

OPINION

Projecting biological impacts from climate change like a climate scientist

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Our ability to project changes to the climate via anthropogenic forcing has steadily increased over the last five decades. Yet, biologists still lack accurate projections about climate change impacts. Despite recent advances, biologists still often rely on correlative approaches to make projections, ignore important mechanisms, develop models with limited coordination, and lack much of the data to inform projections and test them. In contrast, atmospheric scientists have incorporated mechanistic data, established a global network of weather stations, and apply multi-model inference by comparing divergent model projections. I address the following questions: How have the two fields developed through time? To what degree does biological projection differ from climate projection? What is needed to make similar progress in biological projection? Although the challenges in biodiversity projections are great, I highlight how biology can make substantial progress in the coming years. Most obstacles are surmountable and relate to history, lag times, scientific culture, international organization, and finances. Just as climate change projections have improved, biological modeling can improve in accuracy by incorporating mechanistic understanding, employing multi-model ensemble approaches, coordinating efforts worldwide, and validating projections against records from a well-designed network of biotic stations. Now that climate scientists can make better projections of climate change, biologists need to project and prevent its impacts on biodiversity.

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Interactions

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1 | INTRODUCTION

Rising greenhouse gases from human activity are increasing temperatures, shifting precipitation patterns, and acidifying oceans (IPCC, 2013). These climatic changes threaten to alter global species distributions, perturb ecosystems, and initiate species extinctions (Scheffers et al., 2016; Settele et al., 2014). Moreover, as climate change intensifies, these ecological threats are expected to accelerate (Urban, 2015). Consequently, biologists must urgently develop accurate projections to guide effective conservation strategies that protect biodiversity, which encompasses the global variation in genotypes, species, and ecosystems (Rockström et al., 2009; Settele et al., 2014; Urban, 2015).

Whereas climate change projections have steadily improved through time (Jones, 2013), biological projections remain poorly developed. Most biological models still extrapolate correlations between species ranges and current climates (Araujo & Guisan, 2006; Elith et al., 2006) and thus neglect important biological mechanisms known to mediate past and present responses to climate change (Cahill et al., 2012; Hoffmann & Sgro, 2011; Veloz et al., 2012). Biologists usually develop their models independently, with limited coordination or comparison, inadequate funding, and lacking the data needed to inform more realistic models (Schurr et al., 2012; Urban et al., 2016). Consequently, our understanding of future impacts from climate change is uncertain and possibly misleading, thereby challenging efforts to mitigate biodiversity loss and ecosystem change (Buckley et al., 2010; Kearney & Porter, 2009; Urban et al., 2016).

Climate change science faced similar shortcomings and yet emerged to make substantial progress. In the 1970s, climate scientists lacked the data and understanding to project climate change (Kellogg, 1987). A U.S. National Academy of Sciences (1975) report signaled that “our knowledge of the mechanisms of climatic change is at least as fragmentary as our data. Not only are the basic scientific questions largely unanswered, but in many cases we do not yet know enough to pose the key questions.” Yet, the climate science community filled those knowledge gaps, improved atmospheric monitoring, and built increasingly complicated and accurate climate models (Edwards, 2011; Hurrell et al., 2013; Jones, 2013). Here, I compare the histories of projection and prediction in climate change and climate change biology, develop seven conclusions about these differences, and discern what lessons biologists can apply to improve projections for climate change effects. In keeping with Intergovernmental Panel on Climate Change (IPCC, 2014) definitions, I use the term projection rather than prediction to indicate future climate or biological responses to external drivers, especially socio-economic scenarios of greenhouse gas emissions.

2 | A SHORT HISTORY OF PROJECTING CLIMATE CHANGE

2.1 | Discovering greenhouse gases

The effect of greenhouse gases on climate was recognized in 1827 when Fourier compared the Earth's atmosphere to a greenhouse (Figure 1) (Revelle, 1985). Tyndall's (1861) subsequent experiments demonstrated that gases like CO₂ retained heat and thus likely affected global climate. Arrhenius (1896) predicted that doubling atmospheric CO₂ would raise temperatures 5–6°C. In 1938, Callendar wrote that humans were already influencing the climate by increasing atmospheric concentrations of CO₂. However, most scientists still did not think that humans were capable of substantially influencing the climate via CO₂ (Hulme, 2009; Kellogg, 1987).

By the early 1900s, scientists sought to predict climate and weather by solving multiple, linked physical equations. However, these equations could not be solved analytically and thus required intensive numerical searches (Edwards, 2011). A “forecast factory” of 64,000 people was proposed to solve these calculations (Richardson, 1922), but never came to be. Advanced climate projection would await the invention of silicon-based computers.

2.2 | 1950s and 1960s: Computers and alarm

The first general circulation models (GCMs) advanced rapidly under the auspices of newly available computing power and governmental support for predicting weather for agricultural, economic, and military purposes (Edwards, 2011; Schneider & Dickinson, 1974). These 1-dimensional models with latitudinal bands were expanded into 2-dimensional gridded Earth models (the Phillips model; 1955), and eventually the 3-dimensional representations used today. Models improved by including key feedbacks between the atmosphere and the ocean, clouds, freshwater bodies, and vegetation (Edwards, 2011). For instance, early models first ignored the ocean, then included a shallow, non-circulating “swamp ocean,” and modeled oceans with simplistic circulation in 1969.

In the late 1950s, Revelle and Suess (1957) raised the alarm that a “large-scale geophysical experiment” on climate was already underway. Keeling anticipated the need for long-term data, and in 1958 began measuring atmospheric CO₂ at Mauna Loa Observatory, eventually producing the famous “Keeling curve” of rising CO₂ gases (Keeling, Whorf, Wahlen, & Van der Plichtt, 1995).

2.3 | 1970s: Resolving the debate between climate coolers and warmers

In the early 1970s, scientists were divided into two camps: the climate “coolers” and “warmers” (Kellogg, 1987). Climate coolers projected that dust and aerosols from fossil fuel burning would overcome CO₂ impacts and initiate a new ice age (Rasool & Schneider, 1971). In contrast, Manabe (1970) used GCMs to project global temperature increases of 0.8°C by 2000. A Swedish workshop sought to resolve this debate, but consensus was elusive (Study of Man's Impact on Climate,

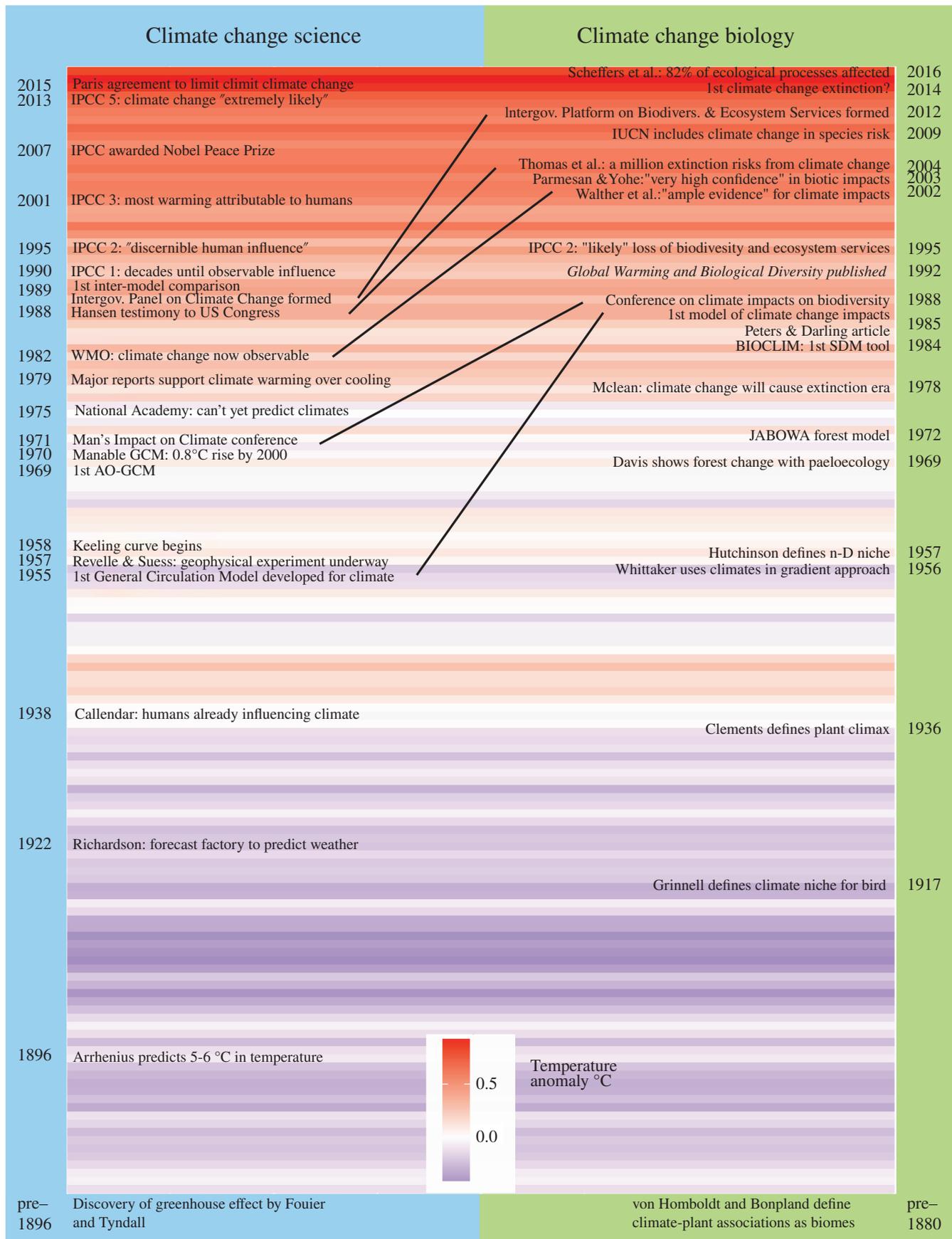


FIGURE 1 Historical milestones in the development of climate science and climate change biology from 1880 to 2017. Background colors depict global temperature anomalies from the 1901 to 2000. Black lines link similar milestones across disciplines

1971). A 1975 U.S. National Academy (NAS) report highlighted the deficient state of current knowledge, including poor understanding of mechanisms and key feedbacks and limited monitoring data. However, they proposed an ambitious plan to project climate by developing new monitoring stations, deploying atmospheric satellites, and coordinating an international research program (U.S. National Academy of Sciences, 1975).

By 1979, better climate models and a better understanding of dust and aerosol impacts pointed convincingly toward a warming climate. A NAS report supported GCM conclusions and projected that doubling CO₂ would increase global temperatures by 3°C (Charney et al., 1979). The World Meteorological Association (WMO, 1979) concurred and further projected that global warming would become detectable by 2000 and significant by 2050.

2.4 | 1980s: A changing climate

Through the 1980s, consensus continued to build that human actions were altering the global climate. Improved data from weather stations and satellites helped a growing international community of modeling groups to produce more accurate and realistic coupled atmosphere–ocean GCM models (Edwards, 2011). Hansen et al. (1981) projected a 2.5°C temperature rise over the next century, and its lead author boldly informed the U.S. Congress in 1988 that he was 99% confident that global warming was occurring. Subsequent news coverage would bring climate change to the attention of the public and policymakers. Still, uncertainties remained. Schneider, Gleick, and Mearns (1990) suggested that it would take another 10 years to project the magnitude of global temperature rise accurately and another 40 years to project precipitation and storm severity accurately.

In 1988, the IPCC was formed to synthesize information on climate change. The IPCC used the new Coupled Model Inter-comparison Project (CMIP) to coordinate simulations using the same emissions scenarios and model outputs, allowing both model comparison and multi-model ensemble projections. Through coordination by the WMO and IPCC, disparate climate models and modeling groups had become linked into a coherent and lasting international collaboration.

2.5 | 1990s until today: Global warming is “extremely likely”

The first IPCC report was cautious, indicating a decade or more for “unequivocal detection of the enhanced greenhouse effect” (IPCC, 1990). Only 5 years later, however, the IPCC would conclude “a discernible human influence on global climate” (IPCC, 1995). Each subsequent IPCC assessment would grow more certain. Concurrently, the number of GCMs grew from 2 to 45, model resolution increased 10-fold, and accuracy increased fourfold (Jones, 2013). By 2013, the IPCC concluded that “it is extremely likely (> 95% probability)” that human activity was increasing global temperatures (IPCC, 2013). In 2007, the IPCC received the Nobel Peace Prize for their work. Today's work includes downscaling climate projections to localized settings and developing more sophisticated representations of mechanistic feedbacks (Hurrell et al., 2013; IPCC, 2013).

3 | A SHORT HISTORY OF PROJECTING BIOLOGICAL IMPACTS OF CLIMATE CHANGE

3.1 | Early climate of ecology

Von Humboldt and Bonpland (1807) proposed that climate determined the location of biomes, such as grasslands and forests, around the world (Figure 1). Clements (1936) renamed the biome the “climax” to emphasize climate's impact on plant assemblages. Whittaker (1956, 1960) extended the climax idea to describe continuous plant distributions along elevational transects. Climate informed the key concept of the niche, which defines how environmental factors determine population persistence (Hutchinson, 1957). For instance, Grinnell (1917) defined the California Thrasher's niche by temperature and humidity, and classic niche experiments also included temperature and humidity (Park, 1954).

In the 20th century, naturalists frequently described changes in the abundance and range boundaries of organisms such as birds, butterflies, and fish in response to natural climate variation (Gushing & Dickson, 1977; Parmesan, 2006). The new field of paleoecology provided a longer perspective. For instance, fossil pollen in lake sediments was used to reconstruct North American forest dynamics during 21,000 years of climate change (Davis & Shaw, 2001).

The applied fields of agriculture, forestry, and fisheries pioneered predictive modeling of climate-species relationships. The mechanistic simulation model, JABOWA, predicted how temperature affected forest growth dynamics (Botkin, Janak, & Wallis, 1972). A mechanistic agricultural model predicted where legume strains might survive using simple relationships between growth and climate (Nix, McMahon, & Mackenzie, 1977). Fisheries models increasingly incorporated natural climate variation as a factor mediating stock recruitment (Sissenwine, 1984).

3.2 | Late 1970s to 1990s: A new risk to biodiversity

McLean (1978) first suggested climate impacts on biodiversity. Drawing inferences from the Mesozoic era or “Time of Great Dying,” McLean suggested that human-induced warming would produce waves of species extinctions, not unlike those ending geologic eras. Still, few ecologists appreciated these threats until the mid-1980s.

In their influential 1985 article, Peters and Darling suggested that climate change would threaten wildlife by forcing them outside protected areas. Two influential conferences, “The First North American Conference on Preparing for Climate Change” in 1987 and “The Consequences of the Greenhouse Effect for Biological Diversity” in 1988 brought together biologists to discuss climate change impacts (Cohn, 1989; Tangle, 1988). By 1992, Soule concluded that “scientists are finally becoming invested in the greatest challenge ever faced by any sentient species—the rescue of the planet” (Peters & Lovejoy, 1992). However, the conservation community lacked the resources, information, and tools to address this challenge (Peters & Lovejoy, 1992; Soulé & Kohm, 1989). Conservation biologists prescribed a general program of monitoring, projecting risks, and developing management strategies (Peters & Lovejoy, 1992). Despite this interest, the golden toad became extinct in 1989, often named the first extinction from climate change (Pounds, Fogden, & Campbell, 1999), although attribution remains uncertain to this day (McMenamin & Hannah, 2012).

Three modeling types emerged to estimate biotic responses to climate change: correlative distribution, species-area richness, and mechanistic models. In one early model, Emanuel, Shugart, and Stevenson (1985) used a correlative approach to project how climate change would shift the global distribution and extent of terrestrial plant biomes. The BIOCLIM program was developed as a generalizable correlative species distribution model in 1984 (Booth, Nix, Busby, & Hutchinson, 2014), and Busby (1988) used it to project climate-induced extinctions in Australian alpine and rainforest species. Using a species-area approach, biologists projected that 20–50% of species would disappear from mountaintop “islands” in the Great Basin desert (Murphy & Weiss, 1992). The mechanistic JABOWA forest model projected the loss of Jack Pine and associated Kirtland's warblers (Botkin, Woodby, & Nisbet, 1991).

3.3 | 2000s: The age of distribution modeling

By 2002, ecologists had found “ample evidence” for climate change effects, including altered phenology, species ranges, and ecosystem processes (Walther et al., 2002). Further reviews would strengthen and quantify these arguments. A meta-analysis suggested that migrations and flowering occurred 2 days earlier per decade, while species ranges expanded 6 km per decade (Parmesan & Yohe, 2003). Accumulating evidence suggested a “very high confidence (>95%)” that climate change was altering biological patterns and a clear “fingerprint” of climate change on ecosystems (Parmesan & Yohe, 2003).

Biotic models, especially correlative distribution models, grew exponentially in number during this period (Figure 2) (Urban et al., 2016). These models relate species' location data to contemporary climate variables and then extrapolate this relationship to future climates (Franklin, 2010; Peterson et al., 2011). Easy access to climate and species distribution data facilitated this approach. A test of species distribution modeling frameworks recommended the MAXENT framework (Elith et al., 2006), which remains dominant today.

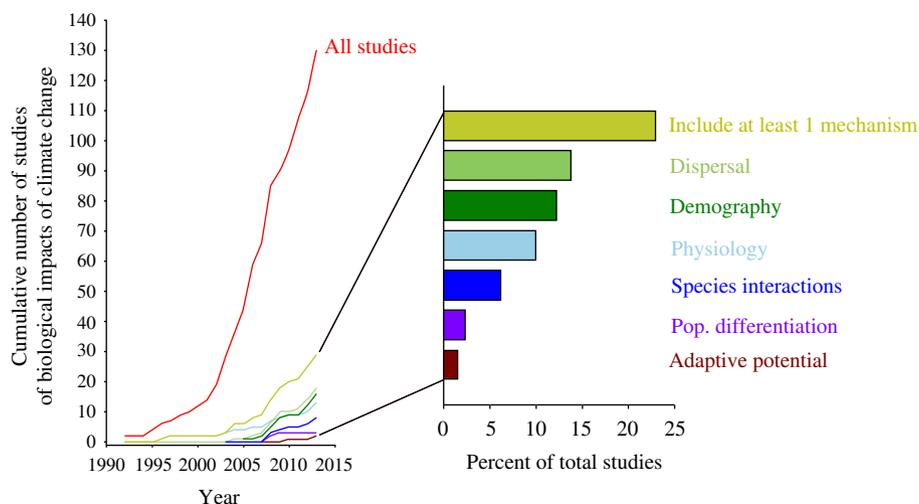


FIGURE 2 Cumulative studies projecting extinction risks from climate change and that include six biological mechanisms. Data from 131 multi-species predictions (Urban, 2015)

Applying the species-area approach to translate habitat losses into extinctions, Thomas et al. (2004) summarized global results to suggest that 9–52% of species would become extinct from climate change. This article spurred debate about modeling techniques and uncertainties, particularly about how to estimate extinction risk from range retractions (He & Hubbell, 2011; Thomas, 2012). Extrapolating these estimates, Thomas suggested that climate change could threaten one million species, which attracted substantial media attention (Hannah, 2012), similar to that generated by Hansen's earlier Congressional testimony. By decade's end, the International Union for the Conservation of Nature (IUCN) began assessing climate change as a major source of global extinction risk (Foden et al., 2009).

3.4 | 2010s: From fingerprint to footprint

Species distribution models remain central to climate change biology. Recent efforts have focused on synthesizing extinction risks across many species. One approach modeled 80,000 species using MaxEnt and projected that extirpations would double from 25% to 50% as temperatures rise from 2 to 4.5°C (Warren, Price, VanDerWal, Cornelius, & Sohl, 2018). Aggregating >500,000 published projections from multiple modeling techniques, I found that extinction risks not only increased with global warming, but accelerated, reaching 16% for the business-as-usual emissions scenario (Urban, 2015).

Despite the many correlative models, skeptics increasingly question their accuracy because they ignore key biological mechanisms known to mediate past climate change responses (Buckley et al., 2010; Kearney & Porter, 2009; Veloz et al., 2012). Mechanistic models that incorporate biological processes are increasingly advocated as more realistic and accurate alternatives (Bocedi et al., 2014; Kearney & Porter, 2009; Purves et al., 2013). These models have grown in complexity to include multiple interacting processes (Bocedi et al., 2014; Okamoto & Amarasekare, 2017) and simulate ecosystem processes (Harfoot et al., 2014). However, these sophisticated models require detailed input data, which are lacking for most species (Urban et al., 2016).

Climate change effects have become even more pronounced. A meta-analysis demonstrated that species were increasing in latitude 17 km per decade (Chen, Hill, Ohlemuller, Roy, & Thomas, 2011), doubling earlier estimates (Parmesan & Yohe, 2003). Phenological changes and population-level extirpations due to climate are now widespread (Cahill et al., 2012; Thackeray et al., 2016). Sea level rise caused a more straightforward extinction of the Bramble Cay Melomys on a low-lying Australian island (Gynther, Waller, & Leung, 2016). Overall, climate change now affects 82% of ecological processes evaluated in an expanding “footprint” of climate change (Scheffers et al., 2016). Although climate change does not yet surmount habitat loss and overexploitation as dominant extinction risks (Ceballos et al., 2015), it is expected to contribute increasingly to “the sixth extinction” in the human-dominated Anthropocene era (Kolbert, 2014). The IPCC suggests “high confidence” that climate change will substantially affect global ecosystems and induce extinctions, but low agreement on how many species, which species, and when (Settele et al., 2014).

4 | COMPARING PROGRESS IN CLIMATE CHANGE AND CLIMATE CHANGE BIOLOGY

In the following, I compare and contrast the development of projections in climate change science and climate change biology (Table 1). In particular, I draw insights from the climate science field that could be applied to expedite progress in climate change biology.

4.1 | Lagging behind

Both disciplines followed a similar trajectory of scientific development (Figure 3): they develop fundamental scientific theories, recognize threats, develop models, capture public attention, and finally generate consensus-building and adopt mitigation

TABLE 1 Comparing climate change and climate change biology

	Projecting climate change	Projecting biological impacts of climate change
Start of modern projection	(Manabe, 1970)	(Emanuel et al., 1985)
Number of systems	1	8–12 million species; 200+ ecosystems
Dominant predictive model	Numerical simulations of gridded coupled atmosphere–ocean–environment mechanistic dynamics (AOGCM)	Statistical correlations between species distributions and climate (e.g., MaxEnt)
International coordinating organization	Intergovernmental Panel on Climate Change (Est. 1988)	Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (Est. 2012)
International infrastructure for standards and model comparison	Coupled Model Inter-Comparison Project	None
Resources	Moderate	Low

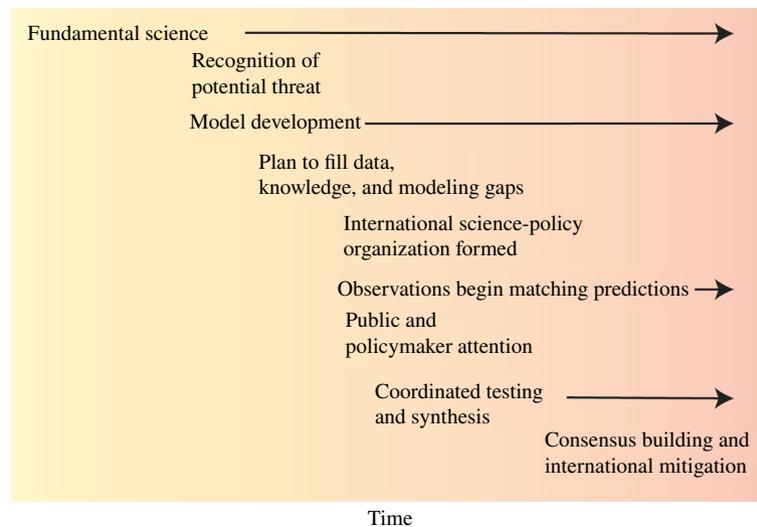


FIGURE 3 A conceptual model of scientific responses to an uncertain crisis derived from the histories of climate change science and biology. Fundamental science develops before recognition of threats. As threats become recognized, projection models are developed and improved, but gaps in knowledge, data, and models are noted and plans developed to address them. As observations begin to support projections, an event occurs which captures the attention of the media, public, and policymakers. An international science-policy organization forms to coordinate global research and policy. The eventual goal is consensus building and adoption of international mitigation measures

measures. Whereas climate science has moved through each of these stages, climate change biology still lags in data collection; model development, comparison, and synthesis; and mitigation. Also, key milestones in climate change biology occurred later than in climate science (black lines in Figure 1). For instance, the “Man’s Impact on Climate” Conference gathered climate scientists together to discuss climate change in 1971 (Kellogg, 1987) whereas biologists attended “The First North American Conference on Preparing for Climate Change” in 1987. The public began to appreciate the climate change threat when James Hansen addressed the U.S. Congress in 1988. Public recognition of biodiversity threats from climate change began in 2004 with media coverage of the Thomas et al. paper (2004) highlighting a million extinctions (Hannah, 2012), a 16-year gap. The IPCC became the governing body for climate science in 1988, and its biodiversity analogue, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), formed in 2012, a 24-year lag. Based on these milestones (Figure 1), climate change biology lags climate science by approximately 20 years.

Recognizing this lag time can help biologists understand what facilitated climate change research and draw on these experiences to facilitate rapid progress in climate change biology. For instance, what milestones have not yet occurred in climate change biology? How can biology make more rapid progress toward these goals? I highlight these and other lessons from climate science in subsequent sections.

4.2 | A multi-dimensional problem

Climate scientists model one climate and its feedbacks with other geophysical systems, whereas biologists model millions of species. Each species is potentially comprised of hundreds of locally adapted populations (Hughes, Daily, & Ehrlich, 1997), which can vary in key functional traits (Des Roches et al., 2018). These populations can adapt to climate change, whereas the climate cannot adapt to higher greenhouse gases. Not only do biologists lack information on model parameters for each species, but these parameters likely differ among billions of populations and can evolve. Hence, projecting billions of biological responses to climate change is more challenging than projecting one climate. Although these differences explain some modeling decisions made by biologists, it does not lessen the importance of developing accurate projections in biology.

4.3 | Differences in approach

Climate modelers did not use the correlation between CO₂ and temperature to project future climates. Instead, they developed mechanistic models to represent key atmospheric processes and their feedbacks with geophysical systems (Farmer & Cook, 2013; Schneider & Dickinson, 1974). In contrast, 82% of biological models used correlations to project species’ responses to climate change scenarios (Figure 2) (Urban, 2015).

By adopting correlative models, biologists choose to maximize model generality over realism. With online climate and species distribution data and automated software, scientists can generate projections in minutes, allowing many species to be

modeled (e.g., 80,000 species, Warren et al., 2018). Correlative modeling usually reproduces a species' contemporary range better than mechanistic models because correlative models are developed expressly for this purpose (see Box 1). The correlations between climate variables and species distributions might capture relevant mechanistic linkages in predictive modeling, especially over short periods over which proxies remain correlated with underlying mechanisms. However, by ignoring processes that alter climate change responses, these models' accuracy likely declines over longer periods.

Mechanistic models trade off realism for generality. Such models often simulate the biology of individuals or populations of particular species (Crozier & Dwyer, 2006; Jenouvrier et al., 2009; Okamoto & Amarasekare, 2017). For example, the RangeShifter model allows researchers to simulate individuals on a changing landscape based on their demography, dispersal, species interactions, and evolution (Bocedi et al., 2014). Ecosystem models can incorporate biologically linked energetics and socioeconomic factors and often model synthetic measures like global fishery harvests (Galbraith, Carozza, & Bianchi, 2017).

Simulations suggest that mechanistic approaches can improve predictive accuracy relative to correlative approaches (Schurr et al., 2012; Zurell et al., 2016). Mechanistic models likely perform better over longer time horizons (Petchey et al., 2015; Zurell et al., 2016), under novel climate regimes (Williams & Jackson, 2007), when new species interact (Gilman, Urban, Tewksbury, Gilchrist, & Holt, 2010), or when populations evolve (Hoffmann & Sgro, 2011). Stochastic mechanistic

BOX 1 MODEL FITTING, PROJECTION, PREDICTION, AND UNCERTAINTY

The goal of a **model** is to represent a natural pattern or process with a relevant subset of important factors.

Statistical (correlative) models derive relationships between proposed explanatory and response variables by finding the best fit.

Mechanistic models are not fit to existing data but are derived from a priori characterizations of important causal factors and parameters. The quality of the mechanistic model depends on how accurately it includes relevant mechanisms, their form, and the parameters that control them.

The variance explained by a statistical model is often called its predictive power. However, we must differentiate description from prediction. A **prediction** (or **projection** when based on a range of potential scenarios of external forcings) describes what will happen in the future or elsewhere. Thus, describing within-sample data is not prediction. A good description of existing data will not necessarily predict future data accurately due to overfitting.

Model overfitting occurs when stochastic vagaries of data are modeled as causation. Data is always better described by more variables and more flexible models. Procedures can be applied to penalize models with more explanatory factors (e.g., Akaike information criterion) to avoid over-fitting and select a parsimonious model. Overfitting is especially problematic for prediction because spurious relationships are extrapolated to values not in the original analysis.

Extrapolation occurs when a model developed for one set of input data is applied to another set that differs in values. Paradoxically, the best model of current data could be the worst model for explaining extrapolated data. Often, models that explain current data better than other models are incorrectly claimed to be superior in prediction, but prediction can only be validated with out-of-sample data.

Validation measures the fit between predictions and observed out-of-sample data. Statistical models will perform poorly when existing correlations no longer describe data because they are uncorrelated with underlying mechanisms. Cross-validation is a useful technique to decrease overfitting. Here, the model is developed on a subset of data, and the correspondence between model predictions and the excluded data estimates model fit.

All **out-of-sample data** are not the same. Often, cross-validation is applied to data subject to the same biases, and thus does not prevent over-fitting to shared vagaries. The greater the separation in space or time, the greater is the probability that underlying mechanisms have operated and temporary correlations have broken apart.

Sensitivity determines how a proportional change in a parameter affects outcomes and provides a measure of how parameter uncertainty affects model results. Refining the most sensitive parameters reduces model uncertainty.

Uncertainty characterizes the confidence in model outcomes and is usually depicted as a probability distribution of predictions. Uncertainty can arise through variation in model structure and inputs as well as stochasticity, and the best models integrate all sources of uncertainty. The average outcome in models of low certainty is less important than the range of potential outcomes.

To summarize, predictive model performance should be assessed with out-of-sample data, and models that are not overfitted and rely on mechanisms rather than correlations can better predict data that is distant in time or space. Model performance is characterized through validation, uncertainty, and sensitivity analyses.

models can better characterize uncertainty (Schurr et al., 2012), which is usually unavailable from unrealistically precise deterministic and correlative models.

Drawing general insights from mechanistic models about many species is more limited versus easily parameterized correlative models. Applying a model developed for one species to another oftentimes requires substantial alterations, recoding, or an altogether different model. Also, mechanistic models require high-quality data for parameters and validation, which are often not available for most species and are often difficult to collect.

Some strategies exist to increase the generality and applicability of mechanistic models. One option is to create hybrid correlative-mechanistic models (Buckley et al., 2010) such as those that adjust outcomes based on the future distributions of interacting species (Schweiger, Settele, Kudrna, Klotz, & Kuhn, 2008) or use species-specific dispersal to determine colonization of future habitats projected by correlative models (Dullinger et al., 2012; Loarie et al., 2009). Trait correlations (e.g., between adult survival and fecundity) can be used to predict missing parameters for species with limited data (Schloss, Nunez, & Lawler, 2012). Researchers also can create virtual species with realistic trait combinations (Santini et al., 2016) or universal size-energy scaling properties (Carozza, Bianchi, & Galbraith, 2016) and test their responses to climate. Minimally, these efforts provide qualitative insights about which types of species are most vulnerable to climate change and should be targeted for future, in-depth study (Pearson et al., 2014).

4.4 | Differences in data

Climate scientists benefit from a system of weather stations and satellites that provide real-time inputs and data for model validation. In contrast, biologists lack detailed information on the long-term dynamics of most species and for parameters underlying mechanistic models (Urban et al., 2016). Monitoring variables are needed to calibrate models and validate outcomes (Araujo, Pearson, Thuiller, & Erhard, 2005), and efforts are underway to coordinate these efforts. For instance, the Essential Biodiversity Variables were developed for monitoring changes in global biodiversity, including variables such as population abundances, traits, and ecosystem properties (Pereira et al., 2013). However, improving the realism of predictive models also requires mechanistic parameters that characterize key biological processes (Buckley et al., 2010; Urban et al., 2016). Their estimation often requires more detailed observations (e.g., food web interactions) or experiments (e.g., adaptive potential) than accomplished via monitoring. By standardizing data collection and specifically targeting knowledge gaps, these global efforts could accelerate our ability to build more biologically informed projections and validate outputs.

4.5 | Organizational culture

Climate science and biology differ in their history, culture, and norms, which affect how each discipline approaches prediction and projection. Early on, climate change modeling involved strong international cooperation, sharing of code, and willingness to accept model-wide standards (Edwards, 2011). This collaborative and international culture likely facilitated its rapid progress. National governments and international agencies often coordinate large groups of collaborating scientists. For instance, more than 50 scientists from 16 institutions contributed to building the land model of the Community Earth Systems Model, representing just 1 of its 12 working groups (NCAR, 2018). Climate change science thus demonstrates how global, collaborative research can yield increasingly accurate projections for climate change.

In contrast, biodiversity modeling is still mostly performed by small research groups with little coordination. Historically, ecologists shared data and collaborated less frequently than other disciplines because disciplinary norms focused on individual scholarship (Rodrigo et al., 2013). Governmental initiatives to organize biological projections are rare, and those that exist usually focus on economically important species (Brown & Rosenberg, 1999). Gradually, biologists are pursuing more collaborative practices such as participating in thematic working groups and sharing model code, software, and data. Moreover, the IPBES is now coordinating biodiversity research and policy. However, international and national funding for collaborative centers, research networks, and model comparison is still needed to shift the culture toward more integrated approaches.

4.6 | Assembling the ensemble

Twenty GCM groups performed coordinated sets of climate change experiments for the recent CMIP (Taylor, Stouffer, & Meehl, 2011). Ensemble projections perform more accurately than single models and constitute the primary IPCC method (IPCC, 2013; Palmer & Räisänen, 2002). Confidence in predictions generally increases if divergent models, each of which are deficient but in different ways, generate similar results. Model understanding is thereby gained via the “intersection of independent lies” (Levins, 1966).

Combining biological models across research groups and modeling types (e.g., mechanistic and correlative) would highlight major sources of variation, characterize uncertainty better, and likely improve accuracy (Kearney, Wintle, & Porter, 2010). An important future step would be to coordinate model development, inputs, and outputs of these ensemble projects by

forming a CMIP-like entity for biological projections. As a start, the Inter-Sectoral Impacts Model Inter-comparison Project developed protocols for comparing outputs from heterogeneous ecosystem models, such as for fisheries (Tittensor, Coll, & Walker, 2018). Similarly, terrestrial modelers created ensembles of mechanistic and correlative approaches to reveal where the greatest uncertainties lie for shifting tree species (Takolander, Hickler, Meller, & Cabeza, 2018). These approaches require an agreement to focus on the same set of species or ecosystem properties. Although ambitious, modeling a set of species representative of taxonomic and functional diversity from each global ecosystem could help us better understand extinction risks (Urban et al., 2016).

4.7 | Biodiversity funding

Although difficult to quantify, one 1997 attempt estimated that governments globally provisioned \$3 billion (\$4.1 billion in 2017 dollars) to climate scientists (Stanhill, 2001). Much of this funding goes toward shared equipment such as satellites and supercomputers. Although no estimates exist for funding biodiversity projections, biodiversity modeling likely receives less funding than climate modeling. Climate research is likely better funded given a clearer link to economics, agriculture, and military strength. Changes to biodiversity and ecosystems can also substantially affect these services (Haines-Young & Potschin, 2010; Pecl et al., 2017), but their impacts are often not as direct. Given the many threats to biodiversity not just from climate change, but also overexploitation and habitat degradation, these synergistic threats are not being adequately addressed under current funding.

A recent paper calls for \$100 billion per year to conserve biodiversity in developing countries from climate change (Barbier, Burgess, & Dean, 2018), matching the amount proposed for promoting climate change solutions in these same countries. Similar past recommendations have failed (Soulé & Kohm, 1989). However, the current proposal asks businesses, especially those that benefit from ecosystem services such as forestry, to support this effort (Barbier et al., 2018). Besides natural-resource companies, opportunities exist for technology companies to develop predictive models for biodiversity while simultaneously learning profitable knowledge about modeling globally complex systems.

5 | CONCLUSION

Projecting responses to climate change biology ranks as one of the greatest challenges in science—a wicked problem of high dimensionality and complexity. This challenge occurs in the context of a lagging response, poor coordination and collaboration, and a shortfall in funding. Biotic systems are already changing in response to climate change, and those threats are likely accelerate and could eventually overshadow current land use threats (Newbold, 2018; Scheffers et al., 2016; Urban, 2015). Hence, we find ourselves much like the climate scientists in the early 1970s, who recognized the deficient state of their field and recommended an ambitious multi-decade plan to make rapid progress (Study of Man's Impact on Climate, 1971; U.S. National Academy of Sciences, 1975).

Although the challenges in biodiversity projections are great, biology can make substantial progress in the coming years by adopting the practices that facilitated progress in climate change science. In short, biology needs an IPCC-like effort to develop next-generation models that incorporate biological realism and fill data gaps in advance of the growing evidence of a climate-fueled biodiversity crisis. The next decade will determine if we have the resolve and the resources to conserve biodiversity and its services to humans.

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CONFLICT OF INTEREST

The author has declared no conflicts of interest for this article.

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