The evolutionary ecology of metacommunities

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Research on the interactions between evolutionary and ecological dynamics has largely focused on local spatial scales and on relatively simple ecological communities. However, recent work demonstrates that dispersal can drastically alter the interplay between ecological and evolutionary dynamics, often in unexpected ways. We argue that a dispersal-centered synthesis of metacommunity ecology and evolution is necessary to make further progress in this important area of research. We demonstrate that such an approach generates several novel outcomes and substantially enhances understanding of both ecological and evolutionary phenomena in three core research areas at the interface of ecology and evolution.

Evolution in metacommunities

Both genetic diversity within populations and species diversity within communities vary from the local spatial scale, where organisms interact with one another, to the regional scale, where populations interact with one another. However, the study of biological diversity has largely been the purview of separate scientific disciplines: evolutionary biologists focus on understanding genetic diversity within populations and often ignore species interactions, whereas ecologists focus on understanding community dynamics and usually ignore evolution [1–3]. Most synthetic efforts to date have concentrated on local scales and simple ecological communities [4,5] (Figure 1; Table 1). Here we argue for a greater emphasis on the interplay between evolution in spatially structured populations and ecological dynamics in spatially structured communities

(termed 'metacommunities'). This is because joint evolutionary and dispersal dynamics can shape the species composition and diversity of natural communities [6–8].

Our overriding thesis is that the study of dispersal is crucial to understanding community assembly and richness because dispersal links focal communities with others that have different community and evolutionary dynamics [7,9]. The evolving metacommunity perspective emphasizes the roles of spatial variation and coupling (both through gene flow within species and dispersal among local communities), which together determine the (i) potential for local adaptation and species sorting (environmental filtering of species according to their traits) and (ii) spatial and temporal patterns of interspecific interactions (and,

Glossary

Evolving metacommunity: a set of local communities linked by the dispersal of multiple potentially interacting species in which genetically determined trait variation within species modifies the outcome of interspecific interactions.
Gene flow: the movement of genes between populations that subsequently contributes to the future gene pool of the recipient population.
Maladaptation: the phenotypic deviation of a population or organism from its potential adaptive peak at a locality.
Mass-effect: the net emigration of individuals from a larger population into a smaller population in a way that influences the recipient community's dynamics.
Metacommunity: a set of local communities that are linked by the dispersal of multiple interacting species.
**Monopolization hypothesis**: local adaptation enhances the rapid monopolization of resources by the first colonizer to a vacant habitat which results in reduced success of future invasions of genotypes or species.
Neutral species: species with identical demographic and evolutionary properties, such as birth, death and speciation rates.
Species sorting: a process by which species come to inhabit the locations most suited to their specific suite of traits owing to colonization and extirpation dynamics across heterogeneous patches.

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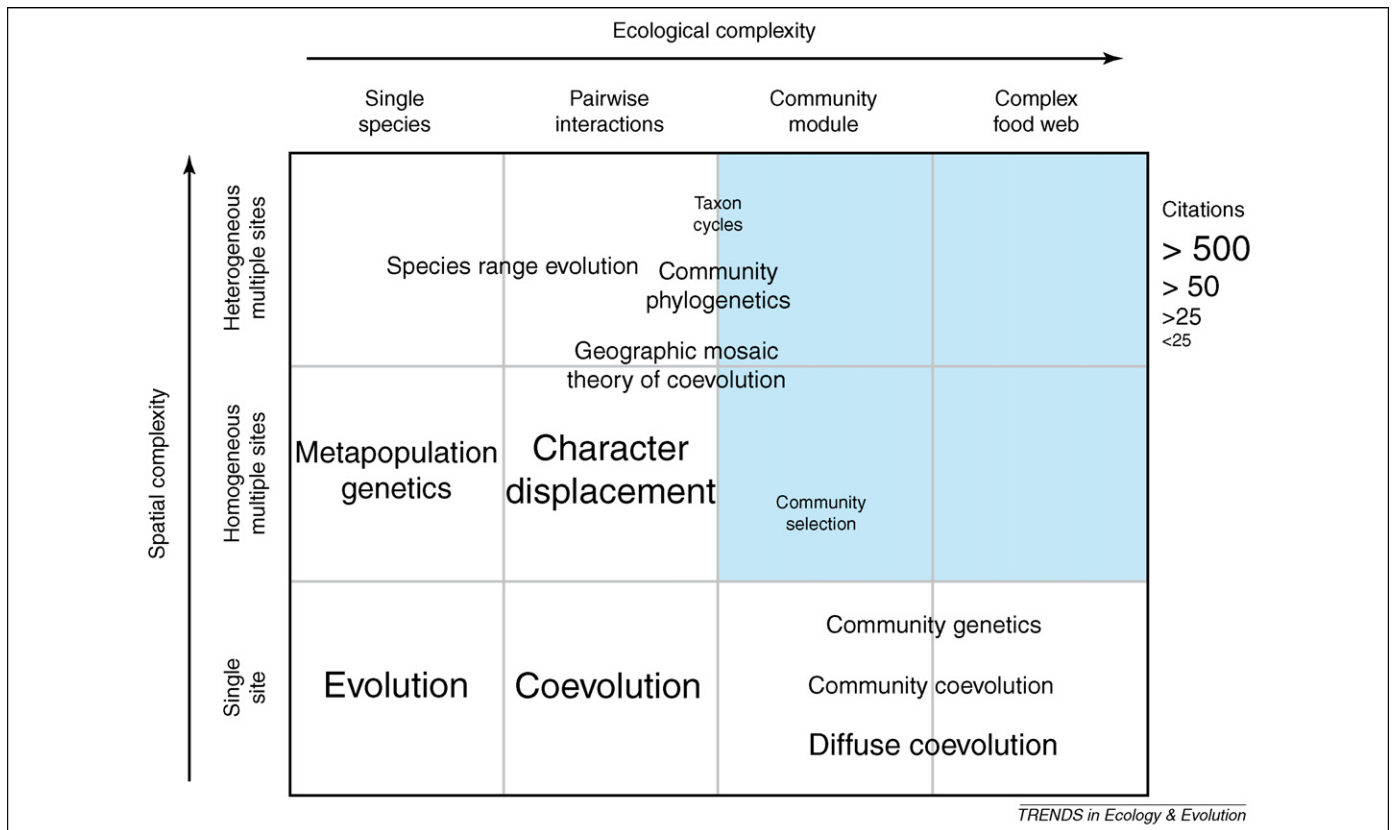
Figure 1. Current evolutionary ecology approaches depicted relative to spatial and ecological complexity. See Table 1 for the underlying premises of these approaches and their key citations. The position of each approach in this parameter space indicates its 'center of gravity' based on our review of literature discussing these concepts. Note that many of these frameworks currently are being extended to include more spatially and ecologically complex scenarios. Font size indicates the number of Web of Science citations (up to and including 2006) attributed to each approach through a search of relevant key words and a review of abstracts. The upper right corner identified in blue encompasses the parameter space relevant to an understanding of evolution in metacommunities.

hence, local selection) experienced by individual species. Our approach thus unites theories from metapopulation genetics [4] and metacommunity ecology [9]. When evolutionary and community dynamics occur at similar spatial and temporal scales, their interaction can generate community patterns that diverge from those predicted based on a separate understanding of ecological and evolutionary dynamics [10–13]. Here we outline three particularly compelling examples of developing research that examine joint evolutionary and ecological dynamics at metacommunity scales: adaptation in metacommunities, the evolution of food web structure in space, and the evolution of neutral and niche-determined mechanisms of diversity. These three cases yield important insights about the effects of dispersal and adaptation on community assembly, food web structure and mechanisms of species diversity. We argue that the 'evolutionary ecology of metacommunities' will facilitate our understanding of how biotas are distributed and how they respond to environmental change at larger spatial scales.

Table 1. Ecological and evolutionary approaches to spatial and ecological complexity, underlying premises and key references

Approach	Underlying premise(s)	Refs
Character displacement	Competition for shared resources among similar species favors evolutionary divergence	[43]
Community coevolution	Multi-species coevolution affects emergent community structure or ecosystem functioning	[44]
Community genetics	Intraspecific genetic diversity, often of a foundation species, influences dependent community patterns and ecosystem processes	[8]
Community phylogenetics	Patterns of genetic ancestry can be used to discern among competing hypotheses about the historical origin of species traits and their ecological distributions and abundances	[37]
Community selection	Multi-level selection on genetic diversity within and among communities can influence community-level trait composition and diversity	[45]
Diffuse coevolution	The evolution of two species in response to each other is altered by the occurrence of a third species	[36]
Geographic mosaic theory of coevolution	Species coevolutionary dynamics are determined by variation in natural selection on interspecific interactions across environments and populations, landscape patterns of reciprocal and nonreciprocal selection and trait mixing through mutation, gene flow, genetic drift and local population extirpations	[7]
Metapopulation genetics	Spatial population structure and extinction and colonization dynamics can shape evolutionary dynamics	[4]
Species range evolution	Spatial evolutionary and ecological dynamics, sometimes assumed to arise from interspecific interactions, determine species range boundaries	[46]
Taxon cycle	Over time, species progress through predictable periods of range expansion and contraction that are accompanied by associated adaptations and changes in ecological distributions	[47]

Adaptation in metacommunities

To understand adaptive evolution in a metacommunity, we must first discern how dispersal interacts with evolution to shape metacommunity processes. Dispersal plays two critical and parallel roles that together influence local community assembly and evolution within a metacommunity [14]. First, dispersal provides novel local trait variation by introducing new species that might drive community assembly and introducing new genotypes that might accelerate adaptation [15]. Second, high dispersal can homogenize communities and gene pools, thereby preventing species from closely tracking local environmental conditions and restricting local adaptation. At the community level, low dispersal keeps species from colonizing sites where their fitness is maximized, whereas high dispersal homogenizes local communities by distributing species into all habitats irrespective of their suitability (termed 'mass-effects') [16]. Therefore, species sorting is most likely to produce a close match between species composition and the environment only at intermediate dispersal levels [17]. Similarly, at the population level, limited gene flow enhances the efficacy of local natural selection and, hence, the process of local adaptation [18]. High gene flow can constrain adaptive evolution by swamping locally adaptive genes [19]. Hence, intermediate levels of dispersal and gene flow can maximize the match between community and population traits with local environments through species sorting and through natural selection.

Despite analogous effects on adaptation and species sorting, gene flow and immigration can affect local population and community trait dynamics differently along the same dispersal gradient (Box 1). These differences arise because not all immigrants become established and therefore contribute to the local gene pool [20], and because different levels of trait variation can be expected within and among species. Also, isolated populations still can respond to changing local conditions through *in situ* mutation, segregation and recombination, whereas species sorting requires colonization. Hence, the magnitude of trait responses at various dispersal rates differs depending on the level of biological organization under study.

This mismatch between the rates of adaptation and immigration is important because it can generate interactions between evolution and community assembly across a metacommunity. Imagine that a species colonizes a vacant habitat to which it is maladapted and that other species exist in the metacommunity that are better adapted to the new patch but have not yet arrived. The fate of the initial species will depend on how quickly it adapts to new conditions before a new species arrives and competitively excludes it [21] (Figure 2). If a species survives the early period of low fitness and better-adapted competitors are not forthcoming, then it might adapt and persist [22,23]. This race between local adaptation and immigration explains the coexistence of consistent sets of ecomorphologically diverged orbweaver spiders (*Tetragnatha*) on separate Hawaiian islands [24]. In this case, the particular species that fill the niches on each island originate from *in situ* speciation or as immigrants from other islands. Similarly, local adaptation and competitive

Box 1. The relative contributions of metacommunity dispersal, gene flow and local adaptation to trait responses in communities

Consider a set of heterogeneous patches populated either by species or populations with different traits that match local environments. Both evolution and species sorting can drive trait value changes that produce a better match between the traits of resident organisms and local habitat conditions [21]. Figure I depicts one expectation [18] of the amount of adaptive trait change (absolute difference between initial and final mean trait values in the population or community) due to selection on a population of haploid organisms subject to mutation, migration and selection (green solid line) and compares it to the expectation for a community (assumed to be clonal organisms) subject to migration and species sorting (red dotted line). We assume that interspecific trait differences are larger than intergenotypic trait differences within species. We also assume equal dispersal rates among all species in the metacommunity. At very low dispersal rates, natural selection changes traits more effectively than species sorting because of extant genetic variation (even more variation will exist if species are sexual) and mutation, whereas species sorting changes traits more effectively at moderate dispersal rates because greater trait variation is assumed between, as compared to within, species. At moderate dispersal rates, adaptability and species sorting might not reach simultaneous peaks because the balance between adaptation by one species versus the invasion and replacement by a better-adapted competitor depends upon many variables. However, in both cases, adaptive trait changes at high dispersal are small owing to maladaptive gene flow and mass-effects for population genetics and communities, respectively.

Figure I represents a highly simplified scenario. Outcomes are likely to be quantitatively affected by mating system (sexual versus asexual species) and assumptions about higher-order genetic interactions. Also, variation in dispersal rates among species or among populations would alter this scenario by allowing for differential adaptive responses across the same gradient in landscape connectivity. However, the key message is that divergent scales of organization and magnitudes of potential trait changes between ecological and evolutionary mechanisms provide significant scope for evolutionary ecological interactions at local and regional scales.
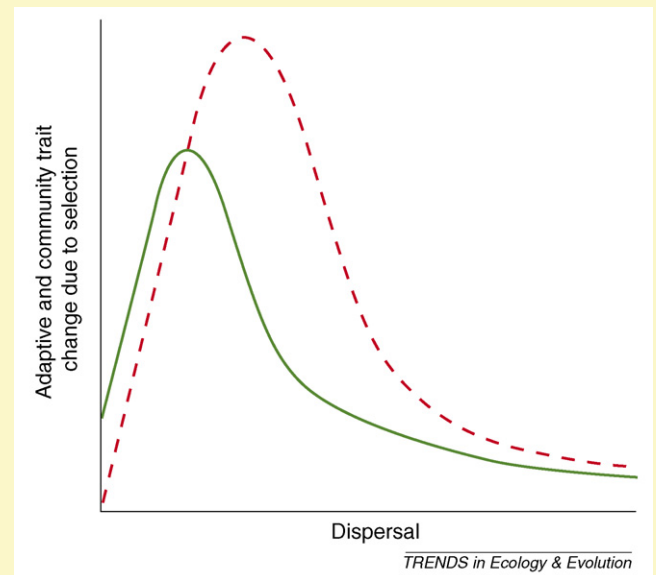
Figure I. Adaptive trait responses in a population (green solid line) and a multi-species community (red dotted line) after a change in local selection across a range of dispersal rates. The take-home point is that adaptation and species sorting need not coincide in their peaks or absolute magnitude, allowing for potential nonadditive evolutionary and ecological outcomes. Where the green line is above the red line, local adaptation is more effective than species sorting and the reverse is true when the red line is above the green line.
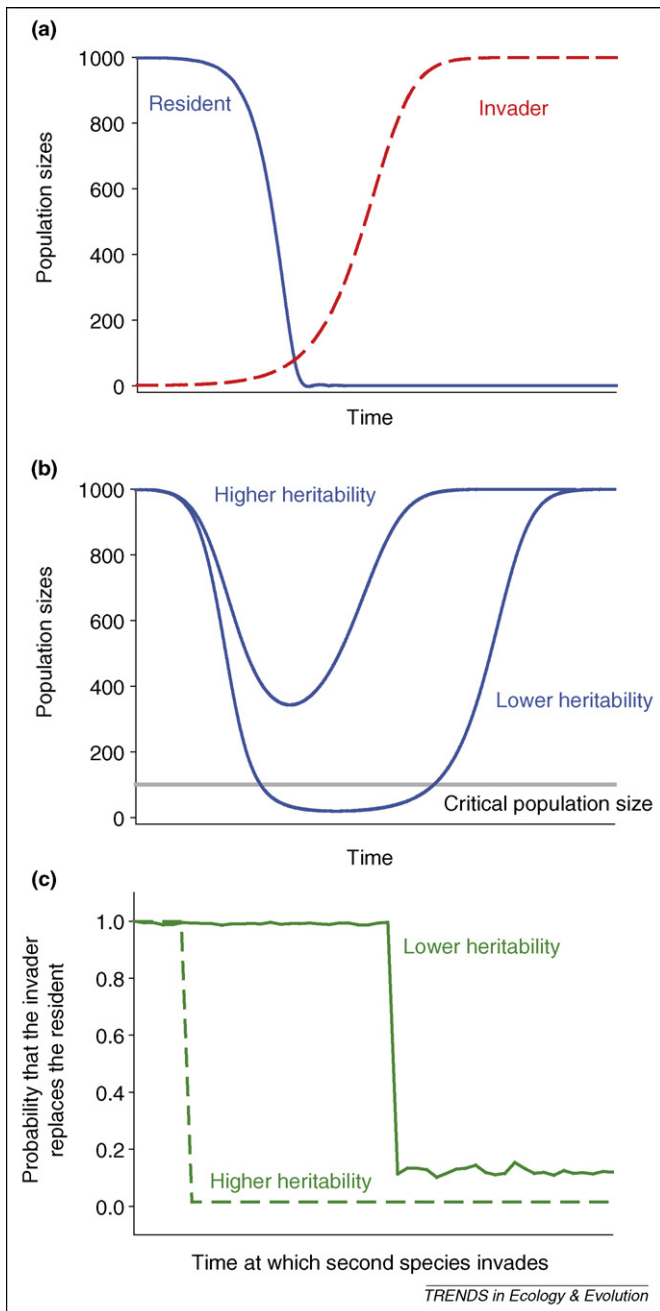
Figure 2. Local adaptation and dispersal determine the persistence of a resident species in a local patch in a discrete-time, stochastic, quantitative genetic model of evolutionary rescue [22]. The original model has been modified to examine the case of an initially maladapted resident and an optimally adapted invader, each competing for space. **(a)** In the absence of the evolution of a critical trait necessary for its survival in the patch, the resident (blue, solid) goes extinct, leaving the habitat vulnerable to invasion by the second species (red, dashed). **(b)** If the trait needed by the resident species to persist is heritable, then the initially maladapted resident can adapt to its new environment and rebound to a fixed carrying capacity. The resident population's scope for adaptation, as measured by heritability, is assumed to determine the period during which the maladapted resident is subject to stochastic extinction below a critical population size (100). At higher heritabilities, the resident population size remains above critical levels, and the resident can adapt faster and is more likely to repel the invader. **(c)** In addition to the resident's trait heritability, the probability that the second species invades and excludes the resident species also depends on when the invader is introduced. The second species is more likely to invade and replace the invader when introduced early and when the critical trait for the resident species is less heritable. In (b), lower heritability = 0.25 and higher heritability = 0.325. In (c), lower heritability = 0.10 and higher heritability = 0.25. Other parameter values are either as described in Ref. [22] or developed for this model extension: $W^{\wedge} = 1.91$, $P = 0.1w$, $N_{resident,0} = 999$, $N_{invader} = 1$, $\beta 0 = 4$ (A,B), $\beta = 3.3$ (C), carrying capacity = 1000.

exclusion can interact to produce a priority effect at shorter timescales, whereby early colonists adapt to the environment and repel future invading genotypes and species (the monopolization hypothesis [25]). Two empirical observations support this idea. In experimental ponds, zooplankton communities assembled differently depending on whether initial water flea (*Daphnia magna*) colonists were adapted to clear or turbid ponds [13]. Also, the timing of invasion of different bacteria (*Pseudomonas fluorescens*) ecomorphs governed the patterns of future niche diversification in experimental communities [12]. Thus, the joint evolutionary and ecological metacommunity perspective provides the key insight that local adaptation and species sorting can synergistically or antagonistically shape the match between community traits and the environment and do so in ways that depend on dispersal.

Altered food webs and ecosystems

We posit that the interplay between adaptation and species sorting might better explain not just community assembly dynamics but also the structure and functioning of complex food webs. It is well known that coevolution alone [26,27] or dispersal without coevolution [28,29] can shape the structure of local food webs by bolstering population sizes or by introducing missing food web components. We expect that the interaction between coevolution and dispersal will structure food web dynamics and the evolution of energy and material flows across ecosystems.

As an example, consider a predator that invades a local community of coevolved herbivores and plants. The herbivores might respond by evolving a preference for a plant species that provides shelter from the predator, which in turn affects the abundance of the plant via increased herbivory. Thus, the adaptation of the herbivores could indirectly affect the fitness and evolution of other predators, herbivores and plants in the local community. If we assume dispersal across a landscape of different predation regimes, then the migration of locally adapted genotypes could generate local maladaptation (a deviation of the population's mean phenotype from its adaptive peak at a site) in other localities. When maladapted species interact differently with other community members, we expect altered selection pressures on various food web components. Thus, the simultaneous consideration of evolution, dispersal and species interactions can lead to predictions about food web structure that would not be predicted if studied in isolation.

Additional dispersal-mediated evolutionary ecological interactions emerge when we consider energy and nutrient flows in a metacommunity [30]. Ecosystem properties such as biomass, productivity and decomposition can evolve because the traits underlying these properties often are heritable [8]. Whereas local adaptation might decrease the complexity of food webs and ecosystems through convergent evolution of ecosystem traits [31], dispersal can produce the opposite effect by introducing species and genotypes with different traits. If these predictions hold over a broad range of conditions, local adaptation and dispersal across heterogeneous sites can maintain multiple functional groups, thereby increasing the

complexity and diversity of pathways in linked ecosystems (N.L. and M.A.L., unpublished). In one such model of evolving consumer aggression, complex food webs emerged only in simulations where dispersal from a regional pool of evolving species was sufficient to replace locally extirpated trophic links [32]. Another metacommunity model suggests that dispersal can also mediate the movement of nutrients among sites in ways that depend on the evolution of the traits of interacting species (N.L. and M.A.L., unpublished). Hence, ecosystem dynamics might often depend on the evolutionary and ecological implications of dispersal.

In conclusion, although we currently know little about how dispersal and evolution affect food webs, early theoretical examples suggest that an evolving metacommunity perspective can predict food web complexity more accurately than approaches that ignore these dynamics.

Neutrality evolves

We argue that the relative importance of different mechanisms of species coexistence depends on a joint consideration of adaptation, gene flow and community assembly. For instance, two mechanisms are typically invoked to explain local species coexistence: a niche-based perspective where species coexist by each depressing their own population growth rates more than the growth rates of other species, and a neutral perspective where species are equivalent in all aspects of their population and evolutionary dynamics [11], which allows for transient coexistence over long time periods. If dispersal and evolution affect the importance of niche versus neutral processes of species coexistence, then our understanding about the underlying reasons for biological diversity will be altered by an evolving metacommunity perspective.

Recent work highlights that both metacommunity and evolutionary processes can affect the relative importance of the niche and neutral processes in maintaining community richness [33,34]. In a simulated metacommunity, high migration rates countered local extinction via demographic stochasticity, thereby allowing near-neutral species with similar niches to co-occur [35]. Another model of a closed community shows that the evolution of competing species along a single niche axis can result in distinct clusters of near-neutral species with similar traits that coexist for long, but transient, time periods [31]. But what happens to the relative importance of niche versus neutral coexistence mechanisms when immigration shuffles evolving species across heterogeneous patches in a metacommunity? One metacommunity model explored this question under different assumptions about environmental autocorrelation and the distribution of niche-related traits among species [11]. With no spatial environmental autocorrelation, all species traits converged to the same value, which was optimal in the average environment (i.e. neutrality evolved). Assuming spatial autocorrelation, species with initially similar traits evolved to be specialists on different environmental conditions because interspecific competition eliminated species with too similar traits in each patch. When species were randomly assigned traits in the same landscape, species evolved to be generalists made up of many locally adapted populations, and hence species were near neutral

but their populations were adaptively niche differentiated. Because this model assumed strong dispersal limitation, its outcomes reflect only one end of the dispersal-dependent continuum. An important future direction is how evolution shapes coexistence mechanisms under less restricted dispersal. High dispersal might support a mixture of niche and neutral mechanisms by maintaining maladapted competitors in sink habitats. Mass-effects and maladaptation would then support near-neutral coexistence of sink species, whereas locally adapted source populations coexist through niche-based mechanisms [10].

As these studies show, dispersal and evolution can provide new insights into the relative importance of the fundamental mechanisms of species coexistence in a metacommunity. Future work should concentrate on understanding the interaction between these two processes in maintaining diverse coexistence mechanisms in metacommunities.

Future directions

The three foci described above illustrate key ways in which metapopulation genetics and metacommunity dynamics interact to affect ecological processes and patterns. Further progress will require development of new theories, enhanced statistical methods for comparative work and novel experiments.

Theory

Future theoretical work should focus on how dispersal and gene flow jointly affect patterns of community richness, assembly, food web structure and ecosystem properties in a metacommunity. We need models that vary in community size from pairwise species interactions [7] to multi-species communities to address what happens when multiple species coevolve in a mosaic landscape [36]. Future work also needs to examine how adaptation and dispersal maintain or destroy complex food webs. From a more dynamic perspective, evolving metacommunity models should allow us to decipher the particular combinations of evolutionary potential and species sorting that allow a species or a community to track changing environments. Lastly, the next generation of evolutionary models should explore how the joint evolution of dispersal and niche-related traits interact to determine metacommunity properties.

Empirical

Empiricists face several challenges in testing emerging theory. First, we need to collect data on variation in environments and genetically determined traits for multiple interacting species across natural landscapes. Statistical work will be needed to guide the design of these sampling efforts (e.g. number and spatial distribution of samples) to ensure that significant patterns can be discerned. Second, we need an integrated set of statistical tools to quantify the interplay of community and evolutionary dynamics in the field. To date, this interplay is documented by an array of ad hoc methods that describe coevolutionary trajectories [7], phylogenetics relationships among interacting species [37] and the communities inhabiting genetically divergent host species [8]. The lack of integration among these approaches makes comparative

studies and meta-analyses difficult and obscures potential generalities.

Manipulative experiments are a third crucial need. Recent experiments show that novel insights about community assembly and evolution are possible by manipulating the genetic composition of colonists, timing of invasions, or dispersal among experimental communities [8,12,13,38]. Not surprisingly, such experiments were conducted under artificial conditions to facilitate the observation of simple evolutionary responses on short timescales. Altering local selection through long-term manipulations of natural metacommunities are also needed to understand the ecological and evolutionary dynamics of metacommunities under natural conditions and over longer timescales [39].

Lastly, an evolutionary perspective on metacommunities is useful even in the absence of rapid microevolution. This is because metacommunity processes are also affected by the macroevolutionary and biogeographic processes that produced regional (metacommunity) species pools. Hence, we need to think more critically about how speciation, historical range shifts, and niche differentiation across environmental gradients shape contemporary community dynamics. We argue that a phylogenetic perspective will facilitate deeper insights into evolutionary metacommunity ecology, as it has in community ecology more generally [1,37], by elucidating the long-term evolutionary stability of communities, testing for matching ancestry patterns among interacting species and revealing patterns of shared ancestry across heterogeneous landscapes [40].

Overall, the insights emerging from this research will inform a community ecology based on evolutionary first principles. This perspective should facilitate more accurate predictions in conservation biology because the interplay between adaptation and species immigration will be crucial for predicting the consequences of biological invasions [41] and global climate change [42], both of which involve a spatial dimension.

Conclusions

The past several decades have seen major advances in the study of spatial ecology and evolution in spatially structured populations. Despite this progress, little attention has focused on extending these approaches to multiple interacting species, complex food webs and ecosystems. Numerous approaches are advancing on this ideal (Box 1), but the theoretical frameworks that accommodate these complexities and the statistical methods that allow integrated comparisons are not yet fully developed. We are not the first to draw attention to the ecology–evolution interface [1]. Our thesis instead is that this synthesis will greatly benefit from increased attention to spatial dynamics. Although much work remains to be accomplished in metacommunity ecology without evolutionary dynamics [16] and geographically structured genetics without the full scope of ecological dynamics [7], we suggest that progress in both metacommunity ecology and evolutionary biology will soon become limited without a more synthetic 'evolving metacommunity' approach.

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