Molecular Ecology (2008) **17**, 1170–1188 doi: 10.1111/j.1365-294X.2007.03659.x

INVITED REVIEW

Genetic variation across species' geographical ranges: the central–marginal hypothesis and beyond

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Abstract

There is growing interest in quantifying genetic population structure across the geographical ranges of species to understand why species might exhibit stable range limits and to assess the conservation value of peripheral populations. However, many assertions regarding peripheral populations rest on the long-standing but poorly tested supposition that peripheral populations exhibit low genetic diversity and greater genetic differentiation as a consequence of smaller effective population size and greater geographical isolation relative to geographically central populations. We reviewed 134 studies representing 115 species that tested for declines in within-population genetic diversity and/or increases in among-population differentiation towards range margins using nuclear molecular genetic markers. On average, 64.2% of studies detected the expected decline in diversity, 70.2% of those that tested for it showed increased differentiation and there was a positive association between these trends. In most cases, however, the difference in genetic diversity between central and peripheral population was not large. Although these results were consistent across plants and animals, strong taxonomic and biogeographical biases in the available studies call for a cautious generalization of these results. Despite the large number of studies testing these simple predictions, very few attempted to test possible mechanisms causing reduced peripheral diversity or increased differentiation. Almost no study incorporated a phylogeographical framework to evaluate historical influences on contemporary genetic patterns. Finally, there has been little effort to test whether these geographical trends in putatively neutral variation at marker loci are reflected by quantitative genetic trait variation, which is likely to influence the adaptive potential of populations across the geographical range.

Keywords: conservation, genetic differentiation, genetic diversity, geographical ranges, range limits

Received 22 July 2007; revision received 18 November 2007; accepted 23 November 2007

Introduction

The genetic characteristics of populations should be dictated by the interplay of genetic drift, gene flow and natural selection. These processes may be strongly influenced by the demography and spatial distribution of populations. Population size and the degree to which size fluctuates through time determines the rate at which genetic variation is lost through stochastic drift. The extent to which neighbouring populations are spatially separated and differ in size influences the replenishment of genetic variation via gene flow. Both population size and spatial isolation are expected to covary geographically with the abiotic and biotic factors that influence the survival and reproduction of individuals. When a nascent species colonizes a geographical gradient of environmental conditions, it should become most abundant where individual survival, reproduction and hence population growth is highest, and increasingly less abundant as conditions depart from this optimum (Hengeveld & Haeck 1982; Brown 1984). Ultimately, the species is expected to achieve highest abundance at the geographical centre of the range, with populations becoming progressively smaller and more spatially isolated towards the range limits (Brussard 1984; Lawton 1993; Vucetich & Waite 2003). This conception of a species' range is commonly referred to as the 'abundant centre' model and has influenced much thinking

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about the ecology and evolution of species' ranges (Sagarin & Gaines 2002).

How an abundant centre distribution is manifested in the amount and partitioning of genetic diversity among populations across the range has been the subject of a long-standing and largely unresolved debate (Carson 1959; Soulé 1973; Antonovics 1976; Brussard 1984; Hoffman & Blows 1994; Lesica & Allendorf 1995; Barton 2001). It is also an issue that bears on one of the most enduring and poorly resolved problems in evolutionary biology (Hoffmann & Parsons 1997; Gaston 2003; Holt *et al*. 2005; Bridle & Vines 2007): why do species exhibit evolutionarily stable limits to their geographical distributions? The simplest extension of the abundant centre model suggests that two key genetic parameters, effective population size (N_e) and the rate of gene flow (m), should be highest at the range centre and lowest at range margins. As a result, geographically peripheral populations should exhibit lower genetic diversity and higher genetic differentiation than central populations. This will be further exacerbated if peripheral populations experience more rapid cycles of extinction, recolonization and associated founder events or severe population bottlenecks than those in less extreme central environments. The resulting stochastic reduction of genetic diversity within populations at geographical range margins may limit their evolutionary potential, thereby inhibiting adaptation to conditions beyond the range limit (Hoffman & Blows 1994; Hoffmann & Parsons 1997; Gaston 2003; Blows & Hoffmann 2005). However, geographical variation in demography may also lead to asymmetries in emigration and immigration among populations. If dispersal is random, there should be more individuals (or gametes) moving from large, productive, geographically central populations into small, sparse, peripheral populations than the other way around. This asymmetric gene flow may also impede adaptation to extreme environments in peripheral populations, thereby limiting spread beyond the range limit (Garciá-Ramos & Kirkpatrick 1997; Kirkpatrick & Barton 1997; Bridle & Vines 2007). However, it will also very likely increase the genetic diversity within, and reduce differentiation among, peripheral populations (Barton 2001). Although drift and asymmetric gene flow are not mutually exclusive explanations for the evolutionary limits to species' distributions, they are expected to have contrasting effects on the pattern of geographical variation in population genetic structure.

Understanding the patterns and processes associated with geographical variation in population genetic structure across species' ranges is also motivated by conservation concerns. Geographically peripheral populations are often rare representatives of relatively widespread species within political jurisdictions (e.g. Bunnell *et al*. 2004). Whether these range-edge populations merit the conservation effort that they are often subject to has been widely debated (Millar & Libby 1991; Lesica & Allendorf 1995; Hunter & Hutchinson 1994). Again, much depends on their evolutionary potential (Vucetich & Waite 2003). If peripheral populations, compared to central populations, are genetically depauperate owing to chronic genetic drift and low gene flow, then perhaps they are of little significance in terms of future evolutionary potential. If, on the other hand, peripheral populations maintain substantial genetic variation, they may adaptively diverge from more central populations owing to different selective pressures and reduced gene flow (Lenormand 2002) and may therefore play a role in the maintenance and generation of biological diversity (Mayr 1970; Channell & Lomolino 2000). Depending on their demographic and genetic properties, peripheral populations may also facilitate shifts in species' geographical distributions in response to rapid climate change (Etterson & Shaw 2001; Parmesan 2006).

The abundant centre model underlies all of the expectations concerning how genetic diversity and differentiation are influenced by the geographical peripherality of populations. However, recent reviews of empirical evidence challenge this widely accepted biogeographical model (Sagarin *et al*. 2006). For instance, Sagarin & Gaines (2002) reviewed the empirical evaluations of the abundant centre model based on analyses of habitat occupancy and population demographic variables and found that only 39% of 145 direct tests supported the predictions that populations are smaller and/or less frequent towards range margins. The very few empirical studies that have estimated demographic parameters from across entire geographical ranges provide even weaker support (Gaston 2003; Sagarin *et al*. 2006; Samis & Eckert 2007). This suggests that the abundant centre model is no longer a safe assumption upon which to make predictions concerning geographical variation in population genetic structure.

The pattern of geographical variation in population genetic diversity and differentiation will be influenced by both historical and contemporary changes to population size and gene flow (Vucetich & Waite 2003). In regions with a recent history of glaciation or some other manifestation of climate change, species are liable to have experienced large-scale fluctuations in N_e and m that may not be reflected among contemporary populations (Pielou 1991; Pamilo & Savolainen 1999; Hewitt 2000). For temperate species, in particular, geographical ranges have shifted, fragmented and/or coalesced in the past 20 000 years, creating a legacy of potentially significant genetic consequences for contemporary populations. However, relatively few studies have attempted to distinguish possible historical effects from those caused by existing geographical variation in population demography and dispersion (Gaston 2003).

Given the discussion above, it is perhaps not surprising that the few attempts to review empirical work on the genetic structure of species' ranges, especially for differences in genetic variation and its partitioning between central and peripheral populations, have produced mixed results. For

instance, Brussard (1984) reviewed the early application of molecular assays of genetic variation to *Drosophila* species and came to the conclusion that 'none of the available studies suggest there is a reduction in levels of allozyme heterozygosity in peripheral populations'. A decade later, Lesica & Allendorf (1995) concluded that 'peripheral populations may have reduced genetic variation, but this is not always the case'. Based on a cursory review of the literature several years later, Gaston (2003) echoed this equivocal conclusion (see also Hoffmann & Parsons 1997). However, there has not yet been a comprehensive review of the available evidence, despite burgeoning interest in genetic characteristics of peripheral populations within the contexts of evolution and conservation.

Here, we report an exhaustive review of the empirical work that investigates variation in population genetic structure across species' geographical ranges. Because most of the available genetic data involves polymorphisms that are assumed to experience little or no natural selection, we focus on a simple extension of the abundant centre model: that effective population size and gene flow among population decline toward geographical range margins. This should result in (i) reduced neutral genetic diversity within peripheral compared to more central populations; and (ii) increased genetic differentiation among peripheral populations compared to among central populations. In addition to providing a general test of these predictions, we suggest improvements to the design of empirical studies and discuss approaches for understanding the processes that generate patterns of geographical variation in genetic structure, with particular attention to distinguishing the effects of historical vs. contemporary variation in population size and isolation. We end by discussing the implications of the empirical work to date for understanding the evolution of geographical range limits and the conservation of peripheral populations.

Review of empirical studies

We exhaustively searched the literature for studies that investigate geographical variation in population genetic structure using molecular genetic assays, including allozymes, dominant and anonymous markers [random amplified polymorphic DNAs (RAPDs), intersimple sequence repeats (ISSRs) and amplified fragment length polymorphisms (AFLPs)], microsatellites and DNA sequences. Because much of the interest in the genetics of peripheral populations revolves around their evolutionary potential, we focused on studies that assayed variation in the nuclear genome. However, we recognize that assays of variation in organellar genes have been widely applied to investigate historical changes in geographical ranges and demographic parameters, and we consider how they can be used in conjunction with assays of nuclear variation below.

We surveyed all studies that tested for a decline in within-population diversity and/or an increase in differentiation among populations towards range margins. Sometimes these predictions were the central goal of the paper, but often they were secondary to some other objective. How geographical peripherality was defined varied greatly among studies. In some cases, peripheral populations were truly at the range limit (e.g. Sjogren 1991) and some were even disjunct (e.g. Hamilton & Eckert 2007). In other cases, populations were classified roughly as relatively peripheral or further towards the range centre. Very few studies used a quantitative measure of peripherality/centrality such as 'distance to range edge' (e.g. Wang *et al*. 2002; Schwartz *et al*. 2003; see discussion in Yakimowski & Eckert 2007). Our analyses are based on the authors' assessment of population geographical location; however, we discuss the importance of clearly defining peripherality below.

To provide a fair evaluation of the predictions stated above, the studies we included in our analyses had to have been designed, at least in part, to explicitly test these predictions. We did not therefore include studies aimed *solely* at describing geographical clines in allele frequencies, genetic differentiation among taxonomic units, genealogical history of species focused exclusively on the effects of Pleistocene glaciations or postglacial colonization (e.g. phylogeography), or general patterns of genetic variation at large geographical scales. Similarly, we did not include studies that investigated the genetic consequences of ecological marginality by quantifying patterns of genetic variation across niche limits (e.g. elevational or edaphic gradients) or studies comparing native vs. introduced populations of invading species (see Bossdorf *et al*. 2005).

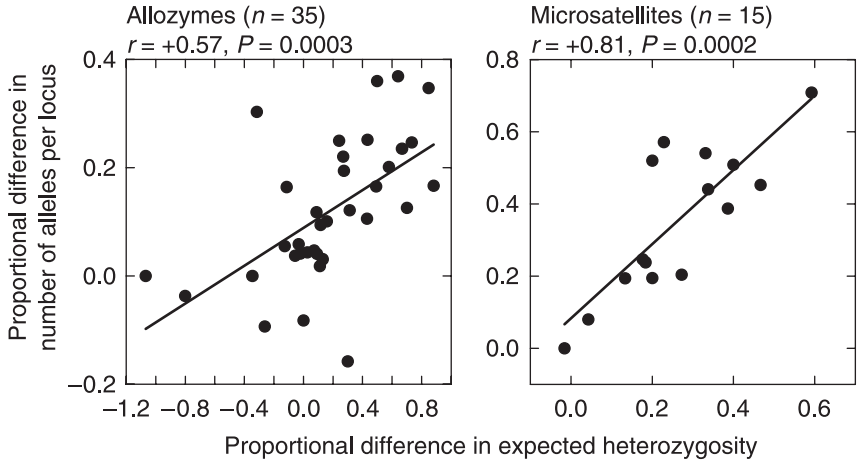
All studies included in our analyses either made some explicit comparison of populations or performed an analysis of geographical variation to test the predictions posed above. This sometimes involved the statistical evaluation of a formal null hypothesis, but very often it did not. We included both qualitative and statistical tests of the predictions and recorded whether the data supported the predictions based on the authors' analysis and interpretation. However, we ignored purely anecdotal evidence derived from singling out individual populations in an attempt to make some association between geographical position and genetic structure. For testing geographical patterns of within-population diversity, most studies estimated expected heterozygosity (H_E), also known as gene diversity. Alternative measures of diversity, especially allelic richness (A), were also analysed in many studies. Because A is more sensitive to variation in sampling effort than H_E and was not used as consistently, our analyses focus on H_E whenever possible (see also Vucetich & Waite 2003). We discuss the degree of concordance between different measures of diversity in Box 1.

We found 134 studies involving 115 species published over the last 35 years. Most studies (57%) were published

Box 1 Which measure of genetic diversity?

Expected heterozygosity (H_E, gene diversity) was the preferred measure of within-population diversity among the studies we reviewed (see also Vucetich & Waite 2003), although most studies reported trends in alternate measures such as the proportion of loci polymorphic (*PLP*) and the average number of alleles per locus (*A*). These three measures are obviously interrelated. However, theoretical studies have suggested that *A* is likely to be reduced by stochastic processes, including those that occur at range limits, to a greater extent than H_E (Nei *et al*. 1975). This is because rare alleles, which influence the estimate of *A* but have a lesser effect on H_E, are readily lost during founder events, population bottlenecks and sporadic fluctuations in population size, which may occur more commonly towards range edges. Some empirical studies have even documented contrasting patterns of geographical variation for H_E vs. *A (*e.g. Cwynar & MacDonald 1987; Comps *et al*. 2001). However, our survey suggests that on the whole, various measures of diversity usually exhibit parallel patterns of geographical variation, at least in the context of comparisons between central and peripheral populations. Among the 54 studies that reported both H_E and *A*, differences between central and peripheral populations were usually in the same direction for both parameters (87.0% of studies); hence there was a strong and significant association between the results based on H_E and those based on *A* (2×2 $\chi^2 = 20.19$, $P < 0.0001$). This is also supported by the figures below. The proportional difference in *A* between central vs. peripheral populations [i.e. (C–P)/C] correlated positively with the proportional difference in H_E among both the 35 studies that assayed allozymes polymorphisms (left panel) and the 15 studies that assayed variation at microsatellite loci (right panel).

However, we found some evidence that the processes reducing diversity at range limits affect *A* more strongly than H_E. A higher proportion of studies found the expected difference in *A* (83.3%) than in H_E (74.1%). When central populations exhibited higher H_E, they almost always (97.5% of the time) had higher *A* ($n = 40$ studies); but when central populations had higher *A* ($n = 45$), H_E was the same or lower than for peripheral populations in 13.3% of cases. The expected difference in *A* was found in 43.9% of 14 studies where the difference in H_E was not detected. Our analysis must, however, be interpreted with caution because very few of the studies estimated *A* using rarefaction to reduce the effect of variation in sample size among populations (Petit *et al*. 1998; see also Comps *et al*. 2001; Coyer *et al*. 2004; Hoffman & Blouin 2004; Johansson *et al*. 2006; Böhme *et al*. 2007).



in the 2000s, with another 26% published in the 1990s, 7% in the 1980s and 10% in the 1970s. Most species (88%) were represented by a single study. In most of the analyses that follow, we used the study as the unit of observation and comment on the consistency of results from multiple studies on the same species below. The 115 species studied included 48 animal species and 67 plant species distributed across a diversity of taxonomic groups (Table 1), although, predictably, 65% of animals were chordates and 67% of plants were angiosperms. Some lower-rank taxonomic groups were also over-represented in the dataset. For instance, 21% of animals species studied were frogs (order Anura) and 22% of plants were pines (order Pinales). There were also biogeographical biases. A disproportionate number of studies (40%) focused on the northern limit of species in the temperate zone of the northern hemisphere (see also Hampe & Petit 2005). None involved an exclusively tropical species. Only 9% of species studied were marine. Most studies

Table 1 Taxonomic representation among the 134 population genetic studies reviewed

Taxonomic rank	Animals	Plants
Phyla/Divisions	4	6
Classes	11	7
Orders	17	21
Families	28	31
Genera	33	48
Species	48	67

(62%) were based on allozymes markers; 23% used microsatellites, 9% used various dominant, anonymous markers (RAPDs, ISSRs and AFLPs) and the remaining few used sequence-based nuclear markers.

Overall patterns

Is diversity lower within peripheral than central populations?

The first prediction, that within-population genetic diversity declines towards at least one range limit, was evaluated by all studies. Qualitative support for this prediction was found by 64% of studies (Table 2), which was much greater than the random expectation of 50% (1-tailed exact binomial test $P = 0.0007$). However, half of all studies (51%) reported only a qualitative assessment of the prediction with no statistical test. Of the 68 studies using some form of statistical analysis, the prediction was supported by 65%. In 17% of cases where there was some qualitative support for the prediction, statistical testing revealed that the trend was not significant. Unexpectedly, however, the frequency of support for the prediction was somewhat higher for studies that used statistical testing (65%) than those that did not (50%), although the difference was not quite significant (2×2 contingency table, likelihood ratio $\chi^2 = 2.97$, d.f. = 1, $P = 0.085$).

The proportion of studies that generated results consistent with a decline in within-population diversity towards range edges did not differ between plants and animals (Table 2) for all studies (2×2 $\chi^2 = 0.00$, $P = 0.99$), those with purely qualitative tests ($\chi^2 = 0.07$, $P = 0.80$) or those using statistical tests ($\chi^2 = 0.66$, $P = 0.41$). For plants, the preponderance of some taxa among the studies analyzed did not seem to greatly bias our results. For instance, the frequency of support for reduced diversity at range margins did not differ between 'pines' (i.e. 54% of 24 studies on Pinales supported the prediction), the best represented plant group, and all other plants pooled (68% of 57 studies on other plants, 2×2 $\chi^2 = 1.47$, $P = 0.22$). Among animals, studies on 'frogs' (Anura), the best represented animal group, yielded a somewhat higher frequency of support (85% of 13 studies) than those on other animals (58% of 40 studies), although this difference was not quite significant (2×2 $\chi^2 = 3.46$, $P = 0.063$).

Table 2 Level of overall support for two main predictions concerning how population genetic structure should vary across species' geographical ranges. Support indicates the percentage of studies that produced results consistent with the prediction. Asterisks indicate statistical departures from random expectations (50% support) assessed using 1-tailed exact binomial tests (***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, †$P < 0.10$)

Prediction/Group		*n* studies	Support
1) Reduced within-population diversity towards range periphery			
All taxa	All studies	135	64.2%***
	Qualitative tests	67	50.0%
	Statistical tests	68	64.7%*
Animals	All studies	53	64.1%*
	Qualitative tests	23	47.8%
	Statistical tests	30	70.0%*
Plants	All studies	81	64.2%**
	Qualitative tests	43	51.2%
	Statistical tests	38	60.5%
2) Increased among-population differentiation towards range periphery			
All taxa	All studies	57	70.2%**
	Qualitative tests	31	74.2%**
	Statistical tests	26	42.3%
Animals	All studies	20	70.0%†
	Qualitative tests	9	88.9%*
	Statistical tests	11	54.5%
Plants	All studies	37	70.3%**
	Qualitative tests	22	68.2%†
	Statistical tests	15	33.3%

Most studies (68%) used a categorical approach to testing the prediction by comparing a sample of geographically peripheral populations with a sample of populations located further towards the geographical centre ('categorical sampling', see below). Of these, many used assays of codominant markers (allozymes, microsatellites, SNPs) for which allele frequencies could be calculated. These were often used to calculate two standard measures of within-population diversity: the number of alleles per locus (A) and expected heterozygosity (H_E). The magnitudes of these measures were greater for central than peripheral populations in 76% of 80 studies that compared H_E and 83% of 58 studies that compared A. Both frequencies are much greater than random expectations (both $P < 0.0001$). Figure 1 compares values of H_E and A based on widely used allozyme polymorphisms between central and peripheral populations. Paired t-tests revealed significantly higher diversity in central than peripheral populations for both measures (both $P < 0.0001$). Although there were some cases where diversity was markedly lower in peripheral populations, most of the differences, although in the expected direction, were rather subtle. Despite sporadic claims in the literature to the contrary, diversity was almost never much

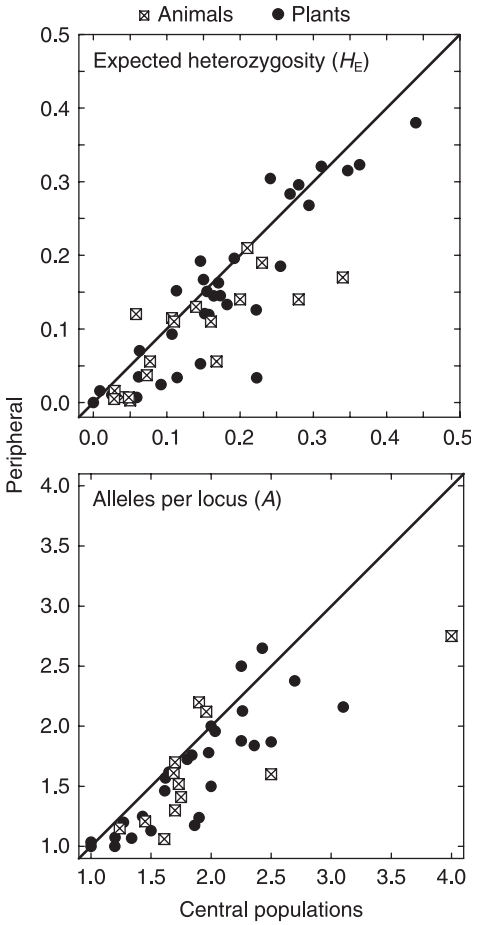


Fig. 1 Comparisons of within-population genetic diversity at allozyme loci between geographically central and peripheral populations, as measured by expected heterozygosity (H_E, also called gene diversity, upper panel, $n = 50$ studies) and average number of alleles per locus (A, lower panel, $n = 40$ studies). Each point is a study, and different symbols differentiate studies on animals vs. plants. Central populations exhibited significantly higher diversity than peripheral populations for both measures (H_E: paired t-test $t = 4.26$, d.f. = 49, $P < 0.0001$; A: $t = 4.69$, d.f. = 39, $P < 0.0001$). The line denotes $\chi = y$.

higher at range edges than in the range core. For instance, the maximum difference in H_E between regions for studies that found unexpectedly higher H_E in peripheral than central populations was 0.063, with a mean difference of 0.022. For studies that found higher H_E in central populations, in contrast, the maximum difference was 0.394, with a mean of 0.082 (see Fig. 1). We found a similar but even stronger pattern from analyses of the smaller sample ($n = 18$) of studies that used microsatellite markers (not shown). Microsatellite diversity was almost always higher in central populations (94% and 93% of cases for H_E and A, respectively), and paired t-tests were strongly significant (both $P < 0.0001$).

Are peripheral populations more genetically differentiated than central populations?

The second prediction, that peripheral populations should become genetically differentiated to a greater extent towards range edges, was evaluated by 57 studies. Seventy percent of these studies supported the prediction (Table 2), which is much greater than random expectations ($P = 0.0016$). Again, more than half of all studies (54%) did not compare estimates of differentiation statistically. Of the 26 that did, only 42% supported the prediction. The frequency of support was lower among statistical comparisons than among qualitative comparisons (74.2% of 31; $2 \times 2\ \chi^2 = 60.5$, $P = 0.014$).

The proportion of studies that generated results consistent with an increase in among-population differentiation towards range edges did not differ between plants and animals (Table 2) for all studies ($2 \times 2\ \chi^2 = 0.00$, $P = 0.98$), those with purely qualitative tests ($\chi^2 = 1.60$, $P = 0.20$) or those using statistical tests ($\chi^2 = 1.17$, $P = 0.28$). The uneven taxonomic sampling of plants did not seem to have biased our results. For instance, the frequency of support for this prediction did not differ between 'pines' (75% of 12 studies) and other plants (68% of 25 studies, $2 \times 2\ \chi^2 = 0.19$, $P = 0.66$). For animals, there was insufficient data to compare 'frogs' ($n = 2$ studies) with other taxa ($n = 18$).

Because differentiation was measured using several different statistics (e.g. measures of the proportion of genetic variation distributed among populations F_{ST}, G_{ST}, or genetic distance), we could not use a paired analysis (as above) to evaluate overall support for the prediction among studies using categorical sampling.

Many of the studies we surveyed found that genetic differentiation between populations increased with the geographical distance between them. However, geographical variation in the distance between sampled populations was almost never accounted for when comparing peripheral vs. central populations. The abundant centre model predicts that populations are more sparsely distributed towards the range edge. However, the range periphery usually encompasses a larger area than the range centre (Hengeveld & Haeck 1982). As a result, the peripheral populations sampled for any given study could be further apart from one another than a comparable sample of central populations, regardless of whether they are truly more isolated from other populations than central populations (e.g. Fazekas & Yeh 2001; Gapare *et al.* 2005). Higher differentiation can therefore arise at least in part as a result of sampling artefact. Box 2 illustrates one approach to dealing with this problem.

Do low diversity and high differentiation go hand in hand at range margins?

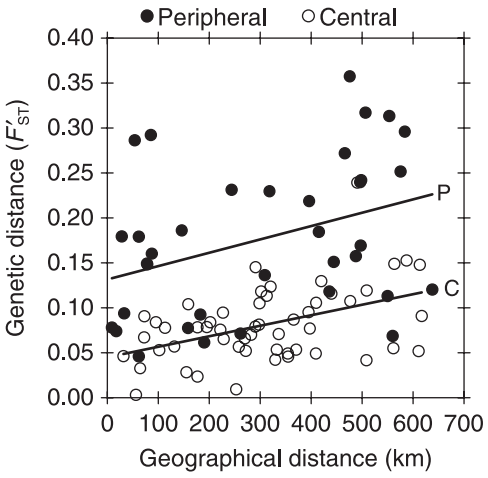
In all, 57 studies qualitatively tested both predictions (Fig. 2). Of these, 74% found evidence of reduced diversity towards

Box 2 Controlling for geographical dispersion when testing for variation in genetic distance among populations

Hamilton & Eckert (2007) compared the level of genetic differentiation between a sample of nine disjunct populations of the perennial plant *Geum triflorum* (Rosaceae) isolated on alvar habitat in the eastern Great Lakes region of North America to 16 populations sampled from prairie habitat throughout the core of the species' distribution in midwestern Canada and the USA. Differentiation among populations was measured by F'_{ST} based on differentiation in allele size phenotypes at five microsatellite loci (*G. triflorum* is an allohexaploid, so phenotypic measures of differentiation were used). They contrasted differentiation between peripheral (P) alvar population pairs and central (C) prairie population pairs by comparing the regressions of pairwise F'_{ST} on geographical distance. Because central populations were sampled over a broader geographical range than peripheral populations, only pairs of central populations within the range of geographical distances between peripheral population pairs were analyzed. To compare differentiation while controlling for geographical distance between populations, randomization tests were used to evaluate the differences in the slope and the y intercept of the regressions of F'_{ST} over geographical distance.

Pairwise F'_{ST} increased with geographical distance within peripheral ($r = +0.36$, $P = 0.03$) and central regions ($r = +0.56$, $P < 0.0001$). The slope of the regression did not differ between regions ($P = 0.29$), but the intercept was higher for peripheral populations ($P = 0.007$). The increase in genetic differentiation with geographical distance was similar between regions, but peripheral populations were more differentiated at all distances. Pairwise F'_{ST} was also more variable for peripheral population pairs across all distances. The variance in the residuals from the regressions was greater for peripheral than central comparisons ($P < 0.0001$).

Differentiation may be higher among disjunct than among central populations due to a simple extension of a common pattern of isolation by distance. However, peripheral populations of *G. triflorum* were more differentiated from each other than were central populations, even after isolation by distance was accounted for, and the variability in differentiation was greater for peripheral populations. This is consistent with a more continuous distribution of *G. triflorum* in the prairie region. The central populations sampled occurred in a landscape containing many other populations of *G. triflorum* (of which only a fraction were sampled), whereas peripheral populations were restricted to patches of alvar habitat that were few and far between. As the isolation of populations increases, genetic drift becomes more influential than gene flow, and the differentiation among populations is expected to become greater and more variable. The nature of the landscape matrix separating populations may combine with geographical isolation to influence the pattern of genetic differentiation.



range edges and 70% found increased differentiation. There appeared to be some association between support for one prediction and support for the other, but this was not statistically significant (2×2 $\chi^2 = 0.97$, $P = 0.32$). For instance, the frequency of support for increased differentiation was higher, but not significantly so, among studies that detected reduced diversity (74%) compared to those that did not detect reduced diversity (60%). Likewise, studies that detected reduced diversity towards range edges seemed more frequent, but not statistically so, among those that found increased differentiation (78%) than studies that did not (65%). When this analysis is restricted to the 24 studies that statistically tested both predictions, there is a significant association between support for one and support for the other (Fig. 2, $\times 2$ $\chi^2 = 4.84$, $P = 0.028$).

Recent theory by Hedrick (2005) suggests that some studies may have overestimated the difference in genetic differentiation between central vs. peripheral populations. As explained in Box 3, G_{ST}, the measure of genetic differentiation most commonly used for loci where more than two alleles are maintained within populations, is influenced by the degree of within-population polymorphism, which is expected to differ between central and marginal populations. This problem can be addressed by scaling the observed value of G_{ST} by the maximum possible value given the level of polymorphism. However, this approach was not

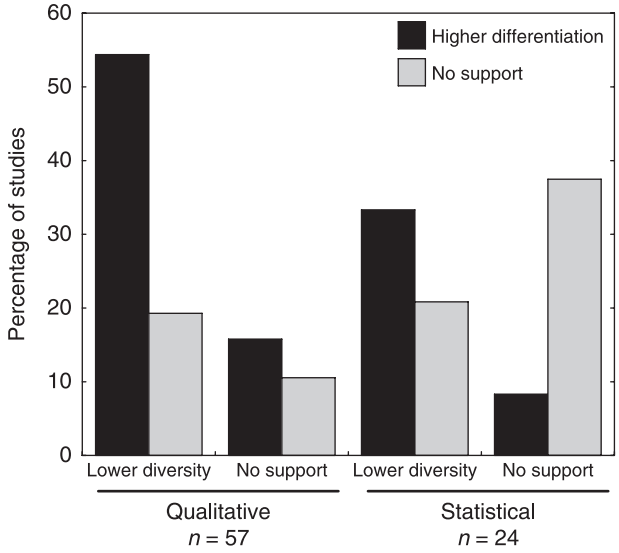


Fig. 2 Association between lower within-population diversity towards range edges and higher among-population differentiation. Studies were first categorized as supporting or not supporting the reduction of diversity towards range margins and then whether they supported the prediction of higher differentiation (black bars) or not (grey bars). Bars show the percentage of studies in each category and sum to 100% within each grouping: qualitative studies ($n = 57$ studies) or the studies where both predictions were subjected to statistical evaluation ($n = 24$ studies). Statistical analysis of these associations is in the text.

adopted by any of the studies we surveyed, and the parameter estimates required for us to perform a *post hoc* correction was provided by only two of 134 studies.

Sampling strategies

Two basic sampling strategies were used to examine geographical variation in genetic diversity and differentiation. Of the 134 studies we surveyed, more than two-thirds (68%) used a 'categorical' sampling approach in which a group of geographically peripheral populations was compared with a group of relatively more central populations, with the classification of populations as central vs. peripheral often based on rather qualitative criteria. Typically, measures of within-population diversity were estimated for individual populations, and group means for these variables were compared qualitatively or statistically (46% of studies), using two-sample tests (e.g. *t*-test, analysis of variance, Mann–Whitney–Wilcoxon nonparametric test). Differentiation among populations within groups (usually measured as F_{ST}, G_{ST} or genetic distance) was estimated for the group of populations as a whole or as the mean of pairwise values and compared between groups.

In most implementations of this categorical approach, peripheral populations were located in one region and central populations in another, such that geographical position was confounded with region. This form of pseudoreplication (Hurlbert 1984) makes it difficult to associate any difference in genetic structure with geographical peripherality/centrality per se. In relatively few studies, the peripheral group included populations from throughout a much larger portion of the geographical range (e.g. Maguire *et al*. 2000; Lönn & Prentice 2002), thereby weakening the association between geographical position and any particular region and thus facilitating interpretation of the results (although see below). In fewer still, a third category of populations, geographically intermediate between central and peripheral, was sampled to relax the confound between group and geographical position (e.g. Prakash 1973; Yeh & Layton 1979; Schiemann *et al*. 2000; Cassel & Tammaru 2003; Hutchison 2003).

The other strategy involved sampling populations that were more continuously distributed throughout the range or at least along some transect through a major dimension of the range. In most cases (56%), the sample only included a portion of the range. Measures of diversity were usually estimated for individual populations and regressed over geographical position, where position was usually represented by latitude or longitude and not by any quantitative measure of peripherality/centrality (but see Schwartz *et al*. 2003). In 60% of these studies, the resulting association was tested statistically, usually with least-squares regression or correlation. This approach yielded evidence of reduced diversity towards range edges less frequently (47%) than studies using categorical sampling (73%; 2×2 $\chi^2 = 8.98$, $P = 0.0027$). Considering only studies using statistical tests of predictions yielded the same result, although the difference between sampling strategies was not quite significant ($P = 0.10$).

Although continuous sampling lends itself to a relatively straightforward test of geographical variation in within-population diversity, a simple test of the prediction that differentiation among populations should increase towards range limits is not as obvious, primarily because differentiation is a property of groups of populations rather than individual populations. Possibly as a result of this, geographical variation in population differentiation was evaluated in only 28% of studies using continuous sampling, compared to 50% of studies using categorical sampling. Compared to categorical sampling, continuous sampling also yielded a lower frequency of qualitative or statistical support for increased differentiation towards range edges, although the differences between sampling strategies were not significant (both $P > 0.12$).

Sampling effort

Investigations of geographical variation in population genetic characteristics encounter a classic problem of how

Box 3 Comparing genetic differentiation among populations when diversity within populations varies geographically

The level of genetic differentiation among populations is widely measured by F_{ST} or its analogue G_{ST} as the proportion of total genetic diversity (H_T) distributed among populations as opposed to within populations (H_S): $G_{ST} = (H_T - H_S)/H_T$, where H_S is the average heterozygosity within populations at Hardy–Weinberg equilibrium and H_T is the expected heterozygosity of all populations pooled. However, as Hedrick (1999, 2005) points out, the magnitude of G_{ST} is strongly influenced by the amount of genetic diversity, especially when individual populations maintain many alleles at the marker loci used. The problem arises because G_{ST} measures the amount of variation among populations ($H_T - H_S$) relative to the total variation (H_T), without taking account of the identity of the alleles involved. As a result, both H_S and H_T can approach 1, even if different populations maintain different alleles. Hence the difference between H_T and H_S and, in turn G_{ST}, will be underestimated.

This problem complicates comparisons of population differentiation between genes with different levels of polymorphism (Hedrick 2005), such as allozymes vs. the more highly variable microsatellites (which have increasingly found use in studies of geographical variation in population genetic structure). This problem also applies to comparisons between geographical regions that may differ in H_S and/or H_T. In the case of comparisons of central vs. marginal populations, the degree of differentiation as measured by G_{ST} will be underestimated for central populations if, as expected, central populations tend to contain more genetic diversity (i.e. higher H_S) than peripheral populations.

Hedrick (2005) suggests controlling for variation in H_S and H_T by scaling G_{ST} by the maximum possible value ($G_{ST(Max)}$) given the level of polymorphism, where $G_{ST(Max)} = (1 - H_S)/(1 + H_S)$. It follows from this that central populations, given that they are likely to have higher values of H_S than peripheral populations, will have lower values of $G_{ST(Max)}$ and potentially lower overall G_{ST}, regardless of the level of population differentiation. A corrected G'_{ST} should therefore be calculated as $G_{ST}/G_{ST(Max)}$. Given that this approach was introduced relatively recently, none of the studies we reviewed had corrected G_{ST} before comparing the level of genetic differentiation for central vs. peripheral populations. Our analyses may possibly overestimate the difference in differentiation of peripheral vs. central populations, especially for studies using highly polymorphic markers. Post-hoc calculation of G'_{ST} is possible, but only in the rare instances where authors reported H_S and H_T for individual loci and central and peripheral populations separately (two of 134 studies) or population-level allele frequencies (21 studies). Our analyses of differentiation must be interpreted with due caution.

sampling effort should be allocated. In principle, the likelihood of detecting a geographical pattern should be influenced by the number of populations sampled (n_{pops}) and the number of individuals assayed per population (n/pop). Increasing n/pop increases the statistical reliability of population-genetic parameter estimates (e.g. H_E and A), whereas increasing n_{pops} provides the statistical power to detect a geographical pattern. When resources and time are limited, as per usual, researchers will have to deal with a trade-off between n_{pops} and n/pop. Broad-scale geographical sampling can be expensive, and decisions about how to allocate funds to costly molecular assays may favour one level of sampling effort at the expense of the other. Sampling effort varied widely among the studies we surveyed with n_{pops} ranging from two to 389 and n/pop ranging from four to 225. Some of this variation was associated with the type of genetic marker used. Log-transformed total sampling effort ($n_{pops} \times n$/pop) was substantially higher for studies using allozymes (back-transformed mean = 477, n = 82 studies), which are relatively inexpensive, compared to more costly polymerase chain reaction (PCR)-based markers (mean = 287, n = 52; t-test $P = 0.0033$). However, this resulted mainly from a higher n/pop (means = 32 vs. 21, respectively; $P = 0.0007$) rather than higher n_{pops} (15 vs. 14, $P = 0.59$). Total sampling effort did not differ between animal and plant studies for either marker type (both $P > 0.18$).

Unexpectedly, sampling effort was not associated with the outcome of the studies we surveyed. We used logistic regression to test for the expected associations between the two components of sampling effort and whether the study detected the predicted geographical pattern. For all studies testing for changes in diversity towards range limits, log-transformed n_{pops} was not associated with the outcome (likelihood ratio $\chi^2 = 0.07$, d.f. = 1, $P = 0.78$), and the odds of detecting a decline towards the margin decreased rather than increased with log-transformed n/pop ($\chi^2 = 7.24$, $P = 0.0071$). Restricting analysis to studies using statistical evaluation yielded similar results except that neither association was significant (both $P > 0.64$). No associations between n_{pops} or n/pop and outcome were detected among studies testing for a change in differentiation towards range limits, regardless of whether they used statistical tests (both $P > 0.08$) or not (both $P > 0.20$). The same results were obtained from analyses that examined allozyme or PCR-based studies separately (not shown).

Allocation of sampling effort at the level of *n*/pop also involves the number of genetic markers assayed. Among the studies we reviewed, marker (loci) number varied widely: 3–43 loci for those based on allozymes and 3–12 for those based on microsatellites. However, logistic regressions performed for each of these marker types separately failed to detect any association between marker number and whether a study detected the expected geographical trend in diversity (allozymes: $n = 82$, likelihood-ratio $\chi^2 = 0.81$, $P = 0.37$; microsatellites: $n = 34$, $\chi^2 = 2.97$, $P = 0.085$ nonsignificant trend in opposite direction) or differentiation (allozymes: $n = 33$, likelihood-ratio $\chi^2 = 1.46$, $P = 0.23$; microsatellites: $n = 15$, $\chi^2 = 0.31$, $P = 0.57$). Restricting analysis to studies using statistical evaluation yielded the same results (all $P > 0.17$).

In addition, to the elements of sampling effort discussed above, tests of whether population genetic diversity or differentiation changes towards range margins are likely to be influenced by how extensively the sampled populations are distributed across the geographical range. Most studies we surveyed sampled only a portion of the focal species' geographical range, with less than a quarter (21%) sampling populations range-wide or along a transect that cut through the entire range. Range-wide sampling was particularly limited (10%) among studies that adopted a categorical approach to comparing central vs. peripheral populations. Strictly speaking, 'partial' coverage of the range cannot provide a clear test of the expected pattern of geographical variation in population genetic structure (see Sagarin & Gaines 2002). As mentioned above, partial studies, especially those using two-group categorical sampling, tend to confound geographical peripherality/centrality with a particular region. This confound often makes it impossible to determine whether any difference in genetic structure is accounted for by geographical variation in contemporary population size and isolation or some historical process, for example postglacial range expansion (see below).

There was a tendency among the studies with range-wide sampling to produce results that were less consistent with predictions based on the abundant centre model. For instance, qualitative evidence of a decline in within-population diversity towards range limits was found in 68% of 106 partial studies compared to only 50% of 28 range-wide studies (2×2 $\chi^2 = 3.00$, $P = 0.083$). The same trend also occurred among studies that tested for an increase in differentiation towards range limits, and was also obtained when analysis was restricted to studies using statistical tests, although none of these trends was statistically significant.

It is notable that a substantial proportion of the 28 range-wide studies (32%) found a decline in diversity towards one range limit but not another; hence the overall pattern failed to support this prediction of the abundant centre model (e.g. Comps *et al*. 2001; Coyer *et al*. 2004; Griffin & Barrett 2004). Inconsistent results have also been obtained from eight of the 14 species that were subjected to more than one test, of whether diversity declined towards the range limit. Of the six species where results were consistent, the multiple studies might have used different samples of populations but they focused on the same range edge, usually the northern limit (e.g. *Decodon verticillatus* Eckert & Barrett 1993; Dorken & Eckert 2001; *Pinus contorta* ssp. *latifolia* Yeh & Layton 1979; Yeh *et al*. 1985; Fazekas & Yeh 2001). Relatively few species exhibited consistent geographical patterns in population genetic diversity towards different range edges in different studies (e.g. *Avicennia marina* Maguire *et al*. 2000; Arnaud-Haond *et al*. 2006; *Fucus vesiculosis* Tatarenkov *et al*. 2005, Perrin *et al*. 2007; *Rana latastei* Garner *et al*. 2003, 2004).

Inferring process from pattern

Typically, factors that structure genetic variation across species' ranges are divided into historical and contemporary ones. However, the lack of an unequivocal line between these time scales creates semantic difficulty. We consider as historical any factor that once impinged on the genetic structure of a species, which is no longer operating, but whose genetic signature may still be evident in contemporary populations. This definition would include range fragmentation caused by glaciation and sequential founder events during postglacial expansion, but also habitat fragmentation or extirpations brought about by human activities in past centuries. Contemporary factors are those that continue to shape the distribution of genetic diversity such as population demography (especially conditions that yield low N_e), or impediments to present-day gene flow. It is these contemporary factors, because they are often influenced by human activities, which are most relevant to the conservation of peripheral populations, so determining their contribution to geographical variation in the genetic characteristics of populations is important.

Regardless, few studies *directly* assess any of the possible causes of reduced peripheral genetic diversity or greater differentiation if they exist, and fewer still attempt to quantify the relative contributions of historical and contemporary factors (Table 3). For example, most studies that compare the genetic structure of geographically central vs. peripheral populations assume, either explicitly or implicitly, that peripheral populations are smaller and more isolated than central populations. However, only 25 (19%) of the 134 studies we surveyed reported any measure of population size (usually a rough estimate) for the populations studied, and of these, only 68% found that peripheral populations were smaller (not quite significantly different from random 50% expectation, binomial test $P = 0.054$). Even fewer studies (7%) estimated the degree of spatial isolation among populations, and only 67% of these (i.e. three) detected

Table 3 Studies that have used statistical modelling approaches to distinguish between the effects of historical processes vs. contemporary variation in population size and isolation on geographical variation in genetic structure

Reference	Species	Region	Markers	Predictor Variables*	Approach	Conclusion
Dolan (1994)	*Silene regia*	Missouri, Arkansas, Indiana, Ohio	Allozymes	Glaciation history (glaciated vs. nonglaciated), population size	ANCOVA and correlation analyses	Greater differentiation and significant relation between population size and genetic diversity in eastern glaciated region; possibly arising from recolonization from Ozark refugium or current habitat fragmentation in eastern range.
Durka (1999)	*Corrigiola litoralis*	France, Germany	Allozymes	Population size, country (France = subcentral, source populations, Germany = peripheral, postglacial colonist populations)	ANCOVA	Both population size and country are significant predictors of genetic diversity. Reduced peripheral diversity is due to founder effects and drift.
Lönn & Prentice (2002)	*Gypsophila fastigiata*	Baltic island of Öland	Allozymes	Population size, population density, position (central. vs. peripheral), plant species diversity, number of adults and juvenile plants	Generalized linear models	Population position (central vs. peripheral) is the most important predictor of genetic diversity and interpopulation differentiation. Cause purported as a mixture of smaller and more variable populations sizes, greater isolation, and potentially recolonization in periphery.
Van Rossum & Prentice (2004)	*Silene nutans*	Sweden, Finland	Allozymes	Latitude, population size	Multiple regression with forward selection	Colonization history is more important than current population size in determining genetic diversity.
Johansson *et al*. (2006)	*Rana temporaria*	Sweden	Microsatellites	Latitude, population density (females/km^2)	Multiple regression	Both latitude and population size explain portions of total variation in genetic diversity. Contemporary demography can override influence of history.

*Latitude is considered by authors as a proxy for colonization history.

greater isolation among peripheral populations ($P = 0.25$). Among the 25 studies that recorded geographical variation in some measure of population size, the frequency of support for declining diversity towards range edges did not differ between cases where peripheral populations were smaller (76%) and cases where they were not (75%; $2 \times 2\ \chi^2 = 0.01$, $P = 0.94$). However, when the analysis was restricted to the 18 studies that measured population size and statistically evaluated geographical trends in diversity, support was more frequent when peripheral populations were smaller (83%) than when they were not (33%; Fisher's exact test $P = 0.057$).

An imperfect relationship between present-day population size and genetic diversity is not unexpected (Lönn & Prentice 2002). The degree to which drift will have reduced genetic diversity depends on the harmonic mean of N_e across multiple generations (Wright 1938) not on the current census population size. Thus, peripheral populations may experience greater fluctuations in size and faster demographic turnover than their central counterparts, with past periods when N_e was smallest exerting the greatest influence on current genetic diversity. This emphasizes the grey area between contemporary and historical processes. With some notable exceptions, few studies have directly compared recent temporal trends in population size and recruitment, and genetic diversity in peripheral populations. For example, Lönn & Prentice (2002) documented a greater proportion of juveniles and dead adults in genetically less diverse peripheral populations of the perennial herb *Gypsophila fastigata*, implying faster yearly turnover of individuals, smaller N_e and thus a larger influence of drift. Sjögren (1991) recorded marked temporal fluctuations in population size and reproductive failure in cold years and concluded that these were responsible for reduced diversity in peripheral populations of the pool frog (*Rana lessonae*).

Some authors suggest that historical, climate-driven range shifts are of overarching importance in determining range-wide genetic structure of species (e.g. Pamilo & Savolainen 1999; Hampe & Petit 2005). Certainly, species distributions in temperate regions of the northern hemisphere were directly and disproportionately affected by global cooling and glaciation during the Pleistocene (e.g. Hewitt 2000; Johnson & Cicero 2004). This implies that contemporary patterns of genetic diversity in peripheral populations of many northern temperate species may largely be the result of recolonization of previously glaciated regions and sequential founder events (Lesica & Allendorf 1995; Hewitt 1999; Hampe & Petit 2005). There is a strong bias in our dataset towards northern hemisphere taxa, with only seven of 134 studies conducted solely in the southern hemisphere. Fifty-four of the studies on northern hemisphere species exclusively considered the northern range boundary. Assuming that many expansions were northward from southern refugia (e.g. Austin *et al*. 2004a; Howes *et al*. 2006), it is very difficult to disentangle the effects of postglacial, sequential founder events from the influence of population isolation and small N_e as all three would correlate positively with latitude. However, we found no difference in the frequency of support for the prediction of reduced diversity between studies that focused only on the northern boundary (53%) vs. those that included one or more other boundaries (59%, $2 \times 2\ \chi^2 = 0.37$, $P = 0.53$). We also did not find difference in support for the prediction of greater peripheral differentiation for studies that considered the northern boundary solely (46%) vs. those that included one or more other boundaries (63%, $2 \times 2\ \chi^2 = 1.51$, $P = 0.22$). For some species, this may in part be because postglacial colonization was not a simple northward progression, especially for species in topographically complex portions of Europe (e.g. Garner *et al*. 2004; Heckel *et al*. 2005; Martinez-Solano *et al*. 2005).

The contribution of colonization history to present-day patterns of population genetic diversity is typically evaluated statistically in three ways: (i) regression or correlation of genetic diversity on distance from a putative refugium (e.g. Zeisset & Beebee 2001; Garner *et al*. 2004); (ii) treating latitude as a proxy for colonization history and regressing measures of genetic diversity on it (e.g. Van Rossum & Prentice 2004; Johansson *et al*. 2006); or (iii) comparing genetic diversity of populations in glaciated vs. unglaciated regions (e.g. Dolan 1994). However, colonization history can be inferred more directly using phylogeographical analysis of variation in organellar genomes. Virtually no studies have used species' genealogical histories based on organellar DNA sequences as historical frameworks for evaluating the central-peripheral hypothesis using nuclear markers. Such an approach allows for statistical tests for the imprint of historical range fragmentation, contiguous range expansion and isolation by distance (e.g. Templeton 1998), and for the identification of secondary contact zones (Petit *et al*. 2003; Austin *et al*. 2004b) and ancestral areas (e.g. Austin *et al*. 2004a); all factors the impact of which may still be present in the genetic structure of contemporary populations. Moreover, geographically bounded, monophyletic lineages within species can serve as independent replicates to evaluate the predictions of the central–peripheral hypothesis; an approach that could be profitably used in future studies.

The most appropriate approach to disentangling causation of patterns of genetic diversity involves the statistical modelling of multiple factors like colonization history, contemporary population size and isolation, with some strategy for selecting the most parsimonious model that provides the best fit to the data (Table 3). The few studies that have adopted this modelling approach suggest that contemporary population size and isolation, as well as colonization history, can contribute to patterns of diversity, but that the relative contributions of these factors vary across species and ecological contexts. For example, Johansson *et al*. (2006)

found a relation between allelic richness and population size, even after controlling for latitude (treated as a proxy for colonization history), in Swedish populations of the common frog *Rana temporaria*. Coupled with observations of increasing among-population differentiation, the authors conclude that contemporary demographic factors '... can override the influence of historical factors on species population genetic structure'. Ultimately, the most powerful and appropriate application of this modelling approach requires a sampling regime that reduces confounds among predictor variables (e.g. colonization history, and population size and isolation). For example, if geographically peripheral populations posited to have the smallest N_e and greatest isolation, are also those most recently founded during sequential colonization from a refugial population, then it is almost impossible to quantify the relative contributions of each because of colinearity. Sampling of multiple range edges with distinct colonization histories is one way of diminishing this problem.

Implications for the evolution of range limits and the conservation of peripheral populations

Much of the interest in contrasting central vs. peripheral populations revolves around the question of whether, compared to central populations, peripheral populations have reduced genetic potential to respond adaptively to the potentially extreme environmental conditions they experience (Hoffmann & Parsons 1997). This question underlies the unresolved issue of why species have limits to their geographical distributions; what prevents adaptation to conditions beyond the range limit (Antonovics 1976; Bradshaw 1991; Hoffmann & Parsons 1997; Gaston 2003; Bridle & Vines 2007)? This issue is also central to developing management strategies for peripheral populations at risk of anthropogenic disruption (Lesica & Allendorf 1995; Channell & Lomolino 2000). Do peripheral populations have the adaptive potential to persist in the face of rapid climate change? If so, they may play a key role in facilitating species' range shifts in response to altered climatic regimes and are therefore well worth conserving (Safriel *et al*. 1994; Parmesan 2006).

Are the rather subtle geographical patterns of variation in the genetic markers used in the studies reviewed here reflected in the amount and distribution of genetic variation for traits that might limit geographical distribution or responses to climate change? Are these patterns significant enough to consider in the management of geographically peripheral populations? The degree of concordance between putatively neutral variation at marker loci and quantitative genetic variation for physiological, morphological or life-history traits has been the subject of ongoing debate (e.g. Lewontin 1984; Fraser & Bernatchez 2001; Merilä & Crnokrak 2001; Reed & Frankham 2001). At the very least, the studies reviewed here suggest that peripheral populations very often experience demographic processes, either historical, contemporary or both, that can lead to somewhat lower genetic diversity and higher genetic differentiation. However, differences in genetic variation between geographically central and peripheral populations are rarely very large. Hence, it is not clear whether the mechanisms that generated these differences are strong enough to influence the pattern of ecologically significant trait variation in the face of natural selection. Moreover, the combined effects of environmental stress, selection, drift and inbreeding due to small population size, as well as gene flow on the various components of quantitative genetic variation, are liable to be complex (reviewed in Hoffmann & Hercus 2000; Blows & Hoffmann 2005). For instance, there are contrasting predictions concerning how selection is expected to influence levels of genetic variation at geographical range margins (Safriel *et al*. 1994; Hoffmann & Parsons 1997). Strong and continuous directional selection in extreme environments might reduce genetic variability for traits related to fitness in peripheral populations, compared to central populations, which are expected to experience a much larger component of stabilizing selection. On the other hand, fluctuating environmental conditions at the range edge may maintain more genetic variation in peripheral populations. It has also been suggested that enhanced spatio-temporal environmental variation in peripheral populations might select for genetic mechanisms that increase the level of additive genetic trait variance. Moreover, the environmental stresses potentially experienced by peripheral populations may influence the generation and phenotypic expression of genetic variation (Hoffmann & Merilä 1999; Hoffmann & Hercus 2000). At this point, there is very little empirical evidence to evaluate these contrasting expectations. Despite the large body of work focused on neutral markers reviewed here, there is only a handful of formal quantitative genetic studies in this context, especially studies conducted under field conditions. Studies that combine quantitative genetics with analyses of selection and spatio-temporal variation in the environment are badly needed (Yeaman & Jarvis 2006).

Several of the studies we surveyed quantified geographical variation in morphological or life-history traits along with patterns of neutral genetic variation at marker loci, primarily to test for geographical variation in trait means rather than variance (Hamann *et al*. 1998). There is also a large body of work on forest trees involving common-garden experiments, where large samples of populations are grown together in one or more common gardens to test for geographical variation in population trait means, often in relation to climate as a selective factor promoting adaptive geographical differentiation (e.g. Rehfeldt 1993). In addition, several studies that we reviewed tested for concordant patterns of population differentiation between morphology and genetic

markers (e.g. Wheeler & Guries 1982; Lagercrantz & Ryman 1990; Allen *et al*. 1996; Hamann *et al*. 1998). However, relatively few studies have tested for geographical variation in the amount of phenotypic or genetic variation. A few compared levels of phenotypic variation as expressed under field conditions across a geographical transect or between central vs. peripheral populations. Agnew (1968) documented higher variation in floral morphology within central than within peripheral populations of the perennial plant *Lysimachia volkensii*. Coyle *et al*. (1982) found higher variance in leaf morphology within central vs. peripheral populations of river birch, *Betula nigra*, although the pattern was not consistent. A few other studies have used common-garden experiments to better compare the genetic component of phenotypic variation within populations between different parts of the geographical range. Wilson *et al*. (1991) grew, in a common environment, field-collected seeds of the shrub *Leptospermum scoparium* from 17 populations representing the breadth of ecological conditions across its geographical range in New Zealand and found no clear evidence of reduced phenotypic variation in ecologically marginal populations for a variety of vegetative traits. Volis *et al*. (1998) found that phenotypic variability for drought stress tolerance among field-collected progeny grown in a common environment was actually higher for six peripheral populations than 12 central populations of the annual grass, *Hordeum spontaneum*. In contrast, Yeaman & Jarvis (2006) detected a negative correlation between phenotypic variation for plant height and distance from range centre among more than 100 populations of lodgepole pine (*Pinus contorta latifolia*) grown in 28 replicate geographically scattered common gardens; a pattern that paralleled the decline in genetic diversity at allozyme and RAPD loci towards the range edge observed in multiple studies surveyed here (Yeh & Layton 1979; Yeh *et al*. 1985; Fazekas & Yeh 2001). Kuittinen *et al*. (1997) also detected a roughly parallel decline in genetic variation at microsatellite loci and phenotypic variation in several morphological and life-history traits towards the range margin among six populations of the annual mustard *Arabidopsis thaliana* compared in a common environment. Determining whether these declines in phenotypic and possibly genetic variation, when they occur or whether they play any role in limiting adaptive potential requires more formal analyses of quantitative genetic variability and evolutionary responses in relation to ecologically relevant selection pressures.

Among the most detailed analyses of the role of geographical variation in evolutionary potential to date have involved the annual plant *Chamaecrista fasiculata* and the fruit fly *Drosophila serrata*. Etterson (2004a, b) reciprocally planted pedigreed populations of *C. fasiculata* at three sites across central North America and measured variation in fitness as well as vegetative and reproductive traits. Evidence of local adaptation and selection favouring resident phenotypes was found at all sites. However, the northern population, which was located relatively close to the species' northern range limit, displayed the lowest levels of heritable genetic variation and suffered the largest declines in fitness when planted at the hotter and drier southern sites. The results suggest that northern peripheral populations may exhibit limited evolutionary response to climate change, which is expected to cause northerly populations to experience environments more typical of southern sites (Etterson & Shaw 2001).

Genetic factors limiting geographical distribution have been investigated in *D. serrata*, a fruit fly endemic to New Guinea and Australia. The concordance between its southern distributional limit and patterns of rainfall suggests that a limited ability to resist or avoid desiccation might prevent expansion beyond the southern range edge. Blows & Hoffmann (1993) imposed artificial selection for increased desiccation resistance in replicate lines from four populations distributed up to the southern limit and found lower realized heritability estimates for peripheral compared to central populations. However, mean desiccation resistance was not higher among flies from peripheral populations sampled in this study, and geographical surveys also failed to detect the expected geographical cline in this trait (Hallas *et al*. 2002). These results support the idea that desiccation is possibly not the principle factor enforcing the southern limit.

Geographical comparisons of genetic variation in a variety of other traits revealed significant differentiation among populations but no evidence of lower heritability, estimated from parent–offspring regressions, in two peripheral compared to two more central populations (Jenkins & Hoffman 2000). This was consistent with the results of an analysis of variation at microsatellite loci suggesting that peripheral populations experience a significant input of genetic variation via gene flow (Magiafoglou *et al*. 2002). Climate modelling of natural distributions (Jenkins & Hoffmann 2001) and analysis of trait clines (Hallas *et al*. 2002; Magiafoglou *et al*. 2002) suggested that resistance to cold might limit the southern edge of the distribution. This was supported by lower cold resistance of *D. serrata* compared to three other related species with ranges that extended further poleward, as well as field-cage experiments demonstrating reduced overwinter survival of *D. serrata* but not of a wider ranging species at the southern limit (Jenkins & Hoffmann 1999). Flies collected from peripheral populations after winter exhibited greater resistance to cold shock than those from central populations, but this pattern was not evident when flies were sampled before winter. Moreover, there appeared to be significant genetic variation for cold resistance within all populations. However, laboratory populations failed to evolve higher cold resistance under a fluctuating temperature regime of 7–18 °C after 20 generations compared to populations held at constant 19 °C for 40 generations, suggesting a limited ability of *D. serrata* to adapt to winter conditions

beyond its southern range limit, but adaptive potential was not particularly low in peripheral populations (Magiafoglou & Hoffmann 2003; see also Kellermann *et al*. 2006).

Achieving adequate replication of populations is a major challenge for investigating geographical variation in quantitative genetic parameters and selective pressures, as reliable parameter estimates require large samples sizes for each population involved (Blows & Hoffmann 1993). In the studies on *C. fasiculata* and *D. serrata* discussed above, population and geographical location were necessarily confounded. Without replicate populations represented in each geographical location, observed differences cannot be extrapolated to general associations between genetic characteristics and peripherality/centrality. Larger-scale and more robust geographical analysis of adaptive trait variation may be most feasible in systems where range expansion is clearly limited by specific traits (e.g. reproductive timing; Griffith & Watson 2006) and for which the genetic architecture of phenotypic variation has been determined (e.g. Stinchcombe *et al*. 2004). For the species that have become model systems, the genetic underpinnings of a wide array of stress-resistant traits have already been investigated in detail (Van Straalen & Roelofs 2006). Efficient genomic assays will enable the pattern of geographical variation at these key loci to be quantified (e.g. Caicedo *et al*. 2004) and to be linked to patterns of phenotypic variation and selection in natural populations (e.g. Korves *et al*. 2007).

Conclusions and recommendations

Since the development of biochemical assays of genetic variation more than 40 years ago, geographical variation in population genetic structure has been assessed for a wide range of plant and animal species (Table 1). We can now conclude that, on average, within-population genetic diversity declines and among-population differentiation increases from the centre of the geographical range to the periphery. As a rough guide, any given species is more than twice as likely to show the predicted pattern as not (Table 2), and usually a change in diversity is accompanied by a parallel change in differentiation (Fig. 2). In most cases, however, the difference in genetic diversity between central and peripheral population is not large (Fig. 1) and the mechanisms that generate this pattern are not clear. Although some broad generalizations have emerged, our survey also revealed some biogeographical and taxonomic biases and common methodological weaknesses in the empirical studies to date.

Most studies have focused on the northern range limit of species in the temperate zone of the northern hemisphere (see also Hampe & Petit 2005). There are very few tests of theoretical predictions involving populations sampled from across the range, so that geographical centrality/peripherality is usually confounded with specific geographical region. Moreover, most studies use a relatively arbitrary categorical definition of peripherality, without consideration of the biology of the focal species (but see Schwartz *et al*. 2003). Almost no studies used 'distance to range margin', a continuous measure of peripherality that permits more sensitive statistical tests, helps to address the aforementioned confound of peripherality and geographical region, and eliminates the sometimes subjective nature of categorical approaches. Many studies assess variation in diversity without evaluating genetic differentiation, and geographical trends in either parameter are rarely subjected to statistical testing.

We were not able to include any study on taxa with an exclusively tropical distribution. Lowland tropical species and low latitude montane species, at least in the Americas, may have ranges that are on average more temporally stable than higher-latitude taxa directly impacted by glaciation (e.g. Winker *et al*. 2000; Bush *et al*. 2004). Thus, the distribution of genetic diversity is potentially less affected by range shifts and founder events. Furthermore, some authors have suggested that the microevolutionary processes driving evolution (drift, gene flow and selection) may covary with latitude and have produced the markedly deeper average divergences among populations and species in the tropics (Chek *et al*. 2003; Martin & McKay 2004). These marked biogeographical biases in our dataset thus further limit our ability to generalize. Uneven sampling of species across taxa may also bias results, although our analyses did not detect significantly different patterns in over-represented taxa (Pinales, Anura) compared to other plants or animals.

There has been relatively little effort to test the possible connections between pattern and process. We have a poor understanding of whether geographical variation in diversity and differentiation is the product of ongoing evolutionary processes in contemporary populations or a legacy of historical fluctuations in effective population size and gene flow associated with shifts in geographical range during periods of climate change. Recent reviews of the empirical evidence suggest that the oft-assumed decline in population size and increase in isolation towards range limits, as predicted by the abundant centre model, occur far less often than previously expected, although direct range-wide tests of the abundant centre model are still very rare (Sagarin & Gaines 2002; Sagarin *et al*. 2006). Perhaps this suggests that geographical patterns in population diversity and differentiation often observed in the studies reviewed here are not generally caused by geographical variation in contemporary population and metapopulation dynamics. Yet, our survey also supports the complaint by Vucetich & Waite (2003) that the results of many studies are arbitrarily interpreted in terms of historical processes without evaluating the possibility that the observed patterns are consistent with contemporary geographical variation in population

size and isolation. Modelling approaches aimed at estimating the relative contribution of contemporary vs. historical processes can profitably use data on population size and population isolation (e.g. Dolan 1994; Durka 1999; Lönn & Prentice 2002; Van Rossum & Prentice 2004; Johansson *et al*. 2006), but these data are rarely collected in conjunction with estimates of genetic parameters. Most studies have not incorporated a phylogeographical framework into their analyses (but see Heckel *et al*. 2005) and thus cannot explicitly evaluate the potential contributions of, for example, sequential founder effects during postglacial colonization (Hewitt 1999), secondary contact zones (e.g. Petit *et al*. 2003), or greater differentiation and diversity in ancestral refugial areas (Hampe & Petit 2005). The wealth of phylogeographical studies for a broad array of taxa (e.g. Soltis *et al*. 2006) and increasing ease of high throughput genotyping of nuclear markers provide excellent opportunities for using robust, independent molecular genealogies to evaluate the importance of history on the current genetic diversity, and to move beyond simple assumptions that latitude is an adequate surrogate for colonization history or population demography.

Finally, there has been little effort to determine whether geographical trends in putatively neutral variation at marker loci are reflected by quantitative genetic-trait variation likely to influence the adaptive potential of populations across the geographical range. This along with uncertainty about the relative contribution of contemporary demographic factors to the geographical variation in population genetic parameters weakens our ability to apply the available empirical results to the management of peripheral populations. Given the tremendous sampling effort required to sort out the potentially complex interactions between geographical variation in population size, isolation and selective pressures, generalizations will likely be slow to emerge, except in model systems where major genes contributing to ecologically significant trait variation are known and can be readily assayed. However, the rapidly growing array of genomic tools (van Straalen & Roelofs 2006) is likely to create new and possibly unanticipated opportunities for the comparative ecological-genetic analysis of populations at geographical range limits.

Acknowledgements

Our own work on the genetic structure of species' across geographical ranges has involved collaborations with Jim Austin, Jill Hamilton, Briar Howes and Sarah Yakimowski. We thank Louis Bernatchez for encouraging us to write this paper; Jim Austin, Louis Bernatchez and Joanna Freeland for comments on the manuscript; the Canada-U.S. Fulbright Foundation for funding a Visiting Research Chair at University of California, Santa Barbara to CGE; and the Natural Sciences and Engineering Research Council of Canada for a postgraduate scholarship to KES and Discovery Grants to SCL and CGE.

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Chris Eckert's research group is interested in the ecological and evolutionary genetics of plants, with a particular fondness for reproductive strategies. Karen Samis just completed her doctoral research in the Eckert lab investigating the ecology and evolution of geographical ranges using Pacific coastal dune plants as an experimental system. Steve Lougheed's group uses a variety of population genetic and phylogeographical approaches to investigate the origins of phyletic and adaptive diversity, primarily in frogs and reptiles. All three authors are exploring how a better understanding of range limits can contribute to the conservation of geographically peripheral populations.
