Review

Empirical approaches to metacommunities: a review and comparison with theory

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Metacommunity theory has advanced understanding of how spatial dynamics and local interactions shape community structure and biodiversity. Here, we review empirical approaches to metacommunities, both observational and experimental, pertaining to how well they relate to and test theoretical metacommunity paradigms and how well they capture the realities of natural ecosystems. First, we show that the species-sorting and mass-effects paradigms are the most commonly tested and supported paradigms. Second, the dynamics observed can often be ascribed to two or more of the four non-exclusive paradigms. Third, empirical approaches relate only weakly to the concise assumptions and predictions made by the paradigms. Consequently, we suggest major avenues of improvement for empirical metacommunity approaches, including the integration across theoretical approaches and the incorporation of evolutionary and meta-ecosystem dynamics. We hope for metacommunity ecology to thereby bridge existing gaps between empirical and theoretical work, thus becoming a more powerful framework to understand dynamics across ecosystems.

Metacommunity theory: a mechanistic approach towards the understanding of local community dynamics

Understanding the mechanisms that underlie patterns of species distribution, abundance and interactions is central to community ecology. Traditionally, community ecology focused on either local processes [1] or dynamics at the regional scale [2,3]. The acknowledgement that community composition within a local habitat is affected by both local interactions and regional processes is one of the major achievements in community ecology within the past 50 years.

This idea of processes at different scales being important and interacting to affect local community composition and diversity embodies the core of metacommunity theory. Metacommunity theory constitutes a theoretical, mechanistic framework to explain the interdependence of local interactions (within species, between species and/or between species and the environment) and regional processes (e.g. dispersal). The term 'metacommunity' describes a set of local communities that are linked by dispersal of multiple potentially interacting species [4], such that both local interactions and regional processes influence local community assembly. Recent interest in metacommunities and metacommunity theory has been fostered by both a review article [5] and a book [6], which have synthetically organised the various approaches to metacommunity theory into four different paradigms (Box 1; Figure 1a).

At present, understanding of metacommunity dynamics is predominantly theoretical in nature, fostered by conceptual paradigms, which have developed more rapidly and stringently compared with corresponding empirical approaches [5,6]. Yet increasing interest has recently led to a growing number of empirical studies, addressing aspects of metacommunity theory by both testing assumptions from its four paradigms (experiments) and assessing and interpreting local community assembly within its theoretical framework (observations). Astonishingly, no review has yet evaluated empirical (i.e. experimental and observational) approaches to metacommunities. A comprehensive and systematic evaluation of empirical and theoretical work is, however, urgently needed to identify and analyse potential gaps between the two [7] and, if necessary, to initiate future research. Here, we scrutinise a broad array of experimental and observational studies for their methodological approaches towards the analysis of metacommunities (see SI1 in the supplementary material online for a detailed description of the analytical procedure). In doing so, we examine whether and to what extent experiments and observations implement the assumptions made by theory and whether and to what extent metacommunity theory captures the realities of natural systems. Finally, we suggest ways to extend empirical metacommunity approaches, to integrate across the theoretical paradigms and to incorporate evolutionary and ecosystem dynamics into metacommunity ecology.

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Box 1. The four conceptual paradigms of metacommunity theory

Four conceptual paradigms have been presented to describe metacommunities. Each paradigm evokes different mechanisms of community assembly to explain local species coexistence within a metacommunity and predicts changes in local community composition based on the rate of dispersal and habitat and species characteristics [5,6].

(i) The species-sorting paradigm acts on the assumption that habitat patches differ with regard to environmental conditions. Where dispersal is not limited (i.e. species arrive at all habitat patches), differences in the ability to cope with these environmental conditions enable species to coexist regionally by means of niche diversification and differences in resource exploitation [77,78]. (ii) The mass-effects paradigm assumes that environmentally heterogeneous habitat patches are tightly interconnected via frequent dispersal in such a way that reproduction in a source habitat allows for persistence within a sink habitat [79,80]. (iii) The patch-dynamic paradigm assumes environmentally homogeneous patches to be inhabited by species that exhibit a trade-off between dispersal and local dominance, such as a colonisation–competition trade-off in which successful competitors are poor colonisers and vice versa [53,81–83]. Finally, (iv) the neutral paradigm implies that species do not differ in their fitness and niche [34]. Community assembly depends entirely on demographic stochasticity, and immigration and speciation is assumed to counteract local extinction processes [34].

Table I gives an overview of the criteria used to identify and differentiate between the four metacommunity paradigms in experimental and observational studies.

Table I. Framework to disentangle metacommunity paradigms in experimental and observational studies[a]

Paradigm	Criteria used in experimental studies	Criteria used in observational studies
Species-sorting (SS)	Habitat patches are environmentally heterogeneous.	
	Dispersal is high enough to enable species to fill niches within habitat patches because of niche diversification.	
	Studies lacking information on dispersal rates or frequencies cannot distinguish between SS or ME.	
Mass-effects (ME)	Habitat patches are environmentally heterogeneous.	
	Dispersal is high enough to override local dynamics (i.e. spatial dynamics are considered explicitly).	
	Studies lacking information on dispersal rates or frequencies cannot distinguish between SS or ME.	
Patch-dynamic (PD)	Habitat patches are environmentally homogeneous.	
	Species differ in their ability to disperse. Along a colonisation–competition trade-off, successful colonisers outcompete poor competitors and vice versa.	
	Experimentally, this requires active mobility or diffusive dispersal based on differing passive mobility rates. Testing PD is counteracted by researcher-mediated bulk dispersal (e.g. via pipetting).	Observationally, differing dispersal abilities among species are considered relevant a priori (although few observational studies have measured dispersal rates). The main criterion here is that habitat patches are environmentally homogeneous. Moreover, dispersal has to be low enough to restrict mobility of the most competitive species.
Neutral-model (NM)	Species do not differ in their fitness or niche (i.e. species composition within habitat patches is not driven by differences in competitiveness or mobility).	

[a]Criteria are listed based on the distinctions given in [5].

Experimental and observational approaches to metacommunity theory

Experimental approaches

Experimental studies were diverse in their approaches towards metacommunities (Box 2). The majority of the 34 experimental studies related to aquatic environments (Figure 2a). Some mimicked certain marine [8,9] or freshwater [10,11] habitat types, whereas others established artificial aquatic microcosms as model communities without referring to a specific type of aquatic system [12,13]. The latter approach was most common (see category 'none' in Figure 2a) and corresponded with the preponderance of unicellular organisms (bacteria, microalgae and protists) in experimental metacommunity approaches (Figure 2b). Metazoans, by contrast, were targeted in 40% of all experimental cases; vertebrate and plant communities, however, were examined only rarely.

Most experimental studies (70%) monitored multiple response variables, usually comprising measures of standing stock (biomass or abundance) and species composition (diversity or evenness) (Figure 2c). Only a few experiments extended this approach to measuring process rates within individual patches or metacommunities, such as productivity [9,14], rates of consumption [8] or dispersal [15]. Regarding dispersal, half of all experimental studies were designed to rely on active dispersal, whereas the other half investigated passive dispersal (Figure 2d).

Of the experimental approaches, 50% were designed to test a specific paradigm, predominantly patch-dynamic (seven studies) or mass-effects (eight studies). More than half (i.e. 19 studies) comprised homogeneous patches without the possibility of regional resource use differentiation, precluding both mass effects and species sorting.

Observational approaches

Most observations were conducted in aquatic habitats, particularly in lentic pelagic environments (Table 1). Furthermore, most studies centred on bacteria, although plants, zooplankton and zoobenthos were also investigated with regularity (Table 1).

Most of the 74 observational studies measured response variables, such as species abundance and composition. Explanatory variables typically comprised physico-chemical habitat parameters, although process rates, such as productivity [16–18], predation [19], resource use [20], or dispersal rates [16,21–24], were also measured. Passive dispersal (via air, through water or by means of a vector) was the predominant mode of dispersal analysed (73%). By

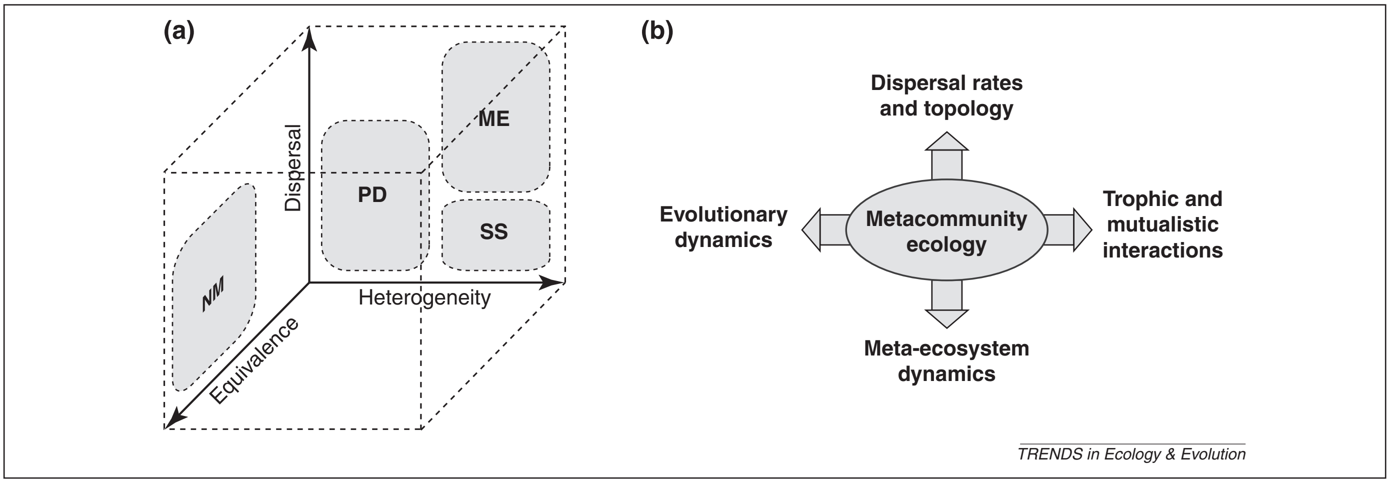

Figure 1. Depiction of the four metacommunity paradigms and areas of potential advances. **(a)** The four formulated paradigms of metacommunity theory placed within a common framework, depicting their differences and overlaps along axes of the rate of dispersal, of the heterogeneity of habitat patches with regard to local environmental and biotic characteristics, and of the equivalence among species regarding niche and fitness. Abbreviations: ME, mass-effects; NM, neutral model; PD, patch-dynamic; SS, species-sorting. **(b)** Four areas potentially advancing metacommunity ecology. Future metacommunity work should explicitly consider dispersal rates and topology, trophic and mutualistic interactions, energy and matter flow in meta-ecosystems, and evolutionary dynamics and constraints.

contrast, only approximately a quarter of the organisms studied dispersed actively.

Only 27 observational studies were not explicitly designed to test a specific metacommunity paradigm, whereas two out of the 74 studies aimed to test all four paradigms simultaneously [25,26]. Among the observational studies that did test metacommunity paradigms, species-sorting and mass-effects were the two paradigms aimed at (35 and 34 studies, respectively) and reflected (66 and 57 studies, respectively) the most. In total, 30 studies observed processes that could be described by two or more metacommunity paradigms, whereas in 16 cases community dynamics could not be related to any of the four paradigms.

Conformity and coherence between the reviewed empirical studies and the four paradigms of metacommunity theory

The two key publications that have synthesised approaches to metacommunity theory [5,6] have provided the theoretical foundation for most of the empirical work reviewed here. The organisation of approaches to metacommunity theory into four paradigms has been both implicitly and explicitly implemented by the empirical studies analysed. This has, however, led to the introduction of a certain degree of incongruence between theoretical and empirical metacommunity research. First, processes of community assembly observed in both experimental and observational studies very often exhibited features that could be attributed not only to one but also to two or more paradigms (see also [27]). This highlights the difficulty of actually disentangling mechanisms of community assembly in nature, where assemblages are obviously structured by a combination of processes. It also relates to the notion that the paradigms were not meant to be exclusive [5] because local communities can, in theory, be structured by a combination of processes ascribed to different paradigms (see ‘Need for integration’, below).

Second, empirical approaches, in particular experiments, were not aligned well enough with the paradigms, which might indicate that the paradigms are too simple an abstraction of processes occurring in nature. Experimenters were often constrained by realistic aspects of their target systems, causing experimental designs to transcend the four paradigms. Matthiessen and Hillebrand [9], for example, mimicked rock pool communities within the laboratory. They created a metacommunity that was assembled by species differing in their ability to disperse and exploit niches and that was structured by the connection of small habitat patches (pools) to a large species-rich region (ocean). Hence, they incorporated aspects of species sorting, patch and mainland–island dynamics.

Moreover, few empirical studies referred to, and found, signatures of either patch or neutral dynamics. Patch dynamics were explicitly analysed in only five observational studies within which they were hardly detected. By contrast, experimental studies addressed patch dynamics more frequently because they often concentrated on physico-chemically simple systems (i.e. homogeneous habitat patches without the possibility of regional resource use differentiation) and allowed for unequal dispersal abilities among organisms. One third of all experimental studies, however, used dispersal treatments that equalised organismal dispersal success, thereby impeding coexistence by colonisation–competition trade-offs [28].

As for neutral dynamics, experimental approaches neither investigated nor found signatures of neutral processes. Although some observational studies intended to assess metacommunities for neutral dynamics, only five observed evidence thereof [29–33]. This is interesting because a large literature on neutral theory does indeed exist [34], including observational [27,35,36] and experimental [37–39] studies. Yet, this literature often does not explicitly include spatial dynamics and substantially differs in its approach compared with the studies targeted in our survey. Although our analytical procedure probably fell short of detecting all studies on neutral dynamics, it

Box 2. Experimental approaches to the study of metacommunities

Experimental studies manipulating aspects of metacommunity dynamics in laboratory and outdoor experiments, comprise a broad array of approaches (Figure I). Well plates (Figure Ia,b) or cell culture flasks (Figure Ic) represent the simplest type of experiment. Patches are, in these cases, not physically connected; thus, dispersal is manipulated by transferring organisms from one patch to another. More complex laboratory systems consist of flasks or bottles connected via tubes (Figure Id,e), which either link all patches with each other (Figure Id) or create a certain topology (i.e. interconnecting some patches more closely than others; Figure Ie). Outdoor experiments use artificial and isolated ponds as patches in which dispersal occurrs through active organismal movement between patches, or is established passively via the exchange of water (Figure If). Alternatively, local patches are placed within a larger vessel, resembling isolated subsystems (e.g. coastal rock pools) in connection with a large regional system (e.g. coastal water body), which functions as a supply of organisms and matter (Figure Ig). Here, dispersal is enhanced by raising the water table to enable organisms to move between patches. Only a few experiments were carried out *in situ*, such as the manipulation of forest fragments (Figure Ih), the use of bivalve shells as habitats (Figure Ii), the construction of a fragmented moss landscape (Figure Ij), or experiments on inquilines metacommunities in the leaves of pitcher plants (Figure Ik).

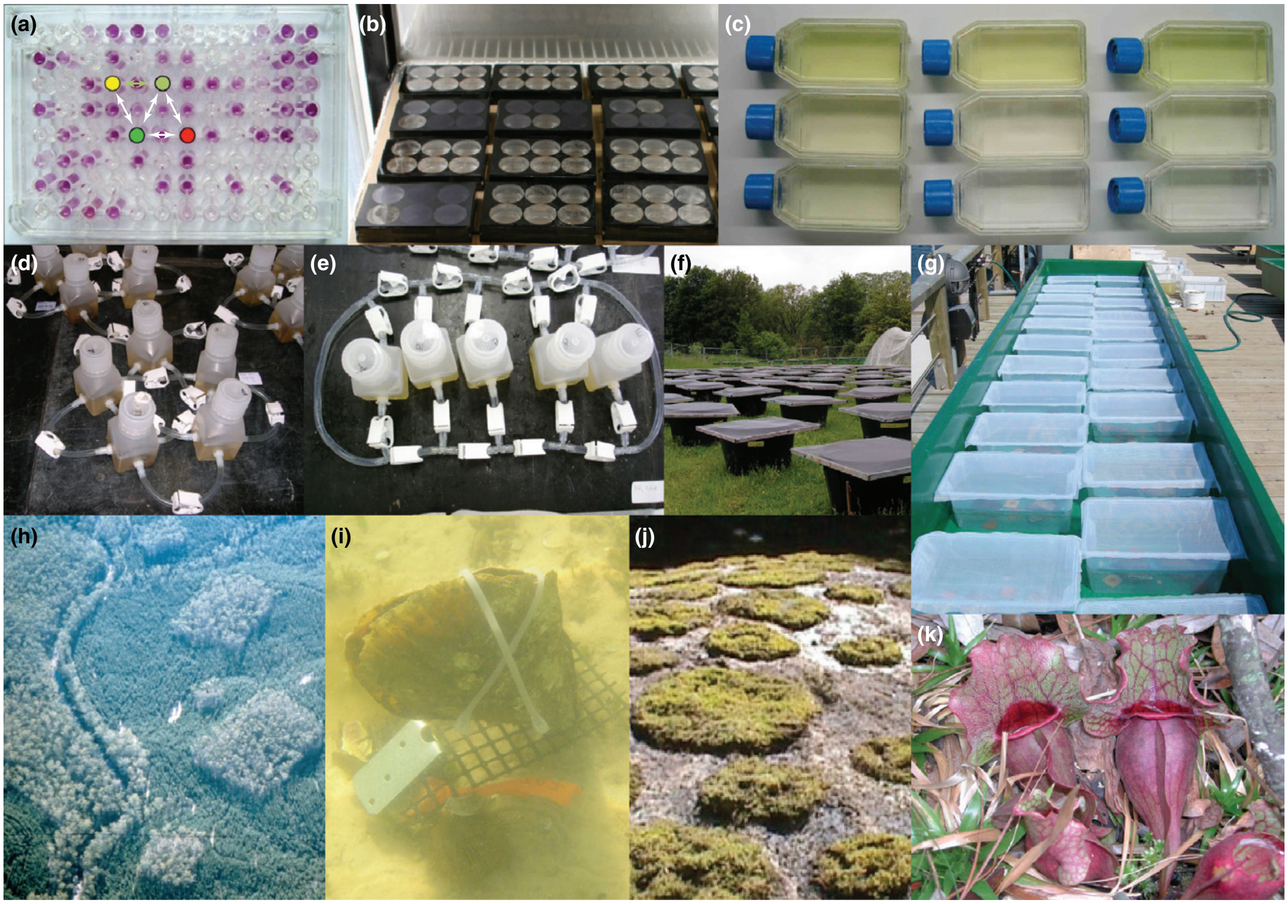

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Figure I. Experimental approaches to metacommunities. **(a)** Bacterial metacommunities in a 96-well plate; wells containing different carbon sources. **(b)** Algal metacommunities in 6-well plates; wells receiving different degrees of shading. **(c)** Algal metacommunities in culture flasks differing in resource ratios. **(d,e)** Protist metacommunities in culture flasks connected via tubes allowing global dispersal **(d)** or including topology in dispersal **(e)**. **(f)** Outdoor pond mesocosms. **(g)** Outdoor metacommunities of marine benthic invertebrates at the Tjärnö Marine Biological Laboratory, Sweden. **(h)** Aerial photograph of a fragmentation experiment in a forested landscape. **(i)** Natural metacommunity within pen shells. **(j)** Moss patches on rocks used for fragmentation experiments. **(k)** Inquiline metacommunities in leaves of *Sarracenia purpurea*. Reproduced, with permission, from Patrick Venail **(a)**, Birte Matthiessen **(b)**, Lars Gamfeldt **(c)**, Marc Cadotte **(d,e)**, Luc de Meester **(f)**, Lars Gamfeldt **(g)**, Chris Margules **(h)** Pablo Munguia **(i)** Andrew Gonzalez **(j)**, Thomas Miller **(k)**.

seems as though spatial community work has grown along two different mind sets, following either a mainland–island perspective at a biogeographical scale [34] or a community-dynamics perspective at a mesoscale [5,40] (see SI2 in supplementary material online). Placing greater emphasis on stochasticity within the framework of metacommunity ecology might propel the assessment of neutral ecological drift. Stochastic events, which are certainly relevant in nature but understudied within metacommunity ecology, are predicted to increase in a globally changing world.

Linking empirical metacommunity literature with processes in nature

Applying metacommunity paradigms to nature, which is not only patchy and heterogeneous [41] but also stochastic [34], is not straightforward [5]. Different organisms respond differently to processes (e.g. at different scales) and

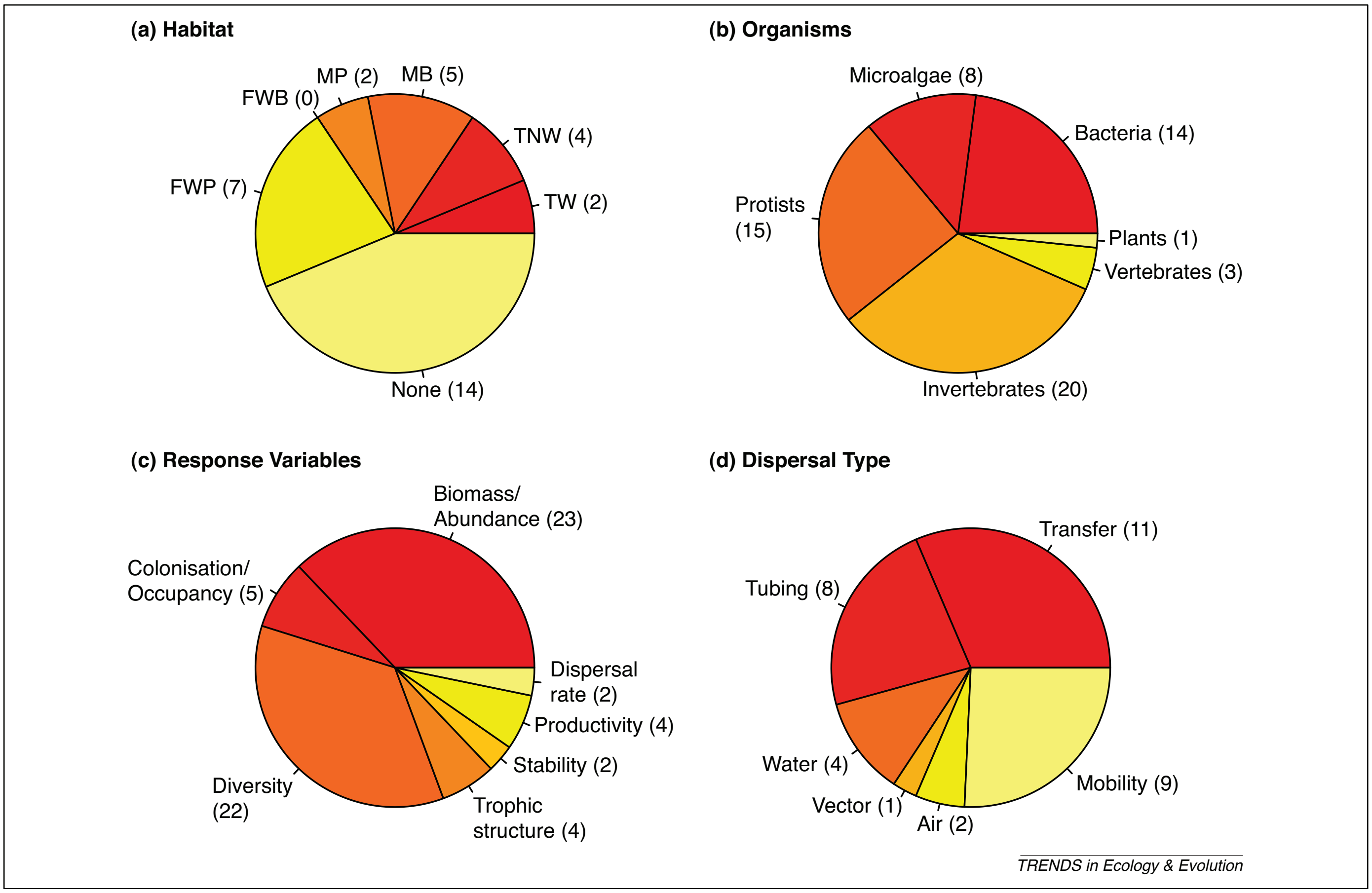

Figure 2. Summary of results for 34 experimental metacommunity studies. The diagrams show the proportion of studies falling into different categories with regard to **(a)** habitat type, **(b)** organism group, **(c)** response variable and **(d)** the dispersal type. Absolute numbers of studies are given in brackets with each text label. However, the sums can deviate from 34 as studies used multiple treatments or organisms, or because studies addressed various response variables or dispersal types. Abbreviations: FWB, freshwater benthic; FWP, freshwater pelagic; none, artificial microcosm that does not reflect any particular system; MB, marine benthic; MP, marine pelagic; TNW, terrestrial non-woody; TW, terrestrial woody. Tubing describes patches linked by tube-like connectors, which are often manipulated by altering the ratio of time closed to time open. Transfer includes all types of transport of water or individuals between habitat patches by the manipulator. Classically, this involves extracting a certain volume of each patch (e.g. via a pipette or a bucket) and transferring this between patches. Mobility identified those metacommunities that lacked any kind of direct connection between patches or direct transfer (i.e. dispersal that depends on organisms actively moving between patches). Other metacommunity experiments included a direct water flow, air connection or some physical vector to mediate dispersal between patches.

local communities often lack discrete boundaries, rendering a direct implemenation of simple theoretical approaches to natural systems difficult. With regard to the latter, most empirical studies addressed permanent habitat patches with discrete boundaries and focused on insular metacommunity types (e.g. lakes, ponds, islands or moss patches). Yet, this preponderance reflects the dominant type of metacommunity paradigms rather than the dominant type of metacommunities observed in nature. Natural habitat patches, however, can be distinct from their surroundings but temporary in character (e.g. pitcher plants, water-filled tree holes or rock pools), lack distinct boundaries yet are permanent (e.g. coral reefs or grasslands), or are hierarchically structured (e.g. streams, rock

Table 1. Summary of 74 observational approaches to metacommunity theory with regard to habitat type and organism group[a]

Habitat type	Organism group									
	Zoobenthos	Zooplankton	Bacteria	Nekton	Fungi	Microalgae	Plants	Terrestrial arthropods	Terrestrial vertebrates	Total
Lentic water bodies, benthos	6						1			7
Lentic water bodies, pelagic	1	12	16	5		4		2	1	41
Lotic water bodies, benthos			1				1			2
Lotic water bodies, pelagic		2	2	1						5
Marine benthos	7			1			1			9
Marine pelagic		1	3							4
Terrestrial woody					1		9	4	2	16
Terrestrial non-woody			2		1		5	4	1	13
Other			1							1
Total	14	15	25	7	2	4	17	10	4	98

[a] Numbers are based on count data.

pool clusters or fragments within a terrestrial matrix). These spatial habitat configurations are as underrepresented in the empirical approaches reviewed here as they are in the theoretical ones. The example of coastal metacommunities (e.g. rock pools or boulders in the intertidal) connected to a large (and almost unlimited) regional pool of colonisers illustrates the difficulty of delineating metacommunities *in situ* because it poses the question of the relative role of dispersal into and between habitat patches compared with that of local interactions: immigration can be either too low (strict dispersal limitation) or too high (panmixis) for metacommunity dynamics to unfold.

In general, experimental and observational studies mostly targeted small, passively dispersed organisms that inhabit aquatic habitats. Larger organisms and terrestrial systems are underrepresented; a bias that can have important ecological consequences. Indeed, in not targeting larger organisms, both experimental and observational approaches neglected large-scale gradients of dispersal, such as dispersal in relation to body size in which passive dispersal decreases and active dispersal ability and range size increase with increasing body size [42]. Smaller sized organisms are not only more readily dispersed passively but also disperse in greater numbers and, hence, are more frequent colonisers. Moreover, larger organisms more often depend on sexual reproduction and, therefore, are more prone to Allee effects [43–45], which can lead to a more complex set of metacommunity dynamics.

Considering the process of dispersal, a distinction has to be made between the locomotion or transport of individuals and effective dispersal [transport plus successful establishment (colonisation)]. This distinction is important to organisms that effectively produce dormant or resting stages. In fact, four observational studies made this distinction and observed differences in the ability of species to colonise newly created freshwater ponds [16,21,22] or to establish themselves in lakes [46]. Distinguishing dispersal from successful colonisation has further implications for biodiversity–ecosystem functioning relationships, as only physiologically active and, thus, successful colonisers execute ecosystem functions. Dormant and resting organisms, however, might be able to react quickly to changing environmental conditions and perturbations and can, hence, act as insurance when the functioning of other members of the community is impaired [47,48].

The order with which a community assembles should also be considered because priority effects are known to interfere with metacommunity dynamics [49] and influence community diversity and functioning [50]. Priority effects arise when early colonisers gain a competitive advantage over late-successional species because of resources being monopolised [51]. This effect can be strengthened by rapid evolutionary adaptation of the early coloniser, allowing them to gain a greater advantage over late arrivals [51]. Stochastic priority effects can mimic patterns of dispersal limitation because initial differences in community composition might be conserved.

Need for integration

The original framework [5,6] provided four main paradigms to metacommunity ecology that are well delineated and separate the main mechanisms of community assembly from a theoretical point of view (Box 1). Yet, as our review illustrates, this classification is not directly operational because it is difficult to link mechanisms to a single paradigm and because natural assemblages are structured by a combination of processes ascribed to different paradigms. In an attempt to reflect processes in nature more realistically, several studies developed hybrid models, illustrating how complexity can arise from combining different mechanisms of coexistence within metacommunities. For instance, mass effects are an extension of niche theory, which underlies species-sorting dynamics [52]. Other examples are links between colonisation–competition trade-offs and mass-effects or species-sorting dynamics [41,53–55] or between mass-effects and neutral dynamics [34,56]. Hence, it is more likely that a continuum between the different mechanisms of community assembly exists within which the four established metacommunity paradigms can be placed (Figure 1a). Expanding metacommunity ecology to such an integrative framework will help shift the focus from separating the four originally postulated paradigms to more concisely testing the mechanisms and relative importance of spatial and local processes. It will, moreover, advance metacommunity ecology to become a more operational tool for empiricists.

Developing an integrative concept for metacommunities along the axes of species differences (equivalence), habitat differences (heterogeneity), and dispersal (Figure 1a), will allow for a generalised view of spatial dynamics. Such a view acknowledges distances in trait and environmental space and a process-oriented approach towards dispersal. Yet, this integration will require different approaches to experimental manipulations along with novel statistical procedures to test the importance of these axes empirically (see Box 3 for an overview of current statistical tests used in observational metacommunity approaches). Hence, observational studies must provide information on not only spatial and environmental distance but also aspects that differ among species and actual dispersal rates.

Need for empirical advancements

The metacommunity concept is a recent addition to community ecology theory. Progress in understanding factors and processes that structure metacommunities has been made beyond doubt. However, we have identified a series of areas within empirical work that need attention and, thus, hope that our review will initiate developments in empirical metacommunity research.

First, the types of habitat and groups of organism focused on in empirical approaches need to be extended. This necessity refers not only to the inclusion of terrestrial ecosystems and larger organisms but also to studying metacommunities that go beyond an insular type with discrete boundaries. Many natural systems influenced by spatial dynamics are more hierarchically structured, have indistinct boundaries, or are of temporary nature. Extending empirical metacommunity approaches to these underrepresented systems also requires the incorporation of metacommunity topology (e.g. differential connectivity between patches or mainland–island dynamics). For example, most experimental studies performed a global dispersal regime in which all patches were connected to each other

Box 3. Overview of statistical tests presently used in observational approaches to metacommunity theory

Variation partitioning is the first and most widely applied test to investigate processes determining dynamics of species abundance and composition within communities across multiple locations [84] (Table I). This method attempts to disentangle the relative effects of environmental and spatial processes via partitioning the variation of species abundance and occurrence data into different components, such as unique environmental or unique spatial variation or an interaction between these two. These variation components have been related to metacommunity dynamics (e.g. [27,85]). However, variation partitioning allows for neither an unambiguous distinction between the four metacommunity paradigms [27], nor a concise assessment of dispersal characteristics [86]; characteristics that conceptually distinguish the four metacommunity paradigms, according to [5]. For instance, spatial signatures observed in local community assembly dynamics can stem from both measured and unmeasured spatially structured environmental parameters; a constraint that makes actual measurements of dispersal all the more necessary.

A second method to evaluate patterns of species distribution uses a site-by-species incidence matrix to try and identify consistent patterns of species co-occurrence [87,88]. Patterns of species distribution are abstracted into six simplified and idealised structures of this incidence matrix. To evaluate whether a given matrix fits any of the idealised structures and to distinguish among them, three aspects of metacommunity dynamics (coherence, species range turnover and boundary clumping) are considered. Advantages are the overall simplicity of the method, its ability to distinguish between a set of idealised patterns and to deduce certain aspects of metacommunity ecology. However, this set of idealised patterns does not comprise all possible patterns and thus natural communities can deviate from them. Although this approach identifies patterns, it does not necessarily imply anything about the processes that led to them. Finally, spatial dynamics are not directly modelled.

The zero-sum multinomial distribution [34] is (aside from general randomisation tests) often implemented to deduce neutral dynamics from species abundance patterns. It derives from the zero-sum assumption (the third of the three assumptions of the neutral theory), which states that constant resource availability implies constant community size (i.e. no species can increase in abundance in the community without a matching decrease in the collective abundance of all other species). It is a simple method that only tests for neutral dynamics (i.e. community dynamics are neutral if relative species abundances follow a zero-sum multinomial distribution).

Table I. Comparison of statistical tests presently used in observational approaches to metacommunity theory

	Definition of metacommunity	Target	Data			Advantages	Disadvantages	Refs
			Species	Space	Environment			
Variation partitioning	Set of ecological communities at different sites linked by dispersal	Species-sorting, mass-effects, patch-dynamic, neutral	Abundance	Yes	Yes	Includes both environmental and spatial characteristics	Species-sorting is the only paradigm that can clearly be distinguished, metacommunities characterised by species-sorting processes can, however, be further scrutinised for high and limited dispersal; the origin of spatial variation can be difficult to assess	[84]
Site-by-species incidence matrix	Set of ecological communities at different sites, potentially but not necessarily linked by dispersal	Checkerboards, nested subsets, Clementsian, Gleasonian, evenly spaced gradients, random	Presence/ absence	No	No	Simplicity, distinction between idealised patterns is possible	Hypotheses are idealisations; spatial dynamics are not directly modelled; method does not necessarily imply anything about the processes underlying the patterns	[87]
Zero-sum multinomial distribution	Set of ecological communities at different sites linked by dispersal	Neutral	Abundance	No	No	Simplicity, clear identification of neutral dynamics	Only answers the question of whether neutral dynamics are important; does not imply processes underlying the pattern other than functional equivalence; environmental and spatial dynamics are neglected	[34]

to equalise the colonisation probability for each patch. Although such an approach has advantages from an experimental design perspective through not introducing systematic variation into the response data, it disregards consequences of metacommunity topology for regional and local processes. Among the few experimental studies that included topology, Cadotte [57] showed that dispersal effects on local and beta-diversity strongly depended on the connection regime. Therefore, we propose to incorporate more complex spatial configurations and community organisation (Figure 1b). With regard to the latter, it can be assumed that different trophic guilds have different levels of mobility and use of space.

Closely associated therewith is the need for empirical metacommunity studies to include concise measures of actual dispersal rates. Out of 74 observational studies, only five measured dispersal rates [16,21–24]. In all other cases, dispersal information was instead inferred indirectly (e.g. via spatial distance, spatial variability in species abundance and composition, connectivity or isolation, or from theoretical measures, such as water retention time). Dispersal rates and distances are indeed inherently difficult to measure in practice [58] and whereas most dispersal might be limited to short spatial scales, distribution and colonisation of new habitats can be strongly dependent on rare long-distance dispersal [59]. Besides, in most cases, only one route of dispersal was examined at a time (e.g. [46]). Ignoring alternative dispersal routes, however, probably leads to an underestimation of immigration, which can, in turn, result in a concealment of the mechanisms influencing community assembly (e.g. [46]; Figure 1b).

Related to topology is the consideration of scales. Although being fully aware of the logistic constraints, we find it noteworthy that regions in experimental studies were, on average, only eight times larger than the single patch. This is important because the scaling of region to patches places strong constraints on how single patch processes affect aggregate properties of metacommunities [60,61]. In the case of a local patch making up a large portion of an area of a region, the emergent properties of that metacommunity are closely and linearly related to the properties of that single patch. At the other extreme, extending the spatial scale to very large regions can involve processes occurring on historic timescales, leading to biogeographic rather than metacommunity dynamics. Obviously, there is a continuum from frequent dispersal to infrequent long-distance dispersal, shifting range boundaries rather than affecting local dynamics. Yet, the current understanding of metacommunities focuses on dynamics upon which spatial and local constraints occur on the same temporal scale. Extending the metacommunity framework to larger spatial scales requires new approaches and concepts. Applying an approach combining phylogeny, biogeography and environmental filtering to zooplankton communities, Leibold and colleagues [62] recently suggested that both metacommunity and biogeography dynamics affect the distribution of species.

Second, empirical metacommunity studies mainly incorporated rather short-term ecological processes. Yet, evolutionary or regional processes (e.g. history of assembly [63,64] or evolutionary history [65,66]) also influence local communities. Incorporating an evolutionary perspective on metacommunity theory (Figure 1b) is warranted [49,67,68] but has rarely been implemented empirically [14]; for instance, evolutionary priority effects might be of importance in structuring many natural metacommunities [51].

Third, in comparison to observational studies, experimental approaches usually included multiple drivers of community assembly as treatments and measured several aspects of community composition as response variables. The factorial manipulation of dispersal constraints (rates, frequency or absence) and of local constraints on coexistence (nutrients, disturbance or predation), in particular, captures the essence of metacommunity dynamics by linking dynamics across scales. In doing so, experimental studies also addressed multiple trophic levels and explicitly approached the trophic structure of metacommunities as exemplified in some models on spatial food-web dynamics [69,70]. Observational studies, by contrast, fell short of including these aspects. Being predominantly based on competition, metacommunity ecology should further comprise non-competitive habitat dynamics, such as trophic and mutualistic interactions, which also have a clear spatial component (Figure 1b). This would also enable metacommunity dynamics to be considered in the context of spatial matter and energy flow (Figure 1b) [69].

Fourth, only a few studies addressed functional consequences of altered community structure in these experiments, such as primary productivity [9,14,71] or consumption rates [72,73]. Theory has already advanced to include elements of ecosystem functioning [70,74,75] through the emergence of meta-ecosystem models [76], linking metacommunity dynamics to ecosystem ecology by considering matter and energy flux. These attempts now have to be approached empirically to move beyond the analysis of community composition and to provide answers to urgent questions regarding ecosystem management, such as how to maintain ecosystem processes and services in the face of species loss and habitat fragmentation (Figure 1b).

Conclusions

Metacommunity theory has enabled a big leap forward in understanding mechanisms of spatial community ecology. We have highlighted this in our review of empirical approaches and their subsequent comparison with metacommunity theory. We have nonetheless revealed major gaps in approaches to metacommunities and discrepancies between theory and empirical approaches. These limitations led to concise recommendations for future metacommunity studies. First, we suggest the extension of empirical approaches to different types of organism and habitat, not only to broaden the basis of inference but also to incorporate more types of spatial dynamics that go beyond competition. Spatial and localised interactions need to be linked based on actual measurements of dispersal rates and mobility. Second, we propose the integration of the established metacommunity paradigms (as reviewed in [5]), which will require co-development of both novel theoretical approaches and more sophisticated ways to test the predictions made by theory. Third, we recommend the incorporation of additional constraints of spatial dynamics, such as evolutionary and meta-ecosystem dynamics. Thereby, metacommunity ecology will develop into a cornerstone of ecology and provide the appropriate tools with which to incorporate spatial dynamics into ecosystem management and conservation biology.

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