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A Practical Guide to the Study of Distribution Limits

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ABSTRACT: Factors that limit the geographic distribution of species are broadly important in ecology and evolutionary biology, and understanding distribution limits is imperative for predicting how species will respond to environmental change. Good data indicate that factors such as dispersal limitation, small effective population size, and isolation are sometimes important. But empirical research highlights no single factor that explains the ubiquity of distribution limits. In this article, we outline a guide to tackling distribution limits that integrates established causes, such as dispersal limitation and spatial environmental heterogeneity, with understudied causes, such as mutational load and genetic or developmental integration of traits limiting niche expansion. We highlight how modeling and quantitative genetic and genomic analyses can provide insight into sources of distribution limits. Our practical guide provides a framework for considering the many factors likely to determine species distributions and how the different approaches can be integrated to predict distribution limits using eco-evolutionary modeling. The framework should also help predict distribution limits of invasive species and of species under climate change.

Keywords: environmental gradients, genetic drift, mutational load, genetic variation, limits to adaptation, population size.

Introduction

The distributions of species are always restricted in space. In this review, we are concerned with the questions of why distributions are geographically restricted, whether distribution boundaries reflect the limits of the realized niche (Hutchinson 1957), why niche evolution is constrained, and what the genetic basis of constraint is. These questions center around extrinsic and intrinsic factors affecting distribution limits: environmental heterogeneity, low genetic variation, and genetic drift leading to mutational load. The answers to these questions have important ecological and

evolutionary implications. For example, restricted distributions create turnover of species composition in space, which is the main source of global biodiversity (Brown et al. 1996). Insights into the limits of niche evolution and the role of small population size are also relevant for long-term conservation of species, managing living natural resources, breeding traits for resistance to environmental change, and predicting future distribution limits of invasive species.

There is no single, general explanation for geographic distribution limits. This has been emphasized in previous reviews of adaptation to marginal conditions (Kawecki 2008), range limits (Case et al. 2005; Bridle and Vines 2007; Gaston 2009; Sexton et al. 2009), and metalevel analyses of the abundant-center hypothesis (Sagarin and Gaines 2002; Eckert et al. 2008; Abeli et al. 2014; Pironon et al. 2017). As we clarify below, empirical studies find examples of factors that are important in certain cases, but multiple factors can be important, and they often differ among species and in different parts of the range. But this does not preclude the existence of generalities about causes of range limits. In fact, it would be helpful to develop an account of factors that are important in certain circumstances or for certain kinds of species. Such an account will require a collection of empirical studies that have systematically quantified multiple factors for a variety of taxa. The goal of this paper is to outline an integrative framework for addressing causes of geographic distribution limits, applicable to nearly any organism. Our prescription may be ambitious, and all aspects will not be applicable in all contexts, but we hope that it helps direct research effort toward understudied questions and toward integrating approaches.

The framework that we suggest for studying distribution limits is summarized in figure 1. Ideally, an investigation should answer five questions. (1) Do range limits coincide with niche limits? (2) Is niche evolution constrained by the spatial pattern of environmental change? (3) Is the distribution limited by the presence of a close relative species? (4) Is evolution constrained by small population size and isolation? And (5) is evolution affected by the genetic architecture of traits that underlie the niche? There are good reasons for addressing the first question at the beginning, whereas

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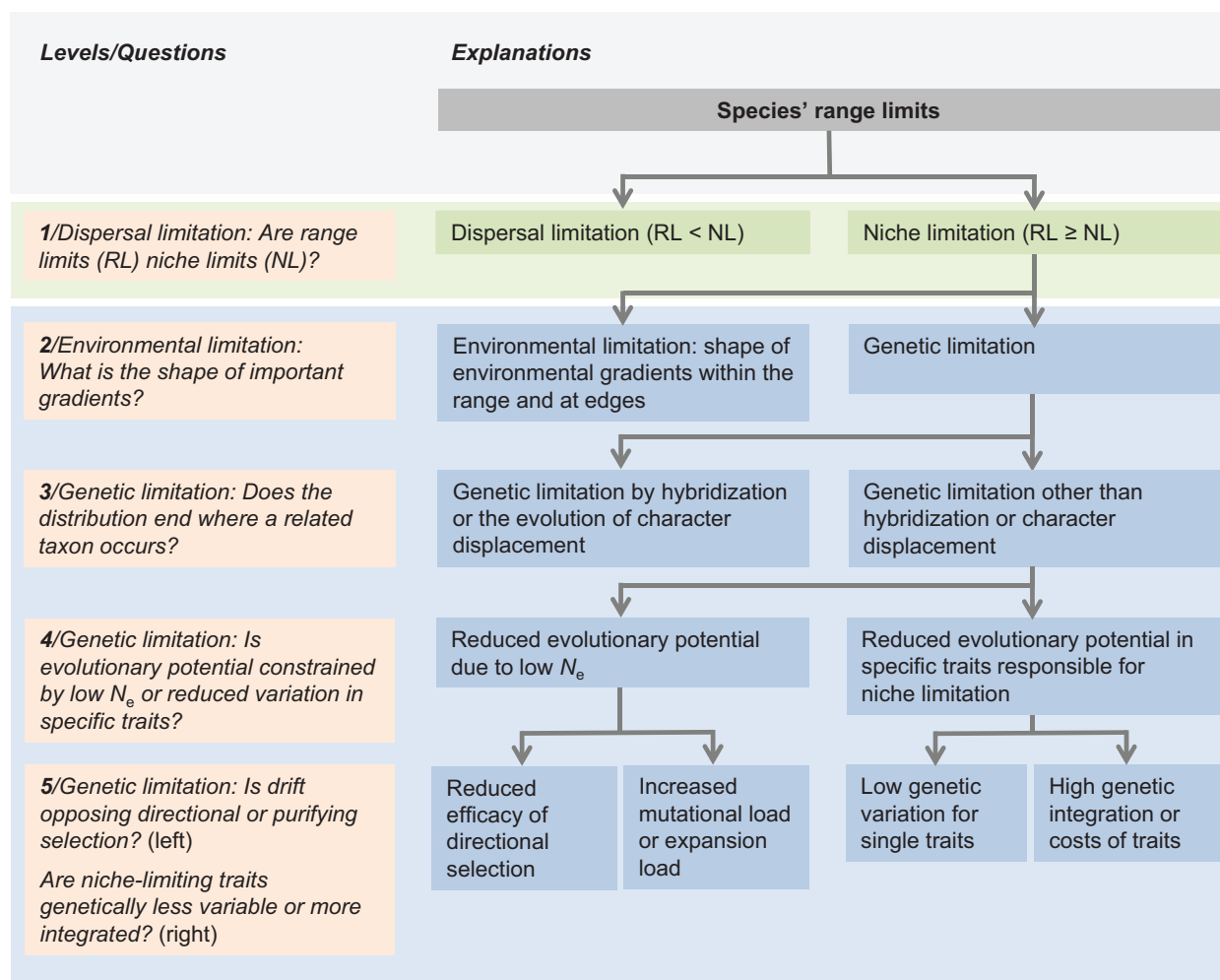


Figure 1: Flow chart guiding the analysis of causes for species' distribution limits. For each node (level), research questions (in reddish boxes) are suggested that help distinguish the importance of two (possibly nonexclusive) explanations for distribution limits (in green or blue boxes). Green coloration highlights questions and approaches that have traditionally fallen within ecology; blue coloration depicts questions and approaches within evolutionary biology.

the other four may be addressed in any sequence. Niche limits must be investigated at the outset because subsequent questions presuppose that the evolution of the niche is constrained. If the range limit is smaller than the species' realized niche limit, then the distribution is currently limited by dispersal, and detailed study of evolutionary constraints is not necessary.

Factors Affecting Distribution Limits: Dispersal Limitation

A prerequisite in any study of range limits is that the distribution of the species is well characterized (Sagarin et al. 2006). An initial step therefore consists of assembling occurrence records to create a distribution map over a predefined

study area. The area need not encompass the entire distribution of the species, but the extent of sampling must be appropriate for the questions under study. For example, separate maps for different portions of a distribution will be needed if the question involves comparing invasive and native ranges of introduced species (Atwater et al. 2018). Range compilation must also include screening for sampling biases and outliers (e.g., Rocchini et al. 2011).

To distinguish dispersal limitation from niche limitation, we test whether the organism could live in nearby regions outside the current distribution (fig. 1, level 1, in green). Dispersal limitation at the edge of a range is difficult to observe directly and is therefore studied by indirect means. The correlative method asks whether observed distribution limits coincide with the limits of environmental conditions toler-

ated by the organism (e.g., Chardon et al. 2015). Those tolerance limits are estimated using habitat suitability models (HSMs; sometimes known as species distribution models), which are algorithms that detect associations between field records of a species and environmental variables. Dispersal limitation is inferred to be unimportant if the multidimensional description of environmental tolerance emerging from the HSM matches closely the location of the geographic range. On the basis of this approach, Lee-Yaw et al. (2016) found that habitat suitability consistently declined from within- to beyond-range sites in 39 of 40 species, providing evidence that dispersal limitation is not very important. Cunningham et al. (2016) and Lee-Yaw et al. (2018) have devised explicit tests of whether range limits coincide with niche limits revealed by HSMs.

The set of environmental conditions predicted to be suitable by an HSM is often interpreted as an operational depiction of the realized niche (Guisan et al. 2017, pp. 21–40). Not everyone is comfortable with this interpretation. One issue is that the spatial resolution and dimensionality of an HSM may be inappropriate for the scale of the niche. Problems with resolution arise when environmental variables are available at a scale far different (usually greater) than that at which the organism experiences its environment. Problems with niche dimensionality can arise when the model is built on a limited set of variables, usually related to climate. But these problems can be surmounted by collecting fine-scale data, including variables that are likely to be important in the context of the organism's natural history and including data on other organisms that may interact with the focal species (Fournier et al. 2017; Mertes and Jetz 2018; Raath et al. 2018). A second issue is that the breadth of the niche may be overestimated for species with high dispersal ability that occur in “sink” habitats, where conditions are unsuitable for supporting population growth (Pulliam 2000). This problem can be overcome, with some effort, by combining the HSM with information on population growth rate or local density (Eckhart et al. 2011; Schliep et al. 2018).

In the end, the most difficult challenge of working with HSMs may be related to their correlative nature. Associations between occurrence and a set of convenient climate variables could reflect causative physiological processes, but they need not do so because climate may correlate with unknown biotic or abiotic transitions (e.g., Sanín and Anderson 2018). An alternative distribution modeling approach, called mechanistic niche modeling, has been developed in part to strengthen the link of causation (Huey et al. 2012; Kumar et al. 2014; Kearney et al. 2018). These models produce an estimate of the organism's fundamental niche using a substantial amount of data on physiology and behavior.

The second approach to detecting dispersal limitation is to experimentally transplant organisms into sites beyond the range edge to determine whether they can persist outside

their range (reviewed in Hargreaves et al. 2014). If population growth rate (λ) is <1 beyond the current edge, it is concluded that the distribution limit must be caused by environmental limitation rather than dispersal limitation. Thus, long-term transplant experiments that include sites within and beyond the range can show unambiguously that organisms are not dispersal limited, at least under the conditions prevailing during the experiment. Their disadvantage is that they are labor intensive and costly when performed at many sites and over many years. Hargreaves et al. (2014) discuss important considerations for designing transplant experiments, including adequate replication of study sites, capturing relevant environmental variables, sourcing organisms from across the range, and estimating lifetime performance along with its separate components. Transplants also run the risk of accidentally releasing organisms beyond their natural range or enabling gene flow between transplanted and local populations. Although rarely discussed, these outcomes are undesirable and should be avoided by implementing proper containment of individuals and propagules.

On balance, evidence from transplant experiments shows that geographic range limits are frequently caused by limits to niche evolution: in a meta-analysis, performance declined beyond the range in 86% of studies that considered lifetime fitness, and no self-sustaining transplants were detected beyond the current range in 25% of studies (Hargreaves et al. 2014).

Future Research Directions

Combining correlative models with transplant experiments can produce compelling evidence for or against dispersal limitation if the two methods concur, as suggested by Lee-Yaw et al. (2016). Alternatively, if a transplant experiment suggests that persistence beyond the range edge is feasible, habitat suitability modeling could help decide whether conditions at transplant sites were exceptional when the experiment was conducted. A strength of HSMs is that they are not sensitive to exceptional environmental conditions because they detect associations between distribution and the environment that have unfolded over many generations; in contrast, an experiment detects the effects of current conditions. Discordance between niche limits and range limits in an experiment could be explained if conditions at beyond-range sites were particularly benign relative to the longer term climate records used by the HSM. This sort of comparison necessitates carefully monitoring the environment during a transplant study.

Limitation by Steep Environmental Gradients

If no clear evidence for dispersal limitation is found for a particular edge of the distribution, the next question is: What

limits the evolution of the ecological niche? We know the organism could move beyond the current range in this region, but it fails to establish new populations. The range limit is then associated with a lack of adaptation to environmental conditions beyond the range. Constraints on adaptation may arise from selection itself, discussed in this section, or from the genetic composition of populations, discussed later (fig. 1, level 2). As explained below, what we call environmental limitation actually consists of three components: steepness of environmental change, dispersal, and change in demography toward the edge.

Environmental conditions encountered at the distribution edge may impose altered natural selection on range-edge populations, and the pattern of change in the environment determines how rapidly selection changes. How must the environment change such that the evolution of niche expansion is prevented? This question has been addressed in models of spatial environmental change and distribution limits in single species or interacting species. Other models predict range limits in the absence of evolutionary change (reviewed in Case et al. 2005); these are not discussed here because they do not address constraints on adaptation to conditions beyond the range limit.

Abiotic environmental gradients and single species. Spatially explicit quantitative genetics models of continuous distribution along linear gradients predict that the range boundary settles at a point where dispersal outward from the core prevents adaptation by forcing the population growth rate below zero. If the gradient (b ; change in trait optimum θ over space x : $\theta(x) = bx$) is steep relative to dispersal distance (σ , the average distance between the birthplaces of a female and her offspring), this point is close to the core and the distribution is small (Kirkpatrick and Barton 1997; Case and Taper 2000; García-Ramos and Huang 2013). In these models, random dispersal from the core is an important constraint on niche evolution. When dispersal is nonrandom and instead sensitive to variation in habitat quality, steep environmental gradients can still attract distribution edges, although the mechanism is different (Armsworth and Roughgarden 2005). Directed dispersal tends to move individuals toward the core and away from edge populations; this reduces the importance of swamping but also erodes population size at the edge and strongly restricts the occurrence of the species to the core area.

Another set of models assumes discrete high- and low-quality habitat patches connected by a demographic source-sink dynamic (reviewed in Kawecki 2008). If the low-quality patch is not self-sustaining and depends on migrants from the source, local adaptation in a quantitative character will fail when the environmental optima differ too much between the two patches (Holt et al. 2003). However, unlike models of linear environmental gradients, source-sink models point to conditions under which adaptation at range edges can be en-

hanced by dispersal. The main constraints on niche evolution in sink habitats are demographic (low survival or fecundity) and genetic (low variation). Higher migration from the source can promote adaptation by boosting population size and importing variation (Kawecki and Holt 2002; Holt et al. 2003). Of course, this outcome is much less likely if organisms can select habitats because few will actively choose to settle in a sink habitat (Armsworth and Roughgarden 2005).

Abiotic environmental gradients and biotic interactions. Models that consider competition among species agree that abrupt range limits can establish along continuous abiotic gradients even under shallow environmental change (Case and Taper 2000; Case et al. 2005). Interspecific competition within contact areas selects for ecological character displacement rather than adaptation to the gradient itself. This causes population density to decline, which in turn may enhance asymmetrical gene flow from the center and cause formation of a range edge. Distribution limits of competing species are especially likely to establish in regions at which the environmental gradient becomes suddenly steeper (Case and Taper 2000; García-Ramos and Huang 2013). Under predator-prey and host-parasite interactions, dispersal may play a more positive role in colonizing and promoting local adaptation within peripheral sink populations (Hochberg and van Baalen 1998; Holt et al. 2011).

Biotic interactions. Simple ecological models indicate that competitive interactions in the absence of an abiotic environmental gradient may create a checkerboard pattern of distribution but cannot account for geographic range limits (Araújo and Rozenfeld 2014). On the other hand, positive interactions, such as mutualism and commensalism, can affect occurrence at both local and geographic scales. Because Araújo and Rozenfeld's (2014) model did not include coevolution, it might be informative to develop a more general kind of model that can simultaneously accommodate evolutionary change, the extent and shape of an environmental gradient, and the type of interaction among species.

The empirical literature provides mostly indirect evidence on how conditions change at the edge of distributions. Environmental suitability sometimes degrades from center to margin (Sexton et al. 2009; Pironon et al. 2017). For example, Lira-Noriega and Manthey (2014) observed that distance to the climatic niche center increased with distance from the center of geographic distribution for 24 of 40 animal and plant taxa surveyed. Comparisons of demography between core and edge have produced inconsistent results (Sexton et al. 2009; Abeli et al. 2014; Pironon et al. 2017). But both habitat suitability and demographic performance decline just beyond range edges in transplant experiments on many species (Hargreaves et al. 2014; Lee-Yaw et al. 2016). These comparisons do not usually reveal the shape of environmental change from within to beyond the range and particularly

whether it steepens near the range boundary (but see Normand et al. 2009; Lee-Yaw et al. 2018). Indeed, this test is not even possible for most studies, which cannot identify which environmental factors limit the distribution (Louthan et al. 2015).

Future Research Directions

Although range limits may occur on shallow environmental gradients, theory suggests that gradients that are steep relative to dispersal or that become steeper are most likely to limit adaptation and cause range limits (e.g., Holt and Gaines 1992; Case and Taper 2000; Holt et al. 2003; García-Ramos and Huang 2013; Polechová and Barton 2015; Polechová 2018). This should motivate studies looking for regions of increasing steepness of change or breakpoints in environmental conditions that coincide with distribution edges. The relevant conditions may be identified with HSMs aimed at detecting environmental factors specifically associated with the edge of the distribution and therefore factors for which the rate of spatial change should reflect the rate of change in the optimum of an evolving trait. Lee-Yaw et al. (2018) determined that the variables predicting the distribution of a plant species in an HSM changed linearly or had multiple breakpoints along replicate transects crossing the range limit. Two key comparisons are, Does the change in limiting environmental variables at the distribution boundary exceed that of other variables that do not predict the species distribution? And does the change exceed that of the same variables along transects at random locations away from the range boundary? Similar studies are needed in many more species.

Future work should also describe the spatial distribution and quality of habitat relative to the dispersal capability of the organism. While characterizing the distribution of potential habitat may be a straightforward mapping exercise, assessing habitat quality requires data on spatial variation in demography or population growth rate, which may be deduced for parts of or entire species ranges by demographic distribution modeling (Merow et al. 2014). Complex environmental heterogeneity within the range is likely; this may be a nuisance in the context of testing theory, but it could help reveal limiting environmental variables and establish a link between habitat quality and demography. Finally, natal dispersal (σ) can be assessed by tracking individuals directly (e.g., Forsman et al. 2002; Rieux et al. 2014) or by estimating the decay of relatedness among densely sampled individuals using molecular markers (Vekemans and Hardy 2004).

Limitation by Hybridization

If there is no evidence of dispersal limitation or clear environmental limitation at the distribution boundary, then failure to adapt to conditions beyond the range edge may

be caused by a set of interrelated factors that we will call genetic limitation. One cause of genetic limitation is hybridization between closely related species in parapatric contact (fig. 1, level 3). The consequences may include hybrid breakdown and the evolution of ecological or reproductive character displacement, and this can create range limits even on shallow environmental gradients without any more direct evolutionary constraint to niche expansion (Goldberg and Lande 2006; reviewed in Case et al. 2005; Bridle and Vines 2007). It is unclear how often range limits are enforced by hybridization, but narrow parapatric hybrid zones are common in some taxa (e.g., Moore 1977; Highton 1995). The implication for empirical studies is that range limits should be inspected for close relatives with parapatric or partially overlapping patterns of occurrence along with indications of hybridization, ecological character displacement, or assortative mating.

Limitation by Low Effective Population Size and Associated Fitness Decline

Genetic limitation may also be caused by the neutral process of genetic drift affecting the entire genome in edge populations that are small over long periods of time or have experienced demographic bottlenecks, or by other genetic constraints specific to traits and genes important for adaptation (Hoffmann and Blows 1994; fig. 1, levels 4 and 5). This section describes genetic limitation due to neutral processes opposing selection (left side of level 5), while the next section focuses on genetic limitation in adaptive traits (right side of level 5).

Low N_e Near the Edge of the Range

Mechanisms causing low N_e . Adaptation at range limits is likely to be limited by population isolation and small effective population size (N_e). Two main mechanisms are hypothesized to be involved. First, the abundance of a species declines toward the range edge because habitat becomes less suitable (abundant-center hypothesis; Brown 1984). The population genetic extension of the abundant-center hypothesis predicts that declining density of individuals and populations at the range edge increases genetic drift and genetic isolation, which leads to declining genetic variation within local populations and increasing variation among populations (Eckert et al. 2008). A recent review of many taxa noted that 51% of studies measured a significant decline in the density of individuals within populations and 81% measured a decline in the density of populations from center toward the periphery (table 1 in Pironon et al. 2017). These values, far higher than expected by chance, support the abundant-center hypothesis but also suggest that the biogeographic pattern is not universal. Data in Pironon et al. (2017) also support the

population genetic extension of the abundant-center hypothesis, especially when studies include populations at the very edge of the distribution.

The second mechanism causing reduced N_e at range edges is related to the geographic pattern of demographic history. Many species were forced by Quaternary glaciation into refugia, out of which they periodically expanded during interglacial periods; this strongly influences the current geographic distribution of genetic diversity (Hewitt 2000). Highest genetic diversity is often found in areas of previous refugia, which may not fall in the center of the current distribution (Hewitt 1996). Several studies have noted that the history of colonization more accurately predicts the decline in genetic variation away from distribution cores than does current habitat suitability (Duncan et al. 2015; Pironon et al. 2015). These results suggest that studies of distribution limits would benefit from a firm understanding of the history of the geographic range, at least over the time horizon required for alleviating the worst consequences of genetic drift (several thousand generations; Peischl et al. 2013).

Low N_e Favors Drift over Selection

Genetic drift opposing directional (positive) selection. An important evolutionary implication of small population size is genetic drift opposing selection. In the theory of range dynamics, this is particularly clear in Polechová and Barton (2015), who discovered that a key parameter affecting distribution in a one-dimensional continuous habitat with an environmental gradient reflects the relative magnitudes of drift and directional selection. In small populations with strong drift, the range edge may be stable or contract toward the core, or the entire range may become fragmented. In contrast, the range is predicted to expand when selection is strong relative to drift. The prediction that selection at the edge is so weak as to be overcome by drift may seem unlikely, but this could be tested by checking for a reduced signature of positive selection within coding genomic regions in populations close to the range edge.

Genetic drift opposing purifying (negative) selection—mutational load. A similar evolutionary implication of low N_e is mutational or drift load, an increase in frequency of deleterious mutations due to genetic drift and less effective purifying selection (box 1; Kimura et al. 1963; Whitlock et al. 2000). Theory suggests that mutational load can contribute importantly to range limits in established ranges. Henry et al. (2015) considered a fully occupied, one-dimensional array of habitat patches along a linear gradient of carrying capacity. When new mutations were deleterious, mutational load sharply curtailed the range, especially when dispersal was limited and population growth rate low. Because of the assumption that the entire range is initially occupied, this model may best apply to stable ranges or rear edges of dynamic distributions.

Mutational load can also increase in nonequilibrium situations, such as during population expansion and bottlenecks (Kirkpatrick and Jarne 2000). Load becomes especially severe over a series of bottlenecks along a geographic expansion route (so-called expansion load; Peischl et al. 2013, 2015; Peischl and Excoffier 2015). In this case, load accumulates due to “surfing” (serial bottlenecks and random increase) of deleterious alleles on expanding wave fronts (Klopfstein et al. 2006; Excoffier and Ray 2008). Under a stepping-stone model, mutational load can moderate the rate of spatial expansion, at some point changing the dynamic from increasing to stable (Peischl et al. 2015). However, the presence of an environmental gradient along the expansion route may reduce the expansion load because the speed of expansion is reduced by increased maladaptation (Gilbert et al. 2017). Taken together, these models predict that mutational load can restrict the range under conditions of range expansion by lowering population growth rate even in the absence of an environmental gradient.

Some of these predictions have been tested by comparing mutational load across geographic ranges. Comparative studies of human populations infer that deleterious mutations within coding DNA regions have accumulated during the range expansion from Africa to Eurasia and the Americas (Lohmueller et al. 2008; Simons et al. 2014; Henn et al. 2016). Heightened genomic estimates of load at both leading and rear edges of the distribution have also been reported in plants (Zhang et al. 2016; González-Martínez et al. 2017; Willi et al. 2018). An alternative approach is to measure heterosis experimentally in natural populations (e.g., van Treuren et al. 1993). In these experiments, individuals are typically crossed with other individuals from the same and different populations, and the difference in fitness between the two cross types estimates heterosis. Offspring of the between-population crosses express higher fitness because their recessive deleterious mutations occur in the heterozygous state (Lynch 1991). These two kinds of estimates of load—genomic and phenotypic—were highly correlated in one recent study (Willi et al. 2018).

Future Research Directions

More information is needed on the role of genetic drift opposing selection in the context of range limits; there are few empirical studies of species other than humans. One should begin by describing the history of the species' range because genetic variation often declines more strongly with past colonization than it does with distance from the geographic core (Duncan et al. 2015; Pironon et al. 2015). This requires a rooted population phylogeny, which can be inferred using sequence or single-nucleotide polymorphism (SNP) data from a representative sample of populations along with at least one closely related species (reviewed in McCormack et al. 2013;

Pickrell and Pritchard 2012). Similar data can be used to estimate the effective population size, N_e , and therefore the magnitude of drift across the distribution of a species. When gene flow is relatively rare, genomic diversity estimates should reflect local N_e . Together with environmental data, genomic estimates of N_e and population history can provide insight into the role of history versus recent environmental conditions in determining N_e (as done by hindcasting distributions in Duncan et al. 2015; Pironon et al. 2015).

Genome-wide signatures of directional and purifying selection come from various statistics estimated with (usually) sequence data from coding regions. In nonmodel organisms, the best option is exome sequencing with some depth; this enables complete de novo assembly, gene prediction, generating SNP data sets, and dividing SNPs into synonymous and nonsynonymous categories (e.g., Blande et al. 2017). The genome-wide signature of recent positive selection may be best evaluated—gene by gene or window by window—by using tests that combine pairs of statistics that cancel each other's sensitivity to (demographic) noise (Zeng et al. 2006). Estimates of mutational load commonly quantify the number of polymorphic and presumably deleterious SNPs weighted by their derived frequency relative to an out-group and scaled to background diversity in SNPs with presumably no effect (Lohmueller et al. 2008). The simplest distinction is between nonsynonymous and synonymous SNPs, but several algorithms predict likely mutational effects of nonsynonymous SNPs based on either the type of amino acid change (Cingolani et al. 2012) or site conservation in homologous sequences in large protein databases (Vaser et al. 2016). Finally, estimates of positive selection and mutational load can be related to the population's range position, the history of range expansion, and habitat suitability.

Phenotypic estimates of mutational load from crossing experiments have not been used to compare range edge with central populations. If the within- and between-population-crossed offspring are reared in a common garden, they reveal the demographic implications of load. The detrimental impact of load may include not only a decline in demographic performance but also an increase in demographic stochasticity (Melbourne and Hastings 2008; Willi and Hoffmann 2009). Moreover, rearing offspring from a crossing experiment in multiple gardens or field sites across the distribution could reveal environmental impacts on the expression of load. As has been shown for inbreeding depression (Armbruster and Reed 2005), the fitness consequences of mutational load may be enhanced under stressful conditions, and this could be especially relevant at the edges of distributions.

Limitation by Low Genetic Variation

The fifth general cause of distribution limits is a genetic constraint specific to traits and genes important for adaptation

within edge habitats (fig. 1, levels 4 and 5, right side). This kind of constraint comes in two forms: low genetic variation for key traits determining distribution, and developmental and functional integration of distribution-determining traits, reflected as genetic correlations.

Low genetic variation of single traits. Genetic variation can vary across a distribution for several reasons. First, N_e may vary geographically, and this affects the expected equilibrium level of quantitative genetic variation (Willi et al. 2006). If populations at range edges have lower N_e , then they should contain reduced (quantitative) genetic variation simply due to drift (Wright 1931; Kimura 1955). In Polechová's (2018) model of range dynamics in two dimensions and an environmental gradient, erosion of genetic variation due to low N_e and isolation from dispersal can cause distribution limits. Second, the strength of natural selection may vary geographically, and for a variety of reasons genetic variation is predicted to decline where selection is strong (Crow and Kimura 1970; Bulmer 1971; Robertson and Hill 1983). Populations experiencing strong selection are especially likely to occur at the distribution margin if the environment changes steeply there or if gene flow from more central populations prevents trait values from reaching the local optimum. In spite of these theoretical expectations, however, there is little empirical evidence that quantitative genetic variation declines in small populations in general or at range boundaries in particular (Willi et al. 2006; van Heerwaarden et al. 2009; Gould et al. 2014; but see Pujol and Pannell 2008).

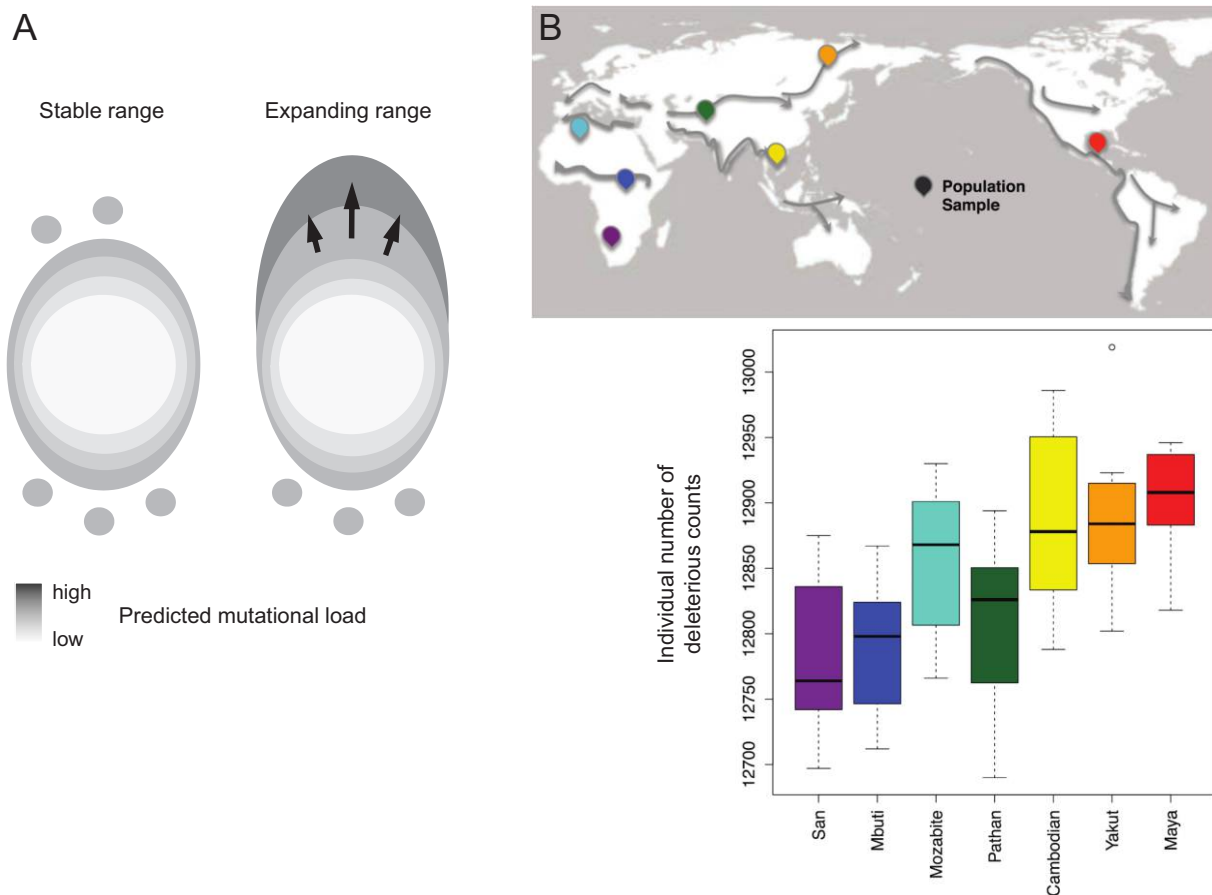
High genetic integration. Even if genetic variation is not directly limiting, adaptation at the margin of a species' distribution could still face constraints arising from genetic correlations caused by developmental and functional integration. A genetic constraint can arise if there is a strong genetic correlation and the direction of selection is antagonistic to the correlation (Antonovics 1976; Lande 1979; Arnold 1992; Schluter 1996; Blows 2007; Walsh and Blows 2009). The potential for constraint is evaluated by quantifying the availability of genetic variance—summarized by the genetic variance-covariance matrix (**G**-matrix)—along the dimensions on which selection is acting. In the context of range limits, the traits that comprise the **G**-matrix must be relevant for adaptation to environmental conditions at the boundary, along with fitness-related trade-offs and costs associated with those traits.

Few studies have estimated **G**-matrices for a realistic number of traits in populations representing edge and central parts of a geographic distribution (Calsbeek et al. 2011; Paccard et al. 2016). Paccard et al. (2016) suggested that genetic drift at range edges can modify genetic integration, which in turn influences evolutionary potential in unexpected ways. Paccard and colleagues estimated **G**-matrices involving 10 ecologically relevant traits in populations from the northern edge, central, and southern edge of the distribution of the

Box 1: Mutational load

Populations at the edge of stable ranges or rear edges are often isolated and small (Hampe and Petit 2005). Small population size is predicted to cause increased frequency and eventual fixation of small-effect deleterious mutations as genetic drift overwhelms purifying selection (Kimura et al. 1963). Increasing frequency of deleterious mutations erodes mean fitness and feeds back to further reduce population size, which accentuates the process of mutation accumulation, finally leading to mutational meltdown and population extinction (Lynch et al. 1995). Mutational load is also predicted to increase during range expansions (“expansion load”; Peischl and Excoffier 2015), after which it can persist for thousands of generations. This time horizon approaches that of major climate oscillations, which implies that expansion load could be relevant for many apparently stable range limits. Hence, edge populations are predicted to bear enhanced mutational load under all scenarios of distribution dynamics: stable, moving, and expanding (box fig. 1A). This may be an important and largely overlooked cause of distribution limits.

One well-studied example is human populations expanding out of Africa. The Human Genetic Diversity Project data revealed that gene diversity declines with distance from central Africa to Eurasia and the Americas (box fig. 1B; Lawson Handley et al. 2007). In parallel, the signature of mutational load increases from Africa along the expansion route. Henn et al. (2016) found that individuals from populations farther from Africa had higher numbers and frequencies of single-nucleotide polymorphisms within conserved, hardly variable coding regions. This reflects mutational load, or expansion load, because these variants are likely to be deleterious.



Box Figure 1: A, Mutational load increasing from the (historic) center of the distribution to the edge, under both stable and expanding range dynamics. B, Expansion route of humans out of Africa (*top*), accompanied by increasing mutational load (*bottom*). Reprint from Henn et al. (2012, 2016), with permission from the publisher.

plant *Arabidopsis lyrata*. Although total genetic variance was reduced in edge populations, there were also weaker genetic correlations at the edge and consequently no reduction in the potential to respond to selection. This may turn out to be a common pattern because genetic integration created by correlational selection is predicted to become weaker under genetic drift in small populations (Jones et al. 2003).

Future Research Directions

A most important step for understanding genetic limits is to identify traits exposed to selection under marginal edge conditions and other traits linked to them by trade-offs (Antonovics 1976; Hoffmann and Blows 1994). Much more progress is needed here. One approach is to use habitat suitability modeling to discover environmental factors that limit distribution (Lee-Yaw et al. 2018). Next, these factors may suggest what traits are important, such as cold tolerance at a range boundary enforced by cold temperatures or foraging effort that allows fast growth during a shorter growing season. A second method comes from associations between niche-determining environmental variables across the species distribution and genetic variation at a large number of SNPs (reviewed in Bragg et al. 2015; Hoban et al. 2016). Alternatively, genome-wide expression differences among organisms reared in a common garden have been linked with their site of origin across species distributions (e.g., Porcelli et al. 2016). These approaches can return lists of enriched gene ontology terms or candidate genes that correlate closely with the environment. A difficulty is that such lists are usually long, and the connection between enriched gene ontology terms and measurable traits may remain elusive. Third, candidate traits can be phenotypically assessed in common-garden experiments or transplants across a species range. Traits measured in a common environment that covary with conditions at the source locality or position away from the core will confirm or further refine the candidate traits involved in constraining niche evolution (e.g., De Frenne et al. 2013). Ideally, a combination of methodologies should help identify traits under selection at the edges of distribution.

Once relevant traits have been identified, the **G**-matrix can be estimated for populations of individuals having known relatedness structure (based on markers, a pedigree, or a crossing design) by experimentally rearing them under near-natural conditions or tracking them in natural populations (Paccard et al. 2016; Delahaie et al. 2017). This must be repeated in core and edge populations. Selection can be estimated from the covariance between phenotype and fitness, preferably at the level of the genotype rather than individual (Rausher 1992; Wilson et al. 2009). Ideally, this would be accomplished at and beyond the edge, probably using experimental or translocated populations. The predicted re-

sponse to selection is obtained by postmultiplication of the **G**-matrix by the vector of linear selection gradients, and constraint is evaluated by comparing selection with the predicted response (Walsh and Blows 2009). One study that comes close to making this comparison is Charmantier et al. (2016); most of the quantities required to estimate genetic constraint have been measured in mainland and island (range-edge) populations of a bird.

Integrating Approaches

The study of species distribution limits will benefit from a combination of three approaches: ecological modeling, population genomics, and quantitative genetics of niche-determining traits (fig. 2). Habitat suitability modeling provides insight into environmental (as opposed to dispersal) limitation, identifies key niche factors and their pattern of change at the distribution limit, and narrows the list of candidate traits limiting the distribution. Population genomic analyses can reveal the phylogeographic history, effective population sizes, isolation, dispersal distances, genome-wide signatures of positive selection, and magnitude of mutational load. Associating genomic variants with environmental gradients or specific environmental factors may, with some luck, highlight aspects of the phenotype involved in niche adaptation. Third, common-garden experiments on central and peripheral populations can estimate the impact of mutational load on declines in performance and vital rates, characterize trait differences across distributions, and reveal the genetic architecture of critical traits. Transplant experiments can reveal the degree of local adaptation of edge populations, constraints on the selection response created by quantitative genetic architecture, and—when beyond-edge sites are included—dispersal limitation.

Once the relevant evolutionary and demographic parameters are known for at least some parts of a species' range limit, eco-evolutionary modeling can help assess the contributions of multiple processes to maintaining range limits. Gradient range models, such as those of Kirkpatrick and Barton (1997), Polechová and Barton (2015), and Polechová (2018), are probably too abstract for this task. These models are strong in illuminating the causes of range limits but too simplistic for integrating data gathered in the steps outlined in figure 1. Cotto et al. (2017) described a model that could be applied to the problem of distribution limits. They combined spatial information on three niche parameters with individual-based stochastic simulations, accounting for species-specific demographic parameters, evolutionary processes, and feedback reactions. The model tracked the dynamics of three hypothetical traits underlying adaptation to each niche parameter and predicted geographic distribution changes under climate change. The relatively fine geographic scale of this model enabled Cotto et al. (2017) to pre-

Methods	Questions to be answered by the method	Questions to be answered by combining methods
1 Habitat suitability modeling <ul style="list-style-type: none"> - Spatial distribution of habitat suitability - Critical niche parameters - Spatial distribution of niche parameters 	1 Are distributions limited by dispersal? What are the important niche parameters? What is the shape of spatial change in niche parameters and habitat suitability at the range edge?	1, 2 Why do populations at edges have reduced N_e ? – habitat suitability and abundance versus history Association between niche parameters and genetic polymorphisms, and subsequent gene ontology or pathway analysis: What are the likely traits of adaptation? 2, 3 Is stress tolerance involved in trade-offs at the genomic level? 1, 2, 3 Relative importance of all factors in an eco-evo modeling framework?
2 Molecular analysis/Sequencing <ul style="list-style-type: none"> - Estimating the dispersal kernel - Population genetics - Population history - GWAS linking variants with niche - Gene ontology/pathway analysis 	2 What are dispersal distances? Do populations at edge have reduced N_e ? Are they more isolated? What is the history of range edges? Are signatures of directional selection weaker and of mutational load higher in range-edge populations?	
3 Demographic and phenotypic trait analysis <ul style="list-style-type: none"> - Transplant experiments, including beyond-edge sites - Demography in relation to environmental parameters - Fitness comparison of crosses in common garden; heterosis - Clinal patterns of trait variation in common garden - G-matrix analysis - Analysis of trade-offs and costs 	3 Are species dispersal limited? What are the important niche parameters? What is the shape of spatial change in demographic parameters at the range edge? Is local adaptation weaker in range-edge populations? Is mutational load higher in range-edge populations? Which traits show clinal variation? Do they trade off with vital rates? How much genetic variation exists? Are traits tightly integrated? Is tolerance of environmental stress involved in trade-offs?	

Figure 2: Research questions that can be answered by one or a combination of three types of analysis: habitat suitability modeling (1), molecular genetic analysis (2), and phenotypic trait analysis (3).

dict details such as the spatial distribution of local population sizes, source-sink characteristics of raster cells, and the role of adaptation and maladaptation in explaining distribution and the demographic composition of local populations. Analogous simulations could be used to integrate factors outlined in figure 1 and explore their relative importance for determining the limits of geographic ranges.

In recent decades, progress in the study of range limits has come from integrating evolutionary with ecological dynamics and adopting a more inclusive perspective on the limits to adaptation. Theory synthesizing ecology and evolution has suggested new empirical approaches by posing predictions that connect genetic mechanisms with demography and history, and this in turn has expanded the range of mechanisms that must be tested empirically. The basic questions about the causes of distribution limits may not have changed much, but the empirical work must be broadened and made more integrative to include connections between spatial variation in the environment and demography, selection, demographic

history and genetic drift, and the genetic architecture of traits constraining niche evolution. As described in the introduction, we envision the development of a taxonomy of factors limiting geographic ranges under various circumstances. Such an account will inform long-standing discussions about limits to adaptation and may be useful for a variety of practical matters, such as assisting gene flow, managing population sizes, and anticipating adaptation of stress resistance under environmental change.

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