

Evolutionary ecology at the extremes of species' ranges

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Abstract: The nature of species at the extremes of their ranges impinges fundamentally on diverse biological issues, including species' range dynamics, population variability, speciation and conservation biology. We review the literature concerning genetic and ecological variation at species' range edges, and discuss historical and contemporary forces that may generate observed trends, as well as their current and future implications. We discuss literature which shows how environmental, ecological and evolutionary factors act to limit species' ranges, and how these factors impose selection for adaptation or dispersal in peripheral populations exposed to extreme and stochastic biotic and abiotic stressors. When conditions are sufficiently harsh such that local extinction is certain, peripheral populations may represent temporary offshoots from stable core populations. However, in cases where peripheral populations persist at the range edge under divergent or extreme conditions, biologically significant differences can arise from historical and contemporary ecological and evolutionary forces. In many such cases reviewed herein, peripheral populations tended to diverge from the species' core, and to display lower genetic diversity or greater stress-adaptation. We conclude that while such populations may be of particular conservation value as significant components of intraspecific biodiversity or sources of evolutionary innovation and persistence during environmental change, small and greatly variable population size, especially combined with low genetic variability, can result in elevated extinction risk in harsh and stochastic peripheral environments. As a result, while peripheral populations should not be dismissed as evolutionary dead-ends destined for local extinction, neither should they be uncritically granted inherently superior significance based only on their peripheral position alone.

Key words: species' range, evolution, ecology, genetic diversity, gene flow, demography.

Résumé : La nature des espèces aux extrémités de leur aire entraîne fondamentalement diverses conséquences biologiques, incluant la dynamique des aires des espèces, la variabilité des populations, la spéciation et la biologie de la conservation. Les auteurs passent en revue la littérature portant sur la variation génétique et écologique des espèces à la limite de leur aire, et discutent les forces historiques et contemporaines pouvant générer les tendances observées ainsi que leurs implications actuelles et futures. Ils discutent la littérature montrant comment les facteurs environnementaux, écologiques et évolutifs agissent pour limiter l'aire des espèces; ils discutent également comment ces facteurs imposent une sélection pour l'adaptation ou la dispersion dans les populations périphériques exposées à des agents stressants biotiques ou abiotiques stochastiques. Lorsque les conditions sont suffisamment sévères pour que l'extinction survienne, des populations périphériques peuvent représenter des rejets temporaires des populations centrales stables. Cependant, dans les cas où les populations périphériques persistent à la limite de l'aire sous des conditions divergentes ou extrêmes, des différences biologiques significatives peuvent survenir à partir des forces historiques ainsi qu'écologiques et évolutives contemporaines. Dans plusieurs des cas revus ici, les populations périphériques tendent à diverger du noyau de l'espèce, et à montrer une moindre diversité génétique ou une adaptation accrue aux stress. Les auteurs concluent qu'alors que de telles populations peuvent représenter une valeur de conservation particulière comme composante significative de la biodiversité intraspécifique ou comme sources d'innovations évolutives et de persistance au cours du changement environnemental, la petite et fortement variable dimension de la population, surtout combinée avec une faible variabilité génétique, peut conduire à un risque d'extinction dans des environnements sévères et stochastiques. Conséquemment, alors que les populations périphériques ne doivent pas être écartées comme cul-de-sac évolutif destiné à l'extinction locale, on ne devrait pas du même coup leur attribuer indistinctement une signification supérieure inhérente basée sur leur seule position périphérique.

Mots-clés : aires des espèces, évolution, diversité génétique, flux des gènes, démographie.

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Introduction

A fundamental issue in evolutionary ecology concerns the nature of populations of species at the extremes of their

ranges (Gaston 2003). Of particular import are questions concerning whether peripheral populations differ fundamentally from conspecifics in other parts of the range and, if so, what factors account for these differences. Answers to these

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questions underpin many theoretical and practical areas of evolutionary, conservation and population biology (Hoffmann and Blows 1994; Hoffmann and Parsons 1997). For example, the study of peripheral populations may help in elucidating processes of range expansion or retraction and speciation (Holt 2003; Kirkpatrick and Barton 1997). Peripheral populations may be of particular conservation concern when they suffer an elevated risk of extinction, possess low genetic variation, are genetically divergent from core populations, isolated from disturbances in central parts of the range, or especially well-adapted to stressful environments (Vecutich and Waite 2003; Lesica and Allendorf 1995).

Many factors have been hypothesized to be responsible for constraining species from continually adapting to overcome the abiotic and biotic factors that impose limits on species' ranges (Hoffmann and Blows 1994; Kirkpatrick and Barton 1997; Holt 2003). In addition to impermeable physical barriers, gradients reaching species' physiological tolerance limits and anthropogenic effects, range limitation can generally be attributed to some combination of environmental, ecological or evolutionary factors (Soule 1973; Hoffmann and Parsons 1997). These range-limiting factors are related to spatial patterns in genetic and ecological variation from the core to the edge of species' ranges (Lesica and Allendorf 1995). However, rather than restricting this review to describing what species are "like" at the extremes of their ranges, our primary intent is to focus on how and, in some cases, whether these differences are adaptively significant.

We begin by examining the general perception that peripheral populations are less genetically variable, but more genetically divergent, than central populations (Gaston 2003). At the core of this approach is the need to identify the forces responsible for generating observed differences and, in particular, to determine the relative importance of deterministic (e.g., selection) and stochastic (e.g., founder effects, bottlenecks, genetic drift, historical contingency, phylogenetic inertia) factors that might account for the distribution of variability (e.g., Hedrick et al. 1976; Yeh and Layton 1979; Shumaker and Babble 1980; Lande 1995; Johannesson and André 2006). Although such a distinction can yield important information about the evolutionary history and conservation significance of peripheral populations, it is often overlooked.

Where ecological variables are concerned, those related to population abundance, density, and temporal variability are of primary concern (Nantel and Gagnon 1999; Sagarin et al. 2006). For example, it is imperative to identify the relative contributions of demographic factors such as founder effects, bottlenecks and effective population size to extant patterns of genetic variation (Lesica and Allendorf 1995). We review the literature to test the hypothesis that abundance and density tend to be lower and more variable in peripheral populations, and that edge populations tend to exhibit life history strategies that act to spread the risk of reproductive failure across temporal patterns of environmental stochasticity.

Lastly, understanding the role of gene flow imparted by the dispersal or migration of individuals among populations is an overarching theme in this area of research. The degree

to which gene flow, or the lack thereof, drives, obfuscates, or otherwise affects clines in both adaptive and neutral variability across species ranges cannot be overstated. We test the hypothesis that the more severe and stochastic character of peripheral environments generates strong selective interplay between adaptation and dispersal. We suggest that understanding this dichotomy is imperative to the correct interpretation of patterns of genetic variation across species' ranges, especially so when considering conservation issues.

Terminology and other caveats

Reference to the "edge" of a species' range can indicate several different manners of boundaries, and it is important to be clear on these terms. Some peripheral populations are not ecologically marginal, e.g., when a coastline defines the edge of an obligate marine species' range. Alternatively, some marginal populations are not peripheral, as is the case when a patch of sub-optimal climate or physical habitat occurs within the central part of a species' range. In other cases, isolated peripheral populations persist in suitable habitat patches disjunct from the species' continuous range (Gaston 2003). In this review we use "peripheral" to indicate the geographical extreme of species' distributions and "marginal" to refer to the particular case defining the ecological extreme of a species distribution which often, but not always, occurs at the geographic periphery. However, as noted by Soulé (1973), marginality is usually assumed, rather than explicitly demonstrated, so the terms are often equated in the literature. The practical limits of species' ranges with respect to conservation and management are often defined by geopolitical boundaries which, more often than not, are biologically irrelevant.

Another challenge is to identify appropriate spatial and temporal scales to define different species' range edges, and to determine the level of sampling sufficient to characterize variability across a species' range (Gaston 2003). Furthermore, the influence of species' delineations on the study of species variability must be acknowledged. Species with broad ecological niches may exhibit a high degree of plasticity, while others may exhibit variation as a result of the initial stages of speciation or undefined (yet biologically relevant) variation. Interactions between historical factors, selection, mutation, gene flow, epigenetic interactions, trade-offs and diverse other factors can obscure adaptive patterns, and it would be naïve to assume that these have not confounded the interpretation of trends in some studies. Lastly, the authors acknowledge that space limitations preclude an extensive consideration of the literature on species variability differences between tropical and temperate environments (e.g., Pianka 1966; Gaston 1996 and references therein) and along elevation gradients (e.g., Hoffmann and Parsons 1997; Rhode 1992 and references therein).

Peripheral versus central components of species' ranges

Peripheral populations are typically characterized as being less abundant and less dense than core populations and as exhibiting higher variability in both of these features (Vecutich and Waite 2003). Environmental conditions at the edges of species' ranges tend to be stressful, or at the very least

different from those experienced by core populations (Lesica and Allendorf 1995). The peripheral environment tends to be more spatially diverse and temporally unstable, and is characterized by relatively depressed niche diversity (Scudder 1989). As a result, it is hypothesized that selection in peripheral populations is dominated by a range of density-independent factors, relative to the predominance of density-dependence at the core (Scudder 1989; but see Gaston 2003). Because of the ebb and flow of species' borders, selection at these locales is generally assumed to favour colonization and dispersal abilities, traits that are not as strongly favoured in stable core areas (Hoffmann and Parsons 1997). Peripheral populations are often genetically and phenotypically divergent, although not universally so (Lomolino and Channel 1995). The general perception that genetic diversity is lower in peripheral relative to central populations is explored in depth herein.

The biological significance of marginal populations

The study of marginal populations is intrinsically and practically important for diverse reasons. Stressful conditions experienced by marginal populations may reveal acute biological phenomena not expressed under more benign conditions, which can render novel phenotypes vulnerable to intense selection and result in evolutionary (Hoffmann and Parsons 1997) and ecological or life history changes (Bears et al. 2009). Moreover, peripheral populations can express unique, polymodal, or otherwise variable genotypes (Hoffmann and Blows 1994), morphologies (Grant and Antonovics 1978; Vermeij 1978), life histories (Lesica and Allendorf 1995), dispersal abilities (Guo et al. 2005), biological tolerances or plasticity (Parsons 1991). Furthermore, the study of trait variability across environmental clines can yield important information, especially where powerful experimental techniques such as common-garden or translocation experiments can help to distinguish genetic, potentially adaptive, differences from environmental effects and phenotypic plasticity (e.g., Merilä et al. 1996). Thus, comparisons between central and marginal populations may yield insight into selection and speciation processes.

The study of the dynamics of peripheral populations can also help to elucidate the process of range expansion. Of particular interest here is the possibility that peripheral populations may be differentially adapted for survival in harsh and spatio-temporally stochastic environments, and may therefore be pre-adapted for dispersal and colonization of newly suitable habitat (Safriel et al. 1994; Thomas et al. 2001). Understanding this process may help in predicting when, where and to what extent species' ranges can be expected to shift in response to climate change (Crozier 2003). While examples of northward range expansions linked to climate warming are already widespread, new evidence shows a disquieting frequency of climate-driven extinctions and range retractions at lower latitudes and lower elevations (Parmesan 1996; Thomas et al. 2006; Sekercioglu et al. 2008). Understanding range-expansion processes may also reveal factors that mediate colonization by invasive species, as well as planned introductions of species for rehabilitation, biological control or recreational opportunities.

Although Mayr (1963) viewed peripheral isolates as "cradles of evolutionary innovation", he suggested that isolation alone is insufficient to complete the process, and that population bottlenecks are also required to accentuate genetic drift and to disrupt epigenetic systems. Carson (1975) built upon Mayr's views concerning the importance of founder events in the evolutionary dynamics of peripheral populations and developed the "founder flush" hypothesis, so named by Powell (1978). Carson differentiated between what he termed "open" (variants with more or less independent effects on fitness that are free to respond to selection) and "closed" (strongly epigenetic) systems, and suggested that the latter could be disrupted by founder effects, bottlenecks, genetic drift, and inbreeding in small (peripheral) populations. As a result, when populations expand their ranges rapidly due to temporarily permissive conditions or sudden genotypic changes due to migrants or mutants, new areas are colonized by small numbers of individuals that exhibit founder effects. If environmental or demographic effects result in repeated crashes in peripheral populations, the effects of serial bottlenecks could result in very strong genetic drift and divergence, initiating speciation (e.g., Keyghobadi et al. 2005). In this manner, drastic events could disorganize closed systems, resulting in new balances that render less fit ancestral genotypes (i.e., reproductive isolation).

Recent models support the view of peripheral isolates as important sites for speciation when gene flow is sufficiently limited, although they suggest that strong selection in the absence of drift is a more likely driving force behind rapid divergence as a first step in species formation (Garcia-Ramos and Kirkpatrick 1997). Strong directional selection during periods of low population size may generate particularly intense evolutionary inertia and the colonization of unusual substrates, which may be commonplace for peripheral or marginal populations, contributing further to divergence (Raven 1964). Levin (1970) suggested that vacillations of species' borders inevitably result in the isolation of populations at the geographic and ecological limits of their range, where they will sooner or later be subjected to severe environmental stress to which they may respond by rapid speciation or extinction.

On the other hand, the perception that selection under extreme conditions accounts for most evolutionary change may simply be attributable to the observation that natural selection is often more detectable under extreme conditions where fitness differences are most evident (Hoffmann and Parsons 1997). Parsons (1991) cautioned that stress-imposed limitations on metabolism and low genetic variation might limit the evolutionary potential of peripheral populations. In effect, he suggested that while populations near species' boundaries may tend to experience high environmentally induced variability, concomitant metabolic costs might preclude evolutionary change or range expansion into even more stressful habitats. He hypothesized that central environments may not generate sufficient stress to induce rapid evolution despite higher genetic variation, such that moderate populations with moderate levels of genetic variation and stress may be those most likely to experience evolutionary change.

It has often been asserted that peripheral populations should constitute important foci for conservation efforts (e.g., Scudder 1989), although some caution against indiscriminate application of this perception (Vecutich and Waite 2003). They often persist in a sub-optimal environment, are often isolated, less abundant, and experience more temporal variability in abundance than core populations. Furthermore, they may exhibit reduced genetic variation compared to central populations, and may be genetically divergent or even distinct. As a result, peripheral populations are generally thought to be at greater risk of extinction due to stochastic or catastrophic genetic, demographic or environmental effects than central populations (Ledig 1986; but see Lammi et al. 1999). Perhaps the best-known example of the negative effects of small population size on genetic variation is that provided by O'Brien et al. (1985) who found that small populations of cheetahs (*Acinonyx jubatus*) have suffered severe genetic homogenization, the consequences of which have brought the species close to extinction. More recent evidence suggests that these effects derive from one or more severe bottlenecks at the end of the last ice-age, and that the species has been reconstituting genetic variation since then (references in Marker et al. 2008). However, low genetic diversity in peripheral populations does not always result in lower fitness or decreased population viability (e.g., Lammi et al. 1999; Milot et al. 2007). Furthermore, the trend of reduced genetic diversity in marginal populations is not ubiquitous, and arguments for the special status of peripheral populations range from their being most vulnerable to loss of genetic diversity to their being considered valuable because genetic diversity is high (Vecutich and Waite 2003).

Peripheral populations tend to diverge strongly from core populations when gene flow is sufficiently limited, and may therefore represent important components of intraspecific biodiversity and endemism, especially when divergence is driven by selection. They may also be isolated from disruptive forces spreading across continuous parts of species' ranges, which might explain why extant populations of many collapsed species tend to be located along the periphery, rather than the centre, of their historic ranges (Lomolino and Channel 1995). Peripheral populations may also have high conservation value if they are pre-adapted to stressful biotic, abiotic, or demographic conditions (Hoffmann and Blows 1994). In this sense, marginal populations may represent an important evolutionary legacy for species. This is particularly true if cases where they: have strongly diverged from core populations (which may indicate adaptive genetic differences), persist in an unusual habitat, exhibit unusual life history or morphology, have been isolated for a long time, are free of genetic introgression from introduced stocks, have avoided severe bottlenecks, or are at or near the ecological extreme of the species' range (Allendorf et al. 1997). They may also represent vital components of ecosystem diversity as members of native assemblages or biogeographical areas that are unusual or rare for the species (Allendorf et al. 1997).

Considering the need for judicious use of conservation funds, it is vital that biological reasons for the conservation of peripheral populations be carefully considered (Lesica and Allendorf 1995). In particular, where geopolitical bound-

daries often set biologically insignificant limits to species' ranges, conservation biologists must be vigilant that limited funds are not expended unnecessarily on peripheral populations of species that are globally secure, unless these populations fulfill criteria, such as those suggested above by Allendorf et al. (1997). A peripheral population may be little more than a transient offshoot (sink) from a stable central (source) population (e.g., Curnutt et al. 1996), persisting in a temporarily permissive environment and ultimately destined for local extinction. When protected areas are selected to maximize species diversity while minimizing the number of protected areas, the resultant bias towards areas of high habitat heterogeneity can result in the indiscriminate protection of peripheral populations, where the species may be quite rare. While the rarity of species in peripheral populations, along with low genetic variation and high probability of extinction, suggests that these may not be the areas to preserve a viable population, they may be genetically divergent, locally adapted, evolutionarily significant, or be of conservation importance to local humans irrespective of their widespread abundance elsewhere (Gaston 2003).

What limits species' ranges?

"The determination of how and why geographical ranges of species are limited should be a central objective of ecological research. . . It is extraordinary that such a fundamental question has received so little attention" (Gaston 2003; but see Sekercioglu et al. 2008). In the simplest cases, range edges are defined by a considerable change in the physical environment, like a coastline, or by the influence of humans limiting or enabling species distributions. In less obviously delineated cases range limits fall along an environmental gradient, presumably because the conditions beyond it exceed the species' tolerance for some feature(s) (Brown 1984). These could include individual or interactive effects of abiotic components of the physical environment, ecological factors including population or community dynamics, and genetic forces limiting the species' ability to evolve to overcome range-limiting factors (Parsons 1991; Hoffmann and Parsons 1997; Case and Taper 2000; Holt 2003).

Environmental range limitations

Despite Darwin's (1859) early suggestion that species' ranges are limited by a combination of abiotic environmental factors and interspecific interactions, it is often assumed that the former, and more specifically climate, is the principal determinant of organismal distributions. MacArthur (1972) was perhaps the first to suggest that this emphasis on climate was misguided, a judgment reiterated by others (Gaston 2003). However, strong correlations between climatic extremes and species' range edges, coupled with historic changes in the abundance and occurrence of species that track changes in climate, provide evidence that range edges can be strongly affected by climate (Hoffmann and Parsons 1997). This is supported further by the occurrence of species outside their continuous range in habitat patches analogous to those in the central environments (Undvady 1969), as well as strong correlations between climatic variables at the latitudinal and altitudinal dimensions of the same species' range (Meisner 1990). Northward expansions and

(or) southern retractions of species' ranges concomitant with climate warming (e.g., Parmesan 1996; Franco et al. 2006; Thomas et al. 2001; Cook and Heath 2005; Rose 2005; Fleischer et al. 2007; Wynn et al. 2007) further bolster this view.

The existence of arboretums and botanical gardens has been invoked as simple evidence that species can persist in foreign climates when other range-limiting factors are controlled (MacArthur 1972). However, this may be due to nothing more than the provision of an artificial climate, and it is often differences in other features of the environment, such as the reduction of biotic interactions (e.g., predation, competition), that allow species to persist in artificial settings. For example, exotic trees persist along many city streets where endemic competitors are excluded by urban landscaping (MacArthur 1972). The salient point is that while climate plays a role in limiting the distributions of most organisms, some interaction between climate and a variety of other factors almost certainly underpins range-limitation dynamics in most cases.

Although more subtle to the human eye than coastlines or other impermeable abiotic habitat transitions, variables such as pH, salinity, moisture, aridity, and trace metals or nutrients can also limit species' ranges where these factors approach the species' tolerance limits. Environmental variability in these and other abiotic (density-independent) factors, which are known to exert a dominant influence on peripheral populations (refs in Beddington et al. 1976; Pianka 1994; Gaston 2003), is often highest at the extremes of species' ranges, and can therefore play an important role in range limitation. Similarly, high levels of environmental stress at species' boundaries have also been invoked as a range-limiting factor (Shumaker and Babble 1980; Parsons 1991; Hummel et al. 1996).

Ecological range limitations

Hutchinson (1957) defined a niche as a combination of physical and biological environmental factors that affect the welfare of individuals of a species, and thereby determine its distribution. Brown (1984) extended this concept to suggest that a multidimensional niche defines species' ranges, and that while the absence of a single component can exclude a species, if the component is present, it will ultimately be a combination of variables that determines density. This manner of thinking is compatible with Darwin's early assertion that a combination of abiotic environmental factors and interspecific interactions define species' range, and is supported empirically (Hanski et al. 1991; Turchin and Hanski 1997).

MacArthur (1972) suggested that more species appear to have their range limited by habitat specialization than by any other factor, at least in the temperate zone, and that species may be unable to adapt to a range of habitats for two main reasons. Firstly, he suggested that biotic interactions with competitors, prey, or parasites might exclude species from habitats where they would otherwise survive. Secondly, he proposed that although species can display multiple genotypes for survival in different habitats, trade-offs between these alternatives limit species' abilities to adjust to abrupt habitat changes. Life history theory predicts that unusually stressful conditions can have significant impacts

on the evolution of life history traits and lead to trade-offs of differing magnitude across a species' range (Hoffmann and Parsons 1997). Although intense directional selection might be expected to drive evolution towards a trait value that would allow the species to overcome a range-limiting factor, the fitness consequences of trade-offs in entrained traits might prevent this.

Caughley et al. (1988) proposed that one could categorize range-limiting factors by the manner in which both the density and well-being of individuals changes from core to marginal areas. However, their somewhat cumbersome categorization of clinal changes as either "ramps" (gradual changes) or "steps" (little change from areas across the range, dropping off sharply at the edge) made it sufficiently difficult to acquire necessary data to categorize potential range-limiting factors that this approach has not been adopted in subsequent studies.

From a demographic perspective, the edge of the species' range is ultimately defined as the point where the death and emigration rates combine to exceed the sum of the birth and immigration rates, and this is set by a wide variety of biotic and abiotic factors (Gaston 1990). Intuitively, birth and death rates are more important determinants of population dynamics in sessile organisms, the dynamics of mobile organisms being more strongly influenced by immigration and emigration. The latter are key factors for peripheral populations because they can mitigate stressors by dampening the effects of local extinction and high temporal and spatial variability (Guo et al. 2005).

Beddington et al. (1976) outlined three possible demographic scenarios to explain range-limitation. Firstly, changing environmental conditions can alter average population parameters to the point where stable population dynamics are impossible. Secondly, the frequency or magnitude of unpredictable environmental events can attain a level where the probability of extinction within a few generations is high or certain. Lastly, the time required for populations to return to equilibrium is prohibitively long, such that small perturbations can lead to extinction. These explanations are consistent with conventional wisdom, models, and empirical evidence which show that core populations are more abundant and less temporally variable than peripheral populations (Vecutich and Waite 2003).

Evolutionary range limitations

Stressful environments, such as those often experienced at the edges of species' ranges, can result in increased genotypic and phenotypic variation in normally canalized traits (Parsons 1987). They can enhance fitness differences among genotypes, lead to associations between heterozygosity and fitness, and result in intense selection (Hoffmann and Parsons 1997). Nonetheless, all species reach a point at which they are no longer able to adapt to overcome range-limiting factors to expand their ranges, and diverse theories exist to address this.

Mayr (1963) and Carson (1975) proposed that genetic and phenotypic changes are most strongly restrained by epigenetic interactions or other homeostatic devices, making genetic units difficult to change radically. Vecutich and Waite (2003) revisited this idea and suggested that stable limits of species' ranges often reflect a balance between the costs of

inbreeding and the benefits of increased evolutionary potential due to the founder-flush phenomenon. In the same way that epistatic interactions among loci can restrict change in certain genetic systems, pleiotropic effects, whereby single genes influence numerous traits, could also limit the effects of selection. Conversely, pleiotropy has also been invoked to explain rapid change under extreme selection via changes in traits other than those directly under selection (Hoffmann and Parsons 1997).

There is an extensive body of literature discussing the “swamping” effect of gene flow as a cohesive force preventing local adaptation at the edge of the range (Soulé 1973; Stearns and Sage 1980; Brussard 1984). The principal of this idea is that asymmetrical gene flow from highly productive core populations outward into less productive peripheral populations can result in the latter receiving centrally-adapted genes that are maladaptive for their marginal habitat. Grinnell (1943) first noted this phenomenon as the out-migration of animals from core to edge populations, but he did not explicitly consider the genetic consequences of centrifugal dispersal. Haldane (1956) was the first to overtly suggest that the swamping effects of gene flow from central to peripheral populations could prevent local adaptation at the range margin. MacArthur (1972) agreed with the concept, but suggested that the obvious question of why any individual would ever migrate to a less favourable area needed to be considered. It is thought that this phenomenon can be sufficiently detrimental to make the peripheral part of species’ ranges act as demographic sinks (Kirkpatrick and Barton 1997), although gene flow may be too weak to exert maladaptive effects in most cases (Gaston 2003). Empirical support for the maladaptive effects of centrifugal gene flow is somewhat equivocal (Stearns and Sage 1980; Magiafoglou et al. 2002; Jump et al. 2003).

Several authors have hypothesized that reduced genetic variability may act to limit range expansion (Gaston 1990; Hoffmann and Parsons 1991; Parsons 1991; Hoffmann and Blows 1994), especially when changes in several independent characters are required for range expansion (these genotypes would be particularly rare). Given that heritability is determined by environmental and genetic variation, it can be reduced in areas of high environmental variation, such as range margins, which may result in diminished heritability for range-limiting traits. Furthermore, negative genetic correlations between stressful and favourable conditions, or among fitness-related traits under stressful conditions, may limit adaptations to stress, especially where the conditions that limit the range occur only occasionally, such that selection for range-expanding genes is short-lived (Hoffmann and Parsons 1991). There may also be a lack of response to directional selection under circumstances of heterozygote-advantage in stressful settings. While it is possible that the accumulation of deleterious mutations under stressful conditions could prevent adaptation, they may also bestow a source of genetic variation, helping to maintain adaptive potential (Lande 1995). Brown (1984) proposed that the repeated flux of species’ ranges out into unfavourable (hard) peripheral areas and back into the favourable (soft) core could result in a net inflow and incorporation of genetic innovations from marginal populations into central populations.

Evolutionary variability at the edge of species’ ranges

From a selectionist perspective, it is generally thought that genetic variation will decrease towards geographical limits of species’ ranges in response to different selection pressures as species reach the limits of their physiological acclimatization (Hoffmann and Parsons 1991), especially if strong directional selection erodes variability (Bellemín et al. 1978). Alternatively, the demographic characteristics of small and temporally variable peripheral populations could also account for reduced genetic variation through neutral mechanisms alone. Therefore, it is important to examine critically the pervasive view that variation declines towards species’ range edges, and to strive to disentangle deterministic (selection acting on adaptively significant variation) from stochastic (migration or dispersal acting on adaptively neutral variation) determinants of extant patterns. However, while most studies acknowledge that quantifying current and historic gene flow between populations is important, few take steps to estimate it. The nature of the genetic marker used can also strongly affect the results, and there remains a consistent concern regarding the possibility of confounding relationships between neutral marker variation and fitness. Alternatively, discordant patterns of variation from neutral and non-neutral markers may indicate that selective forces have strongly affected genetic population structure, whereas correspondence between patterns at neutral and non-neutral markers are more suggestive of stochastic forces. The literature concerning clinal patterns of genetic variation across species’ ranges of plants and animals is summarized (Table 1) and discussed below.

The paradox of chromosomal and allozyme variation clines in *Drosophila*

Early interest in central-peripheral clines in genetic variation focussed on chromosomal polymorphism, mostly drawing attention to the idea that repatterning of chromosomes via translocations, inversions, or changes in chromosome number might provide a basis for speciation in peripheral populations. Initial reductions in the fertility of chromosomally variant individuals may reduce their fitness in large core populations, but they can become established in small peripheral isolates (Soulé 1973). Stressful environments also appear to result in higher rates of crossing-over and recombination (Parsons 1987), although the underlying mechanism is unknown (Hoffmann and Parsons 1997).

Comparative studies of central and marginal populations of chromosomally polymorphic *Drosophila* species began in the 1950s (reviewed in Soulé 1973 and Brussard 1984), and identified a decline in chromosomal inversion polymorphisms towards species’ margins in nearly all species. Early workers observed a positive correlation between environmental complexity and inversion heterozygosity and advanced the ecological hypothesis that more genetically polymorphic individuals can exploit a greater range of environments (Dobzhansky et al. 1950). Carson (1956) proposed the homoselection–heteroselection hypothesis, that optimal conditions in core populations favour structurally heterozygous individuals via heterosis (supported by Wallace 1984), while strong directional selection in marginal populations fa-

Table 1. A summary of clinal central – peripheral/marginal/island population trends in genetic variation within species, identifying studies documenting central-peripheral decreases (–) or increase (+) in addition to those finding genetic uniformity or lacking a discernible pattern (=). The causal basis for the reported patterns (stochastic – S, deterministic – D) is that obtained from the original citation, otherwise specified.

Species	Central – peripheral change in genetic variation	Contributing forces stochastic (S) deterministic (D)	Reference
Plants & Algae			
<i>Avicennia marina</i>	–	S & D	Arnaud-Haond et al. 2006
<i>Lychnis viscaria</i>	–	S	Lammi et al. 1999
<i>Lysimachia volkensis</i>	–		Agnew 1968
<i>Sarracenia purpurea</i>	–	S	Schwaegerle and Schaal 1979
<i>Quercus suber</i>	–		Jiménez et al. 1999
<i>Hordeum jubatum</i>	–		Shumaker and Babble 1980
<i>Avena barbata</i>	–		Jain et al. 1981
<i>Cirsium acaule</i>	–		Jump et al. 2003
<i>C. arvense</i>	–		Jump et al. 2003
<i>C. heterophyllum</i>	=		Jump et al. 2003
<i>Veronica peregrina</i>	–	D	Linhart 1974; Keeler 1978
<i>Betula nigra</i>	+	D	Coyle et al. 1982
<i>Camellia japonica</i>	+		Chung and Chung 2000
<i>Viola pumila</i>	–	S	Eckstein et al. 2006
<i>V. stagnina</i>	–	S	Eckstein et al. 2006
<i>V. elatior</i>	=	S	Eckstein et al. 2006
<i>Lycopersicon pimpinellifolium</i>	–		Rick et al. 1977
<i>Pseudotsuga menzeisii</i>	=		Yeh and O'Malley 1980
<i>Pinus edulis</i>	=	S & D	Betancourt et al. 1991
<i>Pinus contorta</i>	–	S	Cwynar and MacDonald 1987
<i>Pinus contorta</i>	=	D	Wheeler and Guries 1982
<i>Picea abies</i>	=	S	Lagercrantz and Ryman 1990
<i>Picea abies</i>	=		Tigerstedt 1973
<i>Phlox drummondii</i>	=		Levin 1977
<i>Pinus contorta</i> spp. <i>latifolia</i>	–	S: 16/18 loci; D: 2/18 loci	Yeh and Layton 1979
<i>Cladophora rupestris</i>	–		Johannesson and André 2006 (review)
<i>Ceramium tenuicorne</i>	=		Johannesson and André 2006 (review)
<i>Fucus serratus</i>	=		Johannesson and André 2006 (review)
<i>Fucus vesiculosus</i>	–		Johannesson and André 2006 (review)
<i>Zostera marina</i> (3 studies)	–		Johannesson and André 2006 (review)
Invertebrates			
<i>Drosophila</i> spp. (chromosome polymorphism)	–	S and (or) D (study-dependent)	Soule 1973; Brussard 1984 (reviews)
<i>Drosophila</i> spp. (allozymes)	+	S	Soule 1973 (review)
<i>D. willistoni</i>	–	D	Ayala et al. 1971
<i>D. melanogaster</i>	=	D	Gockel et al. 2001
<i>D. melanogaster</i>	=	S: 99/117 loci; D: 18/117 loci	Singh and Rhomberg 1987
<i>D. pseudoobscura</i>	=		Prakash et al. 1969
<i>Hemiargus isola</i>	=		Burns and Johnson 1971
<i>Parnassius mnemosyne</i>	–	S	Descimon and Napolitano 1993
<i>Macoma balthica</i>	–	D	Hummel et al. 1995
<i>M. balthica</i>	+		Hummel et al. 1997
<i>M. balthica</i>	–		Johannesson and André 2006 (review)
<i>M. balthica</i>	=		Johannesson and André 2006 (review)
<i>Cerastoderma glaucum</i>	–		Johannesson and André 2006 (review)
<i>Mytilus edulis</i>	–		Johannesson and André 2006 (review)
<i>Mya arenaria</i>	–		Johannesson and André 2006 (review)
<i>Cyprideis torosa</i>	–		Johannesson and André 2006 (review)
<i>Mysis mixta</i>	=		Johannesson and André 2006 (review)

Table 1 (concluded).

Species	Central – peripheral change in genetic variation	Contributing forces stochastic (S) deterministic (D)	Reference
<i>Crangon crangon</i>	=		Johannesson and André 2006 (review)
<i>Gammarus salinus</i>	=		Johannesson and André 2006 (review)
<i>Gammarus zaddachi</i>	–		Johannesson and André 2006 (review)
<i>Hediste diversicolor</i>	=		Johannesson and André 2006 (review)
<i>Halicryptus spinulosus</i>	–		Johannesson and André 2006 (review)
Vertebrates			
<i>Bufo viridis</i>	=		Dessauer et al. 1975
<i>Acris gryllus</i>	–		Dessauer and Nevo 1969
<i>Uta stansburiana</i>	–		McKinney et al. 1972
<i>Dipodomys merrii</i>	–		Johnson and Selander 1971
<i>Peromyscus polionotus</i>	–		Selander et al. 1971
<i>Alectoris chukar</i>	+		Safriel et al. 1994
<i>Poeciliopsis occidentalis</i>	–		Vrijenhoek et al. 1985
<i>Salmo trutta</i>	–	S	Bouza et al. 1999
<i>Salmo salar</i> (3 studies)	–		Johannesson and André 2006 (review)
<i>Rhinichthys cataractae</i>	–	S	Merritt et al. 1978
<i>Astyanax mexicanus</i>	–	S	Awise and Selander 1972
<i>Catostomus clarkii</i>	–	D	Koehn 1969
<i>Pimephelas promelas</i>	–	D	Merritt 1972
<i>Platichthys flesus</i>	=		Johannesson and André 2006 (review)
<i>Scophthalmus maximus</i>	=		Johannesson and André 2006 (review)
<i>Gadus morhua</i>	–	S	Hardie et al. 2006
<i>Gadus morhua</i> (4 studies)	–		Johannesson and André 2006 (review)
<i>Clupea harengus</i> (2 studies)	=		Johannesson and André 2006 (review)
<i>Zoarces viviparous</i>	–		Johannesson and André 2006 (review)
<i>Acris spp.</i>	–		Dessauer and Nevo 1969
<i>Rana pipiens</i>	–	S	Salthe 1969
<i>Plethodon cinereus</i>	–	S & D	Highton and Webster 1976
<i>Thamnophis sirtalis</i>	–	S & D	Sattler and Guttman 1976; Bellemin et al. 1978
<i>Lacerta spp.</i>	–	S & D (locus-dependant)	Gorman et al. 1975
<i>Lacerta agilis</i>	–	S	Gullberg et al. 1999
<i>Lagopus lagopus</i>	–	S and (or) D	Gyllensten et al. 1985
<i>Passer domesticus</i>	–	D	Väisänen and Lehtväslaiho 1984
<i>Macaca mulatta</i>	–		Goodman et al. 1965
<i>Carduelis chloris</i>	–	S	Merilä et al. 1996
<i>Ovis dallii</i>	–	S	Sage and Wolff 1986
<i>Lynx canadensis</i>	–	S	Schwartz et al. 2003
<i>Phocoena phocoena</i>	=		Johannesson and André 2006 (review)
<i>Phoca vitulina</i>	–		Johannesson and André 2006 (review)

vours particular gene arrangements as homozygotes and, thereby, greater freedom of recombination. He provided empirical support for this by showing that a monomorphic peripheral strain responded to selection for movement towards light more strongly than did a central polymorphic strain (Carson 1958). Similarly, Tabachnick and Powell (1977) demonstrated that monomorphic *Drosophila* populations adapted better to novel stressful environments than did polymorphic populations, but stressed that this may not always be the case, particularly where marginal conditions represent a subset of the central environment, such that recombination would disrupt existing co-adapted gene complexes.

Others took a more neutralist approach, pointing out that morphologically and chromosomally polymorphic species almost invariably show a decrease in polymorphism towards

the species' border where peripheral populations are frequently monomorphic, and considered repeated isolation and low population density as the main factors underpinning this trend (Mayr 1963). Soulé (1971) agreed and advanced the gene flow variation hypothesis, accounting for the observation that peripheral *Drosophila* populations that were not marginal still exhibited lower chromosomal polymorphism. Later, he suggested that because peripheral populations were generally younger than central ones (due to more frequent colonization and (or) extinction) the reduction in heterozygosity was likely transient (Soulé 1973).

Despite the ubiquity of the central-marginal decline in inversion polymorphism in *Drosophila* spp., the advent of electrophoretic techniques painted a paradoxical picture; enzyme variation was equal or higher in marginal fruit fly

populations compared to core populations (the allozyme paradox, reviewed in Soulé 1973). Soulé (1973) offered the explanation that novel environments cause a transient reduction in inversion variability because of directional selection on chromosomes and chromosome segments that are favourable for their production of stress-adapted character states, calling it the Epistasis Cycle. In contrast, he expected similar selection pressures across the species' range for polymorphic loci, as these confer increased fitness via heterosis in *both* central and marginal areas. Brussard (1984) criticized this view on evidentiary and theoretical grounds, proposing instead that rapid return-times from population bottlenecks would minimize effects on average heterozygosity, and that sporadic gene flow from central areas would sufficiently decrease isolation of marginal populations and increase overall effective population size. Interestingly, this paradox only appears to apply to fruit flies. By contrast, allozyme variation has been observed to decrease towards the margins of the ranges of four terrestrial vertebrate species (Soulé 1973) and many other organisms as well (Table 1). Soulé explains this by suggesting that, while there is no inherent difference in genetic systems of *Drosophila* and terrestrial vertebrates, the latter are less vagile, such that genetic drift and low gene flow can act to depress allelic variation in marginal populations.

Increasing genetic variation toward species' range edges

The allozyme paradox highlights the important point that different types of markers and (or) taxa often give discordant results that pertain to the central-marginal problem. Nonetheless, studies identifying elevated measures of genetic variation in peripheral populations are few in number (Table 1). At a local scale, Linhart (1974) advocated a genetic (disruptive selection) explanation for increases in quantitative trait variation in neckweed (*Veronica peregrina*) from the periphery of vernal pools compared to plants from the centre of the pools. Patterns of electrophoretic variation were consistent with Linhart's phenotypic observations and provided support for his selectionist interpretation (Keeler 1978). Other than this and very few other examples, genetic variation among plant populations most often decreases from central to peripheral populations, or shows no consistent trend across species' ranges, and the same is true of most invertebrate and vertebrate species (Table 1).

Prakash (1973) suggested that balancing selection most likely maintained higher heterozygosity and more polymorphic loci among marginal *Drosophila robusta* populations. Although Safriel et al. (1994) reported elevated genetic variation towards the southern periphery of the range of the chukar partridge (*Alectoris chukar*) relative to core populations, genetic data from other peripheral components of the species' range were not reported, so the possibility remains that this is a latitudinal decrease in genetic variation, rather than a central-peripheral pattern. Although Gaston (2003) classified a decline in heterozygosity with increasing latitude among European greenfinch populations (*Carduelis chloris*; Merilä et al. 1996) and lower variability in central European Norway spruce populations (*Picea abies*; Lagercrantz and Ryman 1990) as counter-examples to low marginal genetic variation, the results of both studies can be explained by higher genetic variation within older populations from gla-

cial refugia. Eckert et al. (2008) recently reviewed 134 studies representing 115 species to test for declines in within-population genetic diversity and increases in among-population differentiation towards range margins. Although they found that the majority of studies detected the expected decline in diversity (64.2%) and increased differentiation between central and peripheral populations, they cautioned that these differences were generally small and that there were strong taxonomic and biogeographic biases in the data. Furthermore, they found that few studies attempted to identify the possible mechanisms, to evaluate the historical influences of phylogeography, or to test whether trends in neutral variation were reflected by quantitative trait variation.

While the above examples support the pervasive idea that reduced genetic variation often results from recent population bottlenecks (Lewontin 1965), this may not always be the case, particularly where repeated colonization-extinction cycles have occurred. Experiments by Bryant et al. (1986) showed that repeated bottlenecks could result in increased additive genetic variance in houseflies (*Musca domestica*), although the authors were cautious in interpreting the significance of their results beyond this species.

Homogeneity of genetic variation across species' ranges

In other cases, there exists no clear cline of genetic variation from central to peripheral components of species' distributions, particularly among plants and invertebrates (Table 1). Bentancourt et al. (1991) cited heterosis, large founding population size, multiple founder events, and rapid growth of colonial populations as possible explanations for unexpected genetic homogeneity among central and peripheral isolated populations of Pinyon pine (*Pinus edulis*). Similarly, the genetic uniformity of Lodgepole pine (*Pinus contorta*) populations in Western North America despite near complete isolation and strong morphological divergence among populations is symptomatic of strong local selective pressures (Wheeler and Guries 1982). Likewise, the uniformity of microsatellite variation across the species range of *D. melanogaster* in eastern Australia suggests that selection, rather than population history, accounts for strong clinal increases in body size (Gockel et al. 2001). In an extensive global study of 117 allozyme loci in *D. melanogaster*, Singh and Rhomberg (1987) found that nearly half of the loci were monomorphic, and only 18 showed clinal variation in allele frequencies across continents. They invoked balancing selection to explain clinally varying loci, but cautioned that previously identified patterns may not be supported when a large and unbiased sample of loci is examined.

Decreasing genetic variation toward species' range edges

Most studies are consistent with the general perception that peripheral populations are less genetically variable than those inhabiting central areas (Table 1). Johannesson and André (2006) attributed central (Atlantic) to peripheral (Baltic) decreases in genetic variation in nearly all of their taxonomically diverse review of 29 species from 41 studies to the effects of genetic drift in isolated and size-restricted Baltic populations. Among plants, peripheral populations tend not only to be less genetically variable, but also more

highly differentiated, particularly where they are from previously glaciated areas while central samples derive from glacial refugia (Schwaegerle and Schaal 1979; Cwynar and MacDonald 1987). Based on prior evidence of clinal decreases in population density and seed production away from the centre of the species' ranges, Jump et al. (2003) predicted that peripheral populations of three thistle (*Cirsium* sp.) species would show a concomitant decrease in genetic variation and increase in population divergence. While patterns within two species were consistent with this prediction (*C. acaule* and *C. arvense*), a third (*C. heterophyllum*) showed different genetic variation patterns, suggesting that it can be misleading to draw general conclusions about genetic variation across geographical ranges based solely on present-day characteristics and distributions. Eckstein et al. (2006) invoked stochastic forces, most notably genetic drift, to explain low peripheral genetic variation in two of three species of floodplain violet (*Viola* spp.). Although central-marginal decreases in genetic variation among Lodgepole pine populations were mostly suggestive of neutral forces, some loci appeared affected by selection (Yeh and Layton 1979), and this species was later reported to be genetically uniform across its North American range (Wheeler and Guries 1982).

In addition to the evidence of central-marginal decreases in chromosome inversion polymorphism across many *Drosophila* species' ranges (Soulé 1973; Brussard 1984), Ayala et al. (1971) documented even sharper reductions in chromosome polymorphism on peripheral island populations of *D. willistoni*. They invoked balancing selection to explain this trend, citing the fact that these declines exist despite very large population sizes. By contrast, Descimon and Napolitano (1993) suggested that low allozyme diversity in peripheral populations of the endangered butterfly (*Parnassius mnemosyne*) was consistent with restricted gene flow to peripheral isolates. Interestingly, they suggested that this reduction in genetic diversity could explain the inverse trend of elevated morphological variation in peripheral populations via decreases in canalization power associated with decreased genetic diversity. Hummel et al. (1995) linked strong decreases in heterozygosity in peripheral populations of the Baltic clam (*Macoma balthica*) to a reduction in the frequency of a particular allele associated with stressful conditions in marginal environments.

A central-marginal decrease in genetic variability has also been documented in most vertebrates (Table 1). Bouza et al. (1999) and Merritt et al. (1978) invoked stochastic processes such as founder effects, isolation and (or) low gene-flow to explain decreasing genetic diversity from central to southern peripheral portions of the range of anadromous brown trout (*Salmo trutta*) and similar declines in heterozygosity with latitude in longnose dace (*Rhinichthys cataractae*), respectively. Remarkably, although marginal eyeless cave-dwelling populations of the Mexican tetra (*Astyanax mexicanus*) also have very low heterozygosity relative to eyed surface populations, there is very little evidence of genetic differentiation among them, suggesting an ancient colonization followed by periodic gene-flow (Avise and Selander 1972), and presumably intense selection for eyelessness in the cave environment.

Several studies have linked reduced heterozygosity in northern and southern peripheral populations to a simple two-allele system in fishes. In such cases, northern populations are hypothesized to be selected for a cold-adapted allele in the homozygous state and southern populations for a warm-adapted allele in the homozygous state, with central populations tending to be heterozygous at these loci (*Catostomus clarkii*, Koehn 1969; *Pimephelas promelas*, Merritt 1972).

Although peripheral populations of lacertid lizards (*Lacerta* spp.) consistently exhibit low genetic variation, Gorman et al. (1975) described some interesting trends in these data. As might be expected, island populations exhibit lower genetic variability than mainland populations, and small island populations have lower variation than those on larger islands. Despite their close proximity to mainland populations, some very small islands presented extremely low genetic variability due to drift acting on small population size. Allele frequencies at some loci were suggestive of strong selection, while others appeared driven by genetic drift. Stochastic processes such as population bottlenecks and genetic drift were invoked to explain low genetic variation in peripheral sand lizard (*Lacerta agilis*) populations in Sweden, although the latter did not appear to be more strongly differentiated from each other than populations from central parts of the range, suggesting that gene flow is very limited in all cases (Gullberg et al. 1999). The significant reduction in genetic variability in island populations of the willow grouse (*Lagopus lagopus*) supports both selectionist (directional selection related to mainland-island climate differences) and neutralist explanations (divergence and loss of variation due to low migration and philopatric breeding on islands; Gyllensten et al. 1985) while the absence of genic polymorphism in northern populations of the house sparrow (*Passer domesticus*) lends support to selection-based (directional) hypotheses (Väisänen and Lehtväslaiho 1984).

In other cases, declines in sundry measures of genetic variation with latitude are almost certainly linked to the historic effects of the current glacial cycle (Dessauer and Nevo 1969; Salthe 1969; Highton and Webster 1976; Sattler and Guttman 1976; Bellemin et al. 1978), although these patterns can be interpreted in two non-exclusive ways. The deterministic explanation is that shared ancestry, behavioural grouping, local decimation due to severe peripheral conditions and (or) strong directional selection can account for genetic homogeneity towards the northern periphery. In other cases, the stochastic effects of repeated founder events and population bottlenecks associated with the inherent instability of northern populations (*Carduelis chloris*; Merilä et al. 1996), the historical flux of geographical ranges (*Ovis dallii*; Sage and Wolff 1986), or both (*Lynx canadensis*; Schwartz et al. 2003) have been invoked to explain northward decreases in genetic variation.

Weighing the evidence: genetic variation across species' ranges

Some combination of deterministic or selective and stochastic or neutral factors, whether acting in concert (e.g., Merritt et al. 1978; Wheeler and Guries 1982; Johannesson and André 2006; Raffl et al. 2006) or in opposition (e.g., Johnson 1974), determines clines of genetic variation across

species' ranges. Because peripheral populations are likely to be more recent, smaller, and at least somewhat isolated compared to central populations, they will tend towards genetic homogeneity based on stochastic/neutral mechanisms such as founder effects, population bottlenecks, isolation, genetic drift and inbreeding, independent of selective forces. Moreover, stochastic peripheral population fluctuations may intensify already marked differences between effective and census population sizes, further exacerbating stochastic genetic effects (Johannesson and André 2006). Consequently, with the somewhat tenuous exception of serial bottlenecking (Bryant et al. 1986), it is unlikely that stochastic processes could act to increase genetic variation in peripheral populations. However, multiple founding events, large founding population sizes, rapid growth of colonial populations and maintenance of gene flow can all act to homogenize genetic variability (e.g., Bentancourt et al. 1991).

One is left to assume, then, that clinal central-marginal increases in genetic variation must be due to deterministic forces of sufficient intensity to overcome the stochastic effects discussed above, yet strong support for such forces is difficult to identify. In contrast to the usual interpretation that selection would most strongly favour heterozygotes in dense, optimal central environments (Carson 1956), the idea that heterotic selection increases under stressful conditions (Hoffmann and Parsons 1997) has been invoked to explain non-clinal genetic variation (e.g., Bentancourt et al. 1991) and the maintenance of higher genetic variation in marginal conditions (Lesica and Allendorf 1995). Other authors have invoked selection on adaptively significant polymorphisms to explain genetic homogeneity or variability increases from central to marginal populations (Prakash 1973; Linhart 1974; Wheeler and Guries 1982; Singh and Rhomberg 1987; Gockel et al. 2001).

The observation that most peripheral populations tend towards genetic homogeneity may support the above-mentioned assertion that stochastic forces are most likely to depress peripheral variability acting alone (e.g., Merritt et al. 1978; Bouza et al. 1999; Johannesson and André 2006; Raffl et al. 2006) or in concert with deterministic forces (e.g., Gorman et al. 1975; Bellemin et al. 1978; Gyllensten et al. 1985). Many cases of reduced genetic variation, often concomitant with strong differentiation, among populations on previously glaciated lands are consistent with historical and stochastic interpretations of the effects of isolation and bottlenecks (e.g., Salthe 1969; Highton and Webster 1976; Sattler and Guttman 1976; Sage and Wolff 1986; Merilä et al. 1996). The tendency of marginal-peripheral environments to differ, sometimes acutely so, from core areas often results in intense directional selection, which erodes genetic variability. Centripetal gene flow during range contractions could contribute genetic diversity from ecologically versatile marginal populations, enhancing and enriching the genetic diversity of core populations (Brown 1957; Scudder 1989). However, examples of non-clinality and elevated marginal genetic variation, coupled with evidence that locally adapted peripheral isolates perform relatively poorly in good conditions (Hoffmann and Blows 1994), suggest that the concept of centripetal gene flow cannot be universally applied. The group of hypotheses (Ludwig, Carson's and Niche-Width Variation hypotheses) that link habitat heterogeneity to ge-

netic variability (Carson 1956; Mayr 1963; Wallace 1984) are consistent with widespread evidence of marginal homogeneity, and may account for the loss of variation in marginal populations (reviewed in Soulé 1973). In some cases, this can be linked back to selection for the homozygous state of alleles optimized for extreme conditions (e.g., Koehn 1969; Merritt 1972) or balancing selection (e.g., Ayala et al. 1971; Hummel et al. 1995), while other studies suggest the existence of fitness benefits associated with elevated genetic variability in complex environments (e.g., Powell 1971; Gorman et al. 1975; Yeaman and Jarvis 2006).

Although some have suggested that selection is involved in most geographic clines in genetic variation, and that explanations based on neutral mutations and drift are less important (Gould and Johnston 1972), it is often difficult to disentangle deterministic from stochastic mechanisms unless both neutral and non-neutral markers are employed. Verily, when this is done properly, stochastic factors can prove to be of dominant significance (e.g., Johannesson and André 2006; Raffl et al. 2006). An accurate understanding of the evolutionary dynamics of any population requires awareness of the dynamics of colonization, including founder effects, the duration and severity of population bottlenecks, and the degree of isolation, so it is vital that such studies take steps to understand both neutral and selective influences on extant patterns of genetic variation.

Additionally, more focus is needed on quantitative traits if we are to understand geographic variance in different components of genetic variance. Quantitative morphological characters may be useful indicators of isolation, since they are expected to diverge more rapidly than gene frequencies when gene flow is limited (Lesica and Allendorf 1995). Secondly, partitioning genetic variation into its component parts yields important measures of variability, including broad- and narrow-sense heritabilities (Falconer and Mackay 1996) and trait evolvability (Houle 1989), and can identify maternal or environmental genetic interactions that contribute to phenotypic variation in variable marginal environments (Laugen et al. 2005).

Ecological variability at species' range edges

For our purposes, ecological variables related to the abundance or density of organisms in time and space in different parts of the species' range are of particular interest, as they underpin several important ideas. For example, if one espouses the commonly held belief that abundance is low in peripheral populations, such that density-independent processes exert dominant influence, then one must also expect that peripheral population sizes will be highly variable, resulting in high rates of local extinction (Gaston 2003). Furthermore, elevated population size variability, especially to the degree of repeated local extinction and colonization or population bottlenecks, can have significant evolutionary implications, as discussed above. From a conservation perspective, populations exhibiting source-sink dynamics between core and peripheral areas of a species' range may justify conservation of core populations, especially if peripheral conditions are too short-lived or if gene flow from central areas impedes local adaptation. Because range limits are defined by conditions where the sum of the death and emi-

gration rates exceeds the sum of birth and immigration rates, these variables, as well as recruitment variability and dispersal, are also of great consequence. What is more, high extinction and colonization rates in peripheral populations may select for dispersal ability (Holt 2003). Variability in life-history parameters, including reproductive energy allocation (fecundity, offspring size) and timing (age and size at maturity), frequency of dormancy or diapause and degree of semelparity or iteroparity, can also exert strong influence on peripheral populations. While considerable attention has focussed on how these traits vary across species' ranges, few studies have investigated inter-population differences in variability itself.

In general, there exists theoretical and empirical support for the idea that peripheral populations tend to be less abundant and less dense, yet more temporally variable in these features (Henderson and Seaby 1999; references in Vecutich and Waite 2003; Guo et al. 2005; but see Sagarin et al. 2006). This is consistent with the observation that peripheral environments tend to be more rigorous and unpredictable (references in Leggett and Carscadden 1978; Hoffmann and Parsons 1997; but see references in Rohde 1992), resulting in smaller, more temporally variable populations (Mayr 1963). Although Brown (1984) proposed that density should be highest at the centre of the range, where conditions presumably most fully satisfy the requirements of a species' multidimensional niche, Sagarin et al. (2006) recently cautioned against the indiscriminate application of the 'abundant-centre hypothesis' without large-scale descriptive ecological evidence.

Despite suggestions that rates of population increase should be highest in optimal core conditions, such that one might expect greater population size oscillations than in peripheral populations (May 1981), there is little support for this hypothesis (e.g., Grant and Antonovics 1978). In fact, the preponderance of empirical evidence across diverse taxa reveals low absolute, but highly temporally variable, peripheral population abundance and density (e.g., Beddington et al. 1976; Brown 1984; Thomas et al. 1994; Brown et al. 1995; Enquist et al. 1995; Lesica and Allendorf 1995; Curnutt et al. 1996; Kirkpatrick and Barton 1997; Thomas et al. 2001; Vecutich and Waite 2003; Johannesson and André 2006), often resulting in high local extinction rates in peripheral areas (e.g., Mayr 1963; Shumaker and Babbie 1980; Enquist et al. 1995; Nantel and Gagnon 1999; González-Megías et al. 2005), an observation consistent with the predictions of source-sink dynamics theory (Pulliam 1988). Unlike vagile organisms, which have the ability to disperse or migrate to track changing environmental conditions, sessile organisms are more likely to alter birth or death rates as proximate responses to changing abiotic and biotic conditions (Guo et al. 2005). As a result, one expects birth, death, immigration, and emigration rates in marginal populations to track, to some degree, the high temporal environmental variability characteristic of peripheral environments. The fact that range-edge conditions tend to approach species' tolerance levels suggests that demographic parameters might be particularly sensitive to changes in environmental conditions.

Following on from the generalization that peripheral environments tend to be more temporally variable, one should

expect concomitant clinal increases in recruitment variability towards the edges of species' ranges (Ricker 1958), particularly if density-independent factors are strong determinants of peripheral population dynamics, since these exert a stronger influence on recruitment than density-dependent factors (Myers and Drinkwater 1989). This prediction is borne out at the extremes of some marine fishes' ranges (Myers 1991; Rijnsdorp et al. 1992; Walsh 1994), while others exhibit clinal decreases in recruitment variability with latitude (Walsh 1994) or dome-shaped distributions of greatest recruitment variability in central parts of their ranges (Leggett and Frank 1997; Philippart et al. 1998). Leggett and Frank (1997) cited methodological differences in the calculation of recruitment estimates, time-span of temporal variability data sets, and fundamental dissimilarities in the factors influencing recruitment in different species as explanations for these incongruent results, and stressed the importance of obtaining data spanning entire species' ranges.

Population cycles comprise a form of temporal population size variability that is generally considered uncommon in nature, although they may be more frequent at high latitudes (Kendall et al. 1998). For example, temporal population density variability increases with latitude in Fennoscandian rodent populations and is predictable in northern populations when compared with low but unpredictable variation in southern populations (references in Hanski et al. 1994). It is thought that this difference derives from cyclic predator-prey interactions between rodents and specialist mammalian predators in the north (Hanski et al. 1991) versus rodent interactions with an increasing diversity and pooled density of generalist predators in the south (Hanski et al. 1993). Based on the association between cycle period and body size in herbivorous birds and mammals, and Bergmann's rule (body size increases with latitude), Kendall et al. (1998) analyzed long-term field abundance data from 700 animal populations to test for latitudinal gradients in cyclic population characteristics. They found considerable evidence of cyclic population dynamics (nearly 30% of populations), mostly in mammals and fishes. The incidence of population cycles increased with latitude only in mammals, cycle amplitude decreased with latitude in some fish taxa, and there was no gradient in cycle period. In contrast, Erb et al. (2000) identified a positive correlation between period length and latitude in Canadian muskrats (*Ondatra zibethicus*), citing anthropogenic (hunting and trapping effort), behavioural and life-history (social effects of density), and extrinsic (predation intensity, disease, food availability) factors to explain this clinal variation.

Where peripheral environments tend towards temporal instability and approach species' tolerance limits, one might predict that variable life histories may be advantageous. In particular, bet-hedging strategies that spread the risk of reproductive failure across the potential timescale of catastrophic environmental variation may be favoured. This can include individual-level variation, such as brood asynchrony, or population-level variation, such as variability in germination time (Linhart 1974; Simons and Johnston 2006). However, most studies focus on variation among populations across species' ranges, while data comparing intra-population variability within species' ranges are uncommon. For example, clinal increases in fecundity with latitude are

known from many fish and bird species, but the adaptive basis for these patterns are not obvious. Fleming and Gross (1990) suggested that this trend is driven by selection for small egg size in Pacific salmon, which entrains high fecundity as a trade-off due to the complete utilization of ovarian resources, and that this might explain similar trends in other animal species. There are many other examples of inter-population comparisons of life-history variation that have revealed convincing evidence of strong directional selection across species' ranges, but these are beyond the scope of this review. However, this highlights the important point that the study of life-history trait variability at any level is particularly susceptible to obfuscation by selection on interrelated traits, such that one must be careful when inferring selective mechanisms.

In some cases, clinal increases in frequencies of life-history strategies that are unusual in some part of species' ranges can be viewed as imparting variation (i.e., variation would be considered highest when 50% of the populations adopt each of two alternative strategies). One example of this is clinal changes in the proportion of fish populations that are iteroparous or semelparous. Several fishes that are semelparous at low latitudes grade towards iteroparity at higher latitudes, such that mid-range populations are most variable (Leggett and Carscadden 1978 and references therein), although this is not always the case (Deangelis and Coutant 1982). Similarly, the frequency of diapause or dormancy in certain plant and insect species increases with environmental unpredictability (references in Hoffmann and Parsons 1997). In both cases, the elevated yet unpredictable likelihood of intense juvenile mortality due to unfavourable environmental conditions probably drives range-edge populations to adopt life histories that spread total reproductive effort across the temporal scale of environmental variability. This is consistent with life history theory (Cole 1954) that predicts that mature individuals in the highly competitive, lower latitude populations (where adult survival is less certain) should tend to direct all of their resources into fewer bouts of higher reproductive effort, especially where favourable core conditions intimate high juvenile survival. Another example is that of hatching asynchrony (within broods) of birds, which is thought to be advantageous in unpredictably harsh environments (Lack 1954). In good years, available resources can support the entire brood, including the late hatchlings, and fitness loss relative to a synchronous brood should be minimal. However, in harsh years, late offspring will die, resulting in higher survival of the early hatchlings than if their younger siblings had survived, and higher overall fitness than a synchronous brood. Theoretical and empirical studies support this idea, although explanations unrelated to environmental variability should not be ignored (Hoffmann and Parsons 1997). Northern and southern peripheral populations of walleye (*Sander vitreus*) exhibit steeper regression slopes between egg size and maternal length in central parts of their range (Johnston and Leggett 2002), such that egg size variability is greater in peripheral walleye populations. Other life history traits have been found not to vary with latitude, such as within-population variation in age at maturity in Atlantic salmon (*Salmo salar*; Myers and Hutchings 1987).

Weighing the evidence: ecological variation across species' ranges

The generalization that peripheral populations tend to be smaller, less dense, and more variable (or cyclic) than central populations is strongly upheld. Low peripheral population abundance or density appears related to low resource abundance, harsh conditions approaching species' biological tolerances, and high frequencies of local extinction, which are themselves likely related to high peripheral environmental stochasticity (Soulé 1973). However, simplified interspecific interactions in less diverse, high-latitude populations may also contribute, where individuals in peripheral environments are likely to experience lower diversity of prey, predators, and competitors, thereby reacting strongly and quickly to abundance variation in any of these factors.

The literature reviewed here does not reveal any *consistent* cline of life-history variability across species' ranges. However, there is some support for the prediction that reduced density-dependent interactions and higher environmental stochasticity in peripheral populations may increase the variance in juvenile survival, favouring life-history traits that distribute the probability of reproductive failure across the timescales of environmental variability (i.e., "bet hedging", Slatkin 1974; Boyce 1988; Philippi and Seger 1989, Simons 2009). The study of clinal trends in life history variation across species' ranges is complicated by trade-offs among traits (Holt 2003), in particular by the fact that these trade-offs can limit, allow, or entrain other traits in a manner that may be difficult to reveal. However, given the abundance of data on various life history variables from many populations of diverse taxa, opportunities abound to test hypotheses concerning intra-population variability across species' ranges. Questions concerning the degree to which marginal populations depend on trade-offs among life history traits to contend with high environmental variability near their tolerance limits are of particular interest. For example, the clinal study of life-history variability across species' ranges could address the questions of whether the flexibility conferred by trade-offs among life history traits dampens the effects of high environmental stochasticity at range margins (e.g., Bears et al. 2009; Sandercock et al. 2005).

Dispersal as an overarching idea: take the heat or get out of the kitchen

Individuals faced with environmental stress outside of their tolerance range can respond in two ways. In keeping with the adage that one can either "take the heat or get out of the kitchen", they can either adapt to overcome the range limitation, or move to a more favourable environment. Given that these options are not mutually exclusive, there is likely to be genetic variation in niche requirements and dispersal propensities among individuals within a species. Therefore, the delineation of species' ranges is likely to reflect a co-evolutionary interplay between selection on adaptation to habitats and selection on dispersal (Holt 2003). However, while there is much empirical support for the hypothesis that range expansions reflect responses to changes in the availability of suitable habitat, examples of range expansion via evolutionary innovation are exceedingly rare

(Gaston 2003). Although there is consensus concerning the evolutionary implications of complete isolation (i.e., genetic divergence), the idea that gene flow is continuous and widespread, acting as a cohesive force causing species to evolve as a unit in the absence of geographical isolation, has been questioned for some time (Ehrlich and Raven 1969; Ender 1973; Gaston 2003). In general, it appears that gene flow into many peripheral populations is simply too low for this mechanism to exert a strong maladaptive effect (Gaston 2003).

From a conservation perspective, organisms exposed to variable environments tend to exhibit higher dispersal rates (Hoffmann and Parsons 1997), which may allow them to occupy habitats where their niche requirements are not met (Brown and Lomolino 1998). The protection of peripheral populations that are simply demographic sinks from source core populations could be wasteful and ineffective, especially if the species is left exposed to threats in central parts of its range. On the other hand, evidence of high levels of gene flow between core and peripheral populations, even if it appears unidirectional and outward, is not in itself justification for failing to protect peripheral populations. Moreover, peripheral populations can be of considerable conservation value when they act as sources of recruits for stable central populations, as has been shown for Florida scrub jays (*Aphelocoma coerulescens*; Rangel-Salazar et al. 2008). The question remains whether asymmetrical flow of maladaptive genetic material from core to peripheral populations is sufficient to prevent local adaptation in the latter. This depends, among other things, on the extent and frequency of gene flow and on habitat disparities (and concomitant selection differentials) between core and peripheral populations. All that can be concluded in this regard is that understanding the degree of isolation of peripheral populations is of great consequence, and that this must be approached from divergent perspectives. While lower gene flow can limit the provision of genetic diversity in peripheral populations, it can also act to intensify the effects of genetic drift and diminish the potential for maladaptive swamping of the peripheral gene pool by centrally adapted genes (Hoffmann and Blows 1994). The potential for a conflicting interplay between the provision of genetic diversity upon which selection can act and the maladaptive effects of central genes has led some to postulate that the greatest evolutionary capacity occurs when dispersal is modest (Holt 2003).

Although dispersal impinges strongly on the extent of genetic differentiation among populations, this relationship is complex. In general, there is a negative relationship between gene flow and genetic differentiation. For example, plant populations tend to be significantly less genetically divergent where cultivation intensifies seed dispersal than in adjacent uncultivated lands (Jain and Rai 1980). However, the expectation that low dispersal ability should increase isolation, thereby favouring genetic differentiation, is not always upheld (e.g., Johannesson and André 2006), suggesting that even small amounts of gene flow can prevent differentiation (Schwaegerle and Schaal 1979), even when phenotypic differentiation is acute (Avisé and Selander 1972). Conversely, episodic gene flow events can act to homogenize genetic

structure among seemingly disjunct populations with low apparent connectivity (Fedy et al. 2008).

One might also expect selection to favour strong dispersal ability in peripheral populations because of the higher frequency of local extinction–colonization cycles attributable to stochastic demographic and environmental processes at range edges. The most vagile individuals from central populations should be those most likely to respond to fluctuations in the species' range boundary by tracking the environment through space and time, arriving first at newly available habitat. For example, more recently established populations of lodgepole pine (*Pinus contorta*) exhibit morphological features that impart stronger dispersal ability (small seeds with large wings) than ancient populations from glacial refugia (Cwynar and MacDonald 1987). In addition, contemporary warming at the northern margins of species' ranges may be intensifying selection for dispersal ability. For example, several insect species that have undergone northward range expansions in Britain contemporaneously with climate warming over the past 20 years exhibit elevated fractions of individuals that are better colonizers or dispersers in recently founded populations (Thomas et al. 2001). However, a recent review by Robinson et al. (2009) demonstrated that highly migratory species are more sensitive to environmental perturbations associated with climate warming than their less mobile counterparts. They suggest that this is due to their reliance on high-latitude ecosystems for breeding and foraging where the impacts of climate change are first and most strongly felt.

There are many cases where peripheral populations exhibit no obvious signs of advanced dispersal abilities. Simple explanations for this abound: that the population is an isolated relict of a once-broad distribution of the species (e.g., Schwaegerle and Schaal 1979); that colonization did not require dispersal ability outside that already possessed by central populations of the species; or that no inherent dispersal ability was required for colonization (e.g., intentional or accidental transport of colonizers; Hodkinson and Thompson 1997). However, the possibility also exists that colonial individuals suffered from negative fitness consequences of their enhanced vagility, thereby driving them back toward the less-dispersive phenotype (Thomas et al. 2001). For example, many insect groups include conspecific winged and wingless individuals, those that can migrate, and those that cannot. As one might expect, the winged forms are often found to be more common in temporally unstable and frequently stressful environments. However, under favourable conditions, winged individuals suffer from reduced reproductive output and survival (references in Hoffmann and Parsons 1997). As a result of the significant fitness costs of enhanced dispersal-ability, it is reasonable to assume that intense selection could act to dispel these traits relatively quickly after colonization. This depends, among other things, on the peripheral environment being sufficiently stable for the population to persist for some time, otherwise selection for dispersal is likely to remain high. Homogeneity in dispersal ability across the species' range may also arise where the central, high-quality environment is sufficiently dense so as to be unstable, whereas the low-quality peripheral environment is stable. In this case, the evolutionarily

stable strategy for the species may be to retain enhanced dispersal ability (Holt 2003).

The formulation of hypotheses concerning gene flow and population structure across species' ranges should depend on careful consideration of the inherent dispersal abilities of the species in question. The literature suggests that less mobile organisms tend to have evolved mechanisms to control intra- and inter-specific demographic parameters (e.g., territoriality), whereas vagile organisms are more likely to evolve traits to enhance dispersion. Nonetheless, simply because the vagility of a species has not been empirically demonstrated, one should not assume that it is not possible. Human-mediated translocations, often for the most idiosyncratic reasons, can confound attempts to understand species' distributions or patterns of molecular variation. In other cases, dispersal mechanisms can be even more cryptic. In one recent study, Gittenberger et al. (2006) reported molecular evidence of long-distance (9000 km) trans-oceanic dispersal in land snails (*Balea perversa*) that pre-dated the possibility of human interference. They suggested that the species' extraordinarily tenacious slime and arboreal habits could aid passive dispersal by birds. Given the overarching importance of dispersal ability, it is surprising that the hypothesis that clinal patterns of genetic variability and differentiation across species' ranges should depend strongly on species' dispersal ability has not been rigorously scrutinized.

On the whole, we find that the environmental, ecological, and evolutionary features of populations at the edges of species' ranges can make them particularly vulnerable to extinction, such that peripheral populations that are known or suspected to represent important components of biodiversity should be given particular attention for conservation. However, by the same token that peripheral populations should not be uncritically viewed as temporary offshoots of more important stable core populations, neither should they always be assigned inherently superior importance by virtue of their position at the edge of the species' range alone. While the latter may represent a precautionary approach where resources permit, most realistic scenarios will require a more critical appraisal of the genetic and ecological characters upon which to base management decisions, and the literature reviewed here suggests some fertile approaches by which this might be achieved.

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