














# REVIEW

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## Wildcards in climate change biology

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**Abstract.** Forecasting how climate change will impact biological systems represents a grand challenge for biologists. However, climate change biology lacks an effective framework for anticipating and resolving uncertainty. Here, we introduce the concept of climate change wildcards: biological or bioclimatic processes with a high degree of uncertainty and a large impact on our ability to address the biotic consequences of climate change. Wildcards may occur at multiple points in the progression of research—from understanding, to predicting, to forecasting biological responses. Our understanding of biological responses is limited by the components and processes we exclude to make research tractable. Our ability to predict biological responses often requires integration between biological levels of organization, across

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multiple stressors, and from specific cases to general systems. However, these types of integration can be dramatically affected by, respectively, differences between biological levels in their critical points, nonadditivity of the effects of different stressors, and historical and geographic contingency. Finally, our ability to forecast biological responses to climate change requires incorporating climatic projections in bioclimatic models. Such forecasts are vulnerable to the compounding of biological and climatic uncertainty, especially when biological responses occur in novel areas of bioclimatic parameter space. Both biological responses and climate change are dynamic processes; the potential of biological systems to be buffered against or rescued from the effects of climate change depends on the relative timing of biological and climatic effects—one of the least predictable aspects of both systems. In sum, our framework identifies stress points in the research process where we should anticipate and forestall wildcards. Focusing on universal currencies, like energy and elements, and universal structures, like functional traits and ecological networks, will improve our ability to generalize results. Most importantly, by modeling and communicating uncertainty, climate change biology can identify critical foci for future research.

*Key words:* contingency; ecological surprise; forecast; insurance; multiple stressor; prediction; rescue; uncertainty.

## INTRODUCTION

Predicting how the abundance, distribution, and diversity of life on Earth will respond to rapidly changing climatic conditions represents one of the greatest challenges for biologists today. There is an urgency to this challenge, given that forecasting the biotic impacts of climate change is essential to developing mitigation measures. However, a forecast is only as useful as it is accurate, and climate change biology lacks a coherent framework to identify the most important uncertainties in forecasting. Here we argue that, irrespective of the level of biological organization, there may be universal features of biological systems (or our approach to studying them) that allow us to generalize about the potential wildcards that affect our ability to forecast biotic impacts of climate change.

We use the term “wildcards” purposefully here. In a game of cards, wildcards turn up unexpectedly and infrequently, but can result in major shifts in the outcome of the game. Similarly, the wildcards in climate change biology are game-changing processes, unexpectedly countering the predicted biotic response to climate change. Such dramatic shifts in outcomes are exemplified by rapid changes in biological state in response to small climatic shifts (e.g., from a vegetated to a desertified ecosystem), alterations in the direction of a biological response (e.g., from decreases to increases in population size), and shifts in critical states (e.g., from sublethal to lethal effects on organisms). Excellent examples of wildcards are “black swan events” (Anderson et al. 2017) and “ecological surprises” (Doak et al. 2008). Black swan events have been defined, in an ecological context, as observed, inherently unpredictable events with profound biological consequences (e.g., extreme winters leading to population crashes). Ecological surprises are outcomes that are not predicted from previous results or theory, and this term has particularly been applied to nonadditive effects of multiple stressors on communities and ecosystems (Cote et al. 2016). The concept of climate-change

wildcards extends these ideas to any biological level from an organism to an ecosystem, encompasses both events and processes, and explicitly invokes the dual conditions of high uncertainty and high impact on outcome.

There is an ongoing debate about how predictable biological systems are, ranging from optimism that process-based models of individuals or genes can be scaled to higher levels (Evans et al. 2013) to pessimism that only weak phenomenon-based models are possible (Beckage et al. 2011, Schindler and Hilborn 2015). Low predictability in biological systems may result from inherent stochasticity in the system, uncertainty in the correct model specification (epistemic uncertainty), or limitations to modeling an entire system from component properties (computational irreducibility). Such debates about predictability are occurring simultaneously in cellular physiology (Samoilov et al. 2006), population biology (Crone et al. 2013, Anderson et al. 2017), community ecology (Clark 2009, Vellend et al. 2014), evolutionary biology (Lenormand et al. 2009) and ecosystem modeling (DeFries and Nagendra 2017). However, these debates often occur in parallel, with little attempt to integrate our approaches to uncertainty across these subject areas.

Many other scientific disciplines, such as seismology and tropical meteorology, grapple with modeling complex systems. Yet, unlike biology, these other disciplines have developed ways to express uncertainty in forecasts—for example, odds of an earthquake of a certain magnitude within a certain time frame, probabilistic maps of possible tropical cyclone landfall—in terms that the public can understand and that policy makers can use to develop risk reduction strategies (Gerstenberger et al. 2020). These disciplines have been able to deal with uncertainty effectively through model-building strategies that allow for the propagation of errors but at the same time permit the improvement of models through continual reconciliation of model outputs and observations (Schorlemmer et al. 2018, Gerstenberger et al. 2020).

Such model building begins with the construction of candidate mechanistic model(s) that incorporate current observations, followed by verification of this understanding through cross validation and experimentation to test assumptions, leading to model selection and refinement (Medlyn et al. 2015, Gerstenberger et al. 2020). The verified model may be used to predict responses beyond the original data set, such as other locations or previous time points, and comparisons of predicted and observed responses allow further improvement of the model. This validated model can then be used to forecast future responses, and monitoring of these ongoing responses allows for adaptive improvements to the forecasts (Schorlemmer et al. 2018).

How does such an understanding—predicting—forecasting framework apply to climate change biology? The “understanding” domain of climate change biology focuses on mechanisms, and so asks questions about which processes are most important in determining how (and if) the abiotic environment affects a biological system. In this domain, there is no attempt to apply this understanding to other systems or locations or through

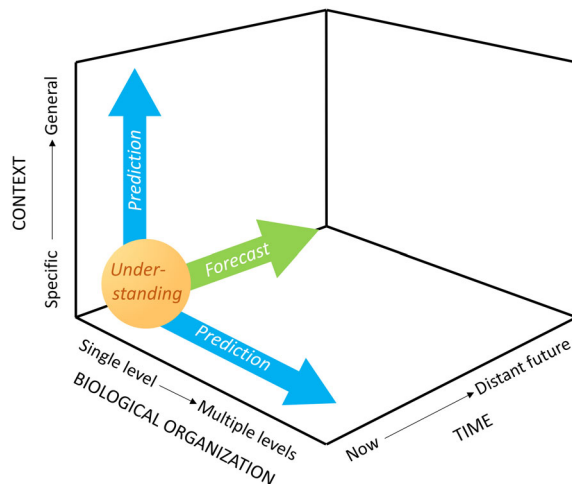


FIG. 1. Most studies are done in the specific, simple, and short-term domain represented by the orange sphere at lower left (e.g., experimental warming establishes that predation rates of a sea star are sensitive to temperature). Studies conducted in this parameter space build “understanding” of the system, but are already vulnerable to Type A wildcards (Table 1); for example, the observed response of the sea stars may have been influenced by a prior infection. The two blue arrows represent use of this understanding to predict system response at higher levels of biological integration (e.g., using individual-level thermal tolerances of sea stars to predict population-level responses) or more general contexts (e.g., predicting effects of warming in other intertidal sites, or in different systems with other invertebrate predators). These “prediction” trajectories may encounter wildcards B1 and B2, respectively (Table 2). The green arrow represents “forecasting,” the special case of prediction over time when new type C wildcards (Table 3) related to the joint application of biological and climatic models become important (e.g., will evolution of higher thermal tolerances in sea stars keep pace with the warming of the intertidal?).

time. Understanding is a valuable objective in itself, and much of climate change biology is currently within this domain. However, if we wish to apply this understanding more broadly, then we must move to the domain of “predicting.” In climate change biology, we often want to apply our understanding of how a driver affects one level of biological organization to another level (e.g., use individual-level thermal tolerances to predict population-level responses to temperature). Another common goal is to develop models and theories that are generally applicable, rather than context-dependent, so that we can apply our understanding to predict the responses of other systems or geographic locations. We can visually represent these two types of prediction as two different axes (organization, context) extending from understanding (Fig. 1). When we predict the future, time is the relevant axis and this special case of prediction is commonly known as “forecasting.” Forecasting is inherently different from other types of prediction because the state of the system at any point depends not just on the exogenous drivers, but also the previous state of the system. In climate change biology, forecasting is particularly challenging because the climate itself is changing dynamically through time with feedbacks between the biotic and climatic dynamics. In our framework, we therefore consider it the final destination of research.

We argue here that widespread adoption of such a framework for understanding, predicting, and forecasting biotic responses to climate change could be an effective way to tackle uncertainty. We will show that there are particular points in this research framework where wildcards are likely to be identified, including when research transitions from one domain of inference to another and when the timing of a biological response is critical to the projected outcome (Fig. 2). Intensive research focused on these stress points may help increase the predictability of the system in terms of application to different contexts, organizational levels, and forecasting through time. Our cross-disciplinary synthesis of wildcards in climate change biology has the aim of focusing future research to both reduce and better communicate uncertainties in biological forecasts.

#### WILDCARDS IN DEVELOPING UNDERSTANDING FROM BIOLOGICAL DATA (TYPE A WILDCARDS)

To forecast biotic responses to climate change we must first understand how biological systems respond to climatic stressors (Fig. 2). Even at this fundamental “understanding” stage several wildcards may originate, often associated with the inherent difficulty in isolating mechanisms without removing important biological complexity (Table 1, in Fig. 2A). Characterizing complex interactions is an active field of research across all levels of biological organization (Ferrière and Fox 1995, Bashan et al. 2012, Komatsu et al. 2019) and so these wildcards are likely the most familiar to the reader.

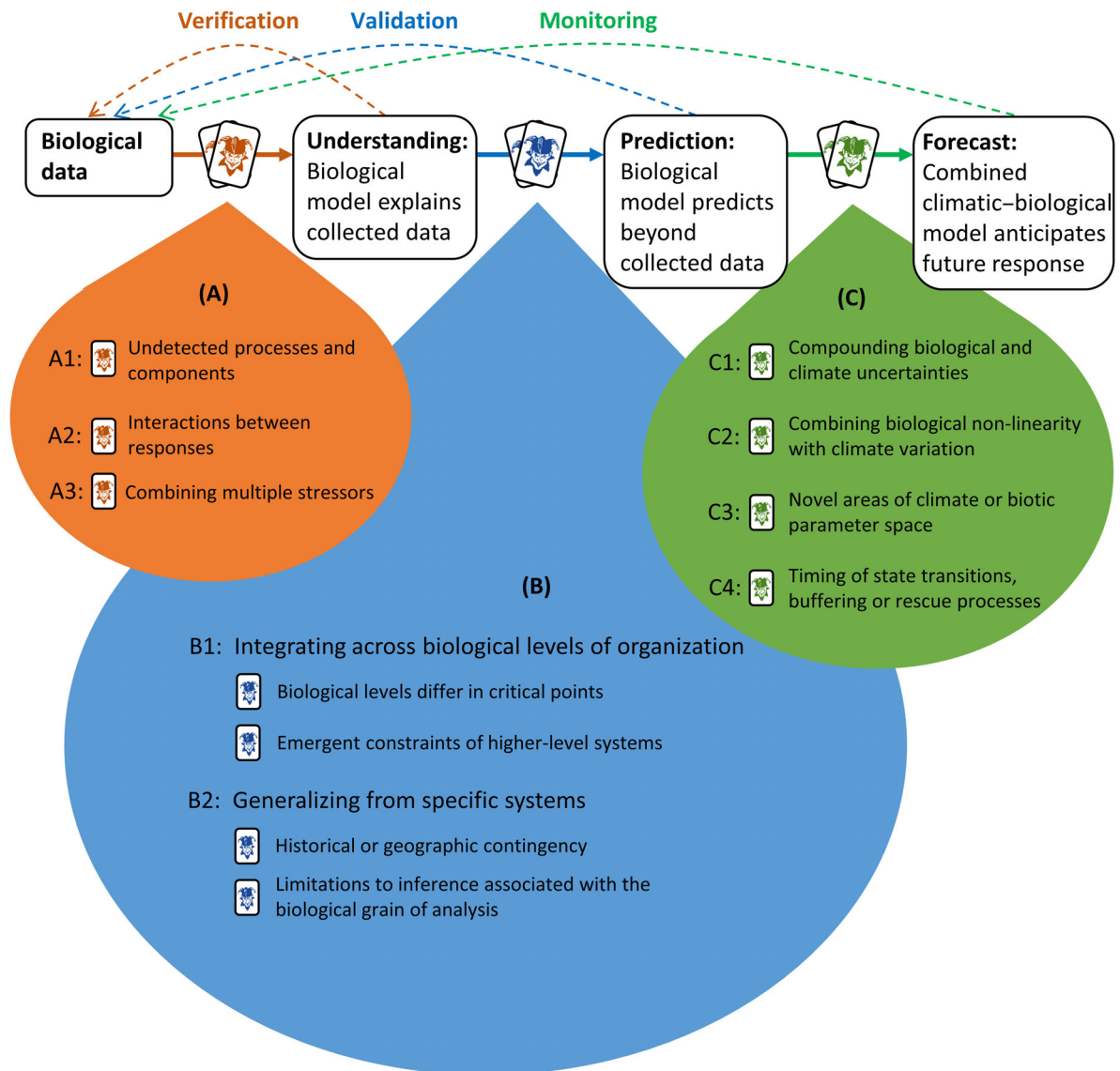


FIG. 2. Forecasting the biotic effects of climate change requires first constructing and verifying specific mechanistic models of how particular climatic stressors affect a biological level (e.g. gene, organism, population, community, ecosystem). Verification of such models can be achieved statistically (cross validation) or methodologically (replication of experiments). This understanding of the system can be used to predict situations beyond the data used initially in formulating the model. Validation of these predictions requires new data, and may result in iterative improvements in model specification, leading to a predictive model. Finally, biological models must be combined with climate models to project the future performance of the system in a changing climate, with such forecasts updated by monitoring. In each of these transitions from understanding to prediction to forecasting, there is the potential for particular wildcards to come into play.

Thus, rather than an exhaustive review, we provide here a brief summary of three common types of Type A wildcards to situate the remainder of our conceptual framework.

#### *Undetected processes and components (A1 wildcards)*

To understand mechanisms, researchers often simplify systems, examining, for example, just one life stage (Byrne 2011) or one population (Sinclair et al. 2012), or

focusing on just one potential process. However, this can mean overlooking key components or processes that may drive the system's response. For example, studies of predator–prey interactions have often ignored the role that chemical cues play in both predators locating prey and prey evading predators. This delayed discovery of important ways that climate change can disrupt the effects of predators on prey—such as high CO<sub>2</sub> reducing the ability of sharks to smell their prey (Dixson et al. 2015) or drought altering how

TABLE 1. Wildcards in developing understanding from biological data occur at all biological levels, from organisms to ecosystems.

Wildcard type	Wildcard subtype	Organism	Population	Community	Ecosystem
A1. Undetected processes and components	Overlooked components	Experimental responses misleading if a biased subset of individuals studied (e.g., life stage, population), or cryptic species included (Garcia-Robledo et al. 2016, Peterman et al. 2016)	Misleading estimates of population dynamics if critical life stages or process not considered (Kimball et al. 2010)	Role of parasites and disease on community responses to climate are understudied (Brooks and Hoberg 2007, Rohr et al. 2011)	Important components that require specialized methods (e.g., microbial diversity) are understudied. (Graham et al. 2012)
	Processes excluded or altered by research approach	Behavioral and physiological responses restricted by experimental setting, or difficult to integrate over lifetime of organism (Schulte et al. 2011)	Short-term or local population responses exclude potential influences of dispersal, selection, drift, and species interactions (Davis et al. 1998)	Small-scale and short-term manipulations may exclude important processes and species (Carpenter 1996), or have misleading transient dynamics (Blonder et al. 2017)	Manipulations may exclude flow of organisms or nutrients between ecosystems, whereas observations may miss extreme events. (Boeck et al. 2015)
A2. Interactions between responses	Combinations of direct and indirect effects of climate	Physiological effects of climate can be moderated by species interactions (Coristine et al. 2014). Analogously, selection on individual traits may be constrained by selection on other traits (Etterson and Shaw 2001)	Direct effects of climate on focal species can be moderated by indirect effects on interacting species (Ockendon et al. 2014)	The ability of one community to shift spatially to track a changing climate is affected by interactions with adjacent communities (Thompson and Gonzalez 2017)	Direct effect of climate change on focal ecosystems may be moderated by response of adjacent ecosystems that provide subsidies (Jeppesen et al. 2009)
A3. Combining multiple stressors	Response to multiple stressors may be nonadditive	Physiological responses to multiple climate stressors are often nonadditive, potentially because they cumulatively push organisms from their optimal allocation of energy (Sokolova 2013)	Population responses nonadditive when adaptation to one stressor affects adaptation to another (e.g., Souther and McGraw 2014)	Community responses nonadditive when species traits that determine sensitivity to one stressor correlate with traits determining sensitivity to a second stressor (Vinebrooke et al. 2004)	Ecosystem response nonadditive when exposure to one stressor erodes ecosystem resilience to another stressor (Scheffer et al. 2001)

Note: Wildcard types and subtypes refer to categories illustrated in Fig. 2 and described in the text.

damselfly odor impacts food webs (Marino et al. 2017). Often, component interactions are unknowingly embedded within studies, as exemplified by cryptic parasite or viral infections that alter the susceptibility of organisms to ocean acidification (Chen et al. 2015, MacLeod and Poulin 2016), or cryptic behaviors following drought that unexpectedly rewire food webs (Amundrud et al. 2019, described in more detail as Example 3 of Fig. 1). Initially undetected components therefore continue to change our understanding of how climatic processes influence biological systems across levels of organization.

#### *Interactions between responses (A2 wildcards)*

A focus on a single, tractable biological component of a system (e.g., a species, a habitat) can result in overlooking complex interdependencies within the system. For example, studies of the distribution and abundance of single, focal species traditionally ignored species interactions, but it is increasingly apparent that nonfocal species can mediate the effects of climate change (Suttle et al. 2007, Ockendon et al. 2014). This insight has now led to advancements in joint species distribution models (Pollock et al. 2014). Similarly, when lakes are viewed as

part of a connected “meta-ecosystem,” then climate-dependent rates of nutrient flow from terrestrial watersheds are recognized as key drivers of the effects of climate change on the aquatic ecosystem (Jeppesen et al. 2009).

#### *Wildcards in combining multiple stressors (A3 wildcards)*

Multiple stressors can interact to produce nonadditive responses. The relative frequency of additive, synergistic (greater than additive expectation) and antagonistic (less than additive expectation) responses is debated, as is how to quantify these effects properly (Cote et al. 2016, Thompson et al. 2018). Nevertheless, meta-analyses have found prevalent nonadditive responses to multiple stressors for individual fitness (Darling and Cote 2008, Harvey et al. 2013) and ecosystem stocks and fluxes (Wu et al. 2011, Dieleman et al. 2012), with some indication that synergism is more common at individual levels compared to antagonism at the community or ecosystem levels (Crain et al. 2008, Jackson et al. 2016). As natural systems have experienced covarying change in multiple climatic variables, as well as other global change stressors (e.g., nitrogen deposition), it may be challenging to use survey data, even from long-term studies, to isolate effects of any particular climate variable. But by failing to build nonadditive effects into models, managing for one stressor could have a range of unexpected consequences (Brown et al. 2013).

#### WILDCARDS IN MOVING FROM UNDERSTANDING TO PREDICTION (TYPE B WILDCARDS)

Understanding a particular system can be a scientific end goal in itself. However, this understanding cannot be externally validated unless we use it to predict a response in a different context, such as a different system or location. As Douglas (2009) argues, “explanations are the means that help us think our way through to the next testable prediction.” Prediction, therefore, is a second goal in science, but one that brings with it a new class of wildcards (Table 2, Fig. 2B).

#### *Wildcards in integrating across biological levels of organization (B1 wildcards)*

Biologists study different levels of biological organization, often with the expectation that knowledge at one level of organization will inform responses at other levels. However, the linking of responses at multiple levels may be fraught with wildcards.

*Biological levels differ in critical points.*—Biological levels can differ in their climate thresholds. A particular climate shift can have nonlethal and monotonic effects on organism performance but, by subtly shifting the balance between birth and death rates, can tip a population over the threshold from viable (stable or increasing

population) to declining (Kroeker et al. 2017), or from stable to outbreak dynamics (e.g., insect pests: Estay et al. 2009). For example, the vital rates (growth, survival, reproduction) of individual tundra plants each respond differently to temperature clines. When these three vital rates are integrated to estimate population growth rates, though, a new pattern emerges: relative insensitivity of population growth rates to moderate differences in temperature through counterbalancing effects on vital rates (termed “demographic compensation”; see Example 2 in Fig. 3 for more details), but rapid declines in populations at temperature extremes—potentially leading to sudden shifts in the geographic range of these plants (Doak and Morris 2010). Such a breakdown in demographic compensation is already being seen for a different species—monkeyflowers—because of recent droughts (Sheth and Angert 2018). The take-home message here is that responses that seem smooth and predictable at one level may actually have dramatic implications for higher-level system stability.

*Emergent constraints of higher-level systems.*—Biological systems often have emergent properties, such that the whole is not equal to the sum of the parts. Such emergent properties can either dissipate or compound the transmission of climate effects between biological levels. We consider two examples of emergent constraints, the first extending from physiology to population growth, the second extending from pairwise species interactions to ecological networks.

For the first example, consider the process of extending an estimate of organismal critical temperature to predictions of population growth rates. Even if we have determined the physiological response to temperature for each life stage of the organism, we still may not be able to determine the population response if we lack information on how each life stage affects population dynamics (van de Pol et al. 2010), how organism behaviour can offset thermal stress (Example 4 in Fig. 3; Schreffers et al. 2014), or how predator presence can increase the thermal exposure of species (Harley 2011).

Another example of an emergent constraint arises when the effects of climate on the stability of pairwise species interactions are found to be insufficient for predicting how climate affects the stability of networks of interacting species. Because of higher-order interactions in networks, there are emergent stability criteria that specifically apply to the network as a whole (Levine et al. 2017); for example, complex networks can often only persist if most species interactions are weak (McCann et al. 1998) and if certain species colonize before others (Fukami 2015). Furthermore, uncertainties in interaction strengths compound. When species are coupled in ecological networks of realistic sizes (>25 species), correctly determining whether a species will increase or decrease in response to a perturbation requires an impossible level of precision for each interaction strength (Novak et al. 2011).

TABLE 2. Wildcards in moving from understanding to prediction occur at all biological levels, from organisms to ecosystems.

Wildcard type	Wildcard subtype	Organism	Population	Community	Ecosystem
B1. Integrating across biological levels of organization	Biological levels differ in critical points	Increased temperature increases energy demands but decreases energy production, leading to threshold effects on organismal performance (Schulte et al. 2011)	Gradual changes in vital rates in response to climate change can lead to threshold effects on population persistence (Kroeker et al. 2017) or regulation (Estay et al. 2009)	Gradual changes in species phenology, if different between interacting species, may lead dramatic changes in trophic dynamics (Winder and Schindler 2004)	Individual communities may appear resistant to climate change, but a perturbation could cause the entire ecosystem to flip between states (Sternberg 2001)
	Emergent constraints of higher-level systems	Whole organism physiological responses to climate stress are not well predicted by enzyme kinetics because of multiple controls and emergent constraints on metabolic networks (Ruoff et al. 2007, Schulte et al. 2011)	Population responses to climate may not be predictable from organismal physiology when vital rates are instead constrained by species interactions (Harley 2011)	Responses of ecological networks to climate stress may not be predictable from pairwise species interactions, due to intransitive and higher-order interactions (Levine et al. 2017)	Ecosystem responses depend not only on species responses, but also effects of biotic–abiotic feedbacks on resilience (Johnstone et al. 2016)
B2. Generalizing from specific systems	Historical or geographic contingency	Prior events in life of an organism (e.g., developmental plasticity) or its ancestors (maternal, transgenerational effects) can affect its response to climate (Love et al. 2013, Vargas et al. 2017)	Historical demographic events (e.g., bottlenecks, introgression, selective sweeps) influence standing genetic variation and therefore adaptive potential (Pujol and Pannell 2008)	Historical effects of assembly order (Clements et al. 2013), past filtering of the species pool (Hawkes and Keitt 2015) affect community response to climate change	History of previous disturbance (Kröel-Dulay et al. 2015) or successional states (Johnstone et al. 2010) affect ecosystem response to climate change
	Limitations to inference associated with the grain of analysis	Climate stressor effects will differ between individuals due to differences in underlying genes or traits (Latimer et al. 2011)	Climate stressor effects will differ between populations of the same species, for example because of differences in underlying age structure (Coulson et al. 2001) or genotypes (Garzon et al. 2019)	Climate stressor effects on communities depends not only on interactions within communities but also dispersal between communities (Thompson and Gonzalez 2017)	Climate stressor effects on ecosystem depends on asymmetry in the sensitivities of interacting species (Gilbert et al. 2014)

Note: Wildcard types and subtypes refer to categories illustrated in Fig. 2 and described in the text.

#### *Wildcards in generalizing from specific systems (B2 wildcards)*

Although individual experiments and surveys contribute to our understanding of particular systems, the diversity of biological systems far outstrips our capacity for study. Therefore, a necessary goal in climate change biology is to extract generalities from individual studies. However, a number of unexpected obstacles can arise when attempting to apply specific models across different contexts. Context dependence arises where the response of a system depends on the state or identity of the organism (e.g., variation between corals in bleaching resistance; Fig. 4 and Box 1), or on the condition of the

environment in terms of time (historical contingency) or space (geographic contingency).

*Historical contingency.*—Historical contingency, the effect of past events on current dynamics, has been cast as the enemy of generalization in ecology (Lawton 1999). At the organismal level, the response of an individual to a climate stressor can be influenced by maternal and epigenetic effects as well as previous exposure (Putnam and Gates 2015, Vargas et al. 2017). At the population level, past demographic events such as bottlenecks, introgression history, and selective sweeps will influence standing genetic variation and potential for adaptation (Alberto et al. 2013). Phylogenetic history

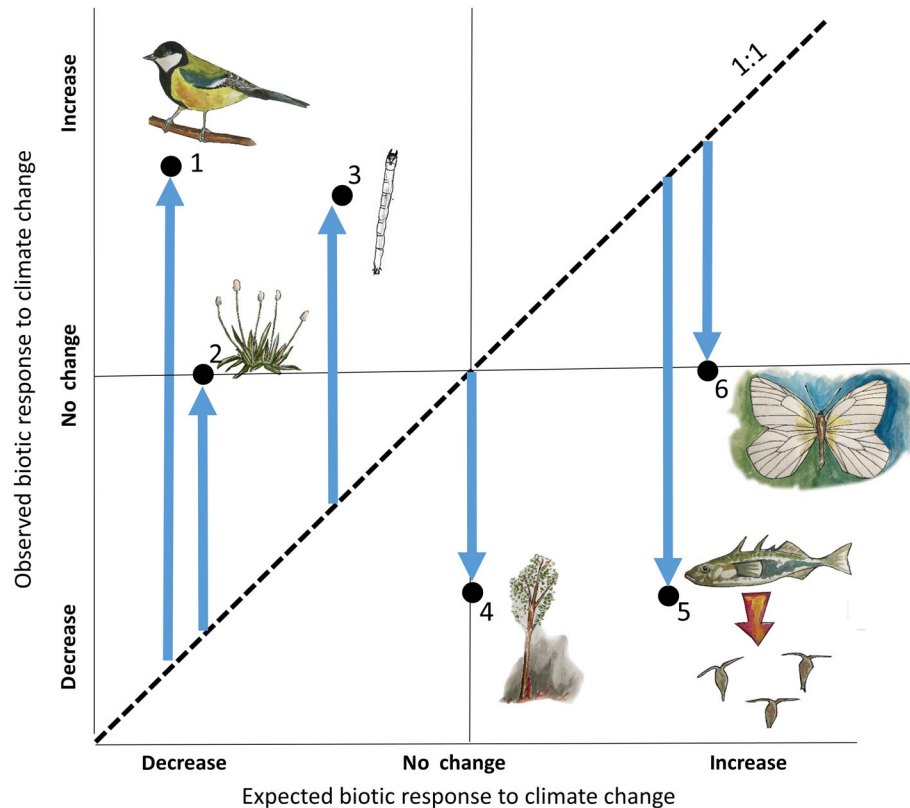


FIG. 3. Wildcard processes cause unexpected and large deviations from the expected biotic effects of climate change (blue arrows). The dashed 1:1 line represents a world without wildcards, where observed biotic effects of climate change are close to expected effects. We illustrate the concept of wildcards here with six examples of qualitative deviations between observed and expected responses to real or simulated climate change. **(1) Wildcard C4: timing of buffering processes.** It is expected that the reproductive success of the Great Tit (*Parus major*) would decline in response to recent warming, as birds cannot rapidly evolve earlier egg hatch times to match the earlier emergence of caterpillars. In actuality, phenotypic plasticity in United Kingdom populations allowed individuals to change the timing of breeding in sync with altered resource supplies, allowing for an observed increase in reproductive success. (Charmantier et al. 2008). **(2) Wildcard B1: biological levels differ in critical points.** In response to recent warming, populations of cold-adapted plants like American Bistort (*Bistorta bistortoides*) are expected to contract at southern range edges, given that adult and seed survival is highest at northern range edges. However, because these effects on survival are counterbalanced by opposite effects on vegetative growth and fecundity, there is currently no difference in population growth rates (i.e., the net effect of survival, growth, and fecundity) between northern and southern range edges. (Doak and Morris, 2010). **(3) Wildcard A2: interaction between responses.** The aquatic larvae of craneflies (Tipulidae) that live in Costa Rican bromeliads are expected to have reduced survival under drought, based on individual assays. However, in a complete community, tipulids are observed to have increased survival following drought because they can become facultative predators at low water levels (Amundrud et al. 2019). **(4) Wildcard C4: timing of state transitions.** Mountain ash (*Eucalyptus regnans*) forests are expected to regrow following drought-induced wildfires in Australia. However, because younger stands are more fire prone, a positive feedback ensues that favors a transition to wattle (*Acacia* spp.) forests (Lindenmayer et al. 2011). **(5) Wildcard B2: geographic contingency.** Experimental warming is expected to increase the effects of predators on their prey, based on studies conducted at colder latitudes. However, the opposite effect is observed in experiments conducted at warm latitudes, perhaps because of a latitudinal shift in the breadth of thermal tolerances (Marino et al. 2018). **(6) Wildcard B1: emergent constraints of higher-level systems.** The black-veined white butterfly (*Aporia crataegi*) is expected to respond to climate warming by shifting upslope, based on the physiological sensitivity of eggs and larvae to warming. However, such an upslope shift is not observed because its host plants are restricted to lower elevations (Merrill et al. 2008).

may also constrain modern adaptation; for example, photosynthetic innovations that allowed some plant taxa to thrive during the low atmospheric CO<sub>2</sub> of cooling phases of glacial cycles may now hinder their adaptation to increasing CO<sub>2</sub> concentrations (Becklin et al. 2016). At the community level, effects of climate change on any particular community can be strongly influenced by historical processes of speciation and colonization (Thompson and Shurin 2012, Clements et al. 2013), and filtering

and selection by past environmental conditions (Hawkes and Keitt 2015). Similarly, shifts in ecosystem state or productivity can depend on antecedent conditions (Johnstone et al. 2010, Sala et al. 2012, Kröel-Dulay et al. 2015). For example, the legacy effects of drought or wildfire can determine the effects of future climate-related disturbance (Kaisermann et al. 2017, Miller and Safford 2020). Such dependence on historical conditions can mean that spatial patterns can give misleading





FIG. 4. After a heat stress event in Fiji, healthy and bleached *Acropora* sp. coral were observed in close proximity, pointing to strong variation in the stress response of coral holobionts. Photo credit: Simon Donner.

predictions if extrapolated to temporal patterns without consideration of legacy effects (Sala et al. 2012).

**Geographic contingency.**—Climate change is a global phenomenon, yet the biotic responses to climate change may be very different in different parts of the world. One reason for this is that climate projections are themselves geographically variable (Loarie et al. 2009)—for example, precipitation will intensify in some areas and decline in others—as are the topological and land-use features that modify the effects of climate (Holmgren et al. 2013). When multiple climate variables are considered, such geographic variation can become much more complex. In the Sierra Nevada Mountains, increased precipitation has tended to shift the elevation range of bird species downslope, whereas warming temperatures have pulled species upslope. The net effect of these forces depends both on how local topography affects temperature vs. precipitation, and which climate factors limit which species (Tingley et al. 2012). Consequently, although 84% of bird species have shown an elevation shift over the last century, this shift is evenly divided between movement downslope and upslope (Tingley et al. 2012). Change in even a single climatic variable includes multiple components (e.g., mean and variance). Amongst ectotherms, midlatitude species show the strongest response to anticipated changes in the mean and variance of temperature because of synergistic effects of these two aspects of temperature on physiological responses (Vasseur et al. 2014). Such a mechanism

may help explain why simulated warming increases predator control of prey at cold, seasonal latitudes but has the opposite effect at warm, nonseasonal latitudes (Example 5 in Fig. 3).

Geographic contingency also occurs because the species pool differs between sites. Although some sites may contain taxa resistant to a climate stressor, such taxa may be missing from other sites if the taxa are dispersal limited or have been extirpated (e.g., via demographic drift, environmental filtering, or biotic exclusion). Such geographic turnover in species can also alter the covariance between functional response traits (i.e., those determining species response to environment) and functional effect traits (i.e., those determining effects of species on the food web and ecosystem). As we show in our case study on bromeliad food webs (Fig. 5 and Box 2), this can result in geographic contingency in the effects of a climate stressor on the functioning of a food web.

**Limitations to inference associated with the biological grain of analysis.**—When biotic response to climate change is studied at a level that aggregates the responses of individual components of the system, failure to model these individual components can result in misleading predictions of the aggregate response. The “biological grain” of a model refers to the level of data aggregation over hierarchical biological units (e.g., cells, individuals, populations, species, etc.). Although there is always a trade-off between model complexity and model

**BOX 1. Case study: Coral reefs and global warming (Type C wildcards)**

Questions about the fate of coral reefs on a warming planet lie at the heart of most coral reef research today. Periods of anomalously warm ocean temperatures have led to widespread episodes of coral bleaching, that is, a loss of color from the reef-building animals due to a breakdown of symbiosis with colourful dinoflagellate *Symbiodinium*.

The response of individual coral species to temperature anomalies has been modeled from field data on coral traits (Kubicek et al. 2019) or genetic variation (Bay et al. 2017), but the results of such models may not apply beyond the specific coral population from which the data were collected, creating a Type B2 wildcard. The variance of coral holobiont response (Fig. 4) to heat stress leads to trade-offs between model complexity and model scalability. In order to make general predictions, it is necessary to coarse-grain the problem by using universal, taxa-independent thresholds for coral response to temperature combined with the simulated frequency of bleaching conditions. Such threshold-based models can be applied globally but are limited to projecting undefined “loss” or “degradation” of coral reefs and the rate of adaptation necessary to avoid such degradation (Donner et al. 2005). These coral-climate models to date project the majority of the world’s coral reefs to degrade this century due to frequent bleaching and associated mortality under even moderate emissions scenarios (Donner et al. 2005, Hoegh-Guldberg et al. 2018).

Researchers developing coral-climate models also encounter Type C1 wildcards when attempting to forecast climate variability accurately as well as characterize the variation in coral and holobiont response to this climate variability. Because bleaching is a response to ocean temperature extremes, future coral reef projections are limited by the ability of climate models to capture the frequency, magnitude, and geography of key modes of variability like the El Niño/Southern Oscillation. This uncertainty can be reduced through careful climate model selection and bias-correcting model output (Logan et al. 2013). Similarly, hydrodynamic modeling can also be used to capture fine-scale heterogeneity of coral reef thermal experience, like local upwelling or topographic shading, but requires high-resolution field data and heavy computation even for an individual atoll. Addressing these types of wildcards requires coral ecologists to partner with climate scientists experienced in climate model analysis.

Bleaching-related mortality can result in a rapid shift to another ecosystem state, often dominated by algae, which can be difficult to reverse. This nonlinearity creates Type C2 wildcards. Such phase shifts are expected to occur as ocean temperatures continue to rise, but depend on the ability of corals and symbionts to adapt. The potential of adaptation and dispersal to slow such transitions is difficult to model, creating Type C4 wildcards. However, broader ecological–evolutionary models (Baskett et al. 2010, Walsworth et al. 2019) have been able to capture aspects of coral and symbiont population dynamics, potential adaptive mechanisms (e.g., shuffling to more temperature tolerant symbionts; evolution of symbiont thermal tolerance), and larval connectivity. The caveat is that no model yet captures all these processes, let alone fine-scale hydrodynamics or effect on fish or other coral-dependent organisms. Because of data and computational limitations, the newer models simulate a limited number (i.e., 2–3) of theoretical coral species and only one (i.e., macroalgae cover) of the many alternative reef states noted in reality. These and more advanced approaches are unlikely to change the dire forecast for the world’s coral reefs in high warming scenarios. However, they may prove more effective at identifying potential refugia and management strategies than the initial threshold-based models.

precision, in some cases models may be unexpectedly sensitive to the biological grain of analysis: a wildcard. For example, the distribution of a species may be composed of populations that vary genetically in their climate niches (Sinclair et al. 2012) or show phenotypic plasticity (Garzon et al. 2019). When distribution models of a plant species are generated from thermal tolerances of individual populations projected on future climate, the species can be predicted to occur in different areas than if it is modelled at the species level (Angert et al. 2011, Garzon et al. 2019). Even when researchers are able to make short-term predictions of aggregate responses without considering the underlying components, any change in the representation of the components can invalidate the prediction. For instance,

changes in the initial age and sex structure of an island population of sheep can lead to opposing predictions of the effects of winter weather on population dynamics (Coulson et al. 2001).

**WILDCARDS IN EXTENDING PREDICTIVE MODELS TO FORECAST BIOCLIMATE DYNAMICS (TYPE C WILDCARDS)**

If a suitable model of how a biological system responds to climate has been created and validated, the next step is to use the model to project future states of the system. Such projections require the combination of two different sets of models, one that projects the expected climate in the future, and the other that predicts the biological response to any specific climate

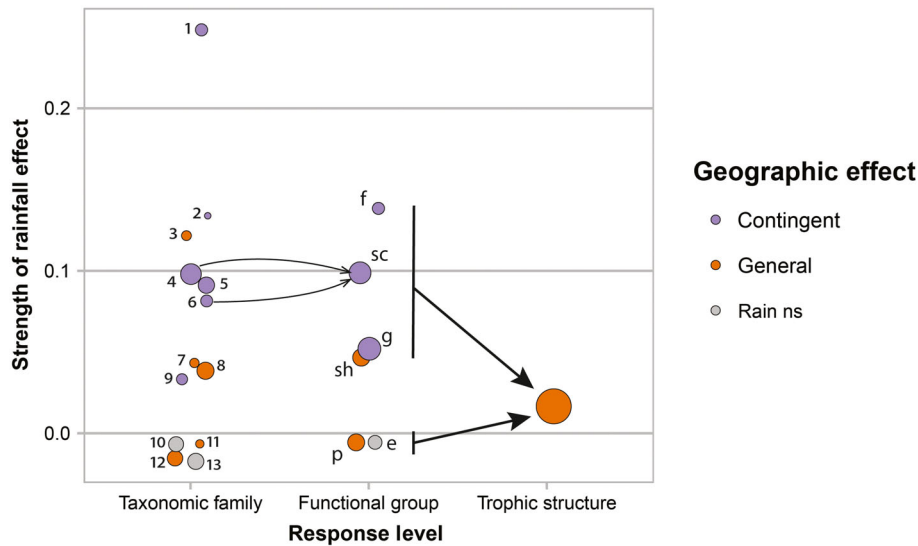


FIG. 5. In a globally distributed experiment (with bromeliad invertebrates; see Box 2), the response of the community to rainfall change in multiple countries could be either geographically “contingent” (i.e., changes between sites), “general” (i.e., similar between sites) or “ns” (nonsignificant). The response of the community in terms of biomass could be determined at the level of taxonomic families (different families indicated by numbers), or taxa could be pooled, as exemplified by the curved arrows, into functional groups (different groups indicated by letter codes). Functional groups could be pooled, as indicated by straight arrows, into predator and prey trophic levels, and the ratio of predator to prey biomass used as a metric of trophic structure. The size of the circles is proportional to mean biomass per bromeliad for each category of response. Taxonomic number codes: 1 = Culicidae; 2 = Empididae; 3 = Corethrellidae; 4 = Scirtidae; 5 = Chironomidae; 6 = Limnocytheridae; 7 = Ceratopogonidae; 8 = Tipulidae and Limoniidae; 9 = Coenagrionidae; 10 = largely Naididae in Oligochaeta; 11 = Psychodidae; 12 = Syrphidae; 13 = Tabanidae. Functional group letter codes: f = filter feeders; sc = scrapers; g = gatherers; sh = shredders; e = engulfing predator; p = piercing predators.

condition. It is at this interface between biology and climate that a host of new wildcards emerges (Table 3, Fig. 2C).

#### *Wildcards from compounding biological and climate uncertainties (C1 wildcards)*

Because both biological and climatological models have uncertainty, these uncertainties can compound, potentially creating bioclimatic predictions with such large confidence intervals as to be unhelpful. Unfortunately, the reliability of climate forecasts is lowest at the small spatial scales relevant to many biological processes, such as species interactions, population dynamics, and local adaptation (Lawler et al. 2010).

Models of future climates forecast changes not only in mean conditions but also in the variation around the mean, such that the frequency of climate events considered extreme by today’s standards will increase, and new extreme records will continue to be set (Hansen et al. 2012). Even when the trajectories of some community and ecosystem responses to extreme events are predictable (e.g., from functional traits of species: Boucek and Rehage 2014), the timing and rate at which state shifts take place can be highly unpredictable for two reasons. First, extreme climate events (e.g., heat waves, windstorms; Smith 2011), or extreme disturbances triggered by climate (fire, floods,

drought), are highly variable in frequency, intensity, and duration over space and time, rendering them difficult to predict even weeks in advance (Steinkamp and Hickler 2015). Second, extreme events can change the internal dynamics of biological systems. Extreme climate conditions can erode the resilience of ecosystems to other perturbations (Scheffer et al. 2001, Sternberg 2001) including invasions (Jimenez et al. 2011), making successional trajectories less predictable (Kreyling et al. 2011). As extreme climatic events are, by definition, rare, the paradoxical situation exists that potentially the most important empirical data are the least available—creating prime conditions for wildcards.

#### *Wildcards from combining biological nonlinearity with climate variation (C2 wildcards)*

Nonlinear responses to climate stressors are common, characterizing biological responses from the fitness of individuals (Wingfield et al. 2017) to the stability of ecosystems (Burkett et al. 2005). Although some of the best characterized nonlinear responses are the effects of temperature on metabolic rates such as respiration and photosynthesis (Angilletta 2009), similar nonlinear metabolic responses are known for other climate-related factors, such as soil moisture (Green et al. 2019) and ocean acidity (Gao et al. 2019).

**BOX 2. Case study: A distributed experiment helps unravel geographic contingency (Wildcard B2)**

One of the thorniest wildcards is geographic contingency, where spatial difference in either the organisms or the abiotic environment prevents generalizing results from one site to other sites. Although comparisons of different studies conducted at different sites can suggest geographic contingency, it is often difficult to exclude the potential effect of methodological differences between studies. A more robust method is a distributed experiment in which a co-ordinated network of researchers uses a common protocol to conduct the same manipulation at different sites. There have been surprisingly few distributed experiments in climate change biology, and most have focused largely on the plant community - presumably because of the logistic challenges in imposing manipulations on an entire food web over multiple sites.

The aquatic food webs in bromeliads offer a useful system for distributed experiments. Water-holding bromeliad plants are distributed throughout the Neotropics, from Argentina to Florida, and contain rich communities of macroinvertebrates (largely insect larvae), protozoa and microorganisms. Members of the Bromeliad Working Group manipulated the rain entering bromeliads, relative to site-specific ambient conditions, in seven field sites in South America, Central America, and the Caribbean (Romero et al. 2020, Srivastava et al. 2020).

The response of the macroinvertebrates to the rainfall manipulation can be summarized with varying levels of aggregation (Fig. 5), starting with the detailed resolution of taxonomic families, which can be aggregated into functional feeding groups, which can further be summarized as a single metric of predator-prey mass ratios. Both the generality and strength of responses change with the level of aggregation. Macroinvertebrate families differed substantially in the strength of their response to rainfall manipulations, with pelagic taxa like mosquito (Culicidae, taxonomic family = 1 in Fig. 5) larvae amongst the most sensitive. However, only a few families showed geographically general responses as the effects of rainfall on organisms were mediated by site-specific hydrological characteristics of bromeliads. In addition, there was strong spatial turnover in family composition, with as few as 32% of macroinvertebrate families in common between sites, further preventing the application of results of one site to other sites. Aggregating families by functional feeding group (i.e., function effect traits) provides a more universal characterization of the functional impact of the macroinvertebrate community. This does not reduce geographic contingency, however, because the taxonomic families that compose certain feeding groups can still differ between sites and this turnover can drive differences in the hydrologic sensitivity (i.e., function response traits) of the entire feeding group (Srivastava et al. 2020). However, detritivore feeding groups were overall more sensitive than predator feeding groups, so when the data are aggregated as the ratio of predator to detritivore biomass there was a geographically general response to rainfall (Romero et al. 2020). This ratio, commonly called the predator-prey mass ratio, was higher in all sites when rainfall became more uneven between days. In summary, these results demonstrate that our ability to generalize from the results of experiments may depend on the ecological response.

When a change in the frequency distribution of climate conditions is combined with nonlinearities in the biological response to climate, there is potential for rapid shifts in biological states. For example, organisms currently living close to their thermal optima are particularly vulnerable to fluctuations in temperature, as their critical limits will be exceeded more frequently (Rummer et al. 2014). Similarly, at the ecosystem level, increases in the variance and temporal autocorrelation of climate drivers, even when the mean is held constant, can erode the resilience of ecosystems, resulting in state shifts (Cueto-Felgueroso et al. 2015, van der Bolt et al. 2018) —as exemplified by coral bleaching (see Box 1).

Furthermore, when nonlinear biological responses to climate are combined with variation in climate, organisms can show different integrated performance than expected based on the mean environment, an example of Jensen's inequality (Denny 2017). For example, including temperature variation in projections of where mean temperature increase will have the greatest effect on ectotherm performance can substantially shift

latitudinal patterns (Vasseur et al. 2014). Organisms also show nonlinear responses to precipitation-related conditions, as exemplified by plant photosynthesis being much more sensitive to decreases than increases in soil moisture relative to mean conditions. This particular nonlinear relationship, when considered at the ecosystem level, results in between-year variation in precipitation reducing the overall ability of terrestrial biomes to serve as carbon sinks, again through Jensen's inequality (Green et al. 2019).

Although these combinations of biological nonlinearities with climatic variation have the potential to result in wildcards, there are promising ways forward. First, although irreducible stochasticity in climate may prevent us from predicting exactly when a state-changing climatic event will occur, we can be more successful if we reframe the question as the likelihood of such an event occurring within a window of time (e.g., threshold-based models of coral reefs; see Box 1). Second, by understanding the conditions under which Jensen's inequality can potentially influence bioclimatic model predictions,

TABLE 3. Wildcards in extending predictive models to forecast bioclimatic dynamics occur at all biological levels, from organisms to ecosystems.

Wildcard type	Wildcard subtype	Organism	Population	Community	Ecosystem
C1. Compounding uncertainty from climate models		Extreme climate events are difficult to forecast yet have the most impact on survival (Vasseur et al. 2014)	Extreme climate events are difficult to forecast but have high impact on population dynamics (black swan events: Anderson et al. 2017)	Extreme climate events can disrupt deterministic community assembly and permit invasions (Jimenez et al. 2011, Kreyling et al. 2011)	Extreme climate conditions increase likelihood of ecosystem altering via inherently unpredictable disturbances (fire, floods, drought)
C2. Combining biological nonlinearity with climatic variation		Temperature variation affects organism performance due to the nonlinearity in thermal performance curves (Vasseur et al. 2014), leading to poor prediction of fundamental niche (Woodin et al. 2013)	Temperature variation reduces population growth due to nonlinear averaging of thermal performance curves (Bernhardt et al. 2018). Temperature autocorrelation combines with exponential population growth to promote population persistence (Gonzalez and Holt 2002)	Temperature variation can combine with nonlinear responses of predators to prey densities to cause unstable predator-prey dynamics (Uszko et al. 2017)	Stochastic fluctuations of climate variables in combination with nonlinear responses of ecosystems (e.g., hysteresis), can result in ecosystem regime shifts (Cueto-Felgueroso et al. 2015)
C3. Novel areas of climatic or biotic parameter space		Climate-induced shifts of organisms into novel habitats can lead to unexpected behaviors (Cannizzo and Griffen 2016)	Novel climate space can result in range loss or expansion with unknown capacity for adaptation (Coristine and Kerr 2015)	Novel co-occurrences or abiotic environments of species can lead to difficult-to-predict community dynamics (Menendez et al. 2008, van Grunsven et al. 2010)	Novel ecosystems, resulting from climate-induced extinctions, invasions or habitat modification, may have difficult-to-predict properties (Hobbs et al. 2006)
C4. Timing of buffering and rescue processes, state transitions:	Timing in state transitions	Physiological state transitions reflect of homeostatic mechanisms (weakening negative feedbacks) combined with increased susceptibility to further stress (positive feedback)	Population viability transitions (Fagan and Holmes 2006) reflect the breakdown of compensatory, density-dependent responses (weakening negative feedbacks) combined with negative genetic and demographic consequences of declining population sizes (positive feedbacks)	Community state transitions occur when climate change allows prey to escape regulation by natural enemies (weakened negative feedbacks, e.g., van Grunsven et al. 2007), and loss of particular species increases the likelihood of further species turnover (Simberloff and Von Holle 1999, Colwell et al. 2012)	Ecosystem state transitions occur when climate change erodes resilience of ecosystems to disturbance, through loss of resistant traits or a change in the abiotic template (Johnstone et al. 2016) reinforced by positive feedbacks between disturbance and ecosystem properties (Lindenmayer et al. 2011)
	Timing of buffering or rescue processes	Uncertainty in organismal responses to climate due to uncertain timeframe for behavioral innovations	Population viability or ranges difficult to predict because of uncertain timing of rescue through evolution or migration (Dullinger et al. 2012)	Uncertain timing of community change reflects lags in species loss (extinction debts), species gain (immigration credits), or species niche shifts (evolutionary rescue)	Uncertain timing of ecosystem change reflects cumulative and connected lags in components, from individuals to populations to communities (Essl et al. 2015)

Note: Wildcard types and subtypes refer to categories illustrated in Fig. 2 and described in the text.

we can work towards better incorporation of nonlinear biological responses. For example, when nonlinear biological functions are based on empirical patterns without an underlying mechanistic model, projections may be highly variable between models—as is the case for bioclimatic models of global productivity that ignore the biomechanics of how soil water affects plant productivity (Trugman et al. 2018).

*Wildcards from novel areas of climate or biotic parameter space (C3 wildcards)*

Another suite of wildcards arises when biological systems enter novel areas of parameter space. Models of long-term climate impacts on biological systems can only be parameterized for current conditions, or in some cases past conditions, creating a problem for predicting biological responses to any future climate conditions (or associated extreme events) outside these bounds. By the year 2100, about 4–39% (depending on projected climate scenario) of the world’s land area will experience a “novel” climate, that is, a climate that does not currently occur anywhere in the world (Williams et al. 2007, Mahony et al. 2017). Species distribution models based on current conditions can fail to inform future distributions in areas with novel climates (Williams and Jackson 2007). Furthermore, if species differ in their spatial tracking of climate (Freeman and Freeman 2014, Gibson-Reinemer and Rahel 2015), novel assemblages of species may occur that have no present-day analog (Williams and Jackson 2007). Such novel interactions are a wildcard in that we have no prior experience of their dynamics (Carrasco et al. 2018). It could be argued that we may be able to draw some insights from existing theory for introduced species. For example, novel communities may have some dynamics similar to invaded communities, including escape from pathogens and parasitoids (Menendez et al. 2008, van Grunsven et al. 2010), exploitation of naïve host plants (Cudmore et al. 2010), and intensification of competition (Alexander et al. 2015). However, inferences may be limited because invasive species have limited or no shared evolutionary history with native species, unlike near-local species undergoing range shifts.

*Wildcards in dynamic responses to climate change (C4 wildcards)*

Time is a critical dimension of forecasting the effects of climate change. Climate change is an ongoing process that shows temporal progression, and biological responses to climate change are themselves dynamic. To explore dynamic wildcards, we start with the simplifying assumption that most biological systems, regardless of biological level, can often be described by transitions between three states—stasis, altered and rescue—even though not all of these states may be realized in every system and some systems may be in non-equilibrium

dynamics between states (e.g., succession). By “stasis,” we refer to a temporally constant state where negative feedbacks tend to limit dynamic change (recognizing that some systems may always be far from equilibria because of intrinsic chaotic dynamics or externally imposed stochasticity). Once these negative feedbacks are overcome, the system may enter a new “altered” state. However, biotic processes may prevent this altered state from persisting, moving the system to a “rescued” state that approximates the original. We argue that wildcards are particularly likely to emerge at the transitions between these three states.

*Wildcards in the timing of state transitions.*—Biological systems are often characterized by negative feedbacks that reduce the impact of stress or disturbance (Thomas and D’Ari 1990). Examples of such negative feedbacks include homeostatic regulation of physiological processes, density-dependence in population growth, frequency-dependent mechanisms of selection and species coexistence, and reinforcing linkages between vegetation and microclimate. However, other biological systems may already be far from any sort of equilibrium (Guichard and Gouhier 2014). In particular, anthropogenic stressors apart from climate change have created a background of flux for many biological systems (Archer and Stokes 2000).

A change in climate beyond some threshold amount can erode the negative feedbacks that exist in a system, or introduce new positive feedbacks, potentially causing rapid state transitions (Fig. 6). Climate extremes can push organisms beyond the ability of homeostatic mechanisms to regulate body temperature, fluid levels, and chemical composition, and lead to critical states such as heat exhaustion and wilting. When climate change causes populations to contract, the fitness of individuals can decrease (e.g., through failure to find mates or inbreeding depression), which further accelerate rates of population decline, sweeping populations into an “extinction vortex” (Gilpin and Soulé 1986). Positive feedbacks can also occur in terms of species interactions, leading to co-extinctions, where the extinction of one species leads to the extinction of interacting species (Colwell et al. 2012, Schleuning et al. 2016), and invasion meltdowns, where the invasion of a community by one species renders the community more susceptible to invasions by other species (Simberloff and Von Holle 1999). These positive feedbacks can be difficult to anticipate, because of the potential for species interactions to propagate among multiple links, emerging unexpectedly in distant locations (Srivastava and Bell 2009, Levine et al. 2017). Positive feedbacks can also ensure state transitions do not reverse. In southeast Australia, drought-induced fires, in combination with overharvesting, have shifted *Eucalyptus regnans* forests from an old-growth state to a young state. Because young trees burn with greater severity than older trees, intense fires keep the forest in a regenerating state, leading to a climate-

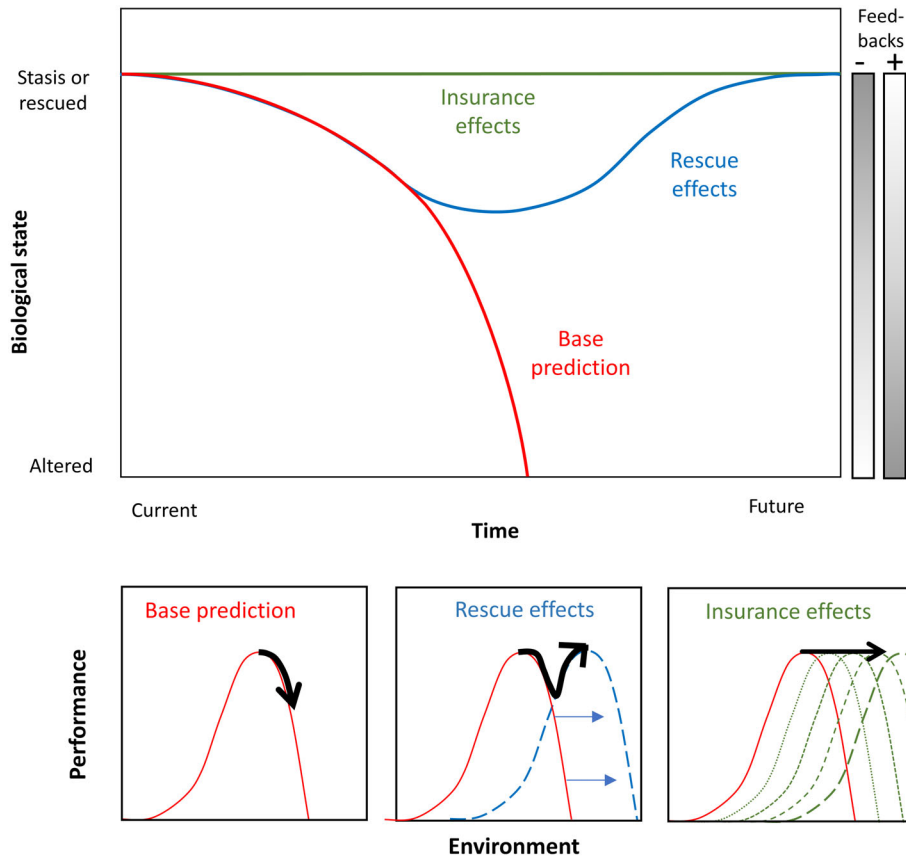


FIG. 6. Biological systems can show a variety of responses to climate change over time (major panel), reflecting how system performance adjusts to a temporally changing environment (minor panels, time reflected by thick black arrows). The “base prediction” is a progressive change in state attributes from a current to altered state as negative (–) feedbacks weaken and/or positive (+) feedbacks strengthen. However, “rescue effects” can allow biological systems to recover by altering (thin blue arrows) the tolerance of the system to environmental conditions. Alternatively, “insurance effects” can buffer effects of climate change when the responses of some system components are offset by other components (dashed and dotted green lines).

induced positive feedback between young forest age and fire severity (Example 4 in Fig. 3: Lindenmayer et al. 2011). Similar climate-induced state changes have been predicted for transitions between tundra and boreal forests (Scheffer et al. 2012) and for coral reefs and benthic macroalgae (Graham et al. 2015).

Although such transitions between states are well-documented in biology, the wildcard arises in predicting the timing of transitions. Timing can be difficult to predict for two key reasons. First, many processes exhibit time lags, meaning that a transition threshold has passed before there is detectable change. Examples of such time-lag phenomena include nonreproductive but long-lived organisms in populations (Pigott and Huntley 1981, Janzen 2001), extinction debts in communities (Dullinger et al. 2012), and functional debts in ecosystems (Isbell et al. 2015), which make it difficult to detect change in population size, species composition and ecosystem functions, respectively. For example, many bioclimatic models have assumed, based on short-term experiments, that C4 grasslands are not affected by

elevated CO<sub>2</sub>, but a long-term experiment shows that effects take over 12 yr to be realized (Reich et al. 2018). Second, when transition thresholds involve the relative effects of multiple processes (e.g., direct effects on reproduction, indirect effects on predation rates), differential effects of climate on each process may be challenging to model (Doak and Morris 2010, Kroeker et al. 2017).

*Wildcards in the timing of buffering or rescue processes.*—Biological systems can be buffered against some of the consequences of climate change when diversity at one biological level creates important redundancy that maintains a higher-level function. Such “insurance effects” (Fig. 6) allow a system to resist change (Yachi and Loreau 1999). For example, genetic and species diversity can help stabilize ecosystem functions such as primary productivity, as long as genotypes or species with similar functional roles differ in their climate sensitivities (Thompson and Shurin 2012). In microbial systems, widespread functional redundancy means that ecosystem-level metabolic functions remain highly

consistent even when community membership is highly variable (Louca et al. 2018). Spatial insurance effects extend this process to a larger spatial scale, in which the regional tracking of environmental change by functionally redundant species facilitates the maintenance of community-level biomass and ecosystem productivity (Loreau et al. 2003, Thompson and Gonzalez 2017). At the organismal level, phenotypic plasticity can be considered an insurance effect, permitting an individual to maintain fitness over a wider range of climate conditions than permitted by any single phenotype (Becklin et al. 2016). For example, individual flexibility in the timing of breeding allow some Great Tit (*Parus major*) populations to track climate change (Example 1 in Fig. 3; Charmantier et al. 2008). The wildcard is whether these buffering processes will be strong enough to prevent a state transition, especially in the context of multiple stressors.

If buffering processes are not able to resist change in the system, then dispersal, evolution, and novel behaviours may still be able to “rescue” a system—even after change has been initiated. Rescue effects (Fig. 6) are an example of system resilience. Long-distance dispersal events may be critical in allowing species to track their climate niche across the world, but are often so rare as to be unsampled—leading to underestimates of migration rates in models (Higgins and Richardson 1999). Like dispersal, evolution has the potential to reverse population decline by generating or increasing the frequency of resistant genotypes within. Such “evolutionary rescue” can occur via de novo mutations, selection acting on standing genetic variation, or gene flow from other populations (Gonzalez et al. 2013). Because both dispersal and evolution involve at least some processes that are irreducibly stochastic (Cain et al. 2000), predicting whether rescue will occur under climate change remains beyond our reach (Carlson et al. 2014). For example, the unpredictability of evolutionary rescue when adequate standing variation is lacking is, in large part, because it is the result of two unlikely phenomena: first, a mutation that increases fitness must arise, and second, that the mutation must sweep through the population rather than be lost to drift while rare (Orr and Unckless 2014). Even in replicate experimental lab populations, some populations experience rescue and others do not (Bell and Gonzalez 2009). A similar argument can be made for dispersal rescue, which requires not only the propagule with the right genotype to disperse to the right spot, but for it to survive and reproduce once it gets there. Thus, evolutionary and dispersal rescue of populations that would otherwise become extinct are high-impact events, but because the timing of their occurrence is very difficult to predict, they are wildcards. Unfortunately, timing is key, as this determines whether the rescue event happens before climate change is able to cause irreversible alterations of the system (e.g., extinction).

A few caveats follow from this dynamic view of dynamic responses. First, climate change will result in

biological winners and losers, so we have intentionally emphasized biotic change rather than change in any particular direction (although some processes like rescue may be inherently directional). Second, although we have laid out phases of stasis, change, and rescue, there is no expectation that any given biological system will experience all of these: Some may never approach equilibrium dynamics, others may simply be insensitive to climate change, and in others rescue may simply not happen fast enough before irreversible change has occurred. Finally, systems will differ in whether transitions between states are gradual or abrupt.

#### RECOMMENDATIONS FOR FUTURE RESEARCH

Here, we have articulated a research framework for climate change biology that links understanding to prediction to forecasting, and have identified specific points along this research arc where wildcards are likely to originate. Going forward, our four key recommendations to identifying and resolving wildcards in climate change biology are as follows.

##### *Begin with integration*

An aim of climate change biology is often to integrate responses from multiple biological levels, such as in the integration of ecophysiological reaction norms into ecosystem bioclimatic models. Because we anticipate wildcards in such vertical integration of responses, we recommend incorporating a multilevel perspective into the planning research programs from the start. When vertical integration occurs early in the research process, it can help determine which components can be safely “black boxed,” where a loss in understanding the variation among individual components is less important than the gain in forecasting accuracy for the whole system. For example, biogeochemical flux rates in a poorly mixed ocean basin can accurately be predicted based on stoichiometry and physiochemical conditions, but without knowledge of the microbial community responsible for these fluxes or reaction kinetics of individual organisms (Louca et al. 2019).

A second recommendation is to facilitate integration between biological levels by using similar currencies. All biological life exists within the constraints imposed by thermodynamics and the conservation of matter. This suggests that general models based on currencies of energy and matter may succeed, even if models based on the specifics of species and allelic identity fail. The metabolic theory of ecology, for instance, uses thermodynamic principles about energy to predict that modest warming should increase metabolic rates (Brown et al. 2004), and has been successfully extended to populations (Bernhardt et al. 2018) and species interactions (O’Connor 2009, Sentis et al. 2015). Similarly, the theory of ecological stoichiometry recognizes that the bodies of organisms must be reassembled from the elements in



their resources, and has been effective in extending elemental constraints from cellular metabolism to organismal growth to species interactions (Hessen et al. 2013). For example, experimental warming results in higher respiration in a number of insect herbivores, necessitating greater carbon intake to meet metabolic requirements (Rosenblatt and Schmitz 2016). This shift affects herbivore interactions with plants, as herbivores will switch their diet from protein-rich plants to carbohydrate-rich plants, as well predator interactions with herbivores, due to the increase in carbon:nutrient ratios of herbivore bodies (Rosenblatt and Schmitz 2016).

Another approach to integrating over biological levels is to find common mechanistic links. Functional traits determine how species interact with their environment and each other, and organisms often show similar trade-offs or covariation between types of traits. Therefore, models explicitly incorporating functional traits generally have broader applicability than those based on species identities (Lavorel and Garnier 2002, Wallenstein and Hall 2012). For example, variation in the response of 50 species of alpine plants to a 2°C increase in mean growing season temperature is well predicted by just four functional traits: species that invest in conserving leaf water and belowground storage responded positively to the warming trend, whereas other species declined (Soudzilovskaia et al. 2013). Such trait-based approaches are also well developed for microbial communities, which show strong functional determinism in terms of the major metabolic pathways (Louca et al. 2016), but are increasingly applied to other taxa, such as birds, where grouping species within functional guilds lends generalizable insight into climate and land-use change responses (Cormont et al. 2011, Zhang et al. 2016).

Models based on universal currencies (elements, energy) and mechanisms (functional traits) have the potential to integrate over multiple biological levels by including fundamental constraints on living systems, yet are still mathematically tractable by blackboxing some of the less influential biological details. For example, the effect of trophic interactions (individual-level process) within food webs (community-level structure) on the carbon cycle (ecosystem-level response) can be modeled by abstracting the interactions in terms of consumer and resource traits and elemental ratios (Schmitz and Leroux 2020). Key to using these abstractions is identifying when it is suitable to combine similar components into functional groups or energy channels, and when they should be kept separate. For example, while ignoring species identity removes the possibility of applying models to conservation of individual species, it enables prediction of system-wide functions. Considerable scope remains to identify and validate new ways of blackboxing processes or components and to develop best practices to apply this approach across biological scales and for specific questions.

### *Mind the gaps and understand contingencies*

We must not only anticipate wildcards, but also detect them. A critical component of our research framework is the comparison of model outputs with empirical data to test and refine each step in the process (“verification,” “validation,” and “monitoring” in Fig. 2). For example, the FACE experiment—which examined forest response to elevated CO<sub>2</sub>—has been used at the model verification step to isolate which model assumptions improve the ability of models to predict empirical results (Medlyn et al. 2015). An important step in generalizing a model is validation: the comparison of model predictions under new conditions (e.g., a new site) with known responses (Fig. 2). For example, experimental results can also be compared with observed patterns in intact, natural systems, to ensure that the mechanisms extend beyond the simplified conditions of experiments (e.g., Amundrud and Srivastava, 2019). Failure at the validation step suggests that the model should be revised to include more context-specific variables or be formulated at a different biological grain (Douglas 2009).

Wildcards can be identified when observations fail to match expectations, such as when contingencies arise. Here we can harness the power of studies replicated across geographic space (e.g., Box 2), studies that use historical data or long-term and extensive monitoring in one location, or meta-analyses of such studies. For example, geographic variance in the response of European shrublands to simulated climate change can be explained by disturbance history, pointing to a need to include anthropogenic disturbance in climate change biology explicitly (Kröel-Dulay et al. 2015). Considerable scope remains for determining the prevalence of contingency using geographical replication of experiments, as most have manipulated climate stressors in plant communities (Walker et al. 2006, Tielbörger et al. 2014, Knapp et al. 2017). As our bromeliad case study demonstrates (Box 2), geographically distributed experiments may be particularly useful in determining which responses are general over space and why. Shifting the analysis to trait or energetics-based responses (e.g., Fig. 5) can provide a way forward when contingency is due to differences in species identity and may lead to the discovery of general patterns (Walker et al. 2006, Romero et al. 2020). When geographically distributed experiments are not practical, meta-analysis of individual studies can be informative. However, we caution that geographic and taxonomic biases are prevalent in climate change biology, often resulting in sparse data for tropical biomes (Marino et al. 2018, Srivastava et al. 2020) and for animal and microbial communities (Cavicchioli et al. 2019). Reporting nonsignificant results or those that may not necessarily fit the prevailing narrative is also critical to generating insights about why certain processes are important in some systems but not others, and will improve the accuracy of meta-analyses.

*Incorporate climate modeling*

Climatologists and biologists rarely collaborate; we need to. To date, both researchers and funding agencies have been slow to embrace tackling questions in climate change biology with teams of multidisciplinary researchers focused on a specific system. Recent advances in modeling extreme climate events have been made possible by improved resolution and better incorporation of physical processes, but biologists have been slow to incorporate these predictions in experiments (Thompson et al. 2013). One potential method is the downscaling of general circulation models to create multiple replicate runs of weather scenarios that can be incorporated in experiments (Thompson et al. 2013). Other methods involve creating orthogonal gradients of climate mean, variance, and extremes within experiments (Kreyling et al. 2014) and model simulations (Rypkema et al. 2019), or characterizing the climate signatures of extreme years for experimental simulation (Knapp et al. 2015). Related, but equally important, is for biologists to develop standardized definitions of climate extremes (e.g., what constitutes a drought; Slette et al. 2019) and to include these definitions in their research. We suggest communicating with climatologists to keep these definitions consistent as a way forward.

*Reframe and communicate uncertainty*

Climate change biology could make headway by formalizing sources of uncertainty. One useful categorization of uncertainty (Spiegelhalter and Riesch 2011) separates uncertainty within models (stochastic events, imprecise parameters, and limited knowledge of model structure) from uncertainty external to models (indeterminacy, unknown limits to knowledge). Climate change wildcards potentially incorporate all these types of uncertainty, but once the source of uncertainty is known, it becomes apparent whether useful progress can be made by further research or only by better communication of the range of potential scenarios or relative risks.

Uncertainty is a given in many areas of science, and climate change biology could learn from other fields that have carefully considered how to incorporate uncertainty in models, and how to communicate the consequences of this uncertainty to the public. In meteorology, the accuracy of a weather forecast declines with time from the present; the forecast horizon defines how far away a forecast can be made before its level of inaccuracy becomes unacceptable. It has been suggested that a similar ecological forecast horizon could be used for populations and communities (Petchey et al. 2015) and this idea could be extended further to genes, individuals, and ecosystems. Depending on the desired forecast horizon, biologists could change the relative weight of information, for example, emphasizing time series for shorter forecast horizons and space-for-time approaches for longer forecast horizons (Adler et al. 2020).

Expressing uncertainty does not give decision makers license for inaction but instead provides the opportunity to take a precautionary approach to climate mitigation strategies.

## CONCLUSIONS

There is no escaping the wildcards in climate change biology. Although we have argued that wildcards may occur at every step in the scientific process, this does not mean that it will be impossible to forecast the future effects of climate change on biological systems. We intentionally used the analogy of wildcards in our framework, drawing on the popular understanding of wildcards in a card game as both unpredictable and potentially game changing. However, unlike players in a game of cards, climate change biologists do not have the luxury of folding. Instead, we must develop strategies to deal with the inevitable wildcards. Here, we have articulated a research framework for climate change biology that links understanding to predictions to forecasts, and have identified specific points along this research arc where wildcards are likely to originate. Our catalogue of wildcard commonalities provides a guide to anticipating wildcards at different biological levels. By focusing intensive research on these stress points, climate change biology can reduce uncertainty, anticipate contingencies, and better communicate the limitations of our knowledge.

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