

## LETTER

# Neotropical birds show a humped distribution of within-population genetic diversity along a latitudinal transect

Matthew J. Miller,<sup>1,2\*</sup> Eldredge Bermingham,<sup>2</sup> John Klicka,<sup>3</sup> Patricia Escalante<sup>4</sup> and Kevin Winker<sup>1</sup>

<sup>1</sup>University of Alaska Museum, 907 Yukon Drive, Fairbanks, AK 99775, USA

<sup>2</sup>Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Panama

<sup>3</sup>Barrick Museum of Natural History, University of Nevada Las Vegas, Box 454012, 4504 Maryland Parkway, Las Vegas, NV 89154-4012, USA

<sup>4</sup>Instituto de Biología, UNAM, AP 70-153, 04511 México, D.F., Mexico

\*Correspondence: E-mail: millerma@si.edu

### Abstract

The latitudinal gradient in species richness is a nearly universal ecological phenomenon. Similarly, conspecific genetic diversity often increases towards the equator – usually explained as the consequence of post-glacial range expansion or due to the shared response of genetic diversity to processes that promote species richness. However, no study has yet examined the relationship between latitude and within-population genetic diversity in exclusively tropical species. We surveyed genetic variation in nine resident bird species co-occurring in tropical lowlands between southern Mexico and western Ecuador, where avian species richness increases with decreasing latitude. Within-population genetic variation was always highest at mid-range latitudes, and not in the most equatorial populations. Differences in demography and gene flow across species' ranges may explain some of our observations; however, much of the pattern may be due simply to geometric constraints. Our findings have implications for conservation planning and for understanding how biodiversity scales from genes to communities.

### Keywords

Centre-marginal hypothesis, genetic diversity, gradient, latitude, mid-domain effect, tropics.

*Ecology Letters* (2010) 13: 576–586

### INTRODUCTION

Biogeography, community ecology and population genetics all attempt to describe how biological diversity is spatially distributed, albeit at different scales of geographic and biological organization. Therefore, it is not surprising that researchers from these disciplines seek common patterns in the distribution of diversity. One of the oldest and likely most recognized patterns of biodiversity is the latitudinal gradient of species richness (Rosenzweig 1995). For most taxa, the number of species occurring in an area increases towards the Equator. The regard for the latitudinal gradient in species richness is due to its ubiquity: the pattern holds at both small and large latitudinal spans, for plants and animals, for terrestrial and marine organisms, for taxonomic richness of genera and families in addition to species, and for fossil assemblages (Willig *et al.* 2003).

In a similar vein, several studies have reported latitudinal differences in genetic variation, including two important meta-analyses (Martin & McKay 2004; Hughes & Hughes

2007). Examples include Nearctic and Palearctic fishes (Bernatchez & Wilson 1998), Palearctic mammals (Jaarola & Tegelström 1995), Palearctic frogs (Johansson *et al.* 2006), Nearctic and Palearctic birds (Merilä *et al.* 1997) and South African corals (Ridgway *et al.* 2008). However, as Eckert *et al.* (2008) noted, single-species studies of geographic variation in within-population genetic diversity are disproportionately focused on taxa at their northern limits in the northern temperate zone. Because of the strong historical effect that Pleistocene-era glaciers had on the biogeography of higher latitudes, it is perhaps not surprising that post-glacial expansion is usually considered primarily responsible for the observed genetic diversity patterns (Hewitt 1996). This empirically demonstrated pattern of decreasing within-population genetic diversity with increasing latitude might be termed the 'poleward model'. Like their temperate zone counterparts, tropical habitats also expanded poleward during the Holocene (Leyden 1984; Hillesheim *et al.* 2005). Thus, as expected by latitudinal diversity hypotheses, it would be reasonable to expect that within-population

genetic diversity should decrease as one samples exclusively tropical taxa poleward along a latitudinal gradient.

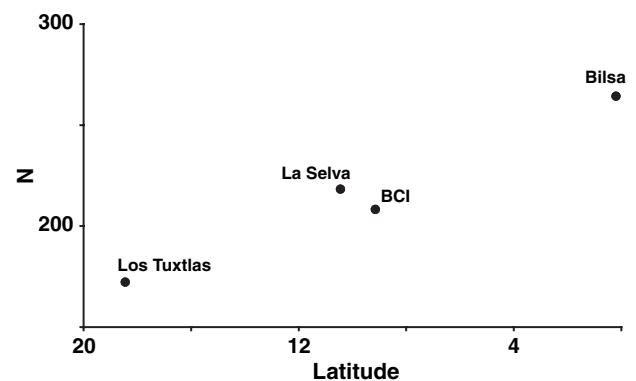
Similarly, latitudinal gradients in genetic diversity are also predicted by recently developed theory that relates species richness in a community to the genetic variation of members of that community. Vellend and colleagues (Vellend 2003; Vellend & Geber 2005) noted that the same biogeographic conditions favourable to high species richness within a community (i.e. high immigration rates and low extinction rates) should promote high genetic diversity within the species comprising that community. Empirical support for this model has come from forest tree communities (Wehenkel *et al.* 2006), butterflies (Cleary *et al.* 2006), and over half of the archipelago species surveyed in a meta-analysis (Vellend 2003). Vellend (2003) termed this positive relationship between species richness and genetic diversity the species–genetic diversity correlation; here, we will refer to it simply as the ‘species richness model’. One of the most intriguing aspects of the latitudinal gradient in species richness is that it can be found within exclusively tropical samples (Willig *et al.* 2003). Therefore, a correlation between species richness and within-population genetic variation should result in a latitudinal gradient in within-population genetic diversity of exclusively tropical taxa.

Models predicting a latitudinal gradient in genetic variation can be compared with the central–peripheral model, an important general model for the distribution of abundance across a species’ range. The central–peripheral model has been most frequently applied in macroecology, where it predicts that a species’ abundance peaks in the centre of its range and diminishes towards the range edges (Brown 1984), but it has also been extended to genetic diversity (da Cunha *et al.* 1950; Brussard 1984). This pattern is believed to be caused by diminishing ecological suitability of habitats at range edges, resulting in greater population fluctuations in edge populations compared with central ones (Brown *et al.* 1995). Reduced abundance and greater variance in abundance should increase genetic drift, thus reducing within-population genetic variation (Vucetich & Waite 2003). The combined consequences of reduced effective population size and lower immigration rates in edge populations should cause a reduction in genetic diversity relative to central populations.

Additionally, geometry predicts that central populations should have higher immigration rates than edge populations (Eckert *et al.* 2008), thus minimizing the diversity-reducing effects of genetic drift in central populations. This geometric effect parallels the macroecological observation that the richness of a local species pool is strongly influenced by the regional species pool richness (Terborgh 1973; Rosenzweig 1995) as well as the notion that species richness gradients are driven largely by geometric constraints or ‘mid-domain’ effects (Colwell & Hurtt 1994; Lees *et al.* 1999; Colwell &

Lees 2000). As noted by Eckert *et al.* (2008), in spite of the strong theoretical support for this model, there is a relative lack of empirical evidence. These authors also noted that they were unable to find a single study of tropical taxa that investigated latitudinal variation in genetic diversity among conspecific populations. To our knowledge, no study to date has addressed how within-population genetic diversity varies across a tropical latitudinal gradient.

Here, we measure within-population genetic diversity along a tropical latitudinal gradient, contrasting central–peripheral and latitudinal gradient models against a null model of no relationship between population genetic diversity and latitude. Our empirical data were developed from nine resident Neotropical landbird species, sampled more or less concordantly across their ranges from Middle America to the Pacific lowlands of northwestern South America. Lowland tropical forest occurs in a narrow band from southern Mexico to western Ecuador, and along this transect avian resident species richness increases with decreasing latitude (Fig. 1). Furthermore, the avian community is relatively biogeographically homogeneous, whereas avian assemblages east of the Andes are more heterogeneous across a similar latitudinal span. Relatively few species co-occur on both sides of the Andes, and we expect gene flow to be non-existent or greatly diminished across the Andes in these cases (e.g. Brumfield & Capparella 1996; Miller *et al.* 2008). These factors combine to make this transect a natural laboratory for observing how within-species genetic diversity varies along the latitudinal and species richness gradient.



**Figure 1** Number of breeding landbirds recorded at four research stations in the Neotropical lowlands from Mexico to Ecuador: (1) Los Tuxtlas (Veracruz, Mexico *c.* 18.6° N); (2) La Selva (Heredia, Costa Rica *c.* 10.4° N); (3) Barro Colorado Island (BCI: Colon, Panama *c.* 9.2° N) and (4) Bilsa (Esmeraldas, Ecuador *c.* 0.4° N) (see Appendix S2 for details).

## MATERIALS AND METHODS

Tropical evergreen forest is more or less continuously distributed from southern Mexico south through Central America and along the Pacific lowlands of South America until western Ecuador, where a strong moisture gradient results in a relatively abrupt transition to tropical dry forest. Blocked by the continental divide along Central America, this narrow band of forest is restricted to the lowlands of the Middle American Caribbean slope until eastern Panama, where a lower continental ridge and increased Pacific rainfall permit this band to cross the continental divide and continue south along a narrow lowland strip of the Pacific coast of Colombia and northwestern Ecuador. Many tropical forest species have a more or less continuous distribution along this transect: 42% of the resident landbirds from the Los Tuxtlas Biological Station in Veracruz, Mexico, can be found in Bilsa Biological Station in Esmeraldas, Ecuador (see Appendix S2). This transect spans over 18° of latitude separating Veracruz and Esmeraldas, and in most places it is less than 200 km wide.

Based on available tissue samples from vouchered museum specimens, nearly all of which we collected, we identified nine species (Table 1) of resident Neotropical landbirds with suitable sample size at various locations along this transect. In most cases, we sampled these species at six sites: Veracruz, Mexico (*c.* 18.5° N), Toledo District, Belize (*c.* 16.5° N), northern Honduras (*c.* 15.5° N), Bocas del Toro, Panama (*c.* 9.0° N), Darién, Panama (*c.* 7.8° N) and western Ecuador (*c.* 0.0° N). One species, *Euphonia gouldi*, occurs only from southern Mexico to Bocas del Toro, and another species, *Glyphorhynchus spirurus*, occurs in our samples northward only to Belize. Additionally, *Myrmeciza exsul* occurs from southern Honduras to western Ecuador; in this case, we included samples from Heredia, Costa Rica (*c.* 10.4° N). In general, for all the nine species, these population samples represent multiple collecting efforts spread over several years at two to four geographic points within a 25-km radius; exact locations are available from the authors and the respective museums. As the range maps in Fig. 3 show, our sampling strategy covered nearly the entire range west of the Andes for these nine species.

As our metric of within-population genetic diversity, we chose nucleotide diversity ( $\pi$ ) of the NADH dehydrogenase subunit II (ND2) mitochondrial gene (1041 bp). Nucleotide diversity equals the average number of nucleotide substitutions between all sequences and is a standard measure of DNA polymorphism (Nei 1987). We sequenced the complete ND2 gene following standard protocols as described by Miller *et al.* (2008). In most cases, DNA was extracted from mitochondrially rich muscle tissue; however, a few western Ecuador samples were from feathers. In

addition, we included one sequence from GenBank (a sequence of *Pipra mentalis*, LSUMZ B18078, from Veracruz, Mexico) which is marked with an asterisk in Appendix S1. All other sequence data were generated by the authors in their laboratories, and the first author reviewed all chromatograms. We estimated  $\pi$  in DnaSP 4.2 (Rozas *et al.* 2003).

We aimed to sample at least 10 individuals per population, but sample sizes varied due to the vagaries of field success (Table 1). To explore the effect of sample size on estimates of  $\pi$ , we subsampled three of our largest population samples that also had varying estimates of  $\pi$  (*Mionectes oleagineus*, Bocas del Toro,  $n = 18$ ,  $\pi = 0.0010$ ; *Myrmeciza exsul*, Bocas del Toro,  $n = 12$ ,  $\pi = 0.0048$ ; *Henicorbina leucosticta*, Darién,  $n = 13$ ,  $\pi = 0.0029$ ). For each of these populations, we created 1000 bootstrapped datasets for each possible sample size value from  $n = 2$  to  $n = 10$ . We plotted the mean, median, standard deviation and mean–median of  $\pi$  against bootstrap sample size.

A null model for the distribution of genetic diversity along a cline predicts no relationship between a population's genetic diversity and that of an adjacent population. In contrast, the latitudinal gradient models (poleward and species richness) both predict an increase in genetic diversity with decreasing latitude. We tested for such an increase in  $\pi$  for our nine Neotropical bird species by calculating the value of the expression:  $\pi_i - \pi_{i+1}$ , where  $i$  refers to a given population and  $i + 1$  is the next population found at a lower latitude. The latitudinal gradient models predict that this difference should be positive more frequently than negative. The frequency of observed vs. expected positive values was compared with a null hypothesis of equal frequency of positive and negative values using an exact binomial test.

An alternative model to latitudinal models (poleward and species richness, as discussed above) is the central–peripheral model, which would produce a humped distribution, wherein the largest value of  $\pi$  is found in mid-range relative to edge populations. A null hypothesis for this model is that, within a species, the largest value of  $\pi$  is equally likely to be observed in any of the sampled populations. We tested for a humped distribution of  $\pi$  by evaluating whether the frequency of a species' highest value for  $\pi$  occurred in the northernmost or southernmost sampling point (i.e. edge populations) at a lower frequency than predicted by the null hypothesis. Specifically, each of our nine species has two edge populations and two to four mid-range populations, so the probability by chance that the maximum observed value of  $\pi$  occurs in a mid-range population varies from 0.50 to 0.66. We calculated the probability that the observed number of species with maximum  $\pi$  in an edge population was due to chance by computing the joint probabilities of all combinations of

**Table 1** Estimated nucleotide diversity for nine species (48 populations) of Neotropical landbirds ranging from SE Mexico to W Ecuador

Scientific name	<i>n</i>	Num Hap	<i>H</i>	$\pi$	$\partial\pi$
<i>Phaethornis longirostris</i> (21.7° N – 4.0° S)					
Veracruz, Mexico	10	1	0.000	0.0000	
Toledo, Belize	10	3	0.511	0.0005	0.0005
N Honduras	10	2	0.467	0.0004	–0.0001
Bocas del Toro, Panama	11	4	0.691	<b>0.0016</b>	0.0012
Darién, Panama	12	4	0.455	0.0005	–0.0011
W Ecuador	5	1	0.000	0.0000	–0.0005
<i>Phaethornis striigularis</i> (18.7° N – 0.4° S)					
Veracruz, Mexico	7	1	0.000	0.0000	
Toledo, Belize	10	5	0.756	0.0014	0.0014
N Honduras	6	4	0.867	0.0018	0.0004
Bocas de Toro, Panama	9	5	0.889	<b>0.0033</b>	0.0015
Darién, Panama	10	8	0.956	0.0022	–0.0011
W Ecuador	3	1	0.000	0.0000	–0.0022
<i>Amazilia tzacatl</i> (18.7° N – 3.4° S)					
Veracruz, Mexico	4	3	0.833	0.0010	
Toledo, Belize	10	5	0.667	0.0010	0.0000
N Honduras	4	4	1.000	0.0048	0.0038
Bocas del Toro, Panama	9	6	0.917	0.0021	–0.0027
Darién, Panama	5	2	0.600	<b>0.0087</b>	0.0066
W Ecuador	2	2	1.000	0.0010	–0.0077
<i>Glyphorhynchus spirurus</i> (18.0° N – 3.8° S)					
Toledo, Belize	10	2	0.200	0.0002	
N Honduras	9	2	0.389	0.0004	0.0002
Bocas del Toro, Panama	10	7	0.933	<b>0.0061</b>	0.0057
Darién, Panama	10	3	0.378	0.0004	–0.0057
W Ecuador	8	3	0.679	0.0024	0.0020
<i>Myrmeciza exsul</i> (14.2° N – 3.5° S)					
Heredia, Costa Rica	10	3	0.600	0.0008	
Bocas, del Toro, Panama	12	6	0.818	<b>0.0048</b>	0.0040
Darién, Panama	11	3	0.564	0.0005	–0.0043
W Ecuador	15	8	0.838	0.0015	0.0010
<i>Pipra mentalis</i> (18.8° N – 0.0° S)					
Veracruz, Mexico	10	2	0.200	0.0002	
Toledo, Belize	12	4	0.561	0.0009	0.0007
N Honduras	10	6	0.889	<b>0.0014</b>	0.0005
Bocas del Toro, Panama	9	3	0.417	0.0004	–0.0010
W Ecuador	2	2	0.100	0.0010	0.0006
<i>Mionectes oleagineus</i> (21.2° N – 4.2° S)					
Veracruz, Mexico	10	5	0.667	0.0014	
Toledo, Belize	10	5	0.822	0.0011	–0.0003
N Honduras	10	5	0.844	<b>0.0015</b>	0.0004
Bocas del Toro, Panama	18	6	0.627	0.0010	–0.0005
Darién, Panama	18	5	0.771	0.0010	0.0000
W Ecuador	5	1	0.000	0.0000	–0.0010
<i>Henicorbhina leucosticta</i> (21.0° N – 0.0° S)					
Veracruz, Mexico	7	5	0.905	0.0018	
Toledo, Belize	10	8	0.933	0.0023	0.0005
N Honduras	9	4	0.583	0.0015	–0.0008
Bocas del Toro, Panama	12	7	0.879	0.0016	0.0001
Darién, Panama	13	6	0.859	<b>0.0029</b>	0.0013
W Ecuador	8	3	0.464	0.0007	–0.0022
<i>Euphonia gouldi</i> (18.7° N – 9.0° S)					
Veracruz, Mexico	9	1	0.000	0.0000	

**Table 1** *continued*

Scientific name	<i>n</i>	Num Hap	<i>H</i>	$\pi$	$\partial\pi$
Toledo, Belize	9	4	0.806	0.0011	0.0011
N Honduras	10	6	0.889	<b>0.0050</b>	0.0039
Bocas del Toro, Panama	10	8	0.933	0.0029	-0.0021

*n* = number of individuals sampled; Num Hap: number of haplotypes; *H*: haplotype diversity;  $\pi$ : nucleotide diversity;  $\partial\pi = \pi_{i+1} - \pi_i$ . Maximum  $\pi$  (per species) **in bold**. Veracruz, Mexico: ( $\sim 18.5^\circ$  N,  $95.0^\circ$  W); Toledo, Belize: ( $\sim 16.0^\circ$  N,  $89.0^\circ$  W); N Honduras (Copán & Atlántida): ( $\sim 15.5^\circ$  N,  $87.5^\circ$  W); Heredia, Costa Rica: ( $10.5^\circ$  N,  $84.0^\circ$  W); Bocas del Toro, Panama: ( $\sim 9.0^\circ$  N,  $82.5^\circ$  W); Darién, Panama: ( $\sim 7.5^\circ$  N,  $78.0^\circ$  W); W Ecuador (Esmeraldas & Manabí): ( $\sim 0.0^\circ$  N,  $79.5^\circ$  W). For each species we have included an estimate of the latitudinal limits of its distribution; see further maps in Figure 3.

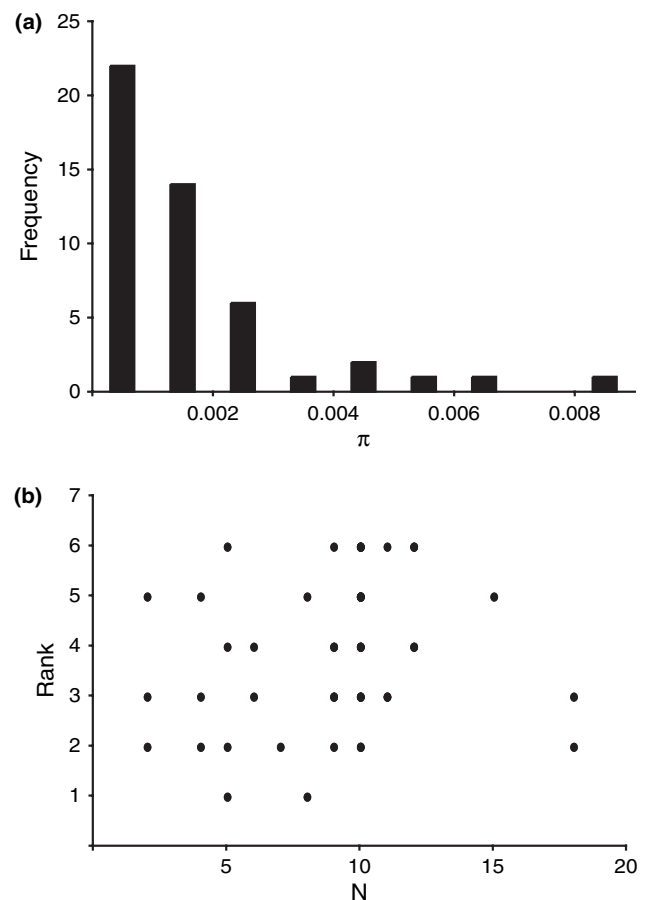
observations that equalled or were less frequent than found in our empirical data.

To visualize the collective pattern of genetic diversity among the nine species along this transect (for heuristic purposes only), we did two simple calculations. First, we standardized site-specific values for each species separately by setting the highest value of  $\pi$  observed in that species to 1.0 and calculating the proportion of this value exhibited at other sampled locations. Second, for each site we averaged the values for all species obtained at that location. This was carried out for the six sites along the transect noted above (Veracruz to western Ecuador); the sampled assemblage at each site included seven to nine species. Although each species has a unique range and not all of those included here match that of our transect, among these particular species they are not so different as to obscure the utility of this heuristic visualization approach. Standardizing ranges into quartiles and performing similar calculations resulted in a similar among-species pattern (not shown). We chose to use the former here because spatially shared attributes among co-occurring species (here, community genetics) are more directly applicable to community ecology and conservation biology.

## RESULTS

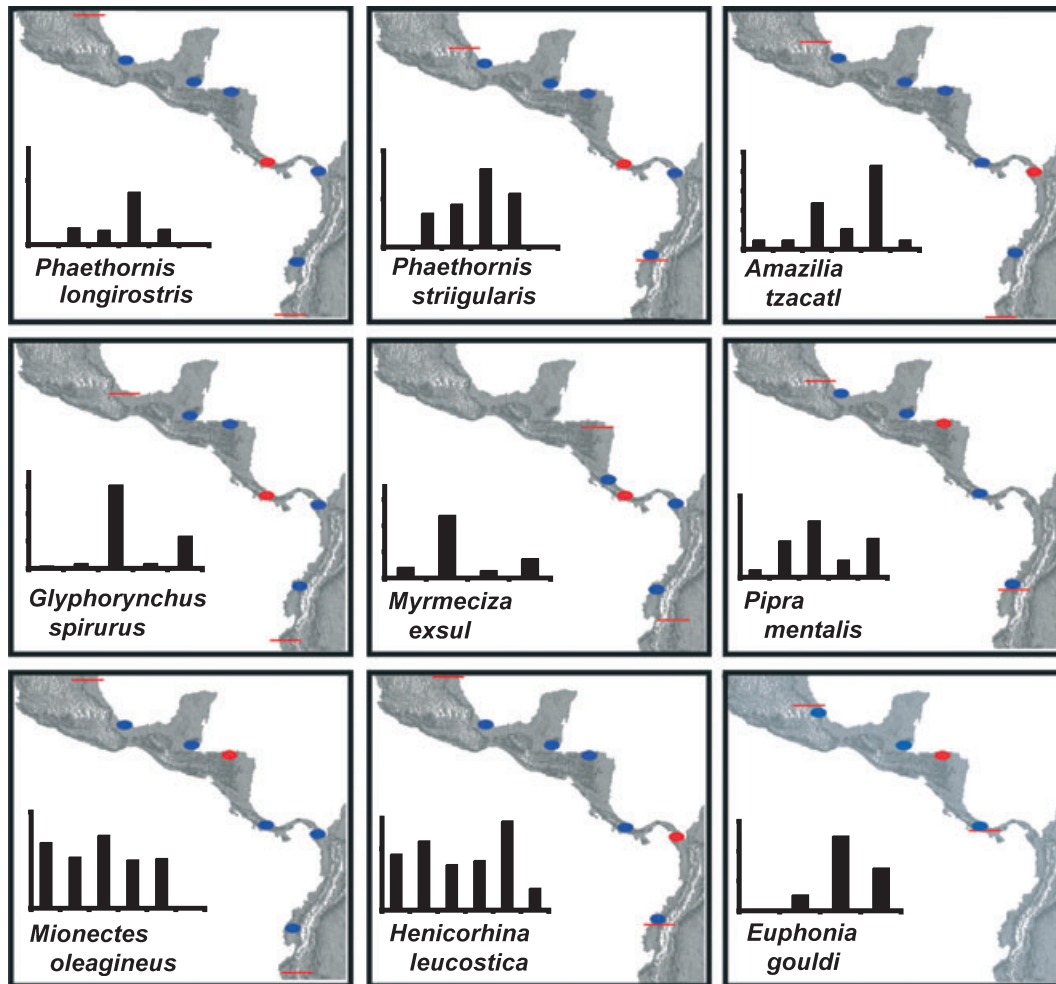
We sequenced ND2 from 48 populations (445 individuals) of the nine species in our study. Among these populations,  $\pi$  varied from 0.0000 to 0.0865 and had a median value of 0.0011. The distribution of values of  $\pi$  was strongly left-skewed and long-tailed (Fig. 2). Values less than 0.001 were most frequent (45%). Only 6% of the populations had  $\pi$  values greater than 0.005.

We found no significant relationship between sample size and the rank of  $\pi$  values within a species (Fig. 2b:  $r^2 = 0.02$ ,  $P = 0.31$ ). Our bootstrap analyses on three of our empirical population datasets did detect a slight downward bias in estimated  $\pi$  in samples of two to three individuals, but this was not observed with sample sizes equal to or greater than 4 (only 3 of our 48 population



**Figure 2** (a) Histogram of estimated nucleotide diversity  $\pi$  from 48 populations (nine species) of Neotropical landbirds. (b) Rank (among populations within species, from largest to smallest) of estimated nucleotide diversity ( $\pi$ ) relative to number of individuals sampled, indicating that sample size and  $\pi$  have a non-significant relationship. Note inverted *y*-axis.

samples had  $n = 2$  or 3; see Table 1; Appendix S4 and Table S1 for details). Based on these two findings, we conclude that sample size did not have an undue effect on our estimates of  $\pi$ .



**Figure 3** Maps for all nine resident Neotropical landbirds surveyed in this study. For each species, the sampled population with the highest nucleotide diversity ( $\pi$ ) is marked in red, other sampled populations are marked in blue. Red lines indicate the species' geographic range latitudinal maximum and minimum (west of the Andes). Inset bar graphs show relative  $\pi$  values for populations, beginning with the northernmost sampled population for each species; data values available in Table 1.

In our comparison of the model of a relationship between genetic diversity and latitude with a null model of uniformity, there were 39 opportunities to evaluate the expression:  $\pi_{j+1} - \pi_j$ . Of these, 22 were non-negative (frequency = 0.56), which is not significantly different from an expected frequency of 0.5 predicted by a null model of random change with respect to latitude (exact test:  $P = 0.26$ ; Table 1). This finding was consistent even in reduced datasets (i.e. sequentially removing populations with sample sizes below three to eight individuals; range of  $P$ -values: 0.10–0.26; see Appendix S4, Table S1 for details). Therefore, there is no evidence for a general trend of increasing within-population genetic diversity with decreasing latitude.

In our comparison of a humped distribution against a null model, we found that zero of the nine species had a maximum  $\pi$  value in an edge population (Fig. 3; see

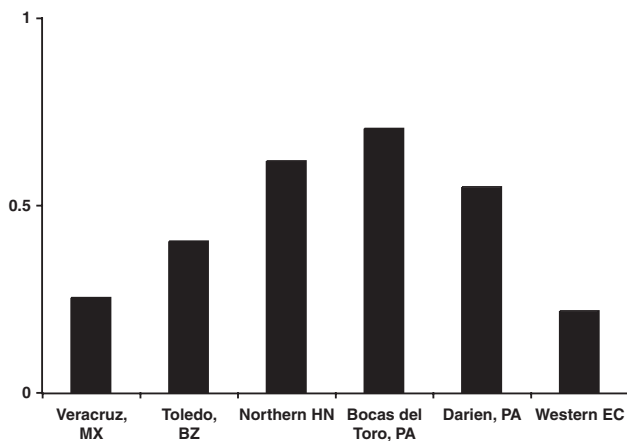
'Materials and Methods'). The  $P$ -value of this result can be calculated analytically as the joint probability of the probability of a mid-range maximum  $\pi$  value for all nine species given a random spatial distribution of maximum values. That result is significant even after a Bonferroni-correction to take into account our previous test of an inverse relationship between latitude and within-population diversity ( $\alpha = 0.025$ ;  $P = 0.01$ ). Likewise, among our reduced datasets (i.e. after sequentially removing populations with sample sizes below three to eight individuals), this probability remained significant in six of seven cases, with the seventh case nearly significant (range of  $P$ -values: 0.006–0.065; see Appendix S4, Table S2 for details). We thus reject the null model of no relationship between latitude and within-population genetic variation in favour of a humped distribution model.

We found no evidence of a secondary effect of latitude on estimates of  $\pi$ . Across our nine species, average  $\pi$  calculated from populations north of each species' latitudinal midpoint did not differ from the average  $\pi$  calculated from populations south of that point (Wilcoxon signed-rank test,  $W = 16$ ,  $P > 0.2$ ). Likewise, we found no difference between the average  $\pi$  for each species calculated from populations in the most poleward quartile of the species' range compared with the average  $\pi$  from populations in the most-equatorial quartile (Wilcoxon signed-rank test,  $W = 21$ ,  $P > 0.2$ ).

Heuristic visualization of the distribution of within-population genetic variation among species along the transect also showed a humped distribution; i.e. collectively, the sampled avian assemblages of largely co-distributed species along this transect (seven to nine species per site) exhibited the pattern observed within these species (Fig. 4).

## DISCUSSION

Among the nine species of resident Neotropical landbirds, our data reject a null model of no relationship between maximum  $\pi$  and latitude in favour of a humped distribution model in which the highest  $\pi$  for a species was found in mid-latitude populations (Figs 3 and 4). In contrast, a model of increasing mitochondrial DNA nucleotide diversity ( $\pi$ ) with decreasing latitude (the poleward or species richness models) was not a better fit to the data than a null model of randomly distributed  $\pi$ . Even after controlling for edge vs. range-centre effects, we found no evidence for a secondary



**Figure 4** Average nucleotide diversity ( $\pi$ ) among nine species of co-distributed resident landbirds across a Neotropical latitudinal gradient showing a humped distribution of  $\pi$ . Values of  $\pi$  are scaled whereby for each species the maximum value of  $\pi$  equals 1. Because our sample points are not evenly spaced across the gradient, the latitudinal midpoint occurs at Bocas del Toro, Panama.

effect of latitude on within-population genetic variation [note that in Fig. 4, Bocas del Toro, Panama (*c.* 9° N) is latitudinally midway between our extreme sampling points Veracruz, Mexico (*c.* 18.5° N) and western Ecuador (*c.* 0.0° N)].

Although relatively few studies have reported within-population  $\pi$  from mtDNA in Neotropical birds, our results appear consistent with values found by others (Brumfield 2005; Aleixo 2006). And although very small sample size can cause a minor downward bias in the estimate of  $\pi$  (see Appendix S3), our findings remain even after populations of varying thresholds of minimum sample size were removed from the analysis.

Many studies focused on temperate zone organisms (e.g. Jaarola & Tegelström 1995; Merilä *et al.* 1997; Bernatchez & Wilson 1998; Milá *et al.* 2000) have suggested that latitudinal patterns of within-population genetic diversity are most likely due to a history of post-glacial poleward habitat expansion. Could our findings similarly result from post-glacial expansion of tropical species west of the Andes both towards the pole and the equator?

The limits of tropical habitats in northern Middle America have shifted northward since the Pleistocene. Studies show that northern Middle America lacked forest and was instead covered with arid habitats (Leyden 1984; Hillesheim *et al.* 2005). Leyden (1984) has documented regeneration of forest cover through the Holocene. In contrast, Colinvaux (1996) provided strong evidence that lower Middle America and northwestern South America remained continuously forested throughout the late Pleistocene and Holocene. In addition, existing biome models for the Chocó forests of western Colombia (and presumably northwestern Ecuador) indicate that this region was continuously covered by wet evergreen forest since the late Quaternary (Berrío 2002; Marchant *et al.* 2004). Further, although no bioclimatic reconstruction has apparently focused on the Ecuadorian coastal lowlands, at least one continental-scale bioclimatic reconstruction suggests that the vegetation in western Ecuador has remained remarkably stable from the Last Glacial Maximum to the present (Adams 1997). Therefore, although the northern populations in our study may have experienced a reduction in genetic variation as a consequence of tracking northward-expanding forests (Hewitt 1996), habitat shifts since the Last Glacial Maximum are unlikely to explain the lower genetic diversity found at the southern edges of the nine species we examined.

If historic habitat shifts do not explain the humped pattern, then latitudinal variation in the demography of central and range-edge populations may be contributing to lower within-population genetic diversity in edge populations. Among the species included in our study, there is some evidence that edge populations may be less abundant

than mid-range populations: of the 18 edge populations, we found abundance estimates for 17 in area checklists. Of these, five (29.4%) were classified as abundant, or common, six as fairly common (35.3%) and the remaining six as uncommon (35.3%), whereas 16 populations surveyed in the centre of the species' ranges were classified as abundant or common 14 times (87.5%) and uncommon twice (12.5%). Paired comparisons among species found that edge populations had lower qualitative rankings for these measures of relative abundance than populations from the range centre (Wilcoxon signed-rank test,  $W = 1.5$ ,  $P < 0.05$ ; see Appendix S3 for details). Thus, mid-range vs. edge variation in relative abundance might be responsible for the observed pattern. If so, this is an interesting observation given that meta-analyses establish that a majority of species do not show a simple pattern of high abundance at mid-range populations and low abundance at range edges (Sagarin & Gaines 2002).

If edge demographics are causing the observed pattern, this would be consistent with models suggesting that reduced abundance and gene flow at range edges may drive central-peripheral models of within-population genetic variation (e.g. Vucetich & Waite 2003; Eckert *et al.* 2008). In fact, while most studies focused on latitudinal variation in genetic diversity in temperate zone species invoke post-glacial expansion to explain reduced genetic variation in poleward populations, at least one study has argued that this factor alone is insufficient: Johansson *et al.* (2006) found a strong latitudinal component to differences in within-population genetic variation among *Rana temporaria* populations. After controlling for latitude, a significant effect of population size on genetic diversity remained, and the authors concluded that demographic patterns in edge populations were principally responsible for their findings. It is important to note if edge effects are responsible for our observation of a humped distribution of genetic variation, they occur on relatively large scales: for six of our nine species at least one 'edge' population occurred greater than 2 latitudinal degrees away from the geographic edge of the species' range.

Lower relative abundance in range-edge populations is not necessary to create the patterns we observed: these patterns can be explained exclusively by the geographical context of contemporary and historical gene flow. On contemporary time scales, immigration counters the loss of genetic diversity caused by genetic drift. For populations that have relatively one-dimensional distributions, such as the birds in this study, range edge populations have functionally half the potential source populations from which to receive immigrants as do mid-range populations. Vucetich & Waite (2003) showed that even in the absence of population size differences, differential migration between central and peripheral populations can diminish

genetic variation in edge populations. Alternatively, the effect of geometry may be historical rather than dependent on contemporary gene flow differences. Haplotypes arise by mutation in a single point in space and then expand to form their current distributions; therefore, they are likely to have a more or less continuous distribution within some portion, or all, of a species' range. The spread of a haplotype across a species' range might be envisioned in purely neutral terms as the spread of a ripple generated from a particular point in a pond. Because these distributions are ultimately bounded by the edges of species' ranges, it is more likely that the majority of haplotypes will overlap in the centre portion of the range. This phenomenon has been coined the 'mid-domain effect' (Colwell & Lees 2000). Proponents of the mid-domain effect (also known as geometric constraints) argue that it is at least partially responsible for other cases in which the geographic distribution of biological diversity is humped, such as latitudinal and altitudinal species-richness gradients (e.g. Jetz & Rahbek 2001; Colwell *et al.* 2004). While controversial (e.g. Colwell *et al.* 2004), geometric constraints can be useful to explain deviations from well-established laws of biodiversity, such as the latitudinal gradient in species richness. For example, Lees *et al.* (1999) argued that geometric constraints explain why, on Madagascar, butterfly species richness peaks at the island's latitudinal midpoint, rather than increasing equatorially as normally occurs with species richness gradients.

We note that six of the nine species examined had a mid-range population comprised of individuals from two clades, one otherwise northward and the second otherwise southward (not shown), consistent with expectations of the mid-domain model. Geometric constraints refer both to the case of secondary contact of two lineages, such as a northern and southern clade in some of the species in our study, or a case in which a single mtDNA lineage is found throughout a species' range. If variants (i.e. mtDNA haplotypes) have relatively continuous distributions and are bound to a discrete area (i.e. a species' range), the greatest number of variants should be found in the middle rather than at the edges of that area, regardless of any particular geographic co-association of variants (i.e. geographic structure). Without finer-scale measurements of contemporary population size and gene flow, we are unable to evaluate the extent to which contemporary vs. historical processes are responsible for the humped mtDNA genetic diversity pattern that we observed. We also note that, as required to compile this dataset, the nine species in this study represent widespread, common birds, and each was reasonably common at our sampling points (which is why they were chosen). Each species does have its own life-history attributes and ecology, but despite their differences they appear to show a common pattern in the distribution of within-population genetic

diversity (e.g. Fig. 4). Future studies will be needed to determine whether the humped distribution found here among common understory forest birds also occurs in rarer or more local taxa.

Differences between the geometric constraints on species and genes may partially explain the decoupling of the gradient in species richness and genetic variation. Haplotypes within our species are geographically bounded by these species' present distributions, which collectively extend from southern Mexico to western Ecuador. However, the processes responsible for the formation of these species have a much wider geographic context. In fact, all of the species included in this study have sister species in regions outside the geographic scope of this study (i.e. northward in Mexico, southward along the Pacific South American coast, into the Andes, or across the Andes into South America), and at these larger geographic scales, Neotropical birds conform to the latitudinal gradient expectation, with highest species richness centred near the Equator (Orme *et al.* 2005). Thus, in cases where the geometry of species formation and genetic variation are coupled, such as island systems, we might expect a coupling between geographic patterns in alpha species richness and within-population genetic variation (e.g. Vellend 2003). However, it seems likely that in most continental cases the geography of conspecific genetic variation will often be decoupled from the geography of the species formation process.

The concept of the 'stable tropics' (Orians 1969; MacArthur 1972) still persists, despite a variety of evidence that tropical populations undergo substantial fluctuations over both contemporary and Quaternary time scales (e.g. Karr & Freemark 1983; Leyden 1984; Phillips *et al.* 1994). Recent reviews continue to posit that effective population sizes of tropical taxa are generally expected to be more stable than those of temperate taxa (e.g. Mallet *et al.* 2005), although the limited genetic evidence for historical stability of tropical populations is mixed (e.g. Schneider & Moritz 1999; Lessa *et al.* 2003; Anthony *et al.* 2007). In contrast, our results suggest that the effective population size (as measured by mtDNA polymorphism) of tropical species is geographically context-dependent: range centres have more genetic diversity than range edges. Because effective population size is proportional to the harmonic mean of the census population size, our results suggest that populations of tropical species near the range centre may have been relatively stable, but that populations on the range edges appear to have been less so.

Our findings have implications for both evolutionary biology and the management of biodiversity, as differences in genetic diversity can have substantial effects on ecological processes (Hughes *et al.* 2008). Further study is needed to determine whether the humped pattern present in mtDNA of

Neotropical birds is also found in potentially adaptive genetic variation. That relationship will be important for conservation and management, because, with respect to the maintenance of genetic diversity, our data predict that consequences of anthropogenic habitat fragmentation and population isolation will likely have differential effects depending on where in a species' range these phenomena occur.

## ACKNOWLEDGEMENTS

We thank A. Johnson for collecting many of the Belizean specimens in this study. M. Lelevier and M. Nuñez assisted in the laboratory work. We also thank the people and governments of the five countries who granted scientific collecting permits; research of this scope is only possible with their continued support. This project was partially supported by NIH Fogarty International Center Award Number U01TW006634; the content is solely the responsibility of the authors and does not necessarily represent the official views of the Fogarty International Center or the National Institutes of Health. Additional financial support for this project came from the University of Alaska Museum, the Smithsonian Tropical Research Institute, and University of Alaska Fairbanks EPSCoR graduate, a Smithsonian Pre-doctoral, Angus Gavin Migratory Bird Research, and an AMNH Chapman Fund fellowships/grants to M.J. Miller. We thank A. Crawford, M. Holyoak, K. McCracken, M. Olson, and three anonymous referees for comments on earlier drafts.

## REFERENCES

- Adams, J.M. (1997). *Global Land Environments Since the Last Interglacial*. Oak Ridge National Laboratory, TN, USA. Available at: <http://www.esd.ornl.gov/ern/gen/nerc.html>.
- Aleixo, A. (2006). Historical diversification of floodplain forest specialist species in the Amazon: a case study with two species of the avian genus *Xipborhynchus* (Aves: Dendrocolaptidae). *Biol. J. Linn. Soc. Lond.*, 89, 383–395.
- Anthony, N.M., Johnson-Bawe, M., Jeffery, K., Clifford, S.L., Abernethy, K.A., Tutin, C.E. *et al.* (2007). The role of Pleistocene refugia and rivers in shaping gorilla genetic diversity in central Africa. *Proc. Natl Acad. Sci. USA*, 104, 20432–20436.
- Bernatchez, L. & Wilson, C.C. (1998). Comparative phylogeography of Nearctic and Palearctic fishes. *Mol. Ecol.*, 7, 431–452.
- Berrio, J.C. (2002). *Late glacial and Holocene vegetation and climate change in lowland Colombia*, PhD Dissertation, University of Amsterdam, Amsterdam.
- Brown, J.H. (1984). On the relationship between abundance and distribution of species. *Am. Nat.*, 124, 255–279.
- Brown, J.H., Mehlman, D.W. & Stevens, G.C. (1995). Spatial variation in abundance. *Ecology*, 76, 2028–2043.
- Brumfield, R.T. (2005). Mitochondrial variation in Bolivian populations of the Variable Antshrike (*Thamnophilus caerulescens*). *Auk*, 122, 414–432.

- Brumfield, R.T. & Capparella, A.P. (1996). Historical diversification of birds in northwestern South America: a molecular perspective on the role of vicariant events. *Evolution*, 50, 1607–1624.
- Brussard, P.F. (1984). Geographic patterns and environmental gradients: the central-marginal model in *Drosophila* revisited. *Annu. Rev. Ecol. Syst.*, 15, 25–64.
- Cleary, D.F.R., Fauvelot, C., Genner, M.J., Menken, S.B.J. & Mooers, A.O. (2006). Parallel responses of species and genetic diversity to El Niño Southern Oscillation-induced environmental destruction. *Ecol. Lett.*, 9, 304–310.
- Colinvaux, P.A. (1996). Quaternary environmental history and forest diversity in the Neotropics. In: *Evolution and Environment in Tropical America* (eds Jackson, J.B.C., Budd, A.F. & Coates, A.G.). University of Chicago Press, Chicago, pp. 359–406.
- Colwell, R.K. & Hurtt, G.C. (1994). Non-biological gradients in species richness and a spurious Rapoport effect. *Am. Nat.*, 144, 570–595.
- Colwell, R.K. & Lees, D.C. (2000). The mid-domain effect: geometric constraints on the geography of species richness. *Trends Ecol. Evol.*, 15, 70–76.
- Colwell, R.K., Rahbek, C. & Gotelli, N.J. (2004). The mid-domain effect and species richness patterns: what have we learned so far? *Am. Nat.*, 163, E1–E23.
- da Cunha, A.B., Burla, H. & Dobzhansky, T. (1950). Adaptive chromosomal polymorphism in *Drosophila willistoni*. *Evolution*, 4, 212–235.
- Eckert, C.G., Samis, K.E. & Loughheed, S.C. (2008). Genetic variation across species' geographical ranges: the central-marginal hypothesis and beyond. *Mol. Ecol.*, 17, 1170–1188.
- Hewitt, G.M. (1996). Some genetic consequences of ice ages, and their role in divergence and speciation. *Biol. J. Linn. Soc. Lond.*, 58, 247–276.
- Hillesheim, M.B., Hodell, D.A., Leyden, B.W., Brenner, M., Curtis, J.H., Anselmetti, F.S. *et al.* (2005). Climate change in lowland Central America during the late deglacial and early Holocene. *J. Quat. Sci.*, 20, 363–376.
- Hughes, A.L. & Hughes, M.A.K. (2007). Coding sequence polymorphism in avian mitochondrial genomes reflects population histories. *Mol. Ecol.*, 16, 1369–1376.
- Hughes, A.R., Inouye, B.D., Johnson, M.T.J., Underwood, N. & Vellend, M. (2008). Ecological consequences of genetic diversity. *Ecol. Lett.*, 11, 609–623.
- Jaarola, M. & Tegelström, H. (1995). Colonization history of north European field voles (*Microtus agrestis*) revealed by mitochondrial DNA. *Mol. Ecol.*, 4, 299–310.
- Jetz, W. & Rahbek, C. (2001). Geometric constraints explain much of the species richness pattern in African birds. *Proc. Natl Acad. Sci. USA*, 98, 5661–5666.
- Johansson, M., Primmer, C.R. & Merilä, J. (2006). History vs. current demography: explaining the genetic population structure of the common frog (*Rana temporaria*). *Mol. Ecol.*, 15, 975–983.
- Karr, J.R. & Freemark, K.E. (1983). Habitat selection and environmental gradients: dynamics in the “stable” tropics. *Ecology*, 64, 1481–1494.
- Lees, D.C., Kremen, C. & Andriamampianina, L. (1999). A null model for species richness gradients: bounded range overlap of butterflies and other rainforest endemics in Madagascar. *Biol. J. Linn. Soc.*, 67, 529–584.
- Lessa, E.P., Cook, J.A. & Patton, J.L. (2003). Genetic footprints of demographic expansion in North America, but not Amazonia, during the Late Quaternary. *Proc. Natl Acad. Sci. USA*, 100, 10331–10334.
- Leyden, B.W. (1984). Guatemalan forest synthesis after Pleistocene aridity. *Proc. Natl Acad. Sci. USA*, 81, 4856–4859.
- MacArthur, R.H. (1972). *Geographical Ecology: Patterns in the Distribution of Species*. Princeton University Press, Princeton, NJ.
- Mallet, J., Isaac, N.J.B. & Mace, G.M. (2005). Response to Harris and Froufe, and Knapp *et al.*: taxonomic inflation. *Trends Ecol. Evol.*, 20, 8–9.
- Marchant, R., Boom, A., Behling, H., Hooghiemstra, H., Melief, B., Van Geel, B. *et al.* (2004). Colombian vegetation at the Last Glacial Maximum: a comparison of model- and pollen-based biome reconstructions. *J. Quat. Sci.*, 19, 721–732.
- Martin, P.R. & McKay, J.K. (2004). Latitudinal variation in genetic divergence of populations and the potential for future speciation. *Evolution*, 58, 938–945.
- Merilä, J., Björklund, M. & Baker, A.J. (1997). Historical demography and present day population structure of the Greenfinch, *Carduelis chloris* – an analysis of mtDNA control-region sequences. *Evolution*, 51, 946–956.
- Milá, B., Girman, D.J., Kimura, M. & Smith, T.B. (2000). Genetic evidence for the effect of a postglacial population expansion on the phylogeography of a North American songbird. *Proc. R. Soc. Lond. B Biol. Sci.*, 267, 1033–1040.
- Miller, M.J., Bermingham, E., Klicka, J., Escalante, P., Raposo do Amaral, F.S., Weir, J.T. *et al.* (2008). Out of Amazonia again and again: episodic crossing of the Andes promotes diversification in a lowland forest flycatcher. *Proc. R. Soc. Lond. B Biol. Sci.*, 275, 1133–1142.
- Nei, M. (1987). *Molecular Evolutionary Genetics*. Columbia University Press, New York.
- Orians, G.H. (1969). The number of bird species in some tropical forests. *Ecology*, 50, 783–801.
- Orme, C., Davies, R., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V. *et al.* (2005). Global hotspots of species richness are not congruent with endemism or threat. *Nature*, 436, 1016–1019.
- Phillips, O.L., Hall, P., Gentry, A.H., Sawyer, S.A. & Vasquez, R. (1994). Dynamics and species richness of tropical rain forests. *Proc. Natl Acad. Sci. USA*, 91, 2805–2809.
- Ridgway, T., Riginos, C., Davis, J. & Hoegh-Guldberg, O. (2008). Genetic connectivity patterns of *Pocillopora verrucosa* in southern African Marine Protected Areas. *Mar. Ecol. Prog. Ser.*, 354, 161–168.
- Rosenzweig, M.L. (1995). *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- Rozas, J., Sánchez-Delbarrio, J.C., Messeguer, X. & Rozas, R. (2003). DnaSP, DNA polymorphism analyses by the coalescent and other methods. *Bioinformatics*, 19, 2496–2497.
- Sagarin, R. & Gaines, S. (2002). The ‘abundant centre’ distribution: to what extent is it a biogeographic rule?. *Ecol. Lett.*, 5, 137–147.
- Schneider, C. & Moritz, C. (1999). Rainforest refugia and evolution in Australia's Wet Tropics. *Proc. R. Soc. Lond. B Biol. Sci.*, 266, 191–196.
- Terborgh, J. (1973). On the notion of favorableness in plant ecology. *Am. Nat.*, 197, 481–501.
- Vellend, M. (2003). Island Biogeography of genes and species. *Am. Nat.*, 162, 358–365.

- Vellend, M. & Geber, M.A. (2005). Connections between species diversity and genetic diversity. *Ecol. Lett.*, 8, 767–781.
- Vucetich, J.A. & Waite, T.A. (2003). Spatial patterns of demography and genetic processes across the species' range: Null hypotheses for landscape conservation genetics. *Conserv. Genet.*, 4, 639–645.
- Wehenkel, C., Bergmann, F. & Gregorius, H.-R. (2006). Is there a trade-off between species diversity and genetic diversity in forest tree communities? *Plant Ecol.*, 185, 151–161.
- Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003). Latitudinal gradients of biodiversity: pattern, process, scale and synthesis. *Annu. Rev. Ecol. Syst.*, 34, 273–309.

## SUPPORTING INFORMATION

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

**Table S1** Effect of removing small sample-size populations on the test of an inverse relationship between latitude and nucleotide diversity.

**Table S2** Effect of removing small sample-size populations on the test of whether the maximum  $\pi$  value occurs in edge populations less frequently than expected by chance.

**Appendix S1** Specimens and tissue samples used in this study, with corresponding GenBank accession numbers.

**Appendix S2** Number of breeding landbirds at four biological stations along a latitudinal gradient in the Neotropical lowlands north and west of the Andes.

**Appendix S3** Relative abundances of populations of nine focal species of Neotropical landbirds near their range limits and in the centres of their ranges.

**Appendix S4** Sample size analysis and permutations.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

Editor, Marcel Holyoak

Manuscript received 11 June 2009

First decision made 17 July 2009

Second decision made 30 December 2009

Manuscript accepted 18 January 2010