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The Role of Mountain Ranges in the Diversification of Birds

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Abstract

Avian faunas vary greatly among montane areas; those at high latitudes are biologically impoverished, whereas those of some low-latitude mountains are biologically very complex. Their high level of species richness is caused by the aggregation of many small-ranged species, which has been difficult to explain from purely macroecological models focusing on contemporary ecological processes. Because the individual mountain tracts harbor species that represent different evolutionary trajectories, it seems plausible to relate these species assemblages to high persistence (or absence of extinction) in addition to high levels of speciation. The distribution of small-ranged species is concentrated near tropical coasts, where moderation of the climate in topographically complex areas creates cloud forests and stable local conditions. The stability underpins specialization and resilience of local populations, and thereby the role of these places as cradles of biodiversity.

1. INTRODUCTION

Montane areas represent rugged landscapes that are uplifted to an extent that affects local climate. Mountains are therefore often viewed as bleak and biologically impoverished environments (e.g., Martin & Wiebe 2004). Mountains at high latitudes are essentially arctic in terms of climate and biota, and many mountains at moderate latitudes harbor relict populations of arctic species, which in most instances have persisted since the Pleistocene ice ages (e.g., Hughes & Eastwood 2006). Even some speciose components of the tropical montane biota are thought to have their origins in temperate environments (see examples in Vuilleumier & Monasterio 1986). Regardless of whether mountains were colonized from higher latitudes or from adjacent lowlands, it has long been acknowledged that some speciation must have taken place by isolation in allopatry or parapatry within montane systems (Vuilleumier & Monasterio 1986, Moritz et al. 2000). However, only recently has the role that mountains play as cradles of biodiversity become fully realized. Mountains contain half of the currently defined biodiversity hot spots (Kohler & Maselli 2009), although they cover only 16.5–27% of the land area (depending on how montane areas are defined). The traditionally delineated montane hot spots are widely recognized as areas of high priority for conservation, primarily as a consequence of the large number of endemic and threatened species they encompass (Stattersfield et al. 1998).

Macroecological analyses on continental distributions of birds have revealed that models based exclusively on contemporary climate fail to explain overall patterns of richness. Thus, it is necessary to incorporate topography relief as a feature to obtain statistical power to account for the unusually high diversity in tropical mountain regions (Rahbek & Graves 2000, 2001). Subsequent analyses have emphasized that models based on contemporary environmental variables explain well only the regional variation in richness of the most wide-ranging species (Jetz & Rahbek 2002, Rahbek et al. 2007). The corollary that models incorporating key variables such as contemporary water and energy availability fail to explain the aggregated occurrence of species with small distributions in montane regions has attracted renewed research effort. The spatial positioning of aggregations of small-ranged species also exceeds what can be predicted by including effects of topography, geometric constraints, and random draws from the total species pool in a given area (Jetz et al. 2004, Fjeldså & Rahbek 2006, Rahbek et al. 2007). As a consequence, effort has centered on better integrating contemporary, evolutionary, and historical variables in an attempt to understand the variation in diversity and composition of avifaunas among montane areas and between mountains and adjacent lowlands.

One influential step toward understanding the difference in biodiversity between high- and low-latitude mountains was formulated by Janzen (1967). He pointed out that high-latitude environments are characterized by seasonal temperature amplitude exceeding that of the elevational temperature gradient, making topographic barriers less important in temperate regions than in the tropics. In the tropics, species could evolve narrower thermal tolerances and thereby be able to permanently reside within distinct elevational zones. His argument of higher species turnover on tropical elevational gradients has been supported by recent studies (e.g., Ghalambor et al. 2006, McCain 2009). Furthermore, Cadena et al. (2012) established that tropical vertebrates tend to have greater evolutionary conservatism in their thermal niches, with sister species generally inhabiting very similar thermal niches.

Most studies of speciation in montane areas have focused on the physical barriers that arose during mountain building, but this approach may not adequately explain the observed variation among montane areas. In northern montane regions, the dispersal barriers are low (in Janzen's sense), and vicariant patterns may be rapidly erased by high levels of climate-driven range dynamics (Jansson & Dynesius 2002, Hawkins & Diniz-Filho 2006). In tropical mountains,

congruent geographic patterns, when placed in a temporal framework, may represent distinct area cladograms, rejecting the idea of generalized vicariance patterns (Fjeldså & Bowie 2008). The problem is exemplified by the pattern of species richness across the Eastern Arc Mountains, a 600-km chain of 13 discrete sky islands in East Africa. Although species richness roughly follows the species-area relationship among the different sky islands, endemism does not, with three sky islands having excessive levels of endemism for their given area (Burgess et al. 2007). Although speciation probably proceeds through divergence in allopatry, the divergences among multiple lineages are not coincident in time (Fjeldså & Bowie 2008, Lawson 2010, Tolley et al. 2011). Most likely, adaptive redistribution and varying rates of extinction among these sky islands have played an important role in generating the observed pattern of endemism. Thus, in order to explain the aggregations of small-range species, we need to consider the whole process of lineage diversification (speciation and extinction). This is particularly relevant from a conservation perspective because the focus on areas where lineages persist (because of low extinction rates) will be more meaningful than the traditional focus on barriers between areas.

Our background for writing this review builds on decades of exploratory field studies in montane regions, notably in the Andes (e.g., Fjeldså & Krabbe 1990) and in the mountains of eastern Africa (e.g., Fjeldså & Bowie 2008, Fjeldså et al. 2010, Voelker et al. 2010), which revealed a much more localized pattern of aggregation of small-ranged species than is apparent from compiling coarse-scale geographical ranges from the literature. We have interpreted the local aggregation of young and old (relictual?) species as signs of local stability, resulting from local climate moderation as prevailing winds and atmospheric stratification interact with complex topography (Fjeldså 1995, Fjeldså & Lovett 1997). This was supported by weather satellite data sampled over a few years (Fjeldså et al. 1999). Furthermore, some descriptions of biodiversity hot spots in tropical coastal mountains (Lovett 1993, Best & Kessler 1995) provided compelling evidence of how the climatic influence from the nearest ocean could provide predictable conditions over longer periods of time.

Nevertheless, this represents an ad hoc explanation, which needs to be supplemented by a search for general patterns supported by quantitative analyses. This was not possible at the time of the first formulation of the above hypotheses, as adequate distributional data had not yet been compiled in digital form. With the recent development of such databases, several thorough continent-wide analyses of variation in species richness now allow a new class of studies that can reveal significant deviation from the expectations of general macroecological models. With the rapid development of phylogenetic data and tools for paleoclimatic modeling, we may now begin to analyze the complexity of the montane biota across the globe.

In this review, we use distributional and phylogenetic data, primarily for passerine birds (order Passeriformes) to illustrate general patterns, and we emphasize some environmental characteristics of the montane biodiversity hot spots. Addressing the possible underlying mechanisms remains a work in progress, although we do broadly outline some interesting patterns and trends. Our passerine focal group is suitable as a model group, as the order is well studied in terms of molecular phylogeny and represents the largest avian radiation with about 6,000 species. Furthermore, passerines are fairly homogeneous in terms of size and gross morphology and yet are highly diverse in their use of terrestrial habitats and in their diet.

2. MATERIALS AND METHODS

Detailed accounts of the montane regions of the world and their biodiversity are described in other published or emerging papers. We therefore provide only a very general outline based on our more detailed continental and especially regional studies from some of the ornithologically most outstanding parts of the world, with the following data primarily derived from our own

extensive fieldwork:

1. The tropical Andes region of South America, a semicontinuous but narrow band of montane habitat covering a large latitudinal range (Fjeldså et al. 1999, Rahbek & Graves 2001, Rahbek et al. 2007, Fjeldså & Irestedt 2009),
2. The Afromontane region, mainly spatially discrete sky islands (Jetz & Rahbek 2002, Fjeldså & Bowie 2008), and
3. The Indo-Pacific region, a complex tropical archipelago that arose during the Neogene Australian-Asian collision, with many montane areas (e.g., Jönsson et al. 2011, Fritz et al. 2012).
4. In addition, significant new data are available for the Sino-Himalayan Mountains, a long mountain chain extending outside the tropics (Johansson et al. 2007a, Price et al. 2011, Päckert et al. 2012).

We defined mountain areas of the world primarily from a GIS (geographic information systems) model based on the range in local elevation and slope developed by the Mountain Research Initiative (Kapos et al. 2000). Because of the fine spatial resolution of this model, large areas appear as mosaics of montane and nonmontane pixels, with hundreds of isolated pixels that marginally qualify as montane scattered far outside the main mountain tracts. Thus, we developed a set of rules to circumscribe broader montane regions, subdivided these according to recognized biogeographic systems, and removed isolated rugged pixels. The biodiversity content (species richness and number of small-ranged species) per region could then be analyzed in relation to latitude, area, placement within continents, and environmental parameters extracted from global environmental models.

For all passerine birds, we compiled a global distribution database (presence-absence data for all species at the spatial resolution of a 1×1 latitudinal-longitudinal degree grid following the approach outlined by Rahbek & Graves 2001). From this we extracted species lists for the defined montane regions. In order to illustrate general patterns of diversification history, we have compiled divergence data for mitochondrial DNA from >150 publications to assess time since most recent common ancestor (TMRCA) for densely sampled groups. Reference to basal and terminal species generally refers to species with short or long root-paths (number of nodes from the base of a phylogeny), unless the TMRCA [in million years ago (Mya)] is specifically mentioned. To highlight different patterns in this review, we used a detailed phylogenetic framework for the endemic radiations of South American suboscine birds (Derryberry et al. 2011; J.I. Ohlson, M. Irestedt, P.G.P. Ericson, and J. Fjeldså, unpublished data) and for some African bird groups: the nonpasserine Galliformes (Cohen et al. 2012, Mandiwana-Neudani 2012), Malaconotidae (notably Fuchs et al. 2004, 2012; Njabo et al. 2008), and Pycnonotidae (Johansson et al. 2007b). Although we can never know the past distribution of a clade, we estimated the paleodistributions of some clades by merging the distributions of all constituent species, assuming diversification by vicariance. Because terminal subclades that obviously represent recent dispersal out of the ancestral area are irrelevant for the reconstruction of paleodistributions, these were removed (Fjeldså & Bowie 2008, Fjeldså 2012).

3. THE GLOBAL VARIATION OF PASSERINE DIVERSITY

Some aspects of the variation in the global diversity pattern of passerine birds are illustrated in **Figure 1**, where panel 1a expresses species richness as relative brightness: old species by purple hues, and recently evolved species by green hues (categories defined in the figure legend). To fully interpret this, one needs to bear in mind the austral origin (in Australia, South America, and almost certainly Antarctica) of passerine birds (Ericson et al. 2003). Whereas the suboscines were moderately successful in colonizing areas outside the Austral area of origin, the oscine passerines

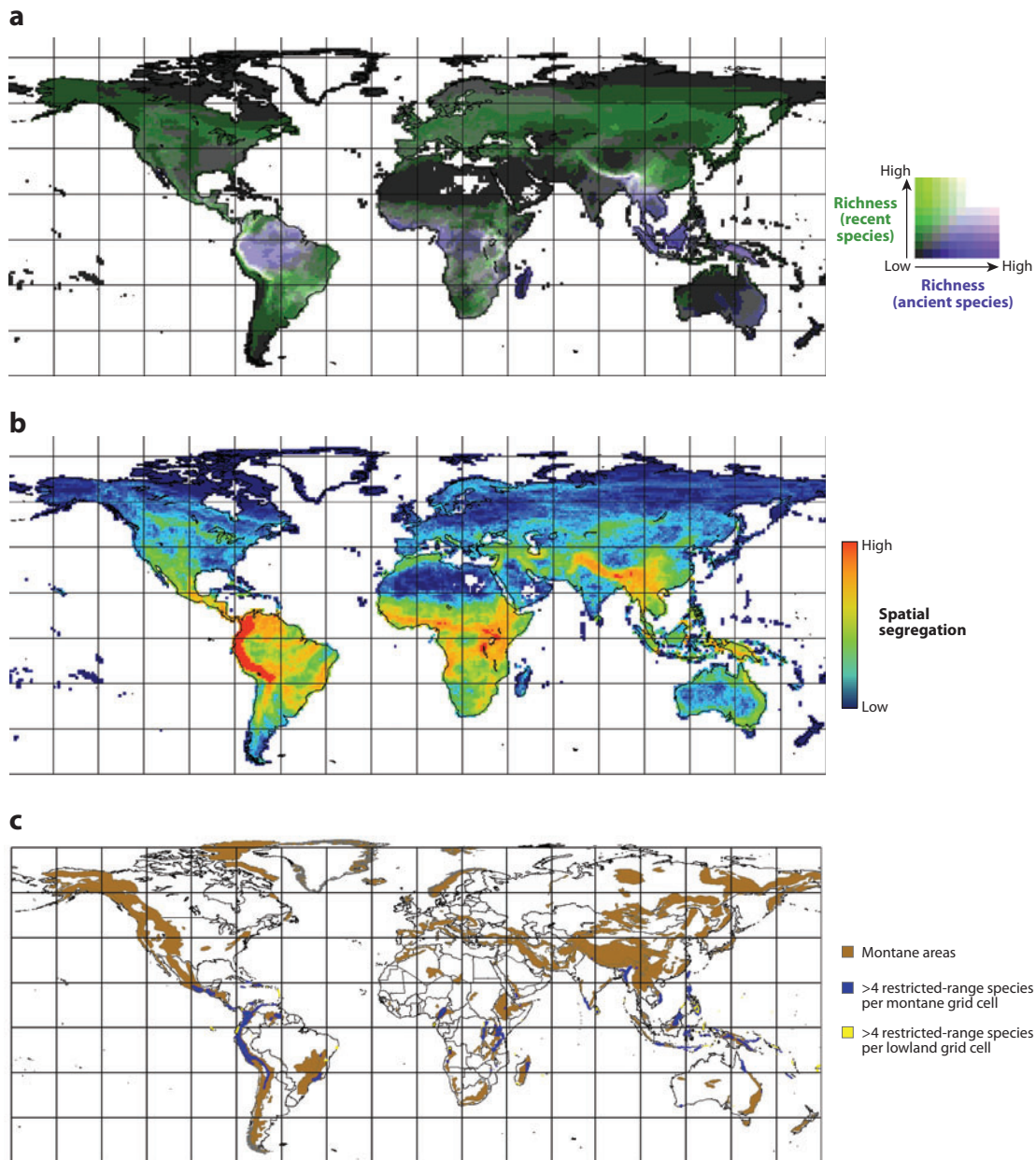


Figure 1

Global patterns of diversification. (a) Diversity of 2,291 species (brightness reflecting species richness; maximum value is 160 species) representing groups where time of diversification is verified by molecular data. Green hues show species with time since most recent common ancestor <3 million years, purple hues show ancient species (small clades originating >15 Mya; such clades may comprise a single species or up to three recently diverged allospecies), and gray hues reflect similar representation of both groups. (b) Spatial segregation of all passerine birds calculated for each grid cell as the species replacement rate in relation to the adjacent 8 grid cells; red represents maximum values. (c) The mountain areas of the world. Dark blue marks areas with >4 restricted-range species occurring together in a montane grid cell, yellow shows similar aggregations in the lowlands (tiny areas near the coasts of Ecuador and Brazil, and on several tropical islands).

(songbirds) underwent a worldwide phylogenetic expansion, initiated in the Oligocene by rapid island radiations in the proto-Papuan archipelago (Jönsson et al. 2011) and multidirectional dispersal across the oceans and the Wallacean archipelago to the Old World tropics. Further expansions went across the Palearctic region to North America and then onward to South America as part of the Great American Interchange (Weir et al. 2009). The historical biogeography of passerine birds explains the predominance of basal lineages in the Indo-Pacific island archipelago, with many relictual forms in the mountains of New Guinea, Sundaland, and the Indo-Burmese foothill mountains. Terminal radiations and high species turnover at northern latitudes (Weir & Schluter 2004), together with range dynamics in the Sino-Himalayan Mountains, would have provided ample opportunity for exchange between high- and low-latitude mountains during the climatically unstable Neogene period (Päckert et al. 2012).

3.1. Species Replacements and Endemism

High levels of species replacement (**Figure 1b**) characterize biome boundaries and are not particularly characteristic of montane regions (**Figure 1c**; see also Hawkins & Diniz-Filho 2006) at high latitudes (in agreement with Janzen's hypothesis). Presumably, the range dynamics at high latitudes and even in some tropical inland regions erased much of the population structure and local adaptations that took place intermittently and locally, leading to a moderate diversity and a predominance of widespread species.

The situation is quite different at low latitudes, where the tropical Andes region and some parts of the Afrotropical and Sino-Himalayan montane regions stand out prominently (**Figure 1b**). These latter areas have particularly high aggregates of small-ranged species (**Figure 1c**) (Stattersfield et al. 1998, Davies et al. 2007, Rahbek et al. 2007). Phylogeographic data suggest a global tendency for a marked reduction in speciation events in the tropical lowlands during the climatically most unstable upper Pleistocene, while speciation continued in the tropical montane areas (Fjeldså & Bowie 2008, Päckert et al. 2012, Fjeldså 2012).

Small-range species apparently survived over time only where they could track their optimal ecological or climatic window by moving short distances (e.g., Tingley et al. 2009), which is typically the case in montane areas. It has been suggested and advocated that the distribution of small-ranged land vertebrates in montane regions may be related to low climate-change velocity (Sandel et al. 2011) and that this metric is a useful reflection of how fast species must move to keep track of climate change since the last Pleistocene glaciation, as well as in the future (Loarie et al. 2009). These are an approach and metric that so far rely exclusively on modeled data and, thus, have yet to be validated with historical empirical data.

As many as 1,116 (73.7%) of the 1,514 small-ranged passerine bird species (species inhabiting 1–20 grid cells, representing the fourth quartile of the 25% of species with the smallest range sizes among all passerine birds) live entirely or partly within the montane regions outlined in **Figure 1c**. In studies of species richness patterns of Africa and South America, the highest residual values of species diversity that could not be explained by the employed ecoclimatic models, notably of small-range species, were found in mountains and near coasts (Rahbek & Graves 2001, Jetz & Rahbek 2002, Jetz et al. 2004, Rahbek et al. 2007). Thus, because rugged landscapes are often found along continental margins, we need to consider what is most important: topography or proximity to the ocean. As many as 1,136 (75.0%) of the small-ranged passerine bird species live (wholly or partially) less than 300 km from sea coasts within 20° latitude (N and S). Of these, 862 inhabit montane regions or their coastal foothills, 39 are found in coastal lowlands, and a further 236 on islands, most of which are mountainous but too small for inclusion in our defined montane regions. The peak aggregations of small-ranged passerines occur in Costa Rica, the Panamanian highlands, the northern Andes, the Cameroon Mountains, mountains around

the northern Indian Ocean, and mountainous islands along the southeast Asian gateway to the Pacific (**Figure 1c**). Globally, the highest density of small-ranged species is near warm coasts with year-round precipitation, but some monsoon coasts and mist-impacted coasts near the cool (upwelling) eastern boundary currents are also important. Farther inland, significant numbers of small-ranged species are found only in the Albertine Rift Mountains of central Africa, along the eastern Andean slope of southern Peru and Bolivia and locally in the Sino-Himalayan Mountains.

It has long been acknowledged that oceanic islands can act as refuges for ancient relictual species because of their thermal stability and slow biotic turnover (Cronk 1997). However, the remarkable aggregation of small-ranged birds outlined above points to a more general trend for such species to be found in rugged landscapes near tropical coasts. The existence of some ancient (relictual) species in the hot spots for small-ranged birds (such as *Sapayoa aenigma* in the South American Chocó region and the Modulatricidae in some African mountains) points to low rates of extinction (Fjeldså & Lovett 1997). There is now a need for a strong statistical approach to determine to what extent the diversification in the terrestrial biota is controlled by thermal inertia and the slow rhythms of variation in oceanic systems (Steele 1985), as well as by the stability of oceanic circulation patterns near the equator (e.g., von der Heydt & Dijkstra 2011).

3.2. Gardens of Eden in the Mist

The most outstanding places of montane endemism all share high air humidity (and thus gain heat from condensation) and high precipitation (at least seasonally). Cloud forests are with few exceptions confined to within 300 km of tropical coasts (Bruijnzeel et al. 2010), but there is a gradual transition to other humid montane forest types in the major mountain ranges extending deeper into the continents. In addition, mist-dependent vegetation types may exist in drier regions, notably on escarpments near coasts affected by cold eastern boundary currents (Bruijnzeel et al. 2010, p. 34). These vegetation formations are highly affected by sea temperatures and relative humidity, which determine where stratified clouds hit the mountain slopes. Persistent mist conditions are mainly found at 2,000–3,000-m elevation, but it is important to note that such habitats can exist below 1,000 m in small coastal mountains (also known as the telescoping effect; e.g., Monteverde near the Pacific coast of Costa Rica; see Foster 2001). Local drainage patterns of cold air may even lead to local development of cloud forest near sea level (Bruijnzeel et al. 2010, pp. 130–133). In these environments, water from wind-driven fog is added to the incident rainfall. This may not add much in places with heavy rainfall, but it is important outside the primary rainy periods and in the mist zones of arid regions. Thus, because of the dense condensation on the complex foliage of tiny, leathery leaves, a significant stemflow is observed even when the rainfall occurs as a fine drizzle or when the forest is cloud enshrouded (see figure 50.2 in Bruijnzeel et al. 2010). Whereas the annual mean precipitation declines slightly with elevation in large highlands, it increases with elevation in small mountains (see figure 3.6 in Bruijnzeel et al. 2010). These mountains are characterized by low evapotranspiration, strong infiltration, and constantly high soil moisture, leading to a large water storage capacity and constant flow of water to the adjacent lowlands.

Thus, cloud forests may represent a distinct habitat from that of the adjacent lowlands at early stages of mountain building, offering early opportunities for the evolution of a montane avifauna. Particular habitat characteristics that are likely to have been present at this stage include stunted/gnarled trees with tiny, leathery leaves and large amounts of epiphytes and mosses (which require constant air humidity). The leached and nutrient-poor soils would provide favorable conditions for nectarivorous birds (Rebello 1991). This is a hypothesis that invites intensive research.

The high relative dominance of species representing mid-Tertiary radiations in many small mountains near tropical coasts (admittedly hard to see in **Figure 1a** because of the spatial

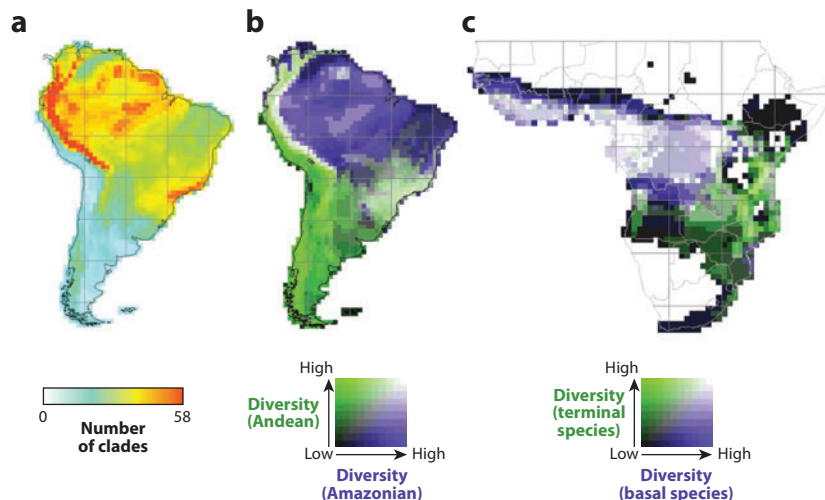


Figure 2

Diversification of South American and African birds. The two left maps show diversity of suboscines (mid-Miocene lineages, at 15 Mya, based on J.I. Ohlson, M. Irestedt, P.G.P. Ericson, and J. Fjeldså, unpublished data). (a) Shows all 76 clades (darkest red representing 58 clades present in one grid cell). (b) 35 clades rooted in the Andean region shown in green, 36 clades rooted in the Amazonian region in purple. (c) Diversity of greenbuls (Pycnonotidae). Basal species in the phylogeny (50% with shortest root paths, e.g., lowest numbers of nodes from the root of the phylogeny) are shown in purple, and the terminal species (longest root paths) are shown in green.

resolution) suggests that this is where the colonization road into the modern highlands started (see Bates et al. 1998 and Sedano & Burns 2010 for the Chocó region) and then extended deeper into the continents. Because of the way the climate is moderated by topography, atmospheric inversions and mist zones, the transition between mountain valleys and large highlands may persist in spite of climate fluctuations. Lush vegetation can under certain conditions exist even in the immediate proximity of glaciers, and some inland montane areas may have maintained refuge habitats for birds during the Pleistocene (see Qu et al. 2010 for the eastern outliers of the Tibet Plateau and Allen et al. 2010 for the Pamir-Tian-Altai Mountains).

4. THE HISTORY OF DIVERSIFICATION

4.1. The Long-Term History of Tropical Montane Avifaunas

Some elements of the long-term diversification history of montane birds is outlined below, starting with South America and the comprehensive molecular phylogenies that are available for suboscine birds (J.I. Ohlson, M. Irestedt, P.G.P. Ericson, and J. Fjeldså, unpublished data; Fjeldså 2012). **Figure 2** illustrates the diversity of suboscine clades in South America at 15 Mya, with a comparison of clades with distinct geographical origins in **Figure 2b**. It is evident that the maximum diversity (red cells in **Figure 2a**, maximum brightness in **Figure 2b**) corresponds to grid cells located at the interface between the Andean and Amazonian biomes. Some (near) endemic clades of the Andean region date back to the Oligocene and early Miocene (Rhinocryptidae, *Chamaeza*, *Geositta*, and *Grallaria/Grallaricula*), and others appeared toward the mid-Miocene. These lineages are best represented in the old parts of the orocline, in Patagonia and in the submontane habitats of western Ecuador and Colombia. Some of them are small clades, suggesting a reduced net diversification

rate since the initial adaptation to montane habitats. Other lineages maintained high rates of speciation throughout the period of orogeny.

Very few taxa among the Amazonian clades (e.g., *Thripadectes*) underwent marked upslope colonization into the Andes, but such an indication of constraining niche conservatism applies also to the Andean clades, which rarely colonized the tropical lowlands. Instead, the Andean avifauna is more strongly connected with the harsh lowland biomes of the Southern Cone of the continent (and with temperate North America). **Figure 2b** excludes some species-rich clades for which the geographical origins could not be precisely determined; however, they were probably south of the Amazon area and involved recent expansions into the tropical Andes region. Here the most intensive recent diversification took place along the *cis*-Andean tree-line zone (Fjeldså & Irestedt 2009). The furnariids (Derryberry et al. 2011) and fluvicoline flycatchers (Ohlson et al. 2008) were constantly able to maintain a high net speciation rate as the geographic center of diversification shifted over time from tropical lowland forests to the new savanna habitats in the south and then onward along the Andes.

At the same time, northern groups, notably the nine-primaried oscines, colonized South America during the Great American Interchange and initially diversified in the moderately high cloud forest ridges of Central America and the northern Andes, from where they proceeded, in a more dynamic way than the endemic South American groups, with several adaptive shifts and colonization of the highest mountain ranges as well as tropical and southern subtropical lowlands (Fjeldså & Rahbek 2006, Sedano & Burns 2010). Similarly, Santos et al. (2011) provide evidence that the Amazonian amphibian diversity arose by multiple colonizations out of the Andes.

Päckert et al. (2012) describe a similar progression for the Asian songbird radiation as outlined above for the Neotropical suboscines. Ancient groups inhabited the tropical lowlands and Indo-Burmese mountain foothills. These clades gave rise to a northward expansion through the interior mountain ranges of China (a connection that has been partly erased by Pleistocene aridification and diversity loss in China's inland mountains; see **Figure 1a**) to the extensive Palearctic forest region. Back colonization took place during the Pleistocene, along the Tian-Pamir-Hindu Kush Mountains to the subalpine Sino-Himalayan *Rhododendron*-coniferous forest zone, leading to the buildup of considerable species diversity in southern China. Thus, gray hues at the Chinese-Indochinese border zone in **Figure 1a** reflect the mix of species of Pleistocene age along the high ridges and ancient fauna in the warm valleys (see also López-Pujol et al. 2011).

Africa was once extensively forested, but savanna habitats expanded during the Miocene, with a tipping point around 5 Mya occurring in response to the formation of the west Antarctic ice sheet (Zachos et al. 2001). The result was severed connectivity of forest habitat across Africa as well as of the forest corridor across the Middle East that once connected Africa with India. Thus, the African montane avifauna has largely evolved in situ, except for rare long-distance dispersal events (e.g., *Hemitesia*; Irestedt et al. 2010) and some putative migratory drop-off from Palearctic radiations whose members winter in Africa (e.g., *Sylvia*; Voelker & Light 2011).

Greenbuls (Pycnonotidae) exemplify the large-scale pattern of lineage divergence in Africa. Here, the 50% most basal species (shortest root paths; *purple* in **Figure 2c**) occur widely across the lowland rainforest biomes, whereas terminal species (*green* in **Figure 2c**) occur primarily outside it, in the East African mosaic of highland habitats (Albertine Rift, Kenyan Highlands, and Eastern Arc Mountains) and savanna thickets (Fjeldså et al. 2007).

Most divergence times between sister taxa of African montane birds center on the Pliocene-Miocene boundary (see **Figure 3c**) (Voelker et al. 2010) and are not clustered in the Pleistocene as suggested in the past by several researchers (e.g., Diamond & Hamilton 1980). This clustering of divergence events in time suggests that most montane speciation events resulted from the rapid isolation of populations in separate sky islands, rather than through immigration from other areas

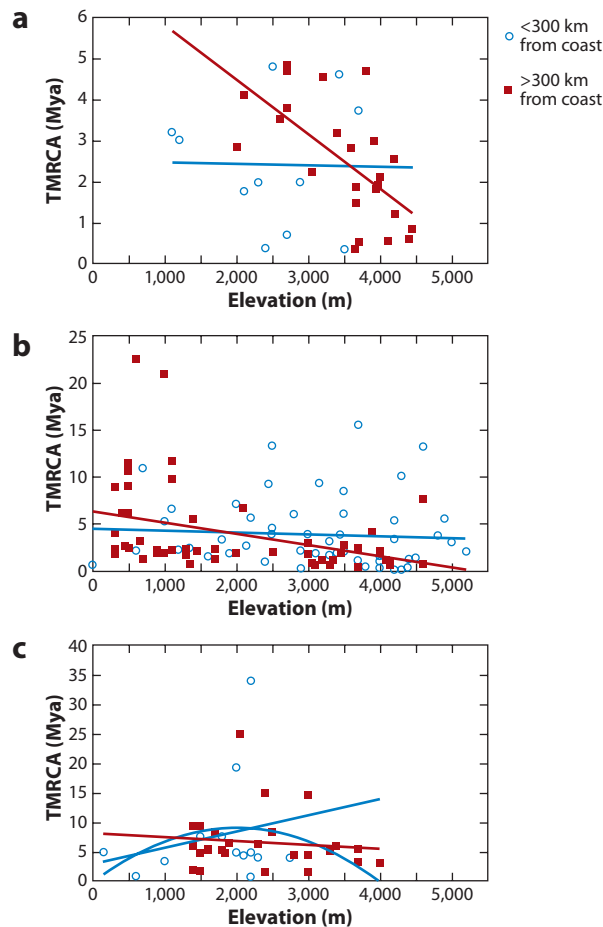


Figure 3

Time since most recent common ancestor (TMRCA) plotted against the upper elevational range of each species; red squares represent species living more than 300 km from the coast, blue open circles are species restricted to the zone less than 300 km from a warm coast. (a) Data for Sino-Himalayan mountains and Taiwan (redrawn from Päckert et al. 2012); (b) furnariid species of Peru and Bolivia, using the chronology developed by Derryberry et al. (2011); (c) data from eastern Africa (see the section on Materials and Methods).

as seen in the Andean and Sino-Himalayan avifaunas (Fjeldså & Bowie 2008, Voelker et al. 2010). This difference may also be a consequence of the isolation of the African montane fauna from that of the Palearctic region due to desert barriers, as well as from temperate environments in the south of the continent (e.g., Bowie et al. 2005).

4.2. Speciation and Species Turnover within Mountain Regions

A recent study of New World vertebrates documented that tropical sister taxa tend to have thermal niches that are both narrower and more evolutionarily conserved than those of temperate sister taxa (Cadena et al. 2012). Therefore, one may expect greater species packing in the tropics as a consequence of increased opportunity for isolation and allopatric divergence across elevational thermal gradients relative to temperate montane regions. However, it remains controversial

whether disruptive selection across an elevational gradient can lead to parapatric speciation, as it requires selection to be sufficiently strong to counter the effects of recurrent gene flow (e.g., Fuchs et al. 2011). For birds in both the Andes and Sino-Himalayan montane systems, the dominant mode of divergence occurs via allopatry rather than parapatry, with sister taxa tending to occupy the same elevation on adjacent slopes across valleys (Weir 2009, Cadena et al. 2012, Päckert et al. 2012) and only tending to co-occur on the same slope as a consequence of secondary contact (García-Moreno & Fjeldså 2000).

Furthermore, the spatial connectivity with high-latitude avifaunas also appears to have played a major role in the diversification of the Andean and Sino-Himalayan birds. In both montane systems, the influx from higher latitudes is likely to have facilitated in situ diversification via isolation from temperate ancestral lineages preadapted to the harshness characterizing the highest elevations (Graves 1988, Sedano & Burns 2010, Price et al. 2011, Päckert et al. 2012), as revealed by the mean age estimate for lineage splits (**Figure 3a,b**). The corresponding plot for eastern Africa recovers a different pattern, and most lineage splits occur at mid-elevation (**Figure 3c**). This contrasting pattern perhaps reflects the fundamentally different spatial structure of the African montane biome, where montane systems typically consist of a series of spatially isolated sky islands and have very little area available above 4,000 m.

Among montane areas of endemism in Africa, most work to date has been conducted on the Eastern Arc Mountains of East Africa (e.g., Fjeldså & Bowie 2008, Lawson 2010, Tolley et al. 2011). Although some spatial concordance is present among area cladograms for several bird species, there is little temporal congruence (Fjeldså & Bowie 2008). For instance, although most lineages of montane birds exhibit a pronounced genetic break between the sky islands of the northern and central Eastern Arc, divergence estimates from mitochondrial DNA data vary from 10% to 1.5% (Fjeldså & Bowie 2008, Fuchs et al. 2011). This extensive variation among sister clades (most of them formally ranked as subspecies!) in adjacent areas questions the validity of a purely vicariance mechanism of diversification and emphasizes instead the role of persistence (lack of extinction).

Although a general tendency for more recent lineage divergence at high elevation seems to exist in the interior of the continents (*closed squares* in **Figure 3**), there appears to be no clear trend in mountains located near warm seas (*open circles* in **Figure 3**). This emphasizes the high lineage persistence in these mountains, as species diversity apparently accumulated over geological time along the entire elevational gradient. In the case of the Eastern Arc, it is remarkable that only three widely separated mountains (Usambara, Uluguru, and Udzungwa) among the 13 sky islands stand out as having particularly high numbers of small-ranged species, including some ancient relictual forms (Fjeldså & Bowie 2008). Among these, the Usambara mountains are located right at the coast and have cloud forest habitat that extends to the coastal foothills. The Uluguru and Udzungwa mountains are located farther inland but have steep and high elevational gradients that effectively capture the incoming precipitation. A climatic explanation is emerging for the Eastern Arc based on a circulation model for the Indian Ocean and is supported by the palynological record demonstrating an absence of vegetation change in the montane forest during the last glacial cycle (Marchant et al. 2007). Similar areas of stability have also been documented in the Andes (Fjeldså et al. 1999) and the montane wet tropics of Australia (Graham et al. 2006). Furthermore, paleoclimatic modeling can now be used to develop a predictive stability (habitat persistence) surface for any system of interest that can then be evaluated by using multilocus DNA sequence data together with phylogenetic and statistical phylogeographic analytical approaches (e.g., Carnaval et al. 2009).

Instead of always searching for barriers to explain speciation, we need to also consider the nature of some habitat configurations, such as the extremely long and narrow band of Andean

tree-line habitat and the potential role that stochasticity and local weather phenomena can play in generating observed patterns of fragmentation (Graves 1988, Fjeldså et al. 1999). It has been suggested that small-ranged montane species could provide recruitment to the regional fauna (Roy et al. 1998). An analysis of range size versus TMRCA for furnariid clades that diversified in the Andes and in the tropical lowlands, respectively (*green* and *purple* in **Figure 2b**) recovered quite similar slopes ($y = 12.215 \times 0.3099$, $R^2 = 0.0472$ for Andean groups; $y = 55.219 \times 0.3679$, $R^2 = 0.0383$ for lowland groups) but different regression levels, with the range-size intercept at 1 Mya being 12.2 grid cells for Andean groups and 55.2 grid cells for lowland groups. The increase in range size over time could reflect higher extinction risks among small-ranged species. However, studies of historical population structures of Afromontane species, at finer temporal and spatial scales (e.g., Bowie et al. 2004, 2006; Voelker et al. 2010), suggest that species, which are now widespread, were fragmented and locally distributed during arid periods in the early Pleistocene. For instance, the Olive Sunbird, *Nectarinia olivacea*, which apparently originated locally in East Africa, underwent range expansion across the entire tropical region of Africa.

5. ADAPTATIONS TO LOCAL CONDITIONS

The geographical range of species is assumed to correlate with their abundance (Brown 1984, Gaston et al. 2000, Borregaard & Rahbek 2010). This occupancy-abundance relationship is considered one of the best-documented relationships in macroecology. Nevertheless, researchers with considerable field experience from tropical hot spots of endemism know that many species with tiny geographical distributions are abundant where they occur and are sometimes the most locally abundant taxon. This is at present poorly documented, probably because few biologists have spent sufficient time in the remaining patches of impenetrable virgin forest on steep, mist-enshrouded slopes to obtain adequate abundance data. However, some documentation has been provided for the Cameroon Mountains (Reif et al. 2006) and Eastern Arc Mountains (Romdal & Rahbek 2009, Fjeldså et al. 2010). Most convincingly, Williams et al. (2009) demonstrated for the montane forests of the Australian wet tropics that species with narrow environmental niches and small geographic ranges have high and uniform local abundance. Many of the narrow endemics are phylogenetically old and are probably locally specialized, and this may enhance the resilience of such species by maintaining high demographic connectivity throughout their ranges.

The analysis of plant-hummingbird mutualistic networks sampled at 31 localities spanning a wide range of climatic regimes across the Americas (Dalsgaard et al. 2011) established that the highest degree of mutualistic specialization among the sampled localities occurs in tropical montane forests (Costa Rica, Colombia, Brazilian Atlantic Forests). Across all 31 sites, the degree of mutualistic connectedness was well explained by the spatial variation of climate change velocity metrics (see above). Thus, such conditions not only benefit individual species but may also extend across communities.

5.1. Safe Havens for Montane Biodiversity?

Many researchers have expressed concern that montane species adapted to narrow elevational zones would be threatened under impending climate change. Montane species should be able to track their climatic niche by moving short distances up or down slope (Loarie et al. 2009, Tingley et al. 2009), but mountaintop inhabitants may have nowhere to go, as suggested by local empirical studies (Foster 2001, Moritz et al. 2008, Colwell & Rangel 2010), as well as by global modeling with different dispersal scenarios (La Sorte & Jetz 2010). The simulations by Williams et al. (2009) and Ohlemüller et al. (2011) project extensive loss of habitat, including within montane regions.

Similarly, the simulations conducted by McCain & Colwell (2011) find high risks of mountaintop extinctions during interglacials and lowland extinction thresholds during glacials, favoring mid-elevation lineages.

We agree that the biota of isolated mountains (conical-shaped, like the classical study sites of Volcan Barva in Costa Rica and Mount Kinabalu on Borneo) may be at risk as climate zones move up, but this may not be universally true. For realistic predictions of the fate of montane avifaunas, we need to know more about the local factors that have allowed small-ranged species to persist in spite of the instability of the global climate.

First, top-ridge habitats, with their distinct, low, gnarled and drought-resistant vegetation may be a consequence of exposure and seasonal dryness rather than elevation as such. Many birds may use this habitat to take advantage of special resources such as seasonal blooming. The recorded elevational distribution of such birds does not necessarily represent a climatic window.

Second, we need to consider whether the lapse-rate-based statistical climate models based on interpolation between widely scattered weather stations can account for the complex topography-driven patterns of temperature and humidity of larger montane regions (Nogués-Bravo et al. 2007). In particular, the models fail to predict the interaction between flows of humid air and topography and the position of significant cloud-affected zones within montane areas (Foster 2001; Bruijnzeel et al. 2010, p. 34). Topography may govern the wind systems in the mountain valleys and cause more or less stable air stratification and local cold air ponding. In the alpine environment, the vegetation is governed by the length of the growth season, temperature and, most importantly, the night-time soil temperatures during the growth season. In steep and complex landscapes, this leads to habitat mosaics, where sites a few meters apart may encompass strikingly different abiotic regimes (Scherrer & Körner 2011). For instance, [Archaux \(2004\)](#) found that elevational distributions of breeding birds in the Alps were related to site-specific factors rather than climatic warming.

5.2. Implications for Conservation

Small-ranged species in tropical montane hot-spot areas have been described in some conservation strategies as the living dead and, hence, deemed to be of low conservation value. However, some of these species are in fact common and well adapted to their local environment, and they represent lineages that have persisted for millions of years in spite of dramatic shifts in the global climate. Some of these birds may represent the last stage in a taxon cycle, as species that were once widespread in the end survive as local remnant populations. We suggest that such birds occur exactly where the chances for long-term survival are best and that they therefore represent viable components of the regional fauna. Whether they may expand again at some point in time and start a new taxon cycle, we cannot know.

DISCLOSURE STATEMENT

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