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REVIEW

Biodiversity conservation through the lens of metacommunity ecology

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Metacommunity ecology combines local (e.g., environmental filtering and biotic interactions) and regional (e.g., dispersal and heterogeneity) processes to understand patterns of species abundance, occurrence, composition, and diversity across scales of space and time. As such, it has a great potential to generalize and synthesize our understanding of many ecological problems. Here, we give an overview of how a metacommunity perspective can provide useful insights for conservation biology, which aims to understand and mitigate the effects of anthropogenic drivers that decrease population sizes, increase extinction probabilities, and threaten biodiversity. We review four general metacommunity processes—environmental filtering, biotic interactions, dispersal, and ecological drift—and discuss how key anthropogenic drivers (e.g., habitat loss and fragmentation, and nonnative species) can alter these processes. We next describe how the patterns of interest in metacommunities (abundance, occupancy, and diversity) map onto issues at the heart of conservation biology, and describe cases where conservation biology benefits by taking a scale-explicit metacommunity perspective. We conclude with some ways forward for including metacommunity perspectives into ideas of ecosystem functioning and services, as well as approaches to habitat management, preservation, and restoration.

Keywords: extinction; rarity; dispersal; ecological drift; biotic interactions; filtering

Introduction

Although its inception started much earlier,[1–4] the field of conservation biology solidified in the 1980s in reaction to the ongoing direct and indirect degradation of populations that occurred via loss and degradation of habitats, harvesting of individuals, introduction of alien and invasive species, and climate change.[5–7] Historically, the primary focus in conservation biology was to understand and mediate the dynamics of threatened and endangered species, with a focus at the population level (e.g., demography).[8] More recently, conservation biology has extended its horizons to become a cross-disciplinary field connecting to metapopulation biology, landscape ecology, biogeography, and biodiversity science.[9]

While the foundations of conservation biology explicitly focused on population-level demography, these parameters (e.g., births and deaths) are often mediated by immigration and emigration within a metapopulation.[10] Indeed, from an ISI Web of Science topic search (mining the title, abstract, and keywords) from 2015 to 2019, we noted 666 papers that used the term “metapopulation OR meta-population” along with the term “conservation” published in the previous 5 years, indicating strong association. Likewise, the spatial field of landscape ecology has been intimately tied with conservation—2364 papers included both “landscape ecology” and “conservation” in our ISI search from the last 5 years—exploring habitat connectivity and how it influences conservation of species and ecosystems.[10–13]

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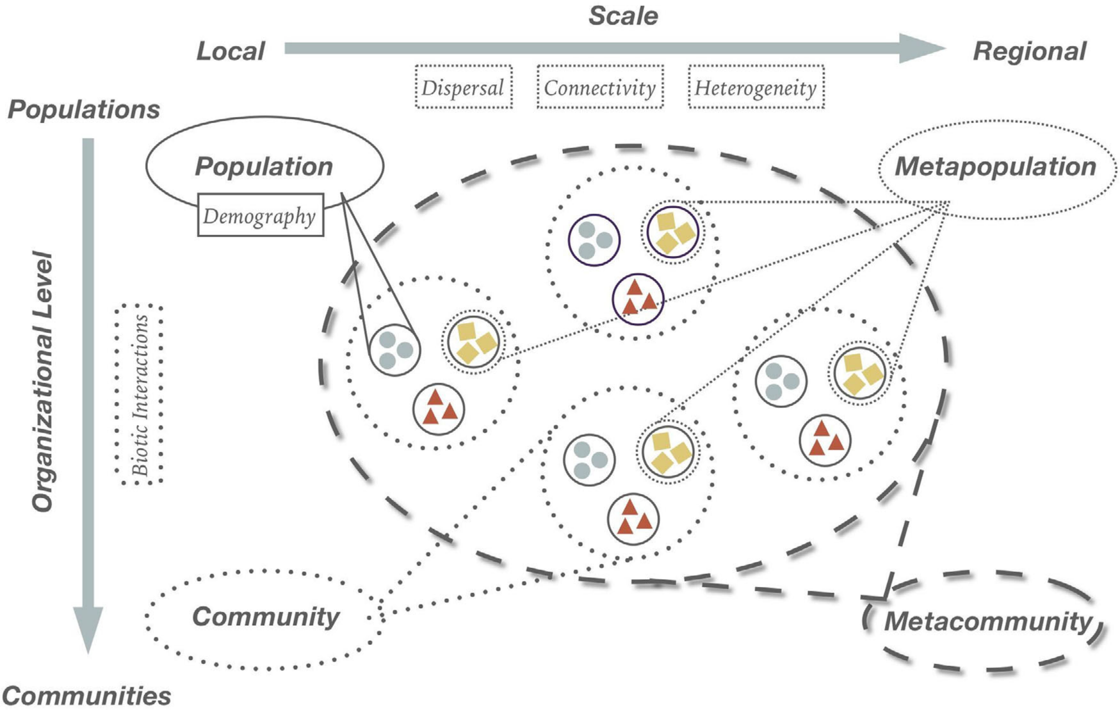

Figure 1. Conceptual figure demonstrating how different levels of conservation are integrated within the metacommunity framework across two axes: scale and organizational level. Populations are embedded within local communities, which are embedded within regional metapopulations and regional metacommunities, respectively. Population-based processes affect communities and metapopulations. Community and metapopulation processes combine to impact metacommunities.

Conservation biology is also connected with community ecology, which is the subfield of ecology primarily concerned with how species interactions influence multiple species' demography and their resulting coexistence and diversity. Our search turned up 2879 papers that included both "community ecology" and "conservation" in the past 5 years. Less well connected to contemporary conservation biology, however, is the emerging field of metacommunity ecology, which considers both spatial and interspecific processes.[14–16] Specifically, metacommunity ecology integrates (1) the local/demographic processes that dominate population biology and conservation biology; (2) dispersal (leading to immigration and emigration) and habitat heterogeneity that have been incorporated into conservation via metapopulation and landscape perspectives; and (3) species interactions and coexistence mechanisms that are at the essence of community ecology (Fig. 1).

The patterns and processes that emerge from the metacommunity level can provide valuable insights in the context of conservation biology, for example, in understanding the abundance and distribution of multiple species (particularly those that are rare and/or declining) in space and time; the degree to which species occupy their available habitat or are dispersal limited; and the biodiversity and composition of species across scales. However, from our ISI Web of Science search, out of the 1075 papers that used the search term "metacommunit* OR meta-communit*," we found only 145 papers that used this term together with "conservation" in the past 5 years.

Probably, the most iconic connection between metacommunity ecology and conservation biology is the equilibrium theory of island biogeography (ETIB),[17,18] emphasizing the key roles of habitat size and habitat isolation (and thus dispersal limitation) in maintaining biodiversity in island-like habitats. Ideas emerging from the ETIB and related theories have been instrumental—albeit not without controversy—in examining the role of habitat loss and fragmentation for patterns of biodiversity, as well as reserve design.[19–26] Spatial and temporal heterogeneities can also be readily incorporated into conservation science. For example, the concept of "keystone communities"[27] allows us to identify habitat patches that have a disproportionate importance for creating environmental heterogeneity and maintaining landscape connectivity, and differences in species composition across sites and through time (i.e., β-diversity) allow us to infer biodiversity change across scales in the face of global environmental change.[28] In addition, spatial and temporal heterogeneity have clear links to ecosystem functioning via community assembly and dynamics[29,30] and as a "spatial insurance" for the maintenance of regional stability and ecosystem services.[31,32]

In what follows, we provide a general overview of how the metacommunity perspective can benefit multiple aspects of conservation biology. Note, we distinguish metacommunity "perspective," which is a general viewpoint that explicitly considers the main tenets of metacommunities[15] (e.g., demography, dispersal, habitat heterogeneity, and species interactions), from metacommunity "theory," for which there are specific and detailed theories that depend on particular assumptions. We identify possible mechanisms by which metacommunity assembly processes are altered by ongoing environmental change, and discuss how these can affect the variables of interest in conservation biology (abundance and diversity patterns, ecosystem functioning). First, we briefly review the main tenets and propositions of the metacommunity perspective that can be of relevance to issues of interest in conservation biology. Next, we discuss how metacommunity processes are potentially influenced by different anthropogenic drivers of major concern in conservation. This includes (1) changes to the local and regional demography of species, particularly those of conservation concern; (2) changes to the biodiversity and composition of species, and the scale-dependence of those changes; and (3) how those changes influence patterns of ecosystem functioning. Finally, we conclude with a discussion of how biodiversity management and planning (e.g., reserve design) can benefit from a metacommunity perspective, and which pieces still need to be placed in order to achieve a deeper understanding of the abundance, identity, and diversity of species, and how to manage them in an increasingly modified world.

A primer of metacommunity ecology's basic processes

In a metacommunity, the occurrence and abundance of species across the landscape are determined by four core processes:[33,34] (1) environmental filtering of species according to local abiotic conditions, (2) biotic interactions resulting from competition and trophic interactions, (3) dispersal among habitat patches, and (4) ecological drift resulting from demographic stochasticity. Note, we here ignore the speciation process, which takes place over much longer time scales.[35] Critically, these basic processes occur in an explicit spatiotemporal context and across scales.[15] Within local habitat patches, population size and local species coexistence are determined by abiotic conditions, biotic interactions, and demographic stochasticity. Under unfavorable local conditions, species have negative growth rates and are eventually filtered out, unless dispersal from the regional species pool (i.e., immigration) compensates for this negative growth. At the regional scale, environmental heterogeneity among habitat patches provides additional niche space for species, and dispersal across the landscape allows species to persist under suitable environmental conditions. Hence, regional environmental heterogeneity, biotic interactions in local patches, and dispersal interact to influence regional species coexistence. Abiotic and biotic processes are often considered under the umbrella of "niche selection"[33,34] as an analogy with selection in population genetics, but we here separate abiotic and biotic processes, as both generate different kinds of dynamics relevant to conservation biology.

Environmental filtering

A species' niche is defined by the set of environmental conditions under which species have intrinsic positive growth rate.[36–38] Niche differentiation among species leads to deterministic fitness differences that influence the likelihood of local coexistence and the geographical distribution of species across spatial scales. This is supported by theoretical formulations of local species coexistence when there are trade-offs in resource utilization and response,[37,39,40] and by empirical evidence of species distributions,[41] species richness,[42] and community compositional variation along environmental gradients.[43,44]

While environmental filtering is typically assumed to be a primary process limiting species distributions, it is clear that a number of other processes, including biotic interactions, dispersal limitation, and ecological drift act in conjunction with, and sometimes in opposition to, environmental filtering. Furthermore, it is important to recognize that the relative importance of environmental filtering depends on the spatial (and temporal) scale in which observations are made. At small scales, and where environmental heterogeneity is minimal, the signal of ecological drift will be stronger than when scales are larger and/or heterogeneity is higher.[45,46]

Biotic interactions

Individuals of the same or different species interact with each other, typically in a density-dependent way, affecting the relative abundance and composition of species among local communities. Competitive interactions have been central in community ecology since its inception,[47] and are the key element in species coexistence theory.[40] Similar principles for coexistence typically form the basis for the majority of metacommunity theories where competitive interactions interplay with spatial processes, including dispersal, and with scale.[48] Despite a focus on competitive interactions, recent efforts have extended the metacommunity perspective to incorporate trophic interactions.[49,50] Thus, habitat suitability is not only determined by the abiotic environment, but also by the presence and abundance of interacting species.[51]

Dispersal

Dispersal connects habitat patches to each other and to the regional species pool. Differences in dispersal rates depend on both landscape connectivity and movement ability of organisms, and underlie a wide range of possible metacommunity dynamics.[15,52] When dispersal is limited, environmental tracking can be disrupted, demographic stochasticity can increase local population extinction, and species occupancy and diversity can be lower. On the other hand, high rates of dispersal can override environmental filtering by allowing species to occupy habitat patches where their intrinsic growth rate would be otherwise negative (i.e., mass effects). Especially in highly heterogeneous landscapes, mass effects can generate source-sink dynamics with spillover of individuals from high- to low-quality habitat patches, where diversity is maintained by transient dynamics (sinks). This can drive more locally adapted species toward rarity or extinction. In addition, within a conservation context, dispersal itself often allows species to persist within a metacommunity. For example, many rare species are specialists within habitats that emerge following disturbances[53,54] and are able to persist in a spatial context by dispersing more rapidly to these habitats, or by tolerating disturbances better than competitors that must reinvade.

Ecological drift

In any given local population, each of the demographic parameters of interest—birth, death, immigration, and emigration rates—are realized with some degree of stochasticity (i.e., pulled from a distribution), which in turn influences metacommunity assembly processes.[55] Small populations are relatively more susceptible to stochasticity, which can ultimately lead to higher chances of local extirpation and altered patterns of species interactions, occupancy, and coexistence.[34,56,57] The effect of demographic stochasticity can also be higher in more isolated communities, where regional dispersal is less likely to rescue populations from local extinction. Environmental stochasticity can also impose abundance fluctuations, but via deterministic environmental filtering. Although both types of stochasticity affect metacommunity functioning, their effects can be substantially different.[55,58]

Anthropogenic drivers altering metacommunity processes

The main global anthropogenic drivers of biodiversity change, and thus the main conservation challenges for the 21st century, include land-use change and water management (including habitat loss and fragmentation), climate change, biological invasions, pollution, and overexploitation.[59–61] Because we advocate for a process-based perspective on metacommunity assembly, we discuss below how these global drivers affect metacommunity processes in multiple ways, which in turn influence the biodiversity variables of interest (Fig. 2). For example, changing climate and physicochemical properties directly influence environmental filtering; changing regional biotas and biological invasions alter biotic interactions; and changing

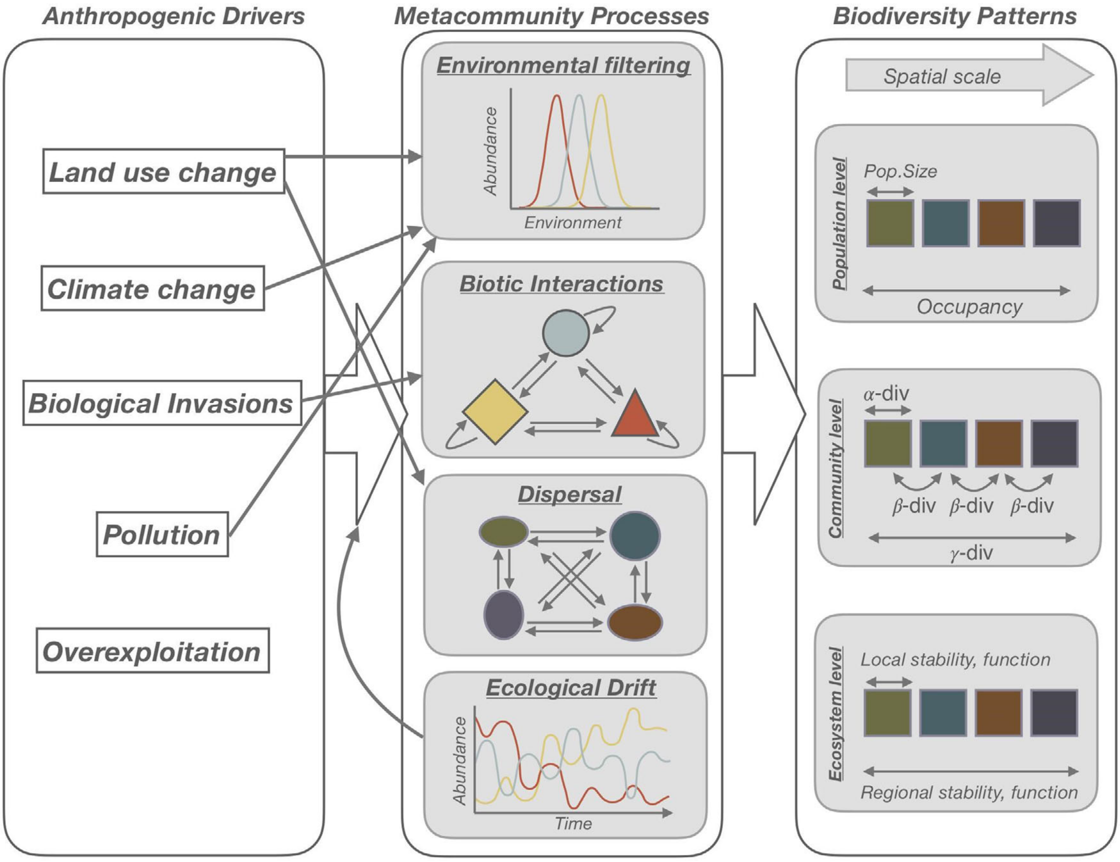

Figure 2. Conceptual illustration of how the metacommunity perspective can aid conservation biology. Global anthropogenic drivers disrupt the natural functioning of metacommunities, altering metacommunity processes and consequently biodiversity patterns at different spatial scales. Arrows from the left panel represent the direct effects of anthropogenic drivers on metacommunity processes, although these direct effects indirectly affect other processes (overexploitation affects demography directly and metacommunity processes indirectly). Ecological drift can amplify the anthropogenic effects through demographic stochasticity in changing populations. This conceptual framework allows us to understand the mechanisms underlying global change effects on biodiversity patterns at different spatial scales and thus at different biological organization levels (i.e., population, community, and ecosystem levels).

landscapes affect dispersal among habitat patches. Furthermore, demographic stochasticity and ecological drift can amplify the effects of other drivers by altering local extinction probabilities of small populations affected by a given anthropogenic pressure. Although there is still a long way to go to fully understand the effects of disturbance on metacommunity functioning and in turn on biodiversity, we identify some general mechanisms for each of the main global change drivers.

Land-use change and water management

Land-use change, such as habitat fragmentation and loss, directly alters habitat and landscape properties, which in turn directly affects dispersal and environmental filtering. A prominent example is urbanization and road expansion, resulting in habitat fragmentation and connectivity loss.[62] Likewise, water-management intensification, including dam construction and water flow modification, is an intense driver of change in aquatic metacommunities.[63,64] In both terrestrial and aquatic environments, these changes affect dispersal and habitat suitability.[65–67] Therefore, the metacommunity perspective can offer tools for understanding complex effects of land-use change for both terrestrial and aquatic conservation in the face of anthropogenic pressures.[68,69]

Climate change

Climate change directly affects metacommunities as an environmental filter, but also indirectly via complex community assembly processes and interactions. Species are extirpated from habitat patches and regions by climatic filtering if they are not able to adapt or disperse to regions with suitable climatic conditions.[70] Changing regions experience both emigration and immigration of individuals, which leads to compositional change and the emergence of novel biotic interactions. For example, a field experiment showed that novel competitors arriving from lower altitudes strongly reduced the performance of plants that failed to disperse upward to colder climates (in contrast to transplanted plants that could track environmental change).[71] Another indirect biotic effect of climate change is the phenological mismatch between consumers and associated trophic resources,[72] which may also affect dispersal if the synchronization between dispersal vectors and propagule production is affected.[73] Similar phenomena are discussed in both marine (e.g., Refs. 74 and 75) and freshwater (e.g., Refs. 76 and 77) ecosystems where shifts in species abundance, timing in phenology, and displacement of suitable habitats result at the metacommunity level in changed niches, modified dispersal/migration paths, and new species interactions.

Biological invasions

Invasive species directly impact biotic interactions in the metacommunity. Nonnative species compete with native species for resources, potentially reducing their performance and causing regional extinctions, as observed in both plants[73] and animals.[78] Likewise, invasive species can establish novel trophic interactions, such as predation[79] and disease.[80] Examples of invasion-driven extinctions are particularly prominent on islands, where species are often evolutionarily naive to these sorts of interactions.[81] In addition, invasive species can be physical ecosystem engineers, having profound effects on habitats that create environmental filtering for native species (e.g., invasive worms[82] and bivalves[83]).

Pollution

Pollution causes habitat alteration and degradation, working directly as a strong abiotic filter through effects on fitness (via changes in growth, health, and behavior).[84,85] It also affects habitat connectivity and suitability by increasing matrix hostility[86,87] and reducing services, such as pollination (e.g., lethal toxicity due to pesticides[88]). Pollution, especially via pesticides, can also interact with spatial processes within metacommunities to repeatedly and cumulatively influence impact, recovery, and regeneration processes.[89,90]

Overexploitation

Overexploitation directly affects mortality, decreasing population size and consequently population viability.[91,92] This effect is exacerbated by associated demographic stochasticity, which can lead to exploited populations experiencing higher levels of uncertainty,[93] particularly under environmental change.[94] Moreover, overexploitation can lead to entire community and ecosystem collapse through the breakdown of dependent biotic interactions if resource exploitation interferes with the trophic structure of communities (e.g., fisheries[95]).

We here stress that the core metacommunity processes are the foundations for a mechanistic approach to understanding and managing the effects of such global change drivers on biodiversity (Fig. 2). However, evidence for the impact of global change on metacommunity processes and functioning has been largely circumstantial. Among the relatively few studies that have explicitly used a mechanistic approach, generalities have been elusive because anthropogenic drivers influence metacommunity functioning in multiple, often interactive, ways.[96–100] This is corroborated by meta-analyses showing that responses after disturbance are highly variable, and depend, among other things, on the type of disturbance, habitat, and trophic role.[101–103] Therefore, to understand global change effects on the conservation of populations and biodiversity, we need to understand how each metacommunity process, alone or in concert, is altered by these global change drivers.

Responses of metacommunities to anthropogenic drivers

In this section, we discuss how the anthropogenic drivers described in the previous section (left panels, Fig. 2), via their influence on the four fundamental metacommunity processes (center panels, Fig. 2), alter a number of patterns in which conservation biologists are interested (right panels, Fig. 2). Three facets of biodiversity conservation are considered through the lens of metacommunity ecology: (1) the population-level patterns (abundance and distribution of species), (2) the community-level patterns and their scale dependence, and (3) the functioning of ecosystems in relation to biodiversity. Critically, the responses at the population, community, and ecosystem levels depend on both the spatial and temporal scales at which the patterns are observed.

Population-level abundance and occupancy

Conservation biology at the species scale is primarily concerned with the abundance and distributions of species, particularly those that are rare or declining. Perhaps the most important thing that a metacommunity perspective can bring to the study of rarity in abundance and occupancy is the issue of spatial scale in defining conservation goals. Rabinowitz[104] codified the scale dependence of species rarity by characterizing rarity along three axes—local abundance, geographic range, and environmental/habitat specificity.[105,106] Species that have narrow habitat specificity or geographic extents might be locally quite common, even if they are considered rare or threatened because their habitats are threatened. Other species may be rare because their local abundances are low or declining throughout their range. Measurements of rarity, and thus local extinction rates, can be similar, lower, or higher than regional or global extinction rates; as a result, studying rarity and extinction at a single scale may fail to capture conservation-relevant dynamics at other scales.[107,108]

The perspective and tools from metacommunity ecology align with Rabinowitz's three axes that influence species' commonness and rarity. Metacommunity ecology (1) embraces scale-dependence to understand multiple species abundance patterns from local to regional scales;[45,46,109] (2) accounts for geographical range of species distributions (species pool concept), as well as for historical effects (e.g., priority effects) to help unravel assembly processes;[37,48] and (3) makes extensive use of niche theory to integrate habitat specialization, species sorting, and environmental filtering (in addition to other processes) to explain biodiversity patterns.[15]

To devise potential conservation and recovery plans, it is critical to know which underlying metacommunity processes limit population abundance and distribution at local and regional scales. At a local scale, if the environment has fundamentally changed, this will influence the basic demographic parameters a species needs to persist in a given patch (i.e., birth rates exceeding death rates). Conservation would need to focus on either mitigating the changes to environmental conditions, or find alternative ways to balance birth and death rates. If biotic interactions have changed, such as via an invasive species, this effect would need to be mitigated, for example, by controlling or eradicating the invasive species, or again, finding alternative ways to enhance the demography of native species. If dispersal is limiting, precluding species from finding suitable habitat conditions, seeding, reintroduction, or assisted migration can be used. Finally, if small populations are at risk of demographic stochasticity, this can be overcome by reducing the uncertainty around birth rates (e.g., seeding, pollination, and population reinforcement) or death rates (e.g., enhancing survivorship).

In addition to a more explicit consideration of scale, the two other elements critical in a process-based metacommunity-based perspective are habitat heterogeneity and spatial connectivity (leading to movement among patches).[15] When dispersal among habitat patches is higher, species can persist in habitats where they otherwise could not, either due to source-sink processes in heterogeneous landscapes[110] or due to reduction of ecological drift and demographic stochasticity in small populations.[111] In the context of conservation, habitat corridors are often intended to minimize the impact of habitat loss by maintaining dispersal among otherwise isolated habitats.[112–114] At the same time, however, spatial processes may have unintended negative consequences for populations of conservation concern.[22,115,116] For example, diseases might be more likely to spread among a population that is more connected.[117,118] Likewise, habitat heterogeneity might allow spillover effects of biotic interactions. For example, Dangremond *et al.*[119] found that patches of invasive grasses could negatively impact populations of an endangered lupine in adjacent patches by providing refuge for seed predators.

Biodiversity change across scales

While a great deal of attention has been paid to biodiversity conservation, the scale-explicit and mechanistic metacommunity perspective allows a more realistic view of how biodiversity is changing in the face of anthropogenic factors. Although it is often assumed that global species losses are reflected, and even magnified, at the smaller (local) scales, recent studies have revealed that this is not always, or even rarely, the case.[120–122] In principle, no net change in species richness through time is expected if losses of species are balanced by gains.[18] Indeed, recent comprehensive analyses of biodiversity time series have suggested that, on average, gains and losses are largely balanced at local scales,[119] explaining the observation that species richness is often unchanged locally, but that the rates by which species turn over can be highly variable in different places.[122]

Local species richness can change in the face of anthropogenic factors, for example, via increased rates of local extinction due to altered environmental filters, biotic interactions, and/or dispersal rates. Often, these changes lead to the canonically expected net loss of local species diversity[123] and shifts in species composition toward more generalist species.[124] In other cases, however, species richness can increase in the face of anthropogenic pressures, particularly when nonnative or disturbance-tolerant species are present,[125,126] or when climate change favors species from the regional species pool.[127]

While there is still debate on exactly how and whether local diversity is changing in the face of anthropogenic pressure,[128,129] a consensus is emerging that biodiversity change is more complex and nuanced and that we need to focus more on how species composition changes through time,[121,122,130,131] as well as on how that temporal change varies across spatial scales within a metacommunity.[109,132] A more explicit focus on scale-explicit patterns of biodiversity change requires an understanding of how anthropogenic drivers influence each of the metacommunity processes described above (Fig. 2).

As an example, consider the case of habitat loss and habitat fragmentation, often considered among the most important drivers of biodiversity change globally.[133] Such changes can (1) alter environmental filtering by influencing local environmental conditions;[134–136] (2) alter species interactions by favoring the colonization of generalist species that can compete with specialist species[137,138] or the extinction of key species (e.g., cascading effects on trophic networks[139–141]); (3) alter dispersal rates into and out of local habitats (e.g., increased habitat isolation via fragmentation);[142] and (4) alter ecological drift by changing population size via altered habitat size.[57] Changes in each of these metacommunity processes alter patterns of coexistence and diversity differently at different spatial scales.[43] Thus, the current ongoing debate in the literature about the influence of habitat fragmentation on biodiversity being positive or negative (or unknown)[22,24] is largely misplaced until one can gain a more definitive focus on the mechanisms being influenced and the scales at which those influences occur.

At a local (α-) scale, the effect of anthropogenic disturbance on metacommunity processes can alter species richness by changing one or more of three components:[109,143–145] (1) the number of species in the species pool, for instance, by changing habitat suitability, or directly removing or adding a species; (2) the number of individuals in a community, which via sampling/rarefaction, leads to a change in the expected number of species; (3) the relative abundances (i.e., evenness) of species in the community, which alters the likelihood species will be observed at small scales in a given sample. For example, environmental filtering and biotic interactions can alter the numbers of individuals, the size of the species pool, and the evenness of the community. Changing dispersal rates can alter the size of the species pool by reducing or removing species (via local extinction) when dispersal is decreased, or by adding species when nonnative species are introduced. Finally, ecological drift can enhance the effects of other metacommunity processes when metacommunity size decreases (Fig. 2).

At the regional (γ-) scale, we also need to consider a fourth component: (4) the intraspecific clumping among local sites, which influences how species accumulate with increased sampled area. Metacommunity processes also influence intraspecific clumping. For example, environmental filtering via spatially autocorrelated environment and dispersal limitation promote intraspecific clumping. At the regional scale, when multiple sites are sampled, all four components influence how species richness increases with sampling effort. Because each component influences the shape of how species accumulate with increasing area, any changes to any of those components via anthropogenic drivers has the potential to influence α- and γ-diversity, as well as β-diversity.[109,146]

β-Diversity describes how species composition varies from place to place and has been of particular interest in metacommunity ecology to infer potential mechanisms underlying metacommunity assembly (e.g., the role of environmental filtering versus ecological drift).[15,43,147,148] In a conservation context, β-diversity can also provide important insights into the spatial structure of biodiversity and how to conserve it.[28] For example, reductions in β-diversity leading to biological homogenization occur when human-altered landscapes favor certain types of species (e.g., human commensals, disturbance-tolerant species, generalists, and nonnative species) and disfavor others (e.g., endemic species and specialists).[64,149,150]

At the same time, there is increasing evidence that anthropogenic factors can sometimes lead to an increase in β-diversity, known as biotic differentiation.[28,132,151,152] This can emerge, for example, when habitat heterogeneity is increased via anthropogenic drivers, or when dispersal limitation and ecological drift lead to decreased population size and local extirpation.[153] To date, there is little evidence available to directly compare and synthesize the relative importance of biotic homogenization versus differentiation, and thus how biodiversity change scales with increasing sampling effort. However, what is available suggests approximately equal evidence for each process.[109,132]

Conservation of biodiversity–ecosystem function relationships

Although the idea is much older,[154] the past 25 years have seen an explosion of research aimed at how biodiversity influences the stability and functioning of ecosystems (reviewed in Ref. 155). A major stimulus for this research program has been the justification for conservation of biodiversity as a means to protect ecosystem functions and services to the benefit of humans and the natural world.[156,157] A large majority of studies on the relationship between biodiversity and ecosystem functioning have either used experiments on artificially assembled communities[158] or have assumed that biodiversity in naturally assembled communities has an independent effect on the functioning and stability of ecosystems.[159] Moreover, as discussed above, local species richness is often unchanged even in the face of dramatic anthropogenic pressures, casting doubt on the frequent justification for studying local biodiversity–ecosystem functioning relationships in the context of conservation.[120,160,161] At the same time, the identity and composition of species can be greatly influenced by human impacts,[121,122,131] and this can have important, albeit complex, influence on patterns of biodiversity at larger scales.[132] Therefore, understanding the relationship between changing biodiversity and composition across scales, and how those changes influence species traits that play a role in the functioning and stability of ecosystems will be a critical next step for linking realistic changes in biodiversity to ecosystems in a conservation context. To this end, we need a more integrative and scale-explicit approach to understanding the role of diversity and composition in maintaining ecosystem functioning, which is provided by the metacommunity perspective.[29,30,162,163]

Although the influence of metacommunity processes on ecosystem functioning has rarely been explored empirically (but see Refs. 164–167), a number of theoretical and conceptual models have been aimed at the problem. Critically, when considered in a metacommunity context, the mechanisms that maintain local and regional species diversity strongly determine the relationship between diversity and ecosystem functioning.[29,31,162,168–170] At the local scale, for example, the assumed positive relationship between species richness and ecosystem function implicitly expects that local diversity is maintained by local coexistence via niche partitioning or other local mechanisms.[168] However, there are many cases where local diversity is maintained by dispersal from the regional species pool. This can allow competitively inferior species to persist in a given community, contributing positively to local diversity, but either having negligible or even negative effects on local productivity (e.g., via mass effects).[15] At the regional scale, habitat heterogeneity can maintain diversity regionally, which can enhance, reduce, or have no influence on local ecosystem functions, while maintaining regional ecosystem functions via a spatial insurance effect.[29,162,171] However, if stochasticity and ecological drift largely determine patterns of local diversity, and species traits are largely neutral with respect to resource utilization or have a weak link with ecosystem functioning,[172] we would expect no relationship between diversity or species composition and any aspect of ecosystem function.

The role of metacommunity perspectives in habitat preservation and management

We have argued that a metacommunity perspective can provide useful tools for conservation biologists when understanding the patterns of abundance and distribution of species and communities of conservation interest. At the same time, many of the concepts that we described, and their application, are still far removed from the "real world" of policy relevant conservation science and practice.[173,174] Here, we outline two prominent examples where a metacommunity perspective can be applied in a more policy-relevant context.

First, as the amount of space for nature and human needs (e.g., agriculture) is a fixed quantity, a pertinent question has been whether future development is best applied in a land sharing versus land sparing[175–177] context: (1) with a "land sharing" context, land is managed to optimize production and natural capital simultaneously, such that agriculture is maintained at relatively low yield across the landscape to allow biodiversity to also persist across the landscape; and (2) with "land sparing," large pieces of land are used for high-yield agriculture, while other pieces are spared that serve as biodiversity reserves. The differences between these ends of the continuum can be thought of as different kinds of metacommunities. Land-sharing metacommunities have small-grain heterogeneities (likely perceived as largely homogeneous to many species) with high connectivity across the landscape. Land-sparing metacommunities have larger-scale heterogeneity with likely higher habitat fragmentation and thus low dispersal rates between habitat patches. Which of these strategies is best for biodiversity conservation will depend on several aspects, namely, the predominant mechanisms and scales underlying the structure of a given metacommunity and the patterns of conservation interest, including particular species (which might have different perceptions of landscape heterogeneity), diversity, and ecosystem function. Indeed, a recent meta-analysis by Gonthier *et al.*[178] indicated complex, scale-dependent biodiversity patterns across more than 200 observations in agroecosystems. Likewise, Renwick *et al.*[179] developed a landscape-level approach to meet multiple objectives incorporating the ecological processes of metacommunities.

Second, interdisciplinary optimizations have been deployed to find solutions for maximizing biodiversity (and other variables of interest) in reserve design while minimizing costs, working within constraints, or efficiently meeting multiple targets simultaneously for quantitative conservation decision support.[180–182] These analytical decision-making tools offer advanced flexibility to incorporate many aspects that are relevant from a metacommunity perspective, including the configuration of habitat heterogeneity and connectivity, as well as population dynamics of multiple species.[183–187] While these complex frameworks are examples of some of the most integrative approaches between ecological theory, economics, land use planning, decision making, and conservation, we advocate that a more explicit and dynamic incorporation of a metacommunity perspective into decision-making support frameworks could be informative. For example, area-based estimates of species conservation and biodiversity often overestimate species persistence in a spatially explicit context (i.e., a metacommunity).[23,188] β-Diversity can also be a useful tool for conservation to improve agri-environmental measures in face of land-use intensification,[189,190] the design of terrestrial and marine reserves,[28,191–194] and river management.[68,69] Furthermore, β-diversity is a good indicator of current and/or historical ecological connectivity in a number of ecosystem types and communities, including in grasslands,[195] invertebrates and amphibians in wetlands,[196] stream fishes,[197] and floodplain river metacommunities.[198,199] While there are many examples of these approaches addressing different aspects of metacommunities in conservation solutions, an explicit integration of these ecological processes together is rare[200] and a complex endeavor for applied conservation. Such an approach could improve both frameworks for land planning and quantitative support for decision making that can influence policy-relevant conservation science. How ecologists and conservation scientists can best bring together theoretical metacommunity ecology and complex spatially explicit biodiversity patterns for real-world conservation solutions will be a future challenge for both fields.[174,201]

Table 1. Examples of empirical studies where understanding the consequences of environmental change drivers on conservation outcomes can be enhanced by a metacommunity perspective

Ecosystem type	Threat/ environmental change driver	Conservation target	Metacommunity concepts involved	Metacommunity tools mobilized	Achievement	Examples from the literature
Terrestrial	Land-use change and overexploitation	Assess relevance of land sparing versus land sharing	Habitat filtering and dispersal	Species richness modeling	Quantified the interaction between habitat availability and landscape configuration	Agroecosystem[214]
Terrestrial	Land-use change	Assist fire disturbance management	Connectivity	Percolation model	Assessed the connectivity threshold needed to maintain ecosystem state	Savanna grasses[215]
Terrestrial	Land-use change	Assess landscape versus spatial effects on metacommunities in 25-year interval	Habitat filtering, dispersal, species turnover, coherence, and species range aggregation	Environmental niche modeling and spatial modeling	Found constant metacommunity structure in a 25-year interval despite environmental and demographic changes	Birds[216]
Terrestrial	Climate change	Predict long-term biodiversity changes at broad scales	Habitat filtering and dispersal	Spatially explicit, dynamic metacommunity model	Projected rates of change in species turnover and local species richness over the next century	Plants[217]
Freshwater	Land-use change	Ecological functioning of urban pond management	Habitat filtering and dispersal	Lottery-based metacommunity model	Inferred the processes determining observed biodiversity patterns	Zooplankton[205]
Freshwater	Land-use change and pollution/ eutrophication	Assess stream alteration effects on metacommunities, including water quality issues	Habitat filtering and dispersal	Spatially and scale-explicit modeling (variation partitioning and asymmetric eigenvector map analysis)	Showed stronger direct effects of dams than indirect effects (on environmental changes induced by the dam presence)	Macroinvertebrates[218]
Freshwater	Land-use change	Guide restoration after dam removal	Habitat filtering and dispersal	Environmental niche modeling and spatial modeling	Identified group-specific effects of dam removal in relation to the environmental context	Fishes and macroinvertebrates[219]
Freshwater	All drivers	Improve stream biodiversity modeling by identifying important processes across scales	Scale-dependence, biotic and abiotic filtering, and mass effects	Null modeling of species co-occurrences and scale-explicit analyses	Assessed that mass effects interfere with species sorting at stream scale, while environmental control and dispersal limitations predominate at larger scales (e.g., across streams)	Macroinvertebrates[220]

Continued

Table 1. ***Continued***

Ecosystem type	Threat/ environmental change driver	Conservation target	Metacommunity concepts involved	Metacommunity tools mobilized	Achievement	Examples from the literature
Marine	Anthropogenic disturbance	Guide marine reserve design	Biotic interactions and dispersal	Spatially explicit metacommunity model	Assessed the regional dynamics of intertidal communities	Bivalves[191]
Marine	Overexploitation and climate	Assist fishery management and fish stock assessment	Source-sink dynamics and species interactions	Spatially explicit food web model	Produced area-specific recommendations by identifying sources from sinks for given species and oriented fishing strategy accordingly	Fishes[221]
Marine	Sea-use changes	Characterize the seascape connectivity for marine conservation planning	Connectivity	Metacommunity connectivity	Characterized the role of each marine area in metacommunity connectivity	Seagrass meadows[222]
Marine	All drivers	Assess human impacts on diversity	Dispersal	Neutral metacommunity model	Inferred the processes determining observed local diversity	Coral reefs[223]

Metacommunity models in action: applied examples across ecosystems

As overviewed here, the metacommunity perspective is a valuable conceptual framework for tackling the complexity and multiscale nature of conservation problems. Table 1 presents a necessarily incomplete list with examples of common environmental change drivers, conservation targets, and key metacommunity processes and tools involved from the literature across terrestrial, freshwater, and marine ecosystems. Aspects of these concepts have been put into practice for different conservation purposes in different ecosystems,[202] but practical approaches integrating these metacommunity concepts remain rare. As more metacommunity modeling platforms become available,[203–206] we expect them to be increasingly operationalized in applied ecology and biodiversity conservation. Applications include explorations of how biodiversity can respond to global change[207]—for example, to predict food web structure,[208] extinction of native species as a consequence of biological invasions,[209] community stability and extinction risk in marine ecosystems,[210] or colonization in aquatic dendritic networks.[211] Likewise, they include more applied contexts in which metacommunity models are used to predict biodiversity patterns in the design of biological reserves and management of land use and biodiversity incentive schemes.[212,213]

As this is intended to be an overview of metacommunity ecology and its relevance to conservation biology, it is beyond our scope to devise new theory. Nevertheless, a number of theoretical approaches are emerging that could provide promising groundwork for a conservation-oriented metacommunity theory.[16,206] For example, Thompson *et al.* developed a framework where each of the processes described above could be varied as part of a single set of equations for each species.[206] This could then be used to examine how anthropogenic factors might influence patterns of local demography (e.g., environmental conditions and harvesting), dispersal (e.g., habitat connectivity), and species interactions in the context of conservation.

Conclusions

Our goal here has been to highlight that a metacommunity perspective can provide a useful framework in which to view issues relevant to conservation biology. Of course, many of the concepts inherent to metacommunity ecology, including habitat heterogeneity, stochasticity and ecological drift, species interactions, and dispersal have all been important and are considered in different aspects of conservation biology in their own right. However, it has been rare to consider them simultaneously, which a metacommunity ecology perspective allows.[15]

Critically, the most important issue that arises from taking a metacommunity perspective in the context of conservation is that of the fundamental role of spatial scale in understanding the conservation of species and biodiversity. All of the variables of interest in conservation biology are implicitly scale-dependent phenomena and should be more explicitly examined as such: whether a species is abundant or rare critically depends on the spatial and temporal context in which observations are made;[104,106,108] the probability and rates of species extinction can be highly scale dependent and nonlinear;[107] and the magnitude and direction of biodiversity change through time in the face of anthropogenic pressures critically depends on the balance of species gains and losses, which again are typically nonlinear and scale dependent.[132] We hope that the concepts overviewed here, and the connections we make, will provide grist for the future development of a more direct link between the metacommunity perspective and scale-dependent issues of critical conservation importance.

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Author contributions

Author order is alphabetical. All authors devised the structure of the manuscript and each wrote first drafts of different sections. J.M.C. performed the literature search, A.J. formulated Table 1, E.L. made Figure 1, and D.V. made Figure 2. All authors revised the whole manuscript.

Competing interests

The authors declare no competing interests.

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