Original article

Fine-scale habitat structure complexity determines insectivorous bird diversity in a tropical forest

Gabriel J. Castaño-Villa [a,b,c], Santiago A. Ramos-Valencia [a], Francisco E. Fontúrbel [c,*]

[a] *Grupo de Investigación en Ecosistemas Tropicales, Universidad de Caldas, Manizales, Colombia*
[b] *Departamento de Desarrollo Rural y Recursos Naturales, Universidad de Caldas, Manizales, Colombia*
[c] *Departamento de Ciencias Ecológicas, Universidad de Chile, Santiago, Chile*

ABSTRACT

Habitat complexity in reforested stands has been acknowledged as a key factor that influences habitat use by birds, being especially critical for habitat disturbance-sensitive species such as tropical understory insectivorous birds. Most studies regarding the relationship between forest structure and species diversity were conducted at the landscape scale, but different diversity patterns may emerge at a finer scale (i.e., within a habitat patch). We examined a tropical reforested area (State of Caldas, Colombia), hypothesizing that insectivorous bird richness, abundance, and foraging guild abundance would increase as intra-habitat complexity increases. We established 40 monitoring plots within a reforested area, measured their structural features, and determined their relationships with species richness, total abundance, and foraging guild abundance, using Generalized Additive Models. We found that the increasing variation in basal area, stem diameter, and number of stems was positively correlated with species richness, total abundance, and foraging guild abundance. Relationships between richness or abundance and structural features were not lineal, but showing curvilinear responses and thresholds. Our results show that heterogeneity on basal area, stem diameter, and the number of stems was more correlated to insectivorous bird richness and abundance than the average of those structural features. Promoting structural variation on reforested areas by planting species with different growth rates may contribute to increase the richness and abundance of a tropical vulnerable group of species such as the understory insectivorous birds.

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1. Introduction

A plethora of studies have addressed the role of vegetation structure on species richness and abundance (e.g., Koh et al., 2006; Pearman, 2002; Sirami et al., 2009; Terborgh, 1985). Most of the studies dealing with the relationship structure-diversity have been conducted at a landscape scale, but diversity patterns emerging from a finer scale (i.e., intra-habitat structure variation) have also been described (Ritchie and Olff, 1999). Such fine-scale diversity patterns may be from critical importance for determining species diversity in a habitat disturbance scenario (Díaz et al., 2005). In this sense, anthropogenic activities (e.g., selective logging) may act as major change drivers in terms of species richness and community structure, by the means of altering forest habitat structure (Banks-Leite and Cintra, 2008; Cleary et al., 2007; Wunderle et al., 2005). However, these ideas have been little explored at the patch scale.

Understanding how diversity patterns emerge due to the structural variation within a habitat patch is particularly relevant for those foraging-specialist species that may be vulnerable to habitat disturbance. A good example of those species susceptible to habitat disturbance are the understory insectivorous birds (Sodhi et al., 2004; Stouffer et al., 2009), known to be particularly vulnerable due to their high habitat specificity, short lifespan, and low mobility that usually confines them to forest interior habitats (Sekercioglu et al., 2002). There are many hypotheses related to the sensitivity of insectivorous birds to habitat disturbance, including food availability, microclimate conditions, and microhabitat features (Canaday, 1996; Sekercioglu et al., 2002). Most studies regarding insectivorous birds are related to habitat fragmentation at a landscape scale (e.g., Sodhi et al., 2004; Stouffer et al., 2009), but the effects of intra-habitat structural variation on insectivorous bird species and their foraging guilds remain poorly studied. For example, insectivorous birds at Mediterranean maquis in Spain

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showed a positive response to silvicultural thinning in terms of species richness but not in abundance (De la Montaña et al., 2006). Conversely, insectivorous bird richness and abundance have negatively responded to forest fuel management in Portugal (Santana et al., 2012). In this respect, intra-habitat structural variation is particularly relevant for insectivorous birds, which are known to forage in specific microhabitats where they establish stable foraging territories (Gradwohl and Greenberg, 1980, 1982; Greenberg and Gradwohl, 1986).

Conducting studies to examine relationships between habitat structure and diversity may be a challenging task in complex environments. However, recent studies have established that forest plantations may act as habitat for native bird species, determined by their understory abundance and complexity (Lindenmayer and Hobbs, 2004; Nájera and Simonetti, 2009). Particularly, habitat complexity (i.e., the variation in habitat physiognomy) may influence the value of forest plantations as avian habitat. Since forest plantations usually constitute simplified ecosystems, they may resemble an early successional stages of natural forests (Kattan and Murcia, 2012), constituting a potential proxy for studying some complex ecological phenomena in tropical forests. Based on these, we used a tropical reforested area to examine the relationship between intra-habitat structure variation and bird species diversity, using understory insectivorous birds (considering both individual species and foraging guilds) as a study model.

We hypothesized that bird species richness, abundance, and foraging guild abundance would increase as intra-habitat complexity increases. We aimed to identify those structural variables relevant to promote species diversity in this highly vulnerable tropical bird group, which in turn may help in restoring degraded areas by managing certain forest structural features positively correlated to insectivorous bird richness and abundance.

2. Material and methods

2.1. Study area

This research was conducted in a 43-ha forest plantation, established around 1970 to protect the watershed of the San Francisco Dam (State of Caldas, Colombia; 05°03′32″N, 75°44′07″W; at 825−1025 m a.s.l.), which is adjacent to a 16.5-ha second-growth forest remnant and embedded in a matrix of cattle pastures, citrus, and tomato farms. The mean temperature is 22.5 °C and the annual rainfall reaches 2245 mm (Morales-Betancourt et al., 2012). The study site plantation consists of four native tree species: *Cupania americana* L. (Sapindaceae), *Cedrela odorata* L. (Meliaceae), *Aegiphila grandis* Moldenke (Lamiaceae), and *Cordia alliodora* (Ruiz & Pav.) Oken (Boraginaceae). Those species were selected to reforest because they were from commercial importance back in 1970. The plantation reaches a canopy height of ca. 23 m, a basal area (i.e., the area of land occupied by the cross-section of tree trunks and stems at their base) of 32.4 m^2 ha^{-1}, and a tree density of 665 individuals ha^{-1}. This plantation has a stratified canopy, with *C. odorata* and *A. grandis* as emergent canopy species (23 m), while *C. americana* and *C. alliodora* are present as co-dominant species (18 m), with some suppressed trees and a few other standing dead trees. The understory is comprised of several shrubs of the families Rubiaceae, Melastomataceae, and Solanaceae (Morales-Betancourt et al., 2012).

2.2. Vegetation sampling

We established 40 sampling plots separated by at least 32 m from each other, and located >100 m from adjacent habitats (i.e., plantation edge or second-growth forest). At each sampling plot we designated two sub-plots of 25 m^2 (12.5 × 2 m), making a total monitoring area of 50 m^2 per plot. Vegetation was sampled once, immediately prior to conducting the first bird sampling. We quantified the following measurements within each plot: (1) understory height, (2) basal area, (3) vegetation soil coverage, (4) number of stems, and (5) average stem diameter; those variables have been previously described as good habitat structure proxies (August, 1983; Cintra et al., 2006). The percentage of soil covered with vegetation was estimated visually in a 1 m^2 sample at 1 m above the ground. The number of stems was determined by counting every tree with DBH ≥1 cm. The average diameter for each stem within the sampling plots was determined using a measuring tape. For each plot we also estimated the coefficient of variation (hereafter abbreviated as CV) of the structural variables just described, using each measured plant within each plot as a study unit. Detailed information of the measured structural variables is available in Table S1, accessible online as Supplementary Material.

2.3. Bird sampling

We set a 12 × 2.5 m mist net at each sampling plot, making a total effort of 40 mist nets. Plots were monitored for nine months (September 2005, April−May 2006, July−August and October−December 2006, and January 2007). Each mist net point was monitored 108 h point^{-1} (12 h point^{-1} month^{-1}), between 06:00 and 17:30 h, making a total sampling effort of 4320 mist net-hours. Mist nets were not operated on rainy days. Captured individuals were identified following the species nomenclature of Remsen et al. (2014). To identify individuals and account for recaptures, we marked captured individuals with a unique color combination of plastic bands. For each mist net capturing point we determined species richness and abundance. With this information we separated the recorded species into five foraging guilds: bark foragers, ant followers, flycatchers, foliage gleaners and ground foragers (classified following Hilty and Brown, 1986); non-insectivorous species captured in the nets were excluded from the analyses.

2.4. Data analysis

We defined the following response variables describing insectivorous bird communities: (1) total species richness (S) measured as the number of insectivorous bird species recorded in each plot, (2) total insectivorous bird abundance (i.e., all species combined), (3) abundance of each species captured at least 10 times, (4) abundance of each foraging guild (bark foragers, ant followers, flycatchers, foliage gleaners and ground foragers) measured as the number of individuals of each guild recorded in each plot (recaptures were not considered in all cases). Our data fitted a Poisson error distribution, and there was no data overdispersion in any case; we checked for overdispersion following the procedure of Zuur et al. (2009; see p. 224), based on the ratio of the residual deviance and degrees of freedom. Consequently, we used Generalized Additive Model (GAM) analyses, with a Poisson error distribution and a log link function in all cases. We ran GAMs using the measured vegetation structure variables as predictors. Explanatory variables were tested for multicollinearity by examining the Variance Inflation Factor (VIF), when VIF >5 we discarded the variable from the analysis; following this procedure we excluded stem diameter and CV vegetation cover from the analyses. We ran separate GAMs for the coefficients of variation derived from the measured structural variables. We also generated GAMs for 12 bird species (the remaining 13 species were not tested due to their low abundances). GAM analyses were performed using R 2.15 (R Development Core Team, 2012) and the packages AER, mgcv and MuMIn, as well as ggplot2 (for visualization). For GAM models, we

used a thin plate spline to smooth explanatory variables by General Cross Validation (GCV).

We used the Akaike Information Criterion (AIC) to quantify the relative support of each competing model obtained from the GAMs fitted. Since the ratio between sample size and the number of parameters was <40, we calculated the second-order AIC (AICc) following Burnham and Anderson (2002). For interpretation purposes we only considered those models in the subset ΔAICc ≤ 2. Once the ΔAICc ≤ 2 subset was defined, we calculated the respective weights (ω_i) and then calculated the relative importance (w_i) of each variable by summing the ω_i values of each model in which the variable i occurred (Burnham and Anderson, 2002), which varied between 0 and 1. $w_i = 0$ means that the given variable was not represented in the competing models, whereas $w_i = 1$ means that the variable was present in all the competing models.

3. Results

3.1. Species richness and abundance

We captured 560 individuals, corresponding to 25 species of insectivorous birds (Table S2). The most abundant species were *Basileuterus culicivorus* (36.6% of the captures), *Dendrocincla fuliginosa* (10.9%), *Microcerculus marginatus* (8.8%), *Myiopagis viridicata* (6.2%), *Xiphorhynchus guttatus* (5.9%), and *Tolmomyias sulphurescens* (4.6%). The remaining 20 species constituted 27% of the total captures. Foliage gleaners were the foraging guild with the greatest species richness ($S = 11$), followed by bark foragers ($S = 5$), flycatchers ($S = 4$), ground foragers ($S = 3$), and ant followers ($S = 2$).

3.2. Effects of habitat structure on species richness, abundance, and foraging guilds

Species richness, total abundance, and foraging guild abundance were positively correlated with four structural variables: basal area, the CV of basal area, CV of stem diameter and number of stems. These variables were highly supported across the competing models derived from the GAMs (Table 1). Species richness was positively correlated with the CV of basal area, showing a continuous increase in richness as the basal area becomes more variable (Fig. 1A). Total abundance was also positively correlated with the CV of basal area, but increasing only after passing a threshold value of 0.5 (Fig. 1B); abundance was also positively correlated with the CV of stem diameter, showing a constant increase until an inflexion point (~1.7) and after this point abundance showed a steep increase (Fig. 1D). Each bird species responded to one or a subset of structural variables which were different for each particular species, with three structural variables (basal area, and the CV of understory height and stem diameter) being the most represented across models (Table S2).

Regarding foraging guilds, ant follower and bark forager abundance were positively correlated with the number of stems (Fig. 1G and H, respectively), showing a constant increase in abundance as stem number increases, becoming steep after a threshold of 30 stems. Ground forager abundance was positively correlated with basal area, which shows a sigmoidal response (Fig. 1I). The abundance of ground foragers is also positively correlated with the CV of stem diameter, resembling an exponential increase function (Fig. 1F). Foliage gleaner abundance was positively correlated with the CV of stem diameter, resembling a sigmoidal function (Fig. 1E). Flycatcher abundance was positively correlated with the CV of basal area until a threshold value of 0.8, decreasing after that value since the abundance function of this guild resembles a parabolic function (Fig. 1C), showing that flycatchers respond positively to a slight variation in basal area but negatively to a strong variation of this feature. In Fig. 1A, C and I, confidence intervals are wide and therefore the smoothing trend may be not significant, we urge caution interpreting those results. Non-parametric estimations (fit and significance values) for each variable are available online in Table S3, and multi-model inferences (based on ΔAICc ≤ 2 subsets) are available in Table S4.

4. Discussion

In concordance with our hypothesis, complexity in intra-habitat structure explained the variation in insectivorous bird species richness and abundance, as well as the abundance of five foraging guilds within this group. Since the seminal work of Karr and Roth (1971) and later Terborgh (1985), habitat structure has been considered to be closely related to tropical bird species richness, with greater richness in more complex habitats. As with previous findings (Banks-Leite and Cintra, 2008; Cintra et al., 2006), our results suggest that mainly the variation in basal area, stem diameter, and the number of stems explained insectivorous bird diversity. Insectivorous bird diversity in our study site responded to intra-habitat structure, similar to other associations previously described for birds (Arriaga-Weiss et al., 2008; Caprio et al., 2009; De la Montaña et al., 2006; Pearman, 2002; Santana et al., 2012) and mammals (Dammhahn and Kappeler, 2008).

The spatial distribution of understory insectivores may be adequately explained by fine-scale habitat structure variation (Remsen and Robinson, 1990), which is related to the variation in foraging microhabitats (Sekercioglu et al., 2002). We found that basal area and basal area variation were the variables that explained most of the understory insectivore richness and abundance, for both individual species and foraging guilds. This is consistent with other findings reporting a reduction in richness and abundance of insectivorous birds after selective logging, which have a strong influence on basal area (Aleixo, 1999; Thiollay, 1992).

Previous studies have described the role of habitat complexity in structuring bird trophic guilds (e.g., insectivores, frugivores,

Table 1
Relative support of predictors of total species richness, total abundance, and abundance of the foraging guilds identified. w_i = sum of Akaike weights across all models where variable i occurs. Figures in bold indicate the most supported variables (CV stands for coefficient of variation).

| w_i	Total species richness	Total abundance	Ant follower abundance	Bark forager abundance	Flycatcher abundance	Foliage gleaner abundance	Ground forager abundance
Understory height	**0.83**	**1.00**		0.14	**1.00**	**1.00**	0.55
Basal area	0.13	**1.00**	0.26	0.15	0.27	**1.00**	**1.00**
Vegetation cover	0.16		0.23	0.33		**1.00**	
Number of stems	0.38	0.27	**1.00**	**1.00**			
CV understory height	0.16		**1.00**		0.16	0.31	0.32
CV basal area	**1.00**	0.55		**1.00**	**1.00**		0.34
CV number of stems	0.29		0.37	0.58	0.23		0.31
CV stem diameter	0.16	**1.00**			0.19	**1.00**	**0.67**
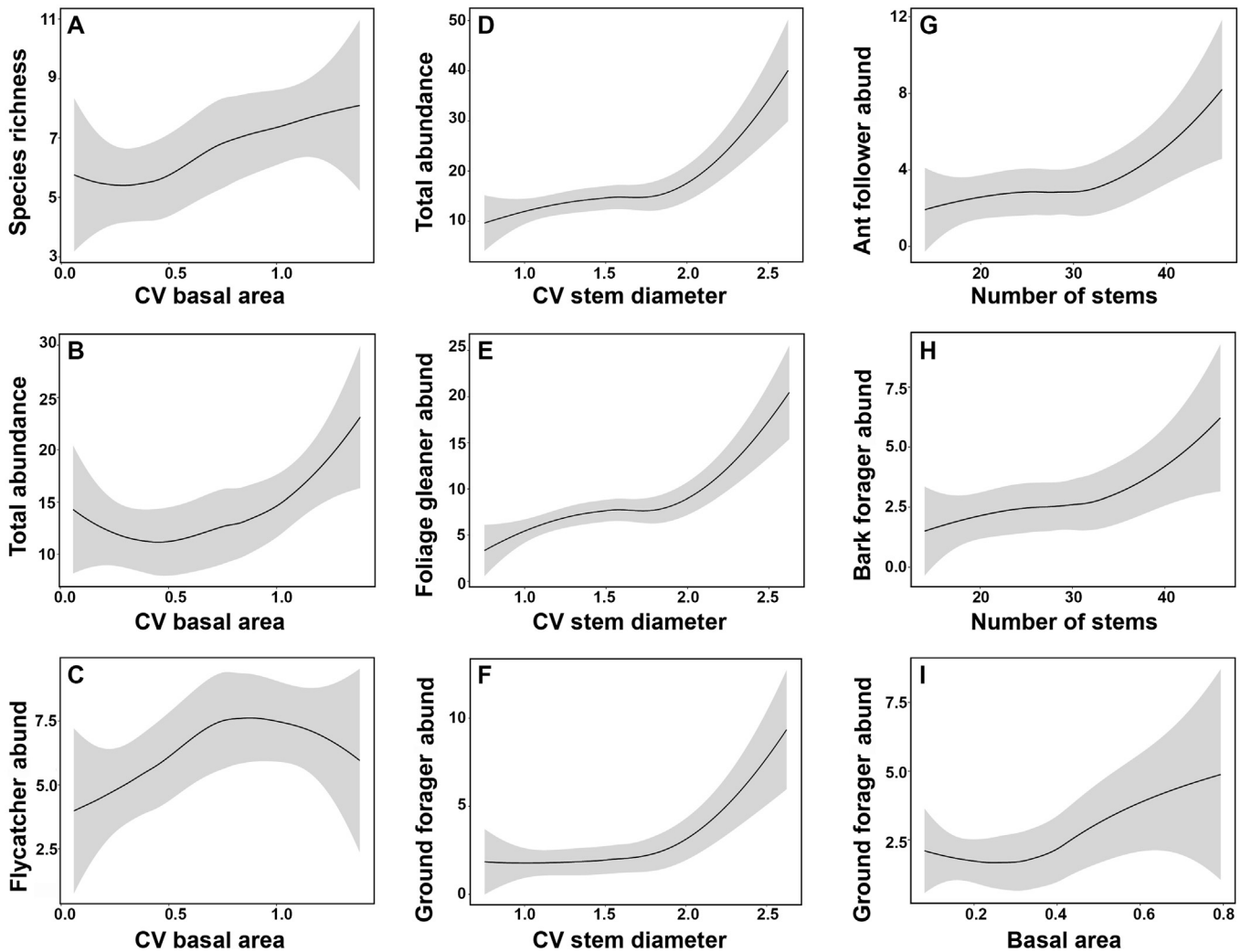
Fig. 1. Response of species richness, abundance, and foraging guild abundance to habitat structure features (CV stands for coefficient of variation). Trends and their confidence intervals were based on GAM model results (based on loess, depicted using the ggplot2 package in R 2.15, parameter settings: size = 1, span = 1).

nectarivores) with respect to habitat associations, because birds choose habitats based on structural features that generate micro-habitats (e.g., favorable temperature conditions) and may also be related to the availability of specific food items (Pearman, 2002). Our results suggest that the five foraging guilds assessed, within the insectivore trophic guild, are responding to a narrow subset of structural variables, in which basal area, stem diameter, and the number of stems explain an important part of the variance in our GAM models. In a heterogeneous environment with many different habitat structures there may be suitable conditions for many insectivorous foraging guilds (e.g., bark foragers, ant followers, flycatchers). This suggests that habitat structure and its variation may be an important factor for understanding why there are so many foraging guilds within a single habitat patch, and how they coexist.

The relationships found between foraging guilds and the structural features of the habitat are supported by the natural history of the species involved, and particularly their life history traits. Bark forager (*Picumnus granadensis* and *Veniliornis kirkii*, Picidae; and *Xenops minutus*, *D. fuliginosa* and *X. guttatus*, Furnar-iidae) abundance varied with the number of stems and the varia-tion in basal area, and this could be related to the fact that these species forage on trees, stems, and branches of different diameters

(showing changes in basal area). Contrarily, small-bodied species *P. granadensis* (12 g) and *X. minutus* (11 g), forage on twigs, woody vines, and sticks at intermediate and lower heights (Remsen, 2003; Winkler and Christie, 2002).

Large-bodied species use the three-dimensional forest space differentially: *V. kirkii* (37 g) forages on trunks to smaller branches in mid-levels of forests (Winkler and Christie, 2002), *D. fuliginosa* (41 g) is usually observed perched on vertical stems of intermediate size, but *X. guttatus* (47 g) climbs larger trees searching for insects in the bark from understory to subcanopy heights (Hilty and Brown, 1986; Remsen, 2003). Small-bodied bird species are usually related dense vegetated habitats, whereas large-bodied bird spe-cies are more common in thinned or open habitats (De la Montaña et al., 2006). Differences of foraging strata within a foraging guild, associated with bird body size, have also been described for ant-birds (Cody, 2000). Also, the abundance of *D. fuliginosa* was corre-lated with the vegetation cover and the variation in basal area, whereas the abundance of *X. guttatus* was correlated with vegeta-tion cover and the variation of understory height. Such microhab-itat segregation might explain why these two tree-climbing species, that are phylogenetically related (Moyle et al., 2009) and have a high dietary overlap (Marantz et al., 2003), may coexist in the same habitat.

We established that insectivorous bird richness and abundance, as well as the abundance of five foraging guilds within this group, were positively correlated with three forest structural features: basal area, stem diameter, and the number of stems. More important than these structural features themselves was their variation. Hence, promoting spatial variation in basal area and stem diameter in reforested areas may increase insectivorous bird richness and abundance. Those structural variables could be managed in both commercial plantations and reforested areas by planting mixed forest plantations, with species differing in growth rates and form. By promoting fine-scale structural complexity, reforested areas could be made more suitable for species depending on habitat structure such as understory insectivorous birds, which are vulnerable and sensitive to habitat disturbance.

Acknowledgments

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.actao.2014.10.002.

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