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PERSPECTIVE

A crucial step toward realism: responses to climate change from an evolving metacommunity perspective

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Abstract

We need to understand joint ecological and evolutionary responses to climate change to predict future threats to biological diversity. The 'evolving metacommunity' framework emphasizes that interactions between ecological and evolutionary mechanisms at both local and regional scales will drive community dynamics during climate change. Theory suggests that ecological and evolutionary dynamics often interact to produce outcomes different from those predicted based on either mechanism alone. We highlight two of these dynamics: (i) species interactions prevent adaptation of nonresident species to new niches and (ii) resident species adapt to changing climates and thereby prevent colonization by nonresident species. The rate of environmental change, level of genetic variation, source-sink structure, and dispersal rates mediate between these potential outcomes. Future models should evaluate multiple species, species interactions other than competition, and multiple traits. Future experiments should manipulate factors such as genetic variation and dispersal to determine their joint effects on responses to climate change. Currently, we know much more about how climates will change across the globe than about how species will respond to these changes despite the profound effects these changes will have on global biological diversity. Integrating evolving metacommunity perspectives into climate change biology should produce more accurate predictions about future changes to species distributions and extinction threats.

Introduction

Global circulation models predict that global temperatures will rise 0.6–4.0°C by 2100 (IPCC 2007). Recent climatic changes have already altered the distribution and diversity of species and threaten to alter future diversity patterns (Walther et al. 2002; Parmesan and Yohe 2003; Menendez et al. 2006; Moritz et al. 2008). To predict these threats, we propose an 'evolving metacommunity' approach that stresses the evolution of interactions with the biotic and abiotic environment across heterogeneous landscape gradients (Urban and Skelly 2006; Urban et al. 2008). We concentrate on global climate change, but our recommendations apply more broadly to other directional large-scale environmental changes (e.g., nitrogen deposition). Most explorations of eco-evolutionary dynamics to date focus on the demographic consequences of evolution for single species or pairwise interactions in a single habitat (Pelletier et al. 2009). Yet, multiple direct and indirect interactions and dispersal between patches characterize most species-rich community dynamics. The evolving metacommunity approach tackles eco-evolutionary dynamics in a multispecies and a spatial context and therefore provides a more realistic – and potentially more accurate – approach to predicting future changes in biological diversity in response to climate change.

Despite the urgent need for accurate predictions of future species distributions to inform management, we have failed to produce realistic models that incorporate the ecological and evolutionary complexity of natural

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systems. Recent work has highlighted that predictions about future biological diversity patterns under climate change need to incorporate species interactions (Davis et al. 1998; Gilman et al. 2010), the evolution of traits that increase local persistence (Skelly et al. 2007), and the evolution of traits that increase dispersal (Hill et al. 2011). Progress is being made in some areas such as species interactions and climate change (reviewed in Gilman et al. 2010), and evolution and climate change (reviewed in Hoffmann and Sgro 2011). But so far, no study has adequately addressed the joint effects of evolution, dispersal, and species interactions. To predict the future responses of communities to climate change, we will need to understand eco-evolutionary dynamics in species-rich communities distributed across changing climatic gradients.

Evolving metacommunities

The evolving metacommunity concept integrates the recent emphasis in ecology on the interplay between local species interactions and regional dispersal (Leibold et al. 2004; Holyoak et al. 2005), with the recent emphasis in evolutionary biology on rapid adaptation that can shape ecological dynamics (Kinnison and Hendry 2001; Hairston et al. 2005; Pelletier et al. 2009). A metacommunity is a regional set of communities connected by dispersal (Leibold et al. 2004). In an evolving metacommunity, each interconnected population also can evolve in response to local biotic and abiotic interactions (Urban and Skelly 2006; Urban et al. 2008). Thus, predicting local community dynamics in response to environmental change in an evolving metacommunity requires integrating two local and two regional processes that strongly interact: (i) local community dynamics, (ii) local genetic adaptation, (iii) immigration of species from the regional species pool, and (iv) immigration of genotypes from the regional genotype pool (Fig. 1).

Recent theory suggests that novel eco-evolutionary interactions can occur in the evolving metacommunity. Adding evolutionary dynamics to metacommunity models can strongly alter patterns of species richness and

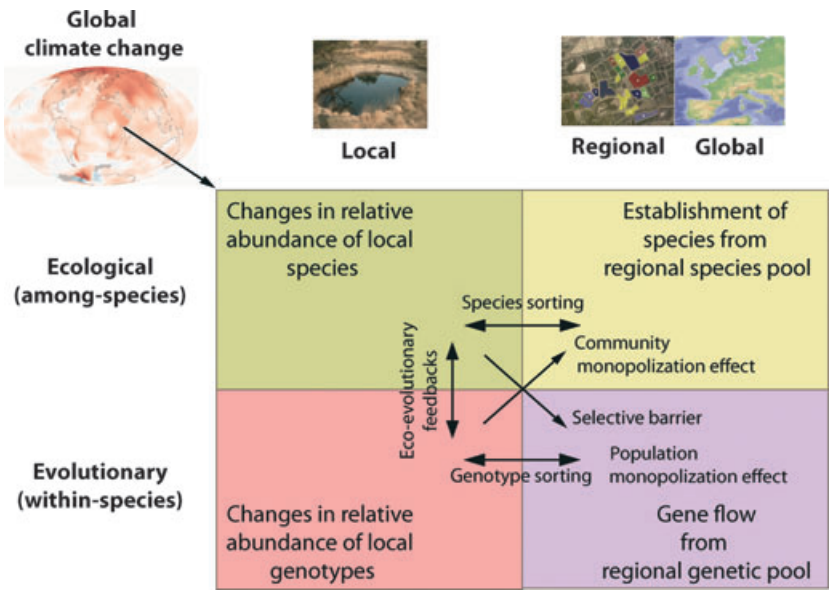

Figure 1 Application of an evolving metacommunity approach to studying biological responses to climatic change depicted relative to ecological and evolutionary mechanisms (upper versus lower row) and spatial scale (from left to right). A community might respond to climate change both by changes in species composition and by genetic adaptation. Regional immigration of species or genes can facilitate the match between local environment and traits (species sorting and genotype sorting, respectively). Both local ecological and evolutionary responses also can interact. If local adaptation allows populations to track climate change, then less community alterations are necessary. However, immigration of species preadapted to the altered local environmental conditions might not allow sufficient time for species to respond through adaptation. Local and regional ecological and evolutionary processes also can interact, as efficient tracking of climatic change by local communities or local adaptation could reduce establishment success of immigrants (ecological priority effect and population monopolization effect, respectively), whereas rapid replacement of resident genotypes and species by preadapted immigrants might not allow time for local species sorting or microevolution. Local adaptation also can prevent the establishment of species through a community monopolization effect, and community composition changes can prevent gene flow by imposing selective barriers. This interplay between local and regional processes and between microevolution and species sorting is the key focus of an evolving metacommunity perspective.

abundance, food web structure, community assembly dynamics, and ecosystem properties (Urban 2006; Vellend 2006; Rossberg et al. 2008; Loeuille 2010). Just taking one example, Loeuille and Leibold (2008a) showed theoretically that the evolution of plant defensive morphs in response to different herbivores altered local and regional patterns of nutrient dynamics, biodiversity, and food web structure. Empirical work also shows that the spatial evolutionary processes that generate trait variation among populations can influence local community (Proffitt et al. 2005; De Meester et al. 2007; Crutsinger et al. 2008) and ecosystem dynamics (Harmon et al. 2009b; Palkovacs et al. 2009). By concentrating on two levels of diversity (within and among species) at multiple spatial scales (local patches, regional metacommunities, geographic clines), the evolving metacommunity framework becomes especially relevant when environmental modifications like climate change simultaneously alter the evolution of traits in populations and the abundances of species with different traits in communities. In this thought piece, we first review how ecological and evolutionary mechanisms at local and regional scales influence responses to climate change when considered independently and then explore how the integration of these mechanisms in an evolving metacommunity framework alters these predictions.

Insights from individual eco-evolutionary mechanisms applied to climate change

Climate change predictions with local ecology and regional dispersal, but no evolution

Species assemblages can persist despite climate change if populations 'track' suitable climates through species sorting (Fig. 2A). Species sorting occurs when regional dispersal and local extinction dynamics match species' traits to the local biotic and abiotic environment (Leibold et al. 2004; Holyoak et al. 2005). Paleontological and niche-envelope empirical studies suggest that species frequently tracked climatic changes in the past (Peterson et al. 1999; Jackson and Overpeck 2000; Davis and Shaw 2001). Modern observations also support that many species compositions have shifted in response to contemporary climate change (Parmesan and Yohe 2003; Hickling et al. 2006; Moritz et al. 2008; Walther 2010) driven both by local shifts in species' abundances and by increased dispersal of warmer-adapted species and genotypes into cooler regions (Hill et al. 2011). For instance, freshwater communities have shifted toward more and smaller fish, smaller zooplankton, a greater dominance of algae and floating leaved macrophytes, and more cyanobacteria in response to climate change as shown by space-for-time, paleolimnological, and experimental studies (reviewed in Jeppesen et al. 2010). Taken together, evidence indicates that species sorting frequently will shape community dynamics in a changing climate.

Predicting biological responses of communities to climate change will require us to know about the interaction between local community dynamics and regional dispersal. Some consensus has emerged that species sorting and, to a lesser degree, mass effects (i.e., multispecies source-sink dynamics) dominate most empirical metacommunity dynamics (Cottenie 2005). Hence, most communities might respond to climate change via dispersal. However, poorly dispersing species will still be threatened, and we might expect that the loss of these poorly dispersing species could have disproportionate effects on communities. The reason for this prediction is that a trade-off frequently occurs between competition and dispersal ability (Tilman 1990), such that the loss of poor dispersers also could mean the loss of competitors with strong effects on community structure. Alternatively, strong competitors might persist long enough to colonize new habitats despite their poor dispersal abilities. Also, the dispersal required by future climate change might surpass that currently required to maintain metacommunity structure. Loarie et al. (2009) projected that species will need to disperse an average of 400 m per year to track climate changes; this distance would exceed the maximum dispersal distance of many species. Dispersal abilities and subsequent metacommunity structure differ strongly across taxa (e.g., from bacteria to vertebrates, Beisner et al. 2006; Van der Gucht et al. 2007) and across landscapes that encompass different connectivities or spatial scales (Muneepeerakul et al. 2008; Caro et al. 2010). Therefore, a better understanding of differences in metacommunity structure among species assemblages, ecosystems, and regions will be critical for predicting future impacts of climate change. For example, any latitudinal trends in the importance of dispersal might predict the character of future metacommunity dynamics in a local site given a space-for-time substitution. At least one study revealed no latitudinal differences in metacommunity structure for bacterial communities separated by 3000 km (Van der Gucht et al. 2007), but much more work is needed in this area.

One exemplary empirical study directly linked changes in metacommunity dynamics and species composition in local habitats to climate change. Altermatt et al. (2008) followed a rock pool metacommunity of three *Daphnia* species over 24 years and found a positive influence of warmer and drier summers on colonization rates. These climate-induced increases in colonization rates were species-specific, and species abundance and composition within this metacommunity changed in accordance with colonization rates, resulting in an increase in metacommunity diversity. The authors proposed that increased

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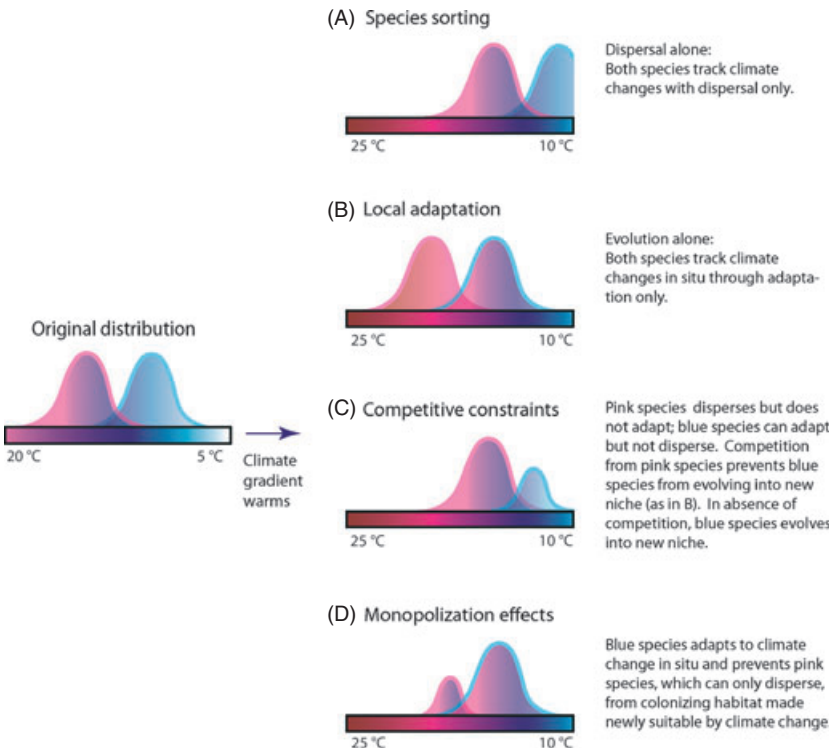

Figure 2 Predicted responses to climate change. Two species (differentiated by outline color) compete for resources along a spatial temperature gradient. Each species has an optimal thermal environment, which leads to a unimodal abundance distribution, and populations within species vary in their optima (indicated by interior color). Temperatures increase along the gradient. In (A and B), we assume dispersal only and local adaptation only, respectively. In (C and D) We assume an interaction between dispersal and adaptation. (A) 'Species sorting,' neither species evolves, and both track optimal temperatures through dispersal. In (B), 'Local adaptation,' both species adapt locally to temperature change; note altered interior colors. In (C), Species sorting prevents an evolutionary response. We assume that the pink species disperses but does not evolve (similar to A), whereas the blue species adapts but does not disperse (similar to B). Without competition, the blue species would adapt locally, and its distribution would match that found in B. However, the pink competitor inhabits the blue species' optimal niche and thereby prevents adaptation by the blue species. As a result, the blue species declines as its local niche disappears and it cannot disperse into its optimal niche. (D) Local adaptation prevents species sorting through monopolization effects. We assume that the blue species does not disperse and adapts to climate change before the pink species colonizes. We assume the pink species can disperse but cannot adapt. The blue species adapts to local climate change and prevents the pink species from colonizing this habitat through a monopolization effect. The evolution of the blue competitor prevents tracking climate change by the pink competitor, which now declines as its local niche disappears. The main difference between C and D is that in C, competition prevents the adaptation of the resident, whereas in D, competition fueled by local adaptation prevents the nonevolving species from invading. In real metacommunities, the different scenarios A–D can be combined, and their relative importance probably differs between species owing to different trophic levels, reproduction systems, generation times, and dispersal abilities that alter evolutionary rates.

colonization rates occurred because dry pools exposed dispersing stages to more wind and animal dispersal. Clearly, much work like this study is needed in a variety of systems.

Climate change predictions with evolution alone

Species might also persist by adapting to local climate change *in situ* (Fig. 2B) (Skelly et al. 2007; Hoffmann and Sgro 2011). Multiple empirical studies report microevolutionary responses to climate in natural populations either along existing climate gradients or, less commonly, in response to temporal changes in climate (Hoffmann and Blows 1993; Huey et al. 2000; Davis and Shaw 2001; Ackerly 2003; Geber and Eckhart 2005; Jump and Penuelas 2005; Balanya et al. 2006; Reusch and Wood 2007; Gienapp et al. 2008). For instance, Franks et al. (2007) showed that *Brassica rapa* rapidly evolved earlier flowering times in response to a multiyear drought. However, not all populations maintain sufficient genetic variation to respond to climate change. Hoffmann et al. (2003) demonstrated little genetic variation and no response to selection in the desiccation resistance of Australian fruit flies; this species probably will not adapt to the projected drying of the Australian climate. Another study showed that evolutionary responses of annual legumes to climatic

selection were slower than rates of climate change owing to substantial negative genetic correlations between otherwise heritable traits (Etterson and Shaw 2001). Hence, evolution will not be a climate change cure-all.

The spatial configuration of environments and climate change also will affect where evolutionary responses might dominate. In general, metacommunities with low connectivity (e.g., large distances between populations or populations surrounded by exceptionally inhospitable matrix) will likely have the most opportunity for local evolutionary dynamics. At temperature maxima (e.g., Equator, valleys, coastal lowlands), adaptation becomes increasingly important because few thermally suitable species exist in the regional species pool, leading to species-poor communities, reduced competition, and the possible persistence of maladapted species for long enough to permit an evolutionary response (Ackerly 2003). Species-poor communities and resultant evolutionary opportunity might also occur with no-analog climates. Assuming evolutionary processes in the absence of dispersal, the species most threatened by extinction are those that cannot evolve quickly enough relative to the rate of climate change owing to inadequate genetic variation, high maladaptive gene flow, antagonistic genetic correlations, or long generation times.

Climate change predictions integrating regional dispersal and evolution

In most cases, natural populations will both evolve and disperse, which generates additional complexities. Gene flow can potentially rescue populations by matching population traits to their translocated climatic niche (genotype sorting) or by fueling adaptation indirectly by provisioning adaptive alleles, gene complexes, or inflating genetic variation (Barton 2001; Polechova et al. 2009). Yet, gene flow also can dilute local gene pools and generate local maladaptation (Wright 1969; Slatkin 1985; Crespi 2000). Alternatively, strong local selection can counter potential gene flow if few immigrants survive to reproduce because of a selective barrier or reproductive isolation (Bolnick and Nosil 2007). Most populations likely lie somewhere between optimal adaptation and maximal maladaptation because most populations have additive genetic variation to fuel adaptation yet also are connected to antagonistic selection regimes through gene flow (Bolnick and Nosil 2007; Moore et al. 2007; Hendry and Gonzalez 2008).

The spatial distribution of selective agents becomes especially important once we consider both gene flow and adaptation in predictions about climate change. Most genes will flow between similar climatic selection regimes because similar climates generally occur near each other on a cline. Therefore, gene flow might entail weaker maladaptive consequences than if selection occurred randomly across space. Species with ranges constrained by climate might peak in population abundances at their thermal optimum and then decline in abundance away from this optimum (Kirkpatrick and Barton 1997). If so, then proportional migration among populations of different size produces an asymmetry in absolute gene flow. Most genes flow from abundant populations at the optimum environmental position into peripheral low-abundance regions, potentially decreasing fitness in the latter, preventing adaptation, and leading to the downward spiral known as migrational meltdown (Kirkpatrick and Barton 1997; Ronce and Kirkpatrick 2001). This asymmetric gene flow along a changing climatic cline also will affect local adaptation differently depending on a population's position on the gradient. If we define a species' optimal temperature as average, gene flow will disrupt local adaptation in warmer areas of the species range because most genes arrive from colder areas. In contrast, gene flow will facilitate evolution in colder areas of the species range that are warming because most genes arrive from warmer regions. However, this asymmetry in number of individuals migrating from one region to the other might be less important than the qualitative effect of gene flow bringing novel additive genetic variance that fuels adaptation (Barton 2001). Also, strong selective barriers or reproductive isolating mechanisms could limit gene flow irrespective of population size asymmetry.

No-analog communities and dispersal

Most climate change predictions ignore the community context of altered species interactions. Species ranges often coincide with thermal gradients, and species often respond individualistically to climate change because they differ in dispersal abilities, climatic requirements, and sensitivities (Sexton et al. 2009; Gilman et al. 2010). These interspecific differences can break apart long-term, perhaps coevolved, species interactions and create novel interactions with naïve participating species in space or time and create no-analog communities (reviewed in Tylianakis et al. 2008; Berg and Ellers 2010; Gilman et al. 2010; Van der Putten et al. 2010; Walther 2010; Yang and Rudolf 2010). Hence, climate change will alter not only the abiotic environment but also the biotic environment comprised of myriad direct and indirect interactions between species.

These altered ecological interactions could in turn create feedback loops between ecological processes and evolutionary dynamics. Novel interactions might prevent some species from colonizing suitable regions or alter their evolutionary dynamics. For example, Geber and

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Eckhart (2005) showed that biotic interactions contributed the most to the decreased fitness of an annual herb outside of its existing range. If biotic interactions commonly play such a defining role in range boundaries, then our job becomes that much more difficult – we cannot just predict responses to climate change based solely on climatic sensitivity. For example, these biotic range limits could prevent direct ecological or evolutionary responses to climate change that would occur in the absence of biotic interactions. Moreover, these biotic range limits will be set dynamically as the species distributions underlying them respond to the climate and other species. The alteration of species interactions along climate gradients could induce selection on additional traits that might have limited genetic variation, with consequent effects on community structure and responses to climate change (Berg et al. 2010). Whereas a species might adapt quite readily to a new climate, they might not adapt so well to climate-induced changes in species interactions. If we know little about the genetic variation needed to respond to climate change, then we know even less about the genetic variation needed to confront altered species interactions. We do not have much evidence yet for these effects, and the effort needed to document them is daunting. However, we suspect that the evolutionary responses of many interacting species, even those involved in diffuse, indirect interactions, might alter predictions about community-level consequences (Case and Taper 2000; Berg et al. 2010).

Insights from evolving metacommunities applied to climate change

To suppose that dispersal, adaptation, and community interactions will operate independently on species' responses to climate change would certainly be convenient, but false. Ignoring the potential interactions among these changing factors could easily produce inaccurate predictions. The likelihood that ecological and evolutionary factors will interact to produce unexpected results is high because fitness links these dynamics across the same temporal and spatial scales and because dispersal simultaneously changes gene flow and species colonization rates. We next address the critical question: Do interactions among evolutionary and community dynamics in space affect predicted responses to climate change?

Five theoretical studies combine adaptation, species interactions, and environmental change (Table 1), though collectively they cover only a narrow range of potential eco-evolutionary dynamics. All models focus on competition. Two models ignore effects of dispersal even though we show this to be a critical feature of natural systems and an important determinant of evolving

Table 1. Community models of eco-evolutionary responses to environmental heterogeneity.

Model	Interaction type	No. of species	Climate change?	Dispersal	Trait evolution	Climate change prediction
Case and Taper (2000)	Competition	2	Step	Clinal	QG; single trait	When species ranges determined by competition, species respond through both local adaptation and dispersal
Goldberg and Lande (2007)	Competition	2	No	Clinal with partial barrier	QG; single trait	If two competing species move in response to climate change and cross a partial dispersal barrier, then the species most affected by the barrier will expand its range at the detriment of the competitor
Johansson (2008)	Competition	2–3	Unidirectional moving optimum	No	Adaptive dynamics and individual-based simulation with explicit genes; single trait	Competition reduces evolutionary responses to climate change
de Mazancourt et al. (2008)	Competition	2, 4, 16	Differs in rate and slope among patches	Global	QG; single trait	Competition reduces evolutionary responses to climate change and results in more species sorting and extinctions
Price and Kirkpatrick (2009)	Competition	2	No; evolution of species into new niche	No	QG; single trait	Competition reduces evolutionary responses to climate change

QG refers to a quantitative genetics approach with fixed genetic variance.

metacommunity dynamics. Most models ignore changes to genetic variance (except for the simulation model of Johansson 2008). However, sexual reproduction, altered selection, and gene flow between populations can release new additive genetic variation, which could affect results considerably. Only two models incorporate three or more interacting species and thus include potential indirect effects (Johansson 2008; de Mazancourt et al. 2008). The empirical study of responses to climatic change in the framework of evolving metacommunities remains in its infancy as well. Searching for literature with the key words 'evolving metacomm*' and 'global warming', 'climate change' or 'global change' only yields a single study (Van Doorslaer et al. 2009b), and this study does not address all aspects needed to integrate community and population responses at local and regional scales. Hence, most of our current understanding comes from theoretical models that await future empirical tests.

Despite the early stages of development of these ideas, we can uncover some preliminary trends. In the broadest sense, local adaptation, dispersal, and species interactions almost always interact to determine responses to climate change; excluding any single factor alters responses to climate change in important ways (Table 1) (Case and Taper 2000; Lavergne et al. 2010). Just taking one example, Case and Taper (2000) theoretically show that without competition, a single species responds almost entirely to climate change through a range shift, whereas two competing species respond via both range shifts and local adaptation. Based on our review of the literature, we highlight two potentially important dynamics that integrate ecological and evolutionary responses in an evolving metacommunity framework: (i) ecological constraints on evolutionary responses to climate change and (ii) evolutionary constraints on ecological responses to climate change.

Ecological constraints on evolutionary responses to climate change

Interspecific competition from a resident can impede adaptation to climate change in an invader in two ways. Competition can manifest either nonspatially as a fitness reduction for species with similar niches or as a lottery-style competition for a spatial resource akin to a spatial priority effect. These two different forms of competition differ in their assumptions: niche monopolization depends on the similarity of resident and invader traits, whereas a spatial priority effect only requires the occupation of space.

In the first case, species are assumed to monopolize resources by inducing selection against individuals that use similar resources via classic niche partitioning (MacArthur 1970; Roughgarden 1972). Two nonspatial models indicate that a competitor can prevent another species from evolving into its niche when the niche of the other species disappears or shifts, even when sufficient additive genetic variation exists to fuel this adaptive response in the absence of competition (Johansson 2008; Price and Kirkpatrick 2009). The particular form of competition assumed here selects against traits that overlap between competing species. The strong fitness reduction associated with being similar to a sympatric species can prevent niche expansion. This reduced fitness can lower population sizes in the inferior competitor, which in turn increases its extinction risks and decreases its future evolutionary potential through reduced genetic variation in small populations. Species that inhabit niches disappearing with climate change might not easily colonize and adapt to the remaining niches if adaptation is prevented by the presence of another competitor. Thus, even if research reveals sufficient evolutionary potential for an adaptive response to climate change, a species might be blocked by a competitor's similar resource use.

In the second case, species monopolize space through an ecological priority effect, whereby the first species in a patch reduces the establishment of later arrivals (Shulman et al. 1983). Although evidence for this effect among species is lacking, a single-species model shows that cooler-adapted populations of long-lived individuals continue to monopolize space even after they become maladapted (Atkins and Travis 2010). Space occupancy in the model slows the invasion of warm-adapted genotypes that would otherwise facilitate local adaptation to changing climates. Competition for local space among species also might slow down invasions and prevent occupancy by a species that would otherwise colonize a patch and adapt to the changing climate, but we lack any sort of theoretical treatment to indicate this suggestion with certainty. If true, then we might observe a more reduced role of evolution in protecting species from climate-induced extinction. In particular, we might expect stronger priority effects for genotypes (Atkins and Travis 2010) or species (Takenaka 2005) when residents live long or their generations overlap. Although such constraints might be transitory, their effects could last long enough to affect equilibrium outcomes if, for instance, they result in extinctions.

Whereas the niche or spatial competitive advantage of a resident species can prevent colonization and adaptation of an invader, a preadapted invader also can outcompete a maladapted resident and prevent its evolutionary response to climate change. If dispersal is high and residents become greatly maladapted, then a preadapted species is more likely to replace residents because these residents do not have sufficient time to adapt (species

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sorting, Fig. 2A). If the local maladapted species cannot evolve into another niche or disperse to another habitat as its niche disappears, then the species could become extinct. The only model evaluating environmental change in a multispecies evolving metacommunity shows that colonization by preadapted species dominates over local adaptation (de Mazancourt et al. 2008). In this model, multiple species adapt to multiple patches, each with a distinct environment. Each patch's climate changes linearly in a random direction and rate (with the restriction that the average climate in the patches changes unidirectionally), creating a web of crossing environments. Some populations adapt to these changes, but the overall contribution of evolution to species' persistence decreases in models with high species richness. Species richness inhibits evolutionary responses because the presence of multiple species increases the probability that one species is preadapted to the new local conditions. Although compelling, local environments change in random directions in this model, and each population has an equal chance of colonizing every patch, which does not apply well to unidirectional and spatially autocorrelated global climate change. Antagonistic selection is also very strong in the model such that most species have an absolute fitness less than one in alternative patches. A metacommunity of harsh sink environments generally impedes niche evolution (Holt 2009). Local adaptation might contribute more to responses when species have broader environmental tolerances and high genetic variance and when dispersal is relatively low.

We next examine empirical evidence that species interactions can substantially alter climate adaptations. Van Doorslaer et al. (2009a, 2010) compared evolutionary responses of *Daphnia* to a temperature increase with and without a community of competing species and found that evolutionary responses to climatic change strongly depended on the community in which populations were embedded. Without competing species, overall performance evolved in the warmer environment. In a natural community, however, performance did not evolve; instead, temperature-dependent body size evolved. Thus, community context can modulate evolutionary response. This outcome also implies that evolutionary potential for a trait to change in response to temperature need not translate into an evolutionary response if climate change also alters the community and associated selection pressures. In contrast, interactions between pea aphids and two predaceous ladybird beetles were not predicted to affect the evolutionary rate of heat resistance because predation affected the relative, rather than absolute, fitness of genotypes (Harmon et al. 2009a). Hence, the effect of community variation on evolutionary responses depends on the types of species interactions and mode of natural selection.

In summary, by consuming shared resources or occupying space even after they become maladapted to the new climate, a resident competitor can prevent the evolution of a nonresident species into a niche. The latter effect of 'space blocking' might be transitory and would disappear when colonization rates are high and the resident becomes strongly maladapted relative to preadapted colonists. Then, we predict species sorting to dominate over evolution. Experiments that evaluate evolution in response to climate change with and without competitors indicate that evolutionary responses can depend on community context. However, the degree to which natural selection is soft or hard mediates the strength of this effect.

Evolutionary constraints on ecological responses to climate change

Besides ecological constraints on evolution, we also expect the opposite feedback of evolutionary constraints on ecology through the so-called community monopolization effect (Roughgarden 1972; De Meester et al. 2002; Gillespie 2004; Emerson and Gillespie 2008; Urban et al. 2008; Urban and De Meester 2009). In the community monopolization effect, early-arriving or resident species adapt to new or changing conditions provided a sufficient delay exists before a better adapted species arrives (Urban and De Meester 2009). Through this local adaptation, a resident species increases its fitness, monopolizes resources (spatial or otherwise), and thereby prevents colonization by other species (Fig. 2D). In this way, local adaptation prevents species sorting. In a climate change context, we could easily imagine a resident species that not only occupies the space but also adapts to the altered climate, thus barring the invasion of the competitor more effectively than through persistence alone.

However, the prevalence of monopolization effects might be limited where climate changes more rapidly than evolutionary rates permit a sufficient response in the resident species. Continuous temporal environmental change has been shown to increase the importance of species sorting relative to evolution in models where evolution proceeds more slowly than environmental change. For instance, Loeuille and Leibold (2008b) modeled an evolving species in one patch with an environment that cycled between the fixed environments of two patches inhabited by species with matching fixed traits. Species sorting dominated over local adaptation in this model except when environmental changes were slow and evolution was rapid. In most cases, the nonevolving species colonized and supplanted the evolving species whenever

the varying environment became similar to the fixed environment of the nonevolving species. Hence, rapid environmental changes, high dispersal, and the presence of preadapted species favor ecological species sorting over monopolization effects. However, Loeuille and Leibold (2008b), like de Mazancourt et al. (2008), assumed crossing environments that reflect cyclical or random environmental changes, unlike the predicted unidirectional climate change.

To what degree do empirical studies support the emergence of monopolization effects? We now know from several empirical studies that differently adapted populations can influence community assembly and structure (Whitham et al. 2006; De Meester et al. 2007; Harmon et al. 2009b) and that the timing of introductions of different ecotypes influences adaptive radiations in bacteria (Fukami et al. 2007) and spiders (Gillespie 2004). No studies have yet shown that adaptations in response to climatic change can alter community assembly as predicted by theory. However, one study on populations of the same species suggests that the mechanism can operate at least at the metapopulation level. Van Doorslaer et al. (2009b) showed that *Daphnia magna* from the United Kingdom evolved rapidly in response to artificial warming. Then, *D. magna* from southern France that were preadapted to warmer temperatures were added to heated mesocosms in different relative abundances. At the end of the experiment, the preadapted French *D. magna* completely displaced the control UK populations not selected to perform well at warmer temperatures. However, the warm-adapted UK population reduced the invasion success of French invaders and dominated when their initial relative abundance surpassed that of their invader. This result suggests that monopolization effects among populations in response to climate change could change the capacity for evolution to provide an advantage to local residents, but tests of the idea are needed among species.

Combined mechanisms

The previous sections show that the outcome of the interaction between ecological and evolutionary processes depends on evolutionary rates, relative adaptation to climate change, competitive abilities, and migration rates, promoting ecology over evolution in some cases and evolution over ecology in others. We expect that in more complex situations both kinds of constraints will play a role and jointly determine the final outcome of genotype and species interactions on climate change. The only model of eco-evolutionary dynamics in response to an environmental change that affects the entire gradient simultaneously (like climate change) shows a mixture of monopolization effects through local adaptation and constraints on adaptation through niche monopolization (Case and Taper 2000). In this model, two species compete along a climate gradient, and the same trait determines their fitness along the gradient and their competition with one another. In sympatry and without climate change, the evolution of character divergence results in a stable range boundary. During a step change in climate, a single species responds almost entirely through dispersal despite genetic potential. However, when two species compete, they both respond to climate change through a combination of local adaptation and range shifts (Case and Taper 2000). In this case, competition prevents adaptation into another species' overlapping niche at the same time as local adaptation prevents species sorting by allowing residents to resist invasion. Future work should seek to understand their separate effects by comparing the theoretical outcome with two evolving species versus that with one evolving and one nonevolving species.

Future directions

Future theoretical directions

Few researchers have produced theoretical models that incorporate eco-evolutionary responses to environmental change along gradients that correspond to the spatial and temporal characteristics of climate change (Table 1). The most applicable model by Case and Taper (2000) indicates a joint role for evolution and dispersal in mediating climate change responses among two competitors. The only model that incorporates more than two species competing among multiple patches (de Mazancourt et al. 2008) assumes multidirectional environmental change and equivalent migration rates among patches, which is more indicative of random regional environmental changes (e.g., resources) than global directional climate change. Therefore, we know little about how dispersal's simultaneous effect on both species sorting and gene flow affects community and metacommunity responses to climate change.

As a result, we need to develop models that build upon Case and Taper's (2000) work to include multiple species and variation in the key factors that control the relative influence of local adaptive evolution versus species sorting: dispersal rate, levels of standing additive genetic variance, genetic architecture, and tolerance of disparate environments. High genetic variance and low dispersal rates should shift dynamics toward local adaptation to climate change and monopolization effects because local adaptation prevents species sorting. Lower genetic variance, high dispersal, and strong environmental gradients should expand the role that species interactions play in decreasing evolutionary responses by limiting absolute

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fitness in the novel environment (de Mazancourt et al. 2008). The genetic architecture of multiple traits in response to climate change (e.g., thermal tolerance, desiccation tolerance, traits involved in novel species interactions) will likely influence evolutionary versus ecological responses also. For instance, negative genetic correlations between climate change–related traits could prevent the evolution of a collective response to multivariate climate change (see Etterson and Shaw 2001).

Despite the handful of significant studies in this area, much remains to be accomplished. The few models that evaluate how environmental change influences evolving species interactions only include competitive interactions. We know almost nothing about how other types of species interactions (e.g., predator–prey, host–pathogen, mutualism) will affect predictions. For instance, adding a trophic level could increase extinction risks if climate change reduces the abundance of a prey species, and the predator population cannot evolve quickly enough to exploit alternative prey species. Tracking climate change for a predator becomes that much more difficult because the predator must track both its optimal climate and its prey. Prey populations, on the other hand, might undergo ecological release if a key predator declines in abundance owing to climatic change. These increased prey abundances could then affect the prey's competitors. Thus, even adding a single trophic level could lead to many currently unexplored, but important, direct and indirect effects.

Another future direction deals with how traits are modeled. Some models treat the environment as a physical gradient (e.g., Case and Taper 2000), whereas others treat it is as a resource gradient (e.g., Johansson 2008; Price and Kirkpatrick 2009). For resources, it makes sense that one trait determines both local fitness regardless of competitors, and the outcome of interspecific competition. For physical environments, separate traits might determine environmental tolerance and resource use. Moreover, many climate and biotic factors could change in a multivariate manner and thereby create no-analog environments (Jackson and Overpeck 2000; Ackerly 2003; Williams and Jackson 2007), which undoubtedly will cause selection on multiple traits. Future models should include multiple traits and varying degrees of correlation between the multiple traits. We should also explore the degree to which dispersal barriers or nonlinear climate gradients determine range responses (Goldberg and Lande 2007). A partial dispersal barrier repels the intersection of competing species' range boundaries such that it might resist poleward movement. Similarly, the position where competing species' ranges meet along nonlinear environmental gradients (e.g., a strong ecotone) might also resist movement in response to climate change.

Empirical future directions

Theory has progressed faster than empirical tests of evolving metacommunity responses to climate change. No single study has yet addressed all four of the components outlined in Figure 1 that need to be integrated to obtain a better picture of the dynamics one can expect under climate change. Dispersal rates and levels of genetic and species diversity should determine the relative importance of regional and local processes. By varying dispersal rates and levels of standing additive genetic variance in experiments, these predictions can be tested. The temporal and spatial scale of the problem limits experimental study systems to species with short generation lengths that can be raised in manageable laboratory vessels or small mesocosms. Evaluating evolutionary dynamics in designs such as that used to examine how dispersal altered *Drosophila* metacommunity responses to climate change would be a logical starting point (Davis et al. 1998).

While manipulating levels of genetic variance is an attractive approach to test general predictions, we also need to carry out experiments with natural populations that capture effective standing genetic variation in the wild. Such experiments do not only allow testing specific hypotheses, they are also needed to document and evaluate the impact of eco-evolutionary processes within an evolving metacommunity framework in shaping responses to climate change in the real world. Combining such studies across natural communities that differ in diversity and composition in a meta-analysis should deliver insights into the relative importance of the different factors in determining responses to climate change.

Two general experimental strategies in natural populations could prove especially rewarding in the context of global climate change. First, in a space-for-time approach, metacommunities could be studied along an elevational or latitudinal gradient to assess how their structure evolves under global warming. This study should be combined with an analysis of (genetic) trait variation in focal species so that responses at the metapopulation and metacommunity level can be assessed at the same time and compared to each other. In addition, these results could be compared with the outcome of a thermal evolution experiment at the community level at the northern latitude in the presence and absence of dispersal at two scales: within the regional metacommunity and across latitudes from more southern communities. In such experiments, the degree of dispersal could be manipulated by transferring a controlled number of organisms across experimental units. In this way, different metacommunity structures could be evaluated for their effect on eco-evolutionary responses. In this experiment too, it would be crucial to also monitor both responses in genotypic trait

values in key species and changes in species composition and associated trait values at the community level. Such a survey combined with an experimental evolution approach is not easy to apply and might best be carried out on systems that are relatively easy to manipulate, such as aquatic communities inhabiting ponds or lakes, soil communities, or plant communities in grasslands.

In a second approach, we suggest that a more direct historical reconstruction of metacommunity structure through time could be achieved by studying the 'resurrection ecology' of several subdivided populations in a region. Resurrection ecology refers to the study of ancestral individuals that can be cultivated from the past (e.g., diapausing eggs or seeds). Historical levels of gene flow could be reconstructed using genetic markers. Comparing metacommunities in regions with high and low habitat connectivity would allow one to test the impact of gene flow on the realized historical changes in metacommunity structure in response to global warming. Such a resurrection ecology approach is limited to organisms that produce dormant eggs or seeds that accumulate in layered sediments. Aquatic communities inhabiting lakes and ponds are obvious candidates, but the seed banks of plant communities also allow reconstruction of events through time. Despite the challenges of incorporating multiple levels of genetic and species diversity into climate perturbation experiments, the most critical current need is empirical research to test theoretical predictions.

Management and policy implications

Given how little we know about eco-evolutionary responses to climate change, we currently find it difficult to translate science directly into policy. Nonetheless, our evolving metacommunity perspective supports calls for increased evolutionary thinking in conservation biology (Stockwell et al. 2003), especially in the context of the interplay between species' movement, local adaptation, and community interactions. In terms of specific conservation issues, the evolving metacommunity perspective suggests the value of exploring 'assisted migration' (McLachlan et al. 2007) and 'assisted evolution' (Jones and Monaco 2009) as potentially important techniques to consider for mediating the impacts of climate change on communities. Such assisted migration or evolution projects could be conducted experimentally (i.e., including control sites where no action is taken, or multiple source populations as 'treatments') to advance both conservation efforts and the fundamental research questions outlined here.

Species sorting will be very important in matching species to preferred climates. Thus, 'assisted migration,' the purposeful introduction of species in regions made newly suitable through climate change, might be especially necessary for poor dispersers (McLachlan et al. 2007; Van der Veken et al. 2008). The genetic composition of introductions will be important in successful application of this technique; individuals should be taken from populations where the current (or recent) climate most closely matches the projected climate at sites of introduction. Assisted migration should be considered on a case-by-case basis rather than applied universally and should only be implemented to support the maintenance of communities or the preservation of rare species that otherwise would be lost. Careless assisted migration projects could lead to collateral damages similar to that occurring with exotic species introductions.

We should also evaluate 'assisted evolution' (Jones and Monaco 2009) as a conservation technique, whereby managers facilitate climate adaptations *in situ*. Such actions might involve limiting immigration of maladapted individuals (e.g., a unidirectional barrier keeping out maladapted cooler genotypes), increasing genetic variation or local adaptation by selective introduction of genotypes, or releases of populations that have been artificially selected in the laboratory. Given the potential importance of community context, enclosures might be needed to prevent exclusion by resident species until adaptation occurs. Assisted evolution has the advantage of not requiring the introduction of species to new geographic regions – species remain in place. Although assisted evolution might incur fewer risks than the assisted migration of novel species in a region, it still needs to be considered carefully, as it could lead to the extinction of specific local genotypes without sufficient foresight.

Conclusions

The evolving metacommunity approach has much to add to the discussion about the distribution and composition of global biological diversity under climate change. By combining dispersal, community interactions, and evolution, novel eco-evolutionary interactions will alter predictions from those made assuming any single mechanism. Admittedly, incorporating eco-evolutionary interactions in space into models promotes realism at the expense of tractability and ease of parameterization (Sexton et al. 2009). However, theory and data to date suggest that in the absence of such complexities, models can make seriously misleading predictions. We will therefore need to build this complexity progressively into experiments and theory. At the same time, we should increase efforts to measure key parameters in wild communities such as dispersal rates and genetic variances for climate-related traits. Predictive models of future climatic change have undergone a similar

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transition from simplistic models to increasingly sophisticated regional models. Unfortunately, we have fallen far behind our meteorological colleagues in our understanding even as climate change increasingly threatens global biodiversity.

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