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ORIGINAL PAPER

Habitat matching and spatial heterogeneity of phenotypes: implications for metapopulation and metacommunity functioning

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Abstract Spatial heterogeneity in the distribution of phenotypes among populations is of major importance for species evolution and ecosystem functioning. Dispersal has long been assumed to homogenise populations in structured landscapes by generating maladapted gene flows, making spatial heterogeneity of phenotypes traditionally considered resulting from local adaptation or plasticity. However, there is accumulating evidence that individuals, instead of dispersing randomly in the landscapes, adjust their dispersal decisions according to their phenotype and the environmental conditions. Specifically, individuals might move in the landscape to find and settle in the environmental conditions that best match their phenotype, therefore maximizing their fitness, a hypothesis named habitat matching. Although habitat matching and associated non-random gene flows can produce spatial phenotypic heterogeneity, their potential consequences for metapopulation and metacommunity functioning are still poorly understood. Here, we discuss evidence for intra and interspecific drivers of habitat matching, and highlight the potential consequences of this process for metapopulation and metacommunity functioning. We conclude that habitat matching might deeply affect the eco-evolutionary dynamics of meta-systems, pointing out the need for further empirical and theoretical research on its incidence and implications for species and communities evolution under environmental changes.

Keywords Gene flow · Dispersal decision · Intraspecific variability · Habitat matching · Environmental conditions · Interspecific interactions

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Introduction

Phenotypic variability is the core material for natural selection to operate since the phenotypes of individuals determine their performance in a given environmental context (Kawecki and Ebert 2004). Differences in phenotypic traits among individuals are therefore of major importance in ecology and evolution (Bolnick et al. 2003; Ridley 2004). Since environmental conditions are largely heterogeneously distributed in the landscape, phenotypes are generally found to be spatially and/or temporally structured in the landscape (Michel 2011; Allen et al. 2012). *Spatial heterogeneity of phenotypes* can impact evolutionary processes, such as population divergence and speciation (Bolnick et al. 2003; Kawecki and Ebert 2004). Furthermore, the phenotypes of individuals can drive the dynamics of populations, communities and ecosystems (Bolnick et al. 2003, 2011; Violle et al. 2012). Local variability should consequently be considered as central in research on population and community ecology (Bolnick et al. 2003).

Spatial heterogeneity of phenotypes in the landscape has mainly been explained by adaptation to local conditions by selection or phenotypic plasticity (Agrawal 2001; DeWitt and Scheiner 2004). Since natural selection favours the phenotypes that best fit a given ecological context, we expect an increase of the phenotypic adaptation of individuals to their local ecological context over generations. In heterogeneous environments, this process, named *local adaptation*, leads to adaptive differentiation of local populations (Kawecki and Ebert 2004). Phenotypic spatial heterogeneity can also occur as a result of *phenotypic plasticity* even without selection of better suited phenotypes, with individuals changing their phenotype during their lifetime depending on their environment (Dufty et al. 2002; West-Eberhard 2003). Additionally, phenotypic plasticity can be favoured by selection in certain environmental contexts, particularly in spatially and/or temporally variable environments, leading to the evolution of adaptive plasticity where individuals improve the match between their phenotype and the local conditions (Agrawal 2001).

Less emphasis has been devoted to the influence of *dispersal* on the spatial heterogeneity in the distribution of phenotypes. This is certainly because dispersal, the movements of individuals potentially leading to gene flow (Ronce 2007), which is a central process in *metapopulation* and *metacommunity* theories (Clobert et al. 2001, 2004, 2012; Hanski and Gaggiotti 2004; Leibold et al. 2004; Urban et al. 2008; Logue et al. 2011), has long been considered as random. In this context, high levels of dispersal are assumed to homogenise metapopulations, and can even prevent local adaptation and population differentiation (Crespi 2000; Bolnick and Nosil 2007; Edelaar and Bolnick 2012). However, dispersal is now largely recognized as a non-random process being dependent on both individual phenotypes and environmental conditions (Bowler and Benton 2005; Clobert et al. 2009, 2012). Dispersal can thus generate spatial heterogeneity of phenotypes when individuals preferentially disperse to environments that maximize their fitness according to their phenotype, a process called *habitat matching* (Edelaar et al. 2008; Edelaar and Bolnick 2012). Provided that phenotypic differences are heritable, high levels of dispersal can thus increase local individual heterogeneity and population differentiation. The role of non-random gene flows generated by dispersal in metapopulation and metacommunity functioning (i.e. the local and global dynamics, connectivity and structure of metasystems) has only recently been acknowledged and is still poorly understood (Edelaar et al. 2008; Edelaar and Bolnick 2012).

In this review, we first define the different scenarios of habitat matching and highlight their potential consequences for spatial heterogeneity of phenotypes. Then, we point out the potential consequences of such phenotype-dependent habitat choice for metapopulation and metacommunity functioning. Finally, we propose important directions for future research in metapopulation and metacommunity ecology in order to better understand the importance of non-random movements in ecological and evolutionary processes.

From non-random dispersal to spatial heterogeneity of phenotypes

Accumulating evidence provides support for the major role played by dispersal in species evolution, ecological processes and ecosystem functioning (Clobert et al. 2001, 2004, 2012; Hanski and Gaggiotti 2004; Leibold et al. 2004; Bowler and Benton 2005; Urban et al. 2008; Logue et al. 2011). Rather than moving randomly in the landscape at a fixed rate, individuals are increasingly recognized to adjust their dispersal decisions according to their phenotype and the environmental conditions encountered (i.e. non-random dispersal) at each of the three dispersal steps, namely departure (emigration), transience and settlement (immigration; Bowler and Benton 2005; Clobert et al. 2009). Therefore, instead of staying in an unsuitable environment where maladapted phenotypes are counter-selected, or plastically change their phenotypes with potential costs (West-Eberhard 1989; Dufty et al. 2002; Kawecki and Ebert 2004; Chaput-Bardy et al. 2014), individuals might move through the landscape in order to find and settle in the environmental context that best match their phenotype, therefore maximizing their fitness. In other words, individuals might perform phenotype-dependent habitat choice during dispersal, the so-called habitat matching theory (Edelaar et al. 2008; Edelaar and Bolnick 2012).

Habitat matching has been mostly discussed as a phenotype-dependent habitat choice at immigration (Edelaar et al. 2008; Edelaar and Bolnick 2012). However, individuals might perform habitat choice at two different steps of the dispersal process: at the emigration step when they decide to stay or leave a habitat, and at the immigration step when they decide to join and settle in a new habitat (post-emigration; Fig. 1). We thus discuss below the implications of habitat matching by focussing on both emigration and immigration.

Dispersal decisions often depend on individual's morphological, behavioural and physiological correlated traits (*phenotype-dependent dispersal* Fig. 1b; Clobert et al. 2009), leading to the extensively discussed *dispersal syndromes* (Clobert et al. 2009; Le Galliard et al. 2012; Stevens et al. 2013, 2014). For instance, dispersers, the individuals that leave a habitat, are often phenotypically different from residents, the individuals that stay in that habitat (e.g. Zera and Denno 1997; Haag et al. 2005; Cheptou et al. 2008; Duckworth and Kruuk 2009; Cote et al. 2010; Le Galliard et al. 2012; Stevens et al. 2014). In the naked mole-rat (*Heterocephalus glaber*), O'Riain et al. (1996) described a dispersive morph that exhibited strong morphological, physiological and behavioural differences with the resident morph. However, this phenotype-dependent dispersal does not necessarily lead to spatial heterogeneity in phenotypes. Indeed, if dispersers always exhibit the same phenotype (e.g. bigger than residents) and choose habitats to settle independently of the environmental context, immigrants and emigrants to and from a patch should have the same phenotype and the phenotypic composition of local populations (mix of big dispersers and small residents) will not vary spatially in a metapopulation at equilibrium (Fig. 1b).

We can expect phenotype-dependent dispersal to lead to spatial heterogeneity under two main circumstances: i) source–sink and colonization-extinction dynamics or range expansion, or ii) habitat selection (Edelaar et al. 2008). First, a disequilibrium between emigration and immigration rates, such as in source–sink dynamics or during range expansions, can create spatial heterogeneity of phenotypes (Fig. 1b). The colonization of an empty habitat might indeed be biased toward individuals phenotypically specialized for

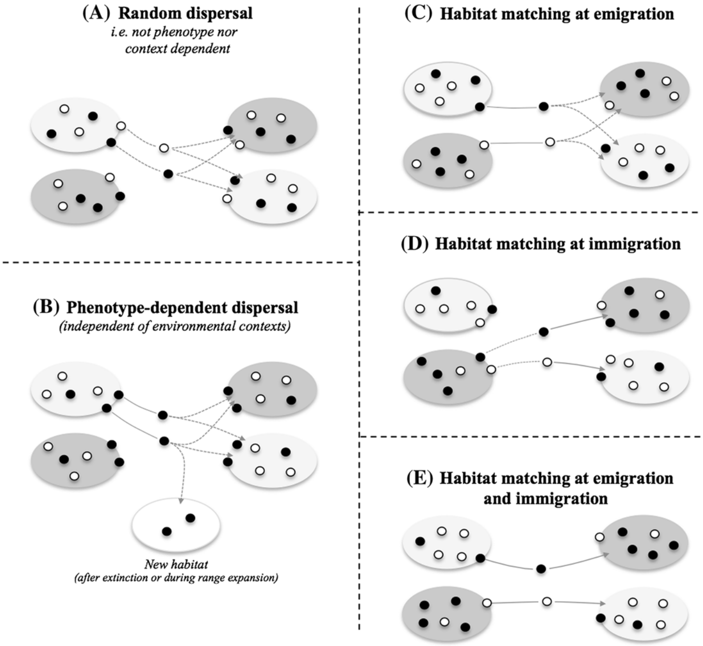

Fig. 1 Illustration of the different scenarios of random and non-random dispersal and their consequences for spatial heterogeneity of phenotypes. In these illustrations, local habitats differ in their environmental contexts (e.g. type of resources, presence/absence of congeners, presence/absence of predators; represented by *dark* and *light grey*). *Arrows* represent dispersal movements between habitats of individuals of two phenotypes (*white* and *black circles*), with continuous arrows illustrating non-random dispersal movements while *dashed arrows* illustrate random movements. **a Random dispersal**: individuals disperse independently of their phenotype and the environmental context. High levels of random dispersal will homogenise metapopulations, and in this case population differentiation might occur only under strong local adaptation and/or phenotypic plasticity. **b Phenotype-dependent dispersal**: Dispersers (*black*) are phenotypically different from resident (*white*), but choose stay or settle in habitats independently of environmental contexts. Phenotype-dependent dispersal can create population differentiation in source sink dynamics, recolonization events or during range expansions. However, this process will not generate spatial heterogeneity in metapopulations at equilibrium between colonisation and extinction. **c Habitat matching at emigration**: Individuals choose to stay or leave a patch depending on the local conditions and their phenotype (*black* individuals decide to leave *light grey habitats*, while *white* individuals leave *dark grey habitats*), but immigration remains random. This first scenario of habitat matching is likely to occur for instance when individuals cannot obtain reliable information about neighbouring patches to adjust habitat choice at immigration (Box 1). Since individuals will here join habitats randomly at immigration, this scenario has relatively low potential to generate spatial heterogeneity of phenotypes compared to habitat matching at emigration and immigration (**e**). However, since the phenotypes that do not match the local contexts will preferentially leave at each generation (either the *black* or *white* individuals depending on the local context), the local populations will contain more phenotypes that match the local context than expected under random dispersal. **d Habitat matching at immigration**: The emigration step does not depend upon individuals' phenotype or local context, while habitat choice at immigration will depend upon individuals' phenotype. Here, *white* individuals engaged in dispersal will settle preferentially in *light grey habitats*, while *black* individuals while choose *dark grey habitats*. In this case, habitat matching can generate population differentiation. **e Habitat matching at emigration and immigration**: individuals choose to stay or disperse according to their phenotype and the local environmental context, and dispersers settle in habitats that match their phenotype. Here, *black* individuals will leave *light grey habitats* to settle in *dark grey* ones, and the reverse for *white* individuals. This scenario of habitat matching at both emigration and immigration can generate population differentiation at evolutionary timescales

Box 1 The role of information in habitat matching

Dispersal is increasingly recognized to be an informed decision based on information obtained about the landscape, with numerous examples showing that the decision to e.g. stay or leave a patch depends on individual phenotype and local context (e.g. Bowler and Benton 2005; Clobert et al. 2009). Dispersing from a habitat without information about the landscape entails risks if no suitable habitats exist in the reachable surroundings. This is particularly the case under habitat matching, when individuals leaving a habitat are searching for specific environmental conditions to settle. While habitat matching reduces the settlement cost of dispersal since individuals are supposed to settle only suitable habitats, the track for optimal habitats might increase the time and energetic costs during the transience phase. As a result, obtaining information about neighbouring patches prior to emigration can be adaptive by reducing the dispersal costs. To do so, individuals might perform prospecting movements in the landscape, gathering information from other populations through assessment of the presence or absence of conspecifics and their performance (Danchin et al. 2004; Doligez et al. 2004; Dall et al. 2005). They might also evaluate neighbouring habitats prior to emigration using information conveyed by immigrants (Cote and Clobert 2007b, 2010; Chaine et al. 2010).

As the degree of fragmentation increases, prospection costs might equal dispersal costs. More sophisticated information acquisition mechanisms, such as using immigrant's traits (Cote and Clobert 2007b; Chaine et al. 2010; Cote and Clobert 2010; Jacob et al. in press), might thus be highly beneficial in highly fragmented landscapes since they do not require costly prospection forays. However, information from immigrants might be less reliable than information obtained through prospecting. Especially, if individuals match habitats at immigration, they will not provide reliable but biased information about the landscape. Interestingly, these information-gathering mechanisms might evolve uniformly or differently among dispersers' types. For example, in Siberian flying squirrel (*Pteromys volans*), long-distance and short-distance dispersers use different mechanisms of information gathering (Selonen and Hanski 2010), with short-distance dispersers prospecting around one location by frequently visiting previously prospected habitats while long-distance dispersers perform sequential searching. Therefore, in a metapopulation context, we can expect colonizers and joiners to use different information acquisition mechanisms. Joiners may prospect more in surrounding patches to acquire information about their social structure. In contrast, colonizers that are searching for empty habitat may engage in long-distance sequential searching. We consequently expect colonizers to personally assess habitat quality, while joiners should rely more on information conveyed by congeners.

dispersal, resulting in a population composed of a subsample of the phenotypes in the source habitats (Duckworth and Badyaev 2007; Clobert et al. 2009; Fogarty et al. 2011; Shine et al. 2011). For instance, newly established isolated populations of the Glanville fritillary butterfly (*Melitaea cinxia*) showed higher frequency of an allele related to a high flight metabolic rate (Haag et al. 2005).

Second, spatial heterogeneity can result from dispersal when individuals' habitat choice at emigration or immigration depends on their phenotype and the environmental conditions (Fig. 1c–e; Benard and McCauley 2008; Rémy et al. 2011; Fernández-Chacón et al. 2013), a process requiring information acquisition from the landscape (Box 1; Cote and Clobert 2007b, 2010; Chaine et al. 2010). Individuals should indeed benefit from living in specific environments that maximize their fitness (Heinz and Strand 2006; Selonen and Hanski 2012). Accumulating evidence provides support for phenotype-dependent habitat choice at the emigration step (i.e. habitat matching at emigration; Fig. 1c). For instance, the decision to stay or leave a patch is both phenotype and context-dependent in the large white butterfly (*Pieris brassicae*; Trochet et al. 2013; Legrand et al. press), but also depends on the interaction between some environmental conditions (weather conditions and habitat quality) and a phenotypic trait (sex; Legrand et al. press). Additionally, phenotype-dependent habitat choice can occur at immigration (i.e. habitat matching at immigration; Fig. 1d), such as in audouin's gulls (*Larus audouinii*) and in common lizards (*Zootoca vivipara*), where dispersers from low-density and poor quality patches are more likely to settle in high-density habitats and display specific phenotypic attributes in comparison to dispersers from high-density habitats (Cote and Clobert 2007a; Fernández-Chacón et al. 2013). This will result in a covariation between phenotypes and the environmental conditions. Importantly, phenotype-dependent habitat choice at immigration can generate spatial phenotypic heterogeneity even without any difference at emigration between residents and dispersers (i.e. habitat matching at immigration; Fig. 1d). Habitat matching might subsequently have important consequences on species range distribution, local adaptation and speciation (Edelaar et al. 2008; Edelaar and Bolnick 2012).

Habitat matching and metapopulation functioning

Metapopulation theory stipulates that individuals live in heterogeneous landscapes where populations occupy suitable habitat patches separated by an unsuitable matrix (Hanski 1999). Dispersal movements between patches maintain connectivity in metapopulations and thus have a major role in metapopulation functioning through reinforcement of small populations (rescue effect) and re-colonization of extinct ones (Hanski 1999; Clobert et al. 2001, 2004; Hanski and Gaggiotti 2004; Bowler and Benton 2005; Ronce 2007; Ronce and Clobert 2012). However, dispersing through an unsuitable matrix is costly and these dispersal costs increase with population isolation and matrix unsuitability (Bonte et al. 2012).

As exposed in the previous section, dispersers often have specialized dispersal phenotypes, which increase dispersal ability and reduce dispersal costs (Clobert et al. 2009; Sih et al. 2012). Such phenotypic specialisations are often coupled with differences in demographic strategies such as a delayed reproductive onset, a faster growth rate or a stronger reproductive effort (e.g. Le Galliard et al. 2012), and these differences may improve colonization abilities. The evolution of such specialized dispersal phenotypes can be generated by increased population isolation and colonization-extinction dynamics (Heidinger et al. 2010; Forsman et al. 2011; Brodin et al. 2013). For instance, geographical isolation from the mainland in island vole populations (*Microtus agrestis*) has selected for genetically-based long feet relatively to body size (Forsman et al. 2011), as a result of the improved dispersal abilities and increased immigration probability provided by this phenotypic specificity (long-distance swimming ability). Selection for this phenotypic specialization therefore resulted in increased connectivity in this island-mainland metapopulation (Forsman et al. 2011).

On top of specialized dispersal phenotypes, we also expect that habitat matching should have important consequences for metapopulation colonization-extinction dynamics. In a metapopulation context, with both colonization and reinforcement movements, some dispersal phenotypes might be specialized in population reinforcement (i.e. joiners; Fig. 2), searching for already established populations with high density, while others (i.e. colonizers; Fig. 2) might look for empty patches to colonize (Wade and McCauley 1988; Clobert et al. 2009; Cote et al. 2010). Colonizing empty patches can be beneficial (Lambin et al. 2001; Le Galliard et al. 2005) but is a risky behaviour since individual fate may depend on others' future settlement decisions. On the other hand, joining existing populations may require different behavioural and morphological specializations such as low aggressiveness or high competitive abilities (Cote and Clobert 2007a; Fernández-Chacón et al. 2013). Colonizers might thus have phenotypic traits enhancing colonization success while joiners might have traits increasing integration success (Bonte et al. 2011). In this case, conspecific density is the habitat characteristic that individuals try to match. We focus on these two strategies, colonizers and joiners, because they specifically matter in metapopulations, but note they are thought to be the two extremes of a density-dependent continuum of preferences (from low density for colonizers to high density for joiners) among dispersing individuals.

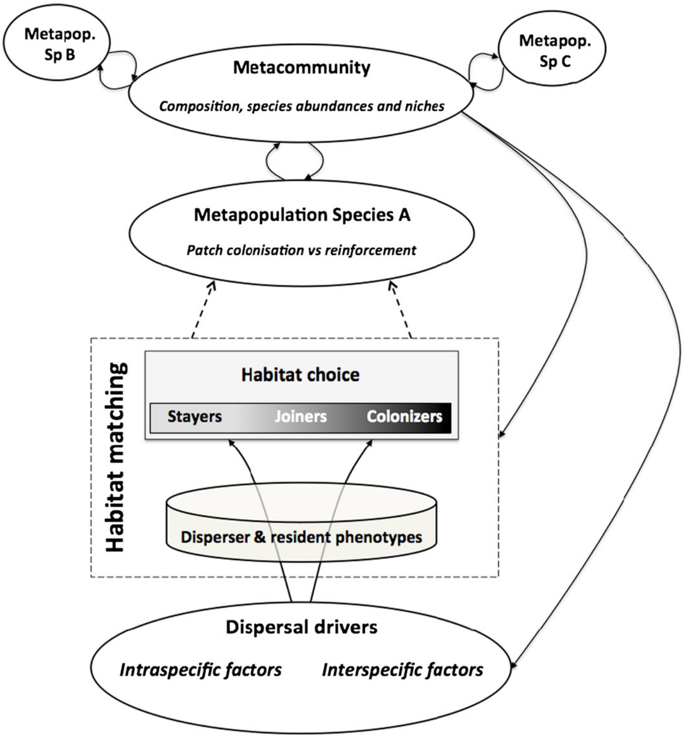

Fig. 2 Schematic outline of the role of habitat matching in metapopulation and metacommunity functioning. Phenotype-dependent decisions at the different phases of the dispersal process are governed by intra and interspecific factors. Phenotype-dependent emigration, together with differences between phenotypes in habitat preferences at immigration (e.g. colonizers vs. joiners), generates habitat matching and can drive patch colonization and reinforcement and therefore metapopulation dynamics. The presence, phenotypic variability and metapopulation dynamics of one species can in turn affect dispersal decisions and therefore habitat matching of other species of the community, making intraspecific dispersal processes likely to drive metacommunity composition, species abundance and niche use

Dispersing individuals are expected to distribute in the landscape according to these dispersal strategies, but empirical evidence for phenotypic differences between colonizers and joiners is still weak. In dispersal studies, phenotypic comparisons are mostly made between dispersers and residents irrespectively of local environmental conditions before and after dispersal. Specifically, the link between dispersers' phenotype and post-emigration decisions (e.g. habitat preferences at immigration) has been relatively overlooked (Duckworth 2008; Clobert et al. 2009; Le Galliard et al. 2012). The only information on colonizers' phenotypic specializations comes from the biological invasion and range expansion literature. For example, in western bluebirds (*Sialia mexicana*) colonizers of new sites are highly aggressive individuals (Duckworth and Badyaev 2007; Duckworth 2008). This phenotype-dependent colonization allowed this species to displace and ultimately exclude an interspecific competitor, the mountain bluebird (*Sialia currucoides*), from invaded sites (Duckworth and Badyaev 2007). Another example is the larger body size of colonizers associated with greater reproductive success, survival and subsequently colonization success (Ebenhard 1990; Cote et al. 2007). Besides, colonizers might not always present highly specialized competitive phenotypes, but instead be individuals with lower competitive ability who would have a reduced fitness in crowded habitats and thus might benefit from dispersing to empty or even sink habitats (Loehle 2012).

A promising direction would be to investigate phenotypes of colonizers and joiners by comparing positive and negative density-dependent dispersers. Indeed, as mentioned above, colonizers and joiners are the two extremes of a density-dependent continuum of preferences with colonizers expected to prefer low density habitats while joiners should prefer high density patches. Dispersal is traditionally thought to increase with density (positive density-dependent dispersal; Gandon and Michalakis 1999; Bowler and Benton 2005; Poethke et al. 2007), but conspecific attraction can lead to negative density dependency (Stamps 2001; Kim et al. 2009; Baguette et al. 2011; Fellous et al. 2012; Pennekamp et al. 2014). Conspecific attraction theory clearly shows that some dispersers search for existing populations (Stamps 2001) and we can expect them to have phenotypic attributes facilitating integration (Dardenne et al. 2013). Interestingly, these two density-dependent tendencies can coexist within a species (Cote and Clobert 2007a; Kim et al. 2009; Pennekamp et al. 2014), and the factors inducing positive and negative density-dependent dispersal are likely to differ (Clobert et al. 2009; Van Allen and Bhavsar 2014, Fig. 2).

We expect that metapopulation persistence should be affected by heterogeneity in dispersal decisions and phenotype-dependent habitat choice, and especially by the enhanced colonization success mediated by colonizers' phenotypic specializations. Indeed, theory shows that heterogeneity in dispersal-related traits at the metapopulation scale may affect metapopulation persistence (Leimar and Norberg 1997). Leimar and Norberg (1997) showed that genetic variation in dispersal-related traits might be detrimental for population persistence during the critical phase right after fragmentation because of the costs endured by high dispersive phenotypes. However, genetic variation may increase the persistence of metapopulations if they overcome this critical phase (Leimar and Norberg 1997). On top of abundance, variability in dispersers' phenotype should then be considered when studying population dynamics and colonization processes (Burgess and Marshall 2011). For example, in the western bluebird, the coupling of colonization ability and heritable levels of aggressiveness has led to a wave of range expansion, with highly aggressive types occupying the front of the range expansion and displacing competitors (Duckworth and Badyaev 2007).

As described in the introduction, habitat matching, local selection and phenotypic plasticity can all generate spatial heterogeneity of phenotypes because they all create covariations between individuals' phenotypes and local environmental contexts. However, the consequences of these different processes for metapopulation dynamics are likely to differ. On one hand, natural selection with random dispersal will lead to high mortality rates for maladapted phenotypes dispersing to a habitat, while on the other hand the degree of plastic changes in phenotype that individuals can reach is usually limited (DeWitt et al. 1998). Consequently, habitat matching will likely involve lower mortality rates, faster adaptive population divergence, and even a better match between phenotype and environment (Edelaar and Bolnick 2012) than local selection and plasticity. Since metapopulation persistence critically depends on effective population size (Hanski and Gaggiotti 2004), habitat matching might decrease extinction risks. Indeed, recent modelling showed that a mix of different disperser phenotypes, with different habitat preferences, allows faster invasion, increases range expansion and favours metapopulation persistence (Elliott and Cornell 2012).

Another scenario where the ecological consequences of habitat matching, local selection and plasticity might deeply differ is under asymmetries in the number of dispersing individuals between patches in a landscape (Amarasekare 2004; Vuilleumier and Possingham 2006; Benard and McCauley 2008). Mainly, models investigating the consequences of dispersal asymmetry in metapopulations found evidence for its negative effects on metapopulation persistence and resistance to fragmentation (Vuilleumier and Possingham 2006). However, if asymmetries in the number of dispersing individuals are coupled with habitat matching, these asymmetric flows might become adaptive since an increased match between individual phenotype and environmental conditions that maximize individual fitness can favour population persistence. Future theoretical and experimental studies will be required to understand the consequences of habitat matching relatively to selection and plasticity on metapopulation persistence.

From intra- to interspecific interactions: non-random dispersal in metacommunities

Local community composition results from both local and regional processes (Logue et al. 2011). While local processes are mainly governed by interactions among and within species, regional processes depend on movements of organisms between localities (Leibold et al. 2004; Urban et al. 2008; Logue et al. 2011). Dispersal between local habitat patches is therefore central in metacommunity functioning. In metacommunity theory, species are classically considered to show fixed dispersal rates with individuals moving randomly in the landscape, regardless of local and regional conditions (Urban et al. 2008; Logue et al. 2011; Lowe and McPeek 2014). However, this review and others (e.g. Bowler and Benton 2005; Clobert et al. 2009; Le Galliard et al. 2012; Stevens et al. 2014), demonstrate that this statement is largely untrue. Assuming dispersal to be random probably leads to misunderstandings and underestimation of the role of dispersal in metacommunity functioning (Urban et al. 2008; Logue et al. 2011; Lowe and McPeek 2014). Recent works indeed provide support for an important role of species habitat selection in the genesis of spatial variability in community composition (Binckley and Resetarits 2005; Leibold et al. 2004; Resetarits and Binckley 2009; Logue et al. 2011). Dispersal directionality toward undisturbed patches negatively affects species richness in experimental communities of protists and rotifers in microcosms (Altermatt et al. 2011). As a result, habitat matching has the potential to influence not only metapopulation but also metacommunity functioning (Fig. 2).

Individual's dispersal propensity can be influenced by multiple external factors related to intraspecific interactions (Bowler and Benton 2005; Clobert et al. 2009, 2012). Although more rarely investigated, interspecific interactions, such as competitive or predator/prey interactions, can also be major drivers of species dispersal tendency (Clobert et al. 2001, 2012; Bowler and Benton 2005; Allen et al. 2012) or dispersal strategies such as short- versus long-distance movements (Goodacre et al. 2009). For example, in a protist predator–prey metacommunity, dispersal decisions vary according to both intra- and interspecific density (Hauzy et al. 2007); in the money spider (*Erigone atra*) the acquisition of maternally transferred endosymbionts reduces the frequency of long-distance dispersal (Goodacre et al. 2009); and in a passively dispersing mite (*Spadiseius calyptrogynae*) the choice of dispersal vector determines its dispersal distance (Fronhofer et al. 2013). Consequently, interspecific interactions might deeply affect species range distribution and ability to reinforce isolated populations or recolonize habitats through their effect on dispersal distances (Johst et al. 2002). A ground-breaking example of the importance of habitat preference variations mediated by species interactions is the reduction of abundance and species richness in an aquatic beetle metacommunity as a result of avoidance of habitats where predator cues was present (Binckley and Resetarits 2005). This study demonstrates that the presence or absence of predators may govern prey habitat selection and in turn metacommunity assemblage.

All species in a community are however not equally sensitive to interspecific interactions. For example, species greatly vary in their ability to detect and escape predators (Wooster and Sih 1995; Binckley and Resetarits 2005; Sih et al. 2010). The interplay between predation modes (e.g. active or passive hunting) and prey escape strategies will thus drive species dispersal reaction to predation risk in the local community and subsequent habitat selection at the regional scale. This should result in habitat matching at the species level, which can deeply change species distribution at local and regional scales and therefore metacommunity and ecosystem functioning (Binckley and Resetarits 2005; Resetarits and Binckley 2009).

Importantly, as demonstrated in the previous section, variability in habitat preferences may occur within species as much as among species. Indeed, within a population, variation in phenotypic traits can be as high and important as among populations or even among closely related species (Estes et al. 2003; Post et al. 2008; Laine et al. 2011; Bolnick et al. 2011; Pruitt et al. 2012; Violle et al. 2012; Allen et al. 2012; Howeth et al. 2013). Therefore, interspecific interactions, and thus community composition, might differently affect dispersal strategies among and within species. The end-result would be within-species habitat matching governed by species interactions.

Species interactions might thus drive phenotype-dependent dispersal within species and phenotypic specializations in dispersers. For instance, predator pressure provokes the production of specialized dispersal morphs in the pea aphid (i.e. winged morph; *Acyrthosiphon pisum*; Sloggett and Weisser 2002) and in the common lizards (Bestion et al. 2014). In common lizards, on top of increasing offspring dispersal probability, maternal predation risk induces offspring dispersers to have longer tails than residents, a specialization reducing predation costs during dispersal (Bestion et al. 2014). This phenotypic specialization is missing in a risk-free maternal environment. In killifish (*Rivulus hartii*), the presence of predators creates a strong positive relationship between body size and emigration probability whereas this relationship is clearly absent in the absence of predators (Gilliam and Fraser 2001). On the contrary, in western mosquitofish (*Gambusia affinis*), dispersal distance is negatively related to social tendency in the absence of predators and this dispersal syndrome is missing when predators are present (Cote et al. 2013). Species interactions such as predator–prey or host-parasites interactions can thus create or disrupt dispersal syndromes within one generation (Gilliam and Fraser 2001; Altermatt et al. 2007; Fellous et al. 2011; Cote et al. 2013; Bestion et al. 2014) and this context- and phenotype-dependent emigration (i.e. habitat matching at emigration, Fig. 1) could induce heterogeneity in phenotypic distribution at both local and regional scales. In cases of strong phenotypic differences among dispersers (Gilliam and Fraser 2001), species composition can thus create an important heterogeneity in phenotypic distribution at a metacommunity scale and, in turn, modify local community functioning. We thus urge the need to integrate intraspecific variation as a new level of biodiversity into metacommunity functioning (Bolnick et al. 2011; Violle et al. 2012; Juette et al. 2014).

While species interactions within communities can mediate non-random dispersal movements in the landscape, habitat matching can in turn affect community assemblage (Box 2). Biased dispersal toward more aggressive western bluebirds displaces less aggressive mountain bluebirds, thus favouring range expansion in the first species while reducing range distribution of the other (Duckworth and Badyaev 2007; Duckworth 2008). Non-random dispersal movements with phenotypes specialized for colonization thus has the potential to play a crucial role in the extension of species range distribution, and

Box 2 Consequences of habitat matching in a metacommunity

We develop a theoretical example describing how habitat matching could affect metacommunity functioning and persistence. We combine the frameworks of within-species individual specialization (Bolnick et al. 2003) and of habitat matching (Edelaar et al. 2008) to predict the intra- and interspecific composition of a two-species metacommunity.

Metacommunity composition: The metacommunity is composed of two species (species A, dashed lines and species B, solid lines; Fig. 3) in competition on a part of their respective niches (grey area in Fig. 3). Individual specialization theory suggests that species with a large niche width (i.e. generalist species) can be composed of individuals specialized in different resources along the niche axis, potentially because of phenotypic differences. In our example, each species is composed of two types of specialized individuals (A1/A2, B1/B2, Fig. 3). As a consequences, individuals at the two ends of their species niche distributions do not share the same resources and are therefore not in competition.

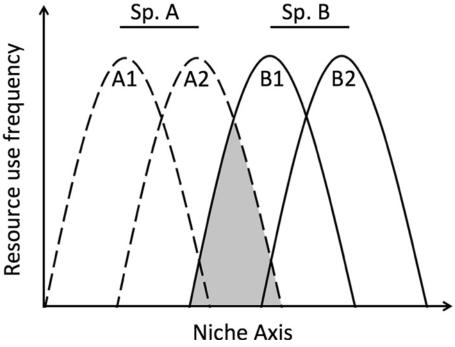

Fig. 3 Illustration of the niches of the two species used in our theoretical example. Each species is composed of two classes of phenotypes (*A1* and *A2* for species A, *B1* and *B2* for species B) that partly differ in their niche, making among species competition occurring mainly between phenotypes *A2* and *B1*

Here, we consider a metacommunity composed of 4 local communities (Fig. 4) without differences in resource type or quantity, covering the whole niche axis (Fig. 3). Local communities can vary at the species (i.e. A or B) and phenotype levels (i.e. A1, A2, B1, B2). These local communities can thus contain two types of phenotypes for each species, but specialists' niches are partly overlapping (Fig. 3), creating among species competition between specialists A2 and B1. Since local communities can be composed of different specialists, the use of resources in local communities and the level of competition for resources might differ. Consequently, total carrying capacities will vary depending on among and within-species competition (e.g. total carrying capacity A1 + B2 > total carrying capacity B1 + B2, B1 + A2 or A1 + A2). In mixed species local communities, we thus assume that specialist A1 and B2 should be more abundant than A2 and B1 as a result of niche overlapping.

Colonization with or without habitat matching: Our scenario starts with an empty patch made available through e.g. extinction (*step 0*, Fig. 4). This scenario also matches a range expansion or a change in matrix viscosity. In *step 1*, one species is (re-)colonizing the empty patch (species A in this example). This patch being similar to the others, except that it is free of individuals, we assume that colonizers would be composed of both types of specialists (A1, A2). We therefore excluded, for this example, any link between colonization ability/preferences and resource specialization.

Box 2 continued

We compared two scenarios for *step 2*, without habitat matching (scenario 1 = ***random dispersal***) or with habitat matching (scenario 2 = ***habitat matching***). In our example, ***habitat matching*** relates to a choice of habitats that depends on the competition level with the other species (niche overlap). In *scenario 1 (Sc. 1)*, the dispersal of species B does not depend on the occurrence of species A. Both B1 and B2 individuals are therefore settling in the recently colonized sub-community (Sc 1; Fig. 4). In *scenario 2 (Sc. 2)*, species performs habitat selection to avoid habitats with a niche already occupied. In our example, B1 specialists are therefore avoiding the recently colonized patch because they would be in competition with A2 specialists. Since the niche for B2 specialists is not overlapping the niche of A1 specialists and is only slightly overlapping the niche of A2 specialists, B2 individuals can settle in this patch (Sc 2; Fig. 4). B and A species will keep joining this every generation according to the given rules (Sc. 1: B1 and B2, Sc. 2: B2 only).

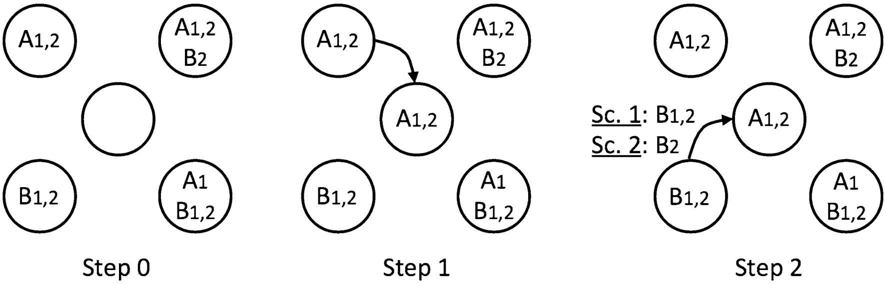

Fig. 4 Metacommunity with two species (*A* and *B*), each one comprising two specialist phenotypes (Fig. 5). At step 0, the metacommunity is composed of four local communities and one empty patch resulting from e.g. local extinction that can then be (re-)colonized. At step 1 (colonization), phenotypes *A1* and *A2* colonize the empty patch. At step 2, two scenarios are envisaged. Under random dispersal (Sc. 1) both *B1* and *B1* colonize, while only *B2* will colonize under the habitat matching hypothesis (Sc. 2)

Predictions for the two scenarios: In the ***random dispersal*** scenario (Sc. 1, Fig. 5), the arrival of individuals of phenotype B1, along with those of B2 individuals, will generate inter-specific competition with A2 individuals. Specialists A2 will thus endure intra-specific competition with A1 individuals and interspecific competition with B1 individuals. Therefore A1 individuals will have to compete on their entire niche width (Fig. 3). Specialists B1 will also endure competition on their entire niche width (with A2 and B2 individuals). Because joining events, through random dispersal, will happen every generation (or continuously), we predict that populations composed of A2 and B1 individuals will not grow to high densities because of intense competition. After a long period, we expect this local community to be mainly composed of A1 and B2 individuals at their respective carrying capacity, while A2 and B1 population sizes will stay low.

In the ***habitat matching*** scenario (Sc. 2, Fig. 5), B1 individuals are avoiding the local community recently colonized by A1 and A2 individuals to avoid competition with A2 specialists, while B2 individuals can settle since their niches are not overlapping the one of species A (Fig. 3). Consequently, A2 individuals only have to compete with A1 individuals on a part of their niches (because of the relaxed competition with B1 specialists). Species A (A1 and A2) will thus reach the carrying capacity on the entire species niche width, which will be higher than under random dispersal (Sc. 1; Fig. 5). On the contrary, species B will reach a carrying capacity corresponding only to the resources used by specialists B2 in this local community.

Box 2 continued

Consequences: Our theoretical example suggests that habitat matching can have different consequences on population size and intraspecific diversity in a metacommunity compared to a random dispersal scenario. In a newly colonized habitat, habitat matching decreases competition, which might benefit species' population size. While all specialists are present in the colonized habitat under the ***random dispersal*** scenario (i.e. A1, A2, B1, B2), specialists suffering within- and between-species competition (A2, B1) have very low abundances (Fig. 5). In the ***habitat matching*** scenario, one specialist is missing (B1) but the remaining specialists (A1, A2, B2) have similar abundances. Consequently, although local intraspecific variability for species B is lower under habitat matching, niche diversity weighted for abundance may be higher. However, in the ***habitat matching*** scenario, specialist B1 is avoiding patches containing specialists A2 to settle in empty patches or containing only species B, or specialists A1. Interestingly, ***habitat matching*** may favour the local persistence of the 3 specialists A1, A2 and B1 at an evolutionary time (extinction risk is reduced because of their higher abundances compared to the random dispersal scenario), which translates into the persistence of the 4 specialists at the metacommunity scale. On the contrary, while ***random dispersal*** leads to the local coexistence of the 4 specialists at an ecological time, the low abundances of the specialists suffering both within- and among-species competition increase their extinction risk at an evolutionary time.

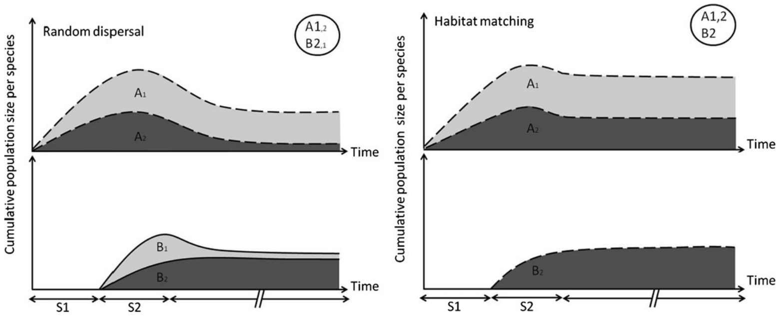

Fig. 5 Illustration of the cumulative population size of a local community along the steps of a (re-)colonization process under a random dispersal scenario (Sc. 1) and a habitat matching scenario (Sc. 2)

Limitations: If colonizing and joining happen only once (i.e. one dispersal event), then, after selection, local communities should soon have similar compositions in the two scenarios. However, it is unlikely that a patch becomes isolated after few dispersal events. On the contrary, random dispersal is expected to bring maladapted phenotypes regularly and dilute the effect of selection. Furthermore, to preferentially select some patches, individuals should be able to assess others' niche width, including individuals of other species, (either through direct recognition of other species characteristics or indirectly by looking at resources). While this is possible for many resources (spatial resources for instance), further studies should investigate whether and how information about neighbouring patches is obtained (Box 1).

indirectly on its reduction in competitive or prey species. More generally, individual dispersal strategies are often linked to individual competitive ability (positively or negatively), foraging rates and trophic position (e.g. Ellsworth and Belthoff 1999; Duckworth and Badyaev 2007; Gloria-Soria and Azevedo 2008; Cote et al. 2010; Cucherousset et al. 2013). In these cases, phenotype-dependent dispersal can affect the speed of invasion and ultimately local populations and communities' dynamics and composition (Fogarty et al. 2011; Juette et al. 2014). Within species variability in habitat preferences might thus be of prime importance for metacommunity assemblages and dynamics.

Effects of dispersal on metacommunities might depend on species' niche breadth, which varies among species from those highly specialized to specific environmental contexts to generalist. Generalists, which are often keystone species in ecosystems (Martín González et al. 2010), are classically considered to better withstand environmental changes because of their ability to cope with various environmental conditions. However, generalist species can be composed of multiple specialized individuals (Bolnick et al. 2003; Box 2). Generalist species, instead of being composed of individuals with large environmental tolerance as a result of high plasticity, can be composed of various types of specialists, each one specialized for specific resources or environments. In this case, the species' niche width result from the sum of inter-individual differences in resource use or environmental tolerance rather than intra-individual variation (Bolnick et al. 2003; Box 2). Because of habitat matching, it is fundamental to distinguish these two options. Generalist individuals should be able to deal with a wider range of conditions and thus should be less inclined to disperse after environmental changes than specialized individuals. As a result, we advocate that a low increase in dispersal rates should occur when generalist species are made of generalist individuals, and in contrast expect an increase of non-random dispersal movements in generalist species made of diverse specialized individuals, given that each specialist should track specific environmental conditions. Total dispersal rates and degrees of asymmetric movements of phenotypes in the landscape should thus differ between these two kinds of generalist species, with potential consequences on species coexistence and metacommunity functioning.

Conclusions

Intraspecific variability is key in evolution (Darwin 1859), but most of the theoretical approaches in population and community biology have surprisingly neglected it. Recent years have seen the resurgence of the importance of phenotypic variability in ecological thinking (Bolnick et al. 2003; Reiss et al. 2009; Bolnick et al. 2011; Logue et al. 2011; Sih et al. 2012; Violle et al. 2012; Wolf and Weissing 2012), but our understanding of how much its incorporation into population and community theories changes our comprehension of ecological and evolutionary processes is still weak. Specifically, the consideration of dispersal as a random process in regard to individual phenotype has led to the underestimation of its role in metapopulation and metacommunity functioning. Instead, dispersal movements are now recognized as non-random at both the intra- and interspecific levels in the landscape. In this review, we have provided evidence that non-random dispersal resulting from phenotype-dependent habitat preferences, the so-called habitat matching, is likely to be of major importance for metapopulation and metacommunity functioning (Figs. 1, 2, Box 2). We thus suggest that a better comprehension of the consequences of habitat matching in meta-systems will improve our ability to predict the consequences of environmental changes on biodiversity. Further theoretical and experimental studies should therefore investigate how intra and interspecific interactions driving decisions at each dispersal stage (departure, transience and settlement) interact with each other to produce dispersers' phenotype, and how this can affect metapopulation and metacommunity functioning.

However, the potential of habitat matching to impact metapopulations and metacommunities might become limited when dispersal becomes challenging, for example in a viscous matrix. If mortality during dispersal is high, or if dispersal rates are low, we predict that habitat matching will not affect the functioning of metapopulations and metacommunities, except under perfect habitat matching (Edelaar and Bolnick 2012), which requires highly efficient information acquisition about the landscape (Box 1). Alternatively, if information acquisition about the landscape remains efficient in spite of the increased costs of dispersal, habitat matching might favour colonization success and therefore deeply affect metapopulation and metacommunity functioning. Moreover, if dispersal phenotypic specializations involve only plastic, non-heritable traits, habitat matching should not lead to population differentiation in metapopulations. However, dispersal behaviour has been shown to be heritable in many species (Zera and Brisson 2012) and is often linked to a large panel of phenotypic traits (Clobert et al. 2012). It seems thus unlikely that dispersal syndromes would only involve a plastic determination. In almost all situations, we believe that habitat matching should create population differentiation, at least for some phenotypic traits. In the other situations, the impact of habitat matching might only be transitional, allowing more efficient (re)-colonization and lower mortality rates at settlement, but without dramatic changes at evolutionary time-scales in comparison with the effects of selection alone.

Future studies in experimental systems with highly controlled conditions will certainly be required to develop our understanding of the role of dispersers' phenotype and habitat matching in ecological and evolutionary processes. Manipulating phenotypic variability while maintaining environmental conditions constant will help identifying the role played by intraspecific variability in spatial phenotypic heterogeneity and metapopulation colonization-extinction dynamics. Moreover, experimental studies investigating the role of dispersal in metacommunities should go beyond the view of random dispersal and compare the effects of various dispersers' phenotypes and strategies in metacommunity assemblages and dynamics. Furthermore, while habitat matching requires individuals to obtain information about their landscape to perform habitat selection, we crucially need to investigate which type of information is used, from which mechanisms this information is obtained, and thus how much this process is affected by changes in environmental conditions (e.g. fragmentation). Experimental work on this topic is at the start, and will certainly benefit from the use of standardized protocols across biological models (Altermatt et al. 2015) and of experimental tools specifically dedicated to the study of dispersal, such as connected micro- and mesocosms (Legrand et al. 2012). Finally, we crucially need empirical studies on phenotype-dependent habitat choice in natural populations to assess the importance and ubiquity of habitat matching processes.

Reviewing literature on metapopulation and metacommunity, we found limited knowledge on the relative contribution of habitat matching, plasticity and natural selection in shaping phenotypes and species distribution in fragmented landscapes. We expect these three processes to act in concert in natural systems (Edelaar et al. 2008), pointing out the necessity of performing experiments designed to quantify the relative contribution of habitat matching, local selection and plasticity in generating phenotypic spatial heterogeneity and driving metapopulation dynamics and metacommunity functioning. Moreover, their relative importance and consequences are likely to depend on the ecological context such as environmental heterogeneity and spatial autocorrelation. For instance, we might expect habitat matching and phenotypic plasticity to evolve under different spatio-temporal environmental conditions. Indeed, the ability of individuals to find and settle in specific environmental conditions should reduce selection for phenotypic plasticity. While phenotypic plasticity is likely to be selected under high temporal variability of environmental conditions, habitat matching might become beneficial when temporal variability decreases and spatial variability increases. Finally, the occurrence of non-random dispersal should vary among species and with dispersal modes. At first, we could expect actively dispersive species to evolve non-random dispersal behaviours more often than passively dispersive species. For instance, in benthic invertebrate communities, species with passive dispersal co-occurred randomly and irrespective of the environmental context, while species with active dispersal showed spatial segregation according to the level of environmental heterogeneity (Heino 2013). However, passive dispersal species may also display non-random dispersal as a result of habitat matching performed by animal vectors or of vector choice when multiple vectors are available (Fronhofer et al. 2013). This passive non-random dispersal will further depend on local community composition, and may lead to non-random distribution of species and phenotypes at the metacommunity level. We thus urge the need to develop theoretical investigations of how different the ecological and evolutionary outputs of habitat matching, selection and plasticity are and how to discriminate them in natural systems.

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Glossary

Context-dependent dispersal	Correlations between dispersal behaviour at each stage and ecological conditions. These conditions include abiotic conditions (e.g. temperature, humidity, soil composition), population/social contexts (e.g. density, relatedness, sex-ratio) and interspecific interactions/community composition (e.g. predation risk, parasitism, prey abundance).
Dispersal syndrome	A suite of morphological, behavioural, physiological and life-history traits characterizing dispersers in comparison to residents. These suites result from the interaction between phenotype- and context-dependencies of dispersal and can thus vary with ecological contexts of dispersal.
Habitat matching	Dispersal decisions consisting in moving through the landscape in order to find and settle in the environmental context that best match their phenotype, providing individuals with higher performances than in other habitats. This process results in a match between individual phenotype and habitat ecological conditions. Habitat matching therefore consists in phenotype- and context-dependent dispersal decisions at emigration and/or immigration.
Local adaptation	Increase of individual's performance driven by genetic adaptation to the local ecological context over generations.
Phenotype-dependent dispersal	Correlations between dispersal behaviour at each stage and individual morphological, behavioural, physiological and life-history traits. These correlations can be genetically determined or can vary with ecological conditions, including conditions involved in context-dependent dispersal.

Phenotypic plasticity	Ability of a given genotype to produce different alternative phenotypes according to the environmental conditions.
Metacommunity	A group of communities that are spatially separated and connected by the dispersal of one or several species. Metacommunity dynamics result from complex interactions between extinctions and re-colonizations for each species constituting communities.
Metapopulation	A group of populations that are spatially separated and connected by dispersal. Metapopulation dynamics result from extinctions and re-colonization events. Metapopulations often result from landscape fragmentation where habitat patches are being surrounded by unsuitable matrix and become more isolated from each other.
Random and non-random dispersal	Random dispersal is active or passive movement from a natal/breeding site to another breeding site regardless of their ecological characteristics and phenotypic attributes of candidate dispersers. Non-random dispersal occurs when dispersal behaviour, at least for one stage (departure, transience, settlement), depends on sites' ecological condition (context-dependent dispersal) or on individual phenotype (phenotype-dependent dispersal).
Spatial heterogeneity	Spatial structure in the distribution of ecological conditions (i.e. spatial environmental heterogeneity) or of phenotypic traits (i.e. spatial phenotypic heterogeneity) in a landscape.

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