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OPINION

Incorporating latitudinal and central–marginal trends in assessing genetic variation across species ranges

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The genetic variation across a species' range is an important factor in speciation and conservation, yet searching for general patterns and underlying causes remains challenging. While the majority of comparisons between central and marginal populations have revealed a general central–marginal (*C–M*) decline in genetic diversity, others show no clear pattern. Similarly, most latitudinal studies (although much fewer, especially those conducted rangewide) also showed latitudinal trends in genetic variation. To date, the *C–M* and latitudinal patterns have often been examined independently and have rarely been considered together when accounting for the observed genetic variation across species ranges. Here, in the light of the most recent findings, I show how latitude might be responsible for some of the deviations from the general *C–M* trends in genetic diversity, and vice versa. In the future, integrating latitude and range geometry with climate-induced species migration would offer important insights into conservation prioritization across species ranges.

Keywords: α-, β- and γ-diversity, climate change, genetic diversity, history, novelty, phylogeography, range geometry and orientation, species invasion

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Introduction

The spatial distribution of genetic diversity is a key aspect and long-standing issue in speciation and biological conservation. There is growing interest in species' rangewide genetic structure, coincident with unprecedented biodiversity loss. Particularly, increasing human influence and climate change constantly alter and redistribute the abundance and genetic centres of species. Thus, identifying and monitoring hotspots of genetic diversity for a species of interest are needed for establishing conservation priorities (Fleishman *et al.* 2002). For allocating conservation efforts with limited resources, perhaps among the most controversial issues is whether central or marginal populations should be given higher priority. Some argue that central populations should be protected first because they often hold the highest genetic diversity and thus represent the major 'sources' of genetic variation (reviewed in Hardie & Hutchings 2010). Others advocate prioritizing marginal populations because they are considered endangered and are more sensitive to environmental changes (Vecutich & Waite 2003; Hampe & Petit 2005). To date, however, marginal populations have been the major focus for both research and conservation because (i) they usually are more isolated and have low density (Lomolino & Channel 1995; Bahn *et al.* 2006), and (ii) they may interact more extensively and intensively with other species (Mcdonald-Madden *et al.* 2008).

Despite considerable progress, recent studies comparing the relative genetic and phenotypic diversity between central (*C*, or core) and marginal (*M*, or peripheral) populations continue to generate discordant patterns and inconsistent explanations (Hardie & Hutchings 2010). Some studies address hypotheses specifically related to the geographical direction of the periphery studied (i.e. few studies have examined the patterns in more than one direction; see review by Eckert *et al.* 2008). As a consequence, these studies have not sufficiently addressed the possible effects of latitude and species-range geometry (e.g. metric, shape and size). However, latitude is not only associated with overall species diversity; it may also be related to speciation rate, the intensity of biotic interactions and the course of species migration (Martin & McKay 2004; Mittelbach *et al.* 2007; Eo *et al.* 2008). Also, range geometry and orientation may control many processes related to gene flow, pollination, migration and relative positions of populations within a species range and distances among them (Brown *et al.* 1996; Gaston 2003). This factor alone could cause some degree of inconsistency among studies as the relative positions and distances (or isolation) among populations to a large extent determine the gene flow (amount and direction), genetic drift, inbreeding and many other genetic processes. For these reasons but particularly for the sake of history, the phylogeographical approach has proved to be a powerful tool with increasing usage in recent years for assessing historical genetic variations, linkages and refuges during past species migration and range shifts that may alter patterns (e.g. *C–M* comparisons) in contemporary populations (Pfeifer *et al.* 2009; Pinheiro *et al.* 2011).

Other major contributing factors for the debates over the spatial genetic variation include discrepancies in sampling

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Despite considerable progress, recent studies comparing the relative genetic and phenotypic diversity between central (*C*, or core) and marginal (*M*, or peripheral) populations continue to generate discordant patterns and inconsistent explanations (Hardie & Hutchings 2010). Some studies address hypotheses specifically related to the geographical direction of the periphery studied (i.e. few studies have examined the patterns in more than one direction; see review by Eckert *et al.* 2008). As a consequence, these studies have not sufficiently addressed the possible effects of latitude and species-range geometry (e.g. metric, shape and size). However, latitude is not only associated with overall species diversity; it may also be related to speciation rate, the intensity of biotic interactions and the course of species migration (Martin & McKay 2004; Mittelbach *et al.* 2007; Eo *et al.* 2008). Also, range geometry and orientation may control many processes related to gene flow, pollination, migration and relative positions of populations within a species range and distances among them (Brown *et al.* 1996; Gaston 2003). This factor alone could cause some degree of inconsistency among studies as the relative positions and distances (or isolation) among populations to a large extent determine the gene flow (amount and direction), genetic drift, inbreeding and many other genetic processes. For these reasons but particularly for the sake of history, the phylogeographical approach has proved to be a powerful tool with increasing usage in recent years for assessing historical genetic variations, linkages and refuges during past species migration and range shifts that may alter patterns (e.g. *C–M* comparisons) in contemporary populations (Pfeifer *et al.* 2009; Pinheiro *et al.* 2011).

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strategy (e.g. sample size, location, intensity, spatial arrangement and timing). For example, the *C–M* pattern in genetic diversity would be quite different if sampled in different cardinal directions from the centre to margin (i.e. *C–N, C–S, C–W* and *C–E*; Fig. S1, Supporting Information). Yet the patterns examined in different directions cannot be simply averaged to generalize the *C–M* patterns for the species with a succinct interpretation (Garner *et al.* 2004; Howes & Lougheed 2008).

For simplicity, here I consider the species with somewhat regular range shapes—circular or near circular, linear or near linear (with both types only loosely defined). The former is exemplified by the strong correlations of populations in many species between the latitudinal (*S–N*) and longitudinal (*W–E*) dimensions (Brown *et al.* 1996), and the latter by coastal or riparian species which tend to be somewhat linear and restricted in width. It is difficult to categorize and quantitatively analyse species' ranges that have highly irregular shapes such as those with multiple, disjunct distributions. A parallel issue also exists in describing density functions within species ranges. Among the most frequently used density functions along *C–M* gradients is the Gaussian-like (density-decay) curve. Other abundance patterns such as random and uniform patterns, though sometimes used in theoretical studies, rarely occur in nature, especially at the whole-range level.

To date, the roles of genetic drift, bottleneck effects, founder effects, inbreeding and isolation related to range edge have received the most attention (Eckert *et al.* 2008). Studies regarding the role of latitude (mostly associated with species migration after glaciations) and those conducted across entire species ranges have been relatively fewer, partly due to recent advances in molecular technology. However, the two dominant forces have almost always been examined separately (James *et al.* 1997; Lammi *et al.* 1999; Vecutich & Waite 2003; Martin & McKay 2004) and have rarely been considered together as an alternative explanation when the expected pattern (e.g. either latitudinal or *C–M*) is not detected. Here, using most recent findings and species with a general decline in density from centre to margins as an example (other abundance functions are not considered here for simplicity and demonstration purposes), I explore how latitudinal processes might alter the *C–M* genetic variations within and among populations across species ranges, and vice versa (Fig. 1). I then make several sampling and conservation recommendations in the light of the linkage between latitude/range geometry and genetic diversity.

General perceptions of genetic diversity vs. novelty

In more or less natural settings, the location and relative position of populations across the species' range indicate the density, size, directions of gene flow and genetic heterogeneity/novelty, to some degree. For species with a general decline in density from range centre to margin, higher genetic diversity (α-diversity) is expected in an individual central population than in a marginal population (Vecutich & Waite 2003). The central populations are surrounded by neighbouring populations in all directions. The marginal populations, in contrast, share a smaller portion of their borders (<50% on average) with neighbours of its own species (i.e. only the interior populations), which could reduce their genetic variation. The greater isolation reduces gene flow not only from central populations ('sources', often asymmetrical) but also from other marginal populations ('sinks'), thus increasing the genetic differentiation among marginal populations (β-diversity; Faugeron *et al.* 2004; Eckstein *et al.* 2006; Fig. 2). Although central populations have higher genetic diversity per unit area, those at the margins may have more unique or novel genetic variations due to isolation and local adaptation (or adaptive radiation; Vecutich & Waite 2003). While most previous studies have focused on genetic diversity within populations, genetic novelty and its conservation value have received far less attention.

For many species, a few large populations occupy a smaller area at the range centre and are geographically closer to each other, and gene flow among populations would be greater and more symmetrical (Wakeley 2004). In contrast, numerous but smaller marginal populations surrounding the central populations and other interior populations occupy a much larger area and are relatively more isolated from each other, especially from populations on the opposite side of the range. The populations in the middle, as a whole, usually receive inputs (gene flow) and asymmetrical feedbacks from both central and marginal populations (Fortuna *et al.* 2009). In addition, when all populations (pooled) in each distance interval from the centre (or margin) are considered, the majority of individuals and populations would exist in the intermediate area along the *C–M* gradients, despite the high population density at the centre and the large geographical extent at the margin (Guo *et al.* 2005). Thus, the populations in the intermediate area may hold the greatest amount of genetic diversity of the species, although the diversity per population or per unit area is the highest at the centre. This is supported by a growing body of evidence showing the positive relations between population size and genetic diversity (Lammi *et al.* 1999). This enhanced diversity may contribute to genetic variation and stability in central, but especially in marginal populations through asymmetrical $C \rightarrow M$ gene flow (Wakeley 2004).

Latitudinal vs. central–marginal (*C–M*) patterns

To date, most studies designed to make comparisons between central and marginal populations have identified some kind of *C–M* trends. For example, 64% of the 134 studies surveyed by Eckert *et al.* (2008) observed the decline in within-population genetic diversity from centre to margin (see also review by Hardie & Hutchings 2010). Latitudinal studies on between-population difference have also found latitudinal trends (73%, or 45 of 62 taxa examined by Martin & McKay 2004). The high proportion of latitudinal or *C–M* patterns in these two surveys is particularly interesting given many alternative patterns that may exist (Table S1, Supporting Information). Nevertheless, while the first-order linear

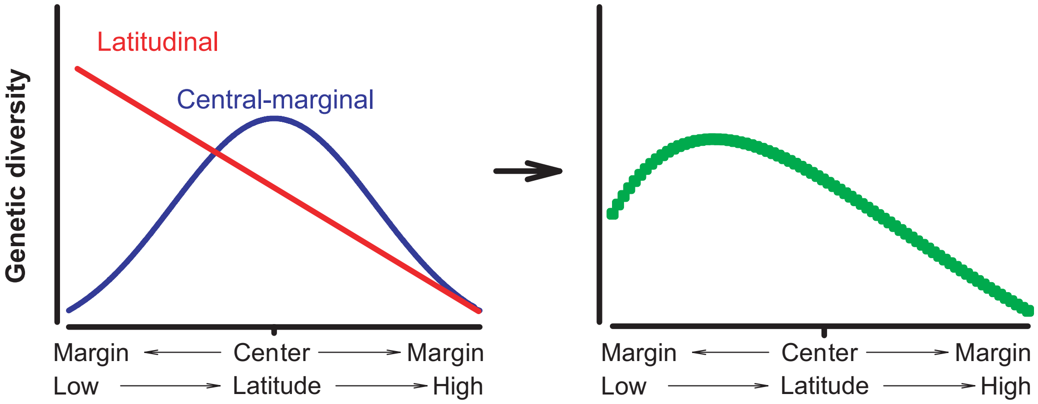

Fig. 1 An example of species with a general central–marginal (*C–M*) decline in density showing how within-population genetic diversity might vary across the whole species range (i.e. from centre to margin) and with the latitude (i.e. low to high). If the latitudinal pattern in genetic diversity is detectable (especially for species with large ranges or latitudinal extents), the *C–M* pattern trend (similar to or may be related to the geometric constraint or mid-domain effect; Colwell *et al.* 2004; Miller *et al.* 2010) is enhanced or overwhelmed by the latitudinal pattern in the higher latitudinal portion of the species range but weakened or obscured in the lower latitudinal portion. The interactive effects of latitudinal and *C–M* processes (left) lead to the intermediary pattern often observed in the field with genetic diversity peaks at lower portion of the species' latitudinal extents (right).

regression analyses reveal the latitudinal trends for all studies examined in this synthesis (Fig. 3 left), quadratic and cubic regressions on the same data also reveal right skewed and hump-shaped curvilinear relationships that largely reflect the *C–M* patterns. Generalized linear models (GLMs) show that for all species showing both latitudinal and *C–M* patterns, the nonlinear regressions provide better fits than the simply linear model (cf. Fig. 3 right vs. left). In other words, the populations at the range margins have lower genetic diversity, although those at the lower latitudinal limits still hold higher diversity than those at higher latitudinal limits (Table S1, Supporting Information; Howes & Lougheed 2008).

For species with large ranges, the populations at *N, E, S, W* and the centre could experience very different physical and biotic conditions and thus would be under different selection pressures. As a result, there would be detectable differences in genetic structure among these populations, especially between *N*- and *S*-populations (Figs 1–3) that may experience the warmest and coldest temperatures within the species' range (cf. elevational diversity patterns on different aspects of the same mountain in the temperate zones). Also, where the decline in genetic diversity with latitude within a species' range is detectable (Martin & McKay 2004), the higher genetic diversity in populations at lower latitudes may be at least partly caused by the same reasons responsible for the higher species diversity at lower latitudes (Mittelbach *et al.* 2007). In such situations, the commonly observed *C*→*M* decline in genetic diversity would be overshadowed by the greater declining trends with latitude (Fig. 1).

Range orientations may be the most important factor for species with linear ranges (e.g. coastal species) although such species are relatively few. If the linear range has a *S–N* orientation with a considerable latitudinal extent, populations at lower latitudes might show higher genetic diversity than *C*- and high latitudinal populations. In contrast, if a species has a range with a dominant *W–E* orientation, the *C* populations may still hold the highest genetic diversity, unless strong longitudinal environmental gradients such as elevation are present. On the other hand, for species with highly dynamic ranges, most of the invading populations are likely to show lower genetic variation than those retreating populations of similar sizes due to historical effects (Petit *et al.* 2003), regardless of range orientation.

The parallel decline of both within-species genetic diversity and overall species diversity with latitude might involve similar mechanisms to some degree (Eo *et al.* 2008; Palma-Silva *et al.* 2009). However, as noted by Miller *et al.* (2010), differential geometric constraints on species and genes may lead to different patterns of species richness and genetic variation (Palma-Silva *et al.* 2009). On the other hand, Hardie & Hutchings (2010) suggest that some of the latitudinal trends might reflect the directions of historical range shifts; for example, when species move poleward, especially under climate warming, older populations often with higher genetic diversity are left at lower latitudes (Table S1, Supporting Information). If this is indeed the case, the overall decline of species diversity from the tropics to polar region should reflect such historical events. Therefore, documentation of latitudinal genetic and species diversity would invoke careful background investigation on species' migration history in both geological past (e.g. glaciation episodes) and that associated with recent climate warming. As Martin & McKay (2004) have noted, re-colonization of previously ice-covered regions alone cannot always explain the latitudinal variation in population divergence within species. Thus, how much genetic diversity can be attributed to gene flow and how much is developed locally within a particular population remains to be explored and may require more direct measurements of migration rate.

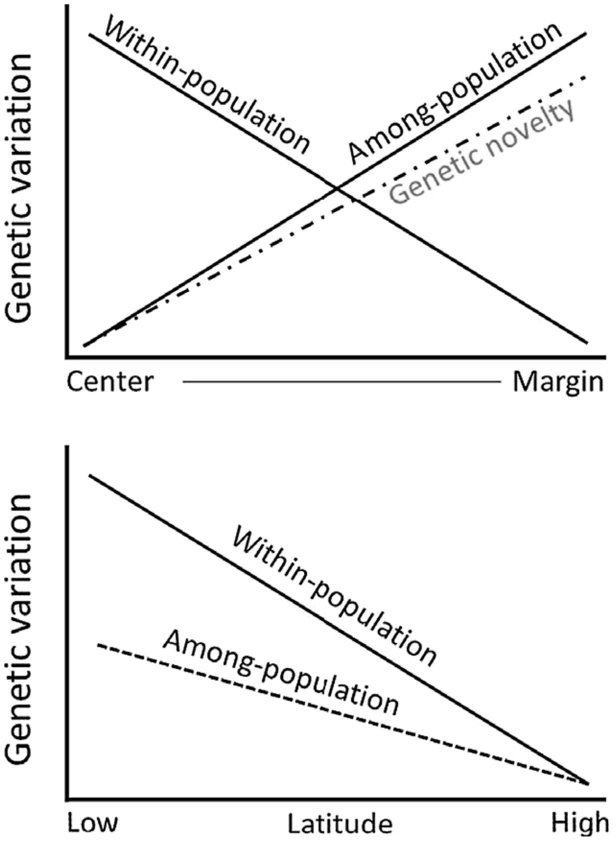

Fig. 2 Diagram showing hypothesized differences in within-population (α-diversity) and among-population genetic variation (β-diversity) along the central–marginal and latitudinal gradients across species ranges. Within- and among-population genetic variations show contrasting patterns from the centre to margin due to joint effects of population density (and size) and isolation (Lammi *et al.* 1999; Zakharov & Hellmann 2008; top). Also, because range margins may be more dynamic in terms of expansion or contraction and have greater chances of hybridization, the adaptive genetic novelty would be higher at range margins, especially the advancing (or colonizing) margins. Everything else being equal (i.e. population size, density, isolation), within- and among-population (given the same levels of isolation and distances among them) genetic diversity may show similar patterns along latitude (Martin & McKay 2004), yet their relative positions and strength would be highly species-specific and may depend on how each is measured (Schrey *et al.* 2011; bottom). The latitudinal trends are based on the assumptions that (i) the same mechanisms responsible for the latitudinal patterns in overall species diversity also lead to similar patterns in within-species diversity (Mittelbach *et al.* 2007; Miller *et al.* 2010), and (ii) much genetic variation and resources are left at lower latitudes following poleward species migration (e.g. after glaciations).

Yet, not all species show the general decline in genetic diversity with increasing latitude (Schiemann *et al.* 2000; Pinheiro *et al.* 2011) due to each species' unique natural and unnatural (e.g. human use) history and phylogenetic position. Relative to overall species diversity pattern, the latitudinal patterns of within-species genetic diversity could be highly species-specific and more dynamic and variable (Hellmann *et al.* 2008). For species with very small ranges, for instance, a latitudinal trend in genetic variation either does not exist or cannot be detected due to narrow latitudinal extents or extremely low abundance (e.g. *Primulina tabacum* Hance, a rare plant; Ren *et al.* 2010).

To date, research on latitudinal intraspecific genetic variation has mainly focused on within-population variation (α-diversity), including Maguirre *et al.* (2000), Ikeda *et al.* (2007), Lihová *et al.* (2010) and Vik *et al.* (2010). Few studies examined among-population variation (β-diversity) over latitude (Martin & McKay 2004). However, for both within- and among-population comparisons, latitude and *C–M* processes may cancel each other depending on their relative strength, making data interpretation more complicated and difficult. For example, some eco-morphological studies show strong latitudinal within-species variation in certain traits (e.g. following within-species Bergmann's rule; Gabriel 1978). In such cases, *C–M* patterns may not be detected or may even be overwhelmed by the latitudinal patterns, that is, genetic diversity may be greater in populations at lower latitudes than those at range centre (Figs 1–3). Equally, the opposite may be true when strong *C–M* trends exist. In fact, the large variation (i.e. large residuals or low r^2) in latitudinal genetic diversity in several recent reports (Miller *et al.* 2010) may be at least in part due to the confounding effects of central–marginal processes.

A major challenge ahead is how to separate and evaluate the relative strength of the latitudinal and *C–M* trends. Unfortunately, evaluating existing studies in this regard is difficult because prior sampling procedures were designed for either latitudinal or *C–M* comparisons (not for both), and the sample size in most cases was relatively small. Future work should focus on improving and increasing sampling across entire species ranges, allowing tests of multiple hypotheses as discussed in the section.

Range geometry and sampling design

The most common weakness in earlier efforts to locate genetic hotspots is insufficient sampling across the entire species range, mainly due to under-developed technology (Eckert *et al.* 2008) and difficulties in obtaining collection permits and funding. As discussed previously, everything else being equal, whether the latitudinal or *C–M* pattern may be detected for a particular species also depends on the range geometry and orientation, and correspondingly survey/sampling procedures. As Fig. 2 illustrates, even though α- and β-diversity may show similar trends with latitude for a particular species, they might be in striking contrast along the *C–M* gradients (Faugeron *et al.* 2004).

In addition to the common *C–M* comparisons, researchers have conducted the central–central (*C–C*) and marginal–marginal (*M–M*) comparisons (Eckstein *et al.* 2006; Fig. S1, Supporting Information). The latter can be analysed by comparing neighbouring and distant populations (i.e. those

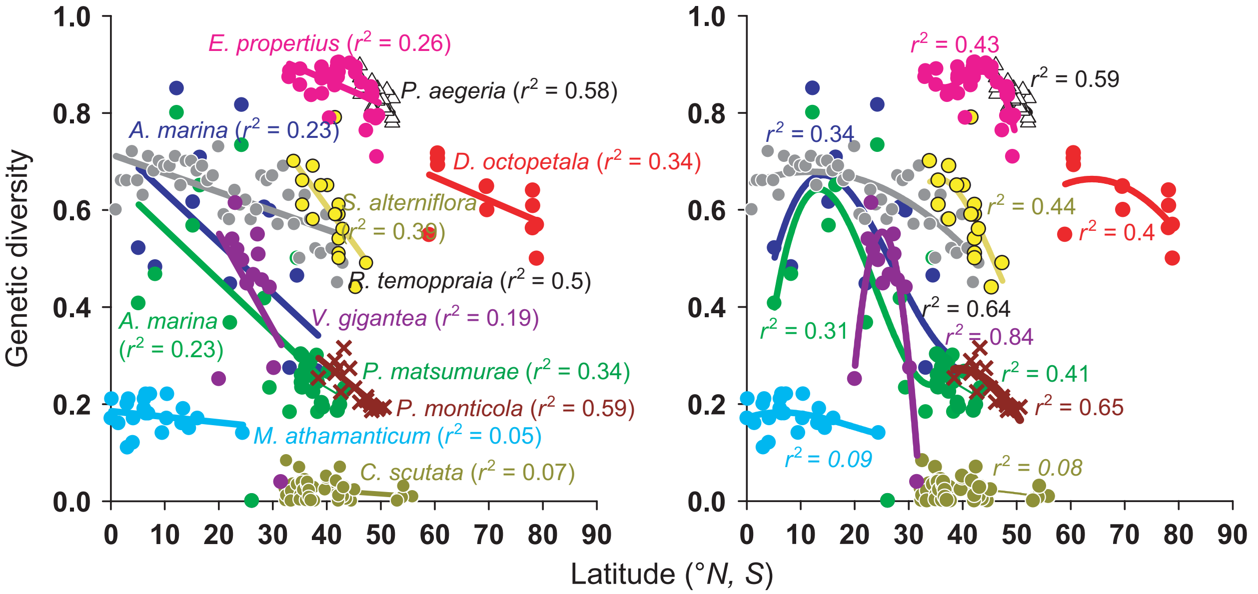

Fig. 3 Examples of the first-order linear regression (left) and quadratic/cubic regression (right) relationships between latitude and genetic diversity using the same data (species' full scientific names are provided in Table S1, Supporting information and in the text). The green and dark blue symbols for *Avicennia marina* represent the observed (H_O) and expected (H_E) proportion of heterozygotes, exemplarily highlighting the varied outcomes from different measures in assessing genetic diversity. The first-order regressions show strong decline in genetic diversity with latitude whereas, the quadratic/cubic regressions show right skewed curve-linear relationships which confirm both the general latitudinal decline in genetic diversity and the central–marginal (*C*–*M*) pattern. However, the drop in diversity towards the species range margins appears to be smaller at the lower latitudinal limit than at the higher limit. Note that the position of each species in the graph cannot be used as an indication of higher or lower genetic diversity relative to others because genetic diversity here is determined by various measures (Schrey *et al.* 2011).

on the opposite edges of the species' range with greater environment disparities). The overall greater genetic diversity in all marginal populations may have been underestimated, although in general the genetic diversity in a single marginal population is relatively low (Hardie & Hutchings 2010). Unfortunately, although a few studies have also sampled locations between centres and margins (Hutchison 2003), available data still do not allow a meta-analysis. For example, the recent analysis based on *C*–*M* comparisons by Eckert *et al.* (2008) revealed that most such studies focused on the higher latitudinal limits of species ranges, often in one direction (*C*–*N*). Nevertheless, while most studies in their survey showed the expected *C*→*M* decline in genetic diversity, this proportion was higher among studies that compared dichotomous *C*- vs. *M*-populations (73% of 91 studies) than among studies using 'continuous' sampling of populations from *C* to *M* (47% of 43 studies), implying the discussed effects of sampling strategy and the use of simple *C*–*M* comparisons.

Besides spatial patterns, as previously discussed, a few emerging issues deserve further consideration. First, species with special or unique distributions resulting from physical boundaries (e.g. coastal species; for an example of a species with a truncated range, Howes & Lougheed 2008), species introductions or biotic invasions (Pattison & Mack 2009), and disjunctions due to habitat fragmentation (Le Roux *et al.* 2008) need special treatment. Second, all spatial patterns vary over time. Third, habitat quality and human activities could significantly affect the genetic structure across species range and complicate or erode the positive relationship between population size and genetic diversity (Fleishman *et al.* 2002). Finally, most, if not all, species have migrated due to accelerated climate changes, but high genetic diversity could be retained in the original locations because of remnant individuals from the former 'core' populations (Garner *et al.* 2004; Hampe & Petit 2005). Thus, sampling time relative to the direction of migration and history (e.g. poleward or upward under warming climates) is essential.

With increased conservation efforts worldwide and highly improved technology, sampling across the entire ranges of many more species with high intensity becomes possible. Not only does such sampling allow different comparisons and tests of multiple hypotheses, it also informs better conservation plans and measures. Before this is accomplished, it is difficult to make generalizations regarding the spatial genetic variation or make comparisons among species. For example, the decline of genetic diversity from *C* to *N* does not separate the latitudinal trends from *C* to *M* patterns (Fig. 1 and Fig. S1, Supporting Information). If sampling covers the entire range, the increased number of samples can be analysed both latitudinally and longitudinally along the central–east (*C*–*E*) and central–west (*C*–*W*) gradients, allowing tests of the presence and even relative strength of latitudinal and *C*–*M* patterns. A multiple regression framework could be useful to identify the relative contribution of the two factors. If no clear pattern is observed (especially through the *C–S* portion of the species' range), the cancellation between latitudinal and *C–M* patterns should be considered as a possible cause.

In addition to the sampling effect, very few comparative studies have been conducted in tropical settings where species ranges may have been relatively stable (Palma-Silva *et al.* 2009; Miller *et al.* 2010). Little effort has specifically focused on the longitudinal trends in genetic diversity, especially along environmental gradients from coastal to interior regions or from low to high elevation. Future research is needed to fill this information gap.

Effects of human activities and climate change and conservation implications

The natural patterns of species genetic diversity are being increasingly altered by human activities, and few studies have examined the possibly dramatic effects of humans such as land use/habitat fragmentation, species introductions and associated recent climate warming (Vandewoestijne & Van Dyck 2010; Schrey *et al.* 2011). This brings an urgent task for conservation geneticists, especially concerning rare and endangered species whose ranges are increasingly fragmented. Knowing where habitat destruction is occurring within species ranges is essential. If fragmentation takes place in the range centre, the genetic diversity could be reduced due to decreased population size and density. If it takes place at the margin, some genetic novelty would be lost, especially at the rear edge (Hampe & Petit 2005). Sampling time is critical because it is possible that genetic diversity may persist at the same level shortly after habitat fragmentation but then would decline over time. In contrast, introductions of species, including invasives, across the globe would increase the species' genetic diversity (Schrey *et al.* 2011). How species introductions might affect the genetic diversity of local (or native) species, especially those closely related, deserves further investigation (Fortuna *et al.* 2009).

Effective allocation of conservation efforts depends on the relative strength of the latitudinal vs. *C–M* trends in genetic diversity, which are often species-specific. When neither a latitudinal nor a central–marginal pattern is apparent, other patterns and associated factors should be identified. For species with strong *C–M* patterns, the long-term persistence of marginal populations is likely linked to central or interior populations, particularly through the source–sink dynamics (Wakeley 2004; Guo *et al.* 2005; Kanda *et al.* 2009). In such cases, conservation should include central populations, as conserving marginal populations alone may not be sufficient. For species with strong latitudinal genetic variation, populations at lower limits usually have higher genetic diversity (Figs 1–3). Such species are most likely to suffer greater impacts from climate warming and are likely to shift poleward; thus, genetic diversity and novelty at lower latitudes may be lost and should be conserved with high priority (Hampe & Petit 2005).

Latitudinal and *C–M* patterns also have important implications for the banking of genetic materials (e.g. seeds) amid changes in climate and land use. It still remains unclear whether genetic diversity often spatially overlaps with novelty. To ensure species adaptation to future climate change and altered landscapes, a balanced collection of genetic resources from the centre and edges (particularly *N* and *S*) would be necessary to effectively preserve enough diverse and sufficient genetic material/novelty. Some less-intensive and balanced collection of genetic materials in more locations across the species range can also help avoid 'cryptic bottleneck' due to dominance of a few genotypes in future plantations for conservation. In addition, restoration or transplantation of certain populations to other locations within the species range could promote genetic diversity and reduce inbreeding depression, thus decreasing the possibility of population or species extinction (Ren *et al.* 2010).

Advances in sequencing make it increasingly possible to examine adaptive radiation due to natural selection using large numbers of loci, not simply neutral variation. To date, the scale and extent of adaptive variation for most taxa still remain poorly understood, but some evidence suggests that only specific genotypes with high genetic variation are responsible for range expansion (Bridle & Vines 2007; Merrill *et al.* 2012), and expansion could in turn deplete genetic variation due to the bottleneck effect (Eckert *et al.* 2008). Thus, knowing to what degree genetic variation may lead to phenotypic difference among populations with adequate plasticity is critical for conservation.

Next generation–sequencing (NGS) technologies are improving our fundamental understanding of genetic variation by offering fast, inexpensive and enormous volumes of data (Gilad *et al.* 2009). NGS enables us to re-sequence entire genomes and/or entire transcriptomes more efficiently. Rather than sequencing individual genomes, it is now possible to sequence large number of related genomes to measure genetic diversity and to decouple genetic variation and novelty within and between large populations. With massive data from NGS including WGS, RNA-seq, RAD-tag (Baird *et al.* 2008), genespace, transcriptome sequencing and related approaches, we will soon be able to test new hypotheses related to the potential links between genetic diversity and novelty and between spatial genetic structure and the biotic and abiotic environments.

Conclusions and further suggestions

Although the relative strength of the latitude vs. *C–M* trend is expected to be highly species-specific and vary with migration history and environmental context, future work jointly considering the two patterns would greatly improve our understanding of rangewide genetic diversity. Given the rapidly accruing genetic data from expanded molecular technologies and the aforementioned dire need for conservation, it becomes easier to identify the true genetically hot and unique spots. Because all populations are somehow related to each other, and each one contributes unique aspects to the overall genetic variation and potentially adapts to a different set of environmental variables, a balanced and dynamic conservation strategy is needed (Mcdonald-Madden *et al.* 2008).

In the future, in addition to the recommendations made by Eckert *et al.* (2008; e.g. 'distance to range margin' sampling, coverage of species in different latitudes and phylogeography), the following issues or priorities need to be emphasized, especially in rangewide and conservation-based research: (i) effects of human activities—this research is urgently needed because the patterns in natural settings are likely to be drastically altered by land use changes or species introductions; (ii) effects of future climate change; (iii) genetic diversifications within and among populations across latitudes; (iv) rigorous comparisons using different measures (e.g. allelic richness, gene diversity) for the same species (Nybom 2004; Petit *et al.* 2005) and the same measure (γ-diversity) across species (Hamrick *et al.* 1992; Petit *et al.* 2003; Fortuna *et al.* 2009); (v) identifying and mapping hotspots for both genetic diversity and novelty (for introduced species, one should compare between native and exotic regions); (vi) temporal variation in spatial patterns and vice versa and (vii) potential links (e.g. possible positive feedbacks) between intraspecific diversity, speciation and overall species diversity, along with the underlying mechanisms (Brown 1995; Vellend & Geber 2005).

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Data accessibility

A list of recent latitudinal studies showing varied trends of within-species genetic diversity: The patterns reported in these studies on individual species were described in Fig. 3 (See also Table S1, Supporting Information).

Supporting information

Additional Supporting Information may be found in the online version of this article.

Table S1 A list of recent latitudinal studies showing varied trends of within-species genetic diversity (mostly after 2006).

Fig. S1 Diagram showing two examples of proposed sampling strategies that may improve our understanding of genetic variation across entire species ranges (The shaded area represents the general location of core populations).