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Looking beyond the mountain: dispersal barriers in a changing world

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Dispersal barriers have demographic, evolutionary, and ecosystem-wide consequences. With ongoing changes in the environment, some dispersal barriers will likely disappear while new ones will appear, and it is crucial to understand these dynamics to forecast species' distributions and adaptive potential. Here we review recent literature on the ecological and evolutionary aspects of dispersal to highlight key dynamics of dispersal barriers in the face of global change. After defining dispersal barriers, we explain that a better understanding of their dynamics requires identifying the barrier types that are most susceptible to change and predicting species' responses. This knowledge is a prerequisite for designing management strategies to increase or reduce connectivity, and maintain adaptive potential. Our intent is to motivate researchers to explicitly consider dispersal barriers in order to better forecast the dynamics of species and ecosystems subject to global change.

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Environmental conditions that prevent organisms from dispersing (ie dispersal barriers) have far-reaching consequences for the organization of life on Earth. Dispersal barriers promote diversification and limit the distribution of populations and/or species (Holt *et al.* 2013). Yet, because dispersal barriers are rarely addressed explicitly in biogeographical models (Engler *et al.* 2012), our ability to accurately forecast the future of biodiversity is impeded.

In a nutshell:

- Dispersal barriers drive many important ecological processes (eg population viability, speciation)
- Such barriers are dynamic features that can vary in strength and location, and can be affected by human intervention and environmental variation; however, they are rarely taken into account explicitly in global change studies
- It is important to be able to predict where they will appear or disappear, to consider their impact on species' distributions and gene flow, and to manage species or landscapes to mitigate their impacts
- Management options that account for population genetics need to be developed to help maintain the adaptive capacity of species when barriers disappear

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In the context of rapid global environmental change, dispersal barriers can affect ecosystems through variations in their strength or location. Human-induced habitat fragmentation creates novel dispersal barriers, leading to decreasing population sizes, decreased species richness, and altered ecosystem functions (Haddad *et al.* 2015). Humans also circumvent or remove natural dispersal barriers by promoting the spread of species via deliberate and inadvertent introductions (Hulme *et al.* 2008) and changes in land use. Finally, the multiple effects of climate change (eg warming and acidification of oceans, changes in wind currents) create opportunities for dispersal barriers to rise or fall (Sorte 2013). The consequences of global change on the dynamics of dispersal barriers are therefore difficult to predict, especially as many of these mechanisms can have synergistic or antagonistic effects.

Although many studies have reviewed the causes and consequences of dispersal limitation (eg Ronce 2007; Travis *et al.* 2013), few have specifically considered the dynamics created by dispersal barriers themselves. Here we review recent literature on the ecological and evolutionary aspects of dispersal to highlight key elements of dispersal barrier dynamics in the face of global change (see WebReferences for the complete list of identified references). After defining dispersal barriers, we develop our synthesis into three points (Figure 1): (1) identifying barriers most susceptible to change, (2) predicting species' responses, and (3) designing species or ecosystem management efforts to increase or reduce connectivity, and to maintain adaptive potential; note that

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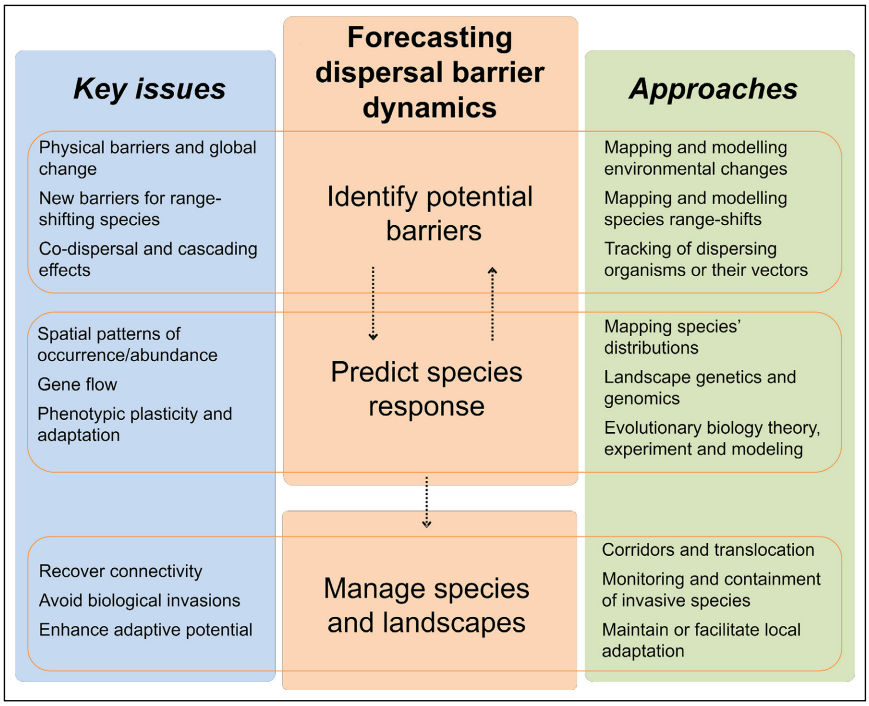

Figure 1. *Studying dispersal barriers in a changing world.*

topics (1) and (2) serve as a basis to develop a framework aimed at understanding the dynamics of dispersal barriers per se.

Defining dispersal barriers

Dispersal barriers have to be defined functionally (Dennis *et al.* 2013): a dispersal barrier is any environmental feature that limits movement through space, and whose effects depend on the interaction with species- or individual-specific traits. For instance, dispersal barriers include oceans for terrestrial species (Holt *et al.* 2013; Burrows *et al.* 2014) but can also be caused by high densities of conspecifics limiting immigration (De Meester *et al.* 2002).

To capture the full complexity of dispersal barriers, scientists must consider two aspects. First, dispersal can be seen as a three-stage process involving the departure of organisms from a natal or previous breeding site, a subsequent transience stage, and finally settlement at a new potential breeding site (Ronce 2007). Dispersal barriers can come into play at any of these stages (Dennis *et al.* 2013), though they are usually regarded as obstacles during the transience stage (eg a mountain between adjacent valleys).

Second, barriers are not binary, permanent obstacles, but rather are dynamic features that can vary in strength (recently illustrated in a proposal to extend the theory of island biogeography to account for surrounding habitat in man-made landscapes; Mendenhall *et al.* 2014) and extent whenever the environment changes (Zeigler and Fagan 2014), species evolve, or individuals adapt. As such, barriers can be affected by human intervention and by climate. In the following sections we emphasize how dispersal barriers (to departure, transfer, and settlement) may appear or disappear as a result of global change, and how species respond to dispersal barriers. Bringing together these two topics allows us to consider how the dynamics of dispersal barriers can be approached. Even though barriers to dispersal may also affect other types of movement, such as seasonal migration or daily foraging, these are beyond the scope of this review.

Falling and rising barriers

Here we explore how the different components of global change may contribute to barrier dynamics either directly, or indirectly, by influencing dispersal vectors or range shifts.

Dynamics of physical barriers as a consequence of global change

Habitat fragmentation caused by land-use change is a well-documented mechanism by which dispersal barriers arise. Terrestrial systems have been particularly well studied, and deforestation (Haddad *et al.* 2015), road construction (Figure 2a; van der Grift and van der Ree 2015), urbanization, and other forms of habitat fragmentation cause major dispersal limitations (Baguette *et al.* 2013). Human regulation of freshwater flows and flooding patterns also has consequences for dispersal of aquatic organisms (Ozinga *et al.* 2009).

Human activities can directly facilitate dispersal and, consequently, remove barriers for other species. Biological invasions are frequently caused by human activities that reduce or remove dispersal barriers, or that elicit direct physical changes in the environment (Hulme *et al.* 2008). The introduction and subsequent removal of river dams create and destroy barriers for aquatic organisms (Branco *et al.* 2014). The construction of the Suez Canal enabled colonization of the Mediterranean Sea by many Red Sea species via a short-circuiting of a previously extensive oceanic barrier (Galil 2007). More often, though, it is the direct and deliberate (eg for biological control or trade) or inadvertent (eg via ship ballast water, air traffic) introduction of species that result in human-facilitated changes in species' dispersal barriers (see Hulme *et al.* 2008 for a review of invasion pathways).

Because many organisms rely on air and water flows for dispersal, any changes in climate have potentially large consequences for dispersal by wind and water

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Figure 2. *Examples of dynamic barriers and associated management options. Road building (a) is a ubiquitous example of dispersal barriers threatening biodiversity, particularly in tropical forests as illustrated by this recent highway, constructed in the heart of the Congo Basin rainforest. Wildlife crossings (b) and other corridors are often proposed to recover connectivity between habitat areas. In Canada, the Elwha River dam (c), which negatively affected ecological processes (including fish dispersal), was removed in 2011 (d).*

(see review by Sorte 2013). In particular, long-distance airborne introduction of new species can be determined by unusual weather events, such as strong winds (de la Giroday *et al.* 2012). Climate affects water movement and therefore barriers to dispersal in aquatic ecosystems, both vertically (eg via stratification) and horizontally (eg currents, eddies, fronts). Retreating glaciers and melting sea-ice open new habitats and dispersal pathways, by removing barriers that are acting at the transience or settlement stages (Clarke *et al.* 2005).

Barriers emerging from distributional shifts

As species' distributions shift following environmental change, new dispersal barriers are likely to appear, such as those that shape species' range limits (Anderson *et al.* 2009). These barriers may prevent organisms from tracking environmental changes sufficiently quickly selection to ensure survival. Delimiting a species' climatic niche and calculating climate trajectories are powerful ways to identify this type of barrier (Burrows *et al.* 2014). Some barriers can be easily inferred, such as large water bodies for terrestrial species ("coastal sinks" in Burrows *et al.* 2014). Other barriers can be deduced from information about geomorphology, land cover, or marine currents, though complementary methods are often needed (see "Detecting the impact of barriers on dispersal patterns" section below).

Co-dispersal

Dispersal of many species depends on the movement of others. Modification of dispersal pathways for species that respond to global change may therefore have cascading effects on other species that would not necessarily be affected otherwise. For instance, global change is having a radical effect on avian migration routes (eg Visser *et al.* 2009), which in turn will affect the dispersal of numerous organisms that rely on migrating

birds as vectors for passive dispersal. Similarly, propagules dispersed by amphibians or fish between distant wetland sites are more likely to exhibit dispersal limitation than those dispersed by water birds (Viana *et al.* 2013), since amphibians and fish are generally more dispersal-limited. Given the current pace of extinctions, many species are losing their dispersal vectors (eg plants that rely on animals for dispersing pollen or seeds; Dirzo *et al.* 2014).

Species' responses

To gain insights into how species may respond to barrier dynamics, researchers must determine the effects of rising and falling barriers on dispersal potential. We suggest two steps: (1) using patterns of dispersal limitation to predict responses to changing barriers, and (2) assessing how plasticity and selection may change species' responses to barriers.

Detecting the impact of barriers on dispersal patterns

Heterogeneity in species' distributions over time and space has provided various opportunities for characterizing dispersal limitations. Barriers are usually assumed to occur when a species is absent from a similar, contiguous area offering suitable habitat (eg Naka *et al.* 2012). For instance, analyses of plant population trends suggest that important barriers to dispersal have been created in Europe owing to the loss of dispersal mechanisms for some plants, such as natural flooding regimes and mass movements of large mammals (Ozinga *et al.* 2009). Dispersal barriers may also be revealed when the spatial distribution of intraspecific phylogenetic lineages can be linked to past climatic changes (Peterson and Nyári 2008).

Geographic information system (GIS)-modeling can help to identify barriers when resistance of specific habitats to movement is known (McRae *et al.* 2012). But predicting how species respond to dispersal barriers – based on species' distributions – is complicated because doing so requires extensive mapping, correctly interpreting what "suitable habitat" or movement costs are (Zeller *et al.* 2012), and knowing about dispersal distances and dynamics. For example, areas of high population density may themselves represent barriers for immigrants of ecologically equivalent competitive species (Urban and De Meester 2009). Density-dependent dispersal complicates inferring dispersal barriers solely from distribution data, and we anticipate that future advances in this field of study may stem from improvements in dispersal modeling (through, for instance, individual-based models; McRae *et al.* 2012) and molecular ecology, as movement and genetic data become more readily available.

Detecting dispersal barriers by identifying their effects on genetic structure is a key objective of landscape genetics (Blair *et al.* 2012; Baguette *et al.* 2013). A major challenge for this approach is to distinguish genetic barriers from the effects of genetic isolation by distance. Existing methods are able to detect genetic barriers to movement (eg linear barriers; Blair *et al.* 2012), such as rivers, roads, dams, or mountains (eg Dudaniec *et al.* 2012). These are examples of symmetric barriers: they constrain dispersal in both directions. However, asymmetric genetic barriers also occur and may be common among organisms dispersed by abiotic means, such as by oceanographic circulation (eg Pringle *et al.* 2011), currents of lotic systems (Pollux *et al.* 2009), or wind. Biotic drivers of asymmetrical gene flow may include priority or monopolization effects (eg where order of arrival of individuals or species in a new area has a long-term impact on genetic structures; De Meester *et al.* 2002). Though rarely used in the context of barrier detection, asymmetric gene flow can be detected with methods that estimate population-specific backward migration rates (reviewed in Broquet and Petit 2009). The detection of barrier dynamics is further confounded by the temporal lag between ecological processes and population genetic structure (Landguth *et al.* 2010). Such temporal mismatches can be avoided by using genetic methods that allow tracking dispersal events in real time (Broquet and Petit 2009).

Finally, because any rising or falling barrier is likely to affect numerous species, multi-species approaches are preferred when characterizing connectivity (Breckheimer *et al.* 2014), and landscape genetic approaches are highly amenable to this (Whiteley *et al.* 2014). The ability to sample assemblages and to characterize and assess signatures of local adaptation by high-throughput sequencing approaches will improve our understanding of how genetic barriers are formed (Rellstab *et al.* 2015). Distinguishing genetic barriers created by the landscape or by behavioral, life-history, or adaptive processes is a formidable challenge. Improvements in the understanding of dispersal limitations will obviously help to construct better predictive models of barrier dynamics.

Evolutionary changes in species' response

Any aspect of dispersal (probability, success, direction, distance) can be seen as the product of the interaction of a disperser's traits and its environment (Clobert *et al.* 2009). Figure 3 illustrates how this interaction creates barriers and affects population dynamics. Traits vary between or within species, such that a barrier for one species or individual may not constitute a barrier for another species or individual of the same species (Clobert *et al.* 2009; Travis *et al.* 2013). These traits are not fixed, however, as organisms can react through

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plastic and/or selection processes to developing or disappearing barriers.

Evolutionary responses to barriers can develop in two different directions. On the one hand, when the probability of crossing the barrier is close to zero, strong selection against dispersing individuals and subsequent reduction in dispersal propensity is expected, and has been documented in the case of severe fragmentation (Bonte *et al.* 2006). On the other hand, when crossing the barrier is possible and confers higher fitness, dispersal is selected for and can be expected to increase; this has been recognized in the case of climate change (Thomas *et al.* 2001) and invasions (Phillips *et al.* 2006) with selection for increased dispersal rate resulting in rapid colonization of newly available habitat (see also Travis *et al.* 2013).

In general, if individuals vary genetically in their ability to cross a dispersal barrier, it should result in non-random gene flow from one side of the barrier to the other (Edelaar and Bolnick 2012). This outcome will decrease genetic diversity among dispersers but might facilitate the colonization of novel habitats by specific individuals displaying a phenotypic disperser or colonizer behavioral syndrome (Clobert *et al.* 2009). In such syndromes, phenotypic and life-history traits that improve the ability to disperse and/or to settle in previously unoccupied habitats can be genetically correlated with dispersal behavior (Cote *et al.* 2010). Taken together, plastic and evolutionary responses to changes in dispersal barriers imply that today's dispersal rates and distances may be different from those of tomorrow.

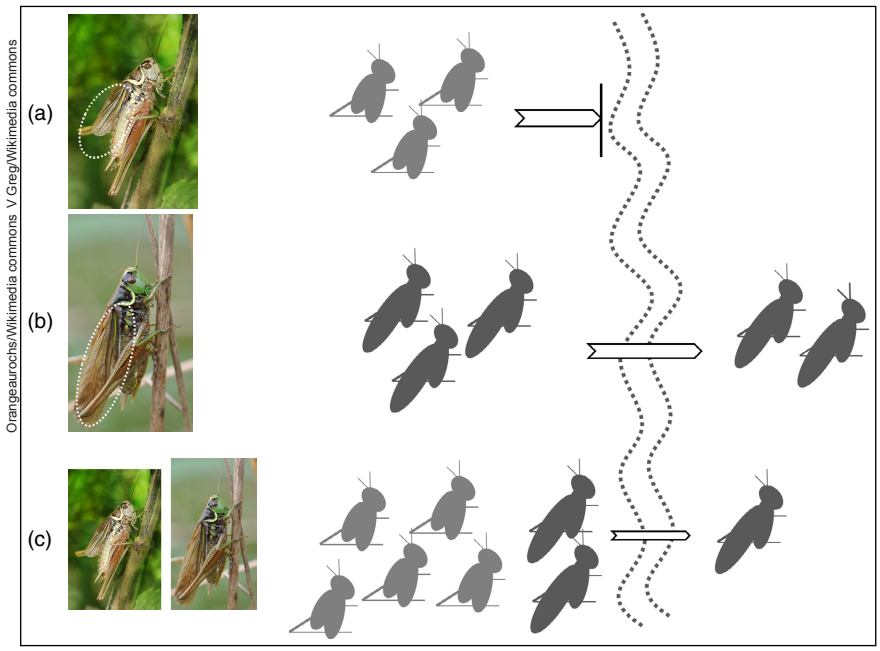

Figure 3. *Dispersal barriers are a result of the interaction between dispersers' traits and the environment. Wing dimorphism in Roesel's bush cricket* (Metrioptera roeselii) *demonstrates that environmental features that act as a dispersal barrier to short-winged individuals (a) may not act as a barrier to long-winged individuals (b). The frequency of these two phenotypes varies as the selection pressure for dispersal capacity changes (c) (Thomas* et al. *2001), and local adaptation occurs on each side of the barrier.*

Forecasting barrier dynamics

Anthropogenic global change and its effects on range distributions and dispersal vectors increase the pace at which dispersal barriers may change. Because dispersal barriers have such profound effects on the species' distributions, the probability that they will persist, and their adaptive potential, tools need to be developed that help forecast where those barriers will rise or fall. This requires combining global change scenarios with likely species' responses. In addition, given that barriers usually affect entire communities, multi-species approaches will likely be needed to effectively forecast the impacts of these barriers, despite the difficulties associated with community-level modeling. Exploring dispersal strategies with spatially explicit individual-based models has already proven useful in recovering known dispersal barriers at a regional scale in the Pacific Ocean (Treml *et al.* 2015). Dispersal traits were not allowed to evolve in this study, which focused on passively dispersed species. The route taken in the modeling of spatial distribution shifts under global change (eg Bocedi *et al.* 2014) shows how dispersal evolution can be taken into account, although such approaches are so far limited to single, actively dispersing species. A combination of functional grouping of species, spatially explicit modeling, dispersal trait evolution, and global change scenarios could serve as a basis for future developments (Marcot *et al.* 2015).

Management options

Notably, most recommendations for managing biodiversity under climate change concern dispersal barrier mitigation (see Table 1 in Heller and Zavaleta 2009). The eco-evolutionary consequences of changing dispersal barriers are numerous, and can be understood directly by looking at the consequences of dispersal limitation (see Edelaar and Bolnick 2012; Baguette *et al.* 2013). Although evaluating every possible effect of rising or

falling barriers on populations and species might be overwhelming, one thing is obvious: removing or maintaining/creating barriers are two management options that should be considered, with the ultimate choice depending on context and management goals (Hermoso *et al.* 2015).

Mitigating the effects of dispersal barriers: recovering connectivity

Management goals often involve alleviating the effects of a developing barrier; this may be achieved by enabling source populations to increase emigration rates, creating dispersal corridors, moving target species (*translocation* or *assisted migration*), or removing barriers. Corridors help increase connectivity (Hale *et al.* 2001; Gilbert-Norton *et al.* 2010) and have therefore been used extensively, particularly in counteracting the negative effects of roads (wildlife crossings; Figure 2b; van der Grift and van der Ree 2015). However, their efficacy depends on their implementation, and species-specific assessments are still needed (van der Grift and van der Ree 2015). Translocations may be the only viable alternative for managing isolated populations, but they are difficult to implement and may increase biological invasion risk; as a consequence, they are still highly controversial (Webber *et al.* 2011). Barrier destruction has become an option when the barrier is of anthropogenic origin and when the potential for restoring connectivity is well understood, as in the case of river dams (Figure 2, c and d). Yet the number of dams is so high that removals need to be prioritized based on ecological and economic constraints (Branco *et al.* 2014).

When barriers disappear: what about adaptive potential?

Management of the results of disappearing barriers has concentrated on controlling invasive species. Invasion biology is a vast discipline that aims to produce management options through the modification of landscapes or by controlling invasion pathways (Hulme *et al.* 2008; Caplat *et al.* 2012). Maintaining or even creating new barriers can have additional benefits, such as preventing disease spread or hybridization between native and introduced species or strains (Hermoso *et al.* 2015). Adaptive potential, which is often presented as a key objective for climate-change adaptation (IPCC 2014), has been overlooked as a basis for management guidelines. We are not aware of any research focused on conserving population genetic structure when dispersal barriers are removed. What strategies could be developed to maintain or improve the capacity of species to track climate? In light of the rapid adaptation exhibited by range-shifting species (see "Evolutionary changes in species' response" section above), it is worth considering that barriers could increase the selection toward dispersers and thereby increase the potential for range shifting. The genetic tools developed in the past decade, the recent interest in dispersal syndromes (Baguette *et al.* 2013), and research on managing micro-evolution (eg Rice and Emery 2003) are likely to improve our understanding of the role of dispersal barriers for adaptive potential.

Conclusions

Dispersal barriers have important consequences for population dynamics and genetics, species' distributions, and community composition, and therefore should be a key focus in evolutionary and conservation biology and biogeography. Here we have outlined the motivational and conceptual means to identify where changes in dispersal barrier strengths and locations are likely to occur. Clearly, the interacting roles of extrinsic (environmental) and intrinsic (organismal) characteristics are mutually influential in defining the properties of a dispersal barrier. Both extrinsic and intrinsic characteristics may also alter under global change, causing the development or disappearance of dispersal barriers in different ways for different species.

This overview is intended to promote future research to identify, understand, predict, and manage the dynamics of dispersal barriers. We suggest a sequence of research objectives that should improve our capacity to predict the effects of global change, based on (1) identifying emerging or disappearing barriers, (2) predicting the response of species, and (3) choosing the appropriate mitigation strategy. Of these, the last is the most challenging, as it requires including knowledge on physical landscapes, species dispersal, and if possible, gene flow, in land management plans. In addition, the interaction between landscape features and species characteristics means that there will be no "one-size-fits-all" management approach, and only concerted efforts across taxa, biomes, and borders will provide the knowledge to manage dispersal barriers for conservation purposes and to maintain ecosystem function.

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