Acta Oecologica 36 (2010) 396–402

Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Original article

Human access and landscape structure effects on Andean forest bird richness

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ARTICLE INFO

Article history:
Received 27 November 2009
Accepted 31 March 2010
Published online 24 April 2010

Keywords:
Akaike's Information Criterion
Cloud forest
Forest birds
Generalized linear models
Habitat fragmentation
Species richness

ABSTRACT

We analyzed the influence of human access and landscape structure on forest bird species richness in a fragmented landscape of the Colombian Andes. In Latin America, habitat loss and fragmentation are considered as the greatest threats to biodiversity because a large number of countryside villagers complement their food and incomes with the extraction of forest resources. Anthropogenic actions may also affect forest species by bird hunting or indirectly through modifying the structure of forest habitats. We surveyed 14 secondary cloud forest remnants to generate bird species richness data for each of them. We also quantified six landscape structure descriptors of forest patch size (patch area and core area), shape (perimeter of each fragment and the Patton's shape index) and isolation (nearest neighbor distance and edge contrast), and generated (using principal components analysis) a synthetic human influence variable based on the distance of each fragment to roads and villages, as well as the total slope of the fragments. Species richness was related to these variables using generalized linear models (GLMs) complemented with model selection techniques based on information theory and partial regression analysis. We found that forest patch size and accessibility were key drivers of bird richness, which increased toward largest patches, but decreased in those more accessible to humans and their potential disturbances. Both patch area and human access effects on forest bird species richness were complementary and similar in magnitude. Our results provide a basis for biodiversity conservation plans and initiatives of Andean forest diversity.

1. Introduction

Anthropogenic activities affect natural ecosystems by altering or creating stress regimes, by generating new disturbances, or even by suppressing natural disturbance regimes (White and Pickett, 1985; Nyström et al., 2000; Lindenmayer and McCarthy, 2001; Stankowich, 2008). Human activities also affect the spatial arrangement of habitats in the landscape as well as the structure of the communities that occur in them. For example, in developing countries, countryside dwellers often complement their income with the extraction of forest resources (Aide and Grau, 2004), promoting the loss and fragmentation of forests and the impoverishment of their biotas (Johns, 1991; Mason, 1996; Turner, 1996; Alvarez, 2002; Köhler et al., 2002; Fahrig, 2003; Barlow and Peres, 2004; Aubad et al., 2008). Moreover, anthropogenically-driven species losses associated with habitat alterations have not only been reported locally, but also at the regional and global extents (Diamond, 1984; Kattan et al., 1994; Turner, 1996; Bierregaard et al., 1992; Pimm, 1998; Hill and Curran, 2003), thus being regarded as one of the most important drivers of the current biodiversity crisis (Groombridge, 1992; Bascompte and Solé, 1996; Turner, 1996; Burgman and Lindenmayer, 1998; Laurance, 1999; Tilman et al., 2002).

Among the many characteristics of landscape structure that change with the loss and fragmentation of habitats, habitat size is considered the most relevant predictor of species richness (reviewed in Fahrig, 2003). Patch size and core-area size (i.e. the amount of interior habitat that is not influenced by edge effects) are both the best known area-related indexes (MacArthur and Wilson, 1967; Bierregaard and Stouffer, 1997; Pimm, 1998; Pimm and Raven, 2000; Hill and Curran, 2003). Habitat size and isolation are frequently associated with patch quality, with high quality patches (i.e. the larger and less isolated ones) commonly performing as source populations and lowest quality patches as sink populations (e.g. see Fauth et al., 2000).

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doi:10.1016/j.actao.2010.03.009

The tropical Andes are considered the most diverse region of the world in terms of bird species (Mittermeier et al., 2000; Hawkins et al., 2003; Boyla and Estrada, 2005; Orme et al., 2005). Almost 10% of all bird species recorded in the Colombian Andes are endemic or semi-endemic (Stiles, 1998) and are mostly restricted to mountain forests above 1000 m a.s.l. In addition, nearly 9% of the 1870 bird species known from Colombia (Salaman et al., 2008) are under some type of threat (Renjifo et al., 2002), mainly due to the loss and fragmentation of forests. This illustrates the high susceptibility to extinction and low tolerance to the degradation of forests of this bird fauna (see Bierregaard and Stouffer, 1997; Renjifo, 2001).

This study was carried out in the Colombian Andes in a landscape that has been proposed as a regional conservation park by local authorities (Corantioquia – UN, 2002). The area suffered intense clearing and fragmentation during the 19th and 20th centuries and is undergoing a slow forest recovery (see Aubad et al., 2008). Our aim was to assess the relative importance of landscape structure and human access and their relationship with forest bird species richness. We hypothesized that forest bird richness was determined by both, landscape structure (i.e. the size, variety and spatial configuration of habitats) and human influences. We generated a battery of landscape structure metrics commonly used in habitat fragmentation research (i.e. variables of patch area, shape and isolation), and we evaluated potential anthropogenic influences by measuring the general accessibility of the forest patches to humans.

We assumed that, if forest bird richness decreases with increasing accessibility to forests, this would indicate that human actions are negatively impacting forest bird fauna and, also, that more accessible forests should be object of special attention by local conservation authorities. From a more general perspective, our goal is to contribute to the establishment of scientifically informed conservation plans protecting the tropical Andean biodiversity through the creation of sustainable regional protected areas.

2. Methods

2.1. Study area and sampling procedures

The landscape, called Parque Arví, comprises 11,431 ha and is located in the central Andes of Colombia, in the province of Antioquia. The landscape (located 6°15′56.00″N and 5°30′11.00″W) is close to Medellín, the second largest city of Colombia. Elevation ranges between 1800 and 2700 m, and mean annual temperature is 14 °C (range 5–20 °C). Annual precipitation varies from 1500 to 2200 mm with a bimodal pattern that includes wet periods in March–May and October–December (see Toro, 2000 for a more detailed description of the area). Potential vegetation consists of tropical Andean cloud forest, characterized by six plant families that contribute 32% of the species; namely, Lauraceae – the dominant tree species group in the altitudinal band occupied by Andean forests (Gentry, 1982) – Rubiaceae, Orchidiaceae, Melastomataceae, Asteraceae and Solanaceae. All mature forests are secondary cloud forests located in a narrow altitudinal belt (the centroids of all forest patches have an altitude ranging between 2300 and 2600 m).

Based on detailed land cover map generated by a conservation project carried out by the Corporación Autónoma Regional del Centro de Antioquia and the Universidad Nacional (UN) (Corantioquia – UN, 2002)- we identified 18 old-growth secondary forest fragments for the study. However, the bird fauna of four of these fragments could not be surveyed because of access restrictions from land owners. The 14 sampled fragments range from 2 to 181 ha (Fig. 1), and we also surveyed four other types of habitats described in the land cover map; i.e. scrubs, arborescent pre-forestal

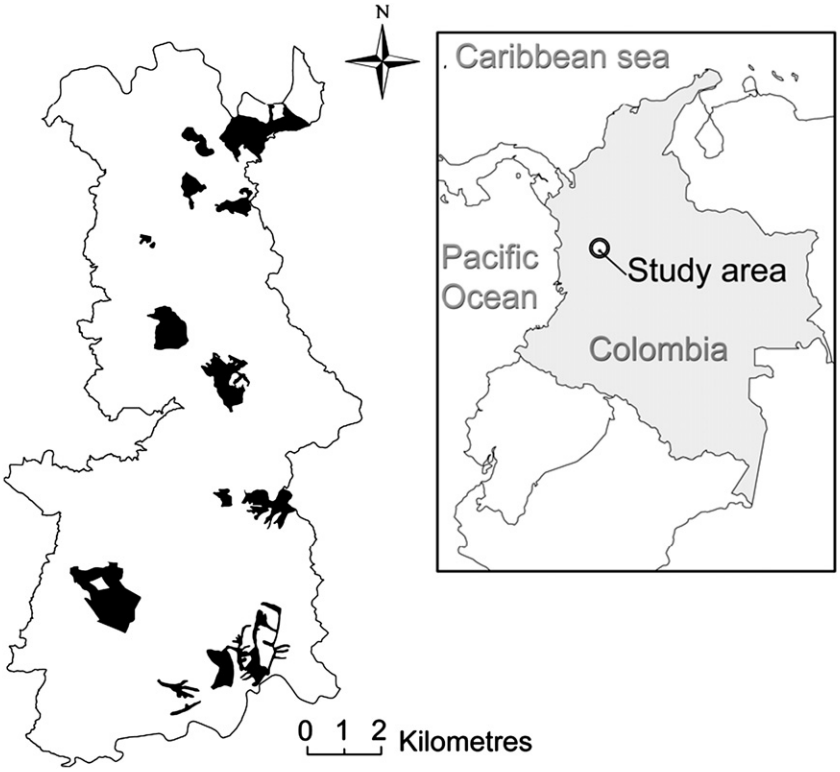

Fig. 1. Map of the study area (park boundary) in the central Andes of Colombia showing the location of the fourteen old-growth secondary forest fragments used in this investigation.

formations locally known as “rastrojos”, forest plantations, and grasslands. Although our analyses were centered on the forest patches, the bird species data obtained for these non-forest habitats were necessary to compute the variable edge contrast, one of the isolation metrics used in this study (see below).

The surveys took place between August 2004, and September 2005, and used two different methods: point counts, which are standardized surveys commonly used for ornithological studies (Bibby et al., 1992; Ralph et al., 1995), and mist-netting. For point counts we randomly established for each forest and non-forest habitat patch ten, 30-m radius plots at least 200 m apart. We used these point counts to survey all bird species that were seen or heard during 15 min. We complemented the surveys with mist-nettings, using 12 m–30 mm mesh-nylon nets. This survey technique allows the capture and marking of forest bird species, including those missed during the point counts surveys due to their quiet behavior. We established five nets per habitat patch, which were surveyed over eleven continuous hours (from 6:00 to 17:00 GTM) until the sampling effort reached 770 net-hours. Nets were placed 30–50 m apart, establishing a line (net series) that started 100 m from the edge, and extended toward the center of the patch (to avoid catching outsider species). In total we recorded 58 bird species, after excluding all species that just overfly the patches or continental migratory species.

2.2. Richness variables

We calculated the total forest bird species richness of each secondary forest patch and used these values as our main response variable (hereafter total richness). We also considered two additional species richness variables after classifying all species according to their occurrence in the forest patches. For this, we used cluster analysis with average linkage as the clustering algorithm (Quinn and Keough, 2002), and the percentage disagreement index between pairs of species as the dissimilarity coefficient (StatSoft, 2005), which is expressed as:

$$D(x_i, y_i) = 100\left(\sum |x_i \neq y_i| / I\right)$$

in which x_i, y_i are two species, I is the total number of forest patches, and $\sum |x_i \neq y_i|$ is the number of forest patches in which a species is present while the other is absent. Therefore, we differentiated two clear groups (Fig. 2), one composed of bird species present in at least eight forest patches (hereafter common species), and the other by species occurring in less than eight patches (rare species). Thus, we calculated the richness of each of these groups in the patches and used common and rare species richness values as complementary response variables. We also considered including feeding guilds as response variables, however statistical analyses based on feeding guilds lacked power due to low species richness.

2.3. Explanatory variables

We processed the Corantioquia – UN (2002) digital cartography with a ArcView 3.2 and Fragstats 3.0 (McGarigal et al., 2002) to generate six landscape structure variables reflecting different aspects of the area, isolation and shape of the forest patches. Area

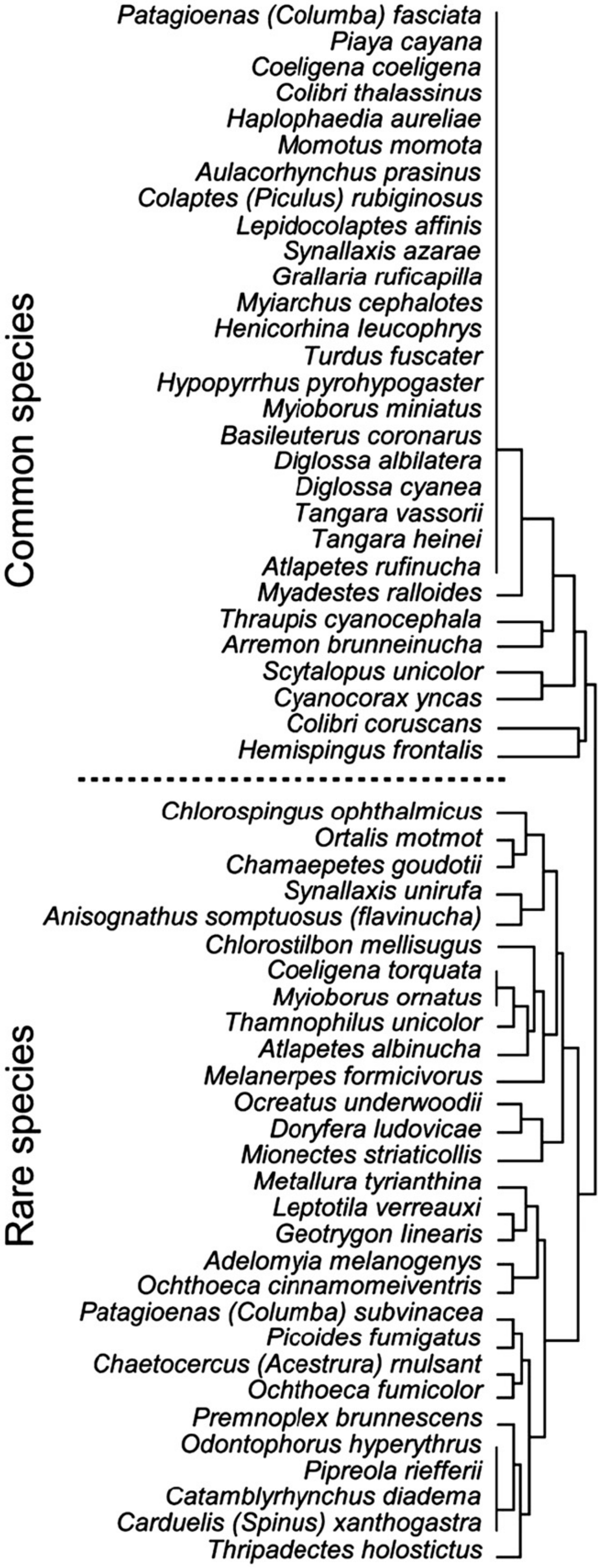

Fig. 2. Hierarchical agglomerative clustering of the 58 bird species present in the fourteen old-growth Andean secondary forests investigated in this study. The analysis used the percentage disagreement index between pairs of species as dissimilarity measure, and average linkage as clustering algorithm. The analysis identified two equally sized groups of 29 species each, one comprising species present in at least eight patches (common species), and the other including species found in a lower number of patches (rare species).

metrics comprised patch area and core area, the first variable corresponding to the total area of each fragment (in hectares), and the second variable reflecting the area that is left after discarding a strip of forest 100 m wide from the edge of the fragment (Forman, 1995; Turner et al., 2001). Isolation variables were edge-to-edge nearest neighbor distance (hereafter NND), and the edge contrast index developed by McGarigal and Marks (1995). NND represents the shortest distance between the focal forest fragment and its nearest forest patch either in the studied landscape or in its surroundings. The edge contrast index considers the habitats that are in contact with the perimeter of each forest fragment and the relative length of this contact. Thus, larger values correspond to forest patches that are surrounded by less suitable habitats for forest birds (see McGarigal and Marks, 1995 for details), taking into account the forest bird species detected by the four previously described land cover classes. Finally, shape variables included the perimeter of each fragment (in meters), and the Patton's shape index, a dimensionless circularity metrics that is theoretically and empirically independent of area (see McGarigal and Marks, 1995).

As a proxy of human influence levels we generated a synthetic metric in a principal component analysis (PCA), combining three different aspects of the accessibility of forest patches to humans; the distance of each patch to the nearest road of any type, its distance to the nearest village, and its average slope. The metric consisted of the first axis, which explained 56% of the variance and was the only axis having an eigenvalue greater than one (1.7); that is, this axis was the one to be chosen according to the interpretability criterion established by Norman and Streiner (1994). This PCA axis is highly negatively correlated with all three accessibility measures (Pearson $r < -0.62$ in all cases), thus indicating that its larger values reflect lower accessibility to humans.

2.4. Statistical analyses

We used generalized linear models (GLMs) to relate species richness values with human access and landscape structure descriptors (see below). However, it is well known that multicollinearity among explanatory variables may strongly affect the outcome of multi-factor linear models. Therefore, we first conducted a cluster analysis to identify a subset of predictors. Specifically, we computed Pearson correlations between each pair of predictors and then used Pearson r as the distance measure and average linkage as the clustering algorithm (Quinn and Keough, 2002). The resulting dendrogram (not shown) classified edge contrast and human access as two independent variable groups. Therefore these variables were selected for further analysis. A third group comprised patch size, core size and NND, which had a significant correlation among them ($r > 0.60$ in all cases). From these variables we selected patch size, which is widely used in studies relating species richness and habitat structure characteristics (e.g. McGarigal and Marks, 1995). Finally, a fourth group included shape index and perimeter ($r = 0.91$), and we selected the first variable to reflect area-perimeter relationships associated to edge effects (Skole and Tucker, 1994; Murcia, 1995; Arango-Vélez and Kattan, 1997; López-Barrera et al., 2006; Broadbent et al., 2008). Pairwise simple correlations among the four variables chosen by this procedure ranged between $|0.02|$ and $|0.50|$, which represents a moderate level of collinearity (see Neter et al., 1996). Furthermore, any remaining collinearity effects are expected to be minimized through the model averaging techniques (see Diniz-Filho et al., 2008). We also checked the level of spatial autocorrelation in the data using the program SAM (Rangel et al., 2006), which is widely used in Macroecology and Biogeography. No significant spatial autocorrelation was found at any distance class for our total and rare species richness variables, indicating that accounting for spatial autocorrelation effects was not needed in these cases.

The error distribution of richness data is expected to be Poisson rather than Gaussian (normal) (Cameron and Trivedi, 1998), and Kolmogorov–Smirnov D tests showed that our three species richness variables did not differ from the Poisson distribution in any case (all observed Ds ≤ 0.329; that is, lower than the tabulated value of 0.349, necessary to assume significant differences between both distributions at $p < 0.05$). Hence, our GLMs consisted on Poisson regressions with a log-link function (McCullagh and Nelder, 1989). The modeling process involved two steps. First, for each species richness variable, we generated all possible models that can be obtained by combining four predictors (i.e. 2^4 models minus the model with intercept only = 15 models). Then, we evaluated the performance of each model through computing three information theory-based indexes: the Akaike's Information Criterion (AIC), ΔAIC and Akaike's weighting (w_i) (Burnham and Anderson, 2002). AIC ranks the models according to their descriptive power, with lower AICs indicating better models. The ΔAIC index compares each model with the model exhibiting the minimum AIC value ($\Delta\text{AIC}_i = \text{AIC}_i - \text{minAIC}$), and a rule of thumb allows identifying those models with $\Delta\text{AIC} < 2$ as good models (see Burnham and Anderson, 2002). Finally, the Akaike's w_i represents the probability that model i is actually the best explanatory model among all possible models.

This model selection protocol allowed us to focus on interpretations for each species richness variable on the standardized regression coefficients of the predictors included in two types of models: the best model (i.e. that with minimum AIC), and the average model obtained after averaging the regression coefficients of all good models (i.e. with $\Delta\text{AIC} < 2$). Higher absolute values of these coefficients correspond to predictors having stronger impacts on species richness. Further, to approximate the proportion of deviance explained by each model, we also computed its *pseudo*-$R^2 \times 100$ value (also known as McFadden's rho-squared) to evaluate model fit. This index varies between 0 and 100, and a rule of thumb is that *pseudo*-$R^2 \times 100$ values larger than 20 indicate good fits (see Terribile et al., 2009 for more technical details). Finally, we complemented these techniques with partial regression analysis to partition the deviance explained by the variables included in the best models into independent and covarying components (e.g. see Hawkins et al., 2003).

3. Results

The correlation between total and rare bird species richness was much higher ($r = 0.97$) than that of each of these variables with common species richness ($r = 0.66$ and $r = 0.47$, respectively). Cluster analysis performed with the presences of the species in the fragments showed that, out of the 29 common species found in the study, 22 species were all clustered in a large group in with zero dissimilarity (Fig. 2). Indeed, this low compositional variability of common species across the fragments explains why this species group had a lower contribution to total richness variation. Conversely, rare species ($N = 29$) were more dissimilar in terms of their distribution (Fig. 2), accounting for the stronger contribution to total richness patterns.

Consistent with this, the multivariate models obtained for both total and rare species richness were very similar, with patch size and human access being the strongest predictors in both cases, as indicated by their respective standardized regression coefficients in the best and average models (Table 1). Positive and negative coefficients for patch size and human access in these models, respectively, indicate that total and rare forest bird richness increase in larger and less accessible forest patches. Conversely, the lower absolute values of the standardized regression coefficients of

Table 1
Best and average multiple GLM models describing the variation of total, rare and common forest bird species richness across fourteen secondary forest patches in an Andean landscape. The standardized regression coefficients of the predictors used for model building are provided, with the absolute value of each predictor in each model indicating its relative importance as descriptor of richness patterns. For each richness variable, the best model corresponds to that with lower AIC. Akaike weighting (w_i) reflects the probability of this model of being actually the best across all possible models. The percentage of deviance explained by each best model is also given (*pseudo*-$R^2 \times 100$). Average models were obtained by averaging the coefficients of all good models (i.e. with $\Delta\text{AIC} \le 2$) found for each species richness variable. Parenthesis indicates the number of good models found in each case.

Model	Patch size	Shape index	Edge contrast	Human access	w_i	*Pseudo*-$R^2 \times 100$
Total richness						
Best	0.105			−0.106	0.324	52.6
Average (4 models)	0.068	0.012	−0.037	−0.125		
Rare species richness						
Best	0.390			−0.382	0.476	37.2
Average (3 models)	0.370	0.048	−0.014	−0.412		
Common species richness						
Best			−0.031		0.171	19.5
Average (9 models)	0.004	0.008	−0.015	−0.016		

shape index and edge contrast in the average models highlight that these are poorer predictors of richness. Table 1 also shows that the best model obtained for the richness of common species explained a lower proportion of deviance (19.5%) than the best models for all and rare species (52.6% and 37.2%, respectively). This, coupled with the similar patterns and relationships of the richness of these two species groups with patch size and human access (Fig. 3) reinforces that variation of total richness mainly reflects rare richness. Finally, according to our partial regression analyses of the relationships described by the best models (Fig. 4), the proportion of deviance jointly explained by patch size and human access was very low for both total and rare species richness (≤2%), thus indicating that the effects of both predictors on richness are independent to a large extent.

For common species, the best model included only edge contrast (Table 1). However, this was a weak predictor, judged by the lower Akaike weighting of this model ($w_i = 0.171$). Moreover, all standardized regression coefficients of the average model showed low absolute values, indicating that common species richness variation was weakly associated with the investigated predictors. This result is consistent with the widespread distribution of the species of this group across the forest patches.

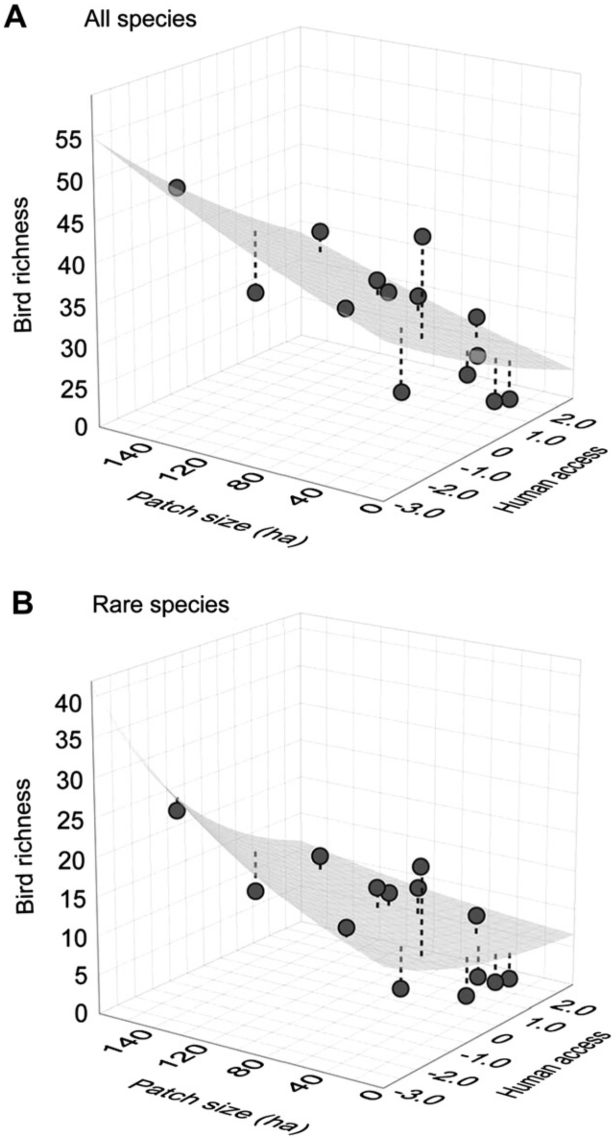

Fig. 3. Bird richness values for all (A) and rare species (B) and their relationships with patch size (in hectares) and human access (higher values indicate greater accessibility to humans; see text) in fourteen remnants of Andean secondary forest in Colombia. The surfaces fitted to the data were generated through Poisson regression with log-link function and represent the best fits of the AIC-based multimodel selection protocols summarized in Table 1.

4. Discussion

We found that the size of the forest fragments and their accessibility to humans were important determinants of bird richness in secondary forest in a highly fragmented Andean landscape. An increase in richness with habitat area was expected, as it is consistent with both the well known species-area relationship, which is one of the basic tenets of island biogeography theory (MacArthur and Wilson, 1967), and a pattern that has been frequently found (Rosenzweig, 1995; Forman, 1995; Laurance et al., 1998; Honnay et al., 1999; Boutin and Hebert, 2002; Hill and Curran, 2003; Fahrig, 2003). On the other hand, the negative effects of forest accessibility to humans on richness can be interpreted as reflecting deleterious anthropogenic impacts on forest bird fauna. Both patch area and human access have complementary effects on total forest bird species richness.

Our analyses also identified two bird species groups, each reacting differently to human influences. Common bird species showed weak relationships with both the accessibility to humans and the landscape characteristics of the forest remnants. Hence, we interpret that these species are common because of their lower sensitivity to anthropogenic impacts, which, of course, does not exclude the possibility that an intensification of such impacts in the future could lead to negative reactions of at least some of these common species. Conversely, the richness of rare bird species was highly correlated with total richness, and both were influenced by forest patch size and accessibility. Thus, total richness patterns are mainly due to the sensitivity of rare species to habitat structure. Moreover, deviance partitioning indicated that the effects of patch area and human access on rare species richness (and hence on total richness) are independent from each other. This suggests that while some species are particularly sensitive to reductions in forest patch size, other species would respond primarily to the accessibility of

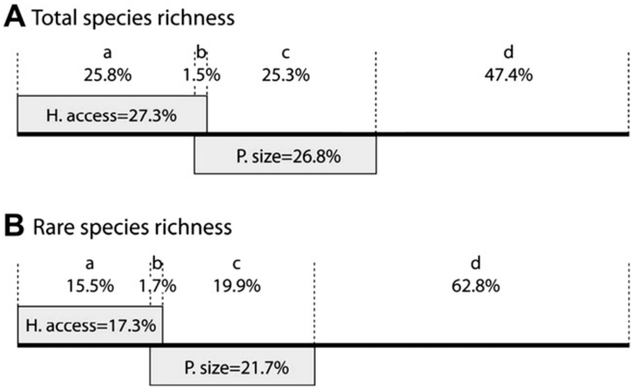

Fig. 4. Partial regression partitioning of the deviance of total and rare Andean forest bird species richness as explained by the independent contributions of human access (a), patch size (c), the overlap between these variables (b), and the proportion of deviance not explained by either factor (d).

humans to the remaining forests (see below). Additionally, from a practical point of view, these results indicate that actions aimed at preserving bird richness in the studied landscape should involve both preventing further forest fragmentation (reduction, perforation and dissection) and controlling human disturbance to the forest patches.

Human access to natural forests may promote the uncontrolled exploitation of forest resources, a phenomenon that seems to be particularly common in developing countries (e.g. Biswas et al., 1987; Rodríguez, 2000; Geist and Lambin, 2001; Cason and Obidzinski, 2002; Aubad et al., 2008). For instance, for the particular case of the studied landscape, we have documented that the unselective cutting of young trees that are used as household fuel causes negative impacts on tree species richness and composition (Aubad et al., 2008). This illegal logging activity may also have indirect effects on the bird fauna, for example by disturbing foraging or reproduction, and/or by altering nesting sites. Likewise, the growing, recreational use of areas in our study region by people coming from the neighboring cities may have similar indirect effects on the forest bird biota (Bautista et al., 2004; Gill, 2007). However, according to the informal interviews with local authorities and forest rangers during field work, a more likely cause behind the negative relationships between human access and total and rare species richness is illegal bird hunting. Although forbidden and prosecuted, traditional hunting practices are still being performed in the area and affect medium and large-sized edible bird species that are consumed locally. Besides these species, illegal hunting also affects vividly colored and/or song birds, in this case with the goal of selling the individuals captured in the Medellín's wildlife black market. Whatever the motivation, both types of bird hunting appear to be highly species selective, a feature that provides a comprehensive interpretation to our results. Indeed, as discussed above, we found nearly independent effects of patch area and human access on rare and total richness, which suggested that the negative effects of forest patch accessibility were mainly due to a negative response of a particular set of our rare bird species. This is consistent with a selective extraction of bird species from the patches and, hence, with the illegal hunting practices that are taking place there.

Our results, coupled with those obtained previously in the same landscape for tree species richness (Aubad et al., 2008), highlight that, along with forest structure characteristics, direct human impacts on the biota have to be taken into account if we want to preserve its richness. Moreover, since those impacts consist on illegal activities which, to a large extent, are related with the general low incomes of the local population, it seems imperative that any actions and initiatives pursuing improving the conservation of this area take into account this economic dimension.

Acknowledgments

We thank Corantioquia and Universidad Nacional de Colombia for partially funding this study, Roberto Parra for his important help during the data collection, and Jennifer Schulz for reviewing a previous version of this paper. Work by M.Á.R. was supported by the Spanish Ministry of Science and Innovation (grant CGL2006-03000/BOS).

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