

Diversification of tanagers, a species rich bird group, from lowlands to Montane regions of South America

J. Fjeldså¹ and C. Rahbek²

Zoological Museum, Universitetsparken 15, DK-2100 Copenhagen, Denmark

Synopsis The process of diversification since the late Tertiary was studied by linking together well-resolved phylogenies and species distributions for tanagers (*Aves*, Thraupini). Species richness patterns reveal very high densities of range-restricted species in the Andes, and to a lesser extent in the Atlantic forests of south-eastern Brazil, and moderate densities of widespread species in the tropical lowlands. Contemporary climate explains well the variation in species richness for the 25% most widespread species; for the remaining 75% of species with more restricted distributions, variation can only be explained well from topography and landscape complexity. Phylogenetically old species are mainly found along the Andes and along the Rio coast of Brazil. Most other areas outside the Andes probably had very moderate rates of later diversification. In contrast, the humid tropical Andes region was a centre of intensive speciation throughout the evolutionary history of the group, and species richness patterns here seem largely to be driven by the rate of speciation, with further diversification from the highlands into adjacent lowlands. The diversification process in montane areas may be related to high persistence of lineages in specific areas, something that may be related to how climatic changes are moderated by local topography.

Introduction

The understanding of relationships between lowland and highland biotas is diffuse, although it is often assumed that highland biota originated as lowland forms specialized to highland conditions and speciated along elevational gradients, or by local isolation within the highlands (*e.g.*, many papers in Vuilleumier and Monasterio, 1986). This view is understandable in the light of the young geological age of many mountain ranges. However, it has also been suggested that mountain regions may represent evolutionary centers, which may feed new species into the adjacent lowland biomes (*e.g.*, Reig, 1986, Roy *et al.*, 1997; Jetz *et al.*, 2004).

In this paper we will analyze the relative roles of montane and lowland regions in the diversification process, using an approach that tries to bridge the chasm between ecological and phylogeny-based (historical) biogeography (Wiens and Donague 2004). Ecological biogeographers (macroecologists) try to explain the large-scale variation in species richness in terms of contemporary environmental factors (*e.g.*, Brown and Lomolino, 1998), but often ignore that every species has an evolutionary history. The historical approach is more concerned with historical area relationships, and the associated methods underpinning the definition of areas (Nelson and Platnick, 1981, Wiley, 1988, Ronquist, 1997). The dichotomy between

these two directions limits the range of questions that is asked and the interpretations of what drives biological diversification, and it is only very recently that some new analytical approaches have been proposed to tease apart evolutionary and environmental causes of species richness patterns (Kerr and Currie, 1999; Jetz *et al.*, 2004; Hawkins *et al.*, 2005).

We chose the tanagers, Thraupinae (*Aves*), as a study group for five reasons:

(1) they represent the most diverse taxonomic group (347 species) for which phylogenetic relationships can be fairly completely reconstructed from deep branches to species level;

(2) they are endemic to one biogeographic region, the Neotropics (The early radiation must have been in South America; Yuri and Mindell, 2002), and because of the restricted opportunities to disperse out of this landmass [*e.g.*, Coates and Obando, 1996] we have excluded from analysis the small “spill-over” [28 endemic species in 11 lineages] to Central America, Caribbean Islands and the Galapagos archipelago, and the diversification of “Galapagos finches” within that archipelago [Burns *et al.*, 2002]; (3) speciation rates are heterogeneous (see Ricklefs, 2003), as some species represent deep lineages and others are part of large radiations, which may help to tell apart patterns of ancestry and later diversification; (4) they show a

From the symposium “Adaptations to Life at High Altitude” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 4–8, 2005, at San Diego, California.

¹ E-mail: jfjeldsaa@snm.ku.dk

² Present address: Institute of Biology, Universitetsparken 15, DK-2100 Copenhagen, Denmark.

Integrative and Comparative Biology, pp. 1–10

doi:10.1093/icb/icj009

© The Society for Integrative and Comparative Biology 2006. All rights reserved. For permissions, please email: journals.permissions@oxfordjournals.org.

wide range of feeding adaptations, with specializations for fruit, nectar, seeds and insects, and colonized all terrestrial habitats in the Neotropics; (5) their evolution falls within a time period from the early to mid Miocene (Burns, 1997; Barker *et al.*, 2004), after the initial uplift of the Andes region (Potts and Behrensmeyer, 1992; Marshall and Sempere, 1993; Moores and Twiss, 1995). New (páramo and superpáramo) habitats were formed through continued mountain uplift and climatic change in the Pleistocene (Hooghiemstra *et al.*, 1993; Hartley, 2003), but over all we assume that the relative distribution of highlands, and vegetation zones, changed little. Persistence of habitats facilitates interpretations about the past based on present-day distributions.

Methods

Phylogeny reconstruction

The tanagers are part of a very large radiation of “New World nine-primaried oscines”, a group with fairly uniform body size and shape, but with prominent variation in colors and bill shapes, which have been important clues for classifying these birds. Modern phylogenetic studies have revealed that the importance of bill-shape was over-emphasized in the past (Remsen, 2003), and that the traditionally defined tanager group is non-monophyletic. The taxon has therefore been re-defined as a lineage, which includes several genera previously placed among the Emberizinae (*e.g.*, *Phrygilus*, *Poospiza*, *Sicalis*, *Sporophila*), Parulinae (*e.g.*, *Conirostrum*), Cardinalini (*Paroaria*), and the “Coeribidae” (*e.g.*, *Coereba*, *Cyanerpes*, *Spiza*), while at the same time some genera previously classified as tanagers are transferred to the Emberizinae (*e.g.*, *Chlorospingus*), Cardinalinae (*e.g.*, *Piranga*), and Fringillidae (*e.g.*, *Euphonia*) (Sibley and Monroe, 1990; Yuri and Mindell, 2002; Burns *et al.*, 2003).

A phylogenetic model for the re-defined taxon was constructed using data from 21 recent molecular studies (mainly Hackett, 1996; Klicka *et al.*, 2000; Lovette and Bermingham, 2002; Yuri and Mindell, 2002; Burns, 1997; Burns *et al.*, 2003; Burns and Naoki, 2004; Lijtmeir *et al.*, 2004; García-Moreno and Fjeldså, 2003 and unpublished), and principles of supertree construction based on points of congruence between several incomplete but partially overlapping phylogenies (Baum, 1992). However, many studies may give a skewed picture of the true phylogeny as only one of the subgroups was well sampled while the rest was represented by a rather arbitrary selection of species (Rannala *et al.*, 1998). Several studies used molecular markers which were too short to confidently

resolve deeper nodes. We therefore did not find it feasible to use existing tree-building programs (*e.g.*, Baum, 1992) that assume equal weighting of source trees, or rigid weighing schemes for constructing a consensus topology. Our approach was therefore to first make a strict consensus tree and then evaluate each part of the tree, assuming that branches well supported by 3.2 kb of mitochondrial DNA sequences (Yuri and Mindell, 2002) should overrule those based on shorter mtDNA sequences, those supported by complex-model analyses should overrule those of parsimony trees, and those of well-resolved species-group studies should overrule nodes from trees with biased taxon sampling. A few odd species, never included in molecular studies, were tentatively placed following plausible suggestions in the literature. For some genera not yet covered by molecular studies to species level, we grouped the species according to morphology (assessed from voucher specimens).

The phylogeny was transformed to a clade-code in our biogeographic software (WorldMap, Williams, 1999), as the sister taxa at each node are assigned “a” and “b” (or additional letters in case of unresolved polychotomies). A full list of species with assigned clade-codes, and supporting references, are provided online as supplementary material at www.icb.oxfordjournals.org.

The age of a species does not follow directly from the number of nodes on a branch, and cannot be calculated in a consistent way when the supertree is based on many kinds of primary data. For a rough definition of species age classes we therefore took into account how earlier taxonomists had arranged the species in genera, defining (1) “ancient species” as those with branch-lengths of maximum five nodes placed in monotypic or two-species genera; (2) “old species” as those with branch-length of maximum 8 nodes, but excluding representatives of genera with >3 species; and (3) “young species” as those with branch-lengths of >10 nodes, but excluding species in monotypic genera (Note that *ca.* 100 intermediate-aged species will fall between the categories of old and young species). A few publications provide a rough age estimate based on molecular clock data (Sibley and Ahlquist, 1990; Burns, 1997; Loughheed *et al.*, 2000; Barker *et al.*, 2004; Lijtmaer *et al.*, 2004; p-distance data for mtDNA in some other papers). This forms the basis for some sweeping statements in the text, referring to the likely geological time of evolutionary events.

Distributional data

Distributional data (for all South American birds) have been compiled over many years in a geographical grid

with a resolution of $1^\circ \times 1^\circ$ (latitude \times longitude) (see Fjelds and Rahbek, 1997; Rahbek and Graves, 2001; updated version of November 2004). Final maps for each species represent a conservative “extent of occurrence,” based on museum specimens, published sight records, data from our own fieldwork and information from colleagues, and interpolation, taking the spatial distribution of prime habitats into account.

We used the WORLDMAP computer program (Williams, 1999) to overlay the distributional data. The software can calculate species richness and various other diversity measures. This includes “mean root path,” which scores the representation of deep phylogenetic branches in a particular cell (inverse value of number of nodes from the root of the tree to each terminal taxon; thus a high index means that the species present in a grid-cell diverged close to the root). “Sub-tree length” is the sum of cladogenetic events (branching points, or nodes) between all the species represented in a cell (Faith, 1994). Thus, the latter value reflects to what extent species in different parts of the tanager phylogeny persist together in the same cell.

Macroecological determinants of species richness patterns

We sought to characterize the relationship between species richness and potential determinants examining the conditional power of six traditionally used independent variables in a stepwise regression (*ad hoc*) model incorporating all independent variables. Variables were considered with forward selection (P to enter = 0.05) followed by a backward elimination (P to removed = 0.05) with tolerance = 0.01. Macroecological data are autocorrelated, which can lead to biased estimators and spurious biological conclusions. For this reason, we emphasize the resulting spatial pattern of our data and results as well as the relative, conditional ranking of variables (F ratios) in our regression model rather than P values (*cf.* Rahbek and Graves [2001], but see also Tognelli and Kelt [2004]). The performance of our model was compared in terms of r^2 and the mapped distribution of residuals.

As independent factors, we included in our model the following six variables: 1) Area calculated as the land surface area within each $1^\circ \times 1^\circ$ latitudinal-longitudinal quadrat, taking topography into account; 2) mean annual temperature and 3) mean annual precipitation extracted from the mean monthly climatic database published by New *et al.*, (1999), which was compiled at a $0.5^\circ \times 0.5^\circ$ lat-long resolution for the period 1961–1990; 4) net primary productivity (NPP) obtained from the DOLY global model compiled at a $0.25^\circ \times 0.25^\circ$ lat-long resolution (Woodward *et al.*, 1995); 5) ecosystem diversity counted as the number

of distinct ecosystems per quadrat from a recent map of global ecosystems (http://edcdaac.usgs.gov/glcc/sadoc1_2.html); 6) Topographic relief calculated as the maximum minus minimum elevation recorded in each quadrat, as a surrogate for topographic heterogeneity based on data from the Global Land One-Kilometer Base Elevation (GLOBE) Digital Elevation Model (<http://www.ngdc.noaa.gov/seg/topo/globe.html>).

Results

Phylogenetic groupings

The phylogenetic data suggest two main groups, with three and five unresolved deep branches, respectively, and *Catamblyrhynchus*, which could not be confidently allocated to any of the two from the available evidence. However, the finer branching pattern was well resolved overall (see Supplementary Material).

The first group comprises mainly rather dull-colored forms, with *Ramphocelus*, *Conothraupis*, and *Creurgops/Orchestius* basally, then the dichotomy between the conebill and flowerpiercer group (*Conirostrum*, *Haplospiza*, *Catamenia* and *Diglossa*, and three monotypic genera), and a large and heterogeneous group. This comprises a clade of yellow-rumped forms (*Heterospingus*, *Chrysothlypis*, *Hemithraupis*) and one of crested forms (*Coryphospingus* basally, then *Lanio*, *Eucometis*, *Tachyphonus*, *Chlorothraupis*, *Trichothraupis*, and *Stephanophorus*), and a largely Andean radiation (basally *Phrygilus*, *Embernagra* and related forms, and then a very diverse assemblage of *Hemispingus*, *Cnemoscopus*, *Poospiza*, *Thlypopsis*, and some small genera).

The other large group has some unresolved basal branches (*Nemosia*, *Sericossyphus/Compsotraupis*, *Tersina* and the nectarivorous *Chlorospiza/Iridophanes* and *Cyanerpes/Dacnis*), and two large radiations of seed-eaters (basal grassquits, including *Tiaris*, *Coereba*, *Volatinia*, some Caribbean species and the “Galapagos finches,” mainly in *Geospiza* [Burns *et al.*, 2002], then *Sicalis* yellowfinches and the *Sporophila* seedeaters and their allies; [Lijtmaer *et al.*, 2004]), and typical multicolored tanagers (a basal clade comprising *Chlorochrysa*, *Paroaria*, *Neothraupis*, *Cissopis* and *Schistochlamys*, and two large radiations of colorful mountain tanagers [*Iridosornis*, *Thraupis*, *Bangsia*, *Buthraupis*, *Anisognathus* and some small genera] and the “superclade” of tropical canopy tanagers [*Tangara*] radiating from the very late Miocene [Burns *et al.*, 2003]).

Geographical patterns

The overall species richness for tanagers (Fig. 1a) shows a predominance in the tropics, and notably in the

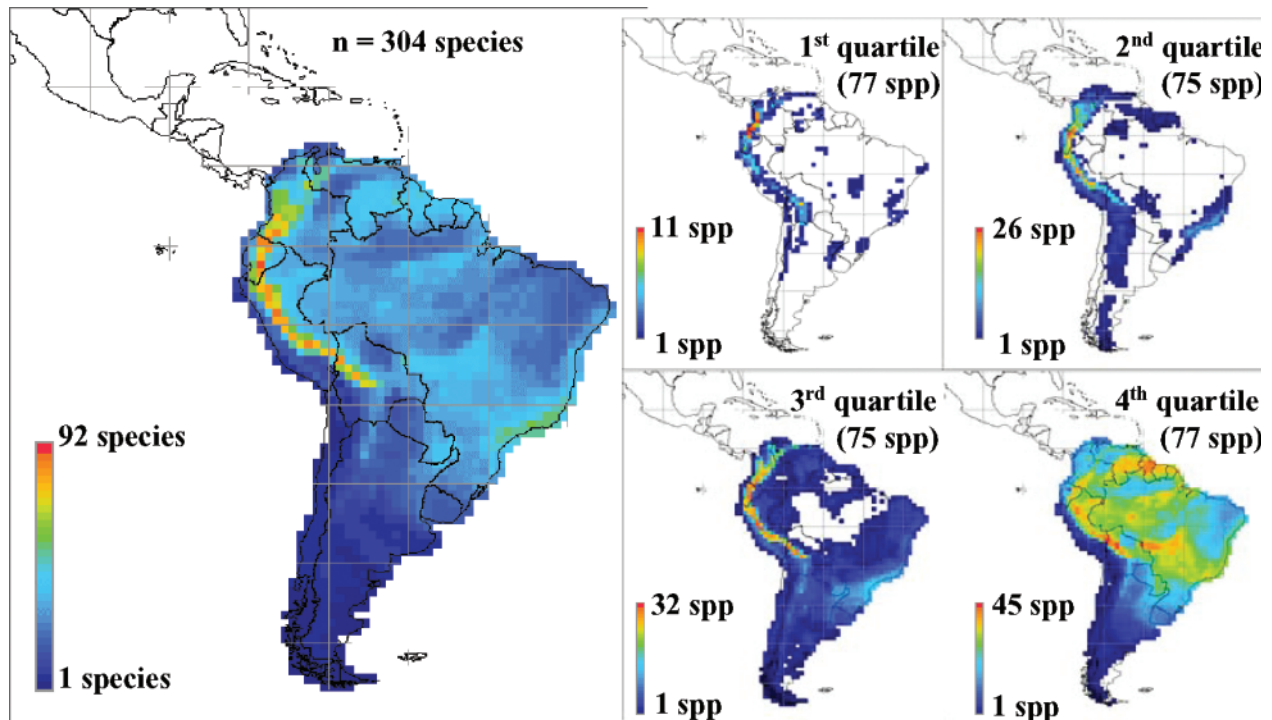


Fig. 1 Continental pattern of species richness for tanagers of South America ($n = 304$ species) measured at a scale of $1^\circ \times 1^\circ$ latitude-longitude quadrats. Red and orange indicate high values, dark blue the lowest values, and white absence of species (see color scale on each map for individual scaling). The left panel illustrates summed species richness for all species, whereas the four maps in right panel is for species partitioned into geographic range size quartiles (first quartile = smallest geographic ranges, fourth quartile = largest geographic ranges). Note that the color scale differs between the map for all species and the maps for each of the four range size quartiles.

Table 1 R^2 of single predictor variables of species richness using linear least square regression

	Topography (Elevational range)	Ecosystem diversity	NPP	Precipitation	Temp (mean annual)	Area (surface)	Contemporary climate model*
All species	0.025	0.187	0.402	0.306	0.285	0.178	0.439
1 st quartile	0.278	0.167	0.004	0.001	0.011	0.008	0.047
2 nd quartile	0.394	0.214	0.005	0.001	0.017	0.002	0.051
3 rd quartile	0.362	0.272	0.004	0.002	0.023	0.005	0.054
4 th quartile	0.093	0.020	0.751	0.507	0.638	0.233	0.783
Deep branch taxa	0.011	0.214	0.216	0.098	0.151	0.083	0.240
Recent radiation taxa	0.121	0.138	0.172	0.217	0.057	0.059	0.254

N = 1676 (grid cells).

Climate + area = (NPP, Precipitation, Temp, and Area).

humid tropical Andes region (absolute peaks Nariño-Imbabura, Morono-Santiago, Huánuco, Apurímac/Cuzco and La Paz), fairly high values also occur in the southern parts of the Brazilian Atlantic Forest, and moderately high values in the Planalto de Mato Grosso of Brazil west to the Bolivian border, and in the Guiana highlands. The species richness is generally low in the Amazon basin, although slightly elevated in the Peruvian part, near Porto Velho and along the lower Amazonas. This pattern is similar for the two main

clades ($r_s = 0.68$) and resembles the overall pattern for all South American land-birds (Rahbek and Graves, 2001).

About half of the tanagers inhabit fewer than 50 one-degree grid-cells, but some species are much more widespread, and species in different range-size groups produce markedly different patterns, something that is very similar for the two subgroups, and for South American land-birds as a whole (C. Rahbek *et al.*, unpublished). Species with very

Table 2 Determinants of Tanager species richness using stepwise regression of variables with forward selection (P to enter = 0.05) followed by a backward elimination (P to remove = 0.05) with tolerance = 0.01

	Variables entering model (F)	model r ²
All species	TOPO (688), NPP (239), ECO (235), T _{mean} (58), PREC (29)	0.693
1 st quartile	TOPO (518), ECO (143), NPP (66)	0.364
2 nd quartile	TOPO (853), ECO (203), PREC (78), AREA (30), T _{mean} (10)	0.514
3 rd quartile	TOPO (650), ECO (293), NPP (63), AREA (14), T _{mean} (7) ^A	0.505
4 th quartile	NPP (317), T _{mean} (148), AREA (64), PREC (33), TOPO (18), ECO (18)	0.791
Deep branch taxa	ECO (319), NPP (130), TOPO (115), T _{mean} (41), PREC (7) ^A ,	0.479
Recent radiation taxa	TOPO (681), ECO (139), NPP (128), PREC (87), T _{mean} (37)	0.599

^Adenotes a negative regression slope.

small distributions are very concentrated in the tropical Andes, and even for the 75% of the smallest to medium-small distributions (up to 151 grid-cells) a very large proportion occurs in the humid tropical Andes, with quite well marked local aggregates (Fig. 1b-d). In contrast, the 25% most widespread species are found mainly in the Amazon basin, and in the Guianan and Brazilian shield areas (Fig. 1e).

The step-wise regression model incorporating surface area, mean annual temperature, mean annual precipitation, net primary productivity, ecosystem diversity, and topographic relief conditionally explain 69% of the variation in tanager species richness, and somewhat less for the subsets of “old” and “young” species (Table 2). R² values progressively decline with quartiles of range-size distribution, having greater explanatory power for those species with large geographical ranges and little for species with the smallest range sizes (Table 2). Topographic relief emerges as the most important predictor, except for deep branch data and for the quartile of wide-ranging species. In general, the importance of climatic variable decreases with range-size quartiles and only Net Primary Productivity (but not temperature and precipitation) remains a weak predictor for species with restricted geographical distributions (Table 2).

As illustrated by the spatial distribution of standardized residuals, there is a relatively good fit of the widespread (4th quartile) species to the regression model (based on net primary productivity, area, precipitation, topographic relief and ecosystem diversity, but noticeably excluding temperature). In sharp contrast, the patterns for the most range-restricted species (1st quartile) are noticeable with “unexplained” peaks, especially in the western Andes near the equator. Only topographic relief, ecosystem diversity and net primary productivity remain significant predictors in the model (Fig. 2 and Table 2).

Similar results as discussed above have also been found in an analysis conducted on all species of

South American birds (Rahbek *et al.* unpublished), mammals (Ruggiero and Kitzberger, 2004), palms (Kreft *et al.*, in press) as well as for African birds (Jetz and Rahbek, 2002).

Historical pattern

“Ancient species” are best represented along an Andean Southeast Brazilian track (Silva 1995; for clade a) but can be found throughout the tropical zone. Some of them are very widespread (*Chlorophanes spiza*, *Coereba flaveola*, *Nemosia pileata*, *Tersina viridis* and *Volatinia jacarina*, all in clade b), others more locally distributed, in humid or dry environments. Some of the “ancient species” can be considered relics, as their distributions are very restricted, or disjunct, with sister taxa in widely separate areas (*e.g.*, *Compsothraupis* and *Sericossypha*). Such forms are found locally in the Andes, in the Tumbes region of south-western Ecuador/north-western Peru, and eastern Brazil, especially in the Río coastal zone.

The index for “mean root path” for all species in a grid-cell is very uniform across the continent (not illustrated), except for very high values in some small areas in the southern cone of the continent (especially for the first sub-group, clade a; see above). This could to some extent be a sampling artifact, as the very few species in these areas represent three genera *Diuca*, *Phrygilus* and *Sicalis*, which are poorly resolved phylogenetically, which means that the clade codes underscore the branch-lengths of individual species. A more interesting trend is found for the second main group (clade b; Fig. 3), where high values characterize the entire southern part of the Amazon basin up to the edge of the Cerrado uplands, as well as the Caatinga dry forest area of eastern Brazil. A similar pattern is seen when this index is applied to all “old species.”

The geographical variation in sub-tree length scores resembles that for species richness. The correlation is particularly close along the humid tropical Andes (pink hue in Fig. 4a) and in a small part of the coastal

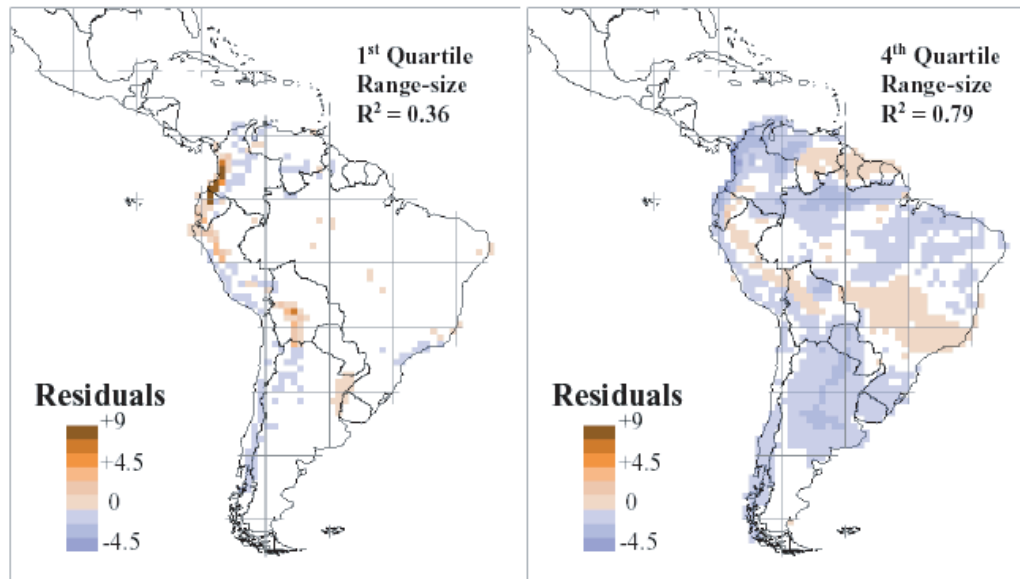


Fig. 2 Spatial distribution of residuals from stepwise multiple regression models presented in Table 2. Left panel shows results for species with small (=1st quartile) geographical range sizes, which is contrasted with patterns for species with large (=4th quartile) geographic range sizes in the right panels.

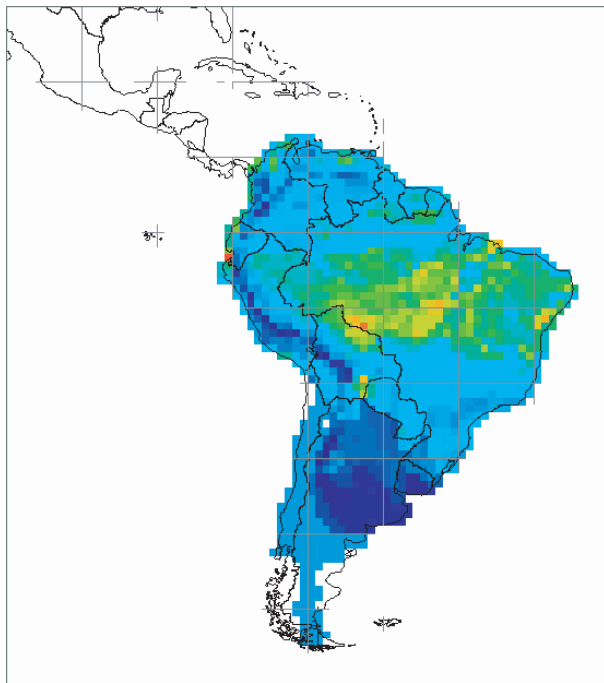


Fig. 3 The variation in the “mean root path” index for clade b.

mountains of southeastern Brazil (and in the Brazilian Cerrados, when applying this index to “old species” only). Elsewhere there is a bias toward sub-tree length (greenish hue in Fig. 4a), meaning that different deep branches are represented in the same grid-cell. However, there is a bias towards species richness

(bluish hue in Fig. 4a) in some sub-Andean foreland areas in the upper Amazon areas, along Río Madeira and locally in Pará, in the coastal zone of Brazil’s Atlantic forests, in the Guiana highlands, and northern extensions of the Andes (Colombia, Venezuela).

This pattern is further supported in Figure 4b, which contrasts the geographical distribution of 61 “old” and 143 “young” species (defined p. 2). Even here there is a clear correlation in the Andes (pink color). In contrast, the Brazilian highlands (Cerrados and upland Atlantic forests) and adjacent Bolivian cerrados and southern Amazon, and some small areas in the north, have relatively more species representing deep branches (blue tinge in Fig. 3b; with slightly different patterns for clades a and b). Some parts of the Amazon area (sub-Andean ridges and white-sands areas in the north), the Guiana Highlands, and the northern Andean ridges, have a slight predominance of species representing recent radiations. However, many species in these latter areas are medium-old and therefore not represented in Figure 4b.

Overall, there is a close correlation between species richness and sub-tree length (broken line in Fig. 5, $r = 0.985$), which means that the most species-rich areas also have a broad representation of lineages. It is particularly interesting in this respect to note that a regression line calculated only for “young” species (fully drawn line in Fig. 5) is particularly steep, which means that recent radiations are particularly characteristic of areas with a broad diversity of lineages present.

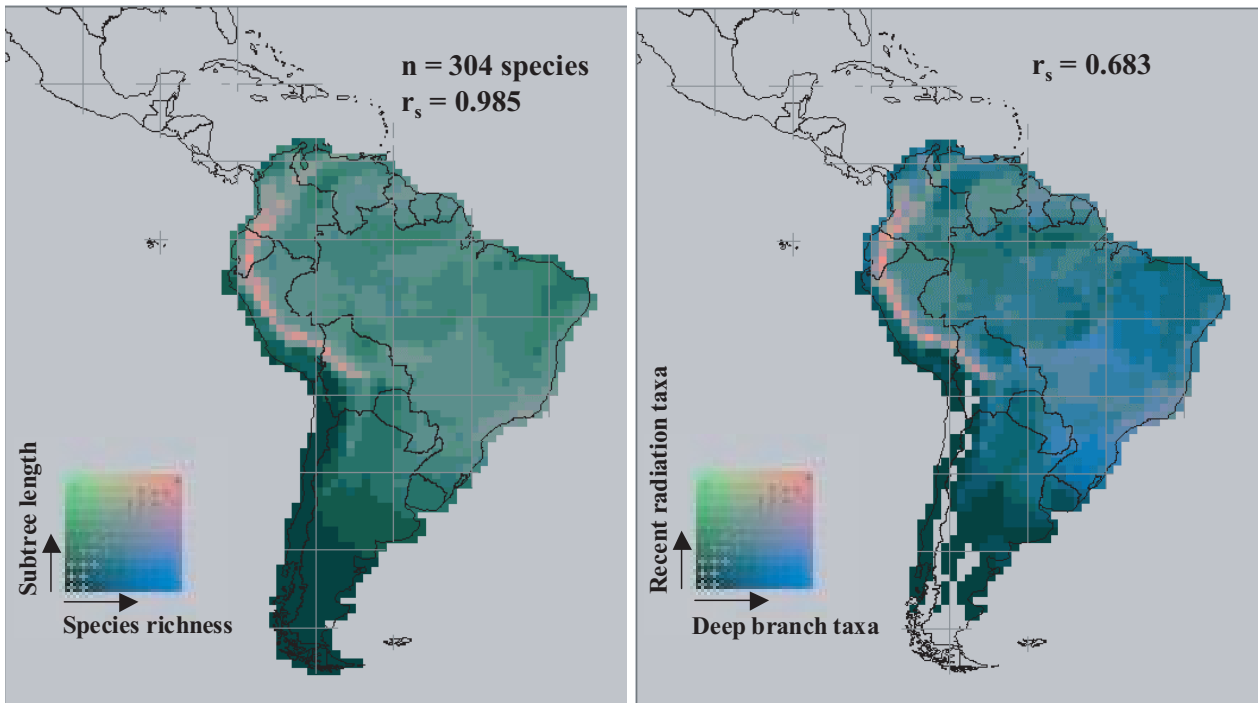


Fig. 4 Historical patterns, A illustrating the relationship between “sub-tree length” (green) and species numbers (blue), B illustrating the relationship between numbers of species defined as “old” (blue) and “young” (green) species (see p. 6). In both diagrams, bright pink represent high values for both parameters.

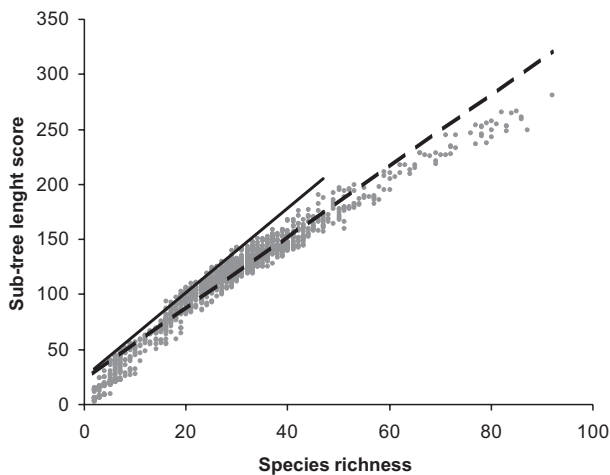


Fig. 5 Scatter plot comparing sub-tree length and species richness per grid-cell. Two regression lines are included for illustrative purposes: The broken line is based on the full set of species, and the solid line is calculated for the “young species” only.

Low sub-tree length scores may reflect sympatry of a few species representing deep branches, or speciation only in a smaller subgroup of tanagers.

Discussion

Popular statements about South American biodiversity often emphasize the importance of the Amazon

rainforest. However, when continent-wide species distribution data are critically examined, it becomes clear that the species richness is not particularly high considering the enormous extent of this biome (Fjelds  and Rahbek, 1997, Rahbek, 1997, Rahbek and Graves, 2001). The α -diversity may be high, especially at forest edges, in secondary growth and on tree-studded clearings, but the number of tanager species per grid-cell is moderate. Many of these species, especially in the southern part of the Amazon basin and the transition toward the Cerrado region, are widespread representatives of early speciation events in the group. However, many ancient species are also found in Andean cloud-forests, in the area that was also the main centre of more recent diversification within the group.

An earlier comparison of the distributions of “old” and “young” species in South America (Fjelds , 1994) described the Amazon area as a “museum” where species could persist over long periods of time in a dynamic habitat mosaic, although it was rather unimportant for diversification in recent geological times. The extraordinary species richness of South America as a whole appears instead to be a consequence of an enormous speciation burst since the Miocene in the humid tropical Andes region (Fjelds , 1994). The tanager group originated in a fairly recent geological time, after the onset of the Andean speciation bursts,

and the tropical Andes region may therefore have played an important role in the entire evolutionary history of tanagers, except that the diversification was more recent in the northern mountain ranges of Colombia and Venezuela (greenish hue in Fig. 4b). Clade b may primarily have radiated in tropical lowlands (including dispersive grassquits, which also colonized Caribbean and Galapagos islands; Burns *et al.*, 2002), but radiations in the Andean Southeast Brazilian region soon followed. After a geological subsidence in the Chaco region in the early Pleistocene (see da Silva, 1995) the Brazilian upland habitats were separated from those in the Andes, and apparently there was very few speciation events in the Brazilian uplands since then.

The low speciation rate and predominance of old species outside the tropical Andes region could be seen as a consequence of geological inactivity. However, there has been a moderate rate of speciation in the Río area, where coastal mountains were uplifted in the Pleistocene (Petri and Fúlvaro, 1983, cit. in da Silva, 1995), and in the Andean forelands in the upper part of the Amazon basin, where sub-Andean ridges have been uplifted since the Mio-Pliocene (Jordan *et al.*, 1983; Räsänen, 1993). Except in the genus *Tangara*, most speciation in the Amazon lowlands probably took place in the upper Miocene and Pliocene. Thus there is no strong signal indicating that postulated changes in Amazonian forest cover in the upper Pleistocene “glacial periods” (Haffer, 1969 and his later papers) affected the rate of diversification in the tanager group.

In the genus *Tangara* there was a fairly high amount of recent (Pleistocene) speciation in the Guianas. Another noteworthy recent radiation outside the Andes was the “capuchinos” group of 11 *Sporophila* species, notably eight species that are present south of the Amazon River. An extremely small sequence divergence among these (Lijtmaer *et al.*, 2004) suggests a rapid radiation within the last half-million years. Lijtmaer *et al.* (2001) suggests that it might have been promoted by marine incursions and regressions in the austral coastal regions in the Late Pleistocene. However, it should be noted that many seedeaters are migratory, or move around rather erratically, but on the other hand require very specific kinds of grassland, and are sensitive to habitat changes (Stotz *et al.*, 1996). The main concentration of seedeaters corresponds to elevated parts of Mato Grosso, so the pattern could also reflect patchy habitats and very local persistence—and population bottlenecks—caused by dramatic habitat changes in this region. It was strongly affected by changing impacts of south polar winds during the cold parts of the Pleistocene (Servant *et al.*, 1993), and by the very

restricted occurrence of savannah habitats in the wettest intervals of the Pleistocene (de Vivo and Carmignotto, 2004).

By combining environmental and historical signals, our approach provides a new avenue for interpreting the complex process of diversification of species-rich groups. Contemporary climate factors provide a strong explanation for the variation in numbers of widespread species. Some lowland areas (the austral and dry-forest regions, the Venezuelan llanos and the very species-poor parts of the Amazon lowland) have fewer widespread species than predicted, and the Brazilian cerrados have slightly more species than predicted (Fig. 2b) but overall the widespread species are distributed in accordance with current climate parameters. In contrast, contemporary climate explains very little of the variation of the 75% less widespread species. Their richness patterns correlate instead with topography, and somewhat with habitat complexity.

Tropical mountains may provide a complex elevational pattern of environments (Ghalambor *et al.*, 2006), but it is questionable whether the correlation between species richness and topography reflects the elevational amplitude as such. It could also be effects of topography on local climates, and thereby on local patterns of persistence of populations and a wide range of lineages. The species richness pattern in the Andes is very locally aggregated (Fjeldså *et al.*, 1999) and this applies especially to the distribution of distinctive (“old”) species (Fjeldså, 1995). Local aggregates of endemic species are especially found in places where the mountain chains make sharp bends, and where rain-capturing ridges are adjacent to warm and dry mountain basins, suggesting that a suitable climate can be maintained constantly over long periods of time. Within such areas, global climate changes may result in small local shifts of the zonal vegetation, maybe few hundred meters up or down the mountain slopes or around local mountain “corners.” The high sub-tree length values (Fig. 4a) and close correspondence of richness peaks of “old” and “young” species (Fig. 4b, and see Fjeldså, 1995) strongly suggest a high local persistence of lineages (or lack of extinction) over long geological time spans. This suggests a “species pump model” of diversification (Jetz *et al.*, 2004), and is also in good agreement with theoretical consideration about what drives speciation in a climatically unstable world (Jansson and Dynesius, 2002). The high peak of unexplained endemism in Figure 2a is very close to the equator, where conditions may be particularly stable, but data from a larger number of species (Fjeldså *et al.*, 1999) suggest other important local environments elsewhere in the humid tropical Andes

region, especially in the Apurimac/Cuzco area in Peru and in the Boopi and Cotacaches basins in the Yungas of La Paz, Bolivia. A significant persistence is also indicated for Río Coast, which may have had a constant impact of humid air.

In contrast, the lowlands lack well-marked topographic structures that can moderate patterns of rain and wind. The zonal vegetation may therefore change dramatically in response to global climatic change, leading to the adoption of wide geographical ranges. Local extinction may sometimes lead to patchy (relictual) distribution, as seen in many species, but the dynamic nature of these ranges may nevertheless provide sufficient opportunities for gene-flow to prevent genetic coalescence and local speciation. Most speciation in the Amazon area and in the Brazilian highland took place in the early and medium-old history of tanager evolution, and the causes of these speciation events are therefore now “buried” by a long history of later range dynamics. Over all, there was little recent (Pleistocene) speciation in the lowlands, except from above-mentioned cases of *Tangara* and *Sporophila* radiations.

The very close correlation between local species richness counts and sub-tree length (Fig. 4) suggest that species richness patterns are driven by a combination of persistence of lineages and speciation. For much of the year, large numbers of tanager species can be seen feeding together in mixed feeding parties, so the number of coexisting species does not seem to be much constrained by limiting similarity between the species. Species originating in different parts of the tropical Andes region may rapidly become sympatric on the same slope (see García-Moreno and Fjeldsá, 2000). Most regions with few opportunities for speciation remain species poor, although details in the variation in the sub-tree length/species richness ratio (Fig. 4a) suggests that the species richness may be raised as adaptive re-distribution brings several old species (with short branch-lengths) together in the same area. The detailed phylogeographic history of *Tangara* species suggest that montane radiations may spur some new radiations in the lowlands (Burns *et al.*, 2004), but the Andes represent the main centre of diversification throughout the evolutionary history of tanagers.

Acknowledgments

We thank Doug Altshuler, Rauri Bowie and David Steadman for comments to earlier versions of this paper. C.R. acknowledges the Danish National Science Foundation (Grant J. 21-03-0221) for support of macroecological research.

References

- Baum, B.R. 1992. Combining trees as a way of combining data sets for phylogenetic inference and the desirability of combining gene trees. *Taxon* **41**:3–10.
- Brown, J. H. and M. V. Lomolino. 1998. *Biogeography*. 2nd ed. Sinauer Ass., Sunderland, MA.
- Burns, K. J. 1997. Molecular systematics of tanagers (Thraupinae): Evolution and biogeography of a diverse radiation of Neotropical birds. *Mol. Phyl. Evol.* **72**:334–348.
- Burns, K. J., S. J. Hackett, and N. K. Klein. 2002. Phylogenetic relationships and morphological diversity in Darwin’s finches and their relatives. *Evolution* **56**:1240–1292.
- Burns, K. J., S. J. Hackett, and N. K. Klein. 2003. Phylogenetic relationships of Neotropical honeycreepers and the evolution of feeding morphology. *J. Avian Biology* **34**:360–370.
- Burns, K. J. and K. Naoki. 2004. Molecular phylogenetics and biogeography of Neotropical tanagers in the genus *Tangara*. *Mol. Phyl. Evol.* **32**:838–854.
- Coates, A. G. and J. A. Obando. 1996. The geological evolution of the Central American isthmus. In J. B. C. Jackson, A. F. Budd, and A. G. Coates (eds), *Evolution and environment in tropical America*, pp. 21–56. Univ. Chicago Press, Chicago.
- de Vivo, M. and A. P. Carmignotto. 2004. Holocene vegetation change and the mammal faunas of South America and Africa. *J. Biogeogr.* **31**:943–957.
- Faith, D. P. 1994. Phylogenetic patterns and the quantification of organismal biodiversity. *Phil. Trans. Roy. Soc. London B* **345**:45–58.
- Fjeldsá, J. 1995. Geographical patterns of neoendemic and relict species of Andean forest birds: the significance of ecological stability areas. In S. P. Churchill, *et al.* (ed.), *Biodiversity and conservation of neotropical montane forests*, pp. 79–87. New York Bot. Garden, New York.
- Fjeldsá, J. and J. Lovett. 1997. Geographical patterns of phylogenetic relicts and phylogenetically subordinate species in tropical African forest. *Biodiver. Conserv.* **6**:325–346.
- Fjeldsá, J. and C. Rahbek. 1997. Species richness and endemism in South American birds: implications for the design of networks of nature reserves. In W. F. Laurance and R. D. B. Bierregaard, Jr (eds), *Tropical Forest Remnants*, pp. 466–482. Chicago Univ. Press, Chicago.
- García-Moreno, J. and J. Fjeldsá. 2000. Chronology and mode of speciation in the Andean avifauna. *Bonn Zool. Monogr.* **46**:25–45.
- García-Moreno, J. and J. Fjeldsá. 2003. Phylogenetic relationships among *Hemispingus* tanagers. *Ornitologia Neotropical* **14**:363–390.
- Ghalambor, C. K., R. B. Huey, and P. R. Martin. 2006. Why mountain passes are higher in the tropics revisited. *Integr. Comp. Biol* **46**.
- Grapputo, A., A. Polastro, A. J. Baker, and G. Marin. 2001. Molecular evidence for phylogenetic relationships among buntings and American sparrows (Emberizidae). *J. Avian Biol.* **32**:95–101.

- Haffer, J. 1969. Speciation in Amazonian forest birds. *Science* **165**:131–137.
- Hartley, A. J. 2003. Andean uplift and climate change. *J. Geol. Soc.* **16**:7–10.
- Hawkins, B. A., J. A. F. Diniz-Filho, and S. A. Soeller. 2005. Water links the historical and contemporary components of the Australian bird diversity gradient. *J. Biogeogr.* **32**:1–8.
- Jansson, R. and M. Dynesius. 2002. The fate of clades in a world of recurrent climatic change: Milankovitch oscillations and evolution. *Annu. Rev. Ecol. Syst.* **33**:741–777.
- Jordan, T., B. Isacks, R. Allmendinger, J. Brewer, V. Ramos, and C. Ando. 1983. Andean tectonics related to geometry of subducted Nazca plate. *Geological Society of America Bulletin* **94**:341–361.
- Kerr, J. T. and D. J. Currie. 1999. The relative importance of evolutionary and environmental controls on broad-scale patterns of species richness in North America. *Ecoscience* **6**:329–337.
- Klicka, J., K. P. Johnson, and S. M. Lanyon. 2000. New world nine-primaried oscine relationships: constructing a mitochondrial DNA framework. *Auk* **117**:321–36.
- Kreft, H., J. H. Sommer, and W. Barthlott. 2005. The significance of geographical range size for spatial diversity patterns in Neotropical palms. *Ecography* In press.
- Lijtmaer, D. A., N. M. M. Sharpe, P. L. Tubara, and S. C. Loughheed. 2004. Molecular phylogenetics and diversification of the genus *Sporophila* (Aves: Passeriformes). *Mol. Phy. Evol.* **33**:562–579.
- Lovette, I. J. and E. Bermingham. 2002. What is a wood-warbler? Molecular characterization of a monophyletic Parulidae *Auk* **119**:695–714.
- New, M., M. Hulme, and P. Jones. 1999. Representing twentieth-century space-time climate variability. Part I: Development of a 1961–90 mean monthly terrestrial climatology. *J. Climate* **12**:829–856.
- Nelson, G. J. and N. Platnick. 1981. *Systematics and biogeography: Cladistics and vicariance*. Columbia Univ. Press, New York.
- Petri, S. and V. J. Fúlfaro. 1983. Geologia do Brasil (Fanerozóico). T. A. Queiroz and EDUSP, São Paulo. T. A. Queiroz and EDUSP, São Paulo.
- Rahbek, C. 1997. The relationship among area, elevation, and regional species richness in Neotropical birds. *Am. Nat.* **149**:875–902.
- Rahbek, C. and G. R. Graves. 2001. Multiscale assessment of patterns of avian species richness. *Proc. Natl. Acad. Sci. U.S.A.* **98**:4534–4539.
- Rannala, B., J. P. Huelsenbeck, Z. Yang, and R. Nielsen. 1998. Taxon sampling and the accuracy of large phylogenies. *Syst. Biol.* **47**:702–710.
- Reig, O. A. 1986. Diversity patterns and differentiation of high Andean rodents. In F. Vuilleumier and M. Monasterio (eds), *High altitude tropical biogeography*, pp. 404–439. Oxford Univ. Press.
- Remsen, J. V. 2003. The “Coerebidae”: A polyphyletic taxon that dramatizes historical over-emphasis on bill shape as a taxonomic character. *J. Avian Biol.* **34**:321–323.
- Ricklefs, R. E. 2003. Global diversification rates of passerine birds. *Proc. R. Soc. Lond. B* **270**:2285–2291.
- Ridgely, R. S. and G. Tudor. 1989. *The Birds of South America* Vol. 1. Oxford Univ. Press,
- Roy, M. S., J. M. C. da Silva, P. Arctander, J. García-Moreno, and J. Fjeldså. 1997. The role of montane regions in the speciation of South American and African birds. In D. P. Mindell (ed.), *Avian molecular evolution and systematics*, pp. 325–343. Acad. Press, New York.
- Ronquist, F. 1997. Dispersal-vicariance analysis: A new approach to the quantification of historical biogeography. *Syst. Biol.* **46**:195–203.
- Ruggiero, A. and T. Kitzberger. 2004. Environmental correlates of mammal species richness in South America: Effects of spatial structure, taxonomy and geographic range. *Ecography* **27**:401–416.
- Servant, M., et al. 1993. Tropical forest changes during the Late Quaternary in African and South American lowlands. *Glob. Planet. Change* **7**:25–40.
- Sibley, C. G. and J. E. Ahlquist. 1990. Phylogeny and classification of birds. A study in molecular evolution. Yale University Press, New Haven, CT. Yale University Press, New Haven, CT.
- da Silva, J. M. C. 1995. Biographic analysis of the South American Cerrado avifauna. *Steenstrupia* **21**:49–67.
- Stotz, D. F., J. W. Fitzpatrick, T. A. Parker, III, and D. K. Moskovits. 1996. *Neotropical birds. Ecology and conservation*. Chicago Univ. Press, Chicago.
- Tognelli, M. F. and D. A. Kelt. 2004. Analysis of determinants of mammalian species richness in South America using spatial autoregressive models. *Ecography* **27**:427–436.
- Vuilleumier, F. and M. Monasterio. 1986. *High altitude tropical biogeography*. Oxford Univ. Press, New York.
- Wiens, J. J. and M. J. Donoghue. 2004. Historical biogeography, ecology and species richness. *Trends Ecol. Evol.* **19**:639–644.
- Wiley, E. O. 1988. Vicariance biogeography. *Annu. Rev. Ecol. Syst.* **19**:513–542.
- Woodward, F. I., T. M. Smith, and W. R. Emmanuel. 1995. A global land primary productivity and phytogeography model. *Global Biogeochem. Cycles* **9**:71.
- Yuri, T. and D. P. Mindell. 2002. Molecular phylogenetic analysis of Fringillidae, “New World nine-primaried oscines” (Aves: Passeriformes). *Molec. Phylogenet. Evol.* **23**:229–243.