
Spatial Components of Bird Diversity in the Andes of Colombia: Implications for Designing a Regional Reserve System

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Abstract: *Beta diversity, or the turnover in species composition among sampling sites in a region, is an important criterion for obtaining adequate representation of regional biodiversity in systems of protected areas. Recently, the additive model for partitioning regional (gamma) diversity (in opposition to the multiplicative model) has been proposed because it allows a direct measure of the contribution of beta diversity to gamma diversity. We determined avian beta diversity along latitudinal (among neighboring river drainages) and elevational axes in a 1347-km² region on the western slope of the Central Cordillera of the Colombian Andes, where a regional system of protected areas is being designed. We then compared avian beta diversity between sites based on rapid versus long-term (>1 year) inventories and between fragmented sites versus continuous forest. Overall, beta diversity represented 63.1% of gamma diversity among 16 sites. Elevational differences in species composition accounted for 43.3% of regional diversity, whereas differences among drainages accounted for 19.8%. A complementary cluster analysis showed that sites grouped by elevational zones. Rapid inventories overestimated beta diversity because of sampling effects, but the effect was biologically small. Estimators of species richness derived from species accumulation curves provided a useful alternative to compensate for undersampling in short-term surveys. Forest fragmentation increased beta diversity because of differential local extinction of populations. Nevertheless, in our region, forest fragments contributed to gamma diversity because they contained complementary sets of species. More importantly, they contained populations of special-interest species. Although the region is relatively small, our analyses indicate that spatial differentiation of the biota is an important factor for deciding number and location of protected areas in the Andean region.*

Keywords: additive partition of diversity, beta diversity, conservation planning, protected-area design

Componentes Espaciales de la Diversidad de Aves en los Andes de Colombia: Implicaciones para el Diseño de un Sistema Regional de Reservas

Resumen: *La diversidad beta, o recambio en la composición de especies entre sitios de muestreo en una región, es un criterio importante para alcanzar una adecuada representación de la biodiversidad regional en sistemas de áreas protegidas. Recientemente, el modelo aditivo para la partición de la diversidad gama o diversidad regional (en oposición al modelo multiplicativo) ha sido promocionado pues permite una medida directa de la contribución de la diversidad beta a la diversidad gama. En este estudio determinamos la diversidad beta de aves a lo largo de ejes latitudinales (entre cuencas hidrográficas vecinas) y altitudinales en una región de 1347 km² en la vertiente occidental de la cordillera Central de los Andes de Colombia, donde se está construyendo un sistema regional de áreas protegidas. También comparamos la diversidad beta de aves entre sitios caracterizados con muestreos rápidos versus inventarios a largo plazo (>1 año) y entre sitios con bosques fragmentados versus bosques continuos. En total, la diversidad beta representó el 63.1% de la*

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diversidad gama encontrada entre 16 localidades. Las diferencias altitudinales en composición de especies representaron el 43.3% de la diversidad regional, mientras que las diferencias entre cuencas representaron el 19.8%. Un análisis de agrupamiento complementario también mostró la diferenciación de especies por elevaciones pues las localidades se agruparon por cinturones altitudinales. Los inventarios rápidos sobre-estimaron la diversidad beta debido al efecto de muestreo incompleto, pero el efecto fue biológicamente pequeño. Los estimadores de riqueza de especies derivados de las curvas de acumulación de especies proveyeron una alternativa útil para compensar el submuestreo en los inventarios rápidos. La fragmentación de bosques aumentó la diversidad beta debido a extinción local diferencial de poblaciones. Sin embargo, en nuestra región los fragmentos de bosque contribuyen a la diversidad gama porque contienen conjuntos complementarios de especies. Además, estos fragmentos contienen poblaciones de especies de interés especial. Aunque la región es relativamente pequeña, nuestros análisis indican que la diferenciación espacial de la biota es un factor importante a la hora de tomar decisiones sobre el número y la localización de áreas protegidas en la región andina.

Palabras Clave: diseño de áreas protegidas, diversidad beta, partición aditiva de la diversidad, planificación de la conservación

Introduction

An important parameter in conservation planning is beta diversity (i.e., the turnover in species composition that occurs among sampling sites within a region; Gering et al. 2003). One of the main criteria used to design regional systems of protected areas is representation of all the ecosystems, communities, and species found in a region (Groves 2003). If beta diversity is high—that is, there are large differences in species composition among sites within a region—then more reserves are required to represent this diversity in the system. In contrast, in a homogeneous region, a few reserves may suffice to represent beta diversity.

Beta diversity was originally defined as the turnover in species composition among samples taken along an environmental gradient or in different habitats in a landscape (Whittaker 1975; Schluter & Ricklefs 1993). Alpha diversity represents the diversity within each sample, and gamma diversity represents the total diversity found in the entire gradient or landscape. The concepts of alpha and beta diversity have also been equated to within-habitat and between-habitat diversities, respectively. The different components of diversity can be defined at different spatial scales. Thus, alpha diversity may be defined as within-habitat diversity in a heterogeneous landscape, beta diversity as between-habitat diversity, and gamma as the diversity of the entire landscape. At a larger spatial scale, alpha may be the diversity of an entire landscape within a region, with gamma representing the diversity of the region and beta representing the differentiation in species composition among landscapes.

There are two ways to relate these spatial components of diversity. The most commonly used relation in the ecological literature is the multiplicative model: $\alpha \times \beta = \gamma$. Numerous ways to calculate β have been proposed under the multiplicative model (Whittaker 1975; Schluter & Ricklefs 1993; Lande 1996; Veech et al. 2002). In these

models, α and γ are expressed in numbers of species and β is a dimensionless number (Schluter & Ricklefs 1993). A problem with these measures is that the different components of diversity are not directly comparable (Lande 1996; Veech et al. 2002).

The spatial components of diversity can also be related with an additive model: $\alpha + \beta = \gamma$. Although the additive partitioning model of diversity was introduced over 30 years ago (Veech et al. 2002), it has been used only recently to characterize patterns of diversity (Loreau 2000; Veech et al. 2002; Gering et al. 2003). An advantage of the additive model is that the different components have the same units. Under this model, α is defined as the mean diversity found in a set of samples and β diversity as the mean diversity not found in the samples (i.e., both measures represent averages that added together represent 100% of gamma diversity). This allows a direct comparison of the contribution of α and β to γ diversity. The additive partitioning of beta diversity can be applied to a range of spatial scales in a hierarchical fashion (Veech et al. 2002; Gering et al. 2003). Samples can be grouped at different spatial levels in a hierarchy (e.g., trees, stands, sites, regions), and beta diversity can be partitioned at different levels in the hierarchy (among trees, among stands, and so on). Alternatively, samples can be grouped according to different factors to explore the contribution of these factors to beta diversity. Samples can also be grouped by temporal units to explore temporal partitioning of diversity (DeVries et al. 1999).

In a conservation context, the additive model provides a simple way to characterize the heterogeneity of a region in terms of beta diversity (Gering et al. 2003). We characterized beta diversity of birds in a region on the western slope of the Central Cordillera of the Andes of Colombia, in the context of designing a regional system of protected areas (Kattan 2005). In addition to protecting overall diversity, an objective of the system is to represent populations of focal species that are of special conservation

concern. The region encompasses an elevational gradient from 980 m to more than 5000 m over 33 km, and several river drainages over a latitudinal extent of 0.62° (67.5 km). Thus, one objective was to determine the differentiation of avian faunas (beta diversity) along the latitudinal and elevational axes.

Decision making in this process has been hampered by poor knowledge of the region. We chose birds as a target group to evaluate beta diversity because they are the best-known taxon (birds may underestimate beta diversity for less vagile groups). Still, gaps in regional knowledge exist, so we conducted a series of rapid biological inventories at several sites to gather data on species composition. Therefore, a second objective of our study was to assess the effectiveness of these rapid inventories compared with sites that have been sampled for longer periods of time. For this we used two approaches. First, we compared beta diversity among sites with rapid surveys and with long-term surveys. Second, we used species-accumulation curves to estimate true species richness. Our study area is in the middle of one of the most economically productive regions of Colombia, which has resulted in extensive landscape transformation and forest fragmentation. Thus, our third objective was to assess the value of small forest fragments for the system of protected areas in terms of their contribution to beta diversity and content of populations of focal species.

Study Area and Methods

The central part of the western slope of the Central Cordillera of the Andes of Colombia is known as the *Eje Cafetero* (cities of Armenia, Pereira, and Manizales) or the main coffee-growing region of the country. Our study region was part of a larger region for which a system of protected areas is being designed (Kattan 2005), and is in itself part of the beta diversity of the Andean region of Colombia (Kattan et al. 2004). The main axis of the Central Andes runs in a general south-north direction, with rivers on the western slope draining in an east-west direction into the north-flowing Cauca River. These montane rivers form a series of transverse drainages separated by ridges, forming rib-like features along the Andean backbone. Our study region was framed by Río Quindío (Municipality of Salento) in the south and Río Blanco (Municipality of Manizales) in the north. The 16 study sites ranged latitudinally over six drainages (4.51° N to 5.13° N; Fig. 1).

Elevationally, the region ranges from the Cauca Valley, 900–1000 m, to several snow-capped volcanos, above 5000 m (75.32° to 75.71°W). Based on previous work (Kattan & Franco 2004), we defined five elevational zones: 900–1500 m, 1500–2200 m, 2200–2600 m, 2600–3200 m, and >3200 m. The lower limit of the uppermost

elevational zone represents the tree line, (i.e., the elevation at which Andean forest gives way to *páramo*, a high-elevation shrubland and grassland ecosystem). This upper zone is open ended because the upper limit of vegetation is variable; however, vegetation is sparse and few bird species are resident above 4000 m.

For each of the 16 sites (Fig. 1), we compiled a list of bird species, which we classified into forest-dwelling species and species of open habitats (pastures and croplands). Eight of these sites were surveyed by ourselves, and for the others we obtained data from published works. Eight of the sites were covered with continuous forest (several thousand hectares), and the other eight were fragmented landscapes, with forest patches of usually <100 ha. In all cases surveys were conducted in forest and adjacent open habitats (mostly pastures with variable levels of tree cover). For 10 sites, bird lists were obtained over a year or longer (long-term sites). Inventories for these sites have been obtained through a combination of methods, including transect sampling, mist nets, and opportunistic observations. Sampling effort varied among these sites, but because data were collected for long time periods, we assumed bird inventories were reasonably complete. For the other six sites, we conducted rapid, 20-day surveys (V.R. et al., unpublished data). In each survey, we operated 20 mist nets between 0500 and 1800 hours for 20 days. Simultaneously we made opportunistic observations throughout the study area in an attempt to record as many species as possible.

We calculated alpha diversity (species richness) as the mean number of species found in all 16 localities. Then we subtracted the number of species in each locality from the total species list (gamma diversity) and calculated beta diversity as the mean number of species not found in sites (Lande 1996; Veech et al. 2002). We used the program PARTITION to generate expected values of beta diversity according to a null model, under the hypothesis that the observed partition of diversity could be produced by random allocation of samples (Crist et al. 2003). We used a hierarchical model, with sites grouped by elevational zones. Thus, we obtained two levels of beta diversity: among sites within elevational zones (beta1) and among elevational zones (beta2). The *p* values generated by the program PARTITION are the number of null values that are greater than or equal to the observed value of beta diversity. Thus, with a two-tailed probability of 0.05, the observed component of diversity is significantly different from the null model if $p < 0.025$ (observed value is greater than expected) or $p > 0.975$ (observed value is smaller than the expected value).

We also evaluated differences in composition among localities by means of a dendrogram constructed from a presence-absence matrix based on a hierarchical cluster analysis. We used the centroid method and Jaccard's coefficient of similarity for grouping localities (SPSS statistical package). Because distances between branches in the

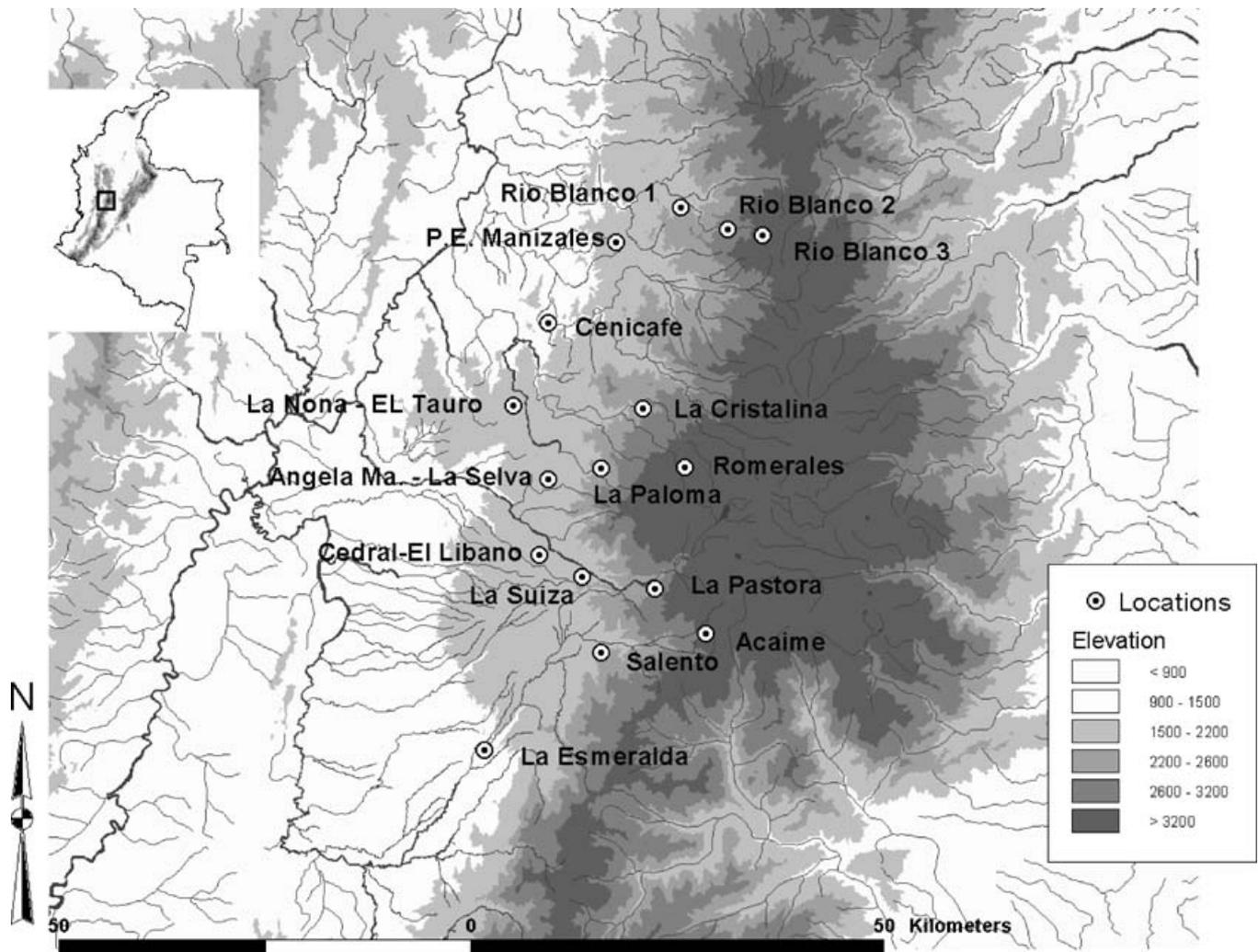


Figure 1. The study region on the western slope of the Central Range of the Colombian Andes, showing the sites included in this study.

dendrogram indicate how different the species composition of the samples is, the cluster analysis is a complementary method of evaluating beta diversity in the region.

To further decompose β along elevational and latitudinal axes, we calculated β separately for three drainages so that each had three or more localities at different elevations (with γ being the total species list for each drainage). Two of these three drainages had long-term species lists, and the other was characterized with rapid surveys. These analyses allowed us to explore the effects of rapid surveys on beta diversity. Because rapid surveys may fail to obtain complete species lists for a locality due to a sampling effect, beta diversity may be overestimated (Lande 1996). To evaluate the effectiveness of these surveys, we used six localities within the 1500- to 2200-m elevational belt. Three of these localities had long-term lists and three had rapid surveys. Assuming that long-term assessment sites had complete species inventories, we tested the hypothesis that beta diversity was different between long-term

assessment sites and rapidly assessed sites with a binomial comparison of proportions (Zar 1999). For this test we constructed a 2×2 contingency table, with values of alpha and beta diversity in rows and rapid and long-term sites in columns. We tested forest and nonforest species separately. The hypothesis was that beta diversity of long-term sites is the "true" beta diversity. Beta diversity values were derived from different sets of sites, so they are independent.

Forest fragmentation may increase beta diversity in a region if there is differential local extinction of species among sites. To test for this effect, we compared beta diversity between continuous-forest sites and fragmented sites (irrespective of elevation or drainage) with a binomial comparison of proportions (Zar 1999), under the hypothesis that continuous-forest sites represent the "true" beta diversity.

To further test for the effectiveness of rapid versus long-term inventories, we used one locality that was surveyed

continuously for 6 years between 1994 and 2000 (La Pastora; G.K., unpublished data). To control for possible seasonal differences in species presence, we compiled lists by quarters corresponding to the bimodal pattern of precipitation of two wet periods (March–May and September–November) and two dry periods (December–February and June–August). In June and July 2004, we conducted a rapid inventory at this site and compared the list we obtained with that of the corresponding quarter in the long-term survey. We used species accumulation curves to compare the two samples. To construct accumulation curves for the long-term survey, each quarter of each successive year was used as the sampling unit. For the rapid survey, we used sampling days. We used the EstimateS (version 6) software (Colwell 2000) to obtain species accumulation curves and estimations of species richness. The estimators selected for comparison were Chao1, Chao2, ICE, and ACE. We calculated the percentage of representation as the average value of all species richness estimates compared with the observed number of species. In the long-term inventory we obtained data on birds through mist netting, visual and aural records in transect surveys, and opportunistic observations. In the short-term survey only mist netting and visual observations in transects were used to obtain data.

Results

Overall, beta diversity accounted for 63.1% of the total gamma diversity of 435 species of birds recorded at the 16 localities. Most of this beta diversity was contributed by species differentiation among elevational zones (beta2, 43.3%; $p = 0.003$). This means that, on average, 188 out of 435 species were not present within an elevational belt. Within individual river drainages, beta diversity among elevational zones ranged between 52% and 57% for forest bird species and between 47% and 55% for species of open habitats (bars C–E, Fig. 2). There was also an important beta component of diversity along the latitudinal (among drainages) axis, represented by differentiation among localities within elevational zones (beta1, 19.8%; $p = 1.0$).

Cluster analysis further revealed the contribution of elevational zones to beta diversity (Fig. 3). Almost all localities clustered by elevational zones, indicating that sites within elevational zones were more similar to each other than to sites in other elevational zones. Two big clusters formed: (1) all localities above 2200 m (montane and páramo life zones) and (2) all localities below 2200 m (premontane and lower montane life zones). Within the high-elevation cluster, páramo sites (>3200 m) formed a separate branch, whereas sites in the two montane elevational zones (2200–2600 and 2600–3200 m) clustered first by elevation and then by drainage. Within the lower-elevation cluster, premontane (1000–1500 m) and lower

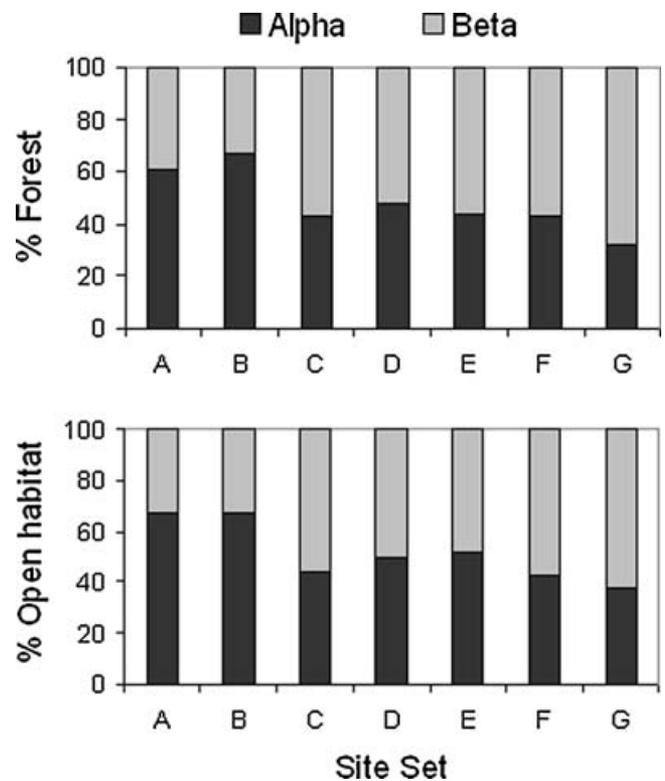


Figure 2. Alpha and beta components of avian diversity for forest and open-habitat species for different sets of sites (A, localities within 1500- to 2200-m elevational zone with rapid surveys; B, localities within 1500- to 2200-m elevational zone with long-term surveys; C, localities within one drainage with rapid surveys; D and E, localities within two drainages with long-term surveys; F, all localities with continuous forest; G, all localities with fragmented forest).

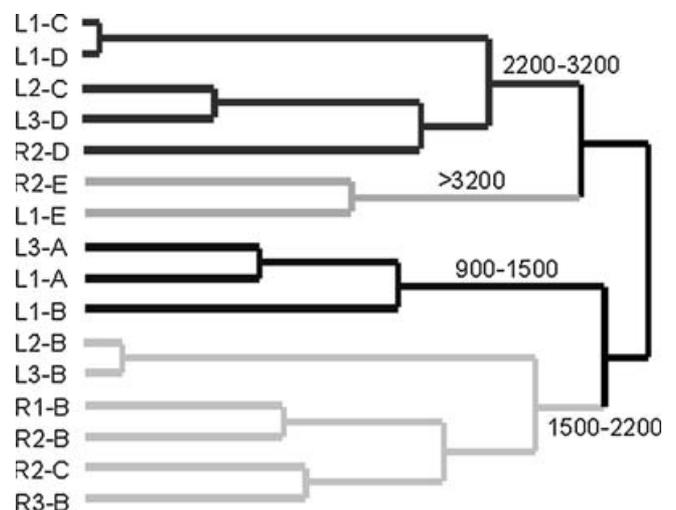


Figure 3. Dendrogram showing clustering of 16 sites (L1-C through R3-B) in the Central Andes of Colombia, based on the avian species presence-absence matrix. See Table 1 for description of site labels.

montane (1500–2200 m) life zones neatly separated into two branches. There were anomalies in these branches: two localities clustered at the “wrong” elevations. Both cases represent fragmented sites that clustered with other fragmented sites at adjacent elevations.

To assess the effect of rapid surveys versus long-term inventories on beta diversity, we compared six sites located in the same elevational belt but in different drainages (Fig. 1). For the three localities with long-term inventories, beta diversity was 33.0% for forest species and 33.3% for open-habitat species (bar B, Fig. 2), whereas the three localities assessed with rapid surveys had beta diversities of 39.2% for forest birds and 32.2% for birds from open habitats (bar A, Fig. 2). Assuming long-term surveys represent the “true” beta diversity, rapid surveys overestimated beta diversity for forest species ($\chi^2 = 5.86$, $p < 0.05$) but not for species of open habitats ($\chi^2 = 0.49$, $p > 0.05$).

To assess the effects of fragmentation on beta diversity, we compared all localities with fragmented forest ($n = 8$) to localities with continuous forest ($n = 8$). Beta diversity was significantly higher in fragmented sites both for forest species (68.4% vs. 54.8%; $\chi^2 = 88.7$, $p < 0.05$) and open-habitat species (62.3% vs. 57.6%; $\chi^2 = 14.4$, $p < 0.05$) (bars F–G, Fig. 2).

The long-term inventory at La Pastora produced a list of 183 species. Estimated species richness was 201 and 203 for the ACE and ICE estimators, respectively, with the observed number of species representing 90.4% of the expected value (Fig. 4). Adjusting for the June–August quarter, the observed number of species was 136. Estimated species richness for this quarter was 149 (ACE) to 162 (Chao2) species. Thus, the observed value represented 86.5% of the estimated species richness for this trimester. In the rapid assessment inventory, 97 species were recorded, representing 56.6% of the 166 (ACE) to 184 (Chao2) species estimated from the species accumulation curve (Fig. 4).

Sixty species recorded in the long-term inventory for the June–August trimester were not recorded in the rapid inventory. These species were grouped in five categories: (1) 9 species with cryptic habits that are difficult to observe, (2) 34 ecologically rare species (i.e., low densities or restricted habitat) or elevational visitors, (3) 6 species that are usually only revealed by their vocalizations, (4) 1 species of poorly known habits, and (5) 10 commonly recorded species. In contrast, 6 species were observed in the rapid inventory but not in the long-term survey. One was a Neartic migrant, 3 were visitors from lower elevation forest, and 2 were accidentals to the region.

Discussion

Although covering a small area, the region we studied had a high beta diversity of birds. Most of this diversity was due to differentiation along the elevational axis.

The cluster analysis also revealed differences in species composition among elevational zones (Fig. 3). Species turnover among drainages, however, also was an important part of regional (γ) diversity. Although only a few kilometers apart in a straight line, there were differences in species composition among localities at the same elevation but different drainages. This reflects patchy distributions of some species. For example, the Red Ruffed Fruit-Crow (*Pyroderus scutatus*), although having a wide geographical distribution, is discontinuously distributed in the Colombian Andes, and some local populations have been extirpated (Kattan et al. 1994). In our region, this species is found in only a few sites.

Species turnover along elevational gradients is a well-known phenomenon (Kattan & Franco 2004), and fragmentation of these gradients causes local species extinctions (Kattan et al. 1994). On a short time scale, these extinctions may occur because movement routes are disrupted. Although elevational migrations are not as well documented in the Andes as they are in other places (e.g., Costa Rica; Chaves-Campos 2004), there is evidence of regional movements occurring at many spatial scales (local to regional) in the Andes and in birds as varied as hummingbirds and parrots (G.K., unpublished data). On a longer time scale, fragmentation of elevational gradients also disrupts the source-sink dynamics that partially generate patterns of elevational diversity (Kattan & Franco 2004).

Some of the beta diversity observed among localities inventoried in short-term surveys can be attributed to a sampling effect because species lists are incomplete. Our comparison of a rapid survey versus a long-term inventory at the same site (La Pastora), revealed that the short-term survey undersampled species richness (97 species in the rapid survey vs. 138 species for the same quarter in the long-term survey). The observed number of species in the rapid survey was 56.6% of the expected number, calculated from the species accumulation curve. This undersampling may be due to several factors. First, resident but rare species may be recorded only after a long, continued sampling effort. Second, species that are mostly recorded by their vocalizations may be seasonally silent. Third, a short-term survey misses seasonal changes in composition because of regional movements of species or changes in activity patterns. Finally, observer experience is a critical factor in short-term surveys. On the other hand, the use of species accumulation curves produced a reasonable estimation of the expected number of species (166 species estimated by the rapid survey vs. 149–162 for the corresponding quarter in the long-term survey). However, for conservation planning purposes, species composition, and in particular the presence of special-interest species, is as important as species richness.

Evaluations of the effectiveness of rapid inventories, in comparison with long-term surveys, are scarce. One

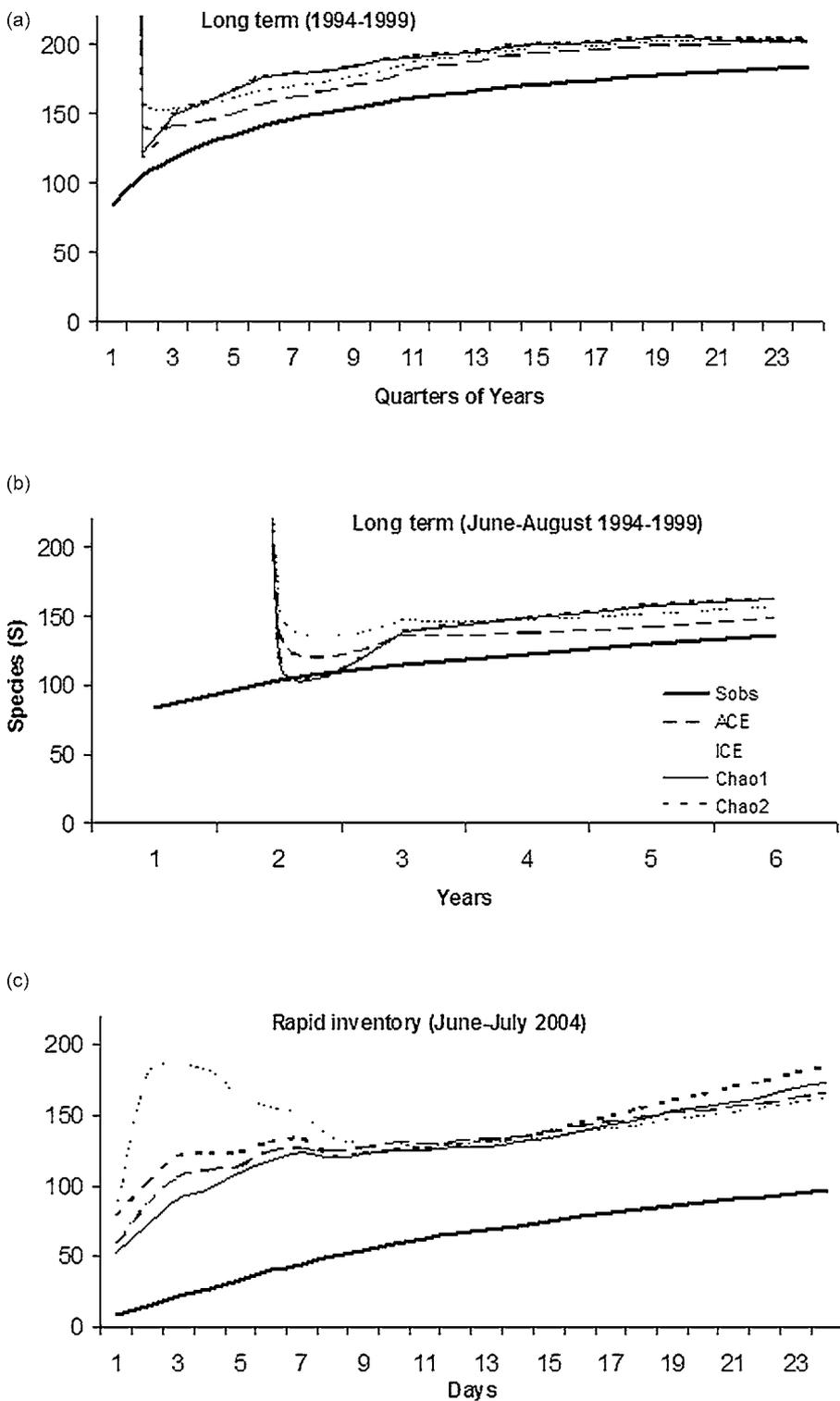


Figure 4. Bird species accumulation curves for La Pastora, 2430 m, Central Andes of Colombia for (a) all species recorded in 24 quarters (6 years), (b) species found only during June-August quarter over 6 years; and (c) species found June-July 2004. The observed number of species (Sobs) and accumulation curves for four estimators (Chao1, Chao2, ICE, and ACE) are shown.

example is a study on the species richness of spiders in a beech forest in Denmark (Scharff et al. 2003), where a 2-year biweekly survey was compared with a 3-day rapid inventory. The two inventories shared close to 92% of species. The differences between the two surveys were attributed to phenological, methodological, and habitat effects for the species observed as singletons and double-

tons or missing in the rapid inventory. A few rare species did not fall into any of these categories and were considered as undersampling bias.

Undersampling in rapid surveys will be more drastic in the tropics, where both total richness and the number of rare species are higher. Nevertheless, rapid inventories help support decision making when there are time and

money constraints in a planning process. Overestimation of beta diversity by rapid surveys in this study, although statistically significant, was small compared with beta diversity observed among localities sampled in long-term studies. Therefore, although rapid surveys underestimate alpha and gamma diversity, beta diversity (as percentage of gamma) is not influenced as much by rapid survey as it is by ecological factors. As alpha and gamma diversities increase with greater sampling effort, there will be only a small change in beta diversity. This characteristic makes the additive model of diversity partitioning a valuable tool for assessing regional heterogeneity.

It must be stressed, however, that there is no quick substitute for long-term and detailed field work. For example, several surveys conducted in the late 1980s and early 1990s failed to find the Brown-banded Antpitta (*Grallaria milleri*), a species thought to be extinct in our study area. Only after several months of intense and continued effort in 1994 was the species rediscovered, even though it was the most abundant of five antpitta species at the site (Kattan & Beltrán 1997, 1999).

Our results also indicated that fragmentation increases beta diversity by creating patchiness in species' distribu-

tions. Differential extirpation of bird populations at a local scale has been documented in the Colombian Andes (Kattan et al. 1994; Renjifo 1999). Fragmentation represents a challenge for conservation because the size of remaining fragments may not be sufficient to sustain a viable ecosystem, but in some cases there are no options. Over 70% of original forest has been transformed in the inter-Andean valleys of the Colombian Andes (Cavelier 1997). In this scenario, even small forest fragments may have value as part of a regional system of protected areas (Kattan & Alvarez-López 1996). In particular, fragments may contain important (or the only remaining) populations of focal species. In our study area, populations of several globally threatened species of birds, such as Moustached Antpitta (*Grallaria alleni*) and Cauca Guan (*Penelope perspicax*) occur in small fragments (Table 1; Renjifo et al. 2002).

We used birds for our study because this taxon is the only one with enough information to conduct detailed comparisons. Beta diversity is expected to be higher in other, less-vagile groups than birds. For example, many species of frogs in the Colombian Andes are known from very small areas (Ruiz et al. 1996), and turnover in species composition among localities may be over 60% (Restrepo

Table 1. At-risk species (according to Renjifo et al. 2002) found in 16 sites in the Central Cordillera of the Colombian Andes.

Species	Sites ^a															
	R1B ^b	R2B	R2C	R2D ^b	R2E ^b	R3B ^b	L1A ^b	L1B ^b	L1C	L1D	L1E	L2B	L2C	L3A ^b	L3B ^b	L3D
Eagles																
<i>Oroaetus isidori</i>												x	x			
Guans																
<i>Aburria aburri</i>		x				x						x				
<i>Penelope perspicax</i>		x	x			x						x			x	
Wood-Quails																
<i>Odontophorus hyperblythrus</i>				x					x	x		x	x		x	x
Parrots																
<i>Bolborbynchus ferrugineifrons</i>					x					x	x					
<i>Hapalopsittaca amazonina</i>									x	x						
<i>Leptosittaca branickii</i>					x				x	x	x	x	x			x
Hummingbirds																
<i>Eriocnemis derbyi</i>				x	x								x			x
Toucans																
<i>Andigena hypoglauca</i>									x	x	x		x			x
<i>Andigena nigrirostris</i>				x	x				x	x	x	x	x			x
Passerines																
<i>Grallaria alleni</i>	x											x				
<i>Grallaria milleri</i>									x	x	x		x			
<i>Grallaria rufocinerea</i>									x	x	x		x			
<i>Grallaricula cucullata</i>		x				x							x			
<i>Chloropipo flavicapilla</i>		x	x									x			x	
<i>Ampelion rufaxilla</i>																
<i>Butbraupis wetmorei</i>											x					
<i>Chlorochrysa nitidissima</i>	x	x										x			x	
<i>Habia cristata</i>		x														
<i>Pseudodacnis bartlaubi</i>												x			x	
<i>Saltator cinctus</i>														x		

^aKey: R, sites with rapid surveys; L, sites with long-term surveys; 1-3, different drainages; A-E, different elevational zones (A, 900-1500 m; B, 1500-2200 m; C, 2200-2600 m; D, 2600-3200 m; E, >3200 m).

^bLocalities with fragmented forest.

& Alberico 1994; Kattan et al. 2004). Similar or higher turnover in species composition over short distances has been reported for plants in the family Araceae (Croat 1992).

Determining quantitative goals is one of the major challenges in conservation planning. Beta diversity is an important tool to support decisions on the number and location of protected areas (Gering et al. 2003; Groves 2003). Previous work shows that at the scale of the Colombian Andes, beta diversity among mountain ranges and even between east- and west-facing slopes of the same range is an important component of total diversity (Kattan et al. 2004). Our analysis indicated this is also the case even at very small spatial scales. Representing this diversity in a system of protected areas is a challenge because a relatively large number of reserves will be required. In particular, our results indicate that reserves should cover the entire elevational gradient on Andean slopes. On the other hand, in Andean ecosystems even small reserves will be valuable, especially if they are integrated in a regional system.

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