

Opinion

Meta-Ecosystems 2.0: Rooting the Theory into the Field

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The meta-ecosystem framework demonstrates the significance of among-ecosystem spatial flows for ecosystem dynamics and has fostered a rich body of theory. The high level of abstraction of the models, however, impedes applications to empirical systems. We argue that further understanding of spatial dynamics in natural systems strongly depends on dense exchanges between field and theory. From empiricists, more and specific quantifications of spatial flows are needed, defined by the major categories of organismal movement (dispersal, foraging, life-cycle, and migration). In parallel, the theoretical framework must account for the distinct spatial scales at which these naturally common spatial flows occur. Integrating all levels of spatial connections among landscape elements will upgrade and unify landscape and meta-ecosystem ecology into a single framework for spatial ecology.

Ecosystem Couplings Outside the Metacommunity Box

Spatial flows of energy, materials, and organisms are ubiquitous in nature: organisms move to forage for food, migrate, or disperse, actively or as propagules [1–3]. All these **organismal movements** (see [Glossary](#)), along with passive flows of inorganic nutrients and detritus, connect ecosystems and influence local ecosystem dynamics [4,5]. Community ecologists have paid particular attention to spatial flows of species (**dispersal**), which connect several communities in a **metacommunity** [6,7]. The metacommunity framework demonstrated how dispersal and environmental heterogeneity determine species coexistence and biodiversity among a set of patches, at local and regional scales [4,8–12]. In parallel, the growing recognition that resources are not stationary, and spatial flows of resources can also play a significant role in the dynamics of various types of biological communities [5], fostered the development of the **meta-ecosystem** framework [13,14]. By explicitly integrating local production and spatial movement of resources within metacommunities, this framework demonstrated the feedback between community and resource dynamics across spatial scales [15]. Organisms moving among ecosystems modify the spatial distribution of resources, and thus **habitat** suitability, through local resource consumption and biomass recycling [16]. In parallel, **resource flows** connect the dynamics of distinct communities via the local production and export of these resources [17], and can trigger trophic cascades in recipient ecosystems [18]. This mechanistic link between community and ecosystem functioning and spatial dynamics makes the meta-ecosystem framework a powerful tool to investigate the dynamics of connected ecosystems. This is especially relevant in the context of increasing perturbations, where disruptions in local processes can spread in space through changes in spatial flows [17,19–22]. However, while the theoretical development of the meta-ecosystem framework has been fast [13,16,23–29], adoption by empiricists has generally lagged behind [11], and mostly consisted of conceptual experiments paralleling the modelling work [17,21,30], or a few applications to coastal systems [31,32].

Trends

Cross-ecosystem movements drive landscape dynamics.

Among-ecosystem couplings are either dispersal- or resource-dominated.

Dispersal-based couplings occur at the regional scale between similar habitat types.

Resource-based couplings occur at the local scale between different habitat types.

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Here, we argue that empirical research on meta-ecosystems is progressing slowly due to the high level of abstraction of the theory. As a conceptual extension of metacommunity theory, meta-ecosystem models usually tend to focus on dispersal to be the driver of organismal flows in space, thereby implicitly considering the couplings between ecosystem patches of similar habitats [16,23,24,26]. Dispersal, however, is but a small subset of all organismal movement types that can couple ecosystems (Box 1). The missing piece – other types of organismal movement – prevents current meta-ecosystem theory from providing predictions specific enough to apply to real ecosystems. Meanwhile, empirical ecology faces challenges in understanding how spatial flows induce mutual feedbacks among different ecosystems, partly due to technical challenges of measuring spatial flows [33]. Empirical ecology is also traditionally divided into independent research domains, which consider spatial flows only as external inputs to ecosystems of interest (e.g., terrestrial vs. aquatic ecology [34]), and have different variables of interest and measurement units to describe the same processes (e.g., individuals or species dynamics in community ecology vs. biomass or nutrient cycles in ecosystem ecology). Given that ecosystems are commonly interconnected in complex networks of spatial flows [5,14], a more holistic spatial perspective, considering potential feedbacks among ecosystems, is critically needed to understand the dynamics of ecosystems and their responses to changes [2,22,35–37].

Incorporating more specific attributes of ecosystem spatial couplings in the meta-ecosystem framework would foster the production of applicable theoretical predictions and bridge previously less-connected empirical fields. Here, we offer a new, synthetic vision of meta-ecosystems. We contend that (i) meta-ecosystems found in nature fall along a gradient of coupling types: some depend mostly on dispersal, and others mostly on spatial flows of resources; (ii) these ecosystem coupling types occur at different spatial scales; with (iii) different underlying drivers, including different types of organismal movement, which might affect meta-ecosystem dynamics in fundamentally different ways than dispersal alone (Box 1). We believe that integrating these organismal movements into meta-ecosystem models will raise the generality–realism trade-off to the appropriate level needed to further understand the mechanisms underlying spatial dynamics across natural landscapes (Box 2). Joining the ongoing effort to build an integrative and predictive ecology [38,39], we propose a comprehensive framework for spatial ecology acknowledging how

Glossary

Dispersal: ‘the tendency of organisms to live, compete and reproduce away from their birth place’ [41].

Habitat: in this paper used as synonymous of biotope, that is, a set of uniform environmental conditions.

Life-cycle movement: cross-ecosystem movement occurring in an organism life to complete its ontogenic development.

Metacommunity: ‘a set of local communities that are linked by dispersal of multiple potentially interacting species’ [4,7].

Meta-ecosystem: ‘a set of ecosystems connected by spatial flows of energy, materials and organisms across ecosystem boundaries’ [13].

Organismal movement: any behaviour that leads to the displacement of an organism from one place to another; here the organismal movement types considered are dispersal, life-cycle movement, foraging, and seasonal migration (Box 1).

Resource flow: spatial flow of inorganic nutrients, detritus, or organisms dying, which constitute an increase of resource for the recipient community. Resource flow can be driven by passive physical processes or organismal movement (Box 1).

Box 1. Feeding Meta-ecosystem Models with Organismal Movement Types

Meta-ecosystem models explicitly consider only dispersal among the possible organismal movement types linking ecosystems. However, other common types of organismal movement are relevant for ecosystem couplings, such as life-cycle movement, seasonal migration, or foraging movement. When focusing on how the spatial flows resulting from organismal movements affect recipient ecosystem dynamics, we distinguish two contrasting types of effects: consumer and resource effects (Table 1). Dispersal, which implies settlement away from the place of birth of an organism [41], essentially conveys consumer effects by adding individuals to the recipient ecosystem (Figure 1A,E). The immigrants and their subsequent offspring, for instance Milu deer individuals recolonising Chinese forests [72], primarily exert a top-down pressure on local resources, even if their production of detritus might ultimately enrich recipient ecosystems. On the contrary, life-cycle movements, such as emerging aquatic insects moving to terrestrial systems for mating, oviposition, and subsequent death, essentially convey resources by transporting individuals which do not settle or consume anything in the recipient ecosystem (Figure 1B,F). For instance, clouds of midges emerging from arctic ponds can substantially enrich nearby tundras in nitrogen by their carcasses [52], and trigger bottom-up effects on local terrestrial herbivores [51]. Seasonal migration and foraging movements involve both consumer and resource effects (Figure 1C,D,G,H). They are distinct from one another by their spatiotemporal scales: migratory animals couple ecosystems across biogeographic scales, for instance with geese feeding on crops in the Mississippi basin and breeding in arctic tundras [73], while the foraging behaviour of large consumers can couple adjacent ecosystems, such as hippopotami grazing in savannahs and defecating in rivers [53]. For both types of movement, the asymmetry in animal activity constitutes a net flow of resource from one ecosystem to another (from feeding to breeding sites, or grazing to resting sites) in addition to the consumption pressure organisms exert where they are. Finally, these movement types, and their effects, can interact across organismal scales: a large consumer, such as an elephant, might couple ecosystem resources through its foraging activity while searching for water points, and in parallel drive the dispersal of small aquatic organisms among ponds via the mud that cover its skin [74]. It is so far theoretically unexplored how the co-occurrence of such contrasting but interacting spatial processes might affect ecosystem dynamics. Lastly, whether other movement types involving complex behaviours, such as mating aggregations or refuges from predation, also commonly induce meta-ecosystem dynamics remains an open question.

Table I. Effects and Empirical Illustrations of the Different Movement Types

	Effect		Some emblematic examples	Refs
	C	R ^a		
Dispersal	X		Meta-population of Milu (a species of deer) re-establishment in China; passive dispersal of plants and small aquatic organisms via birds; all kinds of biological invasions.	[72]; [36,75]; [76]
Life-cycle migration		X	Midge emergence from arctic ponds enriching tundras in Iceland; salmon carcasses or shrimps subsidizing freshwater reproductive sites with marine nutrients.	[52]; [77] or [78]
Seasonal migration	X	X	Geese linking agrosystems in Mississippi and arctic tundras in Canada; all migratory birds and large herbivore herds transporting nutrients across African savannahs or boreal systems.	[73]; [2]
Foraging	X	X	Hippopotami grazing in savannahs and pupping in the Mara river; seabirds bringing nutrients from the sea on islands; large marine mammal defecation or zooplankton vertical migrations transporting nutrients from pelagic to benthic systems.	[53]; [55]; [79] or [61]

^aC and R stand for consumer and resource effects on the recipient ecosystem, respectively. Consumer effects encompass demographic effects (population addition) and consumption pressure, while resource refers to transport of material serving as resources.

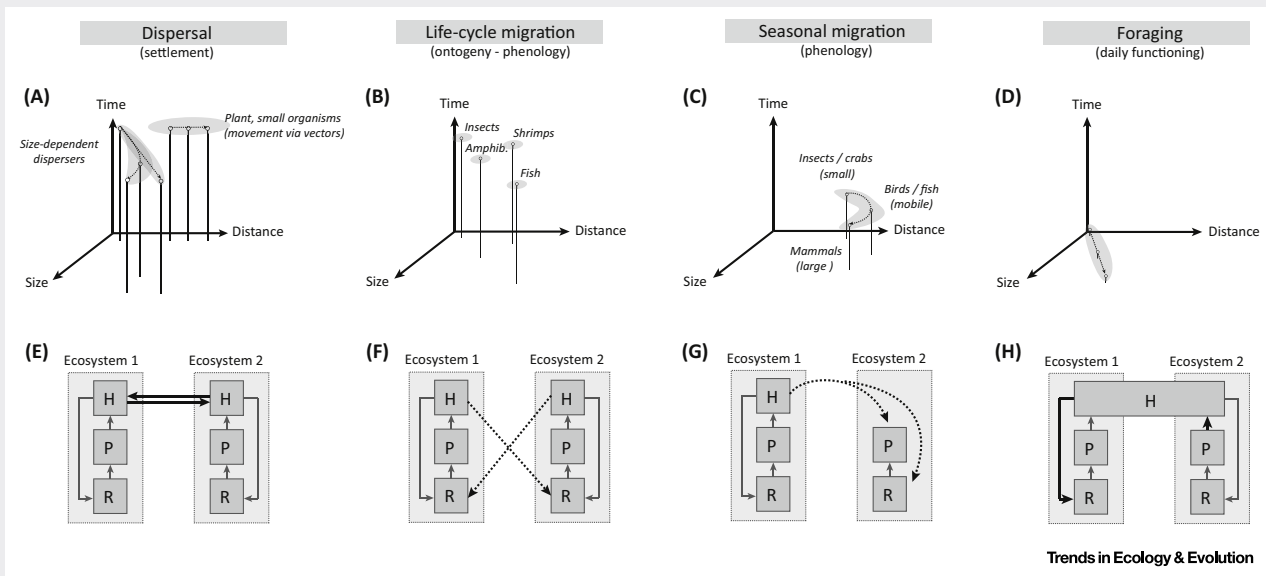


Figure 1. Scales of Organismal Movement Types and Effects on Meta-Ecosystem Dynamics. Top panels (A–D) show the qualitative relationships between organism size, the distance crossed for a given type of movement, and the time spent relative to the lifespan of the organism (inverse frequency). For instance, dispersal movement (A), or life-cycle migration (which corresponds to movement between contrasting habitats associated with specific ontogenic stages) (B), occur only once in a lifetime, whereas seasonal migration (C) occurs several times at regular intervals, and movement linked to foraging (D) occurs on a short time basis and multiple times during the life of an organism. The distance crossed during these movements might depend on the size and the mobility (e.g., flying ability) of the organisms, with larger or more mobile ones dispersing and migrating farther, or foraging on larger spatial scales (A–D) [70,71]. However, small organisms can also cross large distances through passive dispersal driven by air, or water currents, or larger organisms (A). Bottom diagrams (E–H) illustrate how spatial flows of an herbivore H (black arrows) driven by these different movement types might couple two ecosystems in which the herbivore feeds on a plant P, itself up-taking a resource R (grey boxes and arrows). In the meta-ecosystem framework, dispersal corresponds to movement among populations of the same species (E), whereas life-cycle movements represent added resources into the recipient ecosystem, since adults most often die immediately after reproducing (F). Dotted arrows denote that these flows are often as temporally specific pulses. In seasonal migrations, pulsed flows can be of a magnitude that constitutes a shift in the recipient community structure compared to otherwise prevailing local dynamics (G). Lastly, foraging activity can constitute a net flow from an ecosystem to another, even if the animal uses the whole landscape and does not perceive it as a structured meta-ecosystem (H).

spatial flows of organisms and resources occur and interact at contrasting scales in nature. In the next sections we motivate this upgraded meta-ecosystem framework with concrete examples and identify the next theoretical and empirical steps needed for advancing spatial ecology.

Contrasting Natures of Ecosystem Couplings: Dispersal versus Resource Flows

Meta-ecosystem theory has extended the metacommunity framework with general models that include both dispersal and resource flows to connect ecosystems [13]. However, true dispersal, defined as the settlement and successful reproduction of individuals away from their place of birth [1,40,41], can only occur between ecosystems offering similar enough physical habitats for the dispersing organism to survive in both. Clearly, many organisms have some adaptations to deal with variations in habitat conditions, and often can cope with what is considered – and built into models – as environmental heterogeneity. However, all organisms have some physiological limits preventing a successful dispersal across very different physical boundaries (e.g., freshwater to terrestrial or marine to freshwater). Generally, individuals crossing habitat barriers die and enter the detrital pool rather than reproduce and establish new populations in the recipient ecosystem (e.g., whales or algae grounding on beaches). Thus, dispersal primarily links similar ecosystems, while massive flows of resources are reported to cross ecosystem boundaries [5,42], therefore linking contrasting ecosystems. Though implicitly clear to most empiricists, theoreticians often do not explicitly make this distinction ([43] for an exception), thereby ignoring implications for the nature of dominant ecosystem couplings (dispersal vs. resource flows). This has, in our eyes, led to the discrepancy between the theoretical advancements in meta-ecosystem theory and a lack of application to empirical systems.

One can imagine a gradient of meta-ecosystem couplings going from dispersal-based to resource-flow based meta-ecosystems (Figure 1A,B): at one end of the gradient, dispersal is more likely to occur between ecosystem patches of similar habitats, including similar abiotic and biotic characteristics, such as networks of ponds, islands, forest patches, or table mountains (Figure 1A). Organisms dispersing in such fragmented landscapes have to cross what is for them an unsuitable matrix of radically different habitats in order to reach the next acceptable patch. For instance, zooplankton transported by birds can only establish and survive in new aquatic habitats but are doomed to die when released during terrestrial stopovers [36,44]. Given that resources transported along with dispersal are probably negligible in comparison to the consumer effect of individuals founding new populations (Box 1), these dispersal-based meta-ecosystems finally boil down to metacommunity-like dynamics coupled with local recycling (Figure 1A). At the opposite end of the gradient, massive cross-ecosystem flows of resources occur at the boundaries of contrasting ecosystems, such as at aquatic–terrestrial or pelagic–benthic interfaces (Figure 1B). Resource flows can be mediated by physical processes passively transporting detritus or nutrients, such as wind (e.g., windblown

Box 2. Meta-ecosystem Theory at the Landscape Scale

The original definition of a meta-ecosystem as ‘a set of ecosystems connected by spatial flows of energy, materials and organisms across ecosystem boundaries’ [13] is general enough to apply to different scales, from microbial (e.g., mites in soil [80]) to biogeographic (e.g., temperate and arctic grasslands linked by migratory birds; [73]). This flexibility, arising itself from the flexibility of the ecosystem concept, makes meta-ecosystems relevant to address questions on spatial dynamics between any coherent ecological entities linked by biotic or abiotic flows, with the scale varying with the organism or process of interest.

To link this concept and associated theory to empirical ecosystems – with the underlying motivation of facing the consequences of global changes – there is, however, a special interest in focusing on scales adapted to understand human impacts on ecosystems (habitat patches), and to link these spatial dynamics to large-scale processes such as global cycles. The landscape scale is especially interesting in that respect, because it encompasses the environmental heterogeneity produced by human activities, which fragment ecosystems into mosaics of patches (Figure I). These ecosystem patches of different habitat types often correspond to traditionally independent domains of ecology, such as river ecology, agriculture, or forestry. By showing how spatial flows circulating within the landscape generate interdependencies between these different habitats, meta-ecosystem theory has a crucial role to play in identifying efficient actions to control the spread of local perturbations. Moreover, studying the impacts of spatial flows at the landscape scale provides tools to understand the spatial dynamics of regional biodiversity, but also to bridge it, via ecological processes (productivity, recycling), to biogeochemical fluxes (carbon, water, nitrogen) at a larger scale (Figure I).

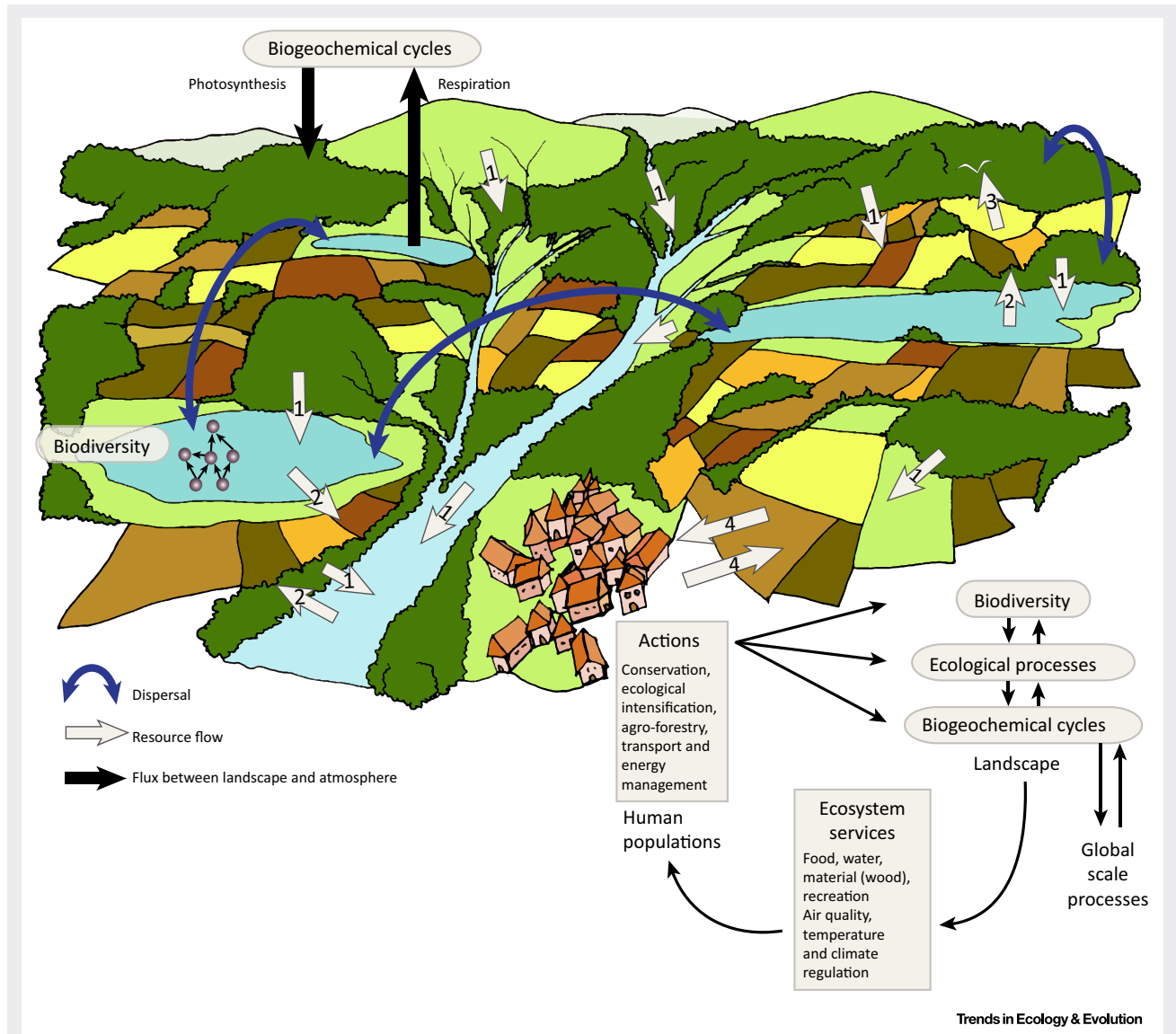
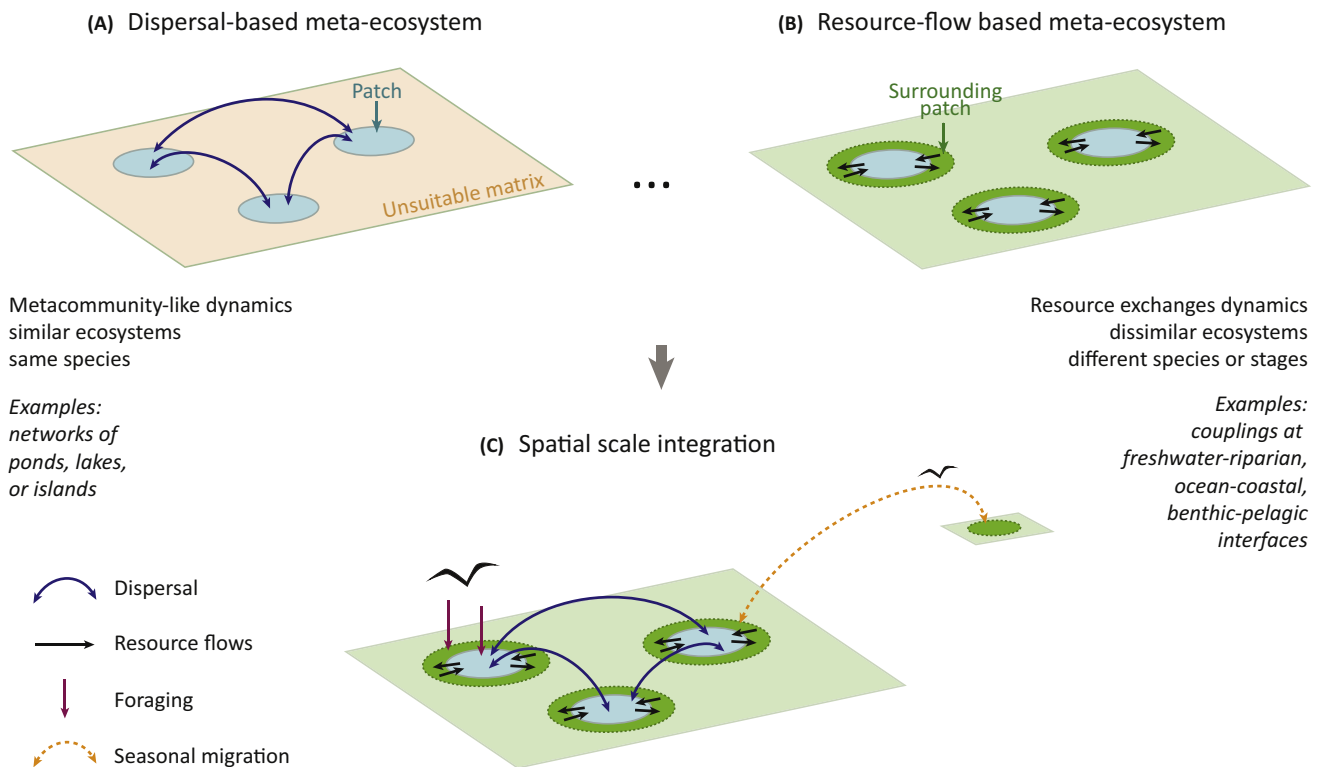


Figure 1. Spatial Dynamics at the Landscape Scale. Both flows of dispersal (curve blue arrows) and resource (white arrows) coupled different types of habitat patches in the landscape, thereby inducing contrasting meta-ecosystem dynamics at regional and local scales, respectively. Flows of resources can be driven by physical forces such as gravity, wind, or water current (arrows 1), by animal movement such as insect emergence (arrows 2) or consumer foraging (arrow 3 next to a white bird), or by human transport (arrows 4). These flows affect biodiversity (e.g., denoted by a food web in a lake) and ecosystem processes (productivity and recycling), which themselves affect global cycles in different ways: example of the carbon cycle depicted by wide black arrows, with net carbon uptake by a forest patch and net carbon release to the atmosphere by a lake. Human populations benefit from ecosystem services provided by the landscape (right box), and human actions (left box) conducted at the landscape scale modulate biodiversity and ecosystem functioning, and ultimately biogeochemical cycles, which in turn induce the services.

leaves from forests accounting for up to 59% of litter nutrient input in adjacent orchards [45], gravity (e.g., nutrient leaching in a watershed, zooplankton faecal pellets sinking from pelagic to benthic systems; [46,47]), or aquatic currents and tides (e.g., benthic nutrients resuspended by upwelling currents, algae or carrion grounding on beaches; [48]). Thus, ecosystems do not have to be suitably similar in order to be connected by these types of resource flows, unlike those connected by dispersal.



Trends in Ecology & Evolution

Figure 1. Gradient of Meta-Ecosystem Types and Their Spatial Integration in the Landscape. Natural meta-ecosystems fall along a gradient along which the pre-eminence of dispersal versus resource flows varies. At one end, (A) dispersal-based meta-ecosystems, displaying metacommunity-like dynamics, connect distant ecosystem patches of similar habitat and functioning via dispersal (curved blue arrows), while at the other end, (B) resource-flow based meta-ecosystems connect adjacent ecosystems of radically different habitats via resource flows crossing their boundaries (horizontal straight black arrows). Resource flows might be driven by physical processes (e.g., gravity, wind, or water currents) as well as biotic processes (e.g., life-cycle movement of organisms). (C) These two types of meta-ecosystem dynamics occur at different scales: dispersal can connect individual resource-flow based meta-ecosystems within landscapes. Foraging activities might trigger consumption pressure as well as transfer of matter between ecosystems within the landscape (vertical pink arrows), while seasonal migrations connect the landscape to more distant ecosystems (curved dotted orange arrow).

Significant resource flows can also consist of organisms approaching the end of their life cycles, such as anadromous fish migrating from oceans to reproduce in streams or insects emerging from freshwater systems and dying on land [49–51]. In Iceland, tundras surrounding lakes receive an additional input of nitrogen of up to 250 kg/ha/year from aquatic midge fall, a level shown to cascade on plant nitrogen content, and eventually increasing the density of herbivorous caterpillars [51,52]. As a product of the life-history cycles of the animals, these flows affect local community dynamics in a fundamentally different way than does dispersal, by primarily acting as resource inputs in the recipient ecosystem instead of contributing to population dynamics (Box 1). Finally, foraging movements of consumers searching for food in one habitat type but otherwise residing in another can also induce massive resource flows. As an example, in Kenya, Subaluski and colleagues estimated that a population of hippopotami grazing in savannahs transfers annually the production equivalent of 260 to 1563 hectares of terrestrial biomass through faeces into the Mara river, where the hippopotami rest and defecate [53]. Even if animal use the whole landscape, this asymmetry in animal activities induces strong resource-based meta-ecosystem dynamics resulting in a huge net flow of resource between two contrasting adjacent ecosystems (other similar and emblematic examples include marine

birds fishing in oceans but defecating guano ashore or bears hunting salmon in rivers and pulling their carcasses into forests [50,53–55]).

Overall, on our gradient of ecosystem couplings with increasing habitat dissimilarity, the two extremes represent widespread types of natural meta-ecosystems with opposing characteristics and dynamics: dispersal-based meta-ecosystems dominated by metacommunity-like dynamics occur between distant ecosystems but of similar habitat types at one end of the gradient (Figure 1A), while at the other end of the gradient, resource-flow based meta-ecosystems occur directly at the boundaries of dissimilar ecosystems (Figure 1B). Along this gradient, intermediate cases exist where dispersal and subsidies are both significant. For instance, uphill and downhill terrestrial habitats, or upstream and downstream sites of river networks are similar enough habitats to be coupled by dispersal of some organisms, while also being linked by passive flows of resources. While the existence of these different flow types structuring spatial dynamics within landscapes are generally acknowledged from field observations (Box 2), we still lack quantitative information about the frequency distribution (bimodal or more continuous) of natural meta-ecosystems along the gradient. Collecting and assembling such data is in our eyes one of the major empirical challenge to make further progress in spatial ecology (see last section for details).

Spatial Scales of Dispersal versus Resource Flows

Dispersal and resource-flow based meta-ecosystems do not necessarily operate in isolation from each other. Rather, the two types of flows and associated meta-ecosystem dynamics occur at different spatial scales within the landscape (Figure 1C). Resource-flow based meta-ecosystems occur at a local scale, across boundaries of adjacent ecosystems (e.g., litter fall or insect exchanges at lake–forest interface; [56]), while dispersal-based meta-ecosystems could connect these local meta-ecosystems at a larger scale via organisms crossing unsuitable matrices to disperse into distant but similar ecosystems (e.g., bird-dispersed plankton among lakes; [44]). Thus, this conceptual framework encompasses spatially nested dynamics and integrates the contributions of landscape and meta-ecosystem ecology in a single framework for spatial ecology. On the one hand, landscape ecology analyses the structure of heterogeneous landscapes, quantifying the surface and relative positions of the different elements (e.g., forest patches, lakes, fields) and their importance for focal species persistence. On the other hand, meta-ecosystem ecology concentrates on the dynamic aspect, by showing how spatial flows connect these structuring elements (Box 2). Acknowledging the different scales at which various spatial flows connect elements in the landscape is crucial both to understand species persistence and ecological processes in heterogeneous landscapes, and to anticipate how perturbations in one location propagate across the landscape [57]. A local perturbation might trigger spatial cascades between apparently unrelated communities or ecological processes [22,58], such as invasive fish affecting terrestrial arthropod communities [59]. Overall, identifying the main paths of spatial flows between ecosystems, and the different scales at which these flows occur, is key to develop an empirically grounded theory of spatial ecology [14]. Notably, this requires incorporating organismal movement types other than dispersal into current theory, and accounting for their respective spatiotemporal scales (next section and Box 1).

A Missing Theory Level

Current meta-ecosystem models have been built on simplest assumptions regarding among-ecosystem spatial flows to identify mechanisms general enough to apply to all systems [13,16,23,25,27,29]. However, model structures and parameterizations are too general to appropriately describe the nature of spatial couplings between real ecosystems. Moreover,

equally limiting are empirical approaches based on system-centred models, which are useful for specific applications but lack generality and restrict any predictions to the focal system. To bridge this gap, an intermediate level of model generality must be found that would better capture the structure of ecosystem couplings by incorporating the main organismal movement types and their specific effects and scale in general meta-ecosystem models.

These spatial flows, at a first glance, look specific to some systems: 'marine snow' made of faecal pellets of phytoplankton and zooplankton sinking from pelagic to benthic systems, for instance [46], or salmon carcasses fished by bears supporting productivity in lowland boreal forests [50]. However, such seemingly specific spatial flows actually share similar functional roles. If we abandon a system-centred perspective to categorise spatial flows by the type of effects they provoke in recipient ecosystems, generalities can be drawn among contrasting systems. For instance, marine snow corresponds to a directional detritus input from autotrophic to heterotrophic systems, for which analogues can be found in inland systems with forest litter inputs to stream benthos [60]. Similar functional equivalences are found between net cross-ecosystem resource flows triggered by bears bringing salmon carcasses on land, hippopotami grazing on savannahs and defecating in tropical rivers [53], or zooplankton feeding in pelagic areas during the night and excreting nutrient at daytime in the deep sea [61]. A commonality of all these cases is the daily net transport of inorganic nutrients or detritus triggered by foraging activity. Such generalisable functional roles of spatial flows are easily identified, incorporated into models, and contribute to build a process-based rather than system-based spatial framework.

Essential features of spatial flows to account for in a process-based spatial framework include consumer versus resource effects, timing (e.g., pulse frequency) and spatial scales. In that respect, the four organismal movement types described in Box 1 each display distinct characteristics (Figure 1C): consumer effects (i.e., demographic + consumption pressure) are the dominant result of dispersal, whereas, on a smaller spatial scale, resource effects dominate common **life-cycle movements**, such as with emerging aquatic midges or spawning salmon [50,52]. Foraging and seasonal migrations trigger both consumption pressure in the recipient ecosystem and potentially net flows of resource, but act at local versus cross-continental scales, respectively, and on continuous versus pulsed time scales compared to local ecosystem dynamics (examples in Box 1). Overall, these ubiquitous movement types fulfil different functional roles in spatial dynamics, and their integration into models would capture essential characteristics of the spatial linkages between ecosystems, without impairing model generality by not being system specific. This effort of depicting more accurately the spatio-temporal and functional complexity of spatial couplings will move meta-ecosystem theory from abstraction to realistic generalities.

Challenges Ahead for Spatial Ecology

Understanding the general effects of spatial flows on ecological dynamics is a first step. Next, theory must identify realistic situations under which spatial flows matter for ecological dynamics by grounding models into empirical knowledge. Extensive data on spatial flows already exist across different fields of the empirical literature, but the broad picture is still missing. A major task is to quantify, unify, and synthesise data across fields.

We currently have only partial knowledge of what kind of flows connect ecosystems, with a bias toward data on resource flows which are easily measured by direct methods, such as passive trapping systems (e.g., terrestrial detritus inputs to freshwater systems, pelagic snow in oceans). In contrast, few studies document active flows of resources (however, see

[53,62]), and dispersal is mostly analysed through its effect on populations or communities rather than estimated as a flow [33]. Improving methods to track animal displacement [63,64] will fill gaps in our knowledge of the spatial scales associated with organismal movement types, but we still have to quantify how much material is conveyed by these movements. When direct measurements are technically challenging, we need to develop and generalise indirect methods combining estimates of the diverse variables and processes involved in spatial flows, such as feeding and excretion rates of organisms, foraging behaviour, population densities in different habitats, average individual body mass, or dispersal kernels [49,53,62,65]. New methods combining isotopic data on diet with consumption rates to estimate resource flows would similarly round out our knowledge of spatial flows.

Synthesising local and spatial data in homogenised units will provide the material to determine which actual spatial flows drive natural meta-ecosystem dynamics, and what the underlying drivers might be (i.e., organismal movement types or physical processes). As a minimum effort towards this necessary homogenisation, we suggest consistently expressing spatial flows in areal units (per meter squared) of both donor and recipient ecosystems, in order to appropriately describe flows linking ecosystems of different sizes. We also need quantifications to be systematically associated with information on timing (i.e., duration and frequency), because whether spatial flows occur as continuous flows or pulses constricted in time (e.g. 15-cycle cicada outbreaks in central US [66]) could provoke contrasting effects on the stability of recipient ecosystem dynamics [67–69].

Using models upgraded by this type of data synthesis to understand the relationship between spatial scales and dominant flow types will improve our ability to forecast changes in connected ecosystems (see Outstanding Questions). This is essential for identifying the relevant spatial flows and species to maintain appropriate levels of connectivity and functioning in the landscape.

Concluding Remarks

By linking contrasting spatial dynamics along a gradient of dispersal versus resource flows occurring at different scales, we propose a unified framework for spatial ecology. Our framework merges the static, but accurate, view of environmental heterogeneity proposed by landscape ecology with the dynamic view from meta-ecosystem theory. We believe this unification is a crucial step toward more fruitful exchanges between theory and empirical ecology. In particular, we advocate that incorporating a wider range of organismal movements into meta-ecosystem models will provide an appropriate balance between generality and realism when describing the prominent features of couplings between ecosystems. While improving our understanding of spatial dynamics and their consequences for ecosystem functioning, our framework also helps refine relevant conservation targets and spatial scales.

Acknowledgements

We thank Dries Bonte and the EMERGE working group for helpful discussions. We thank the editor, Dr. Paul Craze, and two anonymous reviewers for comments on a previous version of this manuscript. Funding is from the Swiss National Science Foundation Grant PPO0P3_150698.

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Outstanding Questions

How are different types of spatial flows distributed within landscapes?

How do community structure and biodiversity affect the quality and quantity of cross-ecosystem flows?

How do perturbations influence cross-ecosystem flows?

How can metaecosystem dynamics explain the spreading of perturbations between ecosystems?

Which organisms play keystone roles in spatial dynamics, and how do they contribute to the spread of perturbations across ecosystems?

How frequent are spatial cascades in natural landscapes?

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