

Patterns of Diversity and Endemism in the Birds of the Tropical Andes

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Well over 2000 bird species, ca. 22% of all known species, inhabit the Andes of Colombia, Ecuador, Peru, and Bolivia from foothills (500 m) to snowline. Almost 600 (28%) of them occur nowhere else on Earth. The northern portion of the tropical Andes, extending from the Huancabamba depression in Peru to the Cordillera de Mérida of Venezuela, holds approximately the same number of bird species as the Amazon basin even though its surface area is 14 times smaller (Kattan et al. 2004). At a continental scale, bird species richness correlates with topographical complexity and ecosystem diversity, which are highest in the Andes. Species richness in $1^{\circ} \times 1^{\circ}$ latitude-longitude quadrats is 30-250% higher in the Andes (peaking at 850 species) than in the Amazon basin (Rahbek and Graves 2001). The tropical Andes are geologically young: Andean cloud forests are estimated to have evolved during the last 20 million years (Sempere et al. 2005), and the region's rich avifauna is undergoing active radiation and speciation since the Miocene (Fjeldså and Rahbek 1997). Therefore, large-scale human impacts such as landscape transformation and climate change are not only a threat to the diversity and uniqueness of the region's avifauna, but also to the evolutionary processes that have generated and maintain this diversity.

Higher-taxon richness in the tropical Andes is exceptional as well. Of the 28 orders and 96 families currently recognized as native to South America (Remsen et al. 2009), 25 orders (89%) and 75 families (78%) occur in the Andes. When excluding three orders and nine families of seabirds, representation increases to 100% and 86%, respectively. A recent taxonomic reference on the birds of the world (Dickinson 2003) recognized 194 families, 36% of which are found in the tropical Andes.

Of the global total of 218 Endemic Bird Areas (EBAs; Stattersfield et al. 1998, BirdLife International 2003), 47 (22%) are situated in continental South America, and 24 of these (51%) are partially or entirely located in the tropical Andes from Bolivia to the Cordillera de Mérida of Venezuela. A total of 355 restricted-range species (whose breeding ranges do not exceed 50,000 km²) distributed in 43 families (45% of all South American families) occur in the tropical Andes (366 species when including the Cordillera de Mérida) (Table 18.1), corresponding to 62 % (64%) of all restricted-range species in continental South America (<http://www.birdlife.org/datazone/>). The prevalence of restricted-range species is a widespread phenomenon in montane areas of the northern Neotropics (Renjifo et al. 1997). In addition to high levels of endemism, montane avifaunas are also unique in terms of ecological roles, as evidenced by the richness of nectarivorous birds and bird-pollinated plants (Renjifo et al. 1997, Krömer et al. 2006).

Table 18.1. Distribution by family of 366 restricted-range species (species whose breeding ranges do not exceed 50,000 km²) in the tropical Andes compared to the total number of species per family in continental South America, all islands within 1200 km of its shores in the Atlantic and Pacific oceans, and several islands in the Caribbean Sea (see Remsen et al. 2009). Eleven restricted-range species endemic to the Cordillera de Mérida in Venezuela are included.

Family	No. of restricted-range species tropical Andes	Total no. of species South America	Percent restricted-range species
Trochilidae (Hummingbirds)	57	254	22.4
Furnariidae (Ovenbirds)	43	283	15.2
Thraupidae (Tanagers)	38	195	19.5
Emberizidae (Sparrows)	33	162	20.4
Grallariidae (Antpittas)	25	49	51.0
Tyrannidae (Tyrant flycatchers)	25	348	7.2
Rhinocryptidae (Tapaculos)	20	53	37.7
Psittacidae (Parrots)	19	126	15.1
Cotingidae (Cotingas)	9	58	15.5
Thamnophilidae (Antbirds)	9	217	4.1
Cracidae (Guans)	8	43	18.6
Troglodytidae (Wrens)	8	47	17.0
Strigidae (Owls)	7	43	16.3
Parulidae (New World wood-warblers)	6	36	16.7
Odontophoridae (Wood-quail)	5	14	35.7
Picidae (Woodpeckers)	5	82	6.1
Turdidae (Thrushes)	4	32	12.5
Tinamidae (Tinamous)	4	45	8.9
Rallidae (Rails)	4	46	8.7
Ramphastidae (Toucans)	3	33	9.1
Fringillidae (Finches)	3	34	8.8
Columbidae (Pigeons and doves)	3	48	6.3
Podicipedidae (Grebes)	2	9	22.2
Capitonidae (Barbets)	2	14	14.3
Vireonidae (Vireos)	2	24	8.3
Pipridae (Manakins)	2	47	4.3
Accipitridae (Hawks)	2	54	3.7
Icteridae (New World blackbirds)	2	60	3.3
Semnornithidae (Toucan-barbet)	1	1	100.0
Cinclidae (Dippers)	1	2	50.0
Melanopareiidae (Crescentchests)	1	4	25.0
Nyctibiidae (Potoos)	1	6	16.7
Formicariidae (Antthrushes)	1	11	9.1
Corvidae (Jays)	1	15	6.7
Trogonidae (Trogons)	1	17	5.9
Galbulidae (Jacamars)	1	18	5.6
Cuculidae (Cuckoos)	1	21	4.8
Cardinalidae (Cardinal grosbeaks)	1	22	4.5
Apodidae (Swifts)	1	23	4.3
Falconidae (Falcons)	1	24	4.2
Tityridae (Tityras)	1	26	3.8
Caprimulgidae (Nightjars)	1	30	3.3
Bucconidae (Puffbirds)	1	35	2.9
Incertae Sedis*	1	—	—

* Species whose familial affinities are uncertain.

Birds are probably the best known group of organisms with respect to their taxonomy, natural history, biogeography, ecology, and conservation. Numerous studies have analyzed diversity patterns of tropical Andean birds at local and regional scales, but no comprehensive review of geographic patterns of species richness and endemism in tropical Andean birds has been published to date. In this chapter we synthesize current knowledge on such patterns in the region and briefly present the most prominent hypotheses on causal factors that underlie the most important patterns. Finally, we point out major knowledge gaps that need to be addressed by future studies. We use the terms ‘species diversity’ and ‘species richness’ interchangeably for the number of species present in a given unit of area. Analyses of restricted-range species are based on information extracted from BirdLife International’s 2009 species factsheets (<http://www.birdlife.org/datazone/>).

Species Richness and Spatial Differentiation Patterns

Species diversity can be partitioned into three components that are defined at different spatial scales (Schluter and Ricklefs 1993). Alpha diversity refers to the number of species in a sample or locality (also termed within-habitat diversity), whereas beta diversity is the spatial turnover in species composition between samples or localities (also termed between-habitat diversity). Gamma diversity is the total species diversity in all samples or in a given region or landscape. The exceptional bird species richness of the tropical Andes is a reflection of high beta diversity or spatial turnover in species composition at all spatial scales (local to regional). Although alpha diversities are relatively low in the tropical Andes when compared to the Amazon basin (see below), beta and gamma diversities are extraordinarily high (Fjeldså 1994, Stotz 1998, Rahbek and Graves 2001, Kattan et al. 2004, McKnight et al. 2007, Melo et al. 2009): as one moves farther from a point of origin, species composition in the tropical Andes changes much faster than it does in the Amazon basin.

Observed patterns of species richness vary with the spatial scale or resolution (e.g., local plots *versus* 1°×1° latitude-longitude grids) of the analysis (Rahbek and Graves 2000) and the spatial extent examined (e.g., partial *versus* complete elevational gradients; McCain 2005, 2009). Methodological approaches to studying patterns of species richness also vary from local field-based studies (e.g., Kessler et al. 2001) to regional meta-data analyses (e.g., Kattan and Franco 2004, Herzog et al. 2005b) to continent-wide grid-based analyses using inter- and extrapolation of species occurrence data from a wide range of primary sources (e.g., Rahbek and Graves 2000, 2001). These different methodologies may produce contrasting results because they rely on different assumptions and have different biases.

Habitat Patterns

In general, bird species richness correlates positively with habitat complexity and rainfall. Humid forested sites at 1800 m in the Colombian Andes harbor >130 species (Kattan et al. 1994, Naranjo 1994), whereas anthropogenic pasturelands at the same elevation have <80 species (Munves 1975). Humid (evergreen) forests, in turn, tend to hold more species per unit area than seasonally dry forests. For example, Schmitt et al. (1997) reported 50 breeding species at 1500 m in an arid valley in the Bolivian Andes, whereas at least twice as many species occur at the same elevation in humid montane forest at similar latitudes (Herzog et al. 2005a). In very wet rainforest on the Pacific slope of Colombia at 1000 m, 271 species have been recorded in 80 ha (Hilty 1997). In some cases, however, excessive precipitation may lead to a reduction in bird species richness (Herzog 2008).

Anthropogenically disturbed or degraded Andean forests are often characterized by lower bird diversity than ecologically equivalent undisturbed forests nearby (Aben et al. 2008). Andean forest bird communities are similarly affected by habitat fragmentation, which has reduced species richness by 30% in two Colombian cloud forests (Kattan et al. 1994, Renjifo 1999). Well matured secondary forest, on the other hand, may harbor greater bird species richness than comparable primary forest (O’Dea and Whittaker 2007), and early to mid-successional forest stages may be species-poor but contain unique species (G.H. Kattan, unpubl. data).

Elevational Patterns at Local Scales

Current knowledge on elevational patterns of tropical Andean bird diversity at local scales is largely derived from a surprisingly small number of empirical studies, particularly from the east Andean slope in Peru and Bolivia (Terborgh 1977, Graham 1990, Patterson et al. 1998, Kessler et al. 2001, Herzog et al. 2005a). Along complete humid forest transects that extend from foothills and adjacent Amazonian lowlands up to the current closed timberline or to the treeline, species richness tends to decrease steadily and linearly with elevation (Terborgh 1977, Patterson et al. 1998). Herzog et al. (2005a) found some deviations from this pattern in the wet Yungas of Cochabamba, Bolivia, where bird diversity peaks around 1000 m and remains fairly constant from about 1800 m to timberline. However, elevation (as a proxy for temperature and ecosystem productivity) is the best single-predictor variable of species richness. The Amazonian *terra firme* forest avifauna in this region is poor due to its semi-isolation at the southwestern terminus of humid lowland forest (Herzog et al. 2005a), which explains the upslope shift of the diversity peak.

In contrast to slopes comprised entirely of humid forest, a peak in bird diversity at some mid-elevation point appears to be the general rule for rain-shadowed inter-Andean valleys (Naranjo 1994, Stiles and Bohórquez 2000, Kessler et al. 2001). These often very steep valleys are truncated at their lower elevational end and characterized by seasonally dry forest on lower slopes, fairly dry evergreen forest on upper slopes, and semi-deciduous forest in the transition between the two. In two such valleys in Bolivia, the location of the bird diversity peak varies between about 2500 m and 3000 m according to local ecoclimatic conditions (Kessler et al. 2001). A hump-shaped relationship between species richness and elevation is also apparent when considering only seasonally dry forest in Bolivia, with maximum species richness at about 1000-1200 m (based on data in Herzog and Kessler 2006).

Bird diversity patterns on the much drier western slope of the central Andes are even more poorly known. In southwest Peru, an extensive mid-elevation section may be so arid that it holds no resident breeding bird species at all, and species richness (and abundance) peaks at an exceptionally high elevation of about 3500 m (Pearson and Pearson Ralph 1978).

Despite these contrasting elevational patterns of bird diversity, the main causes for them are the same. In a global meta analysis of elevational transects McCain (2009) found strong support for current climatic conditions as the main driver of bird diversity. Temperature in combination with water availability were particularly important factors (McCain 2009), resulting in gradients of increasing bird diversity from elevations with cold and dry to those with warm and humid conditions.

Elevational Patterns at Larger Spatial Scales

We know only two studies that examined elevational diversity patterns at regional to continental scales (Rahbek 1997, Kattan and Franco 2004). Both take into account the effect that area has on species richness: an increase in species richness with increasing area is one of the fundamental rules in ecology (Lawton 1999). Because the area of elevational bands decreases strongly as one ascends from Amazonian or Pacific lowlands to páramo or puna, comparisons of regional species richness at different elevations should account for this effect. After controlling for area, Rahbek (1997) found that species richness of South American land birds peaks in the upper foothills around 1000 m, decreasing by about 14% in the lowlands and by about 86% above treeline (4500 m). However, when restricting his analysis to the four tropical Andean countries considered here, species richness remained essentially constant from lowlands up to 1500 m, forming a low-elevation plateau rather than a mid-elevation hump, from where it decreased significantly towards the treeline (see Figure 2C in Rahbek 1997).

Kattan and Franco (2004) examined elevational diversity patterns for eight regions in the Colombian Andes and peripheral mountain ranges. Without controlling for area, species richness decreases linearly with elevation on external slopes that are directly connected to adjacent lowlands, whereas internal Andean slopes were characterized by a slightly hump-shaped relationship between species richness and elevation, with diversity peaks between 1000 m and 2000 m. After controlling for area, a different pattern emerged: similar to the results of Rahbek (1997), species richness remained essentially constant from lowlands up to 2600 m, forming a low- to mid-elevation plateau, from where it decreased significantly towards the treeline.

Latitudinal Patterns

Although the latitudinal gradient of species richness is ecology's longest recognized and one of its best documented diversity patterns (Rohde 1992, Rosenzweig 1995, Willig et al. 2003), latitudinal patterns in avian diversity have largely been neglected in the tropical Andes. We know only four publications that specifically address the topic, three of which examined a rather limited latitudinal gradient (370-530 km). Poulsen and Krabbe (1997, 1998) found essentially constant species richness (alpha diversity) along two trans-equator transects in cloud forest (3000-3350 m) on the east and west Andean slope in Ecuador. Herzog (2008) compared three localities in lower Bolivian Yungas forest (1150-1600 m), finding almost identical species richness at two sites and 28% lower richness at the third, which may be attributable to variations in habitat characteristics and precipitation levels. However, all studies reported considerable turnover in species composition (beta diversity) and community structure despite the limited extension of the gradients. At a much smaller scale, Kattan et al. (2006) found significant turnover in species composition among localities at the same elevation in neighboring watersheds in the Colombian Andes.

Comparisons of alpha-diversity values from more extensive latitudinal gradients are problematic because of differences in survey methods, effort, area, and elevational range employed by different studies. For example, the almost 50 species recorded by Remsen (1985) in a Bolivian cloud forest (3300 m) are not comparable to the 83-92 species in five east Andean cloud forests of Ecuador (Poulsen and Krabbe 1997) for all of the above reasons. However, a survey from another Bolivian cloud forest area (Herzog et al. 2005a) is much more comparable to those of Poulsen and Krabbe (1997). In the same elevational range (3000-3350 m), 76 species were recorded in Bolivia in approximately half the area and with

twice the survey effort, a value similar to the species richness found by Poulsen and Krabbe (1997) in five west Andean sites in Ecuador (65-80 species), but lower than alpha diversity in east Andean cloud forests of Ecuador. Whether this reflects a true latitudinal signal of decreasing alpha diversity with increasing latitude can not be ascertained without further field studies.

Fjeldså et al. (1999: figure 2) did not find a latitudinal pattern of gamma diversity for high-Andean birds that have breeding populations above 2500 m. An updated version of figure 2 in Fjeldså et al. (1999) is shown in Figure 18.1. Species richness in 15'×15' latitude-longitude grid cells is highest on the east Andean slope from northern Ecuador to central Bolivia, where it decreases sharply south of 18°S, with three marked peaks: in Ecuador just south of the equator (southeast of Quito, 265 species), in northern Peru in the Tabaconas Namballe area just south of the Ecuadorian border (257), and in central Bolivia in Carrasco National Park (253). On the west Andean slope gamma diversity is highest around the equator.

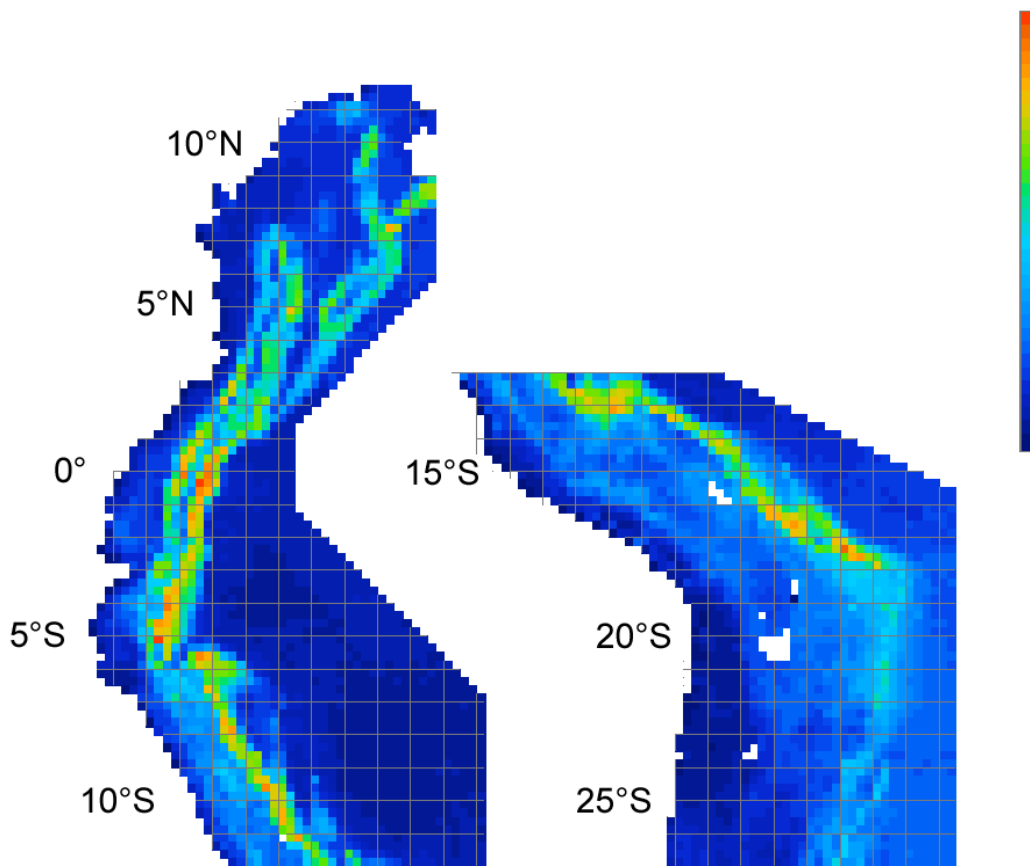


Figure 18.1. Species richness in 15'×15' latitude-longitude grid cells of high-Andean birds that have breeding populations above 2500 m. Red color indicates maximum species richness (265 species just south of the equator). Figure provided by J. Fjeldså in November 2009 (data derived from the distributional data base of the Zoological Museum, University of Copenhagen).

Environmental Drivers of Gamma Diversity Patterns

As for the elevational distribution of bird species richness (McCain 2009), gamma diversity ($1^{\circ}\times 1^{\circ}$ latitude-longitude grid cells) patterns in South American birds are largely explained by contemporary climate, particularly precipitation and energy availability (Rahbek and Graves 2001, Rahbek et al. 2007, although surface area (Rosenzweig 1995), regional and evolutionary history (Ricklefs 2004), as well as interactions between climate and evolutionary history (Rahbek and Graves 2001) can also play a role. It has become clear only recently, however, that the overriding influence of climate is not homogeneous for all groups of species. Rahbek et al. (2007) found that water and energy availability only explain diversity patterns of species with the largest geographical ranges, but not of species with small to moderately large ranges. Because widespread species contribute the largest number of data points they mask patterns of species with small ranges, which contribute little to the overall data. Richness patterns of narrowly distributed species appear to be influenced by topographic complexity and ecosystem diversity (Rahbek et al. 2007).

Endemism: Concepts and Patterns

The concept of endemism has been used in different ways in the biogeographic and conservation literature, but it generally refers to species whose geographic ranges are restricted in their spatial extent. Species with comparatively small ranges constitute an important component of biodiversity and its conservation because they are inherently vulnerable to habitat transformation and climate change. The term endemism has been applied to *political endemics*, i.e., species whose ranges are confined within the borders of a given country (or *near-endemics* when most of a species's range is confined to one country). The term has also been used to refer to species restricted to a biogeographic region such as the Andes. Stotz et al. (1996) divided the Neotropics into zoogeographic regions (dividing the tropical Andes into 'Northern Andes' and 'Central Andes'), and bird species found in only one such region were considered *zoogeographic endemics*. Young et al. (2009) similarly used the term to refer to 115 species restricted to the southwest Amazon watershed of eastern Peru and northern Bolivia.

Endemics are also defined as *restricted-range species* whose global breeding distributions do not exceed 50,000 km² (Stattersfield et al. 1998). Stattersfield et al. (1998) further identified Endemic Bird Areas (EBAs) that encompass the overlapping breeding ranges of at least two restricted-range species. A similar approach to defining areas of endemism in South America, albeit without a range size threshold, was used by Cracraft (1985), who identified 33 areas of bird endemism, including six in the Andes. However, knowledge about the distribution and species-level taxonomy of Neotropical birds has improved so much over the past 25 years that we will not discuss Cracraft's areas of endemism further.

In macroecological studies endemism is often expressed by two different quantitative measures. First, the lower *range-size quartile* of a species assemblage (the 25% of species with the smallest global ranges; Gaston 1994) is considered to be 'endemic', and the spatial distribution in the number of these 'endemic' species is examined. Second, a *range-size rarity* index is calculated as the mean inverse range size of all species combined in a given unit of analysis (Williams and Humphries 1994, Fjeldså et al. 1999), which represents a metric for the community or species pool as a whole.

Large-Scale Patterns of Endemism

Avian endemism in the tropical Andes is higher than anywhere else in continental South America as almost two thirds of the continent's restricted-range species occur in the tropical Andes. The Northern and Central Andes as defined by Stotz et al. (1996) each hold higher numbers of zoogeographic endemics (around 220 species each) than any other Neotropical zoogeographic region. This is partly a result of the peculiar shape of the distributional ranges of many Andean birds. These ranges, which extend along narrow elevational belts over fairly wide latitudinal gradients, favor population isolation and speciation processes (Graves 1985, 1988; Brumfield and Remsen 1996; Johnson 2002).

It can be argued that almost the entire tropical Andes constitute one large area of endemism. Latitudinally, areas of high endemism, as determined by an analysis of the number of lower range-size quartile species in 15'×15' latitude-longitude grid cells, are distributed fairly continuously and evenly from the Sierra Nevada de Santa Marta in northern Colombia south to central Bolivia (figure 4 in Fjeldså and Irestedt 2009; see also figure 1B in Fjeldså et al. 2005). Seven larger areas of peak endemism in the tropical Andes can be identified based on Fjeldså and Irestedt (2009), which overlap to varying degrees with 12 of the 24 EBAs found in the tropical Andes (Table 18.2). The other 12 EBAs cover much of the remaining area of the tropical Andes, the major exception being the Altiplano of Bolivia and southern Peru, which has very low levels of endemism. The top EBAs with the highest numbers of restricted-range species are: (1) Chocó in western Colombia and west-central Ecuador (EBA 041, 49 Andean restricted-range species); (2) Colombian East Andes (EBA 038, 34 restricted-range species); (3) Tumbesian region in western Ecuador and northwest Peru (EBA 045, 30 Andean restricted-range species). These are followed by the Santa Marta Mountains, Cordillera de Mérida, Peruvian high Andes, Colombian inter-Andean slopes, and North-east Peruvian cordilleras, each harboring 20-22 restricted-range species.

Young et al. (2009) identified three areas of endemism in the southwest Amazon watershed of eastern Peru and northern Bolivia, all of them in the Andes: southern Huánuco and central Cusco in Peru and the upper Yungas of northern Bolivia. They coincide at least partly with four Andean EBAs (North-east Peruvian cordilleras, Peruvian East Andean foothills, Bolivian and Peruvian lower Yungas, Bolivian and Peruvian upper Yungas), but due to the fine resolution of their study, Young et al. (2009) were able to identify which portions of a particular EBA likely harbor the largest number of endemic species. In addition, parts of the two Peruvian areas of endemism do not overlap with any EBA, including most of the Southern Huánuco area. In the central Cusco area of endemism, the southwestern Cordillera de Vilcabamba and the region along the Río Mapacho-Yavero east of Cusco do not coincide with an EBA.

Elevational (Local Scale) Patterns of Endemism

Along elevational gradients, endemism as expressed by both the lower range-size quartile and the range-size rarity index generally increases with elevation and peaks near the current closed timberline and, in Peru and Bolivia, in often isolated *Polylepis* forest fragments above timberline (Graves 1985, 1988; Fjeldså and Kessler 1996; Kessler et al. 2001; Fjeldså 2002; Fjeldså and Irestedt 2009). This is likely a consequence of the more fragmented topography and increased climatic harshness at higher elevations, which result in greater risks of stochastic local extinction, more scattered, isolated populations, and correspondingly faster rates of population differentiation (Kessler et al. 2001). Fjeldså and Irestedt (2009) further pointed out that the timber- and treeline zone plays a special role in diversification processes

Table 18.2. Qualitative comparison of the degree of spatial overlap between seven endemism hotspots (taken from figure 4 in Fjeldså and Irestedt 2009) and 12 Endemic Bird Areas (EBAs; Stattersfield et al. 1998, BirdLife International 2003) in the tropical Andes (from north to south). Figure 4 in Fjeldså and Irestedt (2009) is based on the lower range-size quartile of all South American breeding bird species with a spatial resolution of 15'×15' latitude-longitude grid cells (729-775 km²). See text for definition of EBAs.

Endemism hotspots	Endemic Bird Area	Degree of overlap
Sierra Nevada de Santa Marta, Colombia	Santa Marta mountains (EBA 036)	Very high
Cordillera de Mérida, Venezuela	Cordillera de Mérida (EBA 034)	Very high
Pacific slope from southern Cali department, Colombia, to just north of Quito, Ecuador	Chocó (EBA 041)	Moderate
East Andean slope at the equator, Ecuador	Ecuador-Peru East Andes (EBA 044)	Low
Southern Ecuador (Loja and Zamora	Central Andean páramo (EBA 043)	Very low
Chinchi provinces) and adjacent Peru	Ecuador-Peru East Andes (EBA 044)	Low
(Cordillera del Condor to northern	Tumbesian region (EBA 045)	Very low
Cajamarca and eastern Piura departments)	Southern Central Andes (EBA 046)	Very low
	Marañon valley (EBA 048)	Very low
Cordillera Vilcabamba north of Cuzco, Peru	Peruvian high Andes (EBA 051)	Very low
	Peruvian East Andean foothills (EBA 053)	Very low
Upper Bolivian Yungas (Cordillera de	Bolivian and Peruvian upper yungas (EBA	High
Apolobamba to Cordillera de Tiraque)	055)	Very low
	High Andes of Bolivia and Argentina (EBA	
	056)	

(see also Graves 1985, 1988), which underlines the conservation importance of timberline areas. Endemism drops sharply in adjacent puna habitats, where most species are widespread (Fjeldså and Kessler 1996), especially on the Altiplano of Bolivia and southern Peru (see figure 2 in Fjeldså et al. 1999, and figure 4 in Fjeldså and Irestedt 2009); whether this pattern also applies to the northern Andean páramo has not been analyzed. Thus, areas of high endemism usually do not coincide with areas of high species richness.

By contrast, when taking those species that are restricted to the Andes as our measure of endemism (some of which have fairly large ranges), richness of endemic species peaks at mid-elevations and decreases both toward higher and lower elevations (Kattan and Franco 2004).

Environmental Drivers of Endemism Patterns

Patterns of endemism essentially are diversity patterns of species with small geographic ranges. Based on the range-size rarity index, Fjeldså et al. (1999) showed that peak endemism areas in the Andes are characterized by high ecoclimatic stability, i.e., areas where particular topographic conditions moderate the impacts of extreme weather conditions. Such orographic moderation of climatic extremes is thought to have provided refugia for species during Pleistocene climate cycles, which suggests that many endemic species represent relict populations that survived periods of past global climatic change in these stable areas (Fjeldså et al. 1999). Therefore, these same areas may be important conservation targets in the light of ongoing anthropogenic climate change.

As mentioned above, Rahbek et al. (2007) determined that gamma diversity patterns of South American species with small to moderately large ranges (first three range-size quartiles) appear to be influenced by topographic complexity (measured as the elevational range of each grid cell) and, to a lesser degree, ecosystem diversity, rather than climatic factors such as precipitation or energy availability. Thus, topographically and ecologically complex landscapes are conducive to the historical persistence of local populations. However, Rahbek et al. (2007) failed to take into account climatic complexity. On the east Andean slope in southern Peru and Bolivia, climatic complexity (precipitation range and, to a lesser degree, temperature range) explains diversity patterns of first- and second-quartile species better than topographic complexity for the same 1°×1° latitude-longitude grids as used by Rahbek et al. (2007) (S.K. Herzog et al., unpubl. data). Thus, whether topographic complexity or climatic complexity is the driving force behind patterns of endemism still needs to be resolved.

Knowledge Gaps: Challenges for Future Research

Although birds probably are the best known higher group of organisms in the Andes, our knowledge is still rather incomplete. Avian systematics currently are very much in flux and far from resolved (see Remsen et al. 2009). Taxonomic changes are unlikely to alter diversity patterns, but they may lead to a refinement of the details of geographical endemism patterns, especially at larger spatial scales. Quite a number of Neotropical birds that were considered fairly widespread, polytypic species not too long ago have been split recently and some of their subspecies raised to species level (e.g., Brumfield and Remsen 1996, Krabbe and Schulenberg 1997, García-Moreno and Fjeldså 1999, Isler et al. 2007), some of which are now considered restricted-range species (e.g., *Atlapetes melanolaemus* and *A. rufinucha*). Patterns of endemism are further influenced by recently discovered species, which are constantly being described from the tropical Andes and generally have restricted ranges (e.g., O'Neill et al. 2000, Cuervo et al. 2005, Herzog et al. 2008). In fact, the most likely scenario for species still waiting to be discovered is that they have small ranges restricted to particular mountain chains or regions that are poorly (or not at all) studied. Nonetheless, although new species are often found in poorly studied sites, they often occur within areas that are already well known for their high endemism (e.g., Fjeldså 2000) and tend to strengthen known endemism patterns.

Large areas in the Andes have not yet been surveyed, resulting in incomplete knowledge of the distribution of many species. First explorations of such areas often result in numerous new distributional records (e.g., Herzog et al. 1999, MacLeod et al. 2005). Restricted-range species illustrate this: the 24 EBAs that are at least partly located in the tropical Andes were considered to hold 385 restricted-range species by Stattersfield et al. (1998). Just over 10 years later, 96 (25 %) of these are known to have range sizes > 50,000 km², in some cases much greater, and hence no longer qualify as restricted-range species. Although this does not influence the validity of those EBAs themselves, nor questions the EBA concept, it illustrates how much more there is to learn about Andean birds.

Current understanding of local elevational diversity patterns is based on surprisingly few studies, almost exclusively along forested gradients (excluding puna and páramo grasslands), and regional variations in the pattern are thus poorly known. A major obstacle to improving our knowledge are logistical difficulties of accessing entire elevational gradients from treeline to foothills and adjacent lowlands that are reasonably well preserved throughout. The factors and mechanisms that cause elevational patterns of diversity are still debated, especially with respect to the mid-domain effect (e.g., Colwell et al. 2004, 2005,

2009; Hawkins et al. 2005; Zapata et al. 2005; Kerr et al. 2006; McCain 2009). To further our understanding of the mechanisms underlying the observed diversity patterns, more quantitative studies using robust sampling methods along complete or almost complete altitudinal gradients spanning a range of ecoclimatic conditions (e.g., dry to wet) are needed (McCain 2009). The study of latitudinal patterns has fared much worse than that of elevational patterns in the tropical Andes, because there is not a single comprehensive quantitative analysis of large-scale latitudinal patterns.

Studies on historical population structures (phylogeography; e.g., Cadena et al. 2007) to identify places of maximum lineage persistence within the habitat mosaics of the tropical Andes are needed, and the identification of such places is particularly crucial in the face of climate change. Finally, although not directly related to biodiversity patterns, the natural history, ecological requirements, interspecific ecological interactions (see Aguirre et al. Chapter 4, this volume), and dispersal abilities of most species are very poorly known, making it difficult to predict the exact current ranges of species and their responses to environmental changes and habitat disturbance. This is important because local ecological factors significantly shape community composition and species richness patterns (e.g., Herzog and Kessler 2006, McCain 2009).

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Literature Cited

- Aben, J., M. Doerenbosch, S. K. Herzog, A. J. P. Smolders, and G. Van der Velde. 2008. Human disturbance affects a deciduous forest bird community in the Andean foothills of central Bolivia. *Bird Conservation International* 18:363-380.
- BirdLife International. 2003. *BirdLife's online World Bird Database: the site for bird conservation*. Version 2.0. Cambridge: BirdLife International. Available: <http://www.birdlife.org> (accessed 16/6/2009)
- Brumfield, R. T., and J. V. Remsen, Jr. 1996. Geographic variation and species limits in *Cinnycerthia* wrens of the Andes. *Wilson Bulletin* 108:205-227.
- Cadena, D. A., J. Klicka, and R. E. Ricklefs. 2007. Evolutionary differentiation in the Neotropical montane region: Molecular phylogenetics and phylogeography of *Buarremon* brush-finches (Aves, Emberizidae). *Molecular Phylogenetics and Evolution* 44:993-1016.
- Colwell, R. K., C. Rahbek, and N. J. Gotelli. 2004. The mid-domain effect and species richness patterns: what have we learned so far? *American Naturalist* 163:E1-E23.
- Colwell, R. K., C. Rahbek, and N. J. Gotelli. 2005. The mid-domain effect: there's a baby in the bathwater. *American Naturalist* 166:E149-E154.
- Colwell, R. K., N. J. Gotelli, C. Rahbek, G. L. Entsminger, C. Farrell, and G. R. Graves. 2009. Peaks, plateaus, canyons, and craters: the complex geometry of simple mid-domain effect models. *Evolutionary Ecology Research* 11:355-370.
- Cracraft, J. 1985. Historical biogeography and patterns of differentiation within the South American avifauna: areas of endemism. *Ornithological Monographs* 36:49-84.

- Cuervo, A. M., C. D. Cadena, N. Krabbe, and L. M. Renjifo. 2005. *Scytalopus stilesi*, a new species of tapaculo (Rhinocryptidae) from the Cordillera Central of Colombia. *Auk* 122:445-463.
- Dickinson, E. C. (ed.). 2003. *The Howard and Moore complete checklist of the birds of the world*. London: Christopher Helm.
- Fjeldså, J. 1994. Geographical patterns for relict and young species of birds in Africa and South America and implications for conservation priorities. *Biodiversity and Conservation* 3:207-226.
- Fjeldså, J. 2000. The relevance of systematics in choosing priority areas for global conservation. *Environmental Conservation* 27:67-75.
- Fjeldså, J. 2002. *Polylepis* forests – vestiges of a vanishing ecosystem in the Andes. *Ecotropica* 8:111-123.
- Fjeldså, J., M. D. Álvarez, J. M. Lazcano, and B. León. 2005. Illicit crops and armed conflict as constraints on biodiversity conservation in the Andes region. *Ambio* 34:205-211.
- Fjeldså, J., and M. Irestedt. 2009. Diversification of the South American avifauna: patterns and implications for conservation in the Andes. *Annals of the Missouri Botanical Garden* 96:398-409.
- Fjeldså, J., and M. Kessler. 1996. Conserving the biological diversity of *Polylepis* woodlands of the highlands of Peru and Bolivia – a contribution to sustainable natural resource management. Copenhagen: NORDECO.
- Fjeldså, J., E. Lambin, and B. Mertens. 1999. Correlation between endemism and local ecoclimatic stability documented by comparing Andean bird distributions and remotely sensed land surface data. *Ecography* 22:63-78.
- Fjeldså, J., and C. Rahbek. 1997. Species richness and endemism in South American birds: implications for the design of networks of nature reserves. Pp. 466-482 in *Tropical forest remnants: ecology, management and conservation of fragmented communities*, edited by W. F. Laurance and R. O. Bierregaard. Chicago: University of Chicago Press.
- García-Moreno, J., and J. Fjeldså. 1999. Re-evaluation of species limits in the genus *Atlapetes* based on mtDNA sequence data. *Ibis* 141:199-207.
- Gaston, K. J. 1994. *Rarity*. London: Chapman and Hall.
- Graham, G. L. 1990. Bats versus birds: comparisons among Peruvian volant vertebrate faunas along an elevational gradient. *Journal of Biogeography* 17:657-668.
- Graves, G. R. 1985. Elevational correlates of speciation and intraspecific geographic variation in plumage in Andean birds. *Auk* 102:556-579.
- Graves, G. R. 1988. Linearity of geographic range and its possible effect on the population structure of Andean birds. *Auk* 105:47-52.
- Hawkins, B. A., J. A. F. Diniz-Filho, and A. E. Weis. 2005. The mid-domain effect and diversity gradients: is there anything to learn? *American Naturalist* 166:E140-E143.
- Herzog, S. K. 2008. First ornithological survey of Cordillera Mosetenes, with a latitudinal comparison of lower Yungas bird communities in Bolivia. *Revista Boliviana de Ecología y Conservación Ambiental* 23:59-71.
- Herzog, S. K., J. Fjeldså, M. Kessler, and J. A. Balderrama. 1999. Ornithological surveys in the Cordillera Cocapata, depto. Cochabamba, Bolivia, a transition zone between humid and dry intermontane Andean habitats. *Bulletin of the British Ornithologists' Club* 119:162-177.
- Herzog, S. K., and M. Kessler. 2006. Local versus regional control on species richness: a new approach to test for competitive exclusion at the community level. *Global Ecology and Biogeography* 15:163-172.

- Herzog, S. K., M. Kessler, and K. Bach. 2005a. The elevational gradient in Andean bird species richness at the local scale: a foothill peak and a high-elevation plateau. *Ecography* 28:209-222.
- Herzog, S. K., M. Kessler, and J. A. Balderrama. 2008. A new species of tyrannulet (Tyrannidae: *Phyllomyias*) from Andean foothills in northwest Bolivia and adjacent Peru. *Auk* 125:265-276.
- Herzog, S. K., R. Soria Auza, and A. B. Hennessey. 2005b. Patrones ecorregionales de la riqueza, endemismo y amenaza en la avifauna boliviana: prioridades para la planificación ecorregional. *Ecología en Bolivia* 40(2):27-40.
- Hilty, S. L. 1997. Seasonal distribution of birds at a cloud forest locality, the Anchicayá Valley, in western Colombia. *Ornithological Monographs* 48:321-343.
- Isler, M. L., P. R. Isler, and B. M. Whitney. 2007. Species limits in antbirds (Thamnophilidae): the Warbling Antbird (*Hypocnemis cantator*) complex. *Auk* 124:11-28.
- Johnson, N. K. 2002. Leapfrogging revisited in Andean birds: geographical variation in the Tody-tyrant superspecies *Poecilotriccus ruficeps* and *P. luluae*. *Ibis* 144:69-84.
- Kattan, G. H., H. Alvarez-López, and M. Giraldo. 1994. Forest fragmentation and bird extinctions: San Antonio eighty years later. *Conservation Biology* 8:138-146.
- Kattan, G. H., and P. Franco. 2004. Bird diversity along elevational gradients in the Andes of Colombia: area and mass effects. *Global Ecology and Biogeography* 13:451-458.
- Kattan, G. H., P. Franco, V. Rojas, and G. Morales. 2004. Biological diversification in a complex region: a spatial analysis of faunistic diversity and biogeography of the Andes of Colombia. *Journal of Biogeography* 31:1829-1839.
- Kattan, G., P. Franco, C. A. Saavedra, C. Valderrama, V. Rojas, D. Osorio and J. Martínez. 2006. Spatial components of bird diversity in the Andes of Colombia: implications for designing a regional reserve system. *Conservation Biology* 20:1203-1211.
- Kerr, J. T., M. Perring, and D. J. Currie. 2006. The missing Madagascan mid-domain effect. *Ecology Letters* 9:149-159.
- Kessler, M., S. K. Herzog, J. Fjeldså, and K. Bach. 2001. Diversity and endemism of plants and birds along two gradients of elevation, humidity, and human land-use in the Bolivian Andes. *Diversity and Distributions* 7:61-77.
- Krabbe, N., and T. S. Schulenberg. 1997. Species limits and natural history of *Scytalopus tapaculos* (Rhinocryptidae), with descriptions of the Ecuadorian taxa, including three new species. *Ornithological Monographs* 48:47-88.
- Krömer, T., M. Kessler, and S. K. Herzog. 2006. Distribution and flowering ecology of bromeliads along two climatically contrasting elevational transects in the Bolivian Andes. *Biotropica* 38:183-195.
- Lawton, J. H. 1999. Are there general laws in ecology? *Oikos* 84:177-192.
- MacLeod, R., S. Ewing, S. K. Herzog, K. Evans, R. Bryce, and A. McCormick. 2005. First ornithological inventory and conservation assessment for the Yungas forests of the Cordilleras Cocapata and Mosetenes, Cochabamba, Bolivia. *Bird Conservation International* 15:361-382.
- McCain, C. M. 2005. Elevational gradients in diversity of small mammals. *Ecology* 86:366-372.
- McCain, C. M. 2009. Global analysis of bird elevational diversity. *Global Ecology and Biogeography* 18:346-360.
- McKnight, M. W., P. S. White, R. I. McDonald, J. F. Lamoreux, W. Sechrest, R. S. Ridgely, and S. N. Stuart. 2007. Putting beta-diversity on the map: broad-scale congruence and coincidence in the extremes. *PLoS Biology* 5:e272.

- Melo, A. S., T. F. L. V. B. Rangel, and J. A. F. Diniz-Filho. 2009. Environmental drivers of beta-diversity patterns in New-World birds and mammals. *Ecography* 32:226-236.
- Munves, J. 1975. Birds of a highland clearing in Cundinamarca, Colombia. *Auk* 92:307-321.
- Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853-858.
- Naranjo, L. G. 1994. Composición y estructura de la avifauna del Parque Regional Natural Ucumari. Pp. 305-325 in *Ucumari: un caso típico de la diversidad biótica andina*, edited by J. O. Rangel. Pereira, Colombia: Corporación Autónoma Regional de Risaralda.
- O'Dea, N., and R. J. Whittaker. 2007. How resilient are Andean montane forest bird communities to habitat degradation? *Biodiversity and Conservation* 16:1131-1159.
- O'Neill, J. P., D. F. Lane, A. W. Kratter, A. P. Capparella, and C. Fox Joo. 2000. A striking new species of barbet (Capitoninae: *Capito*) from the eastern Andes of Peru. *Auk* 117:569-577.
- Patterson, B. C., D. F. Stotz, S. Solari, J. W. Fitzpatrick, and V. Pacheco. 1998. Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. *Journal of Biogeography* 25:593-607.
- Pearson, O. P., and C. Pearson Ralph. 1978. The diversity and abundance of vertebrates along an altitudinal gradient in Peru. *Memorias del Museo de Historia Natural "Javier Prado"* 18:1-97.
- Poulsen, B. O., and N. Krabbe. 1997. The diversity of cloud forest birds on the eastern and western slopes of the Ecuadorian Andes: a latitudinal and comparative analysis with implications for conservation. *Ecography* 20:475-482.
- Poulsen, B. O., and N. Krabbe. 1998. Avifaunal diversity of five high-altitude cloud forests on the Andean western slope of Ecuador: testing a rapid assessment method. *Journal of Biogeography* 25:83-93.
- Rahbek, C. 1997. The relationship among area, elevation, and regional species richness in Neotropical birds. *American Naturalist* 149:875-902.
- Rahbek, C., N. J. Gotelli, R. K. Colwell, G. L. Entsminger, T. F. L. V. B. Rangel, and G. R. Graves. 2007. Predicting continental-scale patterns of bird species richness with spatially explicit models. *Proceedings of the Royal Society of London B, Biological Sciences* 274:165-174.
- Rahbek, C., and G. R. Graves. 2000. Detection of macro-ecological patterns in South American hummingbirds is affected by spatial scale. *Proceedings of the Royal Society of London B, Biological Sciences* 267:2259-2265.
- Rahbek, C., and G. R. Graves. 2001. Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Science of the United States of America* 98:4534-4539.
- Remsen, J. V. Jr. 1985. Community organization and ecology of birds of high elevation humid forest of the Bolivian Andes. *Ornithological Monographs* 36:733-756.
- Remsen, J. V., Jr., C. D. Cadena, A. Jaramillo, M. Nores, J. F. Pacheco, M. B. Robbins, T. S. Schulenberg, F. G. Stiles, D. F. Stotz, and K. J. Zimmer. 2009. *A classification of the bird species of South America*. Version 06/12/2009. American Ornithologists' Union. <http://www.museum.lsu.edu/~Remsen/SACCBaseline.html>
- Renjifo, L. M. 1999. Composition changes in a sub-Andean avifauna after long-term forest fragmentation. *Conservation Biology* 13:1124-1139.
- Renjifo, L. M., G. P. Servat, J. M. Goerck, B. A. Loiselle, and J. G. Blake. 1997. Patterns of species composition and endemism in the northern Neotropics: a case for conservation of montane avifaunas. *Ornithological Monographs* 48:577-594.

- Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. *Ecology Letters* 7:1-15.
- Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* 65:514-527.
- Rosenzweig, M. L. 1995. *Species diversity in space and time*. Cambridge: Cambridge University Press.
- Schluter, D., and R. E. Ricklefs. 1993. Species diversity: an introduction to the problem. Pp. 1-10 in *Species diversity in ecological communities: historical and geographical perspectives*, edited by R. E. Ricklefs and D. Schluter. Chicago: University of Chicago Press.
- Schmitt, C. G., D. C. Schmitt, and J. V. Remsen, Jr. 1997. Birds of the Tambo area, an arid valley in the Bolivian Andes. *Ornithological Monographs* 48:701-716.
- Sempere, T., D. Picard, and O. Plantard. 2005. Assessing and dating Andean uplift by phylogeography and phylochronology: early Miocene emergence of Andean cloud forest. Pp. 663-665 in *6th International Symposium on Andean Geodynamics, extended abstracts*. Barcelona: SAG 2005.
- Stattersfield A. J., M. J. Crosby, A. J. Long, and D. C. Wege. 1998. *Endemic bird areas of the world: Priorities for biodiversity conservation*. *BirdLife Conservation Series No. 7*. Cambridge: BirdLife International.
- Stiles, F. G., and C. I. Bohórquez. 2000. Evaluando el estado de la biodiversidad: el caso de la avifauna de la serranía de Las Quinchas, Boyacá, Colombia. *Caldasia* 22:61-92.
- Stotz, D. F. 1998. Endemism and species turnover with elevation in montane avifaunas in the Neotropics: implications for conservation. Pp. 161-180 in *Conservation in a changing world*, edited by G. M. Mace, A. Balmford, and J. R. Ginsberg. Cambridge, MA: Cambridge University Press.
- Stotz, D. F., J. W. Fitzpatrick, T. A. Parker III, and D. K. Moskovits. 1996. *Neotropical birds: ecology and conservation*. Chicago: University of Chicago Press.
- Terborgh, J. 1977. Bird species diversity on an Andean elevational gradient. *Ecology* 58:1007-1019.
- Williams, P. H., and C. J. Humphries. 1994. Biodiversity, taxonomic relatedness and endemism in conservation. Pp. 269-287 in *Systematics and conservation evaluation*, edited by P. L. Forey, C. J. Humphries, and R. I. Vane-Wright. Oxford: Clarendon Press.
- Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics* 34:273-309.
- Young, B. E., I. Franke, P. A. Hernandez, S. K. Herzog, L. Paniagua, C. Tovar, and T. Valqui. 2009. Using spatial models to predict areas of endemism and gaps in the protection of Andean slope birds. *Auk* 126:554-565.
- Zapata, F. A., K. J. Gaston, and S. L. Chown. 2005. The mid-domain effect revisited. *American Naturalist* 166:E144-E148.