

REVIEW AND SYNTHESIS

Linking community and ecosystem dynamics through spatial ecology

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Abstract

Classical approaches to food webs focus on patterns and processes occurring at the community level rather than at the broader ecosystem scale, and often ignore spatial aspects of the dynamics. However, recent research suggests that spatial processes influence both food web and ecosystem dynamics, and has led to the idea of 'metaecosystems'. However, these processes have been tackled separately by 'food web metacommunity' ecology, which focuses on the movement of traits, and 'landscape ecosystem' ecology, which focuses on the movement of materials among ecosystems. Here, we argue that this conceptual gap must be bridged to fully understand ecosystem dynamics because many natural cases demonstrate the existence of interactions between the movements of traits and materials. This unification of concepts can be achieved under the metaecosystem framework, and we present two models that highlight how this framework yields novel insights. We then discuss patches, limiting factors and spatial explicitness as key issues to advance metaecosystem theory. We point out future avenues for research on metaecosystem theory and their potential for application to biological conservation.

Keywords

Complex adaptive system, dispersal, food web, grain, landscape, metacommunity, metaecosystem, patch, trait.

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INTRODUCTION

The idea that food webs and ecosystem functioning are intimately linked harkens back at least to the work of Forbes (1887). He pondered, in his 'lake as a microcosm' paper, the complexity of lake ecosystems and how this complexity could be maintained given the complex network of trophic interactions. He also emphasized that spatial structure, both within and among lakes, could be important. Lindeman (1942) built on Forbes' vision of a food web as a microcosm by linking a simplified view of food webs to ecosystem metabolism. Since then, much thinking has gone into understanding food webs and their links to ecosystem attributes (Odum 1957; Margalef 1963), but until recently the importance of space has not sufficiently been integrated into these thoughts. By contrast, the importance of space to populations and communities has been recognized for some time (Watt 1947; Skellam 1951; MacArthur & Wilson 1967), but the connection between this literature and food webs and ecosystems is only now being resolved (Loreau *et al.* 2003; Polis *et al.* 2004; Holt & Hoopes 2005; Pillai *et al.* 2009; Gravel *et al.* 2010a). Some progress has been made (e.g. Polis *et al.* 2004; Holyoak *et al.* 2005), but most of the work on spatial food web and ecosystem properties has progressed along two relatively independent traditions

that separate 'food webs' from 'ecosystems' (Fig. 1; Loreau *et al.* 2003). These two traditions have yet to be united into a more comprehensive view that would fully address the visions of Forbes and Lindeman in a broader spatial setting.

The first of these traditions, initiated by predator-prey ecologists (e.g. Huffaker 1958; Bailey *et al.* 1962) following the path paved by Lotka (1925), Volterra (1926) and Nicholson & Bailey (1935) on predator-prey stability, and Skellam (1951) on dispersal among populations, emphasizes spatial population dynamics in food webs (Fig. 1a). More recently, this tradition has been incorporated in the *metacommunity* framework (see the Glossary for a definition of italicized terms; Hanski & Gilpin 1997; Leibold *et al.* 2004; Holyoak *et al.* 2005) through the study of simple food web modules in a patchy landscape (Amarasekare 2008). While very productive as a source of novel insights into how food webs are structured at multiple spatial scales, this tradition of 'food web metacommunity' ecology focuses on predation and its consequences on community complexity and dynamics, largely ignoring interactions involving abiotic materials and feedbacks on ecosystem functioning (Loreau 2010).

The second tradition comes from 'landscape ecosystem' ecology (Troll 1939), which focuses on the geographical structure of

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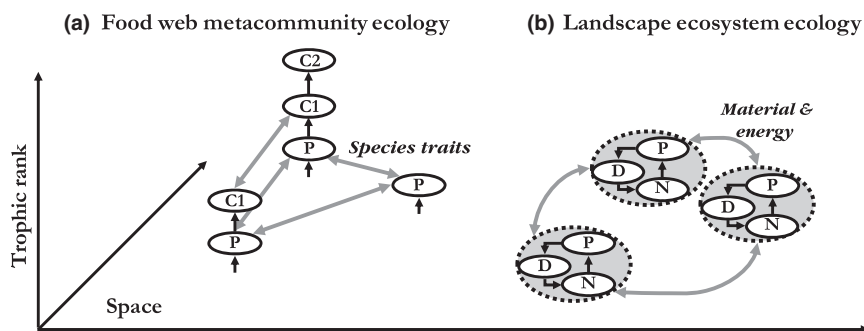


Figure 1 The two traditions of spatial ecology. Agents are presented as ovals with a letter (N for nutrients, P for primary producers, C1, C2, for consumers of a given level, D for detritus). Black arrows represent fluxes due to interactions. Grey arrows represent fluxes due to movements. (a) Representation of the ‘food web metacommunity’ ecology tradition. Primary producers and consumers are explicitly modelled while nutrient pools and detritus recycling are unaccounted. Patch may harbour different food web complexity. Migration fluxes are mostly seen as transfers of species traits through top-down and bottom-up control of local trophic dynamics. (b) Representation of the ‘landscape ecosystem’ ecology tradition. Only primary producers, detritus and nutrients are accounted for, but without much concern for which agents migrate among patches (hence the dotted ovals grouping the three compartments). Fluxes between localities are perceived as purely material couplings, so that it does not matter whether this material flows as detritus, nutrient or plant seeds.

ecosystems, the movements of materials and energy among ecosystems, and how these may affect the functioning of these ecosystems (Naveh & Lieberman 1984; Urban *et al.* 1987; Turner *et al.* 2001). Much of the ‘landscape ecosystem’ ecology literature deals with biogeochemical interactions between primary producers and decomposers (Fig. 1b). Models from this tradition partition the distribution of nutrients among organic and inorganic compartments and quantify nutrient flows, both among compartments and across space (Canham *et al.* 2004). Traditionally, ‘landscape ecosystem’ ecology deals with realistic and complex food webs in a descriptive fashion (i.e. explaining patterns rather than predicting the consequences of processes), and this area has not received as much general theoretical development (Loreau *et al.* 2003). For practical reasons, ‘landscape ecosystem’ ecology studies often ignore higher trophic levels, and thus possibly overlook large effects that might be mediated by the movement of material by migrating animals or with the regulation of primary producers through trophic cascades (Polis & Hurd 1995; Polis *et al.* 1997; Nakano & Murakami 2001; Helfield & Naiman 2002; Polis *et al.* 2004; Fukami *et al.* 2006).

These two traditions differ substantially in the methods and tools being used, on the importance attributed to the different species in the landscape, on the strategy adopted to work with real data, and on the general questions asked about spatial ecosystems. However, the most striking distinction between these two traditions comes from what they hold as the spatial coupling medium (Fig. 2). In ‘food web metacommunity’ ecology, habitat patches are connected by the dispersal of organisms with certain *traits*, which control their interaction with other organisms and abiotic resources at an individual level and thus influence population dynamics and the prospects of species coexistence (Amarasekare 2008). In ‘landscape ecosystem’ ecology, sites are connected by the fluxes of *materials* moving across the landscape, through transport by living organisms, passive diffusion, currents, etc., and these fluxes control the distribution of energy and elements in space, which ultimately determines the range of potential productivity (Cloern 2007) or the length of food chains through productivity and ecosystem size (Post 2002). Because of the existing division between the two traditions, spatial ecosystems are rarely modelled as both trait- and material-coupled entities (Box 1), despite empirical studies that clearly pinpoint the existence of both couplings (e.g. Polis & Hurd 1995; see Table 1).

Box 1 A classification of approaches to spatial ecology

Most studies belonging to the two traditions of spatial ecology can be positioned along two axes: the spatial coupling mediums and the grain (temporal and spatial) considered (Fig. 2, Table 1). *The first axis* concerns the nature of the coupling agent. When two food webs are coupled through the movement of an agent, the coupling may be due to the traits (e.g. interaction coefficients among species or dispersal rates) and/or the material/energy of the shared agent. *The second axis* concerns the rates and scales of the coupling agents (the grain). In living organisms, foraging movement and dispersal affect food web dynamics on different spatio-temporal scales. For abiotic material, diffusion processes may occur at all scales and rates but often at a smaller scale than transport through living organisms. Frequent and close movements (e.g. foraging; diffusion of abiotic material) are distinguished from rare and far movements (e.g. dispersal, upwelling). This distinction is particularly relevant because it applies to both living organisms and abiotic materials and it highlights the potential shortcomings of approaches that would decouple spatial and temporal scales.

This classification reveals missing pathways and gaps in knowledge. For instance, the study by Knight *et al.* (2005) illustrates the importance of rare and far trait movements by organisms on the functioning and diversity of terrestrial ecosystems. They have shown that fish feeding on larval dragonflies enhances nearby plant reproduction because it culls dragonflies that, as adults, feed on pollinators (bees, etc.) and changes their foraging behaviour. It does not, however, envision a connection through material flows while there is evidence that primary production in small lakes is influenced by, e.g. pollen deposition (Graham *et al.* 2006). Thus, there is a possibility of closing the fish-dragonfly-bee-plant loop with a plant-pollen-plankton-fish loop mediated by material flows.

This framework reveals that studies from the ‘food web metacommunity’ and ‘landscape ecosystem’ ecology tend to be isolated from each other (Table 1). The identification of gaps in knowledge should thus help us to link these traditions.

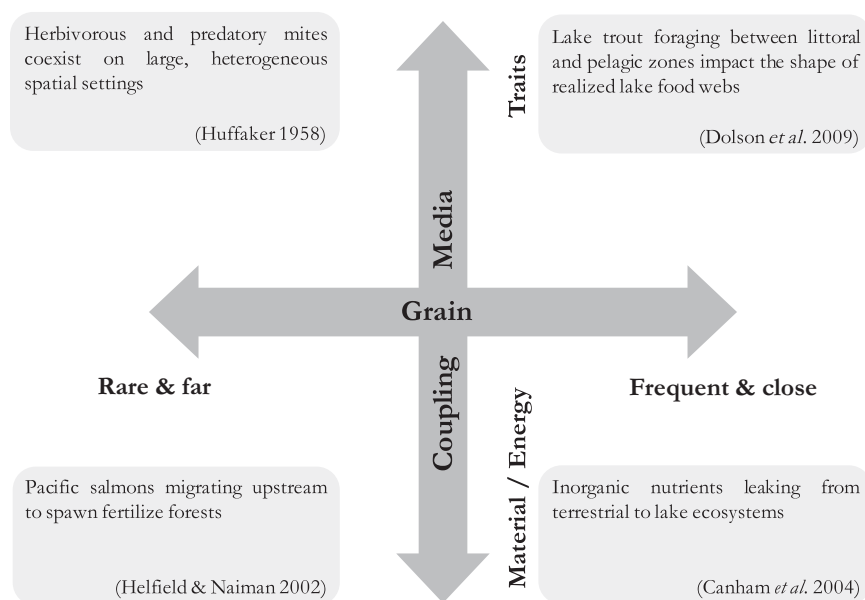


Figure 2 Schematic representation of the two-axis classification for spatial ecology defined in Box 1. The first axis concerns the nature of the coupling agent (either traits or material) and the second axis the rates or scales of the coupling agents (the grain). Studies belonging to the two traditions of spatial ecology can be positioned along this continuum. *Vertical axis:* Along the first axis, food web metacommunity ecology focuses on the movement of living organisms and their traits. Classical example is the seminal work by Huffaker (1958) who found that dispersal among patches allowed both herbivorous and predatory mites to persist at the regional scale despite their tendency for local extinction. Another good example comes from Dolson *et al.* (2009) who found that lake trout foraging between littoral and pelagic zones in lake impact the shape of realized lake food webs. On the other hand, landscape ecology has focused on the passive diffusion of large quantities of abiotic nutrients or on cases where dispersing or foraging of organisms induce a transport of materials among distant locations. Good examples of organism coupling are Pacific salmon migration (Helfield & Naiman 2002). Example of passive diffusion is inorganic nutrients leaking from terrestrial ecosystems to lakes (Canham *et al.* 2004). *Horizontal axis:* Along the second axis, the metacommunity experiment of Huffaker (1958) concerns rare and far dispersal events while Dolson *et al.* (2009) concerns frequent and close movements. In the landscape ecosystem perspective, the salmon migration (Helfield & Naiman 2002) is a rare and far event while the inorganic nutrients from terrestrial ecosystems to lakes (Canham *et al.* 2004) is more continuous and thus analogous to close and frequent movements.

Metaecosystems, defined as a set of ecosystems connected by spatial flows of energy, materials and organisms (Loreau *et al.* 2003), seemingly provide ecologists with the right framework for the reconciliation of trait and material coupling-based approaches of spatial ecosystems. Historically, metaecosystems were an extension of metapopulations and metacommunities incorporating abiotic fluxes and feedbacks stemming from ecosystem functioning (such as recycling). As of today, the concept of metaecosystem, and its associated studies (Loreau *et al.* 2003; Loreau & Holt 2004; Gravel *et al.* 2010a,b), are the only existing attempts at modelling both material and trait flows and their effects on spatial food web dynamics. However, because metaecosystem theory directly extends the metacommunity concept, it has inherited most of its attributes, including concepts such as ‘patch’, ‘dispersal’ or ‘limiting factors’. The fact that these concepts are often loosely defined in the context of metacommunities does not matter strongly, but poses a more serious issue in metaecosystems due to the potential for conflicting definitions and misconceptions. For instance, the notion of patch based on the scale of organism interactions loses its meaning when organisms with different motilities are considered (Holt & Hoopes 2005).

The challenges of ecology as a science are increasingly daunting. They include addressing more complex dynamics, more demanding issues (e.g. ecosystem functioning, resilience) and patterns and processes at larger scales. Tackling these challenges has been difficult within the traditional frameworks of ecological thinking based on local effects and simplified perspectives on species interactions. The existing spatial ecology traditions (Box 1) have considered either the movement of traits or materials among ecosystems, whereas empirical studies highlight the importance of interactions between species traits

and material fluxes. We argue that the key to improve our understanding of such broad scale phenomena is to recast the metaecosystem concept with relevant elements from both traditions of spatial ecology. We illustrate the power of the metaecosystem concept with two simple models that integrate both trait and material couplings. Based on these models, we propose several improvements to the original metaecosystem concept. Finally, we discuss different perspectives for research on metaecosystems, based on the study of emerging principles, phenomena and conservation concepts.

CROSS-TRADITION CASES IN NATURE

If evidence indicated that all spatial food web effects were mediated solely either by the movement of traits or material, the two traditions could exist independently, with each approach being used for its appropriate setting (Box 1). However, because the movement of traits and materials interact to affect food webs, a synthesis of ‘landscape ecosystem’ and ‘food web metacommunity’ ecology would be useful. Here, we illustrate this point with a few studies involving conspicuous interactions between the movements of traits and materials.

A clear cross-tradition situation is provided by Polis & Hurd (1995). This study reported ‘extraordinary’ spider and insect densities on islands of the Gulf of California, despite very low primary productivity. These densities declined with island area. According to Polis & Hurd (1995), two main factors explained this phenomenon: (i) smaller islands have a higher perimeter to area ratio than larger ones, and thus are more open to material inputs from the ocean which, in turn, tend to increase island secondary productivity

Table 1 Classification of some existing study cases on spatially structured food webs/ecosystems

Example	Coupling medium	Grain
Inorganic nutrients leaking from terrestrial ecosystems to lakes ^{1–4}	Material	Rare and far
Lake trout foraging between littoral and pelagic zones impact the shape of realized lake food webs ⁵	Both	Frequent and close
Galapagos sea lions transports nutrients to shorelines when resting, impacting nutrient cycling ⁶	Material	Frequent and close
Introduced seabird predators impact ecosystem functioning on islands by reducing marine inputs ^{7,8}	Material	Frequent and close
Primary production in lakes is influenced by pollen deposition ⁹	Material	Rare and far
Negative relation between island size and spider and insect densities ¹⁰	Both	Both
Dune fertilization by nesting sea turtles ¹¹	Material	Rare and far
Nitrogen transported by migrating Pacific salmon fertilizes neighbouring forests at spawning sites ¹²	Material	Rare and far
Herbivorous and predatory mites coexist on heterogeneous landscape, despite local extinctions ^{13,14}	Traits	Rare and far
Altered arctic food web functioning by migrating snow geese ¹⁵	Both	Rare and far
Grass- and tree-based food webs are coupled by ground-dwelling predators in Kenyan grasslands ¹⁶	Both	Frequent and close
Fish occurrence inhibiting dragonfly predation on bees ¹⁷	Traits	Rare and far
Moving whales influencing the spatial distribution of iron ¹⁸	Material	Frequent and close
Large terrestrial herbivores excreting important nutrient quantities while feeding ^{19,20}	Material	Frequent and close
Upwelling as a flow of abiotic material driving coastal ecosystem productivity and structure ²¹	Material	Rare and far
Co-distribution of plants and ant nests affecting population dynamics of butterflies ²²	Traits	Frequent and close
Southern Alaska kelp decrease due to overfishing in the middle of the Pacific ^{23,24}	Both	Frequent and close
Migrating insects at the water-land interface impact the functioning of terrestrial systems ^{25,26}	Material	Rare and far
Vertical coupling by carnivorous fish foraging in both the benthic and the planktonic food webs ^{27,28}	Both	Rare and far
Downstream communities are shaped by constant inputs from the inefficient upstream ones ²⁹	Material	Rare and far

Twenty examples of natural cases, related to 29 published articles, involving spatially structured food webs and/or ecosystems. This list is by no means exhaustive. 'Coupling medium' relates to the vertical axis in Fig. 2, i.e. whether the observed effect is due to the moving of traits or material/energy. 'Grain' corresponds to the horizontal axis in Fig. 2, that is whether movements occurred rarely but on long distances, or frequently on short distances.

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(i.e. decrease bottom-up constraints); and (ii) smaller islands are less likely to be reached by the predators of spiders and insects (such as lizards) because colonization to extinction ratios increase with island area (MacArthur & Wilson 1967). Factor (i) concerns material-mediated coupling between oceanic and island habitats, whereas factor (ii) concerns trait-mediated coupling between mainland and islands.

Because of agricultural subsidies in Southern Canada and the United States, Lesser Snow Goose population sizes have dramatically increased in the Hudson bay (Abraham *et al.* 2005), leading to harsh negative effects on the vegetation of goose breeding grounds (salt and freshwater marshes). Small goose populations may be beneficial to marshes because of increased recycling (and primary production) through goose grazing and excretion, and microbial decomposition (Cargill & Jefferies 1984; Bazely & Jefferies 1985), but large populations are detrimental to marsh ecosystems because of overconsumption (Jefferies & Rockwell 2002). Interpreting key components of this pattern requires both trait- and material-mediated couplings between staging and breeding grounds. The increase in goose abundance is due to an increase in available energy at the staging ground (material), but is manifested through an increased survival between reproductive events (trait). The degradation of marshes relates to both geese traits (aggregation of individuals while breeding, geese foraging behaviour) and the heterogenizing effect of geese excretion on soil nutrients (leading to hypersalinity, a material-mediated effect). Finally, marshes are degraded for a long period because of nutrient leaching (material) due to the inability of local plants to re-colonize degraded habitats (trait).

Sea otter decline in the Aleutian archipelago and in South Alaska has been well documented. A likely explanation for their long-term decline and/or slow recovery concerns increased predation by killer whales (Estes *et al.* 1998), which was itself likely due to an indirect spatially mediated trophic interaction: (i) the decline of forage fish stocks in the North Pacific due to overfishing (or other causes), which provoked (ii) the decline of large pinniped populations in the Pacific, which in turn caused (iii) transient (i.e. highly mobile) killer whale populations to settle near the shores of Aleutian archipelago and South Alaska and, then, (iv) to prey more heavily on local sea otter populations (Estes *et al.* 1998). This decline in sea otters affected local ecosystems through a trophic cascade, as large otter populations used to keep urchin populations in check and limit overgrazing of kelp by urchins and other herbivores (Estes & Duggins 1995). Overfishing led to a negative impact on kelp populations in Southern Alaska through both trait (mobility of killer whales, attack rate of killer whales on sea otters, attack rate of sea otter on urchins) and material (declines of both forage fish and large pinniped populations) couplings.

COMBINING THE MOVEMENTS OF TRAITS AND MATERIALS

The empirical cases presented above indicate the necessity to merge 'food web metacommunity' and 'landscape ecosystem' ecology into a single framework for the study of spatially structured ecosystems. Such a framework does exist: the metaecosystem concept (Loreau *et al.* 2003) consider all ecosystem compartments in simple patch-based models. Here we illustrate this framework using two theoretical studies that show how novel insights can arise when we simultaneously consider the movements of traits and materials. These two examples are only meant to illustrate that insights can be gained by

such efforts. Future work can and should be performed in more realistic and comprehensive ways (e.g. with a more realistic perspective on trophic interaction, spatially explicit formulation, etc.).

Metaecosystems as extended interaction matrices

In the first example, we take a general, simplistic approach in which we combine spatial movements of traits or materials with classical approaches based on 'interaction matrix models' previously used to evaluate the stability of large complex systems (May 1972; Kokkoris *et al.* 2002). This model links the expected dynamical properties of an ecosystem with the distribution of interaction coefficients among species pairs (values of the interaction matrix components) and the number of species involved (size of the interaction matrix). We show that the dynamical properties of a metaecosystem, described as an interaction matrix involving trophic interactions and dispersal, depend on total system materials.

Consider a large closed system consisting of populations of different agents (species or abiotic material stocks) which interact either through consumption (interspecific interactions) or movement (intraspecific interactions). Let n_i be the biomass of population i . Under the Lotka-Volterra formulation of predator-prey interactions, the rate at which population j biomass is converted into population i biomass through predation is proportional to $n_i n_j$, and noted a_{ij} , where a_{ij} is the rate at which an individual predator from population i preys on preys from population j (this rate summarizes attack rate and energy conversion efficiency). Similarly, the rate at which population j biomass is converted into population i biomass through movements is noted d_{ij} (this only applies between populations of the same agent). Following this simple model and neglecting processes other than predation and migration, the dynamics of agent i biomass are governed by:

$$\frac{dn_i}{dt} = \sum_{j \in A_i} a_{ij} n_i n_j + \sum_{j \in M_i} d_{ij} n_j, \quad (1)$$

where A_i denotes the set of populations interacting with population i (either preys, $a_{ij} > 0$, or predators, $a_{ij} < 0$) and M_i is the set of populations exchanging migrants with population i , including population i itself as a donor of migrants to other populations ($d_{ij} > 0$ for $i \neq j$, and $d_{ii} < 0$).

When the system is assumed closed, the sum of its components' biomass $n = \sum n_i$ is constant, and it is more useful to consider the dynamics of $p_i = n_i/n$ which is the proportion of total system's materials contained in population i . If the metacommunity consists of a single patch (i.e. all d_{ij} coefficients are zero), eqn 1 can be time-scaled by $T = nt$, so that the dynamics of p_i are given as:

$$\frac{dp_i}{dT} = \frac{1}{n^2} \frac{dn_i}{dt} = \left(\sum_{j \in A_i} a_{ij} p_j \right) p_i. \quad (2)$$

Apart from the typical time of the dynamics (which is scaled to n), nothing in eqn 2 is bound to depend on total system's biomass. In other words, dynamical properties of the system governed by eqn 2 will only depend on the interaction coefficients among species, i.e. on traits only.

By contrast, if we consider a system in which some populations harbour the same species and exchange migrants, applying the same time-rescaling to eqn 1 leads to the following dynamics:

$$\frac{dp_i}{dt} = \frac{1}{n^2} \frac{dn_i}{dt} = \left(\sum_{j \in A_i} a_{ij} p_j \right) p_i + \sum_{j \in M_i} \left(\frac{d_{ij}}{n} \right) p_j. \quad (3)$$

In eqn 3, total metacommunity biomass n plays an explicit role: the bulkier the system, the more important predation traits are over migration traits to determine the dynamical properties of the system. Thus, when total biomass is very low, individuals from all species are scarce, and predatory interactions (which occur with a rate proportional to the product of predator and prey abundances) are rare compared with the constant flow of migrants among populations of the same species. By contrast, when total system's biomass is high, predatory interactions occur more often and tend to act on the system more quickly than migration. This phenomenon is similar to the impact of constant prey immigration on the stability of the Rosenzweig–MacArthur model of predator–prey interactions (Murdoch *et al.* 2003). The contribution of constant prey immigration to system dynamics is more important at low prey density (i.e. low biomass) than at high density, thus causing an indirect density-dependence of the prey and stabilizing system dynamics.

This simplistic model highlights one simple fact emerging in spatial food webs: when interactions between populations have different degrees of dependence (here, predation rate scales with predator abundance while migration rate is constant), total biomass influences system dynamics. More precisely, interactions that have a higher degree of dependence on populations' biomass are more important when total biomass is high, whereas simpler interactions are more important when system's biomass is low. It is worth mentioning that, besides favouring migration over predation (a deterministic result), low system biomass will also tend to make all species rarer, and thus to make stochasticity more conspicuous in population dynamics (e.g. Gurney & Nisbet 1978). Because our model is overly simplistic on some aspects (e.g. no mortality terms, functions for interactions were assumed linear), the generality of our conclusions may be questioned, and we hope future models will do. However, the methodology behind our model – considering separate populations for the different agent types and sites, rescaling equations, and comparing trophic interactions with movement interactions – highlights the potential for new insights coming from considering metaecosystems.

Emergent effects of material transports on patch dynamics and persistence

Of critical importance to the metapopulation and metacommunity frameworks is the patch dynamics perspective (Hanski & Gilpin 1997; Leibold *et al.* 2004). Central to this perspective is the idea that a species persists in a region despite local extinctions, given that the colonization rate from occupied patches is larger than the extinction rate. The dynamics of spatial occupancy (the proportion of occupied patches) were first formalized by Levins (1969) as follows:

$$\frac{dp}{dt} = cp(1-p) - mp, \quad (4)$$

where c is the colonization rate and m is the extinction rate. In this context, the metapopulation persists provided that $c > m$. This model captures the essential aspects of metapopulation dynamics, and it has also been extended to communities (Tilman 1994; Calcagno *et al.* 2006) and food webs (Holt 2002). Given a trade-off between competitive ability and colonization rate, such spatial dynamics allow many

species to coexist on a uniform landscape (Tilman 1994; Calcagno *et al.* 2006). The patch dynamics perspective also provides an interesting explanation for the limitation of food chain length and the different slopes of species area relationships of prey and predators (Holt 1997a, 2002).

The patch dynamics perspective is solely based on exchanges of traits. There is no explicit accounting for the amount of material/individuals dispersing between patches. It does not matter how many seeds reach an empty patch as long as there is at least one of them. One feature of this model is that colonization rate (c) is independent of landscape properties. It does not consider for instance that the colonization rate into a small patch having a large perimeter/area ratio should differ from the one of a large patch (Hastings & Wolin 1989). It does not consider either that nutrients and energy could move between patches, having an effect on their local properties. In a disturbed forested landscape for instance, biomass such as leaves, twigs and branches fall from forested areas to canopy gaps, thereby increasing productivity of the newly disturbed locations. Animals may also move nutrients between empty and occupied patches as they forage, like large browsers transporting nutrients when they feed in recently disturbed forest areas and defecate in closed canopy forests (McNaughton *et al.* 1988; Seagle 2003).

In a disturbed landscape, the difference in productivity between empty and occupied patches influences spatial nutrient flows (Gravel *et al.* 2010a). On the one hand, nutrient consumption in occupied patches locally reduces the inorganic nutrient concentration relative to empty patches, making them sinks for the inorganic nutrient. On the other hand, biomass (either dead or alive) mostly flows from occupied to empty patches. Nutrients are thus flowing in both directions and the relative importance of inorganic vs. organic nutrient flows determines whether occupied patches act as sources or sinks (Gravel *et al.* 2010a). Even if the landscape consists of a single habitat type, nutrient dynamics create a strong spatial heterogeneity in resource distribution.

The balance between the different nutrient flows is influenced by spatial occupancy and affects biomass production. For instance, if only detritus are exchanged between patches (e.g. through leaf dispersal), then the amount received in empty patches should increase with spatial occupancy because there is higher regional production, impoverishing the occupied patches. The local biomass B should thus increase curvilinearly with spatial occupancy p when the net flow of nutrients goes from occupied to empty patches, or alternatively decreases when nutrients flow in the opposite direction. Consequently, if the reproductive output in a patch depends only on local biomass production, the effective colonization rate should depend on spatial occupancy and spatial nutrient flows. Gravel *et al.* (2010a) modified Levins' model to introduce the effect of nutrient flows on patch dynamics. Patch dynamics were described by:

$$\frac{dp}{dt} = c'p(1-p) - mp, \quad (5)$$

where the effective colonization rate c' is proportional to the average local biomass, B , which is a function of spatial occupancy, i.e. $c' = cB(p)$. This modification creates a strong feedback between local and regional dynamics. The persistence and the equilibrium spatial occupancy are enhanced when nutrients flow from empty to occupied patches because higher biomass owing to the nutrient redistribution yields higher regional level propagule production. These essential

descriptors of metapopulation properties become a complex function of spatial nutrient flows and local ecosystem properties such as nutrient uptake efficiency and recycling rate.

This slight modification of Levins' model has several, often counter-intuitive, consequences on community assembly, illustrating the importance of accounting for both trait and material flows in spatial food web models. The local–regional coupling studied by Gravel *et al.* (2010a) showed that positive and negative indirect interactions arise between primary producer populations owing to spatial nutrient flows. Plants in this landscape are first limited at the very local scale, as they need enough nutrients to maintain a viable population (R^* minimal resource requirement, see Tilman 1982 for details on resource limitation theory). When detritus have a higher diffusion rate than nutrients, the net flow of nutrients goes from occupied to empty patches, enriching them to the benefit of the good colonizers arriving first. This local enrichment could facilitate the establishment of a weak competitor with low resource uptake ability (it raises nutrient levels above the R^*). Plants are also limited by their regional dynamics, and the enrichment to empty patches increases their propagule production (because of higher biomass). Interestingly, this nutrient redistribution may also facilitate the persistence of a strong competitor/poor colonizer when the weak competitor/good colonizer occupies the landscape first. The persistence of some species may thus rely on the presence of other ones, suggesting that habitat-driven extinctions can trigger cascading extinction events in landscapes characterized by nutrient flows linking local and regional dynamics. The difference between predictions from trait-based models of patch dynamics and this nutrient-explicit model illustrates how integrating ecosystem functioning and spatial population biology leads to novel insights.

ADVANCING METAECOSYSTEM THEORY

Although the metaecosystem concept (Loreau *et al.* 2003) does fit as a potential unifying framework to merge 'food web metacommunity' and 'landscape ecosystem' ecology, there are still some inherent assumptions associated with the metacommunity/metaecosystem tradition that need to be addressed to really bridge the gap between these two traditions. The two models presented in the previous section highlight some of these assumptions. Whereas the first model considers populations of the different agents as completely separate, the ecological unit behind the second model is the 'ecosystem patch' which implicitly defines the meaning of dispersal and interaction ranges for all agents at once. The second model also raises the question of the definition of limiting factors in a metaecosystem, given that some facilitation effects between plant species may result from the balance of detritus and nutrient fluxes among patches. Finally, both models tackle space in an implicit fashion, and thus do not account for neighbouring relationships or gradients in habitat quality among localities. This is not a problem *per se*, as long as physical proximity is not the dominant factor explaining metaecosystem dynamics, but the realism and precision of applied models often depend heavily on how such neighbouring relationships are addressed, thereby linking the potential for application of the theory to its compatibility with spatially explicit formulations.

An inherent assumption associated with the metacommunity/metaecosystem tradition stems from the definition of patches in the metacommunity and metaecosystem literature. As an offshoot of community and population ecology, the metacommunity concept

(Leibold *et al.* 2004) generally emphasizes competitive interactions among individuals over reproduction or perturbations. This emphasis implies that the underlying process defining the spatial unit – the patch – is competition: individuals living in the same patch compete for limiting factors; individuals living in different patches do not. By contrast, metapopulation theory (Hanski & Gilpin 1997) equates the 'patch' with the spatial target of perturbations (i.e. a catastrophic perturbation affects only one patch at a time). The definition of the patch is important because (i) it highlights which processes are assumed to take place solely within a patch and (ii) gives a meaning to dispersal among patches. In a subdivided population context, dispersal is assumed to occur among reproductive units, so that it can be understood as an organism's movement between its place of birth and its place of reproduction (Clobert *et al.* 2009); in a metacommunity, by contrast, dispersal generally characterizes movements of individuals shifting their 'hunting grounds' to compete with different individuals for limiting factors – a glaring exception being metacommunities where perturbations are controlling system dynamics and only one species can live in each patch (e.g. Tilman 1994). In theory, the metacommunity definition of patch would pose a problem even to metacommunity theory as perturbations and reproduction should be allowed to take place at a larger or smaller scale than competition (over several patches or in subdivisions of a patch). However, when studying metaecosystems, this definition holds the potential for a much more serious issue. Indeed, metaecosystems comprise agents that interact not only indirectly through competition for limiting factors, but also directly through trophic and non-trophic interactions which have spatial scales of their own (horizontal axis in Fig. 2): e.g. predation of deers by wolves may occur on a spatial scale that does not match the spatial scale of competition for resources among deers. Moreover, each agent has its own spatial scale for reproduction which, in turn, may be in conflict with the agent's intraspecific competition scale. The multiplicity of processes and the diversity of movement scales among organisms occurring in a metaecosystem (e.g. McCann *et al.* 2005) prevent the definition of a patch as a 'trans-specific' entity (Holt & Hoopes 2005), except perhaps in conspicuously patchy landscapes such as pond systems or mountain heights.

Another concern comes from the definition of limiting factors. In community ecology, limiting factors – resources, predators, parasites, space, etc. – play a preponderant part in the theory of species coexistence (Holt 1977; Armstrong & McGehee 1980; Tilman 1982) and impact the dynamical properties of multispecies assemblages. In metacommunities, dispersal among patches may 'subsidize' populations that would otherwise have gone extinct due to local competitive exclusion, a notion embodied in the concept of 'source–sink' metacommunities (Amarasekare & Nisbet 2001; Mouquet & Loreau 2003), where mass effects substitute other limiting factors (Leibold *et al.* 2004). The case of metacommunities is still relatively simple because true limiting factors directly link the different species – two competing species in the same patch share the same resource pool or the same predator creating apparent competition – and mass effects occur at the same scale for all species involved. In metaecosystems, limiting factors may be highly indirect, e.g. recycling efficiency may impact the sustainability of plant metapopulations (Gravel *et al.* 2010a). Moreover, spatial subsidies due to dispersal among populations of different agents are bound to be a substitute to limiting factors for agents at other levels in the food web, e.g. when the dispersal of an herbivore could enhance local plant primary productivity through source–sink effects (Jefferies *et al.* 2004; Gravel

et al. 2010b). Overall, these considerations suggest that a renewal of the concept of limiting factors should be timely.

Finally, we believe that the next important development for metaecosystem theory is to address space in an explicit fashion. In metacommunity and metaecosystem theory, work to date has been either spatially implicit or has focused on highly simplified cases (e.g. involving only two patches). In 'landscape ecosystem' ecology, by contrast, spatially explicit modelling has been emphasized because it accounts (i) for neighbouring relationships among agent populations and (ii) for the spatial scale of the system studied. While point (i) calls for some adjustments of assumptions on the way interactions and dispersal work in metaecosystems (passing from a very discrete to a more 'continuous' version of metaecosystems), point (ii) suggest a thorough rethinking of the patterns to be studied. Indeed, metaecosystem theory can be key in revealing the rich array of interrelations among community patterns (diversity, stability, etc.) and ecosystem attributes such as ecosystem productivity (e.g. Venail *et al.* 2010), and nutrient cycles, at different spatial scales following the path set by biogeography and community ecology on the link between system size and diversity (MacArthur & Wilson 1967; Shmida & Wilson 1985).

PERSPECTIVES

Our review of topics related to spatial dynamics in food webs indicates that there is a need for a greater integration of 'food web metacommunity' and 'landscape ecosystem' approaches. We have argued that this can be achieved within the context of metaecosystems, but we have highlighted a number of challenges that need to be resolved for this to be successful. In particular, we have argued that a more refined approach to some of the key concepts of ecology including patches, limiting factors and spatial explicitness will be necessary. However, the new approach, once developed, should provide numerous new avenues for research:

Metaecosystem principles

We found no fully satisfying study combining the constraints that come from ecological thermodynamics and mass balance in a landscape with the study of population interactions among species in a metacommunity (Pickett & Cadenasso 1995; Amarasekare 2008). There are two important challenges: (i) the principle of mass balance must be put forward in metaecosystems, in general and in particular following the ecological stoichiometry of abiotic and biotic agents; and (ii) bridging the gap between material and trait effects must be accomplished through theories linking biomass to demographic rates.

In a single ecosystem, the mass-balance constraint implies that the amount of imported nutrients (e.g. through rock weathering, nitrogen fixation and atmospheric decomposition) must balance nutrient exports (e.g. through nutrient leaching, denitrification and volatilization during fires), at least when systems are considered at steady state. In the theory of metaecosystems, nutrient flows create a global mass-balance constraint, with some local ecosystems being net exporters and others being net importers at a given time (Loreau *et al.* 2003). In this framework, nutrient cycles can be complex, as a single molecule goes up and down the food web and among various locations before coming back to its starting location. These cycles become even more complex when different nutrients contribute differently and interactively to population growth, i.e. if ecological

stoichiometry of organismic fitness enters the picture. Ecological stoichiometry deals with how element ratios affect and are affected by organisms (Loladze *et al.* 2000; Sterner & Elser 2002). Spatial ecological stoichiometry (Miller *et al.* 2004) can extend the principles of ecological stoichiometry to spatially structured environments (e.g. water columns, Lenton & Klausmeier 2007), for instance by considering 'biogeochemical hotspots' (McClain *et al.* 2003) where certain molecules are lost or produced. Moreover, because species have different elemental compositions and different movement rates, elements can have different 'dispersal rates' among locations, which in turn may create a spatial heterogeneity in element ratios. By doing so, spatial ecological stoichiometry is likely to affect the diversity and coexistence of organisms (Daufresne & Hedin 2005), how this affects ecosystem stability and functioning (Loladze *et al.* 2000; Miller *et al.* 2004), and possibly food web organization (Woodward *et al.* 2010).

While a global mass-balance constrains how energy and material move among ecosystems, the movements of living organisms also obey the principle of natural selection, so that organism rates and directions of movements are subject to evolutionary forces. Generally, selection tends to favour (i) movements from low- to high-fitness areas to comply with the ideal free distribution *sensu lato* (see e.g. Holt 1997b) and (ii) more frequent movements when local perturbations occur more often (Comins *et al.* 1980). Selection does not act on biomass but on individuals. Thus, to integrate all principles governing the movements of biotic agents, a mechanistic link between ecosystem and demographic variables must be made. For instance, the metabolic theory (Brown *et al.* 2004) links temperature to individual, population and ecosystem rates. Furthermore, linking body size, biological rates and standing biomass (e.g. Cohen *et al.* 2003) may help understand how selective pressures may be translated into ecosystem forces acting on the flow of materials. Metaecosystems may be understood as complex adaptive systems in which natural selection affects ecosystem functioning and connectivity (Levin 1998, 2003; Leibold & Norberg 2004).

Emergent patterns

It is of interest to consider which metacommunity patterns can be extended to metaecosystems. As a first instance of typical metacommunity pattern, diversity among and within communities can be partitioned in α , β and γ diversity components (Whittaker 1972). This partition can be envisioned as an analysis of variance (Lande 1996). A similar partitioning of other descriptors of ecosystems could be implemented for non-negative quantities, such as food web complexity or ecosystem productivity. For example, ' α complexity' would measure complexity within a local ecosystem (e.g. trophic connectance) while ' β complexity' would describe the differences in such attributes at different places. This suggests that it might be possible to analyse variation in any ecosystem property in relation to different aspects of environmental heterogeneity and spatial processes (e.g. biogeography or allopatric speciation, Leibold *et al.* 2010). It also suggests that assessing the major processes determining a given ecosystem property can be looked for in the signal emerging from spatial scaling patterns (e.g. similarly to diversity patterns in communities, Chave *et al.* 2002).

The well-known concept of sources and sinks, formulated by Pulliam (1988), can also be refined in the context of metaecosystems. Indeed, the spatial flows of nutrients, organisms and detritus affect source-sink dynamics of organisms under different trophic organizations (Gravel *et al.* 2010b). This seems to be a fairly general

mechanism (Loreau *et al.* 2003): connections between asymmetric ecosystems, i.e. ecosystems with different productivities and fertilities, generate spatial flows of nutrients that can affect and be affected by community structure. This spatial asymmetry in source–sink dynamics could result from environmental heterogeneity, cross-ecosystem coupling or heterogeneous community structure owing to historical contingencies or disturbances. Whatever the causes of such an asymmetry, the end result is often that a given location can be a source and a sink at the same time, but for different agents. Furthermore, spatial flows of nutrients can transform a sink location into a source for a particular organism via the external supply of resources, even if this organism does not receive immigrants at this location. A viable population could thus establish in an otherwise nutrient-poor environment even in the absence of strong immigration. Another important aspect of the source–sink concept is the control of spatial flows and of their ecological effects on community composition in both source and sink localities. For instance, the introduction of an herbivore in the source patch can result in a spatial trophic cascade where the indirect effects occur in other locations via subsidies of sink populations. Once the source–sink concept is refined from the metaecosystem perspective (vs. a population biology context, see e.g. Holt & Gomulkiewicz 1997), the definition of a sink location no longer depends on the local environmental conditions, but also on the composition, structure and environmental conditions of the neighbouring ones.

In local ecosystem models, the feedback loop from the top species to the basal species of an ecosystem can result in counter-intuitive situations where a consumer (e.g. herbivore) maximizes the productivity of its prey (e.g. the grazing optimization concept, De Mazancourt *et al.* 1998): this situation emerges because factors promoting nutrient cycling efficiency benefit the overall productivity of the system (Loreau 1998). In a metaecosystem, regional mass-balance constraints put this feedback at the regional scale. A metaecosystem with unoccupied locations is inefficient in nutrient recycling because at least some nutrients are moved to empty patches where these nutrients are not consumed and are likely exported (e.g. through leaching). Consequently, increasing spatial occupancy enhances ecosystem functioning at both local and regional scales (Gravel *et al.* 2010a). Given environmental heterogeneity and species sorting along environmental gradients (Leibold *et al.* 2004), this would relate regional diversity and ecosystem functioning through regional complementarity (Venail *et al.* 2010) but such effects would in turn depend on the ways that dispersal mediates species sorting.

A final class of patterns that metaecosystem theory can inform is the complexity–diversity relationship (Cohen & Briand 1984; Williams & Martinez 2000). Spatial segregation of energy channels within the regional food web is likely to affect the stability of the overall system (Rooney *et al.* 2006, 2008) and, consequently, to help the persistence of more complex food webs through weak interactions (McCann *et al.* 1998). Metaecosystem theory will also be able to study how distance between species home ranges affects the strength of their interactions and the complexity of effective food webs at different spatial scales (Pillai *et al.* 2009). Because metaecosystem theory does not focus on trophic dynamics, but also accounts for recycling, matter decomposition and abiotic compartments, it will integrate the effects of recycling efficiency on food web complexity (Moore *et al.* 1993, 2004). Finally, the productive space hypothesis for food chain length (Post 2002) has an intuitive connection with the concept of metaecosystem, suggesting that the study of the determinants of ‘food chain length’ (or

the longest chain from a primary producer to a top predator) will find an appropriate framework with metaecosystems.

Revisiting conservation at the ecosystem level

Biological communities are open to the movement of individuals and materials, and managing such communities requires consideration of these fluxes (Power *et al.* 2004). Many applied fields of ecology, such as conservation biology, restoration ecology, extinction risk assessment and eco-toxicology, already consider spatial processes to some extent, but understanding interactive complex spatial dynamics involving fluxes of nutrients, movements of organisms, and production, feeding and recycling interactions, can lead to a better understanding of the consequences of changes in management strategies or environmental conditions. New ideas for ecosystem management and restoration, as well as methods for whole-ecosystem conservation, will emerge from considering inter-ecosystem connectivity. In particular, the assessment of endangered species’ potential frailty may depend more on metaecosystem characteristics than on population demographic indicators.

The idea of ‘ecosystem-based management’ (Slocumbe 1998) should be revisited in the context of metaecosystems. The general idea behind ecosystem-based, as opposed to species-based, management policies is that the complex network of interactions among organisms can buffer the efficiency of a measure targeted at a particular species. Ecosystem-based management advocates policies that prevent anthropogenic impacts on a whole ecosystem. By accounting for the variability in the movement ranges of species in an ecosystem, metaecosystem theory has the potential to improve the development of management practices that consider both sessile and far-ranging organisms. Metaecosystems may be the right framework for ecosystem-based policies that represent all ecosystem compartments at the regional level (Mac Nally *et al.* 2002).

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GLOSSARY

Agent: An ecological entity that interacts with other agents and can move or be moved among localities. Living organisms, detritus and abiotic nutrients are all ecosystem agents.

Material/energy: The extensive, quantitative properties of an agent. Material relates to the matter content of the agent (usually, in carbon/nitrogen/phosphorus currencies), while energy relates to the maximum chemical energy that can be gained through ingesting or degrading the agent.

Metacommunity: A set of communities connected by dispersal among them. Individuals of all species only interact within each community.

Metaecosystem: A set of ecosystems connected by fluxes of agents (organisms, dead organic matter and mineral nutrients).

Trait: An intensive attribute of an agent, which generally controls some ecosystem fluxes (e.g. dispersal rate, attack rate on a prey species and carbon uptake rate).

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