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Can habitat specialization patterns of Neotropical birds highlight vulnerable areas for conservation in the Atlantic rainforest, southern Brazil?

Luiz dos Anjos [a,*], Cathy D. Collins [b], Robert D. Holt [c], Graziele H. Volpato [d], Edson V. Lopes [e], Gabriela M. Bochio [f]

[a] Departamento de Biologia Animal e Vegetal, Universidade Estadual de Londrina, CP 10011, Londrina, Paraná 86057-970, Brazil
[b] Department of Biology, Colby College, Waterville, ME 04901-8840, United States
[c] Department of Biology, University of Florida, Gainesville, FL 32611, United States
[d] Programa de Pós-Graduação em Ciências Florestais, Universidade Federal de Viçosa, Bolsista de Pós-Doutorado Júnior CNPq, Viçosa, Minas Gerais 36571-000, Brazil
[e] Instituto de Biodiversidade e Florestas, Universidade Federal do Oeste do Pará, Santarém, Pará 68040-070, Brazil
[f] Programa de Pós-Graduação em Ciências Biológicas, Universidade Estadual de Londrina, CP 6001, Londrina, Paraná 86051-970, Brazil

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ABSTRACT

Patterns of habitat specialization can be used to infer conservation risks for species whose habitats are being degraded or lost due to anthropogenic activity. We assigned levels of forest type specialization to birds based on their occurrence and local abundance in three basic types of Atlantic rainforest in southern Brazil: seasonal semi-deciduous forest, mixed rainforest, and dense rainforest. We hypothesized that forest types would contain birds characterized by different levels of specialization. Specifically, we predicted that the dense forest would contain more specialists due to its higher plant species richness. Our study focused on a major clade of the suboscine Passeriformes (Thamnophilidae–Furnariidae), the majority of which are understory insectivorous species. We used field data from 16 locations including 35 sites spanning the major forest types in southern Brazil. We found (1) substantial variation in abundance among sampling locations for a single bird species within and between forest types; (2) species-specific associations with forest types; and (3) spatial aggregation among species that share similar levels of specialization. Using our method of qualitative scoring of forest type specialization, three species were considered habitat specialists (*Xenops minutus*, *Leptasthenura setaria*, and *Cranioleuca pallida*), twelve species were moderate specialists, sixteen were generalists, five were complete generalists, and twelve species were too rare to be included in the analysis. Contrary to our hypothesis, both mixed and dense forests were equally dominated by specialists. We discuss the implications of our approaches for conservation assessment and planning, both at the single-species level and for aggregate species in assemblages.

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1. Introduction

The Atlantic rainforest biome is characterized by high biological diversity (Myers et al., 2000). However, the Atlantic rainforest, is not a homogeneous biome but rather is composed of several different forest types (Veloso et al., 1991). In southern Brazil, plant ecologists subdivide the Atlantic rainforest biome into three main forest types with quite distinct vegetation composition (Fig. 1). In brief, these are mixed rainforest, which occurs farther south in the Atlantic rainforest and is dominated by the conifer *Araucaria angustifolia*; evergreen dense forest, which occurs along the coast;

and seasonal semi-deciduous forest, located largely in the interior. The latter two forest types are not dominated by any single tree species (Veloso et al., 1991; Oliveira-Filho and Fontes, 2000). The Atlantic rainforest is considered one of the most important biodiversity hotspots in the world due to its high rates of endemism and its very considerable forest loss. This pattern of habitat destruction combined with endemism makes this region one of grave conservation concern (Myers et al., 2000; Silva and Casteleti, 2003; Ribeiro et al., 2009; Sloan et al., 2014).

Conservation at the species level requires a quantitative understanding of patterns of habitat specialization. Habitat specialization can occur at hierarchical spatial scales. At a coarse scale, species could be specialized to particular forest types. Moreover, heterogeneity within forest types can permit a finer-scale

* Corresponding author. Tel.: +55 43 33714911; fax: +55 43 33714207.
E-mail address: llanjos@sercomtel.com.br (L. dos Anjos).

specialization. Highly specialized species (among and within forest types) should be more vulnerable to local extinction, particularly in landscapes fragmented due to forest loss and degradation (Henle et al., 2004; Devictor et al., 2008; Colles et al., 2009). Worldwide, habitat loss and degradation may have a disproportionately negative effect on specialists (Clavel et al., 2011). Characterizing spatial patterns of distribution for specialists among and within forest types may help managers prioritize regions for conservation. Specifically, areas harboring more habitat specialists may warrant more attention. In our study, we use local abundance and occurrence data to characterize the degree of forest-type specialization in insectivorous birds.

Understory insectivorous birds of tropical rainforests are of special concern for conservation due to their demonstrable sensitivity to anthropogenic disturbance (Boyle and Sigel, 2015; Bregman et al., 2014; Arcilla et al., 2015; Stratford and Stouffer, 2015). The sensitivity of these species to disturbance has been attributed to their specialized preference for distinct microhabitat foraging substrates; this is particularly true for terrestrial (ground-foraging) insectivores (Stratford and Stouffer, 2015). In Amazonia, for example, insectivorous terrestrial birds occupy microhabitats not found in secondary forests (Stratford and Stouffer, 2013). Although some understory species in Amazonia can use secondary forest after as little as twelve years of recovery after logging, other species may require more than 30 years of secondary growth (Powell et al., 2015). This sensitivity to disturbance makes understory insectivorous birds, and particularly terrestrial species, an ideal and relevant model group for studying the spatial distribution of habitat specialists.

Our first objective in this paper is to characterize bird species in the southern Atlantic rainforest by their degree of forest type specialization. Although some aspects of microhabitat use have been explored for a few bird species in a small number of sites in the semi-deciduous forest (Poletto et al., 2004; Lopes et al., 2006; Volpato et al., 2006), there has been little prior work that characterizes habitat specialization more broadly in this biome. We should note that in this paper, we use the terms "habitat specialization" to include forest-type specialization, but our analyses also suggest finer-scale dimensions of habitat specialization, within forest types.

Our second objective is to assess overall community-level specialization across the three forest types (Julliard et al., 2006). One might a priori expect that forest types differing in plant species diversity could vary correspondingly in bird species diversity and specialization. Broad meta-analyses have revealed that bird species diversity is correlated with plant species diversity (Castagneyrol and Jactel, 2012). There are many possible mechanistic processes that could lead to this correlation, but for our purposes, the existence of this correlation provides the testable hypothesis that the forest type with the highest plant species diversity should also sustain, besides the highest diversity of bird species, higher overall community-level habitat specialization. Dense forest has a higher diversity of tree species in the Atlantic rainforest than mixed and semi-deciduous forests (Thomaz and Monteiro, 1997; Oliveira-Filho and Fontes, 2000). Therefore, our initial hypothesis is that the species in the dense forest tend overall to be more specialized in their use of the regional range of forest types.

Our previous work has demonstrated that a lower average abundance of a species in a forest type is associated with greater sensitivity to fragmentation of that particular forest type, which likely increases the probability of local and even global extinction (Anjos et al., 2011). In this study, we quantify and compare abundances as a tool for assigning species an overall level of specialization to forest types in Atlantic rainforest. Using these assignments, we quantify the degree to which forest types contain specialized versus generalist bird species by characterizing the overall magnitude of habitat specialization in the bird communities of those forest types. We suggest that finding greater habitat specialization within bird communities of particular forest types warrants attention when selecting priority areas for conservation.

2. Methods

2.1. Study area

The Atlantic rainforest stretches along coastal Brazil from the northeast to the far south (Bencke et al., 2006), and reaches into Argentina and Paraguay. The three forest types we studied (mixed, dense, and semi-deciduous forests) characterize the southern Atlantic rainforest in the states of Paraná, Santa Catarina, and Rio Grande do Sul; our study focuses on the first two of these (Fig. 1). Dense forest occurs from sea level to 1200 m in elevation, semi-deciduous forest from 200 to 800 m, and mixed forest from 800 to 1200 m. Overall, dense forest has less variable temperature
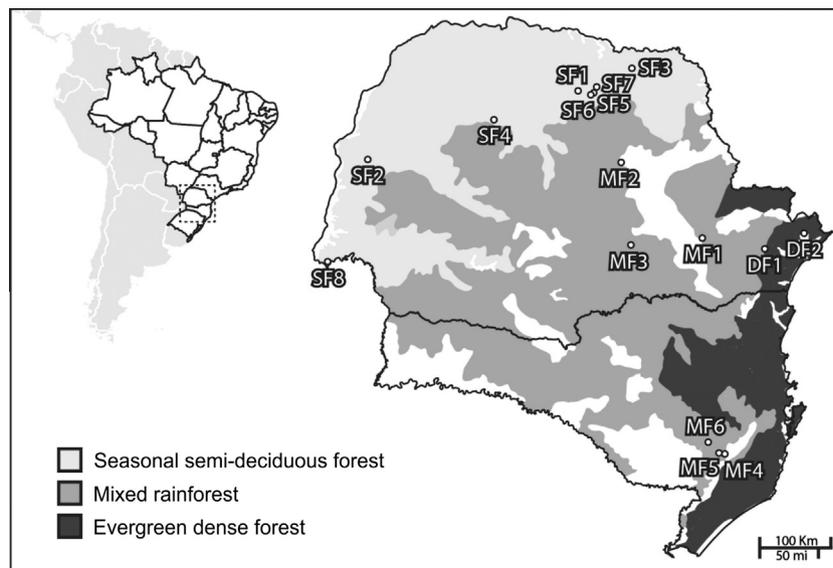

Fig. 1. Map of the locations of the studied areas in the Brazilian Atlantic forest, shading indicates forest types in the natural landscape before modern disturbance (see Table 1); blank represents grassland areas. Map was modified from IBGE, U.S. Geological Survey, 1992.

and rainfall through the year, semi-deciduous forest has a season dry period, and mixed forest is more variable in temperature, sometimes even with several days of frost in the winter (Oliveira-Filho and Fontes, 2000; Mazza et al., 2005). For a more detailed description of these forest types, see Oliveira-Filho and Fontes (2000) and Anjos et al. (2011).

For the present study we selected 16 locations for field work; some are protected as natural reserves, but others are unprotected (Fig. 1 and Appendix Table A1). Our site selection aimed to encompass the largest and best-preserved remnants of continuous forest for each forest type. In fact, three sites are the largest remaining tracts of each forest type in the southern Atlantic rainforest: Iguassu National Park (area SF8; 185,000 ha) for semi-deciduous forest, Floresta Nacional de Irati (area MF3; 3500 ha) for mixed forest; and Área de Preservação Ambiental de Guaraqueçaba (area DF2; 192,000 ha) for dense forest (Fig. 1). The availability of well-preserved areas in the highly fragmented Atlantic rainforest limited our choice of study locations. We assigned our study sites *a priori* to the three forest types, based on an existing vegetation map (modified from IBGE 1992).

2.2. Bird species

We investigated forest type specialization of a major taxonomic group within the suboscine clade of Passeriformes. The New World suboscines – one of the largest endemic vertebrate radiations on the South American continent (Ohlson et al., 2013) – include many taxa of conservation concern. Our study includes antbirds, gnateaters, antpittas, tapaculos, ant-thrushes, ovenbirds, and woodcreepers, in the families Thamnophilidae, Conopophagidae, Grallariidae, Rhinocryptidae, Formicariidae, and Furnariidae (subfamilies Sclerurinae, Dendrocolaptinae, and Furnariinae). These families contain many species in the Atlantic rainforest (Silva and Casteleti, 2003) and collectively comprise a majority of its understory avifauna. We follow the taxonomy of the South American Classification Committee (SACC; Remsen et al., 2014).

This group of species is monophyletic, which is desirable in studies of habitat specialization, because we can largely control for phylogenetic effects that confound comparisons of habitat specialization at broad taxonomic scales (Irschick et al., 2005; Hackett et al., 2008; Moyle et al., 2009; Ohlson et al., 2013). Many suboscines inhabit the forest understory, and several are terrestrial, which may heighten vulnerability to habitat destruction and fragmentation (Stratford and Stouffer, 2013, 2015; Powell et al., 2015). They defend and advertise territories, frequently calling during breeding, which facilitates point censuses (Krabbe and Schulenberg, 2003a,b; Remsen, 2003; Whitney, 2003; Zimmer and Isler, 2003; Chesser, 2004). Some species have specialized foraging requirements, for instance using particular substrates (Krabbe and Schulenberg, 2003a). Although most of the species in our study are insectivorous, several do feed to a degree on non-insect invertebrates and on fruits or small vertebrates. Judging from available distribution maps (Krabbe and Schulenberg, 2003a,b; Remsen, 2003; Whitney, 2003; Zimmer and Isler, 2003; Chesser, 2004), 71 suboscine species might potentially occur in our region in forested habitats, but not all were observed during our study. Overall, the ecology of this group is rather poorly known, so our study should be viewed as a first step toward a rigorous quantification of patterns of habitat specialization in this group.

2.3. Bird sampling

To assess local avian abundance, point counts (Blondel et al., 1970; Bibby et al., 1993) were performed in each area. We located six point counts at 200 m intervals along a 1000 m trail. We considered each trail with its set of six points to be a single site. Because we were working in protected areas, our sampling was limited to existing trails, preventing a fully randomized sample design. However, sites were always located in the forest interior, at least 300 m from the forest edge. More than one site was sampled in large areas. For example, in SF8 (Iguassu National Park), a total of 5 different sites (i.e., 5 trails) were sampled to obtain better coverage of this very large reserve. These sites were sufficiently spaced (by at least 500 m) that censuses at different sites would not detect the same individual birds. In total, 35 sites were sampled; 15 in the semi-deciduous forest, 12 in the mixed forest and 8 in the dense forest. Our sample unit is the site; thus, for a species that occurred in all sites, we would obtain 35 values of its abundance in our study system.

Point counts were performed at each site during the morning, once each spring and summer (September–February), during 2004 and 2005; thus, each site included a total of 24 point samples (4 dates, 6 points per site). Field studies using point counts in the Atlantic rainforest have shown that 3–5 days of sampling suffice to detect more than 90% of the observed species recorded within the sample area over much longer sampling periods (Anjos, 2007; Cavarzere et al., 2013). Points on the trail were sampled consecutively, starting with the first point at each site, which was sampled in the early morning when vocal activities of diurnal birds began. We sampled for 15 min at each point, with a 15 min break between points; surveys for each morning finished 2.75 h after the first sampling point was started. Some authors have recommended a 10 min sampling period when applying point counts (e.g. Buskirk and Mcdonald, 1995). However, a recent study on the evaluation of methodological protocols using point counts in the Atlantic rainforest close to our study area, suggested that sampling periods longer than 10 min were more effective, consistent with our protocol (Cavarzere et al., 2013). Because we obtained a single value of abundance per site, differences in activity among species during mid-morning should have a limited bias, given our broad comparative goals. Care was taken to ensure that the same singing individual was not counted across consecutive points. The detection radius at each point was 100 m; most species can be heard up to 70–80 m, with the exception of *Grallaria varia* (Variegated Antpitta) and *Chamaeza campanisona* (Short-tailed Ant-thrush), which can be heard beyond 100 m. Therefore, when those species were detected to be singing beyond a 100 m distance, they were not included in that particular point sample. This method was found to be appropriate in previous studies (Poletto et al., 2004; Lopes et al., 2006; Volpato et al., 2006). Four observers performed point counts, each of whom had extensive previous knowledge of the avifauna. To minimize bias introduced by multiple observers, the researchers standardized their sampling protocols together in the Parque Estadual Mata dos Godoy, led by L. dos Anjos, who has performed point counts in the reserve since 1995 (for other details of bird sampling, see Anjos et al. (2011).

We recognize that our point count procedure does not consider subtle differences in detectability or allow us to calculate actual densities for each species, but we believe the data are useful for detecting large differences in abundance among populations within a species, and among different forest types (as has been shown in other studies, see Bibby et al., 1993).

2.4. Data analyses

Our index of abundance for a given species at a site was estimated by dividing its total point contact number by the total number of point samples (24) in each site (Blondel et al., 1970; Bibby et al., 1993).

To characterize forest use, we assigned each species a qualitative forest type specialization score (1–4, from most generalized

to most specialized) using one of two approaches. One approach employs abundance and occurrence data (Rank Occurrence–Abundance Profiles, ROAPs, Collins et al., 2009), and the other relies solely on occurrence patterns (used given insufficient data to construct ROAPs). In earlier publication (Collins et al. 2009) the word "occupancy" was used instead of "occurrence" (see Anjos et al., 2011), but because prior usage of the term "occupancy" is slightly different from our usage (e.g. Mackenzie et al., 2002, 2006), we will use the term "occurrence" here.

For the ROAPs we used all the local estimates of abundance (including zeros) within each forest type. We first ranked sites by our index of the local abundance of a species. We then plotted the values of this index against the rank of the sites on the abscissa, including all the sites with zeros. Next, we divided the rank by the total number of sites sampled in each forest type to standardize the abscissa ("relative rank"), which permitted comparison of ROAPs across forest types with different numbers of sampled sites. ROAPs provide a graphical representation of spatial variation in abundance for each species within a forest type. Specifically, by comparing the y-intercepts (maximum local abundance) and shape of the curve, as well as the x-intercept (which provides the spatial extent, occurrence), ROAPs permit a visual contrast of abundance patterns across forest types (examples in Fig. 2).

We tested for differences between the distributions of abundances (ROAPs) among each pair of forest types using a resampling procedure. Following Collins et al. (2009), we sampled the data 1000 times, randomizing forest type among the samples. For each run, we calculated the area between the two ROAPs, a statistic we refer to as D^*. A large value of D^* can reflect differences in mean abundance, or differences in the heterogeneity of abundances among sites, or both. For each species, we calculated the D^* for each of the three possible pairwise combinations of forest types. The area was calculated as the integral of the absolute value of the difference between distributions; if the ROAPs crossed once, the two sub-areas were added (so D^* was always positive). Finally, we compared the empirical D^* to the distribution generated by randomization and considered results significant for $p < 0.05$ using a one-sided test (i.e., a high observed D^*). We applied a correction for multiple tests, controlling for false discovery rate by setting a threshold of 0.05 (61 total tests: 13 species for which we performed one habitat pair comparison plus 16 species for which we conducted three habitat pair comparisons; Benjamini and Hochberg, 1995).

We conducted these tests only for species present at four or more sites (minimal number of occurrence needed to calculate D^*) in either two or three forest types; for these species, the results of the D^* tests were used to assign a specialization score to the species (see below). For species that did not meet this criterion, we based our assignment on occurrence patterns alone. We calculated the occurrence rate for a bird species in a forest type by dividing the number of sites at which it was recorded by the total number of sampled sites, rounding the occurrence measures to the nearest tenth (e.g., to 0.1, 0.2, etc.). A species was considered to have its habitat use associated with a single forest type when the difference in the occurrence measures between the forest types exceeded 0.3. Typically, associations were much stronger than described by this cut-off. We feel it would be unreasonable to make inferences about forest type specialization for very scarce or localized species, which we deemed to be those that occurred in six or fewer sites. Thus these species are excluded from our quantitative analyses. We present data on these species (see Appendix) and in the Discussion reflect on potential biases that not including these rare species might have for our conclusions.

Bird species that occurred in only one forest type were deemed to be forest type specialists and assigned the highest specialization score, level 4. Those species in more than one forest type but with significantly greater abundance in one forest type over another

(using the D^* criterion and visual inspection of the patterns), or with a significant difference in occurrence (for species too scarce to make D^*) are called moderate specialists, and categorized as level 3. Species associated with two forest types with no marked difference in abundance (or occurrence, for species where D^* is inappropriate) between the types are called generalists, categorized as level 2. Finally, those with no significant difference in either occurrence or overall abundance among the three forest types we called complete generalists, categorized with a score of 1.

With these assignments of degree of forest type specialization in hand, we then compared community-level patterns of specialization using two approaches. First, for a given forest type, we aggregated species lists across all sites of that type, and calculated the median specialization scores for this set of bird species. We did this for each forest type, and assessed overall differences among the forest types in degree of specialization using a Kruskal–Wallis test ($p = 0.05$). We compared both median specialization scores and average species richness across each of the three pairs of forest types (i.e., semi-deciduous × mixed, semi-deciduous × dense and dense × mixed) using a Mann–Whitney U-test ($p = 0.05$).

We used multivariate techniques to characterize and compare assemblages at each site with respect to their collective levels of specialization. We did not weight by species abundance, but tallied specialization scores from the species lists. To visualize communities, we used nonmetric multidimensional scaling (NMDS; Clarke, 1993). Using the resemblance matrix from the NMDS, we conducted a one-way ANOSIM, Analysis of Similarities (Clarke, 1993) to test for significant differences in specialization scores among the three forest assemblages. We also performed a similarity profile test (SIMPROF, Similarity Profile; Clarke, 1993) to test whether community structure related to specialization ranks emerged, without the *a priori* assigning of species to their forest types. We drew 1000 random subsets of data and compared the cluster profile (presented as a hierarchical dendrogram) with our empirical data. Groupings detected by SIMPROF are depicted on the NMDS plot (Appendix Fig. A1). For all analyses, data were transformed by dispersion weighting transformation (analogous to square-root transformation in more classical statistical tests), which minimizes the effect of highly abundant and widespread species on the outcome (Clarke, 1993). Bray–Curtis similarities were used to construct the distance matrices between sites. All analyses were conducted using PRIMER 6 (Clarke and Gorley, 2006).

The multivariate tests were performed on the full data set and on a reduced dataset that excluded seven species for which differences in abundance among forest types were no longer significant after correcting for multiple tests (see above). Because both multivariate analyses yielded qualitatively similar results, we chose to retain the full list of species in these analyses and present these results below.

3. Results

Cumulatively, we recorded fifty seven bird species across the 35 study sites. It was not possible to quantify forest type specialization level for twenty one species because they occurred in six or fewer sites. In the Appendix (Fig. A2), we present data for these species and discuss the issue of species not sampled with our field protocol. Among the thirty six species that were assigned levels of forest type specialization, twenty three used the understory and eight were terrestrial foragers (Table 1).

The first fundamental feature of the studied suboscines revealed by the ROAPs is that even for relatively abundant species within their preferred habitat, we observed a wide range of local abundances. Some sites appear to be "hot spots" with high relative abundances of a given species, whereas at other sites the species is
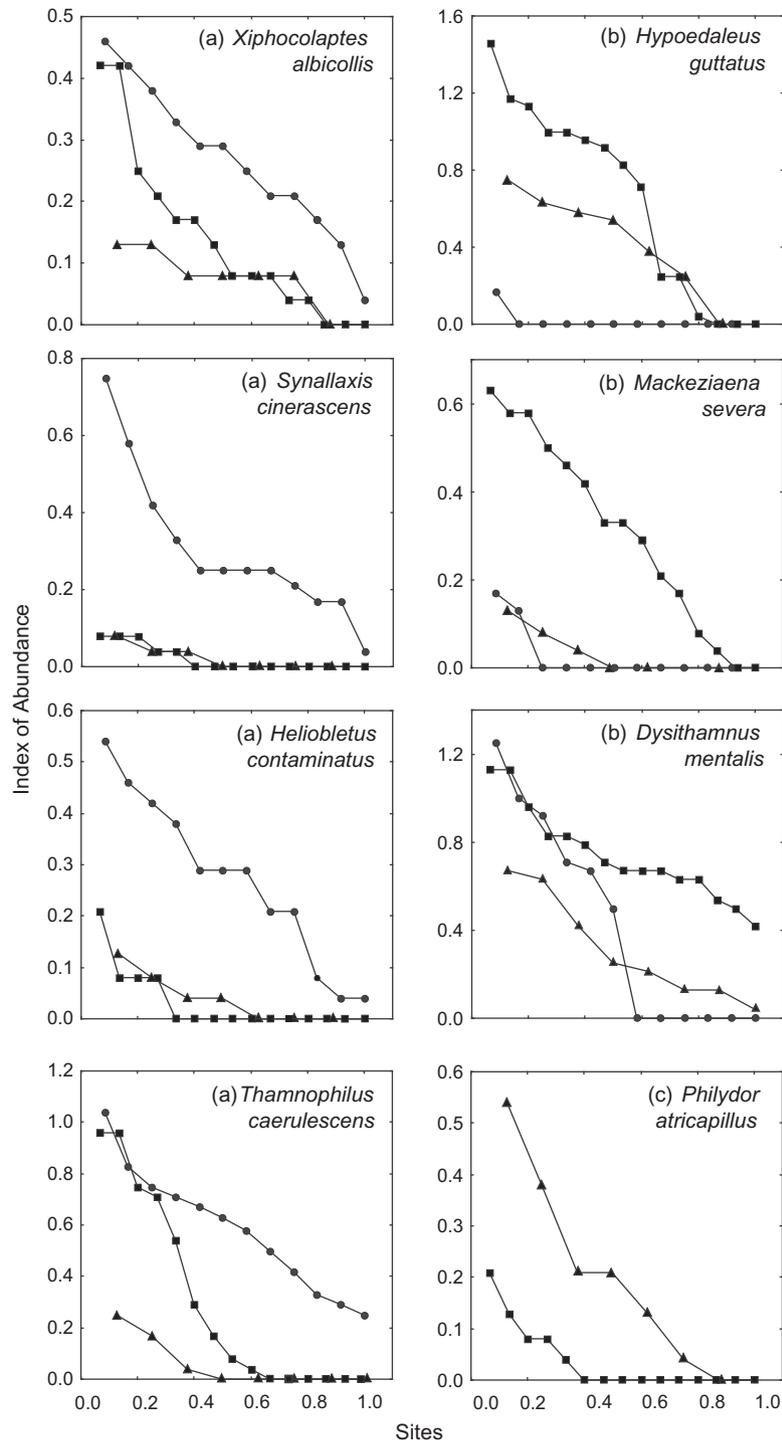
Fig. 2. Index of abundance of bird species plotted against the relative rank of the sites on the abscissa, including all the sites which had zero-value estimates of abundance (ROAPs, see Section 2). Bird species shown are those that appear to have been associated strongly with a particular forest type: (a) species deemed relatively specialized to mixed rainforest (—●—); (b) species that seem specialized to seasonal semi-deciduous forest (—■—), and (c) a species specialized to evergreen dense rainforest (—▲—).

relatively rare. The second basic feature is that the shape of ROAPs differed quite considerably among the thirty six analyzed species (see examples in Fig. 2).

Using our method of qualitative scoring of specialization, three species were considered to be habitat specialists (level 4), twelve species were considered moderately specialized (level 3), sixteen were generalists (level 2), and five were complete generalists (level 1; Table 1). The medians of habitat specialization values for bird assemblages in each site were different among the three forest types (Kruskal–Wallis test, $p = 0.005$). A paired post hoc

comparison revealed, however, that the forest type specialization of bird assemblages is similar between the mixed and dense forests (Mann–Whitney U-test; $p = 0.62$). Bird assemblages in both the mixed and dense forests reached higher levels of specialization than in the semi-deciduous forest ($p = 0.008$ for both comparisons, Mann–Whitney U-test).

Consistent with the univariate tests, bird composition (in multivariate space) among the three forest types differed significantly with respect to the degree of specialization (Fig. 3; one-way ANOSIM, $r = 0.663$, $p = 0.001$). There are three reasonably distinct

Table 1

Forest specialization of each bird species (MF, mixed rainforest; SF, seasonal semi-deciduous forest; DF, evergreen dense rainforest) and levels of forest type specialization (LS; 1, complete generalist; 2, generalist; 3, moderate specialist; 4, specialist). Superscript (1) indicates species that frequently use the understory and (2) indicates terrestrial species. See methods for details.

	Forest specialization	Levels of habitat specialization
Family Thamnophilidae		
Hypoedaleus guttatus	SF, DF	2
Batara cinerea[1]	MF, DF	2
Mackenziaena severa[1]	SF	3
Thamnophilus caerulescens[1]	MF	3
Dysithamnus mentalis[1]	SF	3
Rhopias gularis[1]	DF	3
Herpsilochmus rufimarginatus	SF, DF	2
Drymophila malura[1]	MF, SF	2
Pyriglena leucoptera[1]	SF, DF	2
Family Conopophagidae		
Conopophaga lineata[1]	MF, SF, DF	1
Family Grallariidae		
Grallaria varia[2]	MF, SF, DF	1
Hylopezus nattereri[2]	MF	3
Family Rhinocryptidae		
Eleoscytalopus indigoticus[2]	MF, SF, DF	1
Scytalopus speluncae[2]	MF, DF	2
Family Formicariidae		
Chamaeza campanisona[2]	MF, DF	2
Chamaeza ruficauda[2]	MF, DF	2
Family Furnariidae		
Sclerurus scansor[2]	MF, DF	2
Sittasomus griseicapillus	MF, SF, DF	1
Dendrocincla turdina[1]	SF, DF	2
Dendrocolaptes platyrostris	MF, SF	2
Xiphocolaptes albicollis	MF	3
Xiphorhynchus fuscus[1]	MF, DF	2
Lepidocolaptes falcinellus[1]	MF	3
Xenops minutus	DF	4
Xenops rutilans	SF, DF	2
Lochmias nematura[2]	MF, DF	2
Heliobletus contaminatus	MF	3
Philydor atricapillus	DF	3
Philydor rufum	MF, SF	2
Anabacerthia lichtensteini	SF	3
Syndactyla rufosuperciliata[1]	MF	3
Automolus leucophthalmus[1]	SF, DF	2
Leptasthenura setaria	MF	4
Cranioleuca pallida	DF	4
Synallaxis cinerascens[1]	MF	3
Synallaxis ruficapilla[1]	MF, SF, DF	1

clusters in multivariate space (Fig. 3), with two clusters incorporating two forest types (indicated by different symbols), and one outlier.

The dendrogram resulting from group-average linking and the SIMPROF test (*p* < 0.05; see Appendix Fig. A1) revealed comparable patterns of similarity among sites in community-level specialization scores, as found in the NMDS ordination. For instance, all the mixed forest sites clustered with two well-defined groups (the dark lines indicate significant groupings), and one SF8 site was quite distinct from all the other sites examined. Two of the dense forest sites clustered near the mixed forest sites, while the other dense forest sites clustered with four of the semi-deciduous forest sites.

4. Discussion

Preserving forest types that contain many specialists, compared to other forests types, should be of particular concern to conservationists (see Devictor et al., 2008). We have shown that in both mixed forest and dense forest sites, habitat specialists dominate the studied suboscine bird assemblages. Our work suggests that conservation action should not focus on dense forest areas only, but also encompass tracts of mixed forest.

The highest numbers of moderate specialists and specialists recorded were in the DF1 and MF1 locations (each site in those locations had nine or ten species in these categories). Intriguingly, those locations are in the same general region of our study system (Fig. 1). Both locations are at higher elevation in Atlantic rainforest, between 900 and 1000 m. Thus, we believe that among the study locations, this region of higher altitude encompassing DF1 and MF1 is particularly vulnerable for the studied suboscine species and warrants protection.

Furthermore, the fifteen species identified as moderate specialists and specialists in our study may indicate rainforest health within the southern Atlantic forest. The occurrence of threatened species has often been used to indicate priority areas for conservation; however, threatened species are frequently rare or difficult to detect (see Drummond et al., 2009). We suggest that species with high degrees of habitat specialization, not just those currently deemed to be at risk, should be considered as an additional factor for conservation planning. By relying on more (and easier to detect) species than just scant data on rare, threatened taxa, conservationists may be less likely to underestimate the overall value of certain areas. For instance, given that terrestrial insectivores are highly sensitive to disturbance (Stratford and Stouffer, 2015), *Hylopezus nattereri* (Speckle-breasted Antpitta), a moderate specialist to mixed forest, might be a valuable indicator species.

When data suffice to permit the use of ROAPs, we believe that their ability to simultaneously depict occurrence and local abundance provides a useful tool to reveal hidden dimensions of habitat variability, which warrant more detailed study. For example, within a forest type many distinctive microhabitats can be found. Some sites may be on a slope, others are level; some may contain many fallen trees, others few; patches of bamboo may be present, or not; some may contain the nest of a bird-feeding raptor, and others not. Thus, spatial heterogeneity in abundance could reflect real heterogeneity within a forest type experienced by a species, even for a species found across all forest types such as *Dysithamnus mentalis* (Plain Antvireo; see Fig. 2). Such intra-forest-type variation is visually depicted by ROAPs: for the Plain Antvireo, in both the mixed forest and dense forest, this species occurred in all sites, although its local abundances are generally much lower in the dense forest. By contrast, in the semi-deciduous forest, it only occurred in approximately 50% of the sites, but there are some sites in this forest type where this species is more abundant than in dense forest, and as abundant as at the best sites in the mixed forest. This is an example of a species that is regionally abundant, but nonetheless still expresses qualitative differences in habitat use, as it does not exhibit the same pattern of spatial variation in abundance among sites within a forest type, across all forest types. Consequently, we assigned this species a specialization score of 3 (Table 1), reflecting moderate specialization. Moreover, the pattern suggests that there may be an important unmeasured factor determining local site quality in a given forest type. Other species [(e.g., *Xiphocolaptes albicollis* (White-throated Woodcreeper) and *Thamnophilus caerulescens* (Variable Antshrike)] occurred in all forest types, but showed large differences in overall abundance (as well in the distribution of abundance across sites) among different forest types (see Fig. 2). For specialist species [(e.g., *Synallaxis cinerascens* (Gray-bellied Spinetail)] that occurred in many sites but in just one forest type (in this case, mixed forest), some sites appear to be very much more favorable than others. Future studies aimed at understanding why these species are much more common in these particular sites, within the preferred forest type,
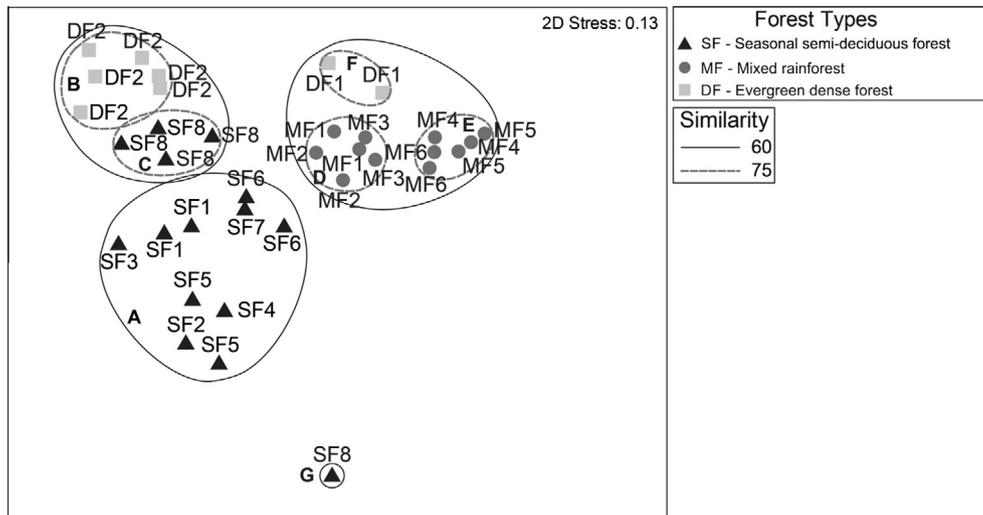
Fig. 3. Nonmetric multidimensional scaling (NMDS) of the bird species assemblages in each site, with the forest types designated as in Fig. 1. The balloons graphically describe grouping resulting from cluster analysis (see text for more details).

could provide important mechanistic underpinnings for conservation strategies.

In this study, we compiled sufficient data to assign levels of forest type specialization for thirty six suboscine species of the Atlantic rainforest. Eight species were understory birds and either specialized (level 4) or moderately specialized species (level 3). The biological reasons for species-specific abundances among forest types are uncertain; elucidating these reasons will require more detailed future studies. We can, however, suggest reasons for several of the patterns we observed. For instance, lower temperature in the mixed forest during winter could be one important factor governing fidelity to this forest type. Foliage-gleaners of the understory, which seek more exposed arthropods (Zimmer and Isler, 2003), such as *Mackenziaena severa* (Tufted Antshrike), Plain Antvireo, and *Rhopias gularis* (Star-throated Antwren), may be more associated with the semi-deciduous forest and dense forest due to the warmer temperature throughout the year providing a more reliable food supply. By contrast, suboscine species that capture concealed prey in the structured bark substrate of trees [(e.g., climbers such *Lepidocolaptes falcinellus* (Scalloped Woodcreeper)] may be able to tolerate harsher winters in the mixed forest if bark provides shelters for arthropod prey. Nicolai (1986) proposed a similar mechanism for birds in temperate forests. He found that temperatures in the bark valleys of fissured bark could remain above the air temperature, which permitted higher abundance in arthropods found in these microhabitats, thus benefiting birds which can forage there. Five of the eight terrestrial foragers were associated with both mixed forest and dense forest (level 2 of habitat specialization). Terrestrial foragers depend mainly on arthropods living in ground litter (Remsen, 2003; Krabbe and Schulenberg 2003a,b). Higher humidity of the leaf litter favors higher abundance of arthropods on the substrate in both mixed and dense forests (Remsen, 2003; Volpato et al., 2006). We suggest that the typical dry period of the semi-deciduous forest depresses soil and litter moisture, reducing ground invertebrate biomass, the primary resource for ground-foraging birds. Thus, soil humidity could interact with vegetation heterogeneity in determining habitat use for these species (Pollock et al., 2015).

When considering broad patterns of spatial variation (e.g., among forest type) in community structure, we might expect that specialists spatially aggregate together, as do generalists. This prediction follows from patterns observed in bird communities in France where habitat specialists tend to reach their highest

abundance in local communities composed of other specialists (Julliard et al. 2006). Consistent with Julliard et al. (2006), we found that for coexisting members of the monophyletic group of suboscines in the southern forests of Brazil, species tend to exhibit somewhat similar levels of habitat specialization: the dense and the mixed forest harbor more forest type specialists, whereas the semi-deciduous forest harbors more generalists.

Additional patterns in structure emerged beyond the three clusters shown in Fig. 3. In particular, the SIMPROF test suggested two subclusters of sites within the mixed forest. Those two subclusters probably reflect two different temperature conditions of mixed forest, warmer temperatures in the northern portion, and cooler in the southern (see Fig. 1). Moreover, there are some interesting outliers. For instance, the sites of DF1 seemed to have levels of specialization more similar to mixed forest sites than to other sites within dense forest. These particular sites in the dense forest were located very close to mixed forest, so some kind of 'spillover' spatial effect might be occurring. Additionally, one site of SF8 did not group with any other site (Fig. 3). This particular site was located at Iguassu Falls; although nominally semi-deciduous forest, this site may have a quite different pattern of water availability for plants, with a constant mist from the massive falls. This may, in turn, influence the supply of insects available for insectivores.

We are somewhat cautious in drawing strong conclusions about forest type specialization in this poorly-studied region. We consider our results to be a first attempt to characterize how assemblages are structured across the major recognized forest types in the Atlantic forest. Importantly, the broad patterns in forest type specialization we report largely accord with our prior experience of which forest types are likely to harbor which species. However, in some cases, detectability could affect the quantitative details of our conclusions (Archaux et al., 2012). For instance, in a previous study in the Parque Estadual Mata dos Godoy, it was verified that some species, such as *Sittasomus griseicapillus*, were more frequently recorded on different days than were others *Synallaxis frontalis*, at sites where both species were known to be present (Bochio and Anjos, 2012). In future analyses, it would be valuable to assess more directly the issue of detectability, and also to utilize some alternative methods of characterizing distribution and abundance patterns that attempt to account for detectability (e.g., Royle, 2004).

We were able to determine the level of habitat specialization for thirty six of the fifty seven species recorded. The twenty one

species (see Appendix Fig. A2) with six or fewer recordings in our sample could either be genuinely rare or, by chance, not included in the study sites. Although sixteen of these species occurred in the semi-deciduous forest (ten and eight species in the dense forest and the mixed forest, respectively; Appendix), many of these species are known from prior studies to be tolerant to forest edge, suggesting habitat generalization. Examples are species such as *Thamnophilus doliatus* (Barred Antshrike), *Lepidocolaptes angustirostris* (Narrow-billed Woodcreeper), *Synallaxis spixi* (Spix's Spinetail) and *Synallaxis frontalis* (Sooty-fronted Spinetail; Remsen, 2003; Zimmer and Isler, 2003). Including these poorly sampled species would not likely change our interpretation that bird communities in the semi-deciduous forest are characterized by generalists.

Moreover, our analysis has deliberately focused on a rather broad brush-stroke characterization of habitat specialization, in terms of major forest types, and heterogeneity in abundance among sites within forest types. In future analyses, it would be valuable to carry out more detailed analyses that take into account factors such as local abundance of bamboo, measures of vegetation structure, elevation, slope, soil type, and so forth, as well as to use more formal approaches that account for spatial autocorrelation. In the NMDS space (Fig. 3), it should be noted, for instance, that the mixed forest sites are found close together, even though they are spatially well-dispersed (Fig. 1). Qualitatively, the community-wide patterns of habitat specialization characterized with this multivariate technique do not seem to closely match spatial juxtaposition. We have categorized forests into discrete forest types, but in reality, sites doubtless exist along a vegetation continuum, so a gradient analysis might be appropriate for assessing patterns of habitat specialization. Site DF1 is near an ecotone with mixed forest, and also this site has patterns of habitat similarity within the bird assemblage that are closer to mixed forest than might be expected (see Fig. 3). It also would be valuable to assess dispersal abilities of the species in these assemblages, since this will influence the ability of species to persist in highly fragmented landscapes. We suspect that many species will not be able to disperse well over the highly modified matrix habitats surrounding these forest fragments, but direct evidence on this point is to date lacking.

Because of the massive perturbation of this region by human land use practices, our study is necessarily constrained to available habitats, rather than an idealized stratified random sampling across a landscape. Moreover, undisturbed forests may themselves represent a non-random subset of historical forests given that steep slopes, poor soils, or difficult access may be reasons particular forests persist in the face of deforestation pressures. And so, the forest remnants we have studied – even the least impacted by human influence – might already be quite disturbed, so we may not be characterizing the original spectrum of habitat specialization patterns in these assemblages, but one already strongly perturbed by anthropogenic effects (we thank an anonymous reviewer for this insight). Thus, one must interpret and use our data with due caution. It is possible that our species abundance and occurrence data depends sensitively on transect location and may not be an accurate assay of bird assemblages in the different forest types, or that the fragments we study do not precisely reflect historical lowland tropical forests prior to degradation. A fully randomized sample design is impracticable, for instance because opening additional trails through forest in protected reserves is restricted by law.

Despite all these caveats, we suggest that a deeper understanding of species' habitat specialization patterns, and those of suboscines in particular, may prove useful in conservation planning and management given the likely sensitivity of many of these species to habitat degradation and fragmentation (Anjos et al., 2011),

and that the results presented here helps identify which species, and species assemblages, have particularly strong patterns of habitat specialization. This conclusion and its practical imperative may seem intuitive, but the approaches provided here allow one to begin to quantify this intuitive insight, providing first steps toward linking patterns of avian habitat specialization among and within forest types with management suggestions for habitat prioritization. Indeed, identifying species' patterns of specialization facilitates focused conservation efforts, both at the species and the habitat scale, for the poorly studied avifauna of the southern Atlantic rainforest of Brazil.

Acknowledgments

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2015.01.016.

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