

Beta diversity along environmental gradients: implications of habitat specialization in tropical montane landscapes

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Summary

1. Understanding how species in a diverse regional pool are spatially distributed with respect to habitat types is a longstanding problem in ecology. Tropical species are expected to be specialists along environmental gradients, and this should result in rapid compositional change (high beta diversity) across landscapes, particularly when alpha diversity is a small fraction of regional diversity. Corollary challenges are then to identify controlling environmental variables and to ask whether species cluster into discrete community types along a gradient.
2. We investigated patterns of avian species' distributions in the Tilarán mountains of Costa Rica between 1000 m and 1700 m elevation where a strong moisture gradient exists. High beta diversity was found with both auditory counts adjusted for detectability and extensive capture data, revealing nearly complete change in community composition over a few kilometres on the Pacific slope. As predicted, this beta diversity was roughly twice as high as on temperate mountainsides.
3. Partial Mantel analyses and canonical correspondence analysis indicate that change in species composition is highly correlated with change in moisture (and correlated epiphyte cover) at different distances from the continental divide on the Pacific slope. Altitude was not a good predictor of change in species composition, as species composition varies substantially among sites at the same elevation.
4. Detrended correspondence analysis and cluster analysis revealed a zone of rapid transition separating a distinct cloud forest community from rainshadow forest. On the Caribbean slope, where a shallower moisture gradient was predicted to result in lower beta diversity, we found lower rates of compositional change and more continuous species turnover.
5. Results suggest that habitat specialization of birds is likely a strong ecological force generating high beta diversity in montane landscapes. Despite overall rapid rates of species turnover, zones of relatively coherent composition could be identified.
6. Landscapes with such high beta diversity are common in the tropics, although little studied. They offer high benefit/cost opportunities for conservation, particularly as climate change threatens to alter the species composition of communities of habitat specialists.

Key-words: cloud forest, conservation, endemic species, reserve design, tropical birds

Introduction

Ecologists have long explored the implications of species' ecological specialization for the spatial organization of biological diversity, and long debated the causes (MacArthur 1969; Orians 1969; Terborgh 1971). When local ('alpha') diversity is a small fraction of regional ('gamma') diversity, then diversity among habitats on a landscape scale ('beta diversity') is expected to be substantial. Avian species richness in Latin America is six times that of North America, in a

similar area, but the multiplier is substantially less on the local scale (3–4; this study, AOU 1998, and see also MacArthur 1969), so that tropical beta diversity is expected to be roughly twice that of temperate landscapes. Narrow environmental tolerances resulting in limited distributions along environmental gradients, coupled with small geographical ranges, help explain this pattern (Whittaker 1975; Stevens 1989; Brown 1995; Gaston & Blackburn 2000). Tropical montane landscapes harbour diverse faunas with many co-existing species within climatic zones or habitat types, and with high species turnover between zones or habitats. High beta diversity along environmental gradients reflects habitat

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specialization by the constituent species, and quantifying beta diversity along such gradients can inform strategies for protecting the biological diversity of a landscape. If beta diversity is high, then even small additions to protected areas could incorporate many new species and improve viability of narrowly adapted local populations in the face of human encroachment and climate change. Spatial variation in species composition within habitat types ('pattern diversity' *sensu* Magurran 2004), although seldom measured, is also important for planning because it indicates the area necessary to protect species of a habitat type. Species in habitats with higher pattern diversity likely have patchy local distributions and viable populations will likely require larger areas. In addition, if sets of species reliably occurred together, and if such sets replaced one another predictably along environmental gradients, then community types and conservation priorities could be mapped objectively.

Beta diversity is often expressed as the ratio of regional ('gamma' diversity) and alpha species richness (Whittaker 1975). This ratio is thought to reflect the degree of habitat specialization among species and possibly the degree to which competitive interactions may have produced 'saturation' of communities (e.g. Caley & Schluter 1997). Divining processes from patterns of beta diversity is, however, fraught with problems beginning with the variety of measurements of diversity at all levels and the definitions of 'habitat' and 'region'. The pool of species on a geographical scale is the raw material for species richness on any smaller scale, and explanations of regional diversity consist of the summed explanations on the smaller scales plus determinants of speciation rates and species exchange among regions. Many studies employ analyses at arbitrarily nested scales, defining beta diversity as variety among cells in a grid (e.g. Lennon *et al.* 2001). These analyses are useful in locating areas of high diversity or compositional uniqueness, but are unlikely to reveal biological mechanism. Beta diversity is most often measured as species turnover without regard for relative abundances of species (Koleff, Gaston & Lennon 2003), but inclusion of the relative abundances of species permits a more biologically informative assessment, especially when abundances vary greatly.

Few analyses of compositional change in animal communities along altitudinal gradients exist, and beta diversity in tropical systems is particularly poorly understood (but see Terborgh & Weske 1975; Terborgh *et al.* 1990; Navarro 1992; Young, DeRosier & Powell 1998; Blake & Loiselle 2000). Among studies of altitudinal gradients in the tropics [e.g. above references for birds; Lieberman *et al.* 1996 (trees); Kitayama 1992, and Vásquez & Givnish 1998 (vascular plants); Brehm, Homeier & Fiedler 2003 (moths)], most have found gradual compositional turnover with altitude, although this can be affected by the coarse sampling regime usually employed (see Kitayama 1992 and Navarro 1992). Fine-scale beta diversity, with sampling distributed continuously over a gradient, is seldom examined. Only Vásquez & Givnish (1998) have explored variation within altitudinal zones, and all others have studied windward altitudinal gradients.

In this study, we investigate changes in avian species composition across a tropical montane landscape in the Tilarán mountains of Costa Rica. We compare beta diversity on the Pacific (rainshadow) and Caribbean (windward) slopes, testing the idea that a steeper environmental gradient would produce greater beta diversity. On the Pacific slope, we ask whether altitude, moisture, topography and vegetation can explain patterns of beta diversity. We also test the hypothesis of gradual change along environmental gradients derived from individualistic models of species' habitat use (e.g. Whittaker 1975). We use patterns of change in species composition to define avian communities and explore implications for conservation planning.

Methods

STUDY SITE

The montane forests of Costa Rica and Panamá have the highest avian species richness in the highlands of Central America (Hernández-Baños *et al.* 1995) and are recognized as a global conservation priority because of their concentration of avian endemism (Bibby *et al.* 1992; Stotz *et al.* 1996; Stattersfield *et al.* 1998). The tropical montane forests of Central America (Mexico-Panamá) contain 147 avian species endemic to that habitat, and the Tilarán mountain range in Costa Rica harbours 41 species narrowly endemic to the highlands of Costa Rica and Panamá (Stiles, Gardner & Skutch 1989; Fogden 1993).

The Tilarán mountain range (10°18' N, 84°45' W; maximum elevation 1850 m) extends for 100 km north west-south east separating the Caribbean slope from the drier Pacific slope. When the dominant north-easterly tradewinds from the Caribbean encounter the Tilarán mountains, adiabatic cooling relieves those air masses of most of their moisture as they are driven up the Caribbean slope. Precipitation on the upper slopes can reach 7000–8000 mm annually (Bolaños & Watson 1993; Haber 2000). As the winds cross the continental divide, much of the moisture is delivered as mist and cloudwater, perhaps equal to precipitation measured in rain gauges, and dripping epiphyte-laden cloudforests grow down to 1500 m on the Pacific slope (Clark, Lawton & Butler 2000; Haber 2000; Häger 2006). The structure of these forests demonstrates the impact of aerial moisture and a moderate dry season, particularly the massive epiphyte community of hundreds of species of ferns, bromeliads, orchids, mosses and vines (Nadkarni, Matelson & Haber 1995). As the air masses cross the ridge, moisture dissipates rapidly over the Pacific slope, and the epiphyte community nearly vanishes below 1400 m, along with moisture from mist.

While there is debate about how to measure moisture in such a hydrological environment, data from conventional gauges and wind-screens suggest that moisture in the ridgetop cloudforests averages 4000–6000 mm annually, and declines to 2000 mm within 4–5 km towards the Pacific (below 1000 m), where there is also a more pronounced dry season. Given that these drier lowlands are also considerably warmer (6 °C/1000 m altitude), higher potential evapotranspiration there further reduces effective precipitation and soil moisture (Clark *et al.* 2000; Haber 2000; Häger 2006). Local topography creates microclimates within this broad picture, as ridges and gaps channel cloud flow. Cloud immersion is common near the continental divide, and recent satellite data show a steep gradient in forest-cloud contact with increasing distance from the divide. Cloud immersion averages above 50% of the day in March on the ridge crest, and declines to one-third that value 3 km away from the

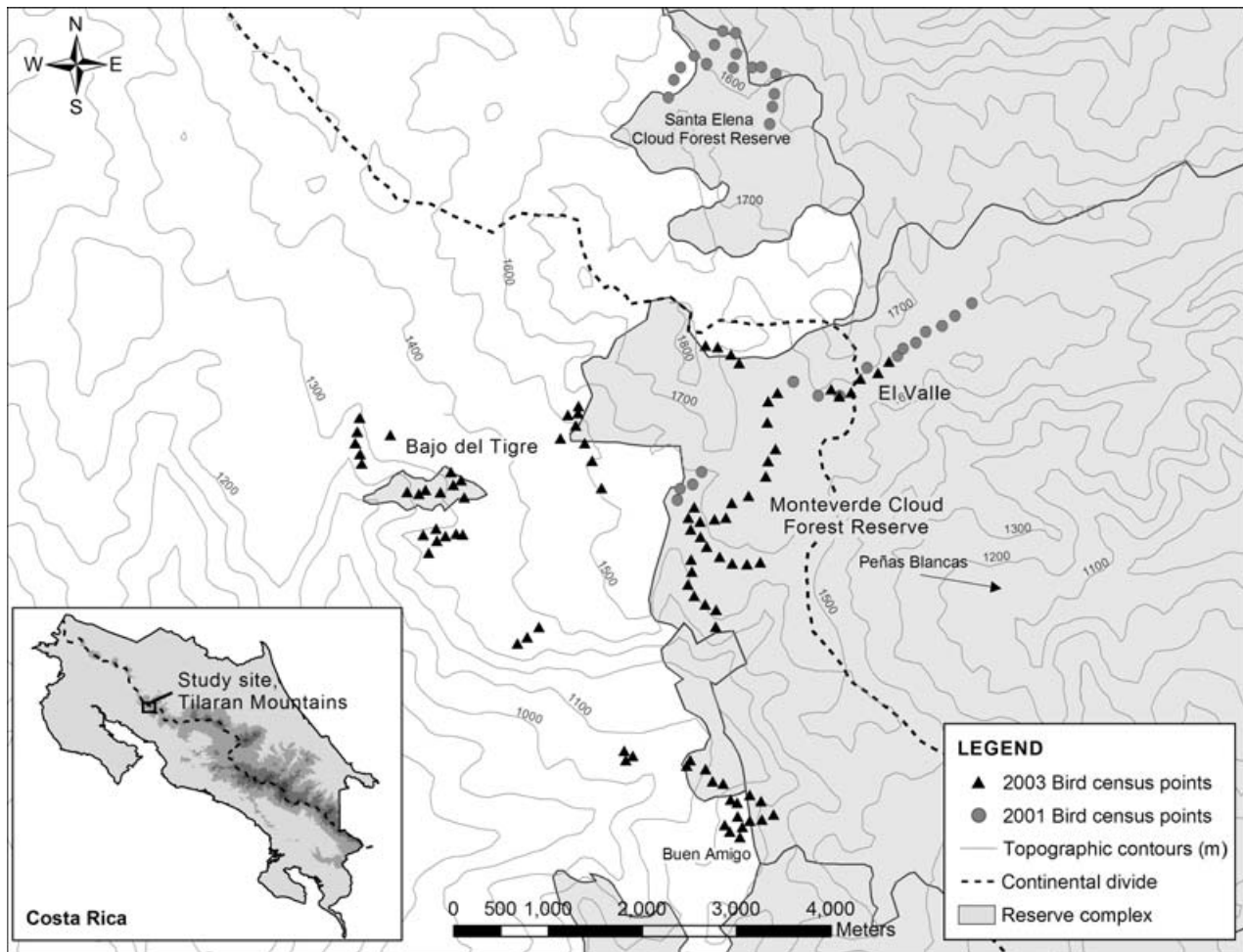


Fig. 1. Map of the Monteverde study area, Tilarán mountains, Costa Rica. Triangles show 89 census points for Pacific slope in 2003. Circles indicate additional auditory census points used in 2001. Netting survey was performed at 33 points at 100-m intervals along the El Valle trail. Arrow indicates the direction of the Caribbean-slope transect. Figure by Dan Majka.

divide (Nair 2008). Using data from this study (at 1 km resolution), cloud immersion is significantly related to both altitude and distance from the continental divide (linear regression; elevation $r = 0.66$, $P < 0.0001$; distance from divide $r = -0.66$, $P < 0.0001$). The overall picture from these various studies is that moisture declines approximately 1000 mm km^{-1} moving along the ground away from the continental divide, and seasonal and daily water balance likely change even more rapidly. Although the physiological mechanisms are unclear, the corresponding changes in plant communities are well understood. There is, for instance, complete turnover in tree species composition within 3 km of the continental divide on the Pacific slope (Haber 2000; Häger 2006). As a result of these well-recognized gradients in moisture, temperature, and seasonality, seven life zones can be recognized in the Monteverde area, although no local mapping of potential evapotranspiration exists. From the Caribbean to Pacific slopes, they are: tropical wet forest transition; premontane rainforest; lower montane rainforest (crest); lower montane wet forest; premontane wet forest; premontane moist forest; and tropical moist forest (Gómez 1986; Bolaños & Watson 1993; Haber 2000).

The protected Monteverde areas, including the Monteverde Cloud Forest Reserve, Children's Eternal Rainforest, and Santa Elena Cloud Forest Reserve, harbour over 27 000 ha of montane forest. Most of this coverage, however, occurs on the Caribbean

slope above 700 m. The Pacific slope, despite its habitat diversity, is relatively unprotected below 1500 m. Although birds have been well studied in Monteverde (e.g. Wheelwright *et al.* 1984; Fogden 1993; Powell & Bjork 1995; Young *et al.* 1998), fine-scale beta diversity of the avian community and its environmental or ecological correlates are still poorly understood.

CENSUS PROCEDURES

We conducted auditory and visual censuses because these sample more of the community than netting (this study; also see Terborgh *et al.* 1990; Robinson, Brawn & Robinson 2000). We censused bird species on the Pacific slope from 1100–1700 m, encompassing forested areas inside and outside of protected areas, during 2001 and 2003. The 36 km^2 Pacific-slope study area was divided into six 100-m altitudinal zones, and within each zone 15 permanently marked census points were established along narrow trails, 200 m apart in unfragmented primary forest ($n = 89$ points; Fig. 1). Ten-min counts at each point were repeated weekly five times in the breeding season (mid-May to late June), 05.30 h–10.30 h on all mornings without heavy wind or rain. Positions of all points were determined with a global positioning system (GPS) receiver with an antenna elevated 7 m to an accuracy of 10 m. These points were entered into a

geographical information system (GIS; ARCVIEW 3.2, ESRI Inc.) data base with digital elevation map. Digital photographs were taken of trunks of the 10 trees > 20 cm in diameter nearest to each point to record epiphyte cover, which was quantified using a superimposed grid, scoring each of 60–100 cells for cover by thick moss or macroepiphytes (ferns, orchids, bromeliads and other families; $n = 890$). Epiphyte cover provides a measure of microhabitat conditions, and should be sensitive to moisture regimes integrated over decades.

Observers had prior experience with the avifauna: three for several years, and the three others during 2001 and 2003. Before each field season, all observers studied recordings of vocalizations (Ross, Rabenold & Simons 1997; Ross 2001; and D. MacDonald, personal communication) for several months, and the team conducted on-site training for another 3 weeks before data collection, including distance estimation verified by laser range finders. Counts were conducted in two teams of three observers with rotating membership. All species seen or heard from each point were identified within a radius of 100 m and distances estimated for all detections. The area sampled for each site was therefore 3.1 ha, for a total of 280-ha coverage in the 36-km² study area. All counts were reviewed using audio recordings, pooling expertise (see Jankowski & Rabenold 2007 for additional details). Censuses did not include raptors, hummingbirds, parrots, swifts or swallows, and these families are not included in our analyses.

We conducted visual and auditory censuses on the Caribbean slope of the Monteverde Cloudforest Reserve using a single 8-km transect from 950–1700 m altitude. Ten-minute stops were made at intervals of 50 m altitude, and the transect was run on six different days. Distances were not recorded so that abundance could not be corrected by detectability. Total detections for species in each 100 m altitudinal zone were used to calculate Sørensen's indices of similarity in species composition between zones (see below). We also conducted point-count and mist-netting censuses between 1500–1700 m near the continental divide on the Pacific slope in the breeding season of 2001, in the Monteverde and Santa Elena cloud forest reserves. Point counts were conducted at 45 points using the same methodology as in 2003, but without detection distances. We mist-netted at 33 points separated by 100 m at 1600–1700 m in the Monteverde Reserve only, using standardized sets of two 7 × 12-m nets, resulting in 854 captures. We use these data for comparative purposes with our 2003 results and with results of previous studies.

ANALYSES OF ABUNDANCE DATA

Analysis of sampling sufficiency indicated that more than five visits to the census points provided little additional information (5–10%) about the number of pairs of each species present at each point (Fig. S1). Abundance data were summarized using the maximum number of individuals detected in a single count (distinguished by simultaneous singing) over five visits to a point. Abundance estimates were corrected by species' detectabilities by the equation $N = C/\beta$; where N is the estimate of true abundance, C is the maximum recorded abundance, and β is the estimate of detectability (≤ 1 ; Williams, Nichols & Conroy 2002). Detectability was estimated for most species ($n = 69$) using the program DISTANCE (version 4.0; Thomas *et al.* 2003; see Jankowski & Rabenold 2007).

We quantified alpha diversity for each zone using Simpson's reciprocal index: $D = 1/\sum p_i^2$ where p_i is relative abundance of species i . We also used the Chao 2 species richness estimator and the incidence-based coverage estimator (ICE) that perform well with moderate patchiness and small sample sizes (Magurran 2004; Colwell 2005). Beta diversity was quantified by the similarity in species composition

between zones using abundance data. Comparisons of species composition, within and between zones, employed the quantitative Sørensen's coefficient of similarity: $S_{or} = 2j_N/(a_N + b_N)$ where a_N and b_N are the total species abundances of zones a and b and j_N is the sum of the minimum abundance for each species between zones a and b . This index, which is equivalent to one minus the Bray–Curtis or the Steinhaus dissimilarity coefficient (Legendre & Legendre 1998), has been shown to be one of the most suitable in numerous comparative studies of similarity indices (see Magurran 2004). Sørensen's index was calculated between every pair of points, and the averages and standard errors were calculated to quantify within- and between-zone variability in species composition. Differences in average values were tested using Kruskal–Wallis and Mann–Whitney tests. We also employed Chao *et al.*'s (2005) modified Sørensen's index that should be less sensitive to differences in sample size, but results were unchanged and we report only the standard Sørensen's values.

To complement analyses using Sørensen's index, we applied a detrended correspondence analysis (DCA) to the site-by-species matrix of abundances (Legendre & Legendre 1998). Site scores for the first axis obtained from the DCA, which indicate similarity of species composition among points, were plotted with altitude and with distance from the continental divide, and the plots were examined for discontinuities with respect to those gradients (see also Lieberman *et al.* 1996). A linear relationship between axis 1 scores and an environmental variable would indicate constant change in the species composition of sites along the gradient.

To relate change in species composition to specific environmental variables, a canonical correspondence analysis (CCA) was conducted (ter Braak 1986). CCA uses a site-by-species matrix and a site-by-environment matrix to extract orthogonal ordination axes that represent linear combinations of environmental variables. We used elevation, distance to the continental divide, and epiphyte cover (percentage cover by thick moss or macroepiphytes) after experimenting with other topographic variables that did not explain significant variation in species composition. Topographic variables were derived from a digital elevation model of the Monteverde region in ARCGIS (version 8.3, ESRI). We examined the variance explained by the ordination axes and the correlation of these axes with environmental variables (indicated by the intraset correlations for each variable). Points were mapped using a biplot with arrows indicating the relative explanatory power of variables.

We employed partial Mantel analyses to determine which environmental variables were correlated with variation in species composition across points on the Pacific slope (Legendre & Legendre 1998). Partial Mantel tests determine correspondence of two distance matrices controlling for the effects of a third factor; in this case we use these tests to examine the relationships between species composition and environmental variables while controlling for geographical distance. Distance matrices for Mantel analyses were calculated using the Bray–Curtis dissimilarity index (1–Sørensen's index) for species abundance data, and Euclidean distance for altitude, distance from the divide and epiphyte cover. To complement ordination and Mantel analyses, an agglomerative, hierarchical clustering algorithm was performed on species abundance data. The Bray–Curtis dissimilarity index and several grouping or linkage procedures (including nearest neighbour, farthest neighbour, average and Ward's method) were used to create cluster dendrograms, and the cophenetic correlation of each dendrogram to the original distance matrix was used to determine the dendrogram that best represented the original similarities in species composition among points (Legendre & Legendre 1998).

Results

PATTERNS OF ALPHA DIVERSITY, WITHIN-HABITAT VARIATION AND ENDEMISM

We recorded 128 species (6430 detections, Table S1) across six 100-m altitudinal zones on the Pacific slope and seven zones on the Caribbean slope. Twenty-nine families were represented, including 104 genera and 27 narrowly endemic species (limited to Costa Rica and Panamá). Species recorded at points only once, including three narrowly distributed endemic species, were excluded from analyses. Several other species characteristic of open habitat but rarely found in forest were excluded from analyses (none detected more than five times).

On the Pacific slope, species diversity, richness and evenness were lowest at the higher elevations and close to the continental divide, with some tendency to peak in the middle of the gradient, especially between 1200 m and 1300 m altitude or between 1200 m and 2400 m from the divide (Table 1). Epiphyte cover peaked at higher elevations closer to the divide, where trees were almost completely covered, and was nearly lacking ≥ 3 km from the divide. The number and proportion of bird species endemic to Costa Rica and Panamá increased with altitude: 7% from 1100 to 1200 m compared to 40% from 1600 to 1700 m. Species endemic to Central America are not similarly concentrated at higher elevations, but comprise a greater fraction of the avifauna below 1500 m.

Variation in species composition among points within altitudinal zones ('pattern diversity' *sensu* Magurran 2004) was higher at lower elevations (Table 1). Within-zone similarity, measured by Sørensen's index between all dyads, is 0.82 in the two highest zones and 0.67 and 0.61 in the two lowest zones. Considering zones by distance from the divide, within-zone similarity is lowest (0.60) in the middle of the gradient at 1800–2400-m distance. Data collected in 2001 from the Monteverde and Santa Elena Reserves also show that species composition is very consistent at higher elevations, both between two halves of a 4-km transect at 1600–1700 m in the former reserve ($n = 33$ points, Sørensen's = 0.84) and between reserves ($n = 50$ points, Sørensen's = 0.82). Variation in epiphyte cover was consistently higher in the lower altitudinal zones (coefficient of variation = 40.6% for 1100–1200 m) and lowest in the highest altitudinal zones (6.6% for 1600–1700 m).

BETA DIVERSITY ON THE PACIFIC SLOPE

The avian community on the Pacific slope showed substantial change in species composition across 500 m of altitude (Fig. 2, Table S2). Most species occurring in the highest altitudinal zone were absent from the lowest zone. A few species occurred only in the middle of the altitudinal gradient. In the 1200–1300-m zone, we found a 'rebound' of some high-elevation species (Fig. 2) because some points in that zone are much closer (1.5 km) to a saddle in the continental divide than other points at that elevation (3 km). Where the continental divide is lower, more wind-driven moisture reaches lower elevations, favouring vegetation similar to higher elevations elsewhere.

Table 1. Alpha diversity, within-zone point similarity and endemism for zones on the Pacific slope, summarized using species detected more than once during the census period. Endemic species are those that are limited to Costa Rica and Panamá. Number of individuals derived from maximum simultaneous, same-species detections at each point

| Altitudinal zone | No. of sites | No. of individuals detected | Simpson's diversity | Species richness | Chao 2 estimator (\pm SD) | ICE (incidence-based coverage estimator) | Within-zone (Sørensen's) similarity | No. of endemics Costa Rica/Pan. (percentage) | No. of Endemics Central Amer. (percentage) | Percentage of epiphyte cover (\pm SD) |
|----------------------------|--------------|-----------------------------|---------------------|------------------|------------------------------|--|-------------------------------------|--|--|--|
| 1100–1200 m | 12 | 335 | 28.4 | 58 | 73.1 \pm 11.9 | 64.6 | 0.67 | 4 (7) | 10 (17) | 15 \pm 10 |
| 1200–1300 m | 16 | 458 | 30.1 | 66 | 68.9 \pm 2.9 | 69.3 | 0.61 | 10 (15) | 11 (16) | 20 \pm 17 |
| 1300–1400 m | 16 | 441 | 24.5 | 63 | 93.9 \pm 18.2 | 89.8 | 0.73 | 9 (14) | 11 (17) | 5 \pm 14 |
| 1400–1500 m | 15 | 492 | 25.0 | 65 | 67.6 \pm 2.7 | 69.0 | 0.75 | 10 (15) | 11 (17) | 24 \pm 23 |
| 1500–1600 m | 17 | 503 | 15.6 | 55 | 67.9 \pm 10.6 | 61.7 | 0.82 | 16 (29) | 8 (14) | 56 \pm 14 |
| 1600–1700 m | 13 | 319 | 13.2 | 43 | 45.9 \pm 2.9 | 48.6 | 0.82 | 17 (40) | 5 (12) | 75 \pm 15 |
| Distance from Cont. Divide | | | | | | | | | | |
| 3000–3600 m | 8 | 220 | 19.6 | 42 | 59.1 \pm 13.0 | 52.2 | 0.82 | 5 (12) | 9 (21) | 3 \pm 5 |
| 2400–3000 m | 14 | 386 | 20.0 | 44 | 46.8 \pm 3.2 | 47.5 | 0.84 | 1 (2) | 9 (20) | 6 \pm 10 |
| 1800–2400 m | 16 | 465 | 30.4 | 69 | 75.6 \pm 5 | 76.1 | 0.60 | 6 (9) | 12 (17) | 20 \pm 15 |
| 1200–1800 m | 17 | 536 | 26.1 | 68 | 72.7 \pm 4.1 | 73.8 | 0.71 | 10 (15) | 11 (16) | 27 \pm 21 |
| 600–1200 m | 20 | 590 | 16.2 | 61 | 71.6 \pm 7.8 | 71.0 | 0.81 | 16 (26) | 10 (16) | 52 \pm 26 |
| 0–600 m | 14 | 351 | 14.0 | 43 | 46.9 \pm 4.1 | 46.8 | 0.83 | 17 (40) | 5 (12) | 68 \pm 17 |

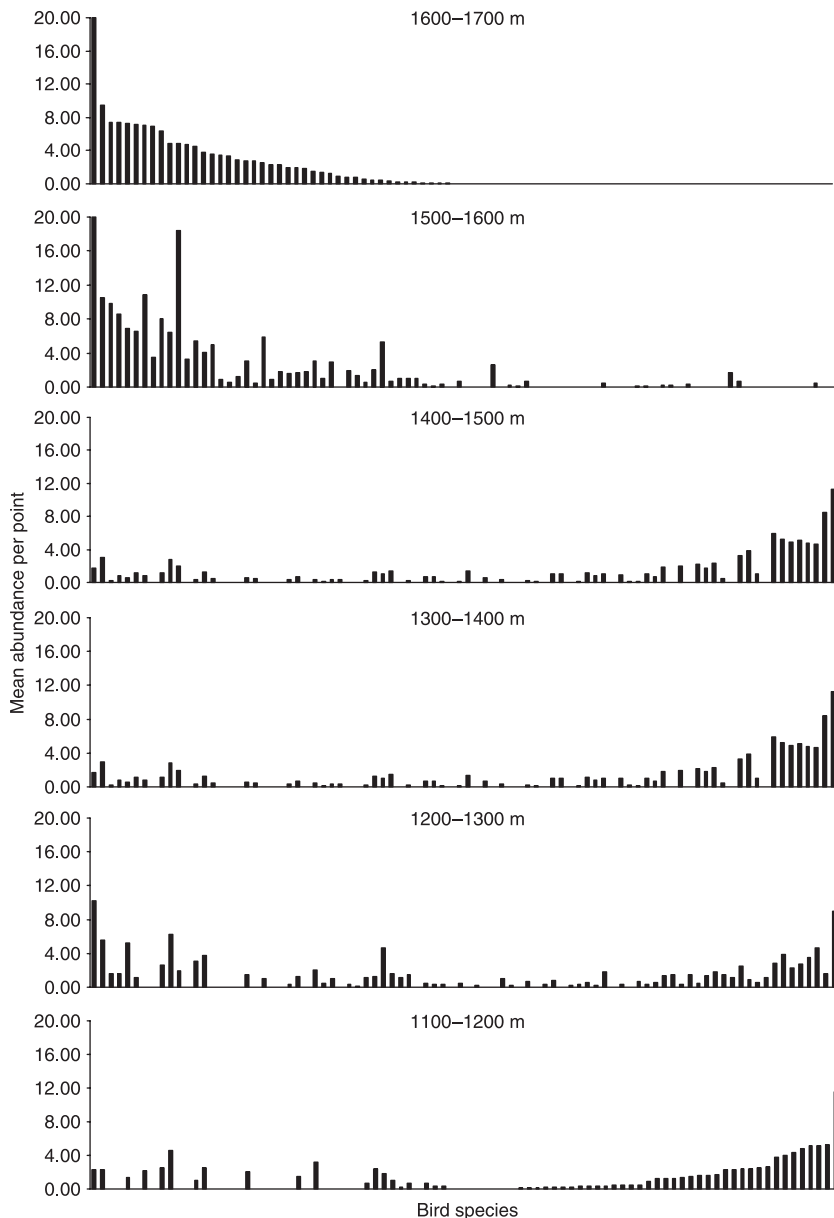


Fig. 2. Abundance per point (3.14 ha) averaged within each altitudinal zone for species (x-axis) recorded in the study on the Pacific slope. Abundances for each species are first ranked for the highest altitudinal zone (1600–1700 m) and then ranked for the lowest altitudinal zone (1100–1200 m). Species absent from the highest and lowest altitudinal zones, occurring only in the middle of the gradient, fall in the centre of the x-axis.

High beta diversity in such a limited area means that many species had narrow local distributions: 20 species occurred at $\leq 10\%$ of point-count locations, and 17 species occurred in just one or two 100-m altitudinal zones. On average, each species was recorded at 26% of the 89 points. Forty-four species occurred mostly below the reserve boundary at 1500 m (75% of abundance).

Using the highest altitudinal zone (1600–1700 m) as a benchmark of comparison to lower zones, we found a steep decrease in Sørensen's index with altitudinal separation until the 1200–1300-m zone, where similarity to the high elevations rebounds before declining again (Fig. 3a). This discontinuity is produced by the high-elevation character of species composition of points between 1200–1300 m that were close to the continental divide. The rate of change in species composition peaked between 1300–1500 m. Comparisons of the species

composition between adjacent 100-m altitudinal zones using Sørensen's index showed an average similarity of 0.58, ranging from 0.35 to 0.78. Average similarity varied significantly among adjacent-zone pairs (Kruskal–Wallis test; $H = 363.8$, d.f. = 4, $P < 0.0001$), due to high divergence in species composition between the 1300–1400-m and 1400–1500-m zones (Mann–Whitney U -test; $Z = -7.44$, $P < 0.0001$).

Similarity in species composition with increasing distance from the continental divide ('distance zones') showed accelerated change at 0.6-km distance followed by nearly continuous change in species composition until 2.4 km from the divide where similarity between the lowest zones and the divide reached a minimum (Fig. 3b). Beta diversity between adjacent distance zones also varied significantly (Kruskal–Wallis' test; $H = 255.6$, d.f. = 4, $P < 0.0001$; Fig. 3b) with highest turnover from 1.2 to 2.4 km from the divide (Mann–

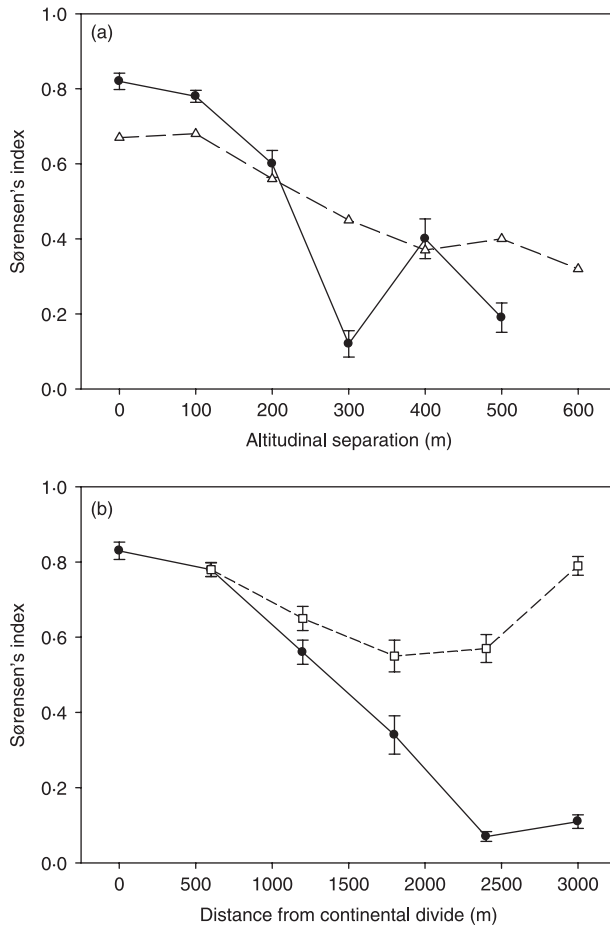


Fig. 3. (a) Sørensen's index of similarity in bird species composition with increasing altitudinal separation from the highest altitudinal zone (1600–1700 m) on the Pacific slope (solid line, with standard errors) and the Caribbean slope (dotted line). Standard error bars were calculated using number of points compared. (b) Sørensen's index (with standard errors) for bird species composition on the Pacific slope with increasing distance from the continental divide (solid line) and between adjacent zones of distance from divide (dotted line; zones compared are those above and below the indicated elevation).

Whitney *U*-test, $Z = -4.352$, $P < 0.0001$). The average similarity between adjacent distance zones was 0.67 and ranged from 0.55 to 0.79 per 0.6 km. The top and bottom altitudinal zones showed 20% similarity by the Sørensen's index, compared to 7% similarity for distance zones.

Variation in beta diversity with altitude and with distance from the divide was also evident in the results of DCA. The first axis in the DCA ($\lambda_1 = 0.70$) was used for the comparison of site scores, representing similarity in species composition among points, with both altitude and distance from the continental divide. A plot of axis 1 scores with distance from the divide showed a tighter clustering of points (Fig. 4) than when the axis 1 scores were plotted against altitude. The relationship with distance to the divide suggests two distinct clusters of compositional similarity near and far from the divide with a transition zone of more rapid compositional change between 1.2–2.4 km.

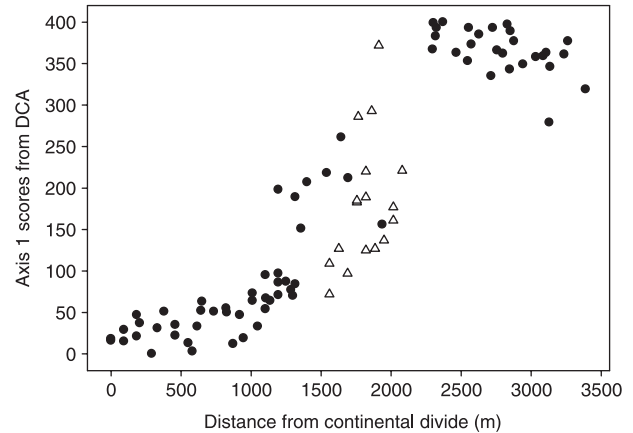


Fig. 4. Axis 1 scores (indicating similarity of species composition among points and placement of points along Axis 1) from the detrended correspondence analysis for the Pacific slope, plotted by distance from the continental divide. Triangles indicate the low-elevation points close to a saddle in the continental divide.

BETA DIVERSITY ON THE CARIBBEAN SLOPE AND COMPARISONS WITH NETTING DATA

Based on 917 detections of 85 species over the 8-km Caribbean-slope transect (including an additional three narrowly endemic species), we found change in species composition across 700 m elevation on the Caribbean slope to be more gradual than on the Pacific slope (Fig. 3a). Sørensen's index between the highest altitudinal zone (1550–1650 m) and the lowest (950–1050 m) was 0.32, compared to 0.20 across just 500-m altitude on the Pacific slope. Sørensen's values between adjacent 100-m zones averaged 0.67 compared to 0.58 on the Pacific slope, and these values did not vary substantially. These results are not affected by the different methods used on the two slopes: if Pacific-slope data are analysed without correction by detectability, between-zone Sørensen's values do not change. The underlying distributions of constituent species also suggest lower beta diversity on the Caribbean slope. Two-thirds of species occurring on both slopes had broader distributions on the Caribbean side. Of 47 common species in the high-elevation cloudforest (1600–1700 m), 60% range below 1100 m on the Caribbean slope in the Monteverde reserve, while only 38% range that low on the Pacific slope. Fogden's (1993) distribution data for 99 species found in cloudforest above 1500 m show the same pattern: 69% and 30% range below 1100 m on the respective slopes.

Our netting data from 2001, at 1600–1700 m elevation near the continental divide in the Monteverde reserve (854 captures in the breeding season), showed that two halves of a 4-km transect did not differ substantially in species composition in this altitudinal zone (Sørensen's index = 0.80). We also compared our capture results to data from Young *et al.* (1998) for 1300–1400 m elevation on the Pacific slope (5061 captures over a 10-yr period; Fig. 5). This comparison is imperfect because of the disparity in sample size, and because the latter data were collected over a greater range of habitats

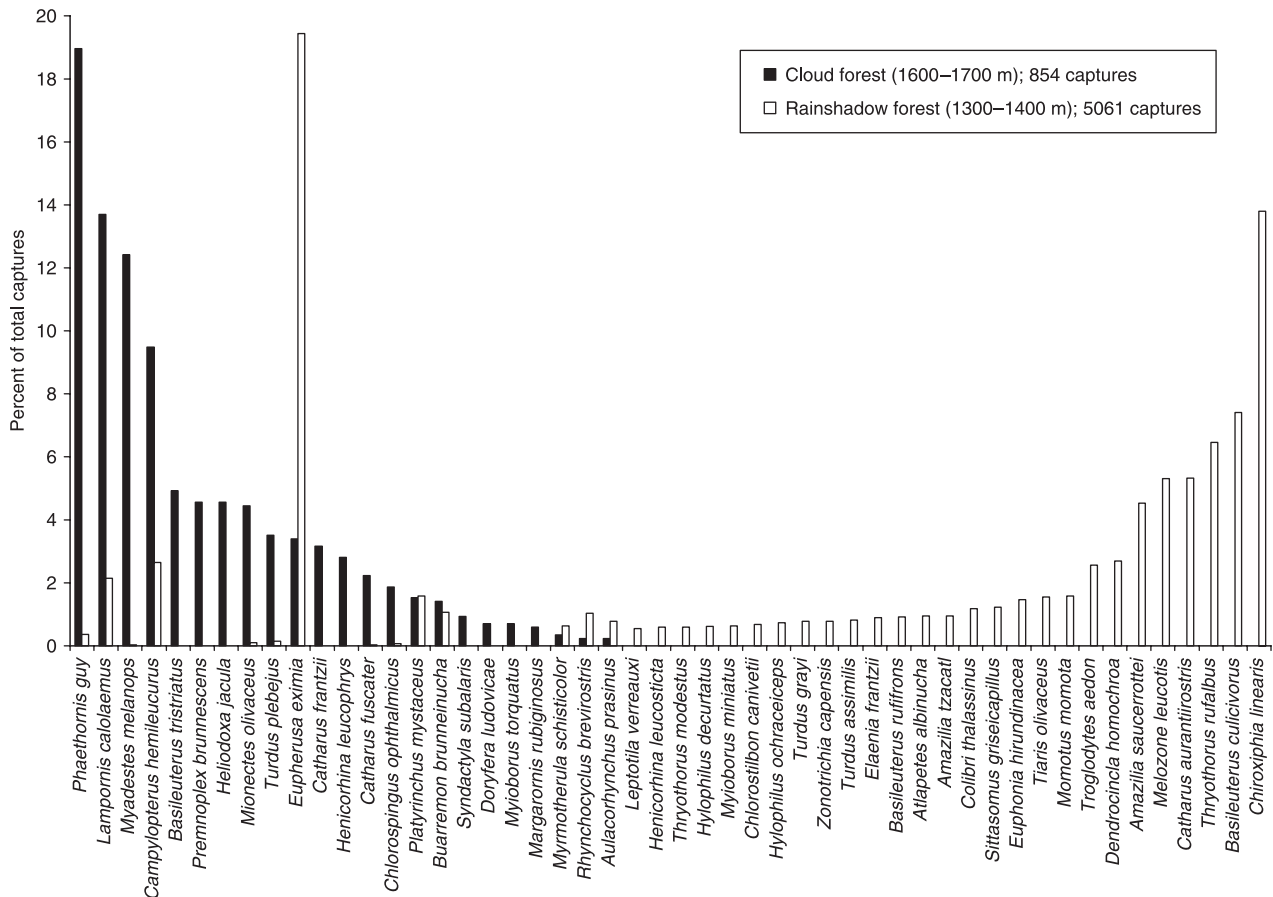


Fig. 5. Comparison of bird communities sampled by mist-netting, comparing data from this study for cloudforest (1600–1700 m; El Valle; $n = 854$ captures) to data from Young *et al.* (1998) for rainshadow forest (1300–1400 m; $n = 5061$ captures by D. MacDonald). Species were omitted if captures were fewer than 0.5% of the total.

(edge, primary and secondary forests) and seasonal times. Nonetheless, the Sørensen's value of 0.13 suggests a very similar decline in avifaunal similarity with distance compared to our point-count data: a nearly complete change in the species composition across the narrow (3 km) plateau of Monteverde (compared to 0.10 in Fig. 3b at 2.5 km distance). On the Caribbean slope, comparing our netting data from 1600–1700 m near the continental divide with that presented in Young *et al.* (1998) from 900–950-m elevation (approximately 3.5 km from the continental divide), we found a similarity of 0.31 over the 750-m gradient, very similar to our value of 0.28 based on the auditory census. This also suggests a substantial, but more gradual, change in species composition on the windward Caribbean slope compared to the leeward Pacific slope.

ENVIRONMENTAL VARIABLES AND COMMUNITY CLASSIFICATION

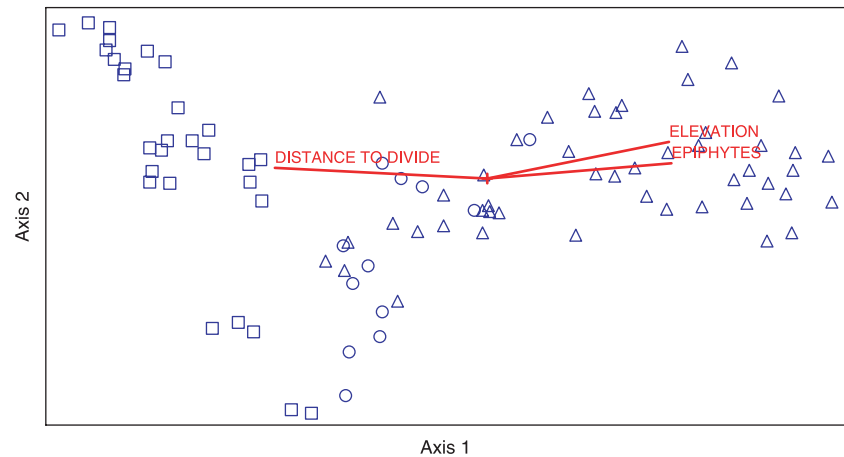
Canonical correspondence analysis explained 30% of the variation in species composition across the 89 points on the Pacific slope. Of the three ordination axes, axis 1 ($\lambda_1 = 0.40$) explained 27% of the total variation in the data set and 90% of the variation explained by all three ordination axes. Axis 1 can be interpreted as a moisture gradient because it relates

positively to distance from the continental divide and negatively to epiphyte cover (Fig. 6). Epiphyte biomass is directly dependent upon relative humidity (Nadkarni *et al.* 1995; Foster 2001). Grouping of sites is also apparent in this analysis, corresponding to cloudforest, rainshadow, and transition habitats (see cluster analysis below and Fig. 6). The correlation of environmental variables to the ordination axis was shown by the intraset correlations and is highest for distance to the divide (0.84) and epiphyte cover (−0.86). The scatter orthogonal to axis 1 (axis 2) is correlated with altitude (0.44) and epiphyte cover (0.50), although it explained very little of the variation in species composition across sites.

Partial Mantel analysis showed a significant and strong correlation between similarity in bird species composition and distance from the continental divide, controlling effects of simple geographical proximity ($r_M = 0.74$; $P = 0.0001$). Species similarity also showed a significant positive correlation with percent epiphyte cover ($r_M = 0.51$; $P < 0.0001$) and with altitude ($r_M = 0.20$; $P = 0.003$), although these relationships were not as strong.

A cluster analysis for Pacific-slope data using Bray–Curtis distances and average linkage method (cophenetic correlation = 0.88) for the 89 points suggests a grouping of sites based on distance from continental divide. Three easily distinguishable

Fig. 6. Biplot of points ($n = 89$) and environmental variables (lines) from canonical correspondence analysis. The environmental variables are: percent cover by thick moss and macroepiphytes (EPIPHYTES); elevation (ELEVATION); and distance of points from the continental divide (DISTANCE TO DIVIDE). The lines represent the direction (orientation with respect to the axis) and strength (length of the line) of the correlations between environmental variables and variation in avian species composition. Symbols for points indicate their grouping in the cluster analysis (squares, rainshadow forest; circles, transition forest; triangles, cloud forest).



groups were formed, corresponding to points farther from the divide with drier conditions (rainshadow forest), points closer to the divide with high moisture (cloud forest), and a smaller group of points representing a transitional zone. Within these three clusters, distinct groupings of points were not apparent. The points represented by the transitional cluster average 1.7 km from the continental divide, ranging between 1.2–2.1 km as in the DCA (Fig. 4). These complementary statistical approaches independently reinforce the conclusion that distinct avian community types are identifiable, arrayed along a moisture gradient corresponding to distance from the continental divide.

Discussion

PATTERNS OF ALPHA DIVERSITY, WITHIN-HABITAT VARIATION AND ENDEMISM

Several studies along tropical altitudinal gradients have found decreasing species diversity with increasing altitude (Lieberman *et al.* 1996; Vásquez & Givnish 1998; Young *et al.* 1998; Blake & Loiselle 2000; Haber 2000) or a peak in species diversity at middle elevations (Terborgh 1971; Kessler 2001; Herzog, Kessler & Bach 2005). It is generally thought that patterns in species richness correspond to changes in productivity governed mainly by moisture and temperature (e.g. van Rensburg, Chown & Gaston 2002), although these patterns can also be influenced by scale effects of individual studies and local human impacts (Nogués-Bravo *et al.* 2008). In this study, a peak in species richness and diversity at the middle distances from the continental divide is in the same cluster of points that are transitional from cloudforest to rainshadow forest, and this appears to result from overlapping tails of altitudinal distributions of species adapted principally to lower rainshadow forests or higher cloud forests (an 'ecotone'). High variability in species composition among points in this zone (patchy species distributions) also contributes to high species richness.

Within-zone variation in species composition is highest at lower elevations and middle distances from the continental divide where the minimum average point-to-point similarities

are similar to average between-zone similarities. This pattern diversity (*sensu* Magurran 2004) could be attributed most simply to species richness (above) or to increased topographic complexity resulting from the cumulative effect of erosion creating deeper valleys and stronger contrast with ridges. This could create greater differences in microclimates determined by exposure, forest composition, vegetation structure including epiphyte cover, and other environmental conditions influenced by the slope and aspect of the terrain. Variation in epiphyte cover was substantially higher within lower altitudinal zones than in higher zones where immersion in clouds is common. Greater variation in forest composition has also been reported in tropical dry forest compared to higher-elevation cloud forest in southern Mexico, from 1500–2500-m elevation (Vásquez & Givnish 1998).

Variation in species composition among sites of the same habitat type should increase as the distance separating these sites increases. At the landscape scale, we found that avian species composition at 1600–1700 m elevation varies little between the Monteverde and Santa Elena reserves, separated by approximately 5 km (Sørensen's index = 0.82), but species composition within that altitudinal zone changes dramatically between the Tilarán and Central mountain ranges, separated by approximately 80 km (Sørensen's index = 0.52; using data from Blake & Loiselle 2000). Cloudforest in the Peruvian Andes harbours an almost completely different avifauna compared to that in Monteverde [binary Sørensen's index = 0.12, proportion of species shared, comparing lists of Fogden (1993) and Weske (1972)]. At this scale, the limited geographical ranges of these montane species create high between-site diversity.

MEASURING BETA DIVERSITY

Quantification of beta diversity on the Pacific slope varies slightly depending upon the way points are grouped into zones and on sampling methodology, but the conclusions are robust that almost complete change in species composition occurs within a few kilometres of the continental divide, and that change is more gradual on the Caribbean slope. The Caribbean slope receives more annual precipitation and is less

seasonal than the Pacific slope, so that Holdridge life zones (defined by potential evapotranspiration) on the Caribbean slope are expected to cover broader altitudinal ranges than on the Pacific slope (Young *et al.* 1998; Haber 2000). Fogden (1993), using a life-zone classification for the Tilarán range based on bird distributions, suggests that life-zone designations are rather arbitrary on the Caribbean slope, but on the Pacific slope changes are rapid and distinct. Our results substantiate these expectations. Blake & Loiselle (2000) used capture and point-count data to calculate the rate of species turnover with altitude on the Caribbean slope of the Cordillera Central in Costa Rica. They found a similarity of 68% from 1000 to 1500 m and 42% from 1500 to 2000 m (recalculated using Sørensen's index), compared to our similarity of 20% across 500 m on the Pacific slope.

From the largest study of an altitudinal gradient in the Neotropics, in the Peruvian Andes, Terborgh (1971) and Weske (1972) found that species composition changed more slowly with altitude than in our study. We calculated binary Sørensen's values from their data and found an average similarity of 74% between adjacent 100-m zones on both sides of the Cordillera Vilcabamba over the entire gradient of 340–3520 m (binary Sørensen's = 0.24 between 500 m zones), compared to our values averaging 58% between 100-m zones. We also re-analysed data for tropical birds along a successional gradient (Robinson & Terborgh 1997) and found lower between-stage variation in species composition than in our study (average Sørensen's = 0.70). Although clearly beta diversity varies among tropical mountain ranges, and the Tilarán gradient could be more pronounced than on larger ranges (the Massenerhebung effect; e.g. Foster 2001), the Pacific slope of the Tilarán range appears to exemplify a general pattern for rapid compositional change in tropical communities along environmental gradients.

For a temperate comparison, we have censused forest avifaunas in Great Smoky Mountains National Park (35°35' N latitude, USA; Rabenold *et al.* 1998 and unpublished data) along an altitudinal gradient and found that species composition changes relatively slowly with altitude in comparison with any of the tropical examples. In fact, beta diversity on this temperate mountainside is roughly half that found in Monteverde (Sørensen's index = 0.30 across 1000 m in Great Smoky Mountains National Park vs. 0.20 across 500 m in the present study). These differences suggest that tropical montane species, on average, have narrower altitudinal distributions than temperate ones, a pattern that is consistent with considerable evidence (Herzog *et al.* 2005; Ghalambor *et al.* 2006) and the longstanding ideas that tropical species are more specialized than temperate ones (MacArthur 1969; Orians 1969; Terborgh 1971). Janzen (1967) proposed that mountains are 'higher' (stronger barriers) in the tropics because of species' narrower physiological tolerances there, in part because stronger seasonality in temperate regions selects for broader tolerances. It would be useful for future studies to test potential mechanisms underlying the restricted altitudinal ranges of tropical species to assess the relative importance of physiology, resource specialization and biological interactions.

PATTERNS OF SPECIES TURNOVER

Results of our ordination and classification analyses suggest that species' distributions are clustered along a moisture gradient. Classic descriptions of species distributions over altitudinal gradients by Whittaker (1975) suggested that species replacement is gradual along such gradients and that species' boundaries are independent of other species (i.e. the individualistic distribution hypothesis). This suggests that each species has its peak abundance at some environmental optimum, and that these optima are distributed randomly along the gradient, creating continuous species turnover. In the tropics, several extensive investigations of species distributions along altitudinal gradients have supported this pattern of beta diversity for various taxa (Terborgh 1971; Lieberman *et al.* 1996; Brehm *et al.* 2003). On the Pacific slope of Monteverde, change in species composition is more rapid in the middle altitudes (1300–1500 m). When the gradient is defined by distance from the continental divide, change appears more continuous, although adjacent-zone Sørensen's values suggest significantly greater change at the middle distances (1.2–2.4 km). Ordination of sites also suggests a zone of rapid community change at these middle distances, bracketed by more homogenous cloudforest and rainshadow forest (*sensu* Haber 2000). This result agrees with patterns of avian species turnover in Sierra de Atoyac, southern Mexico, where upper and lower range limits for birds were concentrated in the transition from semi-deciduous tropical forest to cloud forest (Navarro 1992). Our cluster and canonical correspondence analyses of bird species composition supports a classification of 'cloudforest', 'rainshadow' and 'cloudforest/rainshadow transition' in accord with similar preliminary classification of vegetation types by Haber (2000). Vásquez & Givnish (1998), studying vascular plant distributions along a 1000-m gradient sampled at 100 m altitudinal intervals, also found high rates of compositional turnover in the transition zone between seasonal dry forest and cloud forest (1800–2000 m in Southern Mexico; adjacent-zone Sørensen's values 0.2–0.3, compared to 0.5–0.6 for cloudforest).

Moisture or related plant structure (epiphytes) might be proximate forces determining local range limits, but further study will be required to test possible limiting factors, including interspecific interactions like competition (Terborgh & Weske 1975) and potential interactions with habitat zonation (Graves 1988). We assayed epiphyte cover on tree trunks, but differences among sites are probably much greater in the forest canopy. These differences bring substantial changes in physical complexity that could greatly affect avian foraging (Sillert 1994). Epiphytic cover could magnify the moisture gradient, producing a nonlinear effect on avian species composition. Tree species composition, and therefore fruit (and probably insect) availability also vary dramatically along the gradient (Haber 2000). We have preliminary indications that there is remarkable correspondence between change in bird and tree communities along the moisture gradient. Bird communities, however, change seasonally because of altitudinal migration that is common in many families (Wheelwright

et al. 1984; Loiselle & Blake 1991; Powell & Bjork 1995), and bird communities change substantially over the years (Fogden 1993; Pounds, Fogden & Campbell 1999). Future studies should explore further the year-round composition of communities and the stability of their constituent populations in the face of continuing environmental challenges like habitat fragmentation and climate change.

IMPLICATIONS FOR CONSERVATION

The highlands of Costa Rica and Panamá have one of the highest levels of narrow avian endemism in the world (Stotz *et al.* 1996; Stattersfield *et al.* 1998). High alpha and beta diversities, and spatial variation within zones, contribute to the striking diversity of life across the Monteverde landscape, including half of the bird species of Costa Rica (452 species; Fogden 1993) and more species of trees in a 25-km radius than in all of North America (755; Haber 2000). The number of species endemic to the Costa Rica–Panamá highlands increases sharply with altitude and proximity to the ridge top in Monteverde (Jankowski & Rabenold 2007). Between 1600–1700 m, endemic species represented 40% of detected species ($n = 21$ species) compared to values near 10% 500 m lower.

Three main features of the spatial organization of diversity in this landscape are important for conservation strategy: very high beta diversity driven by a strong rainshadow effect; high variation in species composition within habitat types across the mountainside; and concentration of endemic species at the highest elevations. In addition, the distinctiveness of species composition compared to similar habitats in other mountain ranges increases the importance of local conservation. High beta diversity requires greater care in reserve design, particularly in placement and extent in a heterogeneous landscape (see also Lombard *et al.* 1999), compared to some lowland habitats where species have wide distributions (e.g. Terborgh *et al.* 1990; Robinson *et al.* 2000; Condit *et al.* 2002). The Monteverde Cloud Forest Reserve is well situated for the protection of species narrowly endemic to the highlands of Costa Rica and Panamá, since these species are concentrated at higher elevations, often in narrow zones. Many of these narrow endemics, however, range well below protected boundaries, especially in the nonbreeding season. Even in our breeding-season sample, some narrow endemics were common from 1300–1500 m mostly outside of protected areas, including black-breasted wood-quail (*Odontophorus leucolaemus*), three-wattled bellbird (*Procnias tricarunculata*), ochraceous wren (*Troglodytes ochraceus*), black-faced solitaire (*Myadestes melanops*), golden-browed chlorophonia (*Chlorophonia collopheya*), and orange-bellied trogon (*Trogon aurantiiventris*). In addition, many species endemic to Central America are more prevalent in the less protected rainshadow forests, like the long-tailed manakin (*Chiroxiphia linearis*), yellowish flycatcher (*Empidonax flavescens*), plain wren (*Thryothorus modestus*), black-headed nightingale-thrush (*Catharus mexicanus*), and white-eared ground-sparrow (*Melospiza leucotis*). Overall, half of species' distributions in

the study ($n = 44$) were concentrated below protected areas on the Pacific slope (75% of abundance below 1500 m), where the habitat across the mountainside is also more variable. Fine-scale data like these can be used to pinpoint areas whose protection would maximize conservation of landscape-level biological diversity.

Very high beta diversity is associated with narrow distributions for many species (see also Herzog *et al.* 2005), resulting in small local populations. Combined with small geographical ranges, many of these species can ill afford further disruption of their habitats. Many narrowly endemic species are also threatened by a 'syndrome' of rarity in which they exhibit lower local numerical abundance compared to their more cosmopolitan relatives (Jankowski & Rabenold 2007). Extension of protected areas just 2 km into the middle elevations of the Pacific slope, to include rainshadow forest, would not only afford protection to endemics, but also to a unique and variable community that would approximately double the number of species under protection on the Pacific slope. Forests such as these are poorly understood and poorly protected throughout Costa Rica and Latin America, in part because they occupy climatic zones hospitable to human agriculture. They are also organized along a moisture gradient vulnerable to shifting with global and regional climate change. The specialization that creates high beta diversity also exposes species to risk in the face of climatic shifts that will likely drive species upslope and reorganize communities. Many species in this study are limited to climatic zones at the top of the mountain, so that predicted changes in temperature, precipitation, and seasonality (e.g. Giorgi 2006) could be sufficient to cause local extinctions (Jankowski & Rabenold 2007; Gasner 2008), although biological interactions probably also influence local range limitations. Several recent analyses over large spatial scales suggest widespread risk of avian extinctions and reshuffling of avian communities due to climate change (Peterson *et al.* 2002; Malcolm *et al.* 2006; Parmesan 2006; Jetz, Wilcove & Dobson 2007; La Sorte & Thompson 2007; Sekercioglu *et al.* 2008) and local analyses also forecast significant range shifts and highlight threats to tropical montane landscapes (Pounds *et al.* 1999; Foster 2001; Raxworthy *et al.* 2008). Such landscapes offer high benefit/cost opportunities for conservation, since small downslope increments in reserves can extend protection to dramatically more diverse biological communities, and upslope increments can enlarge specialist populations and enhance population viability. Conservation action will also require long-term studies to assess natural variation in densities and distributions so that population viability and community change can be accurately estimated.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Abundance per hectare, corrected for detectability and averaged over all points for species in each zone of distance to the continental divide. Species are grouped by families and listed in taxonomic order based on the American Ornithologists' Union checklist of North American birds (1998 and successive supplements)

Table S2. Rank of species on *x*-axis of Fig. 2. (from left to right)

Fig. S1. Analysis of sampling sufficiency, showing the proportion of detections representing new maxima for species over the five visits to census points and averaged for each elevational zone. Bars indicate the cumulative number of detections per zone over the five visits, averaged across elevational zones (with standard errors).

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