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Author for correspondence:
Emanuel A. Fronhofer
e-mail:
emanuel.fronhofer@umontpellier.fr

Evolutionary ecology of dispersal in biodiverse spatially structured systems: what is old and what is new?

Emanuel A. Fronhofer[1], Dries Bonte[2], Elvire Bestion[3], Julien Cote[4], Jhelam N. Deshpande[1], Alison B. Duncan[1], Thomas Hovestadt[5], Oliver Kaltz[1], Sally Keith[6], Hanna Kokko[7], Delphine Legrand[3], Sarthak P. Malusare[1], Thomas Parmentier[2,8], Camille Saade[1], Nicolas Schtickzelle[9], Giacomo Zilio[1] and François Massol[10]

[1] ISEM, University of Montpellier, CNRS, IRD, EPHE, Montpellier, France
[2] Terrestrial Ecology Unit (TEREC), Department of Biology, Ghent University, K.L. Ledeganckstraat 35, B-9000 Ghent, Belgium
[3] Station d'Ecologie Théorique et Expérimentale, CNRS, UAR 2029, F-09200 Moulis, France
[4] Laboratoire Évolution & Diversité Biologique, CNRS, Université Toulouse III Paul Sabatier, IRD; UMR5174, 118 route de Narbonne, F-31062 Toulouse, France
[5] Department Animal Ecology and Tropical Biology, Biozentrum, University of Würzburg, Würzburg, Germany
[6] Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, UK
[7] Institute of Organismic and Molecular Evolution, Johannes Gutenberg University, 55128 Mainz, Germany
[8] Research Unit of Environmental and Evolutionary Biology, Namur Institute of Complex Systems, and Institute of Life, Earth, and the Environment, University of Namur, Rue de Bruxelles 61, 5000 Namur, Belgium
[9] Earth and Life Institute, UCLouvain, B-1348 Louvain-la-Neuve, Belgium
[10] Institut Pasteur de Lille, Univ. Lille, CNRS, Inserm, CHU Lille, U1019 - UMR 9017 - CIIL - Center for Infection and Immunity of Lille, Lille, France

Dispersal is a well recognized driver of ecological and evolutionary dynamics, and simultaneously an evolving trait. Dispersal evolution has traditionally been studied in single-species metapopulations so that it remains unclear how dispersal evolves in metacommunities and metafoodwebs, which are characterized by a multitude of species interactions. Since most natural systems are both species rich and spatially structured, this knowledge gap should be bridged.

Here we discuss whether knowledge from dispersal evolutionary ecology established in single-species systems holds in metacommunities and metafoodwebs and highlight generally valid and fundamental principles. Most biotic interactions form the ecological theatre for the evolutionary dispersal play because interactions mediate patterns of fitness expectations in space and time. While this allows for a simple transposition of certain known principles to a multispecies context, other drivers may require more complex transpositions, or might not be transferred. We discuss an important quantitative modulator of dispersal evolution, increased trait dimensionality of biodiverse meta-systems, and an additional driver, co-dispersal.

We speculate that scale and selection pressure mismatches due to co-dispersal, together with increased trait dimensionality may lead to slower and more "diffuse" evolution in biodiverse meta-systems. Open questions and potential consequences in both ecological and evolutionary terms call for more investigation.

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1. Introduction

Dispersal is a central life-history trait [1], defined as the process by which an organism reproduces away from where it is born [2–6]. By definition, dispersal is therefore different from seasonal migration or foraging [7], which do not lead to gene flow. Dispersal can be quantified in multiple ways, such as through dispersal distance, dispersal frequency in long-lived mobile organisms, the proportion of dispersed offspring, or even the proportion of immigrants among a population's reproductive cohort. Dispersal affects many facets of population biology, such as population densities, phenotypic and genotypic composition, species ranges and spatial distributions, their persistence in the face of perturbations, or their ability to adapt to local conditions [1,8–11]. Ultimate and proximate determinants of dispersal have received substantial interest from both empiricists and theoreticians and are integrated in the framework of evolutionary conservation biology [12]. Dispersal also plays a pivotal role at the interface between ecology and evolution and is part of eco-evolutionary feedbacks [13,14].

As an important driver of ecological dynamics, from population to ecosystems, dispersal is under a wide range of selective pressures which we discuss below [6]. Yet, most of our understanding comes from single-species studies (but see e.g., [15,16]; for a review focused on range dynamics see [17]), or theoretical work that considers selection acting within one species [18–22]. Dispersal evolution models that do include inter-specific interactions (e.g., predation, facilitation, parasitism) traditionally consider these interactions only implicitly or in a very simplified manner, such as seed predation accounting for the extra mortality of dispersed and dormant seeds [23]. The lack of a community angle is perhaps not surprising given that the topic of dispersal has been historically entwined with population biology, demography, life-history evolution and the metapopulation framework [24]. Yet, this oversight constitutes a substantial knowledge gap since interactions between organisms extend beyond intraspecific competition for limiting resources, and encompass a continuum of antagonistic and mutualistic interactions with various degrees of immediacy, from event-like (e.g., predation) to lifelong interactions (obligate symbiotic relationships). All interactions are likely to affect selection on, and the consequences of dispersal. For instance, a large proportion of parasitic and mutualistic symbionts disperse thanks to the movement of their hosts [25–27] and plants often make use of animal vectors to disperse their seeds [28,29].

We address this knowledge gap in two parts, focusing on the regional scale traditionally studied in metapopulation and metacommunity ecology (for a discussion of scales and links to ecosystem dynamics, see [30]). First, we set the scene by synthesizing what is already known about dispersal evolution from the single-species perspective. Second, we discuss how far these known mechanisms can be transposed to a multi-species context and highlight novel aspects that may be relevant in driving dispersal in multispecies meta-systems. In both cases, we tackle the ultimate causes of dispersal, i.e., the selective pressures on dispersal, as well as the proximate triggers of dispersal, which include the factors driving dispersal plasticity. We end by discussing new perspectives relevant to a multispecies world and future research directions.

2. A synthesis on dispersal evolutionary ecology in a single-species world

(a) Why disperse?

Comprehensive reviews on dispersal evolution have listed the different selective pressures on dispersal and how their combination results in positive, negative, disruptive or stabilizing selection [3,4,6]. In brief, dispersal is selected for in situations in which there is temporal variability in environmental conditions [31], perturbations [32], kin competition [18], and inbreeding depression [33]. In contrast, stable spatial heterogeneity in fitness expectations [34,35] and direct dispersal costs [36], which can result from a variety of factors including trade-offs, fragmentation and landscape resistance, favour non-dispersing individuals.

Beyond these basic selective forces, demography play a complex role in dispersal evolution. For example, chaotic population dynamics can select for higher dispersal rates [37], while Allee effects can select against dispersal [38]. When populations do not systematically reach carrying capacity as assumed in occupancy models, increasing population extinction rate does not always select for higher dispersal rates, because frequent local extinctions tend to weaken the overall intensity of competition ([39]; but see [40]).

Beyond demography and focusing on more complex life histories, the timing of dispersal has a major impact on both the evolution of dispersal rates and distances [41]. Combining selective pressures on dispersal can lead to complex outcome including disruptive selection. For instance, a combination of spatial heterogeneity, kin competition and dispersal costs can lead to the evolutionary branching of dispersal rates [21,22,42].

The evolution of dispersal can interact with evolution of other traits, like local adaptation [43–46] and self-fertilization [47–49], two traits that are especially sensitive to the spatial scale defined by dispersal (see [50] for a population genetics model which considers dispersal evolution in response to local adaptation and inbreeding depression). The joint evolution of dispersal with local adaptation can result in disruptive selection or alternative evolutionarily stable strategies in temporally variable environments. Indeed, habitat generalists perceive and/or react to this variability to a lesser degree than specialists, hence associating selective pressures for generalism with selective pressures against dispersal ([43]; see also [51], considering selfing individuals as "pollination generalists"). In spatially heterogeneous habitats, generalists tend to disperse more than specialists ([45]; see also [49] for the selfing evolution equivalent).

The evolution of dispersal can thus be affected by the evolution of other traits through reciprocal selective pressures (i.e., joint evolution; as a response to fitness effects imposed by the evolution of another trait, or conversely, other traits evolve in response to the evolution of dispersal). This naturally generates correlations between dispersal and other traits, i.e. "dispersal syndromes". However, this constitutes just one of the reasons behind the existence of dispersal syndromes [52], as syndromes could also emerge from allocation trade-offs (e.g., foraging vs. dispersal), genetic correlations and pleiotropy, structural constraints (e.g., allometric scaling), or shared selective pressures (e.g., inbreeding depression affecting both the evolution of selfing and dispersal when accounting for inbreeding between relatives).

While the evolution of dispersal has traditionally been considered in metapopulations that do not expand in space, dispersal can also evolve during range expansions. In particular, considering the evolutionary dynamics of populations along an invasion front has highlighted the existence of "spatial selection", by which higher dispersal rates are selected at the front of an advancing invasion wave [53–55] for a number of reasons: First, individuals with a higher dispersal rate have a higher probability of ending up at the front of the wave (ecological filtering; [56]). As a consequence, passive assortative mating in sexually reproducing species can further enhance this pattern. Second, dispersal can evolve via trade-offs between competitiveness and dispersal [57] due to gradients of local competition strength, since denser populations far from the front harbour more intense competition. Alternatively, a general trade-off between foraging and dispersal can also generate the same selection for higher dispersal rates at the front [58]. Finally, enhanced kin competition due to repeated "founder effects" at the invasion front also promotes enhanced dispersal [59]. Spatial selection is interesting as it can lead to accelerating range expansions which may explain the rapid recolonization of trees in temperate latitudes since the last glacial period (Reid's paradox; see [60]). The evolution of higher dispersal rates at the invasion front is also reminiscent of the evolution of lower dispersal in ageing demes [61] — in both cases, newly colonised patches harbour individuals with higher dispersal rates than older ones.

(b) Dispersal plasticity: context- and state-dependencies

Dispersal need not be a fixed trait, but can respond plastically to internal and external cues [2]. The biotic and abiotic contexts can affect both emigration and immigration [62]. The extrinsic context typically includes patch-quality proxies (or simply patch types, e.g. [63]), such as patch size [64], patch age [65], population growth rate, population density [66–68], carrying capacity [69], as well as available information about such proxies (number of mated or reproducing conspecifics, e.g. [70]). Information about the habitat matrix can also modulate context-dependent dispersal decisions [71,72]. The reliability of cues is an important parameter affecting the evolution of dispersal plasticity [73].

Intrinsic individual-level conditions affecting dispersal include sex [74–76], age [77], developmental stage [78], body size or condition [79,80], or any proxy of competitiveness, for example. Intrinsic and extrinsic cues can of course be used at the same time and interact to determine dispersal decisions [81].

(c) Consequences of dispersal

In a single-species context, dispersal is known to have multiple consequences, both ecologically and evolutionarily [3,82]. From an evolutionary point of view, dispersal promotes genetic mixing: immigrants bring new alleles into populations and thus increase local genetic diversity. Conversely, a (very) low dispersal rate between populations increases differentiation. The mixing effect of dispersal thereby constrains local adaptation and may lead to "migration load" known from classic population genetics models. This is especially striking in continuous space models of adaptation on environmental gradients, where high dispersal rates tend to impede local adaptation [83–86]. The stage at which dispersal takes place is also critical to the evolution of local adaptation, so that higher dispersal rates might actually not affect local adaptation in certain cases [87–90].

From an ecological point of view, dispersal is also an important parameter controlling the dynamics of metapopulations in at least two different ways. First, dispersal drives the synchrony of local population dynamics, but in a non-linear manner that also depends on other factors such as perturbation frequency, the relative speed of population dynamics of the focal species vs. its natural enemies or resources, or the spatial extent of dispersal [91–96]. Second, dispersal determines the resilience of metapopulations to perturbations as higher dispersal rates can lead to more rapid recolonisation after local extinction.

At the metapopulation level, an important effect of higher dispersal rates is higher occupancy, as long as dispersal translates into higher colonization rates [97–99]. In other words, species occupy more patches when they disperse more. However, this general rule can be counteracted in two important ways. First, when the costs of dispersal are substantial, dispersal rates that are too high can induce a decrease in colonization rate since emigrating effectively leads to a decrease in local birth rate [99]. Put differently, if dispersal is costly, high emigration rates lead to a reduction of total metapopulation size. Second, when local populations experience an Allee effect, dispersal hinders the maintenance of population sizes above the Allee threshold [38].

Overall it is important to note that these general effects are often based on random, unconditional dispersal. They may therefore be counteracted or even inverted by conditional emigration and habitat selection [46,100,101].

(d) Lessons from existing theory

In order to better define future research avenues, we have discussed above what is known from the metapopulation literature. If we summarise our understanding of single species systems to a very abstract level, we can reduce dispersal theory to a single fundamental proposition and two fundamental principles: The proposition is that dispersal and its evolution are driven by the contrast between local (inclusive) fitness expectations and the fitness expectation elsewhere [69,102]. The two general principles, to which most studies looking at more specific effects can be traced back to, are the following: Dispersal will be more frequent in systems where (1) the temporal variance in fitness expectations is large and (2) the spatial correlation in fitness expectations is low [32,35,63], i.e., where the spatio-temporal variance in fitness expectations is large.

3. A more “complex” world — dispersal evolution and plasticity in communities and food webs

The central question we raise here is: What assumptions regarding the determination of dispersal — both at the ultimate and proximate levels — are changed when interspecific interactions are taken into account? Vice versa: Are there novel mechanisms or principles with regards to dispersal evolution if we move from the single-species to the community context? These questions are currently unresolved, both empirically and theoretically. For the sake of simplicity we will first discuss potential impacts in horizontal communities, that is communities defined by competitive interactions [103], before moving on to more complex interaction webs.

(a) Horizontal interactions — metacommunities

In metacommunities [104,105] with horizontal interactions (i.e., non-trophic interactions), the evolution of dispersal has been considered in the context of competition-colonization trade-offs [106,107] and evolution-mediated priority effects [108]. The parallels to single-species work and thinking are unmistakable (see Fig. 1 for an overview), and these parallels also become obvious when considering dispersal plasticity, especially density-dependent dispersal in a metacommunity context, where single-species theory can directly be transposed to the multispecies context taking into account differential strengths of competition (see [109] and Fig. 3).

While the parallels between single- and multi-species drivers of evolution are clear when assuming asexual reproduction since genotypes are then indistinguishable from species, sexual reproduction and kinship may a priori prevent us from extrapolating from single to multispecies meta-systems. However, this added complexity may rather be a matter of quantitative effects than qualitative differences.

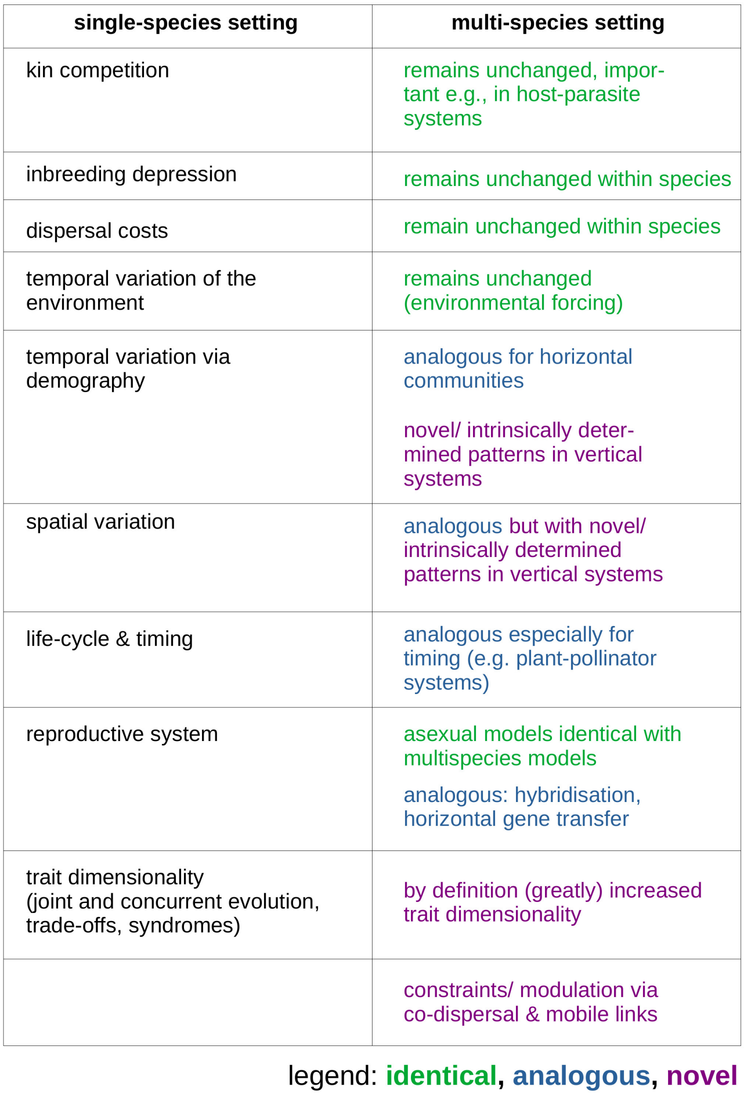
For instance, recombination of genetic material may happen at the interspecific level via hybridisation which is an important eco-evolutionary mechanism [110] and an analogue to sexual reproduction. Inbreeding depression affects single-species dispersal evolution, but it has no clear multispecies equivalent, except maybe if we assume the unlikely case of hybrid vigour, playing a role that is similar to overdominance in single-species models. Similarly, kin competition seems irrelevant at the interspecific level as an ultimate determinant of dispersal, since the probability of sharing the same allele between individuals from different species should, a priori, be very low. However, this may not be the case due to interspecific gene flow from hybridization, as discussed above, or due to incomplete lineage sorting (ancestral polymorphism between species; see e.g., [111,112]), for example. When considering proximate determinants of dispersal, phylogenetic proximity of interacting species might represent an analogous factor to relatedness in single-species cases, because phylogenetically close species might be more likely to have similar niches, and hence compete more strongly for resources (see [113] for a more detailed discussion on the link between phylogenetic proximity and traits).

While these examples are speculative and call for more formal investigations, they highlight that, at least for horizontal communities, the classic mechanisms discussed in single-species models, especially the proposition and two fundamental principles derived above, mostly hold (Fig. 1), however, likely with altered relative importances.

(b) Vertical interactions — meta-food webs

Does the above conclusion hold when moving to vertical interactions such as predation and parasitism? Existing theory can inform us here. For instance, predation affects the evolution of dispersal in predators and prey alike since it intrinsically controls both species dynamics and thus the spatio-temporal dynamics in (expected) inclusive fitness [114–119]. This patterning of spatial fitness expectations, that here relies on predator-prey cycles, is different from what can be expected in a simple horizontal competitive setting or even under mutualism [114] and represents an important driver of dispersal evolution. Note that, as for horizontal communities, the fundamental forces driving dispersal evolution do not differ from those in single species discussed above [120, 121]. This example shows how, in Hutchinson’s [122] words, interspecific interactions can form the ecological theatre in which the evolutionary play of the focal species unfolds [14]. Here specifically, one species’ demography is another species’ temporal variation of the environment when these species interact (Fig. 2). This biotic determination of selection pressures is interesting since it may actually reduce “parameter space”: while theoretically any spatio-temporal autocorrelation of fitness expectations can be assumed, biotic interactions, by generating characteristic population dynamics in interacting species, here determine, and constrain, the nature of this autocorrelation. Importantly, we have models that allow us to capture the essence of these patterns ([41] for a discrete-time discrete-fitness expectation model).

Going one step further, the study of the joint evolution of interaction strength and dispersal has almost never been undertaken. This is of interest because, the strength of interspecific interactions determines the extent to which interacting partner densities impact each other, hence the drivers of dispersal evolution [114,115]. Further, via its feedback on the demography of interacting species, dispersal can impact the evolution of interaction strength. Thus, the joint evolution of dispersal and interaction strength is likely to further constrain population dynamics of interacting partners and dispersal evolution. Calcagno et al. [123] modelled the evolution of colonization rates in a multi-trophic occupancy setting in which colonisation rate trades off with competitive ability, but did not incorporate changes in top-down or bottom-up controls as consequences of colonization evolution (see also [124] for the two-level, predator-prey case). In the case of symbiotic interactions, Ledru et al. [125] tackled the question of dispersal evolution together with that of the evolution of mutualism. They conclude that localized competition favours the evolution of



single-species setting	multi-species setting
kin competition	remains unchanged, important e.g., in host-parasite systems
inbreeding depression	remains unchanged within species
dispersal costs	remain unchanged within species
temporal variation of the environment	remains unchanged (environmental forcing)
temporal variation via demography	analogous for horizontal communities novel/ intrinsically determined patterns in vertical systems
spatial variation	analogous but with novel/ intrinsically determined patterns in vertical systems
life-cycle & timing	analogous especially for timing (e.g. plant-pollinator systems)
reproductive system	asexual models identical with multispecies models analogous: hybridisation, horizontal gene transfer
trait dimensionality (joint and concurrent evolution, trade-offs, syndromes)	by definition (greatly) increased trait dimensionality
	constraints/ modulation via co-dispersal & mobile links

legend: **identical**, **analogous**, **novel**

Figure 1. Comparison of ultimate drivers of dispersal evolution in single-species settings, as known from the metapopulation literature (left), and identical (green), analogous (blue) or novel (red) aspects added when moving to multispecies systems. Some drivers keep their function intra-specifically: For instance, kin competition which is relevant in single species dispersal evolution is a central driver of dispersal evolution in host-parasite systems as well. The same holds true for dispersal costs, although there can of course be the result of interspecific interactions, like predation, during the transfer phase of dispersal. Other drivers are analogous intra- and interspecifically such as temporal variation via intra-specific demography and temporal variation generated via interspecific interactions, such as predator-prey relationships. Finally, some factors are novel at the multispecies level, such as co-dispersal.

mutualism and that mutualistic types tend to be associated with lower dispersal rates, a finding that matches with studies on the joint evolution of intraspecific altruism and dispersal [126,127].

All these examples highlight that knowledge from single-species settings seems applicable, even to meta-food webs. Our proposition and the two fundamental principles introduced above certainly hold. In addition, the multi-species context also introduces the possibility that a given species' abundance or occupancy dynamics and spatial distribution becomes the "environment" in another species' ultimate and proximate drivers of dispersal (Fig. 2).

4. Novel drivers of dispersal evolution and plasticity: co-dispersal and trait dimensionality

Nevertheless, we identify two aspects that go beyond what has been discussed above. One becomes especially clear when considering host-parasite interactions [128]: "co-dispersal". The second one is more quantitative and relates to increased trait dimensionality.

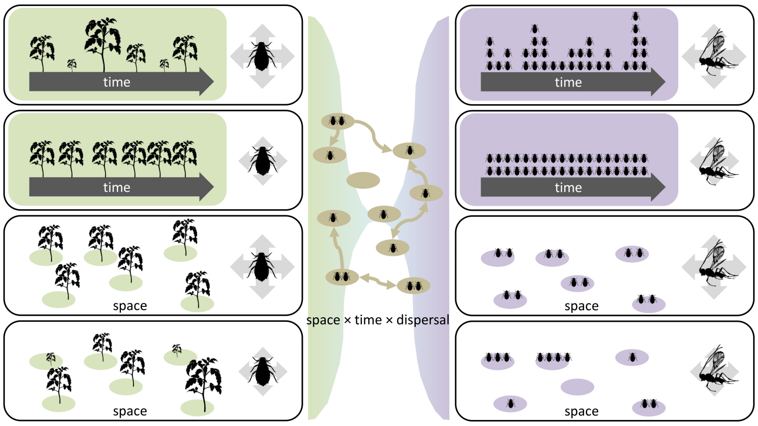
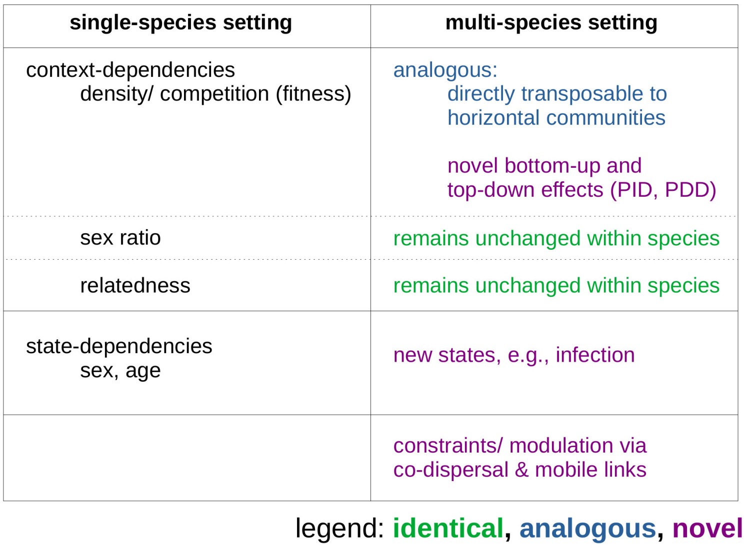


Figure 2. Illustration of the processes affecting the evolution of dispersal in "vertical" systems, here host-parasitoid systems. An aphid species consumes a plant species (represented by tomato plants) and is parasitised by a species of braconid wasps. A higher temporal variability (upper two left-hand panels) or a lower fixed spatial variability (lower two left-hand panels) of tomato abundance selects for higher dispersal of aphids. Selection for dispersal in aphids, combined with spatio-temporal variability of their environment, shapes aphid abundance patterns among and within habitat patches (middle panel). This, in turn, shapes the selection of dispersal in the braconid wasps based on the temporal variability (upper two right-hand panels) and spatial variability (lower two right-hand panels) of aphid abundance. Images of organisms are from phylopic.org.

(a) Biotic proximate determinants of dispersal: co-dispersal and mobile links

As discussed above, proximate biotic drivers of dispersal that lead to context-dependency are clearly present at the interspecific level [129–133] but they can overall be explained relying on theory developed for single-specific systems (Fig. 3).



single-species setting	multi-species setting
context-dependencies density/ competition (fitness)	analogous: directly transposable to horizontal communities novel bottom-up and top-down effects (PID, PDD)
sex ratio	remains unchanged within species
relatedness	remains unchanged within species
state-dependencies sex, age	new states, e.g., infection
	constraints/ modulation via co-dispersal & mobile links

legend: **identical**, **analogous**, **novel**

Figure 3. Comparison of proximate drivers of dispersal, that is, dispersal plasticity, in single species settings, as known from the metapopulation literature (left), and identical (green), analogous (blue) or novel (red) aspects added when moving to multispecies systems. As for ultimate drivers, some will remain identical while other are analogous. New plastic behaviours, such predator-induced (PID) and prevalence-dependent dispersal (PDD), have to be taken into account, as well as modulation of dispersal via co-dispersal.

However, an additional process that is not addressed by classic studies is the occurrence of "co-dispersal" (Fig. 1 and 3), i.e., cases where the two interacting partners disperse together (Fig. 4). This echoes the idea of mobile links [134] — organisms connecting habitats via transport of resources or processes (think of hippopotami linking terrestrial and aquatic ecosystems via transfer of matter; for many more examples see [30], [135] and []). Here, these mobile links transport other organisms and their genes.

For many symbionts, but also for animal-dispersed plant seeds or phoretically dispersed organisms (organisms travelling on other organisms, e.g., [14]), the movements of the host or vector may be unrelated to dispersal (being, instead, related to foraging or

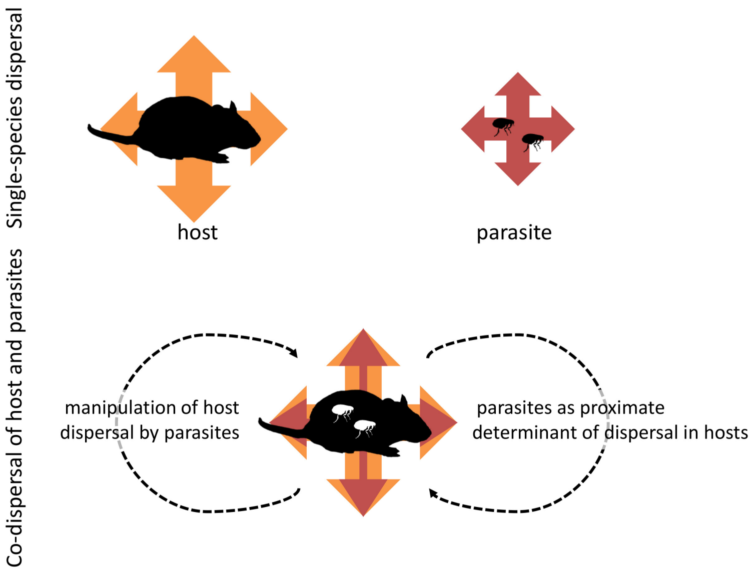


Figure 4. Illustration the processes involved in co-dispersal, here taking the example of a host-parasite system (rats as hosts and fleas as parasites). On their own, both the host and the parasite can display some dispersal rate (here, figured in the top drawings by the orange and red crosses, respectively). When the parasite sits on its host, however, the dispersal of the host-parasite couple can change due to manipulation of host dispersal by parasites and parasites also stand as proximate determinants of dispersal for the hosts (bottom drawing). Images of organisms are from phylopic.org.

seasonal migration), and yet result in dispersal for the symbiont species. For example, foraging pollinators may disperse parasites among plant species [137] or female mosquitoes, blood feeding, may vector different parasites (e.g., viruses or malaria). In such a situation the usual dispersal drivers do not apply, and are replaced by the drivers of movement for the host or vector [138,139]. This mismatch in spatial scale may lead to conflicting selection pressures.

Except in the case of obligate mutualisms, this dependence on dispersal is almost always asymmetric, e.g., plants need animals for seed dispersal, but animals can disperse without seeds; symbionts often need their host to disperse, but symbiont-free hosts can disperse. In these cases, the dispersal of the host organism may be controlled by both its own genes and those of the interacting species, through its extended phenotype. For instance, symbionts might manipulate the dispersal of their hosts, so that infected individuals disperse more or less than uninfected ones [140–142]. Conversely, infection could trigger an adaptive state-dependent dispersal strategy in the host [121,143–146]. Specifically, endosymbionts and, in particular intracellular endosymbionts, on the one hand, will co-disperse with the host, unless disposed of by its immune system. There is evidence that endosymbionts might induce dispersal, select for dispersal in their host, bias immigration success, or affect dispersal distance of their host (e.g., Wolbachia, Rickettsia: [147] and [140]; microbiome and metacommunity: [148]). Ectosymbionts, on the other hand, will not exhibit co-dispersal fidelity with certainty, but can induce dispersal (and co-dispersal). However, the processes and dynamics are different in ectosymbionts since they may be affected by the environment surrounding their host and hosts may attempt to modify symbiotic load by relocating to a different habitat [149].

While manipulation by the symbiont represents one way of addressing the above-mentioned conflict over selection pressures, adaptive dispersal strategies for the host may also lead to curing (i.e., extinction of the parasite; [147]). To make the issue more complex, hosts can be co-infected by multiple parasites where competition between parasites can impact transmission (dispersal) as discussed by Godinho et al. [150]. Finally, parasites may be co-transmitted [151,152], whereby one relies on another for transmission to new hosts. These complexities are beyond the scope of the current paper.

The consequences of co-dispersal can be manifold. From an evolutionary point of view, dispersing with or without a symbiont is known to be different, and can lead to different dispersal and trait evolutionary trajectories [153,154]. These effects can occur under both mutualistic and parasitic symbioses [155], but parasitic symbioses are also prone to evolve towards manipulation of host dispersal [156,157]. Unfortunately, similarly detailed analysis involving more realistic meta-food webs are missing. In conclusion, co-dispersal clearly represents an additional driver at the inter-specific level that cannot occur in single-species systems.

(b) Increased trait dimensionality in metacommunities and meta-food webs

In general, moving from a single- to a multi-species context should increase system complexity and thereby also the dimensionality of the relevant trait space (Fig. 1). Débarre et al. [158] show that increased trait dimensionality tends to destabilise evolutionary equilibria. This in turn increases opportunities for evolutionary branching and can therefore favour diversification, which could lead to polymorphisms of dispersal or other traits [159] with (quasi-)equilibrium reached when the systems settles — across different species — in an ideal-free fitness distribution [160]. By contrast, a more complex biotic environment can be understood as inducing a "cost of complexity" [161], i.e., adaptation is slower when it is required on more dimensions, or, if mutations are more pleiotropic (and thus quicker), phenotypic variation can decrease with the number of dimensions (the "preservation of perfection" effect, [162]).

Taken together, from Débarre et al. [158] we may predict that diversity in species interactions begets diversity (at least in trait distributions; see also [163] outside the context of dispersal evolution). At the same time the cost of complexity [161] and the preservation of perfection [162] introduced above may imply that evolution will be slower in more complex systems, intrinsically, due to increased dimensionality and also due to decreased standing variation in the case of pleiotropy. These impacts on the speed of evolution have interesting consequences for eco-evolutionary feedbacks: Eco-evolution is particularly likely to lead novel, emergent phenomena when ecological and evolutionary timescales are similar [14]. If complexity tends to reduce the speed of evolution as outlined above, it may therefore decouple ecological and evolutionary timescales and prevent eco-evolutionary feedbacks [14]. The ultimate consequence of this interplay may be that dispersal evolution is overall slower and more "diffuse" in multispecies meta-systems. Potentially, this could reduce divergence in dispersal strategies across species or, on the contrary, lead to neutral coexistence of diversity. One can speculate that, as a consequence, dispersal limitation could be less likely overcome by evolution which implies that current models which are largely single species models would drastically overestimate the potential for adaptation and range shifts.

5. Discussion

Despite a strong interest in dispersal, its effects on evolutionary dynamics and many ecological properties, ecologists and evolutionary biologists have yet to properly tackle the determinants of dispersal in the community and food web context. This integration is especially relevant since dispersal has important consequences at the multispecies level. While a detailed discussion of (evolutionary) metacommunity ecology [164,165] is beyond the scope of this article, these consequences include effects on biodiversity and its geographic distribution [17,104,166–171], as well as behavioural effects on biogeography [172] and a potential explanation of the latitudinal diversity gradient based on a dispersal–ecological specialisation trade-off [173]. Further noteworthy effects are related to on system complexity [174], stability [175], coexistence [29] and functioning [135]. For instance, alpha and beta diversity patterns are drastically influenced by dispersal [104,176–178] as well as by evolutionary dynamics under global change [14,179,180]. Yet, how these patterns are affected by dispersal evolution within the metacommunity and meta-food web context, and at larger, biogeographic scales, remains unclear (see e.g. the list of cross-cutting questions in [181]). The same is true for our understanding of how dispersal evolution affects community resilience and assembly (for a detailed discussion see [182]), as well as macro-ecological patterns including the speed of invasion waves, for example.

(a) A proposition and general principles

In order to attain this synthesis of dispersal evolutionary ecology and biodiversity research, we here take a first step in order to understand the drivers of dispersal in biodiverse systems. At the same level of abstraction as the proposition and the two general principles for dispersal evolution in single species systems laid out above, we argue that nothing changes when we consider multi-species systems: Individuals should still emigrate whenever (inclusive) fitness expectations elsewhere are larger than those at the current site of residence and dispersal should occur more often whenever the spatio-temporal variation in fitness expectations is large. Whatever forms the ecological theatre for the evolutionary dispersal play, intra- or inter-specific competition, predation, parasitism or mutualism, does not matter in detail. At a lower level of abstraction, drivers may change in relative importance and additional drivers, such as co-dispersal, may directly impact costs and benefits of dispersal (Fig. 1 and 3).

(b) Directions for future research

Since many points discussed above are largely speculative, they call for more investigation, both theoretically and empirically. In the following we provide a non-comprehensive list of potentially relevant questions and topics.

Going back to the most abstract level mentioned above, it is relevant to determine in general, what the most important drivers of fitness expectations for each species are (abiotic conditions, intra-specific or inter-specific interactions; see e.g. [183]). These define the ecological theatre (selection pressures) for the evolutionary play. Moreover, it is relevant to ask which of these drivers are responsible for the largest temporal variance in fitness expectations and what the characteristic spatial scale of autocorrelation in this variance is. Further, with an increasing number of interactions, is spatio-temporal variance in fitness-expectations likely to increase or decrease? Are fitness expectations at all predictable in a world of highly complex and dynamic interactions?

From a theoretical point of view we have noted that co-dispersal is largely understudied. While some work exists at the interface between evolutionary epidemiology and dispersal evolution, as recently reviewed by [128], a comprehensive theoretical treatment is lacking.

The same holds true for the joint evolution of dispersal with interaction traits, as well as considering higher-order interactions involved in dispersal (e.g. dispersal of parasites with complex life cycles and multiple successive host species). Future work could identify which "parameters" of interactions are important for dispersal (interaction signs, immediacy, effect on abundances, correlations with other traits, to name but a few). Dispersal syndromes with or without co-dispersers (importance of symbiosis for dispersal plasticity and correlation with other traits) may have to be more clearly included into theory. We would also like to highlight that the step from communities and food webs towards ecosystems has to be taken, by taking into account fluxes of matter and studying constraints on dispersal at the ecosystem level, for example [10]. Feedbacks will be interesting to understand, namely feedbacks between the evolution of dispersal in multiple species, but also feedbacks on local and regional community dynamics and realized interaction strengths, which can in turn modify dispersal evolution.

At the opposite end of the continuum of biological organisation levels, the genome, Débarre et al. [158] show that epistasis and trait correlations may to some degree modulate responses, and the "cost of complexity" model suggests that modularity in genetic architecture may be a solution to simplify the problem of adaptation. This overall calls for putting the genetic architecture of traits, including dispersal, at the centre of theoretical and empirical investigations [14,184–186]. Using a multilevel network modelling approach [187] represents a promising way forward.

From an empirical point of view dispersal plasticity certainly requires more investigation. One could imagine, for instance, that a symbiont's dispersal strategy may be less plastic, being more constrained by the host dispersal plasticity, or could it be that symbiont dispersal plasticity is induced by host dispersal plasticity (when the host's environment changes, the same is true for the symbiont)? More generally, it would be relevant to understand what reliable cues, triggers or correlates of fitness-relevant drivers exist at the meta-food web level and how accurately such interspecific information can be perceived. Particularly, increasing the numbers and diversity of interactions may make every single one less fitness-relevant. If dispersal decisions are plastic, external cues may thus become less relevant and reliable as triggers of dispersal in comparison to internal states like body mass/size, hunger level or health status.

(c) Summary and conclusion

We here discussed to which degree theory built for single-species systems also holds at the multi-species level and advance our understanding of dispersal evolution in meta-systems. Are effects exacerbated or averaged out? Do they change in relative importance?

We highlight that at the highest level of abstraction dispersal theory consists of a single fundamental proposition and two fundamental principles that presumably hold within and across species. At a lower level of abstraction, biotic interactions form the ecological theatre for the evolutionary dispersal play: Biotic interactions like trophic interactions mediate patterns of fitness expectations in space and time thereby reducing the realm of possible patterns and providing us with a modelling tool. While this implies a simple transposition of already known drivers to a multispecies context, some drivers may require upscaling or more complex transpositions (Fig. 1, 3). The latter provides interesting possibilities for linking micro- and macroevolutionary dynamics. Above, we have identified an important quantitative modulator of dispersal evolution: increased trait dimensionality which may impact the speed of evolution. Finally, an additional factor to consider is co-dispersal. The latter may lead to scale and selection pressure mismatches between hosts and symbionts. A large number of open questions and important potential consequences in both ecological and evolutionary terms calls for more investigation. Taken together, we hope that these efforts will allow researchers to fully merge dispersal evolutionary ecology with the ongoing push to develop evolutionary metacommunity ecology [164,165]. This merger would allow to better investigate spatial eco-evolutionary feedbacks loops.

Author contributions

All authors discussed the content and topic of the study during a workshop organized by E.A.F. F.M. and E.A.F. wrote a first draft of the manuscript and all authors commented on the draft.

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