

# Limits to evolution at range margins: when and why does adaptation fail?

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**What stops populations expanding into new territory beyond the edge of a range margin? Recent models addressing this problem have brought together population genetics and population ecology, and some have included interactions among species at range edges. Here, we review these models of adaptation at environmental or parapatric margins, and discuss the contrasting effects of migration in either swamping local adaptation, or supplying the genetic variation that is necessary for adaptation to continue. We illustrate how studying adaptation at range margins (both with and without hybridization) can provide insight into the genetic and ecological factors that limit evolution more generally, especially in response to current rates of environmental change.**

## Range margins: an evolutionary paradox

Why do all species have spatially restricted ranges? The simple answer is that populations cannot become established beyond their range because they have negative growth rates in these new habitats. However, it is clear that species can adapt to inhospitable conditions over longer time periods, otherwise there would be no life on land, no mammals in the ocean and only a few species on oceanic islands. Moreover, there is abundant evidence for adaptation to different environments within the range of a species, sometimes over short timescales [1,2]. What then is happening at range edges to prevent adaptation and to stop populations from expanding into new territories?

Populations typically become smaller and more fragmented as species approach their ecological limits [3,4]. There are two contrasting explanations for this failure of local adaptation: (i) if the range edge is highly fragmented, Allee effects (see Glossary), genetic drift and the low rate of mutational input into marginal populations might limit the availability of locally beneficial alleles, preventing adaptation and, therefore, range expansion [5–9]; and (ii) if populations at the margins remain connected to large, well adapted central populations, the continual immigration of these locally deleterious alleles could swamp the establishment of locally adaptive alleles, thus maintaining negative population growth, and again preventing expansion ([10–18], reviewed in [19]). Much discussion of why evolution fails at range margins hinges on determining how much

gene flow is necessary to maintain adaptive potential at the margins without swamping local adaptation (see Ref. [9] for a recent treatment). Answering this question requires a clear and detailed understanding of the genetics of quantitative traits, as well as the nature of selection on these traits.

Here, we describe theoretical models that explore adaptation at range margins, and then examine how they have fared in the light of empirical data. We divide these models by the type of range edge that they consider: environmental margins, parapatric margins and hybrid zones. Although these margins differ in the number and type of factors involved, range expansion in all three depends on locally adaptive alleles becoming established under the ecological or genetic conditions at the range edge. Integrating range margin research into this broader theoretical framework will generate important insights into what limits rates of adaptation in nature, a topic that is particularly

## Glossary

**Allee effect:** inverse density dependence at low density, such that populations below a threshold density are unable to maintain a positive growth rate. For example, below a certain density, encounter rates might be sufficiently low that many females remain unmated.

**Allopatry:** where populations or species are geographically isolated from each other.

**Assortative mating:** the tendency for individuals with similar phenotypes to make preferentially with each other.

**Condition dependence:** where the phenotypic expression of a trait depends on the health of the individual. For example, genes conferring large birth weight will only be expressed in parents with sufficient energy intake.

**Ecological character displacement:** the process of phenotypic divergence caused or maintained by interspecific resource competition [2]

**Ecotone:** a geographical boundary between two different selective environments

**Environmental margin:** where species fail to adapt beyond some point on an abiotic selective gradient.

**Genetic drift:** change in allele frequencies caused by the random sampling of alleles between generations; its effects grow stronger as population size decreases.

**Hybrid zone:** a parapatric margin where two or more populations or species exchange genes through hybridization.

**Introgression:** the movement of alleles between differentiated genomes.

**Linkage disequilibrium:** the tendency for alleles at different loci to be associated within a population. These non-random associations are broken up by recombination between the loci, but are generated and maintained by selection or assortative mating

**Parapatric margin:** where two or more species interact at a shared border, often through competition for resources.

**Sink population:** a population with fewer births than deaths that is maintained only by continual migration from neighbouring non-sink populations.

**Sympatry:** a situation where the presence of a given population or species does not restrict the presence of the other, such that they coexist freely. This is distinct from parapatry in that it involves alpha, rather than beta diversity.

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relevant given the rapid and widespread ecological changes being generated by climate change (Box 1).

### Adaptation to an abiotic environmental gradient

In the simplest models of evolution at range margins, a continuous population persists along a selective gradient in space (e.g. temperature or salinity) that is abiotic in that it is unaffected by interactions with other species. Several important theoretical models have examined the formation of range margins along such a gradient by following changes in the mean of a quantitative trait [17,18]. These models are important because they link population ecology with genetics in that population density is a function of how closely the trait mean matches the trait optimum at that point on the gradient.

In the Kirkpatrick and Barton model [18], when the population tracks the trait optimum, the species expands along the gradient and density remains high (Figure 1a). However, if the optimum changes too quickly relative to the amount of genetic variation available, the population rapidly declines in mean fitness and, therefore, density. Migration now comes mainly from the central, well adapted parts of the range into the margins, so that marginal populations contain a high proportion of poorly adapted immigrants. Population density at the margin is further reduced as selection acts to remove the locally maladaptive alleles, which, in turn, exacerbates the swamping effect of migration (Figure 1b). These low densities also make local adaptation less common, because alleles conferring increased fitness will be unlikely to arise *in situ*. Instead, they will typically arise where populations are already close to their optima (i.e. the range centre), where they will not be favoured by selection. In such models, where gene flow is random, adaptation is effectively biased towards the environmental conditions experienced by the largest number of individuals [14].

These models [18,19] predict that adaptation will be prevented where the selective gradient steepens, population density is locally reduced, or gene flow is locally increased. The problem is that all of these factors are difficult to measure in natural populations [20–22]. In addition, such patterns of gene flow and selection probably operate over small spatial scales, making them difficult to study without intensive ecological surveys or data from a large number of genetic markers (see Ref. [23] for a recent example).

There are some data suggesting that asymmetrical migration load can prevent local adaptation [24,25]. A particularly good example is the evolution of antipredator patterning between parapatric populations of *Timema* walking stick insects [26]. When adjacent host plant patches differed in size, the pattern favoured on the more common host dominated across both patches (Figure 2); only when population sizes were more even did each pattern reach a significant frequency on its respective host. The amount of divergence among populations in different environments and for different traits depends on the relationship between migration and diversifying selection [27,28], and there are many examples of local adaptation despite substantial gene flow (e.g. Refs [29–31]). A recent study [32] of great tits *Parus major* on the Dutch island of

Vlieland quantified the effects of gene flow from mainland populations on local genetic differentiation in clutch size. Small clutch size in the east of the island persists despite 13% of first-year breeders being from the mainland, where clutch size is significantly higher. By contrast, in the western parts of the island, where 43% of first-year breeders were immigrants, clutch size is similar to that observed on the mainland. In addition, mean survival of females born in the east is twice as high as females born in the west, suggesting better adaptation to life on the island, although the traits conferring this increased fitness remain unclear.

In the Kirkpatrick and Barton model [18], genetic variance is assumed to be constant across the entire range. In reality, however, the amount of segregating variance evolves under the joint effects of migration, mutation and selection. Importantly, migration among populations with different trait means increases genetic variance and so facilitates adaptation. Barton [33] extended the model in Ref. [18] to include the effects of population size and migration on genetic variance. He found that, for a range of quantitative genetic models, the swamping effect of gene flow in peripheral populations was outweighed by the associated increase in genetic variance, enabling the population to match the phenotypic optimum even where the selective gradient was steep. A similar rescuing effect of gene flow through its effects on genetic variance is observed in models of poorly adapted sink populations, especially when there is sexual selection [34], or there are brief respites in selection against migrants [35,36].

In nature, however, all species have limited ranges, even though abundant genetic variation is observed for many traits in natural and laboratory populations [21,37,38]. Nonetheless, a species will have a range edge if it fails to adapt in only one important trait [39], and some traits might have limited genetic variation, even if overall genetic variance is high. This might make repeated or sustained responses to rapid selection difficult, as has been suggested for several tree species [40]. Selection experiments in *Drosophila birchii* also found no heritable variation for desiccation resistance, a trait that could constrain the southern range margin of this species [41]. Similarly, many invasive and domesticated species show similar ecological and climatic tolerances in their introduced and native ranges, suggesting a failure to adapt to new conditions, and that invasions typically fail without pre-adaptation [42]. An additional factor that might also limit available genetic variation is condition dependence, as this can reduce heritable variance in environments where a trait is under most selection [43]. Also, if selective gradients in nature change abruptly on a fine spatial and temporal scale, the central population size might be too small to supply the high levels of variance to marginal areas modelled in Ref. [33].

Overall, there is a lack of empirical data concerning how migration among divergent populations really affects adaptive potential. Studies of real populations in hybrid zones often find that mixing two distinct gene pools leads to increased variability (reviewed in Ref. [44]) and, in some cases, the ability to colonize new environments [45], but it is not clear to what extent migration among less divergent

### Box 1. Extinction and evolution in response to climate change

Climate change represents a major immediate threat to biodiversity. Models that project the ecological tolerances of species on future climatic scenarios estimate that at least 11% of species will become extinct during the 21st century, even if one assumes that they can disperse to track the distribution of suitable habitat [69]. However, this figure will be an underestimate in cases where dispersal is limited or if local adaptation already exists throughout a species' range, meaning that ecological tolerance within a given population will be less than the models assume [70]. Conversely, extinctions will be reduced if species can adapt to changing conditions, particularly at range margins, enabling more widespread habitats to be exploited.

Parmesan and Yohe [71] analysed data for over 1700 species and showed that 73% have recently shifted their ranges, mostly in the poleward or upward direction predicted by models of climate change. Detailed studies of European butterflies also reveal similar responses [72,73] (Figure 1), mostly in generalist, high dispersal species. However, poleward range shifts in specialist, low dispersal species tend to be associated with the evolution of increased dispersal abilities [74], or with the ability to use more widespread habitat [75]. Taken together, these studies suggest that, at least in the short term, poleward range shifts are more common than the local adaptation that would enable populations to remain where they are [42].

The remaining 27% of species analysed by Parmesan and Yohe that have not shown the predicted range shifts [71] might be limited by their dispersal abilities, condemning them to extinction as their habitats become increasingly small and fragmented. Some European trees, for example, have yet to reach their predicted distributions following the last glaciation, let alone in response to current climate change [40]. Alternatively, such species could be adapting throughout their range to track changing local conditions, making range shifts unnecessary. However, data from plants [40] and animals [76] suggests that recent adaptation has typically involved shifts in seasonality, rather than the increases in thermal tolerance that are necessary for long-term persistence.

Gene flow might be particularly important for adaptation to climate change, given that many of the alleles required at a species' poleward edge might already exist at the equatorial edge. Sustained evolutionary responses to climate change could depend on such alleles being able to move poleward rapidly. Once again, this focuses attention on how easily alleles can move along selective gradients, and through different genetic backgrounds, to where their fitness is highest. Such movement might be particularly difficult to achieve if population densities are reduced, or selective gradients are locally steepened, by anthropogenic habitat loss [18].



**Figure 1.** The dark-green fritillary *Argynnis aglaja* and purple shot copper *Lycaena alciphron*. The lower elevational limits of these butterflies in central Spain have shifted uphill by 150 m and 400 m, respectively, associated with a 1.3 °C increase in mean annual temperature since 1967–1973 [73]. The loss of such species from lower elevations suggests a failure to adapt to ecological changes at the species' margins. Reproduced with permission from David Gutiérrez.

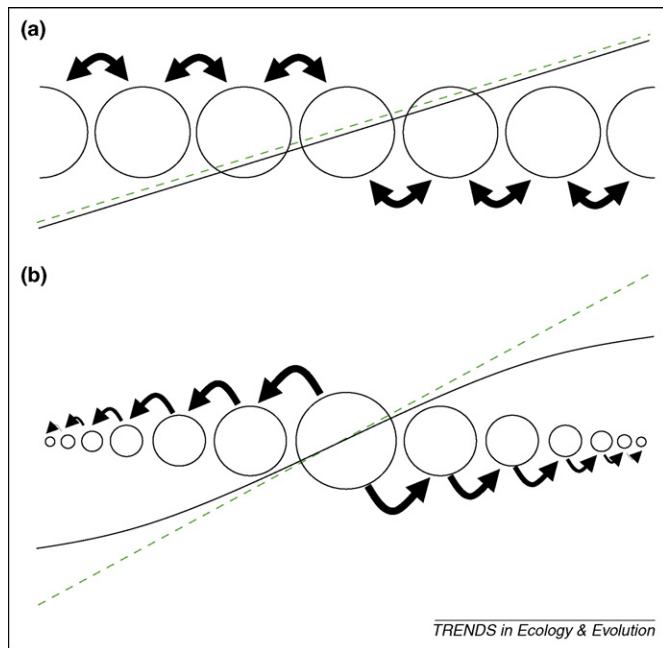
populations increases the potential for adaptation. Swindell and Bouzat [46] showed that immigration enables a greater response to selection in inbred populations, but here gene flow was among highly inbred populations from the same environment. Similar experiments involving outbred populations evolving under different conditions would help determine under what circumstances migration helps or hinders adaptation at range margins.

#### Adaptation at parapatric range margins

The above models examine single species adapting along environmental gradients, yet many species' ranges end where they meet potential competitors. In the classic conception [47], reviewed in Ref. [48], species are excluded from ranges of other species because they compete for resources, although predation or parasitism can have similar effects [49–51]. As with environmental margins, range expansion requires adaptation to conditions at or

just beyond the range edge, which, in this case, includes the presence of other species. Once a viable population can be maintained in the other species' range, the species can coexist in sympatry. For example, this might require evolving to exploit a different ecological niche (ecological character displacement [2]), or the development of new predator avoidance mechanisms. In either case, the margin might be maintained either because such adaptation is prevented by low population density, or because of gene flow from populations away from the range edge that never encounter the competitor.

Case and Taper [52] and Case *et al.* [49] extended the Kirkpatrick and Barton model [18] to include the presence of a competing species, and found that range margins formed at shallower environmental gradients in the presence of a competitor. However, when disruptive selection due to competition was stronger than stabilizing selection towards the environmental optimum, or when the environmental gradient itself was flat, the species became

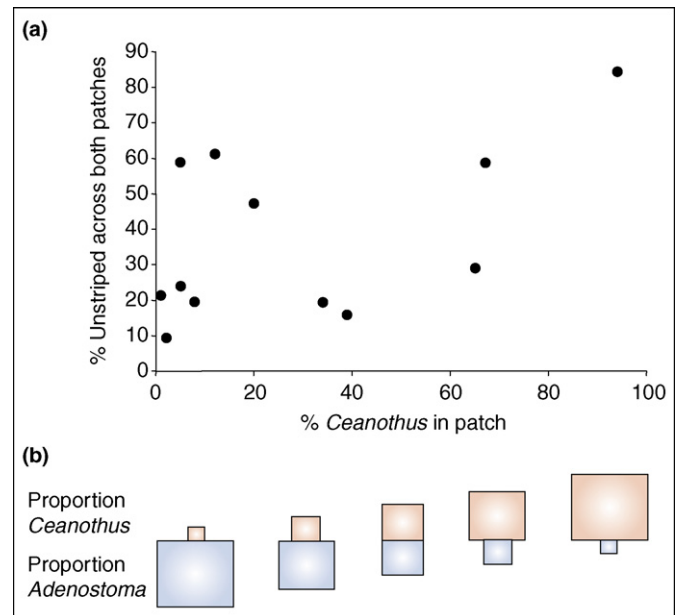


**Figure 1.** Migration load and adaptation along selective gradients. **(a)** Range expansion without limit along a one-dimensional selective gradient in the Kirkpatrick and Barton model [18]. Here, the trait mean (black line) at each point along the gradient matches the environmental optimum (dotted green line) everywhere. Therefore, population fitness is high, population size is uniformly large (indicated by the size of the circles) and the species continually expands along the gradient. The arrows depict the direction and magnitude of migration between adjacent populations. **(b)** Range margins generated by migration load in the Kirkpatrick and Barton model [18]. In this case, the well adapted central population is also the largest, and sends out many migrants to adjacent populations (arrows). These immigrants prevent adjacent populations from reaching their trait optimum (the black line is displaced from the dotted green line), which reduces their fitness and, hence, their population size. These populations, in turn, send out migrants that are even less fit, further reducing the fitness and, therefore, the size of the more peripheral populations. Eventually, the trait mean of the peripheral populations is far from the optimum, and fitness is so low that population growth is negative even with immigration.

sufficiently different to maintain a viable population in the other's range. This divergence enabled the species to spread into full sympatry, eradicating their shared range edge. As in Ref. [18], genetic variance was held constant, although increasing the overall amount of variation made full sympatry more probable.

By allowing the steepness of the selective gradient to be determined by biotic as well as abiotic interactions, the evolution of ecological coexistence (and therefore of ecological communities) can be studied within the framework of evolution at ecological margins. This kind of ecological character displacement, potentially leading to eventual coexistence rather than parapatry, has been observed in response to the Australian range expansion of the toxic cane toad *Bufo marinus* [53]. Within the past 80 years, selection has driven an increase in body size and reduction of gape size in two snake species for which these toads fall well within their usual prey niche. This decreases the fatal probability of eating a toad. By contrast, the prey niches of other snake species that were already morphologically unlikely to ingest these toads, or physiologically immune to their toxins, have remained relatively unchanged.

The importance of competition in maintaining range boundaries is a contentious topic, as many parapatric margins also coincide with transitions between environments (i.e. ecotones) [54–56], making it difficult to determine



**Figure 2.** Gene swamping of anti-predator patterning in host races of *Timema* walking stick insects [26]. The unstriped morph is favoured on *Ceanothus* plants, whereas the striped morph survives better on *Adenostoma*. These host plants sometimes form parapatric patches, enabling migration between them. **(a)** The frequency of the unstriped morph as the *Ceanothus* patch becomes larger relative to the larger *Adenostoma* patch brings in large numbers of striped individuals, which holds the unstriped morph at low frequency (left side of x axis). However, as patch sizes become more even, the unstriped and the striped morphs can coexist. When the *Ceanothus* patch is larger than the *Adenostoma* patch, the unstriped morph dominates on both host plants (right side of x axis). **(b)** Schematic showing the approximate ratio of host plant patch sizes in (a). Data from Ref. [26].

whether competition or environmental selection is maintaining the border. However, these two scenarios can be distinguished with reciprocal transplant experiments, whereby the survival of both species is measured on their non-native side of the ecotone. Many of these studies find reduced viability or fecundity in the other environment [57], whereas others find little or no fitness cost to being transplanted out of their range [54]. Competition is implied as the cause of the range edge in these latter cases, but more compelling evidence would come from additional experiments showing that fitness is reduced in the presence of the native species. For example, the two gorse species *Ulex minor* and *U. gallii* exclude each other where their ranges meet in southern England [58], to the extent that there are no mixed stands even at local scales. Furthermore, both species seem capable of maintaining viable populations in the other's range [59], implying that environmental gradients have little importance in maintaining this margin.

There is, of course, no requirement that the species on either side of a parapatric margin are prevented from expanding their ranges by the same forces. Darwin [47] suggested that species in the northern hemisphere are more likely to be limited by competition at their southern border and by abiotic factors at their northern one, and this pattern has been borne out in at least one study [60]. If this is generally the case, one would predict that parapatric margins often consist of a species at its environmental limit, and a second more environmentally tolerant species that is excluded from the range of the first species by

competition, parasitism or predation [61]. For example, heavy bot fly parasitism prevents the chipmunk species *Tamias umbrinus* from spreading below 2100 metres in altitude in the Front Range of Colorado, whereas the bot-resistant *T. quadrivittatus* is excluded from higher altitudes by the larger and more aggressive *T. umbrinus* [51]. A theoretical exploration of whether these 'mixed' margins form more easily than purely competitive parapatric margins would be useful.

Overall, parapatric margin models [49,52] produce range margins under a wider set of conditions than do environmental gradient-only models [17,18], but their importance as a general explanation for range margins is less clear. To address this question, we need more data on the relative roles of species' interactions and environmental adaptation at parapatric margins on ecotones. In addition, although it is clear that migration can prevent adaptation to local environmental conditions (at least under some circumstances) it would be useful to show that gene swamping can have the same effect on the evolution of character displacement. Lastly, extending the theoretical framework of parapatric models to allow for the evolution of genetic variance and the effects of genetic drift would enable comparisons with equivalent environmental gradient models.

### Adaptation at parapatric margins with hybridization

The third kind of range margin that we consider is a hybrid zone. Hybrid zones also involve two species meeting along a shared border, but, in this case, they also recognize each other as potential mates. This has two consequences for the likelihood that a parapatric margin will form. First, individuals moving into the range of the other species are more likely to mate with the other species than their own, simply because heterospecifics are much more common. Second, if the offspring from hybrid matings are viable and fertile, they can breed successfully and thereby generate gene flow between the two species.

Goldberg and Lande [62] modified Case and Taper's model [52] to include the effects of hybridization without gene flow on parapatric margins. They found that a low rate of interspecific mating led to a sharp parapatric margin even in the absence of an environmental gradient, because migrants into the other species' range rarely reproduced. Under these circumstances, the species cannot establish in each other's ranges until stronger mate discrimination or other hybridization avoidance behaviours have evolved. As in the abiotic and biotic models described earlier, the evolution of these mechanisms can be constrained by gene flow from larger populations away from the range edge [18,52], or by a lack of useful genetic variation in fragmented peripheral populations [9]. Furthermore, range expansion into full sympatry might additionally require ecological character displacement and adaptation to an environmental gradient, as in Case and Taper's parapatric margin model [52].

When hybridization does produce fertile offspring, there is potential for gene flow between the species, and this has additional consequences for evolution at the margin. First, hybrids are expected to be less fit on average than either parental species because their new combinations of alleles

are untested by selection [63]. Hybridization therefore imposes a genetic load on populations in the zone through gene–gene interactions, in addition to the gene–environment migration load explored in the abiotic [18,33] and biotic models [52] described earlier. Both types of load will reduce fitness and therefore density, reducing the chance that locally beneficial alleles will arise within the zone. Second, because species typically differ at many genetic loci, hybridization will generate strong statistical associations (linkage disequilibria) between loci. These linkage disequilibria mean that the fitness of a locus depends on its own effects, on the effects of the loci with which it is associated, and on their interactions [63,64]. The presence of strong linkage disequilibria within the hybrid zone also hampers the fixation of locally beneficial alleles, because new mutations will typically be associated with many deleterious alleles and, therefore, will be removed by selection before they can rise to high frequency [65].

Although there has been no study extending the above models of parapatric margins [52,62] to enable gene flow between the species, many workers have examined the evolution of assortative mating between hybridising taxa. These models are summarized in Box 2. Nonetheless, the likelihood of range expansion at hybrid zones (leading to hybrid zone collapse) is again likely to depend on

### Box 2. The evolution of assortative mating in hybrid zones

There are two significant obstacles to hybridising parapatric species becoming sufficiently distinct to coexist. First, gene flow erodes the differences between the species; and second, linkage disequilibrium hampers the fixation of beneficial alleles by slowing their movement from their parental genomes onto different genetic backgrounds. To overcome both obstacles, the species must stop hybridising and become reproductively isolated from each other. One possible route is the evolution of better mate discrimination, so that individuals avoid mating with hybrids or the other species. This process is known as reinforcement [77].

As hybrid zones are often narrow compared with the rest of the range, beneficial alleles (in this case increasing mate recognition) typically arise away from the hybrid zone. However, because these alleles are not beneficial in the absence of the other species, they might not persist long enough to reach the zone [65]. Even if assortative mating alleles do spread into the zone, or arise *in situ*, they might also fail to establish because they are in linkage disequilibria with unfit alleles, such as those involved in reducing hybrid viability [77]. In addition, as assortative mating alleles become common, and hybrids increasingly rare, selection for the continued spread of such alleles is reduced. However, if the hybrid zone straddles an ecotone, and individuals either move to habitats where they are well adapted, or choose mates that appear well adapted to the local conditions, assortative mating might evolve easily [78]. This movement of individuals to where they are best adapted substantially restricts gene flow, enabling genotypic differentiation over a fine spatial scale, as has recently been shown in great tits *Parus major* in the UK [79].

Finally, assortative mating alleles can arrive in the zone from either species, as introgression can carry them from one species to the other. This is particularly the case for assortative mating alleles that encode for 'mate in your natal habitat' or 'chose a mate resembling your father', as these are equally beneficial in both species. However, the details of mate preferences remain important, as assortment might not be favoured under all conditions [77]. For example, parental and hybrid *Chorthippus* grasshopper females select against intermediate mating signals, which reduces the fitness of hybrid males, and so should favour assortment. However, if hybrid females become locally common, these same preferences will rapidly cause significant gene flow among species [80].

### Box 3. Outstanding questions

We currently lack the empirical data necessary to test the importance of population genetics models to the real margins of species. For this reason, many ecologists consider evolutionary processes to be largely irrelevant to limits to the distribution of species, especially given the fragmented nature of populations at many species' edges. Detailed investigations of how local adaptation and gene flow interact at range margins are required. The following questions are particularly important for rapid progress on this issue:

- Does migration from differentially adapted populations increase or decrease the potential for local adaptation? Is the answer the same when populations are considered at different spatial scales?
- Does genetic variation for adaptive traits generally increase or decrease towards range margins? Is genetic variation more abundant in contracting versus expanding species' edges? If so, does such variation make local adaptation more probable?
- Are range margins found where selective gradients are locally steep and/or populations are reduced in size? How often do interactions with other species determine parapatric range margins? Do the same ecological and genetic factors determine internal as well as external species' edges?
- Is the strength of character displacement at parapatric margins or in hybrid zones negatively or positively correlated with levels of gene flow from nearby allopatric populations? Does this gene flow affect divergence in ecological and reproductive characters differently?
- Which invasive or expanding species have modified their climatic and ecological tolerances in new parts of their range? What ecological or life-history characteristics do these species share?

the steepness of the selective gradient (which here is determined by genetic as well as ecological interactions), the amount and nature of available genetic variation, and the rate of dispersal from populations outside the zone of parapatry.

### Conclusions

Here, we have highlighted some evolutionary and ecological processes shared by different types of species' margin, and have commented on the conditions necessary for range expansion. In Box 3, we summarize research questions where we think rapid progress can be made. In particular, predicting evolution at species' edges depends on understanding the relationship between the swamping and spreading effects of gene flow. These contrasting effects might operate at similar or different spatial scales, and can differ among loci [66]. This means that, whereas gene swamping could prevent local adaptation in adjacent populations, low migration and population extinction might prevent the spread and establishment of beneficial alleles at the scale of the metapopulation. Nevertheless, local adaptation could quickly alter these patterns of gene flow by altering the productivity of patches [67]. Resolving the regions of parameter space where these different effects of gene flow become important, and dissecting how they interact, requires models and data that integrate ecological and evolutionary factors, enabling scaling up from within- to between-population processes.

Ideally, these contrasting effects of gene flow would be studied first in the simplest example (that of abiotic range margins) and then expanded to consider more complex cases where the biotic and genetic background can also vary. Unfortunately, the relatively low levels of ecological and genetic differentiation at abiotic margins make them

less amenable to study than parapatric margins or hybrid zones. This highlights the value of studying the response of range margins to rapid environmental change, especially climate change, because marginal populations must suddenly adapt to ecological conditions that were previously only found outside the range (Box 1). Such situations also enable the exploration of how closely evolutionary or ecological shifts at range edge are associated with, or limited by, range movements of competitors, parasites or predators. Natural experiments of this kind will become depressingly common in coming years (Box 1).

Human modification of habitat also tends to provide environmental gradients that involve fewer selective factors, and that operate over finer temporal scales than those determining large-scale distributional limits of species. For example, Antonovics' pioneering work on local adaptation to heavy metal pollution in *Anthoxanthum* plants [68] remains one of the best examples of evolution along a selective gradient. These situations also enable direct manipulation of selection, making it possible to quantify its effects on gene flow, genetic variance and local adaptation.

The study of adaptation at range edges has reached an exciting point in its development: there are many testable theoretical predictions about how and when range expansion should occur, and there is a range of empirical systems with which to address these questions. Understanding limits to adaptation is essential to predicting rates of extinction owing to climate change, as well as estimating future crop yields, disease and infestation risks, and the effect of environmental change on community ecology and ecosystem services. In addition, the confinement of new adaptations (and, therefore, species) to a small geographical area or particular ecological situation is fundamental to speciation and the evolution of ecological communities [42]. By integrating ecological and genetic interactions with other organisms into an overall measure of gradient steepness, models of marginal adaptation can therefore provide insight into the evolution both of specialization and of species' interactions more generally.

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