

DIVERGENT TIMING AND PATTERNS OF SPECIES ACCUMULATION IN LOWLAND AND HIGHLAND NEOTROPICAL BIRDS

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Abstract.—Late Pliocene and Pleistocene climatic instability has been invoked to explain the buildup of Neotropical biodiversity, although other theories date Neotropical diversification to earlier periods. If these climatic fluctuations drove Neotropical diversification, then a large proportion of species should date to this period and faunas should exhibit accelerated rates of speciation. However, the unique role of recent climatic fluctuations in promoting diversification could be rejected if late Pliocene and Pleistocene rates declined. To test these temporal predictions, dateable molecular phylogenies for 27 avian taxa were used to contrast the timing and rates of diversification in lowland and highland Neotropical faunas. Trends in diversification rates were analyzed in two ways. First, rates within taxa were analyzed for increasing or decreasing speciation rates through time. There was a significant trend within lowland taxa towards decreasing speciation rates, but no significant trend was observed within most highland taxa. Second, fauna wide diversification rates through time were estimated during one-million-year intervals by combining rates across taxa. In the lowlands, rates were highest during the late Miocene and then decreased towards the present. The decline in rates observed both within taxa and for the fauna as a whole probably resulted from density dependent cladogenesis. In the highlands, faunawide rates did not vary greatly before the Pleistocene but did increase significantly during the last one million years of the Pleistocene following the onset of severe glacial cycles in the Andes. These contrasting patterns of species accumulation suggest that lowland and highland regions were affected differently by recent climatic fluctuations. Evidently, habitat alterations associated with global climate change were not enough to promote an increase in the rate of diversification in lowland faunas. In contrast, direct fragmentation of habitats by glaciers and severe altitudinal migration of montane vegetation zones during climatic cycles may have resulted in the late Pleistocene increase in highland diversification rates. This increase resulted in a fauna with one third of its species dating to the last one million years.

Key words.—Climate change, diversification rates, Neotropics, Pleistocene speciation, refuge hypothesis.

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Understanding the historical processes driving the diversification of contemporary faunas is a major aim of biogeography, yet the timing and rate of diversification in some of the most species rich faunas are poorly understood. Species diversity is highest in the Neotropics (Rosenzweig 1995). For example, approximately three thousand species of birds occur there (Haffer 1990), more than all other tropical regions combined. This pattern is repeated in many other groups. A number of theories have been proposed to explain the origin of this diversity (see review in Haffer 1997). These theories differ in their view of what processes promoted speciation and of the age of species in Neotropical faunas, but no consensus has been reached.

Originally, Neotropical forests and climates were believed to have been stable through most of their Cenozoic history (Richards 1952; Fisher 1960; Schwabe 1969). This stability was thought to have promoted low extinction rates and allowed for the gradual buildup of high species diversity (Darlington 1957; Sanders 1969; Schwabe 1969). Under this view, species in Neotropical faunas were thought to be relatively old. This theory was challenged when it became apparent that intense climatic fluctuations during the Northern Hemisphere ice ages also affected climate in the Neotropics. The temperate latitude model of glacial refugia (Rand 1948; Mengel 1964) was applied to explain Neotropical diversification. The resulting refuge hypothesis and its variant forms (e.g., river refuge hypothesis) predicted that the majority of current Neotropical species diversified during recent episodes of climatic fluctuation when Neotropical habitats were believed to have been repeatedly fragmented (Haffer 1969, 1974, 1997; Van-

zolini and Williams 1970; Brown et al. 1974; Prance 1978; Simpson and Haffer 1978; Cerqueira 1982; Whitmore and Prance 1987; Capparella 1991; Ayres and Cluttonbrock 1992; Haffer and Prance 2001). Although the refuge hypothesis has been invoked most often to explain diversification in lowland wet-forest habitats, climatic fluctuations may have also fragmented other Neotropical habitats in both lowland (Meave et al. 1991; Meave and Kellman 1994) and highland faunas (Steyermark and Dunsterville 1980).

Climatic fluctuations have occurred throughout the history of the Neotropics and may have contributed to diversification at any period (Haffer 1997; Haffer and Prance 2001). However, the glacial cycles of the late Pliocene and Pleistocene produced the most intense fluctuations. Beginning about 2.5 million years ago (mya, Bloemendal and Demenocal 1989; Hooghiemstra 1989; Andriessen et al. 1993; van der Hammen and Hooghiemstra 1997; Ravelo et al. 2004; Liu and Herbert 2004), these fluctuations persisted through the late Pliocene (2.5 to 2.0 mya) and early Pleistocene (2.0 to 1.0 mya) and culminated in a series of severe glacial cycles during the late Pleistocene (~ 1.0 mya to recent; Bennett 1990; Hooghiemstra et al. 1993). The intensity of these late Pleistocene glacial cycles led most proponents of the refuge hypothesis to predict that the majority of Neotropical species dated to this time. Recently some proponents have extended this prediction to earlier time periods (Haffer 1997; Haffer and Prance 2001). Nevertheless, if climate fluctuations drove Neotropical diversification, then we would expect the rate of speciation to increase during time periods when the duration and intensity of fluctuations were greatest. Speciation rates should increase

at the onset of glacial cycles 2.5 mya and again at the onset of the late Pleistocene 1.0 mya.

Several other theories have endeavored to link Neotropical diversification to specific geological events that mostly predate the climatic cycles of the late Pliocene and Pleistocene. In the lowlands, events such as uplift of montane barriers in northwestern South America (Sick 1967), formation of the Amazon drainage system (Sick 1967; Capparella 1988; Hoorn et al. 1995; Aleixo 2004; Rossetti et al. 2005), marine incursions (Hoorn 1993, 1994; Irion et al. 1995; Webb 1995; Rasanen et al. 1995; Nores 1999, 2004; Gregory-Wodzicki 2000), or freshwater lake barriers (Vonhof et al. 2003; Rossetti et al. 2005) occurred primarily during the late Miocene (10 to 5 mya) and early Pliocene (5 to 2.5 mya) and are thought to have promoted diversification. The effect of these geological events may have been temporary (e.g., marine incursions) resulting in a burst of diversification at the time of the event or their effect may persist to the present (e.g., mountain and river barriers; see Bates et al. 2004) resulting in ongoing opportunities for speciation. Due to the overlap in the predictions of the timing of diversification, it is difficult to investigate the potential role played by any one geological event.

In the highlands, rapid uplift of the Andes and other highland regions occurred during the last 10 million years (Hooghiemstra and van der Hammen 1998). For instance, 60 to 80% of the current height of the central and northern Andes resulted from uplift during this time period (Gregory-Wodzicki 2000) and the Talamanca highlands of Central America formed within the last five million years (Grafe et al. 2002). This dynamic history of uplift may have provided ongoing opportunities for diversification of highland species to the present. Fjeldsa and Lovett (Fjeldsa and Lovett 1997a,b) proposed that highland regions were the main source of diversification for the Neotropics and that highland species dispersed to lowland faunas where they were preserved from extinction.

Only those hypothesis that stress climatic fluctuations as driving diversification predict that Neotropical faunas should be recently derived with an increase in diversification rates near the recent. With the advent of molecular dating techniques it is now possible to test these predictions. Several molecular based reviews of Neotropical speciation in birds are available but are incomplete and have not addressed patterns in rates of diversification through time. The review by Moritz et al. (2000) suggested that Pleistocene speciation was rare in Neotropical birds and other vertebrates, with the majority of species dating to the Pliocene and Miocene. However, their conclusions were based on only a few genera, and further sampling may find greater support for diversification near the recent. In contrast, a review of speciation in Andean birds suggested a protracted history of diversification from the Miocene to the present with substantial numbers of species dating to the late Pliocene and Pleistocene (Garcia-Moreno and Fjeldsa 2000). The larger sampling design in the Andean study suggests that further sampling of lowland avian genera may provide a more complete picture of Neotropical diversification.

I compared the timing and rate of diversification in lowland and highland avian radiations of the Neotropics. To make

this comparison, patterns of species accumulation were analyzed from mitochondrial DNA phylogenies for 16 lowland and 11 highland radiations. Patterns in the rate of diversification through time were used to determine peak periods of diversification for the faunas in each region and to test for increasing, decreasing, or constant diversification rates through time. The separation of Neotropical taxa into lowland and highland faunas is useful because both regions experienced different geological histories. In addition, climatic fluctuations were more intense in highland regions where extensive glaciation directly fragmented high elevation habitats. In contrast, lowland faunas did not experience direct fragmentation by glaciers but habitats may have been fragmented due to fluctuations in temperature and rainfall that accompanied them (Hooghiemstra and van der Hammen 1998; Bush and Silman 2004). If recent climatic fluctuations drove Neotropical diversification, then the majority of species should date to the late Pliocene and Pleistocene. Additionally, speciation rates should increase through this period and peak during the last one million years when climatic fluctuations were most intense. In contrast, if events that predate the climatic fluctuations were instrumental in Neotropical diversification then we would not expect an increase in diversification during recent periods of climatic instability and a large proportion of species should date to the Miocene and early Pliocene.

METHODS

Phylogenetic Analysis

The Neotropical zoogeographic region extends from central Mexico to the southern tip of South America. In this analysis I excluded the Caribbean and other Neotropical islands because I was interested in analyzing rates of diversification within continental faunas. I included all terrestrial taxa possessing five or more species in highland or lowland regions for which mitochondrial DNA sequences were available for at least 75% of species (Table 1). In some cases recent molecular phylogenetic studies have demonstrated that two or more genera together formed a monophyletic group but individually were paraphyletic. These were analyzed as a single taxon (*Troglodytes* and *Thryorchilus*; *Crax* and *Nothocrax*; *Psarocolius*, *Cacicus*, and *Ocyalus*; *Geositta* and *Geobates*). In addition, a monophyletic assemblage of South American blackbirds (*Macroagelaius*, *Gymnomystax*, *Hypopyrrhus*, *Lamprosar*, *Gnorimopsar*, *Curaeus*, *Amblyramphus*, *Chrysomus*, *Xanthopsar*, *Pseudoleistes*, *Oreopsar*, and *Agelaioides*) and Neotropical swallows (*Progne*, *Phaeoprogne*, *Notiochelidon*, *Atticora*, *Neochelidon*, and *Stelgidopteryx*) were also included and each was analyzed as a single taxon because many of their respective genera were paraphyletic or they did not have enough species to allow for separate analysis.

Wide taxonomic and ecological coverage are included in the sample of Neotropical taxa used in this analysis. In addition, taxon size ranged from taxa with only five species to one of the largest Neotropical genera, *Tangara*, with 49 species distributed in both highland and lowland regions. Nevertheless, this sample is constrained to currently available phylogenies that may not represent a completely random sam-

TABLE 1. Lowland and highland taxa analyzed. Results of the γ statistic, the expected number of lineages for each clade, and phylogenetic sources from which the majority of DNA sequences were obtained for each phylogenetic analysis.

Taxon	Number of species		Youngest species ⁴	γ (P-value)	b^5 (species/lineage per Myr)	d^5 (species/lineage per Myr)	Expected phylogroups per species ⁶	Phylogenetic source
	Region ¹	Available ²						
Lowland								
<i>Amazona</i>	16	14	6	-2.12 (0.033)	0.35	0.00	11.6	Russello and Amato 2004
Blackbird clade	14	13	9	-3.26 (0.001)	0.25	0.00	631.0	Lanyon and Omland 1999
<i>Crax</i>	13	13	3	-1.80 (0.072)	0.65	0.00	0.2	Pereira and Baker 2004
<i>Dendrocincla</i>	7	7	3	0.07 (0.944)	0.51	0.60	0.7	this study
<i>Icterus</i>	16	16	6	-2.06 (0.039)	0.22	0.00	2.3	Omland et al. 1999
<i>Myiarchus</i>	11	10	5	0.27 (0.842)	0.40	0.43	-0.5	Joseph et al. 2003
<i>Nyctibius</i>	6	5	5	-0.34 (0.730)*	0.11	0.00	6.3	Mariaux and Braun 1996
<i>Pionopsitta</i>	9	8	3	1.15 (0.248)	0.32	0.42	-0.1	Eberhard and Bermingham 2005
<i>Psarocolius</i>	19	15	11	-1.79 (0.068)	0.26	0.00	53.7	Price and Lanyon 2002, 2004
<i>Pteroglossus</i>	12	12	4	-0.11 (0.912)	0.49	0.24	0.3	Eberhard and Bermingham 2005
<i>Ramphocelus</i>	7	6	2	0.27 (0.785)	0.80	1.08	0.4	Hackett 1996
Swallow clade	12	12	8	-2.02 (0.043)	0.12	0.00	1.8	Sheldon et al. 2005
<i>Tachycineta</i>	5	5	2	0.56 (0.576)	1.37	2.19	0.7	Whittingham et al. 2002
<i>Tangara</i>	22	19	8	-2.11 (0.032)	0.30	0.00	781.2	Burns and Naoki 2004
<i>Trogon</i>	14	11	5	-1.18 (0.229)	0.13	0.00	0.8	Espinosa de los 1998, this study
<i>Veniliornis</i>	10	8	3	-0.37 (0.707)	0.64	0.39	2.6	Moore et al. 2005
<i>Xiphorhynchus</i>	13	13	6	-1.26 (0.208)	0.25	0.00	7.6	Aleixo 2002
Z-test				-3.92 (<0.0001)				
Average	12	11	5		0.42	0.32	88.3	
Highland								
<i>Anairetes</i>	7	6	5	-1.07 (0.282)	0.30	0.00	0.4	Roy et al. 1999
<i>Carduelis</i>	10	8	5	1.04 (0.290)	4.28	5.59	0.0	van den Elzen et al. 2001
<i>Cinclodes</i>	11	11	3	-0.62 (0.535)	0.49	0.08	0.0	Chesser 2004
<i>Cranioleuca</i>	11	10	3	-1.15 (0.251)	0.83	0.00	0.8	Garcia-Moreno et al. 1999a
<i>Geospiza</i>	9	9	4	0.21 (0.834)	0.33	0.31	0.5	Chevron et al. 2005a
<i>Hemipingus</i>	14	12	7	-1.72 (0.081)	0.12	0.00	1.2	Garcia-Moreno et al. 2001
<i>Metallura</i>	10	9	2	-0.85 (0.394)	0.24	0.00	0.3	Garcia-Moreno et al. 1999b
<i>Muscisaxicola</i>	12	12	6	4.07 (0.000)	5.31	6.64	-0.6	Chesser 2000
<i>Ochthoeca</i>	11	11	7	-0.13 (0.897)	0.32	0.17	0.7	Garcia-Moreno et al. 1998
<i>Tangara</i>	26	23	13	-3.17 (0.032)	0.20	0.00	0.7	Burns and Naoki 2004
<i>Troglodytes</i>	7	6	3	-0.04 (0.968)	0.24	0.03	0.5	Rice et al. 1999
Z-test				-1.03 (0.300)				
Average	12	11	5		1.15	1.17	0.4	

¹ Species in each geographic region of interest.

² Number of species for which DNA samples were available.

³ Maximum number of regionally sympatric species in geographic region.

⁴ Approximation of the lag time to speciation estimated as youngest sister species within the geographic region of interest in each taxon.

⁵ Speciation (b) and extinction (d) rates estimated using a birth death model.

⁶ Expected number of lineages at present if initial rates of diversification remained constant. Initial diversification rates were calculated from the first five nodes in each phylogeny. See text for details.

* Assuming a 2% molecular clock, *Nyctibius* does not speciate during the last 10 million years. It seems unlikely that the speciation process (evolution of reproductive isolation) would require more than a few million years, thus this long time period (g_n) probably represents a genuine slow down in the rate of splitting. However, it is not known if intraspecific splitting events have occurred along g_n . If g_n is not excluded, γ equals -2.3 ($P = 0.02$).

ple of Neotropical taxa. Phylogenetic analyses have mostly been confined to regions amenable to genetic sampling. Species restricted to countries such as Colombia and Venezuela are poorly represented in the phylogenies included here. I do not expect these potential biases to greatly affect the patterns of diversification uncovered in this study. Nevertheless, further sampling undoubtedly will provide a more complete understanding of Neotropical diversification.

For each taxon, phylogenetic trees were generated and calibrated so that branch lengths were proportional to time as follows. Protein coding mitochondrial DNA sequences were obtained from Genbank or were sequenced for this project (see Table 1 in Supplementary Material available online at: <http://dx.doi.org/10.1554/05-272.1.s1>). Phylogenetic analyses were performed with multiple outgroups in MrBayes version 3.0b4 (Huelsenbeck and Ronquist 2001) under the GTR- γ model of evolution. All Bayesian analysis were run for two million generations and were sampled every 200 generations. The first 500,000 generations were excluded as the burn-in period and trees sampled from the remaining 1.5 million generations were used to construct majority-rule consensus cladograms. Parameters of the GTR- γ model were then estimated from the Bayesian consensus trees using maximum likelihood in PAUP* ver. 4.0b10 (Swofford 2002). These parameter estimates were used to obtain maximum-likelihood estimates of branch lengths along the Bayesian consensus topologies. The only exception was that for *Tangara* I used a published Bayesian topology (fig. 2 in Burns and Naoki 2004) and then calculated branch lengths along it using maximum likelihood. Penalized likelihood methods, implemented in r8s (Sanderson 2003), were then used to create ultrametric trees that allow for local rate variation in the molecular clock. The cross validation routine implemented in r8s was used to estimate the appropriate value of the smoothing parameter for each tree. Branch lengths generated using penalized likelihood are proportional to time, but require calibration. The timing of the basal most split within each taxon was used as a calibration point. The timing of this split was estimated with maximum likelihood in PAUP* by determining branch lengths under the assumption of a global clock and applying a molecular clock calibration to date this split.

Uncertainty if the rate of molecular evolution is constant through time and across taxonomic groups needs to be accounted for when dating splitting events. Calibrations obtained for several orders of birds suggest an avian molecular clock of approximately 2% per million years for protein-coding mitochondrial DNA (see note 11 in Klicka and Zink 1997). Nevertheless, the validity of this rate has been challenged due to inconsistent phylogenetic methods used to arrive at this calibration (Lovette 2004a). Moreover, this rate may not be valid for splitting events near the recent (García-Moreno 2004; Penny 2005; Ho et al. 2005). To address these issues, I recalibrated published avian calibrations using GTR-gamma distances. I obtained additional calibrations using fossil material and island ages (Weir, unpubl. data). A total of 47 avian calibrations from 19 families were obtained for the mitochondrial cytochrome b gene. Some calibrations obtained for splitting events less than 0.5 mya were much higher than the 2% rate. However, calibrations obtained for splitting

events between 0.5 and 11 mya closely clustered around a rate of 2.0%. I used this rate throughout this study.

The resulting calibrated, clocklike trees provide useful sources of information for analyzing both the timing and rate of diversification within each geographic region. Nodes in such phylogenies provide estimates of the dates when species diverged (population splitting). Node ages actually measure the coalescence times of DNA haplotypes which may predate population subdivision. The discrepancy results due to the presence of polymorphism within populations at the time of splitting. Assuming that ancestral levels of polymorphism are similar to current levels, then the mean divergence within current populations can be used to correct splitting dates. This is done by subtracting the mean intraspecific divergence from coalescent dates (Nei and Li 1979; Avise et al. 1998). I estimated the average intraspecific GTR-gamma divergence between individuals of a species (see Table 2 in Supplementary Material available online). If species possessed genetic subdivisions then I estimated average divergence between individuals at the phylogroup level following Avise et al. (1998). These estimates were derived from available population level phylogenetic datasets for Neotropical birds and often come from different taxa than those analyzed here. Nevertheless, these corrections are assumed to be reflective of the Neotropical avifauna as a whole. Throughout this study, coalescence dates are reported and are used as a maximum estimate of the age at which population divergence occurred. Estimates of mean intraspecific divergences are then used to explore the magnitude of the discrepancy between node ages and splitting ages.

Ancestor State Reconstructions

I analyzed the timing and rate of diversification in the Neotropics for lowland and highland faunas separately. The division between the lowlands and highlands was drawn at 1000 m, the approximate upper limit of the tropical lowland habitats and the lower limit of subtropical montane habitats. Neotropical species whose elevational distributions were predominantly above or below 1000 m were assigned to highland and lowland faunas, respectively. However, in Patagonia, alpine habitats typical of the high Andes further north descend to sea level. The few species included in this dataset that occur there were considered to belong to the highland avifauna.

Ancestor state reconstruction was used to classify interior nodes to their appropriate faunas. Species in each tree were classified as highland, lowland, Caribbean, North American, or other. Ancestor state reconstructions either assigned nodes to one of these faunas or designated them as dispersal events from one fauna to another. Dispersal events between faunas occur at nodes in which each of the sister lineages occur in different faunas (Fig. 1a). A splitting event within a fauna occurs at nodes in which each of the daughter lineages occur within the fauna. Mesquite (Maddison and Maddison 2003) was used to obtain the most parsimonious ancestor state reconstruction for each phylogenetic tree (see Supplementary Material available online at: <http://dx.doi.org/10.1554/05-272.1.s2>). For several taxa (*Amazona*, *Icterus*, *Tangara*), multiple most parsimonious reconstructions were obtained.

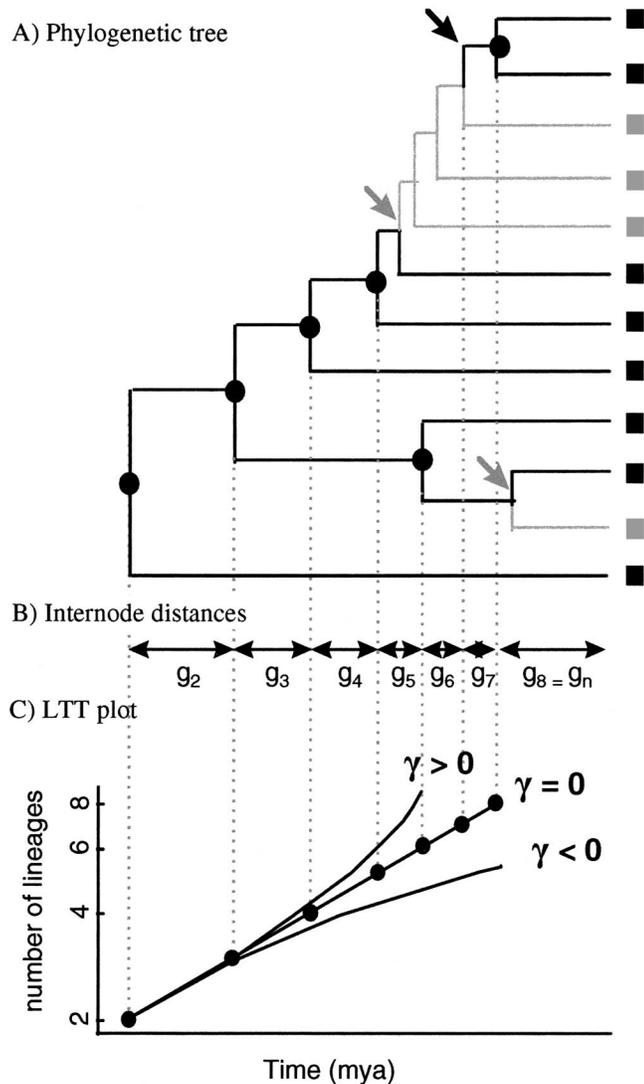


FIG. 1. Example of how patterns of species accumulation are obtained from a reconstructed phylogenetic tree. (A) a reconstructed phylogenetic tree containing species within (black) and outside of (grey) a geographic region of interest. For lineage through time (LTT) analysis, only node ages representing splitting events within the geographic region of interest (black circles) or that represent colonization from an outside source followed by speciation (black arrow) were used. Nodes leading to the formation of a clade outside of the region of interest were excluded (grey arrows) because they do not represent the addition of a new lineage to the fauna. (B) Internode distances for geographic region of interest labelled g_2 to g_8 . (C) LTT plot for taxa in the geographic region of interest. Values of the γ statistic are equal to zero when the slope of the LTT plot is constant through time. Downturns in the slope produce negative γ -values whereas upturns produce positive values.

In such cases a maximum-likelihood method of ancestor state reconstruction was used to differentiate between the competing alternatives. For maximum-likelihood reconstructions of geographic origin, a punctation model is most appropriate because it places character change at the time of splitting (at the node) rather than along branches. This model was implemented by constraining all internode branches to have equal length (Pagel 1994). Node reconstructions with the

highest likelihood were chosen. These methods of reconstructing ancestral states assume that the most parsimonious or the most likely reconstruction is the correct one. This assumption is probably valid for phylogenetic trees with few transitions between states (most taxa in this study). More uncertainty exists when frequent transitions occur (e.g., *Tangara*). In addition, I assume that transitions occur at nodes. However, extinction eliminates nodes and may result in transitions being pushed back to earlier nodes in a tree.

Timing and Rates of Diversification

Analysis within taxa.—To investigate the timing and rate of diversification within taxa, I constructed plots of the log number of lineages (species) through time (lineages through time or LTT plots; Fig 1c) for each taxon. Under a null hypothesis of a constant speciation rate with no extinction (pure birth model), the number of lineages increases exponentially through time (Yule 1924; Nee 2004) and forms a straight line on an LTT plot with slope equal to the speciation rate. I used a method similar to that of Pybus and Harvey (2000) to test the overall fit of a LTT plot to the pure birth expectation of a constant slope. The γ -statistic they develop compares the relative position of node ages in a phylogenetic tree to that expected under the pure birth model. For a phylogeny with n taxa, let g_1 be the distance between the root of the tree and the first node, let g_2, g_3, \dots, g_{n-1} be the internode distances, and g_n be the distance between the most recent node and the present (Fig 1b). The statistic I use here is identical to that developed by Pybus and Harvey (2000), except that it excludes g_n . This last interval should be excluded from real phylogenies because unlike the simulated phylogenetic trees used by Pybus and Harvey there is no splitting event at the present and thus the interval g_n is not drawn from the same distribution as other internode distances (i.e., the next splitting event may occur in the future or it may have already occurred but is not taxonomically recognized as a species). The statistic follows

$$\gamma = \frac{\left[\frac{1}{n-m-1} \sum_{i=m}^{n-2} \left(\sum_{k=m}^i kg_k \right) \right] - \binom{S}{2}}{S \sqrt{\frac{1}{12(n-m-1)}}},$$

$$S = \left(\sum_{j=m}^{n-1} jg_j \right) \quad (1)$$

where S is the sum of the branch lengths in the phylogeny (excluding the interval g_n) and m is the number of initial lineages. Under the pure birth expectation of exponential growth, γ approaches a standard normal distribution with mean equal to 0.

Departures from the pure birth model can be detected by a γ -value that is either too large or too small. Values of $\gamma > 0$ indicate that internode distances are shorter than expected towards the recent, which is also reflected in an upturn in the LTT plot (Fig. 1c). Simulations of phylogenetic trees demonstrate that this can result if the rate of speciation increased through time (see Fig. 1c in Supplementary Material available online). Values of $\gamma < 0$ indicate that internode

distances are longer than expected towards the recent, which is reflected in a downturn in the LTT plot (Fig. 1c). This can result if the rate of speciation has declined through time (see Fig. 1f in Supplementary Material available online). Values of γ greater than 1.96 or less than -1.96 are significantly different at the 5% level from the pure birth expectation.

Extinction may also result in departure from the pure birth model. Simulations using a variety of extinction rates demonstrate that constant or increasing rates of extinction usually increased and more rarely decreased γ -values slightly, but not significantly (see Fig. 1 in Supplementary Material available online). Significantly positive and negative values of γ were only obtained in simulations where speciation rate increased or decreased respectively.

Some of the taxa included in this study possessed one or more clades distributed outside of the geographic region of interest (Fig. 1a, gray arrows). These were simply pruned so that all resulting nodes represented diversification events within the region of interest. However, a small proportion of taxa (four of 26) exhibited a more complex biogeographic history in which a clade distributed outside of a region back colonized into the region (Fig. 1a, black arrow). Lineages resulting from such back-colonization events usually possessed at least one node that represented splitting within the region of interest and were included in the LTT analysis. The node at which the back colonization occurred represents the addition of a new lineage to the fauna following immigration. This node was included in the analysis even though it does not represent splitting within the fauna. Exclusion of this node resulted in similar LTT plots and values of γ .

Missing taxa may result in biased diversification patterns. As many as 23% of species were missing from phylogenetic trees (Table 1). Missing taxa may result in artificial downturns in LTT plots. The effect of missing taxa can be corrected for in the γ statistic using Monte Carlo simulation (Pybus and Harvey 2000). The following method assumes that missing taxa are randomly distributed on the tree. Ten thousand pure birth trees with n tips were simulated in Phyl-O-Gen (Rambaut 2002) and k tips were randomly pruned from each, where n is the number of species in a taxon and k is the number of species sampled. The γ -statistic was calculated for each simulated tree. Average values of γ in simulated pure birth trees equal zero. When tips are deleted in simulated trees, average values are less than zero. The difference is proportional to the expected discrepancy in actual calculated γ -values. Calculated values of γ were corrected by subtracting the mean value in simulated trees. The resulting corrected values were only marginally greater than calculated values suggesting that missing taxa did not have a large effect. The distribution of values in the simulated datasets were used to determine the level of significance.

Lineages through time plots use splitting times from phylogenetic reconstructions of species level taxa. However, there is a lag time between lineage splitting and the time when lineages are recognized as separate species. As a result, older lineages are more likely to be recognized as distinct species today than younger lineages. It follows that there are likely to be recent lineage splitting events in the tree that are not recorded because the resulting taxa are not recognized as distinct species (phylogroups hereafter). Some of these phy-

logroups will evolve to become species in the future and these particular lineages really should be included in LTT plots and the γ -statistic. Failure to include such splits may also result in an artificial downturn in LTT plots towards the present. Most phylogroups are likely to be recent in age and do not confound the LTT analysis because they date to the time interval g_n which is excluded from LTT plots and the γ -statistic. Nevertheless, some of these splits may predate g_n . This is especially true when the interval g_n is short. Because detailed intraspecific sampling was lacking for most of the species in this dataset, I was not able to determine the effect of missing phylogroups on diversification rates.

Fauna wide trends in the mode of diversification within taxa were analyzed using a combined Z test (Whitlock 2005):

$$Z = \sum_{p=1}^l \gamma_p / \sqrt{l}. \quad (2)$$

Under the null model of pure birth, Z has a standard normal distribution where l is the number of taxa being combined and γ_p is the γ -statistic for taxon p . Values of Z greater than 1.96 or less than -1.96 are significantly different at the 5% level from the pure birth expectation. The Z test of combined γ -values identifies trends towards negative or positive values across a series of taxa.

I tested for density dependent cladogenesis in lowland and highland taxa. Density dependent cladogenesis may occur if speciation rates slow through time as ecological niches become progressively occupied. Alternatively, if the processes that promote speciation diminish through time, the speciation rates will slow in a correlated fashion irrespective of species density. Negative values of γ reflect a slowdown in speciation through time. If a fauna experiences density dependent cladogenesis, then a negative relationship should exist between γ and the maximum number of sympatric species. I tested for this relationship using a regression analysis. The maximum number of regionally sympatric species in each taxon was determined by overlaying range maps for each species and determining the geographic location with the highest density of species.

Finally, extinction rates were estimated directly from phylogenetic trees. Equation 17 in Nee et al. (1994) gives the likelihood of an internode distance for a given extinction and speciation rate. Following methods similar to Barraclough and Vogler (2002), I used the “optim” function in R (R Development Core Team 2005) to obtain estimates of extinction and speciation rates that maximized the likelihood of internode distances g_2 to g_{n-1} (Fig. 1) for each tree. The utility of this estimate is limited because it assumes rates are constant, when in reality rates may vary.

Faunawide analysis.—To illustrate fauna wide rates of diversification during different time periods, I used the Kendall/Moran estimator to calculate the net diversification rate during million year intervals for lowland and highland regions separately (Kendall 1949; Moran 1951; Hey 1992; Baldwin and Sanderson 1998; Nee 2001). For each of a series of phylogenetic trees, the per lineage diversification rate during a time window t is

$$b(t) = (n - m) / S \quad (3)$$

where n and m are the number of lineages at the end and beginning of the time period t and S is the sum of branch lengths (excluding the time interval g_n in each taxon; see Eq. 1) occurring within t . A single rate of diversification during each one million year time interval was obtained by summing $n - m$ and S across all phylogenies in lowland and highland regions separately. The variance of the estimate $b(t)$ provided by Nee (2001) is

$$\text{Var} = b^2 / (n - m) \quad (4)$$

and was used to determine 95% confidence intervals (eq. 17 in Nee 2001). Diversification rates were calculated back to eight mya (late Miocene), because not enough nodes were available before this period.

This faunawide analysis is useful for uncovering patterns in net diversification rates through time. If Pleistocene climatic fluctuations were a major factor in promoting speciation, then diversification rates should increase during the late Pliocene and early Pleistocene and again during the late Pleistocene when climatic fluctuations were most intense.

This faunawide analysis of diversification rates assumes that rates (b) are constant across taxa. To test for rate constancy across taxa, I compared overall diversification rates within each taxa using the joint scaling test borrowed from quantitative genetics (Lynch and Walsh 1998, pp. 216). This test compares observed values of a parameter, in this case b , calculated for each of k taxa with the expected value of the parameter \hat{b} if all taxa shared the same value. The expected value is

$$\hat{b} = (\mathbf{M}^T \mathbf{V}^{-1} \mathbf{M})^{-1} \mathbf{M}^T \mathbf{V}^{-1} \mathbf{b} \quad (5)$$

where \mathbf{V} is the covariance matrix with diagonal elements equal to the variance of each b_k (Eq. 4) and \mathbf{M} is a matrix with one column of length k with each element equal to one. The statistic follows a chi-squared distribution with $k - 1$ degrees of freedom

$$\chi^2 = \sum_{i=1}^k \frac{(\hat{b}_i - b_i)^2}{\text{Var}(\hat{b}_i)}. \quad (6)$$

Constant diversification rates across taxa were rejected for both lowland ($\chi^2 = 26.6$, $\text{df} = 16$, $P = 0.05$) and highland ($\chi^2 = 24.57$, $\text{df} = 10$, $P = 0.006$) datasets. To address the error associated with significantly different diversification rates across taxa, I systematically removed outlier taxa with extremely high values of b . When *Crax* was excluded, constant rates in lowland faunas could not be rejected ($\chi^2 = 21.07$, $\text{df} = 15$, $P = 0.13$). When *Carduelis*, *Cranioleuca*, and *Muscisaxicola* were excluded, constant rates in highland faunas could not be rejected ($\chi^2 = 8.7$, $\text{df} = 7$, $P = 0.27$). For both lowland and highland datasets, rates were analyzed through time using both the complete datasets and datasets with outliers excluded.

To determine if faunawide estimates of diversification rate b increased during the late Pliocene and Pleistocene, rates before and after 2.5 and 1.0 mya were compared using the joint-scaling test (Eq. 6). Rates were also compared between highland and lowland faunas before and after 2.5 mya to determine if diversification rates were different in each fauna.

RESULTS

A total of 198 lowland and 146 highland species were included in the 27 taxa. Ancestor state reconstructions recovered 313 nodes with both descendants in the Neotropics. Fifty-two percent of nodes were reconstructed as divergence events within the lowland fauna (Fig. 2a), 33% within the highland fauna (Fig. 2b), and 15% as interchange events between these faunas (Fig. 3). In the lowlands, 26% of nodes (43% of terminal species) dated (coalesced) to the glacial periods of the late Pliocene and Pleistocene and 5% (12% of species) to the late Pleistocene. The frequency of nodes decreased over the past 1.5 million years similar to simulations in which speciation rates declined through time (see Fig. 1f in Supplementary Material available online). In contrast, highland faunas had 42% and 21% of nodes (43% and 27% of species) dating to these periods, respectively. The shape of the distribution of nodes had a strong upturn near the recent that appeared intermediate between simulations in which speciation or extinction rates increased towards the present (see Fig. 1 in Supplementary Material available online). Thus, even though widespread diversification occurred during the periods of climatic instability in both faunas, only the pattern in the highland fauna was consistent with an increase in diversification rate during glacial periods (though extinction may have contributed to this pattern).

Nodes representing dispersal events between highland and lowland regions were most frequent during the last one million years and during the late Miocene and Pliocene (Fig. 3). Figure 3 also includes dates for intraspecific dispersal events for species distributed in both faunas. A few additional intraspecific interchange events are unrecorded because the relevant sequence data was not available. These are expected to date near the recent.

These dates represent coalescent dates. The actual dates of population splitting may occur after the coalescent dates if populations possessed polymorphism at the time of splitting. Current levels of intraspecific polymorphism are low, suggesting that on average lowland and highland coalescent dates predate actual population splitting by only 0.35 and 0.2 million years, respectively (see Table 2 in Supplementary Material available online). These corrections are similar to those reported for Northern Hemisphere taxa (Moore 1995). Applying these corrections did not greatly change any of the results of this study.

Patterns in LTT plots also suggest that the timing of diversification was different in lowland and highland taxa (Fig. 2). Many lowland taxa had very steep slopes between eight and four mya, suggesting rapid diversification during this period. Only one lowland taxon experienced rapid diversification, primarily within the late Pliocene and Pleistocene (*Crax*). The remaining lowland taxa exhibited slower, but relatively constant rates of diversification through time. In contrast, Pleistocene diversification was most prevalent in highland taxa (Fig. 2b). In the LTT plots, four of the 11 highland taxa (*Cranioleuca*, *Carduelis*, *Cinclodes*, and *Muscisaxicola*) displayed steep slopes during the Pleistocene suggesting rapid rates of speciation during this period. The remaining seven taxa diversified primarily before the Pleisto-

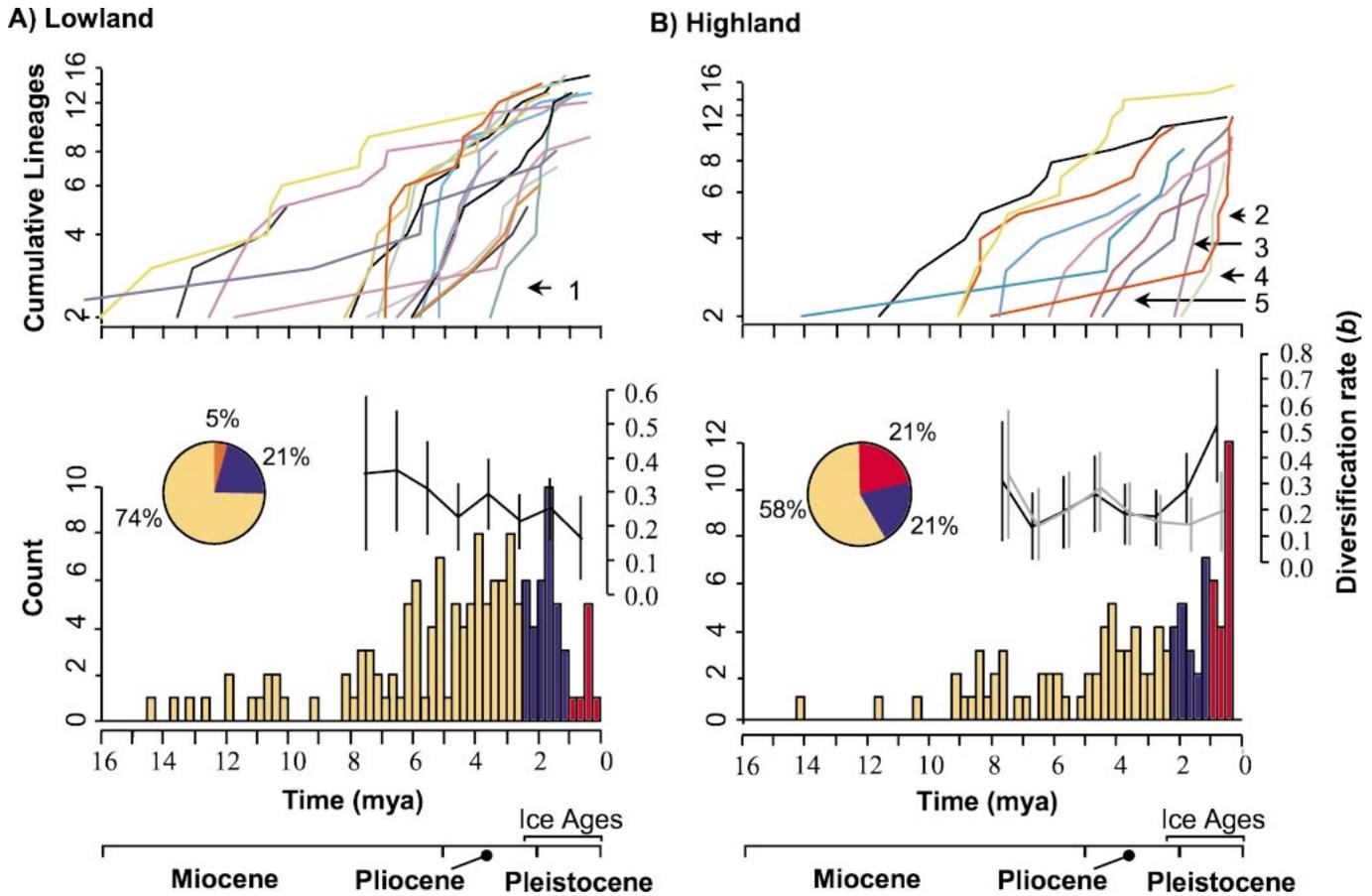


FIG. 2. Lineage through time (LTT) plots and faunawide rates of diversification through time for Neotropical lowland (A) and highland taxa (B). Maximum-likelihood estimates of rates of diversification are plotted with 95% confidence intervals. Two highland datasets were used to analyze faunawide rates: all highland genera (black) and *Carduelis*, *Cranioleuca* and *Muscisaxicola* excluded (gray). Numbers refer to the following taxa: (1) *Crax*, (2) *Muscisaxicola*, (3) *Cranioleuca*, (4) *Carduelis*, and (5) *Cinclodes*. The levels of shading on histograms and pie charts increase from light to dark for warm periods of the Miocene and early Pliocene (in yellow online), mild ice ages of the late Pliocene and early Pleistocene (in blue online) and severe ice ages of the late Pleistocene (in red online).

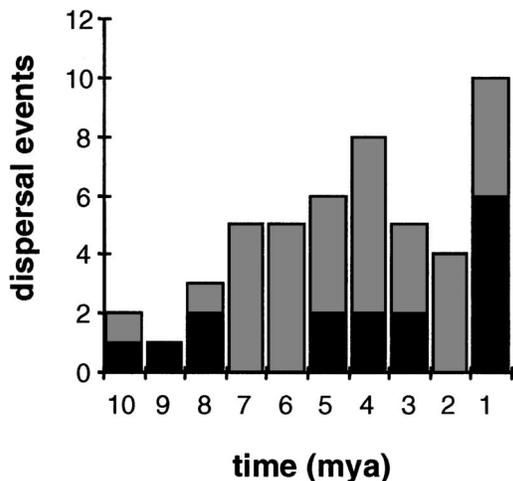


FIG. 3. Nodes representing interchange events between highland and lowland faunas as reconstructed from ancestor state reconstructions for 27 Neotropical taxa. Dispersal from lowland to highland faunas (gray) and highland to lowland faunas (black).

cene and had less steep slopes but, unlike lowland taxa, were not aggregated during any given time period.

Lineage through time plots and the γ -statistic further suggest that the rate of diversification decreased through time in most lowland taxa but remained constant in most highland taxa. Most lowland taxa displayed a downturn towards the recent in their LTT plots, consistent with a decrease in speciation rates through time (Fig. 2a). Values of the γ -statistic were likewise negative in 12 of 17 lowland taxa (Table 1) and were significantly negative in five taxa. No taxa had significantly positive values. The Z test of combined γ -values (Eq. 2) rejected the pure birth process (Table 1) for the lowland avifauna as a whole, suggesting a significant faunawide trend towards decreasing speciation rates through time.

In contrast to the lowlands, the relatively constant slopes in LTT plots for most highland genera were reflected in γ -values closer to zero, the pure-birth expectation. One genus had a significantly positive γ -value and one had a significantly negative value. The remaining genera were not significantly different from the pure birth expectation. The Z test of combined γ -values was negative, but failed to reject the pure birth process for the avifauna as a whole (Table 1),

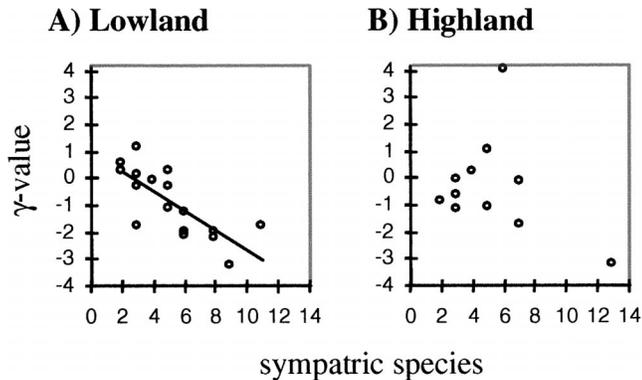


FIG. 4. The relationship between the maximum number of regionally sympatric species in each taxa and values of the corrected γ -statistic for (A) lowland and (B) highland Neotropical faunas.

suggesting that the mode of diversification within highland taxa is not significantly different from exponential growth.

In the lowlands, values of the γ -statistic were negatively correlated with the maximum number of regionally sympatric species in each taxon (Fig. 4; $r^2 = 0.57$, $\beta = -0.360 \pm 0.083$ SE, $T = -4.28$, $P < 0.0007$ two-tailed), suggesting that the rate of speciation declined as the number of sympatric species increased. This relationship remained significant after correcting for taxon size and taxon age (age of first split within taxon) in a multiple regression ($\beta = -0.297 \pm 0.127$ SE, $T = -2.34$, $P < 0.036$ two-tailed). However, highland taxa exhibited no significant relationship between the values of the γ statistic and the maximum number of sympatric species per taxon (Fig. 4; $r^2 = 0.19$, $\beta = -0.192 \pm 0.187$ SE, $T = -1.03$, $P = 0.34$, two-tailed).

Maximum-likelihood estimates of extinction rates (d) were low relative to speciation rates (b) for most taxa in both lowland and highland faunas (Table 1). At face value, these results suggest that extinction has probably not contributed significantly to observed patterns of species accumulation in either fauna. However, extinction rates estimated from reconstructed phylogenetic trees should be viewed with caution because these estimates may be biased. For instance, trees that display a downturn in LTT plots (or negative γ -values) exhibit negative extinction rates when maximum-likelihood searches are not constrained, but extinction rates of zero when they are constrained to positive values (values reported in Table 1 were constrained). In addition, these estimates of extinction assume a constant rate of extinction through time. Although separate rates of extinction for different time periods can be estimated from large phylogenetic trees (Barraclough and Vogler 2002), most of the taxa included here did not have enough nodes.

The Z test of combined γ -values detects common trends toward increasing or decreasing rates through time in a series of taxa. However, because this test lacks a temporal timescale a significant trend does not suggest that all taxa experienced increasing or decreasing rates concordantly. For example, two taxa may exhibit similar γ -values, but if the timing and rate of diversification differ between them, then the resulting net patterns of diversification may give different results. This is best illustrated in the highland fauna where several taxa

exhibit very steep slopes during the Pleistocene period in their LTT plots (*Carduelis* and *Cranioleuca*) yet had similar γ -values to taxa that did not have steep slopes and diverged mostly before the Pleistocene (Fig. 2). Likewise, the significant trend towards negative values of γ in the lowlands does not suggest that diversification rates decline over the same time periods in lowland taxa. Although LTT plots for many lowland taxa do appear to decline somewhat concordantly, this is not true of all taxa (Fig. 2a).

The Kendall-Moran estimator was used to determine faunawide values of diversification rate during million-year intervals. In the lowlands, both the full dataset and the dataset with *Crax* excluded exhibited very similar rates during each time period, thus only the full dataset was used. Faunawide diversification rates declined steadily through time from a high of 0.35 species per lineage/Myr between seven and eight mya to 0.16 species per lineage/Myr between the recent and one mya (Fig. 2a). Diversification rates were almost significantly lower after 2.5 mya ($\chi^2 = 3.60$, $df = 1$, $P = 0.058$), but no difference was found before and after 1.0 mya ($\chi^2 = 2.34$, $df = 1$, $P = 0.126$).

In highland taxa, faunawide rates during the late Pliocene and early Pleistocene were not different from previous rates ($\chi^2 = 0.54$, $df = 1$, $P < 0.46$). However, rates significantly doubled (as high as 0.52 species per lineage/Myr) during the late Pleistocene ($\chi^2 = 7.16$, $df = 1$, $P < 0.008$; Fig. 2b). This late Pleistocene increase was not significant when the three taxa (*Carduelis*, *Cranioleuca*, and *Muscisaxicola*) with the highest birth rates and which diversified primarily within the Pleistocene were excluded ($\chi^2 < 0.001$, $df = 1$, $P = 0.98$). In addition, late Pliocene and Pleistocene rates in the highlands were significantly higher than those in the lowlands when using the complete highland dataset ($\chi^2 = 5.1$, $df = 1$, $P < 0.024$), but when highland outliers were excluded lowland rates were higher ($\chi^2 = 6.51$, $df = 1$, $P = 0.01$). No difference in rates between these faunas occurred before the Pleistocene (all highland taxa included $\chi^2 = 1.88$, $df = 1$, $P = 0.17$, outliers excluded $\chi^2 = 2.58$, $df = 1$, $P = 0.11$). These data suggest that recent climatic fluctuations had an effect on faunawide diversification in the highlands but not the lowlands. However, the faunawide increase in highland faunas resulted from elevated late Pleistocene rates in a subset of highland taxa.

DISCUSSION

Lowland and highland faunas exhibited divergent patterns of species accumulation, suggesting that different processes resulted in their diversification. In the highlands, faunawide diversification rates increased throughout the Pliocene and Pleistocene and culminated in a late Pleistocene diversification rate more than double previous values. This increase in rate resulted in a burst of diversification during the last one million years (Fig. 2b) consistent with the hypothesis that climatic fluctuations resulted in a recent build-up of species in this fauna. In contrast, lowland diversification rates slowed through time (Fig. 2a) and were lowest during the late Pleistocene. Though the faunawide slow down was not quite significant, this result demonstrates that rates did not

increase through the Pleistocene as expected if climatic fluctuations drove lowland diversification.

What processes promoted these divergent patterns of species accumulation in lowland and highland faunas? In lowland taxa, γ -values revealed a significant trend towards decreasing diversification rates (Table 1). This pattern is consistent with the faunawide decrease in diversification rate and suggests that a decline in rates within taxa resulted in the faunawide pattern. Simulations demonstrate that a decline in the rate of speciation was more likely to generate such a strong pattern than an increase in the rate of extinction (see Fig. 1 in Supplementary Material available online). Likewise, estimates of extinction rates, although potentially biased, were low in most taxa (Table 1). The decrease in speciation rates may simply reflect the lack of geographic opportunity for speciation towards the recent. Alternatively, the decrease may reflect density dependent cladogenesis. The significantly negative relationship between the value of γ and the number of sympatric species in each taxon (even after correcting for taxon age and size) suggests that density dependent cladogenesis is responsible for the slowdown in species accumulation in lowland faunas. These preliminary results are consistent with the view that low extinction rates have allowed the accumulation of high species diversity and suggest that the number of species in lowland faunas may be approaching their capacity. Possible low extinction rates for birds contrast preliminary findings from Amazonian paleopollen records in which species diversity may have declined from the Miocene to the present (van der Hammen and Absy 1994; Hooghiemstra and van der Hammen 1998; van der Hammen and Hooghiemstra 2000; Willis and Niklas 2004). Further estimates of extinction rates from other taxonomic groups are needed in order to establish the role of extinction in the build-up of high species diversity in the Neotropics.

Could the observed slowdown in speciation rates through time in lowland taxa be an artifact of not sampling intraspecific splits (i.e., phylogroups) in this study? Indeed, a number of phylogenetic studies have uncovered genetically distinct lineages within many currently named lowland species (Aleixo 2002, 2004; Marks et al. 2002; Joseph et al. 2003; Burns and Naoki 2004; Joseph et al. 2004; Lovette 2004b; Armenta et al. 2005; Cheviron et al. 2005b). However, detailed population level sampling was not available for most species in my dataset. To address this question, I determined the initial diversification rate (slope) for each taxon from its LTT plot using only the first five nodes. I extended this rate to the present to determine the number of expected lineages if diversification rates had remain constant. In highland taxa, the expected number of lineages was very similar to the actual number in all taxa, with 0.4 additional lineages expected within each species on average (Table 1). However, in many lowland taxa the expected number of lineages was much higher than the actual number (88 additional lineages per species on average). It is doubtful that the actual number of lineages in many lowland species approaches, let alone surpasses their pure birth expectation. Thus, it appears that even if unrecognized lineages were included in the LTT plots, there still would be no evidence for a Pleistocene increase in lowland diversification rates. Detailed phylogenies that include all

genetically distinct lineages regardless of taxonomic status are needed for confirmation.

In contrast to the lowlands, LTT analysis suggests that most highland taxa did not exhibit a significant trend away from the pure birth expectation. This is not unreasonable given that continual uplift of highland regions could provide ongoing opportunities for speciation. Likewise, evidence for density dependence was lacking (Fig. 4), further suggesting that ecological opportunity is not currently a limiting factor in highland diversification. This pattern of constant diversification rates within taxa did not match the faunawide pattern of increasing diversification rates during the late Pleistocene. This apparent discrepancy is best explained by the faster speciation rate in taxa that diversified primarily within the Pleistocene (slopes in LTT plots for *Carduelis*, *Crani-oleuca*, *Cinclodes*, and *Muscisaxicola* are steeper than in taxa which diversified primarily before the Pleistocene, Fig. 2b). Thus, it appears that only a subset of highland taxa strongly contributed to the faunawide increase in diversification rates during the late Pleistocene.

Could extinction also generate the apparent late Pleistocene increase in diversification rate? Simulations that included extinction often did result in a recent upturn, although this effect was less pronounced than in models with an increase in speciation rate (see Fig. 1 in Supplementary Material available online). Nevertheless, estimates from highland phylogenetic trees (Table 1) suggest that extinction rates (estimates assume constant rates through time) are low in most highland taxa. Rapid speciation rates in a subset of highland taxa probably drove the late Pleistocene increase. However, until better estimates of extinction rates (i.e., non-constant extinction rates) are obtained, the role of extinction cannot be ruled out entirely.

These differences in species accumulation through time resulted in differently aged faunas (see Fig. 1 in Supplementary Material available online). The most striking difference is the abundance of highland species and scarcity of lowland species dating to the late Pleistocene. Less than one-fifth of lowland species date to this period even after correcting for ancestral polymorphism. Yet, global climatic fluctuations were most intense during this period. If these climatic fluctuations were not enough to promote widespread fragmentation and speciation in the lowlands, then it is unlikely that the weaker climatic fluctuations of the late Pliocene and early Pleistocene were important in lowland diversification either.

In contrast, the late Pleistocene increase in highland diversification rate resulted in a fauna with one-third of its species dating to the last million years. Unlike lowland regions, extensive evidence suggests that widespread alteration of highland habitats occurred repeatedly during the late Pleistocene. Extensive glaciation occurred throughout highland regions (Hooghiemstra and van der Hammen 2004). Glaciers undoubtedly fragmented the ranges of many Andean species by providing a hard barrier between populations displaced along the eastern and western slopes. In addition, cooling resulted in an elevational migration of habitat zones to lower altitudes resulting in an elevational compression of some zones and expansion of others (van't Veer and Hooghiemstra 2000; Hooghiemstra and van der Hammen 2004). The cor-

relation between the onset of severe glaciation in the Neotropics about 0.8 to 0.9 mya (Bennett 1990; Hooghiemstra et al. 1993) and the late Pleistocene increase in speciation rates suggests a causal link.

Interchange between highland and lowland faunas also played an important role in Neotropical diversification (Fig. 3). Dispersal events from the lowlands to the highlands occurred primarily during the late Miocene and early Pliocene when extensive uplift of the central and northern Andes provided new elevation zones and habitats. Thirty-three nodes represent dispersal from lowlands to highlands compared to 146 nodes that represent divergence within highland faunas. This fairly large proportion suggests that dispersal from lowland regions contributed importantly to the build-up of species diversity in the highlands. In contrast, Fjeldsa and Lovett (1997a,b) envisioned dispersal out of highland regions as a major source of species diversity for lowland faunas. Whereas 16 dispersal events from highland to lowland faunas are reconstructed in this dataset, compared to the 198 splitting events that occurred within the lowlands, dispersal from highland faunas represents only a small contribution to lowland diversity. Rather, diversification within lowland regions was the predominant mode by which species accumulated in this fauna. Moreover, most dispersal events from the highlands into the lowlands occurred during the last one million years (Fig. 3) and correlate with major glacial cycles in the Andes (Bennett 1990; Hooghiemstra et al. 1993). Glacial lowering of elevational zones resulted in mixed floras (Colinvaux et al. 1996, 2000; van der Hammen and Hooghiemstra 2000; Bush et al. 2004) and presumably mixed faunas near the base of highland regions that included both lowland and highland components. This mixing may have facilitated adaptation to and subsequent invasion of lowland regions (Rull 2005).

These results are inconsistent with the once prevalent view that late Pliocene and Pleistocene climatic fluctuations drove the recent buildup of species diversity in lowland Neotropical faunas. Many Nearctic avian taxa also display decreasing speciation rates through time (Zink and Slowinski 1995; Zink et al. 2004), suggesting that the processes that promoted speciation in both faunas occurred primarily before the onset of the late Pliocene and Pleistocene ice ages. Nevertheless, this study suggests that the proportion of species of glacial age is much higher in highland regions of the Neotropics where expanding and retracting glaciers directly fragmented habitats. A late Pleistocene increase in faunawide rates of diversification correlates with the onset of severe glaciation in highland regions and resulted in a fauna in which one third of extant species are less than a million years old. Likewise, ice sheets directly fragmented the high latitude boreal forests of the Nearctic where a greater proportion of avian sister species date to the Pleistocene than in subboreal regions (Weir and Schluter 2004). Together, these studies suggest that diversification rates in faunas distributed closest to the expanding and retracting glaciers were most heavily impacted by climatic fluctuations whereas faunas distributed further from the glaciers were impacted to a lesser degree. Further sampling of other glaciated regions is necessary to determine the generality of this pattern.

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