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Opinion

Dispersal syndromes can link intraspecific trait variability and meta-ecosystem functioning

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Dispersal mediates the flow of organisms in meta-communities and subsequently energy and material flows in meta-ecosystems. Individuals within species often vary in dispersal tendency depending on their phenotypic traits (i.e., dispersal syndromes), but the implications of dispersal syndromes for meta-ecosystems have been rarely studied. Using empirical examples on vertebrates, arthropods, and microbes, we highlight that key functional traits can be linked to dispersal. We argue that this coupling between dispersal and functional traits can have consequences for meta-ecosystem functioning, mediating flows of functional traits and thus the spatial heterogeneity of ecosystem functions. As dispersal syndromes may be genetically determined, the spatial heterogeneity of functional traits may be further carried over across generations and link meta-ecosystem functioning to evolutionary dynamics.

Highlights

Dispersal is a key process for the dynamics and functioning of meta-communities and meta-ecosystems. Meta-ecosystem theory, however, does not fully integrate the possible effects of dispersal, largely assuming random diffusion of organisms and nutrients, contrasting with rising empirical evidence for intraspecific variability in dispersal strategies.

Dispersal is often associated with a suite of phenotypic traits, forming dispersal syndromes. Since phenotypic variability is now acknowledged as a key factor mediating ecosystem dynamics, we argue that dispersal syndromes can link trait-based ecology and meta-ecosystem functioning together.

We highlight that the dispersal of individuals can be associated with functional effect traits and can therefore alter trophic and nutrient-mediated interactions in ecosystems. We illustrate how the association between dispersal tendency and functional traits can modify the spatial heterogeneity of ecosystems.

Role of dispersal in meta-communities and meta-ecosystems

The rise of **trait-based ecology** (see Glossary) has emphasised the importance of **individual trait variability** for community structure and **ecosystem functioning** [1,2]. Key frameworks have been elaborated to forecast ecosystem functioning from individual traits, such as the metabolic theory of ecology and ecological stoichiometry [3,4]. Functional traits (particularly **functional effect traits** [2]) indeed allow inferring causal mechanisms (e.g., body size alters resource partitioning) that help understanding of key ecosystem properties, such as the biodiversity–ecosystem functioning relationships. By determining biotic interactions in communities, the variability of functional traits affects species coexistence and matter fluxes (i.e., chemical elements, including nutrients) in food webs, ultimately altering ecosystem processes [5].

Nonetheless, research on the effects of individual trait variability on ecosystems still rarely considers the spatial structure of the environment [6–8]. Food webs in local communities can indeed be connected by spatial flows of organisms forming a food web **meta-community** [7]. **Dispersal** can affect biotic interactions (e.g., predation) in food web meta-communities, modifying species coexistence within communities [9,10]. These exchanges of organisms between local communities can modify nutrient fluxes within the landscape that, added to abiotic energy and material fluxes between and within local ecosystems, form **meta-ecosystems**. Dispersal of organisms is a key process linking populations and communities, and the resulting fluxes of nutrients sequestered in organisms among habitats form a central part of meta-ecosystem dynamics as they affect primary production, consumption, and decomposition [11–13].

While dispersal was mostly considered as a rate in meta-community and meta-ecosystem literature, it is now widely acknowledged to be a nonrandom process resulting from several

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environmental factors, phenotypic traits, and their interactions [14]. For instance, niche breadth and life-history traits are correlated with dispersal variability among species [15]. Within species, dispersal decision of individuals can also depend upon their phenotype, involving morphological, physiological, or behavioural characteristics correlated with dispersal. For instance, in rodents, dispersers are often more active, are bolder, and explore more than residents [16]. Similarly, polymorphism (e.g., wing length of insects) is often associated with dispersal distance [17]. Such correlation or co-occurrence between a suite of phenotypic traits and dispersal forms a **dispersal syndrome** [14,16,18,19], which may result from multiple ecological and evolutionary processes (Box 1).

Dispersal syndromes are known to affect the spatial heterogeneity of functional traits and in turn mediate intra/interspecific interactions and meta-community dynamics [20–22]. However, whether this variability in the movements of organisms and their phenotypic traits in landscapes can in turn modify the flows of energy and materials and affect food web meta-community and meta-ecosystem functioning is rarely studied theoretically or empirically. Here, we build upon empirical evidence on vertebrates, arthropods, and microorganisms to highlight that traits classically integrated into trait-based ecology and known for their role in ecosystem functioning can be linked to dispersal propensity. Based on this evidence for dispersal syndromes as a linkage between trait-based ecology and ecosystem functioning, we point out potential implications of these dispersal syndromes for meta-ecosystem functioning (Figure 1). We explore the consequences of dispersal syndromes and their evolution for the spatial heterogeneity of ecosystem functions.

On the ecosystem importance of dispersal-related traits

The phenotypic structure of populations has received strong consideration from ecologists, and the description of functional effect traits has allowed a mechanistic understanding of the effects of individuals on ecosystems [2,23]. The variability of functional traits within a species can be large [24] and can modify the strength of trophic and nontrophic interactions, such as nutrient recycling within an ecosystem [25]. For example, consistent differences in foraging behaviour in pale chubs

Box 1. Processes generating dispersal syndromes and their consequences for meta-ecosystems

Dispersal is part of large association among suites of phenotypic traits (e.g., pace-of-life framework [34]) whose respective evolution can greatly influence each other. Multiple processes can explain these covariations between phenotype and dispersal [14,19,22], which may generate variability of dispersal syndromes within and between species. First, trade-offs may result in negative correlations between dispersal and other traits, as when allocation of time and energy to dispersal limits investment in other biological functions (e.g., foraging, immunity). Second, syndromes can emerge from structural links between dispersal and other traits, including gene pleiotropy or allometric scaling. Finally, dispersal syndromes can result from selection, when the environment favours both dispersal and other traits (coselection) or when selection on dispersal affects the evolution of other traits or the reverse (joint selection). In addition, both dispersal and related phenotypic traits can be determined by both genetic and environmental factors [19], which can generate different levels of spatial and temporal variability in dispersal syndromes. The level of heritability of traits involved in dispersal syndromes can modify the strength, direction, and variance of correlations between traits and dispersal across generations. Furthermore, plasticity in dispersal and related traits along environmental conditions can result in important and rapid changes in traits and their covariations, potentially generating high variability in dispersal syndromes.

Depending on the relative importance of processes generating dispersal syndromes and their variation across time and space, the extent of intraspecific variation and direction of correlations between dispersal and functional traits might change among localities. Investigating how much dispersal syndromes vary among localities is thus crucial to better understand their importance, for example, on meta-population dynamics [21], species range distribution [73], or the diversity and stability of meta-ecosystems [60]. For instance, landscape fragmentation usually increases dispersal costs and might exacerbate dispersal syndromes that result from trade-offs [19], ultimately potentially increasing the consequences for the spatial heterogeneity of meta-ecosystems. Furthermore, environmental changes can generate different levels of intra- and interspecific variability of dispersal syndromes when dispersal and related traits are plastic [74]. We might expect the resulting variability of dispersal syndromes to determine the strength and type of species interactions, thereby modifying patterns of diversity within communities and potentially meta-ecosystem stability and resilience. Identifying which mechanisms underlie variability of dispersal syndromes is thus one of the key challenges to better understand their effects on meta-ecosystem functioning.

Glossary

Dispersal: any movement of individuals from one population to another that can potentially lead to gene flow. Dispersal should not be confused with migration, that is, a back-and-forth movement (often seasonal but not exclusively) between a reproduction site and a site where other parts of the life cycle are spent.

Dispersal syndrome: suite of phenotypic traits correlated with dispersal (i.e., differentiating dispersers from residents or along dispersal rate or distance).

Ecosystem functioning: set of processes (or functions) describing changes in energy and matter dynamics due to biological, physical, or geochemical factors.

Functional effect trait: individual characteristics affecting community or ecosystem processes (also referred to as functional traits in the text). Can be differentiated from functional response traits allowing organisms to cope with environmental variability.

Individual trait variability (= intraspecific trait variability): variability of trophic, physiological, behavioural, or morphological features displayed by individuals within a species.

Meta-community: set of local communities linked by the dispersal of organisms. Multiple theoretical meta-communities have been studied, such as food web meta-communities or competitive meta-communities.

Meta-ecosystem: set of local ecosystems connected by flows of energy, matter, and organisms.

Nutrient-mediated effects: modification of the dynamics of nutrient elements independent of consumptive effects, for instance through excretion of nitrogen, phosphorus, or carbon.

Trait-based ecology: study of the interactions between organisms' phenotype and their environment.

Trophic interactions: interactions linked to the feeding habits and the consumption of organisms and describing vertical matter fluxes.

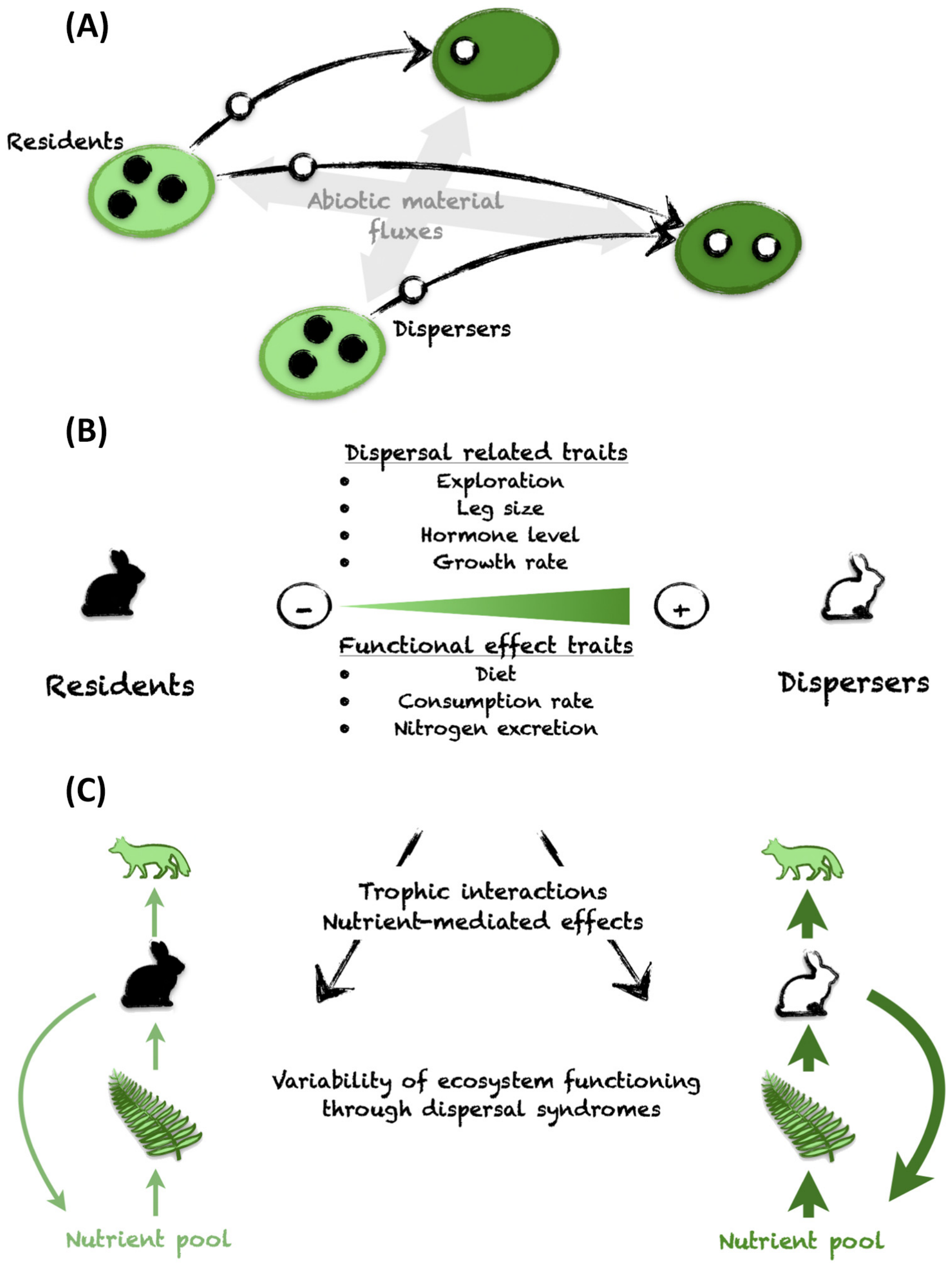

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Figure 1. Overview of the potential linkage between dispersal syndromes and meta-ecosystem functioning through covariations with functional effect traits. (A) Dispersal syndromes consist of dispersers (white circles) with different phenotypes than residents (black circles), potentially leading to a spatial heterogeneity in the distribution of phenotypic traits. Grey arrows represent abiotic fluxes (nutrients and material) that may interact with dispersal in shaping meta-ecosystem functioning. (B) Dispersal syndromes can involve multiple phenotypic traits, such as morphology (e.g., leg size) or physiology (e.g., hormone levels). These traits are known to be linked to key functional effect traits important for ecosystem functions such as consumption rate, nitrogen excretion, and nutrient recycling. The figure illustrates an example where dispersers are more active explorers and consume more resource than residents, but other relationships can exist (see Table 1 in main text). (C) Dispersal syndromes can therefore make local ecosystems differ in key properties such as biomass production, consumption rate, and nutrient recycling, hence increasing spatial heterogeneity of meta-ecosystem functioning.

(*Zacco platypus*) alter trophic cascades [26], and morphology of mandible in shredders (*Gammarus fossarum*) drives decomposition rate [27]. Functional traits and their intraspecific variability therefore have consequences for species coexistence and community structure and subsequently drive the flows of energy and materials within and among ecosystems.

Key functional traits have been found to be related to individual dispersal propensity. In Table 1, we provide a list of relationships within the same species between dispersal and phenotypic traits on the one hand and between these phenotypic traits and functional effect traits (sometimes even ecosystem functions) on the other hand. As such, in a freshwater fish (*Salmo trutta*), higher dispersal propensities are associated with larger body sizes [28], a trait correlated in this species with nutrient excretion rate [29] and known as key for ecosystem functioning [30]. Moreover, movements of dispersers can be associated with higher metabolic costs compared with residents [31] – metabolism is a key trait for ecosystem functioning [3] – which can induce higher consumption rates to counterbalance the energetic expenditure (as found in the butterfly *Melitaea cinxia* [32,33]). Finally, dispersal is often part of a general behavioural syndrome involving multiple traits [34]. In the signal crayfish (*Pacifastacus leniusculus*), individuals staying in core populations (i.e., residents) of an invasion front are more aggressive [35], which can alter multiple dimensions of ecosystems such as **trophic interactions** in food webs [36,37].

Because of dispersal syndromes, individuals moving within a landscape can carry different functional traits from individuals staying locally, and spatially heterogeneous distribution of

Table 1. Traits involved in dispersal syndromes are often linked with functional traits of key importance for ecosystem dynamics[a]

Trait category	Species	Dispersal-related traits	Functional effect traits	Expected relationship between dispersal and functional effect trait
Morphology	Pygmy grasshopper (*Tetrix subulata*, arthropod)	Wing length (+) [17,61]	Diet (+) [41]	Dispersal is positively correlated with trophic position
	Brown trout (*Salmo trutta*, fish)	Body length (–) [28]	Diet/excretion rate (+) [62,29]	Dispersal is negatively correlated with N-excretion rate and trophic position
	Three-spined stickleback (*Gasterosteus aculeatus*, fish)	Stream morphology (+) [63]	Prey biomass (–) [64]	Dispersal reduces prey biomass
Behaviour	Mosquitofish (*Gambusia affinis*, fish)	Sociability (–) [40]	Prey biomass (+) [40]	Dispersal reduces prey density
	Signal crayfish (*Pacifastacus leniusculus*, arthropod)	Aggressiveness (–) [35]	Food consumption (+) [37]	Dispersal is negatively correlated with prey consumption
	Great tit (*Parus major*, bird)	Exploration (+) [65]	Competitive dominance (+) [66]	Dispersal is positively correlated with competitiveness
	Bank vole (*Myodes glareolus*, mammal)	Activity (+) [67]	Food consumption (+) [67]	Dispersal is positively correlated with consumption rate
	Dragonfly (*Libellula spp.*, arthropod)	Colonisation distance (+) [38]	Food consumption (+) [38]	Dispersal is positively correlated with consumption rate
Physiology	Sand field cricket (*Gryllus firmus*, arthropod)	Lipid and amino acid metabolism (+) [17,68]	Nutrient content (+) [47]	Dispersal is positively correlated with lipid and triglyceride content
	Common lizard (*Lacerta vivipara*, squamate)	Corticosterone (–) [69,70]	Food consumption (+) [71,72]	Dispersal is negatively correlated with food intake
	Glanville fritillary (*Melitaea cinxia*, arthropod)	Metabolic rate (+) [32]	Food consumption (+) [33]	Dispersal is positively correlated with food intake
Life history	Common triplefin (*Forsterygion lapillum*, fish)	Growth rate (–) [46]	Nutrient content (–) [46]	Dispersal is negatively correlated with lipid concentration

[a] We present a nonexhaustive list of empirical examples where a trait in a given species is involved in dispersal syndromes and where the same trait (or dispersal directly) is linked to a functional effect trait, therefore potentially sustaining dispersal syndrome effects on meta-ecosystems. Positive and negative correlations are denoted by (–) or (+), respectively.

environmental conditions (e.g., environmental gradients and source–sink systems) can make the fluxes of individual phenotypes asymmetric. Therefore, spatial variability of functional traits can be generated among landscapes, potentially modifying the interactions within meta-communities and in turn material and energy fluxes in meta-ecosystems. These altered fluxes can affect two essential and intertwined dimensions of ecosystems: the strength of trophic interactions and nutrient recycling. Especially, trophic interactions govern food web structure in meta-communities, with subsequent effects on biomass production that are key for meta-ecosystem functioning. First, dispersal syndromes can modify the spatial heterogeneity of traits linked to energy and nutritional needs of organisms, consequently modifying trophic interactions [3,36,38]. For instance, in decomposer species, dispersers may display higher litter consumption, hence affecting the decomposition rate of organic matter, although this effect varies among species [39]. In mosquitofish (*Gambusia affinis*), dispersers are less sociable than residents, which affects prey biomass because sociability is correlated with food intake [40]. Dispersal-related morphological traits can also be important for ecosystem functioning. In pygmy grasshoppers (*Tetrix subulata*), a morphological specialisation for dispersal (i.e., fully developed wings) is associated with a different diet compared with wingless individuals [41]. This can potentially affect the recipient ecosystem through altered trophic interactions. These examples show that dispersal syndromes can affect material fluxes in food webs and thus ecosystem functions, such as decomposition of organic matter, through changes in trophic interactions (Table 1) [42].

Second, dispersal syndromes can produce **nutrient-mediated effects**, modifying nutrient and detritus influxes in ecosystems, both qualitatively and quantitatively [22]. In a freshwater fish (*S. trutta*), larger individuals disperse farther than smaller individuals [28] and display higher nutrient excretion rates (i.e., N and P) [29]. Such intraspecific variability in nutrient excretion rate, resulting from catabolic and homeostatic mechanisms, is large enough to generate functional differences among ecosystems, notably concerning primary production [30,43]. Differences between residents and dispersers may affect the spatial variability of productivity in meta-ecosystems. For example, in phosphorus-limited habitats, individuals with a higher phosphorus excretion rate cause an increased biomass of primary producers [44]. Organic material recycling might also be altered by differential mortality between residents and dispersers induced by the costs of dispersal. For instance, dispersers can have a higher parasite load than residents have [45], which may increase mortality and thus alter the stocks of dead organic matter. Moreover, the stoichiometry of organisms is an important factor governing ecosystem functions [4] and has recently been discussed as a key parameter linking dispersal to meta-ecosystems [22]. Intraspecific variability of stoichiometry has been documented [4], and several studies suggest that differences between residents and dispersers are likely. For instance, differences in chemical composition (e.g., lipid and triglyceride reserves) between residents and dispersers have been found in marine fish [46] and insects [47]. Since chemical compounds within organisms consist of different proportions of the basic elements, differences in molecular traits (e.g., RNA content) and key physiological functions are expected to be associated with variability in organisms' stoichiometry [48,49]. The potential for dispersal syndromes to include stoichiometric variability might thus result in altered nutrient flows among local ecosystems. Studying the three-way association between dispersal, stoichiometry, and ecosystem functioning is an important future challenge [22], especially since dispersal can couple distant (but often similar) ecosystems, while resource flows mostly occur locally [50].

Implications of dispersal syndromes for meta-ecosystem functioning

Meta-community research has emphasised the central role of dispersal as a process linking biotic interactions, and global rates of material flows (through both abiotic and biotic fluxes) among local ecosystems are core to meta-ecosystem theory [10,51]. However, dispersal can be differentiated from abiotic fluxes as it can alter spatial distribution of organisms, mediating directly biotic interactions, in addition to modifying nutrient fluxes. For instance, increasing dispersal rate tends to homogenise food webs and functions across space in a nonlinear manner, above a certain threshold [9,10,51] (although increasing consumer dispersal can also generate spatial heterogeneity [52]). Yet, dispersal is more than just movement rate or distance, it also includes the phenotypic characteristics of resident and disperser individuals, and therefore a potential different package of flowed nutrients (i.e., dispersing individuals). However, the potential for differences between dispersers and residents in multiple functional traits is currently not integrated in meta-ecosystem theory.

As highlighted earlier, dispersal syndromes often involve functional traits of major importance for ecosystem functioning (Table 1). The heterogeneity of phenotypic distributions resulting from dispersal syndromes, that is, when dispersers have different phenotypes than residents in heterogeneous landscapes, may generate spatial differentiation in ecosystem functioning. For instance, the establishment of individuals or species in novel habitats as occurring during recolonisation or range shifts may be associated with a non-random subset of traits, such as body mass or diet. This generates spatial heterogeneity in functional trait distribution [53] and in turn affects resource fluxes and thus ecosystem biomass. Therefore, any biased flow of functional traits carried by dispersers in heterogeneous landscapes may modify the spatial heterogeneity of meta-ecosystems, whose importance could depend upon nutrient flows (Box 2).

The effects of dispersal on meta-ecosystems are known to depend on the rate of dispersal in classic theory. With dispersal syndromes, since dispersers differ from residents, differences in dispersal rate do not only change the total flow of organisms within meta-ecosystems, but also mediate the spatial distribution of functional trait values (Box 2). For instance, in a scenario where dispersers consume more resources than residents (as found in [39]), intermediate dispersal rates would alter the heterogeneity of biomass consumption at the meta-ecosystem scale compared with a scenario in which individuals disperse regardless of their phenotype. Thus, the heterogeneity in resource standing stock can be modified (Box 2). Therefore, developing an integrative framework including dispersal syndromes in a meta-ecosystem might benefit our understanding of spatially structured environments.

Importantly, dispersal syndromes can differ among populations or species [14–16]. Environmental conditions and evolutionary processes can strongly shape dispersal syndromes [19]. The direction and strength of covariations, as well as the traits involved in dispersal syndromes, are the result of an evolutionary history in which biotic interactions and landscape configuration play a key role [19,54] (Box 1). The resulting variability in dispersal syndromes and thus of flows of functional traits might alter meta-ecosystem dynamics through trophic interactions and nutrient-mediated effects. For instance, when dispersal is associated with high competitive abilities (e.g., due to higher aggressiveness as found in bluebirds [55]), an increased dispersal rate would lead to an increase in competition strength in colonised habitats. On the contrary, dispersers can often be poorer competitors (e.g., competition–colonisation trade-off, costs of dispersal, and local exclusion of poorer competitors) [31,56]. If competitive interactions drive community composition, the consequences of dispersal for community composition, and subsequently the level and stability of ecosystem functions, are likely to depend on the form of dispersal syndromes and thus on their ecological and evolutionary drivers.

The role of evolutionary processes for ecosystem functioning has been studied at the local scale [23]. At the meta-community level, Urban and Skelly [57] have drawn a framework integrating the evolution of intraspecific trait variation in meta-communities. They emphasised that genetically

Box 2. A mathematical illustration of the potential effects of dispersal syndromes on a key component of meta-ecosystems: consumption rate

We investigated the consequences of dispersal for the spatial variability of consumption rate, a key component of meta-ecosystems, when dispersal is correlated positively or negatively to this functional trait, as found in many species (see Table 1 in main text). To do so, we constructed a meta-population model with dispersal of a consumer in a landscape consisting of a ten-habitat patch network. Local environmental conditions varied randomly and temporally, leading to random local extinctions. We drew multiple scenarios involving dispersal syndromes (see the supplemental information online). In a scenario of absence of a dispersal syndrome (i.e., residents and dispersers display equal consumption rates; yellow lines) (Figure I), increasing dispersal rate is expected to increase total resource consumption (left panel) and decrease its spatial heterogeneity (nonlinearly; right panel) in meta-ecosystems. We then considered dispersal syndromes, with dispersers showing either higher (competitive advantage) or lower (competition–colonisation trade-off) consumption rate compared with residents, while setting the mean consumption rate constant across different dispersal probabilities. In the case of a positive association of consumption rate and dispersal (blue lines), we observed a slight increase in total resource consumption at intermediate dispersal rates (Figure IA), resulting from increased abundance of the disperser phenotype following recolonisation of extinct patches. Although the effects on resource consumption at the landscape scale (left panel) are weak, they create an important spatial heterogeneity of resource consumption in the meta-ecosystem (Figure IA). While increasing dispersal always has a homogenising effect above a certain threshold, the inclusion of a dispersal syndrome where dispersers are weaker consumers than residents (red curve) could strongly moderate this effect, resulting in higher heterogeneity than previously predicted. On the contrary, higher consumption in dispersers (blue curve) results in a decrease of spatial heterogeneity of ecosystem function and alleviates the effect of dispersal rate. The integration of abiotic nutrient fluxes will be an important next step since they may affect species persistence and interactions. Therefore, further studies should investigate whether abiotic fluxes interact with or blur the effects of dispersal syndromes on local biomass and nutrient recycling. This simple model highlights the potential for dispersal syndromes to significantly affect the spatial variability in ecosystem function, with direction of effects that depends on the type of dispersal syndrome considered, pointing out the potential for further investigation of the integration of dispersal syndromes in meta-ecosystem theory.

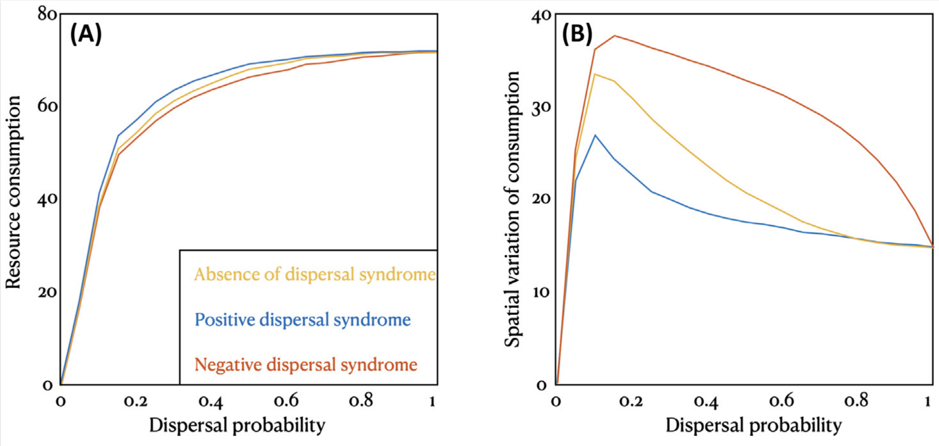

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Figure I. Hypothetical examples of consequences of dispersal syndromes for resource consumption in the meta-ecosystem, concerning both its average value (A) and its spatial heterogeneity of resource consumption (B).

based trait variation might be a major component of meta-community structure affecting species coexistence. Therefore, by extending this concept, dispersal syndromes can have two main roles in the evolutionary dynamics of meta-communities and meta-ecosystems: eco-evolutionary dynamics and local adaptations. First, since the evolution of intraspecific variability of dispersal and its associations with phenotypic variability depend on biotic and abiotic conditions, the existence and form of dispersal syndromes are likely to vary in space and time [19]. Therefore, eco-evolutionary feedback between dispersal and meta-ecosystem functioning can arise because of environmental fluctuations, due to the dependency of dispersal syndromes on abiotic conditions and its effect on ecosystem functions. The consequences of dispersal for meta-ecosystems are expected to differ depending on the nature of the syndrome (Box 2). Therefore, integrating the evolutionary dynamics of dispersal-related traits into meta-ecosystem theories should help understand how ecosystem functioning varies in the face of environmental changes.

Second, dispersal is generally expected to slow down adaptation by homogenisation of local gene pools, at least over a certain threshold. Nonetheless, theoretical and experimental studies have shown that it may instead promote local adaptation and thus population phenotypic differentiation when individuals choose to disperse and settle in habitats that better suit their phenotype [58]. Since dispersal syndromes are also expected to generate spatial heterogeneity of phenotypic traits, the interaction between dispersal syndromes and habitat choice might alter the dynamics of trait variation within and between populations. Whether dispersal syndromes are fixed at the scale of population or species or depend on environmental conditions (Box 1) might generate dynamic phenotypic flows in meta-ecosystems according to evolutionary dynamics (e.g., local adaptation) and ecological context. By modifying trait dynamics within and among populations, dispersal syndromes might hence alter functional divergences among food webs and ecosystems across generations. Indeed, functional traits linked to dispersal propensity may be inherited across generations and so may be the consequences of these traits for ecosystem functioning [59]. Investigating the potential for such eco-evolutionary dynamics of dispersal to affect biotic interactions and as a result food webs and ecosystems is of particular importance.

Concluding remarks

Dispersal syndromes mediate phenotypic distributions and hence interaction strength and nutrient release in ecological networks and thus may play a major role in meta-ecosystem functioning. We especially pointed out that links between dispersal and traits of key importance for ecosystem functioning can modify trophic interactions and material fluxes. For example, dispersal syndromes can make dispersal increase spatial heterogeneity in ecosystem functioning relative to cases without dispersal syndromes. Predictions regarding spatial dynamics of meta-ecosystems may hence benefit from the integration of dispersal syndromes. Yet, dispersal syndromes can vary across species in both direction and traits involved, which might affect the consequences for meta-ecosystems (Box 2). Improving our understanding of the role of dispersal for the spatial dynamics of meta-ecosystems thus requires further effort in integrating dispersal syndromes in meta-ecosystem theoretical frameworks, but also increased investigation of the ecological and evolutionary drivers of dispersal syndromes.

Modelling approaches can be a powerful method to evaluate the role of phenotypic-dependent dispersal for meta-ecosystem functioning. For instance, existing models [22,52] can be modified to implement dispersal syndromes. This would allow us to determine whether the phenotypic differences between dispersing and nondispersing individuals might result in increased complexity in ecological interactions, potentially quantitatively or qualitatively altering meta-ecosystem functioning and stability [60]. Such models should further allow assessment of whether and how the evolution of dispersal syndromes alters meta-ecosystem dynamics. The evolution of dispersal syndromes is important to account for since anthropogenic pressures change the environmental conditions that are known to shape dispersal syndromes (e.g., habitat fragmentation).

Transposition of those predictions to nature is challenging due to the inherent large scale of meta-ecosystem frameworks [8], but correlative approaches in the field coupled with adequate statistics (e.g., structural equation modelling) can bring insights into the relationships between dispersal syndromes, spatially structured diversity, and ecosystem patterns. A further necessary step to identify whether dispersal syndromes directly or indirectly affect meta-ecosystems will be to take

Outstanding questions

Can landscape configuration and anthropogenic modifications of landscapes (e.g., fragmentation) mediate dispersal syndrome effects on meta-ecosystems? How do different regimes of spatial and temporal variability in environmental conditions affect dispersal syndromes and their ecosystem consequences?

Marine, freshwater, and terrestrial ecosystems often differ in their environmental variability and constraints on dispersal movements. Do the evolution of dispersal syndromes and consequences for meta-ecosystems differ across biomes?

In what ways do the mechanisms underlying dispersal syndromes (plastic or genetic) determine the nature and timing of meta-ecosystem consequences? Do meta-ecosystem dynamics affect in turn the evolution of dispersal syndromes? Do eco-evolutionary feedbacks between dispersal syndromes evolution and ecosystem dynamics exist and how do they drive long-term dynamics of ecosystem functioning?

How do differences in mechanisms underlying syndromes and the relative importance of intra- and interspecific variability affect meta-ecosystem dynamics? How do we integrate such variability within and among species in a meta-ecosystem theoretical framework?

Invasion dynamics and range expansions of populations are currently occurring worldwide. Does integration of dispersal syndromes in these theories help predict future impacts on ecosystems?

How do we decipher the effects of population density from those of phenotypic differentiation in natural systems?

Can dispersal syndromes change qualitatively or quantitatively the effects of dispersal for spatial and temporal stability (including resilience and resistance) of meta-ecosystems?

What are the species characteristics (trophic level, functional role, passive or active dispersal, or dispersal distance) that make dispersal syndrome more or advantage of the increasingly used micro/mesocosm experiments. Manipulating dispersal syndromes (i.e., shape and variance) and key characteristics of the environment (e.g., abiotic conditions and habitat fragmentation) in simplified meta-ecosystems is an essential step forward for our comprehension of the effects of dispersal syndromes on biodiversity, biomass production, and stability of meta-ecosystems. Understanding the role of variability of dispersal for meta-ecosystem functioning is an exciting and challenging topic for years to come (see Outstanding questions). In a world where human activities are constantly shaping landscape structure, considering those issues might also help design ecological applications, such as conservation strategies.

less important at the meta-community and meta-ecosystem scales?

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Declaration of interests

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