

Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology

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Abstract

This contribution proposes the meta-ecosystem concept as a natural extension of the metapopulation and metacommunity concepts. A meta-ecosystem is defined as a set of ecosystems connected by spatial flows of energy, materials and organisms across ecosystem boundaries. This concept provides a powerful theoretical tool to understand the emergent properties that arise from spatial coupling of local ecosystems, such as global source–sink constraints, diversity–productivity patterns, stabilization of ecosystem processes and indirect interactions at landscape or regional scales. The meta-ecosystem perspective thereby has the potential to integrate the perspectives of community and landscape ecology, to provide novel fundamental insights into the dynamics and functioning of ecosystems from local to global scales, and to increase our ability to predict the consequences of land-use changes on biodiversity and the provision of ecosystem services to human societies.

Keywords

Dispersal, diversity, ecosystem, landscape, metacommunity, model, productivity, source–sink dynamics, spatial processes.

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INTRODUCTION

A defining feature of ecology over the last few decades has been a growing appreciation of the importance of considering processes operating over multiple spatial and temporal scales. All local systems reflect the imprint of large-scale processes. Ecology has increasingly considered spatial scales larger than that of a single locality, from the scale of the landscape to that of the region (Ricklefs & Schluter 1993; Turner *et al.* 2001). Spatial ecology, however, has developed from two distinct perspectives and traditions with limited overlap.

One perspective comes from population and community ecology, with emphasis on population persistence and species coexistence in spatially distributed systems (Hanski & Gilpin 1997; Tilman & Kareiva 1997). This tradition has a strong background in theoretical ecology and 'strategic' mathematical models. In particular, metapopulation approaches have been increasingly popular (Hanski & Gilpin 1997). Their success comes from the growing concern with the

conservation of fragmented populations in human-dominated landscapes, which they address explicitly, and from their ability to deliver specific testable hypotheses. The metapopulation concept has its roots in island biogeography, but unlike the latter theory, it was until recently largely focused on the dynamics of single species in patchy environments. Metapopulation theory has provided new insights into how the spatial coupling of local populations through dispersal permits the regional persistence of species that experience local extinctions and colonizations.

Another perspective is offered by landscape ecology, which is largely an outgrowth of ecosystem ecology. Landscape ecology is concerned with ecological patterns and processes in explicitly structured mosaics of adjacent, heterogeneous ecosystems (Turner 1989; Forman 1995; Pickett & Cadenasso 1995; Turner *et al.* 2001). It has a strong descriptive basis and focuses on whole-system properties. Its main strengths lie in its realism and its ability to integrate biotic and abiotic processes. Models that

address population persistence and conservation from this perspective are usually of a 'tactical' nature; they consider landscape structure and heterogeneity explicitly, and therefore, aim to be more realistic and directly applicable to concrete problems than the more general, abstract models of classical metapopulation and community ecology (Gustafson & Gardner 1996; With 1997; With *et al.* 1997). A synthesis of landscape ecology and metapopulation ecology is still lacking (Hanski & Gilpin 1997; Turner *et al.* 2001).

A recent development in community ecology is a growing concern with the concept of a metacommunity – a set of local communities connected by dispersal at the landscape or regional scale (Wilson 1992; Holt 1993; Hubbell 2001; Mouquet & Loreau 2002). As local extinctions and colonizations can be influenced by interspecific interactions such as predation and competition, this concept is a natural multispecies extension of the metapopulation concept. In the metacommunity perspective, the focus is on the structural and dynamical properties that emerge at a broad spatial scale as a result of the reciprocal connections among component local communities. Significant novel insights are being gained from this new perspective, particularly on the interrelated dynamics of local and regional biodiversity (Wilson 1992; Holt 1993; Tilman 1994; Leibold 1998; Loreau & Mouquet 1999; Loreau 2000; Codeco & Grover 2001; Hubbell 2001; Shurin & Allen 2001; Forbes & Chase 2002; Mouquet & Loreau 2002, 2003) and the factors governing food-web attributes, such as food-chain length (Holt 1997).

The metacommunity concept, however, has an exclusive focus on the biotic components of ecosystems. There is a growing recognition in community ecology that important properties of ecological communities can only be understood by explicitly embedding communities into ecosystems, including abiotic constraints and feedbacks (DeAngelis 1992; Jones & Lawton 1995; Kinzig *et al.* 2002; Loreau *et al.* 2002; Sterner & Elser 2002). In this study, we propose a natural extension of the metacommunity concept, which includes these abiotic constraints and feedbacks – the meta-ecosystem concept. By focusing on spatial processes at the level of entire ecosystems, the meta-ecosystem concept provides a theoretical framework for a spatial ecosystem ecology that integrates the perspectives of community and landscape ecology.

DEFINITION AND SCOPE OF THE META-ECOSYSTEM CONCEPT

We define a 'meta-ecosystem' as a set of ecosystems connected by spatial flows of energy, materials and organisms across ecosystem boundaries. In contrast to the metacommunity concept, which only considers connections among systems via the dispersal of organisms, the meta-

ecosystem more broadly embraces all kinds of spatial flows among systems. Movements of inorganic nutrients, detritus and living organisms are ubiquitous in natural systems, and are considered explicitly in landscape ecology. In particular, there has been considerable attention to local impacts of spatial subsidies on the structure, dynamics and functioning of communities and ecosystems (Polis *et al.* 1997). Such studies, however, are limited, in that a subsidy entering one local ecosystem must necessarily be drawn from another. Subsidies at one end are losses at another end, and as such should have an impact on both the source and target ecosystems. Moreover, flows are rarely completely asymmetrical. The properties of the higher-level system that arise from movements among coupled ecosystems have seldom been considered explicitly (although there are many concrete examples contained within ecosystem ecology). We suggest that a full appreciation of the importance of spatial flows in ecology and a conceptual synthesis of landscape ecology and metacommunity theory require a meta-ecosystem perspective.

Although there are obvious similarities between our definition of a meta-ecosystem and that of a landscape, the two concepts are not equivalent. First, a landscape is in principle a continuous, if heterogeneous, physical entity whereas a meta-ecosystem need not be so. Metapopulations are, by definition, discontinuous entities as their component populations occupy distinct patches, isolated from each other in a matrix of inhospitable environment. Metacommunities and meta-ecosystems may or may not be continuous, depending on the kind of organisms, ecosystems and processes considered. The local ecosystems that constitute a meta-ecosystem may sometimes behave like 'islands' surrounded by a 'sea' of vastly different ecosystems with which they have little or no interactions for the processes being considered. We recognize, however, that a fully integrated view of meta-ecosystem functioning will often require consideration of the interactions between such islands and the sea, and thus that the difference between the meta-ecosystem and landscape concepts in this respect may often be small.

Second, a landscape is a physical entity that has a characteristic spatial scale intermediate between the local and the regional scales, whereas meta-ecosystems can be defined at different scales, again depending on the kind of organisms, ecosystems and processes considered. When the ecosystems constituting the meta-ecosystem are contiguous and the spatial flows among them occur on small scales, the most direct analogue of the meta-ecosystem concept in landscape ecology is the 'ecosystem cluster', which is defined as 'a spatial level of hierarchical organization between the local ecosystem and the landscape' which 'describes a group of spatial elements connected by a significant exchange of energy or matter' (Forman 1995,

p. 287). For some processes, however, such as spatial flows driven by highly mobile animals or global biogeochemical cycles involving large-scale air or sea currents, the meta-ecosystem concept could legitimately be applied at the regional or global scale, well beyond the conceptual arena of landscape ecology, as it is usually defined.

Last but not least, being a specific spatial level of hierarchical organization, a landscape can be studied from a number of different perspectives, including purely descriptive pattern-centred approaches that ignore spatial flows among component ecosystems. By contrast, the meta-ecosystem concept defines a specific approach to reality. It focuses on the properties of the higher-level, spatially extended dynamic system that emerges from movements at landscape to global scales. Thus, the meta-ecosystem concept is not simply an abstract plea for considering multiple scales in ecology. Just as metacommunity theory is giving new concrete insights into the diversity and structure of ecological communities by explicitly considering the interactions between local- and regional-scale processes, the meta-ecosystem concept provides a new tool to understand the emergent constraints and properties that arise from spatial coupling of local ecosystems. Emergent properties have been widely discussed within the framework of hierarchy theory in ecosystem ecology (Allen & Starr 1982; O'Neill *et al.* 1986). These properties, however, have rarely been studied in a rigorous, quantitative way based on a firm foundation of lower-level interactions. We provide below a simple theoretical meta-ecosystem model, which demonstrates how significant global source–sink constraints arise from spatial coupling of ecosystems through nutrient flows.

SPATIAL FLOWS, SOURCE–SINK CONSTRAINTS AND SUCCESSION: A SIMPLE META-ECOSYSTEM MODEL

Flows of nutrients, whether in the form of inorganic elements, detritus or living organisms, can exert important influences on the functioning of local ecosystems (Polis *et al.* 1997). Less appreciated is the fact that these flows may also impose global constraints at the scale of the meta-ecosystem as a whole, thereby generating a strong interdependence among local ecosystems.

Consider for simplicity a closed nutrient-limited meta-ecosystem consisting of a set of connected local ecosystems, each of which in turn consists of the same set of interacting compartments. These compartments may be defined at various levels of resolution, from that of entire trophic levels up to that of functional groups or species. We further assume for simplicity that spatial flows among ecosystems occur among similar compartments (i.e. from inorganic nutrient to inorganic nutrient, or from plants to plants, etc.), and that they do not modify the nature of local interactions

among ecosystem compartments (such that spatial flows and local growth rate are additive in the dynamical equation for each ecosystem compartment). Let X_{ij} denote the size (in absolute units, e.g. grams) of the nutrient stock of compartment i in ecosystem j , and G_{ij} its local growth rate in the absence of spatial flows among ecosystems. Further, let F_{ijk} be the directed spatial flow of nutrient stored in compartment i from ecosystem j to ecosystem k . Mass balance leads to the following equation describing the dynamics of compartment i in ecosystem j :

$$\frac{dX_{ij}}{dt} = \sum_k F_{ikj} - \sum_k F_{ijk} + G_{ij} \quad (1)$$

with $F_{iji} = 0$ for all i and j .

Local mass conservation in the absence of spatial flows further requires:

$$\sum_i G_{ij} = 0 \quad (2)$$

i.e. if each ecosystem j were to function as a closed system, the limiting nutrient would be recycled entirely within the system, so that what is gained by one compartment would have to be lost by another compartment. It is easy to verify that *global mass conservation* is also automatically satisfied in the meta-ecosystem described in eqns 1 and 2, as it should in any closed system.

Additional constraints emerge from spatial coupling of local ecosystems as the meta-ecosystem reaches equilibrium. At equilibrium the left-hand side of eqn 1 vanishes. Summing these equations over the set of ecosystems j leads to the constraint:

$$\sum_{j,k} F_{ikj}^* - \sum_{j,k} F_{ijk}^* + \sum_j G_{ij}^* = 0 \quad (3)$$

where * denotes functions evaluated at equilibrium. In this equation, the spatial flow terms cancel each other (for each compartment, the summed flows out of all ecosystems are identical to the summed flows into all ecosystems), and hence:

$$\sum_j G_{ij}^* = 0 \quad (4)$$

Equation 4 can be interpreted as a *source–sink constraint within ecosystem compartments*: for each compartment i , positive growth in some ecosystems must be balanced by negative growth in other ecosystems at equilibrium, which means that some local ecosystems must be sources whereas others must be sinks (Pulliam 1988) for that compartment.

Similarly, summing eqn 1 over the set of compartments i at equilibrium leads to the constraint:

$$\sum_{i,k} F_{ikj}^* - \sum_{i,k} F_{ijk}^* + \sum_i G_{ij}^* = 0 \quad (5)$$

which, because of eqn 2, becomes:

$$\sum_{i,k} (F_{ikj}^* - F_{ijk}^*) = 0 \quad (6)$$

As $(F_{ikj}^* - F_{ijk}^*)$ is the net spatial flow of nutrient at equilibrium from ecosystem k to ecosystem j for compartment i , this equation says that the total net spatial flow across the boundaries of ecosystem j must vanish at equilibrium, which means that some compartments must be sources whereas others must be sinks in each ecosystem. Thus, this equation can be interpreted as a *source–sink constraint between ecosystem compartments*.

The combination of the two types of source–sink constraints (within and between ecosystem compartments) imposes a specific pattern of circulation of nutrient in the meta-ecosystem as a whole. For instance, if there are two ecosystem compartments (say, plants P and inorganic nutrient N) and two local ecosystems 1 and 2, it is easy to verify that these constraints result in a global material cycle such that net flows at equilibrium are either in the direction $N_1 \rightarrow P_1 \rightarrow P_2 \rightarrow N_2 \rightarrow N_1$ or in the opposite direction. In this global cycle, although production and nutrient recycling occur within each ecosystem, one ecosystem acts as a net global producer ($N_1 \rightarrow P_1$), whereas the other acts as a net global recycler ($P_2 \rightarrow N_2$). When there are more than two ecosystem compartments and local ecosystems, the pattern of material circulation in the meta-ecosystem may be more complex, but all local ecosystems are embedded in a web of material flows constrained by the functioning of the meta-ecosystem as a whole.

This simple meta-ecosystem model shows that strong constraints are expected to act on local ecosystem functioning because of spatial coupling of ecosystems. When these constraints can be met, they imply that local ecosystems can no longer be governed by local interactions alone. Instead, by being part of the larger-scale meta-ecosystem, local ecosystems are constrained to become permanent sources and sinks for different compartments, and thereby to fulfill different ‘functions’ in the meta-ecosystem. It is also conceivable, however, that these constraints may be impossible to meet in some cases; during transient dynamics parts of the meta-ecosystem will then ‘absorb’ others by progressively depriving them of the limiting nutrient. This means concretely that nutrient source–sink dynamics within meta-ecosystems may drive or accelerate successional changes, until equilibrium is achieved and the final meta-ecosystem state becomes compatible with global source–sink constraints.

This process of ecosystem ‘absorption’ during succession is reminiscent of the hypothesis of Margalef (1963) that mature ecosystems such as forests ‘exploit’ ecosystems from earlier successional stages such as grasslands because animal consumers from late-successional ecosystems move to

nearby early successional ecosystems for foraging. Whether energy and material transfers across ecosystem boundaries are strong enough to drive succession, however, depends on their magnitude relative to that of the colonization processes, which bring new species into local ecosystems and thereby change their properties. This suggests that combining an explicit accounting of spatial flows of energy and materials with the dynamics of colonization of new patches by organisms in an integrated meta-ecosystem approach may provide a promising novel perspective on succession theory.

POTENTIAL APPLICATIONS OF THE META-ECOSYSTEM CONCEPT

Potential applications of the meta-ecosystem concept abound. Here we give just a few examples of the kinds of systems and issues to which it could be fruitfully applied. Large quantities of biomass and nutrients are transported across ecosystem boundaries on land by grazing mammals (McNaughton 1985) and roosting birds (Weir 1969). The meta-ecosystem perspective allows explicit consideration of the impacts of these movements on nutrient cycling, primary productivity and species diversity at both the local and landscape or regional scales. Significant exchanges of materials and organisms also occur at the interface between terrestrial and aquatic ecosystems. Secondary productivity in rivers and lakes is often supported by litter inputs from nearby forests, while adult insects emerging from these lakes and streams feed predatory insects, arachnids, amphibians, reptiles and birds from neighbouring forests and grasslands (Hasler 1975; Nakano & Murakami 2001; Sabo & Power 2002). In many such landscapes, there is potential for significant reciprocal flows. Although these landscapes may not be closed to material exchanges with other systems at a broader spatial scale and therefore, may not meet the particular assumptions of the simple model we presented, formalizing coupled land and water systems as a meta-ecosystem using the kind of modelling approach outlined above offers the potential to assess quantitatively the mutual, reciprocal constraints that the two systems exert on the functioning of each other.

As another example, the pelagic, benthic and riparian or coastal subsystems in lakes and oceans are often studied as distinct ecosystems because they differ substantially in physical habitat, productivity and trophic structure. Yet they are coupled by spatial processes such as sedimentation of detritus, nutrient upwelling and movements of phytoplankton, zooplankton and fish (Boero *et al.* 1996; Schindler & Scheuerell 2002). These spatial flows may be powerful enough to change the nature of the control (bottom-up vs. top-down) of local food webs (Menge *et al.* 1997). Whether one is willing to regard a lake or an ocean as a single

ecosystem or as a set of coupled subsystems is largely a matter of perspective determined by the ecological processes, spatial scales and timescales in which one is interested in. The meta-ecosystem concept allows reconciliation of the two perspectives by focusing on the properties that result from the coupling of various subsystems.

Emergent properties such as the global source–sink constraints discussed above are likely to be found in meta-ecosystems for various types of spatial flows and processes. Recent theoretical work on metacommunities has shown that dispersal by organisms affects patterns of local and regional species diversity, species relative abundances and diversity–productivity relationships in important and non-intuitive ways (Loreau 2000; Bond & Chase 2002; Mouquet *et al.* 2002; Mouquet & Loreau 2002, 2003). Consider a system in which species differ in their niches, such that different species would be expected to dominate different habitat patches, in the absence of dispersal. When dispersal is present, but low, increased dispersal boosts local species diversity through a ‘mass’ or ‘source–sink’ effect while keeping regional species diversity roughly constant, as has been known since Levin (1974). When dispersal is high, however, further increases in dispersal depress both local and regional diversity because of homogenization of the metacommunity, which progressively behaves as a single large community, in which the species that on average is superior across the landscape excludes other species. These non-monotonic dispersal-driven changes in diversity are accompanied by simultaneous changes in local productivity and species relative abundances, leading to a variety of diversity–productivity and species-abundance patterns (Mouquet & Loreau 2003). Total productivity at the meta-ecosystem scale can both rise and fall with increasing dispersal rates. Thus, the spatial coupling of communities generates considerable constraints on their structure, with implications for ecosystem functioning.

Spatial exchanges can further affect the temporal variability of ecosystem processes at both local and landscape scales. Dispersal is known to alter the dynamics of prey–predator systems (Holyoak & Lawler 1996), with increase in dispersal either stabilizing or destabilizing the local interaction, depending on initial conditions (Holt 2002). It can also strongly influence the temporal mean and variability of ecosystem productivity through changes in local species diversity. Increased species diversity driven by changes in dispersal rate allows for functional compensations among species and thereby provides ‘spatial insurance’ for ecosystem functioning against fluctuations in environmental conditions in heterogeneous landscapes (M. Loreau, N. Mouquet & A. Gonzalez, unpublished data). Changes in dispersal rate, however, can either increase or decrease local species diversity depending on initial conditions. Therefore, changes in landscape connectivity following fragmentation or other perturbations may either increase or decrease the average

magnitude and temporal variability of ecosystem processes, depending on the initial level of landscape connectivity and the dispersal abilities of the organisms considered.

Differences among trophic levels in movements across ecosystem boundaries may lead to fascinating although poorly explored indirect interactions among neighbouring ecosystems. Margalef’s (1963) hypothesis discussed above on indirect exploitation of early successional ecosystems by more mature ecosystems through foraging by animal consumers is an example of such interactions. Indirect exploitation of an ecosystem by another may also occur at the land–water interface where aquatic insects feed terrestrial predators, thereby releasing predation pressure on terrestrial prey (Sabo & Power 2002). In this case, however, these may only be short-term effects, because in the long-term organic matter is returned to the river in the form of detritus and invertebrate biomass, and prey subsidies from the water are likely to increase predator populations on land, thereby generating apparent competition between aquatic and terrestrial prey (Holt 1984; Nakano & Murikami 2001). More generally, consumers that forage across ecosystem boundaries can generate apparent competition among resources from different ecosystems, because increased resource abundance in one system can increase consumer abundance, and hence indirectly decrease resource abundance in other systems. More complex interactions, however, are possible if some of the coupled ecosystems receive additional external subsidies (Callaway & Hastings 2002). Conversely, spatial flows of resources may generate indirect exploitation competition among consumers from different ecosystems because increased consumer abundance in one system is expected to decrease resource abundance, and hence reduce consumer abundance in other systems. Cross-habitat movements of consumers may also disrupt the local regulation of ecosystems by inducing or strengthening trophic cascades (Polis *et al.* 1997). They may even generate paradoxical ecosystem configurations in which the bottom is maintained by the top, i.e. in which primary producers are supported by nutrients recycled from immigrating consumers (M. Loreau & R. D. Holt, unpublished data). These hypothetical although plausible examples give only a flavour of the complex interactions that are likely to occur in meta-ecosystems.

CONCLUSION

We feel that the meta-ecosystem concept is an important and timely extension to existing approaches in spatial ecology, which has the potential to integrate the perspectives of community, ecosystem and landscape ecology. At a time when humans profoundly alter the structure and functioning of natural landscapes, understanding and predicting the consequences of these changes is critical for designing appropriate conservation and management

strategies. The meta-ecosystem perspective provides a powerful tool to meet this goal. By explicitly considering the spatial interconnections among systems, it has the potential to provide novel fundamental insights into the dynamics and functioning of ecosystems from local to global scales, and to increase our ability to predict the consequences of land-use changes on biodiversity and the provision of ecosystem services to human societies.

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