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Linking metacommunity theory and symbiont evolutionary ecology

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Processes that occur both within and between hosts can influence the ecological and evolutionary dynamics of symbionts, a broad term that includes parasitic and disease-causing organisms. Metacommunity theory can integrate these local- and regional-scale dynamics to explore symbiont community composition patterns across space. In this article I emphasize that symbionts should be incorporated into the metacommunity concept. I highlight the utility of metacommunity theory by discussing practical and general benefits that emerge from considering symbionts in a metacommunity framework. Specifically, investigating the local and regional drivers of symbiont community and metacommunity structure will lead to a more holistic understanding of symbiont ecology and evolution and could reveal novel insights into the roles of symbiont communities in mediating host health.

Expanding symbiont community ecology

The study of symbionts and symbiont communities, whether these are commensal, mutualistic or parasitic organisms, is vital to our understanding of general host–symbiont dynamics, as well as clinical and epidemiological patterns. Exploring the community-level ecological interactions of symbionts and their hosts has substantially added to our knowledge of host–symbiont relationships [1–4], as well as symbiont evolution [5–7]. Furthermore, symbiont communities themselves have contributed to the fields of ecology and biogeography, for example, in testing of theoretical predictions such as the distance decay of similarity and niche breadth–range size relationships [8]. However, there is an extensive body of other ecological theory that can be applied to and tested with symbiont communities, which would enhance our understanding of host–symbiont interactions, including disease dynamics, and of the structuring of ecological communities in general. Here I advocate the utility of metacommunity theory (Figure 1) [9,10].

The ultimate aim of metacommunity theory is to evaluate patterns of and mechanisms contributing to species diversity across space. Specifically, this theory asks how dispersal of organisms between communities alters local dynamics and subsequently influences community structure both locally and regionally (Box 1; Figure 1). Furthermore, the emerging 'evolving metacommunity' concept explores how genetic variation is distributed across space and how gene flow can influence species interactions and

community composition via (mal)adaptation [11–13]. The metacommunity concept has been integral to our understanding of large-scale trends in community structure and biodiversity [14–16]. The goals of metacommunity theory and the predictions that have emerged from this body of work align well with current research on symbiont communities and host–symbiont interactions.

Interspecific interactions among symbionts, as well as their dispersal and transmission, all influence the ecological

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Glossary

Community structure: refers to the diversity of a suite of species, where diversity is measured by species richness and/or the relative contribution of each species to the community (i.e. evenness).

Dispersal limitation: phenomenon by which species are not able to colonize all available habitats. This can arise via spatial impediments to dispersal (e.g. distance) or species-specific dispersal traits.

Evolving metacommunity: metacommunity in which species interactions are modified by hereditary traits that are allowed to evolve [11]. The primary distinction is that dispersal among patches influences the gene flow and adaptation to various biotic or abiotic conditions of species. These evolutionary processes determine whether or not species can persist in a patch or metacommunity and thus influence how community composition changes over time.

Mass effects: net flow of individuals from patch to patch resulting from differences in local population sizes or densities [9]. Mass effects can alter local patch dynamics. For example, a prey species can be rescued from local extinction due to predation via the influx of immigrants from neighboring patches without predators.

Neutral metacommunity: metacommunity in which species are assumed to have identical demographic rates. Thus, local communities assemble randomly based on the composition of the regional (source) species pool. Differences in local community composition arise primarily via dispersal limitation or evolutionary processes (e.g. speciation events).

Parasitic: the term parasitic is used in a general sense. Here, a parasite must use the resources of a host but may or may not cause pathology in the host as a result of this resource use. Thus, 'parasitic' can be equated to 'pathogenic', depending on the specific effects of the parasite at any given time point.

Resistance: ability of a host to limit infection given a certain exposure to a parasite. In other words, resistant hosts have a lower probability of allowing a parasite to successfully infect and replicate. Resistance can be achieved via a variety of mechanisms including behavioral avoidance of parasites and immunological mechanisms.

Species sorting: essentially niche partitioning, whereby species inhabit areas in which their optimum resources exist. Dispersal is necessary so that species can find their preferred habitat.
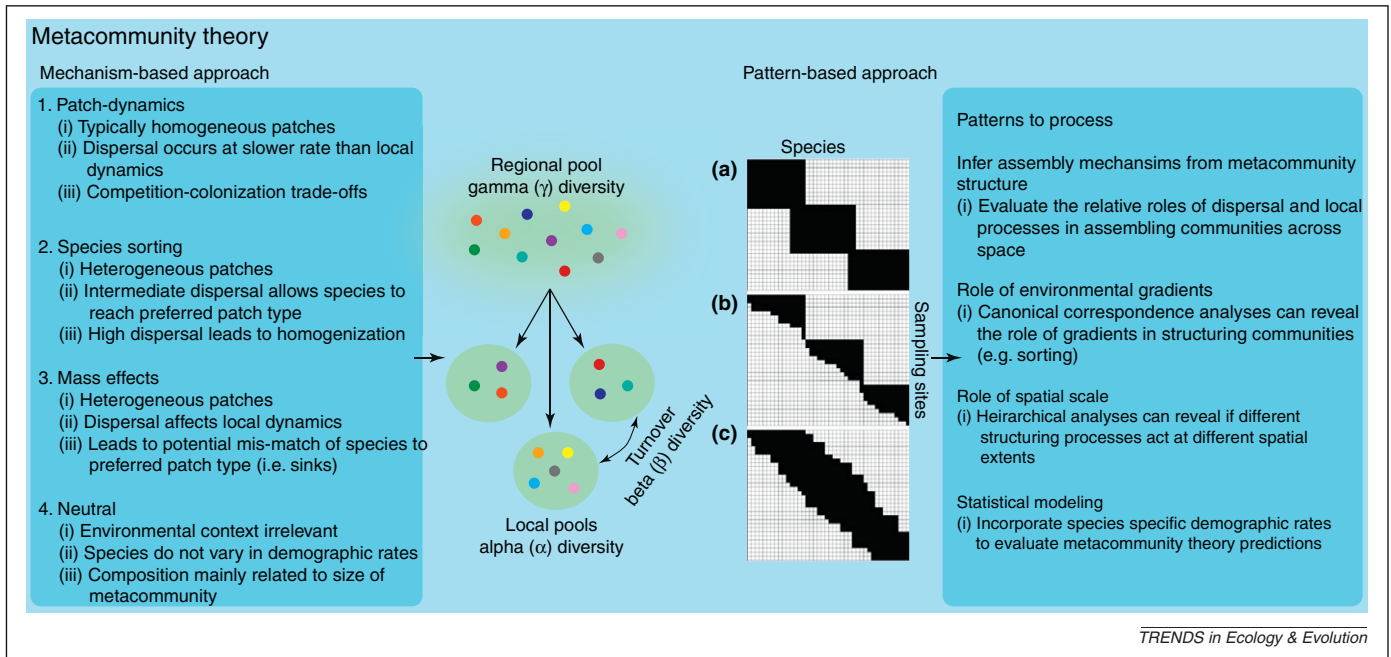
Symbiont: the term symbiont is used in a very general sense to represent all organisms that must infect or inhabit hosts for at least part of their life cycle, including micro- and macro-parasites and non-disease-causing or potentially beneficial micro- and macro-organisms. Here, symbionts are thus the suite of organisms that are encompassed by a mutualism–parasitism continuum (*sensu* [56]).

Symbiont dispersal: passive movement or seeking behavior of symbiont life stages outside of the host. This movement is independent of host movement.

Symbiont transmission: transmission is distinguished from symbiont dispersal in that, in this case, transmission is driven by host-to-host contact. The distinction between symbiont dispersal and transmission in this article differs from traditional epidemiological definitions, but is used to highlight the relative roles of host movement versus movement of the symbiont independent of the host.

Virulence: morbidity or mortality of the host caused by a pathogen. However, virulence is clearly an emergent property of both host and pathogen traits.

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Figure 1. A summary of metacommunity theory. Metacommunity theory can generally be divided into two approaches: mechanism-based and pattern-based approaches. The mechanism-based approach utilizes four modeling paradigms to ask how the regional species pool partitions into local habitats and how these local communities vary across space. The four paradigms differ mainly in the role of patch heterogeneity and the timing and effect of dispersal on local dynamics. The pattern-based approach determines the structures of natural metacommunities. Metacommunities **(a–c)** are cartoon examples of such structures. These represent presence/absence matrices that are ordinated via a process such as reciprocal averaging. Then other ordination methods and null models are used to associate this structure with a variety of potential biotic and abiotic structuring mechanisms.

and evolutionary dynamics of symbiont populations and communities, often in complex ways. For example, direct and indirect interactions among multiple symbionts within an individual host can affect the ways in which symbionts influence host health and can also affect the evolution of symbiont traits, such as the virulence of parasitic symbionts [17–20]. These intra-host dynamics are linked to those of larger spatial scales (e.g. inter-host) via symbiont dispersal or transmission. Understanding how these 'local' and 'regional' processes interact is at the

forefront of symbiont-related research, especially for parasitic symbionts [5,21,22]. Fortunately, merging of local- and regional-scale dynamics is the motivation behind metacommunity theory.

Despite the conceptual similarities with metacommunities of free-living species, the consideration of symbiont metacommunities and their relevance to host health, to symbiont eco-evolution and to the study of ecological communities has not been addressed in depth. Here, I emphasize that considering the metacommunity dynamics of

Box 1. Standard applications of metacommunity theory

In general, ecological metacommunity theory has been approached in two ways (Figure 1). The discussion that follows is not comprehensive but rather is meant to introduce readers to the various ways in which metacommunity theory has been used to date.

Mechanism-based approach

The mechanism-based approach develops and tests theoretical models that generate predictions about how the regional species pool partitions into local habitats and how communities vary across space (Figure 1). Metacommunity models can be separated into four paradigms that mainly differ in the role of patch heterogeneity and the timing and effect of dispersal on local dynamics (Figure 1) [9,10]. Most metacommunity models consider space implicitly, where species can differ in dispersal rates, but it is assumed that all patches are colonized with equal probability. More recent models, however, explore the implications of spatially explicit patch distributions [32]. These paradigms have been tested using a variety of study systems and procedures [51]. The data generally show that community composition patterns are best explained by integrating multiple paradigms.

Mechanism-based theory has been used to investigate many real-world issues. Recent examples include an examination of how habitat destruction alters food web complexity [32], the use of patch

connectedness to determine the best conservation methods [52] and an evaluation of how climate change might alter community compositions [53].

Pattern-based approach

The pattern-based approach examines the structure of natural metacommunities and evaluates the influence of particular environmental gradients in creating those structures (Figure 1). This approach relies on ordinations and null models to determine which 'idealized' metacommunity structures, if any, best fit the observed data [44,54]. Then canonical correspondence analysis is used to test what natural biotic and abiotic factors might lead to the observed structure [46,55].

As a cartoon example, metacommunities (a) and (b) in Figure 1 have a Clementsian structure, in which discrete communities replace each other along a gradient, whereas metacommunity (c) has a Gleasonian structure, in which each species responds individually to any gradient. There are three distinct sub-metacommunities, or compartments, within metacommunity (b), each of which has a nested structure. Interestingly, in natural metacommunities, compartments are probably common, and each compartment can have a unique structure that responds to different biotic and/or abiotic gradients [43,46]. Thus, hierarchical analyses can determine which mechanisms are important at which spatial scales [44].

symbionts will reveal a suite of novel and highly relevant questions pertaining to the structuring of ecological communities and to the influence of symbiont communities on host health and functioning. I explain how symbiont meta-communities fit well within the conceptual framework of the standard free-living organism metacommunity, even though clear differences exist. These differences, however, could actually serve to broaden the scope and test the assumptions of metacommunity theory. I then outline the novelty of metacommunity theory compared to other methods of studying symbiont dynamics and discuss various practical and general applications that stem from linking these two fields.

Defining a (symbiont) metacommunity

Briefly, a metacommunity consists of multiple local communities of interacting species that are connected by the dispersal of at least one of those species. Local communities can be limited to competing 'guilds' of species or can consist of more complex trophic webs. The important aspect here is that dispersal of species among localities changes local community dynamics, leading to community structures that deviate from those expected when considering closed communities. This allows researchers to study community dynamics at larger – and more realistic – spatial scales than previously considered in community ecology [14]. Although the spatial delineation of 'local' communities is stringent in theoretical studies, the principles derived from metacommunity theory have been successfully applied to natural communities that lack definitive boundaries (e.g. grasslands and forests [10]).

'Local' symbiont communities can be designated at various spatial scales, and thus multiple metacommunities can emerge depending on the spatial scale under consideration and the specific questions being addressed (Box 2, Figure I). Although I believe that each spatial scale is worth considering and can lead to novel research initiatives, for clarity I consider the implications of studying

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Box 2. Symbiont metacommunity research topics at multiple spatial scales

I propose ecological and evolutionary research topics that emerge from a consideration of symbiont metacommunities at various spatial scales (Figure I). These questions are diverse and relevant to a general understanding of ecological communities, as well as the effects of symbionts on host health. However, this list is surely not exhaustive.

- **Some important general questions**
  - Which metacommunity processes are most important at the different spatial scales of symbiont metacommunities?
  - How might metacommunity processes that occur at different spatial scales interact to affect symbiont community composition?
  - Is local and/or regional symbiont community structure (e.g. richness, evenness) or metacommunity structure a reliable predictor of disease risk or overall host population health?
- **Intra-host**
  - How does the level of symbiont gene flow between areas within the host (e.g. organs) affect the emergence of novel and/or pathogenic varieties?

- Are the rate and outcome of symbiont evolution influenced by the resident symbiont community composition within different host compartments?
- Could control of symbiont dispersal to certain compartments and/or a spatially directed use of pro-microorganism treatments combat the intra-host evolution of pathogenic strains?
- **Inter-host** (in a host population)
  - How does heterogeneity within a host population (e.g. genetic diversity) influence symbiont gene flow among hosts?
  - Does host heterogeneity influence symbiont community composition within and among hosts and, therefore, the potential for epidemics?
- **Inter-host subpopulation** (in a host metapopulation)
  - How does host dispersal between subpopulations augment local symbiont community composition, and what consequences does this have for population-level disease risk?
  - Considering the effect on host health, how does symbiont β-diversity across host subpopulations affect host metapopulation stability?
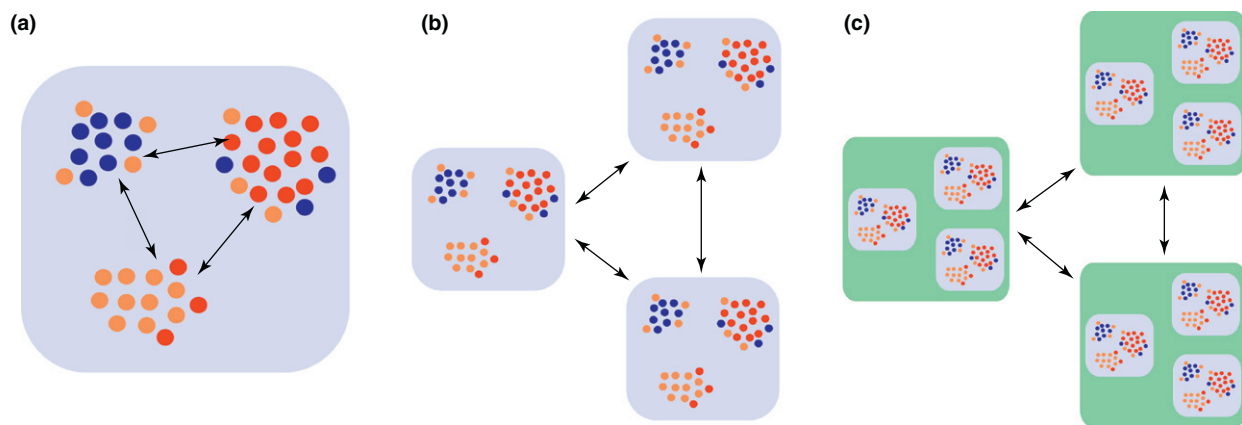
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Figure I. Representations of symbiont metacommunities at various spatial scales. **(a)** Various host compartments (e.g. organs) house different suites of local symbiont communities that are connected by dispersal of symbionts (represented by arrows). **(b)** Host individuals serve as local communities or patches for symbionts. Here, patches are connected by dispersal or transmission of symbionts from host to host (represented by arrows). **(c)** Host subpopulations serve as patches for symbionts, and the suite of symbionts within a host subpopulation constitutes the local symbiont community. In this scenario, patches are connected by the migration of hosts from one subpopulation to another, which augments the local suite of symbionts. Different colored dots represent symbiont individuals and species.

symbiont metacommunities in which a local community consists of the suite of symbionts that inhabit a single host individual (Figure Ib in Box 2). In this way, the local scale is clearly spatially delineated as a single host in which symbiont population dynamics unfold. Emigration from a host is achieved by the release of infective or dormant symbiont life stages. This numerically changes the demographic parameters of resident symbiont populations within the host, and thus potentially changes the community interactions among symbionts. Colonization of a new host occurs via dispersal or transmission of symbionts and the subsequent initiation of population dynamics in the new host, which, as above, can affect the local community dynamics.

There are two clear distinctions between symbiont metacommunities, as defined above, and those of free-living organisms. First, for symbionts the local habitat patch (host) is not necessarily static in space; however, this is not an insurmountable challenge. For example, the metapopulation framework – a single-species perspective that follows the same spatial assumptions as the metacommunity framework – has long been advocated as useful for understanding parasite infection dynamics [23,24]. The disease metapopulation framework has been implemented across spatial scales to explain parasite infection patterns in cases in which parasites infect multiple host tissues (i.e. intra-host metapopulations [25]), hosts are considered patches [26], or parasites are dispersed among host subpopulations via host migration [27,28]. Furthermore, the theory of island biogeography [29], developed with respect to static islands, has been fruitfully applied to explain the prevalence patterns of parasites when mobile hosts are considered islands [30,31].

The success of metapopulation and island biogeography theory in studying parasites makes sense because symbiont population dynamics unfold within a host whether or not the host is mobile. Thus, if hosts were to be considered closed communities, their movement would be irrelevant. The movement of hosts, however, can clearly affect the dispersal and colonization rates of symbionts, especially in cases in which direct host-to-host transmission occurs.

Host movement is a unique feature of symbiont metacommunities that can be integrated into metacommunity theory and lead to interesting research questions. First, the timescale and relative role of dispersal in structuring metacommunities vary, depending on the theoretical paradigm considered, and thus symbiont metacommunities could be analyzed to determine which paradigm is most relevant (Box 1). Second, understanding the role of environmental heterogeneity in structuring communities across space is a principal focus of metacommunity theory (Box 1). The rate of host movement could then be used as a type of patch heterogeneity, in which symbionts in a more vagile host have distinct demographic rates compared to those residing in less vagile hosts. Finally, whereas most theoretical models that have formed the foundation of metacommunity theory consider the spatial distribution of patches implicitly, newer methods explicitly model this distribution [32]. Thus, a variety of host structures could be simulated in which these 'patches' are more or less connected, representing the relative contact rate of hosts.

The second distinction involves the mechanisms that result in patch vacancy. In metacommunities of free-living

organisms, patches become fully or partially vacant and can be subsequently recolonized if, for example, residing species become extinct because of demographic stochasticity or strong interspecific interactions. However, when hosts are considered patches for symbionts, patches can become vacant and subsequently unavailable to recolonization if hosts die because of parasitism or develop strong resistance to parasitic symbionts. Thus, the number of available patches does not remain constant, as is assumed in current implicit-space metacommunity models.

Perhaps the issue above has caused reluctance to use mechanistic metacommunity models to study symbionts, especially because epidemiological models already account for such host–symbiont dynamics. Nevertheless, I feel that, again, this caveat is not intractable. Implicit terms could be added to models for patch destruction (e.g. via pathogen virulence or host resistance) and then balanced with patch creation (e.g. via host immigration or birth rate) (*sensu* [26]). In fact, host resistance to symbiont infection could be modeled more realistically as underlying patch heterogeneity. Then one could explore how intraspecific variation in these host characteristics affects local and regional composition of symbionts [33]. Finally, using explicit space models, host loss could be modeled similarly to habitat destruction (*sensu* [32]). However, the evolution of parasite virulence and host resistance, a common question in epidemiological modeling studies, might be more difficult to address using these methods. The evolving metacommunity perspective, described below, might hold more promise for these important questions. Below I highlight the novel features of metacommunity theory compared to methods of studying infection dynamics in light of their respective research agendas. I also more fully develop the practical and general utility of linking metacommunity theory and symbiont evolutionary ecology.

The utility of considering symbiont metacommunities
The novelty of metacommunity theory
Metacommunity theory differs from current methods of studying symbionts, especially epidemiological models, in both method and agenda. Epidemiological models deal with infectious parasitic symbionts. These are mechanistic models that follow the numbers or densities of infected, susceptible and resistant hosts in a spatially implicit or explicit (e.g. network analysis) manner, incorporating the negative effects of the pathogen. Epidemiological models ask questions about, for example, the probability of epidemics occurring in the host population and the evolution of pathogen traits, such as virulence, in response to within- or between-host dynamics. Importantly, recent models are able to integrate within-host infection processes and between-host transmission dynamics [5,34]. Although some studies have considered the evolutionary consequences of multiple pathogen strains or species at the within-host level [19], few have modeled these dynamics while considering both spatial scales (although see [35]).

Metacommunity models, in a sense, ask more general and larger-scale questions than epidemiological models, although they are similar in many ways (Box 1). This theory makes predictions regarding the roles of local processes and

dispersal among localities in partitioning regional (γ) diversity into local habitats (α-diversity) and how this local diversity varies across space (e.g. β-diversity). Metacommunity models explore general trends, such as how dispersal changes the coexistence of competing species and how dispersal and patch heterogeneity affect β-diversity across the landscape. In other words, metacommunity theory is concerned with the structure of communities and how this structure varies across space in response to various mechanisms. Below, I highlight many specific practical and general applications that stem from considering these types of questions for symbionts.

Practical applications
Linking metacommunity theory and the study of symbionts has many practical applications. In general, an understanding of the structure of symbiont metacommunities, as well as the underlying causes of this structure, could offer new insights into how symbionts affect host health. The diversity of symbionts within a host (α-diversity) might have direct effects on, or be correlated with, host health and general functioning. Understanding the turnover among symbiont communities (β-diversity) is also important, because the effect of symbiont communities on their hosts presumably changes as their compositions change [4].

Incorporating ideas from the 'evolving metacommunity' concept is particularly relevant to the study of symbiont communities because of the overlap of ecological and evolutionary timescales in these systems [36]. The details of this framework are discussed below, and the theory could be used to understand or model, for example, the distribution of symbiont haplotypes among hosts in response to gradients in host genetic diversity, considering the role of host–symbiont genotype interactions in symbiont fitness. This framework would also be relevant in studying kin selection dynamics in the evolution of parasitic symbiont virulence. For example, it is important to understand how multiple related parasite strains interact within a host and how these intra-host interactions and inter-host transmission dynamics influence the evolution of parasite traits [37].

General ecological applications
Linking metacommunity theory and symbiont evolutionary ecology also has implications in understanding the structure of ecological communities in general. For instance, different ecological and evolutionary processes might influence the structure of symbiont metacommunities compared to those of free-living organisms. As revealed by a large meta-analysis, most metacommunity structures for free-living organisms tend to show strong effects of species sorting and mass effects, but both local and regional components of assembly are necessary to explain the majority of variation [38]. Symbiont metacommunities could be compiled and compared to these data to determine if symbiont metacommunities are structured similarly to those of free-living organisms.

Research is already attempting to discern the primary drivers of human microbial symbiont community composition using metacommunity theory. For example, Lindström and Langenheder recently applied the predictions of mechanistic-based metacommunity theory to discuss general trends in bacterial community assembly across a wide range of systems, including the human body[39]. In addition, a model-fitting study used neutral metacommunity theory to explore how microbial α-diversity of the human lungs and digestive tract is structured [40]. Neutral metacommunity theory has also been used to speculate on the structuring mechanisms of parasitic helminth communities [41]. However, these studies could be deepened and extended to encapsulate the full range of metacommunity theory applications (Box 1).

Different structuring mechanisms might act at different spatial scales for symbiont metacommunities compared to free-living organisms. Svensson-Coelho and Ricklefs recently explored how avian host phylogeography relates to haemosporidian parasite community structure across the Lesser Antilles [42]. Host genetic diversity between islands does not predict the β-diversity of these parasites. Furthermore, neither mosquito nor bird β-diversity correlated with parasite β-diversity. Here, the spatial extent of the data analysis might overreach the scale at which the primary structuring processes for the parasite community function. Hierarchical analysis of the parasite metacommunity structure could reveal the relative roles of different structuring processes at different spatial extents (*sensu* [43,44]; Box 1).

Symbiont communities could be used to test metacommunity predictions by using pattern-based metacommunity approaches (Box 1). De Meester speculates that small organisms (e.g. environmental bacteria) might show an even stronger species sorting signal because of their high dispersal capacity and rapid population growth, allowing for the simultaneous influence of dispersal and evolution to match organisms to their environmental optimums across space (see below) [36]. Symbiont dispersal and transmission rates, however, are linked to the dispersal rates of their hosts to varying degrees [45]. Thus, symbiont metacommunities could be divided into 'meta-ensembles' (*sensu* [46]) of varieties with high and low dispersal and the respective structures could be used to test the assumed role of dispersal in the four predominant metacommunity paradigms.

General evolutionary applications
The 'evolving metacommunity' concept considers how gene flow and local adaptation can alter local species interactions and lead to either regional coexistence or monopolization [12]. Consider a simple scenario in which competing species are locally adapted but can disperse to patches with different local conditions [47,48]. Species A invades an empty patch and becomes locally adapted, preventing the establishment of its competitor, species B. This is an example of local monopolization facilitated by adaptation. However, if local conditions vary between patches, gene flow from the new patch for species A to its source could lead to maladaptation in the source. This could then allow species B to invade the source patch of species A. The maladaptation of species A thus facilitates regional coexistence with species B. Similar theory can easily be applied to and tested on symbionts, especially considering their rapid population growth rates and short-term evolutionary dynamics [36]. However, in host–symbiont systems, the

relative rate of gene flow of hosts versus symbionts is important for symbiont adaptation, especially in antagonistic coevolution scenarios [49,50]. Thus, an understanding of the relation between host population gene flow and symbiont gene flow among individual hosts will be essential for predicting and interpreting evolutionary symbiont metacommunity patterns.

Recent conceptual models predict that intermediate levels of gene flow among patches in a metacommunity will maximize the adaptation of community and population traits to the local environment via species sorting and natural selection [12]. In other words, regional biodiversity might be hindered by too little or too much dispersal due to monopolization or maladaptation. Therefore, an understanding of the level of symbiont gene flow among hosts will be crucial for predicting the conditions under which coexistence or monopolization will be favored. Future studies could explore how within-host symbiont community dynamics interact with variable dispersal or transmission rates to influence among-host community structural patterns (Box 2).

Conclusion

Symbiont communities are ripe for a merger with existing and emerging research on metacommunity dynamics. This would simultaneously allow for testing of theories and an understanding of the effects of symbionts on host health, whether positive or negative. Utilization of symbionts in metacommunity research and application of concepts garnered by metacommunity studies to symbiont eco-evolution could aid our general understanding of spatial ecological dynamics, help in determining the processes and spatial scales most relevant to the structuring of symbiont communities, guide studies related to symbiont trait evolution, and offer a framework for exploring the effects of symbiont communities on disease across space. Metacommunity ecology is a new and burgeoning field, and incorporation of symbionts into its theoretical and experimental repertoire is bound to benefit ecologists, evolutionary biologists and medical scientists alike.

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