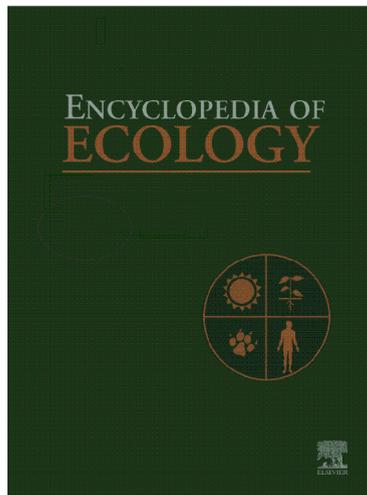


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Metacommunities

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Introduction

Mechanisms of Metacommunity Dynamics
 Metacommunity Topics Extending Beyond Species
 Diversity

Summary

Further Reading

Introduction

A metacommunity is defined as a group of communities that are connected by the dispersal of one or more interacting species. The term was first used in 1991 and since then has grown into an important concept for studies of species diversity and community structure. The concept enlarges the scale at which community dynamics are considered. Metacommunities have several distinctions that make them a valuable unit for consideration in both theoretical and applied ecology, such as in considering the effects of habitat fragmentation on biodiversity and ecological communities.

First, traditional community ecology often relies on the assumption that communities are closed, isolated entities. This assumption arises from consideration of mathematical models such as the Lotka and Volterra competition equations, which are simpler if the community is assumed to be closed to movement. By contrast, theories like source and sink dynamics propose that immigration allows some species to be present even in sink habitats where there are inadequate resources to support viable populations, or where species would be excluded by predators or competitors in the absence of immigration. Therefore opening communities to immigration may change the species present in local communities, such that the conditions assumed in closed models do not apply to open communities. Movement of individuals might also modify species interactions and the local dynamics of individual species. It is widely acknowledged that numbers of individuals moving and the distances they move are some of the most difficult parameters to measure in ecology, and therefore our knowledge of the degree to which real communities are open or closed is limited.

Second, the responses of species diversity to habitat change, including partial destruction and fragmentation,

may arise either because of the responses of individual species or because species influence one another. Hence mechanisms may arise at levels of populations, metapopulations, communities, and metacommunities. If we consider only some of these levels we will have at best an incomplete idea of the effects of habitat change.

Third, it is useful to recognize that regional metacommunity-level species diversity is determined by the sum of both local and regional processes. The local and regional parts merit elaboration. The primary local process influencing species diversity is niche partitioning an idea that is derived from traditional community ecology. A variety of regional processes are possible: (1) There may be a balance between the extinction of species from local communities and their (re)colonization, creating a balance that allows species to persist regionally even if they do not have a predictable place in any given local community. Such dynamics may be rendered more likely if there are tradeoffs in the abilities of species to colonize new or vacant habitat and their ability to compete locally. (2) Immigration may forestall extinction from local communities, as in source and sink models and through so-called rescue effects where immigration raises population size and rescues local populations from extinction. (3) Differences in habitat type among local communities might create different niches for different species. (4) The potential for (1)–(3) may depend on the degree to which dynamics are independent (or asynchronous) in different local communities. There is also the possibility that immigration and emigration modify either the structure of the community (species abundance and composition) or the interactions of species within that community, which represent an interaction between local and regional processes. Although two spatial scales are recognized (local and regional) this is arbitrary and more spatial scales are often represented in

metacommunity models. The feedback between local and regional scales differs sharply from the equilibrium theory of island biogeography where species diversity is viewed as being fixed by a permanent mainland pool of species, and individual habitat islands contain arbitrary subsets of this species pool.

Fourth, interaction among species means that the metacommunity is not simply a collection of metapopulations where species are largely independent from one another. From the 1970s onwards, ecologists tended to view pairwise spatial interactions involving repeated local extinction and colonization as the domain of metapopulations, whereas larger numbers of species are more the domain of metacommunity theory. Many-species spatial competition models were not originally termed metacommunity models but best fit this categorization.

Empirical work on species diversity has long recognized a spatial component to species diversity, through the division of regional (gamma) diversity into local (alpha) diversity and the turnover of species among sites (beta diversity). The existence of differences in species composition among sites (beta diversity) creates the potential for movement to alter local community composition if species are able to move among local communities. The concept of alpha, beta, and gamma diversity also recognizes that regional diversity is made up of local diversity and the differences among local communities. Such diversity patterns do not, however, distinguish what is creating the diversity – in other words, whether local diversity contributes to regional diversity or whether it is a subset of regional diversity.

In the following sections we describe models of species diversity, and then describe some of the factors other than species diversity that are influenced by a metacommunity structure.

Mechanisms of Metacommunity Dynamics

Four broad kinds of metacommunity models have been described, each emphasizing different persistence mechanisms. These are termed neutral community models, patch dynamics, species sorting, and mass effects models. It should be borne in mind that although the discussion is often in terms of patches, the same kind of dynamics can occur in spatially continuous habitats without discrete patches.

The best-known metacommunity models are neutral community models, which assume that all individuals have identical fitness. Neutral models were popularized by the publication in 2001 of Stephen Hubbell's book *The Unified Neutral Theory of Biodiversity and Biogeography*. Hubbell's model includes lottery competition among individuals that are all equal competitors on a spatially

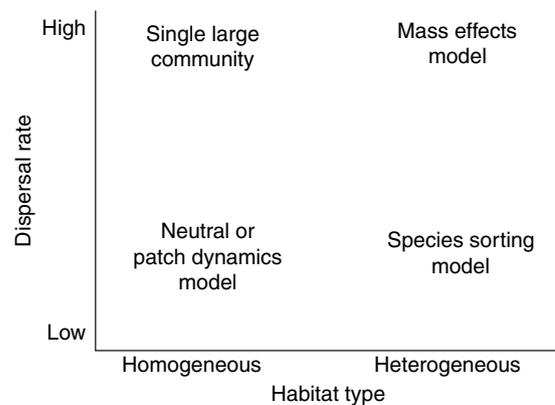


Figure 1 Theoretical types of communities and metacommunities as a response to the similarity of habitat patches and the dispersal rate of species between communities.

uniform habitat plane (Figure 1). Competition in a uniform environment with no differences among species causes species to be transient, and for species diversity to drift through time (termed ecological drift by Hubbell). In Hubbell's model all individuals also have limited movement ability (Figure 1), which causes different species to cluster in different parts of the habitat plane, slowing down competitive exclusion but not preventing it. To replace species that were lost, Hubbell included speciation as a source of new species. The mechanisms maintaining diversity in Hubbell's model are localized dispersal, and speciation that replaces lost species. Hubbell's model was novel in including both ecological and evolutionary processes that might account for species diversity. Neutral models by other authors have often started with a fixed number of species and limited the time span of simulations so that numerous species are still present. Other, so-called neutral models have a fixed pool of species and all individuals are identical, but species cannot go extinct from the regional metacommunity. In such models persistence is determined by the permanent pool of species (like in the equilibrium theory of island biogeography), and this pool of species prevents neutral dynamics from determining diversity. Hence although individuals are neutral, the mechanisms determining diversity that are present in neutral models without permanent species pools cannot play out. Neutral models have surprised ecologists by predicting a number of patterns that are widely observed, such as the distribution of the rank abundance of species, or species–area relationships. Original tests were primarily in tropical trees, but neutral community models have been tested in a variety of taxa, from sedges, to bacteria, to gut parasites, and to bird assemblages. Unfortunately most work has concentrated on testing between neutral models and a single alternate null model, rather than accepting that there might be elements of neutral dynamics that occur along

with other kinds of dynamics. For example, neutral models emphasize stochastic and transient dynamics, but such dynamics are also features of other kinds of models. In tests of a single alternative model, the best evidence leads to the rejection of neutral dynamics in all cases.

A second type of model has been termed patch dynamics, and differs from neutral dynamics because species differ in traits like colonization or competitive ability. Patch dynamics models are multispecies versions of classical metapopulation models. For large numbers of species to coexist permanently there needs to be a trade-off among appropriate traits. Most commonly such models consider competing species that have a tradeoff such that those that are better competitors are poorer dispersers. Inferior competitors can survive by living a fugitive existence where they arrive early at patches unoccupied by superior competitors. The habitat is uniform (**Figure 1**), lacking environmental differences and can either be continuous or subdivided into separate patches. For coexistence a tradeoff would need to be present, and species would need to have localized dispersal (like in neutral community models). Too much dispersal would cause species to show synchronous dynamics across all patches and inferior competitors would occur in the same patches as superior competitors until they are driven regionally extinct and a large single local community is left (**Figure 1**). The model is hard to prove because it relies on the absence of environmental effects (that are present in the two models below) and it is difficult to demonstrate tradeoffs for multiple species. There are recent demonstrations of such a tradeoff among coexisting species in simplified laboratory systems where the environment is uniform but subdivided so that movement is limited.

A third type of model, termed species sorting, is based on classical niche theory, where niches are present either in different habitat types or at points along a habitat gradient (**Figure 1**). Differences in habitats could be due to physical or biotic factors. Physical factors could include things like temperature, nutrient availability, resource availability, and tidal exposure, whereas biotic factors include the presence of habitat-forming species (e.g., trees or corals) or keystone species that exert disproportionate effects on other species. For species sorting to maintain diversity, species would need to be capable of reaching habitat to recolonize if they had gone extinct. If species dispersed so frequently that they often left good habitat, dynamics would become more like the next model, which involves mass effects (**Figure 1**). For species sorting to operate, species could either select habitat actively and behaviorally, or they could have differential success in different habitats. The consequences of either of these would be that species survive and reproduce better in some habitats than others. Species traits that relate to responses to the environment are therefore an

important part of community structure. The persistence mechanism in species sorting models is classical niche partitioning, in this case where niches are in different spatial locations. Niches are often contrasted with neutral models because individual responses to the environment would not be consistent with neutral models where all individuals are equivalent. Therefore species composition varying in response to environmental conditions would be evidence against neutral community models. Some of the best evidence for species sorting comes from differences in zooplankton composition among interconnected ponds with and without predatory fish. Dispersal of zooplankton between ponds seems to be somewhat frequent in such systems but species composition is strongly related to the presence of fish which do not move readily between ponds.

The fourth model, mass effects, results when there are different habitat types present and species are highly dispersive, so that they spillover from the habitats in which they reproduce and survive best to poorer habitats. These kinds of dynamics are described by source and sink models for individual species and are termed as mass effects for multiple species, where there is a mass flow of individuals from one place to another (**Figure 1**). Habitat areas that are suboptimal and more distant in space from good habitat would be less likely to contain species that cannot maintain viable populations in the suboptimal habitat than for similar areas that are close to good habitat areas. This effect arises because species are likely to be limited in their dispersal ability. Where such dynamics are present, there should also be a correlation between population productivity and the environmental factors that make habitat good or bad. The regional persistence mechanism is best described as a spatial storage effect, which Peter Chesson describes as differential survival and reproduction in different locations averaging out the success (finite growth rate) of a species such that the species can maintain a viable population within the metacommunity. Such dynamics have been modeled by Nicolas Mouquet and Michele Loreau in models with differences in habitat among patches and many competing species that differ in their response to environmental conditions.

If dispersal among habitat patches is high and habitats are relatively uniform across space, a single large local community is likely to result (**Figure 1**). In this case it is not clear that anything is to be gained by considering the spatial dynamics of such a community; that is, the system is structured as a community rather than a metacommunity.

The most general form of evidence for and against the various metacommunity models comes from examining whether differences in community composition can be explained by differences in environmental factors or by the distance between the local communities. Species

sorting predicts a purely environmental effect, whereas mass effects predict both environmental effects and effects of distance. Both neutral and patch dynamic models predict effects of distance but not of environmental factors. A complicating factor in such analyses is that the environment may also be spatially structured. A survey of 158 natural community data sets by Karl Cottenie found that 22% of the total variation in community structure was explained by the pure environmental fraction, 16% by the pure spatial component, and 10% by the spatially structured environmental fraction. From these data Cottenie concluded that 69 metacommunities (44%) best fit the species sorting model, 46 (29%) a mixed species sorting and mass effect model, and only 13 (or 8%) the neutral or patch dynamics models; 19 data sets could not be associated with these models, and 11 had no significant components. Therefore it is likely that species sorting and mass effects are relatively frequent in the natural world, but patch and neutral dynamics are less frequent. To date there are no natural communities that have been extensively examined and where we can conclude that the dynamics best fit neutral community models. A book edited by Holyoak, Leibold, and Holt on metacommunities also found that more detailed studies most frequently identified species sorting, followed by mass effects, and with patch dynamics being less common.

There was no system that clearly showed neutral community dynamics. These data, however, should not be regarded as anything other than preliminary because they were usually collected with a different purpose in mind and they are largely correlative rather than coming from manipulative experiments which could more clearly distinguish cause and effect.

It should be noted that the metacommunity models described above are useful as a starting point, but that they are theoretical representations of what is likely a continuum between different kinds of dynamics. Currently the literature lacks models that can represent all of these kinds of dynamics within a single mathematical model, which would be useful for showing how the four different kinds of dynamics relate to each other. The above discussion also relates primarily to species diversity whereas in the following section we consider other aspects of community structure.

Metacommunity Topics Extending Beyond Species Diversity

Food Webs

Historically, food web research has focused on how local deterministic interactions will influence web structure. Considering food webs in a spatial context, however, provides alternative mechanisms for observed phenomena. When species do not interact, we expect that

subdivision will only decrease population sizes and make species more vulnerable to stochasticity. Interacting species, however, can use space as a mechanism of persistence and coexistence thereby promoting a more complex food web structure.

Ultimately, the degree to which metacommunity dynamics influence food web properties over local community dynamics will depend on dispersal, patchiness, and the interaction between the two. Spatial subsidies of immigrants or energy can stabilize or destabilize local interactions that would otherwise be determined by environmental factors. Patchiness in the form of environmental heterogeneity will allow for site-specific demography and alternative food web states within patches, though the resultant food web structure will also depend on the rate of dispersal of and colonization by both competitors and their consumers. Lastly, patchiness in the form of the size and distribution of habitat patches will influence the extent to which species of varying life histories and dispersal abilities experience subdivision. Together, these factors will influence interactions within and between trophic levels. Where they contribute to the stabilization of local interactions, we expect to see longer food chains or more complex food webs.

Though there is a long history of seeking to explain food chain length with productivity, recent work has shown that ecosystem size may be a more consistent predictor of chain length. This could be a result of metacommunity dynamics. If a food web is under donor-control, the criteria for the existence of higher trophic levels will become stricter for each succeeding level. If basal species have low colonization and high extinction rates, and their habitat is rare, we might expect short food chains because, by virtue of being dependent on lower trophic levels for resources, each succeeding trophic level must have extinction rates equal to or higher than the previous trophic level. Increasing colonization rates or the number of habitat patches, or decreasing extinction should enhance regional mechanisms of persistence and coexistence, stabilize local interactions, and allow for greater trophic diversity.

Spatial structure can also influence the impact of consumers on their resources. A consumer's ability to optimize energy intake by switching prey and feeding location can dampen fluctuations in prey populations, stabilizing local food webs. Even when predators are not actively selecting prey and habitat, space can create refugia for prey populations and, in some systems, decrease top predator density and allow other predators to coexist. Dispersal by consumers can also link resources and habitats in ways that are detrimental for some prey species. For example, shared predation by a mobile consumer may cause two species that never co-occur locally to exhibit apparent competition, or,

oppositely, may facilitate the coexistence of two species that otherwise could not coexist locally. All of these factors affect the stability of local interactions and thus the complexity of the food web.

Ecosystem Functioning

Ecosystem functioning reflects biotic effects on the physical and chemical properties of the environment, and an emerging theme has been to link this functioning to metacommunity properties. A common theme in research on ecosystem functioning is the diversity–productivity relationship. Nonspatial models generally predict a positive relationship between diversity and productivity due to increasing niche complementarity, with eventual deceleration due to niche overlap (Figure 2a). Though there is experimental evidence to support these predictions, there are also studies that show a neutral, unimodal, or negative relationship between diversity and productivity. Some of these conflicting results may be reconciled through a metacommunity framework that accounts for the spatial exchanges known to occur in real ecosystems.

Varying rates of dispersal between patches may explain a unimodal diversity–ecosystem functioning relationship at local scales and a positive linear relationship at regional scales. At the local level, diversity may increase productivity because of niche complementarity or sampling effects. This relationship may peak and become negative, however, if dispersal allows inferior competitors to interfere with superior competitors through source–sink dynamics (Figure 2b). At larger scales, increased diversity may allow species to coexist and complement each other regionally, increasing productivity linearly so long as the number of species does not exceed the number of limiting resources. A study examining productivity at the pond (local) and watershed (regional) scale found this scale-dependent relationship between diversity and productivity in nature, evidenced by low local diversity and increasing species dissimilarity between ponds in watersheds with higher productivity.

A form of spatial insurance could also result in a scale-dependent diversity–productivity relationship. If the

dynamics of local communities and environments fluctuate asynchronously, dispersal will supply immigrants to localities where the environment has changed to be unsuitable for the current residents. Increasing regional diversity will increase the likelihood that there will be species appropriate for the various environmental conditions, which will enhance resource-use efficiency and productivity. When levels of dispersal are intermediate, supplying enough immigrants to fill vacancies without leading to dominance by a species with intermediate traits, the temporal mean of productivity across the region will be higher and exhibit lower variability. When the system involves more than one trophic level, consumers that track resources can increase variability in productivity at a local scale, but decrease variability at the metacommunity scale by creating a heterogeneous environment that hosts a more diverse community capable of spatial insurance.

Evolution

Evolution influences communities on many timescales. In a metacommunity context, whether local adaptation promotes or deters coexistence will depend on how influential the change is on a given interspecific interaction and the level of immigration among communities.

Over long periods of time, evolution can promote coexistence through niche partitioning, competition–colonization tradeoffs or mechanisms that make species regionally similar in fitness despite local competitive asymmetries. In addition to shaping the dynamics of interspecific interactions, evolution will impact the connectedness of a community, and thus the frequency of those interactions, by molding dispersal capabilities and habitat preference.

Empirical evidence also suggests that evolution can influence community dynamics within a short, ecologically relevant timeframe. Asymmetrical gene flow from source to sink populations can prevent efficient natural selection, leading to maladaptation in the sink and creating range limits. This type of source–sink dynamics can also decrease niche breadth and inhibit a species' ability to respond to changing biotic and abiotic environmental conditions. In the same way that intermediate dispersal can promote species diversity, intermediate gene flow can promote genetic diversity by supplying new alleles without extirpating the local genetic framework. If environmental conditions in a patch change, the genetic storage effect can provide immigrant genes adapted to the new conditions that can rescue maladapted populations. Therefore, maintaining genetic diversity on a regional scale promotes overall species diversity.

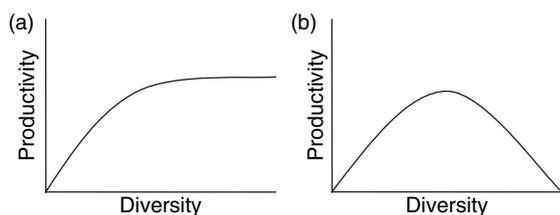


Figure 2 Theoretical relationships between productivity and species diversity. (a) Diversity as a result of niche complementarity or sampling effects. (b) Diversity as a result of source–sink dynamics.

Summary

Metacommunity models offer the most complete view of the factors maintaining species diversity that has been described to date. The metacommunity concept realistically describes how both local and regional forces can contribute to species diversity, and how the structure of local communities can be altered by immigration from other communities within the region. To date, metacommunity models consist of four broad kinds: neutral, patch dynamics, species sorting, and mass effects (or source–sink). There is a variety of empirical evidence for species sorting and mass effects models, whereas patch dynamics appear less common, and there is no good example of a system with neutral community dynamics. A metacommunity structure is likely to alter the composition of local communities, food web structure, species abundances, and the potential for evolution.

See also: Average Taxonomic Diversity and Distinctness; Biodiversity; Community; Island Biogeography; Metapopulation Models; Ordination.

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Metapopulation Models

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Introduction
 Classification of Metapopulation Models
 Four Kinds of Metapopulation Models
 Models for Dynamic Landscapes
 Metapopulation Models for Two or More Species

Application to Landscape Management and Conservation
 Summary
 Further Reading

Introduction

Most landscapes are complex mosaics of many types of habitat. From the viewpoint of a particular species living in such a landscape, only some habitat types, called suitable habitat, provide the resources that are necessary for population growth. The remaining landscape, often called

the (landscape) matrix, can only be traversed by migrating individuals. Often the suitable habitat occurs in discrete patches (also called habitat fragments). Individual habitat patches may be occupied by a local population of the focal species, but many patches are likely to be unoccupied at a particular point in time, because a local population went extinct in the past or the patch appeared in the landscape