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Bird species abundance–occupancy patterns and sensitivity to forest fragmentation: Implications for conservation in the Brazilian Atlantic forest

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ABSTRACT

Developing a predictive theory for species responses to habitat fragmentation is a large, complex challenge in conservation biology, and meeting this challenge likely requires tailoring predictions to specific habitats and taxa. We evaluate the effects of fragmentation on forest birds living in three distinct forest ecosystems found in Brazilian Atlantic forest: seasonal semi-deciduous forest (SF), mixed rain forest (MF), and dense rain forest (DF). We test the hypotheses that (1) bird species most prevalent in SF (relative to other habitat types) will be least vulnerable to population declines in fragmented SF, and (2) species with stronger affiliations with DF or MF will be relatively more sensitive to fragmentation in SF. Using an exploratory statistical technique called "Rank Occupancy–Abundance Profiles (ROAPs)," we compared distribution and abundance of birds among large "continuous" areas of each forest type, then compared abundances in continuous SF forests with patterns of abundance in small fragments of SF, where edge effects could play a marked role in population dynamics. Overall, 39 species showed substantially lower local abundance, occupancy, or both in SF fragments versus continuous SF. As predicted, a higher proportion of bird species associated with DF appeared sensitive to fragmentation in SF; by contrast, species most abundant in SF and MF were similarly abundant in fragmented SF. Our study demonstrates how quantifying distribution and abundance in diverse habitats may enhance managers' ability to incorporate species-specific responses to human disturbances in their conservation plans, and points out ways that even small reserves may have significant conservation value.

1. Introduction

An important objective of conservation science is to identify predictors of species extinctions. The relative importance of factors that influence extinction vary according to the spatial scale over which extinction is assessed, as well as among taxa. For instance, at the global scale, geographic range size, home range size, weaning age, and population density all, to some degree, predict extinction probability among species of primates, marsupials, rodents and ungulates (Purvis et al., 2000a; Cardillo et al., 2008). At a local scale (over several hundreds of kilometers), edge-sensitivity and restricted mobility were shown to be the principal factors predicting local extinction in bats (Meyer et al., 2008) and in birds (Sekercioglu, 2007), respectively. At a continental scale, for Neotropical birds overall, Gage et al. (2004) ranked the relative importance of elevation range, species body mass, and utilization of microhabitats in each of three regions, Central America, the Andes, and southern Amazonia lowlands, and found that different factors best characterized extinction risk in each region. Thus, there may be no universal trait for predicting extinction risk, but rather a suite of traits to consider, depending upon taxa or spatial scale. In this paper, we explore the degree to which avian species' abundance—including both its local density and regional occupancy—in large, continuous areas of forest predicts species' persistence in smaller forest fragments in Brazil, at local to regional scales.

Habitat fragmentation is considered one of the primary drivers of both local and regional extinctions (Davies et al., 2000). There are

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two broad classes of processes at play in habitat fragmentation: (i) island biogeographic, and (ii) edge effects. In island biogeography (MacArthur and Wilson, 1967), the processes influencing species persistence on an island of a given size and position are essentially demographic and spatial. For any given species, small islands have small population sizes and low habitat heterogeneity; both of these factors are expected to increase extinction risks. Isolated islands are rarely colonized, and cannot enjoy demographic rescue effects preventing extinction. These processes operate across a continuum, with no obvious breakpoint as a function of island size. Analyses of continental (="land bridge") island faunas for instance show that there must have been extinctions after sea level rise after the Pleistocene on even relatively large islands, such as Trinidad and Tobago (once part of South America; see Terborgh, 1974). Even large fragments of forest might be expected in the long run to lose species if they are isolated from colonization sources.

In recent years, it has become clear that the processes at play in habitat fragments are not fully captured in this island biogeographic perspective. Laurance (2010) provided a recent summary of the reasons why dynamics of mainland habitat fragments must consider processes that go beyond the traditional scope of island biogeography. In particular, there are distinct physical and biological processes that operate at and near the edges of habitat fragments, which can determine much of what happens in population and community dynamics within fragments.

These edge effects have distinct spatial signatures. A large number of physical and biological processes have been shown (Fig. 8.3 in Laurance, 2010) to penetrate up to 200 m into forest fragments. Many of these processes could affect forest birds. For instance litter depth, moisture level, and the abundance and species composition of leaf litter invertebrates are all influenced by being near an edge; consequently, edges alter the food supply of ground-foraging insectivores. Such effects as these penetrate to around 200 m into fragments. If a forest fragment were a geometrical, round patch equal to 12.56 ha in area, then in some sense it would be "all edge" relative to these processes (its radius – the distance from its center to its edge – would be 200 m). A smaller number of processes, such as elevated tree mortality (which would influence vegetation structure) can penetrate up to 500 m from an edge. So in like manner, a round fragment equal to 79 ha would be all edge, relative to these processes (its radius would be 500 m). Finally, the effects of a few processes (such as episodic fires starting in the matrix) can extend to 1000 m from edges into forest interiors. Indeed, fragments less than 1000 m in radius have an elevated fire frequency (Fig. 8.5 in Laurance, 2010). For these large-scale, physical processes, a round fragment of around 314 ha would be 'all edge'.

These background data suggests that if one dichotomizes fragments into those less than 300 ha, and greater than 300 ha, then the first set should be inflicted by a suite of physical and biological processes which could affect the persistence of forest birds, for reasons quite distinct from (but not mutually exclusive with) those considered in island biogeography. Patches larger than about 300 ha would have a core area, relatively immune to these edge processes and spillover from the surrounding landscape matrix. In our analyses below, we will contrast abundance patterns in forest fragments less than 300 ha in size, with substantially larger areas. This protocol in effect dichotomizes what in reality is a continuum of degrees of habitat destruction and fragmentation. But we suggest that such a dichotomization provides a reasonable partitioning of fragments into those where one might expect dramatic, rapid responses to habitat destruction, and those where such responses play out over much longer time scales.

Local extinctions due to fragmentation have been intensively investigated both experimentally (e.g. see review by Debinski and Holt, 2000) and in comparative observational studies (e.g. Anjos, 2004; Pavlacky and Anderson, 2007). For bird species in Amazonia and the Brazilian Atlantic forest, restricted dispersal ability and/or an inability to survive in the matrix of modified habitats surrounding the fragments (which reduces connectivity) has been linked with population decline in response to fragmentation (e.g. Gascon et al., 1999; Sekercioglu et al., 2002; Ribon et al., 2003). Moreover, Henle et al. (2004) identified population density as one of the strongest predictors for a species' decline in response to forest fragmentation. This empirical observation is consistent with basic theoretical population biology: all else being equal, species with low initial abundances should be negatively influenced by forest fragmentation, which magnifies the impact of demographic stochasticity and other negative consequences of small population size for populations persisting in remnants of suitable habitat surrounded by a hostile matrix (e.g. due to inbreeding, Allee effects, spillover of matrix influences).

Here, we refer to species which show substantially lower abundance in fragmented habitats, over the range of fragment sizes considered here (10–200 ha), relative to continuous areas of those habitats, as "sensitive" to fragmentation; such sensitivity should increase the risk of local extinction (e.g. Purvis et al., 2000b). Studies on birds in the Neotropics have typically assessed the importance of local abundance as a factor in species sensitivity to habitat fragmentation by comparing populations before and after fragmentation (e.g. in Amazonia; Stouffer and Bierregaard, 1995), or by using historical records obtained during some period before deforestation (e.g. in Brazilian Atlantic forest; Christiansen and Pitter, 1997; Ribon et al., 2003), and our assessment of sensitivity to fragmentation is consistent with these previous studies. Of course, one should expect many species which seem insensitive to fragmentation over the range of fragment sizes in our study to be impacted in abundance at very small fragment sizes.

Our study focuses on the southern reach of the Brazilian Atlantic forest (BAF) – widely recognized as one of the biodiversity hotspots in the world, as it contains many endemic species, and many species have been recognized in previous studies to be vulnerable to habitat fragmentation (e.g. Ribon et al., 2003; Bencke et al., 2006). This important region of conservation concern stretches throughout the coast of Brazil from the northeast (the state of Ceará) to the southwest (the state of Rio Grande do Sul; Myers et al., 2000). Due to deforestation, only 10% of the original forest remains in a reasonable approximation of its original state in this biome (Ribeiro et al., 2009).

Within the southern portion of the BAF, plant ecologists have recognized three predominant types of forest ecosystems (Veloso et al., 1991; Morellato and Haddad, 2000; Oliveira-Filho and Fontes, 2000; Castella and Britez, 2004): seasonal semi-deciduous forest (SF), mixed rain forest (MF), and dense rain forest (DF). Although these forest types are different in structure and composition, most bird species occur in more than one forest type (Stotz et al., 1996). In this study, we use Rank Occupancy–Abundance Profiles (ROAPs; Collins et al., 2009) to characterize and quantify differences in abundances between these three forest habitats. ROAPs provide an exploratory tool that can reveal patterns in distribution and abundance that may be obscured using more traditional analyses.

The goals of this study are (1) to describe the distribution and abundance of bird species within and among forest types, and (2) to assess whether overall abundance in continuous SF relative to other habitat types (we call this measure "prevalence") predicts bird species' abundances in fragmented SF. Our protocol involves contrasting distribution and abundance of bird species in habitat fragments with relatively large areas of forest (which we refer to as "continuous") equal to or exceeding 560 ha in area.

Assuming that significantly higher abundance in one habitat type over others reflects suitability, we predicted that species which are more prevalent in continuous SF will be less negatively influenced by (i.e. less sensitive to) fragmentation in SF, than are those species which are instead more prevalent in continuous tracts of MF and DF. The basic idea is that species which are initially most abundant in SF should be particularly well-adapted to that habitat; moreover, higher overall abundance should allow for more potential colonists to rescue vacant patches, should local extirpation occur. We also predicted that species present in similar abundances in two forest types (occupying equally SF/MF, SF/DF, or MF/DF), and species with no perceptible differences in abundance–occupancy distributions across all three forest types (occupying equally SF/MF/DF) will also tend to be less sensitive. The logic behind this prediction is that habitat generalization might decrease sensitivity to habitat fragmentation. Comparable abundances across major vegetation types suggests a kind of versatility in habitat use, which could translate into a degree of resilience in the face of land use change.

2. Methods

2.1. Study area

The study area comprised all forest regions of the state of Paraná and extended into the state of Santa Catarina, southern Brazil. A linear mountain range called "Serra do Mar," occurring along the Brazilian coast, isolates DF on the east side, from MF and SF on the west side, in the southern portion of the BAF. However, isolation is not complete, and indeed contact exists between DF and MF along some river valleys. By contrast, SF and MF come into contact over an extensive area, and there is a clear transitional zone between these forest types in the center of the state of Paraná (Fig. 1). In the southern portions of the BAF, DF occurs from sea level up to about 2000 m, but our study areas were only distributed up to 800 m. DF is very rich in tree species, with more than 700 species recorded, of which around 50% are endemic to this forest type (Morellato and Haddad, 2000; Oliveira-Filho and Fontes, 2000). MF occupies the southern limits of BAF, at elevations ranging from 800 to 1200 m; one tree species, the conifer *Araucaria angustifolia*, represents more than 40% of the individual trees in MF. There are about 350 tree species in MF, with around 13% of these being endemic (Oliveira and Rotta, 1982). Finally, SF, ranging from 200 to 800 m in elevation, has fewer tree species (with about 220 species, about 10% being endemic) and it does not contain *A. angustifolia*. In past eras, the *A. angustifolia* range extended to the central part of Brazil (recordings of fossilized pollen); in the more recent geological era (Holocene), *A. angustifolia* has retracted, presumably due to gradual warming from the Pleistocene to the present (Ledru et al., 1998; Behling, 1998, 2002). Now, in southern Brazil *A. angustifolia* is confined to the cooler climates of higher elevations. This suggests that MF is slowly (over geological time scales) being replaced across this region by SF and DF – the forest types that characterize warmer climates in this part of the Neotropical region (Ledru et al., 1998; Behling, 1998, 2002).

We selected 13 sampling sites in large, continuous areas of the three forest types (Table 1): five sites in SF, six sites in MF, and two sites in DF. The sampled areas include many of the larger and best preserved tracts of continuous forest in their respective regions; some of these sites are designated as Natural Reserves. Three of these Natural Reserves – all under the legal protection of the Brazilian Federal Government – are the largest extant areas with their respective forest types in southern BAF: e.g. the Parque Nacional do Iguaçu (185,000 ha) in SF, the Floresta Nacional de Irati (3500 ha)

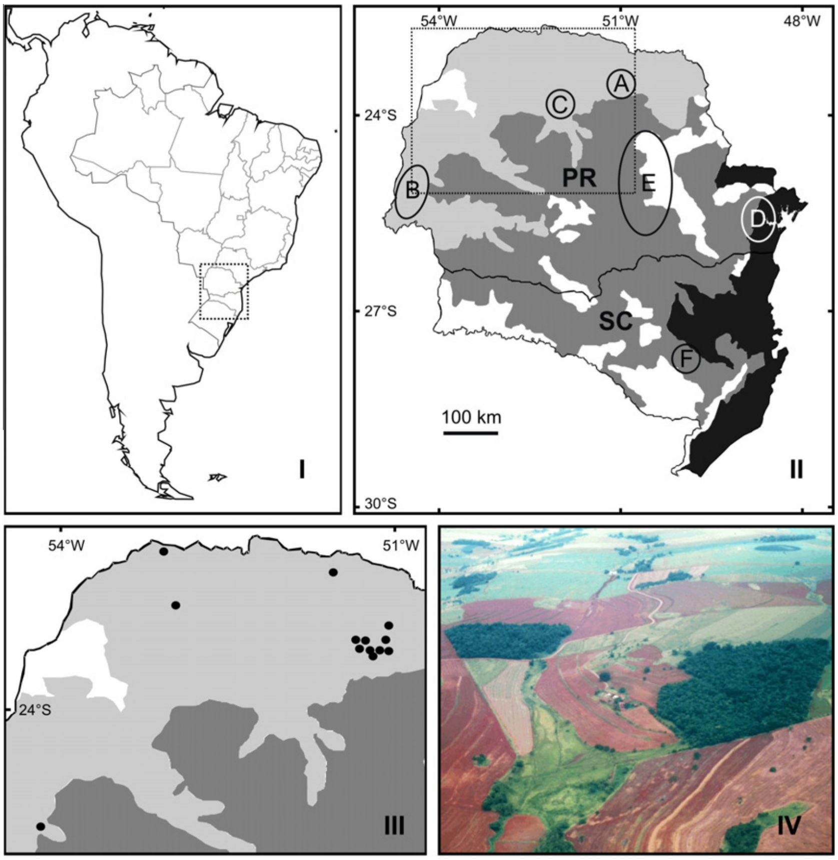

Fig. 1. (I) The location of the study region in southern Brazil. (II) Locations of the studied sites of continuous forests (A–F; see Table 1) in the Brazilian Atlantic forest, in the states of Paraná (PR) and Santa Catarina (SC), southern Brazil. Different shades of color indicate distinct vegetation types: the light shade is for seasonal forest (SF), the dark shade is for dense forest (DF), the middle shade refers to the mixed forest (MF), and white regions refer to open areas (mostly grassland). (III) Locations of the studied forest fragments. (IV) An example of the fragmented forest landscape of the studied region.

Table 1
Studied areas in the Brazilian Atlantic forest, according to forest types, with information on area size (ha), coordinates, locations (L; letters refers to Fig. 1), and numbers of sites (S) sampled. Superscripts indicate which areas are Reserves under legal protection of the Federal Government[a] and of the Government of the state of Paraná[b]. The area refers to the size of the continuous primary forest (see text for explanations).

Forest type/area name	Size (ha)	Coordinates	L	S
Seasonal forest (continuous areas)				
Parque nacional do iguaçu[a]	185,000	25°36′05″S, 54°25′47″W	B	5
Parque estadual do lago azul[b]	1750	24°06′13″S, 52°19′08″W	C	1
Parque estadual mata dos godoy[b]	1500	23°27′08″S, 51°15′08″W	A	2
Patrimônio paiquerê	577	23°29′44″S, 51°05′19″W	A	2
Fazenda colorado	564	23°28′13″S, 51°02′85″W	A	2
Dense forest				
Área de preservação ambiental de guaraqueçaba[a]	192,000	25°19′15″S, 45°42′24″W	D	6
Mananciais		25°26′32″S, 48°58′59″W	D	2
Mixed forest				
Floresta nacional de irati[a]	3500	25°24′03″S, 50°35′11″W	E	2
Pousada panelão	1800	27°53′16″S, 49°35′58″W	F	2
Distrito de são josé	1500	28°01′10″S, 49°27′33″W	F	2
Parque ecológico da klabin[b]	1000	24°21′02″S, 50°34′11″W	E	2
Estrada do corvo branco	1000	28°02′30″S, 49°23′90″W	F	2
Reserva do patrimônio natural do tarumã[b]	840	25°18′12″S, 49°48′53″W	E	2

in MF, and the Área de Preservação Ambiental de Guaraqueçaba (192,000 ha) in DF. But for the reasons discussed above we also considered in our analysis patches to be "continuous" primary forest areas if they had an area equal to or larger than 560 ha. As argued above, the majority of edge effects recorded in Amazonian forest fragments occur within 200 m of the forest edge (Laurance, 2010), and patch sizes equal to or greater than 560 ha should include core areas beyond the effect of nearly all edge impacts. Moreover, given that we are dichotomizing our study areas into 'fragments' and 'continuous forest', if there is data from the latter which actually is in the direction of the former, this makes any effect we report more conservative.

We selected 14 forest fragments in SF which have different levels of connectivity to comparable habitats, judging from their current isolation (Table 2). We consider in this study forest fragments in which primary forest was equal to or smaller than 200 ha in size, less than 50% the size of our smallest "continuous forest" area. Some of the selected forest fragments in the present study are also reserves in the SF vegetation type under the legal protection of the Paraná state government (Table 2). These forest fragments are the result of deforestation that occurred mostly between 50–70 years ago; agriculture and pastures at present dominate the matrix surrounding the fragments, which thus provides habitat that is unsuitable for forest birds. Although sampling irregularly-shaped fragments was sometimes unavoidable, we did avoid elongated fragments which minimize core area and inflate the edge: area ratio (e.g. Fig. 1IV).

All fragments could be considered old-growth/primary forests, but there are four exceptions in which a large portion of the potentially relevant habitat upon close inspection (personal observations) turns out to have substantial areas of scrub or young secondary forest: (1) the Estação Ecológica do Caiuá, legally 1450 ha in size, but we estimate that less than 200 ha is well-preserved; (2) the Parque Estadual de Amaporã, 204 ha in size, with about 150 ha well-preserved; (3) the Fazenda do Bullet, 350 ha in size, with about 180 ha well-preserved; and (4) the Fazenda Ribeirão do Tigre 1, 285 ha in size, with about 200 well-preserved. So these four areas were considered *de facto* forest fragments, because the well-preserved areas of them are about or smaller than 200 ha. Support for this comes from measures of "Biotic Integrity," which represents the ability of a system to maintain its organization in the face of changing environmental conditions (Kay, 1991). This index is calculated using levels of local sensitivity of bird species to fragmentation (high, medium, and low; see Anjos et al., 2009 for details). According to our estimated values for this region (Anjos et al., 2009), forest fragments of up 200 ha provided values of Biotic Integrity of about 50% of continuous forest. Similarly sized forest fragments surrounded by secondary forests also had a Biotic Integrity of close to 50% of continuous forest. Thus, although a secondary forest may be a more permeable matrix and provide better resources than do agricultural lands, we interpret this low Biotic Integrity score to mean that secondary forest is functionally quite distinct from primary forest, and so our measures of fragment size do not incorporate secondary forest or scrub.

Table 2
The studied forest fragments of SF in the state of Paraná and information on their area (ha), connectivity, and coordinates. Connectivity indicates if the forest fragment is isolated or connected by a forest corridor; the distance to the nearest fragment of similar size, when isolated, and the length of the forest corridor, when connected are indicated. An asterisk indicates which areas are Reserves under legal protection of the Government of the state of Paraná(*). The area size refers only to primary forest (see text for explanations).

Forest fragment	Size (ha)	Connectivity	Coordinates
Estação ecológica do caiuá*	200	Isolated; 20,000 m	22°37′02″S, 52°52′16″W
Fazenda ribeirão do tigre 1	200	Connected; 2000 m	23°27′40″S, 51°12′96″W
Fazenda do bullet	180	Isolated; 5000 m	23°24′37″S, 51°19′07″W
Parque estadual de amaporã*	150	Isolated; 3900 m	23°05′01″S, 52°47′42″W
Fazenda santa helena	87	Isolated; 800 m	23°25′45″S, 51°14′73″W
Parque estadual de ibiporã*	74	Isolated; 2000 m	23°15′22″S, 51°01′54″W
Estrada do patrimônio são luis 2	72	Isolated; 800 m	23°29′40″S, 51°11′92″W
Estrada do patrimônio maravilha	70	Isolated; 3300 m	23°26′65″S, 51°00′57″W
Parque estadual cabeça do cachorro*	61	Isolated; 6000 m	24°54′48″S, 53°54′36″W
Parque estadual de ibicatu*	57	Isolated; 7000 m	22°46′50″S, 51°29′23″W
Fazenda ribeirão do tigre 2	56	Isolated; 500 m	23°28′11″S, 51°14′19″W
Fazenda solana	30	Isolated; 3000 m	23°24′25″S, 51°21′56″W
Fazenda do nelson godoy 1	25	Connected; 400 m	23°28′22″S, 51°15′15″W
Fazenda do nelson godoy 2	11	Isolated; 1100	23°28′13″S, 51°15′82″W

If this means we underestimate the 'true' fragment size, again this blurs the dichotomy we are making, and so makes any observed effects conservative.

In addition, two Natural Reserves are contiguous to well preserved forest areas, which expands the area of continuous, high-quality forest. The Parque Estadual Mata dos Godoy, with 656 ha is contiguous to a large area of well preserved forest (though not protected), increasing the total area of continuous primary forest to about 1500 ha. The Reserva do Patrimônio Natural do Tarumã (404 ha) is also adjacent to well-preserved forest, increasing the total area of continuous forest in this location to 840 ha (Table 1).

The resulting 13 areas of continuous forest and the 14 forest fragments we have identified are grouped in five general locations of BAF (Fig. 1). The continuous areas and the forest fragments of SF are relatively well distributed across the state of Paraná; the most distant selected studied areas in our study region are separated by about 500 km (Fig. 1).

2.2. Bird sampling methods

Point counts (Blondel et al., 1970; Bibby et al., 1993) were performed in both the continuous forests and in the fragments. In order to apply the point count method, we plotted six points separated by 200 m along a 1000 m trail. We called a "site" the set of all six points sampled along a trail. In some large areas, more than one site was included in the dataset. For example, in the Parque Nacional do Iguaçu five sites (five different trails) were selected for sampling. This procedure permitted a better representation of the actual avifauna found in the larger areas. In total, 32 sites were sampled in the larger tracts of forest; 12 in SF, 12 in MF and 8 in DF. In fragmented forest, only one trail of six points (one site) was sampled in each fragment, totaling 14 sampled sites. Although point counts do not consider differences in detectability or allow for us to calculate actual densities for each species, we believe they are useful as an index to detect significant differences in abundance among populations within a species, and among different forest types, and thus the data provide information relevant to our hypotheses (Bibby et al., 1993). A previous study in SF showed that four days performing point counts are enough to detect more than 90% of the known local bird species richness (Anjos, 2007).

The point counts were performed in four mornings, two in spring and two in summer, during 2004 and 2005; thus, each site included a total of 24 sampling points. Climatic conditions were similar across sampling days and years. Points along 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 begin. We sampled for 15 min at each point, with a 15 min break between the points. The surveys on each morning finished 2 h and 45 min after the first sampling point. The radius for detection at each point was estimated to be 100 m. Earlier studies applying point counts or evaluating microhabitats of birds in the Parque Estadual Mata dos Godoy (e.g. Anjos 2001, 2007; Poletto et al., 2004) indicate that most of species only can be heard up to 40–50 m from the observer, and some species detected up to 70–80 m. Only certain species, such as *Chamaeza campanisona*, can be heard beyond 100 m, so we excluded from our analyses bird species for which vocalizations are known to propagate to distances greater than 100 m. At a single sampling point, each pair or flock was counted as one contact. Precaution was taken not to count the same pair or group more than once, particularly for highly mobile species. Because our statistical comparisons were intraspecific (see below), interspecific differences in social behavior that may influence point count estimates should not bias our results. The point counts were performed by four observers (L. dos Anjos, E.V. Lopes, R. Boçon, and M.V. Bisheimer), each of whom has had extensive previous knowledge of the avifauna in the location they sampled. To minimize bias introduced by multiple observers, the research team standardized sampling protocols together in the Parque Estadual Mata dos Godoy, led by L. dos Anjos, who has performed point counts in that Reserve since 1995.

We used the published literature (in particular Stotz et al., 1996) and our own extensive field experience to designate bird species as those to be considered as mainly dependent on forests. For the analyses presented below, we focused on forest species for which we had reasonable sample sizes.

2.3. Data analyses

The relative abundance for a single species in a site (a single fragment), called the Index of Point Abundance (IPA), was estimated by dividing its contact number by the total number of points (24) sampled in each site (following Blondel et al., 1970; Bibby et al., 1993).

Distribution–abundance patterns were analyzed using Rank Occupancy–Abundance Profiles (ROAPs; Collins et al., 2009; see also Brown et al., 1995). ROAPs provides a graphical, exploratory tool which displays the distribution of local abundances (number of individuals recorded at a given sampling point, or an index of such abundance) among sites within a habitat category, as well as occupancy. Constructing ROAPs across different habitat categories allows one to compare distribution–abundance relationships. This, in turn, permits discernment of patterns which otherwise are less readily detected using any summary measure of abundance. Further, we can statistically assess the validity of observed differences in ROAPs (e.g. between fragmented and continuous forest areas; Collins et al., 2009) using a randomization protocol.

To construct ROAPs, we first plotted the values of IPA for a given species on the ordinate, against the rank order of the sites (fragments) on the abscissa. We then divided the rank by the total number of sites sampled in each forest type to standardize the abscissa, permitting comparisons of ROAPs constructed for the different forest types or forest fragments of SF that differed in their numbers of sampled sites. We thus generated a graphical representation of all data on abundances (i.e. a ROAP) of each species across the three forest types, and for the forest fragments of SF (see examples in Fig. 2).

Visually inspecting these plots provides valuable qualitative insights into differences in distribution–abundance relationships, but to ensure against reading too much into small differences, we statistically tested for differences between ROAPs for a species present in two forest types, or between the continuous areas of SF and the forest fragments of the same forest type. We used the non-parametric statistic, D^*, calculated as the integral of the area between the two ROAPs, (Collins et al., 2009). If the ROAPs cross, the area is the absolute sum of the areas between ROAPs. To calculate the value of D^* against which we can compare any given observed value, we combine the datasets into one, and then generate a statistical universe of samples drawn at random from this hybrid dataset. For each pair of samples drawn from this combined dataset, we calculate a D^*. Repeating this many times generates a statistical distribution of values of D^* that could have emerged by chance alone, given the observed data. Two empirical distributions are judged to be statistically different if it is highly unlikely that their observed value for D^* could have been produced by chance. Randomization tests provide a powerful tool for making statistical inferences regarding data that does not fit the standard assumptions of classical statistics (e.g. normal distributions).

In our analyses, we re-sampled the data 1000 times, randomly assigning forest type (without replacement) among the samples. For each run, we calculated D^* and compared the empirical D^* to the distribution generated by our randomizations; we considered results significant at $\alpha = 0.05$.

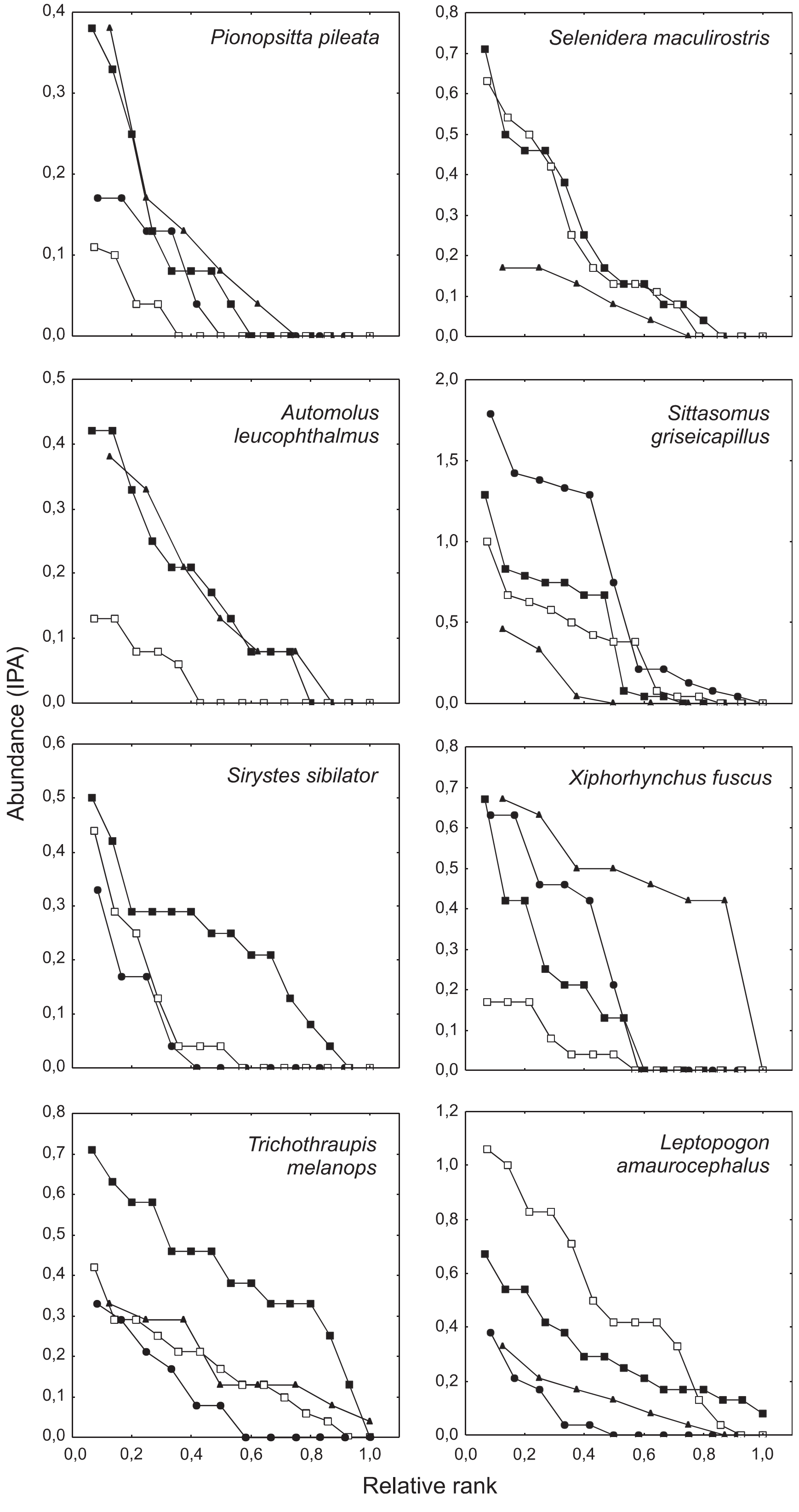

Fig. 2. ROAPs of some bird species categorized as either sensitive (*Pinopsitta pileata*, *Automolus leucophthalmus*, *Sirystes sibilator*, and *Trichothraupis melanops*) or not sensitive (*Selenidera maculirostris*, *Sittasomus griseicapillus*, *Xyphorhynchus fuscus*, and *Leptopogon amaurocephalus*) to forest fragmentation of the Atlantic Semi-deciduous forest. The forest types: —▲—DF; —●—MF; —■—SF (continuous areas); —□—(SF (forest fragments).

We used ROAPs in two distinct ways. First, we compared ROAPs for each bird species among different habitat categories to gauge the association of each bird species with a forest type. A species was deemed to be associated with a single habitat type if it was significantly more abundant (using D^*, and therefore accounting for both local density and occupancy) in one habitat than the others. In some cases, bird species did not show significant differences in abundance among forest types. For these species, we lumped habitat types to create a new category of habitat affiliation. Overall, we determined seven categories of habitat association: species associated mainly with a single forest types (SF, MF, DF); those which straddled a pair of forest types, which were distinctly different than the third (SF/MF, SF/DF, MF/DF), and those which were generalists (SF/MF/DF).

Second, we categorized bird species as sensitive to SF fragmentation based on the differences in their abundance in the continuous forest versus the fragments: species with higher overall abundance in continuous areas of SF compared to fragmented SF (and for which D^* was significant) were deemed "sensitive" to fragmentation, as lower abundance and occupancy likely reflect vulnerability to reductions in habitat area.

We limited our ROAP analyses to species present in at least three sites in each forest type, or in three or more sites of both continuous and fragmented forest. There were several species for which this analysis was not possible due to the low number of sites at which they were recorded. For these species, we used a second method based on species' prevalence to allocate species to one of the eight habitat categories. A species was considered "prevalent" in a forest type when the difference in the occupancies between the forest types was larger than 30%. Similarly, a species is considered "sensitive to fragmentation" when its occupancy in the set of forest fragments was 30% lower than in the continuous forest. A species was also considered prevalent if it occurred in only one forest type, or in only the continuous forest of SF.

We used *G*-tests to evaluate significance ($\alpha = 0.05$) between species numbers of different categories when the expected frequencies were equal or greater than five; Williams' correction factor was used when appropriate (Fowler and Cohen, 1986).

3. Results

A total of 273 bird species were recorded in the three forest types, but only 222 occurred in SF. Among these 222 species (about 78% of bird species that potentially occur in the studied sites of SF), 87 were forest species for which it was possible to address their sensitivity to forest fragmentation using prevalence alone (48 species) or ROAPs (39 species). In total, 39 species were found to be sensitive to forest fragmentation of SF (Appendix).

Among the 39 species evaluated using ROAPs, four species (*Pionopsitta pileata* ($D^* = 7.062$, $p = 0.04$), *Automolus leucophthalmus* ($D^* = 12.44$, $p = 0.007$), *Sirystes sibilator* ($D^* = 12.9$, $p = 0.023$), and *Trichothraupis melanops* ($D^* = 23.64$, $p = 0.001$)) were deemed sensitive. The ROAPs of those four species (Fig. 2) show that their overall abundances (local density at individual sites and collective abundance across them) are higher in SF than in the fragments of this forest type. Closer inspection of the ROAPs suggests that species show distinct, species-specific responses to fragmentation in their abundance–occupancy patterns. *P. pileata* and *A. leucophthalmus* decline greatly in occupancy as well in maximal abundance, on fragments as compared to more continuous forest. *S. sibilator* has a much lower occupancy on fragments, and its mean abundance across occupied areas is reduced, but its maximal local abundance is almost unchanged from that found in continuous forest. This suggests that some fragments may actually provide reasonable habitat for this forest specialist. *T. melanops* by contrast has lower abundance across the fragments, but its occupancy is not really affected by fragmentation.

By contrast, for other species, the distribution of abundances across sites within continuous SF were statistically indistinguishable from the distribution of abundance across sampling points in fragmented SF ($p > 0.05$ for D^* values assessed by randomization tests). Examples of such species include *Selenidera maculirostris*, *Sittasomus griseicapillus*, and *Xyphorhynchus fuscus*. For *S. maculirostris*, the pattern of abundances by visual inspection of the plots is essentially identical in fragmented and continuous forest, and the two are not statistically different, using D^*. For *S. griseicapillus*, occupancy is not affected by fragmentation, but its overall abundance appears somewhat lower. The randomization test, however, suggests that this could have arisen by chance (and the same holds for *X. fuscus*). For some species, abundances were actually higher in fragments than in continuous forest, as is shown for *Leptopogon amaurocephalus* ($D^* = 23.2$, $p = 0.032$; Fig. 2).

Among the 87 species, nearly half (40 species) had significantly higher abundance or prevalence in one forest type over the others, suggesting a degree of habitat specialization: 17 species to SF, 13 to MF, and 10 to DF. Fourteen species were distributed widely among all three forest types, showing no significant differences in abundance among them, while the other 33 were clearly associated with a combination of two forest types: 14 species for SF/DF, 10 for MF/DF, and 9 for SF/MF (see Appendix). *L. amaurocephalus*, *T. melanops*, and *S. sibilator* are examples of species that seem to be tightly associated to only one forest type (all three to SF), and *X. fuscus* (MF/DF) and *A. leucophthalmus* (SF/DF) are examples of species that utilize two (but not all three) forest types. Finally *P. pileata* and *S. griseicapillus* provide examples of generalists, with similar abundances among sites found in all of the three forest types (category SF/MF/DF; Fig. 2).

Interestingly, a species was more likely to be sensitive to fragmentation if it was *not* primarily associated with SF ($G = 4.22$, $df = 1$, $p < 0.05$). Indeed, there appeared to be a gradient of increasing sensitivity to fragmentation across habitat associations (Fig. 3). For instance, only one species (11%) in the category SF/MF was found to be sensitive to forest fragmentation; by contrast, 90% of species of the category DF were sensitive. The proportion of sensitive species was similar for species most prevalent in SF and MF forest types ($G = 0.13$, $df = 1$, $p > 0.05$), but were significantly different between those of SF and DF ($G = 4.85$, $df = 1$, $p < 0.05$).

These results do depend upon the assumption that a given species is equally detectable across all these forest types. Based on our extensive field experience, we believe that the qualitative results we report are genuine and do not reflect such biases. But we do acknowledge that accounting for potential differences in detectability would be a worthwhile direction for future extensions of this work.

4. Discussion

We assessed the potential conservation risks for forest bird species in BAF by comparing species' abundances among different habitats and at multiple spatial scales in continuous and fragmented forests. Our analytic protocol involved a comparison of patterns in abundance and occupancy among species samples, gathered by point-counts using standardized techniques. We found that species with the highest overall abundances and the strongest affiliation to SF as assessed in continuous forest were least likely to show negative effects of fragmentation in SF.

Our results are consistent with conclusions reported by several authors showing that species with large population size in habitats prior to their fragmentation tend to persist longer in remaining fragments (e.g. Purvis et al., 2000a; Henle et al., 2004). It has long been known that average population size is a predictor of extinction risk. Indeed, one explanation for the general cross-species correlation between distribution and local abundance is that a larger local population size can provide sources to replenish populations that are perturbed to low densities (Gaston et al., 1997). Our conclusion of course assumes that abundances in continuous forest today provide insight into the abundances of species in previously continuous forest that currently is fragmented.

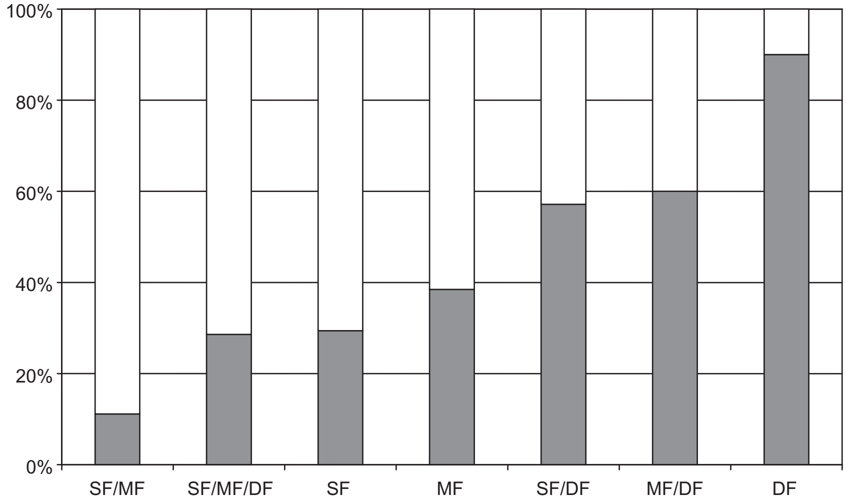

Fig. 3. Percentage of sensitive species in each category of habitat association.

Furthermore, there appeared to be a gradient in sensitivity to fragmentation that corresponded with habitat association (Fig. 3). For example, species associated with DF appeared to be most negatively affected by fragmentation in SF. The relatively low abundance of these birds in SF is probably due to the fact that DF is quite different in structure and phenology from SF. Specifically, SF has a dry season and fewer tree species, in stark contrast to DF, which is the moistest forest among the three analyzed and contains the highest tree species richness. Fragmenting SF may exacerbate the differences between SF and DF (e.g. edges may decrease moisture or increase temperature of the forest and tree richness may decline), making SF even less habitable for species which favor DF. Relative to DF specialists, species well-adapted to somewhat drier conditions such as SF might be, to a degree, pre-adapted to a modicum of fragmentation. Geographic features may also play a role in determining the sensitivity of DF-associated species to fragmentation. DF occupies a narrow strip (50–100 km) between the Atlantic Ocean and Serra do Mar. Thus, species that predominately live in this habitat will have relatively small ranges, which could act as a constraint to hamper (for instance) rescue effects via dispersal among populations.

Species most abundant in both DF and MF (category DF/MF) also showed pronounced declines in SF fragments relative to continuous SF. However, for species associated with DF/SF, few species were significantly less abundant in fragmented SF, suggesting that an increase in suitability to SF is linked with a lack of sensitivity (or delayed, see below) to fragmentation in SF. This pattern is further illustrated by those species that had similar population sizes in all three forest types: these species are presumably adapted to several habitats, and as a group, exhibited the smallest proportion of species responding negatively to fragmentation (Fig. 3). By this measure, habitat generalists are relatively insensitive to fragmented SF.

We also documented several patterns that did not fit our predictions. For example, a large number of MF species – present in relatively low abundance in continuous SF – did not appear to be noticeably sensitive to fragmentation in SF, i.e., the proportion of sensitive species did not differ significantly between MF and SF. We suggest that factors other than abundance/habitat association may contribute to the lack of sensitivity to fragmentation demonstrated by MF species. In particular, the historical background of our system may play a role. MF seems to be in the process of being replaced by SF through a long-term pattern of vegetation replacement driven by climate change during the Quaternary (Ledru et al., 1998; Behling, 1998, 2002). Vegetation changes more slowly than does climate. If bird species are limited to some degree (directly or indirectly) by climate, rather than just vegetation structure, some bird species from warmer forests, in particular from SF, may have expanded their ranges and colonized MF, prior to evident change in the forest. If this hypothesis of a transient disharmony between some bird species' distributions and vegetation types holds, we suggest that the traits of these species that allow them to disperse to and then persist in MF could also allow them to survive more effectively in a fragmented landscape of SF. This interpretation is of course, speculative, and to address it would require tools from other disciplines such as phylogeography.

Notably, using both abundance and distributional information, we found several species that are both closely associated with SF (i.e. they are most abundant in SF) but which are, at the same time, sensitive to forest fragmentation. Conservation planning at the regional scale should consider differences that exist among species in their degree of suitability to forest types so as to better evaluate the location of reserves. The Appendix shows the association of the analyzed bird species to the three major forest types, as well as the sensitivity of these species to the fragmentation of SF. Documenting species associations and sensitivity to fragmentation could help evaluate conservation priorities. Some species which are overall negatively impacted by fragmentation, may nonetheless persist well in a few fragments (e.g. *S. sibilator*). A close analysis of features of these fragments may highlight features of the system important for preserving such species.

Another aspect of our findings that is potentially important for conservation is our observation that many bird species showed no differences in abundance and occupancy between continuous areas and fragments of SF. These data suggest that some species may persist in fragments at similar local densities and occupancies compared to populations of that species found in the continuous areas. This, in turn, highlights the potential importance of even small reserves for conservation. Indeed, the persistence of bird species in even small forest fragments has been suggested to be a frequent feature of species in fragmented landscapes in the Neotropics (Whitmore, 1997). Future research should discern if this pattern reflects local factors permitting persistence in individual fragments, or, alternatively, if fragments are, functionally connected to one another, or to other seemingly distant tracts of forest. Such functional connectivity may permit persistence without unaltering abundance, as assessed at local, within-fragment scales.

The fact that for some species persist in fragments created on the order of 50–70 years ago, at first glance suggests that fragments can sustain species, even at reasonable abundance, for long periods of time. But we caution against over-interpretation of this surprising result. First, our data cannot account for rapid extinctions that likely occurred immediately or shortly following forest fragmentation – our study focused on those species that have in fact survived, which may be a biased subset of the entire community that was initially present. Moreover, the potential existence of "extinction debts" (Tilman et al., 1994; Kuussaari et al., 2009) looms over all such analyses of anthropogenically modified landscapes. Long-lived species (e.g. parrots) may have generation times not that different from the time since fragmentation, and current population trends may not yet reflect a slow decline toward extinction. For other species, local extinction may result from rare, episodic events (e.g. droughts) which can be buffered in continuous habitats, but will unexpectedly push small isolated populations over the edge. For yet other species, transient shifts in community structure might temporarily mask the long-term fate of species. For instance, if a superior competitor went rapidly extinct, this could merely greatly slow down the decline in an inferior competitor, rather than permit it to persist indefinitely.

Rates of abundance decline and thus sensitivity may be linked with fragment size, shape, and connectivity which are all, to some degree, related, and our results must be interpreted with this in mind. Had we evaluated only fragments smaller than 50 ha, more species may have been designated as sensitive, as abundance differences between fragments and continuous regions would almost surely have been more dramatic. Our study includes a number of habitat fragments that are reasonably large in area. Species that seem insensitive to fragmentation in our study could nonetheless prove to be vulnerable to population decline and loss in very small fragments. Furthermore, although we report the distance of our fragments from other forest patches (Table 2) our focus was not to quantify specifically the levels of connectivity based on distance, quality of matrix, or movement data (e.g. Kindlmann and Burel, 2008). Recent studies suggest that in BAF, increased functional connectivity may allow species to persist in forest fragments (Awade and Metzger, 2008; Martensen et al., 2008; Boscolo and Metzger, 2011). Our patches are surrounded by matrix habitats that cannot sustain forest birds. In future studies, extending our sample of fragments to a larger array would be required to assess isolation and connectivity effects.

In our study we evaluated only fragmented landscape of SF and thus can only make inferences for sensitivity to this particular forest type, and over the range of fragment sizes contained in our study. It would be interesting to extend the study by comparing distribution–abundance patterns in fragmented landscapes of the MF and DF as well. If our hypothesis is true, we expect that species associated with (and more abundant in) a certain forest type would be more resilient to its fragmentation than a species which largely occupies a different habitat type. More studies of this nature would help characterize the generality of the patterns we observed for SF.

This study highlights the importance for assessing species-specific conservation risks by evaluating both local density and occupancy of species in different habitats. Using ROAPs instead of simply species occurrences or mean local densities allows a more thorough assessment of habitat suitability to different forest types or forest fragments, thereby providing information crucial for management decisions, and revealing intriguing species-specific differences in responses to fragmentation We here have provided the first example of this approach as applied to bird species in BAF (and indeed in any system). Overall, we believe that evaluating differences in occupancy and abundances among habitat types, landscape treatments, or over time may help provide insight into evolutionary trends of ecosystems, large-scale responses to human-induced global changes, and ultimately aid in establishing priorities for conservation.

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Appendix A. Bird species grouped according to their categories of forest association. An asterisk mark indicates sensitive species

DF: *Patagioenas plumbea**, *Ramphastos vitellinus**, *Philydor atricapillus**, *Myrmotherula gularis**, *Myrmotherula unicolor**, *Drymophila ferruginea*, *Drymophila squamata**, *Formicarius colma**, *Conopophaga melanops** and *Phylloscartes paulista**.

MF: *Crypturellus noctivagus**, *Micrastur ruficollis*, *Veniliornis spilogaster*, *Piculus aurulentus*, *Synallaxis cinerascens*, *Anabacerthia amaurotis*, *Heliobletus contaminatus*, *Xiphocolaptes albicollis*, *Lepidocolaptes squamatus**, *Hylopezus nattereri*, *Phyllomyias fasciatus**, *Vireo olivaceus** and *Cacicus chrysopterus**.

SF: *Trogon viridis*, *Baryphthengus ruficapillus*, *Melanerpes flavifrons*, *Campephilus melanoleucos*, *Philydor lichtensteini*, *Mackenziaena severa*, *Dysithamnus mentalis*, *Psilorhamphus guttatus*, *Myiopagis viridicata*, *Corythopis delalandi**, *Leptopogon amaurocephalus*, *Hemitriccus diops*, *Platyrinchus leucoryphus**, *Sirystes sibilator**, *Pyroderus scutatus**, *Piprites chloris** and *Trichothraupis melanops**.

MF/DF: *Penelope obscura*, *Xyphorhynchus fuscus*, *Batara cinerea*, *Chamaeza campanisona**, *Chamaeza ruficauda**, *Platyrinchus mystaceus**, *Oxyruncus cristatus**, *Chiroxiphia caudata*, *Schiffornis virescens** and *Turdus flavipes**.

SF/DF: *Tinamus solitarius**, *Micrastur semitorquatus**, *Triclaria malachitacea**, *Selenidera maculirostris*, *Pteroglossus bailloni**, *Cichlocolaptes leucophrus**, *Automolus leucophthalmus**, *Xenops rutilans*, *Dendrocincla fuliginosa*, *Hypoedaelus guttatus*, *Herpsilochmus rufimarginatus*, *Pyriglena leucoptera*, *Myrmeciza squamosa** and *Myiobius barbatus**.

SF/MF: *Trogon surrucura*, *Dryocopus lineatus*, *Philydor rufum*, *Dendrocolaptes platyrostris*, *Hemitriccus obsoletus**, *Turdus nigriceps*, *Pyrrhocoma ruficeps*, *Saltator fuliginosus* and *Habia rubica*.

SF/MF/DF: *Crypturellus obsoletus*, *Geotrygon montana*, *Pionopsitta pileata**, *Trogon rufus**, *Ramphastos dicolorus*, *Campephilus robustus*, *Sittasomus griseicapillus*, *Grallaria varia**, *Conopophaga lineata*, *Eleoscytalopus indigoticus*, *Mionectes rufiventris**, *Lathrotriccus euleri*, *Turdus albicollis* and *Cacicus haemorrhous*.

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