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Ecological forecasts of insect range dynamics: a broad range of taxa includes winners and losers under future climate

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Species distribution models are the primary tools to project future species' distributions, but this complex task is influenced by data limitations and evolving best practices. The majority of the 53 studies we examined utilized correlative models and did not follow current best practices for validating retrospective or future environmental data layers. Despite this, a summary of results is largely unsurprising: shifts toward cooler regions, but otherwise mixed dynamics emphasizing winners and losers. Harmful insects were more likely to show positive outcomes compared with beneficial species. Our restricted ability to consider mechanisms complicates interpretation of any single study. To improve this area of modeling, more classic field and lab studies to uncover basic ecology and physiology are crucial.

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Introduction

Humans have drastically altered our living environment, placing many species in peril and ultimately culminating in an ongoing sixth mass extinction [1]. Many stressors, such as land-use conversion, pollution, and the over-exploitation of natural resources, have long been the main factors believed to be driving this crisis. Climate change has emerged as an increasingly dominant stressor [1] as the last ten years have been among the hottest on record [2]. This recent acceleration in climate warming demands that we understand how climate has been and will continue to impact biodiversity and ecosystem function, especially in combination with other ongoing threats [1]. Insects in particular have received a great deal of attention because of recently reported taxon-wide declines that appear to be global in nature [3–5], presenting a risk of widespread loss of ecosystem function [6]. One of the most popular research tools for understanding how global change impacts biodiversity is the use of species distribution models (SDMs), which leverage the relationship between a species' distribution and its putative environmental drivers; SDMs are primary tools for making ecological forecasts [7]. These forecasts allow us to compare possible outcomes of alternative societal decisions and also have a scientific value by allowing iterative improvements of predictive models [8] and sharpening ecological theory [9]. Yet, the approaches to projecting current and future ranges vary substantially and a growing body of research has shown that specific modeling choices have considerable impacts on the reliability of outputs and, ultimately, our ability to anticipate or adapt to ongoing changes [10–14].

There are many different methods associated with SDMs, but terminology and usage vary between practitioners. Here, we adopt the terms 'correlative' [7] and 'mechanistic' [15] and use the following definitions for the purpose of this review. Correlative SDMs are built by combining species locality data (usually presence-only [PO]) and environmental data layers and estimating the correlations between them [7]. The parameterized model is used to predict the expected full extent of their entire range (and also to project ranges into the future) [7]. There are many different modeling approaches available and performance varies substantially [11,12] and variable validation methods can also lead to different modeling choices [16]. Correlative models are often completely 'naive,' meaning that there is no consideration of that species' biology in building the model structure [10]. In contrast, 'mechanistic' SDMs are built and parameterized from *a priori* knowledge of species' biology emerging from natural history observations or lab and field experiments (e.g. thermal constraints, species interactions) [15]. Both correlative and mechanistic approaches have long relied primarily on climate factors to project future species distributions, although other types of layers have often been included, both biotic (e.g. land-use land cover [LULC] and specific interacting species) and abiotic (e.g. soil). When the specific goal is to project ranges or population dynamics into the future, three component steps are required [8]: 1) an SDM that links distributions (correlative) or performance metrics (mechanistic) to environmental covariates; 2) spatial data layers that project key environmental conditions (i.e. the significant covariates chosen during the modeling phase) into the future; and 3) combining the SDM with future environmental layers to project future distributions. Notably, one potential primary driver of recent insect declines, the use of pesticides, is extremely challenging to include in retrospective or future projections because spatial data are sparse and technologies are constantly changing [17].

The challenges of implementing species distribution models

The primary challenge for developing SDMs has always been the limitation of data available to build and validate large-scale distribution models (step 1). By far, the greatest source of distribution data has always been, and likely will always be, PO data from 'opportunistic' collection of field specimens and (more recently) photographs. Unfortunately, the vast majority of historical specimens remain undigitized and so unavailable for model- building [18]. Further, SDMs based on these data have unknown sample biases that are difficult to correct [12,19], although new methods are more effectively tackling these problems, for example, [20,21]. Survey data provide for more robust models [19] but these are extremely limited and, without a global effort to expand them (e.g. [22]), they will rarely be available for SDMs. Correlative SDMs are also criticized for providing little basis to understand the underlying mechanistic drivers [12,23], and are often validated using in-sample tests that show poor transferability when projecting into novel conditions [24] or regions [25]. In contrast, mechanistic approaches provide model variables that are based on known mechanisms and are included as *a priori* factors in a model. With these models, it is possible to validate the model with completely independent distribution data, providing a more robust validation than in-sample tests [12]. However, the reality is that the mechanistic data needed to effectively implement mechanistic SDMs are not available for the vast majority of species.

While much has been written in the ecological literature about the pros and cons of different classes of SDMs (e.g. mechanistic vs. correlative) and distribution data types (e.g. PO data vs. surveys), there has been less exploration of how choices relative to the environmental data layers themselves can impact results, future projections, and their interpretation [12,14,26]. One issue that we believe is particularly important, but is rarely addressed, is the temporal alignment of distribution and environmental data [12,14]. SDMs are structured to overlay spatial data to examine relationships; if these data are temporally disjunct, biases may be introduced into the model. While SDMs assume a system in equilibrium, the reality is this entire field of modeling is predicated on the idea that species' distributions are responding to an environment that is changing directionally over time [27]. Thus, the assumption of equilibrium, especially relative to parameterizing SDMs with retrospective distribution analyses, should be met with great caution [10,12,24] and care should be taken to align data layers temporally.

Another methodological factor that can profoundly impact ecological forecasts is how future climate layers are built for projections (step 2) [26]. Global climate models (e.g. atmosphere–ocean general circulation models [AOGCMs], but hereafter GCMs) are built on physical models and are used not only to forecast future climate conditions, but also to project backward for the purposes of model validation. These GCMs are implemented by a network of collaborating climate centers around the globe under a shared framework organized by the Coupled Model Intercomparison Project (CMIP), part of the Intergovernmental Panel on Climate Change. The output of these projections can vary greatly among the GCMs and some are better suited to a specific region than others [14,26]. Because climate centers also project past conditions [28], these predictions can be used to choose models best suited for a study system by validating retrospective model simulations for the climate metrics found to be most important drivers of a species' range dynamics. While there remains controversy on whether it is better to use a validated subset of models or as many GCMs as is tractable, our opinion is that building ensembles based on validation using retrospective projections produces more defensible results [14]. Even (or especially) without validation, the use of multimodel ensemble dataset for projections is generally considered as current best practice because it minimizes the influence of the variability of individual GCM when making projections [26]. Another particularly acute challenge for making future projections is that while most researchers acknowledge the importance of other environmental factors such as LULC, development of future scenario projections for these variables is either limited or entirely unavailable [29,30]. Finally, propagating uncertainty when combining ecological and future environmental models (step 3) is especially difficult and best practices are only beginning to emerge [13]. Here, we review the recent insect SDM literature for insights about how insect communities may be most likely to change into the future, while accounting for the wide range of methodological differences that can impact output and interpretability.

Survey of the literature

Our goal is to evaluate what the most recent SDM-based forecasts have suggested about potential insect responses to future environmental change while accounting for different modeling approaches and evolving best practices. We took the approach of targeting a comprehensive sweep of all studies we could locate to reduce taxonomic bias in our review, but limited our search to a restricted, recent time period (2018–2022). This is because of how much best practices continue to evolve and the substantial methodological influences on projection outcomes. We conducted a literature search (various combinations of words: GCM, AOGCM, future prediction, insect, and SDM) for studies using Google Scholar and Web of Science. We found additional papers by examining backward and forward citations and located an initial 144 papers published from 2018 to 2022 that project range-wide insect distributions into the future. We only accepted papers that covered a limited number of species (< 30) so that biological realism in the results could be more carefully considered. All papers must have included a retrospective SDM to parameterize the ecological projections (step 1); had future forecasts that were based, at least in part, on climate projections from the CMIP consortium (step 2); and the ecological model was then projected into the future based on the environmental covariates (step 3). Using these criteria, 53 papers were selected to review (each detailed in Supplemental Table 1). We then categorized each of the 53 papers relative to the basic motivation and approach (Table 1). To quantify the methodological approaches, we developed a scoring system that we applied to each paper based on seven criteria related to best practices as described above; the basis for each score is detailed in Table 2.

Our search showed that the use of SDMs to make future projections has grown even in the last 5 years (Figure 1) and their scope includes a broad range of insect taxa, including representatives of 47 families among 8 orders (Supplemental Table 1). Most studies focused on four orders (Coleoptera, Hemiptera, Hymenoptera, and Lepidoptera) and were most often motivated by understanding the ecology of harmful species (pests, invasive species, or disease vectors, n = 36), including species used as biocontrol agents (n = 4). But many other studies were motivated by the understanding of general range dynamics and the ecology or conservation of nonharmful species (n = 13). We separated our summary of study methods and results by whether they were focused on harmful and nonharmful species (Table 1) because there are *a priori* reasons to believe that harmful species may

Table 1

Summary of the category of papers reviewed*, including how each category was broken down and the number of paper representing each type.

Category	Type	Description	# papers
Motivation: H=harmful species; N = not harmful	Pest/invasive (H)	Insects that cause economic damage	31
	Disease agent (H)	Insect that can directly cause disease or serves as a disease vector	5
	Biodiversity/ conservation (N)	Studies that are focused on ecological responses for biodiversity and/or conservation concerns, not control of harmful species	13
	Biocontrol (N)	Biocontrol agents	4
SDM approach; H=harmful species; N = not harmful	Correlative only	Model covariates chosen and parameterized solely based on the relationship between observed distribution and environmental data layers	24H, 12N
	Mechanistic only	Model covariates chosen *a priori* based on known biology and parameterized solely with that information	8H, 4N
	Both correlative and mechanistic components	Model covariates chosen using both methods, or using correlative approaches, but constrained by *a priori* mechanistic knowledge	4H, 1N
SDM distribution data	PO only	PO (e.g. GBIF)	32
	Trait only	Trait only	1
	PO + trait	Also includes consideration of traits in SDM modeling	13
	PA + trait	Presence/absences and trait data used in SDM modeling	2
	SA only	Species abundance data	1
	SA+trait	Species abundances and trait data used in SDM modeling	3
	PO, SA, and trait	Multiple types of data	1
	Change in range size or habitat suitability (NH)	Increase (+), decrease (-), no change (NC), and mixed (M)	39+, 27-, 2M, 2NC
	Shift in range position (NH)	Shift to either cooler (poleward or higher latitude, C) or warmer (opposite, W), or mixed (M)	6C
	Harm risk (H)	For harmful insects, this includes any risk of inhabiting new areas (invasion) or increased/decreased population within the current range (including outbreaks). Increased invasion risk (+), decrease (-), and mixed (M). Also scored separately for reported range shifts (C, W as above).	22+, 9-, 8M; 7C, 1W

The response variable category also includes a score for general outcome. Details for each study are in Supplemental Table 1. Citations for review papers (details for each paper are in Supplementary Table 1): [33,36–39,41–88] GBIF, Global Biodiversity Information Facility.

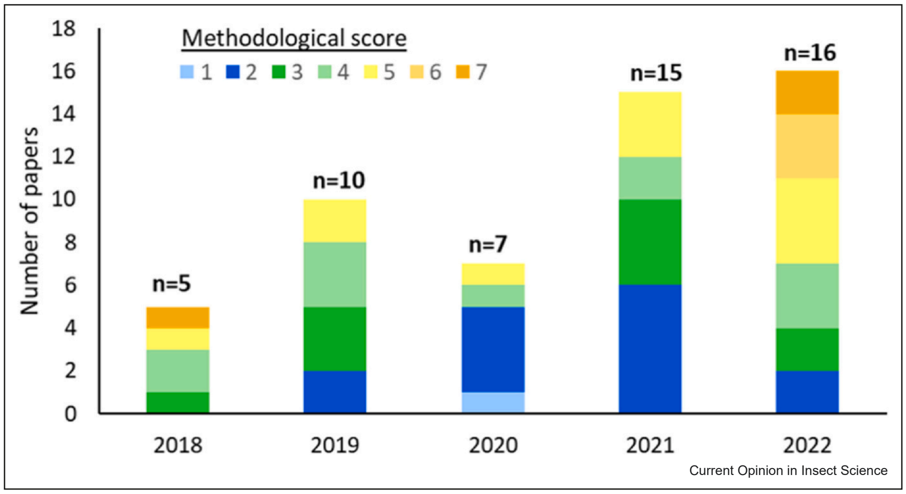
Table 2

Summary of the numeric scores assigned to reviewed papers based on criteria related to our assessment on the rigor of analysis.

Criteria	Category	Score	# papers
Number of SDM modeling approaches	Correlative or mechanistic only	1	48
	Combination of correlative and mechanistic approaches	2	5
Distribution of data type	PO only	0	32
	Not PO only	1	21
Environmental data types	Only climate data	0	34
	Any combination of other factors in addition to climate data (more than one category possible for each paper)	1	19 (12 abiotic, 8 land cover, 4 species interactions, and 2 other)
SDM validation	Validation not obvious	0	7
	Validation using data subsets	1	38
	Validation using independent data	2	8
SDM temporal alignment for distribution and environmental data inputs	No temporal alignment evident	0	41
	Some temporal alignment of data between distribution and environmental data sets	1	12
Use of an ensemble of multiple GCMs	Only 1 GCM used	0	24
	An ensemble of GCMs used (including details on which GCMs were used)	1	2–3 used (10) 4–10 used (10) > 10 used (9)
GCM validation	GCM regional performance not assessed	0	48
	GCM regional performance assessed	1	5

Some of these categories are beyond researchers' ability to choose, especially when data types are limited. Details for each study are in Supplemental Table 1.

Figure 1



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The distribution of methodological scores for each paper published in our 5-year review period. Higher scores indicate greater use of best practices. The explanation for each score is in Table 2 and score details for each of our 53 review papers are in Supplemental Table 1.

be more resilient to (or even benefit from) human-related environmental changes [31]. Correlative, mechanistic, and mixed approaches were well-represented, but correlative models far outnumbered those using mechanistic information (n = 36, 12 respectively), while 5 used elements of both approaches (Table 1). Most of the studies we reviewed used PO data (n = 45), with 32 of these using PO data only (Tables 1,2), not a surprising outcome given that the vast majority of species have only these data available through most or all of their ranges.

Species distribution model practices are becoming more robust over time

Including some mechanisms rooted in *a priori* knowledge of species biology provides a stronger basis for making future projections [12,15,23] and, in our review, studies that focused on species of disease or agricultural importance (including biocontrol agents) were the most likely to use this information (scored as using 'trait data' in Table 1). This is likely because species of economic importance often have a richer mechanistic research history, even leading to a generic software package,

Table 3

Future projection summary scored separately for each species within studies so that there are more results than studies.

Projected change	Direction of change	Tally of results
Shift in range position (NH)	Shift to either cooler (poleward or higher latitude, C) or warmer (opposite, W), or mixed (M)	6C
Change in range size or habitat suitability (NH)	Increase (+), decrease (-), no change (NC), and mixed (M)	39+, 27-, 2M, 2NC
Harm risk (H)	For harmful insects, this includes any risk of inhabiting new areas (invasion) or increased/decreased population within the current range (including outbreaks). Increased invasion risk (+), decrease (-), and mixed (M). Also scored separately for reported range shifts (C, W as above).	22+, 9-, 8M; 7C, 1W

When multiple emission scenarios are used, and also focused on the results of most extreme climate scenario.

Mechanistic Model, that is well-suited to project insect responses based on experimental thermal constraints [32]. Mechanistic Model was used in 8 of 12 purely mechanistic studies, largely for pest species. Of studies motivated purely for ecological or conservation reasons, only studies focused on butterflies were able to include *a priori* mechanistic components, and this likely reflects that, as a group, butterflies are the most comprehensively studied insect taxa and therefore are often used as a model system for understanding insect biodiversity. Most studies used only climate data as explanatory variables (n = 34), which, by far, are the easiest to acquire for future projections. Of the 19 that did use other layers, most were abiotic (soil and/or elevation), which do not tend to vary on ecological timescales, thus making it reasonable to build current data layers into future projections. However, several studies considered more dynamic environmental factors, including LULC (n = 8) or the distribution of specific food resources (n = 4). Most studies (n = 46) clearly stated their validation procedures, but in 7 studies, those were less obvious. Eight studies (mostly mechanistic) used completely independent 'out-of-sample' distribution data sets (see Supplementary Table 1).

SDM modeling frameworks all require distribution data to be spatially aligned with the underlying environmental layers [7], but only 11 studies described any effort to match the temporal extent of the environmental data layers with the available distribution (Table 2). In terms of developing climate data layers based on future emission scenarios, most studies used ensembles (n = 29), but the vast majority did not include any validation procedure for choosing which GCMs to build those ensembles (n = 48), meaning it is unclear if the future climate layers chosen provide the most defensible representation of future regional environmental conditions. However, especially in the case where no validation procedure is used, the more GCMs included in ensembles, the better and 19 used at least 4 (Table 2). It is heartening to note the adoption of many of the listed best practices during our study, including an increase at the end of our short period of review (Figure 1), despite them being relatively rare in the years prior [10].

Grappling with variability in future projections

The most consistent result we observed, unsurprisingly, was that projected shifts were predominantly toward cooler latitudes or altitudes (Table 3). Only one study, focusing on eight invasive bee species, showed that most expansion would be into lower (warmer) altitudes [33]. These results align with many observational studies already documenting such range shifts for insect species [4]. For changes in range size and habitat suitability (or projected population changes), the results were decidedly mixed for nonharmful species, highlighting that species-specific variability (so-called climate 'winners' and 'losers') is expected to be the norm across insect species, as is generally accepted for most taxa [34]. However, pest species showed a greater tendency toward increased invasion or outbreaks (20 increased risk, 8 decreased, and 3 mixed), suggesting that harmful insects may do better, on average, under warming conditions (Table 2), which aligns with a recent review of on-the-ground trends [35]. This is an important result because it shows that species that tend to cause economic or health harms are not only more resilient to anthropogenic changes, but also may not be good indicators of how other species will respond.

Constructed SDMs without any *a priori* consideration of mechanism or without carefully aligning environmental layers to distribution data can lead to unreliable predictions that can be difficult to interpret and thus undermine their individual usefulness [12]. As acknowledged by most authors in our review, studies that rely only on climate are likely missing important factors in species' distributions, yet only about one-third of these studies were able to use nonclimate explanatory variables (Table 2). Including digital data on various other environmental factors, such as LULC, slope, distance to water, or vegetation types, can reduce prediction uncertainties [10,26]. Thus, we encourage future SDM implementations to incorporate diverse explanatory variables whenever possible, especially LULC, which is often the best proxy for species' resource needs. Those types of layers are increasingly the focus of future scenarios [29,30] and so they should be more widely available and easier to access into the future.

The best practices we reviewed are easiest to incorporate when studies are focused on only one or a few species. Studies that incorporate dozens or even hundreds of species in correlative SDMs are common, but in our opinion, these lead to results that may be the most difficult to interpret. In our review, most studies focused on only one (n = 42) or a few species (Supplemental Table 1) and this allowed substantial consideration by the authors of individual species' biology and how relaxing certain assumptions may have influenced their results. The authors often stressed that their models largely made projections based solely on climate and that ignoring other factors could strongly impact the results, but that they were constrained to assume that other drivers remained fixed. In addition to including future LULC scenarios, a key advancement is explicitly modeling range shifts of interacting species as a layer to include in projecting focal species distributions into the future. We found only two examples of this, one showed potential changes in crop distribution on a pest [36]. The other modeled a key host plant as a basis for future modeling of an insect herbivore, specifically modeled futures of milkweed distributions were used as a covariate for projected changes in monarch butterfly distributions [37]. Another substantial advancement was to include dispersal behavior directly into the model and show how this dampened potential range shifts [38], but dispersal data are rarely available. Alternatively, another study stressed the assumption of no dispersal limitation by presenting results solely as the shifting thermal conditions that species would need to track in order to stay within their climate envelope, not a specific projection of future distributions [39]. These caveats and more nuanced framing reinforces a narrative that these projections are generally just for abiotic conditions and do not really model future distributions per se, but capture an altered thermal landscape that species may confront in different ways. This helps better grapple with the variable results of these studies and also presents an intuitive understanding of the uncertainty around what may actually happen without formally quantifying that uncertainty, which remains very difficult [13].

Conclusions

In this review, we examined 53 recent papers that used SDMs to make projections about future insect distributions. This is an inherently difficult task fraught with uncertainties, yet our sweep of this literature highlights that best practices are increasingly being adopted and many predicted outcomes make sense in light of our general understanding of insect ecology. Changes in range boundaries and habitat suitability favor shifts toward the poles or higher elevations, and faster development and additional generations are expected due to higher temperatures. Compared with nonharmful groups, species that cause economic or health harms appear to be more resilient to climate change, or are even expected to benefit from it. But variability in outcomes is projected for both, highlighting the wide variety of outcomes (e.g. 'winners' and 'losers') expected across any taxon. Thus, as we consider how insects as a group may respond to climate change, the variability and complexity of outcomes need to be a dominant component of our summaries, especially to the public. At the same time, it is important to point out that projections suggest that harmful species are more likely to benefit from projected climate change, as has been shown already from retrospective studies [35]. However, we caution against adopting a simplistic narrative that future conditions are expected to uniformly help spread disease and crop damage while causing widespread losses for 'beneficial' species or species of conservation interest.

SDMs can provide valuable insights into species distributions, but require rigorous methods. We emphasize four best practices to improve the reliability of future SDM predictions: (1) incorporating diverse explanatory variables based on species' biology, (2) aligning SDM inputs temporally, (3) conducting SDM validation when possible, or cross-validation as needed, and (4) selecting regionally appropriate climate models for future projections. We acknowledge that these steps can be difficult or, in some cases, impossible. However, by adopting these practices whenever possible, projections based on SDMs will provide more defensible insights into estimations of future outcomes. SDM methods will also continue to become more powerful through continued model development and the application of advancing technologies such as machine learning and artificial intelligence models [40]. Wider adoption of best practices will improve our understanding of the trajectory and uncertainty of insect populations into the future. We especially highlight the importance of using *a priori* knowledge of species' individual biology whenever possible when choosing environmental covariates in order to increase confidence in the underlying drivers represented in the model. This suggests that, as we move into the future, modeling platforms that ease the ability to tailor environmental layers for individual species will help promote more comparable and interpretable research. However, these advances in tool development for large-scale modeling will be most effective if they occur along with a substantial expansion in classic studies of natural history, thermal constraints, and basic ecology that are lacking for most invertebrates but form the basis for the most rigorous models of current and future distributions.

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Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

We declare that we have no conflict of interest. This is purely a research review article.

Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.cois.2024.101159.

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This study also uses the majority of best practices we suggest for implementing SDMs (disclosure: study includes one of us, Neupane, as a co-author). This paper is another of the few papers that includes a validation of the GCMs used in the future scenario projections. It also provides the only example of using the current best methods to propogate uncertainty across all components of the model.

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