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Foraging behavioural traits of tropical insectivorous birds lead to dissimilar communities in contrasting forest habitats

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Many deforested areas worldwide have been planted with *Alnus* spp. to protect watersheds and soils. However, the effects of these plantations on biodiversity are little known yet. Contrasting forest types may impose strong environmental filters to some behavioural traits, leading to dissimilar communities. Insectivorous birds are known to be sensitive to changes in habitat structure due to their specialized foraging behaviour. We contrasted species richness, abundance and composition of insectivorous birds, according to functional behaviour groups (foraging strategy and stratum), between secondary forest stands and Andean alder *Alnus acuminata* plantations, to assess how contrasting forest types affect this bird group in the Colombian Andes. Insectivorous bird species richness and abundance were higher at the Alder plantation rather than at the secondary forest, resulting in dissimilar communities. In this regard, forest plantations act as a positive filter for foliage gleaners and flycatchers, whereas secondary forests act as a positive filter for bark foragers. Secondary forests and alder plantations impose different ecological scenarios to insectivorous birds, related to foraging strategies and foraging stratum, which ultimately leads to a dissimilar species composition.

Keywords: *Alnus acuminate*, Colombian Andes, community similarity, foraging stratum, foraging strategy, understory height

Forest plantations are increasing worldwide, covering millions of hectares across countries and ecosystems, increasing at an average annual rate of 3.6 million hectares during the 1990–2000 period (FAO 2016). Among the most common tree species used to establish forest plantations, the alder (*Alnus* spp.) is becoming increasingly common in 34 countries of Europe, Asia, Oceania and Central and South America (FAO 2006). Alder plantations are intended for productive and protective uses, currently covering 413 000 ha worldwide (FAO 2006). This species is frequently planted due to its fast growing and positive effect on the soil (Mortimer et al. 2015, Rytter and Rytter 2016) and also because of its facilitator role on forest restoration (Murcia 1997, Avendaño-Yáñez et al. 2014). However, its effects on biodiversity are still poorly understood because Alder plantations are remarkably understudied compared to *Eucalyptus* spp. and *Pinus* spp. plantations.

Recent evidence showed that Andean alder *Alnus acuminata* protective plantations are capable to hold a large diversity of bird species, being highly dissimilar to those bird communities found at neighbouring native forest stands (Castaño-Villa et al. 2014a). This could also be the case of insectivore birds, but to the best of our knowledge, no study has assessed this bird group in *Alnus* plantations. Insectivore birds respond drastically to habitat complexity structure (Shahabuddin and Kumar 2007, Moradi et al. 2009, Castaño-Villa et al. 2014b). Consequently, due to their specialized foraging strata and behaviour, it is considered as a highly vulnerable group to habitat disturbance in tropical regions (Bierregaard and Lovejoy 1989, Renjifo 1999). In this regard, forest plantations can act as a strong biodiversity moderator, modifying bird diversity and community composition (Barlow et al. 2007, Faria et al. 2007). These changes on bird communities can be measured using changes in foraging guilds or foraging strategies as a proxy (Barlow et al. 2007, Holbech 2009). Life history traits, such as foraging stratum and strategies, influence aspects related

to resource use as well as matter and energy flows in the ecosystem (Luck et al. 2012). Therefore, these traits can be sensitive and useful tools for assessing the effects of forest plantations on avifauna.

We aimed to compare the richness, abundance and composition of insectivorous birds according to foraging behavioural traits (foraging strategy and stratum) between Andean alder plantations and secondary forest stands. Given that understory insectivorous bird abundance and distribution are known to respond to habitat-specific structural features (Kattan and Murcia 2012), contrasting between alder plantations and native forests (Murcia 1997, Kattan and Murcia 2012), will show if they are subject to different environmental conditions. We hypothesized that insectivorous bird species foraging behaviour would differ between secondary forest stands and alder plantations, as each habitat may favour certain foraging-related responses.

Methods

Study area

The Central Hidroeléctrica de Caldas S.A. E.S.P. (CHEC) Protective Forest Reserve is owned and operated by the public hydropower company. This Reserve is located on the western slope of the Colombian central Andes (05° 01′N, 75° 24′W; altitude 2500 m a.s.l.); and it is part of the basin of the Chinchiná River, in the region of Caldas. This zone has an average annual temperature of 13°C and an annual precipitation of 2500 mm. The Reserve covers 3890 ha, comprising stands of native secondary growth forests in diverse successional stages (however, there are no accessible primary growth forest stands in the area, as the few remnants that still persist were not disturbed due to their inaccessibility), as well as some exotic (*Eucalyptus* spp., *Acacia* spp., *Pinus* spp. and *Cupressus lusitanica*) and native (*Alnus acuminata*) tree plantations (Castaño-Villa et al. 2014a). Those plantations are intended for a protective use only (Castaño-Villa et al. 2014a). Central Hidroeléctrica de Caldas provided the necessary permissions to carry out fieldwork.

We set eight capture points at each forest type, being careful to select stands of about the same age (35–40 years old, based on information provided by the local people) to avoid confounding effects related to forest maturity and habitat structure, which are associated with the resident avian community (Styring et al. 2011). The eight capture points at the alder plantation were located in four stands (i.e. two points per stand), ranging between 6 and 7 ha (covering ~26 ha in total). Similarly, the eight capture points at the secondary forest were located in four stands (two points per stand), where the most common species are *Montanoa quadrangularis* (Asteraceae), *Saurauia cuatrecasana* (Actinidiaceae) and *Lippia schlimii* (Verbenaceae), ranging between 5 and 9 ha (covering ~30 ha in total). In both cases, sampling locations were separated from each other by 500 m to 1 km. Common understory tree and shrub species found in the plantations included *Bocconia frutescens* (Papaveraceae), *Miconia theaezans* (Melastomataceae), *Palicourea acetosoides* (Rubiaceae), *Palicourea calophlebia* (Rubiaceae), *Sapium stylare* (Euphorbiaceae). The most common species found in the understory of the native forest stands were *Palicourea deviae* (Rubiaceae), *Hoffmannia glabra* (Rubiaceae), *Chamaedorea linearis* (Arecaceae), *Siparuna laurifolia* (Siparunaceae) and *Piper* spp. (Piperaceae) (Ramos 2010).

Bird sampling

We used mist nets to determine the avifauna present in each forest type. This method has been used in similar investigations in the tropics (Barlow et al. 2007, Holbech 2009) since it allows conducting multiple sampling, independently from observer bias (Blake and Loiselle 2001). It also allows performing direct comparisons among studies, and allows detecting silent, cryptic and cautious species (Karr 1981) such as insectivores birds. Between October 2008 and April 2009, we established four mist nets (12 × 2.5 m × 36 mm) on a monthly basis at each capture point (separated 100 m from other). Each capture point was operated for 56 h per month, with a total capturing effort of 3136 h net^{-1} at each forest type. Captured birds were marked using bands with a unique colour combination for later identification, and then individuals were released at the same capturing place. Bird species were classified following Remsen et al. (2018). Resident and migratory insectivorous bird species (i.e. those birds that have a diet mainly based on insects) were included in the analyses. Bird species were then categorized according two behavioural groups: foraging strategy (bark foragers, flycatchers, foliage gleaners and ground foragers) and foraging stratum (intermediate + canopy, and understory) following Del Hoyo et al. (1992), and corroborated with field observations. Sampling effectiveness was assessed using the average of four species richness estimators commonly used (Chao1, ACE, Jack1 and bootstrap, calculated in EstimateS 9.1.0), our field sampling effectiveness was expressed as the ratio between the number of observed and expected species (Castaño-Villa et al. 2014a, b). Using this criterion, overall sampling effectiveness in this case was 84% (sampling effectiveness in the secondary forest was 81% and in the plantation was 79%), therefore we considered our sampling representative of the insectivorous species richness present at the study area.

Data analysis

We contrasted insectivore bird diversity between both forest types (i.e. secondary forest and Alder plantation sites) and among foraging strategy and stratum through the visual inspection of the estimated species richness (S_{est}) and the lower and upper bounds of its confidence intervals (when confidence intervals do not overlap we assume significant differences at an alpha level of 0.05) (MacGregor-Fors and Payton 2013, Hanula et al. 2015). To statistically compare bird community composition between secondary forests and alder plantations, we performed a one-way analysis of similarity (ANOSIM; using the Euclidean distance as similarity measure). ANOSIM is a non-parametric test based on similarity matrices that estimates the significance level upon 9999 permutations, which is commonly used for comparing bird communities (Barlow et al. 2007, Fontúrbel and Jiménez 2014). For the general between-habitat comparison we conducted a one-way ANOSIM, whereas for the foraging

strategy and stratum comparisons we performed two-way ANOSIM tests, nesting foraging strategies and strata within habitat types. Further, to visualize potential composition differences among groups we used a non-metric multidimensional scaling (nMDS hereafter) approach. ANOSIM and nMDS tests were performed using the software PAST 3.20 (Hammer et al. 2001).

All references to abundance in this document refer to the number of captured individuals, which were reported as mean values. Recaptured individuals were not included in the analyses. Bird abundance between the alder plantation and the secondary forest was compared using a one-way nested analysis of variance (ANOVA), with mist-net capture points nested within each stand according to forest types (Murcia 1997). Goodness-of-fit to a normal distribution was assessed through a Shapiro–Wilk test. Homogeneity of variances was assessed using a Levene test. These analyses were performed using R ver. 3.4.2 (<www.r-project.org>).

Data deposition

Original data is freely available at the figshare digital repository: <https://doi.org/10.6084/m9.figshare.6900665>.

Results

We registered a total 45 insectivorous bird species (Supplementary material Appendix 1 Table A1). From those, 37 species were captured in the alder plantation stands and 28 in the secondary forest stands, being 21 species captured in both forest types (47% of the total species pool). Only two migratory species were recorded in the study area (*Setophaga fusca* and *Cardellina canadensis*). Species richness was significantly higher at the alder plantation than at the native forest (Fig. 1a). Regarding foraging strategy, estimated species richness of bark foragers was significantly higher at the native forest, whereas estimated species richness was significantly higher for foliage gleaners and flycatchers at the alder plantation (Fig. 1b); due to the low number of ground forager species present, we cannot perform any formal comparison in this case. Examining species richness by foraging stratum, there were no significant differences on species richness for understory birds, but those foraging at the canopy and intermediate heights showed a significantly higher species richness at the plantation (Fig. 1c). We captured a total of 352 individuals, 220 were captured at the alder plantation and 132 at the native forest. Overall, the average number of individuals captured per point was greater in the plantations (27.50 ± 3.54) than in the secondary forests (16.50 ± 2.04; $F_{1,8} = 10.94$, $p = 0.011$). Regarding foraging strategy and stratum, plantations had a significantly higher abundance of foliage gleaners and those birds foraging at the canopy and intermediate heights, but abundances of the other functional groups were similar between forest types as well as those foraging at the understory level (Table 1).

Bird species composition was significantly different between plantations and native forests (ANOSIM $R = 0.22$, $p = 0.004$; Fig. 2). From the 17 species exclusive to alder plantations, 65% corresponded to foliage gleaners (*Scytalopus spillmanni*, *Phyllomyias nigrocapillus*, *Poecilotriccus ruficeps*, *Mecocerculus poecilocercus*, *Vireo leucophrys*, *Cinnycerthia unirufa*, *Hemispingus atropileus*, *Conirostrum albifrons*, *Catamblyrhynchus diadema*, *Myioborus ornatus* and *S. fusca*), while from the nine species exclusive to the native forests, 56% corresponded to bark foragers (*Campephilus pollens*, *Dendrocolaptes picumnus*, *Anabacerthia striaticollis*,

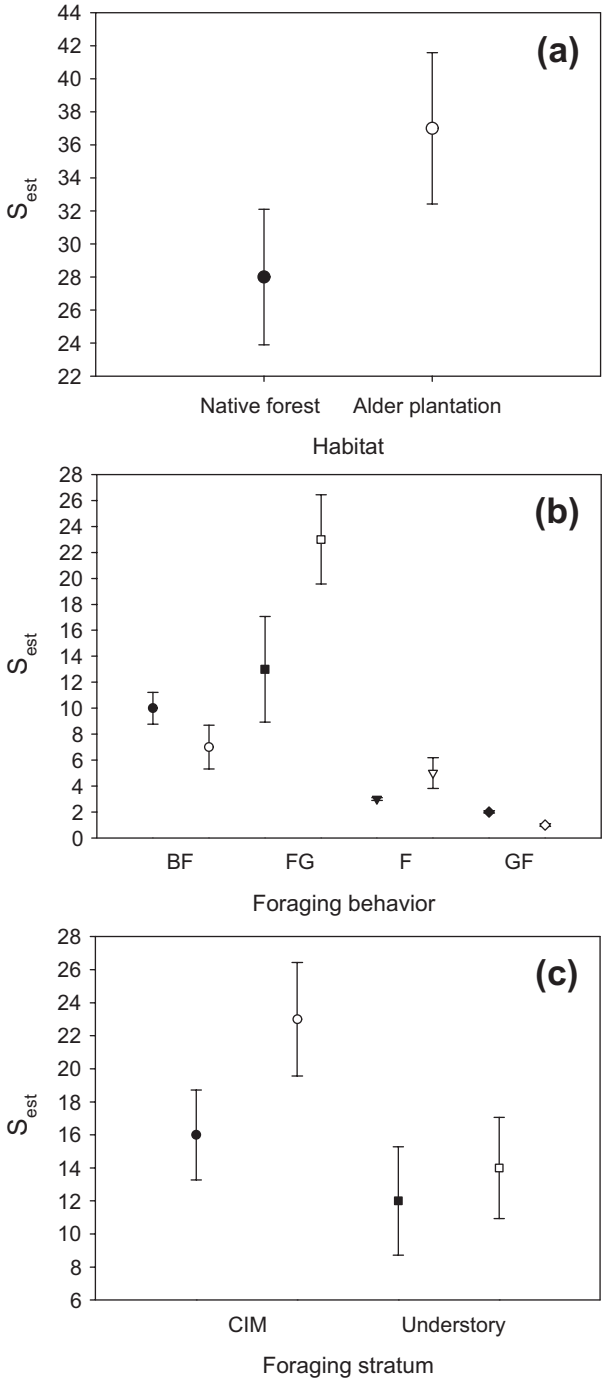

Figure 1. Estimated species richness (S_{est}) for (a) the overall comparison between native forest (black symbols) and alder plantation (white symbols); (b) comparison among foraging strategy: BF = bark foragers (circles), FG = foliage gleaners (squares), F = flycatchers (triangles) and GF = ground foragers (diamonds); (c) foraging stratum: CIM = canopy and intermediate (circles) and understory (squares). Error bars represent the 84% confidence interval of the richness estimations.

Table 1. Abundance comparison between native forest and alder plantation examined by foraging strategy and stratum. Significant comparisons after a nested ANOVA analysis are denoted with an asterisk.

Group	Alder plantation	Native forest	Test
(a) Foraging strategy			
Bark forager	3.63 ± 1.31	4.25 ± 1.44	$F_{1,8} = 0.32$, $p = 0.584$
Flycatcher	4.25 ± 1.19	2.88 ± 0.48	$F_{1,8} = 4.17$, $p = 0.075$
Foliage gleaner	19.50 ± 1.87	8.88 ± 1.89	$F_{1,8} = 9.16$, $p = 0.016$*
Ground forager	5.50 ± 2.08	1.75 ± 0.50	$F_{1,8} = 4.32$, $p = 0.071$
(b) Foraging stratum			
Intermediate + canopy	12.00 ± 3.24	7.00 ± 1.47	$F_{1,8} = 15.38$, $p = 0.004$*
Understory	15.50 ± 3.37	9.50 ± 1.87	$F_{1,8} = 4.99$, $p = 0.056$

Thripadectes holostictus and *T. flammulatus*). Examining bird composition data by foraging strategy, both forest types (ANOSIM $R = 0.08$, $p = 0.019$) and foraging strategy ($R = 0.46$, $p < 0.001$) showed significant composition differences (Fig. 3); foliage gleaners, which form a clearly separated group from the remaining ones, mainly explaining those differences. Also, when examining data by foraging stratum we detected significant differences in composition for forest type ($R = 0.23$, $p < 0.001$) and foraging stratum ($R = 0.75$, $p < 0.001$) (Fig. 4).

Discussion

Insectivorous bird diversity found in the alder plantations was dissimilar to that of the secondary forests. This results is opposite to previous reports on this matter, as similar insectivorous bird species compositions were found in native *Araucaria* plantations in Brazil (Volpato et al. 2010), native *Eucalyptus* plantations in Australia (Loyn et al. 2007, Law et al. 2014), and exotic tree plantations in Ghana (Holbech 2009). The dissimilarity in species diversity and abundance between alder plantations and secondary forests could arise as result of different environmental conditions affecting bird foraging behaviour. Alder plantations are likely to positively affect foliage gleaners and flycatchers, and negatively affect bark foragers. In the case of foliage gleaners and flycatchers, the dense understory found at the alder plantation, dominated by common pioneer and secondary plant species (Ramos 2010) with large leaf production and high vulnerability to insect attack (Newbery and Deforesta 1985), could be favouring the abundance and diversity of insectivorous birds (Holbech 2009, Sheldon et al. 2010). The dense understory composed of pioneer and early secondary species in alder plantations results from the physiognomy of its trees (mainly determined by its canopy type), and the plantation location on sunny slopes, allowing abundant light to enter through the understory. On the other hand, the reduced bark forager diversity may result from the homogeneity in tree size within plantation (e.g. diameter at breast height is similar among most of the planted trees). Bark forager diversity is known to respond to the variation on tree diameter values and not to the diameter values itself (Castaño-Villa et al. 2014b).

Structural differences between the forest types can also explain the low bird assemblage similarity between the alder plantations and the secondary forests (only 47% of the species were present in both forest types). This pattern may emerge from strong differences in richness and abundance of particular foraging groups. For instance, foliage gleaners are the most common group at the alder plantations, with 23 species detected and 12 of them (52%) being found only there. It is possible that vertical vegetation structure within the alder plantations (having only two strata: understory and canopy) is influencing foliage gleaner habitat use. It is likely that this understory discontinuity from the ground to the canopy will force foliage gleaner birds (including

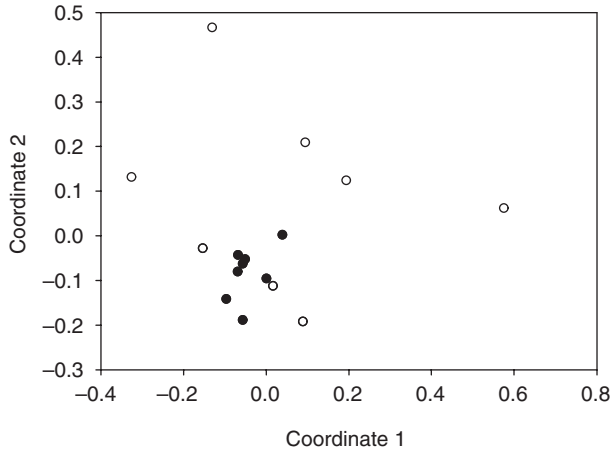

Figure 2. Non-metric multidimensional scaling (nMDS) plot of the overall species composition between native forest (black symbols) and alder plantation (white symbols). Ordination stress = 0.12.

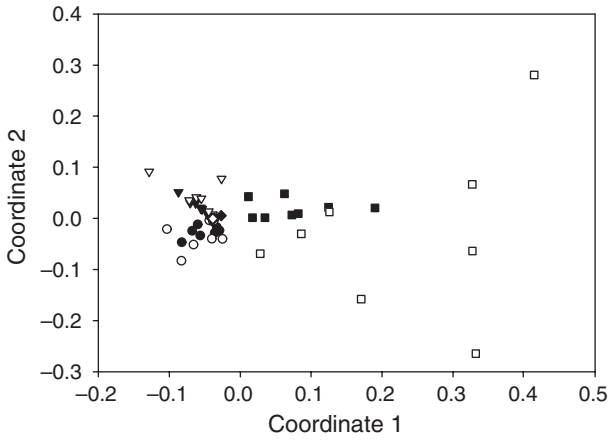

Figure 3. Non-metric multidimensional scaling (nMDS) plot of the species composition between habitats (black symbols = native forest, white symbols = alder plantation) and among foraging strategies (circles = bark foragers, squares = foliage gleaners, triangles = flycatchers, diamonds = ground foragers). Ordination stress = 0.08.

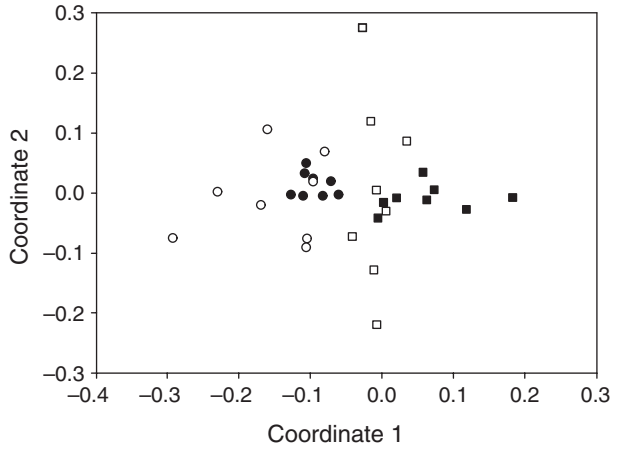

Figure 4. Non-metric multidimensional scaling (nMDS) plot of the species composition between habitats (black symbols = native forest, white symbols = alder plantation) and between foraging strata (circles = canopy and intermediate, squares = understory). Ordination stress = 0.11.

those canopy or sub-canopy foragers such as *P. nigrocapillus*, *M. poecilocercus*, *V. leucophrys*, *H. atropileus*, *C. albifrons* and *M. ornatus*) to forage more intensively at the plantation understory, where vegetation and insects are usually more abundant. This also may be conditioning species from other foraging strategies (such as flycatchers: *Pyrrhomyias cinnamomeus* and *Myiarchus cephalotes*, or bark foragers: *Colaptes rivolii*, *Xiphorhynchus triangularis* and *Margarornis squamiger*) to forage at the understory, where they are able to find perching sites and shelter against predators. Such idiosyncratic responses may be responsible of the larger functional space observed in Fig. 2–4, despite the plantation represents a more homogeneous habitat, microclimate conditions are likely to create a patchy distribution of food resources (i.e. insects), increasing the variation on bird species richness among capturing points. Another non-mutually exclusive explanation for this pattern is territoriality, as many insectivorous species actively defend territories, they may have to defend larger areas in lower quality habitats. Besides, the higher capture numbers at the alder plantation should be interpreted with caution, as this pattern is likely to result from the association between habitat structure and foraging behaviour (Pearson 1975), which may be leading insectivorous birds to be more frequently captured at the plantation understory, compared to the native forest, simply because they are frequently flying at the mist net height (Blake and Loiselle 2001).

Management implications

The Colombian central Andes is one of the most biodiverse areas in the world, but it is one of the most threatened ecosystems as well. Past deforestation and land-use changes have significantly altered this area during the 20th century, making its present conservation and management a challenging issue. In this sense, our results show that forest plantations based on native tree species (such as the Andean alder) are able to hold a non-random subset of species, but they cannot replace native forests. Therefore, aiming to preserve bird diversity in this hotspot, it is crucial to: 1) protect the extant native forest remnants, 2) encourage reforestation with native species, and given that both forest types are complementary in terms of bird diversity, 3) provide landscape-level connectivity between both habitat types. If these three conditions are met, properly-managed landscapes could take advantage of the complementary role of native forest plantations and act as a relief to native habitat loss and land-use change pressures. Therefore, this information may be used by policy-makers to think about biodiversity-friendly landscapes and their long-term implications.

Conclusions

Alder plantations and secondary forests seem to impose different environmental conditions to birds, which result in differences on diversity of foraging behaviour as well as in species composition. While alder plantations may constitute suitable habitat for many insectivorous bird species, they do not constitute a substitute of native forest stands, but rather act as complementary habitat for the regional insectivorous avifauna. Examining foraging strategies in addition to species diversity may depict a more complete and accurate scenario of the actual conservation value of forest plantations across countries and ecosystems, as plantations are likely to modify bird ecological scenario, and its effects can widely vary depending on the tree species planted and how the plantation was established.

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Supplementary material (available online as Appendix wlb-00483 at <www.oikosjournal.org/appendix/wlb-00483>). Appendix 1.