

IDEA AND PERSPECTIVE

Towards a multi-trophic extension of metacommunity ecology

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Abstract

Metacommunity theory provides an understanding of how spatial processes determine the structure and function of communities at local and regional scales. Although metacommunity theory has considered trophic dynamics in the past, it has been performed idiosyncratically with a wide selection of possible dynamics. Trophic metacommunity theory needs a synthesis of a few influential axis to simplify future predictions and tests. We propose an extension of metacommunity ecology that addresses these shortcomings by incorporating variability among trophic levels in 'spatial use properties'. We define 'spatial use properties' as a set of traits (dispersal, migration, foraging and spatial information processing) that set the spatial and temporal scales of organismal movement, and thus scales of interspecific interactions. Progress towards a synthetic predictive framework can be made by (1) documenting patterns of spatial use properties in natural food webs and (2) using theory and experiments to test how trophic structure in spatial use properties affects metacommunity dynamics.

Keywords

dispersal, food webs, foraging, migration, networks, patch dynamics, spatial information processing, spatial scale, spatial use properties, trophic interactions.

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INTRODUCTION

Metacommunity theory formalises the role that dispersal plays in determining the diversity, stability and function of ecological communities at local and regional scales (Leibold *et al.* 2004; Holyoak *et al.* 2005). This rich body of theory has allowed ecologists to understand that ecological dynamics observed at the scale of local habitat patches are, in part, determined by dynamics in other habitat patches via the exchange of dispersing individuals. To date, metacommunity ecology has been most successful at providing a theoretical predictive framework for competitive metacommunities (Holyoak *et al.* 2005). However, we still lack a cohesive framework for trophic metacommunities (Leibold & Chase 2018). The need for a general theory of trophic metacommunity arises (1) when we need to predict food web properties, which are incompatible with a competitive framework and (2) when interacting species use space at different scales; for example when a predator population interacts with multiple smaller scale prey populations.

A growing effort has been dedicated to exploring the consequences of trophic interactions in metacommunities (e.g. Holt 2002; Beger *et al.* 2010; Gravel *et al.* 2011; Pillai *et al.* 2011; Tremblay *et al.* 2012; Haegeman & Loreau 2014). Despite recent empirical and theoretical advances that have laid a solid foundation for a synthetic theory of trophic metacommunities, our understanding remains fragmented due to the diversity of response variables (e.g. diversity, stability, network structure,

energy flow) and representations of spatial constraints (e.g. perception of scale, types of movement). Traditional metacommunity theory focuses on only one type of movement: dispersal. Dispersal is often related to reproduction (e.g. seed, larvae and gamete dispersal, or dispersal in search of mates), and therefore relates to only one particular component of life history. A recent review of metacommunity ecology suggested that future development of this theory must allow species to vary in their abilities to experience the spatial environment (Leibold & Chase 2018). As a consequence, we suggest that it is time to rebuild trophic metacommunity theory, using spatial processes as pillars of a more cohesive theory for metacommunity dynamics. We focus on five characteristics of 'spatial use properties' that we suggest should be at the centre of a coherent and broad theory of trophic metacommunities. We define 'spatial use properties' as population-level properties that reflect how species use space, and include three forms of movement relevant to trophic metacommunities – dispersal, migration and foraging (Gounand *et al.* 2017). We emphasise that species vary in their responses to the environment and to each other, that movement is not just about dispersal, but an array of processes that each have their own consequences for population dynamics and, we highlight that differences in the way species use space – a dynamic critical to metacommunity dynamics – is due to differences in these spatial use properties.

We propose a framework as a first step to bridge the rapidly advancing fields of spatially structured food web

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ecology, movement ecology and metacommunity ecology. This framework: (1) builds on competitive metacommunity theory to make it applicable to trophic dynamics and (2) explicitly considers a set of five spatial use properties relevant to the spatial and temporal dimensions of trophic interactions. We emphasise the distinction between the three forms of movement – dispersal, migration and foraging – because they occur at different stages of an organism's life cycle, they couple different habitat types (e.g. different nearby habitat patches vs. summer and winter habitats), they are initiated by different environmental cues, and they generally occur over different spatial and temporal scales. Therefore, we expect each form of movement to differ in their consequences for metacommunity dynamics. Future progress in trophic metacommunity ecology can be made by documenting the distribution and variation in these five spatial use properties within and among food webs. With this knowledge, we can generate empirical and theoretical predictions for how patterns in spatial use properties within a food web can affect metacommunity dynamics, the diversity, and structure of food webs at local and regional scales. We also outline empirical and theoretical avenues to test our predicted consequences of spatial use properties in trophic metacommunities.

PAST AND PRESENT METACOMMUNITY THEORY

Recent advances and challenges in trophic metacommunity research

While the theory for competitive metacommunities offers clear predictions, trophic metacommunity theory is remarkable in the diversity of topics explored despite lacking an overarching organisational framework. The first models were inspired by Huffaker's (1958) famous experiment exploring the population dynamics of herbivorous and predatory mites in an experimental metacommunity. Seminal metapopulation models by Holt (summarised in Holt & Hoopes 2005), Hanski (reviewed in Hanski 1999), and others investigated how spatial predator–prey dynamics can contribute to regional coexistence. For example predators may stabilise prey populations that would otherwise overexploit their resources in the absence of predators (Holt 2002). The spatial nature of food webs has also been considered previously (Holt 2007). A greater geographical range of higher trophic level populations was noted by Elton (1966) and its implications for the spatial scale of communities by Holt (1996) and Polis *et al.* (1997). Species (and resources) moving on different scales was recognised to result in spatial subsidies between otherwise seemingly discrete food webs (Polis *et al.* 1997). Despite these early advances, the effects of spatial processes on food webs dynamics has not been explored in a metacommunity context though they are becoming increasingly apparent (i.e. a 'multi-channel process', Ward *et al.* 2015). Metacommunity configurations can determine whether dispersal stabilises or destabilises predator–prey dynamics (Jansen 2001; McCann *et al.* 2005; Amarasekare 2008; Gravel *et al.* 2016b) and this understanding has pushed food web models towards a more general patch dynamics approach of predator and prey assembly. In an effort to map different metacommunity paradigms to food webs, Baiser *et al.* (2012) found that pitcher

plant inquiline community structure is best explained by the species sorting archetype (because of covariation in response to the environment) and patch dynamics (because of a predominance of local interactions). Other studies have used the source-sink framework to investigate the maintenance of food web structure, not only directly through the dispersal of individuals to poor quality patches, but also indirectly via the spatial exchange of nutrients and energy (Gravel *et al.* 2010a, b). Such exchanges were further shown to buffer spatial variation in patch productivity, potentially stabilising trophic metacommunities subject to the paradox of enrichment (Gounand *et al.* 2014).

Emerging models of trophic metacommunities have demonstrated how trophic interactions can help to understand basic ecological patterns and processes, such as species–area relationships, the co-distribution of predators and prey, range limits and the restructuring of food webs in response to global change. For example Holt *et al.* (1999), followed by Ryberg & Chase (2007), proposed that predator species richness should accumulate faster with increasing area than prey species richness. Similarly, Stier *et al.* (2014) showed that predator species richness is less sensitive to isolation than prey species richness. This difference between trophic levels has significant consequences for the interaction network–area relationship (Galana *et al.* 2018). This phenomenon results from a sequential assembly of food webs, starting with generalist species at the trophic base of the food web, followed by higher trophic levels and more specialised species (Gravel *et al.* 2011; Pillai *et al.* 2011). The co-distribution of predators and prey in trophic metacommunities appears to be a key to understand the spatial variation in local network structure (Cazelles *et al.* 2016). In addition to species turnover among patches, interaction networks also vary in space due to spatial turnover in the realisation of potential interactions (Poisot *et al.* 2012), with cold and hot spots of network beta-diversity (Stier *et al.* 2014; Poisot *et al.* 2016).

Although existing metacommunity theory provides a guiding predictive framework for how spatial processes affect the dynamics and structure of species belonging to the same trophic level [Table 1A; (Mouquet & Loreau 2003; Calcagno *et al.* 2006 Table 2)], those predictions are not applicable to the unique response variables that arise when trophic levels interact. When trophic levels interact, the local and regional food webs that are formed can be characterised by network properties, such as connectance (Dunne *et al.* 2002), diversity at each trophic level (Gamfeldt *et al.* 2005), and spatial turnover in pairwise interactions in a network (Poisot *et al.* 2012). Local communities that contain identical numbers of species might differ in their ratio of predators to prey, or in the average number of prey species that predators consume [i.e. linkage density (Winemiller *et al.* 2001; Banasek-Richter *et al.* 2009)]. Additionally, because trophic levels are linked through consumption, the flow of energy and matter through local food webs might differ through space (Table 1B). The greater array of metacommunity properties that characterise multi-trophic systems may reveal spatial processes that are missed by the traditional suite of metacommunity response variables (Pillai *et al.* 2010) despite being essential to food web stability (Dunne *et al.* 2002; Rooney & McCann 2012).

Table 1 Comparison of response variables of competitive metacommunity vs. trophic metacommunity theory

Response class	A. Competitive metacommunity ecology	B. Trophic metacommunity ecology
Structure	Coexistence Diversity Species distribution	Coexistence Diversity Species distribution Species co-distribution Complexity/connectance Trophic length Trophic modules
Dynamics	Stability Synchrony Species turnover	Stability Synchrony Species turnover Interaction turnover Trophic regulation (top-down vs. bottom up)
Energy	Energy flow Productivity	Energy flow Productivity Trophic biomass pyramid

Reformulating the assumptions of competitive metacommunity theory

Leibold *et al.*'s (2004) proposal of four metacommunity paradigms has guided empirical research for much of the past decade (Table 2A) though, subsequent research demonstrates that communities rarely conform to any single archetype (Cottenie 2005; Leibold & Loeuille 2015). Rather, the distribution of organisms across habitat patches can reflect a combination of mechanisms, such as species sorting into some patches and mass effects into others, even within a single species (Thompson *et al.* 2017). Others have suggested that metacommunity dynamics do not fit into discrete paradigms and instead are better represented as a continuum (Cottenie 2005; Holyoak *et al.* 2005; Logue *et al.* 2011; Thompson *et al.* 2017). We argue that this continuum perspective is more critical when we are interested in studying the dynamics of trophic metacommunities, since different trophic levels are more likely to differ in the way species use space than single trophic levels. Therefore, adopting this continuum perspective is necessary to extend metacommunity theory to encompass trophic interactions.

Competitive metacommunity theory assumes that the suitability of habitat patches is determined only by the abiotic environment, and competition can allow species to exclude one another (Leibold *et al.* 2004). In a trophic metacommunity perspective, patch suitability also depends on the interactions between species, because predators can only persist in patches that have sufficient prey (Gravel *et al.* 2011). Effectively, the presence of prey increases predator persistence (i.e. a form of 'niche construction'), whereas the presence of predators decreases their persistence (i.e. 'niche destruction') (Holt 2009). Because the population dynamics of species linked by trophic interactions are interdependent, patch suitability is dynamic through space and time, even in the absence of abiotic heterogeneity. In this context, distinguishing among patch dynamics and species sorting archetypes becomes difficult (Table 2A) because species sort into habitat patches based on the presence of predators and prey.

It is clear that these systems where scales of movement and dispersal differ among interacting species violate the

assumption inherent in most metacommunity theory: species interacting and coexisting within the metacommunity experience the environment at the same spatial and temporal scales. This assumption is reflected in three ways in competitive metacommunity models: (1) by forcing species to share a common dispersal rate (the proportion of the population that disperses to another population in each generation), (2) by considering only dispersal and not other forms of movement among populations, such as migration or foraging and (3) by assuming species share the spatial resolution at which they perceive the environment and their ability to act on this information. Variation in dispersal rates has generally been considered in competitive contexts where competition-colonisation trade-offs promote coexistence (Cadotte 2006). In empirical studies, however, bulk dispersal is the most commonly used method for altering dispersal rates, which prevents detection of interspecific differences in dispersal abilities (Grainger & Gilbert 2016). Grainger & Gilbert (2016) argue that the heterogeneity that many experimenters choose to remove is necessary to detect metacommunity processes, leading to an inability to robustly test a growing body of theory. Variation in dispersal rates has also been applied to simple predator-prey systems where coexistence is promoted by a higher colonisation rate in the prey species (Holt & Hoopes 2005). In particular, studies of host-parasite interactions revealed that differences in dispersal rate and/or scale could have huge impacts on metacommunity dynamics because parasitoid infection was found to be dependent on host dispersal rate (Holt & Hoopes 2005) and differences in host vs. parasitoid dispersal rate was found to destabilise dynamics (Rohani *et al.* 1996). In a two-parasitoid model, the less mobile species was able to persist only in small pockets of high host density, resulting in a competition-colonisation trade-off for the competing parasitoids (Nee *et al.* 1997). However, beyond two-species systems, differences in dispersal between species of different trophic levels are only recently being considered (Haegeman & Loreau 2014; Pedersen & Guichard 2016; Jacquet *et al.* 2017; Thompson & Gonzalez 2017). Differences in dispersal rates between trophic levels are expected to be much greater than differences within trophic levels because, for example species at different trophic levels tend to differ in body size and life history (Haskell *et al.* 2002; McCann *et al.* 2005). This has consequences for the structure of local and regional trophic networks (Woodward *et al.* 2005). With larger body size also comes longer life spans and greater energetic requirements (Speakman 2005), and thus the need for other forms of movement, such as foraging and migration, to track daily and seasonal variation in resource supply respectively. It is for these reasons that we will explore the consequences of differences between interacting species not only in dispersal but also in foraging and migration, and how species-specific differences in these 'spatial use properties' affect the structure of food webs.

Metacommunity theory has not yet explicitly integrated the effects of movement governed by perception of the environment on spatial biodiversity processes, even though perception and behaviour are central to the interactions between species (Table 2B). Existing metacommunity models implicitly assume

that demographic consequences of behaviour are captured in local population dynamics. Metacommunity models based on patch dynamics and species sorting assume that the probability that an organism exists in a habitat patch (often equated to a population) is based on its colonisation and extinction probabilities (Levins & Culver 1971; Law & Morton 1993). In reality, this probability is not fixed but varies with patch quality and the experience of the dispersing organism through prey seeking, predator avoidance, avoidance of competition and selection of suitable habitat, all of which occur at the level of the organism but which have consequences for stability of the entire food web (Kondoh 2003). For example predators might leave habitat patches when their prey reach low abundances, buffering prey populations from extinction (Holt 1984), or prey might avoid dispersing to habitat patches that contain predators, bolstering the prey's regional fitness and allowing predators and prey to coexist regionally (Resetarits 2005). Similarly, individuals may choose to leave patches with high densities of intra or interspecific competitors allowing more stable, regional coexistence (Fronhofer *et al.* 2015). Movement and behaviour of individuals that link patches can

affect the population dynamics and persistence of other species. The latter is traditionally the domain of metacommunity concepts, but a food web perspective highlights that individual decisions about movement in space can couple these population dynamics (e.g. McCann *et al.* 2005).

SPATIAL USE PROPERTIES AND THEIR CONSEQUENCES FOR PAIRWISE TROPHIC INTERACTIONS ACROSS SCALES

Spatial use properties must be considered beyond abiotic niches and dispersal in order to expand metacommunity theory. We propose to incorporate additional ones related to temporal and spatial scales of migration, foraging, and spatial information processing, all of which have very different implications for population dynamics. We propose to differentiate these forms of movement since they happen at different times in an organism's life, they couple different habitats in space and in time, they occur at different temporal frequencies and each may have varied consequences across scales of observation. In this section, we draw on theory from movement

Table 2 A synthesis of ideas in metacommunity ecology [formalised in (Leibold *et al.* 2004)] and food web ecology

Process	Application to competitive communities	Extension to trophic metacommunities	Incompatibility with trophic metacommunities	Spatial use properties relevant to coexistence
A. Metacommunity ecology				
Patch dynamics (Levins & Culver 1971; Levin & Paine 1974)	Competition-colonisation trade-offs allow the regional coexistence of species that differ in competitive ability	Prey must disperse more than their predators; predator distributions must be a nested subset of their prey	None	Dispersal; niches (incl. biotic environment)
Species sorting (Tilman 1982; Leibold 1998; Chase & Leibold 2003)	Species differ in which patches are suitable, with suitability defined by abiotic conditions and competitive interactions	The presence of predators and prey (i.e. trophic interactions) also affect patch suitability	Patches must contain prey to be suitable to a predator, thus predators and prey can never completely sort into different patches	Dispersal; niches (incl. biotic environment)
Mass effects (Shmida & Wilson 1985)	High dispersal erodes the effects of species sorting such that abundance does not fully reflect patch suitability	The presence of predators and prey also affects patch suitability; predators and prey maintained in neighbouring patches can impact each other	None	Dispersal; niches (incl. biotic environment)
Neutral interactions (Hubbell 2001)	Species are competitively equivalent, consuming the same resources	Not extendable	Neutral interactions are not possible between species that do not consume the same resources	Dispersal
Process	Application to food web ecology	Extension to trophic metacommunities	Incompatibility with trophic metacommunities	Spatial use properties relevant to coexistence
B. Food web ecology*				
Spatial coupling (McCann <i>et al.</i> 2005)	Predators forage at larger spatial scales than their prey, linking local food webs together	Promotes food web stability when predators are generalists	Predators forage at larger scales than prey	Foraging scale
Behavioural adaptive foraging (Kondoh 2003)	Dynamic shifts in foraging strategies to optimise prey capture	Currently not incorporated	Current formulations of metacommunity theory do not allow for changes in interspecific interactions and the response to space due to behaviour	Foraging scale and spatial information processing

*We present two examples of food web phenomena out of the many spatial and behavioural phenomena that have been explored in food web ecology.

ecology and food web ecology to consider explicitly how to integrate the consequences of species' differences in spatial use properties (Figs 1 and 2), and provide examples where spatial use properties vary with trophic level in natural systems. We also consider how spatial use properties may be estimated in terms of measurable organismal traits.

Abiotic niches

Species' abiotic niches, and their overlap, play a major role in determining the spatial distribution of species in metacommunities. Interactions are only possible between species that overlap in their abiotic niches, except for species that can transiently forage in or disperse through environments that are otherwise lethal (Holt 1993; Rahel & Nutzman 1994; Mouquet & Loreau 2003). We expect abiotic niches to correlate between trophic levels when predators are specialists and need to track their prey. Generalist predators are not constrained to their prey distribution and therefore their abiotic niches may not correlate with their prey's abiotic

requirements. Incomplete overlap of abiotic niches may allow for spatial refugia from predation or competition, or constrain species ranges for species that depend on other species for persistence (e.g. specialist predators). In addition, we expect that changes in environmental conditions will determine not only a species' spatial distribution, but also food web responses such as food chain length and the shape of biomass pyramids (Tunney *et al.* 2012).

We expect that the consequences of partial overlap in abiotic niches should depend on which trophic level has the narrower niche. If species belonging to lower trophic levels have wider niches, then prey populations might benefit from spatial refugia in environments outside their predators' niche envelope. For example mosquitofish are more tolerant to warm temperatures compared to their bass predators, which allows them to escape predation by residing in warm habitats (Grigaltchik *et al.* 2012). Conversely, the abiotic niches of species at higher trophic levels may be limited if their prey have lower abiotic tolerances (e.g. Fig. 2b). For example a butterfly with the physiological tolerance to handle high elevations, can be limited to low elevations by the low elevation range of its host plant (Merrill *et al.* 2008).

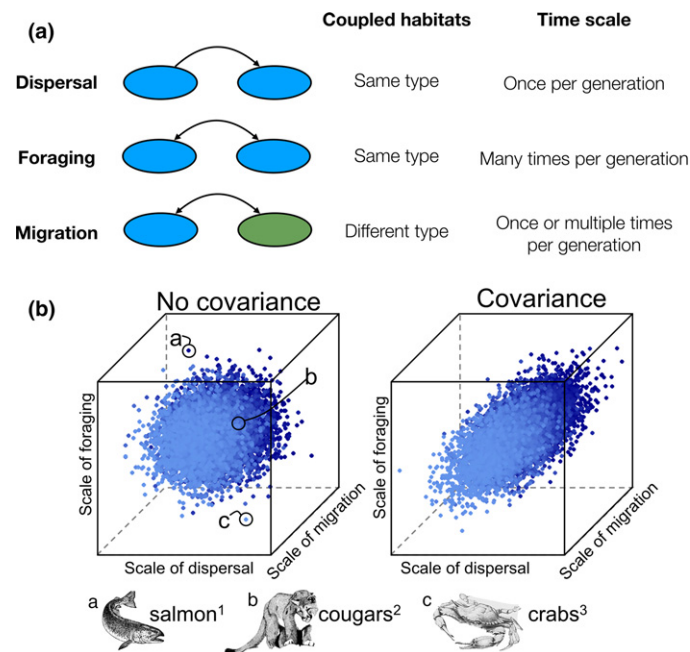


Figure 1 (a) Schematic representation of the three forms of movement highlighting the differences of the three forms of movement based on habitat and timescale. The differences between the types of movement for spatial scale are dependent on the organism. (b) A hypothetical distribution of species spatial use properties, where each axis dimension is one of the three movement types, and each point is a species' characteristic movement distance. Dark blue points correspond to those with high levels of migration, and light blue to those with low levels of migration. Data are simulated with multivariate normal distributions, and the empty regions represent ecological or evolutionary constraints. We present two scenarios with no covariance between movement types or covariance between movement types. When there is no covariance between movement types, knowing the scale of one type of movement can not allow for predictions about the others. We highlight three examples of organisms that vary in their scales of movement among the three movement types (1 = Tallman & Healey 1994, 2 = Dickson & Beier 2006, 3 = Pineda *et al.* 2007). Three spatial use properties are shown for visualisation, but all five are possible.

Three forms of movement

Dispersal, migration and foraging differ in their frequency and timing within an organism's life cycle; more importantly they have different consequences for the dynamics of trophic metacommunities (Fig. 1a). We first define each movement process, and then unpack their unique consequences for spatial food web structure, particularly when they differ among trophic levels.

The first form of movement, dispersal, occurs once in a lifetime via the movement of individuals to new habitat patches. When an individual disperses, it permanently leaves a patch and enters another patch of the same type of habitat. As such, dispersal can allow a species to colonise a patch that was previously unoccupied or can contribute individuals to existing populations, affecting population size and stability. The second form of movement, migration, is the tracking of seasonally available resources or mates by individuals, and typically occurs annually or once in a lifetime. Unlike dispersal, individuals or their progeny complete migration by returning to their original habitat type; migration does not act to link populations together like dispersal but tends to move single populations through many food webs. Migration is a more predictable event, with proximate cues depending on body condition and climatic and phenological processes. The last form of movement, foraging, is the frequent exploration of space by organisms as they search for resources. Species differ in the spatial scales over which foraging takes place, from very localised for some (e.g. plants through roots) to highly mobile and integrating resources across many habitat patches in a region (e.g. the movements of large herbivores on the Serengeti: Dobson 2009). Foraging behaviour is highly variable, with decisions depending on the availability and preference of different prey types as well as predator risk (Fig. 1a). We provide the following example to clarify the differences between the types of movement: Dragonflies forage when they are

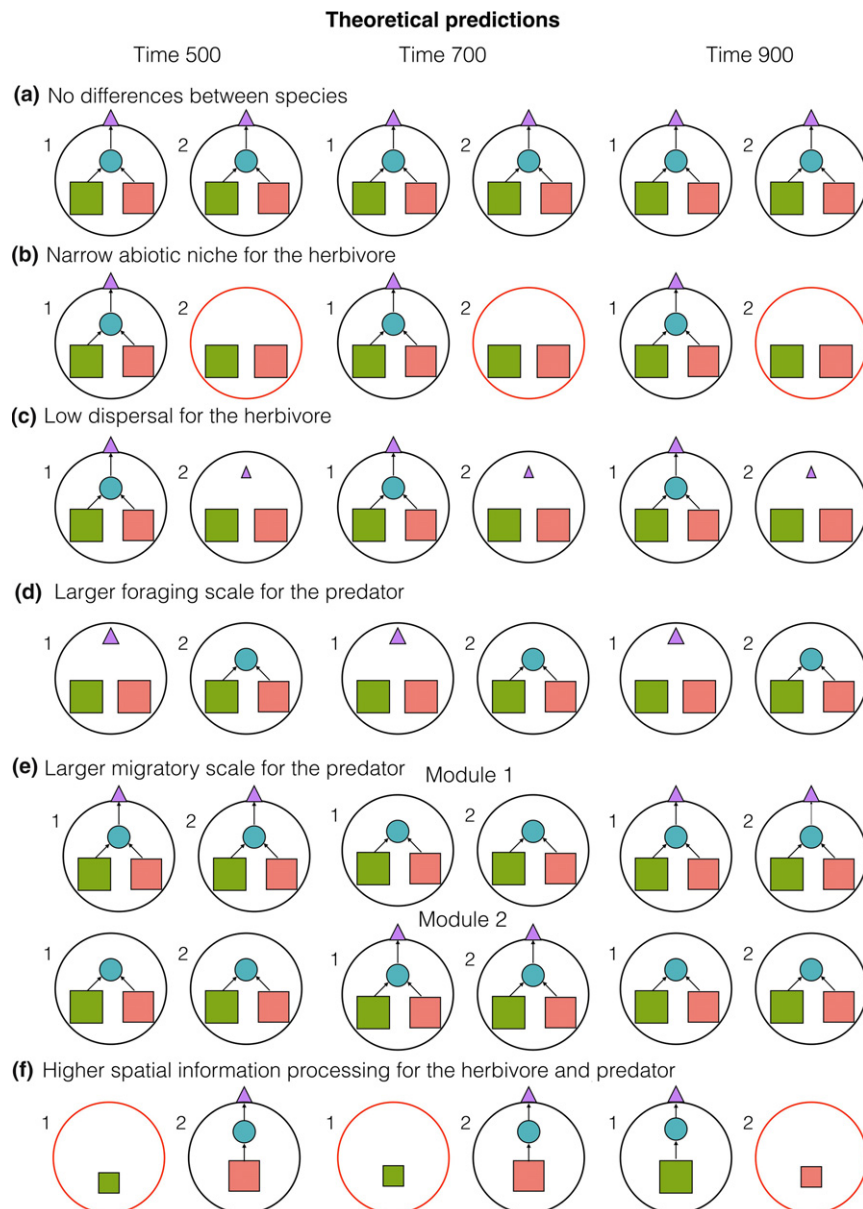


Figure 2 Schematic representation of simulation outcomes for food web structure in two patches and three time points. The food web consists of two primary producers (squares), one herbivore (circle) and one predator (triangle). We show five scenarios of species differences in spatial use properties. (a) The species in this food web do not vary in spatial use properties and therefore the food web does not vary through space or time. (b) The environment varies between patch 1 and patch 2 and because the herbivore has a narrower abiotic niche, it cannot persist in the red patches. The predator consequently also goes extinct in these patches. (c) In this food web, the herbivore has a much lower dispersal than any other species in the food web. Over time, the herbivore is able to reach distant patches. (d) In this food web, the herbivore has a larger foraging scale than any other species in the food web. The herbivore alternates foraging between patches, frequently enough to allow the predator to persist. (e) The top predator migrates in and out of the region, (here presented as a module, each module has two patches) with little effect on the persistence of other species (although abundances may change). (f) In this food web, plants have lower spatial information processing and they are unable to track changing abiotic conditions in patches. The herbivore and the predator track the abundance of the plants.

larvae within ponds. Although they are sit and wait predators, they can still forage within ponds to find higher abundances of prey (Johansson 1991). Then they undergo metamorphosis, an ontogenetic habitat shift. We categorise this ontogenetic habitat shift as the first part of migration, as aquatic habitats and terrestrial habitats are different types of habitats, and terrestrial adults will eventually return to ponds to oviposit, completing the cycle between habitats. Finally, adult dragonflies may stay in their natal pond, or disperse to a different

pond (McCauley 2007). Here the movement as adults between ponds is a dispersal event since they are moving between habitats of the same type. While each of these three forms of movement may occur over distinct spatial and temporal scales, each form of movement will likely have different consequences for food web structure and stability across multiple scales of space and time. For example at the local scale of a marine rocky reef system, sea urchins may be extirpated by foraging sea otters, however, urchins may recover locally due

to the dispersal of urchin gametes from distant populations or alternatively, by the migration of transient orcas that eat sea otters. Here, multiple types of movement, each primarily occurring over different scales of space and time and by organisms at different trophic levels, interact to produce dynamics at a single scale that could not be fully understood without consideration of each simultaneously. We consider dispersal, migration and foraging to be different types of movement (1) because they are not necessarily correlated, and therefore, it is difficult to infer anything about the scale or dynamic consequences of these processes from knowledge of another of these processes; (2) they have dramatically different effects on the trophic dynamics of a metacommunity since they occur at different stages in an organism's life cycle and because they couple different habitats. These three spatial use properties have recently been highlighted as key to understanding spatial flows of energy in meta-ecosystems (Gounand *et al.* 2017), but their effects on metacommunity dynamics and coexistence are not well understood.

Consequences of dispersal

Differences in dispersal rates among trophic levels may stabilise population dynamics and lead to more complex food webs than would exist in the absence of dispersal (Hauzy *et al.* 2010). Spatial asymmetries in dispersal among interacting consumer and resource populations can produce distinct spatial distribution of resources. For example when resource populations have limited dispersal and the consumer has global dispersal, the resource density becomes highly variable in space (e.g. Fig. 2c). On the other hand, when the consumer has limited dispersal and the prey disperses regionally, the prey is able to persist in subsets of patches that do not contain their predators (McCauley *et al.* 1993; de Roos *et al.* 1998; Pedersen & Guichard 2016). It is expected that rates of dispersal often vary systematically with trophic level, for example larval dispersal is greater in predator vs. prey species in Pacific reefs (Stier *et al.* 2014). More generally, we expect that specialist predators require a higher dispersal rate than generalist predators because they need a particular prey species to be present before it can colonise new habitats (Holyoak *et al.* 2005).

Consequences of migration

Species' migration determines the movement of species among habitat type patches, for reproduction and resource consumption. Migration links patches of different habitat type, where species composition is different. In contrast, when individuals disperse and forage, they typically move between habitats of the same type, with similar species composition. In the case of foraging, the movement of individuals between these compositionally similar habitats may be driven by variation in resource abundance. Classic examples of migration include whales migrating towards the poles in the search of food resources during the summer and migrating towards the tropics during their breeding season in the winter months (Stone *et al.* 1990), wildebeest following the flush of grass growth across the Serengeti (Holdo *et al.* 2009), and waterfowl migrating across latitudes to follow the growing season of plants (Si *et al.* 2015). In addition, some species switch

habitats at some point in their life cycle if they require sequential hosts (i.e. parasites) or resources to complete development (Molnár *et al.* 2013). For example many insects transition between aquatic and terrestrial life histories, or between belowground and aboveground dwellers as they develop from larvae to adults. We aggregate migration and habitat switches as both act as spatial subsidies for the receiving food web and link different habitats.

Migration can influence the structure and dynamics of local food webs, involving non-migrating species, by providing a temporal influx of energy, nutrients and temporary competitors, natural enemies or facilitators. For example migration may allow the maintenance of populations in low productivity ecosystems such as the Arctic, where large populations of migratory birds disrupt the trophic interaction between terrestrial carnivores and small rodents (Giroux *et al.* 2012). These spatial subsidies can occur at different trophic levels, for example a prey species may migrate into a community and provide resources to predators, which can release local prey from risk. Alternatively, predators may migrate which can depress prey populations and have either stabilising or destabilising effects (Polis *et al.* 1997).

Consequences of foraging

Foraging movements are within-population movements of one species that can affect the dynamics of other species. Food webs across habitats may be coupled when predators and prey differ in the spatial scales at which they forage (e.g. Fig. 2d) (Polis *et al.* 1997; McCann *et al.* 2005). For example if predators forage at broader spatial scales (meaning, over greater areas) than their prey, prey populations in one habitat patch can increase the abundance of predators in an adjacent habitat patch. Because organisms can forage in habitat patches that are outside their abiotic niches (Rahel & Nutzman 1994), a predicted outcome of linking local food webs via foraging activities is the realisation of a greater range of trophic interactions than a given habitat patch would otherwise support. As a consequence of spatial coupling among habitat patches, local dynamics may be coupled, leading to stable food web structures (McCann *et al.* 2005).

The consequences of foraging on metacommunity structure depend on the mismatch between species at different trophic levels in the use of space; some predators forage over smaller spatial areas than their prey, whereas others forage over larger areas than their prey. We must first consider two general constraints to understand the causes of mismatches in foraging extent among trophic levels: i) consumptive interactions are energetically inefficient, with only ~10% energy transfer from food consumed into the bodies of individuals of the consumer population (Trebilco *et al.* 2013), ii) foraging is also costly because of energetic demands and lethal risks of movement (Anderson & Karasov 1981; Pyke 1984). The spatial scale of foraging should therefore reflect the minimum area needed to meet energetic and nutritional requirements given the spatial distribution of prey (Laca *et al.* 2010; DeLong *et al.* 2014). Foraging can be highly localised for predators with locally replenishing prey (e.g. web-building spiders with a sit-and-wait strategy), or integrate over much larger spatial scales for predators with scarce, depleted and patchily distributed prey

(e.g. predatory birds that must actively seek prey). Mismatches in the spatial scale of foraging occur among trophic levels when their constituent species differ in spatial scales at which energetic/nutritional requirements are met (Higginson & Ruxton 2015). Such differences in foraging scale between trophic levels will create spatiotemporal dynamics in food webs, and therefore are a critical part of understanding trophic metacommunities.

Spatial information processing

Traditional metacommunity ecology assumes that dispersal is passive. This assumption becomes problematic when studying food webs, especially for higher trophic levels where movement involves cognitive and information processing systems that allow organisms to actively determine when and where to move (e.g. Fig. 2f). Movement therefore often requires the capacity to receive, store, and process spatially explicit information about the environment; we refer to this capacity as spatial information processing. Spatial information processing can affect any of the three forms of movement – dispersal, migration and foraging – and encompasses ‘habitat selectivity’, or the degree to which individuals control their movement based on local conditions. However, spatial information processing requires organisms not only to sense their local environment (requiring ability to perceive environment), but also the environment of adjacent patches (requiring spatial memory to integrate perceptions). Organisms must then use this information to aid their navigation and decide where to go (Nathan *et al.* 2008a). Spatial information processing can have large consequences for the distribution of species in space. For example colonisation rates can depend not only on the perceived quality of one patch, but also that of surrounding suitable patches, leading to spatial contagion (Resetarits & Silberbush 2015). Mathematical models of animal movements suggest that perception of environmental stimuli affects movement decisions (Hein & McKinley 2012), and that increased spatial memory optimises time spent foraging in suitable patches (Fagan *et al.* 2013).

The ability to process spatial information likely differs between trophic levels. In general, we expect selectivity to increase with trophic level, with plants and microbes being the least selective and top predators being the most selective (but there are also counter examples). Organisms at higher trophic levels tend to have greater cognitive function and brain size, both of which correlate with greater habitat selectivity (Rooney *et al.* 2008). In particular, actively foraging consumers require more spatial memory to efficiently exploit their environment (Edmunds *et al.* 2016), and so have larger hippocampal complexes and putative hippocampal homologues both across and within taxa (Krebs *et al.* 1989; Baird Day *et al.* 1999). Similarly, animals with larger brains, for example mammals, have a greater degree of behavioural flexibility and are better able to successfully colonise new environments (Sol *et al.* 2008). However, increased brain size also comes with increased energetic demands (Fagan *et al.* 2013) and thus the need for increased foraging.

The scale at which organisms perceive their environment reflects the scale at which they use that environment. Some

organisms, such as seabirds, forage across multiple habitat types to meet their nutritional requirements (Orians & Wittenberger 1991) and so must be able to perceive the patchiness of the landscape and select for certain patches. Habitat specialists may perceive a higher degree of habitat heterogeneity than generalists, resulting in their restriction to small amounts of suitable habitat surrounded by perceived barriers (Holyoak *et al.* 2005). Larger species have longer viewing distances and therefore a wider scale of perception (Kiltie 2000), allowing them to move farther and survive for longer in novel environments (Sol *et al.* 2008). However, faster moving animals also have less accurate perception, potentially explaining changes in visual acuity with trophic level (Chittka *et al.* 2009). Indeed, the ability to navigate through sensory perception and memory has likely co-evolved with movement capacity, and together these factors influence how and where an individual may move (Nathan *et al.* 2008a; Fagan *et al.* 2013).

PREDICTED EFFECTS OF (CO)VARIATION IN SPATIAL USE PROPERTIES ON TROPHIC METACOMMUNITY DYNAMICS

Predicting the consequences of different distributions of spatial use properties will require deeper theoretical investigation than is possible here, but we nonetheless propose a few general patterns as a starting point. As an illustration, we examine the dynamics of a simple food web of four species (two plants consumed by one herbivore, which itself is preyed upon by one predator) in two patches using the model presented in Appendix S2. We parameterised this model with simple scenarios where at least one species in the food web varies in their spatial use properties from the rest of the food web (Fig. 2 and Fig. S3). The same food web will occur in all patches at all time points if species do not differ in their spatial use properties, the environment is homogenous and dispersal between patches is null (Fig. 2a). Changes in diversity and food web composition through space or time arise with variability in spatial use properties (Fig. 2). For example the herbivore cannot persist in the red patch of Fig. 2b, only on the black patch when it has a narrower abiotic niche and species do not disperse between patches. Since the herbivore is permanently absent from the red patch, the predator is also absent because of starvation. Similarly, the herbivore will be absent from the second patch if it has very low dispersal (Fig. 2c). In this case, however, the predator is only present via dispersal, where the second patch becomes a sink population for the predator, given that there is no prey present (Fig. 2c). The predator can persist if it has a larger foraging scale because of the consumption of herbivores on both patches. Even if there are no herbivores on the patch that contains predators, the predator will be able to persist by coupling the two patches and foraging on the second patch (Fig. 2d). In the case where the predators migrate in and out of a metacommunity module, they will affect the abundance of the herbivores only when they are present in that module (Fig. 2e). Finally, when the plants have lower spatial information processing, they will be slower at tracking changes in the abiotic conditions of patches. This inertia could cascade to other trophic levels if upper trophic levels track their

Table 3 Spatial use properties and how they correspond both to measurable traits and parameters in the modelling framework described in the text

Spatial use properties	Measurable organismal traits	Model parameters
Abiotic niches	Temperature tolerance (Magnuson <i>et al.</i> 1979; Huey & Kingsolver 1989) Drought tolerance (Schimper <i>et al.</i> 1903; Engelbrecht <i>et al.</i> 2007) Range limits (Parmesan <i>et al.</i> 2005; Sexton <i>et al.</i> 2009; Ehrlén & Morris 2015) Stoichiometric niche (Sterner & Elser 2002; González <i>et al.</i> 2017)	Species-specific environmental optima and environmental breadth
Dispersal scale	Maximum dispersal distance (Cain <i>et al.</i> 2000; Levin <i>et al.</i> 2003; Nathan <i>et al.</i> 2008b) Dispersal rate (Hanski 1991) Number of propagules (Shanks <i>et al.</i> 2003; Simberloff 2009) Gene flow (Slatkin 1987; Palumbi 2003) Mode of locomotion (Ronce & Clobert 2012; Stevens <i>et al.</i> 2014)	Dispersal rate and distance
Migration scale	Migration propensity (Alerstam <i>et al.</i> 2003; Hanski <i>et al.</i> 2004) Migration distance (Webster <i>et al.</i> 2002) Stable isotopic ratios (Hobson 1999)	Migration rate and distance
Foraging scale	Home range size (Mitchell & Powell 2004; Börger <i>et al.</i> 2008) Radio collars for daily movement (Harris <i>et al.</i> 1990)	The number of patches that each species uses to forage
Spatial information processing	Relative brain size (Fagan <i>et al.</i> 2013) 2d vs. 3d perception (Pawar <i>et al.</i> 2012) Sensing appendages (Vickers 2000; Mitchinson <i>et al.</i> 2007) Active vs. passive dispersal (Cottenie 2005; Van de Meutter <i>et al.</i> 2007)	Changes to movement due to environmental variation or other species.

resources more closely than they do their environment (Fig. 2f). Overall, we expect increased network diversity, complexity, and stability when trophically linked species are dissimilar in their spatial use properties. This should coincide with greater difference in the spatio-temporal dynamics of each species. These results, based on a relatively simple model, show how differences in spatial use properties across trophic levels can impact the dynamics, diversity and food web structure of trophic metacommunities. Further work is now needed to fully integrate spatial use properties into trophic metacommunity models and theory.

FUTURE DIRECTIONS: BUILDING AND TESTING FUTURE METACOMMUNITY THEORY BASED ON SPATIAL USE PROPERTIES

We have argued that incorporating spatial use properties will provide a deeper understanding of trophic metacommunities; our challenge is now to use this perspective to develop, test and refine a body of trophic metacommunity theory. To accomplish this goal, efforts are now needed to (i) document these five spatial use properties within food webs, (ii) use meta-analytical approaches to investigate patterns of spatial use properties across scales of space time and organisation, within and among food webs, (iii) develop new theory for how the relative scales of spatial use properties across trophic groups affects metacommunity dynamics and their outcomes and (iv) test whether empirical biodiversity patterns in trophic metacommunities can be explained by the scales of ecological processes related to spatial use properties.

Goal i: Documenting spatial use properties within food webs

Before new theory about trophic metacommunity dynamics (goals iii-iv) can be tested, we require quantitative measures of spatial use properties (using traits) within food webs. This is a challenge, because spatial use properties themselves are rarely quantified directly in empirical studies. We propose a set of

measurable traits that can be used as proxies of spatial use properties (Table 3), to quantitatively compare differences in the spatial scales and extents movement among interacting species. A single measurable trait may not be suitable to estimate differences in spatial use properties across all trophic levels ranging from microbes to top predators. Experiments coupled with observations from multiple techniques may be required to estimate spatial use properties for whole food webs. For example bacterial movement can be studied using microfluidic devices (Englert *et al.* 2009), insect movement with harmonic radar (Chapman *et al.* 2011), and mammal movement with radio tags (Millsbaugh 2001).

Goal ii: Using meta-analytical approaches to investigate patterns of spatial use properties within and among food webs

Documenting the scales and mechanisms associated with spatial use properties will provide the empirical evidence needed to answer the question of whether these properties vary systematically within and across food webs, using meta-analytical approaches. It will also allow us to test whether spatial use properties are constrained by physiological, morphological or evolutionary trade-offs. In other words, can we use knowledge of one spatial use property within a food web to infer the structure of another spatial use property in that food web? (Fig. 1b).

The synthesis of metacommunity and spatial food web concepts we have reviewed here implies that within a food web, organisms vary in their spatial use properties and that this variation affects metacommunity dynamics. Species at different trophic levels have very different energetic needs and life-history strategies (Trebilco *et al.* 2013). Furthermore, both trophic level and spatial use properties such as dispersal, migration and foraging scale with body size (McCann *et al.* 2005; Hein *et al.* 2012; Kalinkat *et al.* 2015). However, these scaling relationships have been generated by aggregating species across many food webs and therefore little is known about how spatial use properties are structured within

Box 1 Trophic metacommunities in bromeliad-dwelling insects

We use a food web module from water-filled bromeliads in Costa Rica to consider how shifts in the relative abundances of species along a habitat size gradient can be understood in terms of species differences in their spatial use properties (colonisation rates, abiotic niches) and susceptibility to predators. *Culex* spp. and *Wyeomyia* spp. mosquitoes are potential competitors and are both preyed upon by *Mecistogaster modesta* damselflies. All three taxa show strong patterns with bromeliad size, with the abundance of *Culex* and *Mecistogaster* increasing with bromeliad size, and *Wyeomyia* decreasing with bromeliad size (Fig. 3a). Bromeliad size affects species in three ways. (1) Numerical effects on colonisation. If colonisation probability is related to available habitat, as often assumed in competitive metacommunity models, we would expect larger bromeliads to be colonised more frequently than small bromeliads, such that species with small regional populations and thus few colonists (*Mecistogaster*) occur entirely in the large bromeliads whereas species with larger regional populations (*Culex*, *Wyeomyia*) occupy mainly large but also some medium-sized bromeliads. Although such numerical effects explain the distribution of *Culex*, *Mecistogaster* still occurs in larger bromeliads than expected and *Wyeomyia* in smaller bromeliads than expected. (2) Abiotic niche differences. Small bromeliads are at risk of drying out, whereas insects are still aquatic larvae, and this risk is particularly acute for *Mecistogaster*, whose larvae require ca. 9 months to develop. *Culex* and *Wyeomyia* larvae require ca. 3 weeks to develop and have less exposure to drought risk (Fig. 3b). After correcting species abundance for numerical effects on colonisation probability, residual *Mecistogaster* abundance is positively related to bromeliad size in a structural equation model – presumably reflecting its greater likelihood of drought exposure at some point during the larval stage. *Wyeomyia* residual abundance is negatively related to bromeliad size, potentially because drought-resistant eggs in this genus (unlike *Culex*) enable it to preferentially colonise small bromeliads. (3) Trophic interactions. Finally, bromeliad size may affect species indirectly via predation or competitive interactions. In our structural equation model, *Wyeomyia* occurs in smaller than expected bromeliads because it is negatively affected by its predator, *Mecistogaster*, which in turn occurs disproportionately in large bromeliads. In contrast, *Culex* abundance is unaffected by effects of bromeliad size mediated by *Mecistogaster* (Fig. 3c). This is consistent with the documented ability of *Culex* – but not *Wyeomyia* – to chemically detect *Mecistogaster* and avoid predation through a change in foraging behaviour (Hammill *et al.* 2014). This example shows the power of combining statistical analyses with documented differences between species in their response to abiotic stress and predation to understand the distribution of the food web module between habitat patches. Deeper understanding of this module could be achieved by studying how other spatial use properties differ between these species, such as spatial information processing by ovipositing adults, or dispersal (pupation) cues for mosquito larvae.

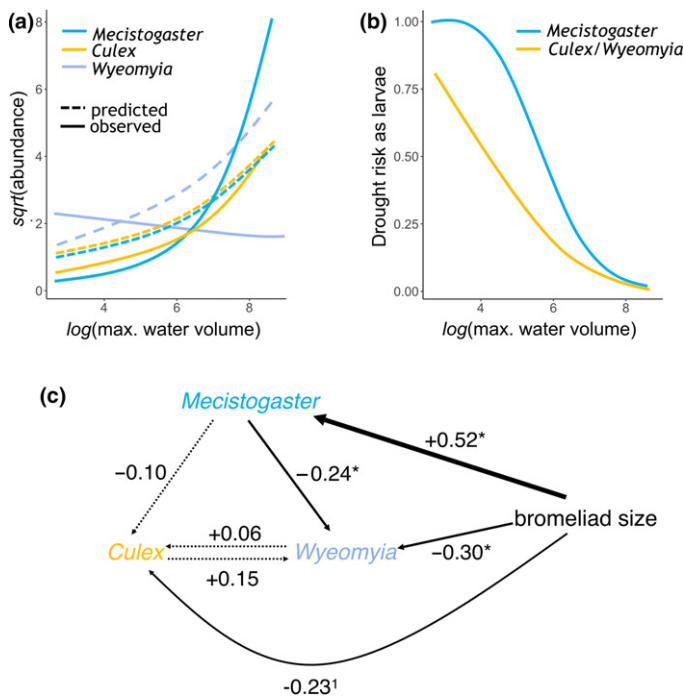


Figure 3 (a) The observed abundance of three genera of insects changes across a gradient in the maximum volume of bromeliads. A null model that assumes no per capita differences in colonisation probability, but purely numerical differences driven by differences in regional abundance ('predicted abundance'), can account for some of the positive effects of bromeliad size on *Culex* and *Mecistogaster*. (b) The *Mecistogaster* damselfly larvae experience greater risk of drought during their 9 month larval phase than the *Culex* and *Wyeomyia* mosquito larvae with a 3 week larval duration. (c) After correcting for the numerical

effects of bromeliad size on colonisation rates, residual abundance of species may be related to bromeliad size either directly, for example by drought risk associated with small bromeliads, or indirectly, through effects on competitors and predators. Bromeliad size was corrected for numerical effects on colonisation. Path coefficients are standardised effect sizes from structural equation models described in full in the Supplementary Material; path widths are proportional to absolute standardised effect sizes. Significance of path coefficients: $*P < 0.05$; $^1P < 0.10$.

individual food webs. A related question that could be answered through meta-analysis of is whether trophic structure in spatial use properties varies systematically across different ecosystem types. We might expect such systematic differences between ecosystem types to arise because of differences in the evolutionary histories of their constituent species (e.g. aquatic vs. terrestrial), regional environmental structure (e.g. patchiness) or bioclimatic differences on larger geographical scales (e.g. temperate vs. tropical). Identifying additional scaling relationships, and their causes, will not only allow application of this framework with efficient use of data for parameterising models, but will also help understand how macro-ecological and physiological constraints may influence spatial processes in metacommunities.

Understanding covariances in spatial use properties across species can reveal biological or evolutionary constraints and trade-offs of these properties, as well as variation in those constraints among ecosystems (Díaz *et al.* 2016). For example relative brain size (a proxy for spatial information processing) is smaller in migratory than in non-migratory birds due to an energetic trade-off between neural tissue volume and migratory flight (Vincze 2016). Similarly, traits relevant to particular types of movement (foraging, migration, dispersal) might be positively correlated (Bowman *et al.* 2002) as each has been shown to increase with body size (Kelt & Van Vuren 1999; Alerstam *et al.* 2003; Greenleaf *et al.* 2007; De Ryck *et al.* 2012; Hirt *et al.* 2017); for this reason, we refrain from assigning body size as a proxy for any specific spatial use property (Table 3). A high degree of covariation among spatial use properties might simplify predictions in some ecosystems. Non-random covariation among traits will constrain the range of local food web structures that are possible for theoretical studies (Gravel *et al.* 2016a).

Goal iii: Developing new theory for how the relative scales of spatial use properties across trophic groups affects metacommunity dynamics and their outcomes

We can use theoretical models to explore the consequences of different trophic structures in spatial use properties for the stability and network structure of food webs. By constraining this exploration based on documented patterns of spatial use properties (goals i and ii) will allow us to focus on and contrast the predicted outcomes of patterns that are found in specific food webs or ecosystem types. We have outlined how this could be done using a modelling approach that incorporates the five spatial use properties (Fig. 2, Appendix S2). This constrained exploration will allow us to ask what are the commonalities and differences in how the five spatial use properties affect food web stability? and how does trophic

metacommunity structure and persistence respond to environmental change and habitat loss? Given the importance of spatial use properties for the dynamics and stability of trophic metacommunities as we suggest here, we hypothesise then that diversity of spatial use properties associated with trophic status might be a particularly important dimension of diversity for spatially structured food webs (McCann *et al.* 2005). For example McCann *et al.* (2005) showed that when predators forage at larger spatial scales than prey, they can stabilise food webs. Similarly, differences in dispersal between predators and prey can result in stability of the interactions (e.g. Pedersen & Guichard 2016). We suggest that it should be addressed with theory that is guided by observational patterns of spatial use properties (i.e. goals i and ii) and then tested using experiments. If, for example fish in ponds are observed to forage at larger scales but disperse at smaller scales than invertebrate prey, we can develop models that provide theoretical predictions for how these movement differences affect the spatial distribution of the two trophic levels. We can test these predictions by experimentally manipulating fish foraging and dispersal via movement restriction (i.e. size-specific mesh) and assisted dispersal respectively.

Movement is a key process that determines how communities respond to environmental change and habitat loss (Loreau *et al.* 2003; Norberg *et al.* 2012; Grilli *et al.* 2015; Thompson *et al.* 2017). Despite the fact that we know that trophic level is a key predictor of how species will respond to such changes, we have limited theory that links this response to movement within a food web context (but see Thompson & Gonzalez 2017). Theoretical models offer the opportunity for developing expectations of how different patterns of spatial use properties affect the response of food webs to different forms of environmental change or habitat loss. This theory is needed for informing and interpreting experiments since the presence of predators has often interfered with our ability for experiments to match theoretical predictions (Grainger & Gilbert 2016).

Goal iv: Testing whether empirical biodiversity patterns in trophic metacommunities can be explained by the scales of ecological processes related to spatial use properties

Inferring the spatial processes that govern the diversity and functioning of communities is a major goal in metacommunity ecology (Leibold & Chase 2018). Yet, methods for linking patterns of abundance to different metacommunity paradigms (Cottenie 2005; Ovaskainen *et al.* 2017) do not have a systematic way of incorporating trophic interactions, nor variation in movement between trophic levels. We demonstrate how our framework can be used to link patterns of abundance to spatial use properties with a food web module from a

metacommunity of bromeliad-dwelling invertebrates (Box 1). This example shows how observational data may be coupled with structural equation models to untangle how space affects food web structure. Additional efforts to formalise these links in other systems with existing data would be one way to rapidly advance our empirical understanding of trophic metacommunities.

The questions and avenues of research we highlight are underexplored and promise rich research opportunity. The feasibility of answering these questions will undoubtedly vary among food webs, particularly those for which spatial use properties are difficult to quantify with reasonable certainty. Trophic metacommunities are complex and models will need to deal with the rich natural history that underlies species interactions and movement (such as omnivory, territoriality, ontogenetic niche shifts, non-consumptive effects and cross-ecosystem subsidies). Experiments and observational studies will guide theoretical studies to manage that complexity. Further development of trophic metacommunity theory requires a feedback between empirical observation, theory and experiments. We believe that this approach offers exciting possibilities and has the potential to guide the development and testing of the next generation of trophic metacommunity theory.

CONCLUSION

We argue that metacommunity theory must incorporate trophic interactions to encompass the full range of dynamics that occur in real-world communities. We began by outlining challenges to extending metacommunity ecology beyond competitive systems, with suggestions for how to overcome those challenges by reformulating some basic assumptions. We then proposed that progress towards a trophic metacommunity framework could be achieved by accounting for a wider array of spatial use properties than the traditional metacommunity framework allows. These spatial use properties are (1) abiotic niches, (2) spatiotemporal scales of dispersal, (3) scales of migration, (4) scales of foraging and (5) spatial information processing. We end by reiterating priority questions to be answered towards a robust trophic metacommunity theory. Answering these questions would allow metacommunity ecology to fulfil its promise as a truly synthetic theory of food web ecology.

AUTHORSHIP

All authors participated in discussions and writing of the manuscript. D.S.S. contributed bromeliad data and performed analysis.

DATA AVAILABILITY STATEMENT

The data supporting the results are archived at <https://doi.org/10.5281/zenodo.1410460> and the code is archived at <https://doi.org/10.5281/zenodo.1410473>

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Additional supporting information may be found online in the Supporting Information section at the end of the article.

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