

DIVERSIFICATION OF THE NEOTROPICAL AVIFAUNA: DISENTANGLING THE GEOGRAPHICAL PATTERNS OF PERSISTING ANCIENT TAXA AND PHYLOGENETIC EXPANSIONS

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Resumen. – **Diversificación de la avifauna neotropical: desentrañando los patrones geográficos de taxones persistentes antiguos y las expansiones filogenéticas** – Con el desarrollo de bases de datos digitales de distribución de especies y de filogenias moleculares, ahora es posible analizar los procesos espacio-temporales de diversificación. Esto se puede hacer mediante el análisis de la distribución geográfica de especies evolutivamente próximas en los árboles filogenéticos, de los patrones de diversidad de clados antiguos y de especies de diferentes edades. La “conservación de nicho tropical” parece estar relacionado con el desequilibrio de la suma neta de los procesos de nacimiento y muerte, y con la mayor persistencia de clados con bajas tasas netas de especiación en las tierras bajas tropicales, en comparación con tasas más elevadas en otros lugares. Las distribuciones geográficas divergentes de los grupos que sufrieron expansiones filogenéticas durante el Neógeno sugieren una fuerte capacidad de acceder a nuevas regiones ecológicas, en particular en el sur y en la región tropical de los Andes, donde los pulsos de especiación más intensos tienen lugar ahora en el límite de la vegetación arbórea. La especialización y densa compartimentación de los nichos podrían ser los procesos que explican las continuadas elevadas tasas de especiación en los Andes.

ABSTRACT. – With the development of digital distribution databases and comprehensive molecular phylogenies it is now possible to analyze diversification processes in time and space. This can be done by contrasting geographical distributions of sister groups up through the phylogenetic hierarchy, patterns of ancient clade diversity and species representing different ages. The “tropical niche conservatism” appears to be linked with the imbalance of the net sum of birth-death processes and the higher persistence of clades with low net speciation rates in the most productive tropical lowlands, compared with a higher turnover elsewhere. Divergent geographical distributions in groups that underwent phylogenetic expansion during the Neogene suggest a strong ability to access new ecoregions, notably in the south and in the tropical Andes region, where the most intensive speciation now takes place in the tree-line zone. It is suggested that specialization and dense niche packing forms the basis for continuous high speciation rates in the Andean “hotspot”.

Keywords: Suboscine birds, species diversity, lineage diversity, root-path groups, tropical niche conservatism, speciation, endemism.

Biogeographic research has long been hampered by the lack of communication between disciplines. While the macroecologists have set out to explain the large-scale trends in species diversity from present-day ecological conditions, ignoring that every species has a history, the historical biogeographers were most con-

cerned with the methods for tracing generalized patterns of vicariance and identifying underlying barriers. Although a significant proportion of the large-scale variation in species richness is well explained from climate-based environmental models, this correlation is mainly caused by the many data points representing the most

widespread species (Rahbek et al. 2006). On the other hand, the very aggregated distributions of range-restricted species represent high residual values that are hard to explain from present-day environmental parameters and therefore require historical explanations (Jetz et al. 2004, Rahbek et al. 2006, Hawkins et al. 2006). Over the last two decades, the rapid development of digital distribution data and molecular phylogenetic data has opened new perspectives for teasing apart the environmental and evolutionary causes of biogeographic patterns (Jetz et al. 2004; Hawkins et al., 2005; Weir 2006).

Interpretations of large-scale patterns of diversification have until recently been hampered by lack of phylogenetic data. Thus, biogeographic interpretations were often based on simple assumptions, such as centers of species richness representing centers of origin (dispersal centers; Müller 1976). With the emergence of modern phylogenies, this was replaced by area cladograms and recently by more sophisticated ancestral area reconstructions that take into account dispersal and uncertainties in the phylogenetic reconstructions (e.g., Burns & Haricot 2009; Santos et al. 2011). Such methods cannot remove the uncertainty about how much of the ancestral distributions that have been erased by extinctions and range dynamics caused by past climatic perturbations, such as the disappearance of the species-rich tropical-like forest of the Argentinean Patagonia until the end of the Eocene (Wilf et al. 2003). Because of this uncertainty, I will illustrate here more general tendencies based on comparison of spatial diversity patterns for ancient and terminal lineages. This will first of all be done for the endemic radiation of suboscine birds. On this background I will address more general questions about the relative roles of extinction, speciation, niche conservatism and phylogenetic expansion.

METHODS

Species distribution data are part of a comprehensive global distributional database de-

veloped at the Centre for Macroecology, Evolution and Climate (version July 2010). The geographical range of each species has been mapped at a resolution of 1° x 1° lat-long quadrates, following the approach outlined by Rahbek & Graves (2001). Maps represent a conservative extent-of-occurrence for the breeding range based on museum specimens, published sight records and spatial distribution of habitats between documented records (>1000 references used for South America), and has been validated by many experts. The species level taxonomy is updated according to Remsen et al. (2011). The software used (Worldmap) calculates various diversity measures, such as species richness in grid-cells, range centers, mean range-size and endemism (either number of species representing the 1st range-size quartile, viz., the 25% of all species with smallest distributions, or the sum of inverse range-size values). The species distribution data can then be linked with tree-spanning measures such as mean root path (sometimes used as evidence of tropical niche conservatism, although biased towards species poor areas), based on a supertree for all birds (compiled through review of most of the published phylogenetic studies), and densely sampled molecular phylogenies for some groups. Special attention will given here to the endemic suboscine radiations, because of the well resolved and densely sampled phylogenies (notably Irestedt et al. 2009; Ohlson et al. 2009, in review; Moyle et al. 2008; Tello et al. 2008; Derryberry et al. 2011), and because this is the largest endemic radiation that evolved in splendid isolation through most of the Tertiary, until the establishment of the Panama Isthmus allowed a limited amount of phylogenetic expansion to the north.

In addition, dated phylogenies can be used to reconstruct patterns of clade diversity at particular points in time. We cannot know the past distribution of a clade, but assuming that it diversified *in situ*, by vicariance, we may esti-

mate the ancestral distribution by merging the ranges of all constituent species and removing only the peripheral areas (notably outside South America) that evidently represent dispersal in a terminal subclade. Time windows for reconstructions of clade diversity maps were defined from earth history data: Assuming that modern bird groups flourished during the Eocene climatic maximum (when species-rich tropical-like forests existed south to Patagonia; Wilf et al. 2003) but suffered a serious set-back at the Eocene/Oligocene transition (34 Mya) during the first Antarctic chill. New crown group radiations started again late Oligocene up until the mid-Miocene optimum (15 Mya) (see Zachos et al. 2001). Past diversity patterns were therefore assessed by mapping:

- 1 the diversity of small clades (of all birds; defined as lineages with 1-3 allospecies) that date back to the warm Eocene and
- 2 the clade diversity for suboscine groups in the late Oligocene (26 Mya), after the Oligocene chill and just before the onset of intensive diversification in crown groups, and
- 3 the clade diversity of suboscines in the mid-Miocene (15 Mya).

These geographical patterns can be compared with diversity patterns for all South American birds, as a general measure of representativeness (Tab. 1; r values refer to compari-

son with the total diversity and with range size groups, from the 1st to 4th quartiles [25%] of least to most widely distributed). This provides an indirect assessment of the ecological determinants of the illustrated pattern, which is well documented for all endemic South American birds and analyzed Rahbek et al. [2006] with respect to environmental models that best explain the geographical patterns.

Recent diversification can be illustrated for groups with densely sampled phylogenies. Fjeldså & Irested (2009) illustrated the spatial diversification of Furnariidae using root-path quartiles as a surrogate measure of age, but this can now be supplemented with molecular age estimates of all terminal species taxa thanks to the very densely sampled phylogeny by Derryberry et al. (2011). During the preparation of this manuscript, most other phylogenies of South American birds have been examined for general trends.

RESULTS

Patterns of large scale variation in avian diversity in South America is illustrated in Fig. 1. The phylogenetic relict species (Fig. 1a) are most strongly represented in the most extensive areas of lowland rainforests and floodplains, corresponding well to the diversity of the most widespread quartile of South American bird species (Tab.1). The other maps are

Table 1. Comparison of geographical diversity patterns (r values) of the illustrated diversity patterns (Figs 1, 2 and 3) with patterns for all endemic South American birds, as presented in Rahbek et al. (2006) (1st quartile is the 25% of species with the smallest geographical ranges; 4th quartile is the 25% of most widespread species). Because of the high autocorrelation in such datasets, it was not considered relevant to present p values).

	Fig1a	b	c	d	Fig.2a	Fig.3 ^a	b	c	d	e
All	0.82	0.91	0.98	0.24	0.94	0.87	0.82	0.84	0.15	0.28
1 st	0.12	0.30	0.29	0.82	0.33	0.11	0.09	0.14	0.12	0.01
2 nd	0.21	0.27	0.23	0.71	0.30	0.15	0.11	0.16	0.08	0.05
3 rd	0.62	0.47	0.45	0.43	0.51	0.74	0.28	0.43	0.49	0.20
4 th	0.88	0.90	0.98	0.31	0.94	0.74	0.79	0.82	0.33	0.29

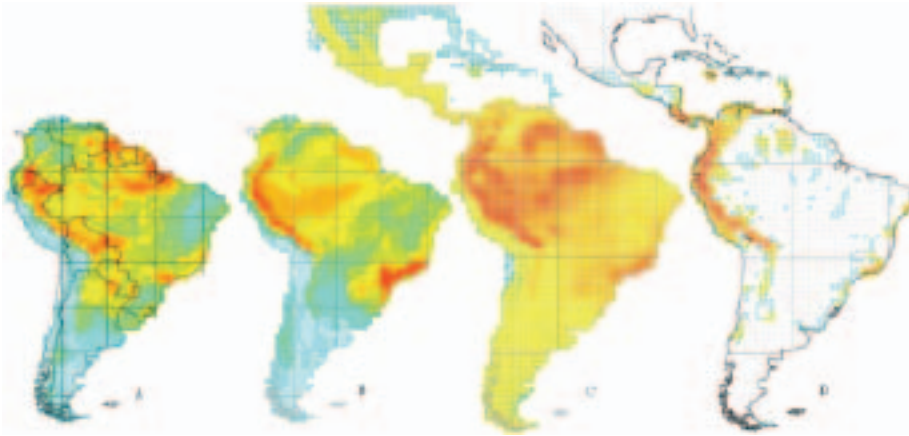


FIG. 1. General characteristics of diversity of South American birds. A, variation in distribution of 65 phylogenetic relict avian species of Eocene age; b, diversity of 19 suboscine clades as of 26 million years in the late Oligocene; c, diversity of extant species; and d, of the 25% species with the most restricted distributions. Proportional colour scale, red colour representing the highest number of taxa (which is 180-285 species in map c).

based on suboscine birds only. The highest lineage diversity from the early phase of the diversification of suboscine crown groups (late Oligocene; Fig. 1b) is rather concentrated in the southern Atlantic forests of Brazil, with many small clades, and in the western Amazon area up to the sub-Andean zone; many of the old lineages being disjunctly distributed in both areas (Batalha-Filho et al. 2013). These ancestral patterns are also evident in the map of terminal species taxa (Fig. 1c), with the quartile of most range-restricted species in the tropical Andes region (Fig. 1d). Very similar species richness patterns are found when comparing the richness patterns of Tyrannides versus Furnariides ($r = 0.94$), Suboscines versus Oscines ($r = 0.85$), and Suboscines versus hummingbirds, Trochilidae ($r = 0.89$; Rahbek & Graves 2001). The geographical patterns for range-restricted suboscines (Fig. 1d) is closely similar to that for all range-restricted birds (Tab. 1).

Basal suboscine clades are widely distributed in the mesic tropics, notably in the ancient cratonic areas north and south of the Amazon

basin. However, some clades of Andean origin appear from the Oligocene and early Miocene (Rhinocryptidae, *Chamaeza*, *Geositta*, and *Grallaria* / *Grallaricula*), and several other appear towards the mid-Miocene. Some of these are rather small clades (*Ampelion* group, *Ampelioides*, *Teledromas-Rhinocrypta-Acropternis*, *Pygarhicas/Ochetorhynchus*, *Pseudocolaptes-Premnornis-Tarphonimus*), suggesting a down-scaling of diversification rates, other clades maintained high speciation rates throughout the upper Tertiary.

Interestingly, by the mid-Miocene (15 Mya), most suboscine clades can be classified as either based in the Andes region (or Andean-South Brazilian uplands) or Amazonian/Guianan. Fig. 2 presents diversity of clades at 15 Mya, with separate colours for the two geographical origins in Fig. 2b (this graph excludes, though, some clades of other, or uncertain, geographical origin; see legend). It is evident from this illustration that the maximum diversity (white cells, or red cells in Figs 1 b and c) are in grid-cells located along the borderline between the Andean and Amazonas faunas, and that there

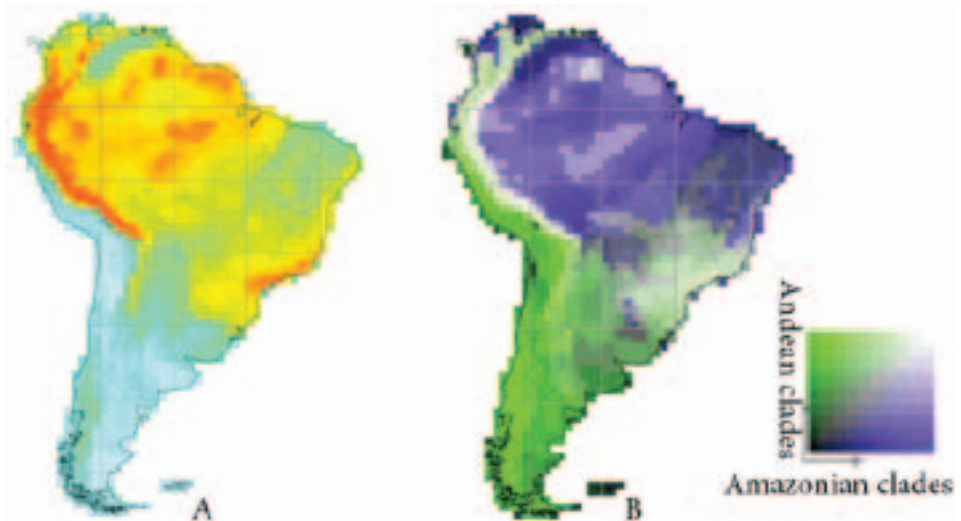


FIG. 2. Diversity of suboscine clades at 15 Mya. To the right, these have been split up into 35 clades rooted in the Andes region (green), and 36 clades rooted in tropical lowlands (purple) (q^2 0.416). Note that mixing of these groups produce grey hues, and overall lineage diversity is expressed as brightness, with the most diverse areas appearing white. (This comparison excludes the south Brazilian *Calyptura* and *Carpornis* and five larger groups whose biogeographic origin is difficult to place although it is most probably rooted in a broadly defined southern savanna region, namely the crown group of spinetails, thornbirds and elaenine, tyrannine and fluvicoline flycatchers).

has been very limited geographical mixing of these faunas. Among the Amazonian clades, some species have apparently dispersed north of the Colombian Andes or crossed the Andes to the Chocó region, but only very few have developed a decided tolerance for montane conditions. Similarly, only few terminal species in Andean clades colonized the Amazonian lowlands.

The densely sampled and time calibrated phylogeny for Furnariidae (Derryberry et al. 2011) is used in Fig. 2 to illustrate the historical progress of speciation events. The oldest species, representing speciation events around the mid-Miocene, are mainly found in the Amazon basin and along its ancient drainage channel to the north, and in the Chocó and to some extent in the Guianas and southern Atlantic forest (Fig. 3a). The diversification then continued in the Guiana highland and in the upper (Solimões/Pebas) Amazon basin, with a concentration in the sub-Andean forelands becoming

increasingly prominent towards the Pliocene. An apparently high diversity along the lower Amazonian channel east of the Purus Arc (Fig. 3 b-d) marks the in-grid-cell overlap of species inhabiting the northern and southern banks (thus this does not reflect local endemism, as no range-restricted species are centered in this area). Also the local peaks at Río Sao Francisco in eastern Brazil and along the western edge of the Brazilian shield (Fig. 3d) represents points of marginal overlap between regional faunas. Recent diversification took place throughout the southern savannas (Fig. 3d) and in the Andes (Fig. 3e). The high levels of Pleistocene speciation along the humid eastern edge of the highest parts of the Andes (Fig. 3 d and e). Areas with no new species originating during the upper Pleistocene (white in Fig. 3e) correspond to areas of highest median range-size.

The Tyrannida follow a similar pattern, with basal radiations (Cotingidae, Pipridae,

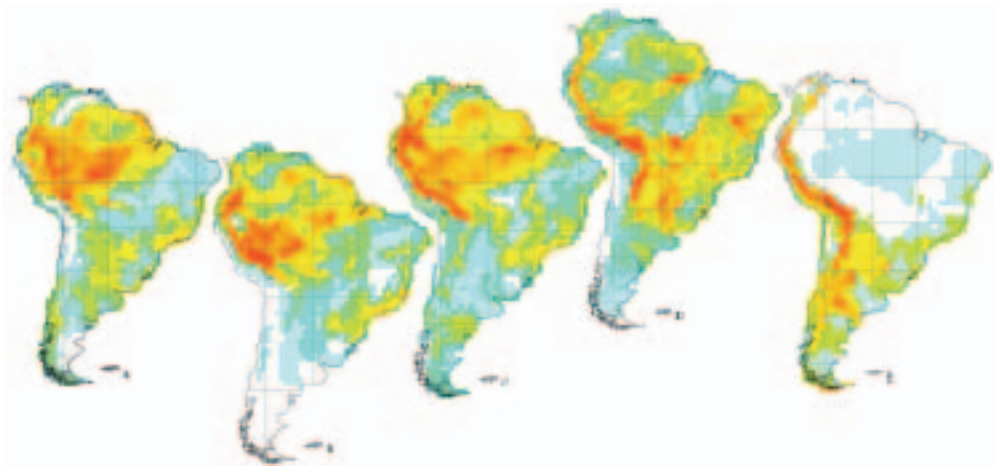


FIG. 3. Diversification of South American furnariids, illustrated as spatial variation in richness of species in groups based on time to the most recent common ancestor, following molecular phylogenies of Derryberry et al. (2011) and Ohlson et al. (2013). A, 45 species lineages with origin 20-7.5 million years ago; B, 34 species age 7.5-5 my; C, 79 species age 2.5-5 my; D, 86 species age 2.5-1.5 my; E, 48 species age <1.5 my.

Tityridae, Rhynchocyclidae and various small old clades) mainly in the mesic tropical lowlands, and elaenines, tyrannines and fluvicolines expanding out in the open, first in the southern tropical woodland savannas, but continuing in the southern cone of the continent (Xolmiini) and in the Andes (Fluvicolini and Xolmiini), and with phylogenetic expansions out of South America in Tyrannini and Contopini (Tello et al. 2009; Ohlson et al. 2008 and in review). The tapaculos diversified along the entire Andes (with gaps in the arid highlands), with three colonizations to S Brazil and one old colonization to the Amazon lowlands.

DISCUSSION

Imbalanced distribution of old and young taxa. The illustrated species richness pattern for the endemic suboscine radiation (Fig. 1c) resembles that for groups that colonized in recent geological times (tanagers; FjeldsÅ & Rahbek 2006), and for other taxonomic groups, such as mammals (Tognelli & Kelt 2004) and plants (Barthlott et al. 2005). Thus, this appears to represent

a fairly general pattern of variation in terrestrial biodiversity in South America, at this scale of spatial resolution. The diversity pattern for the most ancient avian species (Fig. 1a) resembles the pattern for the most widespread birds (Tab. 1), corresponding to extensive mesic lowland habitats and well explained from net primary productivity (Rahbek et al. 2006 fig. 3). Most of the ancient, small clades are relatively large birds that may have required extensive areas to persist over such a long time, which may explain their general absence inside the montane regions.

The mid-Tertiary lineage diversity pattern (Figs 1b and 2a) appears to be reflected in the current species diversity pattern ($r = 0.91$ and 0.94 ; Tab. 1). Using the same distributional and phylogenetic data as this study, Sanín et al. (in review) found that 81% of the variation in species diversity at a spatial resolution of $10 \times 10^\circ$ could be explained from the lineage diversity as far back as 40 mya. This would seem to suggest a strong role of regional variation in speciation rates. This may notably be the case near the geologically dynamic western edge of the continent. However, part of the

explanation may also be range-dynamics: A high loss of diversity in the south as a consequence of major climate perturbations, and a higher persistence of lineages in the areas that remained warm and humid. The disappearance of the diverse tropical-like forests of Patagonia during the abrupt global cooling (Terminal Eocene Event, 34 Ma; Wilff et al. 2004; Zachos et al. 2001) must have put an end to many warm-adapted groups. The Tyrannides phylogeny (Ohlson et al. 2009, 2013) has a long basal branch, a single species surviving up until 32 Ma. This ancestor was probably a rainforest frugivore (judging from the ecology of the basal tyrannid groups of manakins, cotingas and some small clades). Frugivory is also widespread (as a diet supplement) in other tyrannid groups. Such frugivorous birds may have become brutally restricted by the global cooling at the Terminal Eocene Event, and the early radiation of the Tyrannides crown group therefore took place near the equator. As the old groups were thus shuffled together in the remaining tropical forest regions, the continuing diversification in the south was constrained by the development of a large rain shadow area that developed as a consequence of the Andean uplift.

The asymmetries of many phylogenies suggests that early bursts of diversification were followed by apparent down-shifts, leading to the emergence of many small clades (Ricklefs 2005), which mainly survived in the southern part of the Brazilian Atlantic forest and in the sub-Andean Amazon Basin (Fig. 1b). The high persistence of old lineages in this region has given rise to the idea of tropical niche conservatism as a historical narrative for explaining such broad species richness gradients (Fig. 1 a, b; Hawkins et al. 2005; Weir 2006). However, the distinct pattern in Fig. 2b suggests that also the Andean clades may also be constrained by niche conservatism. The Andes contains an interesting mix of radiating groups and small/old clades that persisted in

situ, mainly in the lower montane forest (e.g., *Laniisoma*, *Snowornis*, *Thamnistes*, *Premnoplex*, *Margarornis*, *Hellmayrea* and *Pseudocolaptes*, and *Aphrasture* in the south), with little or no net diversification, at least not during the Pleistocene.

As illustrated in Fig. 3, the geographical patterns of diversification changed in time. The lowland rainforest clades diversified mainly during the Miocene, with some shifts over time, but apparently there was a down-shift in the radiation of rain-forest groups, and these groups were only moderately elevation tolerant and successful in colonizing the rising tropical Andes region. The philydorine genus *Thripadectes*, which radiated in the Andes since 8-9 Mya (Derryberry et al. 2011), is the most noteworthy exception. World wide, it seems that speciation in tropical lowland biomes ceased during the last million years of great climatic instability (Päckert et al. 2011 for Asia; Fjeldså et al. 2007 for Africa).

In contrast, the Andean clades continued to diversify, and various synallaxine groups (as well as the Tyrannidae flycatchers, sensu Tello et al. 2009 and Ohlson et al. 2013) diversified strongly during the upper Miocene in the mosaic habitats that developed with the spread of savannah vegetation and grasslands in the southern subtropical zone (Zachos et al. 2001). This shift of the frontier of diversification to the south is reflected in the low r values in the right column in Tab. 1. Apparently, the southern savanna region was a center diversification and expansion to riparian habitats and edge habitats in the Amazon (*Cranioleuca*, *Synallaxis*) as well as to the central parts of the Andes. There has been a significant exchange between Andean-Pampean region and the South Brazilian highland forest. Interestingly, as the involved groups are strongly associated with rugged terrain (or well-drained soils), this Andean-Brazilian track was broken by the development of hydrologically unstable plains in the Beni-Pantanal region (Fig. 2b). During the

climatically most unstable upper Pleistocene the diversification continued only in some clades and mostly at 13–18° south in Peru and Bolivia, and mainly at the upper tree-line and upper montane valleys (Fjeldså & Irestedt 2009).

In the New World flycatcher group, phylogenetic expansions outside the topical lowlands, and in open habitats, happened only from the mid-Miocene, and only in one major clade (*Tyrannidae sensu stricto*; Ohlson et al. 2009), with different subclades moving into distinct areas, thus the Xolmini radiating mainly in southern open habitats and the barren Andean puna, while the Ochothocini radiated in the montane cloud-forest zone (García-Moreno et al. 1998) and the Contopini dispersed to North America.

Oscine groups arriving from the north (Weir et al. 2009) diversified first of all in mountain ridges of Central America and Colombia (Fjeldså & Rahbek 2006; Klicka et al. 2007; Sedano & Burns 2009; Lovette et al. 2010) and after a rapid initial burst of speciations in this region several lineages of finches and tanagers underwent phylogenetic expansion further south in the Andes and in the tropical and southern subtropical lowlands (like in amphibians; see Santos et al. 2011). Other colonizing groups arrived through trans-oceanic sweepstakes dispersal (vireos, thrushes, mockingbirds, euphonias), radiated mainly in the lowlands, but over all with significant flexibility in their life zone associations. Although oscine and suboscine groups have markedly different biogeographic histories, the coarse-scale diversity patterns are remarkably similar.

Linking diversity patterns and earth history. The most basal members of the extant suboscine groups inhabit ancient cratonic areas (Guiana and Brazil Shields) and some parts of the southern Andes and there is significant connectance in the east between the Guianan and Brazilian shield faunas. Apparently some of the old rainforest

groups may have their origin in the southern Atlantic forest of Brazil but expanded along the western edge of the Brazilian cratonic shield into the western Amazon basin (Batalho-Filho et al. 2013). The tropical lowland groups invaded the Andean habitats only marginally (*Thripadectes*); yet some clades of the mesic tropics colonized the Chocó region by circumventing the Colombian cordilleras, or by crossing the low passes of southern Colombia or northern Peru (Haffer 1974).

The comparison of Andean and Amazonian clades that diverged in the mid-Miocene, well before the final uplift of the northern Andes, is a novel demonstration of long historical isolation of clades in the Andean orocline and specialization for this misty environment. The extraordinary biodiversity at the Andean-Amazonian interface (Fig. 1) emerges as an effect of overlap (at the spatial resolution of this grid) of faunas with different histories.

To understand the historical separation of Andean and Amazonian clades we need to look into the geological history. The Andean habitats are often described as young environments, but the orocline as such has a long history (Garzzone et al. 2008; Mamani et al. 2010). As a consequence of the convergence of South America with the oceanic Nazca Plate, marine terranes were accreted to the north-western margin of the continent (Ecuador to Venezuela) and a proto-Andean chain developed along the entire western plate boundary. Here we need to acknowledge that even small mountains near tropical coasts will be distinct from the surrounding lowlands in terms of climate and habitat structure with stunted, microphyllic and epiphyte-laden cloud forest down below 1000 m elevation (Foster 2001; Bruijnzeel et al. 2010). This may have allowed physiological specialization for these cool/wet habitats and development of a distinct highland avifauna from already from an early stage.

Increasing uplift of mountain chains lead to formation of several thrusting planes and thick-

ening of the continental crust, and this load caused a subsidence of the lowlands to the east, first with formation of a narrow axial groove, whereby the water from the Andes could flow north to the Caribbean (Maracaibo) or south to the Paraná. Thus, the early fauna of the tropical Andes (Fig. 2b) may have been more or less isolated from that of the Brazil-Guiana area.

During the mid-Tertiary the Bolivian orocline underwent significant crustal thickening and bending (Mamani et al. 2010). The contact (“Chapare Buttress”) between the thrust front of the Bolivian Andes and the subsurface edge of the Brazilian Shield formed a structural divide between the Amazonas and Paraná systems and faunal exchange between the Andes region and uplands of southern Brazil, which explains why many clades are shared between the Andes region and the southern Brazilian uplands (Fig. 2b). As the weight of the Bolivian Andes continued to rise there was a large geological subsidence, leading to the formation of the present Beni plains (Hanagarth 1993, Silva 1994), and today only small fragments are left in southeastern Bolivia of the former high land surface, and the divide between the Amazon and Paraná basins shifted south (Lundberg et al. 1998: 42). The new, hydrologically unstable environments in the Beni-Chaco region became an insurmountable barrier for the birds adapted to rugged and well-drained landscapes, leading to the divergence from the late Miocene to early Pleistocene of Andean and South Brazilian sister taxa (see Fig. 2b).

Within the tropical Andes, the most recent diversification took place in the young eastern Cordillera of Colombia-Venezuela (Fig. 3e) and Bolivia (Fig. 3d and e). In the southern parts, this corresponds to where jagged configuration of the eastern Andean ridges form climatic pockets that are well protected against the ecological disturbance by south polar winds, notably during glacial periods (Fjeldså et al. 1999). This led to an extraordinary peak of species diversity 12-18°S of the equator.

Opportunities for diversification in the Amazon Basin may have shifted much in the course of the conversion from the wide-northwest-flowing flood basin to the current eastward-running Amazon basin since the late Miocene (Hoorn & Wesselingh 2010) or even as late as the Pliocene (Latrubesse et al. 2010). In the early Tertiary, this region was characterized by a sub-Andean groove draining north to Maracaibo (Venezuela), but gradually shifting east to form large tectonically controlled sedimentation basins (Solomões/Pebas) over large parts of western Amazonia. Some disagreement exists over the nature and timing of these wetlands, but apparently there were enormous freshwater swamp habitats and marine incursions (Lundberg et al. 1998; Hoorn & Wesselingh 2010) and in the late Miocene some tectonic deformation of foreland ridges (Divisor-Contamana ranges) in northern Peru are reflected in Figs 3 b and c. We must therefore assume that the Amazonian avifauna persisted by moving around, taking advantage of the patch dynamics and high productivity of the floodplains but generally within the same region, until the wetlands were filled up by megafans of sediment and the drainage towards the Atlantic Ocean was finally established. Thus, the diverse Amazonian and Andean faunas could finally merge, leading to the incredible present species diversity in the transition zone (Fig. 2b). The establishment of new rivers channels finally lead to distinct vicariant patterns and raised species richness in grid-cells that include para-species occupying opposite river banks (see Figs 3 c and d).

Diversification is tightly linked with geology and landscape evolution in the upper Amazon basin up through the Miocene and Pliocene, and in general there has been a slow-down in diversification after the present drainage pattern was established. In general, the bird populations inhabiting the Brazilian and Guianan shields are widespread and have undergone little diversification in recent geological times.

Speciation mechanisms. Low mean root-path distance in the tropical lowland biota has been taken as evidence of the tropical niche conservatism hypothesis, as opposed to assumed innovative adaptations characterizing the more terminal radiations in the Andes (Hawkins et al. 2006; FjeldsÅ & Irestedt 2009; Löwenberg-Neto et al. 2011). The high diversity in the lowlands is mainly associated with the enormous extent and complex geological history of the Amazon basin, but the lack of recent speciation in the Amazon lowlands suggests that Pleistocene forest refuges (Haffer 1974), if they existed, were not drivers of speciation. During the upper Pleistocene there was intensive speciation (among furnariids) only in the western Pampean region and in the Andes (Fig. 3e). The recent radiations are closely associated with the upper montane forest and tree-line zone (FjeldsÅ & Irestedt 2009), mainly in clades that originated south of the Amazon area (a similar situation has now been described for the upper montane forest zone in the Sino-Himalayan mountains, where lineages of northern temperate origin diversified intensively during the Pleistocene; see Päckert et al. 2011). This represents a habitat band that may be easily fragmented because of the narrow configuration of this habitat band and the steep terrain with many physical barriers (Graves 1988). In addition to this comes the complex ways in which the topography creates a mosaic of local climates, with local pockets of very predictable conditions. Areas with intensive recent speciation in the Andes corresponds closely with areas with many small distributions (Fig. 1d), in contrast to the lack of recent speciation in areas with high mean range-size on the tropical savanna regions and much of the Amazon/Guiana region (Fig. 3e).

Apparently, few groups were well adapted to cope with highland condition and to radiate in this harsh environment, leading to phylogenetically clustered communities in the highlands (Graham et al. 2009; Parra et al. 2010).

Most speciation took place within a narrow climate window, with sister species generally replacing each other at similar elevations on different slopes (Cadena et al. 2011). This suggests niche conservatism in the terminal niches, while segregation in different elevational zones (or in different structural habitats) on the same slopes were often delayed by several million years (García-Moreno & FjeldsÅ 1997). There are few cases of marked elevational shifts (e.g., *Cinclodes*, *Leptasthenura*, *Cranioleuca*). Thus, the key to understand intensive radiation may be related to conditions that allow remnant populations to persist in constantly favorable local environments within the montane habitat mosaic. This is rarely possible outside the tropics. Speciation has traditionally been explained physical barriers between areas, but many replacements appear to be secondary contact zones (in places with no obvious physical barriers) and it is important to note the importance of factors that promote local persistence during periods of environmental stress, when many species survive only as local relict populations. The most prominent local aggregation of restricted range species in the southern half of the tropical Andean hotspot are in valley systems that are protected by sharp bends on the eastern Andean ridges against the impacts of south polar winds, which represent a disturbing agent in the Pleistocene climate (FjeldsÅ et al. 1999). The most intensive recent radiation took place in resident species of dense thickets and elfin forest patches (*Scytalopus*, *Cranioleuca*, *Schizoeaca*), where the amount of gene flow may be limited (cf. Kisel & Barraclough 2010), but interestingly also the widespread *Cinclodes* and *Muscisaxicola* species of the barren alpine habitats maintain rapid speciation.

Because of the restricted distributions of many Andean endemics, each species can accumulate local adaptations that allow them to become more abundant, whereas in more widespread species the gene flow across sub-

optimal environmental gradients and over long distance may restrict local adaptation and thus the local abundance. Species must either be sufficiently generalist to utilize a broad habitat mosaic, including suboptimal sites, or they must survive *in situ*, by tracking specific habitat zones where they can maintain dense populations and remain resilient (Williams et al. 2009; Reif et al. 2010). The abundance of many range-restricted species, which should be well known among Andean ornithologists (although not documented quantitatively for these difficult habitats) is contrary to general theory of range-abundance relationships (Brown 1984; Gaston et al. 1997). Analyzing the mutualistic networks of plants and hummingbirds at 31 study sites spanning a wide range of climate regimes, Dalsgaard et al. (2011) found that the highest degree of mutualistic specialization in montane forests in Costa Rica, Colombia and coastal mountains in southern Brazil. Across all 31 study sites, the degree of mutualistic connectedness was well explained from “climate change velocity” (Loarie et al. 2009), which, based on global climate models, describes the rate at which species must migrate to keep track of climate change. Comparing present-day conditions with a global climate model for the last glacial maximum, the lowest levels of “climate change velocity” were found in tropical montane regions, and explains well the global variation in occurrence of local endemic species of amphibians, mammals and birds (Sandel et al. 2011). Thus, high local endemism can be explained from conditions that allow species to remain in the same geographical area, and specialize to local biotic and abiotic conditions, in spite of the instability of the global climate.

It has been predicted that the current global change may drive montane species out of the local elevational gradient, leading to large-scale extinction of montane birds (Sekercioglu et al. 2008, La Sorte & Jetz 2010). This might well apply to isolated, cone-shaped mountains, but may

be less relevant in large and complex montane regions, where conditions may vary over very short distances in the complex habitat mosaic (see Scherrer & Körner 2011). Global climate models based on interpolation between widely scattered weather stations cannot capture the complex local variation within the habitat mosaics of large mountain regions, where pockets of extremely stable conditions may exist locally because of interactions between wind systems, atmospheric stratification and topography.

Are communities saturated? The terminal radiations of the super-diverse clades of hummingbirds, tyrannids, furnariids and tanagers all took place in areas characterized by low climate change velocity within the tropical Andes region. Some subclades (coquette and brilliant hummingbirds; *Cranioleuca*, *Asthenes/Schizoeaca*, *Scytalopus* and mountain tanagers) are really outstanding, considering the short time span and the limited geographical space within which they have radiated. With the intense speciation in this region we may wonder whether diversification can continue.

Several studies have demonstrated declining diversification rates over time, suggesting a saturation as the ecological niche space is filled up (e.g., Phillimore & Price 2008; Rabosky 2009; Rabosky & Lovette 2008; Sedano & Burns 2010). McPeck (2008) considered that slow-down may be a general trend, and Raboski (2010) went on to suggest ecological limits as an alternative to speciation and extinction in explaining diversity patterns. Against this view, Morton et al. 2010 and Wiens (2011) argues that biological diversity continues to grow, and indeed the great speciator groups of South America (core tyrannids, furnariids and tanagers; Barker 2011) could be good examples. In all groups, the most intensive diversification takes place within a rather limited geographical area in the tropical Andes region. The analysis of furnariid diversification (Derryberry et al. 2011) suggests a continuously high rate of spe-

ciation as the diversification has shifted from the Amazon lowlands to other ecoregions with a very high landscape complexity. The most recent phylogenetic expansion in this group, as well as of crown group tyrannids, moves northwards in the tropical Andes region, into the areas with maximum diversity of nine-primaried oscines. Although these groups often feed together in mixed feeding parties, they differ markedly in feeding methods and microhabitats, and may therefore not interfere much in their use of food resources. Other examples of continuously high diversification rates are emerging (e.g., Fritz et al. 2011) for groups that have undergone large geographical expansions into new geographical areas.

It is more questionable what happens in ecoregions that are structurally less complex and where the species are widespread, move in response to climatic harshness and instability and thus are under shifting selective pressures. Here, the general range-abundance relationships (Brown 1984) could well apply, and the generalist species may squeeze out the local specialists.

Further studies of diversification rates need to be comprehensive, covering large taxonomic assemblages at continent-wide or global scale, and should include data on community structure, phylogenetic clustering as well as niche segregation. This next generation of studies can start now, as large distributional databases and large phylogenies become available, and as we obtain more ecological data: we now need to look at networks and community structure, analyzing packing of niches according to morphological segregation (as done already for furnariids; Derryberry et al. 2011) and resource use, and relatedness within local communities, and also on large geographical scales.

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