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The relationship of tropical bird communities to tree species composition and vegetation structure along an Andean elevational gradient

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ABSTRACT

Aim Understanding patterns of species turnover along environmental gradients and their consistency across taxonomic groups is central to the study of biodiversity. We may expect congruence in diversity patterns across groups whose ranges could be influenced by species interactions. We explore associations between bird and vegetation communities in the tropical Andes to determine whether patterns of species richness and turnover in birds and trees are congruent with elevation, and whether tree species composition, vegetation structure, elevation, or a combination of these best predicts bird species composition.

Location A forested 2600-m elevational gradient on the eastern slope of the Peruvian Andes.

Methods Bird surveys and vegetation measurements were conducted at 172 points, and a subset of these were spatially matched with fourteen 1-ha tree inventory plots. Diversity patterns were described for trees, birds, and avian foraging guilds. We used dissimilarity matrices to examine patterns of turnover and nestedness. Turnover of birds and trees was examined by comparing compositional change of adjacent plots along the gradient. Multiple regression on distance matrices was employed to determine contributions of tree species composition, vegetation structure and elevation to explaining variation in bird species composition.

Results Species richness was higher for trees than for birds, and whereas diversity in both taxa decreased with elevation, tree richness showed a low-elevation plateau before declining at higher elevations. Tree species had narrower distributions compared to birds, but patterns of turnover were largely congruent between taxa. Nestedness contributed much less to dissimilarity than turnover, although birds showed higher nestedness, particularly at high elevations. Tree species composition, elevation and vegetation structure were all important predictors of bird species composition; the best model explained 78% of bird dissimilarity across plots. Tree species composition was always included in the best models, for all birds and foraging guilds.

Main conclusions Our assessment of Andean bird and vegetation communities suggests strong correspondence, perhaps due to direct interactions or similar underlying drivers. We hypothesize that with climate change, range shifts in these groups may not occur independently. Rather, birds may have delayed upslope shifts or may be limited to high-elevation patches where appropriate vegetation communities exist.

Keywords

Andes, avian guilds, beta diversity, climate change, habitat use, montane forest, Neotropics, nestedness, species turnover.

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INTRODUCTION

Evaluating patterns of species turnover in relation to environmental gradients can reveal underlying drivers of regional diversity and primary factors that influence species range boundaries (Buckley & Jetz, 2008). Such knowledge is essential for informed conservation planning and can be used to predict how species' ranges may shift with climate-driven changes in abiotic factors and biotic interactions (Kissling *et al.*, 2010). Montane landscapes have consistently served as valuable testing grounds for hypotheses to explain patterns in species richness and turnover and how these two aspects combine to influence regional diversity (Janzen, 1967; Terborgh, 1971; Whittaker, 1975). Furthermore, montane landscapes are widely recognized as global biodiversity hotspots due to high regional diversity and endemism (Myers *et al.*, 2000) and have become a principal focal landscape for assessing impacts of climate change on species distributions (Colwell *et al.*, 2008; La Sorte & Jetz, 2010; Tingley *et al.*, 2009; Feeley *et al.*, 2011).

Whereas numerous studies have examined species compositional turnover (i.e. beta diversity) along elevational gradients (e.g. Patterson *et al.*, 1998; Jankowski *et al.*, 2009), less is known about the correspondence of diversity between taxa and how communities that vary in their degree of environmental specialization or capacity for dispersal respond to elevational gradients. Importantly, if one species group is dependent upon another for resources or provides services such as dispersal or pollination, then aspects of species' distributions and patterns of turnover could be constrained by such interactions. Correspondence in species turnover patterns across groups may also be derived from indirect relationships linked to common underlying mechanisms responsible for ecological sorting of species.

The relationship between birds and vegetation has been a natural starting point for understanding the influence of biotic interactions on bird species distributions (Wiens, 1989). Vegetation forms a fundamental component of terrestrial avian habitats and provides cues that guide habitat selection (Lee & Rotenberry, 2005), as well as food and substrates used for shelter and foraging (Robinson & Holmes, 1984). Likewise, many plants rely upon birds for pollination and fruit dispersal (e.g. van Schaik *et al.*, 1993). In temperate regions, there is evidence for a strong correspondence between avian assemblages and both structure and species composition of vegetation (Lee & Rotenberry, 2005; Fleishmann & Mac Nally, 2006). In contrast to temperate regions, the correspondence between tropical bird and plant communities is poorly studied, although generally the type and structural complexity of habitats are known to influence avian diversity and composition (MacArthur & MacArthur, 1961; Terborgh, 1985a; Jayapal *et al.*, 2009). It has been proposed that different guilds of birds should be more sensitive to structural versus compositional changes in vegetation (Terborgh, 1985a), with insectivorous birds that rely on specific foraging substrates responding to structural changes

and frugivores being linked to plant community composition (Hasui *et al.*, 2007).

In tropical montane regions, plants and animals are confined to narrow elevational ranges, producing belt-like distributions that may extend hundreds to thousands of kilometres in distance, but span only a few hundred metres in elevation (Stotz *et al.*, 1996). Vegetation changes dramatically in structure and composition with elevation (Grubb *et al.*, 1963), and the coincidence of range limits in some bird species with habitat shifts along gradients (e.g. ecotones) suggests that vegetation may influence avian species distributions (Terborgh, 1985b; Jankowski *et al.*, 2009). In their survey of the Vilcabamba range of Peru, Terborgh & Weske (1975) reported that one-sixth of avian elevational range limits coincided with vegetation ecotones, affecting upper or lower range boundaries of 28% of bird species. Thus, to some degree, birds respond to recognizable changes in vegetation along elevational gradients, but the extent of correspondence of birds and plants and the relative influence of vegetation structure and species composition on avian communities remain unknown.

The study of taxonomic congruence along elevational gradients takes on a practical importance in the face of climate change. In response to warming climates, montane species are expected to show upslope range shifts to track optimal abiotic conditions (Parmesan, 2006; Feeley & Silman, 2010; but see Lenoir *et al.*, 2010). Upslope movements have been confirmed in various ectotherms (e.g. Wilson *et al.*, 2005; Chen *et al.*, 2009), but responses by endothermic species have been mixed, with some studies revealing upslope shifts (Moritz *et al.*, 2008; Tingley *et al.*, 2009; Maggini *et al.*, 2011) and others finding little or no evidence of shifts (Archaux, 2004; Popy *et al.*, 2010). Trees and other long-lived plants, unlike birds, may shift distributions more slowly due to substrate specificity, shorter dispersal distances, and longer generation times (Iverson *et al.*, 2004; Ibáñez *et al.*, 2009). Even under scenarios of rapid plant migration, given that bird and plant distributions are set by factors that differ in intensity and kind, it is unclear to what extent bird distributions will track rapidly changing abiotic conditions versus slowly changing tree distributions.

Here we investigate the correspondence of bird and tree assemblages for a forested elevational gradient from 800 to 3400 m a.s.l. in the southeastern Peruvian Andes, one of the world's biodiversity hotspots. Using datasets of bird and tree species composition and vegetation structure along the same gradient, we describe changes in richness and community composition for these taxa with elevation and determine the extent to which their patterns of richness and turnover are congruent. Then we ask how well species composition of birds across sites can be explained by composition of trees, vegetation structure, elevation, or a combination of these factors. We also examine foraging guilds of birds to determine whether guilds that rely on plants directly for food resources (i.e. frugivores, nectarivores and granivores) are more closely linked to plant composition, whereas insectivorous or

omnivorous birds are more influenced by structural changes in vegetation. If relationships between bird and vegetation communities are weak, as would be indicated by incongruent patterns of species turnover or low explanatory power of vegetation structure or tree species composition on bird species composition, then we should expect greater flexibility in bird–vegetation interactions. As a corollary, we would also expect range shifts of birds with changing climates to be more independent of vegetation change on tropical mountains. Alternatively, a high correspondence between birds and vegetation, in terms of tree species composition or vegetation structure, would suggest that bird species may be constrained spatially or temporally as climate regimes change.

MATERIALS AND METHODS

Study region

Our survey sites were distributed along an elevational gradient on the eastern slope of the Andes in and adjacent to Manu National Park, in the department of Cuzco, Peru. The highest survey sites ($13^{\circ}11'44''$ S, $071^{\circ}36'26''$ W, 3400 m a.s.l.) were located at tree line and the lowest sites ($12^{\circ}57'17''$ S, $071^{\circ}32'00''$ W, 800 m a.s.l.) are located in the Andean foothills (Fig. 1). Sites were established on trails in primary forest or contiguous older secondary forest.

Vegetation along the gradient undergoes striking transitions within this range, changing from montane rain forest to cloud forest to *puna* grassland with increasing elevation

(Terborgh, 1971). Within these broad forest classifications are patches of distinctive vegetation. Bamboos, including *Guadua* spp. below c. 1500 m a.s.l. and *Chusquea* spp. above c. 1500 m, form dense stands within forest. At mid- and high elevations, exposed, windswept ridges are covered in shrub-like vegetation with a canopy < 3 m, and landslides leave scars in various stages of succession. The result is a patchwork of low- and high-canopy forest with distinct structure, even at similar elevations. While logistical constraints prevented us from surveying all vegetation types at each elevation, we included substantial structural variation in vegetation across survey sites to evaluate structural versus elevational effects on bird species composition.

Tree censuses

Trees were recorded in fourteen 1-ha plots, established approximately every 250 m along the elevational gradient (Farfan Rios, 2011; Girardin *et al.*, 2010). Plots at 1500 and 3000 m a.s.l. had two replicates on different transects that were separated by approximately 3–9 km. Within each 1-ha plot, every individual tree ≥ 10 cm diameter at breast height (d.b.h.) was measured, tagged and identified to species or morphospecies.

Bird surveys

During field seasons from 2006 to 2008, we established 172 forest bird survey points along the elevational gradient, with

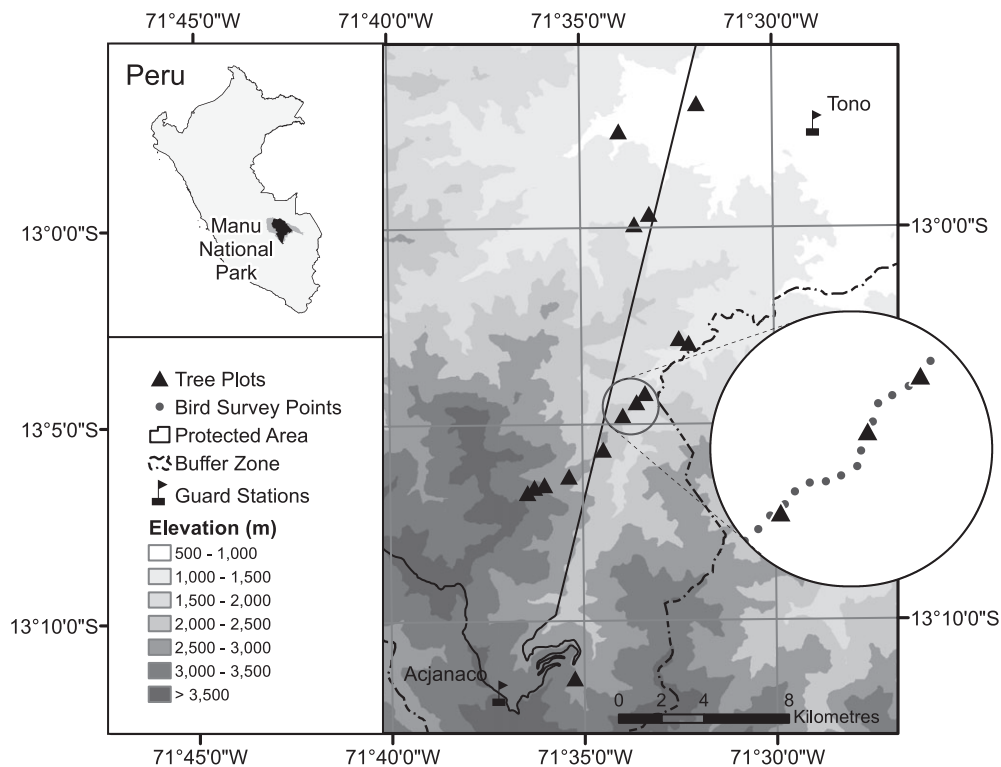


Figure 1 Map of the study area in Manu National Park, Peru, with locations of 1-ha tree plots (triangles) and bird survey sites (circles; see magnification) along the elevational gradient.

an average of 43 points (min. 38, max. 53) within each of four 650-m elevational zones. Forty-two survey points were associated with 1-ha tree plots. Points were placed 130 m apart (horizontal distance) along narrow trails, visually marked with flags and their geographical coordinates were recorded using a Garmin GPSMap 60CSx unit (Garmin International, Olathe, KA, USA). Elevation (m a.s.l.) and vegetation structure data were recorded at each point. All points were visited four times during the avian breeding seasons (July–November) of 2006–2008, with visits occurring across multiple field seasons. On mornings without heavy wind or rain, 10-minute counts were conducted at each of 10 points between 05:00 and 09:00 h. The order of visitation to points was reversed between visits to reduce bias due to temporal variation in species' detectability. During each count, all individuals detected were identified and their distances from the point were estimated using a laser range-finder. Counts were recorded using an Edirol R-09 WAV/MP3 digital recorder (Roland Corporation, Los Angeles, CA, USA) for later review of species identifications. For analysis, we restricted the survey dataset to detections ≤ 65 m from the point centre, approximately half the distance between consecutive points, to avoid double-counting of individuals across points. Species detected within this distance during any visit were considered present at the survey point.

Vegetation structure

Vegetation structure was measured at each bird survey point using a protocol adapted from Martin *et al.* (1997) within the same months in which bird surveys were performed during 2007–2008. Forest vertical structure variables included mean canopy height, number of trees > 10 cm d.b.h., and percentage canopy cover, obtained from hemispheric photos at the point centre taken 1 m above ground level using a Nikon D-50 digital camera (Nikon, Inc., Melville, NY, USA) and fish-eye lens mounted on a tripod and analysed using GAP LIGHT ANALYZER 2 (Frazer *et al.*, 1999). Average canopy height and number of trees were estimated from a 20 m \times 20 m plot surrounding each survey point. Understorey variables were measured within a nested 10 m \times 10 m plot and included density of small stems (< 2.5 cm d.b.h.; ≥ 1 m in height), large stems (≥ 2.5 cm d.b.h.), and bamboo (*Chusquea* and *Guadua* spp.). A principal components analysis (PCA) was used to reduce these potentially correlated variables into orthogonal principal components. The first four principal components explained 78–91% of the variance (see Appendix S1 in Supporting Information) and were retained for analysis.

Avian foraging guild classification

Birds were classified into foraging guilds using foraging observations, faecal samples of birds captured with mist nets, and references on diets of tropical birds (Appendix S2). We designated species as frugivorous, nectarivorous, granivorous,

omnivorous or insectivorous. Carnivorous and piscivorous species (e.g. raptors, kingfishers) were not included in foraging guild analyses.

Data summary and analyses

Analyses were performed at the level of 1-ha tree plots ($n = 14$; hereafter 'plot-level') to compare diversity patterns in birds and trees and to examine variation in bird species composition explained by trees, vegetation structure and elevation, and also at the level of bird survey points ($n = 172$; 'point-level') to examine small-scale variation in bird species composition and relationships to vegetation structure within elevational zones. For plot-level analyses, bird survey data and vegetation structure data were assigned to 1-ha tree plots. Three bird survey points were assigned to each of the 14 tree plots (utilizing 42 of the 172 survey points); these points were located within 250 m horizontal distance and within 150 m elevation of the centre of the plot to which they were assigned. Bird species presence–absence data from associated survey points were combined to create a plot \times species matrix. Likewise, tree occurrence data for each plot were used to create a presence–absence plot \times species matrix. To summarize plot-level vegetation structure, values of variables were averaged across the three bird survey points associated with each plot. Point-level analyses used bird survey data from all 172 survey points and vegetation structure data collected at each point. Bird occurrences at survey points were used to create a presence–absence point \times species matrix.

Measurements of change in species composition across sites (i.e. beta diversity) expressed as dissimilarities can reflect change due to species loss, including nestedness of sites, where one set of species is a subset of another set, and change due to replacement of one set of species by another (i.e. turnover). We distinguished these processes by partitioning total beta diversity (Sørensen's dissimilarity index, β_{sor}) into contributions by turnover (Simpson's dissimilarity, β_{sim} ; Lennon *et al.*, 2001) and nestedness-resultant dissimilarity (β_{nes}) following Baselga (2010). β_{sim} describes turnover without the influence of richness gradients, and β_{nes} is derived from the difference between β_{sor} and β_{sim} which accounts for the nestedness component of beta diversity. Each index varies between 0 and 1, with lower values indicating a greater proportion of shared species and larger values indicating greater dissimilarity between two locations.

We examined patterns of species richness in trees and birds (overall and within each guild) across plots. We then used dissimilarity matrices to examine variation in bird species composition and evaluate correspondence between bird and tree communities. We tested for significant peaks in dissimilarity between adjacent plots by using a Monte Carlo simulation (Bach *et al.*, 2007) to create a null distribution of 1000 dissimilarity values generated by random placement of observed elevational ranges across range classes ($n = 12$ as two of the 14 plots are elevational replicates), while

constraining the number of species per range class to observed plot richness. Dissimilarity was calculated between adjacent plots for each randomization using Sorensen's index (β_{sor} ; equivalent to the Wilson–Shmida index used by Bach *et al.*, 2007). Significance was determined by dividing the number of null values greater than the observed value by the number of permutations plus one (Kraft & Ackerly, 2010).

At the point level, we summarized overall beta diversity (β_{sor}), turnover (β_{sim}) and nestedness (β_{nes}) for survey points within each of four 650-m elevational zones to determine how beta-diversity components changed with elevation. Zones of 650 m were chosen because this range best reflects clustering patterns in bird species composition across plots (Appendix S1) while allowing for zones of equivalent elevational range.

We examined the relationship of bird species composition to tree species composition, elevation and vegetation structure through multiple regression on distance matrices (MRM; Lichstein, 2007). The dissimilarity matrix of tree species composition (β_{sor}), distance matrix of elevation (from elevational difference), and distance matrix of vegetation structure (from the Euclidean distance of the first four principal components of the vegetation PCA) were used as predictors to explain variation in bird species dissimilarity (β_{sor}). MRM analyses at the plot level were performed for all birds and for each foraging guild. MRM analysis was also performed at the point level for each 650-m elevational zone, where predictors included distance matrices of vegetation structure and elevation across points in each zone. Each analysis used all combinations of explanatory variables and model evaluation was based on Akaike's information criterion (AIC) model selection (evaluated using change in the corrected AIC, ΔAIC_c), with consideration of the weights of models and predictors (Burnham *et al.*, 2011). Predictor weights (ranging from 0 to 1) allowed evaluation of the relative importance of predictors across models and were calculated as the sum of Akaike weights for all models that include a given predictor. All analyses were performed in R 2.11.0 using packages VEGAN, STATS and ECODIST (R Development Core Team, 2010) and functions provided by Baselga (2010).

RESULTS

Species richness

Our surveys revealed high regional richness across the fourteen 1-ha plots in both bird and tree communities. Overall, 872 species of trees were identified from plots and 211 species of birds were identified from the 42 survey points associated with plots. A total of 325 bird species were detected across all 172 survey points (Appendix S3). Plot richness was nearly three times higher in trees compared with birds; the average number of tree species per plot was 100 (ranging from 38 to 171), and the average number of bird species per plot was 35 (ranging from 12 to 58). Species richness across

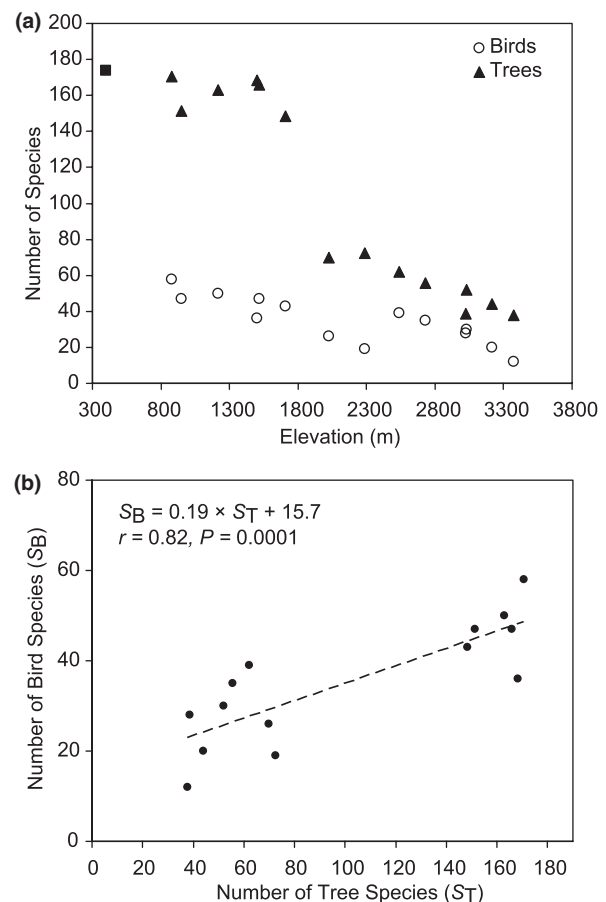


Figure 2 (a) Species richness for trees (solid triangles) and birds (hollow circles) with elevation for fourteen 1-ha plots. An estimate of tree species richness for lowland *terra firme* in Manu National Park (approximately 400 m elevation; solid square) is given as a reference (from Pitman *et al.*, 2001; averaged across twenty 1-ha plots). (b) Relationship between plot species richness of birds (S_B) and trees (S_T). The equation for the linear relationship, Pearson correlation coefficient (r) and P -value are shown.

plots was highly correlated between birds and trees ($r = 0.82$; $P = 0.0001$; Fig. 2), and the number of species per plot generally decreased with increasing elevation for both taxa, although there was a low-elevation plateau in tree richness between 800 and 1750 m a.s.l., above which species richness dropped linearly with elevation (Fig. 2a). For birds, analysis of individual foraging guilds showed that the pattern of decreasing richness with elevation was driven primarily by loss of insectivores (Fig. 3a). Declines in species richness of frugivores, granivores and omnivores, in absolute numbers of species, were marginal compared to the loss of insectivores, and nectarivores showed little trend in richness with elevation. Similar patterns across guilds are shown when bird species richness is plotted against canopy height (Fig. 3b). Generally, canopy height decreased with elevation ($r = -0.68$; $P < 0.0001$) and bird species richness increased with increasing canopy height.

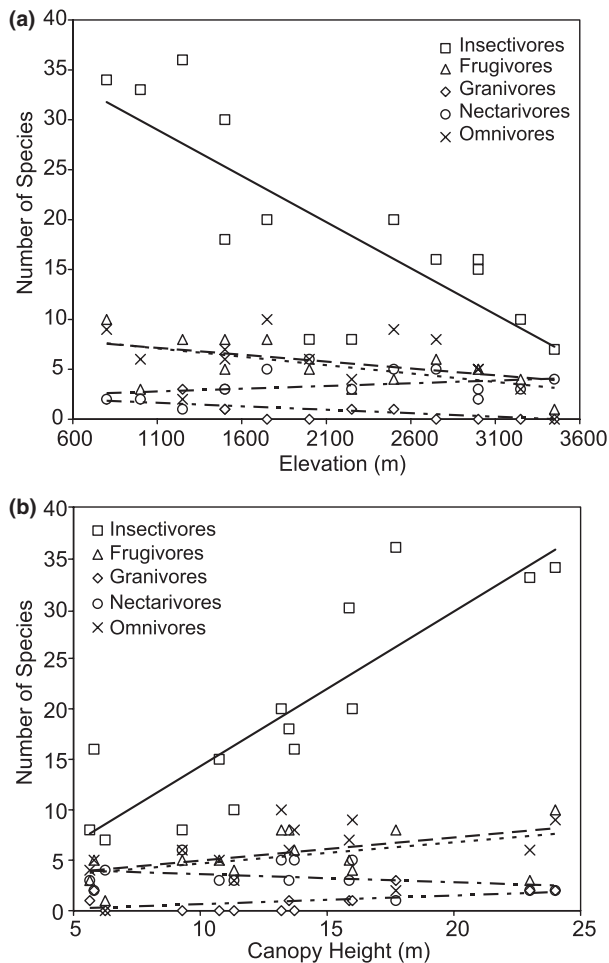


Figure 3 Species richness of avian foraging guilds across plots in the Manu study region varying in (a) elevation and (b) average canopy height. Best fit lines are shown for each guild, including nectarivores, granivores, omnivores, frugivores and insectivores.

Species occurrence, turnover and nestedness

Most species of trees and birds showed narrow elevational distributions, generating high species turnover. On average, individual tree species occurred in 1.7 (12%) of the 14 plots, and bird species detected at plots occurred in a mean of 2.3 plots (17%). Over half of tree species (58%) and two-fifths of bird species (41%) were restricted to a single plot, and 85%

of tree species and 65% of bird species were restricted to two or fewer plots. Only four bird species and not a single tree species occurred in half or more of the plots.

At the plot level, pairwise dissimilarity values of species turnover (β_{sim}) ranged from 0.2 to 1 in birds (mean = 0.80) and from 0.49 to 0.98 in trees (mean = 0.87). For both taxa, nestedness dissimilarity (β_{nes}) made up a much smaller component of change in species composition compared to species turnover. Values of β_{nes} across plots ranged from 0 to 0.28 (mean = 0.05) in birds and from 0 to 0.12 (mean = 0.03) in trees.

At the point level, pairwise bird dissimilarity values varied more than at the plot level, with β_{sim} ranging from 0 to 1 (mean = 0.78) and β_{nes} ranging from 0 to 0.86 (mean = 0.05). Mean pairwise dissimilarity values across points within 650-m elevational zones varied with elevation (Table 1). Dissimilarity attributed to turnover (β_{sim}) declined with elevation, such that pairwise points in high-elevation zones, on average, reached only two-thirds the level of dissimilarity found in the low-elevation zone. Dissimilarity due to nestedness of species (β_{nes}), however, was two to four times greater in high-elevation zones and negligible between points in low-elevation zones.

Congruence in birds and trees

Analysis of dissimilarity indices between adjacent plots revealed higher dissimilarity in trees compared with birds for both β_{sor} and β_{sim} (Fig. 4; Appendix S1). β_{sor} values ranged from 0.54 to 0.85 for trees and 0.3 to 0.62 for birds, and β_{sim} values ranged from 0.49 to 0.77 for trees and from 0.26 to 0.60 for birds. Dissimilarity due to nestedness (β_{nes}), however, was generally higher in birds (range: 0.01–0.20) than in trees (range: 0.01–0.09; Appendix S1).

Regions of significantly higher dissimilarity, compared to expected values under a null model of simulated elevational ranges, were spatially consistent across birds and trees. In birds, dissimilarity was higher for the foothills between 1000 and 1500 m a.s.l. and for cloud forest between 1750 and 2500 m (Fig. 4a). In trees, dissimilarity between adjacent plots was higher than expected for the entire elevational range between 1000 and 2500 m (Fig. 4b). Comparisons of β_{sor} , β_{sim} and β_{nes} values in birds show that dissimilarity peaks were generated both by species turnover (β_{sim} ; 1000–1500 and 2000–2250 m a.s.l.) and by nestedness between

Table 1 Pairwise dissimilarity values for Sørensen's (β_{sor}), Simpson's (β_{sim}) and nestedness-resultant (β_{nes}) dissimilarity indices across bird survey sites within four 650-m elevational zones in the Manu study region on the eastern slope of the Peruvian Andes. Number of sites per zone, mean, minimum, and maximum dissimilarity values are shown for each index.

Elevational zone (m a.s.l.)	No. of sites	Sørensen's index (β_{sor})			Simpson's index (β_{sim})			Nestedness-resultant index (β_{nes})		
		Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
800–1450	43	0.76	0.35	1	0.73	0.30	1	0.03	0	0.24
1450–2100	38	0.62	0.23	1	0.55	0.07	1	0.08	0	0.30
2100–2750	53	0.63	0.24	1	0.49	0	1	0.14	0	0.82
2750–3400	38	0.60	0.21	1	0.46	0	1	0.14	0	0.79

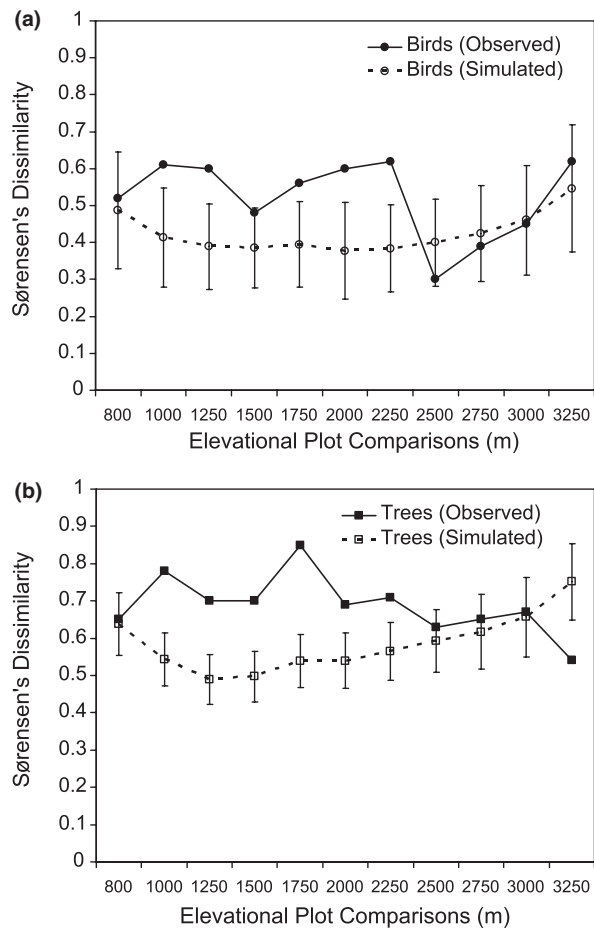


Figure 4 Observed (solid line, filled symbols) and expected (dotted line, open symbols) dissimilarity values of Sørensen's dissimilarity index (β_{sor}) for (a) birds and (b) trees between adjacent plots in the Manu study region, where the expected values are mean β_{sor} dissimilarities (with error bars showing range of values within two standard deviations of the mean) under the null model of randomized placement of elevational ranges of species along the gradient generated using 1000 Monte Carlo simulations (see Bach *et al.*, 2007). The x-axis indicates the elevation of the lower of the two adjacent plots compared.

adjacent plots (β_{nes} ; 1750–2000 and 2250–2500 m). In trees, dissimilarity peaks were generated by species turnover; nestedness made little contribution to overall dissimilarity among adjacent zones. Turnover peaks (β_{sim}) were coincident between birds and trees in the foothill elevations of 1000–1250 m and were nearly coincident in the cloud forest elevations of 1750–2250 m, where the turnover peak in trees was 250 m lower than the turnover peak in birds (Figure S1.4 in Appendix S1).

Roles of vegetation structure, elevation and trees in explaining bird dissimilarity

Multiple regression on distance matrices showed that a combination of vegetation structure, elevation, and tree dissimilarity best explained variation in bird dissimilarity across

Table 2 Model selection results from multiple regression on distance matrices (MRM) for all birds across plots in the Manu study region. Explanatory variables include distance matrices of elevation (Elev) and vegetation structure (Veg) and dissimilarity in tree species composition (Tree). For each model, the proportion of explained variation (R^2), number of parameters (k), change in corrected AIC from the model with the lowest AIC value (ΔAIC_c) and model weights (w_i) are shown. Model weights are equivalent to the probability of that model being the best approximating model.

Model	R^2	k	ΔAIC_c	w_i
Elev + Tree	0.78	4	0.0	0.693
Elev + Tree + Veg	0.79	5	1.7	0.303
Tree + Veg	0.75	4	10.3	0.004
Tree	0.72	3	16.7	0.000
Elev	0.65	3	36.8	0.000
Elev + Veg	0.66	4	38.7	0.000
Veg	0.27	3	105.4	0.000

1-ha plots (Table 2). For the group 'all birds', and for all avian foraging guilds except one (omnivores), the best-fit model included both tree species composition and elevation. Models that included all three variables (i.e. tree species composition, vegetation structure and elevation) had $\Delta\text{AIC}_c \leq 1.7$ for all birds (Table 2) and $\Delta\text{AIC}_c \leq 4.1$ for other foraging guilds (Appendix S1). For omnivores, the best model consisted of tree species composition and vegetation structure. Overall, our models explained a large proportion of the total variation in bird species dissimilarity (78% for all birds and 65–73% for most foraging guilds, with the exception of omnivores, where the best-fit model explained only 40% of the variation in bird species dissimilarity). The granivore foraging guild was the least diverse, consisting of 20 species surveyed, and principally included species with low densities and patchy distributions (e.g. parrots, tinamous, some doves). This created a large proportion of zeros within the dissimilarity matrix, and as a result, granivores could not be analysed using MRM. For all groups analysed, tree species composition had the highest predictor weight, ranging from 0.85 to 1.0 (Table 3). Elevation was also consistently an important predictor, although less so for omnivores (0.38). Vegetation structure was an important predictor principally for omnivores (0.84) and insectivores (0.45).

Bird species dissimilarity (β_{sor}) at the point level within 650-m elevational zones was best explained by a combination of vegetation structure and elevation, and this was consistent for all zones (Table 4). The variation explained in bird dissimilarity ranged from 34 to 67% across 650-m zones, and, generally, a larger proportion of variation was explained at lower elevations compared to higher elevations. Models that included both vegetation and elevation as predictors were consistently ranked highest among candidate models, and any model using only one of these two predictors had $\Delta\text{AIC}_c > 12$.

Table 3 Relative importance of predictor variables in multiple regression on distance matrices (MRM) analyses for all birds and for each foraging guild* across plots in the Manu study region, calculated as the sum of the Akaike weights for models that include each predictor. Predictor weight ranges from 0 to 1 and is equivalent to the probability that the predictor is included in the best model.

Predictor	All birds	Frugivores	Insectivores	Nectarivores	Omnivores
Elevation	1.00	0.99	0.86	0.91	0.38
Tree Species Composition	1.00	1.00	1.00	1.00	0.85
Vegetation structure	0.31	0.13	0.45	0.12	0.84

*Granivores could not be included due to insufficient detections across plots.

Table 4 Model selection results from multiple regression on distance matrices (MRM) for all birds across points within 650-m elevational zones in the Manu study region. Explanatory variables include distance matrices of elevation (Elev) and vegetation structure (Veg). For each model, the proportion of explained variation (R^2), number of parameters (k), change in corrected AIC from the model with the lowest AIC value (ΔAIC_c) and model weights (w_i) are shown. Model weights are equivalent to the probability of that model being the best approximating model.

Elevational zone (m)	Model	R^2	k	ΔAIC_c	w_i
800–1450	Elev + Veg	0.67	4	0.0	1.000
	Elev	0.66	3	27.3	0.000
	Veg	0.06	3	950.9	0.000
1450–2100	Elev + Veg	0.50	4	0.0	0.998
	Elev	0.49	3	12.5	0.002
	Veg	0.07	3	434.6	0.000
2100–2750	Elev + Veg	0.12	4	0.0	1.000
	Elev	0.10	3	22.6	0.000
	Veg	0.01	3	159.0	0.000
2750–3400	Elev + Veg	0.34	4	0.0	1.000
	Elev	0.25	3	81.9	0.000
	Veg	0.16	3	163.5	0.000

DISCUSSION

Our analysis of bird and vegetation communities along the Manu elevational gradient revealed correspondence between birds and trees in both species richness, particularly for mid- and high elevations, and species turnover, such that areas with high beta diversity and peaks in species turnover occurred in similar locations for birds and trees. Changes in vegetation structure, tree species composition and elevation explained up to 78% of variation in bird dissimilarity across plots. The hypothesis that insectivores are more influenced by vegetation structure whereas frugivores and nectarivores are more influenced by vegetation composition was only partially supported. Across foraging guilds vegetation structure had the highest relative importance for insectivores and omnivores, and the lowest for frugivores and nectarivores. However, tree species composition was an important predictor for all foraging guilds and had a higher relative importance compared to vegetation structure, irrespective of guild. Our results may instead suggest that changes in tree species

composition, perhaps driven by underlying changes in primary productivity or by direct biotic relationships, affect different avian guilds in similar ways.

Species richness in trees and birds

Species richness in trees and birds decreased with elevation; however, whereas bird species richness declined continuously above 800 m a.s.l., tree communities showed lowland-level richness up to 1500–1700 m. This discrepancy could be explained by several changes that occur independently of tree diversity at these plots. The foothill elevation of approximately 1250 m marks the loss of canopy-emergent trees, reducing the complexity of forest canopy structure, with consequences for canopy birds and foraging flocks. This elevation also marks a decrease in tree growth rates and fruit crop production (M. Silman, unpublished data; Girardin *et al.*, 2010), reflecting decreases in above-ground net primary productivity. Reduced productivity could have consequences for the resource base of many avian guilds, and especially for insectivores, which can have species-specific, inflexible, and time-consuming foraging behaviours for seeking out cryptic prey (Naoki, 2007). From an energetic perspective, increasing foraging area to compensate for lower productivity at these elevations should be comparably easier for frugivores and granivores (often large-bodied), and trap-lining nectarivores, which travel widely in search of food (Stiles, 1975).

In general, we found that the loss of insectivores dominates the pattern of decreasing bird richness with elevation; changes in richness of other guilds are relatively slight. These patterns match those found by Terborgh (1977) in the Vilcabamba range of Peru, one of the few tropical studies that have examined guild richness with elevation. One plausible driver, discussed above, is decreasing temperature and associated declines in primary productivity, factors which are correlated with a reduction in insect abundance with elevation in other Andean ranges (Garibaldi *et al.*, 2011). Diversity at higher elevations may also be affected by reduced canopy height and structural complexity (MacArthur & MacArthur, 1961; Goetz *et al.*, 2007), factors which may be particularly important for insectivores, where reduced forest vertical structure limits opportunities for specialized foraging strategies.

Global analysis of elevational patterns in bird diversity has revealed that patterns of decreasing richness (as opposed to

mid-elevation peaks) are most likely to occur along humid gradients (McCain, 2009), and our results show no exception. Suggested ecological and evolutionary mechanisms operating across gradients to generate these patterns include physiological limitations for upward range expansion, reduced resource availability with elevation, historical effects on timing of diversification and phylogenetic niche conservatism (McCain, 2009). None of these mechanisms, however, has received rigorous analysis. The ecological and evolutionary correlates of elevation and their impacts on richness need further investigation, but at least in Neotropical birds, any explanation for decreasing richness with elevation should address the overwhelming loss of insectivores.

Species turnover, nestedness and patterns of compositional similarity

Although local species richness for trees is generally higher than for birds, these differences alone do not account for the much larger discrepancy in regional diversity; regional richness in trees is more than four times that of birds. This estimate of regional richness is probably conservative, as our spatial extent of sampling for birds at tree plots was slightly larger than that of trees, with some bird survey points located just outside plot boundaries. Differences in regional diversity may instead be explained by higher beta diversity of trees compared to birds along the gradient. Given the short distances between plots and the high dispersal capacity of trees (Clark *et al.*, 1999), this pattern is not likely to be driven by dispersal limitation. Rather, increased turnover may result from higher diversity in tree communities combined with greater specialization to environmental conditions, including temperature and rainfall, as well as indirect effects on soil nutrient cycling and geological substrate (Aiba & Kitayama, 1999).

Despite differences in levels of species turnover in birds and trees, we found that regions of higher dissimilarity were consistent between taxa, with similar patterns in the location of turnover peaks, suggesting that birds and trees are either associated, or that both communities respond in parallel fashion to some other aspect of the gradient. The matching peaks of species turnover of birds and trees in the foothills (1000–1250 m a.s.l.) are especially notable, where there is 10% greater dissimilarity between adjacent plots compared with dissimilarity values between adjacent plots above and below this elevation. A second region of elevated turnover occurs in cloud forest between 1750 and 2000 m for trees and only slightly higher for birds (2000 and 2250 m). These peaks in turnover are probably influenced to some extent by local factors such as soil differences for trees (e.g. granite-derived soils at 2000 m versus Palaeozoic shales and slates found across other plots) and habitat structure for birds (the location of the 2250-m plot on an exposed ridge with short, dense vegetation and open canopy). More generally, species turnover in birds and trees is likely to be influenced by the presence of persistent clouds at these elevations, even in the

dry season. For birds, the lower range boundaries of many high-elevation species are concentrated in this zone (Jankowski, 2010), perhaps indicating that these species respond to the position of the cloud base or associated changes in vegetation (Jankowski *et al.*, 2009). The third region of higher turnover for birds occurs at the tree line; bird surveys associated with the highest tree plot (3400 m) sampled areas just above the tree line in *puna* grassland and reflect this transition in vegetation. The plot itself, however, was located just below the tree line, necessarily, so our analysis does not represent the tree line shift from forest to *puna*, with the loss of stems ≥ 10 cm d.b.h. above this ecotone.

Nestedness contributed much less than turnover to dissimilarity in birds and trees. Nestedness was higher for birds compared with trees, however, and the contributions of nestedness to bird dissimilarity were greater above 2100 m. Thus, variation in species composition at high elevations, to a greater extent, was determined by differences in richness: birds found at less diverse sites were more often subsets of the species at more diverse sites. Broader sampling will allow a more detailed examination of habitat associations for high-elevation generalist versus specialist species.

Importance of tree species composition, vegetation structure and elevation

Multiple regression on distance matrices revealed that tree species composition, vegetation structure and elevational position are all important predictors of bird community composition. The best-fit models, for all birds and avian foraging guilds, typically included tree species composition and elevation as predictors, although models including all three predictors could also be considered suitable. Across points within 650-m elevational zones, the best-fit models always included elevation and vegetation structure. While species composition patterns in birds were well predicted, it is difficult to attribute the major portion of explained variation to any single variable. That said, models with elevation as a sole predictor perform considerably worse than any model that also includes tree species composition or tree species composition and vegetation structure, suggesting an important role for these habitat features in predicting changes in bird species composition.

We find partial support for the hypothesis that avian foraging guilds with diets based on plants (e.g. frugivores and nectarivores) are more closely associated with tree species composition (Hasui *et al.*, 2007) whereas insectivorous or omnivorous birds are more influenced by structural changes in vegetation. Across foraging guilds the relative importance of vegetation structure as a predictor was highest for insectivores and omnivores (many of which include insects as a major dietary component). However, tree species composition was an important predictor in models for all foraging guilds, and vegetation structure was usually less important than tree species composition. The result that tree species

composition was consistently an important predictor of bird species composition suggests that bird and tree communities are either directly associated, respond to similar underlying drivers that influence compositional change across sites, or both.

One aspect that was unexplored in our analysis is the influence of vegetation functional diversity and composition on bird communities. Montane communities, like their lowland counterparts, are expected to have keystone tree species or functional types that are essential for avian diversity. Rather than correlated changes in richness or turnover in birds and trees, bird species diversity and composition could be largely unaffected by changes in tree species composition if functional groups of plants are maintained. For example, in the Amazonian lowlands, tree species diversity decreases by one-third over 12 degrees latitude from Yasuni, Ecuador to Manu, and by another one-third over four degrees from Manu to Beni, Bolivia (Silman *et al.*, 2005). Keystone species and functional types in those forests, however, remain nearly identical. Correspondingly, mammal and bird richness decrease only slightly over this lowland gradient, and at a much lower rate than tree richness, pointing to the importance of plant functional types rather than plant diversity *per se* in influencing avian diversity. We might expect similar patterns in montane forests. Importantly, patterns of decoupled changes in species *diversity* across taxonomic groups do not necessarily indicate an absence of biological process. Similarly, evidence for congruent changes in species *composition* between bird and tree species may be the result of underlying functional relationships.

Prospects for montane birds and trees with climate change

Most projections of species range shifts with climate change use abiotic variables (e.g. temperature and moisture) to predict future 'climate landscapes' in which species are likely to be distributed. Given predictions of a 4–6 °C temperature increase for the study region over the next century (Urrutia & Vuille, 2009) and an adiabatic lapse rate of *c.* 5.6 °C per km for tropical montane landscapes (Bush *et al.*, 2004), we should predict that within 100 years, a given location will reflect present-day thermal environments of areas *c.* 700–1100 m lower in elevation. If the correspondence of bird communities with vegetation structure and tree communities is driven by avian habitat selection, however, tropical birds may not show the expected upslope range shifts. At least two other studies have found no evidence of significant upslope movement of birds due to climate change (Archaux, 2004; Popy *et al.*, 2010), and another study from a nearby tropical mountain shows that over four decades, bird species have shifted much less than expected based on patterns of climate change in the region (Forero-Medina *et al.*, 2011). The change in climate observed in Manu and observed migration rates of trees will allow us to test this hypothesis over the next few decades (Feeley *et al.*, 2011).

Even if bird species distributions do shift upslope in response to climate change, vegetation structure may impose community-wide constraints. If structural complexity is linked to bird diversity, as suggested by our results and elsewhere (Goetz *et al.*, 2007; Lesak *et al.*, 2011), and if there is a time lag with shifts in vegetation structure, then there may not be sufficient vertical space for numerous lower elevation species to move into structurally simpler highland forests without increased competition, resulting in reduced species richness or population densities. Vegetation ecotones along elevational gradients with corresponding peaks in present-day species turnover (e.g. tree line) may pose particularly challenging hurdles for upslope movement of communities.

Generally, we can expect that avian range shifts will rely on shifting forest dynamics, successional pathways, and major vegetation types found along mountainsides. When possible, species distribution models should consider alternative projections of range shifts under scenarios of habitat constraint (Araújo & Luoto, 2007; Kissling *et al.*, 2010). With the narrow elevational distributions that many Andean species exhibit in these heterogeneous landscapes, local-scale projections that include information on habitat associations and behaviour will be necessary for precise evaluations of the threats that tropical montane species face.

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SUPPORTING INFORMATION

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

Appendix S1 Discussion of survey protocols and analyses pertaining to variation in vegetation structure, distribution of elevational zones, and plot dissimilarities and model selection.

Appendix S2 References providing information on tropical bird diets.

Appendix S3 Bird species detected along the 2600-m elevational gradient in the Manu region.

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BIOSKETCH

Jill E. Jankowski is an assistant professor at the University of British Columbia, Canada. This study was conducted as part of her dissertation work in the Department of Biology at the University of Florida and also as part of the Andes Biodiversity and Ecosystem Research Group.

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