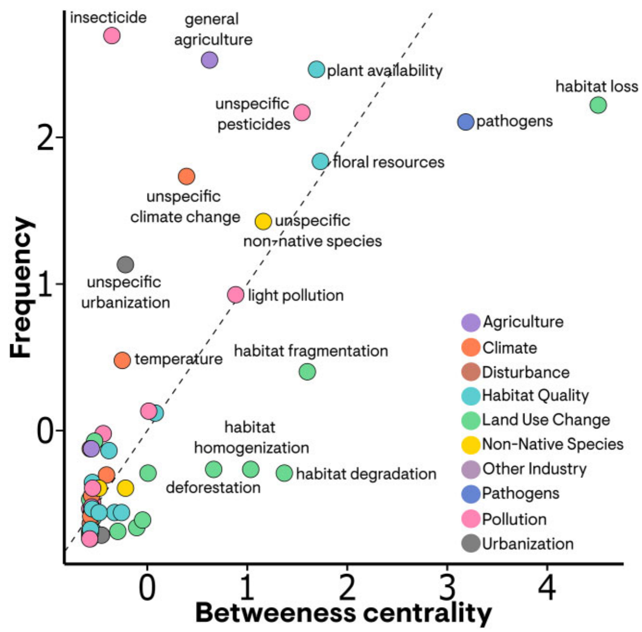

Figure 3. The relationship between the frequency of a node and its centrality in the network of potential drivers of insect decline. Frequency describes how many edges emerge from a node, whereas betweenness centrality describes how often a variable is an intermediary in a pathway. Both axes have been scaled, and the dotted line shows a one-to-one relationship.

Second, we examined the overall tendency of nodes to be clustered using the clustering coefficient, which measures how likely neighboring nodes are to be connected. We found a global clustering coefficient of .31, half of that expected from random chance (assessed via permutation by generating 1000 random networks with the same structure; see supplemental material for complete methods). Therefore, we did not find that certain small groups of drivers were proposed almost exclusively together and not with other threats. The shape of the network of proposed drivers of insect decline is well connected, and the proposed stressors are widely connected to each other.

Finally, we examined the betweenness centrality of each node, which measures how often an intermediate node is part of the shortest path between two other nodes. The two most connected proposed drivers of decline by this measure were habitat loss and pathogens. Habitat loss was often part of the shortest paths between drivers of land-use change, such as agriculture and urbanization, and insect outcomes, whereas pathogens were often part of the shortest paths between agriculture and non-native species impacts, largely from the literature on spillover effects from managed bees. Comparing the betweenness centrality of each idea to the overall frequency revealed how the commonness of an idea relates to its potential importance as a mediating variable (figure 3). For instance, insecticides were the most frequently proposed high-resolution stressor but were not well connected to other stressors. Hypotheses about insecticides are primarily linked directly with individual-level outcomes with no mediating downstream variables and often only agriculture as an upstream factor. Alternatively, a high ratio of betweenness centrality to frequency indicates drivers that are well connected, even if they are mentioned relatively infrequently in the recent literature. Drivers in this category were mostly related to habitat. Although habitat loss was an often-mentioned node, other related threats such as degradation, fragmentation, and homogenization are more connected than expected, given their frequency in the network. For example, habitat homogenization was connected to pollution, land-use change, climate, and agriculture while also being hypothesized to have impacts across all outcome variables (Henríquez-Piskulich et al. 2021, Méndez-Rojas et al. 2021) but was only mentioned in 22 of the 175 articles. These centralized nodes may be critical in a conservation context, because multiple connections allow more opportunities for intervention, which, in turn, may have a broad impact as these central nodes are more connected to outcome variables across levels of biological organization. The centrality of habitat variables reinforces the notion that habitat loss and quality declines remain dominant threats to biodiversity loss and that this is as true for insects as other organisms (Wilcove et al. 1998, Caro et al. 2022).

Insect outcomes are focused on individuals and populations

At the terminal end of the hypothesized causal pathways are nodes representing the outcome variables, describing how insects are expected to respond across different levels of biological organization. The proposed response variables ranged from genes to communities but were predominantly focused on individuals and populations. Hypotheses related to individual-level outcomes were strongly biased toward pollution, a pattern driven by a preponderance of hypotheses about pesticides (figure 1a). Pesticides have been negatively linked with nearly every individual-level response variable, including mortality, reproduction, health, and various aspects of behavior such as cognition and food acquisition (Lehmann and Camp 2021, Singla et al. 2021). Hypotheses for how stressors affect genetic-, population-, and community-level outcomes were more evenly distributed, where all major stressor categories have been hypothesized to have effects at these levels, but none have received disproportionate attention (figure 1a). Of these categories, population-level responses were the most common but were often described using terminology that was less specific than that for individual outcomes and specific mechanisms pinpointing the impacts on different aspects of population-level outcomes, such as total abundance or density, were often missing. Genetic effects and changes in community interactions have received far less attention (Eggleton 2020, Kelemen and Rehan 2021, Bascompte and Scheffer 2023, Webster et al. 2023) than individual and population responses and remain essential areas for future research.

Pollinators drive hypotheses about insect biodiversity loss

Substantial taxonomic and ecological guild biases in the literature present a significant challenge to broad consensus about drivers of insect decline. Reports of decline have focused mainly on bees, butterflies and moths, and ground beetles (Saunders et al. 2020, Wagner 2020). In our meta-synthesis, we found this same pattern in the discussion of drivers, with many synthesis papers about Hymenoptera, fewer on Coleoptera and Lepidoptera, and virtually none on other groups (figure 4). Only 7 of the 26 orders of insects were directly connected to a hypothesized causal pathway, with minimal attention paid to the diverse orders Hemiptera, Diptera, and Orthoptera. Even orders well represented in the literature exhibited taxonomic bias: For instance, nearly half (48%) of all taxon-specific hypotheses in the network came from pathways about *Apis* and *Bombus*, despite these two genera representing

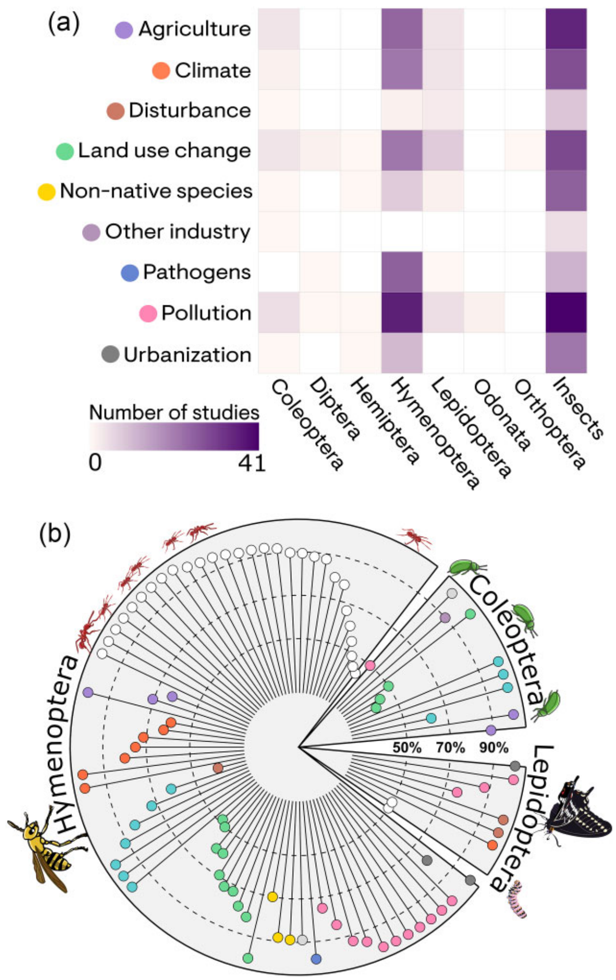

Figure 4. Taxonomic bias in the treatment of hypothesized drivers of insect declines from 106 articles containing taxon-specific hypotheses. (a) The distribution of hypotheses about broad classes of drivers of decline across insect taxonomic groups. (b) The distribution of higher resolution driver and outcome nodes across taxonomic groups. Each colored point shows a node in the network in figure 2 that was said to affect at least two different orders. The nodes are plotted in the taxonomic section where they are most frequently mentioned. Therefore, all taxon-specific nodes are most associated with Coleoptera, Hymenoptera, or Lepidoptera. The line length from the center indicates how biased a term is. The dashed lines indicate which nodes are mentioned about a given taxonomic group more than 50%, 70%, or 90% of the time. The nodes are colored the same way as in figures 1, 2, and 3 (see supplement for node labels). Insect icons were designed by Suyeon Jang.

approximately 0.2% of described Hymenopterans (Klopfstein et al. 2013, Forbes et al. 2018, Stork 2018). Likewise, the Lepidoptera articles were focused mainly on butterflies (Rhopalocera), despite non-butterfly moths representing more than 93% of described Lepidoptera. Put another way, for all but the most considered taxa, species-specific networks are very sparse, with very few hypothesized drivers (see our interactive tool). Although this biased pattern could arise from a few well-studied topics that are heavily anchored to focal taxa, we found that most nodes in the network showed strong taxonomic bias where ideas were rarely shared evenly across taxa (figure 4b). Of the 97 nodes that applied to at least two insect orders, 47 were mentioned in reference to a single order over 90% of the time. For instance, the nodes associated primarily with Hymenoptera included pathogens, immune function, nesting locations, and the gut microbiome, but these potential causes of decline were rarely mentioned in connection with any other insect order. This pattern should be expected for some hypotheses, such as beekeeping and colony health. However, variables such as winter temperature, microhabitat, floral resources, and many others apply to many taxonomic groups (Bale and Hayward 2010, Merten et al. 2014, Raguso 2020) but exhibited a similar skew toward a limited subset of hymenopterans.

Strong taxonomic bias in thinking about the hypothesized drivers of decline could have consequences for insect conservation planning, because funding and solutions will likely favor taxa that are more often discussed (i.e., bees and butterflies). These pollinators are among the most charismatic insects in the public consciousness (Shipley and Bixler 2017), and their agricultural services make them an attractive focus for conservation. Still, action to mitigate insect declines must consider more than just the plight of these two lineages. Although some lessons learned from bees and butterflies could apply widely, many insects, even other pollinators, have vast differences in their life histories and conservation needs. As one example, flies are important global pollinators (Orford et al. 2015), but in their larval stages, they are often carnivorous or scavengers that require very different environments from, for example, those needed by colony or ground-nesting bees or phytophagous butterflies and moths. Conservation of floral resources for pollinators may positively affect adult flies but has little relevance to the survival of the immature stages. More unrelated still are aquatic insects that spend their nymphal or larval stage underwater and are vulnerable to drivers such as water pollution, which is sparsely represented in our current network of hypotheses. Although economic importance and public appeal are important motives for selecting study organisms, these reasons are not necessarily indicative of a species' imperilment, which is an essential criterion for further understanding of the drivers of insect decline.

Missing hypotheses may be important research gaps

Although the meta-synthesis approach is useful for identifying underrepresented topics and taxa that are a part of the network, it cannot identify hypotheses entirely missing from the literature that built it. To explore these gaps, we reclassified hypothesized stressors into new categories using the International Union for Conservation of Nature (IUCN) threat classification scheme (version 3.3) for abiotic stressors and the IUCN stresses classification scheme (version 1) for biotic stressors. We also reclassified hypothesized outcomes into new categories using the essential biodiversity variables framework (Pereira et al. 2013). We then aligned our terminology with these classifications, mapping our findings onto this more extensive framework that is independent of our data (figure 5). IUCN stressor classifications are presented at multiple levels of nested specificity, where some stressors have more levels than others. We linked our terms with the most specific label whenever possible. A more detailed assemblage is presented in figure 5a, whereas the same information is summarized more broadly in figure 5b. Given the preponderance of pollution hypotheses, we present an even more detailed breakdown of gaps for that category in figure 5c.

The IUCN categories for agriculture, residential development, pollution, and climate change have received the most comprehensive attention; however, even these well-studied categories contain many gaps when described more precisely (figure 5a–5c). For instance, pollution is one of the most abundant drivers in our

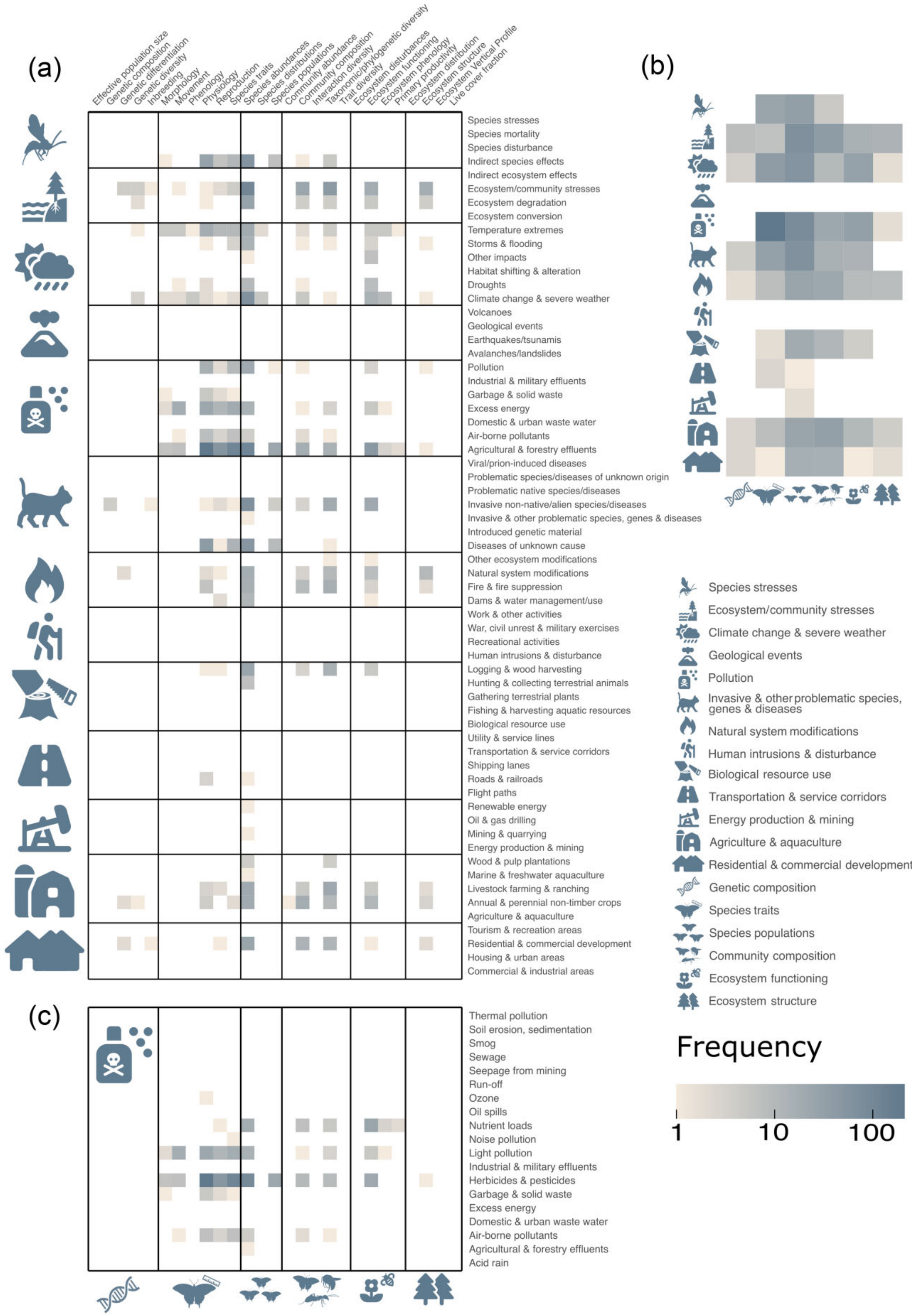
(a)
Effective population size
Genetic composition
Genetic differentiation
Genetic diversity
Inbreeding
Morphology
Movement
Phenology
Physiology
Reproduction
Species traits
Species abundances
Species distributions
Species populations
Community abundance
Community composition
Interaction diversity
Taxonomic/phylogenetic diversity
Trait diversity
Ecosystem disturbances
Ecosystem functioning
Ecosystem phenology
Primary productivity
Ecosystem distribution
Ecosystem structure
Ecosystem Vertical Profile
Live cover fraction
Species stresses
Species mortality
Species disturbance
Indirect species effects
Indirect ecosystem effects
Ecosystem/community stresses
Ecosystem degradation
Ecosystem conversion
Temperature extremes
Storms & flooding
Other impacts
Habitat shifting & alteration
Droughts
Climate change & severe weather
Volcanoes
Geological events
Earthquakes/tsunamis
Avalanches/landslides
Pollution
Industrial & military effluents
Garbage & solid waste
Excess energy
Domestic & urban waste water
Air-borne pollutants
Agricultural & forestry effluents
Viral/prion-induced diseases
Problematic species/diseases of unknown origin
Problematic native species/diseases
Invasive non-native/alien species/diseases
Invasive & other problematic species, genes & diseases
Introduced genetic material
Diseases of unknown cause
Other ecosystem modifications
Natural system modifications
Fire & fire suppression
Dams & water management/use
Work & other activities
War, civil unrest & military exercises
Recreational activities
Human intrusions & disturbance
Logging & wood harvesting
Hunting & collecting terrestrial animals
Gathering terrestrial plants
Fishing & harvesting aquatic resources
Biological resource use
Utility & service lines
Transportation & service corridors
Shipping lanes
Roads & railroads
Flight paths
Renewable energy
Oil & gas drilling
Mining & quarrying
Energy production & mining
Wood & pulp plantations
Marine & freshwater aquaculture
Livestock farming & ranching
Annual & perennial non-timber crops
Agriculture & aquaculture
Tourism & recreation areas
Residential & commercial development
Housing & urban areas
Commercial & industrial areas
(b)
Species stresses
Ecosystem/community stresses
Climate change & severe weather
Geological events
Pollution
Invasive & other problematic species, genes & diseases
Natural system modifications
Human intrusions & disturbance
Biological resource use
Transportation & service corridors
Energy production & mining
Agriculture & aquaculture
Residential & commercial development
Genetic composition
Species traits
Species populations
Community composition
Ecosystem functioning
Ecosystem structure
Frequency
1
10
100
(c)
Thermal pollution
Soil erosion, sedimentation
Smog
Sewage
Seepage from mining
Run-off
Ozone
Oil spills
Nutrient loads
Noise pollution
Light pollution
Industrial & military effluents
Herbicides & pesticides
Garbage & solid waste
Excess energy
Domestic & urban waste water
Air-borne pollutants
Agricultural & forestry effluents
Acid rain

Figure. 5. Coverage of research topics in the recent synthesis literature that describes the drivers of insect declines. For each heat map, stressors are organized by IUCN stressor category (***y***-axis) and essential biodiversity variables (***x***-axis). The color of each tile in the heat maps indicates the number of instances in which a given combination occurred in the network (on the log scale); white space indicates that there are no occurrences of that combination. (a) Heat map of all IUCN categories presented in moderate detail. (b) Heat map of all IUCN categories presented in the broadest detail. (c) Heat map of only the pollution category presented at the highest detail.

network, a pattern driven by hypotheses about agrochemicals, light pollution, and nutrient loads. Other potential pollutants, such as noise and many non-agricultural effluents, however, have received relatively little attention (figure 5c). In fact, all of the most proposed categories in the network contain major gaps, especially when considering combinations of stressors and outcomes (figure 5b). Perhaps more serious, we also identified entire IUCN threat categories that have received almost no attention in our sample of studies, including human-caused disturbance, geological events, and energy production (figure 5b). Although perhaps not as globally important as other drivers, each of these categories is listed as a threat by the IUCN for hundreds of vulnerable or endangered insect species. Finally, this approach highlighted the gaps in studying genetic- and community-level outcomes. The impacts of stressors on variables such as effective population size, inbreeding, trait diversity, and interaction diversity have not been recently reviewed, even for well-studied stressors such as pollution and climate change. If sufficient primary studies are available, synthesis articles on insect-relevant topics such as these would fill critical gaps. When and where such data are unavailable, these topics warrant further primary investigation.

Where to from here?

The recent surge of attention to the status of insects has generated many hypotheses about the threats they face. Since 2017, at least 175 reviews, meta-analyses, and perspectives have been published on the drivers of insect decline, forming a highly connected network of proposed drivers, mediators, and outcomes. It is clear that threats are considered to be a collection of interacting and potentially synergistic drivers; therefore, management strategies focused on a single threat and disregarding other connected stressors may lead to undesired outcomes because of unexpected interactive effects (Brook et al. 2008). Our approach has limitations, and substantial gaps remain. Still, we are encouraged by the sustained scientific and public interest in disentangling the drivers of insect biodiversity loss and proposing solutions to conserve insect biodiversity.

Our meta-synthesis has identified important features of the literature on the drivers of insect decline and can help guide future directions. First, the overall network of proposed stressors is highly connected. Centralized nodes such as habitat loss and habitat degradation remain critical threats to insect biodiversity, and interventions on highly connected stressors may require careful consideration because they are also associated with more opportunities for interactive effects. Second, we found that many common hypotheses are often repeated using imprecise descriptors of causes and without mechanistic language, limiting the capacity for effective design of management responses. Much would be gained if future studies and reviews addressed hypothesized drivers with as much detail as possible. Third, we want to emphasize the importance of continued work on quantitative assessments of the effects of drivers of insect decline, because our approach cannot test the support for highly represented hypotheses. Only through meta-analyses, where the effects of drivers are synthesized quantitatively to draw broad generalities, can we more rigorously understand the relative impacts of drivers in different contexts and better understand how the stressors interact. Finally, our meta-synthesis quantified to what degree many proposed drivers have received disproportionate attention because of their perceived importance and association with commonly studied taxa, regions, and other elevated research priorities. Such established ideas can receive more scientific attention because they are seen as more likely to be funded and published, perpetuating further research in the same areas rather than encouraging researchers to pursue novel research directions (Fortunato et al. 2018). We suggest that funding and research should prioritize taxa, life histories, and regions that are currently underrepresented or entirely absent from the literature, because research into these unexplored areas may provide greater returns for our understanding of threats to insects and how to respond.

The drivers of insect declines are many, interconnected, and context dependent. Even if the geographic and taxonomic breadth of research is expanded and pathways are quantified, there will still be more that we would like to know. However, amid vast uncertainty, we know that many insects are declining at alarming rates (Hallmann et al. 2017, van Klink et al. 2020); we also know the broad drivers, that many of the threats are connected, and we understand many of the consequences. It is essential that conservation action proceeds in parallel with research so that the two realms have mutually reinforcing and informative outcomes (Forister et al. 2019). There is no doubt, for example, that efforts should be underway to limit the rate and impacts of habitat loss, reduce the atmospheric accumulation of greenhouse gasses, and advance the sensible uses of pesticides, even as we acknowledge that additional research will refine our actions. Further research, guided by the conceptual landscape described in the present article, will make conservation actions more effective and impactful, especially in the tropics and across the Southern Hemisphere, where actions are especially needed.

Supplementary data

Supplementary data are available at *BIOSCI* online.

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Author contributions

Christopher A. Halsch (Data curation, Formal analysis, Investigation, Methodology, Project administration, Visualization, Writing - original draft, Writing - review & editing), Chris S. Elphick (Conceptualization, Writing - review & editing), Christie A. Bahlai (Writing - review & editing), Matthew L. Forister (Writing - review

& editing), David L. Wagner (Writing - review & editing), Jessica L. Ware (Writing - review & editing), and Eliza M. Grames (Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Project administration, Supervision, Validation, Visualization, Writing - original draft, Writing - review & editing)

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