

## PATTERNS AND MAGNITUDE OF TEMPORAL CHANGE IN AVIAN COMMUNITIES IN THE ECUADORIAN ANDES

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**Abstract.** The tropical Andes rank first among the world's 25 "hotspots" of biodiversity and endemism yet are threatened and little studied. We contrast population trends in avian diversity in montane cloud forest (*bosque altoandino*) and similar forest degraded by the planting of introduced tree species (*bosque introducido*) in the Mazán Reserve, Ecuador. We describe changes in bird diversity and abundance in these habitats over 12 years and evaluate the nature of change within these avian communities. On the basis of 2976 count detections and 419 net captures of 76 species of landbirds, indices of similarity between the habitats were low, with only 47.6% of species occurring in both forest types. From 1994–95 to 2006–07, species richness decreased from 54 to 31 in *bosque introducido* and from 67 to 30 in *bosque altoandino*. Capture rates also declined from 56.0 to 28.5 birds per 100 mist-net hr in *bosque introducido* and from 38.0 to 22.4 birds per 100 mist-net hr in *bosque altoandino*. We explore various potentially interacting factors that might have caused the observed changes in bird communities, including changes in vegetation within the Mazán Reserve and environmental changes resulting from global warming. But our results also suggest that local and regional changes in habitat outside of the Mazán Reserve were likely responsible for some community changes within the reserve. We argue for increased population monitoring to verify trends and to strengthen the effectiveness of conservation efforts in the Andes.

**Key words:** avian abundance, climate change, habitat change, land use, monitoring, páramo, protected areas.

### Patrones y Magnitud del Cambio Temporal en Comunidades de Aves de los Andes Ecuatorianos

**Resumen.** Los Andes tropicales ocupan el primer lugar entre los 25 "puntos calientes" de biodiversidad y endemismo a nivel mundial, pero se encuentran amenazados y han sido poco estudiados. En este estudio contrastamos las tendencias en la diversidad de aves en un bosque altoandino y en un bosque similar pero degradado por la siembra de especies exóticas de árboles en la reserva Mazán, Ecuador. Describimos los cambios en la diversidad y abundancia de aves en estos ambientes a lo largo de 12 años y evaluamos la naturaleza del cambio en esas comunidades de aves. Con base en 2976 detecciones obtenidas durante conteos y en 419 capturas con redes de 76 especies de aves terrestres, los índices de similitud entre los hábitats fueron bajos y sólo el 47.6% de las especies se encontraron en ambos tipos de bosque. Desde 1994–95 hasta 2006–07, la riqueza de especies disminuyó de 54 a 31 en el bosque con especies introducidas y de 67 a 30 en el bosque altoandino. Las tasas de captura también disminuyeron, de 56.0 a 28.5 aves por 100 horas-red en el bosque con especies introducidas y de 38.0 a 22.4 aves por 100 horas-red en el bosque altoandino. Exploramos varios factores que potencialmente interactúan y podrían haber causado los cambios observados, incluyendo cambios en la vegetación en la reserva Mazán y cambios ambientales resultantes del calentamiento global. Sin embargo, nuestros resultados también sugieren que cambios locales y regionales en el hábitat sucedidos por fuera de la reserva Mazán probablemente fueron responsables de algunos de los cambios en las comunidades de la reserva. Aducimos que es importante incrementar los monitoreos poblacionales para verificar las tendencias y para fortalecer la efectividad de los esfuerzos de conservación en los Andes.

## INTRODUCTION

South America is the world's richest continent for birds with 3200 species, of which approximately 658 have breeding ranges that are restricted to <50 000 km<sup>2</sup> (Stattersfield et al. 1998). The center of this diversity is the tropical Andes, which harbor the greatest concentration of restricted-range species

in South America (Stotz et al. 1996, Stattersfield et al. 1998), have one of the highest concentrations of the world's threatened bird species (Stotz et al. 1996), and therefore ranks first among the world's 25 "hotspots" of diversity and endemism (Myers et al. 2000). The tropical Andes contain three major terrestrial vegetation types at elevations above 3000 m: high montane cloud forest or *bosque altoandino*, páramo grassland,

Manuscript received 23 December 2009; accepted 22 September 2010.

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which in some regions is accompanied by patches of *Polylepis* forest (Jorgensen and León-Yáñez 1999, Baquero et al. 2004), and puna grasslands (which occur in Peru and farther south).

Like other major biodiversity hotspots, the tropical Andes region has suffered extensive habitat loss because of inappropriate land use. In southern Ecuador, the burning of grasslands to promote regeneration for the benefit of grazing cattle is an ancient tradition that is still commonly practiced (White and Maldonado 1991). In addition, habitat has been lost to urbanization, road building, deforestation, the cultivation of exotic Mexican pine trees and *Eucalyptus* forests, and other causes. Human-induced disturbance is so widespread in the area that native montane forest is now confined to the least accessible areas. Continued destruction of forests is projected to lead to further fragmentation of bird populations and to local extinctions (Kattan et al. 1994, Brooks et al. 1999, Wiegand et al. 2005).

As elsewhere, protected areas have been established in Andean habitats to protect local floral and faunal diversity, contributing to the approximately 8% of the earth's land surface that is now in a protected status (Hansen and DeFries 2007a). These reserves are considered the cornerstone of global conservation strategies, but questions have arisen concerning the effectiveness of protected areas in the context of growing human pressures (Redford et al. 1998, Ghimire and Pimbert 1997, Hansen and DeFries 2007b). Numerous studies have addressed the effects of human encroachments inside protected areas (Dompka 1996, van Schaik and Kramer 1997, Liu et al. 2001), resulting in a widespread sense that parks are simply not working (but see Bruner et al. 2001). Assessments of protected areas have also addressed issues surrounding the adequacy of the design of park systems to maintain species' viabilities and support ecological processes and functioning (Craighead 1979, Newmark 1985, Ervin 2003, Hansen and DeFries 2007b). Quantitative information about the ecological deterioration of protected areas is, however, scant (van Schaik et al. 1997).

Global climate change has become a more recently understood threat to species and protected areas (Root et al. 2003, Hannah et al. 2007). Climate change has caused reductions and expansions in the ranges of a variety of animals, and it has altered community composition and dynamics (Root et al. 2003, Parmesan 2006, La Sorte and Thompson 2007). The climate of the Andes in particular is predicted to become drier and more seasonal, so vegetation types that require less rainfall are likely to become more common (Foster 2001, Barnett et al. 2005, Hannah et al. 2007, Sekercioglu et al. 2008, Graham et al. 2011). Therefore, it is essential to know how persistence of species varies by vegetation type and condition in order to predict how climate change will influence species. Acquiring such information is particularly critical to park planners and managers precisely because of the inherent effect of climate change on ecological processes and ecological functioning and because of the global reach of causes and effects.

Despite the establishment of protected reserves, few investigators of the Andes have analyzed avian assemblages quantitatively or sought to determine population trends either inside or outside of protected areas. Some attention has focused on various aspects of avian community structure, habitat use, and effects of environmental degradation on bird communities in high-altitude *Polylepis* forest (e.g., Herzog et al. 2003, Cahill and Matthysen 2007, Jameson and Ramsay 2007, Lloyd 2008a,b), and in lower-elevation montane forest (e.g., Arango and Kattan 1997, Renjifo 1999, O'Dea and Whitaker 2007, Kikuchi 2009). But beyond surveys of species' occurrence and distribution (e.g., King 1989, Bonaccorso 2004, Creswell et al. 1999, Tinoco et al. 2009), very little research has addressed bird communities in high montane cloud forest (but see Remsen 1985, Poulsen 1996, Poulsen and Krabbe 1997, 1998) or assessed the effects of loss of this critical habitat on avian diversity (but see Kattan et al. 1994, Kessler and Herzog 1998). In addition, despite the fact that many international, regional, and local organizations have agreed on the value of long-term avian monitoring (Latta et al. 2005), and there has been much discussion over the past decade about the need for standardized methods for monitoring bird populations so that comparisons can be made across space and time, we have seen no published attempts to determine population trends in the Andes at any scale of analysis (Renjifo 1999).

Here our goal is to examine change in avian diversity over a 12-year period in high montane cloud forest and in forest dominated by introduced tree species in the Andes of southern Ecuador. To accomplish this we (1) describe and contrast current species richness and avian diversity in high montane cloud forest and forest characterized by introduced trees, (2) describe patterns of changes in the bird communities in terms of species and their body mass, diet, foraging stratum, primary habitat occupied, habitat breadth, and rarity, and (3) assess conservation needs of birds in these habitats. We conclude with a discussion of the importance of protected areas as parts of larger ecosystems and argue for increased population monitoring to strengthen the effectiveness of conservation efforts in the tropical Andes, as global warming and land-use change in the unprotected portion of an ecosystem may lead to changes in biodiversity and ecosystem functioning within an otherwise protected reserve (Liu et al. 2001, Root et al. 2003, Sekercioglu et al. 2008, Graham et al. 2011).

## MATERIALS AND METHODS

### STUDY SITES

We conducted this study in the 2700-ha Mazán Reserve adjacent to Cajas National Park in the high Andes of Azuay Province, Ecuador. Both the Mazán Reserve and Cajas National Park are managed by ETAPA (Empresa Pública Municipal de Teléfonos, Agua Potable y Saneamiento Ambiental), under a co-management agreement with the Ecuadorian Ministry of Environment. Cajas National Park covers more than

28 000 ha and is situated on the continental divide approximately 35 km west of Cuenca at 2° 50' S, 79° 15' W. Elevation in the park ranges from 3100 to 4450 m, and the topography of the area is markedly irregular. About 90% of the park is *páramo* interspersed with small patches of *Polylepis* forest. The original vegetation of the remaining area below 3500 m was high Andean cloud forest (*bosque altoandino*), but much of this area has been affected for several decades by human disturbances including forestry and grazing. Evidence of the effects of the last glacial maximum is widespread and seen in remnant glacial lakes, U-shaped valleys, and glacial cirques (Harden 2007). This area receives 1200–1500 mm of precipitation annually. Daily temperatures can fluctuate greatly, often changing from 0 to 20 °C, while the monthly mean temperature varies from 5 to 12 °C (IERSE 2004). The park is designated as a wetland of international importance (RAMSAR) and an internationally important bird area (Freile and Santander 2005). It is home to at least 144 bird species, including 9 threatened species (Tinoco and Astudillo 2007).

The Mazán Reserve, located in a U-shaped valley that runs from an elevation of 3100 m in the east to 3500 m in the west, is a highly protected area dedicated to biological research and closed to all other activities. Bisected by the Mazán River, the site contains primary high-elevation cloud forest on the south bank of the valley and mature secondary high-elevation cloud forest (hereafter *bosque altoandino*) with a 15- to 20-m canopy on the north bank of the valley. The extreme upper reaches of the valley consist of *páramo* and a small extent of *Polylepis* forest, while the lower reaches of the valley are dominated by introduced tree species (hereafter *bosque introducido*) and characterized by mixed stands of mature *Eucalyptus*, pine, and remnant native species with a canopy of 15 to 20 m. A small (<5 ha) patch of grassland succeeding to shrubs lies between the *bosque altoandino* and the *bosque introducido*.

#### HISTORICAL DATA

As a baseline for comparison, we report here data recorded in the Mazán Reserve in 1994 and 1995 by Toral (1996). He established transects in representative patches of *bosque altoandino* from 3150 to 3250 m elevation (transects T2 and T4) and in *bosque introducido* from 2950 to 3100 m elevation (transect T1). He set ten mist nets (12 m × 36 mm mesh) in pairs with 50–100 m between pairs. Although he did not report the exact distance covered by nets, his method suggests that the nets covered a minimum of 320 m and a maximum of 520 m, with the greater figure more likely given the team's effort to cover the majority of the 1000-m transect. Nets were opened from sunrise for 4 hr one day each month from October 1994 through February 1995. All birds captured were identified, marked with a colored plastic band, and recorded. Counts consisted of strip transects in the same habitat patches and were 1000 m long, with all birds counted within 20 m of either side of the transect. Each transect was walked slowly for 150 min

each month from October 1994 through May 1995, and all birds seen or heard were recorded.

#### SAMPLING BIRDS

We relocated the transects of Toral (1996) and established fixed locations for mist nets and point counts along these transects to obtain complementary indices of abundance of birds (Ralph and Scott 1981, Ralph et al. 1993). We established one study site in *bosque altoandino* encompassing transects T2 and T4 of Toral (1996) and another in *bosque introducido* to coincide with transect T1. We limited our sampling to months also sampled by Toral (1996) to eliminate potential problems associated with seasonal migrations or changes in abundance but increased sample sizes by pooling data across 2 years. We sampled in *bosque altoandino* 28–29 March 2006, 11–12 November 2006, 26–27 March 2007, and 20–21 November 2007 and in *bosque introducido* 30–31 March 2006, 13–14 November 2006, 28–29 March 2007, and 22–23 November 2007.

In each habitat, we sampled birds with 20 mist nets (12 × 32 mm mesh), placing them along or perpendicular to existing paths over ~510 m in interior *bosque altoandino* and ~575 m in *bosque introducido* to sample each habitat with similar intensity. In the *bosque introducido* the path was along or adjacent to a single-lane grass and gravel track that had been closed to all but the most occasional traffic since 1994. At each site, nets were opened from dawn to dusk of day 1, and dawn to 1100 of day 2. We identified all mist-netted birds to species and sex by plumage characteristics as presented in Ridgely and Greenfield (2001) and to age (juvenile or adult) by plumage or molt limits (after Pyle 1997) whenever possible. All birds, including hummingbirds, were uniquely banded with a numbered metal band for identification of recaptures. To maintain mist-netting effort similar to that of Toral (1996), in all analyses we used only captures recorded in the first 4 hr of net operations because capture rates are known to decline with time (Ralph and Scott 1981, Terborgh 1985). We then expressed the abundance of birds, or capture rate, as the number of birds captured per 100 mist-net hours, where one 12-m mist net opened 1 hr = 1 mist-net hr.

Mist nets are subject to several additional biases (Ralph and Scott 1981, Karr 1981, Remsen and Parker 1983). For example, in some habitats nets do not sample all strata of the vegetation, very small or very large birds may be ineffectively sampled, and nets may overestimate the abundance of species that travel widely in search of food over that of more sedentary foragers (Remsen and Parker 1983, Remsen and Good 1996). While recognizing these potential biases, in this study we minimized most of these problems because the vegetation in these habitats is similar in structure and we limit analyses of net-capture frequencies to comparisons within species and assume that the probability of a species being captured is equal in the two habitats.

Recognizing the limitations of mist nets, we also used point counts as an index of bird abundance. We conducted 10-min, 50-m fixed-radius point counts (Hutto et al. 1986)

at six points in each study site each sampling period, with each point set along the transects sampled by Toral (1996). We categorized the distance to each bird observed to one of three bands: <15 m, 15–29 m, and 30–50 m. Although results from counts from the <30-m and the ≤50-m circles were highly correlated ( $r = 0.98$  in *bosque introducido*;  $r = 0.91$  in *bosque altoandino*), indicating little risk of an area effect in point-count samples, we sought to reduce potential error associated with increased difficulty in identification of birds at greater distances in dense vegetation (Ralph et al. 1993, Wunderle 1994) and limited analyses to those birds recorded at <30 m. Points were equidistantly spaced at 150-m intervals. All point counts began at sunrise and were completed by 09:30, and no point counts were conducted in inclement weather. For some analyses we calculated the mean number of detections of birds per point ( $\times 100$ ) at each site and in each habitat, while in others we used presence/absence data. We restricted our studies to landbirds occurring within our count circles and eliminated flyovers, including raptors, psittacids, swallows, and swifts.

We classified birds captured in mist nets or recorded in audiovisual counts into groups based on body mass, diet, foraging stratum, primary habitat occupied, habitat breadth, and rarity. Body mass was determined by reference to Toral (1996), Ridgely and Greenfield (2001), Dunning (2007) and our unpublished data. Birds were grouped by diet on the basis of principal food items consumed (Ridgely and Greenfield 2001; pers. obs.), as insectivores, nectarivores, granivores, frugivores, and omnivores. The foraging stratum of each species, from Stotz et al. (1996), was understory and/or terrestrial, mid-story, or canopy. Where a species was reported to use two strata in foraging we assigned the species to the lower stratum. We assigned species reported to use all strata to the mid-story. We assigned all species to a single preferred habitat on the basis of Stotz et al. (1996). For species whose primary habitat was not represented at the Mazán Reserve, we selected the next most preferred habitat recognized by Stotz et al. (1996) that was present. Habitats were montane evergreen forest, scrub and secondary forest, edge habitat, high-elevation elfin forest, and *páramo* grasslands. Species whose primary habitat was aquatic ( $n = 2$ ) were omitted from habitat analyses. Habitat breadth was also derived from Stotz et al. (1996) and was expressed as the number of habitats occupied by the species across its range, with more specialized species occupying fewer habitats.

Finally, following Renjifo (1999), we evaluated rarity at three different scales: geographic range size, local relative abundance, and relative abundance in the neotropics. We categorized the geographic range as small ( $\leq 60\,000\text{ km}^2$ ) or large ( $> 60\,000\text{ km}^2$ ) as assessed by BirdLife International ([www.birdlife.org/datazone/index.html](http://www.birdlife.org/datazone/index.html)). Local relative abundance was based on records from Cajas National Park (Tinoco and Astudillo 2007) and personal observation, with species scored

on a scale of 0 to 5 (rare, unusual, moderately common, common, abundant). Relative abundance across the neotropics was based on data from Stotz et al. (1996).

#### STATISTICAL ANALYSES

We used Excel 2003 and on-line worksheets provided by McDonald (2009) to perform various statistical tests described by Sokal and Rohlf (1995). We tested data for normality with normal probability plots and tests of skewness and kurtosis. When data were not normally distributed and could not be transformed to achieve normality, we used nonparametric statistics. We accepted a probability of type I error of 0.05 or less as significant unless otherwise noted. We did not analyze data within a sampling period (1994–95 or 2006–07) systematically to determine annual variation in bird populations within each period but pooled them by period for each habitat type to increase sample sizes. Some analyses are based on presence/absence of species or proportions of birds captured or observed, while other comparisons are based on capture rates or mean number of individuals recorded in counts.

We used rarefaction (Simberloff 1972) to compare species richness in different habitats and different time periods with data obtained from counts and mist-net samples. Rarefaction curves are essentially idealized species-accumulation curves that use the accumulated number of individuals to allow the direct comparison of results between groups that differ in patterns of abundance and were sampled by very different techniques (Gotelli and Colwell 2001, Barlow et al. 2007, Cleary et al. 2007). Rarefaction calculates the expected species richness of the different groups for a constant sampling effort but does not provide an estimate of asymptotic richness. Rather, for each species' accumulation curve we calculated a Chao 1 nonparametric estimator of richness with its variance (Chao 1984, Colwell and Coddington 1994). Chao 1 estimates do not require that sample sizes be equal, but with more data and larger samples the confidence interval is narrowed (Chao 2010; A. Chao, pers. comm.). We evaluated the significance of observed differences in species richness between the periods by comparing Chao 1 estimates of species richness and their associated 95% confidence intervals. This provided an indication of the statistical significance of the difference between pairs of species-richness curves.

We also compared species diversity by habitat and period by calculating the Shannon diversity index (Magurran 1988) for each group. We used the  $t$ -test of Hutcheson (Magurran 1988) to test whether pairs of indices of diversity were significantly different. Because the diversity index is based on entropy and gives the uncertainty in the outcome of a sampling process (Jost 2006), we followed Jost (2006) and converted the diversity to the “effective number of species.” This transformation represents the number of equally common species and thus represents a true diversity with mathematical properties that allow comparison among groups and facilitates



interpretation. We then used the effective number of species to determine the magnitude of the difference between paired groups of interest by calculating the percent change in effective numbers of species.

Finally, to help understand the nature of changing avian communities, we calculated an index of evenness in each habitat and time period (Magurran 1988). Evenness is a measure of the distribution of individuals among taxa, with absolute evenness = 1.0. We used similarity measures to determine if bird communities in the two habitats and two periods differed from one another, and we used Jaccard's index to compare the similarity of bird communities on the basis of species' presence or absence in samples from nets or counts.

We used a chi-squared test, a  $G$ -test of independence, or, when expected values were small, a Fisher's exact test of independence to test for significant heterogeneity between habitats or periods in the proportion of individuals in diet categories, body-mass classes, foraging strata, preferred habitat, habitat breadth, regional rarity, and rarity in the neotropics. We completed the tests for both mist-net samples and point-count samples from 2006–07. Similarly, we used row  $\times$  column tests of independence to test for significant heterogeneity between the proportions of apparently extirpated and extant species in each of these categories or classes. For these tests we used presence/absence data to compare the group of species present in both periods (extant species) with those species present in 1994–95 but not encountered in 2006–07 (apparently extirpated). Our use of the term “apparently extirpated” recognizes that these species may still be present at our study sites in low numbers (and some “extirpated” species have in fact been seen or captured outside of our sampling periods), but they were not recorded in the more recent period by methods and sampling intensity comparable to those of 1994–95. In fact, mist-net sampling in 2006–07 was more intensive than in 1994–95 (see Results), so apparent extirpations revealed by net captures are in fact conservative.

We used the Kruskal–Wallis  $H$ -test to compare the abundance of individuals captured in mist nets (capture rate) and the abundance of individuals detected in point counts (detection rate) by habitat in 2006–07, with capture rates and detection rates within each period averaged. We also used the Kruskal–Wallis  $H$ -test to compare the abundance of individuals captured in mist nets in 1994–95 with capture rates in 2006–07 for both *bosque introducido* and *bosque altoandino*. Finally, we used the Kruskal–Wallis test to compare capture rates in 1994–95 and 2006–07 of the 13 most common birds in *bosque introducido* and *bosque altoandino*. Because these tests entailed 13 planned comparisons for each habitat, we used the sequential Bonferroni technique (Rice 1989) and decreased the table-wide level of  $\alpha$  in order to reduce the probability of committing a type I error (Sokal and Rohlf 1995).

## RESULTS

We report here on patterns of change in the distribution of birds generated by 2976 count detections and 419 net captures of 76 species of landbirds in *bosque introducido* and in *bosque altoandino* during surveys in the Mazán Reserve (Table 1). Count detections were 1009 in *bosque introducido* and 1967 in *bosque altoandino*; net captures were 202 in *bosque introducido* and 217 in *bosque altoandino*. All species-accumulation curves appear to have reached or have approached their asymptote (Fig. 1), indicating that the intensity of sampling was appropriate and that few additional species would have been added with continued sampling by mist net (Fig. 1a, b) or counts (Fig. 1c, d) in either habitat in either 1994–95 or 2006–07.

### PATTERNS OF DISTRIBUTION BY HABITAT

During the 2006–07 sampling period, detections of birds in the two habitats were similar but not equal. Combining both detection methods, we recorded 31 species in *bosque introducido* and 30 species in *bosque altoandino* (Table 1). Capture rates were higher in the *bosque introducido* (28.5 birds captured per 100 mist net hr) than in *bosque altoandino* (22.4 birds captured per 100 mist-net hr), but this difference was not significant ( $H_{\text{adj}} = 0.75$ ,  $df = 1$ ,  $P = 0.386$ ). A similar pattern was seen in point counts, with detection rates higher in the *bosque introducido* (7.1 birds detected per point count) than in the *bosque altoandino* (5.2 birds detected per point count), but this difference also was not quite significant ( $H_{\text{adj}} = 3.036$ ,  $df = 1$ ,  $P = 0.081$ ).

Evenness was high and similar in the two habitats and by both detection methods (Table 2). Evenness in *bosque introducido* was 0.88 for birds captured in mist nets and 0.87 for birds recorded on point counts. Evenness in *bosque altoandino* was 0.90 for birds captured in mist nets and 0.88 for birds recorded on point counts. The extent of numerical dominance of species within a habitat also suggests the degree of evenness within that habitat. In terms of mist-net captures, seven species accounted for 67.8% of captures in *bosque introducido*, while seven species accounted for 66.1% of captures in *bosque altoandino*. In terms of point-count detections, seven species accounted for 58.2% of observations in *bosque introducido*, while seven species accounted for 65.6% of observations in *bosque altoandino*. Various hummingbirds (Trochilidae), warblers (Parulidae), and flowerpiercers (Emberizidae) dominated both the net captures and the counts (Table 3).

Similarity indices based on combined survey methods of species' presence/absence in a habitat were low, with only 47.6% of species occurring in both the *bosque introducido* and the *bosque altoandino*. In Fisher's exact test of differences in birds occurring in the two habitats, mist-netting results (but not audiovisual surveys) showed significant differences in numbers of individuals from different trophic groups in the

TABLE 1. Body mass, ecology, rarity, capture rates (birds/100 mist net hours) and count detections (presence/absence) of birds in *bosque introducido* and *bosque altoandino* in the Mazán Reserve of the southern Ecuadorian Andes in early (1994–95) and late (2006–07) sampling periods.

Species	Body-size class <sup>a</sup>	Diet <sup>b</sup>	Foraging stratum <sup>c</sup>	Primary habitat <sup>d</sup>	Habitat breadth <sup>e</sup>	Range size <sup>f</sup>	Rarity		Captures					
									Bosque introducido			Bosque altoandino		
							Local abundance <sup>g</sup>	Neotropical abundance <sup>h</sup>	1994–95	2006–07		1994–95	2006–07	Bosque altoandino
Andean Guan ( <i>Penelope montagnii</i> )	4	O	M/C	F	1	L	F	F			×			×
Andean Snipe ( <i>Gallinago jamesoni</i> )	4	I	T	A	2	L	F	F						×
Band-tailed Pigeon ( <i>Patagioenas fasciata</i> )	4	F	C	F	3	L	R	F			×			
White-tipped Dove ( <i>Leptotila verreauxi</i> )	4	O	T/U	N	5	L	R	C			×			
Andean Pygmy-Owl ( <i>Glaucidium jardinii</i> )	4	C	C	F	1	L	U	F	0.50					×
Rufous-banded Owl ( <i>Ciccaba albitarsis</i> )	4	C	C	F	1	L	R	F						×
Band-winged Nightjar ( <i>Caprimulgus longirostris</i> )	4	I	T	N	4	L	U	F	0.25					×
Sparkling Violetear ( <i>Colibri coruscans</i> )	1	N	U/C	N	4	L	F	C	0.50		×		×	
Shining Sunbeam ( <i>Aglaeactis cupripennis</i> )	1	N	U/C	N	3	L	F	C			×			×
Mountain Velvetbreast ( <i>Lafresnaya lafresnayi</i> )	1	N	U	F	2	L	F	F	4.50	1.58	×	1.33	×	×
Great Saphfirewing ( <i>Pterophanes cyanopterus</i> )	2	N	U/M	D	2	S	R	F						×
Rainbow Starfrontlet ( <i>Coeligena iris</i> )	1	N	U/M	F	4	L	F	F	3.50	4.11		2.25	3.33	×
Sword-billed Hummingbird ( <i>Ensifera ensifera</i> )	2	N	U/C	F	2	L	R	U						×
Purple-throated Sunangel ( <i>Helianthus viola</i> )	1	N	U/M	F	2	L	U	F	2.00	0.63	×	0.75	1.33	×
Sapphire-vented Puffleg ( <i>Eriocnemis luciani</i> )	1	N	U/M	F	2	L	F	F	1.50	2.22	×	0.75	0.33	×
Black-tailed Trainbearer ( <i>Lesbia victoriae</i> )	1	N	U/C	N	3	L	U	F	0.50		×			×
Green-tailed Trainbearer ( <i>Lesbia nuna</i> )	1	N	U/C	N	4	L	R	F					×	
Purple-backed Thornbill ( <i>Rhamphomicron microhynchum</i> )	1	N	M/C	F	2	L	R	U			×			×

(continued)

TABLE 1. Continued.

Species	Body-size class <sup>a</sup>	Diet <sup>b</sup>	Foraging stratum <sup>c</sup>	Primary habitat <sup>d</sup>	Habitat breadth <sup>e</sup>	Range size <sup>f</sup>	Rarity		Captures						Counts			
									Bosque introducido		Bosque altoandino		Bosque introducido		Bosque altoandino			
							Local abundance <sup>g</sup>	Neotropical abundance <sup>h</sup>	1994–95	2006–07	1994–95	2006–07	1994–95	2006–07	1994–95	2006–07		
Tyrian Metaltail ( <i>Metallura tyrianthina</i> )	1	N	U/M	D	3	L	C	C	4.00	6.01	2.00	2.00	×	×	×	×	×	
White-bellied Woodstar ( <i>Chaetocercus mulsant</i> )	1	N	U/C	E	2	L	R	F							×			
Masked Trogon ( <i>Trogon personatus</i> )	4	F	M	F	1	L	U	F					×	×	×			
Gray-breasted Mountain-Toucan ( <i>Andigena hypoglauca</i> )	4	I	C	F	1	L	U	U						×	×			
Crimson-mantled Woodpecker ( <i>Piculus rivolii</i> )	4	I	M/C	F	2	L	U	U					×	×	×			
Bar-bellied Woodpecker ( <i>Veniliornis nigriceps</i> )	4	I	M/C	F	2	L	R	F	0.50							×		
Bar-winged Cincloides ( <i>Cincloides fuscus</i> )	3	I	T	P	4	L	C	C							×			
Azara's Spinetail ( <i>Synallaxis azarae</i> )	3	I	U	E	2	L	C	C	4.00	1.90	2.50	1.00	×	×	×	×	×	
White-browed Spinetail ( <i>Helmayrea gularis</i> )	2	I	U	F	2	L	U	U			2.25		×		×			
Line-cheeked Spinetail ( <i>Craniolaeca antisiensis</i> )	3	I	M/C	F	1	L	U	F	0.50	0.63			×	×				
Streaked Tuftedcheek ( <i>Pseudocolaptes boissonneautii</i> )	4	I	M/C	F	2	L	U	F							×			
Pearled Treerunner ( <i>Margarornis squamiger</i> )	3	I	M	F	2	L	F	C	0.50		0.75				×			
Flammulated Treehunter ( <i>Thripadectes flammulatus</i> )	4	I	U	F	2	L	R	U				0.33	×	×	×	×	×	
Undulated Antpitta ( <i>Grallaria squamigera</i> )	4	I	T	F	2	L	U	U					×		×		×	
Chestnut-crowned Antpitta ( <i>Grallaria ruficapilla</i> )	4	I	T	E	2	L	U	C				0.33	×		×			
Rufous Antpitta ( <i>Grallaria rufula</i> )	4	I	T	F	2	L	F	C	1.00		1.00	1.33	×	×	×	×	×	
Unicolored Tapaculo ( <i>Scytalopus unicolor</i> )	3	I	U	F	1	L	C	C	0.50	0.32	0.25	0.33	×	×	×	×	×	
Tawny-rumped Tyrannulet ( <i>Phyllomyias uropygialis</i> )	2	I	C	F	3	L	U	U			0.50	0.33	×			×		
White-crested Elaenia ( <i>Elaenia albiceps</i> )	3	O	C	E	4	L	R	C	1.50				×		×		×	

White-banded Tyrannulet ( <i>Mecocerculus stictopterus</i> )	2	I	C	F	1	L	F	C	0.50			X	X
Tufted Tit-tyrant ( <i>Anairetes parulus</i> )	1	I	U/C	N	4	L	R	C	0.32	0.50	X		
Cinnamon Flycatcher ( <i>Pyrrhomyias cinnamomea</i> )	1	I	C	F	2	L	U	C	0.50		X		
Crowned Chat-tyrant ( <i>Ochthoeca frontalis</i> )	2	I	U	F	2	L	U	F	1.00	1.00		X	X
Rufous-breasted Chat-tyrant ( <i>Ochthoeca rufipectoralis</i> )	3	I	U/C	D	4	L	R	C	0.25		X		
Slaty-backed Chat-Tyrant ( <i>Ochthoeca cinnamomeiventris</i> )	2	I	U/M	F	2	L	U	F	0.63		X	X	
Streak-throated Bush-Tyrant ( <i>Myiotheretes striaticollis</i> )	2	I	C	E	4	L	R	F			X		
Smoky Bush-Tyrant ( <i>Myiotheretes fumigatus</i> )	2	I	C	F	1	L	R	U				X	
Red-crested Cotinga ( <i>Ampelion rubrocristatus</i> )	4	O	C	D	3	L	U	C	0.25		X		
Turquoise Jay ( <i>Cyanolyca tucosa</i> )	4	O	C	F	2	L	F	C	0.32		X	X	
Great Thrush ( <i>Turdus fuscater</i> )	4	O	T/C	F	5	L	C	C	1.00		X	X	X
White-capped Dipper ( <i>Cinclus leucocephalus</i> )	4	I	T	A	2	L	U	F			X		
Grass Wren ( <i>Cistothorus platensis</i> )	2	I	U	P	5	L	U	F	0.25		X		
Mountain Wren ( <i>Troglodytes solstitialis</i> )	2	I	M	F	2	L	U	F	1.00		X	X	
Spectacled Whitestart ( <i>Myioborus melanocephalus</i> )	2	O	M/C	F	2	L	C	C	2.50	0.63	1.00	0.33	X
Black-crested Warbler ( <i>Basileuterus nigrocristatus</i> )	2	I	U/M	E	4	L	F	C	1.50	0.95	1.00		X
Russet-crowned Warbler ( <i>Basileuterus coronatus</i> )	2	I	U	F	2	L	C	C	3.50	0.63	1.25	3.33	X
Cinereous Conebill ( <i>Conirostrum cinereum</i> )	2	I	U/C	N	4	L	U	C	0.50		X		
Blue-backed Conebill ( <i>Conirostrum sitticolor</i> )	2	I	C	D	2	L	U	F			X		
Masked Flowerpiercer ( <i>Diglossa cyanea</i> )	2	O	C	F	2	L	F	C	3.50	1.27	1.00	1.67	X
Black Flowerpiercer ( <i>Diglossa humeralis</i> )	2	O	U/C	N	4	L	F	F	2.50	1.90	2.50		X
Rufous-chested Tanager ( <i>Thlypopsis ornata</i> )	2	I	U/C	N	3	L	U	F	4.50		1.00	0.67	X
Blue-and-black Tanager ( <i>Tangara vassorii</i> )	3	O	C	F	3	L	F	F	2.00		1.00	0.33	X

(continued)



TABLE 1. Continued.

Species	Body-size class <sup>a</sup>	Diet <sup>b</sup>	Foraging stratum <sup>c</sup>	Primary habitat <sup>d</sup>	Habitat breadth <sup>e</sup>	Range size <sup>f</sup>	Rarity		Captures						Counts			
							Local abundance <sup>g</sup>	Neotropical abundance <sup>h</sup>	Bosque introducido	Bosque altoandino	Bosque introducido	Bosque altoandino	Bosque introducido	Bosque altoandino				
Scarlet-bellied Mountain Tanager ( <i>Anisognathus igniventris</i> )	4	O	U/C	F	3	L	F	C	2.00	0.63	0.50	0.33	×	×	×	×	×	
Black-chested Mountain Tanager ( <i>Buthraupis eximia</i> )	4	O	C	D	1	L	R	U								×		
Buff-breasted Mountain Tanager ( <i>Dubusia taeniata</i> )	4	O	U/M	D	2	L	R	U	1.00	0.63	0.25		×	×	×			
Superciliated Hemispingus ( <i>Hemispingus superciliaris</i> )	3	I	C	F	3	L	F	F	1.50		0.25	1.00	×	×	×	×	×	
Black-headed Hemispingus ( <i>Hemispingus verticalis</i> )	2	I	C	D	2	L	R	F			1.75					×		
Plushcap ( <i>Catamblyrhynchus diadema</i> )	3	G	U	D	2	L	R	F			0.25					×		
Golden-bellied Grosbeak ( <i>Pheucticus chrysogaster</i> )	3	O	C	E	4	L	F	F					×			×		
Páramo Seedeater ( <i>Catamenia homochroa</i> )	2	G	T/U	N	4	L	R	U				0.33						
Plain-colored Seedeater ( <i>Catamenia inornata</i> )	2	G	T/U	N	5	L	C	F			0.25		×		×			
Band-tailed Seedeater ( <i>Catamenia analis</i> )	2	G	T/U	N	3	L	R	C								×		
Plumbeous Sierra-Finch ( <i>Phrygilus unicolor</i> )	2	G	T	P	3	L	C	F					×					
Rufous-naped Brush Finch ( <i>Atlappetes latinuchus</i> )	4	O	U	E	3	L	F	C	2.50	1.58	1.00		×	×	×	×	×	
Stripe-headed Brush Finch ( <i>Buarremon torquatus</i> )	4	O	T/U	F	2	L	U	F	1.50	0.63	0.50	0.67	×	×	×	×		
Rufous-collared Sparrow ( <i>Zonotrichia capensis</i> )	3	G	T/U	N	7	L	C	C							×	×		
Yellow-bellied Cacique ( <i>Amblycercus holosericeus</i> )	4	I	U	F	3	L	R	F		0.95	0.25					×		
Hooded Siskin ( <i>Carduelis magellanica</i> )	2	G	C	N	5	L	F	C					×			×		

<sup>a</sup>1, 3–9 g; 2, 10–15 g; 3, 16–21 g; 4, >22 g.<sup>b</sup>C, carnivore; F, frugivore; G, granivore; I, insectivore; N, nectarivore; O, omnivore (after Ridgely and Greenfield 2001 and pers. obs.).<sup>c</sup>C, canopy; M, mid-story; T, terrestrial; U, understory (from Stotz et al. 1996).<sup>d</sup>A, aquatic; D, elfin forest; E, forest edge; F, montane evergreen forest; N, montane scrub and secondary forest; P, páramo (from Stotz et al. 1996).<sup>e</sup>The degree of specialization of the species as represented by the number of habitats occupied (from Stotz et al. 1996).<sup>f</sup>S, <60 000 km<sup>2</sup>; L, >60 000 km<sup>2</sup> (from www.birdlife.org/datazone/index.html).<sup>g</sup>Across Cajas National Park: R, rare; U, unusual; F, fairly common; C, common (from Tinoco and Astudillo 2007).<sup>h</sup>Relative abundance across the neotropics: R, rare; U, unusual; F, fairly common; C, common (from Stotz et al. 1996).

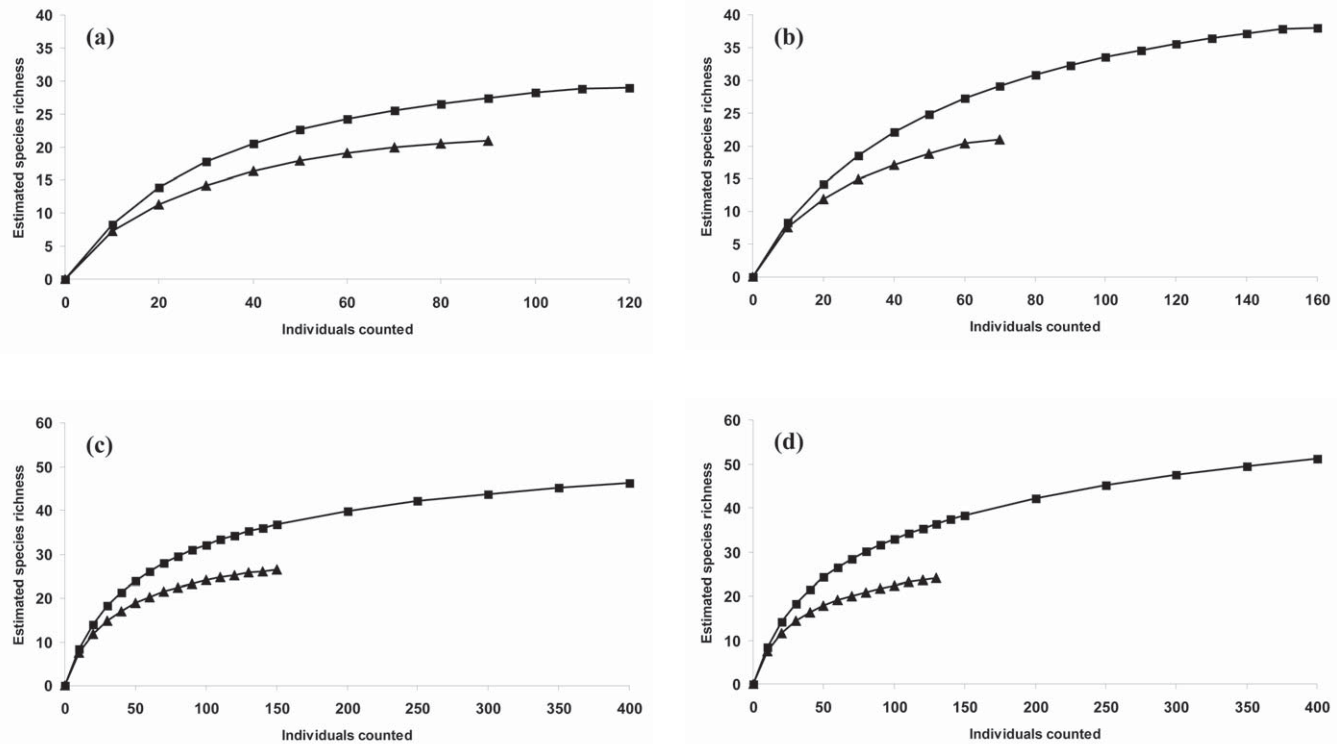


FIGURE 1. Species richness in 1994–95 (squares) and 2006–07 (triangles) estimated through (a) mist net captures in *bosque introducido*, (b) mist net captures in *bosque altoandino*, (c) audiovisual counts in *bosque introducido*, and (d) audiovisual counts in *bosque altoandino*. Analyses of Chao 1 indicators of diversity indicate that all paired comparisons are statistically significant with the exception of (b).

two habitats ( $P = 0.008$ ). Mist nets revealed that *bosque introducido* was dominated by nectarivores (51.1% of captures), while the *bosque altoandino* was dominated by insectivores (44.6% of captures). Mist-netting results (but not audiovisual surveys) also suggested that species captured in *bosque introducido* and *bosque altoandino* differed significantly in habitat preference ( $G_3 = 12.465$ ,  $P = 0.006$ ). Birds captured in the *bosque altoandino* were overwhelmingly (80.0%) species whose preferred habitat was montane evergreen forest, while

*bosque introducido* was occupied by species with a wider diversity of habitat preferences, including not only montane evergreen forest (53.3% of individuals), but also forest edge (15.6%), montane scrub and secondary forest (7.8%), and even higher-elevation habitats (23.3%). Results of audiovisual surveys suggested that the habitat breadth or degree of specialization of the species in *bosque introducido* and *bosque altoandino* differed significantly ( $G_4 = 11.699$ ,  $P = 0.020$ ). Birds recorded in the *bosque introducido* tended to be species

TABLE 2. Measures of species richness and diversity from mist net-captures and audiovisual counts in *bosque introducido* and *bosque altoandino* of southern Ecuador, 1994–95 and 2006–07.

	Species richness	Evenness	Chao 1 estimator	SD	95% CI	Shannon index	Effective number
Nets							
<i>Introducido</i> 1994–95	29	0.93	35.1	4.96	25.4–44.8	3.14	23.1
<i>Introducido</i> 2006–07	21	0.88	21.6	0.84	20.0–23.2	2.68	14.6
<i>Altoandino</i> 1994–95	38	0.90	45.1	4.91	35.5–54.7	3.28	26.6
<i>Altoandino</i> 2006–07	21	0.90	41.3	13.99	13.8–68.7	2.73	15.3
Counts							
<i>Introducido</i> 1994–95	51	0.86	52.0	1.23	49.6–54.4	3.72	41.3
<i>Introducido</i> 2006–07	27	0.87	28.6	1.84	25.0–32.2	2.87	17.6
<i>Altoandino</i> 1994–95	67	0.83	75.0	6.02	63.2–86.8	3.47	32.1
<i>Altoandino</i> 2006–07	24	0.88	32.2	6.52	19.4–45.0	2.78	16.1

TABLE 3. Rank of the most common species (capture rate expressed as birds per 100 mist-net hr) in *bosque introducido* and *bosque altoandino* in 1994–95 and 2006–07 in the Mazán Reserve of the southern Ecuadorian Andes.

English name	<i>Introducido</i>		<i>Altoandino</i>	
	1994–95	2006–07	1994–95	2006–07
Mountain Velvetbreast	1 (4.5)	6 (1.58)	1 (5.5)	5 (1.33)
Rainbow Starfrontlet	5 (3.5)	2 (4.11)	4 (2.3)	1 (3.33)
Purple-throated Sunangel				5 (1.33)
Sapphire-vented Puffleg		3 (2.22)		
Tyrian Metaltail	3 (4.0)	1 (6.01)	6 (2.0)	3 (2.00)
Azara's Spinetail	3 (4.0)	4 (1.90)	2 (2.5)	
White-browed Spinetail			5 (2.2)	
Rufous Antpitta				5 (1.33)
Russet-crowned Warbler	5 (3.5)			1 (3.33)
Masked Flowerpiercer	5 (3.5)			4 (1.67)
Black Flowerpiercer		4 (1.90)	2 (2.5)	
Rufous-chested Tanager	1 (4.5)			
Black-headed Hemispingus			7 (1.8)	
Rufous-naped Brush Finch		6 (1.58)		

typically occurring in a greater variety of habitats than those recorded in the *bosque altoandino*. Patterns of mist-netting results were similar but the difference was not quite significant (Fisher's exact test,  $P = 0.075$ ). We found no significant differences between habitats in terms of proportion of birds in each body-mass class, foraging stratum, category of abundance estimates for the entire Cajas National Park region, or category of abundance across the neotropics (all  $P > 0.05$ ). Combining presence/absence data from both sampling periods, we found that the number of locally rare species was higher in *bosque altoandino* than in *bosque introducido*, but this difference was not quite significant (Fisher's exact test,  $P = 0.104$ ). The pattern for the occurrence of regionally uncommon species was similar (Fisher's exact test,  $P = 0.093$ ).

#### CHANGES IN PATTERNS OF DISTRIBUTION SINCE 1994–95

We compared our bird detections (presence/absence) and capture rates to those we derived from Toral (1996) to assess changes in abundance and distribution patterns over 12 years. Both methods of detection combined, the number of species recorded was 54 in *bosque introducido* (compared to 31 in 2006–07) and 67 in *bosque altoandino* (compared to 30 in 2006–07). In *bosque introducido*, the rate of capture in 2006–07 (28.5 birds per 100 mist-net hr) was lower and only half that of 1994–95 (56.0 birds per 100 mist-net hr), and this difference was significant ( $H_{adj} = 3.84$ ,  $df = 1$ ,  $P = 0.050$ ). Capture rates in *bosque altoandino* in 2006–07 (22.4 birds per 100 mist-net hr) were also significantly lower than in 1994–95, when 38.0 birds were captured per 100 mist net hr ( $H_{adj} = 3.96$ ,  $df = 1$ ,  $P = 0.046$ ).

Our rarefaction curves suggested that species richness in both the *bosque introducido* and the *bosque altoandino* was

lower in the more recent sampling period than in the earlier period (Fig. 1), and this held true for both mist-netting and audiovisual counting techniques. Results from the Chao 1 estimators of richness ( $\pm 95\%$  confidence interval) largely support the observation of significant changes in bird communities over time (Table 2, Fig. 2). Results from mist-net captures supported the observed pattern in the *bosque introducido*: estimated richness in the later period (21.6) was significantly lower than in the earlier period ( $35.1 \pm 9.73$ ), but estimated richness in the *bosque altoandino* in the later period (41.3) was not significantly lower than in the earlier period ( $45.1 \pm 9.62$ ). Among birds recorded by audiovisual methods, estimated richness in

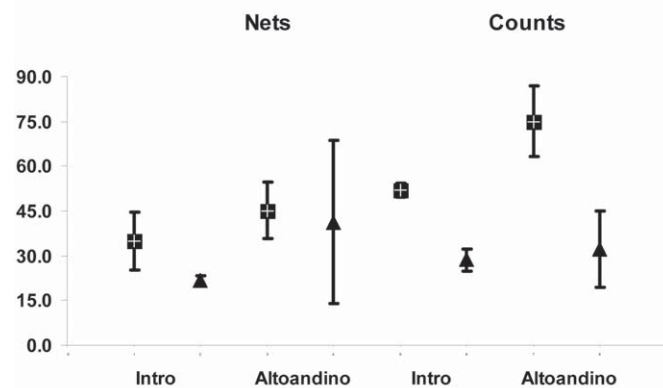


FIGURE 2. Chao 1 indicators of diversity ( $\pm 95\%$  confidence intervals) for bird species captured in mist nets or recorded on point counts in *bosque introducido* (Intro) and *bosque altoandino* (Altoandino) in 1994–95 (squares) and 2006–07 (triangles). Analyses of Chao 1 indicators of diversity indicate that all paired comparisons are statistically significant with the exception of mist net captures in *bosque altoandino*.

the *bosque introducido* in the later period (28.6) was significantly lower than in the earlier period ( $52.0 \pm 2.40$ ). Similarly, estimated richness in the *bosque altoandino* in the later period (32.2) was also significantly lower than earlier ( $75.0 \pm 11.8$ ).

Changes in avian communities were also suggested by analysis of Shannon diversity indices and the effective number of species (Table 2). We found significant differences in diversity indices based on mist-net captures from 1994–95 and 2006–07 in *bosque introducido* ( $t_{151} = 4.56$ ,  $P < 0.001$ ) and *bosque altoandino* ( $t_{110} = 5.09$ ,  $P < 0.001$ ), as well as in diversity indices based on audiovisual counts in *bosque introducido* ( $t_{82} = 15.84$ ,  $P < 0.001$ ) and *bosque altoandino* ( $t_{153} = 9.41$ ,  $P < 0.001$ ). By converting the diversity to the “effective number of species” (Jost 2006), we determined the magnitude of the difference between these paired groups of interest. In all cases the fractional drop in diversity was  $>35\%$  and was most often close to 50%. Mist-net captures indicated a 36.7% drop in *bosque introducido* from 1994–95 to 2006–07 and a 42.5% drop in *bosque altoandino*. Audiovisual counts indicated a 57.4% drop in *bosque introducido* over this same period and a 49.8% drop in *bosque altoandino*.

This decline in numbers of species and capture rates was also reflected in low indices of similarity between new and old data sets. Similarity indices based on presence/absence in *bosque introducido* showed only 48.3% of species occurred in both the earlier and later sampling periods, while in the *bosque altoandino* only 41.0% of species occurred in both the earlier and later periods.

We attempted to identify where in the community these changes took place by comparing characteristics of species apparently extirpated since 1994–95 with those of species that persisted (or were extant) in each habitat. We analyzed patterns of distribution of trophic groups under the hypothesis that certain trophic groups may be more susceptible to habitat change and may be declining more rapidly at our study sites. In *bosque introducido* the number of species in each diet category of apparently extirpated species did not differ from that in each diet category of extant species (exact test,  $P = 0.425$ ). We also found no significant difference between the apparently extirpated and extant species in the proportion of birds in each mass class ( $G_3 = 6.332$ ,  $P = 0.100$ ), foraging stratum ( $G_2 = 2.051$ ,  $P = 0.359$ ), primary habitat preference (exact test,  $P = 0.349$ ), degree of specialization of the species as represented by the number of habitats occupied (exact test,  $P = 0.739$ ), or range size of the species (exact test,  $P = 0.492$ ). We did, however, find a significant difference between apparently extirpated and extant species in their estimated abundance in the Cajas National Park region (exact test,  $P = 0.007$ ). This difference was driven by a pattern of species apparently extirpated from Mazán being significantly more often rare or unusual in the region (exact test,  $P = 0.001$ ) and extant species being significantly more often fairly common or common in the region (exact test,  $P = 0.001$ ). In addition, we found a nearly

significant difference between apparently extirpated and extant species in their relative abundance across the Neotropical Region (exact test,  $P = 0.079$ ), with apparently extirpated species again being scarcer regionally and extant species being more common across the Neotropical Region.

In *bosque altoandino* the number of species in each diet category of apparently extirpated and extant species did not differ (exact test,  $P = 0.271$ ), and we found no significant difference between apparently extirpated and extant species in terms of the proportion of birds in each mass class ( $G_3 = 0.834$ ,  $P = 0.841$ ), foraging stratum ( $G_2 = 3.810$ ,  $P = 0.149$ ), degree of specialization of the species as represented by the number of habitats occupied (exact test,  $P = 0.445$ ), or range size of the species (exact test,  $P = 0.571$ ). We did, however, find a significant difference between apparently extirpated and extant species in their primary habitat preference (exact test,  $P = 0.008$ ). This difference was driven by a pattern of species apparently extirpated from Mazán being significantly more often associated with high-elevation elfin forests and páramo (exact test,  $P = 0.017$ ) as their preferred habitat and extant species being significantly more often associated with montane evergreen forest (exact test,  $P = 0.007$ ). We also found a significant difference between apparently extirpated and extant species in their estimated abundance in the Cajas National Park region ( $G_3 = 14.281$ ,  $P = 0.002$ ), with apparently extirpated species more often being rare in the region (exact test,  $P = 0.004$ ) and extant species being regionally fairly common or common (exact test,  $P = 0.001$ ). But there was no significant difference between apparently extirpated and extant species in their relative abundance across the Neotropical Region (exact test,  $P = 0.340$ ).

In addition to identifying characteristics of apparently extirpated species, we analyzed patterns of occurrence of common species to determine changes in their abundances from 1994–95 to 2006–07. We compared rates of capture of all of the most common birds in *bosque introducido* and *bosque altoandino* in each period (Table 3). Only the Rufous-chested Tanager (see Table 1 for all scientific names) had declined significantly ( $H_{\text{adj}} = 6.67$ ,  $df = 1$ ,  $P = 0.0098$ ), falling from one of the most abundant species in 1994–95 to one never recorded in the *bosque introducido* in 2006–07. No other common species underwent a statistically significant decline (all  $P > 0.05$ ). Similar comparisons between sampling periods on the basis of count data were not possible because of differing methods.

The addition of species to an avifauna could also indicate habitat change. In 2006–07 we captured four species in *bosque introducido* and three species in *bosque altoandino* that were not captured in 1994–95 (Table 1). However, transect surveys indicated that four of these seven species were present in the earlier period. Only the Slaty-backed Chat-Tyrant and Yellow-bellied Cacique appear as new additions to *bosque introducido*, the Paramo Seedeater to *bosque altoandino*, but in each case the numbers captured were very low.



## DISCUSSION

### PATTERNS OF DISTRIBUTION BY HABITAT

High Andean forests provide critical habitat for numerous species of birds, but native forests and forests dominated by introduced trees support distinctly different avian communities. *Bosque introducido* tended to have more species and more individuals than *bosque altoandino*, but there was substantial variation in census numbers within the habitat, and this difference was not significant. Nevertheless, the relatively high diversity of the *bosque introducido* was surprising; we suggest that some of this diversity is due to the location of *bosque introducido* next to the *bosque altoandino* with both located in a closed valley. This juxtaposition of habitats in the landscape may have facilitated short-term movements of birds between habitats. We predict that if we sampled an isolated *bosque introducido* we would find substantially lower diversity and abundance of birds, but no censuses in isolated disturbed forest in the region were available to test this prediction.

Evenness was similarly high in both habitats and by both census methods (Table 2), indicating that no one species or small group of species dominates the avian community. In fact, we found that a variety of hummingbirds, warblers, and flowerpiercers were all common in our net captures and counts (Tables 1 and 3). Nevertheless, each habitat was distinct and supported a unique avifauna that shared <50% of its species. Nectarivores made up >50% of the individuals in *bosque introducido*, while *bosque altoandino* was dominated by insectivores. Birds occurring in the *bosque altoandino* were also species that preferred this type of montane evergreen forest, while birds recorded in the *bosque introducido* were more generalists with a wider diversity of habitat preferences. Not surprisingly then, locally rare and regionally uncommon species were more frequently found in the *bosque altoandino*.

### CHANGES IN PATTERNS OF DISTRIBUTION SINCE 1994–95

We found marked declines in the number of species and individuals, and we found statistically significant declines in species richness, as suggested by Chao 1 indicators for mist-net captures and count detections in *bosque introducido* and for count detections in *bosque altoandino* (Table 2). Only mist-net captures in the *bosque altoandino* did not indicate a significant decline in species richness, although here too the trend was toward fewer species. While this result obscures somewhat conclusions regarding temporal change in bird communities in the *bosque altoandino*, it should also be noted that far more individuals and more species are recorded through audiovisual sampling, lending weight to the decrease in richness suggested by audiovisual counts in *bosque altoandino*.

This pattern of comprehensive decline is surprising given the relatively short ~12-year interval between sampling. For mist-net captures, decline of birds can not be attributed to

differing effort or undersampling in either period. As previously described, mist-net sampling was more intensive in the later period, so estimated declines in the number of species and individuals should be conservative. Although effort invested in transect surveys and point counts is not so directly comparable because of the different methods, the rarefaction curves' approach toward their asymptotes suggests nearly complete sampling of the habitat, and with the noted exception of net captures in *bosque altoandino* the Chao 1 estimators indicate that species richness differed significantly. These curves provide no indication that we are missing nearly half of the species that were present in the 1994–95 samples. The patterns we uncovered are common to both mist-net and count data, further suggesting that our sampling regimes were adequate. Nevertheless, it should be noted that differences in survey effort may affect estimates of species richness and their confidence intervals to a certain degree (Gotelli and Colwell 2001, Herzog et al. 2005), and inflation of the observed decline in species richness is a possibility.

Several potentially interacting factors might have caused observed changes in bird communities, including changes in vegetation within the Mazán Reserve, changes in vegetation outside the reserve, and other environmental changes such as global warming. Without additional information we can not definitively state which factor, or combination of factors, is responsible for the observed changes, but we can evaluate which factors might be particularly important and use this evaluation to guide future research.

There are several lines of evidence suggesting that the declines we observed are only minimally influenced by changes in habitat structure and composition within the reserve over the past 12 years. First, the Mazán Reserve has been tightly controlled by Cajas National Park authorities, by a guard posted at the entrance gate and by regular patrols. Because the reserve is located in a deep valley, access is also restricted by the nature of the terrain. We have seen no evidence of extraction of trees or other disturbances by humans other than occasional light grazing by a few head (<6 total) of horses and cattle. Habitat change by natural succession within the reserve could also be a factor in changes in bird populations. Although vegetation surveys to quantify our observations are lacking, we believe that succession was minimal because our sites were not located in early-successional habitats but rather in well-established *bosque altoandino* and *bosque introducido*. In each habitat, transects avoided edges, but the previously mentioned small (<5 ha) patch of grassland succeeding to shrubs lay between our study sites and may have affected birds recorded in the adjoining habitats. A number of grassland species appear to have been extirpated from the sampled sites, including the Grass Wren, Plain-colored and Band-tailed seedeaters, Plumbeous Sierra-Finch, and Hooded Siskin, and these may have responded to the conversion of the grasslands to shrubs. However, even if this was a factor in community



change, generalized successional change can not explain the majority of the observed differences. If successional changes were driving the observed changes in bird abundance and distribution, then we should see specific patterns of declines among particular trophic groups or species with specific habitat preferences. For example, natural succession might be expected to eliminate habitat for species partial to scrub habitats as growth of trees eliminates their habitat. Similarly, birds of the mid-story and canopy might be expected to benefit from natural successional change. However, such patterns were not realized. Rather, we recorded widespread declines in a variety of species, with regional rarity being their common denominator.

The observed pattern of decline of birds in both *bosque introducido* and *bosque altoandino*, characterized by the decline and loss of species rare and uncommon at the regional level, is more likely a result of changes in habitat outside of the Mazán Reserve. In both habitat types in Mazán we found a significant difference between apparently extirpated and extant species in their estimated regional abundance, with species apparently extirpated from Mazán more often considered regionally rare and extant species considered regionally fairly common or common. We found a similar pattern relating status in Mazán's *bosque introducido* (but not in *bosque altoandino*) to abundance across the neotropics. For the great majority of species common in both *bosque introducido* and *bosque altoandino*, we recorded no decline, but the large number of individuals of less common species that we failed to find in either habitat points to systematic changes in abundance across the broader region. This interpretation of regional factors affecting local abundance of birds is supported by studies of land use in Azuay Province (which includes Cajas National Park) and adjoining Cañar Province. Rodas (2001) used LANDSAT imagery to quantify changes in vegetative cover in the western Andes of Azuay and Cañar from 1991 to 2000 and to relate these changes to human activities. He found an annual rate of deforestation of 4.0%, amounting to a 34% decline in total forest cover across the study area over the 9 years. He found that the decline in *bosque altoandino* was caused principally by burning of forest edges to expand grasslands at lower elevations.

Land-use change may also influence these high-elevation species because many species that prefer elfin forest, *páramo*, and *Polylepis* are not limited to a single preferred habitat but rather may be found in a suite of often adjoining habitats (Table 1). *Páramo*-associated birds that respond negatively to the burning of grasslands are common in both the *páramo* itself and the forest edges in *bosque altoandino* (Koenen and Koenen 2000). In addition, *páramo* birds in Cajas National Park may be negatively affected by aggressive efforts to reduce and eliminate introduced grazing livestock. García et al. (2008) have shown that when livestock are excluded from montane Andean habitats adapted to extirpated large native

herbivores, bird density and richness decrease. Thus, just as for species common in *bosque altoandino*, these regional effects might also influence *páramo* species.

Finally, global climate change must be considered as a possibility to explain differences between bird communities in 1994–95 and 2006–07. We found a pattern of species apparently extirpated from Mazán significantly more often being those whose preferred habitat is high-elevation elfin forests and *páramo* and extant species being those whose preferred habitat is lower-elevation montane cloud forest. The result that species preferring higher-elevation habitats declined more than lower-elevation species is consistent with the possibility that species may be moving up in elevation as a result of climate change or may be perishing as habitats dry with increased temperatures (Foster 2001, Barnett et al. 2005, Hannah et al. 2007, Sekercioglu et al. 2008, Graham et al. 2011). Range shifts associated with global warming have been documented among birds in Europe and North America (e.g., Root et al. 2003, La Sorte and Thompson 2007, Tingley et al. 2009) and among various taxonomic groups in tropical mountains (Epstein et al. 1998, Pounds et al. 2009, Chen et al. 2009). However, virtually nothing beyond modeled predictions is known about how climate change might be affecting Andean birds. Our results suggest climate change might be one possible explanation of observed changes in species' abundances in Mazán through time, but additional regionwide monitoring is necessary to confirm such changes.

#### CONSERVATION IMPLICATIONS

Our results support the predictions of Brooks et al. (1999) and Wiegand et al. (2005) that continued destruction of forest habitats in the Andes should lead to further fragmentation of bird populations and to local extinctions. Studies at Mazán show that extirpations are apparently taking place in high Andean forests, even in those forests, like Mazán, that are apparently healthy and where human access is highly restricted. But even the strict management of forest reserves like Mazán may not be able to prevent habitat changes on a larger, regional scale from reducing avian diversity and richness in remaining forest fragments. Furthermore, these high-elevation habitats might be particularly susceptible to climate changes. Given the apparent rapid decline in some species in Mazán, it is urgent that we study the declining species in detail to evaluate what might be causing changes in abundance patterns and that we monitor additional sites over longer periods to obtain more robust data sets.

Beyond its direct relevance to bird populations and their conservation in the high Andes, this study has important broader relevance to management of national parks and reserves. Our finding that regional factors may be contributing to local declines in bird populations augments a growing understanding that protected areas are parts of "greater ecosystems" and can not be managed in a vacuum (Keiter and Boyce

1991, Liu and Taylor 2002, Schneider et al. 2002). Although burning to promote forage for the benefit of grazing cattle is an “ancient tradition” (White and Maldonado 1991), the apparent increase in the intensity of burning and the concomitant changes in montane cloud forests and *páramo* grasslands (Rodas 2001) likely have had a negative effect on bird populations in the region. As land-use change reduces habitat in the unprotected portion of the ecosystem, ecosystem function and biodiversity within the protected area may be degraded. Recognizing that protected areas are parts of greater ecosystems helps to clarify the effects of agriculture, human settlements, and other land uses in the unprotected part of the ecosystem. Future work in these habitats should include long-term monitoring to test observed population trends and demographic studies across multiple habitats to clarify spatial aspects of ecological interactions between protected areas and the surrounding habitat matrix.

#### ACKNOWLEDGMENTS

We acknowledge the assistance of Danilo Mejía, Ramiro Carpio, and many volunteers from Escuela de Biología, Ecología y Gestión, Universidad del Azuay, who helped to record field data. We thank J. Faaborg, J. M. Wunderle Jr., and two anonymous reviewers for comments on an earlier draft of this paper. Anne Chao generously commented on analytical methods. Logistical support was provided by Paul Vintimilla, Francisco Sanchez, and Franklin Bucheli from Parque Nacional Cajas and by Gustavo Chacón from Universidad del Azuay. Funding was provided by Stony Brook University, National Aviary (USA), Cajas National Park, and PRBO Conservation Science.

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