

LATITUDINAL VARIATION IN GENETIC DIVERGENCE OF POPULATIONS AND THE POTENTIAL FOR FUTURE SPECIATION

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Abstract.—The increase in biological diversity with decreasing latitude is widely appreciated but the cause of the pattern is unknown. This pattern reflects latitudinal variation in both the origin of new species (cladogenesis) and the number of species that coexist. Here we address latitudinal variation in species origination, by examining population genetic processes that influence speciation. Previous data suggest a greater number of speciation events at lower latitudes. If speciation events occur more frequently at lower latitudes, we predicted that genetic divergence among populations within species, an important component of cladogenesis, should be greater among lower latitude populations. We tested this prediction using within-species patterns of mtDNA variation across 60 vertebrate species that collectively spanned six continents, two oceans, and 119 degrees latitude. We found greater genetic divergence of populations, controlling for geographic distance, at lower latitudes within species. This pattern remained statistically significant after removing populations that occur in localities previously covered by continental glaciers during the last glaciation. Results suggest that lower latitude populations within species exhibit greater evolutionary independence, increasing the likelihood that mutation, recombination, selection, and/or drift will lead to divergence of traits important for reproductive isolation and speciation. Results are consistent with a greater influence of seasonality, reduced energy, and/or glacial (Milankovitch) cycles acting on higher latitude populations, and represent one of the few tests of predictions of latitudinal variation in speciation rates using population genetic data.

Key words.—Genetic divergence, glaciation, latitudinal variation, speciation, species richness.

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The spectacular increase in biological diversity from polar to tropical regions is well known across a diverse array of taxa and environments (von Humboldt 1808; Wallace 1878; Dobzhansky 1950; Fischer 1960; Pianka 1966; Rohde 1992; Rosenzweig 1995; Gaston 2000; Schemske 2002; Willig et al. 2003). This latitudinal gradient in richness is present across taxonomic levels (Fischer 1960; Simpson 1964; Stehli et al. 1969; Willig et al. 2003), has been found in the fossil record as far back as 270 million years before present (BP) (Stehli et al. 1969), and reforms after decimation by mass extinction events (Stehli et al. 1969; Hecht and Agan 1972). Despite the robustness of latitudinal variation in taxonomic richness, the gradient remains one of the least understood patterns in biology (Rohde 1992; Futuyma 1998; Gaston 2000; Schemske 2002; Willig et al. 2003). The many hypotheses for the origin of this global pattern address two general themes: (1) the origin of high tropical species richness and (2) the ability of more species to coexist in the tropics (cf. Terborgh 1992), or in other words, the paucity of species at high latitudes and the inability of many species to coexist at higher latitudes. Here we focus on (1) the origins of variation in species richness, examining the hypothesis that speciation events occur more frequently at lower latitudes (i.e., lower latitudes have more speciation events per species, per unit time). We address this hypothesis by testing the prediction that population divergence, an important component of cladogenesis, varies latitudinally within species.

Allopatric speciation is the major mode of speciation for vertebrates and other taxa (Mayr 1963; Futuyma 1998; Barraclough and Vogler 2000; Turelli et al. 2001; see also Whitaker et al. 2003). If species originate at a greater frequency

moving from the poles towards the equator, we predicted, a priori, that populations within species should show greater genetic divergence at lower latitudes because genetic divergence is an important component of allopatric speciation (Mayr 1963; Slatkin 1987; Futuyma 1998; Barraclough and Vogler 2000; Turelli et al. 2001). We examined genetic divergence of populations using mtDNA data from 62 vertebrate taxa (60 species), sampling a diverse array of taxonomic classes (birds, fishes, mammals, and herps) (Table 1), environments (marine, freshwater, and terrestrial), and continents and oceans, across a broad span of latitudes (populations spanning 45°S–74°N). We used mtDNA divergence estimates as an index of the relative evolutionary independence of populations within species, recognizing that the mitochondrial genome may play no direct role in speciation. Our explicit assumption is that the evolutionary independence of populations, as measured by mtDNA divergence, positively covaries with the likelihood of future speciation within a species. Support for this assumption comes from ring species, where mtDNA divergence of populations within a species positively covaries with divergence in phenotypic traits associated with reproductive isolation (Wake et al. 1986; Moritz et al. 1992; Irwin et al. 2001). Recognizing this assumption, we used mtDNA population genetic data to test the prediction that lower latitude populations within species exhibit greater genetic isolation, after controlling for geographic separation.

MATERIALS AND METHODS

We reviewed studies on the population genetics of vertebrates that examined 200 or more base pairs of mtDNA, using either sequences or haplotypes. We limited our analysis to

studies with at least three individuals per population and four populations per species, spanning at least eight degrees of latitude, where results showed some genetic variance among populations, and where the necessary genetic data were publicly available. A latitudinal span of eight degrees was selected as a minimum because the latitudinal gradient in species richness is evident along latitudinal transects at least as small as eight degrees (e.g., Sharrock 1976 and see Results). We examined mtDNA studies because the great majority (80%) of phylogeographic studies examine mtDNA (Avice 2000). We excluded studies that described human-induced bottlenecks or reintroductions, and excluded samples taken from captive animals or hatcheries that could obscure natural population genetic patterns. Within studies, we excluded island populations from analyses. For migratory species, we examined only breeding populations.

We only examined populations occurring on the same continents or within the same oceans (except for contiguous North and South Americas). In two cases (green turtle and harbor seal), species were sampled from the Atlantic and Pacific Oceans, each represented by many populations. In these cases, populations in different oceans were treated as independent taxa in the analyses. We used either pairwise genetic divergence data presented in each paper, or genetic data obtainable from the paper or Genbank, to calculate pairwise genetic divergence (F_{ST} , p_{xy} , see Table 1) among populations using the Arlequin software package (Schneider et al. 2000). Divergence parameters were the same for all populations within species, and thus our within-species comparisons were appropriate and not influenced by variation in the parameters used across studies. All parameter estimates controlled for within-population levels of genetic variation when calculating among-population differentiation. For 24 taxa, nucleotide divergence [$p_{xy(ner)}$] was calculated where $p_{xy(ner)} = p_{xy} - 0.5(p_x + p_y)$ (following Avice and Walker 1998; Avice et al. 1998). For species using restriction-fragment length polymorphisms (RFLPs), or where both sequence data and the alignment used by the authors were available, we calculated F_{ST} based on a haplotype distance matrix using the Arlequin software package (Schneider et al. 2000). For details of other metrics used, please see original references in the Appendix available online at: <http://dx.doi.org/10.1554/03-611.1.s1>.

For each study that met our criteria, we separated populations into high and low latitude groups by dividing the latitudinal span of the populations by two (Fig. 1). In cases in which only one population was represented in high or low latitudes, the lone population was compared to the population closest in latitude, with all other populations compared among each other in the opposite latitudinal group. After splitting populations into two latitudinal groups, we calculated pairwise estimates of genetic divergence [(genetic distance) ÷ (geographic distance between populations in km)], and calculated mean values for low and high latitude groups within each species. We tested our hypothesis that genetic divergence of populations (controlling for geographic distance) is greater at lower latitudes, by comparing mean genetic distance per kilometer between high and low latitude groups ($n = 62$ taxa). Thus, comparisons were effectively made within species using data from the same study, which

helped to control for variation in ecology, mating systems, taxonomy, and different methods of sampling that can confound across species and across study comparisons.

We tested the statistical support for our hypothesis (that lower latitude populations show greater genetic divergence per kilometer) using a type-III analysis of variance (ANOVA), with latitudinal block (high or low) and species as factors. The response variable, genetic distance per kilometer, was cube root transformed prior to analysis to normalize the distribution of data. To address the potential role of glacial ice cover in our test of latitudinal variation in population divergence, we ran a second analysis excluding all populations that now occur in areas that were covered by ice sheets during the last 22,000 years (Clark and Mix 2002). This reduced our sample size to 47, and reduced the number of populations for some of the taxa. We ran the same analyses described above for this subset of taxa, using the exact same methodology. Finally, we addressed whether the mean latitude of the sampled species influenced the patterns that we found using a regression, with the standardized difference between low and high latitude groups (i.e., [(low genetic distance/km – high genetic distance/km) / ((low genetic distance/km + high genetic distance/km) / 2)]) as the dependent variable, and mean latitude of populations (Table 1) as the independent variable.

RESULTS

We found greater genetic divergence of populations at lower latitudes within species ($F = 11.0$, $df = 1,61$, one-tailed $P = 0.0008$)—a pattern that was evident in 45 of the 62 (73%) taxa examined. Greater genetic divergence per kilometer at lower latitudes was not driven by bias in population sampling, as geographic distance between populations (km) did not differ between high and low latitude groups ($F = 0.02$, $df = 1,61$, $P = 0.88$), while genetic divergence alone was significantly higher among low latitude populations ($F = 11.2$, $df = 1,61$, one-tailed $P = 0.0007$).

Greater genetic divergence per kilometer at lower latitudes was not the sole result of glacial ice during the most recent glaciation, because the pattern remained after removing all populations that occupied areas covered by continental ice sheets at the last glacial maximum ($F = 5.2$, $df = 1,46$, one-tailed $P = 0.014$). Populations examined in our analysis were distributed from the equator to 44.5°S in the southern hemisphere, and 74.3°N in the northern hemisphere, with mean latitude of populations within taxa ranging from 39.0°S to 66.2°N (Table 1). Despite this broad latitudinal variation, there was no significant relationship between mean latitude of the taxon examined and the difference between high and low latitude groups (linear regression, slope = +0.012, $t = 1.5$, $P = 0.15$). Overall, the pattern of greater genetic divergence per kilometer in lower latitude populations occurred in 60% of exclusively southern hemisphere taxa ($n = 10$), 79% of exclusively northern hemisphere taxa ($n = 43$), and 58% of taxa that occurred in both hemispheres ($n = 19$).

DISCUSSION

The majority of vertebrate taxa examined in this study (73%) showed greater genetic divergence per kilometer

TABLE 1. Summary of results for vertebrate species examined in this study.

Species	Common Name	Continent /Ocean ^a	Environment ^b	Taxa ^c	Hemisphere ^d	Mean latitude ^e	Lat. span	No. of pops.
<i>Acanthochromis polyacanthus</i>	Spiny damselfish	PO	m	f	S	18.0	9.4	12
<i>Acanthurus bahianus</i>	Ocean surgeon	AO	m	f	B	15.4	19.0	6
<i>Acanthurus coeruleus</i>	Atlantic blue tang	AO	m	f	B	14.5	19.0	4
<i>Acrocephalus arundinaceus</i>	Great reed warbler	EU	t	b	N	50.1	21.0	6
<i>Agama atra</i>	Southern rock agama	AF	t	m	S	29.9	8.4	8
<i>Alca torda</i>	Razorbill	AO	m	b	N	60.4	15.0	5
<i>Alcelaphus buselaphus</i>	Hartebeest	AF	t	m	B	7.5	21.9	10
<i>Ambystoma maculatum</i>	Spotted salamander	NA	t	a	N	37.8	8.8	22
<i>Ammodramus savannarum</i>	Grasshopper sparrow	NA	t	b	N	35.1	14.3	5
<i>Aulostomus strigosus</i>	Atlantic trumpfish	AO	m	f	B	9.1	20.5	5
<i>Balaenoptera physalus</i>	Fin whale	AO	m	m	N	51.0	28.5	5
<i>Barbus barbus</i>	Barbel	EU	f	f	N	47.1	10.5	19
<i>Branta canadensis</i>	Canada goose	NA	t/f	b	N	53.7	25.3	7
<i>Bufo marinus</i>	Marine toad	NA/SA	t	a	N	10.8	11.7	7
<i>Calidris alpina</i>	Dunlin	EU	t	b	N	66.2	18.3	8
<i>Caretta caretta</i>	Loggerhead turtle	AO	m	r	B	27.4	21.8	9
<i>Chelonia mydas</i> -Atlantic	Green turtle	AO	m	r	B	9.4	35.2	8
<i>Chelonia mydas</i> -Pacific	Green turtle	PO	m	r	B	4.6	44.6	5
<i>Connochaetes taurinus</i>	Wildebeest	AF	t	m	S	11.0	23.0	10
<i>Coregonus artedii</i>	Lake Cisco	NA	m/f	f	N	55.4	8.5	7
<i>Cottus gobio</i>	Bullhead	EU	f	f	N	60.7	15.2	12
<i>Damaliscus lunatus</i>	Topi	AF	t	m	S	6.6	17.9	5
<i>Dendroica discolor</i>	Prairie warbler	NA	t	b	N	34.2	14.5	6
<i>Dendroica petechia</i>	Yellow warbler	NA	t	b	N	50.4	20.5	6
<i>Leuciscus cephalus</i>	Chub	EU	f	f	N	51.2	20.5	20
<i>Macropus rufus</i>	Red kangaroo	AU	t	m	S	22.5	11.5	6
<i>Malaclemys terrapin</i>	Diamondback terrapin	NA/AO	m	r	N	31.4	9.6	6
<i>Micropterus salmoides</i>	Largemouth bass	NA	f	f	N	35.1	16.3	6
<i>Microstomus pacificus</i>	Dover sole	PO	m	f	N	41.0	25.3	6
<i>Microtus pennsylvanicus</i>	Meadow vole	NA	t	m	N	47.9	15.2	6
<i>Nemadactylus macropterus</i>	Jackass morwong	PO	m	f	S	39.0	12.5	9
<i>Odocoileus virginianus</i>	White-tailed deer	NA	t	m	N	30.2	8.0	11
<i>Odontesthes argentinensis</i>	Silverside	SA	m	f	S	34.4	13.2	6
<i>Oncorhynchus kisutch</i>	Coho salmon	NA	f/m	f	N	52.2	25.5	17
<i>Paralabrax maculatofasciatus</i>	Spotted sand bass	PO	m	f	N	29.0	8.7	5
<i>Passerella iliaca</i>	Fox sparrow	NA	t	b	N	48.0	31.6	31
<i>Perca fluviatilis</i>	European perch	EU	f	f	N	53.6	28.4	40
<i>Phoca vitulina</i> -Atlantic	Harbor seal	AO	m	m	N	54.9	21.1	14
<i>Phoca vitulina</i> -Pacific	Harbor seal	PO	m	m	N	44.3	24.8	7
<i>Phocoena phocoena</i>	Harbour porpoise	AO	m	m	N	50.8	22.0	4
<i>Poecile carolinensis</i>	Carolina chickadee	NA	t	b	N	34.5	8.9	6
<i>Pomatostomus temporalis</i>	Grey-crowned babbler	AU	t	b	S	24.8	20.3	4
<i>Potamorhaphis guianensis</i>	Needlefish	SA	f	f	B	1.9	10.4	5
<i>Procavia capensis</i>	Rock hyrax	AF	t	m	S	28.5	12.3	9
<i>Salmo salar</i>	Atlantic salmon	EU	f/m	f	N	60.0	27.4	37
<i>Salmo trutta</i>	Brown trout	EU	f	f	N	45.3	18.4	12
<i>Sciurus aberti</i>	Tassel-eared squirrel	NA	t	m	N	35.4	10.1	15
<i>Sebastes helvomaculatus</i>	Rosethorn rockfish	PO	m	f	N	50.1	20.4	5
<i>Sebastolobus alascanus</i>	Shortspine thornyhead	PO	m	f	N	40.4	27.4	7
<i>Sebastolobus altivelis</i>	Longspine thornyhead	PO	m	f	N	37.2	10.6	5
<i>Sorex ornatus</i>	Ornate shrew	NA	t	m	N	34.4	16.8	17
<i>Sternotherus minor</i>	Musk turtle	NA	f	r	N	32.7	8.1	9
<i>Sternotherus odoratus</i>	Stinkpot turtle	NA	f	r	N	33.4	9.0	13
<i>Strix occidentalis</i>	Spotted owl	NA	t	b	N	38.1	14.8	12
<i>Syncerus caffer</i>	African buffalo	AF	t	m	B	4.9	21.8	9
<i>Thymallus arcticus</i>	Arctic grayling	NA	f	f	N	57.0	19.0	5
<i>Trichechus manatus</i>	West Indian manatee	NA/SA	m/f	m	N	15.1	21.5	7
<i>Uria aalge</i>	Common murre	AO	m	b	N	57.2	25.1	4
<i>Ursus americanus</i>	Black bear	NA	t	m	N	49.3	25.7	8
<i>Wilsonia pusilla</i>	Wilson's warbler	NA	t	b	N	45.1	27.3	13
<i>Xenopus laevis</i>	African clawed frog	AF	f	a	S	29.5	10.7	10
<i>Xerobates agassizi</i>	Desert tortoise	NA	t	r	N	33.1	9.9	8

^a AF, Africa; AO, Atlantic Ocean; AU, Australia; EU, Eurasia; NA, North America; PO, Pacific Ocean; SA, South America.

^b f, freshwater; m, marine; t, terrestrial.

^c a, amphibian; b, bird; f, fish; m, mammal; r, reptile.

^d N, north; S, south; B, both.

^e Mean latitude of all populations examined in this study.

^f Metric for genetic divergence of populations; $F_{ST}^1 = F_{ST}$ estimated by REAP (McElroy et al. 1991); $F_{ST}^2 = F_{ST}$ estimated by arlequin (Schneider et al. 2000) or equivalent (Φ_{ST} ; Excoffier et al. 1992); $F_{ST}^3 = F_{ST}$ estimated by DNASP (Rozas and Rozas 1997); $p_{xy} = p_{xy} - 0.5(p_x + p_y)$; see Materials and Methods or original references for further details.

^g Mean [population genetic divergence/distance (km)] between populations for high and low latitude populations; see Materials and Methods for details.

^h +, taxa with increased genetic differentiation per kilometer at lower latitudes.

ⁱ References are listed in the Appendix available online at: <http://dx.doi.org/10.1554/03-611.1.s1>.

TABLE 1. Extended.

No. of individuals	Divergence metric ^f	Divergence per km-high latitude ^g	Divergence per km-low latitude ^g	Pattern ^h	Reference ⁱ
126	F_{ST}^3	2.6×10^{-3}	4.4×10^{-3}	+	Planes et al. 2001
112	F_{ST}^2	7.5×10^{-6}	1.0×10^{-4}	+	Rocha et al. 2002
82	F_{ST}^2	1.5×10^{-6}	2.6×10^{-5}	+	Rocha et al. 2002
93	F_{ST}^2	3.1×10^{-5}	2.3×10^{-4}	+	Bensch and Hasselquist 1999
30	F_{ST}^2	2.1×10^{-3}	2.4×10^{-3}	+	Matthee and Flemming 2002
123	d_A	1.1×10^{-5}	0	-	Moum and Árnason 2001
125	F_{ST}^1	7.8×10^{-4}	7.7×10^{-4}	-	Arctander et al. 1999
258	F_{ST}^2	1.1×10^{-3}	2.1×10^{-3}	+	Phillips 1994
171	F_{ST}^2	1.3×10^{-5}	8.2×10^{-5}	+	Bulgin et al. 2003
90	p_{xy}	0	5.7×10^{-5}	+	Bowen et al. 2001
237	F_{ST}^1	0	3.6×10^{-6}	+	Bérubé et al. 1998
73	p_{xy}	5.2×10^{-4}	7.2×10^{-4}	+	Kotlík and Berrebi 2001
52	p_{xy}	2.4×10^{-7}	2.4×10^{-6}	+	Van Wagner and Baker 1990
27	p_{xy}	9.0×10^{-4}	7.4×10^{-4}	-	Slade and Moritz 1998
95	F_{ST}^2	5.5×10^{-5}	1.6×10^{-4}	+	Wenink et al. 1996
228	F_{ST}^2	5.7×10^{-4}	1.7×10^{-4}	-	Encalada et al. 1998
137	p_{xy}	3.0×10^{-4}	2.4×10^{-4}	-	Bowen et al. 1992
75	p_{xy}	3.8×10^{-7}	9.4×10^{-7}	+	Bowen et al. 1992
121	F_{ST}^1	4.3×10^{-4}	4.6×10^{-4}	+	Arctander et al. 1999
139	p_{xy}	8.9×10^{-7}	1.6×10^{-6}	+	Bernatchez and Dodson 1990
45	F_{ST}^2	0	3.9×10^{-3}	+	Kontula and Väinölä 2001
59	F_{ST}^1	4.9×10^{-4}	2.4×10^{-4}	-	Arctander et al. 1999
61	F_{ST}^2	2.5×10^{-5}	3.1×10^{-4}	+	Buerkle 1999
124	\hat{g}_{ST}	1.4×10^{-5}	5.2×10^{-5}	+	Milot et al. 2000
154	F_{ST}^2	9.3×10^{-4}	7.1×10^{-4}	-	Durand et al. 1999
27	p_{xy}	5.9×10^{-7}	7.4×10^{-6}	+	Clegg et al. 1998
41	p_{xy}	0	2.3×10^{-6}	+	Lamb and Avise 1992
60	D_{xy}	4.9×10^{-6}	6.6×10^{-5}	+	Nedbal and Philipp 1994
112	D_{xy}	7.0×10^{-7}	2.0×10^{-6}	+	Stepien 1999
74	p_{xy}	4.6×10^{-5}	6.2×10^{-5}	+	Plante et al. 1989
>166	D_{xy}	1.6×10^{-4}	2.5×10^{-5}	-	Grewe et al. 1994
102	F_{ST}^2	1.8×10^{-3}	2.8×10^{-3}	+	Ellsworth et al. 1994
196	F_{ST}^2	6.8×10^{-5}	2.7×10^{-4}	+	Beheregaray and Sunnucks 2001
311	F_{ST}^2	6.8×10^{-5}	3.8×10^{-4}	+	Smith et al. 2001
63	F_{ST}^2	1.7×10^{-3}	1.5×10^{-3}	-	Stepien et al. 2001
253	F_{ST}^2	6.2×10^{-4}	6.8×10^{-4}	+	Zink 1994
386	F_{ST}^2	6.0×10^{-4}	5.5×10^{-4}	-	Nesbø et al. 1999
176	p_{xy}	2.3×10^{-6}	2.4×10^{-6}	+	Stanley et al. 1996
50	p_{xy}	3.9×10^{-6}	2.1×10^{-6}	-	Stanley et al. 1996
212	F_{ST}^2	0	7.0×10^{-5}	+	Rosel et al. 1999
52	p_{xy}	1.8×10^{-5}	2.2×10^{-5}	+	Gill et al. 1993
34	p_{xy}	1.7×10^{-5}	2.6×10^{-7}	-	Edwards and Wilson 1990
36	p_{xy}	2.4×10^{-4}	4.5×10^{-5}	-	Lovejoy and Araújo 2000
54	D_{xy}	1.7×10^{-5}	7.8×10^{-5}	+	Prinsloo and Robinson 1992
1625	F_{ST}^2	8.7×10^{-4}	1.4×10^{-3}	+	Nilsson et al. 2001
87	D_{xy}	0	2.2×10^{-5}	+	Apostolidis et al. 1997
86	p_{xy}	2.9×10^{-4}	4.6×10^{-4}	+	Lamb et al. 1997
88	F_{ST}^1	6.7×10^{-5}	2.2×10^{-5}	-	Rocha-Olivares and Vetter 1999
93	F_{ST}^2	7.9×10^{-6}	1.5×10^{-4}	+	Stepien et al. 2000
55	F_{ST}^2	4.8×10^{-5}	1.3×10^{-3}	+	Stepien et al. 2000
194	p_{xy}	1.0×10^{-4}	5.1×10^{-5}	-	Maldonado et al. 2001
48	p_{xy}	2.3×10^{-3}	1.6×10^{-3}	-	Walker et al. 1995
88	p_{xy}	2.1×10^{-5}	4.3×10^{-5}	+	Walker et al. 1997
70	F_{ST}^2	2.8×10^{-4}	6.8×10^{-4}	+	Barrowclough et al. 1999
227	p_{xy}	7.0×10^{-6}	1.5×10^{-5}	+	Simonsen et al. 1998
102	d_A	1.6×10^{-7}	2.5×10^{-6}	+	Redenbach and Taylor 1999
79	p_{xy}	1.6×10^{-5}	2.4×10^{-5}	+	García-Rodríguez et al. 1998
130	F_{ST}^2	9.8×10^{-8}	1.1×10^{-6}	+	Friesen et al. 1996
98	p_{xy}	7.4×10^{-8}	9.2×10^{-6}	+	Wooding and Ward 1997
152	F_{ST}^2	3.0×10^{-5}	3.7×10^{-4}	+	Kimura et al. 2002
30	p_{xy}	6.4×10^{-5}	1.5×10^{-6}	-	Grohovaz et al. 1996
44	p_{xy}	5.0×10^{-5}	1.6×10^{-4}	+	Lamb et al. 1989

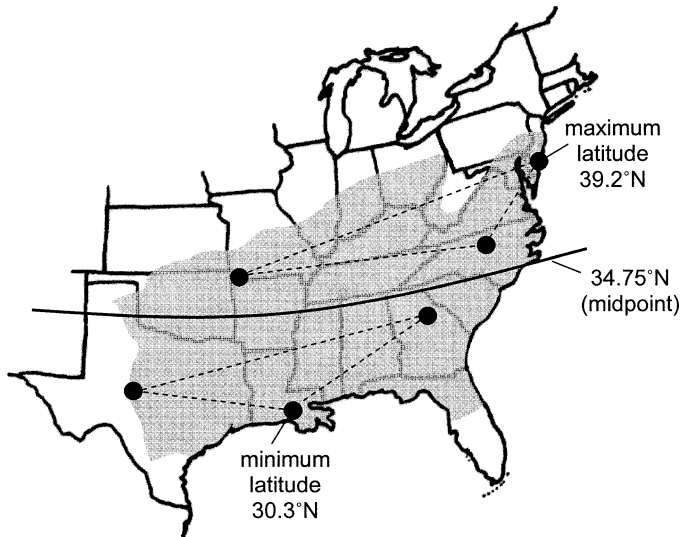


FIG. 1. An example of the methodology using Carolina chickadee, *Poecile carolinensis*, data from Gill et al. (1993). Shaded area represents the breeding range (Mostrom et al. 2002). Population genetic data were available for six populations (with three or more individuals sampled per population; black circles), spanning 8.9° latitude (30.3°N–39.2°N). We divided the six populations into high and low latitude groups by splitting populations in half latitudinally (split at 34.75°N; two groups spanning 4.45° each). Within high and low latitude groups (independently), we measured genetic distance [$p_{xy(net)}$] and geographic distance (km) between all populations in pairwise comparisons (3, 3 pairwise comparisons for high and low latitude groups, respectively). We then calculated genetic distance per kilometer for each pairwise comparison [$p_{xy(net)} \div \text{geographic distance}$], and subsequently calculated an overall mean [$p_{xy(net)} / \text{km}$] for high and low latitude groups. We tested our hypothesis that genetic divergence of populations (controlling for geographic distance) is greater at lower latitudes, by comparing mean genetic distance per kilometer between high and low latitude groups ($n = 62$ taxa; see Materials and Methods; Table 1).

among low latitude populations as compared with high latitude populations, suggesting that the potential for future speciation is greater at lower latitudes within species. These results support previous evidence that the tropics may act as a ‘‘cradle’’ for new taxa (Stehli et al. 1969; Stehli and Wells 1971; Hecht and Agan 1972; Jablonski 1993; Flessa and Jablonski 1996; Cardillo 1999). Results are also consistent with studies showing greater genetic structuring of populations in some tropical versus high latitude species (Seutin et al. 1994; Braun et al. 1996; Chek et al. 2003), and a positive correlation between mtDNA variation within species and overall species richness (Indo-West Pacific, Palumbi 1996).

Although genetic divergence of populations does not define a speciation event (Mayr 1963; Futuyma 1998), it is both a component and a correlate of factors important in speciation (Slatkin 1987; Turelli et al. 2001). We show greater mtDNA divergence among lower latitude populations, suggesting greater evolutionary independence of lower latitude populations within species. Greater evolutionary independence would allow lower latitude populations to follow independent evolutionary trajectories, increasing the likelihood that mutation, recombination, selection, and/or drift will lead to divergence of traits important in reproductive isolation and speciation (cf. Wake et al. 1986; Moritz et al. 1992; Irwin

et al. 2001; see also Coyne and Orr 1989; Tilley et al. 1990; Sasa et al. 1998; Wu and Hollocher 1998).

Overall, we expect a greater chance of speciation in lower latitude populations of a given species for a given time period. This does not necessarily imply a difference in the rate at which individual lineages diverge, because differences among populations reflect both the rate of divergence (among lineages) and time since isolation. Thus, our results do not imply or assume faster rates of molecular evolution or population divergence at lower latitudes. Instead, greater genetic divergence among the populations suggests a higher likelihood of future speciation among lower latitude populations because these populations are and/or have been evolving more independently as compared with higher latitude populations within the same species.

Causes of Variation in Population Divergence

Although increased population divergence at lower latitudes may provide insight into the proximate origins of tropical diversity, we can further ask what environmental variation over latitude causes variation in population divergence. Our results are consistent with several hypotheses (Pianka 1966; Rohde 1992; Schemske 2002; Willig et al. 2003). Janzen (1967) argued that increased seasonal variation in climatic conditions at higher latitudes resulted in broader tolerance of higher latitude organisms to conditions across spatially separated populations. Greater adaptation to conditions separating populations could reduce costs to dispersing between populations at higher latitudes, resulting in higher levels of gene flow and reduced genetic differentiation among high latitude populations. A second possibility is that cold temperatures and low energy availability during high latitude winters or during the cooling phase of glacial cycles could cause higher mortality and population extinctions at higher latitudes (Simpson 1964). Higher population extinctions coupled with subsequent recolonization could result in the reduced genetic divergence among higher latitude populations (Maruyama and Kimura 1980; but see Whitlock 1992 and references within). A third possibility follows from climatic changes during glacial (Milankovitch) cycles that resulted in geographically shifting ranges at higher latitudes (Huntley and Webb 1989). The geographic shifting of species’ ranges could reduce population divergence at higher latitudes through a variety of mechanisms, including population mixing (McGlone 1996; Walter and Epperson 2001; Dynesius and Jansson 2000; Jansson and Dynesius 2002), population bottlenecks (Cwynar and MacDonald 1987; Hewitt 1996, 1999, 2000; Bernatchez and Wilson 1998), sampling bias during recolonization (Davis 1981; Bennett 1985; Cwynar and MacDonald 1987), and selection for high dispersal individuals, particularly during recolonization (Cwynar and MacDonald 1987; Dennis et al. 1995; Dynesius and Jansson 2000; Jansson and Dynesius 2002).

Evidence strongly suggests that the last glaciation had profound effects both on current distributions of populations, and patterns of genetic variation (Hewitt 1996, 1999, 2000; Bernatchez and Wilson 1998; Ray and Adams 2001; Jansson and Dynesius 2002). The often discussed ‘‘southern richness to northern purity’’ pattern in the northern hemisphere (Hew-

itt 1996, 2000) resulted from the rapid expansion of organisms recolonizing regions that had been covered by glacial ice (Hewitt 1996, 2000). Organisms in these newly colonized regions frequently show low genetic variation both within and among populations (particularly pronounced in fish; Bernatchez and Wilson 1998), reducing the potential for speciation in these regions and potentially contributing to the latitudinal gradient in species richness (Hewitt 2000). Our results support the importance of recolonization following glacial ice expansion for patterns of genetic divergence among populations. However, without these populations, results remain significant, illustrating that latitudinal variation in population divergence within species is not driven simply by recolonization of previously ice-covered regions. Ample paleoecological evidence illustrates that postglacial recolonization and the shifting of species' distributions was not confined to ice-covered regions, high-latitude regions, or the northern hemisphere (Ray and Adams 2001). Thus, our results are entirely consistent with the influence of glacial cycles on species' distributions, both through glacial ice expansion and retraction, and through other climatic changes (Kutzbach et al. 1993; Ruddiman and Mix 1993) that cause shifts in the distribution of taxa—shifts that generally increase latitudinally towards the poles (cf. Dynesius and Jansson 2000; Ray and Adams 2001). Although these effects of glacial cycles undoubtedly influence patterns of population divergence, testing among alternative hypotheses (e.g., glacial cycles vs. seasonality) must await a stronger data set than we present here.

Origins of the Latitudinal Gradient in Species Richness

Hypotheses to explain the latitudinal gradient in species richness usually address one of two questions: (1) Why are there more species at lower latitudes, and (2) How are more species able to coexist at lower latitudes? (cf. Terborgh 1992). Our results presented here address only the first question, and suggest that higher speciation rates result in higher diversity at lower latitudes. The role of speciation in the origins of tropical richness is supported by fossil evidence of higher origination rates of post-Palaeozoic orders of marine invertebrates in tropical versus high latitude regions (Jablonski 1993; see also Wei and Kennett 1986), as well as other less conclusive evidence for higher origination rates in tropical regions (Stehli et al. 1969; Stehli and Wells 1971; Hecht and Agan 1972; Flessa and Jablonski 1996).

Other studies have suggested that elevated extinction rates at higher latitudes contribute to more species occurring in the tropics (Gaston and Blackburn 1996; see also Chek et al. 2003). This argument was based upon shorter branch lengths of avian tribes in contemporary species occurring at higher latitudes (Gaston and Blackburn 1996). However, the cause of this pattern (and others, including Cardillo 1999) is open to other alternative explanations (Chown and Gaston 2000), including latitudinal variation in patterns of speciation, hybridization across lineages, and shifts in the distributions of younger versus older taxa over the past several million years. In contrast, fossil evidence fails to support notably higher rates of extinction at higher latitudes through glacial cycles (Coope 1995; Bennett 1997), with other evidence instead

showing higher extinction rates of tropical species (Stanley 1984; Jablonski 1985; Jablonski et al. 1985), and more generally, higher turnover (origination and extinction) of tropical taxa (Flessa and Jablonski 1996). Higher extinction rates of tropical species are consistent with their smaller ranges and population sizes which make species more susceptible to extinction (Hansen 1980; Jablonski et al. 1985 and references within; see also Soulé 1986), and are also consistent with current patterns of species extinctions in the face of human perturbations (Gentry 1986; Terborgh 1992). Overall, patterns of extinction over latitude support the idea that an increase in the rates of speciation from the poles towards the equator is the primary cause of high tropical diversity.

The second question of how more species can coexist in the tropics is an equally important issue in determining the cause of the latitudinal gradient in species richness. Recent work by Francis and Currie (2003) building upon previous research (Currie and Paquin 1987; Currie 1991; cf. Gaston 2000; Schemske 2002; Willig et al. 2003 and references within) shows strong correlations between available energy and the estimated tree species richness (based on familial richness) across the globe. Available energy is undoubtedly the best predictor of latitudinal variation in species richness, although the relationship is likely dependent upon the regional availability of species. Regional availability of species may in turn be strongly influenced by geographic variation in speciation rates (cf. Ricklefs 1987; Latham and Ricklefs 1993; Ricklefs et al. 1999).

Implications for Evolutionary Patterns over Latitude

Latitudinal variation in population divergence has implications for other biogeographic patterns and evolutionary processes beyond species richness. For example, increased population divergence at lower latitudes could lead to the subdivision of large-ranged species into sister taxa occupying smaller, allopatric ranges (Mayr 1963; Jansson and Dynesius 2002). Thus, latitudinal variation in population divergence should increase the frequency of smaller-ranged endemics both at lower latitudes and in regions of highest taxon diversity—patterns that have been observed across many taxa (Gentry 1986; Brown et al. 1996; Dynesius and Jansson 2000; Jansson and Dynesius 2002).

Perhaps most importantly, greater divergence among lower latitude populations within species (this study; Armbruster et al. 1998; Bernatchez and Wilson 1998) and among species (Seutin et al. 1994; Braun et al. 1996; Chek et al. 2003) suggests that the relative influence of processes driving evolution (e.g., gene flow, genetic drift, and selection) may vary as a function of latitude (see Dobzhansky 1950; Fischer 1960). If so, a bias towards high latitude taxa in studies of evolution may obscure our understanding of how evolution and speciation occur in the majority of the earth's organisms.

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