RELATIONSHIP OF GENETIC DIVERSITY AND NICHE CENTRALITY: A SURVEY AND ANALYSIS

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The distribution of genetic diversity within and among populations in relation to species' geographic ranges is important to understanding processes of evolution, speciation, and biogeography. One hypothesis predicts that natural populations at geographic range margins will have lower genetic diversity relative to those located centrally in species' distributions owing to a link between geographic and environmental marginality; alternatively, genetic variation may be unrelated with geographic marginality via decoupling of geographic and environmental marginality. We investigate the predictivity of geographic patterns of genetic variation based on geographic and environmental marginality using published genetic diversity data for 40 species (insects, plants, birds, mammals, worms). Only about half of species showed positive relationships between geographic and environmental marginality. Three analyses (sign test, multiple linear regression, and meta-analysis of correlation effect sizes) showed a negative relationship between genetic diversity and distance to environmental niche centroid, but no consistent relationship of genetic diversity with distance to geographic range center.

KEY WORDS: Central-peripheral hypothesis, ecological niche, genetic diversity, geographic range.

The study of species' geographic distributions has been approached from many different perspectives in ecology, evolutionary biology, biogeography, and macroecology (Udvardy 1969; Rapoport 1982; Brown et al. 1996; Gaston 2003; Holt and Keitt 2005). Particularly important are geographic range edges, because they represent frontiers where populations interact with marginal environmental conditions, to which they may or may not adapt (Holt 2003; Bridle and Vines 2007; Kawecki 2008; Sexton et al. 2009; Paul et al. 2011).

Along distributional limits, populations are often sparse, fragmented, and prone to local extinction (Gaston 2003); they may represent demographic sinks maintained by immigration from higher-quality core habitats, which makes them demographically and genetically dependent on other populations (Pulliam 1988). Peripheral sites may also receive gene flow that can counteract

local selection pressures and local adaptation (Kawecki 2008). As a consequence, these populations may be more prone to loss of genetic diversity (Kawecki 2008; Keller et al. 2010).

This pattern has been illustrated as a hypothesized relationship between local abundance and geographic centrality, in which abundances would be higher in central populations versus peripheral ones (e.g., Brown 1984; Brussard 1984; Vucetich and Waite 2003). This idea is called the abundant-center hypothesis (Hengeveld and Haeck 1982). However, exceptions to the pattern have been reported frequently (e.g., Sagarin and Gaines 2002; Gaston 2003; Martínez-Meyer et al. 2013). Although higher genetic diversity may be expected at range centers than at range edges, empirical patterns have been mixed (Eckert et al. 2008; Kawecki 2008; Moeller et al. 2011).

The distance to the center of the geographic distribution per se should perhaps not be expected to cause abundance or genetic variability differences. Demographic processes may relate more

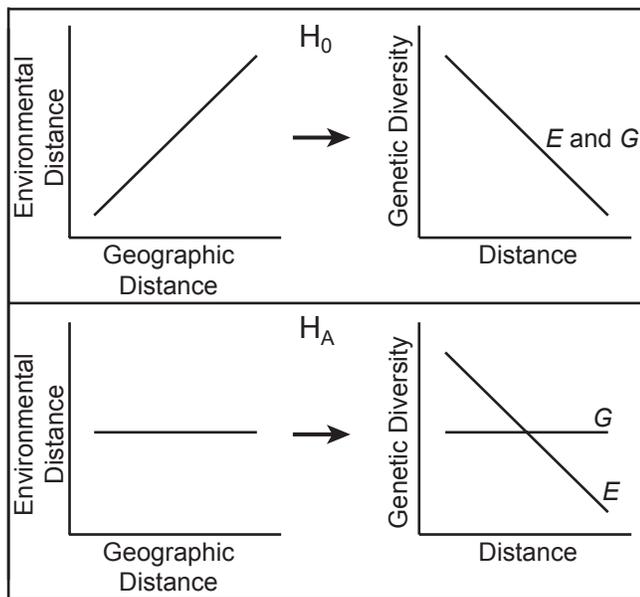*Both authors contributed equally to this work.
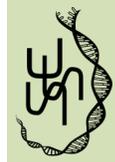
Figure 1. Hypothesized relationships between distance to ecological niche centroid, geographic range center, and genetic diversity. Under H_0, environmental and geographic marginality coincide, leading both to be negatively correlated with genetic diversity. Alternatively, under H_A, environmental and geographic marginality are decoupled, leading to the lack of a relationship between genetic diversity and geographic centrality.

directly to the quality of local conditions, as expressed by the fundamental ecological niche of the species (Hutchinson 1957, 1978; Pulliam 2000; Soberón 2010; Martínez-Meyer et al. 2013). The fundamental niche is the set of environmental conditions under which the species shows positive population growth rates without immigration; outside of those conditions, the species shows zero or negative population growth. Under this alternative framework, populations under conditions closer to the core of the fundamental ecological niche would achieve higher growth rates or greater stability than those far from the optimum conditions (VanDerWal et al. 2009). Of special note is that environmentally "central" conditions frequently are not located at the center of the geographic range. Therefore, an important question arises as follows: are demographic and genetic effects of peripherality manifested more consistently in geographic or environmental spaces?

Under one hypothesis (H_0 in Fig. 1), geographic marginality and ecological marginality are positively linked, creating a relationship between geographic marginality and population characteristics (e.g., local abundance or genetic diversity). Alternatively, geographic marginality and ecological marginality may be decoupled (H_A in Fig. 1), leading to a lack of a relationship between geographic marginality and population characteristics. The key assumption behind these hypotheses is that environmental marginality causes adverse population effects. Here, environmen-

tal marginality may lead to small population sizes (i.e., an environmental version of the abundant-center hypothesis), which in turn causes population genetic processes to reduce genetic diversity. Increased genetic drift in small populations, source-sink dynamics of unsustainable populations, or strong selection in marginal environments could all contribute to environmental marginality reducing genetic diversity within a species.

Little has been done to explore this ecological niche-based version of the abundant-center hypothesis, that is, that population dynamics or genetic structure are functions of environmental conditions associated with ecological niches of species (Martínez-Meyer et al. 2013). To our knowledge, only one study has explored the central-peripheral hypothesis regarding genetic variability in relation to environmental suitability (Diniz-Filho et al. 2009). However, these authors related genetic variability to measures of environmental suitability (not centrality within the niche), which they estimated from an average of ecological niche model suitability scores from multiple niche modeling algorithms; they found no clear relationships.

The above situation suggests that reassessment of the traditional geographic abundant-center hypothesis (Sagarin and Gaines 2002; Gaston 2003; Garner et al. 2004; Eckert et al. 2008) in terms of ecological niches is necessary. Particularly important to this point are differences between environmental conditions near the core of the geographic distribution versus those at its periphery, because these contrasting environments are where key components of selection, adaptation, and evolution are—or are not—taking place (Bridle and Vines 2007; Kawecki 2008; Bozinovic et al. 2011). Soberón and Miller (unpubl. ms.) extended models originally presented by Holt and Gomulkiewicz (1997), and obtained equations for genetic variance–covariance matrices in spatially explicit population-genetic models. The main equation predicted that phenotypic variance should decrease as a function of the geographic distribution only if strong spatial covariance exists in the direction of selective pressures. This result suggests that geographic centrality will be associated with higher genetic diversity only when correlated with environmental characteristics.

Here, we test whether genetic diversity is higher near the core or at the periphery of habitable conditions (the niche) versus the geographic distribution in 40 species for which some measure of genetic variability in multiple natural populations has been published. We contrasted relationships among genetic diversity, distances to three estimates of niche centroids, and distances to seven measures of geographic range centers.

Methods
SPECIES' OCCURRENCES AND GENETIC DIVERSITY
We assembled data from 40 species from numerous taxonomic groups for which both genetic diversity and geographic locations

Table 1. Species used in this study, their taxonomic affinities, measure of genetic diversity used (Div.), and the original publication for each species.

Species	Taxonomic Group	Div.	Reference
Arenaria humifusa	Magnoliopsida: Caryophyllaceae	GD	Westergaard et al. (2011)
Bombus bifarius	Insecta: Apidae	AR	Lozier et al. (2011)
Bombus bimaculatus	Insecta: Apidae	AR	Lozier et al. (2011)
Bombus impatiens	Insecta: Apidae	AR	Lozier et al. (2011)
Bombus occidentalis	Insecta: Apidae	AR	Lozier et al. (2011)
Bombus pensylvanicus	Insecta: Apidae	AR	Lozier et al. (2011)
Bombus vosnesenskii	Insecta: Apidae	AR	Lozier et al. (2011)
Cardellina pusilla	Aves: Parulidae	π	Kimura et al. (2002)
Cardellina ruber	Aves: Parulidae	π	Barrera-Guzmán et al. (2012)
Cardinalis cardinalis	Aves: Cardinalidae	π	Smith et al. (2011)
Cassiope tetragona	Magnoliopsida: Ericaceae	GD	Eidesen et al. (2007b)
Certhia americana	Aves: Certhiidae	π	Manthey et al. (2011)
Dalbergia nigra	Magnoliopsida: Leguminosae	π	Ribeiro et al. (2011)
Eucryphia cordifolia	Magnoliopsida: Cuconiaceae	π	Segovia et al. (2012)
Fraxinus angustifolia	Magnoliopsida: Oleaceae	AR	Temunovic et al. (2012)
Himantoglossum hircinum	Liliopsida: Orchidaceae	H_E	Pfeifer et al. (2009)
Hymenaea stigonocarpa	Magnoliopsida: Fabaceae	π	Ramos et al. (2007)
Lampornis amethystinus	Aves: Trochilidae	π	Cortés-Rodríguez et al. (2008)
Lynx rufus	Mammalia: Felidae	π/AR	Reding et al. (2012)
Melampodium leucanthum[1]	Magnoliopsida: Asteraceae	AWD	Rebernig et al. (2010)
Microtus miurus	Mammalia: Cricetidae	π	Weksler et al. (2010)
Microtus oeconomus	Mammalia: Cricetidae	π	Galbreath & Cook (2004)
Oxalis alpine	Magnoliopsida: Oxalidaceae	π	Pérez-Alquicira et al. (2010)
Pelecanus erythrorhynchos	Aves: Pelecanidae	π	Oomen et al. (2011)
Peripatopsis capensis	Onychophorida: Peripatopsidae	π	McDonald & Daniels (2012)
Peromyscus attwateri	Mammalia: Cricetidae	π	Lack et al. (2010)
Pheropsophus jessoensis	Insecta: Carabidae	π	Li et al. (2012)
Picoides albolarvatus	Aves: Picidae	π	Alexander & Burns (2006)
Poecile gambeli	Aves: Paridae	π	Spellman et al. (2007)
Quercus engelmannii	Magnoliopsida: Fagaceae	AR	Ortego et al. (2012)
Rhodiola alsia	Magnoliopsida: Crassulaceae	π	Gao et al. (2012)
Rubus chamaemorus	Magnoliopsida: Rosaceae	GD	Ehrich et al. (2008)
Sagina caespitosa	Magnoliopsida: Caryophyllaceae	GD	Westergaard et al. (2011)
Setophaga caerulescens	Aves: Parulidae	π	Grus et al. (2009)
Sitta carolinensis	Aves: Sittidae	π	Spellman & Klicka (2007)
Sitta pygmaea	Aves: Sittidae	π	Spellman & Klicka (2006)
Spermophilus parryii	Mammalia: Sciuridae	π	Galbreath et al. (2011)
Stipa capillata	Liliopsida: Poaceae	H_E	Wagner et al. (2011)
Toxostoma redivivum	Aves: Mimidae	π	Sgariglia & Burns (2003)
Vaccinium uliginosum[1]	Magnoliopsida: Ericaceae	GD	Eidesen et al. (2007a)

GD, genic diversity; AR, allelic richness; π, nucleotide diversity; HE, expected heterozygosity; AWD, average distances within populations.
[1]Alternative ploidy levels were removed from analysis.

of populations were reported (Table 1). These data come from insects (seven), birds (15), mammals (three), plants (14), and an onychophoran velvet worm, distributed in North and South America, South Africa, Eurasia, the Mediterranean region, and the Arctic. The collection of data was done by searching for phylogeography papers in the Web of Science; papers with poor locality data, individuals from a single population spread over many kilometers (e.g., >10 km between individuals in a single population), or small sample sizes for all or most populations were excluded. Genetic diversity measures were taken directly from the original publications (Table 1, Appendix S1); most indices of genetic diversity were from putatively neutral genetic markers.

One assumption of this study is that the reported values of neutral genetic variation have some relationship with fitness, which has been shown in some taxa (Reed and Frankham 2003; Leimu et al. 2006), but not in others (Chapman et al. 2009).

We obtained occurrence data for all species through the Global Biodiversity Information Facility (www.gbif.org), in addition to the occurrence data associated with the phylogeographic or population genetic data from the original publication. All occurrence data were inspected carefully to detect and correct problems associated with mistaken taxonomic identification (including all lower taxonomic forms of recognized species), duplication, lack of precision, or geographically discordant localities (Chapman 2005). In the case of some plants, we eliminated populations that exhibited alternative ploidy levels (Table 1). Ploidy was only considered when investigating the genetic data (and not the occurrence data) because of possible inflation of genetic diversity measures with an increase in chromosomes. This only impacted two species in the analyses.

NICHE CHARACTERIZATION AND DISTANCES TO NICHE AND GEOGRAPHIC CENTROIDS

To estimate ecological niches of species and measure environmental space distances of each population to the species' niche centroid, four steps were necessary as follows: (1) create ecological niche models for each species, (2) extract background points and associated environmental data, (3) perform a principal components analysis (PCA) on each dataset, and (4) measure multivariate Euclidean distance to niche centroids and geographic range centers.

For ecological niche modeling, 19 bioclimatic layers were obtained from the WorldClim database at a spatial resolution of 2.5′ (Hijmans et al. 2005; www.worldclim.org). These layers contain worldwide precipitation and temperature information, including minima, maxima, and ranges of values. These datasets, however, were highly intercorrelated; hence, only seven were included (annual mean temperature, mean diurnal range, maximum temperature of warmest month, minimum temperature of coldest month, annual precipitation, and precipitation of wettest and driest months) for modeling, owing to high correlations between some pairs of variables ($r > 0.7$, tested in ENMTools; Warren et al. 2008, 2010). Because we focus on climatic dimensions, our analyses are of the Grinnellian or scenopoetic fundamental niche, which is in essence a suite of abiotic, range-wide determinants of the population status of the species being modeled (Soberón 2007). Here, we assume that the niche we model is a good estimator of the fundamental niche, although we recognize that it is not possible to capture the true fundamental niche without physiological experiments for each species (Peterson et al. 2011).

To reduce model overfitting owing to spatially autocorrelated occurrences, we rarefied numbers of points per species using a minimum distance between points of 10′. For species with >100 occurrences, we selected 11 sets of points at random without replacement from the set of unique values of longitude and latitude, but with replacement between sets. Species' occurrences and environmental layers were then used in Maxent (Phillips et al. 2006) to build one model per set of points. We calibrated models via 11 bootstrap replications, using a threshold of $E = 10\%$ of training data to convert the models to binary (Peterson et al. 2008), with remaining parameters left as default. The median of each set of thresholded models (i.e., presence predicted in ≥ 6 of 11 models) was used as the final estimate of suitable area, considering that each thresholded model was derived from different sets of points. Because calibration areas influence outcomes of niche model predictions given differences in background sampling, and these areas should be biogeographically relevant for the species (Barve et al. 2011), we designed three calibration areas for each species: a 500 km buffer around occurrence points, and 200 and 500 km buffers around the terrestrial ecoregions (Olson et al. 2001) in which species' occurrence points fell (labeled "500 km," "ER + 200 km," and "ER + 500 km," respectively, in tables and figures). We used these buffers to keep methodologies consistent among species, as well as to test for effects of changing the calibration areas on overall results. These polygons were used to mask environmental layers for ecological niche modeling in Maxent; niche models were calibrated for each species over three geographic areas.

To characterize ecological niches and estimate niche centroids, we created a data matrix including known occurrence data and 5000 points sampled at random from the suitable area for the species as estimated in Maxent. From this matrix, we extracted values of the 19 bioclimatic layers at each point, and then transformed the matrix via PCA based on the correlation matrix. To ensure that 5000 points, rather than a smaller number, did not impact the output, we replicated this step using smaller samples of 2500, 1000, and 500 points sampled from the suitable extent for each species (see Appendix S1). The mean of scores along the first six principal components was used as an estimate of the species' niche centroid. From this vector, we estimated the multivariate Euclidean distance of each population for which we had genetic variation estimates. In all cases, the first six principal components explained the great majority (>95%) of the variance in the environmental data.

Geographic centrality of populations was estimated in relation to seven geographic ranges: the centroid of the minimum convex polygon encompassing all occurrence points, centroids of the three suitable areas obtained from thresholded Maxent models, and centroids of the three polygons of the calibration areas used for niche modeling. These measures allowed us to contrast among competing hypotheses associating genetic diversity with distance to geographic or ecological niche centroids. This

may be especially important because species' geographic ranges have traditionally been delimited using different approximations (Rapoport 1982), and this task is frequently accomplished via gridded outputs of ecological niche models (Fortin et al. 2005).

To identify relationships between genetic diversity and distances to ecological niche and geographic centroids, we used linear regressions between these variables, using distance to ecological niche or geographic centroids as the independent variable. We used linear regression only to derive simple patterns from the overall dataset, not attempting to derive best models, to avoid complicating comparisons between species unnecessarily. To reduce effects of outlier points in regressions, we removed points with a Cook's distance (Cook 1977) of ≥ 0.95, followed by rerunning the linear regression.

To investigate overall trends in the data, we used three methods. First, we used a sign test across all linear regressions to determine whether negative or positive slopes were unexpectedly overrepresented in each dataset. Second, we fit a generalized linear model including all genetic diversity and distance data for each species. Distance to niche centroid and distance to geographic range center (e.g., E distance and G distance for ER + 200 km calibration area) were used as predictors of genetic diversity to disentangle the effects of each variable with the following model: genetic diversity $\sim$ distance to niche centroid + distance to geographic range center. Prior to regression, all variables were z-standardized within each species.

Finally, we calculated mean effect sizes of correlation coefficients between genetic diversity and distance to either ecological niche centroid or geographic center (Borenstein et al. 2009). First, we transformed the correlation coefficient (r) to Fisher's z, using the following equation:

$$z = 0.5 \times \ln\left(\frac{1+r}{1-r}\right), \tag{1}$$

which gave an effect size for each individual species. The variance of z (VZ) was calculated as:

$$VZ = \frac{1}{n-3}, \tag{2}$$

where n is the number of populations for each species. Lastly, the mean effect size was calculated as the weighted mean of each species' effect size:

$$ES = \frac{\sum_{i=1}^{k} VZ_i z_i}{\sum_{i=1}^{k} VZ_i}. \tag{3}$$

Confidence intervals were calculated with 10,000 bias-corrected bootstrap replicates. Following calculation of grand mean effect sizes and associated 95% confidence intervals, values were back transformed from Fisher's z to correlation coefficients for visualization.

For every species, we checked for separate clusters of points in both geographic and environmental space. For one species, *Stipa capillata*, we detected clearly separate clusters of points along geographic distance, which corresponded to the central and peripheral populations analyzed in the original publication (Wagner et al. 2011); in this case, we calculated linear regressions separately to understand if relationships within each cloud differed from those in the whole dataset for the species. For *Lynx rufus*, for which both mtDNA and nuclear DNA (microsatellites) data were available (Reding et al. 2012), we repeated analyses to assess whether different molecular markers showed contrasting results. Finally, we calculated correlations between niche centrality and geographic centrality to assess the degree to which the two vary independently of one another. Spatial data were handled in ArcMap 10.1 (ESRI 2011) and R (R Development Core Team 2012); all statistical computation was done in R.

Results

Most species showed negative relationships between distance to niche centroid and genetic diversity; results were consistent across the three alternative training regions for niche models (Tables 2 and 3). Conversely, we found no general trend between genetic diversity and distance to geographic centroid (Tables 2 and 3). Similarly, the grand mean correlation effect sizes of distance to environmental centroid were negative and significantly different than zero, whereas effect sizes of distance to geographic center, although all negative, were not significantly different from zero (Fig. 2).

Overall, 24 species showed similar patterns of associations of genetic diversity between environmental and geographic space (Table 2). We illustrate results for two species, *Bombus bifarius* and *L. rufus*; in both cases, genetic diversity was negatively associated with distance to niche centroids, but patterns in relation to geographic centroids were inconsistent (Figs. 3 and 4). The mitochondrial (mtDNA) and nuclear DNA available for *L. rufus* yielded consistent patterns ($r = 0.41$, $P = 0.0028$; Fig. 4), although they differed in frequency distributions, as mtDNA was slightly biased toward east-to-west genetic structure, whereas nuclear DNA (microsatellites) was normally distributed. In *S. capillata*, the species with distinct clusters in geographic space, regression analyses showed significantly negative slopes for peripheral populations for all estimates of distance to the niche centroid and to the three distances from the geographic center estimated from Maxent models, a pattern which was hidden when both central and peripheral populations were pooled together. We identified outlier points for seven species in environmental space and for 10 species in geographic space; however, regression analyses following removal of outliers did not change in overall pattern (Appendix S1).

Table 2. Species used in this study, number of populations for each species (*N*), number of occurrence records used for modeling ecological niches (*N* Occ.), whether geography and environment show similar relationships with genetic diversity (Agree), pattern(s) observed between genetic diversity and distance to centroid of the niche (*E*), number of significant comparisons for *E* (*E**) out of three total, pattern(s) observed between genetic diversity and distance to geographic center of a species (*G*), number of significant comparisons for *G* (*G**) out of seven total.

Species	*N*	*N* Occ.	Agree	*E*	*E**	*G*	*G**
Melampodium leucanthum	68	360	X	−		−	6
Cassiope tetragona	62	418	X	−	1	−	2
Vaccinium uliginosum	54	833	X	−	2	−	7
Lynx rufus	52	1096		−	3	+/−$_C$	3$_C$
Stipa capillata	43	295		+		−	
Rubus chamaemorus	41	625		−		+/−$_C$	
Spermophilus parryii	34	207	X	−	3	−	
Bombus bimaculatus	34	197		−		+/−	
Bombus bifarius	33	947		−	3	+/−	3
Bombus impatiens	33	390		−	3	+/−	
Bombus pensylvanicus	25	451	X	−	3	−	3
Poecile gambeli	25	396	X	−		−	
Pheropsophus jessoensis	25	27		−	3	+/−	1
Peromyscus attwateri	22	94		+		+/−	
Eucryphia cordifolia	22	32	X	−		−	6
Cardinalis cardinalis	20	1458	X	−	3	−	7
Himantoglossum hircinum	20	619		−		+	1
Oxalis alpina	20	107	X	−		−	6
Certhia americana	19	871	X	+		+	
Dalbergia nigra	19	27	X	−		−	
Rhodiola alsia	18	27	X	+	3	+	1
Hymenaea stigonocarpa	17	83	X	+		+	
Peripatopsis capensis	17	12	X	−		−	
Bombus vosnesenskii	16	511		−		+/−	3
Pelecanus erythrorhynchos	16	344	X	−		−	1
Sitta carolinensis	14	1611		+/−		+	2
Microtus oeconomus	14	464	X	−		−	
Setophaga caerulescens	14	395	X	+		+	
Sagina caespitosa	14	80		+/−		+/−	
Bombus occidentalis	13	939		+/−		+	
Lampornis amethystinus	13	98		+		+/−	
Quercus engelmannii	13	26	X	+		+	
Cardellina pusilla	12	855	X	−		−	
Picoides albolarvatus	12	73	X	−		−	
Fraxinus angustifolia	11	590		−		+/−	
Sitta pygmaea	11	238	X	−		−	
Arenaria humifusa	11	59	X	−		−	
Toxostoma redivivum	9	61	X	+		+	
Cardellina ruber	9	44		−		+	3
Microtus miurus	8	110	X	−		−	
Total consensus positive				7	9	10	
Total consensus negative				18	28	19	
Total mixed pattern				16	3	11	

A (−) or (+) indicates negative or positive relationships, respectively, while a (+/−) indicates mixed patterns. A (C) subscript indicates conflicting patterns between model-based and other geographic center measures.

Table 3. Binomial tests of slopes (sign test).

	No. of negative slopes (*P*-value)	# − Sig.	# + Sig.
Environmental distance			
500 km	29 (0.0064)	8	1
ER + 200 km	31 (0.0007)	8	1
ER + 500 km	29 (0.0064)	8	1
Geographic distance			
500 km	26 (0.0807)	6	2
ER + 200 km	25 (0.1539)	6	2
ER + 500 km	24 (0.2682)	4	1
MCP	25 (0.1539)	6	3
500 km (Mx)	24 (0.2682)	9	1
ER + 200 km (Mx)	24 (0.2682)	8	1
ER + 500 km (Mx)	25 (0.1539)	10	1

"# − Sig." indicates the number of significant negative results; "# + Sig." indicates the number of significant positive results. Training areas compared included 500 km = 500 km buffer around occurrence points, ER + 200 km = 200 km buffer around terrestrial ecoregions, and ER + 500 km = 500 km buffer around terrestrial ecoregions.

MCP, minimum convex polygon; Mx, centroid estimated from Maxent prediction.

No consistent correlation (among calibration areas) existed between distance to geographic centroid and distance to environmental centroid in all species (Appendix S1). Twenty-four species had consistent, positive correlations between distance to geographic and environmental centroids, with 14-21 of those correlations significant depending on model-calibration area. Additionally, different methods of estimating geographic centroids provided conflicting distance-diversity relationships in 11 of 40 species (Table 2). For example, estimating geographic centroids from minimum convex polygons versus thresholded suitability models yielded relationships with different signs between geographic centrality and genetic diversity.

Results from the generalized linear models (Table 4) indicated that distance to niche centroid was the only relevant predictor of genetic diversity for the dataset of points buffered with 500 km, and showed higher significance than distance to geographic range center for the datasets of ecoregions buffered by 200 and 500 km. When only cases in which slopes showing same signs were considered (see Table 2), both distances were significant predictors. In contrast, distance to the ecological niche centroid was the only significant predictor in models of cases in which regression slopes showed contrasting patterns (Table 4).

Regressions between genetic diversity and distance to geographic centroids showed no significant dependence on sample size (Table 5), whereas relationships between genetic diversity and distance to ecological niche centroid showed a strong relationship to sample size (Table 5). Limiting analyses to species with
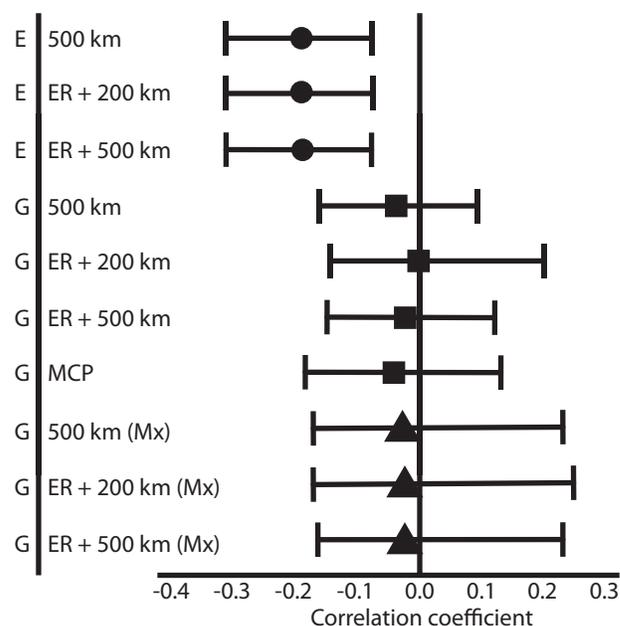

Figure 2. Mean grand effect sizes of the relationship between genetic diversity and either environmental (*E*) or geographic range (*G*) centrality. These are displayed for distance to environmental centroid with three different calibration areas for modeling (circles), and seven different estimates of distance to geographic center based on model calibration areas (squares) and modeled suitable areas (triangles). See Methods for more details.

25 or more populations sampled, 12 of 13 species showed negative relationships between genetic diversity and distance to niche centroid ($P = 0.003$, binomial test), with eight of these showing a significant relationship (Table 2). Conversely, only seven of 13 species showed negative relationships between genetic diversity and distance to geographic centroid (four of seven significant; Table 2); three of which showed conflicting significant results between different geographic centroid estimates.

Discussion

Reviewing published phylogeographic studies for 40 species, we identified a clear pattern of negative relationships between genetic diversity and distance to ecological niche centroids, but mixed or no relationships between genetic diversity and distributional centrality. Using three methods to evaluate the entire dataset, the sign test of results of linear regressions of the two distances separately (Table 3), the generalized linear models combining both distances (Table 4), and the meta-analysis of mean effect sizes (Fig. 2), distance to niche centroid showed higher predictive ability of genetic diversity than distance to geographic range center. Only about half the species showed a strong correlation between environmental and geographic marginality (Appendix S1). This decoupling in
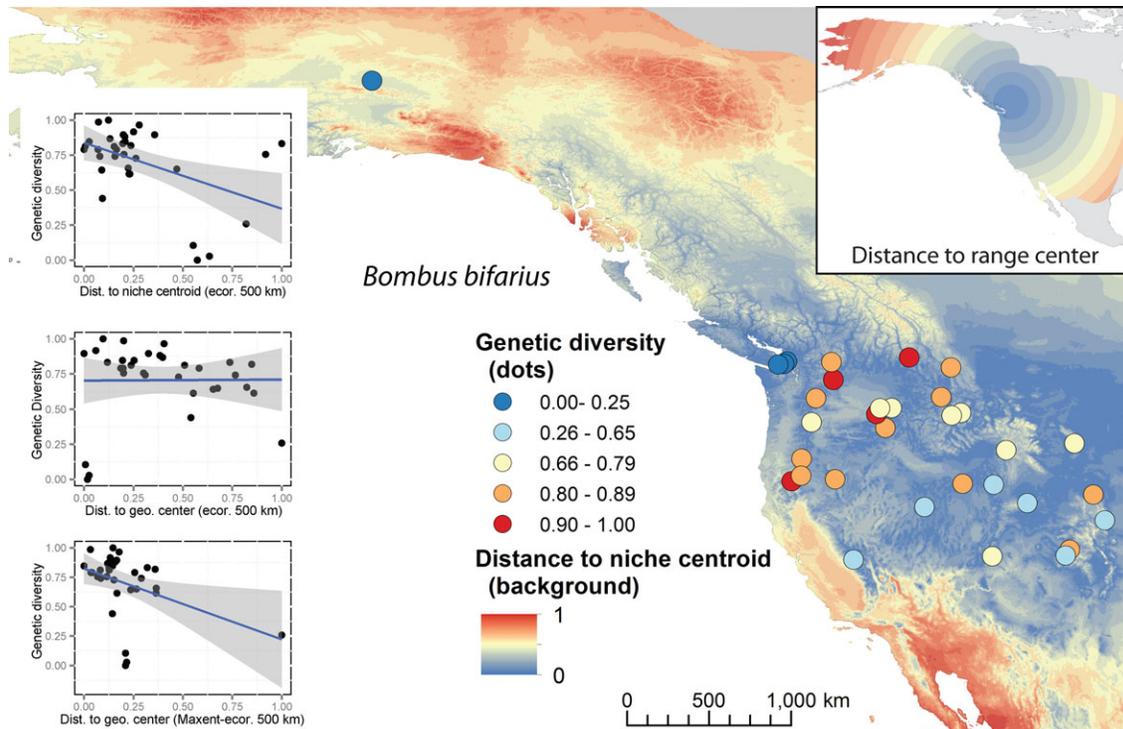
Figure 3. Relationships between genetic diversity and centrality in *Bombus bifarius*. Points indicate populations sampled, with warmness of colors symbolizing higher genetic diversity; the map is colored as distance to niche centroid, with warmer colors representing further distance from niche centroid. Top right inset shows the distance to the range center (based on 500 km buffer around ecoregions). Left panel shows linear regressions between genetic diversity and distance to niche or geographic centroids.

some situations likely led to the pattern where distance to geographic range center was a predictor of genetic diversity only when it agreed in sign with environmental distance (supporting H_0 in Fig. 1) but showed no predictivity when environment and geography disagreed in sign (supporting H_A in Fig. 1). These results support the hypothesis that peripherality within the set of habitable conditions (ecological niche) represents an important determinant of geographic patterns in species' genetic variation.

Although we found consistent negative relationships between genetic diversity and ecological niche centrality, we do not imagine that environmental conditions alter levels of genetic variation in species directly. Rather, we envision a cascade of environmental impacts on population dynamics (e.g., effective population size, gene flow, population stability), leading to changes in genetic variation likely causing observed patterns (Kawecki 2008). Two recent studies identified negative relationships between relative abundances and distances to niche centroid (Martínez-Meyer et al. 2013) or environmental suitability (VanDerWal et al. 2009), which demonstrate part of the set of causal links that we envision.

Lower genetic diversity at the periphery of the set of suitable ecological niche conditions translates into lower potential for genetic differentiation and expansion beyond environmental conditions of a species' niche, where positive feedback with population density occurs (Antonovics et al. 2001; Barton 2001). In

consequence, persistence of locally adapted genotypes may be unachievable given lower population densities and incoming gene flow, resulting in long-term stabilizing selection on niche-related traits and consequent conservatism (Haldane 1956). On broader time scales, niche stability (or lack thereof) has been shown to impact geographic variation in population genetic diversity (Carnaval et al. 2009; Ortego et al. 2012); however, it would be difficult or impossible to measure the environmental suitability that individual populations experience through time.

It is interesting that, for many species, high levels of genetic diversity were observed in geographically distant populations. Interpreting this pattern in the context of historical and ecological evidence of species' dispersal capabilities and genetic diversity or structure, as many phylogeographic studies do, supports the hypothesis of a set of optimal conditions within which populations are more likely to survive and reproduce, with greater population stability and higher levels of genetic diversity.

Because we found a strong tendency toward greater statistical power as more populations (≥ 25) were sampled for a species, studies investigating these relationships based on fewer populations may simply have lacked statistical power to detect relationships. These results suggest that future phylogeographic studies should focus on sampling designs that incorporate not only large numbers of populations spread across geographic distributions
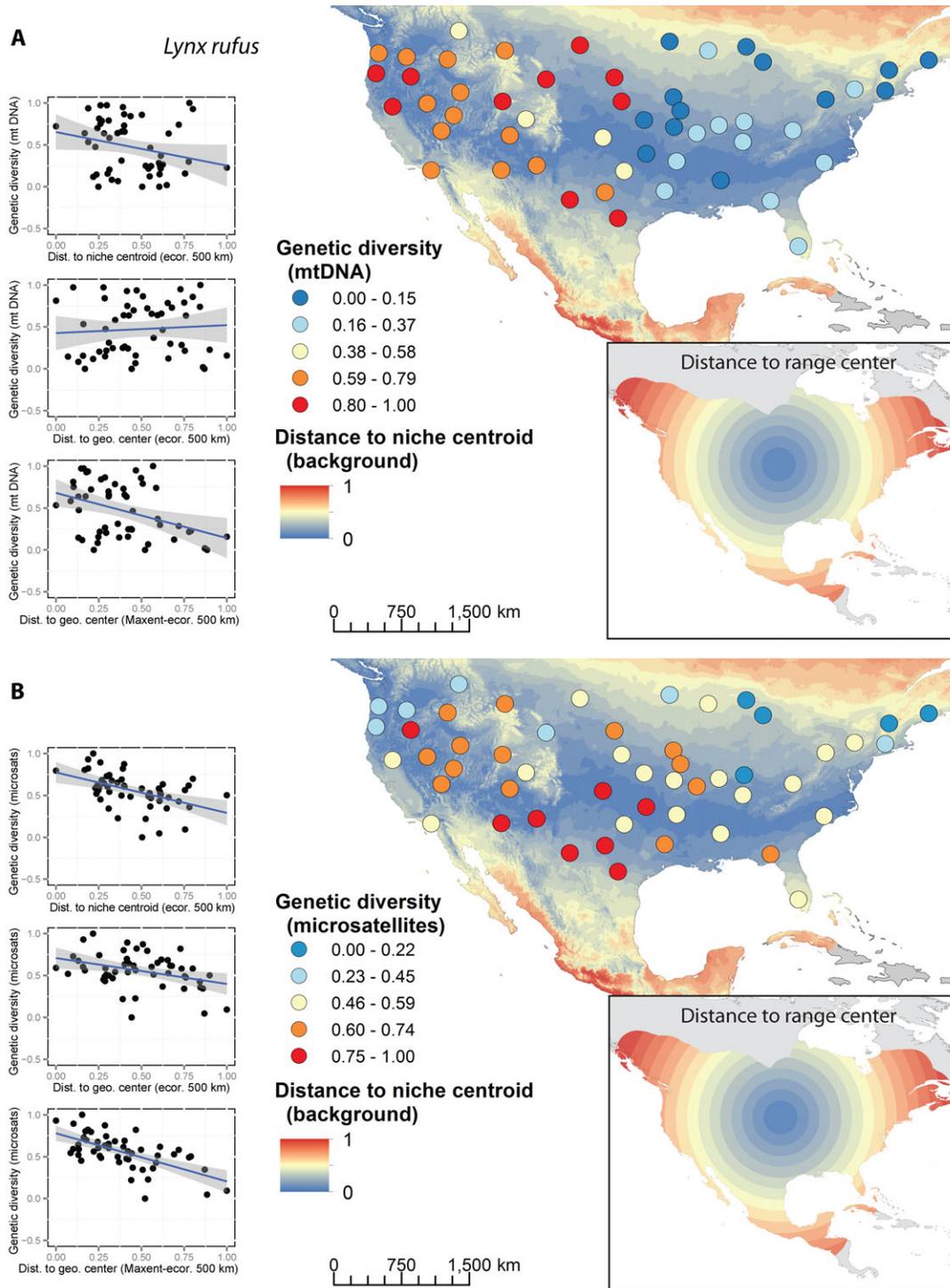
Figure 4. Relationships between genetic diversity and centrality in *Lynx rufus* for mitochondrial DNA (A) and microsatellites (B). Points indicate populations sampled, with warmness of colors symbolizing higher genetic diversity; the map is colored as distance to niche centroid, with warmer colors representing further distance from niche centroid. Bottom right inset shows the distance to the range center (500 km buffer around ecoregions). Left panel shows linear regressions between genetic diversity and distance to niche or geographic centroids.

Table 4. Results of generalized linear models using data from all species (*z*-standardized).

Dataset		*E* distance	*G* distance
500 km	All species	−0.475***	−0.161
	Consistent	−0.330*	−0.495**
	Mixed	−0.628**	0.229
ER + 200 km	All species	−0.460***	−0.247*
	Consistent	−0.287	−0.570***
	Mixed	−0.541**	−0.063
ER + 500 km	All species	−0.478***	−0.232*
	Consistent	−0.332*	−0.519***
	Mixed	−0.551***	−0.056

Values are contributions in the regression model of distance to niche centroid or geographic range center to explain genetic diversity. Regressions were performed for separate datasets where distance to geographic center and distance to niche center showed consistent or mixed patterns in sign of the slope (see Table 2).
Asterisks indicate significance at 0.05 (*), 0.01 (**), and 0.001 (***) levels. Training areas compared included 500 km = 500 km buffer around occurrence points, ER + 200 km = 200 km buffer around terrestrial ecoregions, and ER + 500 km = 500 km buffer around terrestrial ecoregions.

of species, but should also represent the different environments where populations occur across species' geographic ranges. Better still, empirical studies designed explicitly to test relative effects of environmental versus geographic centrality should be developed.

Finally, as an important component of biodiversity, as well as a strong predictor of fitness (Reed and Frankham 2003), genetic diversity is an important conservation target (Primack 2006).

Table 5. Relationship between number of populations and *P* values of the relationships between distance to niche centroid and distance to geographic center.

	R^2	*P*-value
Environmental distance		
500 km	0.2009	0.0037
ER + 200 km	0.2029	0.0035
ER + 500 km	0.1899	0.0049
Geographic distance		
500 km	0.0006	0.8747
ER + 200 km	0.0004	0.8945
ER + 500 km	0.0001	0.9412
MCP	0.0106	0.5269
500 km (Mx)	0.0886	0.0621
ER + 200 km (Mx)	0.0823	0.0726
ER + 500 km (Mx)	0.0800	0.0771

Training areas compared included 500 km = 500 km buffer around occurrence points, ER + 200 km = 200 km buffer around terrestrial ecoregions, and ER + 500 km = 500 km buffer around terrestrial ecoregions.
MCP, minimum convex polygon; Mx, centroid estimated from Maxent prediction.

As such, the capacity to predict genetic diversity across species' distributions may prove useful to conservation biologists. Phylogeographic studies have shown mixed results in anticipating genetic diversity patterns based on peripherality or centrality of populations (Eckert et al. 2008; Kawecki 2008; Moeller et al. 2011). Our results, in conjunction with studies focused on abundance (VanDerWal et al. 2009; Martínez-Meyer et al. 2013), suggest that a focus on environmental centrality, rather than geographic centrality, will provide greater insight into populations as foci of conservation initiatives. Preserving populations central in a species' niche (but not necessarily central in the geographic range) may protect populations with higher abundance and that maintain relatively higher genetic diversity than populations that are environmentally peripheral.

LITERATURE CITED

Alexander, M. P., and K. J. Burns. 2006. Intraspecific phylogeography and adaptive divergence in the White-headed Woodpecker. Condor 108:489–508.

Antonovics, J., T. J. Newman, and B. J. Best. 2001. Spatially explicit studies on the ecology and genetics of population margins. Pp. 91–116 *in* J. Silvertown and J. Antonovics, eds. Integrating ecology and evolution in a spatial context. Blackwell, Oxford.

Barrera-Guzmán, A. O., B. Mila, L. A. Sánchez-González, and A. G. Navarro-Sigüenza. 2012. Speciation in an avian complex endemic to the mountains of Middle America (*Ergaticus*, Ayes: Parulidae). Mol. Phylogenet. Evol. 62:907–920.

Barton, N. H. 2001. Adaptation at the edge of a species' range. Pp. 365–392 *in* J. Silvertown and J. Antonovics, eds. Integrating ecology and evolution in a spatial context. Blackwell, Oxford.

Barve, N., V. Barve, A. Jiménez-Valverde, A. Lira-Noriega, S. P. Maher, A. T. Peterson, J. Soberón, and F. Villalobos. 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecol. Model. 222:1810–1819.

Borenstein, M., L. V. Hedges, J. P. T. Higgins, and H. R. Rothstein. 2009. Introduction to meta-analysis. John Wiley and Sons, Chichester, U.K.

Bozinovic, F., P. Calosi, and J. I. Spicer. 2011. Physiological correlates of geographic range in animals. Annu. Rev. Ecol. Evol. Syst. 42:155–179.

Bridle, J. R., and T. H. Vines. 2007. Limits to evolution at range margins: when and why does adaptation fail? Trends Ecol. Evol. 22:140–147.

Brown, J. H. 1984. On the relationship between abundance and distribution of species. Am. Nat. 124, 255–279.

Brown, J. H., G. C. Stevens, and D. M. Kaufman. 1996. The geographic range: size, shape, boundaries, and internal structure. Annu. Rev. Ecol. Syst. 27:597–623.

Brussard, P. F. 1984. Geographic patterns and environmental gradients—the central—marginal model in Drosophila revisited. Annu. Rev. Ecol. Syst. 15:25–64.

Carnaval, A. C., M. J. Hickerson, C. F. B. Haddad, M. T. Rodrigues, and C. Moritz. 2009. Stability predicts genetic diversity in the Brazilian Atlantic forest hotspot. Science 323:785–789.

Chapman, A. D. 2005. Principles and methods of data cleaning—primary species and species-occurrence data, version 1.0. Global Biodiversity Information Facility, Copenhagen.

Chapman, J. R., S. Nakagawa, D. W. Coltman, J. Slates, and B. C. Sheldon. 2009. A quantitative review of heterozygosity-fitness correlations in animal populations. Mol. Ecol. 18:2746–2765.

Cook, R. D. 1977. Detection of influential observation in linear regression. Technometrics 19:15–18.

Cortés-Rodríguez, N., B. E. Hernández-Baños, A. G. Navarro-Sigüenza, A. T. Peterson, and J. García-Moreno. 2008. Phylogeography and population genetics of the amethyst-throated Hummingbird (*Lampornis amethystinus*). Mol. Phylogenet. Evol. 48:1–11.

Diniz-Filho, J. A. F., J. C. Nabout, L. M. Bini, T. N. Soares, M. Pires de Campos Telles, J. P. de Marco, and R. G. Collevatti. 2009. Niche modelling and landscape genetics of *Caryocar brasiliense* ("Pequi" tree: Caryocaraceae) in Brazilian Cerrado: an integrative approach for evaluating central-peripheral population patterns. Tree Genet. Genomes 5: 617–627.

Eckert, C. G., K. E. Samis, and S. C. Lougheed. 2008. Genetic variation across species' geographical ranges: the central-marginal hypothesis and beyond. Mol. Ecol. 17:1170–1188.

Ehrich, D., I. G. Alsos, and C. Brochmann. 2008. Where did the northern Peatland species survive the dry glacials: cloudberry (*Rubus chamaemorus*) as an example. J. Biogeogr. 35:801–814.

Eidesen, P. B., I. G. Alsos, M. Popp, O. Stensrud, J. Suda, and C. Brochmann. 2007a. Nuclear vs. plastid data: complex Pleistocene history of a circumpolar key species. Mol. Ecol. 16:3902–3925.

Eidesen, P. B., T. Carlsen, U. Molau, and C. Brochmann. 2007b. Repeatedly out of Beringia: *Cassiope tetragona* embraces the Arctic. J. Biogeogr. 34:1559–1574.

ESRI. 2011. ArcGIS desktop: release 10. Environmental Systems Research Institute, Redlands, CA.

Fortin, M. J., T. H. Keitt, B. A. Maurer, M. L. Taper, D. M. Kaufman, and T. M. Blackburn. 2005. Species' geographic ranges and distributional limits: pattern analysis and statistical issues. Oikos 108:7–17.

Galbreath, K. E., and J. A. Cook. 2004. Genetic consequences of Pleistocene glaciations for the tundra vole (*Microtus oeconomus*) in Beringia. Mol. Ecol. 13:135–148.

Galbreath, K. E., J. A. Cook, A. A. Eddingsaas, and E. G. DeChaine. 2011. Diversity and demography in Beringia: multilocus tests of paleodistribution models reveal the complex history of Arctic ground squirrels. Evolution 65:1879–1896.

Gao, Q. B., D. J. Zhang, Y. Z. Duan, F. Q. Zhang, Y. H. Li, P. C. Fu, and S. L. Chen. 2012. Intraspecific divergences of *Rhodiola alsia* (Crassulaceae) based on plastid DNA and internal transcribed spacer fragments. Bot. J. Linn. Soc. 168:204–215.

Garner, T. W. J., P. B. Pearman, and S. Angelone. 2004. Genetic diversity across a vertebrate species' range: a test of the central-peripheral hypothesis. Mol. Ecol. 13:1047–1053.

Gaston, K. J. 2003. The structure and dynamics of geographic ranges. Oxford Univ. Press, Inc., New York.

Grus, W. E., G. R. Graves, and T. C. Glenn. 2009. Geographic variation in the mitochondrial control region of Black-throated Blue Warblers (*Dendroica caerulescens*). Auk 126:198–210.

Haldane, J. B. S. 1956. The relation between density regulation and natural selection. Proc. R. Soc. B Biol. Sci. 145:306–308.

Hengeveld, R., and J. Haeck. 1982. The distribution of abundance. I. Measurements. J. Biogeogr. 9:303–316.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25:1965–1978.

Holt, R. D. 2003. On the evolutionary ecology of species' ranges. Evol. Ecol. Res. 5:159–178.

Holt, R. D., and R. Gomulkiewicz. 1997. The evolution of species' niches: a population dynamic perspective. Pp. 25–50 *in* H. Othmer, F. Adler, M. Lewis, and J. Dallon, eds. Case studies in mathematical modelling: ecology, physiology, and cell biology. Prentice Hall, Englewood Cliffs, NJ.

Holt, R. D., and T. H. Keitt. 2005. Species' borders: a unifying theme in ecology. Oikos 108:3–6.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harb. Symp. 22:415–427.

———. 1978. An introduction to population ecology. Yale Univ. Press, New Haven, CT.

Kawecki, T. J. 2008. Adaptation to marginal habitats. Annu. Rev. Ecol. Evol. Syst. 39:321–342.

Keller, S. R., M. S. Olson, S. Silim, W. Schroeder, and P. Tiffin. 2010. Genomic diversity, population structure, and migration following rapid range expansion in the Balsam Poplar, *Populus balsamifera*. Mol. Ecol. 19:1212–1226.

Kimura, M., S. M. Clegg, I. J. Lovette, K. R. Holder, D. J. Girman, B. Mila, P. Wade, and T. B. Smith. 2002. Phylogeographical approaches to assessing demographic connectivity between breeding and overwintering regions in a Nearctic-Neotropical warbler (*Wilsonia pusilla*). Mol. Ecol. 11:1605–1616.

Lack, J. B., R. S. Pfau, and G. M. Wilson. 2010. Demographic history and incomplete lineage sorting obscure population genetic structure of the Texas mouse (*Peromyscus attwateri*). J. Mamm. 91:314–325.

Leimu, R., P. Mutikainen, J. Koricheva, and M. Fischer. 2006. How general are positive relationships between plant population size, fitness, and genetic variation? J. Ecol. 94:942–952.

Li, X. C., H. Yin, K. Li, and X. Y. Gao. 2012. Population genetic structure and historical demography of the ground beetle *Pheropsophus jessoensis* from the Tsinling–Dabashan Mountains, central China based on mitochondrial DNA analysis. Zool. Sci. 29:238–246.

Lozier, J. D., J. P. Strange, I. J. Stewart, and S. A. Cameron. 2011. Patterns of range—wide genetic variation in six North American bumblebee (Apidae: *Bombus*) species. Mol. Ecol. 20:4870–4888.

Manthey, J. D., J. Klicka, and G. M. Spellman. 2011. Cryptic diversity in a widespread North American songbird: phylogeography of the Brown Creeper (*Certhia americana*). Mol. Phylogenet. Evol. 58:502–512.

Martínez-Meyer, E., D. Díaz-Porras, A. T. Peterson, and C. Yáñez-Arenas. 2013. Ecological niche structure and rangewide abundance patterns of species. Biol. Lett. 9. doi: 10.1098/rsbl.2012.0637.

McDonald, D. E., and S. R. Daniels. 2012. Phylogeography of the Cape velvet worm (Onychophora: *Peripatopsis capensis*) reveals the impact of Pliocene/Pleistocene climatic oscillations on Afromontane forest in the Western Cape, South Africa. J. Evol. Biol. 25:824–835.

Moeller, D. A., M. A. Geber, and P. Tiffin. 2011. Population genetics and the evolution of geographic range limits in an annual plant. Am. Nat. 178:S44–S61.

Olson, D. M., E. Dinerstein, E. D. Wikramanayake, N. D. Burgess, G. V. N. Powell, E. C. Underwood, J. A. D'Amico, I. Itoua, H. E. Strand, J. C. Morrison, et al. 2001. Terrestrial ecoregions of the world: a new map of life on Earth. Bioscience 51:933–938.

Oomen, R. A., M. W. Reudink, J. J. Nocera, C. M. Somers, M. C. Green, and C. J. Kyle. 2011. Mitochondrial evidence for panmixia despite perceived barriers to gene flow in a widely distributed waterbird. J. Hered. 102:584–592.

Ortego, J., E. C. Riordan, P. F. Gugger, and V. L. Sork. 2012. Influence of environmental heterogeneity on genetic diversity and structure in an endemic southern Californian oak. Mol. Ecol. 21:3210–3223.

Paul, J. R., S. N. Sheth, and A. L. Angert. 2011. Quantifying the impact of gene flow on phenotype-environment mismatch: a demonstration with the scarlet monkeyflower *Mimulus cardinalis*. Am. Nat. 178:S62–S79.

Pérez-Alquicira, J., F. E. Molina-Freaner, D. Piñero, S. G. Weller, E. Martínez-Meyer, J. Rozas, and C. A. Domínguez. 2010. The role of historical factors and natural selection in the evolution of breeding systems of *Oxalis alpina* in the Sonoran desert "Sky Islands." J. Evol. Biol. 23:2163–2175.

Peterson, A. T., M. Papeş, and J. Soberón. 2008. Rethinking receiver operating characteristic analysis applications in ecological niche modeling. Ecol. Model. 213:63–72.

Peterson, A. T., J. Soberoʹn, R. G. Pearson, R. P. Anderson, E. Martiʹnez-Meyer, M. Nakamura, and M. B. Arauʹjo. 2011. Ecological niches and geographic distributions. Princeton Univ. Press, Princeton, NJ.

Pfeifer, M., B. Schatz, F. X. Pico, N. G. Passalacqua, M. F. Fay, P. D. Carey, and F. Jeltsch. 2009. Phylogeography and genetic structure of the orchid *Himantoglossum hircinum* (L.) Spreng. across its European central–marginal gradient. J. Biogeogr. 36:2353–2365.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190:231–259.

Primack, R. 2006. Essentials of conservation biology. Sinauer, Sunderland, MA.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. Am. Nat. 132:652–661.

Pulliam, R. 2000. On the relationship between niche and distribution. *Ecol. Lett.* 3:349–361.

R Development Core Team. 2012. R: a language for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramos, A. C. S., J. P. Lemos-Filho, R. A. Ribeiro, F. R. Santos, and M. B. Lovato. 2007. Phylogeography of the tree *Hymenaea stigonocarpa* (Fabaceae: Caesalpinioideae) and the influence of Quaternary climate changes in the Brazilian cerrado. Ann. Bot. Lond. 100:1219–1228.

Rapoport, E. H. 1982. Areography: geographical strategies of species. Pergamon Press, Oxford, U.K.

Rebernig, C. A., G. M. Schneeweiss, K. E. Bardy, P. Schonswetter, J. L. Villasenor, R. Obermayer, T. F. Stuessy, and H. Weiss-Schneeweiss. 2010. Multiple Pleistocene refugia and Holocene range expansion of an abundant southwestern American desert plant species (*Melampodium leucanthum*, Asteraceae). Mol. Ecol. 19:3421–3443.

Reding, D. M., A. M. Bronikowski, W. E. Johnson, and W. R. Clark. 2012. Pleistocene and ecological effects on continental-scale genetic differentiation in the bobcat (*Lynx rufus*). Mol. Ecol. 21:3078–3093.

Reed, D. H., and R. Frankham. 2003. Correlation between fitness and genetic diversity. Conserv. Biol. 17:230–237.

Ribeiro, R. A., J. P. Lemos, A. C. S. Ramos, and M. B. Lovato. 2011. Phylogeography of the endangered rosewood *Dalbergia nigra* (Fabaceae): insights into the evolutionary history and conservation of the Brazilian Atlantic Forest. Heredity 106:46–57.

Sagarin, R. D., and S. D. Gaines. 2002. The 'abundant centre' distribution: to what extent is it a biogeographical rule? Ecol. Lett. 5:137–147.

Segovia, R. A., M. F. Pérez, and L. F. Hinojosa. 2012. Genetic evidence for glacial refugia of the temperate tree *Eucryphia cordifolia* (Cunoniaceae) in southern South America. Am. J. Bot. 99:121–129.

Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. Evolution and ecology of species range limits. Annu. Rev. Ecol. Evol. Syst. 40:415–436.

Sgariglia, E. A., and K. J. Burns. 2003. Phylogeography of the California Thrasher (*Toxostoma redivivum*) based on nested-clade analysis of mitochondrial-DNA variation. Auk 120:346–361.

Smith, B.T., P. Escalante, B. E. Hernández Baños, A. G. Navarro-Sigüenza, S. Rohwer, and J. Klicka. 2011. The role of historical and contemporary processes on phylogeographic structure and genetic diversity in the Northern Cardinal, *Cardinalis cardinalis*. BMC Evol. Biol. 11:136.

Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. Ecol. Lett. 10:1115–1123.

———. 2010. Niche and area of distribution modeling: a population ecology perspective. Ecography 33:159–167.

Spellman, G. M., and J. Klicka. 2006. Testing hypotheses of Pleistocene population history using coalescent simulations: phylogeography of the Pygmy Nuthatch (*Sitta pygmaea*). Proc. R. Soc. B Biol. Sci. 273:3057–3063.

———. 2007. Phylogeography of the White-Breasted Nuthatch (*Sitta carolinensis*): diversification in North American pine and oak woodlands. Mol. Ecol. 16:1729–1740.

Spellman, G. M., B. Riddle, and J. Klicka. 2007. Phylogeography of the Mountain Chickadee (*Poecile gambeli*): diversification, introgression, and expansion in response to Quaternary climate change. Mol. Ecol. 16:1055–1068.

Temunovic, M., J. Franjic, Z. Satovic, M. Grgurev, N. Frascaria-Lacoste, and J. F. Fernández-Manjarres. 2012. Environmental heterogeneity explains the genetic structure of continental and Mediterranean populations of *Fraxinus angustifolia* Vahl. PloS ONE 7:e42764.

Udvardy, M. D. F. 1969. Dynamic zoogeography. Van Nostrand Reinhold Company, New York.

VanDerWal, J., L. P. Shoo, C. N. Johnson, and S. E. Williams. 2009. Abundance and the environmental niche: environmental suitability estimated from niche models predicts the upper limit of local abundance. Am. Nat. 174:282–291.

Vucetich, J. A., and T. A. Waite. 2003. Spatial patterns of demography and genetic processes across the species' range: null hypotheses for landscape conservation genetics. Conserv. Genet. 4:639–645.

Wagner, V., W. Durka, and I. Hensen. 2011. Increased genetic differentiation but no reduced genetic diversity in peripheral vs. central populations of a steppe grass. Am. J. Bot. 98:1173–1179.

Warren, D. L., R. E. Glor, and M. Turelli. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62:2868–2883.

———. 2010. ENMTools: a toolbox for comparative studies of environmental niche models. Ecography 33:607–611.

Weksler, M., H. C. Lanier, and L. E. Olson. 2010. Eastern Beringian biogeography: historical and spatial genetic structure of singing voles in Alaska. J. Biogeogr. 37:1414–1431.

Westergaard, K. B., I. G. Alsos, M. Popp, T. Engelskjon, K. I. Flatberg, and C. Brochmann. 2011. Glacial survival may matter after all: nunatak signatures in the rare European populations of two west-arctic species. Mol. Ecol. 20:376–393.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Appendix S1. Lira-Noriega and Manthey.