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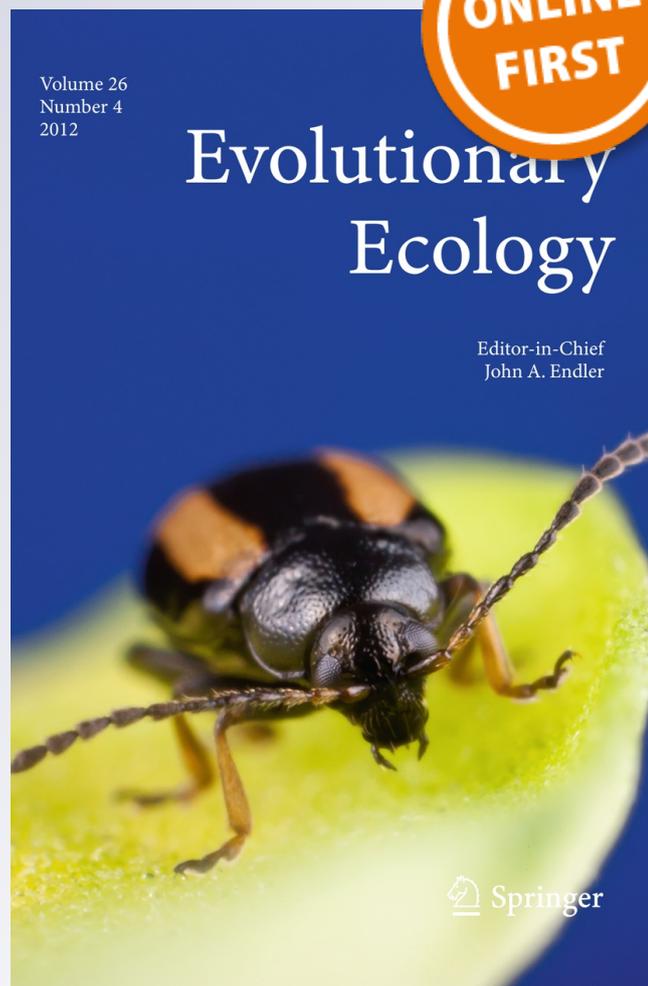
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Genetic diversity within vertebrate species is greater at lower latitudes

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Abstract The latitudinal gradient of species diversity is one of the oldest recognized patterns in biology. While the cause of the pattern remains debated, the global signal of greater diversity toward the tropics is widely established. Whether the pattern holds for genetic diversity within species, however, has received much less attention. We examine latitudinal variation of intraspecific genetic diversity by contrasting nucleotide distance within low- and high-latitude animal groups. Using mitochondrial DNA markers across 72 vertebrate species that together span six continents, two oceans, and 129 degrees of latitude, we found significantly greater genetic diversity at low latitudes within mammalian species, and trends consistent with this pattern in reptiles, amphibians, fish, and birds. The signal held even after removing species whose current geographic ranges include areas recently covered by glaciers during the late Pleistocene and which presumably have experienced colonization bottlenecks in high latitudes. Higher genetic diversity within species was found at low latitudes also for genera that do not possess higher species richness toward the tropics. Moreover, examination of a subset of species with sufficient sampling across a broad geographic range revealed that genetic variation demonstrates a typical gradient, with mid-latitude populations intermediate in genetic diversity between high and low latitude ones. These results broaden the pattern of the global latitudinal diversity gradient, to now include variation within species. These results are also concordant with other studies indicating that low latitude populations and species are on different evolutionary trajectories than high latitude ones, and we speculate that higher rates of evolution toward the equator are driving the pattern for genetic diversity within species.

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Introduction

On a global scale, species richness is highest near the equator and decreases poleward. First appearing in published form in 1807 when Alexander von Humboldt wrote of his travels in the New World tropics, this biogeographical observation may be the oldest recognized pattern in ecology (Hawkins 2001), as well as the most prominent. At the species level, the latitudinal diversity gradient is consistent across marine and terrestrial habitats, trophic levels, hemispheres, thermoregulatory mechanisms, and body size, among other traits (Rosenzweig 1995; Hillebrand 2004). Moreover, it has been present for at least 270 million years, thus re-forming after mass extinctions (Stehli et al. 1969), and is known to apply to taxonomic levels higher than species, including those of genera (Powell 2007) and families (Stevens 2004). Here, we ask whether the pattern of co-variation of latitude with biodiversity around the globe, with decreasing richness toward the poles, is also found in the genetic diversity within species.

Explaining this global distribution of biodiversity is a fundamental goal of ecological and evolutionary biology, and thus the primary cause(s) of the latitudinal gradient continue to be studied (Willig et al. 2003; Mittelbach et al. 2007). Proposed mechanisms, which have increased in the literature at a striking rate (Pianka 1966; Rohde 1992; Palmer 1994), typically fall into either an ecological or evolutionary category. Ecological explanations focus on factors that promote species coexistence, such as variation in predation pressure (e.g., Freestone et al. 2011), while evolutionary explanations draw on the generation of species diversity, including the time required for this generation to occur (Mittelbach et al. 2007).

Investigating the pattern of diversity at finer taxonomic levels than that of species (i.e., intraspecific genetic diversity) offers several potential rewards for those wishing to explain—and conserve—the global distribution of biodiversity. First, considering patterns and processes of genetic diversity can offer insights into the mechanisms behind the observed patterns of species richness (e.g., Wright et al. 2006). Second, the processes that shape species diversity may also influence genetic diversity (Antonovics 2003), and elucidation of such common processes can bridge traditionally disparate fields (community ecology and evolutionary biology) into a more comprehensive view on the maintenance of diversity (Vellend 2005; Johnson and Stinchcombe 2007). Third, in a concern for the conservation of diversity, geographic areas of high diversity and endemism receive special attention in order to minimize the loss of biodiversity (Myers et al. 2000), of which genetic diversity is a part and thus would need to be recognized. Moreover, conservation managers may need to identify populations most resilient to future environmental change, and genetic diversity can be one index of adaptive potential (McLachlan et al. 2007).

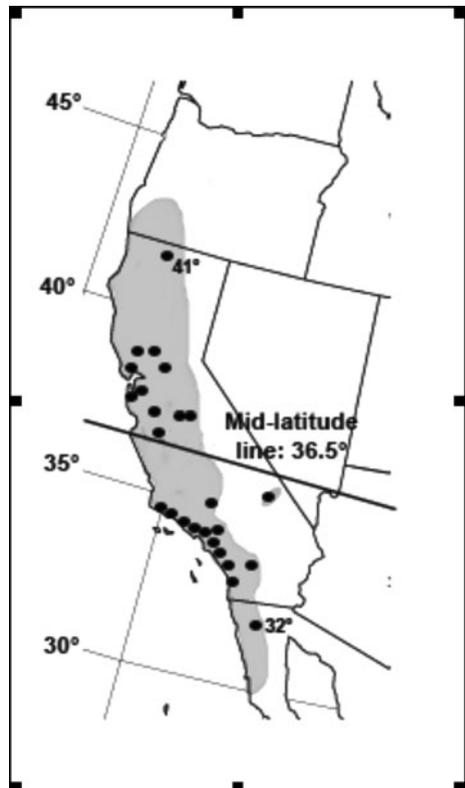
We hypothesized that genetic diversity within species would show the typical latitudinal gradient apparent in higher classifications. Our approach was to focus on vertebrate species across an array of taxonomic classes, environments, and latitudes. By clustering populations of over 70 vertebrate species by latitude, our objective was to determine whether we could identify consistent patterns between distance from equator and intraspecific genetic diversity.

Materials and methods

The methodology largely follows one employed by Martin and McKay (2004), who demonstrated greater population divergence (e.g., greater F_{ST} values) of vertebrates at lower latitudes than higher latitudes. In brief, we included animals from different classes and different environments (terrestrial, freshwater, marine) that inhabited both the northern and southern hemispheres. We assigned mitochondrial haplotypes from phylogeographic studies of these animals to a latitudinal group (low vs. high, or low vs. mid vs. high) and determined the evolutionary distance between sequences within a latitudinal group to determine if there was a consistent signal of higher genetic diversity at lower latitudes. An example of this methodology for one species is depicted in Fig. 1.

In more detail, we searched the scientific literature for phylogeographic studies in which corresponding mitochondrial haplotypes had been deposited in Genbank (www.ncbi.nlm.nih.gov/genbank) and could be georeferenced to a particular locality through either the source information in Genbank or in the original publication. We created latitude groups by dividing the latitudinal span of the sampled populations by two or three (Table S1). For those species that spanned the equator and for which the sampling spanned the entire range, three groups were delimited: one for low latitude, and one each for north and south high latitude groups. For those species that occurred on several continents, we grouped individuals onto the same continent. For migratory species, we grouped animals into latitudinal groups based on breeding sites, following Martin and McKay (2004) and

Fig. 1 A depiction of the methodology employed in this study, using as an example the California vole, *Microtus californicus*, with data from Conroy and Neuwald (2008); Adams and Hadly (2010). The shaded area represents the geographic range of the species in western North America, spanning from southern Oregon and through California in the United States to northern Baja California in Mexico. Black circles represent sampling localities included in published phylogeographic studies. The sampled latitudinal range, 32°N–41°N, was split in half, at 36.5°N. Within the high and low latitude groups, genetic diversity was measured using the Kimura 2-parameter correction of nucleotide distance



because that is how sampling in the original phylogeographic studies occurred. We excluded species that had been relocated or had their ranges expanded by human intervention (e.g., the black bear, *Ursus americanus*, in North America). While we found phylogeographic studies that specifically noted a correlation between genetic diversity and latitude within a species, if not enough information was included to assign haplotypes to a particular location, those studies were not included here (e.g., Kimura et al. 2002; Borden and Krebs 2009).

We had originally set a cut-off of at least 10 individuals per latitudinal grouping to ensure sufficient sampling; however, excluding studies with less ($n = 18$) did not change the outcome, and thus results for all species are included here. Molecular loci were limited to the mitochondrial genome, with a minimum length of 250 basepairs, because mitochondrial markers are persistently used in phylogeographic studies and because, generally speaking, they represent similar rates of neutral evolution between species (Avice 2000). We defined intraspecific genetic diversity as the mean nucleotide diversity between sequences within a latitudinal group, and thus this metric can incorporate both intra- and inter-population components of genetic variation within each species. Distance values for Kimura's two-parameter model (i.e., K80) for inferring evolutionary distance (Kimura 1980)—a model that assumes equal base frequencies and accounts for differences in the rates of transitions and transversions—were estimated using *MEGA* v4 (Tamura et al. 2007). Qualitative results were identical if the descriptive statistic Nei's nucleotide diversity, π (Nei 1987), was used instead. Repeat haplotypes were included in the analysis (i.e., a monomorphic population of 10 individuals with the same haplotype was represented with 10 counts of the same haplotype) in order to better capture the intra- and inter-population genetic diversity.

We used the Wilcoxon signed-rank test to test for statistical support that low latitude populations have higher genetic diversity than high latitude groups. In order to consider the possible role of glaciations in accounting for global patterns of genetic diversity, since many populations are documented to have experienced colonization bottlenecks in glaciated areas (Hewitt 2000, 2004; Lessa et al. 2010), we performed the analysis again excluding those species whose geographic range extends into areas covered by ice sheets during the Last Glacial Maximum, 20,000 ybp (Clark and Mix 2002) and 18,000 ybp (Hulton et al. 2002) in the northern and southern hemispheres, respectively. To determine if the genus of the sampled species demonstrated the typical latitudinal variation in species diversity, we consulted the International Union for Conservation of Nature's Red List of Threatened Species (www.iucnredlist.org), as well as Fishbase (www.fishbase.org) and the Neotropical Birds database at Cornell University (www.neotropical.birds.cornell.edu). For the trinomial pattern, we considered northern hemisphere species whose sampling spanned a minimum of 15 degrees and whose clustering in three latitudinal groups resulted in no less than 5 individuals per group. We chose this subset to ensure sufficient latitudinal variation between groups and sufficient haplotype representation within groups.

Results

Seventy-six taxa, representing 72 terrestrial, freshwater, and marine species, were used in our analysis (Table S1). Approximately half of the taxa were mammals ($n = 41$), and the remaining taxa were comprised of amphibians ($n = 4$), birds ($n = 19$), fish ($n = 9$), and reptiles ($n = 3$). Sampled populations ranged from 54°S to 74°N. Species were found exclusively in the northern hemisphere ($n = 43$), exclusively in the southern hemisphere

($n = 22$), and in both ($n = 11$). Geographic distributions were varied, with some exclusively tropical or temperate and others spanning multiple regions. The predominant genetic marker was cytochrome *b* ($n = 47$), with the control region ($n = 13$) and NADH dehydrogenase subunit 2 ($n = 9$) also well represented. Levels of genetic diversity within taxa largely matched previous comparisons across groups (Nevo 2001), with reptiles and amphibians demonstrating higher genetic diversity than fish, birds, and mammals (Fig. 2).

Within-species comparisons of genetic diversity between latitudinal groups showed a clear pattern: intraspecific genetic diversity was found to be higher in low latitude populations in 55 cases of the 76 comparisons (72.4 %; Table 1; Fig. 2). For those species with greater diversity at lower latitudes, the magnitude of the effect ranged from $1.02\times$ to $17.56\times$ higher genetic diversity towards lower latitudes, with a median of $2.02\times$ and an average of $3.27\times$ (Table S2—excluding one taxa with an outlier effect size of $66.68\times$). Those species with a high magnitude of effect (i.e., $>3.00\times$ higher genetic diversity towards lower latitudes; $n = 18$) included mammals, fish, and birds, occurred in both the Northern and Southern hemispheres, and tended not to be glacial. Mammals and birds were the only taxonomic groups represented with sufficient sampling for individual statistic comparisons,

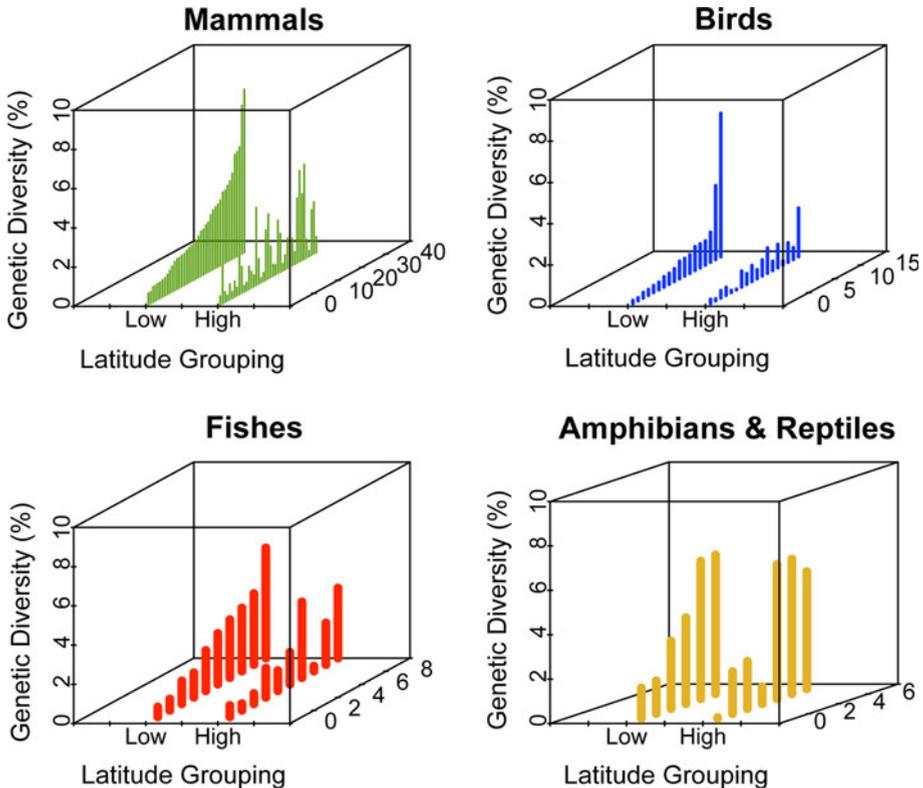


Fig. 2 The correlation between low latitude populations and higher genetic diversity within individual species grouped by clade. The *x* axis blocks taxa into low and high latitude groups, and the *y* axis depicts taxon index, rank ordered by increasing genetic diversity in the low latitude group. All graphs have the same scale for the *z* axis, Kimura 2-parameter genetic diversity, in percent. Note the differing levels of genetic diversity across clades and the consistent pattern that low latitude groups tend to demonstrate higher genetic diversity than high latitude groups

Table 1 *P* values for one-tailed Wilcoxon signed-rank test for tests of latitudinal variation in genetic diversity within species

Comparison	Total (n)	n	W	<i>P</i> value	Effect size
All	76	55	2,342	<0.00001	3.27
Non-glacial	39	27	611	0.00077	3.49
Glacial	37	28	573	0.00026	3.00
Mammals	41	32	684	0.00035	3.60
Birds	19	11	130	0.08440	3.22
Fish	9	6			3.21
Amphibians	4	3			1.31
Reptiles	3	3			1.72
Species in general showing a species-richness latitude gradient	40	30	706	0.00001	4.11
Species in general not showing a species-richness latitude gradient	36	25	684	0.00838	2.27

A significant *P* value indicates that in paired samples within a species, nucleotide diversity in the lower latitude group is higher more often would occur from random sampling. The n column corresponds to the number of taxa that show higher genetic diversity at low latitudes

with birds demonstrating marginal significance; however, in all taxa the majority of cases demonstrated the trend (Table 1). The pattern was not driven by differences in sampling, as there was no correlation between sample size and latitudinal grouping ($F = 0.95$, d.f. = 1,74, *P* value = 0.333). Moreover, there is no link between the latitudinal span and the magnitude of the effect; that is, greater genetic diversity in low-latitude populations is just as likely to be found when the latitudinal range is 5 degrees as when its 35 degrees.

Results remain significant even when excluding species with some part of their present distribution extending into areas that were recently glaciated (Table 1). In addition, we observed the latitudinal variation of genetic diversity in our data set even for those genera that do not show the typical latitudinal variation of species richness (Table 1). Moreover, for the 15 North American species (16 comparisons) with sufficient sampling to partition haplotypes into three latitude groupings, the far majority ($n = 14$) showed a gradient in genetic diversity, with mid-latitude populations intermediate in genetic diversity between the low and high latitude populations (Fig. 3). Species that did not show latitudinal variation in two groups also did not show it in three.

Discussion

Our data shows that genetic diversity within an array of vertebrate species, particularly mammals, is higher toward to equator. The latitudinal gradient of diversity thus spans tiers of biodiversity, from intraspecific variation to families. While the pattern is strongest for mammals in this data set, the trend is present in the other taxonomic groups. Greater diversification rates toward the tropics have been found for non-mammals as well as mammals (see next section), and the latitudinal species gradient holds for all these taxonomic groups. Therefore, while the data do not preclude the possibility that this pattern occurs primarily in mammals, it is more likely that limited sampling in non-mammals prevents full corroboration of the trend in these groups.

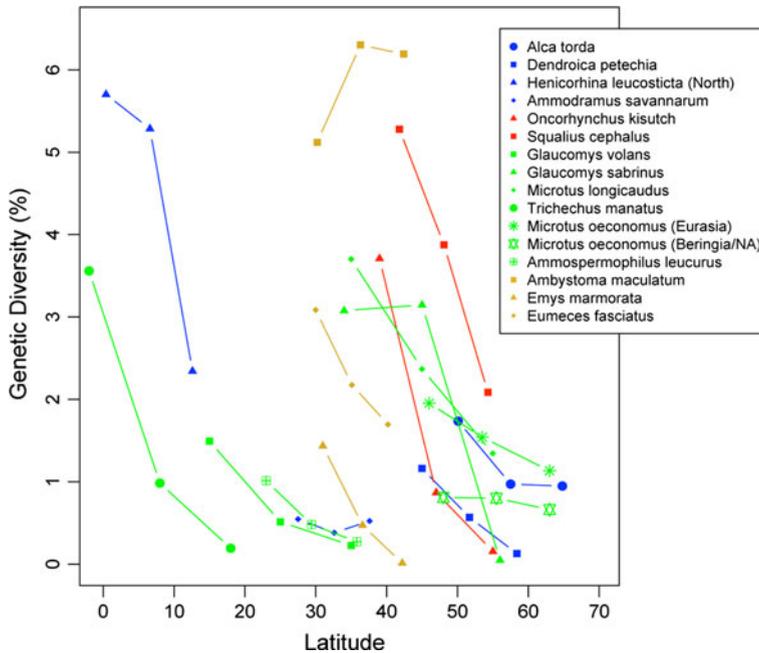


Fig. 3 A gradient of genetic diversity with latitude analyzed for a subset of species used for the full analysis. The majority of comparisons (14/16) showed a strong gradient in genetic diversity (Kimura 2-parameter, in percent) with latitudinal-intermediate populations demonstrating intermediate levels of genetic diversity. Animals are grouped by clades (with colors matching those in Fig. 2)

Higher genetic diversity at the lower latitude areas of a species range, just like overall species richness at lower latitudes, can be explained by many processes. In fact, it seems likely that many processes are operating simultaneously in a combinatory fashion to produce the global pattern. Here, we discuss several prominent mechanisms to explain the latitudinal diversity gradient in the context of intraspecific genetic diversity.

Intraspecific genetic diversity and increased rates of genetic evolution

Rohde (1992) proposed that higher temperatures result in greater “evolutionary speed” brought about through shorter generation times, higher mutation rates, and acceleration of selection in the tropics. The metabolic theory of biodiversity more explicitly links temperature to mutation rate (Gillooly et al. 2005; Allen et al. 2006), arguing that high temperatures lead to high metabolic rates, which increase the availability of kinetic energy at the molecular level. Our results are consistent with this model, as are studies showing that intraspecific genetic diversity is higher for tropical bird species than for temperate or arctic ones (Chek et al. 2003; Hughes and Hughes 2007), and highest in general for species that occupy exclusively tropical life zones, intermediate for temperate species, and lowest in arctic species (Nevo 2001). Faster overall rates of DNA evolution have been found at lower latitudes for plants, foraminifera, mammals, and amphibians (Allen et al. 2006; Wright et al. 2006, 2010; Gillman et al. 2009) but not for birds (Bromham and Cardillo 2003; Weir and Schluter 2008). Coupling the increased raw nucleotide diversity and rate of evolution with increased population differentiation at lower latitudes (Martin and McKay

2004; Eo et al. 2008), there is compelling evidence that speciation rates are higher in the tropics (Jablonski et al. 2006).

Interestingly, genetic diversity and species richness may be linked but show contrasting patterns because of different time scales in which population differentiation and speciation operate. We observed the latitudinal variation of genetic diversity in our data set even for those genera that do not show the typical latitudinal variation of species richness (Table 1). For example, voles of the genus *Microtus* demonstrate higher genetic variation at low latitudes, even though the genus is holarctic and has higher species richness in more polar regions. Buckley et al. (2010) have shown that the extent of latitudinal variation in species richness in mammals varies considerably by clade, with bats showing greater latitude variation than, for example, rodents. We found increased genetic diversity at lower latitudes in both these clades. These data would then predict that given enough time and barring any overriding of other processes at play, those genera that do not show the typical species gradient but do show greater sequence divergence at lower latitudes would eventually show the typical species gradient.

Climatic and geographic constraints on intraspecific genetic diversity

One hypothesis for the species gradient is that periodic changes in earth's climate have resulted in glaciations and higher rates of extinctions toward the poles. Historical perturbations of glaciations may have led to reduced genetic variation in poleward-expanding species in spite of the larger geographic area available during interglacial periods. This trend is a well-documented component of genetic diversity patterns for some northern hemisphere species (Hewitt 2000, 2004), as well as southern ones (Lessa et al. 2010), including some of the same species included here. Clearly, range expansion after global perturbations can leave a mark on the genetic diversity within species, where only a subset of populations within a species acts as the genetic source for novel habitats, otherwise known as a colonization bottleneck. However, the latitudinal variation in genetic diversity is not caused exclusively by this process, as species not directly affected by glaciations, including ones with an all-tropical distribution, still demonstrate clear and significant decreasing latitudinal variation in genetic diversity toward the poles.

Another explanation for the latitude diversity gradient is the mid-domain effect, which attributes latitudinal variation to the constrained nature of species' ranges: a random placement of ranges in one- or two-dimensional geographic domains will result in a peak of richness toward the center (Colwell and Lees 2000). Although its role in explaining species diversity pattern varies (Colwell et al. 2004), greater genetic diversity at the center of a species range has been reported (Eckert et al. 2008; Miller et al. 2010). Eckert et al. (2008) consider central and peripheral populations of animals and plants, without specific consideration to latitude, while Miller et al. (2010) looked at birds of the narrow Central American land bridge. Here, considering different groups of animals across a wider geographic range in specific latitudinal groups, we did not observe the same trend (Fig. 3).

The fact that our data do not support these two hypotheses does not, of course, mean that these processes are never the cause for latitudinal trends in diversity. More likely, the biogeography and ecological and evolutionary history of the particular taxa dictates which process is the most influential in producing the latitudinal gradient, or even if there is one. We would argue that variation in diversification rates through higher speciation rate is the broad background process onto which other taxon-specific ecological (such as predation, e.g., Freestone et al. 2011) and evolutionary process (such as time-for-speciation and niche conservatism, Wiens et al. 2006) operate.

Conservation

One objective for understanding the ecological and evolutionary drivers of diversity in all its guises is conservation of the planet's biodiversity. Conservation priorities often focus on high-diversity and endemism, low latitude areas, with the argument being that anthropogenic impact in these locations causes more extinctions than in poor biodiversity areas (Dirzo and Raven 2003). The focus has historically been on preserving diversity at the species-level. A more recent push to consider the loss of populations highlights that (1) the benefits of biodiversity often depend on a reservoir of different populations of species rather than a clustering of the species in a single locality (Hughes et al. 1997), and (2) the major pulse of current biological extinction lies in population loss (Dirzo and Raven 2003). Here, we demonstrate that genetic diversity shows a similar pattern to species diversity, indicating that loss of populations at low latitudes would entail greater genetic diversity loss than at higher latitudes. In fact, our estimates for vertebrates are that the loss in genetic diversity would be 2–3× greater from the low-latitude populations than for the high latitude populations. In other words, preserving land in low latitude areas may disproportionately save within-species biodiversity than preserving an equal area in high latitudes. Thus, conserving tropical areas, many of which are less protected than higher latitude regions, is most likely to protect high genetic diversity within species. This is important also for agrobiodiversity conservation—agriculturally important crops, domesticated animals and the wild relatives of both (Dirzo and Raven 2003; Food and Agriculture Organization 2010)—and as source populations for assisted migrations of species, thus providing a greater repertoire of adaptive potential for warming climates of the future.

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