

REVIEW SUMMARY

CLIMATE CHANGE

Improving the forecast for biodiversity under climate change

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BACKGROUND: As global climate change accelerates, one of the most urgent tasks for the coming decades is to develop accurate predictions about biological responses to guide the effective protection of biodiversity. Predictive models in biology provide a means for scientists to project changes to species and ecosystems in response to disturbances such as climate change. Most current predictive models, however, exclude important biological mechanisms such as demography, dispersal, evolution, and species interactions. These biological mechanisms have been shown to be important in mediating past and present responses to climate change. Thus, current modeling efforts do not provide sufficiently accurate predic-

tions. Despite the many complexities involved, biologists are rapidly developing tools that include the key biological processes needed to improve predictive accuracy. The biggest obstacle to applying these more realistic models is that the data needed to inform them are almost always missing. We suggest ways to fill this growing gap between model sophistication and information to predict and prevent the most damaging aspects of climate change for life on Earth.

ADVANCES: On the basis of empirical and theoretical evidence, we identify six biological mechanisms that commonly shape responses to climate change yet are too often missing

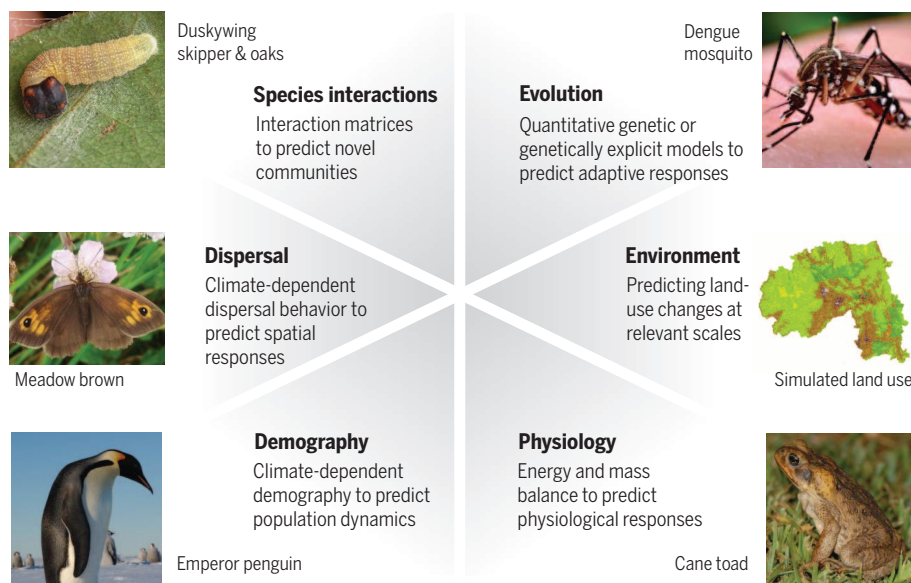
from current predictive models: physiology; demography, life history, and phenology; species interactions; evolutionary potential and population differentiation; dispersal, colonization, and range dynamics; and responses to environmental variation. We prioritize the types of information needed to inform each of these mechanisms and suggest proxies for data that are missing or difficult to collect. We show that even for well-studied species, we often lack critical information that would be necessary to apply more realistic, mechanistic models. Consequently, data limitations likely override the potential gains in accuracy of more realistic models. Given the

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enormous challenge of collecting this detailed information on millions of species around the world, we highlight practical methods that promote the greatest gains in predictive accuracy. Trait-based approaches leverage sparse data to make more general inferences about unstudied species. Targeting species with high climate sensitivity and disproportionate ecological impact can yield important insights about future ecosystem change. Adaptive modeling schemes provide a means to target the most important data while simultaneously improving predictive accuracy.

OUTLOOK: Strategic collections of essential biological information will allow us to build generalizable insights that inform our broader ability to anticipate species' responses to climate change and other human-caused disturbances. By increasing accuracy and making uncertainties explicit, scientists can deliver improved projections for biodiversity under climate change together with characterizations of uncertainty to support more informed decisions by policymakers and land managers. Toward this end, a globally coordinated effort to fill data gaps in advance of the growing climate-fueled biodiversity crisis offers substantial advantages in efficiency, coverage, and accuracy. Biologists can take advantage of the lessons learned from the Intergovernmental Panel on Climate Change's development, coordination, and integration of climate change projections. Climate and weather projections were greatly improved by incorporating important mechanisms and testing predictions against global weather station data. Biology can do the same. We need to adopt this meteorological approach to predicting biological responses to climate change to enhance our ability to mitigate future changes to global biodiversity and the services it provides to humans. ■



Emerging models are beginning to incorporate six key biological mechanisms that can improve predictions of biological responses to climate change. Models that include biological mechanisms have been used to project (clockwise from top) the evolution of disease-harboring mosquitoes, future environments and land use, physiological responses of invasive species such as cane toads, demographic responses of penguins to future climates, climate-dependent dispersal behavior in butterflies, and mismatched interactions between butterflies and their host plants. Despite these modeling advances, we seldom have the detailed data needed to build these models, necessitating new efforts to collect the relevant data to parameterize more biologically realistic predictive models.

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Improving the forecast for biodiversity under climate change

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New biological models are incorporating the realistic processes underlying biological responses to climate change and other human-caused disturbances. However, these more realistic models require detailed information, which is lacking for most species on Earth. Current monitoring efforts mainly document changes in biodiversity, rather than collecting the mechanistic data needed to predict future changes. We describe and prioritize the biological information needed to inform more realistic projections of species' responses to climate change. We also highlight how trait-based approaches and adaptive modeling can leverage sparse data to make broader predictions. We outline a global effort to collect the data necessary to better understand, anticipate, and reduce the damaging effects of climate change on biodiversity.

We need to predict how climate change will alter biodiversity if we are to prevent serious damage to the biosphere (1). Biologists develop predictive models to anticipate how environmental changes might affect the future properties of species and ecosystems (2, 3). Many models have been developed to understand climate change impacts (fig. S1) (4), but biological responses remain difficult to predict (5, 6). One reason is that most models forecasting biodiversity change ignore underlying mechanisms, such as demographic shifts, species interactions,

and evolution, and instead extrapolate correlations between current species' ranges and climate (Fig. 1) (4). These omissions are troubling because we know that these missing biological mechanisms played key roles in mediating past and present biotic responses to climate change (7–9). Moreover, models ignoring biological mechanisms often become unreliable when extrapolated to novel conditions (10–13). As climates and ecological communities without historical precedent become more common and correlations between current species distributions and climate become uncoupled (10, 14, 15), we cannot rely on tools based on statistical descriptions of the past. Given the essential role of biological processes in mediating species' responses to climate change, accurate forecasts of future biodiversity likely will require more realistic models.

Emerging models incorporate fundamental biological mechanisms rather than relying solely on statistical correlations (16–19). Unlike correlative approaches, mechanistic models do not assume that a species' range reflects its niche perfectly, has reached equilibrium with the environment, or is independent of species interactions—all commonly violated assumptions (7, 13, 20, 21). Mechanistic models can also integrate multiple, interacting biological processes, as well as non-linear and stochastic dynamics (Fig. 2) (17, 18, 22), and can better characterize uncertainty by directly modeling error sources (2, 21, 23).

By incorporating realistic features such as demography and dispersal, mechanistic models commonly outperform correlative approaches in projecting climate change responses (13, 20). For example, mechanistic models consistently predicted simulated species' range dynamics over a period of 75 years, whereas correlative models became increasingly inaccurate over this same time frame (20). Mechanistic models improve predictive accu-

racy, especially when species face strong biotic interactions, experience novel climates, or cannot disperse far (13, 20, 24). Moreover, mechanistic models can inform predictive efforts by indicating processes (e.g., biotic limits on ranges) hidden by current associations between environments and species distributions (24). Although more work is needed to craft more sophisticated and accurate mechanistic models that are customizable for individual species and ecosystems, the tools are already mature enough to improve projections (2, 16, 19).

Mechanistic models, however, require high-quality data about how a species' unique biology governs its responses to climate. Parameters provide this information. For example, a parameter such as population growth rate determines how population abundances change through time. In contrast, a model variable such as population abundance describes emergent properties. Differentiating between parameters and variables is important given the recent focus on harmonizing efforts to collect variables that monitor the state of global biodiversity (25). We believe that such endeavors should focus not solely on collecting variables that indicate the state of biodiversity, but also on measuring mechanistic parameters critical for predicting future responses.

Here, we identify the mechanistic data needed to make substantial gains in predictive modeling. Rather than focusing on one particular mechanism (15, 18, 22, 26, 27), we take a comprehensive approach, assess data availability for each mechanism, prioritize data needs, demonstrate how to leverage sparse data to make general predictions, and suggest how global coordination could facilitate these efforts. By synthesizing this information in one framework, we aim to inspire the future research agenda needed to develop the full predictive potential of mechanistic models. Consistent with the Intergovernmental Panel on Climate

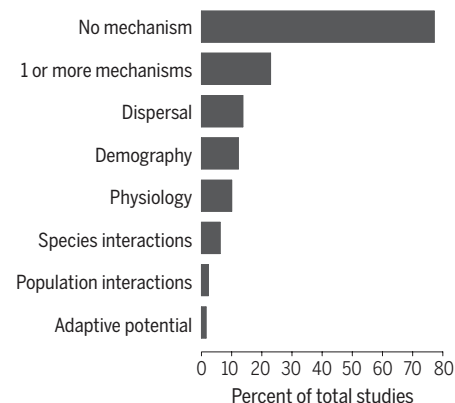


Fig. 1. Most models of biological responses to climate change omit important biological mechanisms. Only 23% of reviewed studies (4) included a biological mechanism. Models that included one mechanism usually incorporated others, but no model included all six mechanisms. All models included environmental variation, generally via correlations, but usually did not explicitly incorporate species' sensitivities to environmental variation at relevant spatiotemporal scales.

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Change (IPCC), we use “projection” to define all descriptions of the future and reserve “forecast” for the most likely projections.

Crucial biological information

In Table 1, we identify six mechanisms that determine biological responses to climate change. On the basis of these mechanisms, we assess data availability for four well-studied species (Fig. 3). We find that although information on the six key mechanisms partly exists for species with high economic value, it is incomplete for even the best-studied species and absent for the vast majority of Earth's species. Consequently, the most realistic models usually rely on sparse data or data extrapolated from nonrepresentative populations, environments, or species.

We next describe each mechanism in further detail, highlighting key parameters and discussing challenges of measurement, uncertainty, and sen-

sitivity. Here, uncertainty encompasses both limited knowledge and random outcomes; sensitivity denotes how changes in a parameter value influence model outcomes. After describing these mechanisms, we recommend how to collect data efficiently and leverage imperfect data.

Physiology

Physiology mediates how climate conditions such as temperature, growing degree-days, water availability, and potential evapotranspiration influence survival, growth, development, movement, and reproduction (18, 28–30). Physiological parameters include critical thermal minima or maxima (the low and high temperatures at which organisms cease organized movement), evaporative water loss, photosynthetic rate, and metabolic rate. These individual physiological responses often are used to inform higher-level processes such as population persistence and range shifts (29, 31). For example,

knowledge of the proportion of time a lizard remains active outside its burrow, where it is thermally neutral, can help in predicting its extinction risk under future climates (32).

Physiologists measure parameters from natural observations or experiments in climate-controlled chambers (28). However, using natural observations risks confounding responses to climate with other environmental factors (28). High-priority traits include responses to extreme heat or dryness, where survival often declines steeply. Uncertainty about physiological responses increases when we lack information on habitat heterogeneity, local adaptation, and physiological impacts on overall fitness.

Demography, life history, and phenology

Demographic (birth, death, migration), life history (schedule of life cycle events), and phenological (timing of life history events) traits play critical

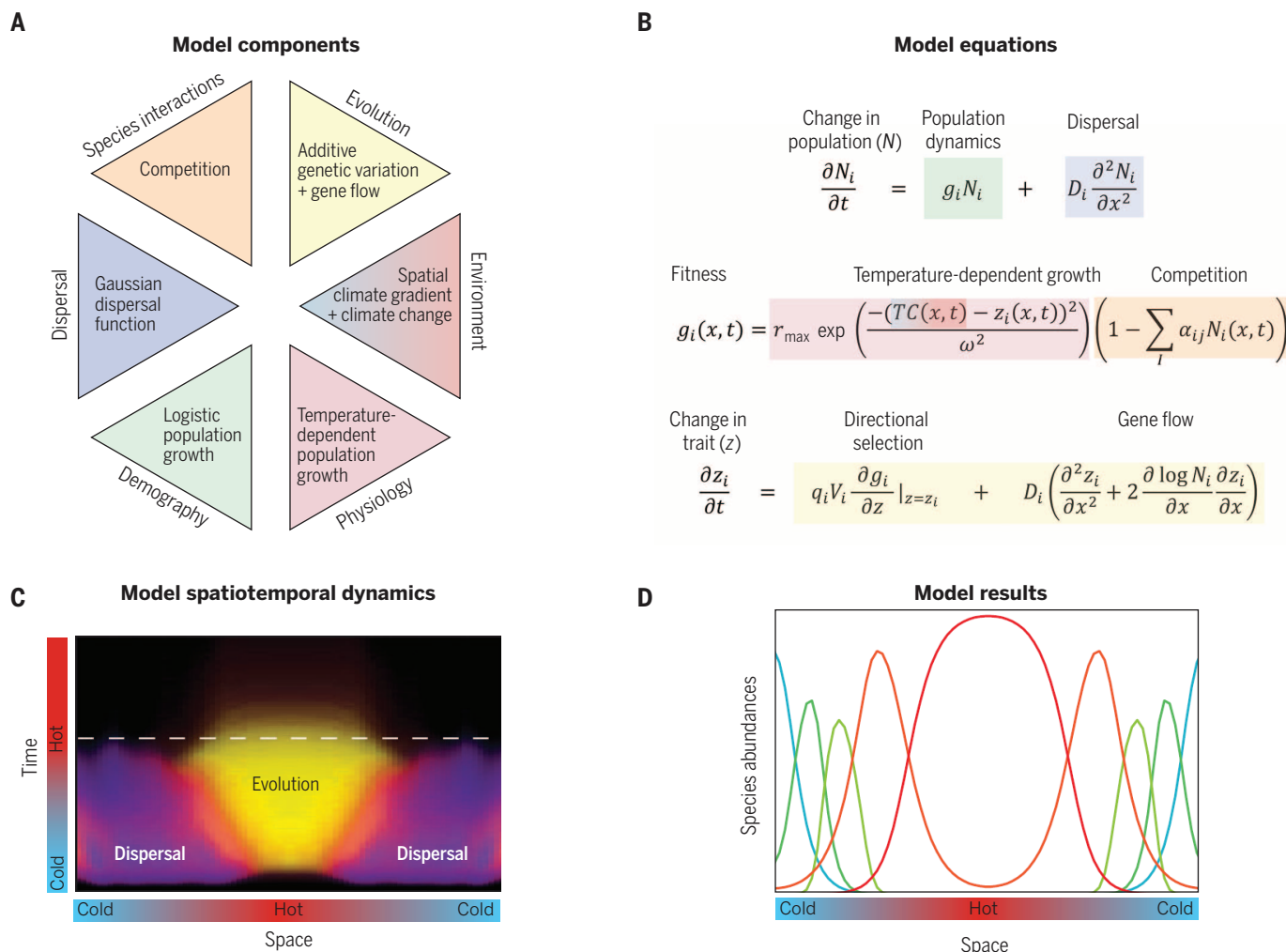


Fig. 2. A generic model integrates six biological mechanisms to predict climate change responses. (A to C) The six mechanisms (A) are matched by color to their representation in equations (B) simplified from (11) (see table S1 for symbol descriptions). Results suggest how dispersal (blue-purple), adaptive evolution (yellow), and their combination (red-orange) determine the match between community-wide thermal traits and changing local temper-

atures (C). Temperatures increase before stabilizing at the white dashed line. Black indicates no trait change. In cold regions, warm-adapted species disperse into newly suitable, warmer habitats. In warm regions, evolution dominates because no species with higher thermal tolerances exist. (D) Equilibrium abundances of five hypothetical species (each indicated by differently colored lines) after climate change.

roles in climate change responses (29, 33, 34). Important parameters include birth and death rates, age at maturity, development rate, and reproductive investment. Parameters are best collected on marked individuals across representative populations spanning different densities and climates.

However, these efforts require long-term, costly commitments. Changes in population abundances from short-term weather variation can provide proxies, but these become unreliable over time. Long-term vegetation plots can provide detailed demographic information for plants. Citizen sci-

tists can collect data over large regions, on traits such as flowering time or breeding date, but concerns about data quality likely limit their usefulness for less easily measured traits such as genetic variation.

Certain demographic parameters are especially important. For example, adult survival often affects population growth rate more than fecundity does in long-lived species (35). Density dependence and generation length also strongly affect extinction risk from climate change (22). Additional uncertainty stems from local adaptation, responses to novel environments, mismatched phenology, community shifts, and interactions with nonclimate stressors (15, 36, 37).

Evolutionary potential and local adaptation

Assaying genetic variation is crucial for predicting future responses (27, 38) because it could allow populations to adapt to climate change in situ. Unfortunately, scientists seldom know if, or how quickly, populations can evolve climate-sensitive traits (36). Moreover, species usually comprise many locally adapted populations that each respond differently to climate change (39). Species might not shift their ranges with climate change if locally adapted populations become isolated and cannot colonize new habitats (39). Alternatively, individuals dispersing from locally adapted populations might track optimal climates across landscapes, and thus might not need to adapt locally (Fig. 2) (11).

The breeder's and Price equations can be used to predict responses to natural selection based on selection strength and genetic (co)variances (40). Genetic (co)variances are commonly measured through controlled breeding experiments or pedigrees. However, these estimates can become unreliable over long time scales or in novel environments if selection regimes or adaptive potential change (41). Also, genetic (co)variances often vary among populations and environments, thus requiring broad sampling and careful sensitivity analyses. Other approaches involve tracking evolution using long-term observations, reconstructing evolution from layered propagule banks, or applying experimental evolution (42, 43). For instance, comparing *Brassica rapa* plants grown from seeds collected before and after a drought revealed rapid evolution of flowering time (43). Past local adaptations to spatial climatic gradients are easier to assess. However, these patterns suggest past adaptive potential, not future evolutionary rates (36). By scanning entire genomes, next-generation sequencing offers a promising tool to uncover fine-scale evolutionary diversification (44), and declining cost for genomics could rapidly expand our limited knowledge of adaptive potential. Other frequently applied approaches include common garden experiments, natural transplants, and observations of phenotypic variation (Table 1).

Adaptive potential and population differentiation represent high-priority parameters because ignoring them contributes high levels of uncertainty (12, 27, 36, 43). For example, the Quino

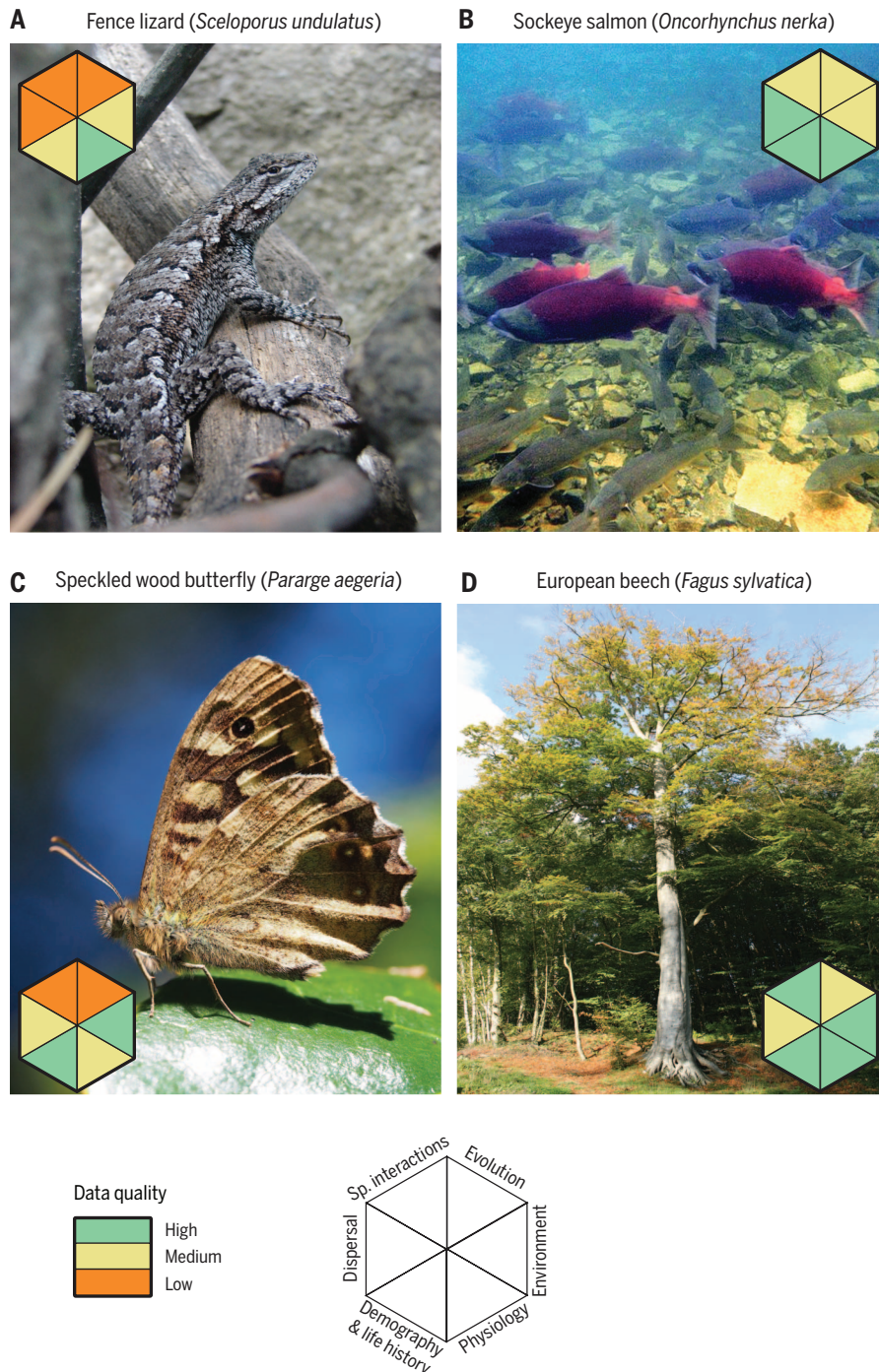


Fig. 3. Data gaps exist even for well-studied species. We rated data quality for some of the best-studied species in climate change research: (A) fence lizard, (B) sockeye salmon, (C) speckled wood butterfly, and (D) European beech. Data quality: high = near-complete information; medium = information available but missing critical components; low = information mostly absent. We evaluated data availability by examining models of climate responses, reviewing species-specific literature, and contacting experts.

checkerspot butterfly was expected to become extinct from climate change, but it persists after adapting to live on a new host plant (45). Given limited genetic and evolutionary information, we will often need to generalize adaptive rates across species based on characteristics such as generation time, genetic isolation, phenotypic variation, and phylogenetic position. Fortunately, even coarse estimates of maximum adaptive rate compared to climate change suggest tipping points, where minor changes in climate initiate major biological disruptions and thus represent targets for facilitating adaptation in threatened populations (46).

Species interactions

Species interactions often underlie unexpected responses to climate change (10, 15), and most extinctions attributed to climate change to date have involved altered species interactions (47). Surprises occur when specialist interactions such as mutualism constrain species' responses (48), phenological mismatches alter species interactions (37), or top consumers propagate climate change effects throughout food webs (8). For instance, high temperatures along the Pacific Coast exacerbated predation by sea stars on mussels, which caused local extirpations (49). Yet few models account for species interactions explicitly, instead assuming that each species responds independently to climate change (6, 15) (Fig. 1).

High-quality information on species interactions requires well-resolved information about interacting species, interaction types and strengths, spatiotemporal variation, and phenology. Unfortunately, such detailed information is usually missing. One approach to overcome this deficit is to analyze important subsets of strongly interacting species (15). Less robust alternatives include estimating trophic position using isotopes, understanding competition via diet breadth or species co-occurrence patterns, extrapolating from correlations between body size and trophic level, or discerning species co-occurrence patterns from metagenomics. High-priority parameters include those characterizing specialist interactions, top-down food web interactions, and timing mismatches among interacting species. High uncertainty arises from changes in species interactions themselves (e.g., shifts from competition to facilitation) and complex indirect effects that propagate through food webs (9). Additional uncertainties arise from species' differential abilities to track climate change in space, creating previously unseen communities as coevolved interactions disappear and novel interactions form (10).

Dispersal, colonization, and range dynamics

To persist, species often must track suitable climates into new regions through dispersal, colonization, and subsequent range shifts (50, 51). Most models unrealistically assume that all organisms disperse comparably and across any landscape (Fig. 1) (26). In reality, dispersal depends on the interplay among individual behavior, fitness, habitat quality, and landscape configuration

(52). Range shifts are particularly sensitive to dynamics at range boundaries where low abundances challenge accurate estimation (53).

Global positioning system units can record fine-scaled individual movement but are costly and unsuitable for many small organisms. Passive integrated transponders, acoustic tags, and telemetry devices track smaller individuals at lower cost, but these require strategically placed recorders.

Neutral genetic variation across landscapes can indicate movement patterns, but demographic history can confound these estimates. Citizen science sometimes enables cost-effective, coordinated, and large-scale data collection, assuming adequate quality control. Dispersal distances also can be inferred from proxies [e.g., body size–dispersal relationships in animals (51) and growth form, seed mass, and vegetation type in plants (54)] until

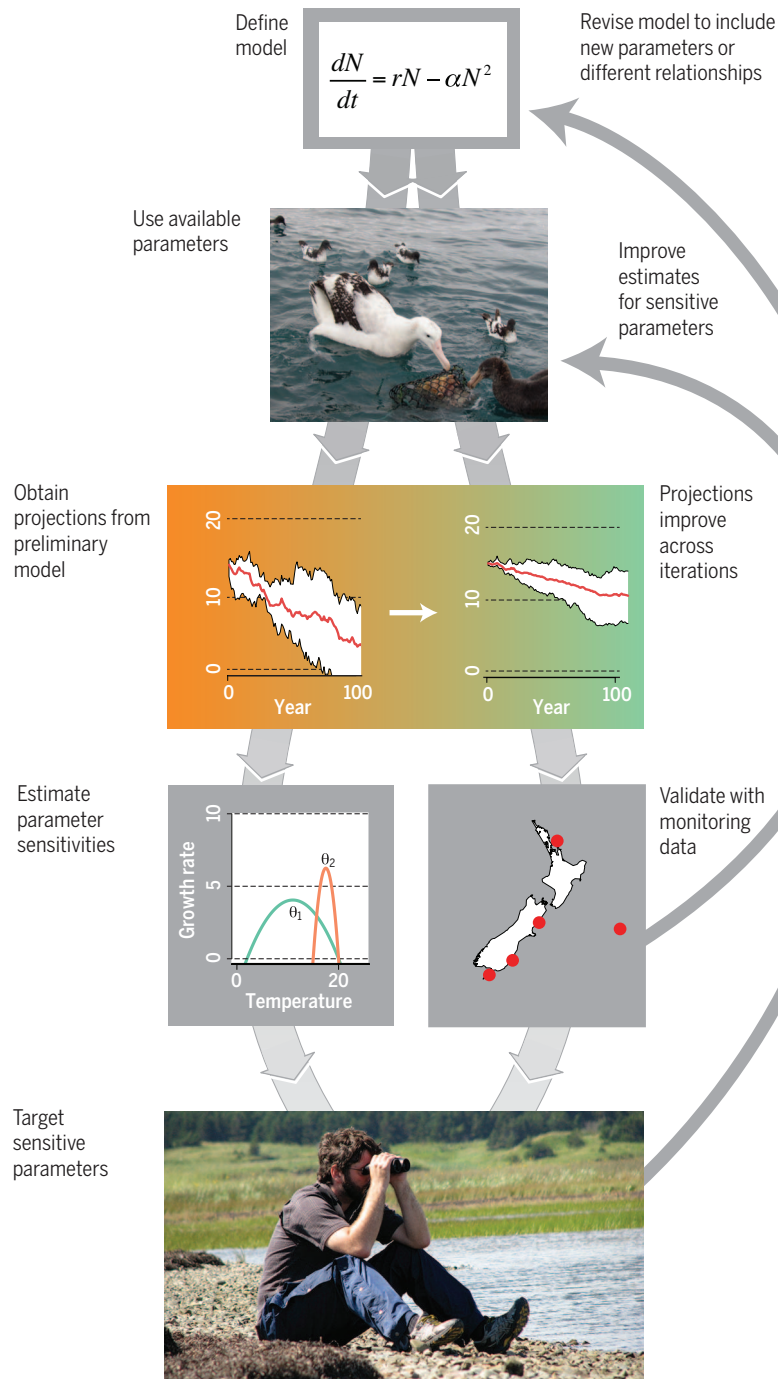


Fig. 4. Biological models improve iteratively through time by applying an adaptive modeling scheme. Steps include parameterizing models using available data, estimating parameter sensitivities, targeting better measurements for sensitive parameters, validating projections with observations, and iteratively refining and updating the model to improve predictive accuracy and precision through time.

Table 1. Biological parameters, collection methods, proxies, priorities, and key uncertainties. We list six classes of biological mechanisms, example parameters, methods to collect them, possible proxy relationships that could fill in gaps for poorly studied taxa, priority parameters, and key remaining uncertainties. We list methods in an illustrative descending order of data accuracy. The ordering of collection methods is illustrative only and will clearly change depending on the particular attributes of species and systems. The best methods, however, might not be easily implemented for some taxa, necessitating more practical methods followed by sensitivity analysis. They will also change through time—for example, as emerging methods become less costly. In reality, the ideal

approach for collecting data on a key process will involve joint use of more than one method. For example, for dispersal we might currently want to collect high-quality telemetry data for the movement of a relatively small number of dispersers because of cost constraints while also obtaining population-level estimates of dispersal through either landscape genetics or mark-release-recapture methods (or both). We encourage readers to tailor costs and benefits of the alternative and complementary approaches to their own system and adjust decisions for investment of resources appropriately. Note that each of these mechanisms likely interacts with other mechanisms.

Biological mechanisms	Example parameters	Alternative and complementary methods	Proxy relationships	Priority parameters	Key uncertainties
Physiology	Thermal, desiccation, and chemical tolerances; environment-dependent performance and metabolic rate; photosynthesis	<ul style="list-style-type: none"> • Experimental understanding of physiological responses to environmental conditions in nature or the laboratory • Observed correlations between physiological responses and environmental conditions in time or space • Trait-based proxies (e.g., body mass for metabolism) 	<ul style="list-style-type: none"> • Body mass correlates strongly with energy requirements • Water and light requirements in vegetation models 	Physiological responses in extreme environments (e.g., performance under hot or dry conditions)	<ul style="list-style-type: none"> • How does behavior modify physiology? • To what degree do organisms evolve different physiological responses across a range? • How do physiological sensitivities of different performance traits scale to whole-organism fitness?
Demography, life history, and phenology	Birth and death rates, including age or stage structure, age of maturity, development and growth rates, environmental dependence, timing, and individual variability	<ul style="list-style-type: none"> • Long-term mark recapture parentage studies or long-term demographic data from vegetation plots • Experimental studies of environment-dependent birth and death rates in nature (best) or the laboratory • Population growth rates from observed abundance data 	<ul style="list-style-type: none"> • Demographic parameters correlate with life history traits (e.g., slow-fast continuum) and niche specialization 	<ul style="list-style-type: none"> • Vital rates that most influence population growth rates (e.g., adult survival for long-lived organisms, generation length, mismatches in timing of life history events) 	<ul style="list-style-type: none"> • To what degree do organisms evolve different life histories across a range? • Does rapid adaptation to climate change play a role? • When does phenology depend on climate versus nondimate triggers (e.g., day length)? • How do other environmental changes (e.g., habitat degradation) interact with climate responses? • To what degree is trait change determined by genetics versus environment? • How well do short-term measurements of adaptive mechanisms perform in the long run? • How does local adaptation within a range alter species-level responses to climate change?
Evolutionary potential and local adaptation	Additive genetic trait (co)variance/heritability and additive genetic covariance between traits and fitness	<ul style="list-style-type: none"> • Quantitative genetic variation in key traits estimated from controlled breeding designs, from populations with pedigrees, or from individuals raised under common conditions • Experimental or correlational estimation of selection gradients • Gene expression patterns for understanding functional trait variation under different environmental conditions 	<ul style="list-style-type: none"> • Evolutionary rates correlate negatively with generation length • Genetic variation within populations positively correlates with population size • Space-for-time substitutions 	<ul style="list-style-type: none"> • Adaptive potential, local adaptation of climate-sensitive parameters across species range 	
	Fitness differences among populations and environments; genetic variation among populations; phenotypic variation, including plasticity among populations	<ul style="list-style-type: none"> • Phenotypic variation within populations • Reciprocal transplant and common garden experiments that reveal fitness and trait differences among populations in response to relevant environmental gradients • Statistical search for variation in loci under selection 	<ul style="list-style-type: none"> • Genetic variation among populations positively correlates with range size 		

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Biological mechanisms	Example parameters	Alternative and complementary methods	Proxy relationships	Priority parameters	Key uncertainties
Species interactions	Interaction webs with spatiotemporal variation and phenology, interaction types and strengths, community module, diet or resource overlap, trophic position	<ul style="list-style-type: none"> Gene expression patterns for understanding functional trait variation under different environmental conditions Population genetics with neutral loci to understand population differentiation through barriers to gene flow Observation of phenotypic variation within and among populations Experimental evaluation of species interaction strength and direction in nature (best) or the laboratory Natural history observations of interactions Isotope analysis to reveal trophic levels and food web links Statistical co-occurrence patterns (e.g., checkerboard patterns for competition) Satellite telemetry of moving organisms to reveal landscape movement tracks Mark-recapture and relocations to evaluate absolute movement Experiments (e.g., linked mesocosms) to understand movement Landscape genetics to reveal landscape connectivity among populations Historical reconstruction of movement patterns during expansion Incidence functions in metapopulations to determine population connectivity Citizen science to track organisms (e.g., tagged birds) 	<ul style="list-style-type: none"> Trophic level increases with body size Similar trophic levels are shared by phylogenetically similar species 	<ul style="list-style-type: none"> Specialist interactions, sensitivity of top consumers, phenological mismatches between interacting species 	<ul style="list-style-type: none"> What happens as coevolved interactions disappear and new species interactions form? How sensitive are food webs to top-down versus bottom-up climate disturbances? To what degree can species adapt to novel species interactions?
		<ul style="list-style-type: none"> Dispersal behaviors; movement and settlement rules; interindividual variability; environment-, density-, and condition-dependent dispersal; landscape permeability (e.g., least-cost path analysis) 	<ul style="list-style-type: none"> Larger-bodied animals disperse farther Smaller seeds travel farther Animal-dispersed seeds travel farther Larger-winged organisms disperse farther Pelagic animals disperse farther than benthic ones 	<ul style="list-style-type: none"> Long-distance dispersal, fitness at range boundaries 	<ul style="list-style-type: none"> How important is long-range dispersal for range dynamics? How does fitness vary across a range?
Responses to environmental variation	Functional relationships between traits and environments; identification and quantification of key environmental gradients across species-relevant scales of space and time	<ul style="list-style-type: none"> Experimental manipulation of key environments to understand functional responses Statistical analysis of environmental gradients and responses Characterization of environmental gradients at biologically relevant scales Surveys of environmental parameters conducted at relevant spatial and temporal scales Ground-truthed maps to be used in environmental gradient analyses Statistical interpolation of coarse map data 	<ul style="list-style-type: none"> Determining networks of co-acting environmental variables Correlating easily collected remotely sensed data to other factors such as resources 	<ul style="list-style-type: none"> Identifying key gradients, spatial scale dependence of environmental responses, dynamic change in gradients 	<ul style="list-style-type: none"> Are there general ways to predict the relevant scales at which different species will respond to environmental variation? What biological parameters are linked with the environmental factors and how? How are important environmental gradients changing through time?

better estimates become available. Long-distance dispersal and fitness at range edges are high-priority parameters because they introduce high uncertainty in model outcomes (26), yet are difficult to measure.

Responses to environmental variation

Responses to climate change depend on species-specific sensitivities and exposures to climate and habitat variation at relevant spatiotemporal scales. For instance, birds respond idiosyncratically to different climate variables, depending on their individual sensitivities to temperature and precipitation change (55). Researchers must carefully identify which specific climate components actually affect species. Many organisms respond not to average annual temperature or precipitation, but rather to temperature thresholds, season length, humidity, potential evapotranspiration, or extreme events such as droughts. Species also differ in the relevant spatiotemporal scales of environmental variation. Researchers should evaluate the environment through the eyes of the organism. The scales relevant to focal organisms often are meters and minutes rather than the measurements in kilometers and months typically available. Despite the increasing availability of fine-scaled information, most predictions are still made at coarse scales, which can substantially reduce predictive accuracy (56). Hierarchical sampling can maximize information content by combining large-scale sampling with targeted fine-scale measurements that capture relevant gradients. Species characteristics such as body size or generation length also can provide proxies for missing data on species' environmental responses.

In addition, we need to integrate predictions of climate change with other human disturbances, including land use, pollution, invasive species, and harvesting, to gauge the full extent of future environmental change. Improving predictions of these disturbances [e.g., (57)] and downscaling data to relevant ecological resolutions are critical for reducing future uncertainty.

Interacting mechanisms

Each mechanism potentially interacts with many others. Specifically, climate responses depend proximately on dispersal and demography; demography in turn depends on physiology, species interactions, and environments; and each trait can evolve. For example, great tit birds in the Netherlands do not lay eggs earlier in warmer springs (involving demography, phenology, and environmental responses), whereas their caterpillar prey (species interaction) emerge earlier. This phenological mismatch between birds and their prey decreases nestling fitness (demography) (37). Yet great tits from the United Kingdom do breed earlier in warmer springs, suggesting population genetic differentiation (58). A challenge is to integrate multiple interacting mechanisms without unnecessarily increasing model complexity (Fig. 2).

A practical way forward

We recognize that the complexity of natural systems will add uncertainty to even the best-

parameterized and most realistic models (59). Collecting the relevant information and developing realistic biological models will require substantial investment in time and resources. Despite these challenges, we believe that collecting mechanistic data will both enhance our fundamental understanding of the biological processes that underlie climate responses and contribute to more accurate, longer-term projections that facilitate more effective conservation. Mechanistic models might not make accurate predictions initially, but learning from those failures provides the insights that ultimately improve projections. Predictive science advances most quickly via iterative prediction-failure-improvement cycles, and mechanistically grounded models often quicken the pace of these advances (2, 3, 19). Even small gains in understanding can improve future models by indicating critical missing information, highlighting key uncertainties, suggesting general trait-based predictions for nonmodeled organisms, and delimiting the best options for retaining biodiversity under a range of future policy scenarios.

Given limited time and resources, however, we need to develop strategies that leverage existing data and target essential information. Toward this end, we advocate for an adaptive modeling scheme that facilitates cost-effective model development and data collection (Fig. 4). The process of model testing and revision—steps rarely taken today, but facilitated by a more systematic approach—can reveal data of particular importance for improving predictions. Researchers first parameterize models with available data. In Table 1, we demonstrate how to tailor data collection efforts to system-specific constraints by listing ideal methods along with more easily collected proxies. Researchers then use independently collected variables from monitoring efforts to test outcomes and fit uncertain relationships. Sensitivity analyses identify the most important parameters to collect, ensuring that resources go toward producing the greatest gains in accuracy. On the basis of these analyses, researchers can collect improved or new parameter estimates and revise the model through successive iterations of the approach. Crucially, results from multiple independent models should be combined because ensemble forecasts often prove more accurate (3, 60). Researchers also need to articulate clearly how uncertainty in parameter estimates and model choice propagates at each modeling step. We recommend adopting the IPCC's standards (1) for classifying model confidence and probabilistic uncertainty.

Several approaches are available to extend projections from a few carefully studied species to many unstudied ones. We often possess extensive information that is spread across many species but is incomplete for any particular species. Emerging phylogenetic and trait-based approaches could fill these data gaps. Trait-based approaches use trait correlations (e.g., between adult survival and fecundity) to predict missing parameters for species (50). Researchers also can simulate the climate responses of virtual species with realistic combinations of traits. For example, this virtual approach predicted that 30% of terrestrial mam-

mals might not keep pace with climate change (61). Minimally, these efforts provide qualitative insights about which types of species are most vulnerable to climate change and therefore should be targeted for future, in-depth study (22). Another cost-effective strategy is to prioritize research on species with both high climate sensitivity and disproportionately large impacts on ecosystems. These so-called biotic multipliers—often, top predators and other keystone species—amplify small changes in climate to produce large ecological effects (8) such that their future dynamics drive overall ecosystem changes (9).

Conservation sometimes focuses on overall biodiversity rather than focal species. Estimates from subsets of species might be cautiously extrapolated to overall biodiversity, assuming suitable representation across taxonomic and phylogenetic diversity. However, trait-based approaches might more efficiently suggest species that have vulnerable trait combinations or amplify community-wide impacts of climate change. For example, focusing on top consumers and other keystone species can indicate how their responses reverberate through entire food webs (8), thus further extending the value of single-species forecasts.

Lastly, hybrid correlative-mechanistic approaches offer a pragmatic initial approach to improving predictions by adding key mechanisms to simple models. For example, adjusting predicted ranges from correlative models with species-specific dispersal abilities (62) or interacting species' ranges (48) can add realism and improve predictions. Given the simplicity of most current approaches (Fig. 1), even minimally more realistic models might improve projections until more complicated models can be developed (13, 19).

Global coordination

Global coordination will be critical at all stages, including defining projection goals, developing better models, collating and incorporating existing data, determining which additional data might improve forecasts, collecting new data, monitoring biodiversity changes, and organizing and maintaining data. Researchers and policymakers first must agree on the nature of the projection itself, including the accuracy, coverage, and time horizon of forecasts. A global clearinghouse would be useful to organize trait data, standardize terminology (e.g., dispersal versus migration), and monitor climate responses.

It would also be useful to form regional working groups with local experts. Regional working groups would define representative ecosystems and climatic and environmental gradients in their region, while taking advantage of existing data and long-term monitoring sites. Groups would select species representing a broad range of regional trait diversity and build initial models with available data to estimate parameter sensitivity. To address immediate extinction threats, regional working groups might also characterize the climate change risk for threatened species on the International Union for Conservation of Nature Red List. Groups should then develop plans to refine sensitive parameters through targeted funding opportunities and citizen

science. Collected biological information must be accessible, quality-checked, standardized, and maintained in databases such as Encyclopedia of Life's TraitBank (traits) and Global Biodiversity Information Facility (species occurrences).

The IPCC's development of climate change predictions provides a template for how to achieve comparable progress in biodiversity projections. The IPCC's biodiversity analog, the Intergovernmental Platform on Biodiversity and Ecosystem Services, can also help to coordinate this effort. Already, the Group on Earth Observations–Biodiversity Observation Network is developing a list of essential biodiversity variables (EBVs) for monitoring global biodiversity (25) and is working to address monitoring gaps (19). Despite some overlap between the modeling parameters outlined here and EBVs, the two collection schemes have divergent objectives. The EBVs monitor changes in biodiversity and provide variables for initializing and testing mechanistic predictions. Mechanistic models, however, also require parameters governing key processes, which often mandate more detailed observations or experiments than monitoring programs currently entail.

Combining predictive modeling with robust scenario analysis

Collecting the data necessary to inform mechanistic biological models presents an enormous challenge given the vast diversity of life, its complexity, and our inadequate knowledge about it. This inherent complexity and stochasticity limits the accuracy of biological predictions for policy and management (59, 63), especially over long forecast horizons (3). We must accept that even the best-informed predictions could fail for a variety of unanticipated reasons.

An alternative approach to planning for climate change develops conservation strategies robust to a broad range of future scenarios (64), thus insuring against inevitable surprises. For example, applying this “robust scenario” approach might include maintaining dispersal corridors, preserving existing natural habitat and genetic diversity, and facilitating monitoring and flexible, adaptive management (59, 65). This strategy broadly protects biodiversity and depends less on accurate predictions. However, practical considerations will often limit the number of options that are feasible, especially when management options for one species trade off against another.

The two approaches are not mutually exclusive, and we believe that they work best in tandem. Mechanistic approaches likely will improve predictions at intermediate time horizons (e.g., 25 to 50 years), when current environmental correlations break down and correlative approaches become less accurate (3). Beyond this time frame, even the best mechanistic models become uncertain as key parameters can shift and uncertainty propagates. Yet predictive models are still needed to delimit plausible expectations, place bounds on uncertainty, and direct limited resources toward strategies that target the most threatened regions and species (23, 59). Hence, a tandem approach builds general insights from key representative

species while preserving flexible options that work when models fail.

Conclusions

Climate scientists in 1975 acknowledged their inability to predict climate accurately and highlighted the many challenges to reaching this objective (66). Despite these challenges, they outlined an ambitious long-term research program aimed at understanding key mechanisms governing climate change and collecting key pieces of missing information. This program ultimately produced the improvements in forecasting weather and climate change that society benefits from today. We believe that biology can and must do the same.

We advocate for a renewed global focus on targeting the natural history information needed to predict the future of biodiversity. Such efforts would more than compensate for their cost by improving our ability to understand, anticipate, and thereby prevent biodiversity loss and damage to ecosystems from climate change as well as other disturbances. Ultimately, understanding how nature works will provide innumerable benefits for long-term sustainability and human well-being.

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SUPPLEMENTARY MATERIALS

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Fig. S1

Table S1

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Improving the forecast for biodiversity under climate change

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