**Adaptation and dispersal interactively determine the composition, structure, and biodiversity of future ecological communities.**

How do ecosystems reorganize when the environment changes? This question remains one of the greatest and most pressing challenges facing ecologists today (Urban et al. 2016). When the environment changes, organisms must adapt, move, or attempt to persist in the new conditions (O'Connor et al. 2011). Species are likely to differ in these responses and so we expect that communities of the future will differ in their composition from those that we see today (Williams and Jackson 2007). It is, however, unclear whether ecosystems will retain their biodiversity, food web structure, and functioning as this reorganization plays out. To address this challenge, we must develop theory on how ecological and evolutionary processes combine to determine how ecological communities reorganize when the environment changes.

From an ecological perspective, community reorganization largely depends on species sorting, the process by which species shift their distributions to track favourable environmental conditions (Leibold et al. 2004). Species sorting allows for the maintenance of biodiversity and ecosystem functioning in changing conditions (Loreau et al. 2003), and can maintain the structure and composition of ecological networks, such as food webs, if species track environmental conditions at the same rate (Thompson and Gonzalez 2017). Species interactions generally impede species sorting, which rewires ecological networks by causing asynchronous range shifts and extinctions

(Tylianakis et al. 2008, Urban et al. 2012, Alexander et al. 2015). However, metacommunity theory suggests that the degree to which species interactions can impede species sorting is highly dependent upon the rate at which species move between local habitats on the landscape; when dispersal rates are sufficiently high, species interactions have minimal impacts on species sorting, so ecological networks remain intact as their component species respond to environmental change (Thompson and Gonzalez 2017).

Species can also deal with changing environmental conditions through adaptation, which, if fast enough, can provide evolutionary rescue (Gomulkiewicz and Holt 1995, Gonzalez et al. 2012). Evolutionary rescue is promoted by low rates of dispersal across a gradient of environmental conditions (Bell and Gonzalez 2011), because by combining species sorting and adaptation, lower rates of evolution are required for rescue. However, dispersal can also hinder adaptation if dispersal rates are sufficiently high to cause maladaptation through gene swamping (Lenormand 2002). When species compete for resources and local habitats span a gradient of environmental conditions, dispersal can impede adaptation because species sorting offers an alternative strategy for dealing with environmental change (de Mazancourt et al. 2008, Norberg et al. 2012). However, despite considerable knowledge of the processes that allow for evolutionary rescue, we have little understanding of how evolution affects the reorganization of ecological networks in changing environments.

Current theory that incorporates both ecological and evolutionary dynamics highlights the interactive nature of these processes in determining the response of communities to environmental change. Broadly, the relative contribution of ecological vs. evolutionary processes in determining the response of communities to environmental change should depend on whether the future conditions that they experience have a present-day analogue; species sorting is a viable option in regions where future conditions have a current analogue but in regions with no current analogue, evolutionary processes should dominate (Norberg et al. 2012). Experimental evidence from soil microbe metacommunities suggests that evolutionary rescue can allow for viable communities to be maintained in novel stressful environments, and that this is promoted when local communities are connected by dispersal (Low-Décarie et al. 2015). However, this community rescue was characterized by considerable compositional reorganization and possibly a loss of diversity at the metacommunity scale. Clearly, community reorganization under environment change will depend on the interplay between species interactions, dispersal, and evolution. Understanding this interplay is therefore critical for making predictions about the composition, structure, and functioning of future communities.

Here we ask: how do evolution and dispersal jointly affect the reorganization of communities as they respond to environmental change? Other than in the unlikely scenario where rates of adaptation are equal across all species, evolution is likely to cause regional biodiversity loss as fast evolving species impede species sorting by slower evolving species, making them more likely to go extinct (de Mazancourt et al. 2008) (hypothesis I). Furthermore, we expect that evolution should lead to the rewiring of ecological networks as novel species combinations and interactions are formed and current ones are lost (hypothesis II). In addition, rates of evolution for many species, such as those in higher trophic levels, will be too slow for evolutionary rescue. However, we predict that these species may persist better if species that they rely on (e.g. as prey or through mutualist relationships) are able to evolve (hypothesis III) (Abrams and Matsuda 2005, Schröder et al. 2014). Finally, we expect that dispersal and evolution, both independently and in concert, will act to maintain the structure of ecological networks, even if there is turnover in the biotic interactions that make up that structure. These hypotheses mainly apply to communities in environments that have a historical analogue and so we mainly focus on these cases, although we do consider the implications of evolution and dispersal in non-analogue conditions.

**Methods**

*Model description*

The evolving metacommunity dynamics were simulated in R v. 3.4.2 using an individual based model. The model consists of species in patches, spanning an environmental gradient. The reproductive output of each individual is determined by a random draw from a poisson distribution. The expected value of this distribution for individual of species at time is equal to:

1. ,

where is its intrinsic rate of increase, is the effect of the local environment on its fitness, is the per capita effect of individuals of species on individuals of species , and is the abundance of species in patch at time . This assumes that per capita interaction strengths are equal across all individuals in a species and that all individuals in a patch interact equally. Equation 1 is formulated such that when the positive (, positive species interactions) and negative parameters balance each other (, negative species interactions) individuals produce, on average, one offspring. Because the per capita interaction strengths are multiplied by the population abundances , negative interactions result in density dependence.

The effect of the local environment on individual fitness is governed a Gaussian response curve:

1. ,

where is the environment in patch at time , is the environmental optima of individual , and is the rate at which fitness decreases as the distance between and increase. We assume an equal value of for all species for simplicity and to focus fitness differences in our model on the match between each individual and its local environment as well as its interactions with other individuals.

We assume that reproduction is asexual, and that is drawn from a normal distribution with a mean value equal to that of the parent, and a standard deviation equal to a mutation value of . Mutation values for each species are drawn from a normal distribution with a mean of and a standard deviation of to allow for interspecific differences in evolutionary potential. This is not intended to replicate any specific mutation process, but rather acts as a simple mechanism by which to generate variation in which can be selected upon by the local environmental conditions. For simplicity, and to focus our analysis on the effects of local environmental adaptation, we do not allow other species traits to evolve.

Dispersal occurs following reproduction, and the chance that an offspring disperses is governed by a binomial distribution, with a probability equal to . Values of are drawn from a normal distribution with a mean of and a standard deviation of . Values of are constrained to the range of 0 to 1. We draw values of from this fixed distribution rather than based on the values of the parent to prevent dispersal rates from evolving. Allowing dispersal to evolve would be an interesting next step, but we have elected not to allow it so that we can focus on the interaction between species sorting and local adaptation. Dispersing individuals leave their natal patch and disperse to one of the adjacent patches with equal probability. Following dispersal, individuals remain in the same patch for the remainder or their lives. At each time step, each individual has a 50% probability of surviving to the next time step. We chose to allow individuals to survive more than a single time step to prevent populations that are above carrying capacity (i.e. ) from going extinct because all individuals fail to reproduce.

Patches in the metacommunity are arranged in a ring with each patch connected to it’s two adjacent patches. This ring arrangement allows us to avoid edge effects in our landscape. We assume that the ring spans an environmental gradient such that:



where is amount to which the environment has changed from its initial state at time . This results in the environmental value increasing linearly from patch to , and then decreasing linearly in the same fashion for the remainder of the patches, so that the difference in the environment between patch and is equal to the difference between and . Environmental change is constant across all patches in the metacommunity, so that the initial environmental gradient is maintained through time, and occurs such that:

1. ,

where is the total amount of environmental change in that occurs in the simulation, is the duration of the period prior to environmental change, is the duration of the period when the environment is changing.

*Simulations*

We simulated metacommunities consisting of patches and 80 species. Species interaction parameters were generated such that most, but not all, species could co-exist locally. This was achieved by setting the per-capita effect of intraspecific competition, to be -1, and drawing rates of interspecific competition, from a uniform distribution between 0 and -0.5. We then randomly drew species pairs and gave them rates of interspecific competition drawn from a uniform distribution between – 1.18 and –1.22. This generated co-existence (provided that local environmental conditions were favourable) for species pairs where rates of interspecific interactions were weaker than rates of intraspecific interactions and led to alternative equilibria in cases where rates of interspecific interactions we stronger than rates intraspecific competition. In these alternative equilibria, the species that first colonized a patch could exclude their strong competitor, resulting in priority effects. In all cases we scale rates of interspecific interactions to . This allows for more stable dynamics, because it makes less sensitive to small changes in . We assumed that = 0.5 for all species.

We initialized the landscape by randomly choosing 5 patches for each species and adding 5 individuals to each of those patches. We then allowed the model to initialize for 1000-time steps, while we added a single individual from each species to each patch every 100-time steps. This allowed us to vary the order in which species colonized the patches, which allowed for priority effects to occur, but while still giving every species the chance to access every patch. We assumed that the initial environmental optima of the species spanned were equally spread across the initial range of environmental conditions, and that all initial individuals of a species shared the same value of .

We ran the simulation for a total of 30,000-time steps, with and . This gave sufficient time for the metacommunity to reach a quasi-equilibrium state before the environment began to change. It also ensured that environmental change was slow enough so that both dispersal and adaptation were viable strategies for persistence, depending on the specific parameters in the simulation scenario. We set to be equal to so that half of the patches would have a pre-change analogue for their environmental conditions.

We contrasted nine mean dispersal rates spanning the range from 0 to 0.1. We combined this with a factorial comparison of five levels of evolutionary potential spanning the range from 0 to 0.02. We also included a case where values of were drawn from a uniform distribution between 0 and 0.01 to explore the consequences of increased interspecific variation in evolutionary potential. For each combination of dispersal and evolutionary potential , we ran 50 replicate simulations, each time drawing a new set of species interaction values .

*Response variables*

We calculated the following summary statistics: local species richness, regional species richness, local biomass, ecological network similarity, ecological network link density, and the amount of evolution in the species’ environmental optima. In all cases other than for the evolution of species’ environmental optima, we estimated these as proportional change; the final value ( divided by the pre-change value (**.**

The ecological network in patch consisted of nodes, which were the species present in that patch at time , and the links were the interactions between those species, weighted by their realized interaction strengths, . We calculated link density using the NetIndices package in *R*. We calculated network similarity as the similarity between each final network and its most similar pre-change network. This similarity was calculated as the Bray-Curtis similarity of the weighted ecological networks:

where and are two different networks and is the weight of interaction in network .

In all cases, we averaged the response variables over all patches based on whether their final environmental conditions had an initial analogue or not. An analogue environment was define as being present within the initial range of environmental conditions in the metacommunity, while a no-analogue environment was defined by being outside of this range.

Abrams, P. A., and H. Matsuda. 2005. The effect of adaptive change in the prey on the dynamics of an exploited predator population. Canadian Journal of Fisheries and Aquatic Sciences 62:758–766.

Alexander, J. M., J. M. Diez, and J. M. Levine. 2015. Novel competitors shape species' responses to climate change. Nature 525:515–518.

Bell, G., and A. Gonzalez. 2011. Adaptation and Evolutionary Rescue in Metapopulations Experiencing Environmental Deterioration. Science 332:1327–1330.

de Mazancourt, C., E. Johnson, and Barrowman. 2008. Biodiversity inhibits species’ evolutionary responses to changing environments. Ecology Letters 11:380–388.

Gomulkiewicz, R., and R. D. Holt. 1995. When does evolution by natural selection prevent extinction? Evolution.

Gonzalez, A., O. Ronce, R. Ferriere, and M. E. Hochberg. 2012. Evolutionary rescue: an emerging focus at the intersection between ecology and evolution. Philosophical Transactions of the Royal Society B-Biological Sciences 368:20120404–20120404.

Ives, A. R., and B. J. Cardinale. 2004. Food-web interactions govern the resistance of communities after non-random extinctions. Nature 429:174–177.

Leibold, M. A., M. Holyoak, N. Mouquet, P. B. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–613.

Lenormand, T. 2002. Gene flow and the limits to natural selection. Trends in Ecology & Evolution.

Loreau, M., N. Mouquet, and A. Gonzalez. 2003. Biodiversity as spatial insurance in heterogeneous landscapes. Proceedings of the National Academy of Sciences of the United States of America 100:12765–12770.

Low-Décarie, E., M. Kolber, P. Homme, A. Lofano, A. Dumbrell, A. Gonzalez, and G. Bell. 2015. Community rescue in experimental metacommunities. Proceedings of the National Academy of Sciences 112:14307–14312.

Norberg, J., M. C. Urban, M. Vellend, C. A. Klausmeier, and N. Loeuille. 2012. Eco-evolutionary responses of biodiversity to climate change. Nature Climate Change 2:747–751.

O'Connor, M. I., E. R. Selig, M. L. Pinsky, and F. Altermatt. 2011. Toward a conceptual synthesis for climate change responses. Global Ecology and Biogeography 21:693–703.

Schröder, A., A. van Leeuwen, and T. C. Cameron. 2014. When less is more: positive population-level effects of mortality. Trends in Ecology & Evolution 29:614–624.

Thompson, P. L., and A. Gonzalez. 2017. Dispersal governs the reorganization of ecological networks under environmental change. Nature Ecology and Evolution 1:0162.

Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. Ecology Letters 11:1351–1363.

Urban, M. C., G. Bocedi, A. Hendry, J. B. Mihoub, G. Peer, A. Singer, J. R. Bridle, L. G. Crozier, L. De Meester, W. Godsoe, A. Gonzalez, J. J. Hellmann, R. D. Holt, A. Huth, K. Johst, C. B. Krug, P. W. Leadley, S. C. F. Palmer, J. H. Pantel, A. Schmitz, P. A. Zollner, and J. M. J. Travis. 2016. Improving the forecast for biodiversity under climate change. Science 353:aad8466–aad8466.

Urban, M. C., J. J. Tewksbury, and K. S. Sheldon. 2012. On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. Proceedings of the Royal Society B-Biological Sciences 279:2072–2080.

Williams, J. W., and S. T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. Frontiers in Ecology and the Environment 5:475–482.