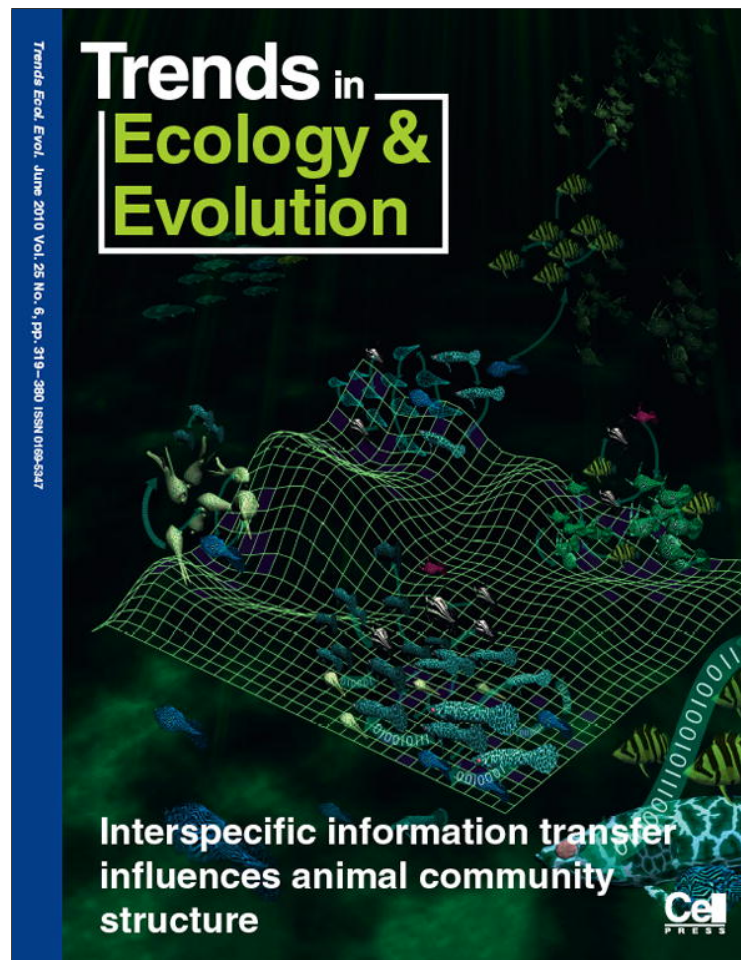


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A framework for community interactions under climate change

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Predicting the impacts of climate change on species is one of the biggest challenges that ecologists face. Predictions routinely focus on the direct effects of climate change on individual species, yet interactions between species can strongly influence how climate change affects organisms at every scale by altering their individual fitness, geographic ranges and the structure and dynamics of their community. Failure to incorporate these interactions limits the ability to predict responses of species to climate change. We propose a framework based on ideas from global-change biology, community ecology, and invasion biology that uses community modules to assess how species interactions shape responses to climate change.

Climate change and species interactions

Global climate change affects natural [1,2] and human-modified [3,4] environments, and is progressing faster than previously recorded [5]. Predicting and ameliorating the consequences of climate change presents a major challenge for ecologists, but we have largely failed to generate comprehensive predictions or clear suggestions for amelioration. We argue that this failure stems from the lack of a strong theoretical and empirical foundation for incorporating species interactions into climate-change predictions.

Species interactions are among the most important forces structuring ecological communities and are commonly climate-dependent [6–8]. Davis et al. (Box 1) elegantly demonstrated that sets of species respond differently to temperature if reared together rather than alone. More recently, a review of >600 studies [9] found that climate change influenced virtually every type of species interaction, yet most models of climate effects on species ignore biotic interactions. It is unsurprising that many such models produce inaccurate results [10–12], but often improve if species interactions are incorporated [12,13]. We believe that a ‘community modules’ approach (*sensu* Ref [14], see Glossary) that simplifies entire food webs into tractable sub-webs of strong interactors can help

elucidate how species interactions will influence (and be influenced by) climate change.

Direct and indirect effects of climate change

Throughout this contribution we emphasize the effects of temperature change, but our ideas pertain equally to other aspects of climate change such as precipitation, atmospheric carbon dioxide, and ocean pH. Temperature can directly cause extinctions or geographic range shifts, but

Glossary

Apparent competition: A three-species interaction in which two prey species negatively affect each other's fitness through interactions with a shared predator.

Boltzmann factor: The quantity $e^{-E/kT}$ where E is the activation energy of a reaction (broadly defined to include interlinked sets of reactions, such as biological growth processes), T is temperature (in Kelvin), and K is Boltzmann's constant.

Climate envelope model: An algorithm that predicts how climate variables relate to the present or future distribution of a species.

Community module: A small number of species (2–6 species, often interacting strongly) encapsulating a commonly encountered configuration of interactions, such as a predator–prey or host–pathogen pair, keystone predation, or a trophic cascade.

Ecological release: Increased fitness of a species owing to the lack of negative species interactions, often after a range expansion or invasion that leaves some negatively interacting species behind.

Facilitation: The increase in fitness of one species owing to positive interactions with another species.

Keystone predation: A multi-species interaction in which a predator mediates the coexistence between two asymmetrically competing species by selectively preying on the competitive dominant, permitting persistence of the subordinate.

Leading range margin: The edge of a species distribution where abiotic factors are changing to favor its expansion; usually in the direction of the poles or higher altitudes because warming temperatures allow species to colonize previously unsuitable colder habitats.

Parapatric distribution: Two species with contiguous but non-overlapping ranges.

Priority effect: When an early-arriving species gains an advantage over late-arriving species.

R*: The resource level necessary for a species to persist in a location. If two species are in competition for a single limiting resource, all else being equal, the one with the lowest R* will exclude the other, at least in simple models of exploitative competition (e.g. with no unstable dynamics).

Realized niche: The n-dimensional set of abiotic and biotic factors (including species interactions) that determine the positive rate of increase of a species.

SIR model: An epidemiological model of a pathogen in a host population that tracks the density of host individuals that are susceptible (S), infected (I), or recovered (R).

Trophic cascade: The effect of one higher trophic level on a lower one through an intermediary trophic level.

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Box 1. Temperature and species interactions among *Drosophila*

Davis *et al.* [29,30] conducted manipulative experiments on three competing *Drosophila* species and their shared hymenopteran parasitoid in an enclosed laboratory environment along a thermal gradient. Each replicate ecosystem included eight cages, housed in pairs in adjacent incubators, connected by tubing to allow movement. Two sets of experiments were run: cold gradients with incubators at 10, 15, 20 and 25 °C, and warm gradients with each incubator set 5 °C higher. *Drosophila melanogaster* had highest fitness in warmer cages, *Drosophila simulans* did best at intermediate temperatures, and *Drosophila subobscura* preferred cooler cages. The parasitoid *Leptopilina boulardi* had highest fitness at high temperatures. The drosophilids were mixed in various one-species, two-species and three-species ensembles, with and without parasitoids, and with and without dispersal.

The results were striking. First, dispersal allowed source-sink dynamics, extending thermal ranges beyond those observed without dispersal. Competitive interactions changed local abundance and thermal range, shifting the 'optimal' conditions for a species in some cases. The parasitoid affected the host assemblage directly at high temperatures, and indirectly at low temperatures through changes in dispersal. Simulated warming altered the relative abundances of species along the gradients in non-intuitive ways, dependent partially on the assemblage of species present. The authors

concluded that dispersal and species interactions significantly altered the realized thermal ranges of species within the cool gradient and in the transition from the cool to the simulated warming gradient. *D. subobscura* remained dominant under the coolest conditions and *D. melanogaster* was dominant under the warmest conditions in all experiments. The presence and absence of other species altered local abundance and overall range, but not the relative dominance of species along the gradients. This suggests that temperature changes and species interactions act independently in at least some cases.

This laboratory-based study illustrates the potential for interactions to significantly alter species distributions, but extrapolating these results to natural communities is difficult. The strength of competition between these species in wild populations is unknown, but it is unlikely to be as strong and consistent as in mesocosm experiments. The mesocosm system has limited opportunities for habitat partitioning, so interactions are unavoidable, making the success of one competitor necessarily constrained by another. In natural systems, habitat selection and microhabitat partitioning could provide competitive refuges, moderating the effects found in the laboratory. However, mesocosm studies remain a potentially powerful and underutilized tool for understanding the impacts of climate change on complex multispecies modules.

more subtle organismal or population changes are also possible. Such changes can affect other members of a community *via* species interactions. These indirect effects can be more important than direct effects. For instance, temperature can alter the metabolic rates of ectotherms or the energetic requirements of endotherms, which affect activity patterns, survival, individual growth, or reproductive rates [15–17]. Changes in activity can modify encounter rates among species [18] if individuals avoid exposure to stress or increase foraging to meet metabolic needs. Changes in growth rates can alter body sizes, and influence the outcome of species interactions [19]. Phenological traits (e.g. emergence or flowering time) can be temperature-sensitive such that climatic changes disrupt seasonally

timed species interactions [11,20]. For example, flowering times might no longer coincide with pollinator presence [11]. Moreover, a given abiotic change can differentially affect species in a community because each species has its own physiological optimum [17] and experiences abiotic conditions differently [21].

Predicting the effects of climate change is dependent upon identifying those interactions between species that are most vulnerable to changing climate and are key determinants of the structure and function of a community [22]. The use of community modules (see Glossary) provides one tool to explore these questions. Community modules offer a conceptual framework for integrating species interactions with climate change because they

Box 2. Modeling modules

Community modules can be used to examine the interplay of interactions between the climate and species by making model parameters functions of abiotic variables. This exercise provides heuristic insights even without a detailed understanding of the thermal dependence of model parameters. For instance, using a SIR model for a pathogen specializing on a single host, Lafferty and Holt [23] explored the hypothesis that thermal stress from climate change will amplify host–pathogen interactions [48]. Thermal stress could increase susceptibility to infection, but also affect host carrying capacity (e.g. by reducing resource availability or increasing host mortality). Given these multiple potential effects, negative, positive and even non-monotonic relationships between thermal stress and disease prevalence are possible. Consider the rate of change in infected host numbers when a parasite is introduced, as shown in Eqn I:

$$\frac{dI}{dt} = \beta SI - LI = \lambda I \quad \text{[Eqn I]}$$

where *S* and *I* are the susceptible and infected host densities; β the transmission coefficient; and *L* the loss rate from mortality and recovery. $\lambda = \beta S - L$ is the intrinsic growth rate of the pathogen. Assume the host is initially at its carrying capacity, *S* = *K*. In principle, each parameter can be dependent upon temperature such that: $\lambda(T) = \beta(T)K(T) - L(T)$. The effect of a small increase in thermal stress on the growth rate of the infection is shown in Eqn II:

$$\frac{\partial \lambda(T)}{\partial T} = \left(\frac{\partial \beta}{\partial T} \right) K + \beta \left(\frac{\partial K}{\partial T} \right) - \left(\frac{\partial L}{\partial T} \right) \quad \text{[Eqn II]}$$

If thermal stress increases the vulnerability of healthy hosts, the first term is positive, and a warming climate facilitates disease spread. If thermally stressed individuals move less, healthy and infected hosts encounter each other infrequently, slowing the increase of the pathogen. Decreases in *K* or increases in *L* from thermal stress also dampen the infection growth rate. Probable outcomes are dependent upon biological details. However, models clarify which features of natural systems one should examine.

These results provide heuristic insights, but more detailed models with realistic parameterizations of temperature effects and more species are needed [19,24]. For example, Vasseur and McCann [19] used the Rosenzweig–MacArthur predator–prey model with logistic prey growth and a saturating functional response and added mass-specific rates and a Boltzmann factor scaling thermal rate dependency. Their model predicts destabilized predator–prey interactions and greater extinction risks with increasing temperature. Few studies have moved beyond exploring thermal impacts on pair-wise interactions. A richer array of effects might ultimately characterize more complex modules [23]. In all such theoretical exercises, a critical issue is characterizing functional relationships between model parameters and temperature. Articulating how the physical environment (including climate change) affects interspecific interactions thus requires much stronger linkages between physiological and community ecology [8].

can partition complex communities into manageable sub-units. Because each module represents a distinct set of species interactions, conceptual [18] or mathematical (Box 2, see also [19,23,24]) models coupled with comparative and experimental studies, can be used to uncover general predictions for module-specific responses to climate change. This provides an important step towards understanding the responses of entire communities.

Closed communities

We begin with closed communities, in which we assume that populations cannot track changing climates along geographical gradients by dispersal. Species therefore either persist or become extinct. Closed communities offer insights into the dynamics of isolated habitats (e.g. islands, mountaintops) and provide a starting point for understanding more complex, open communities. The central issue is how species interactions alter the probability of local extinction. Empirical evidence suggests that climate-driven changes in interacting species, including pathogen prevalence [25], phenologies or behaviors of competitors or mutualists [2,11], predator or competitor efficiency [17], and changes in the body size of prey [19,26] can drive local extinctions, but surprisingly few general patterns have emerged.

Dominance versus tolerance

The often-cited 'trade-off' between competitive ability and stress tolerance [8,27,28] predicts that competitive dominants are more susceptible to climate change provided that the novel climate is more stressful. Climate-mediated shifts in competitive success occur in a wide range of plant and animal taxa (Box 1, [8,29–31]). However, sometimes climate change reduces stress (e.g. cold-sensitive species [32,33]), thereby favoring the dominant. For example, differences in competitive ability among freshwater salmonid fish were magnified at warmer water temperatures, allowing one to become competitively dominant [34]. In other cases, the rank order of dominance among species is unchanged by climate [29,30,35]. Climate can also shift competitive interactions to facilitation [2,36], changing dominance to dependence.

Increased sensitivity of higher trophic levels

Empirical [37–39] and mathematical [19] studies often show that higher trophic levels are more sensitive to climate change than lower levels. The reasons for this are unclear; it might be due to relatively greater metabolic needs or smaller population sizes of top consumers [38,39], or due to bottom-up effects [40]. However, in systems with strong top-down control, the loss of top consumers leads to predictable changes in trophic cascades [39,41]. For example, Kishi *et al.* [41] showed that reduced feeding at warmer temperatures by a top fish predator increased herbivory and indirectly diminished benthic algal abundance even though benthic algae increased with temperature in the absence of other trophic levels.

Larger modules

Specialized species should be more sensitive than generalists to the loss of a partner from climate change [11,20], and small modules, by definition, have many specialized

species. Increasing module size may therefore strengthen module resilience to climate change by increasing opportunities for species to replace lost interactions [38,42]. However, this is dependent upon the degree of specialization and the pattern of linkages within the module. Empirical studies show that large communities are often dominated by asymmetrical interactions in which many specialists interact with the same generalist partner [43]. Community size is therefore not always a buffer to climate change [44].

Stability and transient dynamics

Climate change can reduce the stability of community modules [19] and magnify the importance of transient dynamics [2]. For example, Vasseur and McCann [19] modeled the changes to metabolism and body size in a predation module and found that species biomass and the stability of the system declined under warming temperatures. Suttle *et al.* [2] discovered that increasing spring precipitation in an experimental grassland initially favored native plants over invasives, but the former ultimately facilitated the latter by increasing soil nitrogen. Concurrently, herbivore biodiversity first increased, and then declined as invasive plants increased. Thus, an abiotic change altered species interactions in unexpected ways that cascaded to other modules across the community. Such transient dynamics pose substantial challenges for accurately predicting how communities will respond to climate change.

Summary and recommendations

Our present understanding of the effects of species interactions on responses to climate change in closed systems remains mired in idiosyncratic case studies and focused primarily on very small modules. Species interactions clearly modulate the effects of climate change, but robust generalizations that transcend more than a few cases are difficult to identify. A broadly conceived modules approach applied across many taxa and systems could identify such generalizations. If mathematical models address modules from as general a perspective as possible (e.g. Box 2), they can efficiently consider a wide range of climate-change scenarios. This will establish the range of conditions that can modify the persistence of a species beyond those predicted by just its physiology, and provide hypotheses for testing in natural systems using experimental or comparative methods. To date, such a tight coupling of modeling and empirical studies has not occurred, but we believe this is a promising approach for understanding the community effects of climate change.

Scaling the results of small modules up to larger modules or ecosystems remains challenging [22] given the potential number of species and the complexity of their functional relationships. The key question for larger systems is not the just fate of individual species, but the stability and persistence of the system as a whole. This requires a better understanding of the limits of food web resilience to species loss, the extinction risks of generalists, and the extent to which interactions among modules within a community will influence resilience to climate change [22].

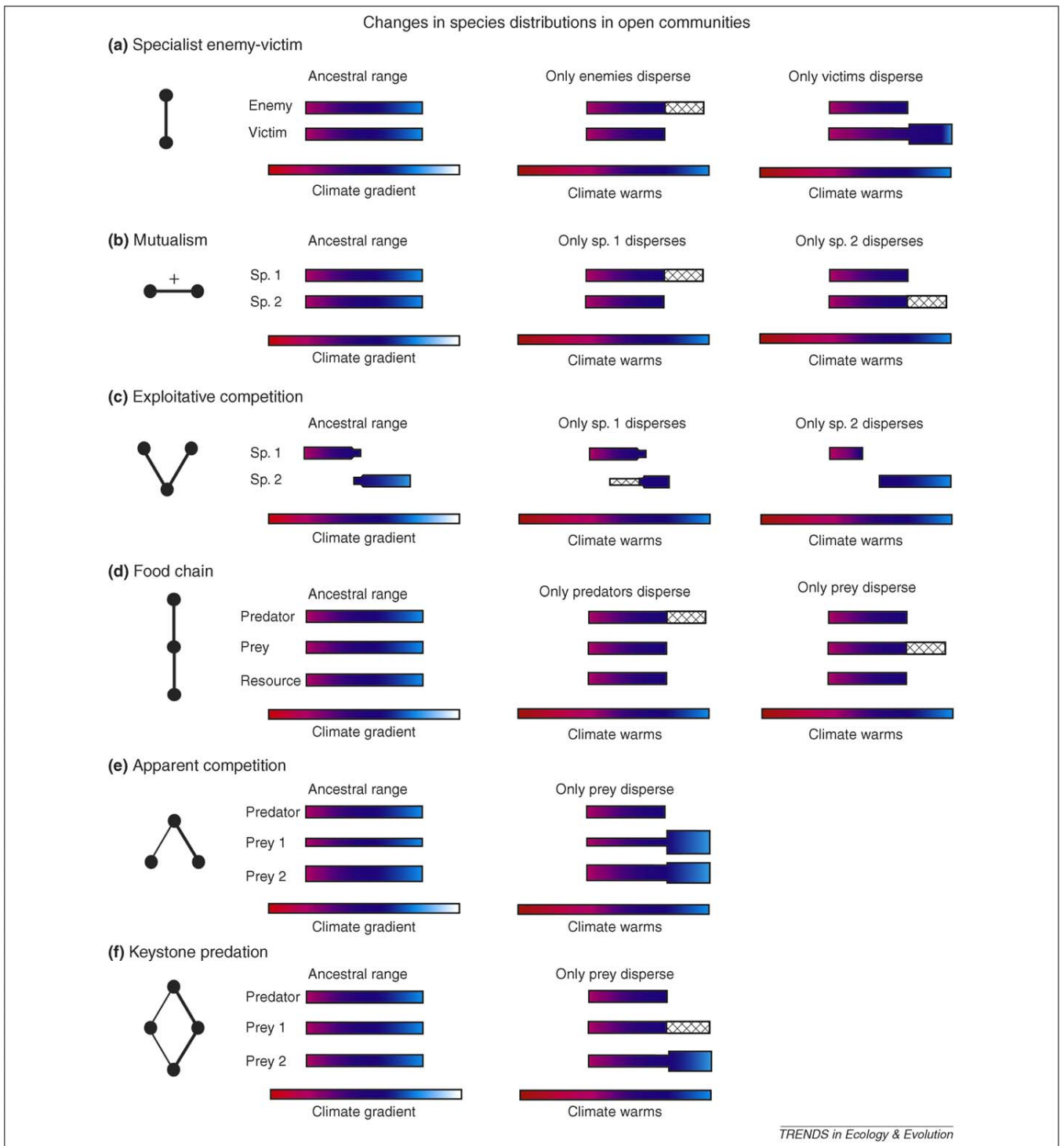


Figure 1. Modules along climatic gradients. We explore how climate change along a temperature cline could affect several community modules. The first column of each row depicts a particular module. Vertical lines indicate negative interactions between species. Line thickness reflects the strength of the association. The second column shows the initial conditions for each interaction along the current climatic gradient, from warm to cold (red to white). Colored horizontal bars indicate the geographic range of each species. The remaining columns show what happens if one or more species tracks warming temperatures along the gradient (indicated as changes in colors), whereas others do not. We assume species cannot survive in cold (white) and hot (red) areas, but can maintain positive population growth in the blue-purple areas of the thermal gradient. The width of the range bar is proportional to abundance. Hatching indicates a region that a species should inhabit based on dispersal ability and tolerance, but cannot because of altered species interactions. In **(a)**, a specialist enemy cannot disperse farther than its victim, limiting the enemy's range. If the victim disperses more than its enemy, it can expand its range and increase in density through enemy release (thickened line). In **(b)**, specialist mutualists limit each other's ability to track a changing climate. In **(c)**, we assume a temperature-based R^* (resource level at which population growth is zero) for each species that allows a narrow range of coexistence (e.g. owing to modest 'spillover'). The expansion of the warm-adapted species decreases the range for the cold-adapted species, whereas the expansion of the cold-adapted species moves it outside the region of interaction. In the food chain in **(d)**, upper trophic levels cannot track changing climates beyond the dispersal-limited lower trophic levels. In **(e)**, prey 1 has an initially reduced abundance owing to the positive effect of prey 2 on the predator. Once the prey expand beyond the predator, prey 1 experiences a larger increase than prey 2 because this indirect negative effect disappears. For keystone predation **(f)**, asymmetric competition between prey species occurs once both move beyond their keystone predator, which allows the competitive dominant to exclude the subordinate. These predictions are based on many simplifying assumptions and actual dynamics will be dependent upon specific formulation and parameterization of models (Box 2). Even in simple two-species models, instabilities can alter predictions about coexistence. For instance, hosts can become extinct in productive regions when parasitoids disperse well [70].

Open communities

Movement and climate-change responses

In open communities, dispersal differences among species could dissolve existing species interactions, eliminating some modules and communities and creating new ones [45–47]. This ‘re-mixing’ of interactions can occur rapidly because the abiotic thresholds constraining range margins shift across space, leading to large-scale changes in species dynamics [48,49]. Broken and novel interactions will probably alter the abundances, distributions, and extinction probabilities of species under climate change [33,50]. Even short-lived transient dynamics could cause long-term changes in species distributions through extinction or priority effects. Priority effects occur when an early arriving competitor usurps available resources and prevents a later-arriving competitor from colonizing [51], thus making transient changes permanent. Novel species combinations can form under rapid climate change if species differ in their ability to track changing climates through dispersal, increasing the risk of extinction even if historical communities eventually re-assemble once poor dispersers catch up. Although the exact responses of a particular community are dependent upon the specific traits of its members, a community modules perspective, together with empirical insights from invasion biology, can elucidate general patterns. We suggest five predictions for how species interactions will influence abundances in open communities, assuming that species ranges contract near the equator and expand poleward with warming temperatures (Figure 1).

Sensitivity of specialists

First, specialist enemies or mutualists with obligate interactions can be limited by other species [47,52], whereas generalists are not similarly constrained. For example, invasions by specialist species are often facilitated by the presence of other invaders, or hindered by their absence [53]. Similarly, obligate specialists might not track changing temperatures if they are dependent upon a poorly dispersing species (Figures 1a and b). Conversely, obligate species might disappear unexpectedly from warmer portions of their range if they are more tolerant of warming climates than their partner. Similarly, in a three-species food chain (Figure 1d), higher trophic levels can track climate no faster than their basal resources (although the reverse need not be true). These effects will be greatest among species combinations with large asymmetries in physiological tolerances or dispersal potentials [53,54]. For instance, terrestrial plants might not track climate as fast as their insect herbivores or mutualists [47,54]. Unfortunately, limited data exists on the dispersal abilities and degree of specialization of most species.

Ecological release

Second, climate change could create ecological release for species that track changing temperatures better than their enemies or competitors (Figures 1a and c). Inferior competitors are often superior dispersers [27,55,56], and enemies are often predicted to lag their victims during a range expansion [51]. Under climate change, many species might

invade new regions due to altered climates and species distributions. Ecological release has occurred during biological invasions [57] and in contemporary range expansions [58]. More complex modules such as apparent competition and keystone predation could also create conditions for ecological release (Figures 1e and f). Ecological release could also allow species to expand even faster than expected by climate-envelope models or into regions with harsher abiotic conditions than tolerated with enemies present. The absence of natural enemies in a newly colonized region might facilitate enhanced physiological performance under extreme conditions, as has been suggested for invasive species [59].

Increased antagonism

Third, differences in dispersal among species can exacerbate antagonistic interactions through indirect mechanisms and cause extinctions. If two species compete exploitatively, the dominant species is the one persisting at the lowest resource level, but such dominance can vary with abiotic conditions [8,31]. If relative dominance shifts along a temperature gradient, sharp parapatric distributions can emerge (Figure 1c); each species will track the changing climate only if relative thermal tolerance is lower for the competitor. A good disperser could drive a competitor extinct if it overtakes the latter during climate change [29,30]. The outcome of environment-specific competitive interactions for species with dissimilar dispersal rates remains an important research area that requires attention.

Novel interactions

Fourth, independent range shifts could create encounters with novel species that further restrict or promote range shifts. Novel interactions can strongly affect fitness because species lack a coevolutionary history with the new partner [e.g. 60]. They can cause local extinctions or hamper the ability of a species to track climate, leading to increasingly restricted ranges [51,61]. In other cases, novel species (e.g. a novel prey expanding into a predator's range) might permit persistence that is otherwise impossible. Similarly, novel interactions among native and exotic species can hinder and help invasions [62]. To assess the potential effects of novel interactions precipitated by climate change, experiments should be designed to measure the demographic responses of species to potential novel interacting species located just beyond current range boundaries.

Metacommunity dynamics

Fifth, if species coexistence is dependent upon ongoing dispersal in a metacommunity [63], climatic changes restricting movement can cause extinctions. Inferior competitors sometimes persist because of their colonization abilities after disturbance, and prey might likewise persist because of dispersal into empty patches. Good colonizers might benefit from climate change, particularly if disturbance increases. However, if climate change heightens stress and mortality during dispersal, colonization success might be reduced. Additionally, climatic influences on movement rate [64] could alter the likelihood of persistence

of interacting species in a metacommunity. The relative role of competition–colonization dynamics in determining broad-scale species responses to climate change needs to be better explored by empirical and theoretical means.

Summary

Precious little is known about the effect of species interactions on responses to climate change in open systems. Accurate predictions require overcoming three major uncertainties: the variation in dispersal abilities among species; the frequency of specialization within communities; and the influence of climate on both. Dispersal can often be estimated qualitatively even if quantitative data are unavailable, but basic information on specialization in species interactions is often lacking. Despite these *lacunae*, we believe the modules approach holds promise as a strategy for developing a broad understanding of the influences of dispersal and specialization on climate-change responses. Using basic modules and assuming specialized interactions, we have made some simple predictions about the outcomes of climate change along a shifting thermal gradient. Future theoretical work should explore models for these modules in more detail using a fuller range of functional forms and assumptions about climatic dependencies. A greater range of outcomes than presented in [Figure 1](#) will probably emerge from such a systematic analysis. As in closed systems, an additional challenge will be to scale-up modules to larger food webs with varying levels of generalist and specialist interactions, embedded in more complex landscapes. Carefully designed experiments, including those on invasive and native species, will provide important tests of theory.

Applying community modules to human-modified systems

Determining the influence of species interactions on biotic responses to climate change is vitally important for human-modified systems such as agriculture and human disease. For example, climate change will influence crop yields directly [3], but also indirectly *via* changes to the population dynamics and geographic distributions of pests, pathogens, and pollinators. Pests account for 30–40% of all crop losses [65], yet their responses to climate change are not routinely considered in crop-yield models [66]. Similarly, agricultural systems reliant upon insect pollinators might be particularly sensitive to climate change directly *via* changes in pollinator numbers and indirectly *via* pathogens, predators, and competitors of those pollinators.

Infectious diseases in humans are likewise subject to direct and indirect effects of climate change on species interactions [67]. Disease prevalence might increase or decrease under warming temperatures dependent upon the relative thermal sensitivities of hosts and pathogens ([Box 2](#)). Vector-borne diseases (e.g. malaria, Lyme disease) are frequently predicted to increase at higher latitudes and altitudes under warming temperatures [4,48,68]. Climate change allows for community reorganization, so pathogens might collect novel vectors or hosts [4,69] and expand farther than expected beyond their original range. A module approach could sharpen the recognition of possible

outcomes for agriculture and human diseases under climate change.

Conclusions

We have shown that species interactions can dramatically alter species responses to climate change. The exact consequences for focal species are dependent upon the: (i) direct effects of climate change on the species; (ii) direct effects on interacting species; (iii) degree of specialization of the species; (iv) strength and climatic sensitivity of interactions; (v) impacts on mobility; and (vi) potential for novel community composition. We suggest that community modules are powerful conceptual tools for elucidating the effects of this rich array of possibilities (particularly if a combined theoretical–empirical research framework is employed). We suspect that community modules will work best if only a few strong interactions exist and weak interactions can be ignored. In other cases, a more complex network approach might become necessary that will require scaling from modules to entire food webs. Accurate predictions of responses to climate change are crucial for conserving and protecting natural and human-influenced ecosystems, and cannot be considered complete without a deep understanding and recognition of the pervasive importance of species interactions.

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