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Habitat fragmentation, an important element of current global change, has profound repercussions on population and species extinction. Landscape fragmentation reduces individual movements between patches (i.e. dispersal) while such movements connecting patches enhance the persistence of metapopulations and metacommunities. Through the recognition of non-random movements, dispersal has recently been recognized as a highly complex process. This complexity likely changes the predictions on the evolution of dispersal in spatially structured populations and communities. In this article, we emphasize the effects of fragmentation on the evolution of non-random dispersal. Habitat fragmentation may shape local and global selective pressures acting on a large array of phenotypic traits known to covary with dispersal behaviors. On top of changes in dispersal propensity, habitat fragmentation could therefore modify dispersal syndromes (i.e. dispersers' phenotypic specializations). Habitat fragmentation often leads to spatial structuring of local conditions and consequently may lead to the evolution of different dispersal syndromes at the landscape scale. By neglecting impacts on dispersal syndromes, we might underestimate the impacts of fragmentation on a crucial biodiversity level for metapopulation and metacommunity functioning. We highlight a set of priorities for future empirical and theoretical work that together would provide the understanding of eco-evolutionary dynamics of dispersal syndromes required for improving our ability to predict and manage spatially structured populations and communities.

Introduction: the multidimensional dispersal process

Habitat conversion from natural ecosystems to agriculture, forestry and human settlements has taken over large amounts of land, leaving species with an increasingly shrinking world (Foley et al. 2005, Newbold et al. 2015). Beyond direct negative effects on taxonomic, functional and genetic diversity (Foley et al. 2005, Newbold et al. 2015), this indirectly erodes biodiversity through the fragmentation of large, continuous habitats into smaller isolated patches in a sea of often heterogeneous matrix (Fahrig 2003, Haddad et al. 2015, Wilson et al. 2015, Resasco et al. 2017, Thompson et al. 2017). Fragmentation modifies landscapes in four ways – reducing habitat quantity; increasing the number of patches; decreasing their size; and, increasing isolation (Fahrig 2003) – with diverse effects on population dynamics. Smaller patches have smaller populations, increasing stochastic risks of extinction from demographic and genetic processes, e.g. inbreeding depression, leading to an extinction vortex (Gilpin 1986, Fagan and Holmes 2006). Moreover, increasing inter-patch distances magnifies dispersal risks; fragmentation may reduce movements among patches (Fahrig 2007) and worsen the extinction vortex. Dispersal between patches (Fahrig and Merriam 1994, Baguette et al. 2013), enables recolonization after local extinction and may even reduce the likelihood of stochastic extinctions (Fahrig and Merriam 1994, Bowne and Bowers 2004, Baguette et al. 2013). The precise influence of dispersal on population persistence depends on both landscape and dispersal traits (Johst et al. 2002, Vuilleumier and Possingham 2006). Increased dispersal may even hamper persistence, given trade-offs with reproduction (Baguette and Schtickzelle 2006), effects on synchrony (Heino et al. 1997), or the swamping of local adaptation (Lenormand 2002). Understanding how dispersal will change post-fragmentation (including via evolution) is essential for forecasting the fate of populations and communities (Caplat et al. 2016).

Dispersal is increasingly recognized to be a complex process. A major advance is recognizing inter-individual variability in dispersal (Clobert et al. 2009). Dispersers are not a random draw from a population, moving across a landscape at fixed rates. Rather, dispersal decisions depend on individual phenotypes and environments (i.e. context- and/or phenotype-dependent dispersal) at each of three dispersal steps: departure (emigration), transience, and settlement (immigration) (Holt 1987, Armsworth and Roughgarden 2005a, Bowler and Benton 2005, Benard and McCauley 2008, Clobert et al. 2009, Delgado et al. 2010, Lowe and McPeek 2014). Inter-individual variability in dispersal arises from variability in phenotypic traits (e.g. morphology, physiology, behavior) through: 1) *enabling traits* – phenotypes required to disperse at all (e.g. presence of wings, ballooning behavior; 2) *enhancing traits* – phenotypes facilitating dispersal or reducing its costs (e.g. longer wings, higher energy reserves); 3) *matching traits*, leading to non-random movements, conditional on these phenotypic traits and dispersal drivers (e.g. local conditions). The phenotype of an individual may imply higher fitness in specific environments (Levins 1962), which should select for inter-individual movement differences in a heterogeneous landscape (Baguette and Van Dyck 2007, Clobert et al. 2009) and covariances between dispersal decisions and a suite of phenotypic traits, which we call dispersal syndromes (Clobert et al. 2009). Such phenotypic dependency may arise at any of the three steps of dispersal so that individuals find and settle in habitats that best match their phenotypes and maximize their fitness (Maynard-Smith 1966, Holt 1987, Ruxton and Rohani 1999, Ravigné et al. 2004, Armsworth and Roughgarden 2005a, Edelaar et al. 2008). Non-random dispersal (i.e. context- or phenotype-dependent dispersal) is likely the rule rather than the exception. Species dispersal decisions at any stage should depend on external factors (abiotic and biotic conditions) or internal factors (genetic, physiology, morphology and behavior), well beyond habitat matching (i.e. phenotype-dependent habitat preference, Berner and Thibert-Plante 2015). Despite mounting empirical evidence of non-random dispersal (Edelaar and Bolnick 2012), it is not yet often incorporated into empirical and theoretical studies of spatially structured population and community dynamics (but see Fogarty et al. 2011, Bolnick and Otto 2013, Bocedi et al. 2014, Henry et al. 2015, Gibert 2016).

A major challenge is to replace the current unidimensional representation of dispersal with a multi-dimensional viewpoint built on multiple external and internal drivers. To date, most studies focus on how mean dispersal behaviors (leaving, moving, and settling) change after fragmentation, assuming that environmental conditions are homogeneous among patches. However, landscapes can be heterogeneous independent of fragmentation; by reducing movements, fragmentation will alter the heterogeneity in biotic and abiotic conditions experienced by individuals and lineages. We hypothesize that habitat fragmentation should reduce variability (at any one point in time) of conditions within patches, but increase variability among patches. Although this effect likely depends on the detailed characteristics of fragmentation and species traits (below), fragmentation should at the least influence spatial structuring and ultimately divergence across all levels of biological organization, from metapopulations, to metacommunities, to even metaecosystems. We conjecture that one effect of fragmentation is greater heterogeneity in local selective pressures. Reduced movements weaken the spatial averaging of local conditions, and should alter the means and variances of traits under selection, and how those variances are partitioned across space. Because of strong covariances of dispersal behavior with multiple phenotypic traits (Clobert et al. 2009), the evolution of dispersal syndromes may be deeply driven by these changes. Dispersers' phenotypic specializations should evolve in response to conditions experienced at each of the three steps of dispersal: the local conditions inducing dispersal decisions; matrix characteristics over which individuals move; and, the conditions encountered during settlement (Clobert et al. 2009). Habitat fragmentation, by decreasing connectivity, and effects on the kind of heterogeneity experienced by individuals, should shape evolution of dispersal syndromes across multiple spatial scales.

After considering the evolution of dispersal as a unidimensional trait, we present a multi-dimensional viewpoint on how fragmentation influences dispersal evolution (Fig. 1). We develop predictions for how habitat fragmentation should shape the mean and variance of phenotypic traits locally and globally, as well as change dispersal syndromes (Fig. 1) in relation to proximal causes (e.g. genetic and environmental factors, Fig. 2). Finally, we underscore the importance of considering trait variation, and changes in such variation, for understanding metapopulation functioning.

Evolution of dispersal strategies in a fragmented landscape

Direct effects of fragmentation features

The dispersal phenotype that evolves is determined by the balance between benefits and costs. Dispersal provides the benefits of escaping: competition with kin and/or non-kin conspecifics (Aars and Ims 2000, Cote et al. 2007, Hauzy et al. 2007), inbreeding (Szulkin et al. 2013), and adverse abiotic and biotic conditions [e.g. food availability: (O'Sullivan et al. 2014), predation risk: (Hauzy et al. 2007, Baines et al. 2014, Bestion et al. 2014), interspecific competition (Fronhofer et al. 2015)]. However, dispersal incurs multiple costs. While there are costs associated with emigration and settlement, such as the lack of social bonds or adaptation to local conditions after immigration, costs inflicted by transience across the matrix are likely particularly influential following fragmentation (Bonte et al. 2012). Dispersing between habitat patches may cost considerable time and/or energy for a low likelihood of success. Most empirical and theoretical studies on dispersal in fragmented landscapes have thus focused on the effect of matrix suitability and habitat patch geometry (e.g. distances among habitat patches, number, shape and aggregation of habitat patches, Travis et al. 2012).

Intuitively, the first prediction from theory is that reduced dispersal should be selected for in fragmented landscapes due to the increased costs and risks of moving across fragmented landscapes (Olivieri and Gouyon 1997, Travis and Dytham 1999), and indeed this is often found in empirical studies. Reduced dispersal propensity and distance moved have been reported when fragmentation increases, due to increased inter-habitat distances or reduced matrix permeability

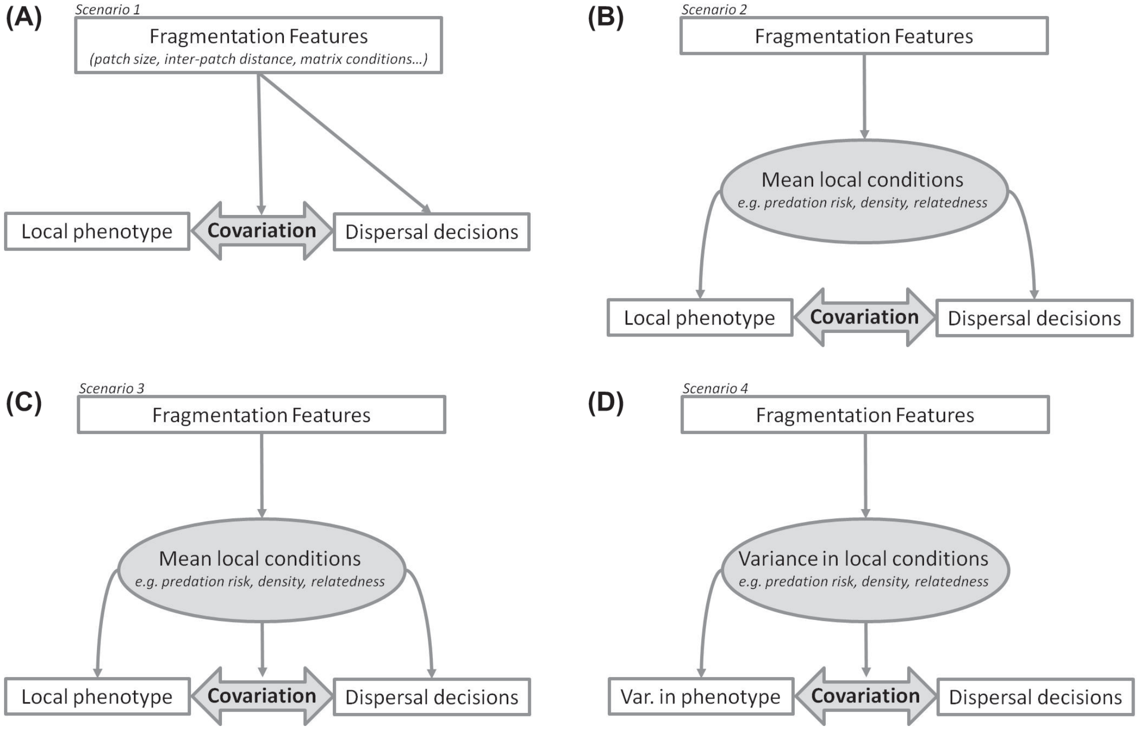

Figure 1. Direct (A: scenario 1) and indirect (B and D: scenario 2 and 4) impacts of fragmentation features on the evolution of dispersal decisions, other phenotypic traits and their covariances (i.e. dispersal syndromes). In scenario 1, habitat fragmentation directly acts on dispersal decisions (i.e. propensities and distance moved) by increasing dispersal costs. In addition, fragmentation selects for dispersers with phenotypic specializations improving their abilities to cross a matrix and travel longer distances (i.e. enabling and enhancing traits, e.g. wing size, muscles, metabolic fuels). In scenarios 2 to 4, habitat fragmentation acts on the evolution of dispersal decisions and syndromes through changes in the mean and variance of local environmental conditions. Fragmentation creates a patchwork of habitats with different mean local conditions at a global scale. Changes in mean local conditions (scenarios 2 and 3), such as predation risk, population density or relatedness, may select for higher or lower dispersal rates. These changes could also select for phenotypic attributes improving local adaptation (i.e. matching traits). These changes do not necessarily modify covariations between dispersal decisions and phenotypic traits if all individuals (dispersers and residents) display the phenotypic adaptations (scenario 2). A modification of covariations can occur when individuals less adapted locally disperse to escape local conditions (scenario 3). Covariations may also be modified through a decrease in variance of local conditions and therefore the local diversity of phenotypes (scenario 4).

(Dempster 1991, Lens and Dhondt 1994, Diffendorfer et al. 1995, Matthysen and Currie 1996, Haddad 1999, Debinski and Holt 2000, Mennechez et al. 2003, Schooley and Wiens 2004, Bonte et al. 2006, Schtickzelle et al. 2006, Smith and Batzli 2006, Matter 2006, Cheptou et al. 2008, Bowler and Benton 2009, Ahlroth et al. 2010, Bergerot et al. 2012, Eycott et al. 2012, Banks and Lindenmayer 2014).

However, theoretical studies also highlight the potential for more complex relationships between dispersal and habitat fragmentation (Olivieri and Gouyon 1997, Gandon and Michalakis 1999, Travis and Dytham 1999, Heino et al. 2001, Ronce and Olivieri 2004, Travis et al. 2012). Model results suggest that on already highly fragmented landscapes, further habitat loss sometimes selects for higher dispersal. This occurs because of the increased benefits that dispersal provides, at the point where local patch extinctions become common. Increased habitat loss raises the cost of dispersal, but the benefits gained through dispersal enabling recolonizations can outweigh these additional costs (Olivieri et al. 1995, Gandon and Michalakis 1999, Travis and Dytham 1999). While direct empirical tests of this prediction are lacking, there are a few indirect tests (Schtickzelle et al. 2006, Williams et al. 2016). A recent experimental study on *Arabidopsis thaliana* showed an impressive evolution for longer dispersal distance in highly fragmented system (Williams et al. 2016), while in the butterfly *Proclossiana eunomia* there was a twofold short-term evolutionary response to increased fragmentation (Schtickzelle et al. 2006). Although the propensity of emigration was lower in highly fragmented landscapes, actual emigrants dispersed faster with straighter movements. This increased the probability that emigrants find another suitable habitat, and also decreased dispersal mortality. Importantly, these results emphasize that the two behavioral strategies may evolve in concert in fragmented landscapes, leading to non-linear patterns of dispersal responses (Schtickzelle et al. 2006).

Species can also evolve dispersal polymorphisms (e.g. sharp phenotypic distinctions between short- and long-distance dispersers) in response to increasing fragmentation. Theoretical studies predict that short and long distance dispersal strategies can emerge and coexist for moderate degrees of fragmentation, with frequencies varying with local conditions (Mathias et al. 2001, Hanski et al. 2004, Bonte et al. 2010, Hovestadt et al. 2011). For example, a clumped distribution of habitats can favor short-distance dispersal over long-distance dispersal (Mathias et al. 2001, Bonte et al.

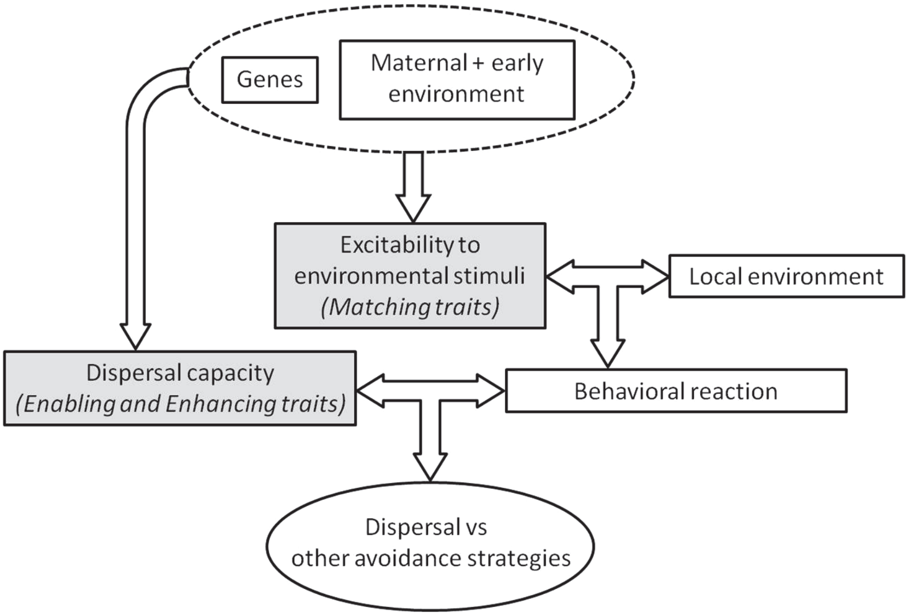

Figure 2. A scenario to explain context-dependent (aka condional) dispersal syndromes. Context-dependent dispersal syndromes refer to covariations between dispersal behavior and phenotypic traits varying with local conditions. In this scenario, the two concepts in grey boxes, dispersal capacity and the excitability to environmental stimuli, are driven by different sets of genes and environmental conditions and involve different types of traits (i.e. enabling, enhancing and matching traits). Depending on their excitability to different environmental stimuli, individuals may react to local conditions and this reaction should covary with matching traits. The type of reaction, dispersal or other avoidance strategies (e.g. hiding), depend on dispersal capacity which depends on individuals' enabling and enhancing traits (e.g. wing presence or size, muscles).

2010). Empirical examples demonstrate that while long distance dispersal shrinks as habitat fragmentation increases, both strategies persist even under high fragmentation. In the weed *Crepis sancta*, long-distance dispersing seeds have a 55% lower chance of settling in a suitable patch within a fragmented urban environment (Cheptou et al. 2008). Following 5–12 generations of selection this dispersal cost resulted in a 4.5% reduction of long-distance dispersing seeds in fragmented habitats. In the dune wolf spider *Pardosa monticola* the percentage of spiderlings performing tiptoe behavior, a behavior inducing long-distance aerial dispersal, is negatively correlated with the degree of landscape fragmentation (Bonte et al. 2006). Notably, in both examples, long-distance dispersers persisted in fragmented landscapes (% long-distance dispersers in fragmented vs continuous landscape: 85% vs 89% in *Crepis sancta*, 4–6% vs 14% in *Pardosa monticola*), suggesting that the two strategies stably coexist.

Habitat selection behaviors should also be selected in fragmented landscapes and likewise lead to mixed strategies. Such polymorphisms should be distributed between two extremes (Armsworth and Roughgarden 2005a): random dispersers, moving and settling independently of environmental conditions, and directed dispersers, who select patches that increase their expected fitness. In a spatially variable and temporally stable landscape, random dispersers endure the cost of moving away from suitable habitats to reach another habitat. In a highly fragmented environment, these costs may be particularly high. In temporally variable landscapes, random dispersers may, however, benefit from a bet-hedging strategy and the colonization of empty habitats (Armsworth and Roughgarden 2005b). Directed and conditional dispersers can track environmental conditions and avoid the cost of moving away from suitable habitats (Armsworth and Roughgarden 2005b). Although directed dispersers endure dispersal costs less often (e.g. following environmental changes), they likely suffer from the additional costs of gathering enough information (Stamps 2001) and of relying on potentially inaccurate information (Hale and Swearer 2016). Given the increased costs that random dispersers incur as habitat begins to fragment, we might expect to see an initial decrease in the frequency of random dispersers, for increasing habitat loss. However, as these random dispersers likely provide benefits in terms of recolonizing distant empty patches, we also predict that at higher levels of fragmentation, their frequency will increase with additional fragmentation. Importantly, the evolution of strategies at different dispersal phases are not independent; the evolution of movement and settlement strategies is likely to feedback on the evolution of emigration behavior (Travis et al. 2012).

Effects of fragmentation through a modification of local conditions

Landscape fragmentation effects more than connectivity (Fahrig 2003), including changing habitat and population characteristics locally and globally. The relative influence on dispersal of different fragmentation effects is rarely considered (but see Delattre et al. 2013), with the notable exception of patch quality and size (Andreassen et al. 1998, Matter 2006, Bowler and Benton 2009, Baguette et al. 2011, Rémy et al. 2011). Because changes in patch size or quality often occurs as a function of landscape fragmentation, it is important to disentangle their relative influences on both biodiversity (Fahrig 2013, Haddad et al. 2017) and dispersal evolution (Travis and Dytham 1999, North et al. 2011). An important consequence of reduced patch size and quality is reduced population size (North et al. 2011), accompanied by increasing demographic stochasticity, kin competition and inbreeding (Keyghobadi 2007, North et al. 2011, but see Sumner 2005). Increases in these three factors should all select for increased dispersal (Hamilton and May 1977, Perrin and Mazalov 2000, Ronce et al. 2000, Lambin et al. 2001, Cadet et al. 2003), particularly when fragmentation reduces local population size and connectivity (Heino et al. 2001, Mennechez et al. 2003, Cote and Clobert 2010, Bitume et al. 2013, Kubisch et al. 2013). For example, reduced gene flow among patches may increase relatedness and kin competition within patches (Keyghobadi 2007) which should drive evolution towards higher dispersal rates (Hamilton and May 1977, Perrin and Mazalov 2000, Ronce et al. 2000). This may be reinforced if rare immigrants are sexually selected over more related resident mates (i.e. for inbreeding avoidance, Pusey and Wolf 1996). However, immigrants may in some cases be avoided by sexual partners to prevent outbreeding depression (Pusey and Wolf 1996), reducing selection for increased dispersal. Despite these clear theoretical predictions, the influence of habitat/population size, kin competition, or relatedness are rarely teased apart from effects of fragmentation on connectivity (Matter 2006, Ahlroth et al. 2010). In one interesting study, Banks and Lindenmayer (2014) assessed the degree to which the decisions of agile antechinus *Antechinus agilis* to emigrate and settle depended on relatedness and patch characteristics (size, quality and isolation). They found that inbreeding avoidance was as important for emigration and immigration decisions as were patch isolation and inter-patch distances (Banks and Lindenmayer 2014).

In addition to changing patch sizes and thus local demography and genetic structure, landscape fragmentation may slice habitat into patches in a quite unpredictable way, consequently reducing variability of environmental conditions in local patches and increasing variability among patches. The increased spatial variation between patches together with increased temporal variation in local populations sizes due to higher demographic stochasticity (Lande et al. 2003) will exert selection on dispersal strategies (Gadgil 1971, Paradis 1998, Heino et al. 2001, Mathias et al. 2001). Although temporal and spatial variability are often predicted to select for and against dispersal respectively (Duputié and Massol 2013), the temporal and spatial scales of fluctuations (e.g. spatial and temporal autocorrelation), the frequency and magnitude of fluctuations, and the combination of temporal and spatial variations will determine the direction and speed of dispersal evolution (McPeek and Holt 1992, Travis 2001, Duputié and Massol 2013). Interestingly, different dispersal strategies are more likely to coexist when environmental conditions are both spatially and temporally variable (Cohen and Levin 1991, McPeek and Holt 1992, Mathias et al. 2001, Parvinen 2002, Massol et al. 2011). For example, dispersal polymorphism can result from disruptive selection in landscape with heterogeneous perturbation rates, carrying capacities and patch sizes (Parvinen 2002, Massol et al. 2011). There are currently few empirical studies assessing this theory by quantifying environmental fluctuations and their consequences for dispersal evolution. In one exception, an experimental approach using *Caenorhabditis elegans* showed that spatiotemporally variable conditions favor the evolution of increased dispersal propensity in a patchy environment (Friedenberg 2003).

In a highly fragmented environment, different local populations may experience distinctive ecological conditions, e.g. social structure (density, sex-ratio, and age structure), predator/prey densities and diversities, abiotic conditions; these local conditions may contribute to driving dispersal behaviors, blurring predictions made simply from local patch size and connectivity alone. For example, resource availability and diversity may vary among patches, leading to increased emigration rate from a subset of patches through a plastic response (Benard and McCauley 2008). This conditional dispersal should also have consequences for habitat selection in a fragmented landscape. After leaving a patch, emigrants will search for the most suitable habitats and select habitats matching their phenotype (i.e. habitat matching, Edelaar et al. 2008), or their natal habitat (i.e. natal habitat preference induction, Davis and Stamps 2004) or lacking the environmental condition that induced emigration. The reduced within-patch variation and increased environmental heterogeneity among patches should make optimal habitat selection harder, leading to higher dispersal mortality, imperfect habitat selection, and/or the selection for improved detection skills.

The above predictions assume that fragmentation reduces within-patch variability, but increases among-patch heterogeneity. These effects should depend on characteristics of the landscape (e.g. degree of heterogeneity, spatial autocorrelation), of the fragmentation (e.g. degree of isolation, patch size), and of the focal species (e.g. movement abilities and occurrence). Edge effects, a common by-product of fragmentation, may increase environmental variability within patches. Several abiotic factors (e.g. light, temperature) and biotic factors (e.g. species composition, population density) are altered at patch borders (Murcia 1995). However, when patches are sufficiently small, effectively the whole patch is edge and then in within patch variability will match that of the matrix.

Regardless of the exact nature of changes, fragmentation will directly and indirectly act on the evolution of dispersal strategies, inducing a diversification of unconditional and conditional dispersal strategies. We suggest that the evolution of dispersal strategies in fragmented landscapes can only be understood from a multi-dimensional perspective integrating those different phenotypic specializations (e.g. locomotor, competitive, orientation skills) that may covary with dispersal behavior at each of dispersal's three stages.

Evolution of trait variance and covariance with dispersal strategies

Direct effects of fragmentation features

Non-randomness of dispersal decisions results from the interaction between environmental context and individual phenotypes, at each of the three steps of dispersal (Edelaar and Bolnick 2012, Jacob et al. 2015). Individuals disperse in response to various local conditions (e.g. kin- and non-kin interactions, habitat quality, interspecific interactions), and not all individuals are equally influenced by these conditions (i.e. phenotypic attributes may shape an individual's expected success in diverse ecological conditions). This observation pertains to conditions encountered during transience and settlement. For instance, the ability to move across different landscapes may reflect a disperser's phenotype (e.g. locomotor and orientation skills), resulting in dispersal syndromes varying with dispersal costs and thus fragmentation features (level of fragmentation, but also matrix quality). In this section, we illustrate how landscape fragmentation may directly act on the evolution of dispersal syndromes (Fig. 1).

Impacts of fragmentation may act directly on phenotypic specializations of dispersers that facilitate movements across the landscape (Fig. 1A, scenario 1, Table 1). Landscape fragmentation leads to increased distances among habitat patches. Depending on the degree of isolation, different dispersal strategies should be selected for (e.g. long-distance versus short-distance dispersers, directed versus random dispersers, active versus passive dispersers). These strategies represent a polymorphism in dispersal behaviors covarying with several phenotypic attributes related to enhancing and enabling traits.

In general, travelling longer distances and travelling across a fragmented landscape requires enhancing traits such as higher movement abilities and correlated phenotypic attributes, e.g. different metabolic fuels, muscle development (Zera and Denno 1997), body shape (Hill et al. 1999b), longer wings (Harrison 1980, Taylor and Merriam 1995, Zera and Denno 1997), longer legs (Trochet et al. 2016b) or better orientation and navigation skills (Vuilleumier and Perrin 2006, Merckx and Van Dyck 2007). For example, a recent study found larger eyes in dispersing than in philopatric individuals of the bog fritillary *Boloria eunomia* (Turlure et al. 2016). Interestingly, in the context of habitat fragmentation, the same study also found that the related cranberry fritillary, *Boloria aquilonaris*, a species that evolved within a naturally highly fragmented landscape, has larger eyes than the bog fritillary, suggesting that investments in physiology and morphology improving navigation may be selected under conditions of habitat fragmentation. Another study comparing populations of the silver-spotted skipper butterfly *Hesperia comma* showed that relative investment in thorax, a trait linked to flight ability, was higher for individuals in landscapes with patches further apart (Hill et al. 1999b). Phenotypic specialization improving long-distance dispersal

Table 1. Predicted effects of fragmentation on dispersal decision, on phenotypic traits and on their covariances (i.e. dispersal syndromes).

	Environmental condition[a]	Dispersal traits changed[b]	Potential traits changed[c]	Whose phenotype changed?[d] Are covariances changed?	Scenario (Fig. 1)[e]
Landscape conditions	Fragmentation level (+) Habitat loss (+) Inter-patch distance (+) Matrix viscosity (+) Isolation (+)	Emigration prob. (–)[3,4,6,7,8,10,11,12,13,14,15,19,22,27] Emigration prob. (+) Distance moved (+)[3,20,24,27] Distance moved (–)[8,9,18,19,24] Dispersal timing (+)[1,2] Return prob. (+) Immigration prob. (–)[1,2,6,7,10,12,13,22] Transience success (–)[6,7,10,11,12,23]	Body size and shape (+)[20,97, 98] Wing length and width (+)[20] Condition/energetic resources (+) Musculature/metabolism (+)[24] Mobility traits (+)[20,24] Mobility traits (–)[4,5,7,9,24] Locomotor endurance/ speed (+)[16,17] Boldness/Exploration(+) Orientation skills (+)[25,26] Movement straightness (+)[6,16,17, 21]	Dispersers Covariance changed[4,6]	Scenario 1 (Adaptive disp. syndrome)
	Matrix risk level (+) (e.g. predation risk)	Emigration prob. (–) Distance moved (–) Dispersal duration (–) Return prob. (+) Immigration prob. (–) Transience success (–)[10,23]	Body size/mass (–/+) Antipredator traits (+) Boldness (+) Locomotor speed (+) Movement straightness (+)	Dispersers Covariance changed [4]	Scenario 1 (Adaptive disp. syndrome)
	Matrix resources level (–)	Emigration prob. (–) Distance moved (–) Dispersal duration (–) Return prob. (+) Immigration prob. (–) Transience success (–)	Body size (–) Condition/energetic resources (+) Locomotor speed (+) Locomotor endurance (+) Movement straightness (+)	Dispersers Covariance changed [4]	Scenario 1 (Adaptive disp. syndrome)

This table reports predictions for effects of fragmentation on dispersal traits. Fragmentation features can act directly on dispersal and related phenotypic traits (scenario 1 in Fig. 1) or can act indirectly through modifications of the mean (scenario 2–3 in Fig. 1) and the variance (scenario 4 in Fig. 1) of local conditions. We first report environmental conditions that can be changed by fragmentation at the landscape or local scales (a). The sign ± describes an increase or a decrease of this condition (a) and the direction of predictions on changes in dispersal traits (b) and phenotypic traits (c). We further report in (d) whether we expect the phenotypic traits (c) to change in dispersers, residents or in similar intensity in residents than dispersers (Residents = Dispersers) or not (Residents > Dispersers). It should therefore result into changes of covariances between dispersal and phenotypic traits or not (d). We finally associate these predictions with scenarios in Fig. 1.

Table 1. (Continued)

	Environmental condition[a]	Dispersal traits changed[b]	Potential traits changed[c]	Whose phenotype changed?[d] Are covariances changed?	Scenario (Fig. 1)[e]
Local conditions	Predation risk (+)	Emigration prob. (+)[28,29,36,37,40,89] Distance moved (+)[38,40] Immigration prob. (–)[41]	Body size/shape (+)[28,35,39] Antipredator traits (+)[28,31] Boldness/Exploration (–)[34] Activity (–)[30,32] Activity (+)[28] Social behavior (+)[33] Aggressiveness (+)[31] Locomotor speed (+)[35] Stress level (+)[31]	Residents = Dispersers Covariance unchanged[36] Residents > Dispersers Covariance changed [28,29,40]	Scenario 2 (Random dispersal) Scenario 3 (Habitat matching)
	Density (+) Competition (+) Food availability (–)	Emigration prob. (–)[10,42,43,44,45] Immigration prob. (–)[10,42] Emigration prob. (+)[37,42,43,47,48,54,89] Immigration prob. (+)[42] Distance moved (+)[46] Dispersal timing (–)[51,52] Dispersal duration (–)[51]	Body size (–)[49,53,55,56] Energy requirement/ metabol.(–)[56] Activity (+)[50,55] Competitive/fighting skills (+)[57] Social behavior (+)[42,50] Foraging activity (–/+)[54] Diet specialization (+)[58,59]	Residents = Dispersers Covariance unchanged[44,52] Residents > Dispersers Covariance changed [42,43,45,48,51]	Scenario 2 (Random dispersal) Scenario 3 (Habitat matching)
	Sex ratio (more males) Density of males (+) Density of females (–)	Emigration prob. (–/+)[60] Immigration prob. (–/+)[60] Transience success(–/+)[60] Sex-biased dispersal (+)[61,62,63]	♂/♀ body size/mass (–/+)[64,68] ♂ fight skills (+)[65] ♂ secondary sexual character (+)[66] ♀ mate choosiness (+)[64,66] ♀ coercion avoidance skills (+)[67]	Residents = Dispersers Covariance unchanged Residents > Dispersers Covariance changed[60]	Scenario 2 (Random dispersal) Scenario 3 (Habitat matching)
	Relatedness (+) Kin competition (+)	Emigration prob. (+)[13,71] Emigration prob. (+)[71,72] Immigration prob. (–)[13] Distance moved (+)[46] Sex-biased dispersal (–/+)[73]	Cooperation (+)[69] Mate choosiness (+)[70]	Residents = Dispersers Covariance unchanged[73] Residents > Dispersers Covariance changed[72]	Scenario 2 (Random dispersal) Scenario 3 (Habitat matching)

may also be under selection in passively dispersed species, such as in *Arabidopsis thaliana* where highly fragmented systems conjointly select for greater height and dispersal distance (Williams et al. 2016).

Information gathering and processing abilities can be important enhancing traits, especially for individuals actively moving across complex landscapes and engaging in habitat matching. While we are not aware of studies comparing information processing skills between fragmented and continuous landscapes, comparisons have been made between long-distance and short-distance dispersers in the Siberian flying squirrel *Pteromys volans*. Short-distance dispersers frequently revisited previously prospected sites to gather information and compare sites before making a settlement decision (Selonen and Hanski 2010). Long-distance dispersers performed a sequential search, staying over a longer period of time in prospected sites without revisiting them. A possible explanation is the cost of revisiting sites when moving far from natal sites. A similar cost is likely to exist in fragmented landscape and we can expect a similar information processing and habitat selection strategy for dispersers in fragmented landscapes.

Long-distance dispersers can also display enabling traits, i.e. morphological structures or behaviors dedicated to the mode of dispersal (above, e.g. wings in flying versus walking dispersers: Lombaert et al. 2006) and such traits might also be under selection in a fragmented landscape. For example, in several spider species, individuals may perform short-distance dispersal through walking or rappelling, or long-distance dispersal through ballooning or silk ball formation (Bonte et al. 2008, Clotuche et al. 2011). These strategies involve completely different behaviors and dispersal modes, as long-distance dispersers climb to a platform and perform tip-toe behavior or group themselves together in order to be passively dispersed by wind. The frequency of these dispersal strategies can vary with landscape fragmentation (Bonte et al. 2006); selection acts against individuals dispersed randomly over long-distance due to unpredictable wind currents.

Both enhancing and enabling dispersal traits can be costly to produce and may trade off against other life history traits. A recent meta-analysis showed that trade-offs between dispersal and other life-history traits occur across terrestrial and semi-terrestrial animals, but the nature and shapes of the relationships strongly vary among high taxonomic categories (i.e. orders, Stevens et al. 2014). In the wing-dimorphic field cricket *Gryllus texensis*, long-winged males fly better than short-winged males, at the expense of higher aggressiveness and fighting propensity, postponing access to reproduction (Zera and Denno 1997). Although reproductive penalties

Table 1. (Continued)

	Environmental condition[a]	Dispersal traits changed[b]	Potential traits changed[c]	Whose phenotype changed?[d] Are covariances changed?	Scenario (Fig. 1)[e]
Local conditions	*Abiotic conditions:* Temperature/hygrometry Soils Topography Water level Wind speed/direction	Emigration prob.[54,75,76,77,78] Immigration prob. Distance moved[74,75,79,80,40]	Thermal physiology[86] Water balance[83] Stoichiometry[85] Physiology[82,87] Activity/movement[54,79] Body size/shape[81,84,85]	Residents = Dispersers Covariance unchanged Residents > Dispersers Covariance changed[77,80]	Scenario 2 (Random dispersal) Scenario 3 (Habitat matching)
	Spatial heterogeneity of: Predation risk (–) Food availability (–) Competition (–) Abiotic conditions (–)	Variance in emigration (–) Emigration prob. (+)	Variance in above traits (–)[88]	Residents = Dispersers Covariance removed	Scenario 4 (Phenotype monomorphism)
	Predator diversity (–) Prey diversity (–) Competitor diversity (–)	Emigration prob. (–)[90,92] Immigration prob. (+)[91] Distance moved (+)[90] Emigration prob. (+)[90]	Antipredator specialization (+)[93] Handling/Digestive specialization (–/+)[94,95,96] Diet specialization (–/+)[94]	Residents = Dispersers Covariance unchanged Residents = Dispersers Covariance removed Residents > Dispersers Covariance changed	Scenario 2 (Random dispersal) Scenario 4 (Phenotype monomorphism) Scenario 3 (Habitat matching)

Numbers refer to articles illustrating the effect of environmental conditions on dispersal traits (b) and on phenotypic traits (c). For (d), the references report effects of environmental conditions on covariances. 1: Lens and Dhondt 1994; 2: Matthysen and Currie 1996; 3: Mennechez et al. 2003; 4: Bonte et al. 2006; 5: Maes et al. 2013; 6: Schtickzelle et al. 2006; 7: Cheptou et al. 2008; 8: Ahlroth et al. 2010; 9: Bergerot et al. 2012; 10: Smith and Batzli 2006; 11: Matter 2006; 12: Bowler and Benton 2009; 13: Banks and Lindenmayer 2014; 14: Eycott et al. 2012; 15: Schultz and Crone 2001; 16: Stevens et al. 2005; 17: Goodwin and Fahrig 2002; 18: Schooley and Wiens 2004; 19: Merckx et al. 2003; 20: Taylor and Merriam 1995; 21: Schtickzelle et al. 2007; 22: Haddad 1999; 23: Matter et al. 2004; 24: Hanski et al. 2004; 25: Turlure et al. 2016; 26: Merckx and Van Dyck 2007; 27: Diffendorfer et al. 1995; 28: Bestion et al. 2014; 29: Cote et al. 2013; 30: Teyssier et al. 2014; 31: Bell et al. 2010; 32: Moses and Sih 1998; 33: Krause and Ruxton 2002; 34: Bell and Sih 2007; 35: Langerhans et al. 2004; 36: Baines et al. 2015; 37: Baines et al. 2014; 38: Hakkarainen et al. 2001; 39: Coslovsky and Richner 2011; 40: Gilliam and Fraser 2001; 41: Morris 2003; 42: Cote and Clobert 2007a; 43: Cote and Clobert 2007b; 44: Kuussaari et al. 1996; 45: Pennekamp et al. 2014; 46: Bitume et al. 2013; 47: Baguette et al. 2011; 48: Byers 2000; 49: Einum et al. 2011; 50: Le Galliard et al. 2015; 51: Kim 2000; 52: Rémy et al. 2011; 53: Mugabo et al. 2010; 54: Tuda and Shima 2002; 55: Cote et al. 2008 56: Bohlin et al. 1994; 57: Knell 2009; 58: Svanbäck and Persson 2004; 59: Evangelista et al. 2014; 60: Trochet et al. 2013; 61: Barros et al. 2013; 62: Sandell et al. 1990; 63: Steifetten and Dale 2011; 64: Dreiss et al. 2010; 65: Kvarnemo et al. 1995; 66: Jirotkul 1999; 67: Gossum et al. 2001; 68: Le Galliard et al. 2005b; 69: Ruch et al. 2009; 70: Blyton et al. 2016; 71: Cote et al. 2007; 72: Davis 2012; 73: Le Galliard et al. 2003; 74: Damschen et al. 2014; 75: Delattre et al. 2013; 76: Bestion et al. 2015b; 77: Legrand et al. 2015; 78: Bonte et al. 2007; 79: Kuefler and Haddad 2006; 80: Niitepold et al. 2009; 81: Sheridan and Bickford 2011; 82: Dillon et al. 2010; 83: Kearney et al. 2013; 84: Bestion et al. 2015a; 85: Norlin et al. 2016; 86: Huey et al. 2012; 87: Meylan et al. 2012; 88: Moran 1992; 89: Hauzy et al. 2007; 90: Fronhofer et al. 2015; 91: Binckley and Resetarits 2005; 92: Sih and Wooster 1994; 93: Relyea 2003; 94: Araújo et al. 2011; 95: Olsson et al. 2007; 96: Persson 1985; 97: Thomas et al. 1998; 98: Hill et al. 1999b.

also exist in female wing dimorphic insects (Zera and Denno 1997), the nature and strength of dispersal syndromes is likely to vary by sex (Hill et al. 1999a). For example, in the bog fritillary, there are sex differences in investment in the eye and, regardless of whether these are driven by differences in requirement for dispersal or are driven by requirements for better eyesight for another component of behavioral ecology (e.g. need to locate and identify host plants), it illustrates the importance of sex in dispersal syndromes. In male butterflies, for example, a high allocation to thorax may reflect mate location strategy (perching versus patrolling males) which might be linked to male dispersal or patch use in a fragmented landscape (Thomas et al. 1998). Females and males may incur different dispersal costs, leading to sex-biased dispersal (Gros et al. 2008). Sex-biased dispersal can therefore evolve after landscape fragmentation if habitat isolation is more costly to female or male dispersers.

Habitat isolation is just one aspect of fragmentation and other biotic and abiotic characteristics of the landscape matrix may act on the evolution of covarying dispersal traits (Fig. 1, Table 1). For instance, higher predation risk is a dispersal cost in fragmented landscapes (Smith and Batzli 2006) and it might select for dispersers with a phenotype enhancing survival during movements. In common lizards *Zootoca vivipara*, higher predation risk produces dispersers with a longer tail, a phenotype decreasing mortality from predation (Medel et al. 1988, Bestion et al. 2014).

Effects of fragmentation through a modification of local conditions

Fragmentation may result in narrower ranges of environmental conditions at the local patch scale and in variation among patches. These local conditions should select for dispersers with different phenotypes (matching traits, Fig. 1, scenarios 2 and 3, Table 1). Local conditions can affect dispersers' phenotypes in two different ways. First, local conditions may create patch-specific selective pressures and act as 'plastic modifiers' of a suite of phenotypic traits, which alter dispersal propensities and dispersers' phenotypes (Fig. 1 scenario 2 and 3, Table 1). Dispersal could arise as a by-product of selection on other traits such as foraging activity, mate location or the search for predation refuges (Benard and McCauley 2008, Burgess et al. 2016). Local conditions may thus select for increased (or decreased) foraging activity or predator avoidance strategies and indirectly modify dispersal propensity and disperser phenotypes. For instance, local predation risk induces important behavioral and morphological anti-predator adaptations (Agrawal et al. 1999, Verdolin 2006, Bestion et al. 2014) altering individual departure from local habitat patches (Cronin et al. 2004, McCauley and Rowe 2010, Cote et al. 2013, Baines et al. 2014, Bestion et al. 2014). Among-patch variation in local predation risk may therefore create a phenotypic divergence between populations on different patches (Dingemanse et al. 2007, Bell et al. 2010); dispersers from populations with different local conditions (e.g. risk level) would carry different phenotypic adaptations even without any effect on a dispersal syndrome (Fig. 1 scenario 2, Table 1). Indeed, if all individuals (residents and dispersers) display these adaptations, covariation between dispersal and these adaptations may not necessarily vary with local predation risk. Such differences may also result from phenotypic plasticity, induced by developmental conditions, of traits related to dispersal capacity (reviewed by Benard and McCauley 2008).

Second, local conditions may change the covariance between dispersal decisions and other traits when locally less adapted individuals disperse to escape local conditions. Given that different phenotypes vary in their abilities to cope with different ecological factors (e.g. competition for food or mates, predation), the phenotype of individuals should shape the reaction to local conditions, producing context-dependent (i.e. conditional) dispersal syndromes (McPeek and Holt 1992, Cote and Clobert 2007a, Edelaar et al. 2008, Clobert et al. 2009). Context-dependent dispersal syndromes at the departure and settlement phases have been documented in several species (MacCallum et al. 1998, Byers 2000, Gilliam and Fraser 2001, Cote and Clobert 2007a, 2007b, Bonte et al. 2008, Bolnick et al. 2009, Cote et al. 2013, Maes et al. 2013, Pennekamp et al. 2014, Bestion et al. 2015b, Camacho et al. 2015, Myles-Gonzalez et al. 2015, Wey et al. 2015, Jacob et al. 2016). For example, Pennekamp et al. (2014) investigated the role of genotype and environment interactions on dispersal propensity in a ciliate. They found marked differences in dispersal among genotypes, plasticity (in response to density) and evidence of genetic variability in this plastic response. This variability in plastic reaction norms likely reflects variability in aggregation behavior among genotypes (Jacob et al. 2016). After fragmentation, local populations may experience divergent external drivers of dispersal and exhibit different dispersal syndromes. We predict two major mechanisms for fragmentation to change dispersal syndromes through modifications of local conditions.

First, the degree and grain of environmental heterogeneity in the landscape, the degree of fragmentation, and patch size will determine the mean abiotic and biotic conditions within a patch. Given the multiplicity of dispersal drivers and of phenotypic traits correlated to dispersal, the external factors acting locally on emigration, phenotypic traits and their covariances are likely to vary across space (Fig. 1 scenario 3, Table 1), this dissimilarity increasing with inter-patch distance and patch size. For example, landscape fragmentation may change thermal conditions in patches due to the edge effect (Tuff et al. 2016). Small patches, with a high edge-to-interior ratio, may have warmer and less spatially variable climatic conditions. In common lizards, the thermal phenotypes of emigrants vary with the local thermal conditions (Bestion et al. 2015b). In warmer conditions, emigrants had lower thermal preferences at birth, and conversely, higher thermal preferences at birth when leaving cooler local conditions. Variability in patch size should thus induce variability in dispersers' thermal phenotypes. The realized variability in dispersal syndromes will depend on divergence of local conditions among patches resulting from fragmentation.

Second, fragmentation overlaying environmental heterogeneity should jointly shape the local diversity of conditions (Li and Reynolds 1995) and therefore the maintenance of phenotypic diversity (Moran 1992). Less variable local conditions may reduce the local diversity of phenotypes with subsequent consequences for covariances between emigration behavior and phenotypic traits (Fig. 1 scenario 4, Table 1). Continuing our previous example, fragmentation-induced homogenization of climatic conditions for warmer conditions may select against individuals with cooler thermal optimum (Huey et al. 2012), reducing among-individual variation in thermal optimum and the potential for covariation with emigration behavior. These predictions illustrate how multiple environmental changes can modify the covariance of emigration with other traits from no covariation to covariations in opposite directions among patches.

Changes in local conditions may also affect covariation between matching traits and settlement decisions. Conditional immigration decisions should mirror conditional emigration decisions; for example, individuals leaving high density population should settle in low density populations (Cote and Clobert 2007a). Traits linked to emigration decisions should also be linked to habitat preference. For example, in three-spine stickleback *Gasterosteus aculeatus*, stream and lake individuals differ morphologically (Bolnick et al. 2009). A transplant experiment showed that, while most fish returned to their native habitats, stream fish moving into the lake were morphologically similar to lake fish (and conversely, Bolnick et al. 2009). Phenotype-dependent habitat preferences may therefore reinforce phenotypic and genotypic divergences among demes of a spatially-structured population (MacCallum et al. 1998, Bolnick et al. 2009). Higher among-patch variation in environmental conditions may also select for dispersers with improved skills to process and memorize private and social information acquired while prospecting across the landscape. Such skills would help maintain the accuracy and efficiency of habitat selection while dispersing across a risky landscape. Overall, landscape fragmentation may change the covariance of dispersal strategies with other phenotypic traits directly or indirectly through modifications of local conditions.

Although there are many complexities, two major predictions emerge about how dispersal should evolve in fragmented landscapes: there should be 1) the diversification of unconditional dispersal strategies and 2) the sharpening of conditional dispersal strategies. The first prediction emerges from the non-monotonic cost–benefit balance of dispersal in fragmented landscapes (direct effects of fragmentation) and from the increased spatiotemporal variation at a local scale (indirect effects of fragmentation). Dispersal polymorphisms will likely span a resident strategy and a 'super-disperser' strategy (Baguette and Van Dyck 2007), creating a continuous suite of dispersal strategies varying for enabling and enhancing traits (e.g. moving and orientation abilities). The second prediction emerges from the divergence of local dispersal drivers among patches (indirect effects of fragmentation), inducing context-dependent dispersal decisions and syndromes, i.e. conditional dispersal syndromes. While dispersal polymorphisms and conditional dispersal are both predicted to evolve in patchy environments (Cohen and Levin 1991, McPeek and Holt 1992), we believe that examining dispersers' phenotypic traits may help to reconcile these two predictions, and in particular the proximate pathways connecting dispersal behavior to other phenotypic traits.

Proximal causes of dispersal syndromes and their evolution along fragmentation gradients

Dispersal syndromes can arise from genes (G), environment (E) and G × E interactions (Langellotto et al. 2000, Cote et al. 2010, Shine et al. 2011, Ronce and Clobert 2012, Ducatez et al. 2012). To explore these pathways, we need to disentangle the determinants of dispersal, related enabling, enhancing and matching traits and their covariations.

The proximal causes of dispersal behavior have become a central focus of dispersal studies (Zera and Brisson 2012). Dispersal behavior has both genetic and environmental determinants (Li and Margolies 1993, Pasinelli et al. 2004, Braendle et al. 2006, Sinervo et al. 2006, Tschirren et al. 2007, Zera and Brisson 2012, Pennekamp et al. 2014). Traditionally, dispersal studies aimed to identify environmental determinants of dispersal (Clobert et al. 2001), for instance in conditional dispersal. A growing number of studies now demonstrate a significant heritability of dispersal behavior and the major influence of several candidate genes has now been reported (Zera and Brisson 2012). The phenotypic traits covarying with dispersal behavior are also likely to be both genetically and environmentally determined (Trefilov et al. 2000, Gloria-Soria and Azevedo 2008, Niitepold et al. 2009, Duckworth and Sockman 2012, Korsten et al. 2013, Edelsparre et al. 2014), although the multiplicity of candidate traits and the types of covariation (enabling, enhancing, matching covariations) make generalization difficult.

The proximal causes of covariances between dispersal and other traits are more complex than either genes or the environment, alone (Cote et al. 2010, Ronce and Clobert 2012). These covariations can result from immutable associations between dispersal behavior and phenotypic traits as predicted for enabling traits. The presence of enabling traits (e.g. wings) conditions dispersal (e.g. dispersal vs residency, long- vs short-distance dispersal). The proximal causes of covariations thus depend on the proximal causes of the traits involved. Enabling traits often have an important genetic and epigenetic determinism and so should their covariations with dispersal. Landscape fragmentation and local conditions should thus constitute selective pressures acting on the different dispersal morphs and change the proportion of dispersal strategies locally and across the landscape.

Second, dispersal syndromes can evolve in response to dispersal costs as predicted for enhancing traits. For example, dispersers with enhanced locomotor or orientation skills will better survive dispersal, especially in fragmented landscapes, than dispersers with poorer skills, leading to the evolution of dispersal syndromes. The evolution of dispersal syndromes could be accelerated by diverse processes such as assortative mating in colonized habitats or at invasion fronts (Shine et al. 2011). These covariations are predicted to have an important genetic and epigenetic determinism and can arise from genes with pleiotropic effects or from linkage disequilibrium between genes involved in the two covarying traits. For example, in western bluebird *Sialia mexicana*, aggression and dispersal are phenotypically and genetically correlated; while the integration of aggressiveness and dispersal is coordinated by shared genes, the actual strategy that emerges also depends on environmental variation (Duckworth 2009, Duckworth and Kruuk 2009). The strength of dispersal costs may not necessarily change the occurrence of dispersal strategies, but instead adjust the strength of associations between dispersal strategies and enhancing traits. As predicted for the direct effect of fragmentation, a polymorphism in dispersal strategies may be maintained through disruptive selection for skills dedicated to the different strategies.

Third, local environmental conditions can influence the strength and the direction of covariations between dispersal behavior and other phenotypic traits (i.e. matching traits), resulting in the labile expression of dispersal syndromes. Benard and McCauley (2008) suggested that local conditions may shape the phenotypic skills needed to disperse (i.e. dispersal capacity) and the motivation to disperse (i.e. dispersal propensity) resulting in covariation between phenotypic traits and dispersal behavior. For example, in a damselfly *Enallagma boreale*, high-quality habitats produce larger individuals at emergence and, as body size is positively related to dispersal abilities, these habitats produce better dispersing individuals (Anholt 1990). However, a phenotype-dispersal covariance can only arise locally when some individuals change jointly their dispersal tendency and other traits, while others do not. Inter-individual variation can result from individuals experiencing locally different environmental conditions or from individual variation in 'sensitivities' to environmental conditions reflecting complex environment–phenotype–genotype interactions (Baguette et al. 2015) acting on dispersal capacity and propensity. We suggest that individual variation in sensitivities may be important and that dispersal can be one of the behavioral responses to 'excitabilities' (i.e. sensitivities) to different environmental stimuli (Fig. 2). A suite of matching traits, genetically and environmentally determined, could underlie individuals' excitability to environmental conditions and whether individuals would react 'negatively' to local conditions or not. An individual would disperse away from local conditions rather than opt for another stressors avoidance strategy (e.g. hiding in a predator context, submissive behavior in a competition context, Dantzer 1989, Koolhaas et al. 1999) depending on its dispersal capacity. This dispersal capacity would result from a suite of enabling and enhancing traits. This framework differentiates two categories of phenotype-dispersal associations.

The first compiles phenotypic traits (i.e. enabling and enhancing traits) that are linked to dispersal capacity (e.g. locomotor skills). Such covariations with dispersal behavior 1) would vary in strength, not in direction (e.g. dispersers have similar or better, but not worse, locomotor skills than residents); 2) would have a significant genetic determinism and; 3) would have a strong potential to evolve in a fragmented landscape towards a polymorphism of dispersal strategies. These phenotypic specializations would therefore be carried by most dispersers.

The second category groups together phenotypic traits (i.e. matching traits) that appear genetically uncoupled from dispersal. These traits 1) can covary positively, negatively or not with dispersal behavior depending on local conditions. Their covariations with dispersal behavior are 2) less likely genetically determined and; 3) in a fragmented landscape, should reflect the evolution of conditional dispersal. Excitability to certain environmental conditions, leading to emigration or other risk avoidance behavior, could genetically covary with phenotypic traits. Dispersers would display these phenotypic attributes in a context-specific manner, as dispersal would be indivisible from its local dispersal inducer (density-dependent dispersal, predator-dependent dispersal, kin competition dependent-dispersal and so on).

Although this framework requires theoretical enrichment and empirical demonstrations, this classification could conciliate 1) the evolution of dispersal polymorphisms and conditional dispersal in fragmented landscapes and 2) the genetic determinism and the context dependency of syndromes. By altering dispersers' attributes, landscape fragmentation should modify gene flow between patches. Conditional and unconditional dispersal syndromes only exist because some individuals more readily disperse in response to landscape features and local conditions. It is likely that a single gene underlies such inter-individual variation in dispersal response, related phenotypic traits, or excitability. Modified dispersal syndromes should therefore lead to non-random gene flows in a metapopulation with potential consequences on its dynamics (Jacob et al. 2015).

Consequences for spatially-structured populations

A better understanding of the evolution of dispersal syndromes and its consequences requires discussing how dispersal syndromes may vary across ecological and spatial scales. We predict that an unsuitable and risky matrix, coupled with increased spatiotemporal variation, should lead to the evolution of diverse strategies including emigration, transience and settlement decisions. Distributed between a resident strategy and a 'super-disperser' strategy, these strategies would covary with a suite of phenotypic specializations. Abiotic and biotic conditions in the matrix shape the selective pressures acting on the ability of dispersers to successfully cross the matrix. We expect the evolution of a general dispersal syndrome at the metapopulation scale, but with local variation. For example, patch clumping can induce looser associations between dispersal behavior and moving ability locally, altering the dispersal syndrome across the entire metapopulation. The evolution of a dispersal polymorphism should improve metapopulation persistence, because only individuals with a dedicated phenotype should attempt to cross the matrix, increasing the success of movements among local populations and likely homogenizing local populations in a landscape. Aside from moving skills, these strategies should co-evolve with other traits, especially habitat/resource specialization (Kisdi 2002, Ravigné et al. 2009, Nurmi and Parvinen 2011). Although individuals with low dispersal propensity are predicted to be habitat specialists (Kisdi 2002, Nurmi and Parvinen 2011), the degree of habitat specialization in dispersers will depend on the rules for habitat choice (Ravigné et al. 2009) and landscape features. For example, random dispersers should likely be habitat generalists, while directed dispersers should display some degree of specialization.

A second set of predictions relates to increased heterogeneity in local conditions among patches. We might expect no general dispersal syndrome at the metapopulation scale, but a diversity of syndromes tailored to local conditions. A diversity of dispersal syndromes can be maintained in a metapopulation because of habitat matching (Edelaar et al. 2008, Jacob et al. 2015). In a fragmented, heterogeneous landscape, dispersers will benefit from selecting local patches that better match their phenotypes. As proximal causes of dispersal capacity and environmental excitability are uncoupled in our framework, the settlers can propagate their dispersal capacity genes and allow individuals of the next generation to disperse when they are less adapted to local conditions (i.e. high excitability). This non-random gene flow could hasten local adaptation and population differentiation at the metapopulation scale (Edelaar et al. 2008, Jacob et al. 2015, but see Holt and Barfield 2015). However, habitat matching requires dispersers to prospect different habitat patches before settling and therefore they might incur higher dispersal costs especially in hostile matrices. Habitat matching could enhance the adaptiveness of gene flow at the expense of immigration rates. Merging the first set of predictions with this one, we expect evolution towards both efficient dispersal and habitat matching, which would result in the fastest local adaptation and population differentiation in a metapopulation.

Predicting the persistence and dynamics of spatially-structured populations is a major goal for contemporary ecologists and evolutionary biologists, especially given rapid environmental changes. An improved ability to forecast species' responses to environmental changes (Urban et al. 2016) requires precise estimates of the mean and variance of species dispersal among patches and, for a local patch, the balance between the mean and the variance of emigration and immigration rates. Many models now just assume that an immigrant equals an emigrant and that dispersal asymmetry results from unbalanced rates. However, this may not be valid when considering covariances between individuals' dispersal and functional traits. Immigrants may display a totally different set of phenotypic traits than emigrants, and asymmetric dispersal can result from the phenotypic composition of immigrant and emigrant pools (Benard and McCauley 2008). In such a situation, the emigration–immigration balance is harder to gauge. As contrasted dispersal phenotypes might have different fitness in different patches, phenotype-dependent emigration and immigration decisions could influence source–sink dynamics and the speed of adaptation in spatially-structured populations (Holt and Barfield 2015). How such differences might impact dynamics is a key question with important consequences. Consider sex-biased dispersal. Local conditions, such as local competition, predation risk or inbreeding, as well as spatiotemporal variability, may lead to a pool of dispersers with a biased sex-ratio if males and females suffer differently from these conditions (Gros et al. 2008, Henry et al. 2016, Trochet et al. 2016a). In a fragmented and heterogeneous landscape, some patches may experience female-biased emigration and male-biased immigration. Emigration and immigration might seem balanced at first glance, but this asymmetry could strongly bias sex-ratio and endanger population persistence (Le Galliard et al. 2005a). By neglecting dispersal syndromes, we might underestimate the impacts of fragmentation on population and community persistence. Overall dispersal distances and rates might not be changed by landscape fragmentation, even while some dispersal syndromes disappear or emerge, causing cryptic changes in functional biodiversity within metapopulations and metacommunities (Stevens et al. 2014). Below, we provide a few promising future directions for incorporating the multi-dimensionality of dispersal syndromes into studies predicting and quantifying the consequences of fragmentation.

Developing theory on the causes and consequences of dispersal syndromes in fragmented landscapes – key challenges

Modeling frameworks are now available for exploration of the joint evolution of traits at each of the three stages of dispersal, but have not yet been used to gain a general understanding of how emigration, transfer and settlement rules/behaviors jointly evolve as a function of the degree and spatial pattern of habitat fragmentation. A priority should be to develop a general understanding of the interplay between the evolution of behaviors for each stage under a broad range of environmental conditions. For example, it would be relatively straightforward to apply existing methods (Travis et al. 2012, Bocedi et al. 2014) to determine under what range of life histories, and for which spatial environmental configurations we might expect evolution of a dispersal strategy comprising low emigration rate together with high distance (and high risk) transfer. It is particularly important to understand which species' life history characteristics and fragmentation attributes lead to dispersal evolution improving population persistence), and when it leads to negative impacts, including the potential for evolutionary suicide (Delgado et al. 2011). While we have a reasonable understanding of these effects for the evolution of emigration rates (Delgado et al. 2011), there appear to be no studies that consider how the balance between positive and negative effects changes for more complex dispersal syndromes.

A further priority is developing models that allows for dispersal (at the three stages) to coevolve with other life history characteristics and phenotypic traits. A few models do incorporate trade-offs between dispersal and competitive ability, reproductive ability, and/or habitat specialization (Burton et al. 2010, Nurmi and Parvinen 2011) but these typically model dispersal in a rather simple way (Burton et al. 2010, Nurmi and Parvinen 2011). The priority now, given the urgent need for modeling that yields quantitative ecological forecasting predictions (Evans 2012, Evans et al. 2012, Urban et al. 2016), is to allow covariances between dispersal traits and other phenotypic and life history traits to emerge from a more biologically realistic model. This requires incorporation of physiological costs that properly represent trade-offs between, for example, investment in larger eyes to improve navigation and fecundity. It is also critical to recognize and account for the fact that not all dispersal traits are solely for dispersal (Benard and McCauley 2008, Burgess et al. 2016). For example, navigation capability gained by having larger eyes may under some conditions become less important for dispersal. However, if this visual capability remains critical for foraging efficiency, finding mates or avoiding predators, it will not necessarily be the case that investment in eye size can be traded off to gain, for example, greater fecundity. These constraints are not currently embedded within models focused on dispersal. A further key issue is to ascertain the genetic basis for the covariances between the traits that make up a dispersal syndrome. In particular, the enabling, enhancing and matching framework entails assessing both genetic and plastic components of phenotypic covariances. The manipulation of environmental variability and of landscape features would allow predictions of the emergence of different trait associations in dispersers. Developing a quantitative genetic and/or explicit genetic framework for modeling dispersal syndromes is essential for better understanding of dispersal evolution in fragmented landscapes and assessing how such evolution impacts population dynamics (Legrand et al. 2017).

Advancing the empirical evidence for dispersal evolution in fragmented landscapes

We need to better understand both proximal and ultimate causes of dispersal behaviors and syndromes, which is challenging for dispersal syndromes and their conditionality. How can labile dispersal syndromes concord with heritable dispersal behavior and with the few reported genetic covariances with phenotypic traits? To answer this question, empiricists need first to quantify covariation between the phenotype and dispersal behaviors. This requires targeting a suite of phenotypic traits that can depict different functions linked to movements (e.g. locomotion, orientation) and to dispersal drivers (e.g. sexual secondary characters, competitive and social abilities) and monitoring their covariation with emigration, transience and immigration behaviors. A related step is to apply reaction norms techniques (Martin et al. 2011) to quantify variation of dispersal syndromes with a suite of ecological conditions (e.g. population density, sex-ratio, community composition). This task can be done at two temporal scales: a short-time scale to measure plastic reaction norms, and, a longer time scale, to quantify evolved dispersal syndromes (e.g. for uni-cellular organisms, see Pennekamp et al. 2014, Jacob et al. 2016) and quantify the selection for covariation in different contexts. Combining these studies with functional genetics would allow disentangling the respective and interactive influences of genome, epigenome and phenome on dispersal behaviors and syndromes (Baguette et al. 2015). We expect some phenotypic traits to monotonously and genetically covary with dispersal decisions (enabling and enhancing traits), while matching traits would contextually covary with dispersal behaviors. Genetic covariations could only be tracked down after controlling for the multiple drivers of dispersal. The estimation of genetic covariatons would allow dismantling the proximal causes of dispersal capacity and of excitability to environment stimuli.

Second, our framework may help identify key fragmentation features that influence dispersal behaviors and syndrome and therefore help empiricists distinguish widespread from case-specific effects. Following recommendations from theorists (Martin and Fahrig 2015), we should empirically study the relative influence of matrix quality, patch size, patch isolation and edge effects on dispersal behaviors, phenotypic traits and their covariances. More information on within- and among-patch variation in conditions may be particularly important to quantify. This is empirically challenging, but we recommend going beyond quantifying emigration and immigration in continuous and fragmented landscapes to assess underlying suites of key traits. These traits can have ecological consequences as important as the number of dispersers (e.g. in disease spread, predation strength). These data can also help experimenters to design novel experimental landscapes. Experimental semi-natural systems (Debinski and Holt 2000, Legrand et al. 2012, Altermatt et al. 2015, Haddad et al. 2015, Resasco et al. 2017) have much to offer in this respect, in particular to disentangle plastic from selective effects of habitat features. Joint theoretical and experimental studies should further quantify how the evolution of various dispersal syndromes alters gene flow under different environmental contexts. Ascertaining whether fragmentation driven selection on dispersal syndromes leads to adaptive trait covariations and dispersal decisions, or instead modifies patterns of traits covariation so as that reduces fitness and/or effective gene flow is a central question for further research. Finally, semi-natural experiments offer the possibility to study eco–evo feedbacks induced by landscape fragmentation (Legrand et al. 2017), beyond evolution of dispersal syndrome. Accurate predictions of biodiversity futures require the implementation of eco–evo feedback loops in empirical and theoretical studies.

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