Is dispersal neutral?

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Dispersal is difficult to quantify and often treated as purely stochastic and extrinsically controlled. Consequently, there remains uncertainty about how individual traits mediate dispersal and its ecological effects. Addressing this uncertainty is crucial for distinguishing neutral versus non-neutral drivers of community assembly. Neutral theory assumes that dispersal is stochastic and equivalent among species. This assumption can be rejected on principle, but common research approaches tacitly support the 'neutral dispersal' assumption. Theory and empirical evidence that dispersal traits are under selection should be broadly integrated in community-level research, stimulating greater scrutiny of this assumption. A tighter empirical connection between the ecological and evolutionary forces that shape dispersal will enable richer understanding of this fundamental process and its role in community assembly.

What do we really know about dispersal?

Dispersal (see Glossary) is a fundamental process in population biology, ecology, and evolution [1,2]. Broadly defined as permanent movement away from an origin, dispersal in most animals and plants is characterized by many individuals that stay close to their origin and large variation in the distances moved by those that leave [3,4]. This produces dispersal distributions with high peaks around a distance of 0 (the 'stayers') and fat tails encompassing variation in dispersal distance (e.g., Figure 1). The high frequency of stayers is generally attributed to the energetic cost and risks of dispersal, but we have less understanding of why individuals disperse and why dispersal distances vary [5,6].

Darwin [7] saw that variation in dispersal propensities and distances had a key role in range expansion, and theory shows that these factors contribute to local abundance [8], range shifts [9], and patterns of species coexistence [10]. We also know that individuals and species differ in traits affecting dispersal propensity and ability (e.g., winged versus wingless insects [11] or variation in seed morphology [12]), including traits governing settlement decisions [13]. However, low detectability and small post-dispersal sample sizes have impeded research on how dispersal propensity and distance affect individual fitness and phenotypic evolution [6,14]. Consequently, empirical understanding of the role of natural selection in shaping dispersal traits is limited [1,5,15].

Many areas of ecology and evolutionary biology would benefit from better empirical understanding of the adaptive drivers of dispersal traits, but this information is especially valuable for understanding questions of local and regional community structure. For over a decade, the unified neutral theory has strongly influenced research addressing these questions [16]. This and related theory posit that diverse species assemblages can be maintained by stochastic dispersal and extinction dynamics alone, without strong niche differences among species [16,17]. In neutral models, dispersal is lumped with other traits that are functionally or demographically equivalent among species; interspecific differences in dispersal propensity and distance alone cannot promote coexistence or lead to dominance.

The most forceful critiques of the unified neutral theory focus on the assumption that traits mediating local competitive interactions are unimportant, which conflicts with a long history of work on species coexistence [18,19]. Just as central to neutral theory is the assumption that dispersal is a purely stochastic process, but reaction to this assumption has been less intense. It is unlikely that this muted reaction reflects acceptance: most researchers who work on dispersal would be quick to reject this assumption based on evolutionary or ecological principle. For example, in his overview of the future of neutral theory, Clark [20] points out that 'dispersal is a real process that differs among species and evolves by natural selection'. Yet the lack of an empirical challenge to the 'neutral dispersal' assumption implies tacit acceptance that is worth examining, to advance understanding of both community assembly and, more broadly, the interaction of ecological and evolutionary forces that shape dispersal.

The 'neutral dispersal' assumption might be unacceptable based on evolutionary and ecological principle, but we

Glossary

Connectivity: a concept based on the dispersal of individuals among discrete populations, communities, or, more generally, 'patches' of suitable habitat.
Deterministic: determined by starting condition or initial state.
Dispersal: permanent movement away from an origin and long-term settlement at a new location.
Dispersal kernel: probability function describing the likelihood of dispersal to different distances.
Metacommunity: a group of spatially discrete communities of multiple species linked by dispersal.
Metapopulation: a group of spatially discrete populations of one species linked by dispersal.
Neutrality: species independence of individual demographic rates (e.g., survival, fecundity, or dispersal) or functional traits.
Niche differences: variation among individuals and species in demographic response to the environment, or effects on the environment.
Stochastic: randomly determined, either wholly or partially.
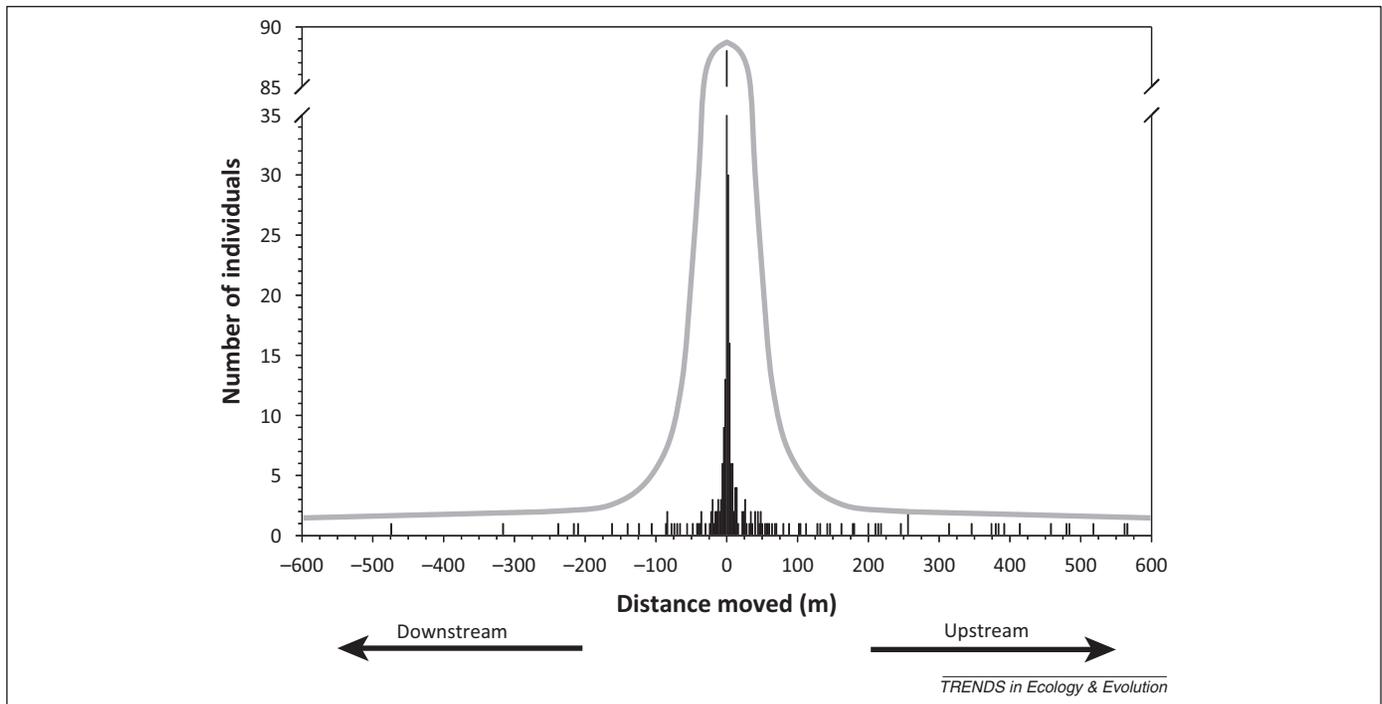
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Figure 1. A fat-tailed dispersal distribution. Dispersal distribution of the stream salamander *Gyrinophilus porphyriticus* in Merrill Brook, a first-order stream in northern New Hampshire, USA. Data are net movements of marked individuals over a 6-year period. The leptokurtic or 'fat-tailed' distribution of dispersal distances, with a high peak comprising stayers and fat tails encompassing variation in dispersal distance, is a believed to be shared by most species.

believe that it is consistent with treatments of dispersal in many spatial ecological studies, whether deliberately or due to a lack of empirical data on individual dispersal traits. Most studies of spatial community dynamics and landscape connectivity focus on stochastic and extrinsic controls on dispersal, rather than on variation in individual traits (e.g., behavior, morphology, or physiology) that determine population-level dispersal distributions (e.g., Figure 1). Likewise, studies that have documented individual traits affecting dispersal do not, in general, address the community-level implications of those traits, despite a growing body of research documenting effects at the population level.

We believe that these two factors are the primary obstacles preventing empirical assessment of the 'neutral dispersal' assumption: (i) the treatment of dispersal as a process controlled primarily by stochastic and extrinsic forces in spatial ecological studies, and (ii) a lack of research linking individual dispersal traits to emergent patterns of community structure and, to a lesser extent, population dynamics. These factors perpetuate a neutral view of dispersal, one that fails to consider the importance of eco-evolutionary feedbacks in producing variation in individual dispersal traits and their ecological effects. Although we acknowledge that dispersal likely has a stochastic component in most systems, we advocate a more balanced, bottom-up approach to dispersal research that addresses both stochastic, extrinsic drivers and deterministic, intrinsic drivers.

Here, we identify specific approaches in spatial ecology research that we believe maintain this neutral view of dispersal. To shift this view, we then highlight compelling predictions from ecological theory on the causes and consequences of variation in dispersal traits, and compelling

evidence that these traits are under selection. We hope to stimulate empirical scrutiny of the 'neutral dispersal' assumption and of the broader ecological and evolutionary implications of individual dispersal traits, leading to a richer understanding and, thus, richer analyses of this fundamental biological process.

Perpetuating a neutral view
One kernel might not fit all
Probability functions of dispersal distance, known as dispersal kernels, are often used to model the exchange of individuals among populations and communities, but rarely account for individual variation in dispersal traits, thus supporting the neutral view of dispersal. The use of dispersal kernels extends beyond basic science to land-use planning, where they are used in large-scale wildlife connectivity models. These connectivity models identify habitat corridors for protection, based on an assumption that dispersal (and migration) is critical to maintaining target populations and biodiversity [21].

The amount of empirical data used to develop dispersal kernels varies, but is usually low. Instead, dispersal kernels are often based on simple observations or assumptions about the movement behavior of the focal species (e.g., sedentary or vagile, maximum dispersal distance, or home-range size), or inferred from landscape-level patterns of occupancy, abundance, or genetic relatedness [22]. More importantly for this discussion, the use of dispersal kernels reinforces a purely stochastic and extrinsically driven view of dispersal by disregarding deterministic variation in dispersal traits within and among populations.

Dispersal kernels are generally assumed to be fixed attributes of a focal species and, consequently, do not account for variation among populations in dispersal

frequencies and distances. Likewise, application of dispersal kernels is random with respect to individuals within populations. Individuals vary in dispersal propensities and distances, but these attributes are assigned randomly. Thus, the use of dispersal kernels does not account for phenotypic differences among individuals, whether adaptive or plastic, that can underlie differences in individual dispersal propensities and distances. Acknowledging this variation in dispersal phenotypes is a key step toward understanding adaptive variation in dispersal [23] and variation in the demographic and ecological effects of individual dispersers [13].

By not incorporating deterministic variation in dispersal traits, most applications of dispersal kernels are consistent with the 'neutral dispersal' assumption. These applications are appropriate for systems where stochastic and extrinsic forces are the dominant drivers of dispersal (e.g., wind or water currents), and where individuals and populations do not differ deterministically in their response to these forces [24,25]. However, we know that individuals within populations can differ in ways that

influence dispersal propensities and distances, leading to population-specific dispersal kernels [26]. Incorporating deterministic processes in applications of dispersal kernels, including simulation studies, might be a productive way to probe the 'neutral dispersal' assumption and the eco-evolutionary feedbacks that shape dispersal.

Looking beyond the landscape

Spatial ecological models commonly predict and simulate interpatch exchange based solely on the geographic distribution of focal patches and related attributes of the physical landscape (Figure 2A), disregarding ecological and evolutionary processes acting within patches that can affect individual dispersal traits and population-level dispersal distributions (Figure 2B). Interpatch distance is seen as the key predictor of dispersal rates, whether patches are populations or communities [27–29]. This same emphasis on geography can be seen in studies identifying barriers to dispersal and gene flow, whether barriers are specific features (e.g., ridges, rivers, or roads) or areas of low-suitability habitat. Recently, indices of
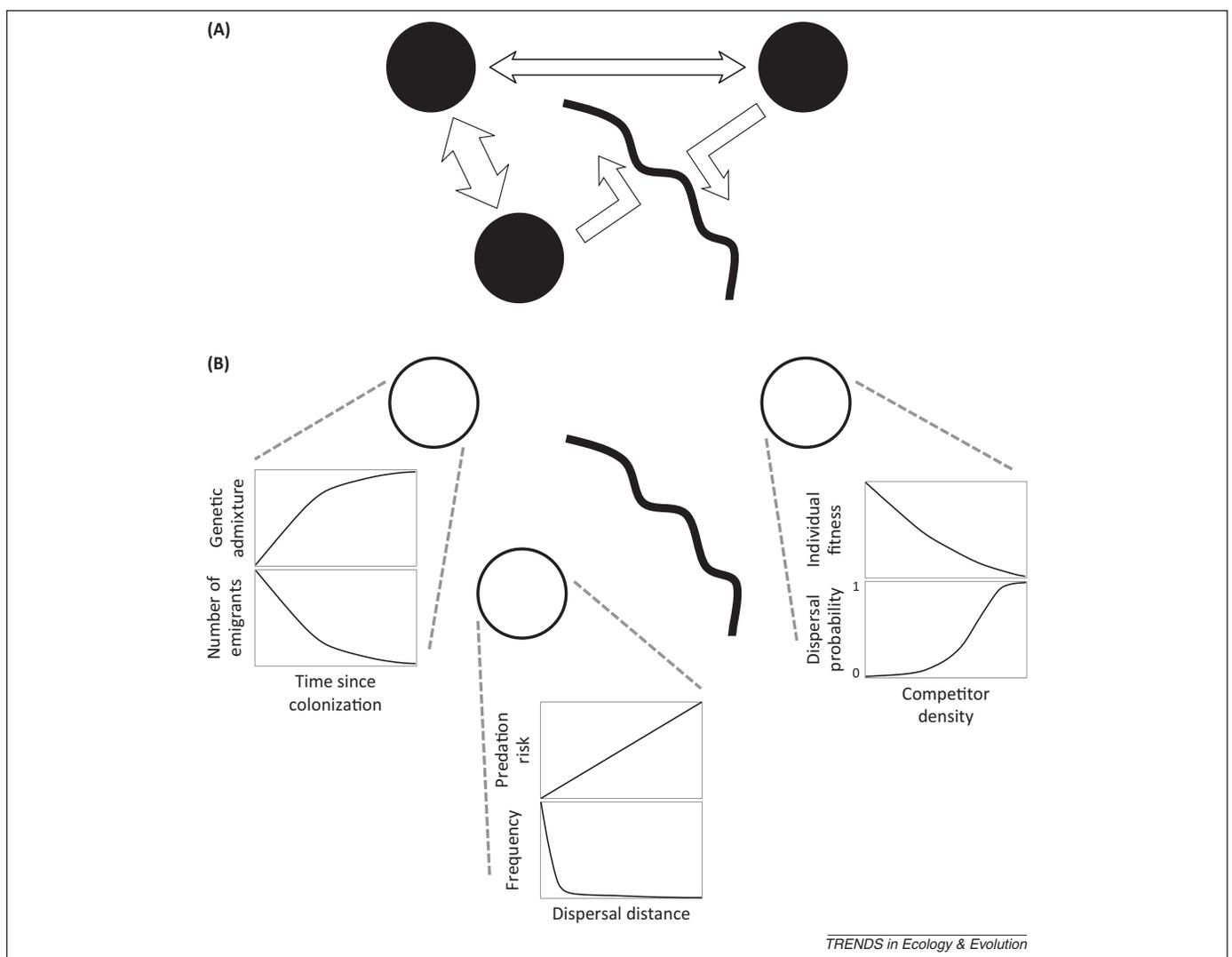

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Figure 2. Different perspectives on dispersal in spatial models. Schematic representations of **(A)** the traditional approach to dispersal and gene flow in spatial models, emphasizing extrinsic controls, such as geographic distance and barriers, and **(B)** patch-specific processes that might affect dispersal rates and distributions as functions of the change in genetic admixture over time, the change in individual fitness with competitor density, and the change in predation risk with dispersal distance. Along with extrinsic geographic factors, these processes can be crucial to understanding patterns of interpatch dispersal and gene flow.

landscape permeability have been used to capture both interpatch distance and habitat suitability [30].

There is no doubt that patch geography influences dispersal and resulting population and community dynamics in most systems. It can also be argued that geographic factors, including interpatch distance and major barriers, affect diverse species, further justifying their prominence in spatial models. Finally, interpatch distances and potential barriers are relatively simple to quantify using GIS and remote-sensing tools, making them an economical centerpiece of both single- and multispecies spatial models [31].

Despite its mechanistic and methodological appeal, broad acceptance of a geography-centered view of dispersal comes at a cost. This view draws attention away from the many factors acting within patches that can produce variation in dispersal traits among individuals and populations, independent of purely geographic factors (Figure 2B). For example, variation in competitive performance can influence rates of emigration and immigration [32], setting the stage for evolutionary feedbacks between individual dispersal traits and local ecological interactions [33]. By disregarding these feedbacks and (more directly) deterministic variation in individual- and population-level dispersal traits, the geography-centered view obscures the dynamic nature of dispersal, both as an ecological process and a 'real trait that...evolves by natural selection' [20].

Studying the effects of dispersal on community dynamics

Despite early recognition that dispersal traits shape and are shaped by species interactions, common methods for examining the role of dispersal in community dynamics do not account for individual- and population-level variation in these traits. Field studies of spatial community dynamics generally rely on indirect indices of dispersal, lacking the resolution to reveal variation in dispersal traits among individuals or populations [34]. These indices include population genetic data, spatial or temporal variation in local abundance, and even measures of spatial isolation alone (e.g., distance to nearest patch).

Use of indirect indices is often necessary because dispersal cannot be quantified directly at the scale of interest [6,14]. Nevertheless, interpretation of these indices is based on a purely stochastic, extrinsically controlled view of dispersal. Dispersers are assumed to be random with respect to individual- and population-level traits, and geographic variables (e.g., distance or barriers) are assumed to be the primary predictors of interpatch dispersal rates (Figure 2A). Consequently, these indirect indices limit insight into the deeper, eco-evolutionary causes and consequences of dispersal at the community level, that is, those mediated by traits of individual dispersers.

Experimental approaches have also been used to explore the role of dispersal in community dynamics. There is a long history of experimental work on dispersal limitation in plant communities (reviewed in [35]), and we have seen this approach applied more broadly with the expansion of metacommunity theory [10]. Experimental approaches generally rely on dispersal treatments where individuals are randomly drawn from source populations, then added to experimental units to simulate immigration. Dispersal treatments can vary in the frequency of immigration events and number of immigrants per event, thus capturing variation in dispersal rates. Applications of this approach are diverse, including immigrant additions to experimental communities of invertebrates [36], bacteria [37], and plants [38].

Experimental approaches provide mechanistic insight into spatial community dynamics that indirect dispersal indices cannot. However, this approach decouples dispersal from individual traits, consistent with the neutral view of dispersal, because individuals added in dispersal treatments are drawn randomly from source populations. These treatments are based on an implicit assumption that species interactions in recipient communities are not affected by the traits of individual immigrants, only by the immigration rate. In cases where individual dispersal traits are linked to competitive performance (e.g., when dispersers are poor competitors), this assumption will obscure mechanisms underlying patterns of coexistence and diversity. Perhaps the clearest illustration of the relation between dispersal and local competitive interactions is the process of establishment. Fundamentally, establishment depends on the combined probability of: (i) an individual arriving at a specific location; and (ii) surviving to reproduce. This creates an evolutionary interconnection between dispersal traits and competitive traits in any system where postsettlement survival is influenced by interactions with other species.

Reliance on indirect indices and experimental treatments promotes the view that dispersal happens *to* individuals, independent of local competitive interactions and related evolutionary history. Although not deliberate, this methodological disregard of covariation in competitive and dispersal traits is surprising considering broad recognition that competitive traits often covary with other traits [39]. In designing these studies, more consideration must be given to the properties of dispersing individuals and why these individuals are moving in the first place.

Moving beyond 'neutral dispersal'
Dispersal theory in the community context

Since the pioneering work of Huffaker [40], ecologists have recognized that dispersal can have a central role in community assembly and structure, but theory has far outpaced empirical work on how ecological and evolutionary forces interact to produce variation in intra- and interspecific dispersal patterns, and in the community-level effects of dispersal. For example, the competition–colonization trade-off is seen as broadly relevant for explaining biological diversity in ecological communities [39,41,42]. This trade-off predicts that competitive asymmetries between species can be offset by differences in immigration, promoting coexistence (Figure 3). Similar arguments can be made about predator–prey interactions in patchy environments [43]. Crucially, these trade-offs imply that dispersal traits evolve in concert with competitive or predation-related traits in co-occurring species [33,44]. In these scenarios, dispersal is an integral component of the adaptive mechanisms promoting species coexistence.
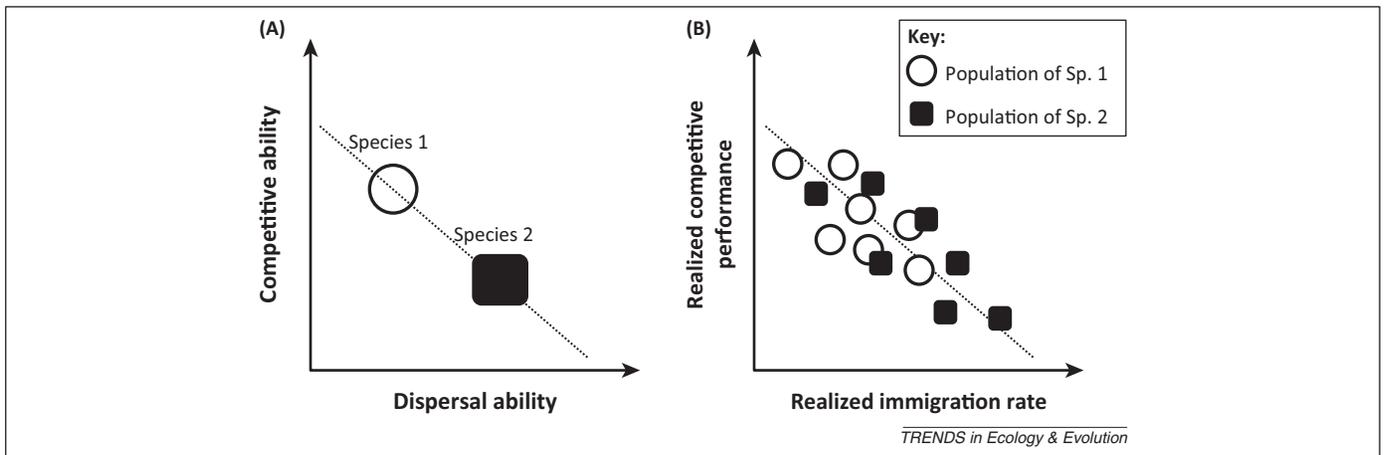
Figure 3. The competition–colonization trade-off. **(A)** Structure of the classic competition–colonization trade-off, which emphasizes interspecific variation in competitive and dispersal abilities. **(B)** Hypothesized structure of the competition–colonization trade-off when accounting for intraspecific, population-level variation in dispersal distributions. This variation might result from extrinsic, landscape factors or patch-specific eco-evolutionary processes affecting individual dispersal traits.

If movement of individuals between communities is passive, selection on dispersal propensities within a given species will be defined by the spatial and temporal variability in its population sizes across the metacommunity. Low-dispersal propensities are predicted for species with population sizes that vary spatially but not temporally, particularly when dispersal is costly [45,46], reducing connectivity among patches. By contrast, high-dispersal propensities should evolve in species with population sizes that vary both spatially and temporally, and patch-specific and polymorphic dispersal propensities are favored under certain forms of spatiotemporal variability [47]. In all these cases, the set of species-level dispersal traits favored by natural selection should demographically balance local immigration and emigration such that population sizes do not deviate from those favored by local ecological conditions [48].

Dispersal can also establish source–sink structure among populations of a given species: source populations have positive growth rates at low population size, whereas sink populations have negative population growth rates at all sizes and are maintained by immigration [49]. Source–sink structure can arise in passively dispersing species, species with density-dependent dispersal, and species that make active habitat choices (e.g., habitat traps [50]). Source–sink structure can make a species more prone to extinction if the fitness differences between sources and sinks are too great, so that persistence hinges on the constellation of patch types in the metacommunity [51]. Moreover, source–sink dynamics imply a strong deviation of species abundance from what is favored by local conditions, with concomitant effects on co-occurring species. Source populations will tend to be smaller because of net emigration, and sink populations are larger than expected (which is zero). Sink populations can have especially large community-level effects when supported by large nearby sources (e.g., 'mass effects' [52]).

Whether species passively disperse or actively choose among patches can also fundamentally alter community dynamics (reviewed in [53]). For example, prey populations found in different habitat patches are demographically coupled if predators disperse passively between the patches, but prey populations are demographically uncoupled if predators forage optimally among the patches [54]. Similarly, habitat selection by prey can fundamentally alter predator–prey dynamics [55].

Recognition that local communities are linked by dispersal has provided new insights into community structure at local and landscape scales [10]. However, not all environments select for the same dispersal propensities and distances, and not all species disperse according to the same rules. Thus, any particular metacommunity can comprise a diverse collection of species expressing many different dispersal capabilities, propensities, and strategies. How and why species move among local communities can affect the overall dynamics of the system as much as the type and strength of species interactions within local communities. Moving beyond 'neutral dispersal' will require better empirical resolution of these effects.

Building up from the individual
There is a rich literature linking dispersal to behavioral, physiological, and morphological phenotypes [56,57], and methods for exploring these connections continue to expand [22,58]. Empirically, however, this work is largely divorced from research on the community-level consequences of dispersal. This rift is likely related to deeper, historical divisions between ecology and the more organismal subdisciplines of biology. Regardless of cause, deeper understanding of the interplay between evolutionary and ecological forces affecting dispersal will require overcoming these divisions. We need to not only quantify individual variation in dispersal traits, but also understand the processes that maintain variation in these traits.

Phenotypes affecting dispersal fall into two broad categories, and traits in both categories are likely to influence and be influenced by community dynamics: (i) traits affecting dispersal propensity, or the discrete response of moving away from an origin; and (ii) traits affecting dispersal distance, including phenotypes that determine where settlement occurs [5,13,59]. Evidence that selection mediates

dispersal propensity has come from studies of dimorphisms between dispersive and nondispersive individuals. Dimorphisms affecting dispersal propensity have been documented in many different organisms, including plants [12], insects [11], fish [60], and small mammals [61]. These dimorphisms manifest in diverse traits and suites of correlated traits; however, variation in dispersal propensity is often linked to behavioral syndromes (e.g., shy versus bold personalities) and morphology (e.g., non-winged versus winged seeds).

Unlike traits affecting dispersal propensity (the discrete response of moving away from an origin), we know relatively little about traits affecting dispersal distances, or the evolutionary basis of these traits [6,59]. Traits affecting dispersal propensity and distance might be related in some species (e.g., those with shy versus bold personalities), but not others (e.g., when dispersal is a single, discrete event in the life of an individual), creating the possibility of independent effects at the population and community levels, and different evolutionary origins. Haag *et al.* [62] identified a candidate locus underlying variation in flight metabolic rate in the butterfly *Melitaea cinxia*, and individuals with higher flight metabolic rates moved more and were more likely to colonize open patches [63]. In the spring salamander (*Gyrinophilus porphyriticus*), individual survival and growth rate increase with dispersal distance, and dispersal distance is correlated with limb morphology [64].

Additional studies have linked dispersal distance to phenotype without assessing fitness consequences. Fraser *et al.* [65] linked dispersal distance to behavioral syndromes in the Trinidad killifish (*Rivulus hartii*), and Phillips *et al.* [66] linked dispersal rate to leg length in cane toads (*Bufo marinus*). Settlement rules, both behavioral and nonbehavioral, can also influence dispersal distances [13,67], and there is empirical evidence for individual variation in these rules [68]. Although there appears to be considerable plasticity in settlement behavior, broader conclusions about the evolutionary basis of settlement traits will require more data on their fitness consequences and heritability.

Overall, these findings suggest not only that natural selection has a role in maintaining variation in dispersal propensity and distance, but also that dispersing individuals often differ from nondispersers in phenotype and, thus, ecological performance capabilities. These phenotypes can mediate individual fitness through localized eco-evolutionary feedbacks and emergent population and community dynamics (Figure 2B). For example, there might be selection for high-dispersal phenotypes within a patch as local competition intensifies across generations [69], increasing emigration to neighboring patches and thereby influencing metapopulation and metacommunity dynamics [44]. Alternatively, the frequency of high-dispersal phenotypes within a patch might decrease with time since colonization and, assuming ongoing immigration, a related increase in genetic admixture [70]. This would influence not only within-patch demographic and evolutionary process, but also the effects of dispersal on ecological and evolutionary processes in neighboring patches [71].

Concluding remarks

There is little doubt that stochastic and extrinsic forces influence dispersal in many species and systems. Therefore, it is both reasonable and productive to view dispersal, in part, as a 'neutralizing force' in natural communities, one that affects biodiversity independent of adaptive mechanisms of coexistence. However, we will miss many opportunities for deeper ecological and evolutionary insight if we allow this neutral view to dominate empirical research on the causes and consequences of dispersal. Instead, we need to test the relative importance of neutral and adaptive forces in determining individual dispersal propensities and distances, population-level dispersal distributions (e.g., Figure 1), and resulting effects on populations and communities.

This bottom-up approach to dispersal research poses empirical challenges because it requires a foundation of data on individual dispersal traits. However, conceptual and methodological tools for examining the evolutionary basis and ecological consequences of individual trait variation are expanding rapidly [72,73]. With these new tools and a more balanced approach to the forces shaping dispersal, we can help distinguish between niche and neutral controls on biodiversity and build a richer understanding of this fundamental biological process.

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