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Eco-evolutionary dynamics in fragmented landscapes

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It is widely recognized that ecological dynamics influence evolutionary dynamics, and conversely that evolutionary changes alter ecological processes. Because fragmentation impacts all biological levels (from individuals to ecosystems) through isolation and reduced habitat size, it strongly affects the links among evolutionary and ecological processes such as population dynamics, local adaptation, dispersal and speciation. Here, we review our current knowledge of the eco-evolutionary dynamics in fragmented landscapes, focusing on both theory and experimental studies. We then suggest future experimental directions to study eco-evolutionary dynamics and/or feedbacks in fragmented landscapes, especially to bridge the gap between theoretical predictions and experimental validations.

Recognizing that ecological and evolutionary changes can occur at similar time-scales has led biologists to the conclusion that not only ecology can influence evolution (hereafter referred as 'eco → evo'), but also the reverse (hereafter referred as 'evo → eco') (Schoener 2011, Hendry 2016a). A recognition of the intertwined nature of ecological and evolutionary processes was present even in Darwin's theory (1859), and it has long been implicit in many biological fields such as population genetics (Hartl and Clark 2007) and community ecology (Vellend 2010). However, a formalized 'eco-evolutionary dynamics' framework has emerged only very recently (see historical syntheses in Pelletier et al. 2009, Schoener 2011, Shefferson and Salguero-Gómez 2015). There has been an exponential growth in the number of both theoretical and empirical studies at this interface of ecology and evolution over the last 10 yr (see Fig. 1 in Shefferson and Salguero-Gómez 2015). As both ecological and evolutionary processes play out over space, changes in spatial structure due to habitat destruction and fragmentation can potentially alter eco-evolutionary interactions.

The term 'eco-evolutionary dynamics' can broadly refer to any unidirectional change in an ecological factor that provokes a heritable change in phenotypic distribution due to microevolutionary processes such as selection or gene flow, or any heritable change in a trait distribution (shape, mean and higher moments) that provokes a change in ecological factors (Pelletier et al. 2009, Schoener 2011). This definition inherently implies that 'phenotypes are the nexus of eco-evo dynamics' (Hendry 2013). When interactions between ecology and evolution become reciprocal or cyclical, i.e. 1) changes in ecological factors drive evolutionary change in organismal traits that, in turn, alter some ecological factors, or 2) evolutionary changes in organismal traits drive changes in ecological factors that, in turn, alter some organismal traits, they lead to 'eco-evo feedbacks' (Post and Palkovacs 2009). Eco-evo feedbacks can occur if an evolutionary change in a trait will then impact the ecological factor responsible for the trait change in the first place (the narrow sense of eco-evo feedback), or if an evolutionary change in a trait will change any other ecological factor than the one directly responsible for the evolutionary change (the broad sense of eco-evo feedback). While selection is traditionally considered as the main articulation of eco-evolutionary feedbacks, other evolutionary forces may similarly shape the change in phenotypic distributions and be modulated through ecological change associated with phenotypic changes. This is the case in particular of well-known extinction vortices where ecological conditions reduce population size, which subsequently increases the strength of genetic drift, reduces the efficiency of selection, and leads to the fixation of mildly deleterious mutations in the population, depressing mean fitness and leading to further reductions in population size in a process of mutational meltdown (Lynch et al. 1995).

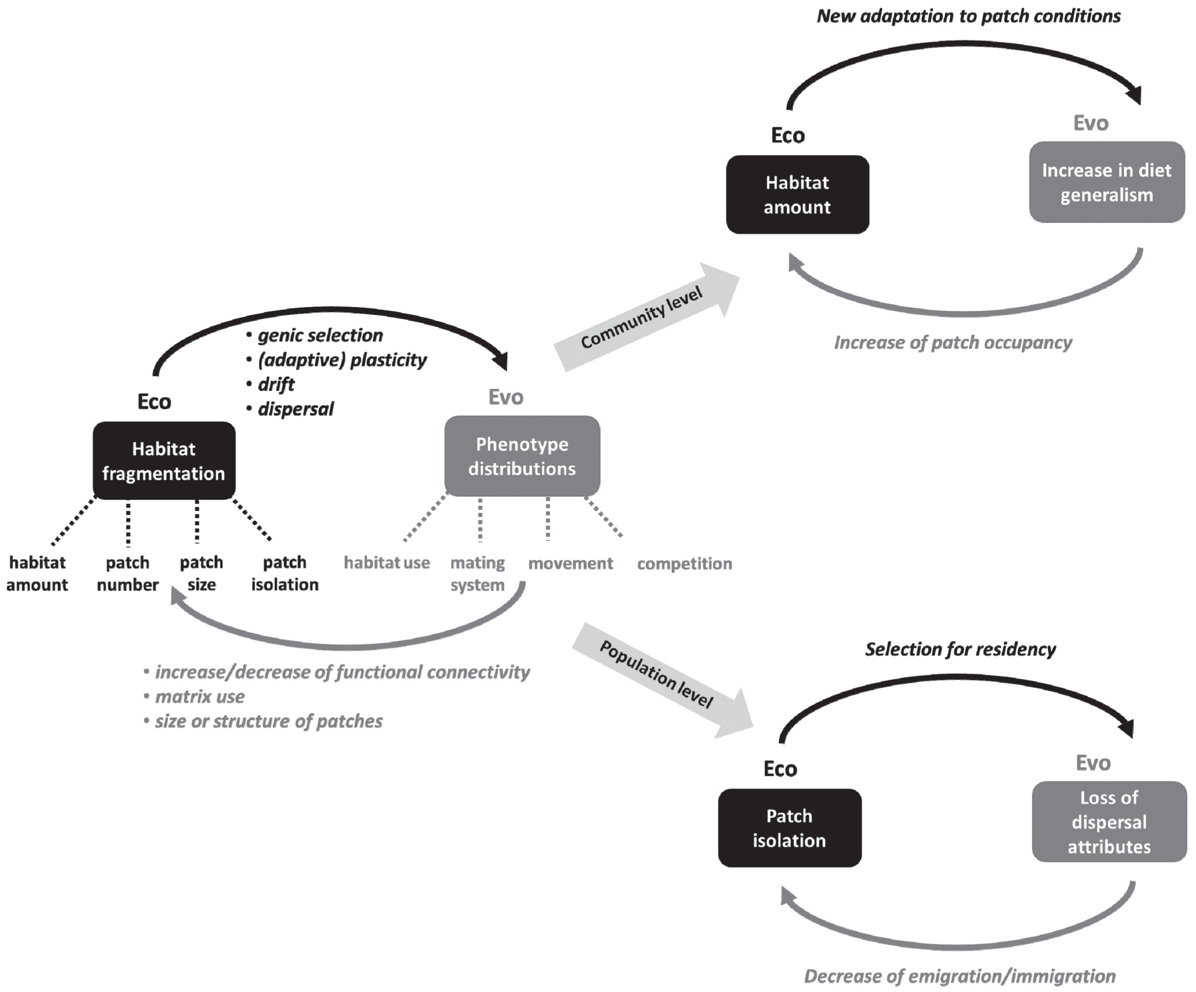

Figure 1. Interactions between ecology and evolution in fragmented landscapes. The diagram on the left synthetizes how the four aspects of habitat fragmentation can modify the distribution of phenotypes through several processes (eco → evo, black arrow). In turn, changes in phenotype distribution can modify habitat/matrix characteristics and functional connectivity and act on fragmentation (evo → eco, grey arrow), with potential cyclical feedbacks across time. The two diagrams on the right represent specific types of eco-evo links in the context of fragmentation. The upper right diagram illustrates a feedback loop at the community level in which selection favours an adaptation toward diet diversification when habitat amount is reduced, which allows a species to increase its occupancy within a patch, in turn decreasing the amount of resource available for other species. The lower right diagram illustrates a feedback loop at the population level in which patch isolation selects for residency and thus decreases emigration and immigration, in turn increasing patch isolation.

Eco-evo dynamics and feedbacks have been studied across all levels of biological organization (molecules, individuals, populations, communities and ecosystems), with a particular focus on the required conditions for eco-evo interactions to occur, their impact on population, community and ecosystem structuring and functioning, and, to a lesser extent, their consequences for species divergence or convergence (see reviews in Fussmann et al. 2007, Kinnison and Hairston Jr 2007, Post and Palkovacs 2009, Ellner 2013, De Meester and Pantel 2014, Fontúrbel and Murúa 2014, Hendry 2016a, b). Other authors have pointed out that eco-evo interactions cannot be dissociated from the spatial context in which they occur (Urban et al. 2008, Morris 2011, Hanski 2012a, Fontúrbel and Murúa 2014, Kubisch et al. 2014, Tack and Laine 2014), in particular because their consequences vary with spatial scales (e.g. at local versus regional scales, Garant et al. 2007). If we elaborate on the mutational meltdown example, a reduction in population size at the local scale can increase the population extinction risk and change local distribution of phenotypes. At the metapopulation scale, the strong changes at a local scale can have weak effects on the population size or on the traits distribution at a metapopulation scale. Therefore, the spatial structure of the landscape has to be considered when studying eco-evo interactions, especially in our rapidly changing world. Many natural environments are currently cut into fragments by human activities, from agricultural practices and urbanization in terrestrial ecosystems, to the massive disruption by damming and degradation of aquatic ecosystems. This fragmented structure can influence genetic variation (DiBattista 2008), and can induce a 'meta-functioning' at the levels of populations, communities and ecosystems, which modifies both ecological interactions and most evolutionary forces (such as the force of drift, selection and gene flow) and in turn the outcomes of eco-evo interactions. Especially, this fragmented structure can deeply change the evolution of dispersal and the covariations between dispersal and multiple phenotypic traits (see synthesis focused on this particular theme in Cote et al. 2017a). These changes play a particularly central role in modulating eco-evo interactions, because dispersal in itself and through its covariation with multiple phenotypic traits has important effects on both ecological and evolutionary processes. Therefore, although many phenotypic traits can affect, and be affected by fragmentation (in particular those traits related to mating systems, competitive skills, movement abilities or habitat use, Fig. 1), dispersal evolution has been one of the most studied examples of eco-evolutionary feedback in fragmented landscapes. Especially, fragmentation can reinforce or disrupt dispersal syndromes (see synthesis focused on this particular theme in Cote et al. 2017a).

In this article, we discuss how the spatial dimension influences eco-evo dynamics and feedbacks, and focus on the consequences of habitat fragmentation for the reciprocal interplay of ecology and evolution as well as on the consequences of integrating eco-evo interactions into fragmentation studies. We first introduce the role of spatial structure on eco-evo interactions by showing how different aspects of fragmentation can change patterns of trait distribution through their influence on eco-evo processes. We then detail selected examples of studies (both unidirectional and cycling dynamics) on the influence of the spatial context on eco-evo dynamics and feedbacks using theoretical, empirical and combined approaches. This short synthesis highlights the limited number of empirical studies considering the interplay of fragmentation and eco-evolutionary interactions, despite the fact that studies of eco-evo dynamics and feedbacks would be more realistic if performed in spatially explicit contexts. Finally, we suggest future research directions to merge theory and experiments, including the utilization of molecular approaches, to better understand the consequences of habitat fragmentation for eco-evo interactions.

Spatial heterogeneity of habitats and phenotypes

A consideration of spatial context has long been recognized to be important in ecology and evolution. Hanski and Gaggiotti (2004) modified the famous quotation by Dobzhansky (1973) to read ‘Nothing (or little) makes sense in ecology and evolution without a spatial perspective’. Landscapes in which individuals live, reproduce and move are comprised of a heterogeneous mosaic of local environmental conditions (Wiens 1976, Turner 2005). Such spatial heterogeneity of habitats can encompass many structural or functional aspects (Li and Reynolds 1995). Even in apparently homogeneous habitats, micro-spatial heterogeneity in biotic and abiotic conditions can occur (Lechowicz and Bell 1991, Bell et al. 1993), and spatial heterogeneity in the genetic composition of population regularly emerges as the result of stochastic events and limited dispersal, generating spatial heterogeneity in phenotypes that does not necessarily tightly match corresponding heterogeneity in the environment (Richardson et al. 2014).

Here, we will mostly focus on patchy environments, i.e. landscapes made of favourable patches (more or less ecologically distinct) that are separated by an unfavourable matrix in which individuals cannot sustain viable populations. Such patchy environments represent a spatial structure that is a sensible metaphor for many fragmented landscapes, including landscape experiments (Robinson et al. 1992, Brudvig et al. 2017). In these fragmented landscapes individuals face three kinds of spatial and temporal heterogeneity: habitat vs matrix, variation across space within the matrix in its properties, and variation among suitable habitat patches. Spatially structured biological entities are connected by movements, mostly dispersal (Hanski and Gaggiotti 2004, Leibold et al. 2004), i.e. movements of individuals potentially leading to gene flow (Ronce 2007), but also by foraging of individuals within their home ranges (which may include matrix habitats, Cook et al. 2004), and migration, i.e. the coordinated behaviour of a large number of individuals that move together through time and space in a synchronized fashion and can occur across broad regions under particular social and habitat conditions and traversing matrix conditions (Burgess et al. 2016, Cote et al. 2017b). Among these behaviors, only dispersal is supposed to induce gene flow even if the other behaviors can interact with dispersal evolution (Burgess et al. 2016, Cote et al. 2017b).

Translated into an evolutionary perspective, this spatial ecological heterogeneity among patches may entail a mosaic of partially isolated populations, along with spatial variation of selective pressures endured by individuals across the landscape. Ecological heterogeneities may generate spatial heterogeneity of phenotype distributions in a landscape through four eco-evolutionary processes, provided that random gene flow is sufficiently low (i.e. it will not oppose the other processes).

1) Geographic isolation of populations can lead to their phenotypic divergence due to genetic drift. The force of drift and the speed of divergence will be inversely related to the size of isolated populations, and directly related to the degree of isolation: when gene flow is limited, individuals that are spatially close are expected to be more genetically related and phenotypically similar than are distant individuals, even if evolutionary processes are entirely neutral (Hartl and Clark 2007).

2) Natural selection favours phenotypes that best fit local environmental conditions, and therefore local adaptation can increase divergence between populations facing different local conditions, even at micro-scales (Richardson et al. 2014), when selection is strong enough to oppose the forces of genetic drift (and gene flow, Kawecki and Ebert 2004).

3) Spatial heterogeneity of phenotypes can result from phenotypic plasticity, i.e. changes in phenotypes according to local conditions without the need for evolutionary changes. Interestingly, plasticity itself can be selected and become adaptive, especially in spatially heterogeneous environments (Ghalambor et al. 2007, Scheiner et al. 2012, Hendry 2016b).

4) Dispersal can also lead to spatial heterogeneity of phenotypes by spatial sorting (Shine et al. 2011), and when individuals emigrate from and/or immigrate toward environmental conditions that match their phenotypes (i.e. habitat matching, Holt 1987, Ravigné et al. 2004 or 2009, Edelaar et al. 2008, Jacob et al. 2015). Habitat matching challenges the idea that dispersal is always a random process

homogenizing phenotypes among populations (Lenormand 2002, Garant et al. 2007) and, on the contrary, permits dispersal to be a non-random process producing spatial heterogeneity of phenotypes (Clobert et al. 2004, Garant et al. 2007, Edelaar et al. 2008, Edelaar and Bolnick 2012, Jacob et al. 2015). The detailed behavioural rules underlying habitat matching can strongly influence the outcome of adaptive evolution in heterogeneous landscapes (Holt and Barfield 2015).

Local adaptation, phenotypic plasticity, non-random dispersal and drift, however, are not independent processes, and interrelations among those processes can be complex (Hendry 2016c). For example, dispersal can limit or favour local adaptation depending on the degree of non-randomness in movements and the intensity of drift (Lenormand 2002, Räsänen and Hendry 2008, Nosil 2009); drift can limit local adaptation depending on dispersal rates (Yeaman and Otto 2011, Blanquart et al. 2012); and plasticity itself can be adaptive (Ghalambor et al. 2007) or maladaptive (e.g. in novel environments). Further, dispersal itself can be plastic or can genetically evolve as function of local and regional conditions (Cote et al. 2017a). Whether or not dispersal facilitates or impedes local adaptation can also be influenced by density-dependence, and whether or not local population sizes shift and thus alter local density-dependence in fitness is dependent upon dispersal (Holt 1996, Gomulkiewicz et al. 1999).

A crucial point is to determine the tipping points at which processes will influence each other, as for example above or below which threshold will dispersal have positive or negative effects on local adaptation (Garant et al. 2007, Räsänen and Hendry 2008, Hendry 2016c). Another crucial and challenging task in studies about eco-evo interactions is to disentangle the relative effects of these different processes, which can act independently or all together, so as to better predict the changes in phenotypic distributions in fragmented landscape (Lenormand 2002, Cheviron and Brumfield 2009) and how these changes affect metacommunity and even metaecosystem functioning (Hanski and Gaggiotti 2004, Leibold et al. 2004, Urban et al. 2008). Fragmentation has several distinct impacts on habitats (patch isolation, reduction in patch size, alterations in environments within patches due to coupling with the surrounding matrix). The following section discusses the effects of these different aspects of fragmentation on the initiation, modulation and inhibition of the above-discussed processes in order to clarify their interrelations, and to better understand their impact on phenotypic evolution.

Different aspects of fragmentation, different eco-evolutionary dynamics

In this paper, fragmentation will be considered as a historical process that has cut a once large area into several smaller fragments scattered over a landscape, now separated by a markedly different (often anthropogenic) kind of habitat (the matrix). This dynamic view of fragmentation is inherently coupled with a loss of habitat area over some time scale. As a result, we will not discuss fragmentation per se, i.e. the breaking apart of habitat independent of any loss of habitat.

In this context, habitat fragmentation can be defined as ‘a large expanse of habitat transformed into a number of smaller patches of smaller total area, somehow isolated from each other by a matrix of habitats unlike the original’ (Wilcove et al. 1986, Fahrig 2003). This definition implies four effects of fragmentation on habitat pattern: global reduction in the amount of habitat, increase in the number of habitat patches, decrease in size of habitat patches, and increase in isolation among patches (Fahrig 2003, Fig. 2). It has been pointed out that teasing apart the effects of the different aspects of fragmentation on biodiversity can be challenging (Fahrig 2003). Especially, the increase in number of patches and the decrease in patch sizes are difficult to separate (although in practice, as habitat destruction proceeds, eventually the number of remnant patches also typically declines). In this section, we discuss the potential impact of 1) global habitat loss, 2) the combination of decrease in patch size and increase in patch number, and 3) increase in patch distance on phenotype distributions (eco → evo), with a focus on the eco-evo processes responsible for these changes and their influence on each other.

Reduction in amount of habitat

A starting scenario is that the pure loss of habitat at the regional scale will cause a proportional loss of individuals in the remaining habitats (and also at the regional scale) (Wiegand et al. 2005). If habitats were heterogeneous before fragmentation and individuals ranged widely over the pre-fragmentation landscape, then the decrease in habitat

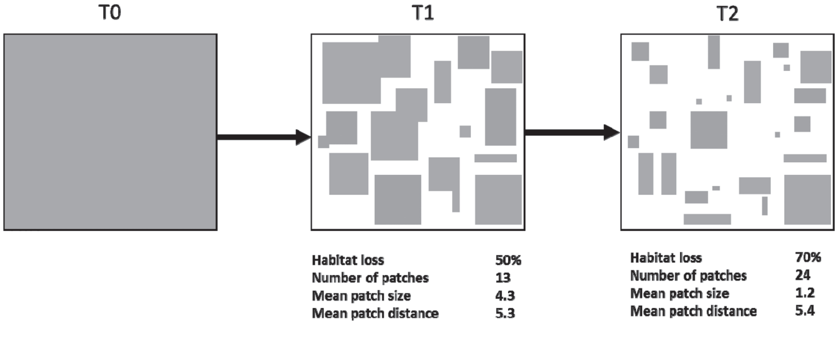

Figure 2. Illustration of the effect of the fragmentation process in a given landscape. Throughout the fragmentation process (Time 0 to 2), habitats (in grey) are cut into a number of smaller isolated fragments.

surface also likely induces a decrease in habitat diversity experienced by the remaining individuals. Considering interspecific interactions, local extinctions can lead to cascading effects among persistent members of the original community. Therefore, reduction in habitat amount is expected to change trophic cascades, as well as metapopulation and metacommunity composition and dynamics via a direct negative effect (through the removal of individuals) or a range of indirect effects (e.g. increased competition for resources, reduced predation, constrained movements of individuals) on population sizes and inter-individual variability, especially as the diversity of habitats decreases. Such effects have been confirmed by several theoretical models, which further show that habitat loss can induce metasystems decline and even extinction (Nee and May 1992, Keymer et al. 2000, Wiegand et al. 2005, Mouquet et al. 2011, Astegiano et al. 2015, Thompson et al. 2017).

On top of these ecological effects, such extinction due to straightforward habitat loss is predicted to be greatly accelerated by the negative effect of inbreeding in previously outbred populations, and the fixation of deleterious mutations in metapopulations (Higgins and Lynch 2001, Robert 2011, Henry et al. 2015). Mutational meltdown is much faster in subdivided populations with limited dispersal than in well-mixed continuous populations, and a reduction in total metapopulation size through habitat loss can cause the rapid collapse of the whole system (Higgins and Lynch 2001). Modifications of phenotypic distributions when global habitat amount is reduced are therefore strongly linked to drift effects. A consequence is that among-population divergence within metapopulations may be less impacted by habitat loss than by the other aspects of fragmentation, i.e. inter-patch distance and patch number, which strongly affect the dispersal process and thus the connectivity between patches (Cushman et al. 2012), at least if local populations in the fragments are sufficiently large that drift is weak.

If the original landscape is heterogeneous, some local habitat conditions may be spatially rare. If there is local adaptation to these conditions (i.e. edaphic conditions for plants), then with an overall reduction in area, these parts of the landscape-wide phenotypic distribution could be lost, simply because these rare local habitats are not retained in the resulting fragmented landscapes. This is a chance effect that can occur very rapidly, unlike the loss of phenotypic variation due to drift, which plays out over many generations.

Empirical studies in natural populations have abundantly confirmed that habitat loss can reduce the size and modify the composition of populations and communities, with correlated changes in phenotypic traits. Horn breadth and length as well as body mass of the mouflon *Ovis gmelini musimon* changed in response to habitat loss (Garel et al. 2007), as did body and growth of the lemon shark *Negaprion brevirostris* (DiBattista et al. 2011). In damselfly communities, habitat loss changed species composition, and the effects on traits were different depending on the degree of habitat loss (Rodrigues et al. 2016, see also Carrié et al. 2017). In general, a loss of species is expected to shift the milieu of interactions such as competition and predation that drives much of trait evolution.

Increase in number/decrease in size of habitat patches

Fragmentation induces the breaking apart of large habitat patches into a number of smaller ones. If dispersal across the matrix is limited, this local scale reduction of habitat has a direct negative effect on local effective population sizes, because losing resources entails a reduction in population carrying capacities, and this loss in numbers can be exacerbated because emigration from patches into the matrix will not be matched with corresponding inputs of immigrants. If a single large patch is trimmed in area, as noted above, this is expected to shrink local population sizes, even if habitat quality per se does not correspondingly change. As a result, the level of population genetic diversity will be locally reduced, and both genetic and demographic stochasticity increased. As one empirical observation of this, Dixo et al. (2009) showed in natural populations of the toad *Rhinella ornate* that population genetic diversity was lower in small forest fragments than in larger ones. Such reductions in local genetic diversity can in turn limit local adaptation, and change phenotype distributions in a maladaptive manner (Crespi 2000). When an originally outbred population is strongly reduced in abundance, inbreeding depression moreover is also transiently expressed, depressing fitness traits. A meta-analysis of patterns of local adaptation in plants found that local populations of small size (< 100) were unlikely to show any local adaptation (Leimu and Fischer 2008). In Daphnia, metapopulations made of smaller populations had reduced genetic diversity, lower fitness, faster aging and showed much improved fitness in between-population crosses, all patterns consistent with strong fixation load affecting phenotypic traits in those populations (Walser and Haag 2012, Lohr et al. 2014, Lohr and Haag 2015). As landscape become fragmented, those species which remain out of the original pool might increasingly be maladapted, leading to an emergent extinction debt that plays out over much longer time-scales than the original ecological processes.

An increased number of smaller patches might produce a mosaic of distinctive local conditions in the long term, because it might locally modify the interactions between the abiotic and biotic dimensions of patches, and also change in a non-homogeneous manner patch characteristics across the landscape (for example, through changes in local microclimatic conditions, species composition or resource availability). This could in turn increase local adaptation and population divergence, provided that selection intensity is high enough and population sizes sufficient to limit stochastic effects (e.g. in the maintenance of adaptive genetic variation), or if individuals perform habitat choice (Holt 1987, Edelaar et al. 2008, Richardson et al. 2014, Jacob et al. 2015). The extent of local (mal)adaptation and population differentiation will thus highly depend upon dispersal rates and movement decisions in such fragmented landscapes. By increasing competition within patches, the reduction in patch size can also directly affect dispersal driven by density-dependent phenomena (Poethke and Hovestadt 2002). Finally, by affecting the genetic and thus phenotypic resemblance among individuals in the same patch, reduction in patch size and number of patches also affects the selection pressures on many phenotypic traits, including dispersal (Cote et al. in 2017a);

increased kin competition due to increased relatedness has been shown to select for higher dispersal in many models (Frank 1986, North et al. 2011). High heterosis, i.e. higher fitness of crosses involving immigrants, as regularly found in small populations, is a second factor that is predicted to favour the evolution of higher dispersal (Gandon 1999, Perrin and Goudet 2001), and this might be enhanced in fragmented landscapes because of increased risk of inbreeding (Cote et al. 2017a).

A decrease in patch area will entail a greater perimeter:area ratio. If there are processes coupling patches to the surrounding matrix, these processes are likely to be much stronger in small patches. In some cases, resources flowing in from the matrix can sustain larger populations on small fragments than would otherwise be expected, or individuals residing in patches can make foraging forays into the matrix (e.g. rodents found in small patches of successional vegetation in the Kansas fragmentation project utilized the surrounding mowed matrix, Cook et al. 2004). In other cases, there can be negative effects, e.g. due to generalist predator 'spillover' into the fragments. Variation across space in the matrix can lead to corresponding quantitative and qualitative variation among patches in their local ecological conditions. This paves the way for corresponding variation in the strength and nature of local eco-evo dynamics.

Increase in isolation of patches

An increase in physical distance and/or degradation in matrix quality between patches translates into an increase in dispersal costs (Bonte et al. 2012). The evolution of dispersal traits is shaped by the balance between its costs and benefits (see both theoretical and empirical discussion in Clobert et al. 2012, Cote et al. 2017a). Therefore, any increase in patch isolation is likely to modify the distribution of dispersal phenotypes, depending on their evolvability, and the isolation dimension of fragmentation should strongly affect this process. For instance, Cheptou et al. (2008) found that increasing dispersal cost in fragmented urban areas has selected for decreased dispersal ability of seeds in the plant *Crepis sancta*. Yet in some cases, increased isolation between patches can select for increased dispersal ability, as was found in the Glanville fritillary butterfly (see review in Hanski 2011 and more details below). In the butterfly *Boloria eunomia*, a combination of reduced emigration and increased survival during dispersal was found as fragmentation increased (Schtickzelle et al. 2006). Theoretical studies confirm that fragmentation can select for either increased or decreased dispersal, and further show that the relationship can be non-monotonic (see reviews in Ronce and Olivieri 2004, Baguette et al. 2012, Cote et al. 2017a). Increase in the isolation of patches all by itself should have weak direct effects on intra-patch local conditions, at least if the matrix is spatially homogeneous, but will have strong antagonistic effects on the evolution of local adaptation and the intensity of drift and inbreeding depression (Lopez et al. 2009). In small populations, increasing isolation will have the most detrimental effects on fitness traits, while intermediate levels of isolation can enhance fitness evolution in larger fragments by allowing the evolution of local adaptation (in part by the beneficial effects of a small trickle of genetic immigration, providing variation but without so much input that local selection is overwhelmed, Gomulkiewicz and Houle 2009).

How does fragmentation change eco-evo interactions, and the reverse?

As described in the previous section, different aspects of fragmentation can generate different eco-evo dynamics because they act differently on local adaptation, drift and dispersal processes, and the interactions among these processes. Some studies have now convincingly demonstrated the effects of different aspects of fragmentation on phenotype distributions and metasystem functioning, the eco → evo pathway, as discussed above (and see Haddad et al. 2015, Haddad et al. 2017). Unfortunately, far less emphasis has been devoted to the evo → eco pathway (i.e. the effects of changes in the distribution of phenotypes on the ecological consequences of fragmentation, Fig. 1). Importantly, the vast majority of these studies do not formally integrate their results into the eco-evo dynamics framework. In addition, eco-evo dynamics studies rarely take the landscape structure into account. However, predictions on the fate of populations, communities and landscapes would change when considering eco-evo approaches in fragmentation studies, or when including the spatial context in eco-evo studies. This point was recently raised in the context of island biogeography. Farkas et al. (2015) showed that the incorporation of (mal)adaptation and island isolation can generate new predictions on species richness. They propose that (mal) adaptation can either exacerbate or invert the effects of isolation on immigration and extinction rates depending upon the studied organisms and contexts. Here, we provide a few examples in which we use a parallel conceptual approach to demonstrate how predictions on the effect of fragmentation on population, community and landscape properties can differ when considering eco-evo dynamics.

Priority effects

Priority effects occur when the first colonist or genotype influences the structure of community or population (Fukami 2015, De Meester et al. 2016). It has been emphasized that adaptation following colonization has the potential to generate eco-evo feedbacks promoting monopolization (Urban and De Meester 2009, De Meester et al. 2016). Fragmentation has the potential to accelerate monopolization of populations or species, and even modify the outcome of assemblies. Indeed, by increasing distances between patches, it increases time lags between the first and the second immigrants (De Meester et al. 2016). As a result, the first immigrants have more time to acquire adaptation favouring their initial rate of increase and promoting its long-term dominance. In addition, as habitat amount decreases, the race between the local adaptation of early colonists and immigration of pre-adapted genotypes or species has more chance to be won by early colonists because the global pool size of pre-adapted genotypes that can immigrate into the target patches decreases, either by pure loss of individuals or by drift. Besides, if fragmentation creates a number of small divergent patches within a landscape, we can predict that genotypes that will evolve adaptive plasticity will monopolize patches more often at the landscape scale.

Competitive interactions

The outcome of individual or species competition may be different throughout the fragmentation process because it can create spatial segregation of competitors across the landscape, change their demography, and/or modify the time for competitors to acquire new adaptations. In a continuous landscape where competitor A (individual or species) has some fitness advantage relative to competitor B (i.e. A is a better competitor than B), A should rapidly exclude B provided that its abundance is sufficient to oppose the effect of drift, whatever the dispersal abilities of A and B (Table 1). At a moderate level of fragmentation (Time T1 and T2 of Fig. 2), the creation of a number of small patches that are relatively isolated could allow competitor B to occupy some patches, by spatial sorting, a loss of competitor A locally, and/or a higher dispersal ability for B than A. A high level of fragmentation increases the probability for B to occupy more patches because, as patches become smaller and highly isolated, drift puts competitor A at risk of extinction more often, and increases the probability for B to evolve competitive ability or to occupy free patches. The probability for B to occupy patches will be even more important as its own dispersal ability increases and the one of A decreases.

Evolution of dispersal and functional connectivity

Functional connectivity is the degree to which an organism's behavioural response to both the landscape structure and the landscape matrix facilitates or impedes movements among resource patches (Taylor et al. 1993, Taylor et al. 2006, Baguette et al. 2013). Any changes in phenotypes that modifies dispersal ability will thus impact on functional connectivity, and the reverse. A simple example of a feedback loop in this context would be strong selection for specialized dispersal phenotypes in response to increased patch isolation (eco → evo). The evolution of increased dispersal in turn increases functional connectivity, implying that movements across the matrix may be easier, and in any case, patch isolation will be decreased (evo → eco). We can also think about the opposite case where increased patch isolation will strongly select for residency (due to very high dispersal costs), which will in turn decrease functional connectivity and thus increase population fragmentation (Fig. 1), potentially even leading to increased risk of regional population extinction (e.g. through evolutionary suicide). In a metacommunity, some interacting species may persist only because of heterogeneity among species in dispersal rates (e.g. colonization–competition tradeoffs), and evolutionary shifts in dispersal can alter the likelihood of species coexistence. The dynamics of strong predator–prey, host–parasitoid, and host–pathogen interactions are particularly sensitive to changes in dispersal (Hassell 1978, Gandon and Michalakis 2002), and so are likely to show emergent ecological effects of evolutionary changes in dispersal rates or either interacting partner.

Table 1. Effects of levels of fragmentation and dispersal ability on the outcome of competition at the landscape scale. In this example, A has greater competitive ability than B (A and B can represent individuals or species). In a continuous landscape, B should rapidly disappear, whatever the dispersal ability of the two competitors. At moderate levels of fragmentation, B would be found in some patches of the landscape, provided that A disappears from them through stochastic effects and that it has low dispersal ability. B could also have time to locally evolve competitive ability. At high levels of fragmentation, B has high probability to be present in some patches in all cases, because fragmentation increases the time left for B to evolve new competitive abilities. B could even be more frequent than A at the landscape scale if B has high dispersal ability and A has low dispersal ability. In this case, B has the potential to immigrate within most patches left empty by A (because of stochastic effects and its low dispersal ability). It is noteworthy that these predictions will be highly context- and system-dependent (De Meester et al. 2016).

	Dispersal ability of A/B competitors			
	high/high	low/low	high/low	low/high
Fragmentation level				
continuous	A	A	A	A
moderate	A	AB	A	AB
high	A (B)	AB	A (B)	B (A)

Selected examples of spatial eco-evo dynamics and feedbacks

In the previous sections, we have shown that the ability of fragmentation to generate eco-evo interactions depends on how changes in the structural features of landscapes (e.g. patch isolation, patch distance) have emergent effects on eco-evo processes (e.g. adaptation, drift, dispersal). In this section, our aim is to examine in more detail a few theoretical and empirical examples of eco-evo dynamics or feedbacks in fragmented landscapes. We specifically (but not exclusively) dwell on examples of the evolution of dispersal itself in response to fragmentation, because this eco-evo interaction is certainly the most documented.

Theoretical models

A large number of theoretical studies have dealt with eco-evolutionary dynamics and feedbacks in the past without being explicitly labelled as such. One noteworthy example is the 'metapopulation paradox' (Poethke et al. 2011). Poethke and colleagues (2011) explored theoretically the consequences of a typical conservation measure: improving the quality of a limited number of patches in a large spatially structured population. The authors showed that increasing the quality, size or stability of a few patches may lead to the rapid evolution of reduced dispersal rates in the entire metapopulation (eco → evo). These adaptive changes subsequently lead to the 'evolutionary suicide' of the entire metapopulation, as reduced dispersal rates imply reduced occupancy and ultimately metapopulation extinction (evo → eco). This negative ecological consequence of evolution of reduced dispersal in fragmented landscapes has been shown in several theoretical studies that include different degrees of complexity ranging from simply modelling an emigration propensity (Gyllenberg et al. 2002, Rousset and Ronce 2004, Delgado et al. 2011, Poethke et al. 2011) to a model that simulated the dispersal distances of plant seeds using a semi-mechanistic wind-dispersal model and incorporated the evolution of seed release height (Travis et al. 2009). This latter model also demonstrated that, under some conditions, the response to fragmentation (either evolutionary rescue driven by an increase in dispersal distance through greater release height or evolutionary suicide driven by selection for reduced release height) can be unpredictable with eco-evo trajectories going in both directions for the same amount of fragmentation (Travis et al. 2009, Fig. 3).

A further intriguing result obtained in this model of seed release height (Travis et al. 2009) is the potential for eco-evolutionary cycles to occur on fragmented landscapes (Fig. 4d in Travis et al. 2009 and Fig. 3d). It was speculated that the following processes might drive this observed cyclic dynamic: initially there is a low release height and thus a low dispersal distance; this results in low patch occupancy as patches that become locally extinct are unlikely to be colonized. However, as the availability of empty patches increases, selection can favour increased release height (and greater dispersal distance) as the benefits of a seed reaching a new patch are much greater (as it and its progeny are likely to benefit from plentiful resources). However, as dispersal distance evolves upwards, patch colonization rates increase to the point where most patches are occupied. At this point, the benefit of being a colonizer is massively diminished and selection again favours the less risky short dispersers (reducing the loss of seeds in the inhospitable matrix). As dispersal distance reduces, the rate of colonization of locally extinct patch declines and we end up at the starting point with low patch occupancy and low dispersal distance; and the cycle can start again.

With a different focus, Fronhofer et al. (2012) and Fronhofer and Altermatt (unpubl.) showed how landscape structure and connectivity select for a given dispersal rate (eco → evo). In landscapes characterized by variation in connectivity (varying numbers of connections per patch), such as dendritic landscapes, the local densities and therefore fitness expectations vary from patch to patch, as the number of connections varies. This leads to spatial variation in fitness expectations and may select against dispersal. The

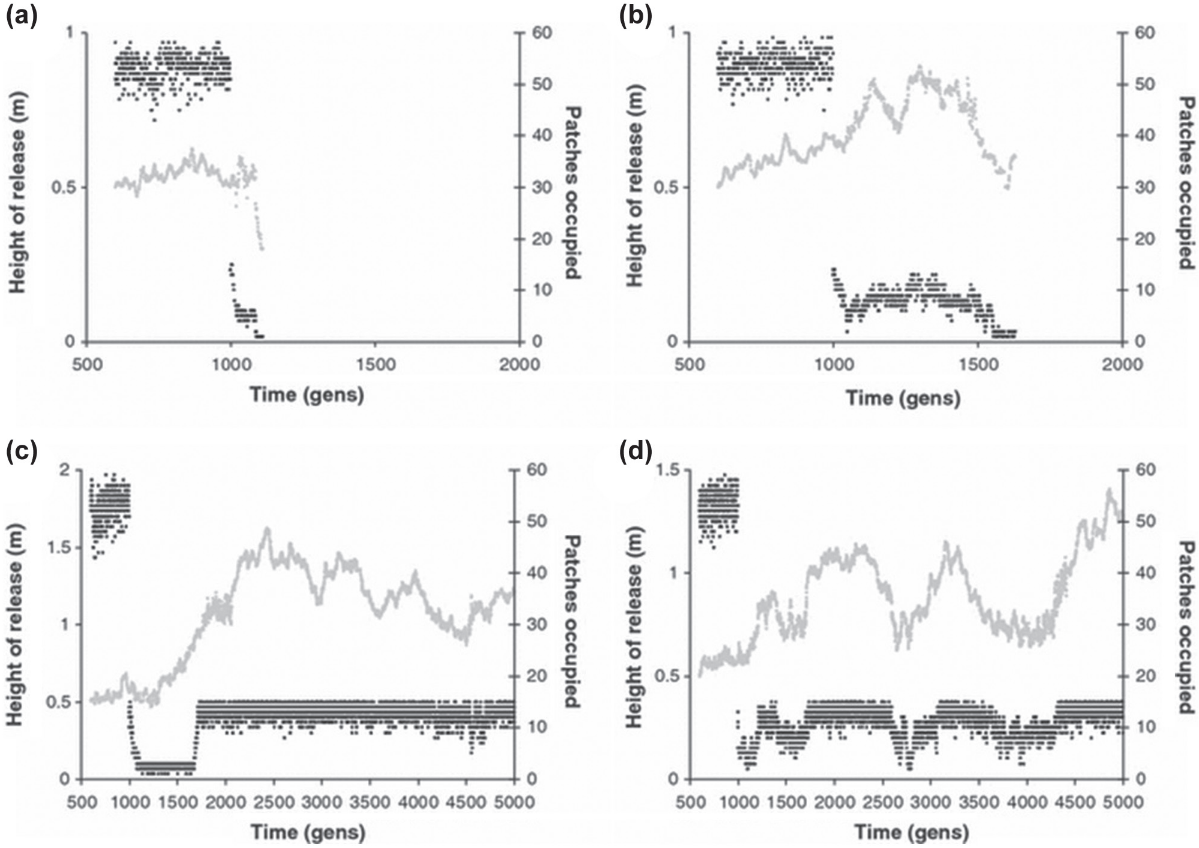

Figure 3. Evolutionary suicide (a, b) and evolutionary rescue (c, d) following fragmentation. Using the same theoretical model, Travis et al. (2009) showed that both evolutionary outcome can arise under the same fragmentation process, here destruction of habitat patches, for the same initial parameters of the model. Grey depicts the height of release and black the patch occupancy. Typically we see two types of response. First, the height of release evolves downwards making the population more vulnerable to extinction (a). Second, the height of release evolves upwards, increasing patch occupancy and securing long term population persistence (c). In some instance the dynamics are somewhat more complex. In (b) an example is shown where there is a moderate initial increase in release height, but at around time = 1300 this trend is reversed and evolution towards lower release height ultimately drives the population extinct. In (d) evolution of increased height results in population persistence but there is a suggestion of cyclic dynamics with periods where taller plants dominate followed by periods with shorter plants. In the periods when plants are shorter the patch occupancy is lower.

evolutionarily stable dispersal strategy in turn impacts turnover, occupancy and genetic structure of the spatially structured population (evo → eco). The authors furthermore show that 'classical metapopulation dynamics' – which has traditionally been characterized by intermediate rates of turnover and occupancy as well as some genetic spatial structure – are an emergent phenomenon that may be globally rare (Fronhofer et al. 2012) and most likely to occur in dendritic landscapes, such as riverine systems (Fronhofer and Altermatt unpubl.).

Empirical studies

An interesting study of an herbaceous plant species shows the evolution of plant dispersal-traits in a fragmented landscape (Cheptou et al. 2008). The weed *Crepis sancta* has colonized the patches around trees in the sidewalks in an urban fragmented area in the south of France. This weed species produces two types of seeds: dispersive (seeds with a parachute-like structure called a pappus) and non-dispersive seeds (seeds without a pappus). In this urban habitat, dispersive seeds are disadvantaged since many of them fall on the pavement, an unsuitable matrix for the seed (50% lower survival rate than non-dispersive seeds). This increased cost of dispersal resulted in selection against dispersive seeds. When grown together in a common garden, individuals originating from the urban patchy habitat produced less dispersive seeds than did individuals from continuous natural habitats. This study system illustrates how habitat fragmentation has resulted in rapid evolution of dispersal-related traits in this species, consistent with strong selection against the most dispersive genotypes. Similarly, Riba et al. (2009) report that wild-lettuce plants *Mycelis muralis* produce less dispersive seeds in more isolated populations, and in metapopulations showing lower average connectivity of populations. These two examples show that species can rapidly modify their dispersal rates in response to fragmentation (Cote et al. 2017a).

Under laboratory conditions, Bell and Gonzalez (2011) studied the consequences of varying dispersal rates on the rate of local adaptation to environmental deterioration in metapopulations. They first exposed genetically-limited and isolated yeast populations to different amounts of salt, creating a 'north-south stress gradient' in the artificial landscape. They then applied a second set of treatments consisting of 1) three rates of further environmental deterioration: no, slow and high southward shifts of the salt gradient, and 2) three rates of unidirectional and assisted dispersal: no dispersal, limited dispersal by introduction of individuals from neighbouring patches, and global dispersal by movement of individuals across all patches. They found that the likelihood of evolutionary rescue (adaptation through natural selection leading to persistence in the changed environment) in their metapopulations depended on the interaction between the magnitude and rate of deterioration, on the one hand, and dispersal rates, on the other: a low amount of salt during the first exposure to stressor combined with local dispersal fostered the evolution of tolerance to environmental stressors. This means the way that patches are connected to each other through dispersal might change phenotypic and genetic adaptation to local conditions. Interestingly, they also showed evidence for a U-shaped relationship between the rate of adaptation and the level of stress across all treatments, highlighting that the rules of eco-evo interactions can be different along environmental gradients.

Quite recently, Carazo et al. (2014) showed experimentally that population subdivision and limited dispersal, as is characteristic of fragmented habitats, could significantly alter sexual conflicts over reproduction between males and females in *Drosophila melanogaster*. Competition between males in that species is known to lead to female harming. In particular, toxic ejaculates improve male immediate reproductive success but shorten female lifespan. By manipulating relatedness among competing males, Carazo et al. (2014) found that they can adjust their reproductive behaviour such that brothers fight less than unrelated males, and females mated with brothers aged more slowly and had higher lifetime reproductive success than those mated with unrelated males. This change in female life history can have profound demographic consequences, allowing faster population growth. Population genetic structure associated with fragmentation could thus lead to variation in the intensity of sexual conflicts, with multifarious consequences on the evolution of phenotypes and population dynamics.

Mixed approaches

Examples of mixed approaches of eco-evo interactions in fragmented landscapes are scarce. One of the most completely examined example is undoubtedly the study of the Glanville fritillary butterfly in Finland (Hanski 2011, 2012b). This species inhabits a large network of patchy dry meadows in the Åland Islands where it functions as a classical metapopulation, with high extinction and recolonization rates. It has been shown from field observations and experiments that such colonization–extinction dynamics have selected for increased dispersal abilities (Hanski et al. 2002, 2004, Saastamoinen and Hanski 2008). At the molecular level, heterozygotes at one SNP of the *pgi* gene (which encodes a glycolytic enzyme) have higher flight performance than do homozygotes, and are in higher frequencies in new-established populations (Hanski and Saccheri 2006, Orsini et al. 2009). Altogether, these empirical results establish a link between fragmentation and the evolution of dispersal at both phenotypic and genotypic levels. Zheng et al. (2009) constructed an individual-based model to test for putative reciprocal effects of the perturbation in population sizes (such as those induced by fragmentation) and evolutionary dynamics (changes in the relative frequency of different alleles of *pgi*). The authors found that both effects were detected, but that demographic changes had a stronger immediate effect on allele frequencies than did the reverse. Although these reciprocal eco-evo effects have not been explicitly validated with experiments, these demographic and genetic predictions match with the most recent empirical data from this system (Hanski 2011).

Another example of a mixed approach was published by Farkas et al. (2013) on the impact of camouflage maladaptation in *Timema cristinae* walking sticks. These flightless insects live on two host plant species, presenting very different leaves, and accordingly have evolved a dimorphic camouflage pattern (presence vs absence of a dorsal white stripe). In natural metapopulations, a degree of maladaptation in camouflage persists because gene flow via dispersal and founder effects can perturb the outcome of natural selection. As expected, empirical data showed that maladaptation negatively impacted both individual survival (via increased avian predation, which imposes density-dependent selection, Farkas and Montejo-Kovacevich 2014) and the population size of *T. cristinae*. Furthermore, such maladaptation in this one species also affected the community. The abundance of other arthropod species decreased alongside *T. cristinae*, although *T. cristinae* is a competitor of many of them and the opposite trend might thus be expected. The cause has been identified as shared predation leading to apparent competition: the higher bird predation inflicted on maladapted *T. cristinae* populations by generalist predators also could lead to higher predation pressure on the other arthropod species. This shift in the community in turn affected the overall herbivory pressure imposed on plants. Using a spatial eco-evolutionary model (Hanski and Mononen 2011), the authors showed that the demographic consequences of maladaptation (lower survival and hence local population size), translated into a lower probability of habitat patch occupancy at the metapopulation level and an overall smaller metapopulation size. It also affected the spatial scale of adaptation, promoting adaptation at a larger scale than the local patch, which might push ongoing speciation in *T. cristinae* towards fruition, by further reducing gene flow between the two morphs. Unfortunately, so far as we know, experimental validation of these predictions is still lacking.

To illustrate the potential of mixed approaches to understand eco-evo interactions within spatially explicit contexts, we have picked an example from the range expansion literature that illustrates an eco-evo feedback occurring as a result of landscape heterogeneity. Fronhofer and Altermatt (2015) experimentally showed that the colonization process during range expansion selects for increased dispersal abilities at the expanding range front. This phenomenon, termed 'spatial selection', has long been theoretically known (see Kubisch et al. 2014 for an overview) and inferred in comparative analyses (Phillips et al. 2006). Spatial selection implies that during a range expansion highly dispersive genotypes are located at the expanding front leading to assortative mating. Since patches are empty beyond the range front, competition is also relaxed, which confers a fitness advantage and ultimately selects for higher dispersal rates at the scale of the whole expanding population. Fronhofer and Altermatt (2015) further showed indirect empirical evidence for a trade-off between dispersal and competitive ability during range expansion, where competition is captured by the parameters of the functional response of a consumer–-resource model. The concurrent evolution of dispersal and competitive ability subsequently feeds back on population densities throughout the range, resulting in an evo → eco feedback. Interestingly, higher competitive abilities in the range core lead to resource depletion and, as a consequence, lower equilibrium population densities. It implies lower population densities in the range core and increasing densities towards the range front, because denser areas are inhabited by weaker competitors. The degree to which such eco-evo feedback loops are likely to occur during range expansion into fragmented landscapes is undoubtedly the next question to answer. It has been shown that high levels of habitat loss and fragmentation might change the evolution of dispersal rate during range expansion (Hughes et al. 2007).

This brief overview of spatial eco-evo studies shows that experimental approaches lag behind theoretical approaches and natural population surveys, and that both the description and prediction of eco-evo interactions within fragmented landscapes need to be further investigated. Besides, these examples show that dispersal and its evolvability are key in such a context. However, we are far from capturing all the complexity of this process (including plasticity in dispersal), which may limit our ability to understand and predict spatial eco-evo dynamics and feedbacks. Indeed, dispersal comprises three steps (emigration, transience and immigration, see review in Clobert et al. 2009), each being modulated by a plethora of phenotypic and environmental factors (Trochet et al. 2013, Legrand et al. 2015). Furthermore, we have shown in this section that traits determining dispersal phenotypes can rapidly evolve in response to fragmentation (see also Cote et al. 2017a). As a result, it would also be valuable to consider, theoretically and empirically, the interplay of dispersal evolution and local adaptation in heterogeneous fragmented landscapes, especially because the evolution in dispersal alters rates and patterns of gene flow at loci all across the genome, not just those related to dispersal directly.

Understanding the molecular mechanisms generating eco-evo dynamics and feedbacks

We have no doubt that, in the upcoming years, the number of studies describing evo → eco and/or eco → evo pathways will continue to accumulate (as shown in Shefferson and Salguero-Gómez 2015). As recently outlined (Hendry 2013, Baguette et al. 2015), a genotypic and molecular approach is now required to deepen our understanding of eco-evo dynamics. Phenotypes are the nexus of eco-evo dynamics, which expressions are determined by their (epi)genomes. The recent developments of 'omics' have opened new perspectives in eco-evolutionary studies because they enable one to detect the molecular changes responsible for phenotypic adaptations, as well as the general genomic signatures of both adaptation and drift (Pearse et al. 2014, Galtier 2016). In addition, the molecular pathways of phenotypic adaptation also shed light on the way evolution generally proceeds, e.g. a single mutation with major effects versus many mutations with small effects, or epigenetic changes (Nadeau and Jiggins 2010, Stapley et al. 2010), and thus on the speed of successive retroactive loops. For instance, a transcriptomic analysis performed in rotifer-alga microcosms showed that during successive eco-evo feedbacks (predator abundance → prey defense trait → predator abundance), the changes in gene expression responsible for changes in prey defense traits occurred for different suites of genes (Becks et al. 2012). The authors suggested that the studied phenotype may be rapidly produced by several different gene transcription pathways.

To date theory on the evolution of life-history traits (including dispersal) has made highly simplifying assumptions related to the underlying genetics. Very often haploid individuals are still assumed and dispersal is controlled by a single locus (Bocedi and Travis 2016, Poethke et al. 2016). Even when diploids have been modelled, a single locus has typically been assumed (Guillaume and Perrin 2006, 2009). Some very recent work has begun relaxing these assumptions. Henry et al. (pers. comm.) have demonstrated that the number of loci involved in determining dispersal has a very substantial influence on the eco-evolutionary dynamics of a range shift. With few loci of large effect, dispersal evolves upwards more rapidly at the expanding front and results in a greater acceleration of range expansion than when dispersal is under the control of many, smaller effect loci. In contrast, after range shift (e.g. when climate change has stopped), dispersal evolves back down to a lower rate more rapidly when it is controlled by many loci. These results highlight the importance of developing theory for the eco-evolutionary dynamics of life histories in fragmented landscapes within which the influence of genetic architectures is explored. Currently, we have no such theory, yet it will be vital as we strive to develop models that can predict complex ecological systems (Evans et al. 2013).

Further, we should also begin to develop eco-evolutionary models that incorporate epigenetic control of life histories on heterogeneous landscapes. We have empirical studies that point towards the likely importance of non-genetic inheritance of dispersal, such as maternal and grand-maternal effects on dispersal distance in spider mites (Bitume et al. 2014) and plants (Li et al. 2013), and on dispersal probability on lizards (Massot and Clobert 1995, Bestion et al. 2014). A noteworthy recent paper (Kronholm and Collins 2015) explored how epigenetic mutations influence evolutionary responses to environmental change and demonstrated that they can both speed up or slow down evolution. In another interesting recent theoretical study addressing sexual selection, Bonduriansky and Day (2013) explored how non-genetic inheritance can result in the maintenance of costly female preference for mates. These two theoretical studies point the way forwards in terms of combining classical evolution and epigenetic mechanism but neither incorporate ecology (both make the common, simplifying evolutionary assumption of constant population sizes). There is a real opportunity to develop novel theory on eco-evo dynamics in relation with epigenetic changes on fragmented landscapes by integrating (and extending) the approaches taken by Bonduriansky and Day (2013) and Kronholm and Collins (2015) with spatially explicit eco-evolutionary modelling.

To our best knowledge, 'omic' eco-evo studies have not been described in spatially explicit experimental systems, except those concerning the Glanville fritillary butterfly (Wheat et al. 2011). At present, spatial eco-evo studies mostly rely on landscape genomics (Manel and Holderegger 2013) or landscape community genomics (Hand et al. 2015) approaches. These two frameworks aim at studying the influence of landscape features on neutral and adaptive genetic variation on natural populations or communities, and can thus provide relevant information on the way eco-evo processes shape genetic and phenotypic diversity. For instance, genome scans of *Daphnia* populations performed in a geographic mosaic of environments where dispersal is very limited revealed that repeatable patterns of local adaptation, i.e. parallel evolution, can arise in patchy landscapes (Orsini et al. 2012).

An interesting individual-centered 'omic' framework that echoes back to the multidimensional view of the phenotype has been very recently proposed by Ritchie et al. (2015) in the context of medical research, and further transposed to the context of evolutionary ecology (Baguette et al. 2015). This framework proposes to integrate all levels of molecular variations, i.e. genome, epigenome, transcriptome and proteome, in a complex and interactive way to unravel the molecular pathways by which phenomes (the complex associations between phenotypic traits) are produced (Fig. 4). Going beyond the now commonly used genome scans by using such a multi-omic approach has the potential to link the processes at work in eco-evo interactions, (e.g. adaptive plasticity, genic selection, dispersal) to their underlying molecular mechanisms, although we recognize that it requires expertise that many evolutionary ecologists are not familiar with. By coupling such mechanistic determination of the molecular bases of phenotypes to population (epi) genomic analyses, we should be able to entirely unravel the effects and consequences of the processes involved in eco-evo dynamics and feedbacks.

Bridging the gap between theoretical predictions and experimental validations

In conclusion, we have observed that the proliferation of theoretical models dealing with spatial eco-evo dynamics or feedbacks contrasts strongly with the relatively few experimental examples on the same topic. A corollary to this

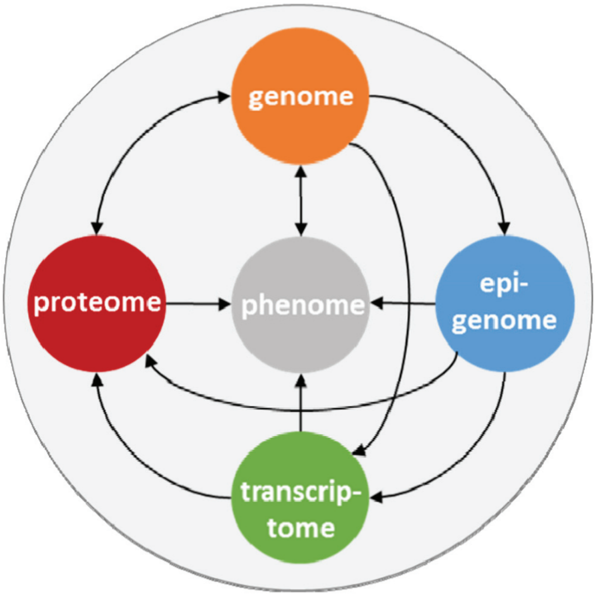

Figure 4. Relationships between complex phenotypes (phenomes) and 'omic' levels, as proposed in the interactive framework of Ritchie et al. (2015). This framework suggests that it is the combination of variation across all possible molecular compartments in concert that leads to phenotypes, and not only their linear relationships as historically proposed (Lewontin 1974, see more details in Baguette et al. 2015).

observation is that many major theoretical predictions on eco-evo dynamics in fragmented landscapes have not been empirically verified.

Fronhofer and Altermatt (2015) provide a good illustration of how experimental approaches can be used to test major theories in the context of range dynamics, but we unfortunately lack similar examples in the context of fragmentation (aside from the Glanville fritillary butterfly system). However, we advocate that experimental evolution using fragmented micro-, meso- or macro-cosms could more efficiently decipher the rules of ecology-evolutionary games in fragmented landscapes because it allows to monitor 1) changes in phenotype distribution over relevant time and spatial scales in highly controlled systems in response to ecological changes, 2) changes in individual fitness necessary to demonstrate adaptation by natural selection, and 3) alterations in individual movements across the landscape.

This review has also highlighted that the evolution of dispersal and its interaction with the other eco-evo processes are fundamental issues to tackle in the context of fragmentation, but we still lack realism in our study of dispersal. Theoretical models have long oversimplified dispersal rules, for example by fixing a constant dispersal rate performed by a random fraction of individuals (see synthesis in Travis and Dytham 2012, Duputié and Massol 2013). Such oversimplified models may incorrectly explain or predict eco-evo interactions (Hendry 2016a). The emergence of individual-based eco-evo models accounting for inter-individual variation in dispersal at each of its three stages is a giant step forward for tackling this issue (Bocedi et al. 2014). Empirical studies also suffer from this lack of 'dispersal realism', because

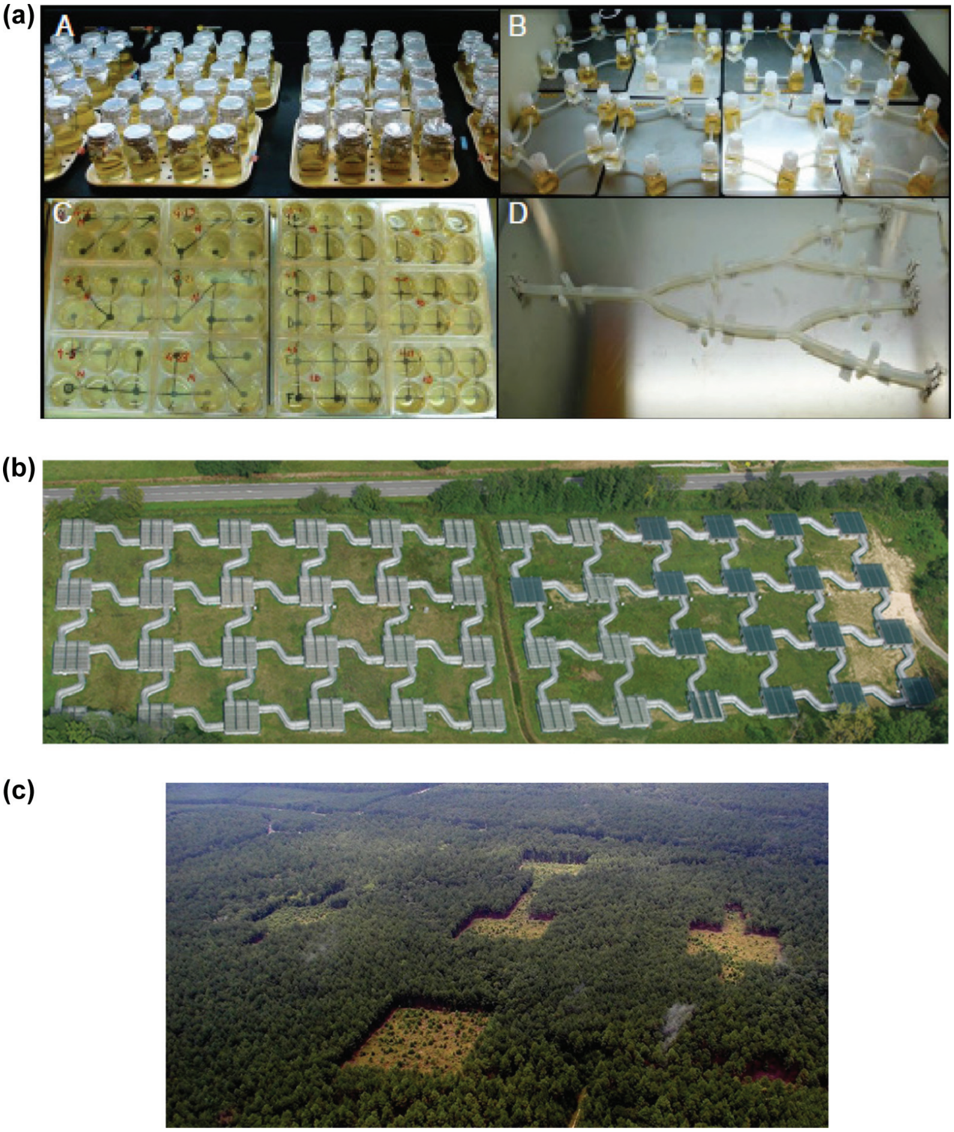

Figure 5. Examples of platforms that can be used to study eco-evo interactions within fragmented contexts. (a) Laboratory microcosms have the advantage of high spatial modularity and control of most biotic and abiotic parameters, as show in designs A to D (Altermatt et al. 2015). (b) The Metatron platform can be used to study a large number of terrestrial species under semi-natural conditions, with possibility of control of climatic parameters (Legrand et al. 2012). (c) The Savannah River Site experimental site proposes a macro-scale forest fragmentation with the advantage of monitoring of species under natural conditions. Photo credits are due to Florian Altermatt (a), Quentin Besnard (b) and Ellen Damschen (c).

they often measure dispersal at only one of the three steps or ignore inter-individual variation in dispersal (Baguette et al. 2013, Cote et al. 2017a), often as a consequence of technical limitations (Haddad 2012, Legrand et al. 2012, Haddad et al. 2015). There is also urgent need to develop experimental designs to determine the role of dispersal in eco-evo interactions within fragmented landscapes by teasing apart the effects of dispersal from those of drift and adaptation. This could be achieved by comparing experiments and models with and without dispersal. At present, most eco-evo studies did not tested for the effect of dispersal (Yoshida et al. 2003) or relied on assisted dispersal movements (Bell and Gonzalez 2011, Low-Décarie et al. 2015). We suggest that a more comprehensive approach would allow active movements of individuals among populations in order to test for the effect of non-random dispersal on eco-evo interactions in realistic and complex fragmented systems (Fig. 5). Standardized protocols in fragmented microcosms have been developed (Altermatt et al. 2015), but they are restricted to the study of small organisms like protists or mites (Schtickzelle et al. 2007, De Roissart et al. 2016). The Metatron platform has recently been built to offer such experimental facilities under semi-natural conditions for larger terrestrial organisms at a meso-scale (Legrand et al. 2012, 2015, Bestion et al. 2015). Fully-controlled or semi-natural systems have however some limitations because they cannot capture the complexity of ecological factors that shape phenotypic distributions (Haddad 2012, Haddad et al. 2015, Hendry 2016a), and the effects of phenotype evolution on realistic ecological dimensions such as habitat connectivity, patch quality and shape, and population and community dynamics may be hard to fully assess. Controlled experiments should thus be performed hand in hand with long-term monitoring of biodiversity changes in large-scale fragmentation programs (Urban et al. 2008, Haddad 2012).

Finally, we are convinced that the temporal changes of multiple omic compartments is fundamental to reveal the hidden diversity of eco-evo feedbacks occurring in complex metasystems and to better understand the processes at play in these feeders, including the role of the understudied plasticity in this eco-evo context (Hendry 2016b). Furthermore, characterizing the molecular mechanisms of phenotypic changes should help to parameterize and validate models about spatial eco-evo feedbacks at various levels of biological organization (genetic, individual, population, species or community). This approach echoes back to the necessity to adopt a multidimensional view of the phenotype (Laughlin and Messier 2015), i.e to consider phenotypes as assemblages of traits that can coevolve as the result of constraints, plasticity or correlational selection (Ronce and Clobert 2012, Legrand et al. 2016, Cote et al. 2017a). By raising this point, we would like to emphasize that spatial eco-evo dynamics should benefit from a better knowledge of fitness landscapes of both traits impacted by fragmentation (e.g. foraging behaviours, mating attributes, body size) and dispersal traits. Overall, such multidimensional view of phenotypes and omic compartments would improve our predictions of metasystem dynamics, from populations to ecosystems, in response to habitat fragmentation.

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