Evolution and Ecology of Species Range Limits

Jason P. Sexton,[1] Patrick J. McIntyre,[2] Amy L. Angert,[3] and Kevin J. Rice[1]

[1] Department of Plant Sciences, University of California, Davis, California 95616;
email: jpsexton@ucdavis.edu, kjrice@ucdavis.edu

[2] Department of Evolution and Ecology, University of California, Davis, California 95616;
email: pjmcintyre@ucdavis.edu

[3] Department of Biology and Graduate Degree Program in Ecology, Colorado State University,
Fort Collins, Colorado 80523; email: angert@mail.colostate.edu

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Abstract

Species range limits involve many aspects of evolution and ecology, from species distribution and abundance to the evolution of niches. Theory suggests myriad processes by which range limits arise, including competitive exclusion, Allee effects, and gene swamping; however, most models remain empirically untested. Range limits are correlated with a number of abiotic and biotic factors, but further experimentation is needed to understand underlying mechanisms. Range edges are characterized by increased genetic isolation, genetic differentiation, and variability in individual and population performance, but evidence for decreased abundance and fitness is lacking. Evolution of range limits is understudied in natural systems; in particular, the role of gene flow in shaping range limits is unknown. Biological invasions and rapid distribution shifts caused by climate change represent large-scale experiments on the underlying dynamics of range limits. A better fusion of experimentation and theory will advance our understanding of the causes of range limits.

INTRODUCTION

Species range limits are essentially the expression of a species' ecological niche in space. The challenge is to identify the environments within which births are greater than deaths, how those environments are distributed across the landscape, and how they are connected by dispersal. This requires understanding how spatial variation in fitness results from the fit between phenotype and environment and how differences in fitness translate into population-level differences in abundance. Focusing on fitness variation helps to link ecological limitations and evolutionary processes. A central goal in evolutionary biology is understanding conditions that facilitate adaptive diversification versus those that promote niche conservatism. Adaptation to novel habitats at the range margin is akin to niche evolution (see Holt & Gomulkiewicz 1997 for a classic introduction to this issue). Thus, range limits can serve as testing grounds to understand the conditions by which populations can adapt—or fail to adapt—to novel conditions.

A long-standing interest in the ecology of range limits is reflected in seminal works (e.g., Darwin 1859, MacArthur 1972). The study of geographic ranges has enjoyed a recent resurgence, spurred by the need to accurately forecast responses to large-scale, anthropogenic alterations to climate and habitat. This renewed interest has been facilitated by the development of extensive online databases compiling species' occurrences and environmental variables. However, many questions remain about the ecological and evolutionary processes that give rise to range limits.

Here we review the major hypothesized causes of range limits and the empirical approaches used to test them. We discuss the theory of range limits and review the predictions and hypotheses generated by theory for natural systems. We end by highlighting important frontiers in range limits research, including biological invasions and climate change responses.

NATURE OF SPECIES RANGE LIMITS

Species ranges are highly mobile, often shifting, expanding, and contracting over time (Brown et al. 1996, Davis & Shaw 2001, Gaston 2003). Range mobility could reflect gradual niche evolution over time or spatial tracking of the environmental niche in response to changing environmental conditions (Pfenninger et al. 2007). Some studies suggest that spatial tracking of the niche is more common (Davis & Shaw 2001, Pease et al. 1989), although range shifts can lag behind environmental changes (Svenning et al. 2008).

Range boundary disequilibria with environmental niches is often attributed to dispersal limitation, where populations cannot expand as quickly as the environment becomes favorable (e.g., recolonizing formerly glaciated areas; Fang & Lechowicz 2006). Species differ markedly in their extent of climatic disequilibrium; this may reflect differences in dispersal (Tinner & Lotter 2006), life history (Araujo & Pearson 2005), recolonization history (Stewart & Lister 2001), or stochasticity (Clark 1998). Although there are clear examples of range disequilibrium, it is certainly not the rule. Range equilibrium is suggested by transplant experiments beyond species' current range boundaries; many species have low fitness and exhibit negative population growth in areas beyond present distribution limits (e.g., Angert & Schemske 2005, Geber & Eckhart 2005, Griffith & Watson 2006, but see Carter & Prince 1985, Van der Veken et al. 2007).

Despite centuries of interest in range limits, little is known about basic differences in the evolutionary ecology of edge and central populations. Such differences could have important effects on range limit dynamics and could arise by several mechanisms. First, edge populations may exhibit reductions in the diversity and number of immigrants by virtue of spatial arrangement alone, resulting in an isolation-by-distance effect. At range edges spanning ecological gradients, gene flow from different selection regimes may be limited to nearby populations from just inside, or at, the
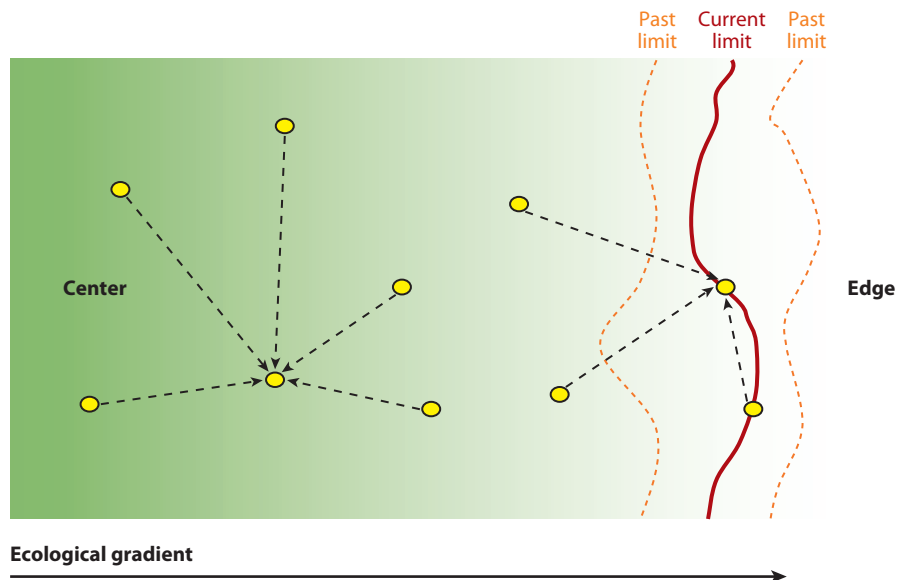
Figure 1

Potential differences between central and marginal populations. Populations are shown equally distributed among selection regimes produced by an ecologically important gradient (e.g., temperature, precipitation, competitor density, or symbiont density) across the species range. Example populations from central and edge areas are shown with potential sources of gene flow (*arrows*) and illustrate how gene flow to edge populations can be limited by the number and diversity (that is, from fewer selection regimes) of source populations. Central populations are more likely to receive immigrants from opposite ends of their selection gradient, whereas edge populations are more likely to receive immigrants from only one end. The spatial position of the range limit may vary through time, caused by increased temporal variance in critical habitat quality near the range limit.

species range limit (**Figure 1**). Such an effect could alter the distribution of variation within and among populations (Eckert et al. 2008). Second, the mode of selection may differ between edge and central areas (Bridle & Vines 2006, Hoffmann & Blows 1994). If ecological stress gradients create range limits, then directional selection may dominate at edges, whereas stabilizing selection may be more common in central populations. Third, assuming range boundaries are near equilibrium, edge populations may experience greater variability in survival and reproduction because they more frequently experience strong, limiting factors. Habitats with variable environments that exceed individual tolerances might select for developmental switches, producing a mixture of phenotypes (that is, increased adaptive plasticity) (Levins 1968). Selection for increased dispersal is also expected in such environments (Darling et al. 2008). In the following sections, we explore these and other concepts as we review theoretical and empirical literature on ecological and evolutionary mechanisms underlying the dynamics of range limits.

THEORETICAL MODELS OF RANGE LIMITS

Theoretical investigations have revealed a number of ways to generate stable or transient range limits (see reviews by Bridle & Vines 2006, Case et al. 2005, Holt et al. 2005b). These models have their origins in early work on spatial dynamics such as reaction-diffusion equations (Fisher 1937, Skellam 1951) and spatially implicit epidemiological/metapopulation models (Kermack & McKendrick 1927). We divide models on range limits into three groups: (*a*) models without

Adaptive plasticity: beneficial adjustments in the phenotype to different conditions

Reaction-diffusion model: models the abundance of a population in space as a result of diffusion and a function of local population dynamics

environmental heterogeneity or evolution, (*b*) models with environmental heterogeneity but without evolution, and (*c*) models with both environmental heterogeneity and evolution. After a brief discussion of the first two, we more extensively analyze the third class of models that address the failure of species to adapt to conditions beyond range edges. We discuss how empirical studies can test these models and inform future ones. A summary of models directly addressing range limits is presented in **Table 1**; additional models relevant to specific aspects of range limits are discussed in the text.

Priority effect:
occurs when initial colonizer to a site gains a demographic advantage and excludes subsequent colonists by monopolizing limiting resources

Models without Environmental Heterogeneity: Allee Effects and Ecological Interactions

At least two classes of models can generate range limits without environmental gradients (Holt et al. 2005a). Incorporation of Allee effects into a reaction-diffusion model (Lewis & Kareiva 1993) can yield an unstable range limit if expansion via dispersal is precisely balanced by an inability for a population to grow when small. Keitt et al. (2001) explore how discrete space analogs to these diffusion models can result in Allee effects producing stable range limits when the spatial pattern of occupied patches limits expansion into new areas. Multispecies interactions can also produce range limits without environmental variation (Case et al. 2005). For example, priority effects among competitors dispersing within a homogenous environment can lead to stable ranges if species cannot invade areas previously colonized by a competitor (Levin 1974, Yodzis 1978). Similarly, reproductive interference between species may also cause parapatric range limits if low hybrid fitness prevents invasion of one species into the range of another (Case et al. 2005, Goldberg & Lande 2006).

Models with Environmental Heterogeneity but No Evolution

Single- or multispecies spatial models with deterministic environmental gradients or stochastic environmental heterogeneity produce range limits (Hochberg & Ives 1999, Pulliam 2000, Roughgarden 1979). Although these models do not address the failure of a species to adapt to conditions beyond the range, they do address proximate causes and patterns of range limits. In single-species models with environmental gradients, range limits correspond to fundamental niche limitation; population growth is negative at some point along the gradient. For multispecies models, patterns of occurrence may reflect an altered realized niche. Range limits in these nonevolutionary models can also reflect dispersal disequilbrium. Heterogeneity in dispersal or habitat suitability (e.g., dispersal barriers) can limit range expansion and produce semistable, nonequilibrium ranges (Holt et al. 2005b, Shigesada et al. 1986). These models may also produce complex patterns of abundance across the range. For example Hastings et al. (1997) found in a model combining diffusion and predator-prey dynamics that prey densities could be highest at the edge of the range. Holt & Barfield (2009) found that incorporating predation into models of competition along gradients could increase the geographic range of prey species. In metapopulation models, shallow gradients of extinction and colonization may result in sharp range limits, with suitable patches existing beyond the range border (Carter & Prince 1981, Holt & Keitt 2000). These unexpected patterns resulting from interactions between dispersal and environmental heterogeneity suggest that it may be challenging to identify underlying gradients contributing to range limits.

Adaptation at Range Limits: Models that Incorporate Environmental Heterogeneity and Evolution

Given sufficient genetic variation to respond to selection, edge populations may adapt to environments beyond those within the range (reviewed in Kawecki 2008; see Antonovics 1976 for a classic

Table 1 Summary of major theoretical models addressing geographic range limits, with key findings

MODELS OF RANGE LIMITS[a]		
No evolution and without underlying environmental heterogeneity		
Framework	**Key findings**	**References**
Random dispersal (diffusion) with an Allee effect	Negative growth at low density can prevent a population from dispersing beyond its current range	Keitt et al. 2001, Lewis & Kareiva 1993
Spatially explicit competition	Parapatric ranges form owing to competitive exclusion (e.g., colonization patterns maintained by priority effects)	Case et al. 2005, Fowler & Levin 1984, Yodzis 1978
Random dispersal of hybridizing species	Parapatric ranges form owing to reduced hybrid fitness limiting population expansion	Case et al. 2005, Goldberg & Lande 2006
No evolution and with environmental heterogeneity		
Framework	**Key findings**	**References**
Demographic parameters vary along gradients (single- or multispecies models)	Limits to population growth along an environmental gradient result in a range limit. Corresponds to fundamental (single species) or realized niche limitation (multispecies)	Case et al. 2005, Hochberg & Ives 1999, Holt & Barfield 2009, Pulliam 2000, Roughgarden 1979
Environmental gradients in metapopulation models	Variation in colonization and extinction along gradients can result in range limits. Sharp range limits are possible even over shallow gradients owing to patch extinction-colonization dynamics	Carter & Prince 1981, Case et al. 2005, Holt & Keitt 2000, Lennon et al. 1997
Temporal or spatial heterogeneity in dispersal	Range limits result from environmentally determined patterns of dispersal (ocean or air currents)	Gaylord & Gaines 2000
	Spatial or temporal variation in dispersal can stall population expansion and create temporary range limits	Holt et al. 2005b, Shigesada et al. 1986
	Dispersal barriers can "attract" parapatric range limits owing to competition or hybridization over otherwise homogenous space	Goldberg & Lande 2007
With evolution and environmental heterogeneity		
Framework	**Key findings**	**References**
Gene flow (dispersal), selection, and adaptation along an environmental gradient	Gene flow from large, well-adapted populations may prevent adaptation in marginal populations. Depends on the rate of adaptation (genetic variance, selection) and steepness of the gradient. Assumes constant genetic variance	Kirkpatrick & Barton 1997
	Range limits are harder to achieve if genetic variation is not constant, because migration can increase variation in peripheral populations and facilitate adaptation	Alleaume-Benharira et al. 2006, Barton 2001
	Incorporation of competitive interactions among species makes range limits easier to achieve, as presence of a better-adapted competitor along a gradient can reduce peripheral populations and increase asymmetry in gene flow	Case & Taper 2000
	Dispersal barriers limit gene flow and allow for local adaptation and spread. If gene flow is restricting a species range, species borders should not be associated with dispersal barriers	Goldberg & Lande 2007
	The strength and form of density-dependent population regulation can influence the likelihood that a species adapts to peripheral populations by influencing demographic asymmetries in peripheral and central populations	Barton 2001, Filin et al. 2008
Selection and gene flow in a source sink scenario	Gene flow can provide a demographic and genetic "rescue effect" in sink populations, facilitating adaptation. Niche expansion may proceed in a punctuated fashion	Holt 2003, Holt & Gomulkiewicz 1997, Gomulkiewicz et al. 1999

(Continued)

Table 1 (*Continued*)

MODELS OF RANGE LIMITS[a]		
With evolution and environmental heterogeneity		
Framework	**Key findings**	**References**
Selection and gene flow with two habitat types	Gene flow dynamically linked to selection and adaptation to different types of habitat can influence the evolution of specialist or generalist strategies or result in global extinction	Filin et al. 2008, Holt & Gaines 1992, Ronce & Kirkpatrick 2001
Selection and resource competition without gene flow	Competition for resources of varying distribution (e.g., biomodal) can result in stabilizing selection for resource use, producing stable range limits	Price & Kirkpatrick 2009

[a]Models are described in terms of conceptual frameworks, as key findings can cut across specific theoretical approaches (e.g., continuous and discrete space). Models are also grouped according to whether they include evolution and environmental heterogeneity. Citations are representative and not exhaustive.

introduction to selection at range limits). Two approaches have been used recently to address evolutionary dynamics in the formation of species ranges: (*a*) reaction-diffusion frameworks with continuous environmental gradients, and (*b*) models of adaptation to a series of habitat patches (usually two) of discretely varying quality or optima.

Kirkpatrick & Barton (1997) incorporated evolutionary dynamics into a reaction-diffusion model to address the role of selection and gene flow in forming range limits along an environmental gradient. Their single-species model examined the evolution of a quantitative trait along a continuous environmental gradient. Demographics along the gradient were linked to selection differentials by how well the trait distribution of a population matched an optimum value along the gradient. If environmental gradients are steep enough, migration from populations adapted to the center of the gradient can prevent local adaptation in peripheral populations, resulting in a stable range limit. Subsequent studies found that the model is sensitive to the assumption of constant genetic variation (Alleaume-Benharira et al. 2006, Barton 2001). When this assumption is relaxed, local adaptation and migration can inflate genetic variation, facilitating adaptation in peripheral populations. Other extensions of this model found that multispecies interactions such as competition can increase the parameter space predicting stable ranges (Case & Taper 2000, Case et al. 2005), that hybridization can increase the likelihood of parapatric range formation (Goldberg & Lande 2006), and that incorporation of more complex population dynamics can lead to nonequilibrium range limits (Filin et al. 2008).

Some models treat the evolution of range limits as adaptation to a series of discrete habitat patches varying in quality (e.g., Holt & Gomulkiewicz 1997, Ronce & Kirkpatrick 2001). Rather than producing range limits in continuous space, these models examine how adaptation to a habitat is facilitated or inhibited by processes such as gene flow, selection, and population regulation. If patches represent sources and sinks, adaptation to the sink environment corresponds to expansion of the ecological niche and, thus, expansion of the species' range. In these models, migration can facilitate adaptation by increasing genetic variation and sustaining a population in a sink environment (Gomulkiewicz et al. 1999, Holt & Gaines 1992, Holt et al. 2003). Temporal variation may also facilitate adaptation when periods of greater habitat suitability allow advantageous alleles to spread (Holt et al. 2004). As with the continous space models, migration may also inhibit adaptation to novel habitats by reducing absolute fitness and contributing to density-dependent mortality (LoFaro & Gomulkiewicz 1999). Viewing range limits as adaptation to discrete habitats suggests the interesting possibility of periods of niche stasis followed by rapid range expansion once adaptation to sink habitats is achieved (Holt et al. 2003). In both continuous and discrete models, the sharper the selective difference along the gradient or between patches, the harder it is to

adapt (R.D. Holt, personal communication). This suggests that factors that modify the strength of selective gradients, such as resource depletion by competitors (Price & Kirkpatrick 2009) or other dynamic effects of biotic interactions on environmental gradients, may be important to consider.

As the complexity of models has increased to include evolutionary dynamics and multispecies interactions, their usefulness as heuristic tools for identifying potential factors in range-limit formation has increased; however, the list of assumptions relevant to empirical research has also expanded. For example, incorporation of evolutionary dynamics into range-limit models is usually based on simple quantitative trait or single-allele models, highlighting the lack of empirical knowledge of the role of macroevolutionary processes (Roy et al. 2009) or genetic constraints to adaptation (Antonovics 1976, Hoffmann & Blows 1994). Factors such as genetic correlations, network complexity, and how traits are governed by varying numbers of loci may influence the adaptive potential of peripheral populations (reviewed in Kawecki 2008). Two broad areas of needed theory in range limits are the nature of genetic variation, described above, and the incorporation of biotic feedbacks and coevolutionary dynamics into multispecies models of range limits (but see Case & Taper 2000, Nuismer & Kirkpatrick 2003, Price & Kirkpatrick 2009).

EMPIRICAL RESEARCH ON THE CAUSES OF RANGE LIMITS

Many of the models described above share common elements that are amenable to empirical investigation. For example, many predict that species are increasingly maladapted to an environment that varies from the center to the edges of the range. Here we describe empirical approaches that have been used to investigate species range limits. In doing so, we assess the level of support for various assumptions and predictions highlighted by range-limit theory and point out areas that require greater study.

We queried the ISI Web of Science database on July 8, 2008 using four sets of search terms: geographic range limit, geographic range boundary, geographic distribution limit, and geographic distribution boundary. We excluded studies on topics beyond the scope of this review, including species delimitation, records extending known limits, range size, non-native ranges, stratigraphic ranges, community/biome boundaries, local/habitat limits, and genetic variation across the range (see recent thorough review by Eckert et al. 2008), and we supplemented results with studies from our personal files. Studies of marginal populations alone, with no comparison to central regions, also were excluded; 321 studies were used to explore expected differences between range centers and margins. **Table 2** lists major assumptions and predictions that underpin range-limit theory, the ways that they have been investigated, and the degree of support for each category. Notable example references from this search are listed in Supplemental **Table 1**. (Follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**.)

▶ Supplemental Material

Limiting Abiotic and Biotic Factors and Their Interactions

Many empirical approaches have been used to identify factors causing range limits. Although it is generally unrealistic to confine ecological factors into opposing categories (Gaston 2009), many studies explicitly define and test factors as being abiotic or biotic from long-standing traditions (e.g., Darwin 1859). We review findings studied under these two categories, and group these findings by the common approaches used to study them. We end the section with a discussion of abiotic and biotic interactions in determining range limits.

Correlations and associations. Associations between distribution boundaries and climatic variables have a long history (e.g., Merriam 1894) and remain the most common subject of range-limit

Table 2   Summary of empirical studies addressing geographic range limits[a]

EMPIRICAL STUDIES OF RANGE LIMITS			
Association of range limit with environmental parameter(s)			
Hypothesis/Prediction	**Support**	**Partial support**	**No support**
Limiting abiotic variable(s)	**112**	**17**	**17**
Response variable:			
Presence(/absence)	41	6	2
Abundance	16	2	0
Fitness component(s)	34	4	5
Physiological response	21	5	10
Limiting biotic variable(s)	**31**	**8**	**12**
Explanatory variable:			
Competition	17	6	3
Predation	6	1	3
Disease or Parasitism	4	0	3
Host	4	1	3
Limiting abiotic $\times$ biotic interaction(s)	**7**	**0**	**1**
Variation in individual and population fitness			
Hypothesis/Prediction	**Support**	**Partial support**	**No support**
Fitness declines	**56**	**8**	**48**
Response variable:			
Recruitment	7	0	5
Survival	8	3	10
Size, growth or development	19	1	14
Fecundity	15	1	15
Lifetime fitness (or lambda)	7	3	4
Abundance declines	**31**	**17**	**24**
Response variable:			
Population size	5	1	3
Density within populations	20	13	17
Frequency of populations	6	3	4
Population dynamics more variable	**16**	**2**	**8**
Response variable:			
CV(lambda)	1	0	2
CV(abundance)	6	2	3
Recruitment more irregular	4	0	0
Extinction more likely	5	0	3

[a]Per line, cell counts are the number of studies that reported support, partial support, or no support for a given range limit hypothesis or prediction. Partial support arose when multiple species were examined within a single study and only some species provided support for the hypothesis. Studies that examined multiple range-limit hypotheses appear on multiple lines of the table.

investigations (**Table 2**). Sophisticated statistical treatments have gradually supplanted visual or verbal associations (e.g., Arntzen & Espregueira Themudo 2008). The advent of environmental niche modeling has rapidly increased the number of correlative studies over the past decade. Although little doubt remains that distribution boundaries are often significantly associated with aspects of climate (**Table 2**), disentangling direct and indirect effects and pinpointing climatic

features of relevance to organisms still pose considerable challenges (Kearney & Porter 2009). Additionally, objectively defining range boundaries is difficult; many criteria have been employed based on the scale of interest (Gaston 2003). In general, support for climatic limitation at distribution boundaries weakens as we move from studies documenting pattern (e.g., presence) to those documenting process (e.g., fitness or physiological response) (**Table 2**, lines 1 to 4).

Competition is the biotic factor examined most frequently at range limits, and 23 out of 26 studies provide support for its role in range limitation (**Table 2**). Support for the role of other biotic factors, such as predation or parasitism, is more limited. At the broad scale, negative correlations between the abundances of potential competitors (e.g., Bullock et al. 2000), or predator and prey (deRivera et al. 2005), suggest that biotic interactions structure distributions. However, the observation of negative associations cannot rule out the possibility that species are responding differently and independently to an underlying abiotic gradient.

Mechanistic models. In contrast to correlative approaches that model the realized distribution as a function of climate, some mechanistic models seek to characterize the fundamental niche based on biophysical principles (Kearney & Porter 2009). For biophysical models to convert energy and water fluxes to distribution predictions, a threshold value is chosen below which a population is assumed to be unable to persist. Alternatively, demographic parameters such as survival and fecundity have been modeled as a direct function of abiotic variables (Crozier & Dwyer 2006) and then projected across the landscape. Some analyses draw features from both model types. For example, Buckley (2008) created a foraging model that incorporated morphology, physiology, energetics, and population dynamics to predict the distribution of the fence lizard, *Sceloporus undulatus*. Although this model overpredicted the species range in some dimensions, overprediction may be informative by suggesting areas where biotic interactions or dispersal limits the realized distribution to a smaller area than is physiologically tolerable (Buckley 2008).

Experimental manipulations. Experimental manipulation of environmental variables provides a more direct means to examine how factors contribute to range limitation. Climate anomalies or long-term directional changes can be seen as natural, large-scale experiments that reveal how climate regulates distributions directly or indirectly. Convincing evidence that recent climatic warming has caused poleward or upward shifts in distributions has accumulated for large numbers of species (Parmesan 2006). Other studies have documented expansion or contraction of a range boundary during episodes of climatic warming or cooling (e.g., Crothers 1998). Climate may have both direct and indirect effects during range expansions and contractions. For example, during the range contraction of the southern flying squirrel, *Glaucomys volans*, at its northern range boundary, population crashes resulted from energetic limitations owing to both direct effects of climate (energetic demands of low winter temperatures) and indirect effects (mast crop failure caused low energetic input) (Bowman et al. 2005).

Spatial or temporal variation in community composition also provides natural experiments that reveal the role of biotic interactions. Altitude or habitat ranges of some bird and fish species are greater in mountain ranges where parapatric congeners are absent rather than in mountain ranges where congeners are present (Cadena & Loiselle 2007). Temporal variation in the position of interacting species' range limits also suggests that competitive interactions may shrink the realized range of some species to a smaller spatial area than is physiologically tolerable (Hersteinsson & Macdonald 1992). Alternatively, species may show concerted but independent (opposite) responses to a temporal abiotic change (Dawe et al. 2007).

At smaller scales, more controlled field and lab experiments have examined how single or factorial combinations of variables affect physiological processes or fitness components (**Table 2**).

Although the majority of these studies seem to support abiotic limitation, the likelihood of mechanistic support is somewhat lower than when simply associating presence or abundance with climate (**Table 2**). Mechanistic studies often gain power of inference through a comparative design by asking how environmental responses differ between congeners or sympatric species with contrasting distributions (e.g., Matson & Edwards 2007) or populations of a single species from different areas of the species range (Griffith & Watson 2006). A major challenge for experimental manipulations is the realistic simulation of relevant environmental parameters; organisms may exhibit integrated responses to environmental fluctuations, extreme values, and duration of exposure. Moreover, multiple factors can interact, for example, when thermal tolerance depends on resource availability (Bowman et al. 2005, Gilman 2006). The merger of lab and field experimentation with spatiotemporal modeling is required to determine whether responses measured in simplified environments are sufficient to explain the distribution boundary (Parker & Andrews 2007).

Experimental manipulations also have provided some of the most definitive evidence that biotic interactions can be important determinants of species range limits. A series of transplant experiments and removal treatments demonstrated that the barnacle *Chthamalus fragilis* can survive when transplanted beyond its northern range limit, but only in the absence of competition from *Semibalanus balanoides* (Wethey 2002). Similarly, transplant experiments with and without herbivory suggest that increasing slug herbivory at lower elevations is responsible for the lower elevation range limit of the subalpine plant *Arnica Montana* (Bruelheide & Scheidel 1999).

Interactions between biotic and abiotic factors. All biotic interactions take place within a landscape of varying abiotic conditions, but surprisingly few studies have explicitly examined abiotic and biotic interactions at range limits (**Table 2**). Similarly, although the relative importance of biotic and abiotic factors has long been hypothesized to differ between northern and southern range limits (Darwin 1859, MacArthur 1972), our search returned no studies that examined both factors at both limits. Clearly, more work is needed. Condition-specific competition, wherein the relative competitive abilities of species depend on the abiotic environment, is one mechanism by which the interaction between biotic and abiotic variables may determine distributions along environmental gradients (Taniguchi & Nakano 2000). Competitive interactions are often asymmetrical, and examples exist where the range of a superior competitor appears to be set by the abiotic environment, whereas the inferior competitor is restricted to areas not physiologically tolerable to the superior competitor (e.g., Arif et al. 2007). Species may also become more susceptible to pathogens or predation when physiologically stressed at the range margin (Briers 2003). Spatiotemporal interactions between biotic and abiotic factors add an additional layer of complexity. The giant kelp, *Macrocystis pyrifera*, experienced population declines at its southern range limit owing to high temperatures and large waves during a strong El Niño event, yet was unable to recolonize formerly occupied areas after the El Niño owing to preemption by a competitor less affected by the abiotic change (Edwards & Hernandez-Carmona 2005).

Fitness Across the Species Range

A widely held assumption is that fitness should be reduced toward the edge of the range; the results shown in **Table 2** do not provide strong support for this generalization. Individuals in marginal populations may have high fitness if they reside in patches of favorable habitat, even if favorable habitat is sparse toward the range edge. Periodic bad years not captured in a short-term study may also be important for the dynamics of marginal populations. In addition, the fitness component(s) examined may be high, but unexamined life stages may yet be limiting (Kellman 2004). The latter possibility appears particularly relevant because growth and reproductive components of

fitness have received the most attention, while relatively few studies examine recruitment or survival. Even fewer studies report a quantitative estimate of lifetime fitness or population growth rate based on multiple fitness components across the life cycle (but see Purves 2009). This is of particular significance when the accumulation of small fitness differences across the life cycle yields substantial differences in overall fitness (Marshall 1968). When studies are grouped by species (rather than separated by fitness components), 49 out of 73 found at least one of the examined fitness components to be lower at the range edge compared to the range center. However, this still leaves a moderate number of studies with no evidence of lower fitness at the range margin, and in these cases it may be necessary to consider extinction-recolonization dynamics (Carter & Prince 1981, Lennon et al. 1997) or dispersal limitation (Svenning et al. 2008).

If ranges exist at migration-selection equilibria, species should have low fitness not just at the range margin but also beyond present-day ranges. Of 39 studies that transplanted individuals to areas beyond the present range, 28 reported that fitness was lower beyond the range edge compared to that within the range, as expected. Reciprocal transplants are often used to examine local adaptation, in which case relative fitness is an appropriate metric for comparison between populations and environments. However, for investigations of niche and demographic constraints beyond range boundaries, absolute fitness is also meaningful and warrants greater explicit consideration than it has received to date (R.D. Holt, personal communication). Even if population growth rates are too low for long-term persistence beyond the range edge, the ability of even a few individuals to survive and reproduce creates a window of opportunity for the evolution of novel adaptations to the sink environment (discussed below).

Migration-selection equilibrium: equilibrium state between gene flow and natural selection so that differentiation does not occur between populations experiencing different environments

Abundance Across the Species Range

Another generalization is that species abundances are greatest at the range center and lowest at the range margin (Brown et al. 1995). Empirical approaches to quantify abundance vary widely, and tests of the abundant center hypothesis include a mix of response variables such as population size, individual density within populations, and frequency of populations (**Table 2**). Sagarin & Gaines (2002) did not find strong support for the abundant center pattern, and our survey is largely consistent with their findings across different metrics of abundance (**Table 2**). Methodological limitations may contribute to the lack of clear support; range edges are usually undersampled relative to the range center (Sagarin & Gaines 2002). In addition to methodological issues, there are biological reasons why the abundant center pattern may not occur. The abundant center hypothesis assumes environmental suitability is spatially autocorrelated such that: (*a*) species abundance is greatest where the environment is most favorable, and (*b*) the environment is most favorable at the range center. Because patterns of fitness variation are similarly equivocal, the assumption that the environment of the range edge is less favorable than the range center may not hold. Most investigations of abundance focus on local density within populations (**Table 2**). The spatial distribution, pattern of dispersion, and patch structure of population density are also likely important in determining range limits. This basic level of heterogeneity is often minimized in range limits studies and is in need of more empirical and theoretical work. It is possible that the relative number of source or sink populations increases or decreases toward the range edge and that these dynamics contribute to range limits. Capturing this level of heterogeneity throughout a species' range should improve models of the spatial dynamics of range limits as well as increase our capacity to develop realistic and relevant experimental tests of those models.

Finally, temporal variation in abundance is likely to introduce error to snapshot estimates of spatial trends in abundance across the range. In theory, central populations may exhibit greater temporal variability if intrinsic rates of increase are high in optimal habitat or if biotic regulation

is stronger when population density is high (although this has rarely been reported). Conversely, marginal populations may be near the species' limit of environmental tolerance and will exhibit greater temporal variability when environmental fluctuations exceed the species' tolerance in some years; this is a pattern more strongly supported by our literature survey (**Table 2**). Gaston (2009) calls for studies to estimate all essential parameters of the single-population model (population size; number of immigrants; number of births; number of deaths; number of emigrants) to improve understanding of how population processes may or may not change systematically among centers and edges.

Adaptation at Range Limits

Theory suggests that species range limits can act as (*a*) diversifying areas where niche evolution occurs during adaptation to novel environments, or (*b*) depauperate sinks where adaptation is prevented by small population size and maladaptive gene flow from central populations (**Table 1**). Empirical studies have described individual components of the above scenarios (see Gaston 2003), lending support to both viewpoints. Nevertheless, simultaneous examination of the major hypothesized factors for understanding population differentiation at range limits (gene flow, selection, ecological gradient, and the heritability of important traits) has been lacking.

Empirical testing of evolutionary dynamics at range edges has been impeded by at least three major obstacles. First, studies of range limits generally do not replicate central and edge populations—especially edges—and therefore suffer from limited power to draw robust conclusions. It is important to consider multiple edges of the range and to include replicate populations from each type of edge. Second, organisms examined in range-limit research are seldom optimal for studying population genetics—they lack controllable breeding systems, sufficiently short generation times, and enough variable genetic markers—thus, it is difficult to estimate fitness, trait heritability, or gene flow. Third, because environmental factors often covary (Bradshaw & Holzapfel 2008) and may influence adaptive traits in complex ways, the geographic ranges of study species may lack a simple environmental or ecological gradient against which to test for the effects of counter-gradient gene flow.

With recent advances in genomic resources and spatial analyses, we are poised to combine molecular data with phenotypic trait data to test opposing hypotheses of range-limit adaptation. Range edges may create distinct adaptive patterns under certain conditions. However, definitive tests of this hypothesis hinge on analyses of gene flow, selection, and the underlying genetic architecture of adaptations. In particular, the structure of adaptive genetic variation across a species range and the influence of immigration on genetic variation in peripheral populations are poorly understood. Empirical studies to date have focused almost solely on quantifying levels of neutral genetic variability within and among marginal populations. These studies provide some support for greater differentiation among and lower variation within peripheral populations (Eckert et al. 2008). Drawing on powerful analytical approaches from landscape and population genetics, molecular genetics can now be used to estimate both recent and historical asymmetrical gene flow between populations (see references within Pearse & Crandall 2004). A study on adaptation at range margins in rainforest *Drosophila* (Bridle et al 2009) suggested that the effects of gene flow on local adaptation may depend on the steepness of the environmental gradient. Gene flow along a steep altitudinal gradient appeared to swamp phenotypic divergence in traits conferring stress resistance. In contrast, gene flow across a more shallow gradient increased genetic variation that, in turn, may have fostered adaptive responses in cold tolerance. These indirect estimates can be contrasted to experimental manipulations of gene flow to determine whether gene flow is likely to facilitate or hinder local adaptation at the range margin. Barton (2001) suggested limiting gene

flow into peripheral populations and testing for a decrease in genetic variation and an adaptive shift in response to selection. Alternatively, experimental gene flow (that is, manipulated matings or introductions) can be used to test alternative models of adaptive enhancement or gene swamping at range edges, not unlike genetic rescue experiments. Experimental matings facilitate the comparison of selection differentials across gene flow treatments as well as within multiple environments.

Understanding the dynamics of range margins requires further examination of adaptive genetic variation in quantitative traits. By imposing artificial selection on male reproductive traits, Pujol & Pannell (2008) recently demonstrated that marginal populations with lower neutral genetic diversity compared to that of central populations also exhibited reduced evolutionary response to selection on quantitative traits. Gene flow should affect (positively or negatively) fitness at range limits as well as the heritability of traits under selection, which can be estimated using the genetic (co)variance matrix (as in Etterson 2004). Coupled with transplant experiments, these are powerful tools for understanding the scale and intensity of selection, the nature of adaptations (complex versus simple traits), and the importance of local adaptation in setting range limits. Angert et al. (2008) demonstrated that fitness trade-offs between environments can forestall range expansion by transplanting hybrid populations of *Mimulus cardinalis* and *M. lewisii* to different elevations and assessing local adaptation after selection. The evolution of traits that could increase fitness beyond the elevation range would incur a fitness cost within the present range. Jenkins & Hoffmann (1999) demonstrated an existing genetic trade-off between fecundity and cold performance traits within edge populations of *Drosophila serrata* that may, in part, explain its southern range limit. Nevertheless, heritable genetic variation was found in cold resistance traits, suggesting that the species range is not necessarily limited by a lack of genetic variation in these traits.

Studies that replicate edge-center comparisons, although demanding, are necessary to improve understanding of evolutionary range-limit dynamics because the effects of gene flow on edge populations may vary in different portions of the species range (e.g., gene swamping at one edge population, migrational enhancement at another). Replication of edges is also important to disentangle equilibrium limitations from nonequilibrium characteristics of range margins. For example, the bias of empirical work toward north-temperate range margins makes it difficult to discern whether observed patterns (or lack of expected patterns) reflect lasting signatures of post-glacial range expansion or whether they are characteristic of peripheral populations per se (Eckert et al. 2008). Additionally, although theoretical investigations of gene flow have focused primarily on center-to-edge dynamics, migration along edges may also strongly affect the evolution of range limits. Thus, the inclusion of among-edge population comparisons will be informative.

Localized selection gradients, or internal range limits, are often found nested within the larger-scale fitness gradients measured across geographic scales of central and marginal populations. The value of these internal range limits in understanding factors limiting geographic ranges has been little explored (Gaston 2003). Co-occurring environmental gradients are likely to be complicated, yet experimental studies of internal range limits may be useful in teasing out both agents of selection and the relative intensity of selection along external range limits. If replicate internal gradients in the primary environmental factors (e.g., soil, climate, competition) thought to restrict the geographic range of a species could be identified, it may be possible to examine the relative importance of each factor in geographic range restriction. This would likely involve the reciprocal transplant of populations from locations along the different internal gradients to external edge locations. Gene flow rates among populations along these localized internal gradients are also likely to be higher than among more widely spaced populations at the scale of the geographic range. Gene flow regimes in these localized gradients may offer replicated model systems to examine the strength of selection and the effects of antagonistic gene flow for different environmental factors thought important for geographic range limits.

Genetic (co)variance matrix: multiple regression approach to estimate the multivariate (multitrait) response to selection

Lastly, the adaptive significance of cross-generational plasticity (that is, maternal environmental effects) in range limits is largely unexplored. Given differences in environmental quality across the range, maladaptive gene flow may be mitigated by adaptive cross-generational plasticity. Poorly adapted migrants to edge environments may persist because they are fostered by enhanced maternal provisioning produced in a less stressful maternal environment (Stanton & Galen 1997).

RANGE LIMITS AND BIOLOGICAL INVASIONS

Biological invasions, while regrettable, provide useful experiments in the dynamics of range limits. Dynamics of the spread of invasives can give clues as to what factors restrict range expansion in their native range. In particular, human-induced disturbance (Hobbs & Huenneke 1992) and escape from predators and pathogens (Maron et al. 2004a) may foster invasions (Mack et al. 2000). There are some examples of invasions reaching geographic and environmental limits. These species provide an opportunity to use a correlative approach to test hypotheses about range limits by comparing environmental conditions in the new range with those of the species' native range. Although there are ethical concerns, there is the potential to experimentally manipulate conditions at newly established margins to tease out factors limiting further spread (Pierson & Mack 1990). Of course, there are important differences between invasion dynamics and native-range equilibrium. Cross-continental invasions involve human-facilitated transfer of species across broad biogeographic scales (Mooney & Cleland 2001), and the invaders are not coevolved with the competitors, predators, pathogens, and mutualists in their new range. Although the role of contemporary adaptive change in invasion dynamics has been less studied, there is a rapidly growing body of evidence that suggests the importance of these processes (Cox 2004, Lee 2002).

Adaptation During Invasive Spread

Adaptation during invasive spread can be likened to adaptation (niche evolution) at range limits. The number of examples of rapid evolutionary change occurring during the invasive spread of a species has grown exponentially over the last 10–15 years (Cox 2004, Lee 2002). Cases of rapid evolution of clinal variation in novel, invaded ranges have been particularly revealing. Populations of St. John's wort (*Hypericum perforatum*) from North America exhibited similar clinal variation to populations within its home range in Europe (Maron et al. 2004b). This suggested rapid adaptation because the climatic regimes of novel populations differed greatly from those of source populations. Multiple introductions have increased genetic variation in this invasive plant and have probably facilitated adaptive responses. In a study on California poppy (*Eschscholzia californica*), Leger & Rice (2007) found similar patterns of trait variation in poppy populations across abiotic gradients in temperature and rainfall within native (California) and invasive ranges (Chile). Although trait responses to the gradients were similar in both ranges, there were also significant differences in trait combinations suggesting that historical contingencies may influence adaptive responses. Similar results indicating the repeatability and contingency of adaptation to latitudinal clines were reported for the fruit fly *Drosophila subobscura* in its new range in North America (Huey et al. 2000). We might expect that patterns of adaptive differences across environmental gradients between center and edge populations may be similar in terms of fitness effects, but the mechanisms underlying adaptive responses may vary widely within a given species' range. Specifically, analyses of the evolution of adaptive clines at the leading edge of invasions should elucidate the process of niche evolution in these demographically and perhaps environmentally unique areas.

One might expect selection for increased dispersal ability along range edges, especially if range edges are dynamic and not static (Darling et al. 2008). Modeling studies of invasive spread found

strong selection for increased dispersal ability along invasion fronts (Travis & Dytham 2002). Empirical studies on phenotypic variation in dispersal capacity along invasion fronts have also found evidence for increased dispersal ability in initial colonizers. Populations of two bush cricket species (*Conocephalis discolor* and *Metrioptera roeselii*) currently expanding their range in England exhibit a higher frequency of a long-winged morph than in resident populations not undergoing range expansion; increases in the long-winged morph probably reflect both phenotypic plasticity as well as genetic differentiation (Thomas et al. 2001). A study on the morphology and dispersal rates of cane toads, *Bufo marinus*, in Queensland, Australia found that longer-legged toads dispersed more rapidly and were more frequent at the edges of invasion fronts (Phillips et al. 2006). A 10-year study of invasion of islands by three weed species in British Columbia found that initial colonizers exhibited traits that facilitated long-distance wind dispersal (Cody & Overton 1996). Interestingly, once populations were established on the island, there was strong selection in the opposite direction for traits that reduced wind dispersal. Taken together, these studies suggest that selection for increased dispersal along range limits may depend on whether the range edge is expanding or static.

Since introduction of the concept of the "general purpose genotype" (Baker 1965), there has been considerable interest in assessing the role of phenotypic plasticity in fostering the establishment and spread of invasive species (Rice & Mack 1991, Sultan 2004). In particular, recent interest focuses on comparing the degree of plasticity between populations of an introduced species in its home and invaded range (e.g., Maron et al. 2004b); such studies provide insight for the general study of adaptive plasticity at range limits. In plants, results are somewhat mixed on whether invasive populations of a species are generally more plastic than populations in the species home range; expression of greater plasticity in invasive populations seems to be both trait and environment dependent (Richards et al. 2006). A better understanding of central and marginal populations, as well as better data on spatial and temporal patterns of resource availability along range edges, is needed to test the role of plasticity at range limits.

Time Lags During Invasive Spread

It has long been noted that there is often a lag phase at the initial stages of a biological invasion where local population growth is low and there is minimal range expansion in the newly introduced species (Cox 2004). Despite a fair amount of speculation on the likelihood of evolutionary processes in creating prolonged lag times, the importance of adaptive constraints on initial range expansion in invasives has yet to be empirically demonstrated (Williamson 1999, but see Griffith & Watson 2006 for an example of experimentally overcoming range limits in a weedy, native plant). The paucity of examples probably reflects the difficulty in identifying a truly prolonged lag coupled with the fact that few experimental studies have been attempted. As noted by Baker (1965), the injection of additional genetic variation into populations through repeated introductions will also increase the capacity of a population to adapt genetically. The larger the effective size of the founding populations, the less likely that genetic drift or inbreeding depression will reduce the capacity of the founders to adapt locally. It has been suggested, for example, that the successful spread of the cladoceran *Bosmina coregoni* throughout the Great Lakes resulted from repeated ballast water introductions (Demelo & Hebert 1994). Finally, augmentation of additive genetic variation by mutation might be an under-appreciated factor in promoting adaptive spread (Bataillon 2003). If edge populations along range limits are dynamic and characterized by nonequilibrial demography and genetics, then lag phase studies may represent useful models for understanding the evolutionary ecology of range edges.

GLOBAL CHANGE AND RANGE LIMITS

Rapid climate change will teach us volumes about the stability or mobility of range limits. Geographic range shifts are widely expected, although many species may not be able to track their fundamental niche (Loarie et al. 2008, Parmesan 2006). Models predicting future species range shifts generally assume range equilibrium with the present environment. Climate change will thus inform us on how many species are actually at equilibrium, the importance of range equilibrium to species persistence, which types of organisms adjust quickly, and the relative importance of abiotic and biotic niches. Additionally, rapid climate shifts will provide "opportunities" to examine the dynamics of expanding versus trailing range limits and the role of peripheral populations in conservation biology.

Conservation under climate change will require accurate estimates of the positions of future range limits. Species distribution modeling combines environmental data sets and species occurrences to estimate areas of climatic suitability (Pearman et al. 2008). In some cases, one to a few environmental variables are selected based on a priori hypotheses for their role in limitation; in other cases, all available variables are evaluated for their relative predictive abilities. Recent simulation studies demonstrate that automated model selection strategies may not discriminate well between truly causal and spatially autocorrelated variables (e.g., Meynard & Quinn 2007). Further, covariation among variables and indirect effects operating through unexamined variables make even strong associations suggestive at best (Gaston 2003). Changes in the realized distribution of a species, and its associated environmental correlates, may be influenced by interactions with other species. Therefore, presence data at edges should be combined with performance data to improve predictive power.

Edge populations may be key in providing adaptations to novel environmental extremes expected to occur during rapid climate shifts (Ackerly 2003). Channell & Lomolino (2000) reviewed species range contractions in 309 mammal species and found that declining species are as likely to collapse into peripheries of their original range as collapse into the center. Hampe & Petit (2005) discussed how trailing-edge populations can be more stable under shifting environments than is generally thought; they argue for increased conservation of these areas and more theoretical work on these dynamics. Species responses will be tested as never before in future climates, as multiple environmental variables are likely to interact in novel ways (Williams & Jackson 2007).

SUMMARY POINTS

1. Range limits are highly mobile and dynamic. Edge populations exhibit increased genetic isolation and differentiation, and greater variability in individual and population performance. Population dynamics may be more variable at range limits, but the reliability of this pattern, and its effect on creating limits, is unknown.

2. Theoretical models predict many ways for range limits to arise, with and without environmental heterogeneity, including competitive exclusion, Allee effects, hybridization, and swamping gene flow. Most models, and their underlying assumptions, remain empirically untested.

3. The abundant center hypothesis is not a general explanation for the formation of range limits. Abundance and fitness often do not appear to decline toward range limits, but more studies that integrate fitness across multiple life-history transitions are needed.

4. Abiotic and biotic factors are clear determinants of range limits, and although there are examples of interacting factors creating limits, the importance of interactions remains largely unexplored. Despite long-standing predictions, the relative importance of biotic versus abiotic factors limiting differing ends of ecological gradients (e.g., elevation and latitude) remains largely untested.

5. Invasive species can act as experiments on the formation of range limits, the adaptation to novel conditions, and the mechanisms of range equilibrium and expansion.

FUTURE ISSUES

1. Climate change will inform us on the importance of range equilibrium to species persistence, which types of organisms adjust fastest, and the relative importance of abiotic and biotic niches. The dynamics and scale of transient range limits (e.g., during invasions and rapid climate shifts), including expanding and retreating boundaries, are in need of further study.

2. Adaptation at range limits (that is, niche evolution) is in need of empirical research, including the importance of gene flow in facilitating or preventing adapation. There is limited evidence that a lack of genetic variation creates range limits. More examinations of adaptive variation (e.g., genetic covariance matrix) and the strength and mode of selection at range limits are needed. The underlying genetics of adaptation at range limits is unknown. Can adaptation in sinks involve many genes of small effect or mostly few genes of large effect?

3. There are major gaps between theoretical predictions and empirical tests of the causes of range limits. Theoretical models can be complex and are difficult to empirically parameterize. Nevertheless, key findings and predictions of the models are conceptually amenable to empirical investigation. Empirical studies that can make use of theory will greatly benefit range-limit research, as will theoretical models that incorporate empirically testable assumptions and ecological constraints.

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Errata

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