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1 Meta-ecosystems 2.0: rooting the theory into the field

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19 **Keywords**

20 resource flow; metaecosystem; metacommunity; subsidy; animal movement; landscape

21 **Abstract**

22

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

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35

36 Ecosystem couplings outside the metacommunity box

37 Spatial flows of energy, materials and organisms are ubiquitous in nature: Organisms
38 move to forage for food, migrate or disperse, actively or as propagules [1–3]. All these
39 organismal movements along with passive flows of inorganic nutrients and detritus connect
40 ecosystems and influence local ecosystem dynamics [4,5]. Community ecologists have paid
41 particular attention to spatial flows of species (dispersal; see Glossary), which connect several
42 communities in a metacommunity [6,7]. The metacommunity framework demonstrated how
43 dispersal and environmental heterogeneity determine species coexistence and biodiversity among
44 a set of patches at local and regional scales [4,8–12]. In parallel, the growing recognition that
45 resources are not stationary and spatial flows of resources can also play a significant role in the
46 dynamics of various types of biological communities [5] fostered the development of the meta-
47 ecosystem framework [13,14]. By explicitly integrating local production and spatial movement of
48 resources within metacommunities, this framework demonstrated the feedback between
49 community and resource dynamics across spatial scales [15]. Organisms moving among
50 ecosystems modify the spatial distribution of resources, and thus habitat suitability, through local
51 resource consumption and biomass recycling [16]. In parallel, resource flows connect the
52 dynamics of distinct communities via the local production and export of these resources [17], and
53 can trigger trophic cascades in recipient ecosystems [18]. This mechanistic link between
54 community and ecosystem functioning and spatial dynamics makes the meta-ecosystem
55 framework a powerful tool to investigate the dynamics of connected ecosystems. This is
56 especially relevant in the context of increasing perturbations, where disruptions in local processes
57 can spread in space through changes in spatial flows [17,19–22]. However, while the theoretical

58 development of the meta-ecosystem framework has been fast [13,16,23–29], adoption by
59 empiricists has generally lagged behind [11], and mostly consisted of conceptual experiments
60 paralleling the modelling work [17,21,30] or a few applications to coastal systems [31,32].

61 Here, we argue that empirical research on meta-ecosystems is progressing slowly due to
62 the theory's high level of abstraction. As a conceptual extension of metacommunity theory, meta-
63 ecosystem models usually tend to focus on dispersal to be the driver of organismal flows in
64 space, thereby implicitly considering the couplings between ecosystem patches of similar habitats
65 [16,23,24,26]. Dispersal, however, is but a small subset of all organismal movement types that
66 can couple ecosystems (Box 1). The missing piece – other types of organismal movement –
67 prevents current meta-ecosystem theory from providing predictions specific enough to apply to
68 real ecosystems. Meanwhile, empirical ecology faces challenges in understanding how spatial
69 flows induce mutual feedbacks among different ecosystems, partly due to technical challenges of
70 measuring spatial flows [33]. Empirical ecology is also traditionally divided into independent
71 research domains which consider spatial flows only as external inputs to ecosystems of interest
72 (e.g. or terrestrial vs. aquatic ecology [34]) and have different variables of interest and
73 measurement units to describe the same processes (e.g. individuals or species dynamics in
74 community ecology vs. biomass or nutrient cycles in ecosystem ecology). Given that ecosystems
75 are commonly interconnected in complex networks of spatial flows [5,14], a more holistic spatial
76 perspective, considering potential feedbacks among ecosystems, is critically needed to
77 understand the dynamics of ecosystems and their responses to changes [2,22,35–37].

78 Incorporating more specific attributes of ecosystem spatial couplings in the meta-
79 ecosystem framework would foster the production of applicable theoretical predictions and

80 bridge previously less connected empirical fields. Here, we offer a new, synthetic vision of meta-
81 ecosystems. We contend that (1) meta-ecosystems found in nature fall along a gradient of
82 coupling types: some depend mostly on dispersal, and others mostly on spatial flows of
83 resources; (2) these ecosystem coupling types occur at different spatial scales, with (3) different
84 underlying drivers, including different types of organismal movement, which might affect meta-
85 ecosystem dynamics in fundamentally different ways than dispersal alone (Box 1). We believe
86 that integrating these organismal movements into meta-ecosystem models will raise the
87 generality-realism trade-off to the appropriate level needed to further understand the mechanisms
88 underlying spatial dynamics across natural landscapes (Box 2). Joining the ongoing effort to
89 build an integrative and predictive ecology [38,39], we propose a comprehensive framework for
90 spatial ecology acknowledging how spatial flows of organisms and resources occur and interact
91 at contrasting scales in nature. In the next sections we motivate this upgraded meta-ecosystem
92 framework with concrete examples and identify the next theoretical and empirical steps needed
93 for advancing spatial ecology.

94

95 Contrasting natures of ecosystem couplings: dispersal versus resource flows

96 Meta-ecosystem theory has extended the metacommunity framework with general models
97 that include both dispersal and resource flows to connect ecosystems [13]. However, true
98 dispersal, defined as the settlement and successful reproduction of individuals away from their
99 place of birth [1,40,41], can only occur between ecosystems offering similar enough physical
100 habitats for the dispersing organism to survive in both. Clearly, many organisms have some
101 adaptations to deal with variations in habitat conditions, and often can cope with what is

102 considered – and built into models – as environmental heterogeneity. However, all organisms
103 have some physiological limits preventing a successful dispersal across very different physical
104 boundaries (e.g., freshwater to terrestrial or marine to freshwater). Generally, individuals crossing
105 habitat barriers die and enter the detrital pool rather than reproduce and establish new populations
106 in the recipient ecosystem (e.g. whales or algae grounding on beaches). Thus, dispersal primarily
107 links similar ecosystems, while massive flows of resources are reported to cross ecosystem
108 boundaries [5,42], therefore linking contrasting ecosystems. Though implicitly clear to most
109 empiricists, theoreticians often do not explicitly make this distinction ([43] for an exception),
110 thereby ignoring implications for the nature of dominant ecosystem couplings (dispersal vs.
111 resource flows). This has, in our eyes, led to the discrepancy between the theoretical
112 advancements in meta-ecosystem theory and a lack of application to empirical systems.

113 One can imagine a gradient of meta-ecosystem couplings going from dispersal-based to
114 resource-flow based meta-ecosystems (Figure 1A–B): at one end of the gradient, dispersal is
115 more likely to occur between ecosystem patches of similar habitats, including similar abiotic and
116 biotic characteristics, such as networks of ponds, islands, forest patches, or table mountains
117 (Figure 1A). Organisms dispersing in such fragmented landscapes have to cross what is for them
118 an unsuitable matrix of radically different habitats in order to reach the next acceptable patch. For
119 instance, zooplankton transported by birds can only establish and survive in new aquatic habitats
120 but are doomed to die when released during terrestrial stopovers [36,44]. Given that resources
121 transported along with dispersal are probably negligible in comparison to the consumer effect of
122 individuals founding new populations (see Box 1), these dispersal-based meta-ecosystems finally
123 boil down to metacommunity-like dynamics coupled with local recycling (Figure 1A). At the

124 opposite end of the gradient, massive cross-ecosystem flows of resources occur at the boundaries
125 of contrasting ecosystems, such as at aquatic-terrestrial or pelagic-benthic interfaces (Figure 1B).
126 Resource flows can be mediated by physical processes passively transporting detritus or
127 nutrients, such as wind (e.g. windblown leaves from forests accounting for up to 59% of litter
128 nutrient input in adjacent orchards [45]), gravity (e.g. nutrient leaching in a watershed,
129 zooplankton faecal pellets sinking from pelagic to benthic systems; [46,47]), or aquatic currents
130 and tides (e.g., benthic nutrients re-suspended by upwelling currents, algae or carrion grounding
131 on beaches; [48]). Thus, ecosystems do not have to be suitably similar in order to be connected
132 by these types of resource flows, unlike those connected by dispersal.

133 Significant resource flows can also consist of organisms approaching the end of their life
134 cycles, such as anadromous fish migrating from oceans to reproduce in streams or insects
135 emerging from freshwater systems and dying on land [49–51]. In Iceland, tundras surrounding
136 lakes receive an additional input of nitrogen of up to 250 kg ha⁻¹yr⁻¹ from aquatic midge fall, a
137 level shown to cascade on plant nitrogen content and eventually increasing the density of
138 herbivorous caterpillars [51,52]. As a product of the animals' life-history cycles, these flows
139 affect local community dynamics in a fundamentally different way than does dispersal, by
140 primarily acting as resource inputs in the recipient ecosystem instead of contributing to
141 population dynamics (Box 1). Finally, foraging movements of consumers searching for food in
142 one habitat type but otherwise residing in another can also induce massive resource flows. As an
143 example, in Kenya, Subaluski and colleagues estimated that a population of hippopotami grazing
144 in savannahs transfers annually the production equivalent of 260 to 1563 hectares of terrestrial
145 biomass through faeces into the Mara river, where the hippopotami rest and defecate [53]. Even if

146 animal use the whole landscape, this asymmetry in animal activities induces strong resource-
147 based meta-ecosystem dynamics resulting in a huge net flow of resource between two contrasting
148 adjacent ecosystems (other similar and emblematic examples include marine birds fishing in
149 oceans but defecating guano ashore or bears hunting salmon in rivers and pulling their carcasses
150 into forests [50,53–55]).

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

166

167

168 Spatial scales of dispersal versus resource flows

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

190 organismal movement types other than dispersal into current theory, and accounting for their
191 respective spatio-temporal scales (next section and Box 1).

192

193 A missing theory level

194 Current meta-ecosystem models have been built on simplest assumptions regarding
195 among-ecosystem spatial flows to identify mechanisms general enough to apply to all systems
196 [13,16,23,25,27,29]. However, model structures and parameterizations are too general to
197 appropriately describe the nature of spatial couplings between real ecosystems. Moreover,
198 equally limiting are empirical approaches based on system-centred models, which are useful for
199 specific applications but lack generality and restrict any predictions to the focal system. To bridge
200 this gap, an intermediate level of model generality must be found that would better capture the
201 structure of ecosystem couplings by incorporating the main organismal movement types and their
202 specific effects and scale in general meta-ecosystem models.

203 These spatial flows, at a first glance, look very specific to some systems: ‘marine snow’
204 made of phytoplankton and zooplankton’s faecal pellets sinking from pelagic to benthic systems
205 for instance [46], or salmon carcasses fished by bears supporting productivity in lowland boreal
206 forests [50]. However, such seemingly specific spatial flows actually share similar functional
207 roles. If we abandon a system-centred perspective to categorize spatial flows by type of effects
208 they provoke in the recipient ecosystem, generalities can be drawn among contrasting systems.
209 For instance, marine snow corresponds to a directional detritus input from autotrophic to
210 heterotrophic systems, for which analogues can be found in inland systems with forest litter
211 inputs to stream benthos [60]. Similar functional equivalences are found between net cross-

212 ecosystem resource flows triggered by bears bringing salmon carcasses on land, hippopotami
213 grazing on savannahs and defecating in tropical rivers [53], or zooplankton feeding in pelagic
214 areas during the night and excreting nutrient at daytime in the deep sea [61]. A commonality of
215 all these cases is the daily net transport of inorganic nutrients or detritus triggered by foraging
216 activity. Such generalizable functional roles of spatial flows are easily identified, incorporated
217 into models, and contribute to build a process-based rather than system-based spatial framework.

218 Essential features of spatial flows to account for in a process-based spatial framework
219 include consumer versus resource effects, timing (e.g. pulse frequency) and spatial scales. In that
220 respect, the four organismal movement types described in Box 1 each display distinct
221 characteristics (Figure 1C): consumer effects (i.e. demographic + consumption pressure) are the
222 dominant result of dispersal, whereas, on a smaller spatial scale, resource effects dominate
223 common life-cycle movements, such as with emerging aquatic midges or spawning salmon
224 [50,52]. Foraging and seasonal migrations trigger both consumption pressure in the recipient
225 ecosystem and potentially net flows of resource, but act at local versus cross-continental scales,
226 respectively, and on continuous versus pulsed time scales compared to local ecosystem dynamics
227 (examples in Box 1). Overall, these ubiquitous movement types fulfil different functional roles in
228 spatial dynamics, and their integration in models would capture essential characteristics of the
229 spatial linkages between ecosystems, without impairing model generality by not being system-
230 specific. This effort of depicting more accurately the spatio-temporal and functional complexity
231 of spatial couplings will move meta-ecosystem theory from abstraction to realistic generalities.

232

233

234 Challenges ahead for spatial ecology

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

240 We currently have only partial knowledge of what kind of flows connect ecosystems, with
241 a bias toward data on resource flows which are easily measured by direct methods, such as
242 passive trapping systems (e.g. terrestrial detritus inputs to freshwater systems, pelagic snow in
243 oceans). In contrast, few studies document active flows of resources (but see [53,62]), and
244 dispersal is mostly analysed through its effect on populations or communities rather than
245 estimated as a flow [33]. Improving methods to track animal displacement [63,64] will fill gaps
246 in our knowledge of the spatial scales associated with organismal movement types, but we still
247 have to quantify how much material is conveyed by these movements. When direct
248 measurements are technically challenging, we need to develop and generalize indirect methods
249 combining estimates of the diverse variables and processes involved in spatial flows, such as
250 organisms' feeding and excretion rates, foraging behaviour, population densities in different
251 habitats, average individual body mass, or dispersal kernels (see examples in [49,53,62,65]). New
252 methods combining isotopic data on diet with consumption rates to estimate resource flows
253 would similarly round out our knowledge of spatial flows.

254 Synthesizing local and spatial data in homogenized units will provide the material to
255 determine which actual spatial flows drive natural meta-ecosystem dynamics and what the

256 underlying drivers might be (i.e. organismal movement types or physical processes). As a
257 minimum effort towards this necessary homogenization, we suggest consistently expressing
258 spatial flows in areal units (per meter squared) of both donor and recipient ecosystems, in order to
259 appropriately describe flows linking ecosystems of different sizes. We also need quantifications
260 to be systematically associated with information on timing (i.e. duration and frequency) because
261 whether spatial flows occur as continuous flows or pulses constricted in time (e.g. 15-cycle
262 cicada outbreaks in central US [66]) could provoke contrasting effects on the stability of recipient
263 ecosystem dynamics [67–69].

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

269

270 Conclusion

271 By linking contrasting spatial dynamics along a gradient of dispersal versus resource flows
272 occurring at different scales, we propose a unified framework for spatial ecology. Our framework
273 merges the static, but accurate, view of environmental heterogeneity proposed by landscape
274 ecology with the dynamic view from meta-ecosystem theory. We believe this unification is a
275 crucial step toward more fruitful exchanges between theory and empirical ecology. In particular,
276 we advocate that incorporating a wider range of organismal movements into meta-ecosystem
277 models will provide an appropriate balance between generality and realism when describing the

278 prominent features of couplings between ecosystems. While improving our understanding of
279 spatial dynamics and their consequences for ecosystem functioning, our framework also helps
280 refine relevant conservation targets and spatial scales.

281
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286

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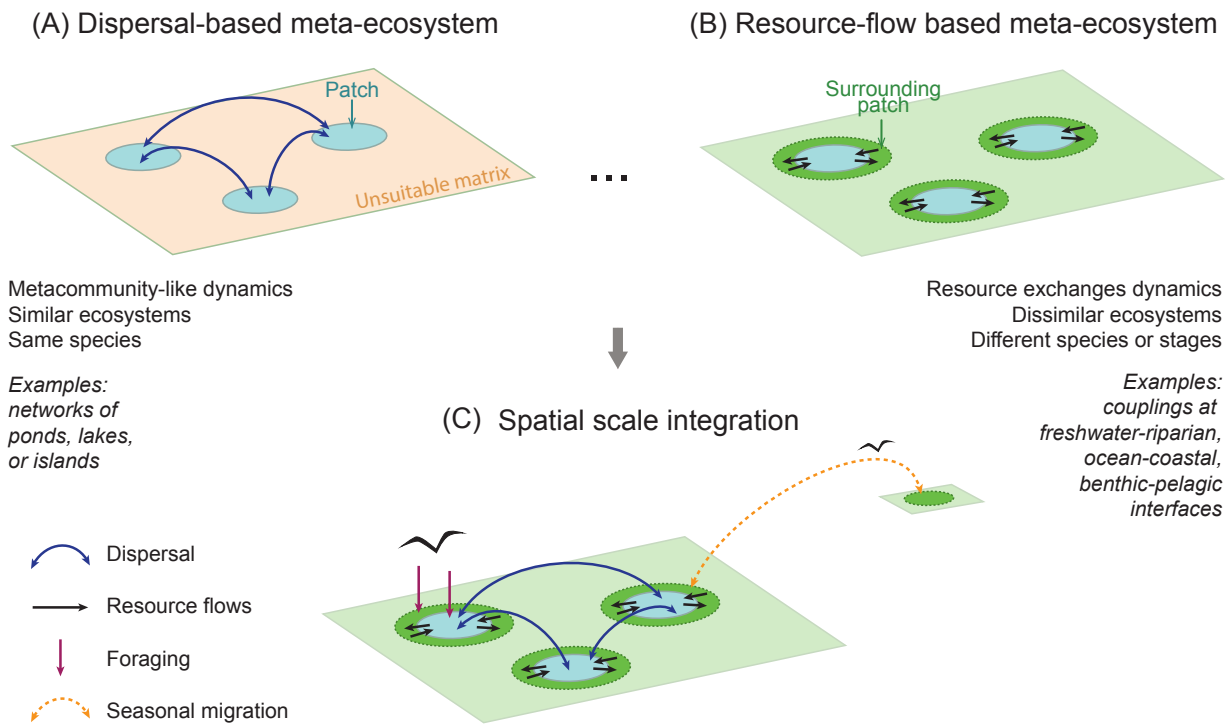
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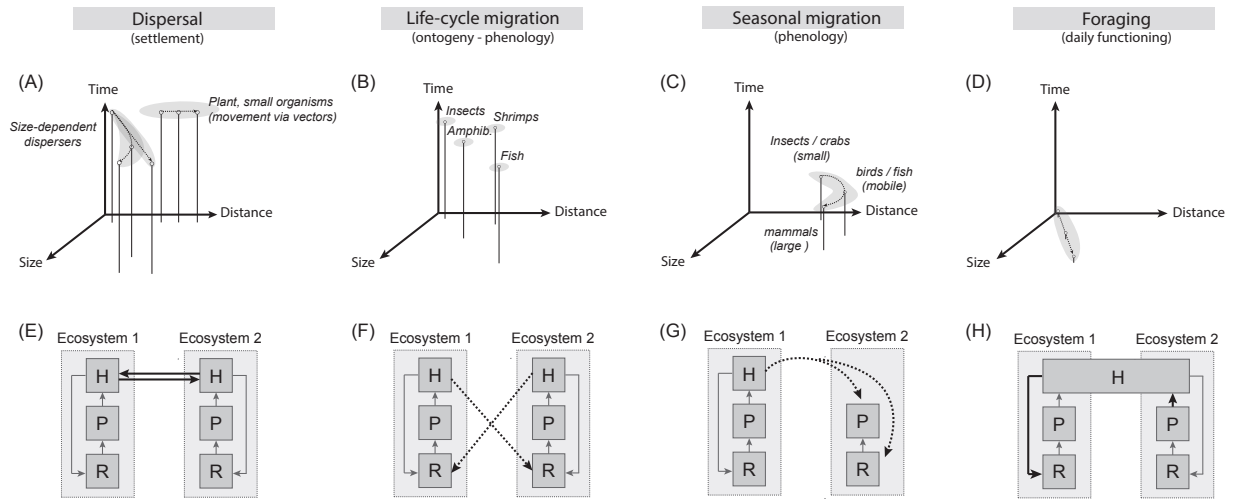
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458 **Figure 1:** Gradient of meta-ecosystem types and their spatial integration in the landscape.
 459 Natural meta-ecosystems fall along a gradient along which the pre-eminence of dispersal versus
 460 resource flows varies. At one end, (A) dispersal-based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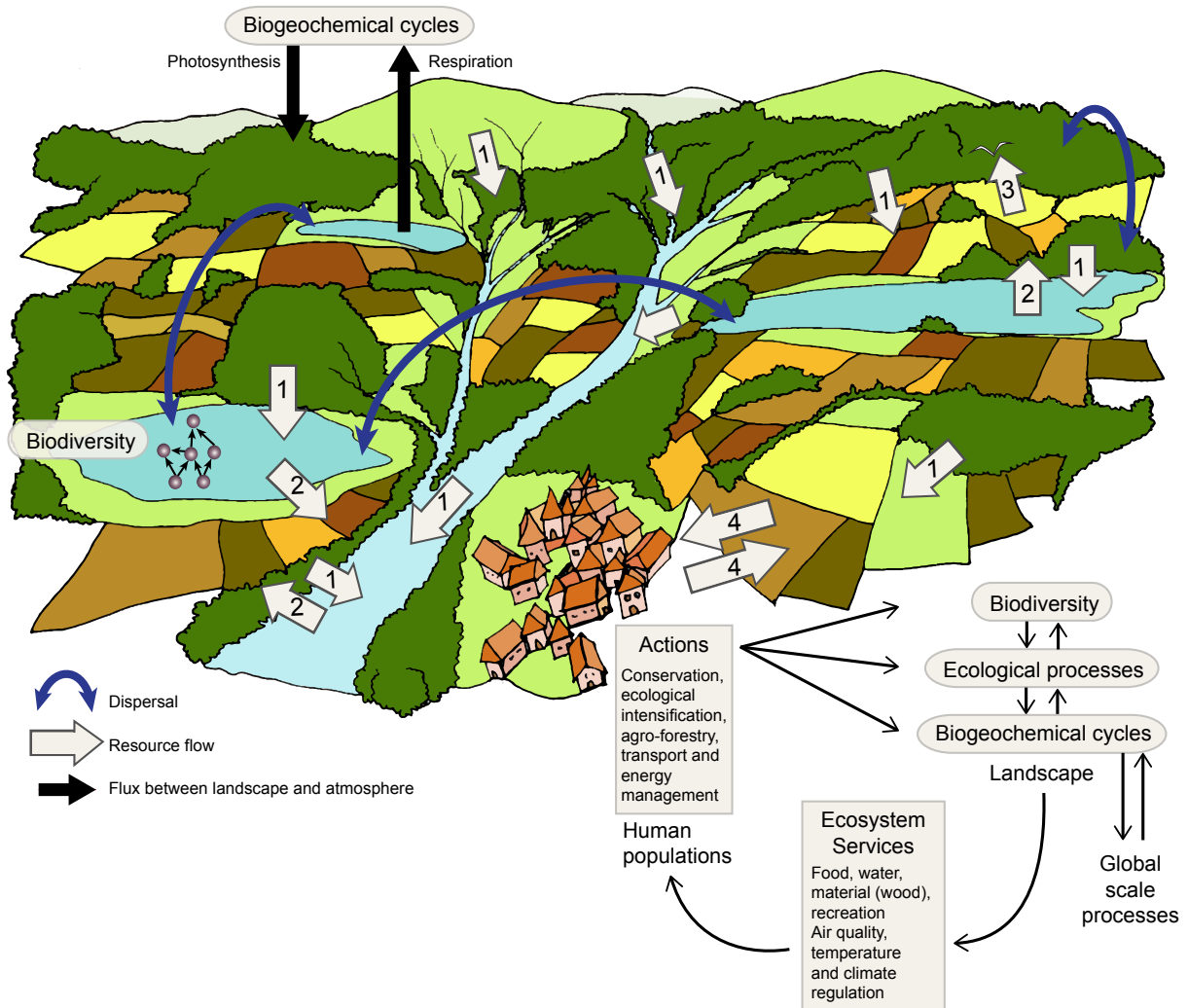


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474 **Figure I. Scales of organism movement types and effects on meta-ecosystem dynamics.**

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

496



497

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

510 Boxes

511 **Box 1. Feeding meta-ecosystem models with organismal movement types**

512 Meta-ecosystem models explicitly consider only dispersal among the possible organismal
513 movement types linking ecosystems. However, other common types of organismal movement are
514 relevant for ecosystem couplings, such as life-cycle movement, seasonal migration, or foraging
515 movement. When focusing on how the spatial flows resulting from organismal movements affect
516 recipient ecosystem dynamics, we distinguish two contrasting types of effects: consumer and
517 resource effects (Table I). Dispersal, which implies settlement away from an organism's place of
518 birth [41], essentially conveys consumer effects by adding individuals to the recipient ecosystem
519 (Figure IA, E). The immigrants and their subsequent offspring, for instance Milu deer individuals
520 re-colonizing Chinese forests [72], primarily exert a top-down pressure on local resources, even if
521 their production of detritus might ultimately enrich recipient ecosystems. On the contrary, life-
522 cycle movements, such as emerging aquatic insects moving to terrestrial systems for mating,
523 oviposition and subsequent death, essentially convey resources by transporting individuals which
524 do not settle or consume anything in the recipient ecosystem (Figure IB, F). For instance, clouds
525 of midges emerging from arctic ponds can substantially enrich nearby tundras in nitrogen by their
526 carcasses [52], and trigger bottom-up effects on local terrestrial herbivores [51]. Seasonal
527 migration and foraging movements involve both consumer and resource effects (Figure
528 IC,D,G,H). They are distinct from one another by their spatio-temporal scales: Migratory animals
529 couple ecosystems across biogeographic scales, for instance with geese feeding on crops in the
530 Mississippi basin and breeding in arctic tundras [73], while the foraging behaviour of large
531 consumers can couple adjacent ecosystems, such as hippopotami grazing in savannahs and

532 defecating in rivers [53]. For both types of movement, the asymmetry in animal activity
 533 constitutes a net flow of resource from one ecosystem to another (from feeding to breeding sites
 534 or grazing to resting sites) in addition to the consumption pressure organisms exert where they
 535 are. Finally, these movement types, and their effects, can interact across organismal scales: a
 536 large consumer, such as an elephant, might couple ecosystem resources through its foraging
 537 activity while searching for water points, and in parallel drive the dispersal of small aquatic
 538 organisms among ponds via the mud that cover its skin [74]. It is so far theoretically unexplored
 539 how the co-occurrence of such contrasting but interacting spatial processes might affect
 540 ecosystem dynamics. Lastly, whether other movement types involving complex behaviours, such
 541 as mating aggregations or refuges from predation also commonly induce meta-ecosystem
 542 dynamics remains an open question.

543

544 **Table I. Effects and empirical illustrations of the different movement types.**

	Effect ¹		Some emblematic examples	References
	C	R		
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].

545

¹ C 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.

546

547 **Box 2. Meta-ecosystem theory at the landscape scale**

548 The original definition of a meta-ecosystem as “*a set of ecosystems connected by spatial flows of*
549 *energy, materials and organisms across ecosystem boundaries*” [13] is general enough to apply

550 to very different scales, from microbial (e.g. mites in soil [80]) to biogeographic (e.g. temperate

551 and arctic grasslands linked by migratory birds; [73]). This flexibility, arising itself from the

552 flexibility of the ecosystem concept, makes meta-ecosystems relevant to address questions on

553 spatial dynamics between any coherent ecological entities linked by biotic or abiotic flows, with

554 the scale varying with the organism or process of interest.

555 To link this concept and associated theory to empirical ecosystems—with the underlying

556 motivation of facing the consequences of global changes—there is, however, a special interest in

557 focusing on scales adapted to understand human impacts on ecosystems (habitat patches) and to

558 link these spatial dynamics to large-scale processes such as global cycles. The landscape scale is

559 especially interesting in that respect, because it encompasses the environmental heterogeneity

560 produced by human activities, which fragment ecosystems into mosaics of patches (Figure I).

561 These ecosystem patches of different habitat types often correspond to traditionally independent

562 domains of ecology, such as river ecology, agriculture or forestry. By showing how spatial flows

563 circulating within the landscape generate interdependencies between these different habitats,

564 meta-ecosystem theory has a crucial role to play in identifying efficient actions to control the

565 spread of local perturbations. Moreover, studying the impacts of spatial flows at the landscape

566 scale provides tools to understand the spatial dynamics of regional biodiversity, but also to bridge

567 it via ecological processes (productivity, recycling) to biogeochemical fluxes (carbon, water,

568 nitrogen) at a larger scale (Figure I).

569

570 Glossary Box

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

573 **Habitat:** in this paper used as synonymous of ‘biotope’, that is a set of uniform environmental
574 conditions.

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

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

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

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

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

587

588 **Highlights**

589

590 Cross-ecosystem movements drive landscape dynamics

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

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

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

594

595 **Outstanding Questions Box**

596

597 How are different types of spatial flows distributed within landscapes?

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

599 flows?

600 How do perturbations influence cross-ecosystem flows?

601 How can meta-ecosystem dynamics explain the spreading of perturbations between ecosystems?

602 Which organisms play keystone roles in spatial dynamics, and how do they contribute to the

603 spread of perturbations across ecosystems?

604 How frequent are spatial cascades in natural landscapes?

605