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Climate change and species interactions: beyond local communities

Benjamin Gilbert[1] and Mary I. O'Connor[2]

[1]Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario, Canada. [2]Department of Zoology and Biodiversity Research Centre, University of British Columbia, Vancouver, British Columbia, Canada

Address for correspondence: Benjamin Gilbert, University of Toronto, Department of Ecology and Evolutionary Biology, 25 Harbord St., Toronto, Ontario M5S 3G5, Canada. benjamin.gilbert@utoronto.ca

It is increasingly recognized that the wide-scale modification of habitats caused by climate change requires scientists to consider how species and species interactions change both locally and at larger, regional scales. Metacommunity approaches explicitly link local and regional dynamics for communities of species, providing a conceptual and mathematical framework for global change biologists. These approaches can scale between community-level impacts and the regional distributions and movements of species, and likewise determine how changes to regional processes, such as dispersal and habitat configuration, influence local abundances and occurrences. This review discusses several lessons that have recently emerged from climate change studies and metacommunity theory to identify some of the key processes that link local-scale studies to regional-scale properties of communities, and vice versa. We then use simple models to highlight how these linkages function and to identify where research could gain most by studying specific local and regional processes. Finally, we propose methods for the field to move forward by clarifying how to incorporate metacommunity approaches into empirical research, and by identifying important gaps in metacommunity research.

Keywords: metacommunity; metapopulation; climate change; dispersal; abundance; competition; facilitation; spatial ecology

Introduction

Climate change impacts survival and fitness, occasionally with catastrophic consequences of species extinction.[1] Whether species persist, thrive, or become extinct reflects physiological responses to local abiotic conditions and how these conditions alter the biotic processes that facilitate persistence.[2] Together, these processes play out across a range of scales where species interact locally, where populations exchange genes to evolve, and where individuals and populations migrate.[3–5] The full effects of climate change on species persistence and evolutionary trajectories cannot be understood without considering the importance of both biotic and abiotic processes across these spatial scales.[1,6] For example, global changes that decrease local abundances may eventually drive species extinct even when local population growth rates are positive on average because these local changes lead to lower colonization and higher extinction rates.[7] Some processes, such as fine-scale individual physiological responses and species interactions, are receiving increased attention.[3,8–10] However, other processes, such as the interplay between broad-scale dispersal and community dynamics, remain understudied in the climate change context.[2,11]

Species persistence in heterogeneous environments can be understood using metacommunity models and approaches.[12] A metacommunity is a set of local communities linked through dispersal of individuals among habitat patches, where dynamics within each local community may be related to other communities.[13–16] Well-defined metacommunity models incorporate local population dynamics into community interactions within habitat patches, and explicitly link these patches through dispersal of individuals over the landscape.

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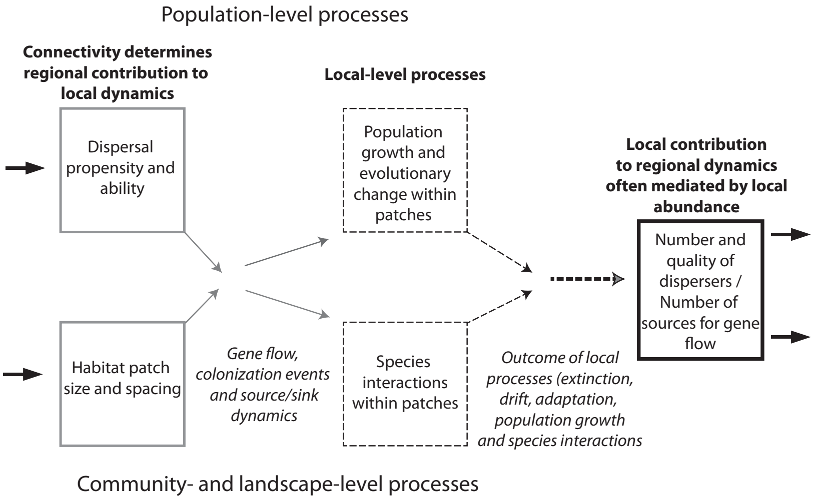

Figure 1. Population-, community-, and landscape-level processes. The effect of climate change on species' traits and demographic processes (top boxes), as well as its effect on landscape structure and other community members (bottom boxes), jointly determines the overall impact on species in metacommunities. Metacommunity dynamics are particularly susceptible to climate change because they are driven by regional processes (gray lines and boxes) and local processes (dashed lines and boxes). A common measure of species viability that reflects local processes and affects regional processes is local population abundance (thick black box).

Metacommunity spatial structure, or the degree of isolation among local communities, impacts species' dynamics and viability both within local communities and at the regional scale across all communities considered.[15–17] Spatial structure can also create complexity in communities by influencing the rate and endpoint of evolutionary processes,[18–21] changing the outcomes of competitive or consumptive interactions at the regional scale relative to local outcomes,[22,23] and creating extinction debts that persist long after their putative causes.[24–26] It is therefore unsurprising that species dynamics in spatially patchy communities, or metacommunities, have yet to be incorporated into predictions about the effects of climate change on species. This challenge of incorporating metacommunity processes into a global change framework is arguably one of the largest faced by ecologists.[11,26]

Relating local climate responses to regional changes is a key challenge in climate change ecology.[6] Still, metacommunity dynamics have been considered in very few climate change studies,[6,11] possibly because of the scale and complexity of systems required to test metacommunity dynamics; understanding the effects of climate change on species interactions alone is difficult,[4,10] and the research required to quantify dispersal dynamics of even a few species is considerable.[27,28] In addition, recent theoretical and synthetic work has proposed that numerous factors need to be quantified in order to understand metacommunity ecological and evolutionary dynamics.[2,21] To understand eco-evolutionary processes, for example, the factors needed include genetic diversity within and among populations, gene flow, and ecological differences between resident and away populations.[21] Moreover, metacommunity modeling has often relied on parameters that are abstract or very difficult for empirical biologists to interpret or measure.[16,29]

In this synthesis, we propose methods that allow researchers to overcome hurdles to adopting a metacommunity approach in climate change research. We begin with a general framework for understanding how local and regional processes influence metacommunity dynamics (Fig. 1). Using this framework, we identify how climate change is likely to alter both local and regional processes and the feedbacks between them. We then use heuristic models to examine the scaling of local dynamics to regional processes, and vice versa, under climate change scenarios. In the first scenario, we consider how climate may impact local abundances, which ultimately scale up to alter regional dynamics of interacting species. Abundance at the local scale often provides a strong indication of the ecological and evolutionary trajectory of species in a metacommunity;[30–32] we focus on changes in abundance for this reason and because it is relatively well studied. In the second scenario, we investigate how the effect of climate on colonization rates of a single species alters its own success, as well as the persistence or success of interacting species. For both scenarios, we examine how changing local or regional processes can render species in metacommunities vulnerable to extinctions, and how this vulnerability depends on the type of species interactions considered. Finally, we describe approaches to studying climate impacts on species in metacommunities, and highlight future directions for this field.

How could climate change affect species persistence in metacommunities?

Species persistence in a changing climate depends in large part on how demographic processes respond to biotic and abiotic conditions. Key demographic processes are those contributing to persistence in the historical range, and those that facilitate evolution and spatial tracking of climate conditions. These processes operate differently for species in metacommunities compared to those that are members of communities lacking strong spatial structure.[21,26] The difference stems from the relationship between demographic processes operating primarily at local scales, and those operating across locales at regional scales. Local dynamics concern birth and death rates of closed populations. Variation in birth and death rates resulting from climate-driven changes in species interactions or abiotic conditions affect abundance, population growth, and evolutionary trajectory.[4,8,33] Regional processes connect local populations, linking ecological and evolutionary dynamics over a landscape[12,14,18,34] (Fig. 1), and include connectivity among spatially separated populations, spatially structured species interactions, and spatially heterogeneous patterns to disturbance.

Climate change could affect species' persistence, distribution, or evolution by altering local community processes, regional processes, or both.[2,6,11] Regional processes are particularly important in metacommunity research because they determine the degree to which local and regional abundances are correlated. In particular, the coupling of local and regional abundances depends on the isolation of populations, and varies with species-specific dispersal traits, physical and physiological barriers, and distance between habitats (Fig. 1, gray boxes). Climate change can alter isolation by affecting any of these factors, independent of direct effects on population size or growth trajectory of local populations.[35,36]

The effect of climate change on local dynamics also impacts the regional abundance of species (Fig. 1, dashed boxes). These impacts may be direct, through physiological responses to climate change, or may occur indirectly through species interactions. As we show below, metacommunity impacts that arise from altering local dynamics often generate correlated patterns across spatial scales. In the extreme case, local climate change responses may scale directly, or linearly, to regional responses if the isolation of local communities is minimal. For many species, however, the magnitude of regional climate change responses will differ from those seen locally due to the nature of scaling. As a result, local effects are often indicative of the direction, but not the magnitude, of regional species responses.[26]

The dynamic feedback between local and regional processes (Fig. 1) makes metacommunities particularly vulnerable to global changes.[26,37] This vulnerability arises because each type of process is vulnerable to climate change in unique ways, and their synergy determines the ultimate risk of extinction and evolutionary potential of species (Fig. 1). For example, in continuous habitat, the potential to realize range shifts in response to climate change is constrained by population growth rate and maximum dispersal distance.[38] In metacommunities, range shifts are additionally constrained by habitat patchiness (isolation), dispersal through nonhabitat areas,[26] and inter- and intraspecific limitations on population sizes within patches.[38] Similarly, the ecological viability of species and their evolution in metacommunities depend on habitat patchiness and interspecific interactions within patches.[21,26]

The challenge in studying metacommunities is to determine the effects of climate change on processes at different scales, and to account for their synergy. Isolation and local abundance are two practical focal points for advancing a conceptual and empirical approach to understanding climate change impacts. Isolation and local abundance can be estimated empirically and related to ecological and evolutionary theory, and their responses to climate change can

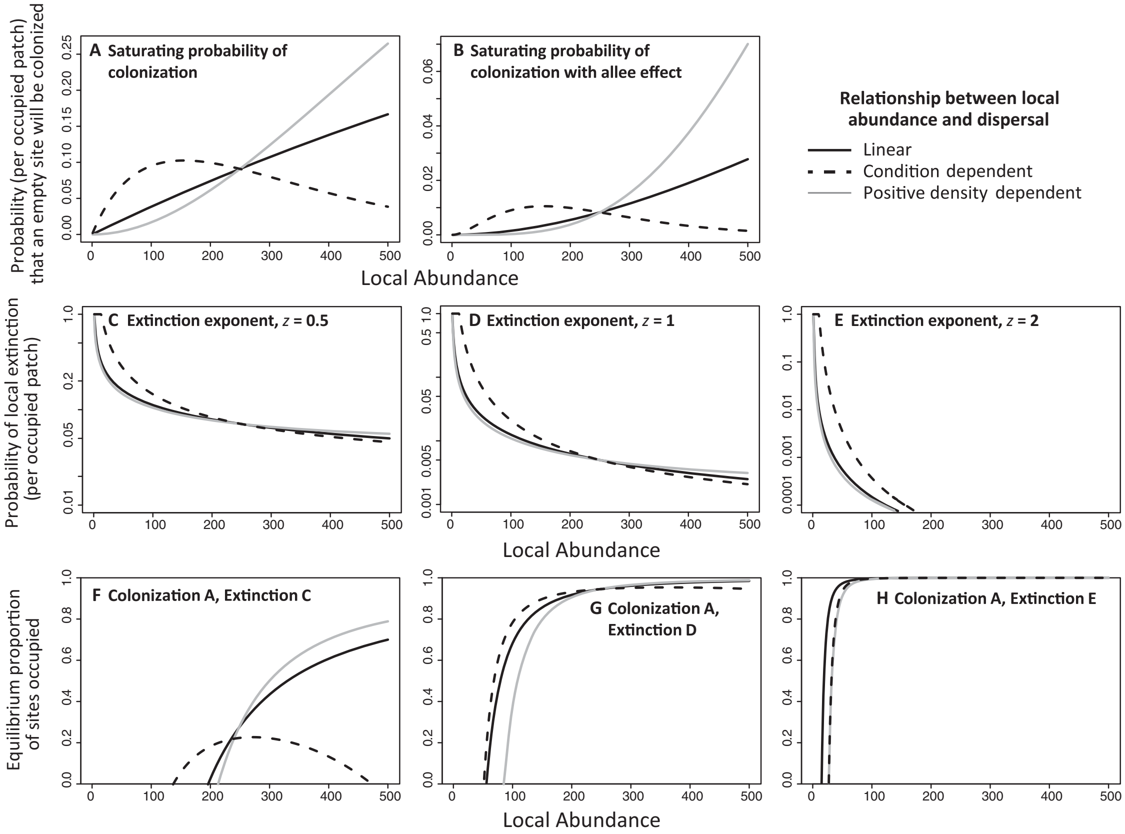

Figure 2. The relationship between local abundance, extinction, colonization of new sites, and regional frequency. Three dispersal strategies are shown, where the proportion of individuals dispersing shows a linear relationship to local abundance (black), a positive density-dependent relationship so that the proportion dispersing increases with local population size (proportion $= 1 - e^{(-\text{abundance} \times \text{constant})}$; gray), or a condition-dependent relationship where the proportion dispersing decreases as local abundance increases (proportion $= e^{(-\text{abundance} \times \text{constant})}$; dashed). All dispersal strategies are standardized to have the same proportion of individuals dispersing at a mid-level abundance (250 individuals). (A) Colonization is a saturating function of number of seeds successfully dispersing (s) and is described by a Monod function ($P(\text{colonization}) = s/(b + s)$, where b is the half-saturation constant). (B) Colonization is reduced by an Allee effect (using the Monod function in A raised to the exponent 2). Panels C–E show extinction functions as $P(\text{extinction}) = 1/n^z$, where z is the extinction exponent. Panels F–H give the equilibrium abundance that results from the combination of the saturating colonization function and each extinction exponent.

be studied using experiments, models, and observations. We illustrate how they can be used to estimate species climate change responses both locally and regionally.

Scaling from local to regional processes in metapopulations

The challenge of understanding local and regional dynamics, and how they interact, requires a method for integrating changes at both scales. We can move toward this understanding for metacommunities by first considering the simpler case of how local and regional population dynamics are related in metapopulations. Although climate change can influence local and regional processes in surprising ways,[3,10,36,39] the abundances of local populations provide a clear link between the local and regional dynamics of most metapopulations[26,30,40–43] (Fig. 2). For example, local extinction rates are well predicted by local population size;[30,40,44,45] the number of dispersing individuals from a patch is often a positive function of local abundance[26,46] (Fig. 2A and B); and the genetic variance and fitness of populations are correlated to population size.[31,47] As a result, regional abundance scales monotonically with mean local abundance in most metapopulations, although the functional form of this scaling depends on the exact relationships between abundance, dispersal, and extinction.

Despite the importance of local abundance for linking local and regional dynamics, predicting the regional implications of changes in local abundances is not trivial. As an example, consider the hypothetical species illustrated in Figure 2G. For the gray species, a drop in local abundance from 200 to 100 individuals/patch would cause a drastic regional decline, causing it to disappear from about 75% of previously occupied patches. In contrast, if the black or dashed species experienced the same drop in local abundances, their regional frequencies would only drop by 10–15%. However, a mere 20% decline in local abundance of the black species would drive it to extinction if it initially had a local abundance of 70 individuals. These scenarios highlight the need to quantify how local processes scale to regional abundances, and vice versa, in order to predict the effects of climate change.

Just as changes in local abundances impact regional distributions in metapopulations, changes in the dispersal of individuals among habitat patches can have surprisingly large impacts. For example, warmer temperatures are sometimes associated with a decrease in the size of individuals within a population;[48] smaller individuals have shorter dispersal distances for plants[49] and some insects,[50] effectively reducing the connectivity of the landscape. Similarly, temperature alters development rates of the larvae of marine animals, modifying survival and dispersal rates, and potentially reducing connectivity in warming oceans by decreasing the length of time that larvae disperse.[35,51] The same phenomenon may result from physical changes to the landscape, such as decreases in the number and connectivity of vernal pools with increased warming or drought.[39]

Changes in connectivity may be coincident with decreases in local abundance. However, the impacts are distinct. Because dispersal kernels often decay exponentially with distance, changes in connectivity can have disproportionate impacts on the viability of metapopulations.[26] In addition, certain patches in a landscape can have far larger impacts on overall metapopulation viability than other patches of equal carrying capacity simply because they create important spatial links.[37,41,52] These details of metapopulations are too complex to capture in simple (spatially implicit) models, but are nonetheless critical to understanding the viability of metapopulations. Fortunately, recent mathematical and statistical advances in spatial ecology[52,53] allow for these impacts to be quantified.

Although the exact regional dynamics of metapopulations depend critically on the distribution of habitats, these dynamics can still be qualitatively captured with heuristic models (Fig. 2).[37] These models highlight two critical metapopulation processes that must be well understood to predict the effects of climate change. First, absolute local abundance and change in this abundance need to be known to correctly scale the impacts of local dynamics to regional outcomes. Second, this scaling will depend on regional processes of colonization and extinction, which cannot be inferred from local dynamics alone. Although complete knowledge of these two processes is lacking for the vast majority of organisms, biologists cannot ignore them and still hope to predict the long-term consequences of climate change.

Fortunately, there are several methods available for quantifying the metapopulation processes that link local and regional abundances. The most appropriate approach for a given study area depends on the data available. For well-studied species, information may be available to model both local and regional dynamics. For example, work by Clark *et al.*[54–57] provides estimates of the local impacts of climate change on tree communities as well as species' dispersal abilities; this work can be coupled with landscape information to model metacommunity processes in a given region.[54–57] In cases where data are more scarce but include patch-occupancy data from one or more time periods, the incidence-function approach can be used to parameterize metapopulation models.[40,46] The incidence-function approach relies on regional abundances reflecting quasi-equilibrium conditions, and is appropriate when at least one snapshot of patch-occupancy data is from historical (predisturbance) sampling. Unfortunately, these types of data are not present for many species, as data are often collected following changes to metapopulation dynamics, such as reductions in species abundances or alteration of the landscape.[26,58,59]

A third approach to estimating the impact of global change on metapopulations, the relative viability approach, was recently developed for metapopulations that have undergone some degree of change.[26] It couples experiments with sampling data to determine the change in metapopulation viability that results from a given change such as species invasions or climate change. The relative viability approach requires measurement of comparatively few parameters and can be used to partition the effects of local and regional processes on metapopulation viability.[26] As the name implies, this approach provides a measure of the relative viability of a species, which is used with information on the species before climate change to estimate extinction risk and long-term viability.

Species interactions in space: moving from metapopulations to metacommunities

There are a number of important processes that structure metacommunities (Fig. 1). First, when considering a single focal species, any change to local dynamics that increases carrying capacity will scale up to a higher regional abundance when the local to regional scaling is a positive function. Similarly, any change that increases local extinction rates, such as an increase in temporal environmental variability, will cause a decrease in regional abundances. Finally, increasing the connectivity of patches, either by changing the dispersal success of the species or altering the landscape, results in higher regional abundances. These predictions are intrinsic to all metapopulation models, and are sufficient when researchers are interested in a single species. However, they are not sufficient to capture the dynamics of multiple interacting species in a community.

Understanding how species interactions influence local and regional processes is key to scaling from metapopulations to metacommunities. Clearly, interactions that alter local abundances of one species have a direct effect on that species' extinction and colonization rates within a patch.[26] More difficult to predict is how this direct effect changes the probability of the two interacting species co-occurring in other patches, and thus the regional outcome of local interactions.[13,60,61] In addition, one species in a metacommunity may influence another species' regional dynamics more directly, by altering establishment rates within patches,[32] emigration rates from patches,[62] or changing its ability to disperse through the matrix area between patches.[26] The processes that can affect a metacommunity are too diverse to comprehensively review, and often researchers' insights into the natural history of a system expose novel processes. For example, Altermatt *et al.*[36] demonstrated that dispersal among rock pools increased for several *Daphnia* species with warming, but that warming nonetheless favored some species more than others because of differences in dispersal dynamics.

Despite the diversity of processes that can alter metacommunity dynamics in a changing climate, the impacts on species in metacommunities may be fairly general. To consider these impacts, we introduce two metacommunity modules that have qualitatively different local dynamics.[2,13] The specific models and assumptions are given in the Appendix. In general, the models differ in that one considers competitive interactions between two species, whereas the other examines facilitative interactions. In both cases, we consider two scenarios: how gradual, temperature-dependent decreases in carrying capacity alter local and regional dynamics, and how gradual changes in colonization of one species influences the local and regional dynamics of both species. The changes in dispersal or carrying capacity that we model are predicted from the gradual physiological changes that result from the temperature-dependency of metabolic rates.[4,66,67] The case studies that we highlight were chosen to illustrate when these gradual changes generate dramatic changes in regional dynamics.

When climate change gradually decreases carrying capacity of competing species (see Appendix), species can have very different responses regionally even if their local responses are similar to each other (Fig. 3A–C versus Fig. 3D–F). Local declines in both species result in the rapid regional decline of one competitor, but a relatively small decrease in the abundance of the other competitor (Fig. 3A–C). For example, when temperatures change from 20 to 24 °C, the hypothetical gray species in Figure 3A becomes extinct, dropping its regional abundance by more than 20%. This large drop in regional abundance coincides with a fairly small change in local abundance (Fig. 3B). This apparent contrast between local and regional impacts of temperature change results from the change in realized competition that the more abundant species experiences; as its competitor decreases regionally, the number of patches where it experiences competition falls, which compensates for the direct negative effect of temperature change. Meanwhile, the

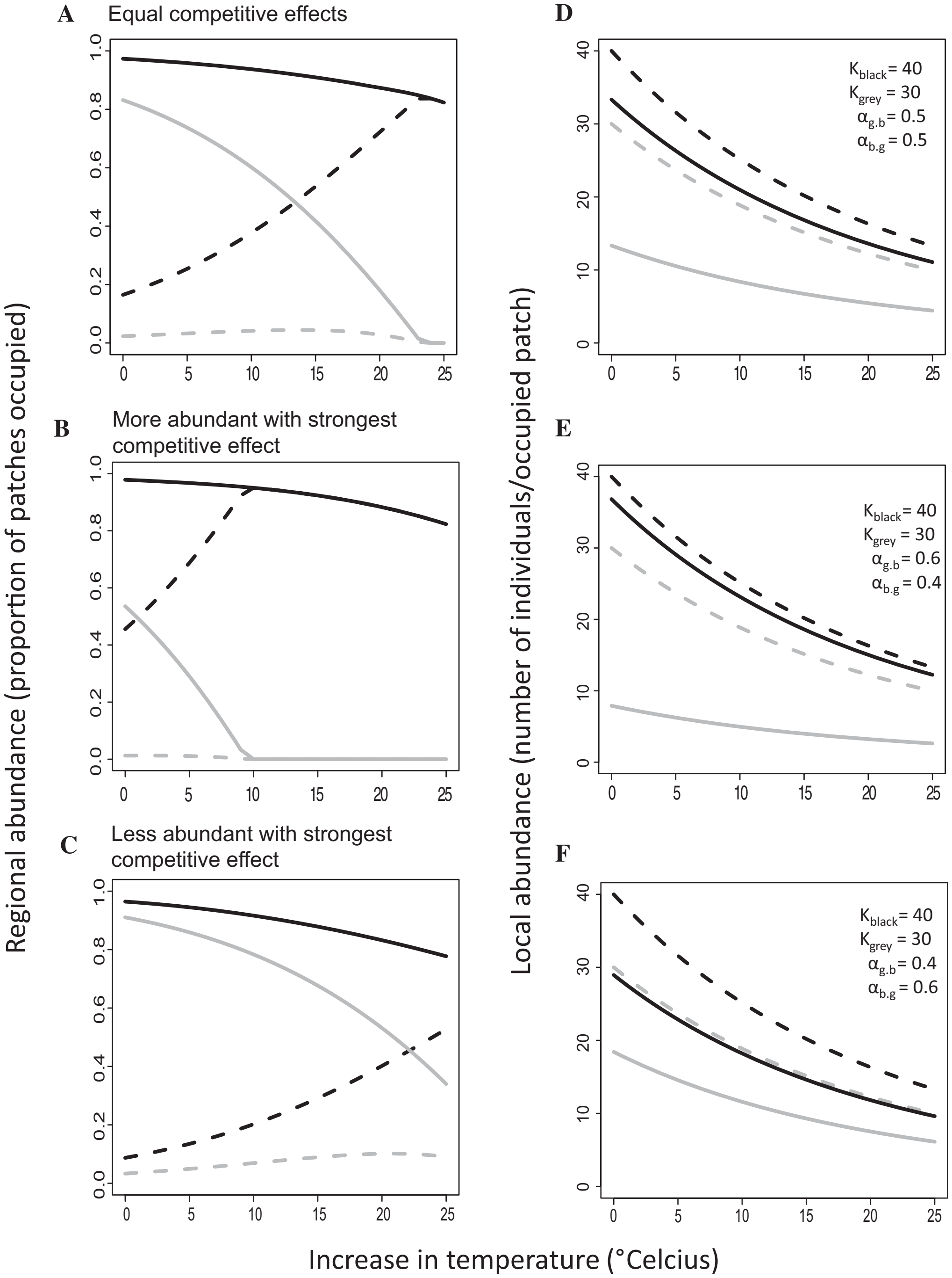

Figure 3. Changes in regional and local abundance in competitive metacommunities with warming. When carrying capacities of competing species decrease with warming, metacommunity processes cause divergent responses in regional abundances (A–C; solid lines represent the total proportion of sites occupied and dashed lines represent sites in which a species occurs alone). Local dynamics for each regional outcome are given in panels D–F, with solid lines representing abundances when species occur together and dashed lines representing abundances when a species is alone. Parameters for the competition model (Appendix) are given in each panel, with the proportion of individuals dispersing set at 0.2, and the proportion successfully colonizing other sites set at 0.04.

less abundant species experience local abundances that are low enough for its extinction rate to approach its colonization rate when its competitor is present, causing rapid declines that ultimately help its competitor. This general trend occurs when per capita competition coefficients favor the more abundant (Fig. 3B and E) or less abundant species (Fig. 3C and F).

The effect of a decrease in carrying capacity following climate change is markedly different for species that facilitate each other (Fig. 4). In this case, regional abundances of both species decrease as carrying capacity declines, and this decrease is on average steeper than observed for competing species (Fig. 4A–C versus Fig. 3A–C). The steeper regional decline results from positive feedback between local and regional processes, whereby decreases in local abundances decrease colonization and increase extinction rates. This results in lower regional abundances, and thus less co-occurrence within patches, which further reduces local abundances (Fig. 4D–F, solid versus dashed lines). As a result, species that facilitate each other can show very steep and correlated declines in abundance when carrying capacities decline even gradually, as could occur with small shifts in temperature. This phenomenon can cause species to go from relatively abundant (present in 20–40% of patches) to regionally extinct with a fairly small (3 °C) change in temperature (Fig. 4A–C), even though changes in local abundance over this temperature are minor and no acute thermal stress is invoked (Fig. 4D–F).

Climate change can also impact metacommunities by altering dispersal dynamics directly (Fig. 5). In the example of *Daphnia* dispersing among rock pools, the authors noted that dispersal is more sensitive to climate for some species than others.[36] We model these dynamics for two interacting species that vary in how temperature impacts their dispersal success (Fig. 5A and B). A change in a species' per capita colonization rates always strongly affects its regional abundance (Fig. 5C and E), and can often have a large effect on interacting species as well. For example, when the colonization rate of the species with the larger carrying capacity falls, the species' regional abundance also decreases, promoting its competitor (Fig. 5D). This competitive release at the regional scale could be falsely interpreted as one species driving the other extinct. The same effect on colonization in a facilitative metacommunity has the opposite effect on the partner, lowering its regional abundance either slightly or to a larger degree (Fig. 5E and F).

The simultaneous response of local and regional dynamics to climate change has a multiplicative effect on species viability.[26,52] In other words, if a loss in carrying capacity (Fig. 3D) were to occur simultaneously with a decrease in per capita colonization rates (Fig. 5A), the overall effect would be much greater than what we would expect by simply adding the effect of each of these processes in isolation.[26] When other nonlinear processes, such as Allee effects (Fig. 2A), are included, the overall effects are still greater.[52] Although it is often difficult to study multiple processes simultaneously, the multiplicative nature of metacommunity dynamics highlights the need to identify and jointly quantify the important local and regional effects of global changes.[26]

Lessons for global change biologists

The challenge of incorporating metacommunity approaches into global change science is significant. Research to date highlights the importance of considering multiple processes at various scales simultaneously,[20,26,36,39,63] what we have loosely termed local and regional processes. Although it is clear that understanding local population and community processes is a good starting point, it is essential that biologists take the next step to link these to regional processes. For example, explicitly relating local and regional dynamics requires understanding how colonization and emigration rates depend on intra- or interspecific interactions[52,62] (Fig. 2). Similarly, estimates of regional processes, such as individual dispersal distances, are essential to fully understand metacommunity dynamics.[28,34,35,57]

Despite the importance of correctly identifying and quantifying both local and regional processes, many studies would greatly benefit from incorporating metacommunity processes even when some of these processes are not completely understood. For example, seed dispersal plays an important role in plant metacommunities but is very difficult to quantify.[63] One approach that can be used is to incorporate general dispersal kernels into this research,[27,28,35,49,57] and test the sensitivity of predictions to reasonable levels of variation in dispersal estimates. Similarly, although it is important to understand the relationship between abundance and

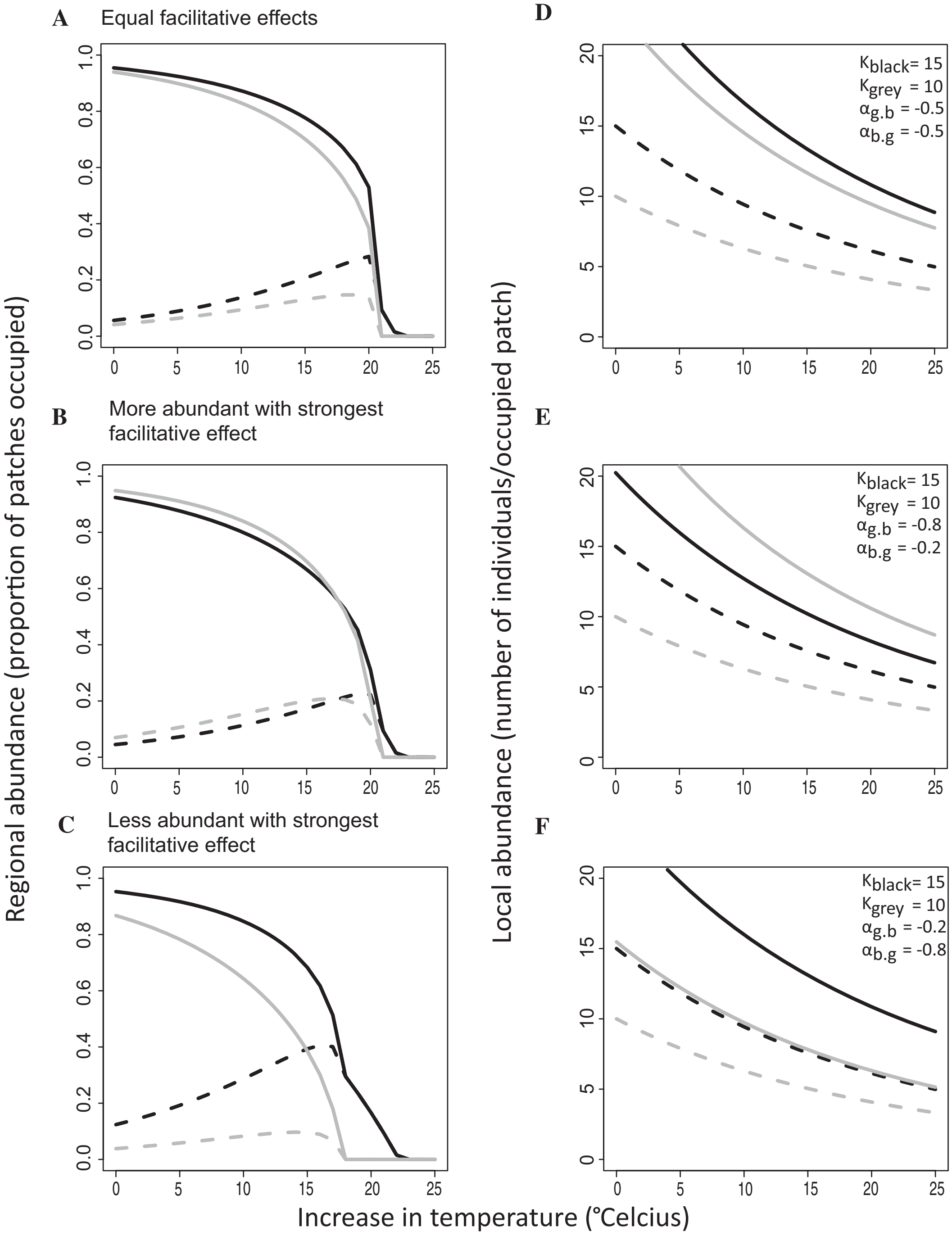

Figure 4. The direct effect of temperature on carrying capacity and the resulting regional dynamics in a mutualistic metacommunity. Lines (solid vs. dashed) are as in Figure 3. Parameters for each species are given in the top right corner, with the proportion of individuals dispersing set at 0.2 and the proportion successfully colonizing other sites set at 0.04. Full model details are given in the Appendix. Species carrying capacities were chosen so that the mean local species abundance for co-occurring species was similar for the facilitative and competitive (Fig. 3) scenarios.

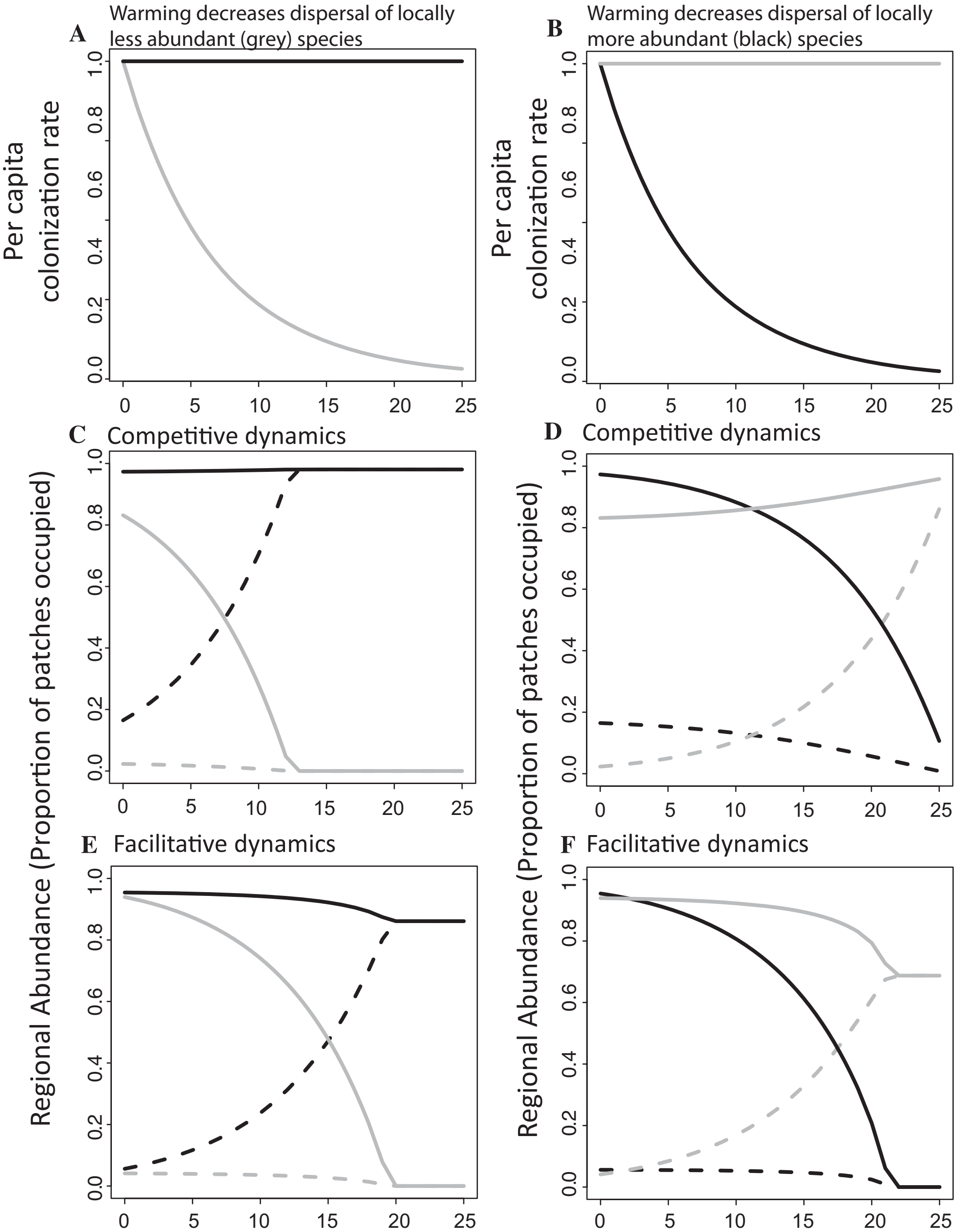

Figure 5. Warming influences dispersal. The direct effects of temperature on per capita colonization rate (A, B) and the resulting regional dynamics in a competitive (C, D) and mutualistic (E, F) metacommunity. Panels C–E illustrate regional abundances (proportion of sites occupied) at each temperature, with solid lines representing the total number of sites occupied and dashed lines representing sites in which a species occurs alone. Panels C and E correspond to the changes shown in panel A, and panels D and F correspond to panel B. Local dynamics for the competitive metacommunity are modeled with parameters $\alpha_{1,2} = \alpha_{2,1} = 0.5$, $K_{\text{black}} = 40$, $K_{\text{gray}} = 30$. Local dynamics for the mutualist metacommunity are modeled with parameters $\alpha_{1,2} = \alpha_{2,1} = -0.5$, $K_{\text{black}} = 15$,$K_{\text{gray}} = 10$. Full model details are given in the Appendix.

number of individuals dispersing[39] (Fig. 2), most biologists use a linear relationship as a starting hypothesis.[37,46]

The approach of incorporating metacommunity processes before they can all be fully tested requires biologists to recognize that our understanding of every ecosystem is simply a working hypothesis that needs improvement. We advocate beginning with the simplest metacommunity models, and then building on or revising these models as their predictions or assumptions are proven to be inadequate. Although simple models may be incomplete, they have provided insights into the effects of global changes ranging from habitat loss[37,41,64] to invasions[26,65] to climate.[36] Moreover, including even an incomplete knowledge of regional dynamics into research is likely more correct than ignoring them altogether, and this process will lead to a more rapid increase in understanding how to jointly consider local and regional dynamics.[11]

Metacommunity research has not only highlighted gaps in traditional research programs, but also has identified key concepts that are important but poorly understood even in well-developed metacommunity models. One of these concepts is the link between metacommunity dynamics and range shifts. Although species in metacommunities must have reasonable dispersal abilities to persist, their movement into new areas (i.e., range shifts) is also more restricted than that of species in continuous habitat. This restricted movement occurs because dispersal into patchy landscapes relies heavily on the rate of population build-up in the new area, with larger populations more able to jump to new habitat patches.[38] As a result, we expect species in patchy habitats to shift ranges in discrete jumps. The role of fat-tailed dispersal kernels may be less relevant to population spread in such cases, at least for species that disperse passively or that show an Allee effect.[38] The interplay between this slower, discontinuous dispersal and interactions with resident species requires more theoretical and empirical research.[61]

Extinction debts are also important but poorly quantified in metacommunities. An extinction debt arises any time a change to the metacommunity causes the delayed but deterministic extinction of species. For example, early research showed how habitat destruction could drive the extinction of species in a metacommunity 50 to over 1000 years after habitat destruction.[24] Subsequent work has shown that this delay depends on how close a given species is to its extinction threshold, the point at which habitat destruction is sufficient to drive it extinct.[41] Despite these examples from models, biologists have relatively little data on extinction debt timelines in real ecosystems.[59] Without these, it will be difficult to understand whether short-term persistence may in fact lead to extinction in metacommunities.[26]

In summary, metacommunities represent a great challenge and opportunity to global change biologists. The interplay of local and regional processes that is central to metacommunities is also increasingly important for all species faced with changing local habitats, range shifts, and changing interactions with other species experiencing similar processes. The growth of metacommunity research in global change biology promises to further our understanding of fundamental ecological concepts as well as provide a backbone for predicting and mediating the biotic effects of global climate change.

Appendix

Our heuristic model assumes that the dynamics of each species when alone is modeled by consumer-resource dynamics. Within a patch occupied by species i

$$\frac{dN_i}{dt} = ucN_iR - mN_i, \quad \text{(A1a)}$$

$$\frac{dR}{dt} = s - uN_iR, \quad \text{(A1b)}$$

where R is the resource, N is the population abundance, u is the uptake rate, c is the conversion rate, and m is the per-capita mortality rate. The parameter s describes the supply rate of the resource. With nontrivial equilibria of

$$\hat{R} = \frac{m}{uc}, \qquad \hat{N}_i = \frac{sc}{m}, \quad \text{(A2)}$$

the parameters u and m (the species uptake and mortality) are temperature dependent, whereas conversion (c) is not.[4,66,67] The supply rate of (abiotic) resources (s) depends on the processes that provide the limiting resources; here, we assume either that the supply rate is independent of temperature or that it changes at the same rate as plant mortality. The equilibrium value for the resource (Eq. A2) is also termed the $R*$ of the species. This value determines competitive outcomes when species are competing for a single resource, with the species with the lowest $R*$ being the best competitor.[68] Mortality increases with temperature and is well modeled by the Boltzmann–Arrhenius function:

$$m(T) = be^{\frac{-E_{\mathrm{m}}}{kT}}, \tag{A3}$$

where b is a species-specific parameter, k is Boltzmann's constant, T is temperature in Kelvin, and E_m is the activation energy of mortality that specifies the species temperature response curve.[67] Incorporating (Eq. A3) into the equilibrium N (Eq. A2) has no effect on the carrying capacity of the focal species (K) when the supply rate changes at the same rate. However, when the supply rate does not change, it changes the equilibrium abundance at the rate:

$$K \propto e^{\frac{E_{\mathrm{m}}}{kT}}. \tag{A4}$$

For plants, we use 0.32 as the activation energy of mortality.[4] A similar result is obtained when considering herbivores that eat common plant species so long as the activation energies of the plants are lower than those of the herbivores. In this case, an approximate change in carrying capacity of the herbivore is given by the quotient of the activation energies of the herbivore feeding rate (E_h) and the plant growth rate (E_p), $e^{(E_{\mathrm{h}}-E_{\mathrm{p}})/(kT)}$, which is 0.33 on average.[4]

Our two metacommunity models examine facultative mutualisms and competitive dynamics that are not sufficiently strong to drive species extinct locally (weak competition[13]). Local dynamics are modeled with the general Lotka–Volterra competition model

$$\frac{dN_{\mathrm{i}}}{dt} = rN_{\mathrm{i}}\left(1 - \frac{N_{\mathrm{i}} + \alpha_{\mathrm{ij}}N_{\mathrm{j}}}{K_{\mathrm{i}}}\right). \tag{A5}$$

In this model, r is the population growth rate and α measures the competitive (facilitative) impact of species j on i when positive (negative). Note that, in the competitive model, the interaction coefficients can emerge from species having partial overlap of resource use or by interfering directly with each other. In the facilitation model, the interaction coefficients are best understood by the decrease in mortality rates that occurs when species co-occur. The two-species, nontrivial equilibrium for species i is:

$$\hat{N}_{\mathrm{i}} = \frac{K_{\mathrm{i}} - \alpha_{\mathrm{ij}}K_{\mathrm{j}}}{(1 - \alpha_{\mathrm{ij}}\alpha_{\mathrm{ji}})}. \tag{A6}$$

And the equilibrium for j is identical with subscripts switched. For these two models, we assume that interaction coefficients (α) are independent of temperature so that changes in interactions with temperature are only modified by changes in resource consumption and K (Eqs. A2 and A4). When carrying capacity changes with temperature (Eq. A4), the functional form of the equilibrium populations (Eqs. A4 and A6 appear as in Figures 3D–F and 4D–F).

Metacommunity dynamics: We use a simple, spatially implicit metacommunity with equal patch qualities to illustrate the commonalities and differences between competitive and facilitative models. For our exploration of metacommunity processes, we use the following rules to scale from local to regional dynamics:[41]

$$c_{\mathrm{A}} \propto K_{\mathrm{A}},\ e_{\mathrm{A}} \propto \frac{1}{K_{\mathrm{A}}} \tag{A7a}$$

$$c_{\mathrm{AB}} \propto \hat{A}_{\mathrm{Bpresent}},\ e_{\mathrm{AB}} \propto \frac{1}{\hat{A}_{\mathrm{Bpresent}}}. \tag{A7b}$$

Here, c_A represents the colonization rate of species A from sites occupied by species A alone or by both A and B (c_{AB}), and e is the extinction rate. The dynamics for species B are symmetric (i.e., the subscripts are switched).

For species A and B, the scaling of local to regional dynamics are given by Eqs. A7a and A7b, and the regional dynamics are defined a:

$$\begin{aligned}\frac{dA}{dt} &= c_{\mathrm{A}}A(1 - A - B - AB)\\ &\quad + c_{\mathrm{AB}}AB(1 - A - B - AB) + e_{\mathrm{BA}}AB\\ &\quad - e_{\mathrm{A}}A - c_{\mathrm{B}}B \times A - c_{\mathrm{BA}}AB \times A,\end{aligned} \tag{A8a}$$

$$\begin{aligned}\frac{dAB}{dt} &= AB(c_{\mathrm{AB}}B + c_{\mathrm{BA}}A) + c_{\mathrm{B}}B \times A + c_{\mathrm{A}}A\\ &\quad \times B + (1 - A - B - AB)\,t(c_{\mathrm{A}}A \times c_{\mathrm{B}}B\\ &\quad + c_{\mathrm{A}}A \times c_{\mathrm{BA}}AB + c_{\mathrm{AB}}AB\\ &\quad \times c_{\mathrm{B}}B + c_{\mathrm{AB}}AB \times c_{\mathrm{BA}}AB) - e_{\mathrm{BA}}AB\\ &\quad - e_{\mathrm{AB}}AB,\end{aligned} \tag{A8b}$$

where AB represents patches occupied by both species A and B, and the regional dynamics of species B are symmetric to those of A (i.e., Eq. A8a with subscripts switched). To model the effect of changing colonization rates, we specify the proportionality constant in Eq. A7 and vary this constant as a function of temperature (Fig. 5A and B).

Conflicts of interest

The authors declare no conflicts of interest.

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