

## Spatial diversity patterns of birds in a vegetation mosaic of the Pantanal, Mato Grosso, Brazil

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**ABSTRACT.** In this contribution we characterize the spatial diversity of bird populations in a heterogeneous landscape with respect to vegetation in the northern Pantanal region of Brazil. The method of additive partitioning of species diversity ( $\gamma = \alpha + \beta$ ) was used. Samples were collected in a grid with 30 sampling plots within a 25 km<sup>2</sup> area (5 x 5 km). A total of 163 bird species were found, comprising 114 resident species and 49 regional migrants. Most species were restricted spatially, with 58% found in a maximum of five sampling plots, while 15% were found in only one plot. The beta diversity comprised 77% of total diversity and was lower for residents than for regional migrants (66% and 88%, respectively). This suggests greater spatial heterogeneity in diversity patterns for regional migrants. Seasonal availability of resources caused by changing water levels as well as anthropogenic influences may also play a role in species diversity patterns by influencing species composition across sampling plots. High beta diversity and species-specific habitat occupancy suggest that conservation and management strategies should be implemented at a regional spatial scale and focus on the conservation of this environmental mosaic.

**KEY WORDS.** Additive diversity; beta diversity; flood plains; regional migration.

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Spatial patterns of species diversity are the result of distinct environmental processes at different spatial scales such as topography, climate heterogeneity and differences in vegetation (SEOANE *et al.* 2004, VAN RENSBURG *et al.* 2004, CLEARY *et al.* 2005, COREAU & MARTIN 2007, VEECH & CRIST 2007). In general, habitat heterogeneity is positively correlated with species diversity (see review by TEWS *et al.* 2004), being one of the most important factors to consider while examining species diversity patterns at different spatial scales (ATAURI & LUCIO 2001, SEOANE *et al.* 2004, CLEARY *et al.* 2005).

The ecological consequences of habitat heterogeneity may vary considerably for different species, depending on how vegetation patterns are recognized (TEWS *et al.* 2004, COREAU & MARTIN 2007). This, in turn, may lead to variations in the patterns of land usage and occupancy of a species (WIENS 1989, COREAU & MARTIN 2007). Spatial diversity patterns are fundamentally important for the design of conservation and management strategies (KATTAN *et al.* 2006). These patterns have proved useful in describing differences in spatial or temporal species richness and diversity, since they obviate the need to examine each of the several processes that may determine these differences (GERING *et al.* 2003).

Alpha ( $\alpha$ ), beta ( $\beta$ ) and gamma ( $\gamma$ ) diversities are all used to describe species diversity patterns (LOREAU 2000, GERING & CRIST 2002, GERING *et al.* 2003, CRIST & VEECH 2006, KATTAN *et al.*

2006, VEECH & CRIST 2007). Alpha diversity is defined as the diversity measured within a sample or community, whereas  $\gamma$  refers to the regional diversity. Beta diversity quantifies the differences in species diversity across locations and provides a simple characterization of heterogeneity in a region. For this reason, it is used to plan conservation strategies and circumscribe protection areas (GERING *et al.* 2003, KATTAN *et al.* 2006). Beta diversity, or between-habitat diversity, seems to reflect the effects of landscape heterogeneity, such as that resulting from variations in climate or habitat (MACNALLY *et al.* 2004, ERÖS 2007, VEECH & CRIST 2007).

The Pantanal, in central South America, is the world's largest seasonally flooded region. There, flood cycles vary in intensity among years, and often result in long periods of either severe drought or heavy floods (HECKMAN 1999, NUNES DA CUNHA & JUNK 2004). The result of this variable water regimen is a seasonal variation in resource availability, which in turn leads to different patterns of usage and occupancy of Pantanal habitats by resident and regional migrant birds (FIGUEIRA *et al.* 2006).

The Pantanal landscape has a wide variety of vegetation types that form mosaics of different habitats (PRANCE & SHALLER 1982, SILVA *et al.* 2000, CUNHA *et al.* 2002). It also harbors the greatest bird species richness among similar flood plains, featuring 463 species, of which at least 133 have some migratory behavior (TUBELIS & TOMAS 2003, NUNES & TOMAS 2004).

Bird seasonal migration patterns associated with flood cycles are among the most interesting phenomena observed in the Pantanal. Understanding how species with different movement patterns use habitats is extremely important for the planning of conservation strategies. Therefore, we developed this study to quantify the  $\alpha$  and  $\beta$  diversity of both resident and regionally migrating species inhabiting a heterogeneous vegetation landscape, in the northern Pantanal. Our aim was to examine how migrant and non-migrant bird species varied spatially in their use of habitat mosaics.

## MATERIAL AND METHODS

The study area is located in Pirizal (16°15'S, 56°22'W), in the municipality of Nossa Senhora do Livramento, state of Mato Grosso, Brazil (Fig. 1). This region is part of the Poconé sub-region of the northern Pantanal (ADÁMOLI 1982). Here, the dry season lasts from May to September, and the rainy season from October to April. Annual rainfall averages 1,400 mm. Maximum and minimum monthly rainfalls are in January and July, respectively (NUNES DA CUNHA & JUNK 2004).

Similar to other areas of the Pantanal, a variety of habitat types is found in Pirizal, and, depending on topography, vegetation may change within very short distances (NUNES DA CUNHA *et al.* 2006).

Samples were collected in a mosaic of five different vegetation types (Appendix 1 and Figs 2-7) in the seasonally flooded savannah. The study area includes three forest types, savannah and pasture, as described below:

**Landis** (LAN) ( $n = 5$  sampling plots) are continuous and sinuous geomorphologic depressions located in negative relief, 8-15 m in depth (NUNES DA CUNHA & JUNK 2009). They function as a drainage line during flood periods and are not flooded during the dry season. Landis are always close to "cambarazais", "cordilheiras" and "murunduns" (savanna park). The following species are characteristic of Landi forests: *Licania parviflora* (Chrysobalanaceae), *Alchornea discolor* (Euphorbiaceae) and *Calophyllum brasiliensis* (Guttiferaceae) (NUNES DA CUNHA *et al.* 2007) (Figs 2-3).

**Cordilheiras** (COR) ( $n = 3$ ) are deciduous or semi-deciduous forests in which the ground is densely covered by bromeliads (*Bromelela balansae*). These bromeliads only occur in areas that are never flooded (NUNES DA CUNHA *et al.* 2006). Cordilheiras also harbor a dense undergrowth of up to 2 m, and a 5-6-m canopy of *Petiveria tetrandra* (Phytolaccaceae) and *Adelia membranifolia* (Euphorbiaceae). These forests are continuous, long, winding strips of vegetation (Fig. 4) and have dense composite trees with a 8-20 m tall (SILVA *et al.* 2000).

**Campos de Murundus** (Murundus fields, MUR,  $n = 14$ ) are seasonally flooded savannah fields with a small, round canopy (small "islands" that are never flooded, called murundus, with cover an area between 1 and 15 m<sup>2</sup>) in grassy flood plains (NUNES DA CUNHA *et al.* 2006, 2007). The upper stratum

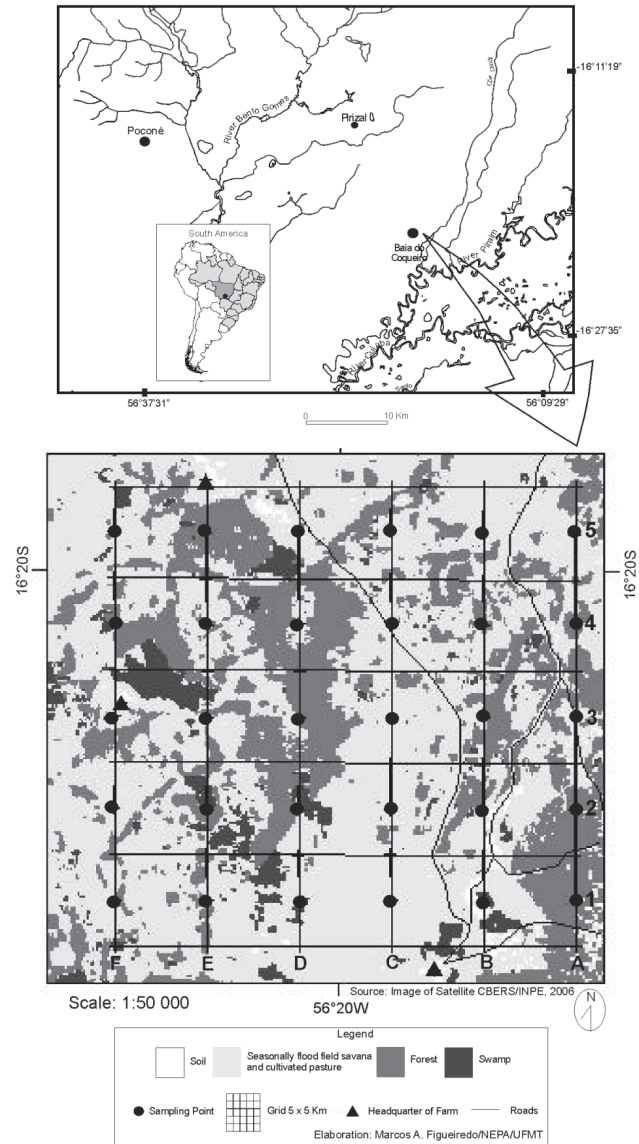


Figure 1. Map of the study area located in the Pantanal, near Poconé, and map of the sampling grid showing the 30 sampling plots distributed in different habitats.

tum is composed of shrubs and trees from 0.8 to 10 m high (SILVA *et al.* 2000). The tree *Curatella americana* (Dilleniaceae) is locally abundant (Fig. 5).

**Campos Limpos** ( $n = 1$ ) are sometimes flooded open fields with few trees and shrubs. Two additional sampling plots were edges of open and dense savannah (Fig. 6).

**Pasto Cultivado** (Cultivated Pasture, CUL,  $n = 5$ ) are pastures for cattle, with exotic grasses (predominantly *Brachiaria humidicola*) and occasionally a few trees and shrubs (Fig. 7).



Figures 2-7. The five types of vegetation found in the study area are *Landis*, during the dry season (2) and flooded (3), *Cordilheiras* (4), Murundus fields (5), Campos Limpos (6) e Cultivated Pasture (7). Photos: Izaías Fernandes (2, 3 and 5-7) and Mônica Aragona (4).

Samples were collected in 30 sampling plots in a 5 x 5 km grid (Fig. 1). The grid was formed by a system of six, 5 km long trails covering a total area of 25 km<sup>2</sup>. A sampling plot was established every 1 km on the trails in the east-west direction. The 250 m long sampling plots were demarcated in order to follow the contour in linear sections 10 to 10 m. The 30 sampling plots did not have a definite shape, for each sampling plot is the same corner of the field level and aim to minimize the variation of topography within each plot (MAGNUSSON *et al.* 2005).

Birds were sampled during three sampling periods: August and September 2006 (dry weather, no rainfall, reproduction period of most bird species), February and March 2007 (floods), and May and June 2007 (runoff, with low rainfalls and some cold spells). Each sampling plot was surveyed once in each period. During sampling, birds were captured with mist nets or counted by sight and auditory recognition.

Birds were captured using 25 mist nets (36-mm mesh), 10 m long, 2.75 m in height, along each sampling plot. Nets

were in a line along the sampling plot, and just above the ground or water level to avoid drowning during high water. Nets were opened from 6:00 to 10:00 a.m., for a total of 9,000 h/net (100 h/net for each sampling plot in each collection season).

Birds were counted by sight or sound at three points counts, for 10 min each, along each sampling plot. During counting we strived to keep a maximum of 30 m between the observer and the subjects. Birds that flew over the canopy were ignored. Points were separated by 125 m and sampled in the same order, after the sunrise. Birds were counted in a total of 2,700 min (30 min in each sampling plot, in each collection season). When an unknown call or song was heard, we recorded the vocalization for later identification from a sounds library. One observer (C.A.S), trained on the methodology and familiarized with bird sounds conducted all sampling.

Estimates of species richness were calculated with the Jackknife 1 estimator by the program EstimateS 6.0 (COLWELL 2005). Species richness estimates were compared with the observed total species richness in the study. In order to compare the relative contribution of the  $\alpha$  and  $\beta$  components of diversity with species diversity patterns, we compared the observed species richness with the respective richness estimate obtained using the Jackknife 1 estimator, for each sampling plot.

Nocturnal birds and some large bird species were excluded from the analysis because mist-nets may not be the appropriate sampling method for these species. The status of migration was defined based on the study of João B. Pinho (unpubl. data). Resident species were defined as those captured during  $\geq 10$  months per year and regional migrants were those in the area for three to nine months. Vagrants (only seen in  $\leq 2$  months) were excluded from the analysis. We consider those species as seasonal residents who were not registered in the grid of study in a least one of the three sampling stations. We compared patterns of spatial occupation ( $\alpha$  and  $\beta$  components) among sampling plots (beta diversity) between residents and migrants using the Kolmogorov-Smirnov test, and among habitat types using the chi-square test. We used the chi-square test for habitats because there are few categories of habitats. Three plots were excluded from the analysis once habitat type was not defined.

We tested for a correlation between the relative abundance of each species and the number of sampling plots where each was recorded. Relative abundance is calculated by dividing the total number of individuals of a given species by the total number of individuals of all species. This correlation was used as a tool to check whether the patterns of diversity of resident species and migrants vary according to the relative abundance of both.

Regional diversity ( $\gamma$ , species richness) was partitioned as  $\alpha$  and  $\beta$  diversities and expressed as  $\gamma = \alpha + \beta$ . Both  $\alpha$  and  $\beta$  diversities are expressed as means (LANDE 1996, VEECH *et al.* 2002). Here,  $\alpha$  diversity is the mean number of species recorded in the

30 sampling plots, whereas  $\beta$  represents the mean number of species recorded between sampling plots. Alfa and  $\beta$  diversity, and expected species diversity based on the random occurrence of individuals in samples were estimated using the unrestricted individual-based randomization option with the program PARTITION (VEECH & CRIST 2006). This test generates a significance value ( $p$ ) that serves to show if alpha and beta diversity values found are significantly different from those expected by random occurrence. Our null hypothesis is that species are widely distributed on the sampling grid, and therefore we should expect a low beta diversity value.

Since the definition of  $\beta$  diversity does not explicitly acknowledge the differences in samples or habitats (VEECH *et al.* 2002), we estimated similarity between different sampling sites, using non-metric multidimensional scaling (NMDS), with the program PCORD (MCCUNE & MEFFORD 1999). Sampling plots were ranked in order of relative abundance and presence of species and Bray-Curtis similarity indexes (for abundance) and Sorensen similarity indexes (for presence) were calculated.

## RESULTS

### General diversity patterns

A total of 3,551 individuals (2,594 observed and 957 captured) in 132 genera and 163 species were recorded. Sixty four species were non-Passeriformes and the remainder (99) was Passeriformes (Appendix 1). The family with the most species was Tyrannidae (29 species), followed by Trochilidae (12), Columbidae (9) and Icteridae (9). Resident species comprised 114 species, of which 12 (found in only one season) and 30 (found in two seasons) were seasonal. Seventy two species were recorded in three seasons. In turn, regional migrants comprised 49 species, of which 22 were found in one season, 23 in two and four species were in all seasons. Overall, 77% species were residents, 12% were seasonal residents and 10% were regional migrants.

Most species were spatially restricted: 58% were found in two to five sampling plots, and 15% were found in only one plot (Fig. 8 and Appendix 1). Residents and migrants had different patterns of spatial occupation on sampling plots (Kolmogorov-Smirnov Two Sample test:  $p = 0.004$ ). All residents recorded in one season only (12) were in one to four sampling plots, except for the toco toucan, *Ramphastos toco* Statius Muller, 1776, which was found in twelve sampling plots. Among the residents recorded in two seasons, 73% were noted in 1-5 sampling plots. Of the 72 residents in the three collecting seasons, 34 were noted at  $\geq 10$  sampling plots, with 23 in  $\geq 15$  or more sampling plots. Among the residents with the greatest spatial occupancy were the narrow-billed woodcreeper, *Lepidocolaptes angustirostris* (Vieillot, 1818); the great kiskadee, *Pitangus sulphuratus* (Linnaeus, 1766); the glittering throated emerald, *Amazilia fimbriata* (Gmelin, 1788); and the short-crested flycatcher, *Myiarchus ferox* (Gmelin, 1789).

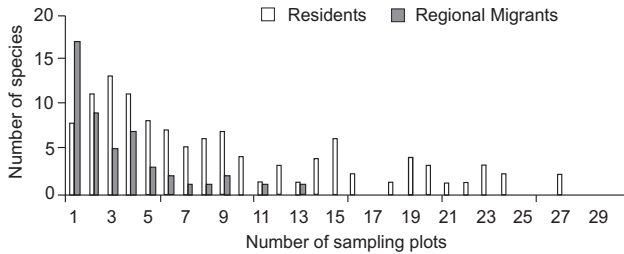


Figure 8. Number of sampling plots occupied by resident and regional migrant species near Poconé. Resident species were found in a significantly greater number of sampling plots than regional migrants (Kolmogorov-Smirnov test,  $p = 0.004$ ).

As for the regional migrants, 86% were at a maximum of five sampling plots (Fig. 8). Relative abundance was positively correlated with the number of sampling plots at which the resident ( $r = 0.794$ ,  $p < 0.001$ ) and regional migrants ( $r = 0.54$ ,  $p = 0$ ) species were encountered. Residents and migrants had different patterns of spatial occupation on habitat types ( $\chi^2: 889.1$ ; df: 4  $p \leq 0.0001$ , Fig. 9).

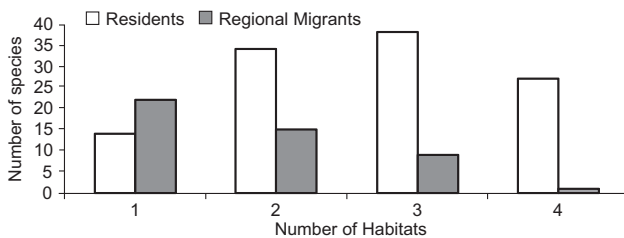


Figure 9. Number of habitats used by resident and regional migrant species near Poconé, MT, Brazil. Resident species were found in a significantly greater number of habitats than regional migrants ( $\chi^2: 889.1$ , df: 4,  $p \leq 0.0001$ ).

The average species richness per habitat type was 41 species for Landis ( $n = 5$ ), 38.1 for Murundus fields ( $n = 14$ ), 34.3 for the Cordilheiras ( $n = 3$ ) and 33.8 for Cultivated Pasture ( $n = 5$ ) (see Appendix 1).

### Species richness estimates

The number of observed species (163) represented 89% of the number expected to be found in our study (184 species, according to Jackknife species richness estimator). On average, there were 38 species (SD = 9.12) at each sampling plot.

### Additive partitioning of species diversity

The beta diversity accounted for 77% of the total species diversity (gamma diversity) and was always greater than a randomly expected value ( $p < 0.0001$ ). The alpha diversity was 23% of the total diversity and was always lower than that expected ( $p < 0.0001$ ). The beta was lower for residents ( $\beta = 66\%$  of total

diversity) as compared with regional migrants ( $\beta = 87\%$  of total diversity). This suggests greater spatial heterogeneity in diversity patterns for regional migrants.

### Ordination

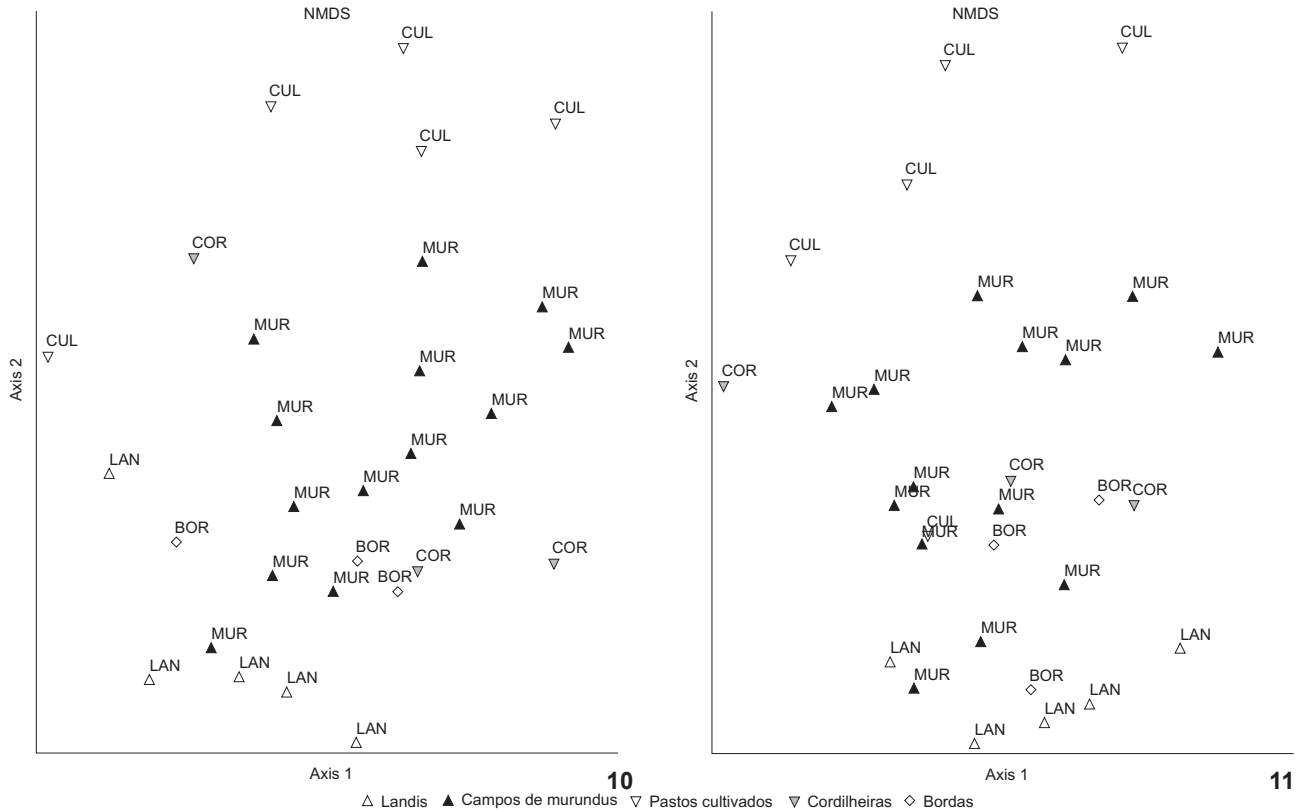
NMDS explained 81.4% of the variation in bird species presence (Fig. 10) and 86.1% of the variation in species abundance (Fig. 11). The 30 sampling plots had marked variation in species richness and composition (Appendix 1). Sampling plots were grouped by habitats using both presence and abundance, with Murundus fields and two Landis (seasonably flooded forests) near water (Figs 10 and 11). Cultivated Pasture was also different from the rest and two of those sampling plot had the lowest species richness.

## DISCUSSION

The comparison between the observed and the estimated species richness, for the entire study area ( $\gamma$ ) and for every sampling plot ( $\alpha$ ), as well as the small variation in estimated species richness across all sampling plots, reveals that the sampling approach was satisfactory, and suggests that the diversity patterns observed are consistent.

### Use of habitats and $\beta$ diversity

The high  $\beta$  diversity value obtained reveals considerable spatial heterogeneity of bird diversity patterns. The effect of habitat heterogeneity on bird spatial diversity patterns is supported by the fact that some species occupy certain habitats in particular. Among these species are some residents, such as the Mato Grosso ant bird, *Cercomacra melanaria* (Menetries, 1835); the band tailed ant bird, *Hypocnemoides maculicauda* (Pelzeln, 1868); and the Cerrado endemic helmeted manakin, *Antilophia galeata* (Lichtenstein, 1823), which were restricted to two Landis areas (seasonably flooded forests-LAN), near one permanent water course. In the Pantanal, *C. melanaria* and *H. maculicauda* had been found in association with wet forests occurring near water courses (PINHO *et al.* 2006). The presence of these and other species in those two areas indicates that the suppression of forest habitats near water courses may be extremely deleterious to the bird fauna of the Pantanal, especially to *C. melanaria*, a species found almost exclusively in the biome (STOTZ *et al.* 1996). Other species such as the ruby topaz hummingbird, *Chrysolampis mosquitus* (Linnaeus, 1758), and the buff-throated woodcreeper, *Xiphorhynchus guttatus* (Lichtenstein, 1820), occur only in Cordilheiras (non-flooded forests-COR). These species are certainly not confined to the non-flooded areas. For instance, *C. mosquitus* was observed in the four forest types sampled by João B. Pinho (unpubl. data) in Pirizal. Nevertheless, these and other species are restricted to forest environments, demonstrating the importance of preserving these forests to maintain the bird fauna. A similar circumstance is observed in Murundu fields, the only habitat where species such as the white-throated kingbird, *Tyrannus albogularis* Burmeister, 1856; the Cerrado endemic species white rumped



Figures 10-11. NMDS Ordination of the 30 sampling plots based on their bird species composition: (10) species presence or absence data; (11) relative abundance.

tanager, *Cypsnagra hirundinacea* (Lesson, 1831); and black throated saltador, *Saltator atricollis* Vieillot, 1817, were found.

Most species in the Pantanal seem to depend on multiple habitats to survive throughout the year, due to the seasonality of habitats and resources brought in by seasonal floods, as already suggested by FIGUEIRA *et al.* (2006). Reliance on multiple habitats is more intense among resident species, which have to find additional resources in different habitats during the year in order to deal with yearly oscillations in resource availability. In fact, residents occupy a larger number of sampling plots (greater  $\alpha$  values) as compared with regional migrants, though  $\beta$  diversity remained high. Therefore, even though residents tend to occupy several habitat types throughout the year (which would lower their respective  $\beta$  diversity values), spatial occupancy in a given period was shown to be highly heterogeneous. This stresses the need for the conservation of multiple environments for the sake of maintaining species diversity in the Pantanal, throughout the year.

Among the residents, non-seasonal species, such as the white-wedged piculet, *Picumnus albosquamatus* Orbigny, 1840, were most widely distributed among sampling plots. On the other hand, most seasonal residents and regional migrants oc-

cupied few sampling plots – e.g., the spot-backed puffbird, *Nystalus maculatus* (Gmelin, 1788), and the white-crested elaenia, *Elaenia albiceps* (Orbigny & Lafresnaye, 1837). The strong correlation between abundance and occupation suggests that restricted occupation of regional migrants is due to the low abundance of these species. A study accessing four forest environments in the same area found that bird species that remain in the Pantanal during a greater number of seasons occupy a greater the number of different forest habitats (João B. Pinho, unpubl. data). Species abundance is greater where ecological conditions are more favorable (WIENS 1989), which suggests that residents have adapted to the seasonality of the Pantanal. However, they do not seem so rare to justify the low value of alpha diversity, and so it is not possible to rule out that this effect is due to preference for the use of certain habitats by these species.

Seasonal usage of habitats by seasonal residents and regional migrants also seems to reflect seasonality in resource availability. For instance, some aquatic or semi-aquatic seasonal residents, such as *H. maculicauda* and the yellow-chinned spinetail, *Certhiaxis cinnamomea* (Gmelin, 1788), were observed in the area only during flood periods, which coincide with the

reproductive period of these species (C.A. Signor, pers. obs.). Several other species occupy different habitat types only in specific flood seasons, such as the frugivorous blue-crowned trogon, *Trogon curucui* Linnaeus, 1766, which occurred only in dry periods, in forests habitats. Therefore, the different specific resource requirements exhibited by some species, some of which are related to distinct flood periods, side by side with the temporal seasonality of the Pantanal, increased the spatial heterogeneity of bird diversity in the sampling grid. This was manifested as the greater  $\beta$  and  $\gamma$  diversity values measured. Therefore, changes in water flow and in the Pantanal hydrological regimes – caused chiefly by development projects implemented by the government, such as hydroelectric power dams and the transformation of natural Cerrado habitats adjacent to the Pantanal into agricultural zones – may alter the seasonal dynamic of habitat occupancy by birds. In turn, these alterations may lead to the local extinction of some representatives of native birds that depend on this seasonality, apart from the related environmental and economic losses (HARRIS *et al.* 2005, GALDINO & VIEIRA 2006), which are a burden to the government and to the society.

Apart from the different resource requirements, vagility levels determine how different species or groups of species sense and use a mosaic of habitats (LAW & DICKMAN 1998, BENNET *et al.* 2004, 2006). In a survey of several mosaics of 25-km<sup>2</sup> forest fragments in England, migrant bird richness was strongly influenced by ecological factors at the regional scale, especially habitat patterns and availability of habitats, whereas resident species richness was more intensely affected by local ecological aspects (BENNET *et al.* 2004). These considerations suggest that the starting point for the establishment of migrants may be the availability of habitats and resources at the regional level. Therefore, lower richness, abundance and spatial occupancy of regional migrants may be the consequences of the response of these species to the availability of resources and habitats at larger spatial scales. The same may happen with seasonal residents, which were also uncommon and in few places. Thus, to conserve bird diversity and the seasonal dynamic of occupancy by different species in the Pantanal, conservation strategies should be planned at regional levels.

The uncommonness of regional migrant birds may also be due to the greater energetic requirements of these species with respect to migration, which would compel them to be more habitat-selective. The influence of habitat selection on  $\beta$  diversity, as seen in the additive model, was also seen in moths and host plants. Here, generalist moth species had lower  $\beta$  diversities in comparison with specialists at several spatial scales (SUMMERVILLE *et al.* 2006).

Finally, part of the notion that the difference in the  $\alpha$  and  $\beta$  components of diversity between resident and regional migrants may be due to a sampling bias cannot be entirely ruled out, since spatial patterns for regional migrants are more susceptible to errors, due to their shorter stay in the study area.

### Anthropogenic influence on beta diversity

The marked differences in species composition between the sampling plots in Cultivated Pasture suggest that at least part of the  $\beta$  diversity may be explained by human disturbance (Figs 10 and 11). In Cultivated Pasture, exotic grasses are dominant, and only occasionally trees and shrubs are also present. Apparently, the presence of scattered shrubs and trees was the main factor determining the presence of many species in the pasture areas. In the Cerrado biome, the number of species in pastures with shrubs was 120% greater than in those without shrubs (TUBELIS & CAVALCANTI 2000). This difference is due to the fact that birds which depend on shrubs and canopy layers are absent from the Cultivated Pasture. Isolated trees, typical of natural pastures, favor animal diversity (TEWS *et al.* 2004) by providing perches for birds and frugivorous bats (GUEVARA *et al.* 1986). A reduction in the number of trees and shrubs in Pantanal pastures may lead to a loss of resources deemed important for the reproduction, feeding and sheltering of several species. Also, such reduction may influence movement patterns of species that use trees and shrubs as ecological facilitators when traveling over different areas and habitats in the Pantanal. During floods, fields lacking trees and shrubs become unavailable to aquatic and semi-aquatic birds. This was particularly clear at one sampling plot in a pasture area with almost no trees and shrubs, in which no birds were captured in the rainy season and during runoff.

In pastures, how dominance of exotic grasses influences birds has not been investigated. We found that birds typically associated with fields, such as the black throated saltator, *S. atricollis* and the rusty-collared seedeater, *Sporophila collaris* (Boddaert, 1783), are present in areas with exotic grasses. More specific studies are needed to shed more light on how exotic grasses influence native birds in the Pantanal.

### Final considerations

The model of additive partitioning of species diversity appears to be an excellent tool to evaluate regional diversity using species diversity patterns. Understanding these patterns will help in decision-making for conservation and management of natural landscapes. In the Pantanal, high  $\beta$  diversity and locally restricted occupation suggest that conservation and management strategies should be implemented at regional scales and focus on the conservation of this mosaic of environments. Due to the urgent need for national conservation and research priorities for Brazilian birds (MARINI & GARCIA 2005), we believe that investing in the study of diversity patterns may be an efficient pathway to understanding regional heterogeneity. With that understanding, it will be easier to design effective conservation strategies. In the Pantanal, migratory movements associated with environmental seasonality lead to seasonal variations in species richness and composition. Since species composition is the most important factor determining community patterns (WIENS 1989), further research should be conducted to investigate how these seasonal variations may

affect the patterns of spatial use of habitat mosaics during the different seasons, in the different sub-regions of the Pantanal, and at distinct spatial scales.

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Appendix 1. List of the bird found during this study, and species abundances by habitat and counting method. Species status: Resident (R) and Regional migrants (M); Number of sampling plots (N Plots) and number of habitats (N habitats) occupied by each species. Seasons when seen: dry season (Dry), rainy season (Rai) and runoff (Run). Habitats: Landis (LAN, n = 5)-seasonally flooded forest); Cordilheiras (COR (n = 3)-Dense-canopy savannah); Murundus fields (MUR, n = 14)-Seasonally flooded field savannah, of which three were invaded by the tree species cambará, *Vochysia divergens* Pohl. (Vochysiaceae); Cultivated Pasture (CUL, n = 5)-Open pastures; Two borders between Cordilheiras and Murundu fields (Bord) and one border between Cordilheiras and open field (flood open field areas-Bord1).

Taxon	Status	N Points	N Habitats	Abund	Dry	Rai	Run	Habitat					
								LAN	COR	MUR	CUL	BORD	BORD1
Tinamiformes													
Tinamidae													
<i>Crypturellus undulatus</i> (Temminck, 1815)	R	7	2	9	X	X	X	1	0	5	0	1	2
<i>Rhynchotus rufescens</i> (Temminck, 1815)	M	6	1	7	X		X	0	0	7	0	0	0
Falconiformes													
Accipitridae													
<i>Rostrhamus sociabilis</i> (Vieillot, 1817)	M	3	1	3		X		0	0	3	0	0	0
<i>Busarellus nigricollis</i> (Latham, 1790)	R	1	1	1			X	1	0	0	0	0	0
<i>Rupornis magnirostris</i> (Gmelin, 1788)	R	14	3	19	X	X	X	3	0	12	2	1	1
Falconidae													
<i>Caracara plancus</i> (Miller, 1777)	M	2	2	3	X			0	0	2	1	0	0
<i>Milvago chimachima</i> (Vieillot, 1816)	R	2	2	3	X	X		0	0	1	2	0	0
<i>Herpotheres cachinnans</i> (Linnaeus, 1758)	R	2	2	2		X		0	1	1	0	0	0
<i>Falco rufigularis</i> Daudin, 1800	M	1	1	1		X		0	0	0	1	0	0
Gruiformes													
Rallidae													
<i>Aramides cajanea</i> (Statius Muller, 1776)	R	7	4	15	X		X	1	1	4	7	2	0
<i>Porphyrio flavirostris</i> (Gmelin, 1789)	M	4	1	9		X		0	0	0	7	0	2
Eurypygidae													
<i>Eurypyga helias</i> (Pallas, 1781)	M	1	1	1			X	0	0	0	1	0	0
Charadriiformes													
Jacanidae													
<i>Jacana jacana</i> (Linnaeus, 1766)	R	3	2	9		X	X	0	0	2	7	0	0
Columbiformes													
Columbidae													
<i>Columbina minuta</i> (Linnaeus, 1766)	M	4	3	5	X		X	1	0	2	2	0	0
<i>Columbina talpacoti</i> (Temminck, 1811)	R	17	3	86	X	X	X	12	30	41	0	3	0
<i>Columbina squammata</i> (Lesson, 1831)	R	6	2	15	X	X	X	0	0	6	1	5	3
<i>Columbina picui</i> (Temminck, 1813)	R	4	3	24	X		X	0	18	1	5	0	0
<i>Claravis pretiosa</i> (Ferrari-Perez, 1886)	R	4	2	7	X		X	3	0	3	0	1	0
<i>Uropelia campestris</i> (Spix, 1825)	M	4	3	12	X	X	X	0	1	7	4	0	0
<i>Patagioenas cayennensis</i> (Bonaterre, 1792)	R	3	2	5	X	X		0	0	2	3	0	0
<i>Leptotila verreauxi</i> Bonaparte, 1855	R	15	4	28	X	X	X	3	4	7	8	4	2
<i>Leptotila rufaxilla</i> (Richard & Bernard, 1792)	R	2	2	2	X		X	1	0	1	0	0	0
Psittaciformes													
Psittacidae													
<i>Primolius auricollis</i> (Cassin, 1853)	R	4	2	9	X		X	0	0	4	2	0	3
<i>Aratinga leucophthalma</i> (Statius Muller, 1776)	M	1	1	6		X		0	0	6	0	0	0
<i>Aratinga aurea</i> (Gmelin, 1788)	R	3	2	6		X	X	0	0	2	4	0	0
<i>Brotogeris chiriri</i> (Vieillot, 1818)	R	7	3	23	X	X	X	0	11	5	7	0	0
<i>Amazona aestiva</i> (Linnaeus, 1758)	R	15	4	50	X	X	X	11	11	16	4	8	0

Continue

## Appendix 1. Continued.

Taxon	Status	N Points	N Habitats	Abund	Dry	Rai	Run	Habitat					
								LAN	COR	MUR	CUL	BORD	BORD1
<i>Amazona amazonica</i> (Linnaeus, 1766)	R	3	3	19		X		0	12	5	2	0	0
Cuculiformes													
Cuculidae													
<i>Piaya cayana</i> (Linnaeus, 1766)	R	3	3	3	X	X		1	1	1	0	0	0
<i>Crotophaga major</i> Gmelin, 1788	M	3	3	16		X		2	6	8	0	0	0
<i>Crotophaga ani</i> Linnaeus, 1758	R	11	3	91	X	X	X	0	21	29	41	0	0
<i>Guira guira</i> (Gmelin, 1788)	R	16	4	58	X	X	X	3	2	18	33	2	0
<i>Tapera naevia</i> (Linnaeus, 1766)	M	1	border	1	X			0	0	0	0	0	1
Apodiformes													
Trochilidae													
<i>Glaucis hirsutus</i> (Gmelin, 1788)	R	6	2	7	X	X	X	2	0	5	0	0	0
<i>Phaethornis nattereri</i> Berlepsch, 1887	M	2	2	2		X	X	1	0	1	0	0	0
<i>Phaethornis ruber</i> (Linnaeus, 1758)	R	1	1	1	X			1	0	0	0	0	0
<i>Phaethornis pretrei</i> (Lesson & Delattre, 1839)	M	1	1	1	X			1	0	0	0	0	0
<i>Eupetomena macroura</i> (Gmelin, 1788)	R	8	3	11	X	X	X	0	2	7	2	0	0
<i>Anthracothorax nigricollis</i> (Vieillot, 1817)	M	2	2	2	X		X	0	0	1	1	0	0
<i>Chrysolampis mosquitus</i> (Linnaeus, 1758)	M	2	1	2		X	X	0	2	0	0	0	0
<i>Hylocharis chrysura</i> (Shaw, 1812)	R	13	4	30	X	X	X	1	6	14	4	2	3
<i>Polytmus guainumbi</i> (Pallas, 1764)	M	3	2	7		X	X	0	0	1	6	0	0
<i>Amazilia versicolor</i> (Vieillot, 1818)	M	1	1	2	X			0	0	2	0	0	0
<i>Amazilia fimbriata</i> (Gmelin, 1788)	R	27	4	98	X	X	X	14	23	42	8	7	4
<i>Heliomaster furcifer</i> (Shaw, 1812)	M	1	1	1			X	0	1	0	0	0	0
Trogoniformes													
Trogonidae													
<i>Trogon curucui</i> Linnaeus, 1766	R	4	2	10	X			6	0	2	0	0	2
Coraciiformes													
Alcedinidae													
<i>Megaceryle torquata</i> (Linnaeus, 1766)	R	6	3	12		X	X	6	0	2	2	0	2
<i>Chloroceryle amazona</i> (Latham, 1790)	M	2	2	2		X	X	0	0	1	1	0	0
<i>Chloroceryle aenea</i> (Pallas, 1764)	M	8	3	12		X	X	6	0	3	2	0	1
<i>Chloroceryle americana</i> (Gmelin, 1788)	M	5	4	7		X	X	3	1	1	2	0	0
<i>Chloroceryle inda</i> (Linnaeus, 1766)	M	7	2	11		X	X	4	0	3	0	1	3
Momotidae													
<i>Momotus momota</i> (Linnaeus, 1766)	M	1	1	1	X			0	0	1	0	0	0
Galbuliformes													
Galbulidae													
<i>Galbula ruficauda</i> Cuvier, 1816	R	4	2	8	X	X	X	1	0	3	0	1	3
Bucconidae													
<i>Nystalus maculatus</i> (Gmelin, 1788)	M	5	2	7	X	X		2	0	4	0	1	0
<i>Monasa nigrifrons</i> (Spix, 1824)	R	8	3	28	X	X	X	5	1	16	0	0	6
Piciformes Meyer & Wolf, 1810													
Ramphastidae Vigors, 1825													
<i>Ramphastos toco</i> Statius Muller, 1776	R	12	3	20	X			0	2	9	7	0	2
<i>Pteroglossus castanotis</i> Gould, 1834	R	2	2	6	X	X		4	0	2	0	0	0

Continue

## Appendix 1. Continued.

Taxon	Status	N Points	N Habitats	Abund	Dry	Rai	Run	Habitat					
								LAN	COR	MUR	CUL	BORD	BORD1
Picidae Leach, 1820													
<i>Picumnus albosquamatus</i> d'Orbigny, 1840	R	22	3	67	X	X	X	14	8	31	0	9	5
<i>Melanerpes candidus</i> (Otto, 1796)	M	4	2	6	X			0	0	4	1	1	0
<i>Veniliornis passerinus</i> (Linnaeus, 1766)	R	8	3	16	X	X	X	0	2	9	1	4	0
<i>Colaptes campestris</i> (Vieillot, 1818)	M	9	2	15	X		X	0	0	10	3	2	0
<i>Celeus lugubris</i> (Malherbe, 1851)	R	14	4	31	X	X	X	11	5	8	1	2	4
<i>Dryocopus lineatus</i> (Linnaeus, 1766)	R	3	3	4	X	X		1	0	2	1	0	0
<i>Campephilus melanoleucos</i> (Gmelin, 1788)	M	4	2	6	X		X	0	0	1	2	3	0
Passeriformes Linné, 1758													
Thamnophilidae Swainson, 1824													
<i>Taraba major</i> (Vieillot, 1816)	R	5	3	10		X	X	1	3	3	0	0	3
<i>Thamnophilus doliatus</i> (Linnaeus, 1764)	R	5	3	6	X	X	X	2	0	2	1	1	0
<i>Thamnophilus pelzelni</i> Hellmayr, 1924	R	4	2	11	X	X	X	6	0	4	0	1	0
<i>Herpsilochmus longirostris</i> Pelzeln, 1868	R	6	2	31	X	X	X	27	0	4	0	0	0
<i>Formicivora rufa</i> (Wied, 1831)	R	21	4	91	X	X	X	3	28	45	2	13	0
<i>Cercomacra melanaria</i> (Ménétrières, 1835)	R	2	1	9	X	X	X	9	0	0	0	0	0
<i>Hypocnemoides maculicauda</i> (Pelzeln, 1868)	R	1	1	5		X	X	5	0	0	0	0	0
Dendrocolaptidae Gray, 1840													
<i>Sittasomus griseicapillus</i> (Vieillot, 1818)	R	9	4	15	X	X	X	1	5	3	1	5	0
<i>Xiphocolaptes major</i> (Vieillot, 1818)	R	7	4	12	X	X	X	1	1	8	2	0	0
<i>Xiphorhynchus picus</i> (Gmelin, 1788)	R	10	2	23	X	X	X	14	0	8	0	0	1
<i>Xiphorhynchus guttatus</i> (Lichtenstein, 1820)	M	1	border	3	X		X	0	0	0	0	0	3
<i>Lepidocolaptes angustirostris</i> (Vieillot, 1818)	R	24	4	74	X	X	X	3	14	48	2	5	2
<i>Campylorhamphus trochillostris</i> (Lichtenstein, 1820)	M	2	2	2	X		X	1	1	0	0	0	0
Furnariidae Gray, 1840													
<i>Furnarius leucopus</i> Swainson, 1838	R	10	3	27	X	X	X	14	0	5	6	0	2
<i>Furnarius rufus</i> (Gmelin, 1788)	R	14	3	61	X	X	X	0	8	28	25	0	0
<i>Synallaxis frontalis</i> Pelzeln, 1859	M	1	1	1			X	0	0	1	0	0	0
<i>Synallaxis albilora</i> Pelzeln, 1856	R	15	3	67	X	X	X	29	0	27	3	2	6
<i>Cranioleuca vulpina</i> (Pelzeln, 1856)	R	2	2	8		X	X	2	0	0	6	0	0
<i>Certhiaxis cinnamomeus</i> (Gmelin, 1788)	R	2	2	5		X		0	3	0	2	0	0
<i>Phacellodomus ruber</i> (Vieillot, 1817)	R	5	2	10	X	X		0	0	6	4	0	0
<i>Pseudoseisura unirufa</i> (d'Orbigny & Lafresnaye, 1838)	R	5	2	10	X		X	0	0	4	5	1	0
Tyrannidae Vigors, 1825													
<i>Hemitriccus margaritaceiventer</i> (d'Orbigny & Lafresnaye, 1837)	R	20	3	103	X	X	X	20	17	44	0	20	2
<i>Poecilotriccus latirostris</i> (Pelzeln, 1868)	R	3	2	7	X	X	X	6	0	1	0	0	0
<i>Todirostrum cinereum</i> (Linnaeus, 1766)	R	2	2	4		X		2	0	2	0	0	0
<i>Myiopagis gaimardii</i> (d'Orbigny, 1839)	R	19	4	79	X	X	X	28	3	27	3	16	2
<i>Myiopagis viridicata</i> (Vieillot, 1817)	R	8	2	13	X	X	X	3	0	10	0	0	0
<i>Elaenia flavogaster</i> (Thunberg, 1822)	M	11	3	19	X	X	X	2	0	10	7	0	0
<i>Elaenia albiceps</i> (d'Orbigny & Lafresnaye, 1837)	M	3	2	6	X		X	4	2	0	0	0	0
<i>Elaenia cristata</i> Pelzeln, 1868	M	1	1	1	X			0	0	1	0	0	0
<i>Camptostoma obsoletum</i> (Temminck, 1824)	R	23	4	72	X	X	X	4	2	45	9	12	0

Continue

## Appendix 1. Continued.

Taxon	Status	N Points	N Habitats	Abund	Dry	Rai	Run	Habitat					
								LAN	COR	MUR	CUL	BORD	BORD1
<i>Suiriri islerorum</i> Zimmer, Whittaker & Oren, 2001	M	2	2	2	X			0	0	1	1	0	0
<i>Phaeomyias murina</i> (Spix, 1825)	M	2	1	2	X			0	0	1	0	1	0
<i>Euscarthmus meloryphus</i> Wied, 1831	R	7	3	11	X		X	3	4	3	0	1	0
<i>Sublegatus modestus</i> (Wied, 1831)	M	4	1	15	X	X	X	0	0	4	0	2	9
<i>Tolmomyias sulphurescens</i> (Spix, 1825)	R	3	1	10	X	X	X	1	0	0	0	8	1
<i>Cnemotriccus fuscatus</i> (Wied, 1831)	R	18	4	62	X	X	X	26	2	25	2	3	4
<i>Xolmis velatus</i> (Lichtenstein, 1823)	R	6	2	11	X	X	X	0	0	3	8	0	0
<i>Machetornis rixosa</i> (Vieillot, 1819)	R	5	3	21	X	X	X	0	5	3	13	0	0
<i>Legatus leucophaeus</i> (Vieillot, 1818)	R	3	1	3	X			0	0	2	0	1	0
<i>Myiozetetes cayanensis</i> (Linnaeus, 1766)	R	5	3	21	X	X	X	2	0	9	3	0	7
<i>Myiozetetes similis</i> (Spix, 1825)	R	1	1	1	X	X		0	1	0	0	0	0
<i>Pitangus sulphuratus</i> (Linnaeus, 1766)	R	24	4	102	X	X	X	6	8	47	30	6	5
<i>Philohydor lictor</i> (Lichtenstein, 1823)	R	8	4	21	X	X	X	5	1	6	3	4	2
<i>Myiodynastes maculatus</i> (Statius Muller, 1776)	R	6	3	9	X	X	X	0	1	4	4	0	0
<i>Megarynchus pitangua</i> (Linnaeus, 1766)	R	15	3	30	X	X	X	4	0	21	1	1	3
<i>Tyrannus albogularis</i> Burmeister, 1856	M	1	1	2	X	X		0	0	2	0	0	0
<i>Tyrannus melancholicus</i> Vieillot, 1819	R	1	border	1	X			0	0	0	0	1	0
<i>Casiornis rufus</i> (Vieillot, 1816)	R	20	3	60	X	X	X	11	6	30	0	10	3
<i>Myiarchus swainsoni</i> Cabanis & Heine, 1859	M	9	3	18	X	X	X	4	5	9	0	0	0
<i>Myiarchus ferox</i> (Gmelin, 1789)	R	27	4	87	X	X	X	14	13	41	10	6	3
<i>Myiarchus tyrannulus</i> (Statius Muller, 1776)	R	23	4	82	X	X	X	9	7	54	1	7	4
Pipridae Rafinesque, 1815													
<i>Neopelma pallescens</i> (Lafresnaye, 1853)	R	2	1	6	X	X	X	6	0	0	0	0	0
<i>Antilophia galeata</i> (Lichtenstein, 1823)	R	2	1	6	X	X	X	6	0	0	0	0	0
Tityridae Gray, 1840													
<i>Tityra inquisitor</i> (Lichtenstein, 1823)	M	3	2	4	X		X	2	0	2	0	0	0
<i>Tityra cayana</i> (Linnaeus, 1766)	R	9	3	11	X	X	X	2	0	4	1	3	1
<i>Pachyrhamphus viridis</i> (Vieillot, 1816)	M	6	1	10	X			0	0	8	0	1	1
<i>Pachyrhamphus marginatus</i> (Lichtenstein, 1823)	R	6	3	9	X	X	X	2	2	4	0	1	0
Vireonidae Swainson, 1837													
<i>Cyclarhis gujanensis</i> (Gmelin, 1789)	R	2	1	5	X	X	X	0	0	5	0	0	0
<i>Vireo olivaceus</i> (Linnaeus, 1766)	R	3	2	14	X	X		11	0	3	0	0	0
<i>Hylophilus pectoralis</i> Sclater, 1866	R	3	2	7	X		X	6	0	1	0	0	0
Corvidae Leach, 1820													
<i>Cyanocorax cyanomelas</i> (Vieillot, 1818)	R	23	4	102	X	X	X	16	13	53	4	8	8
Troglodytidae Swainson, 1831													
<i>Troglodytes musculus</i> Naumann, 1823	R	10	3	21	X	X	X	0	4	6	10	1	0
<i>Campylorhynchus turdinus</i> (Wied, 1831)	R	9	3	43	X	X	X	0	14	15	8	0	6
<i>Pheugopedius genibarbis</i> (Swainson, 1838)	R	2	1	2		X		0	1	0	0	0	1
Donacobiidae													
<i>Donacobius atricapilla</i> (Linnaeus, 1766)	R	1	1	1		X		0	0	0	1	0	0
Poliophtilidae													
<i>Poliophtila dumicola</i> (Vieillot, 1817)	R	19	4	143	X	X	X	25	14	73	2	29	0

Continue

## Appendix 1. Continued.

Taxon	Status	N Points	N Habitats	Abund	Dry	Rai	Run	Habitat					
								LAN	COR	MUR	CUL	BORD	BORD1
Turdidae													
<i>Turdus leucomelas</i> Vieillot, 1818	M	1	1	1	X			0	0	1	0	0	0
<i>Turdus amaurochalinus</i> Cabanis, 1850	R	15	4	54	X		X	32	1	15	1	3	2
Mimidae													
<i>Mimus saturninus</i> (Lichtenstein, 1823)	R	4	2	11	X	X	X	0	0	1	10	0	0
Coerebidae													
<i>Coereba flaveola</i> (Linnaeus, 1758)	R	9	2	12	X	X		4	0	8	0	0	0
Thraupidae													
<i>Nemosia pileata</i> (Boddaert, 1783)	R	3	2	7	X	X		0	0	4	1	2	0
<i>Cypsnagra hirundinacea</i> (Lesson, 1831)	M	1	1	3			X	0	0	0	3	0	0
<i>Ramphocelus carbo</i> (Pallas, 1764)	R	9	3	36	X	X	X	11	0	18	2	0	5
<i>Thraupis sayaca</i> (Linnaeus, 1766)	R	15	4	57	X	X	X	3	3	30	10	11	0
<i>Thraupis palmarum</i> (Wied, 1823)	R	1	1	2	X	X		0	0	2	0	0	0
<i>Conirostrum speciosum</i> (Temminck, 1824)	R	19	3	113	X	X	X	30	15	40	0	23	5
Emberizidae													
<i>Ammodramus humeralis</i> (Bosc, 1792)	M	13	3	95	X		X	0	1	46	48	0	0
<i>Sicalis flaveola</i> (Linnaeus, 1766)	M	4	3	5	X		X	0	1	1	3	0	0
<i>Emberizoides herbicola</i> (Vieillot, 1817)	R	4	2	10	X	X	X	0	0	4	5	1	0
<i>Volatinia jacarina</i> (Linnaeus, 1766)	R	19	4	97	X		X	2	4	49	39	3	0
<i>Sporophila collaris</i> (Boddaert, 1783)	R	5	3	12	X	X	X	0	1	1	10	0	0
<i>Sporophila angolensis</i> (Linnaeus, 1766)	R	9	3	25	X	X	X	6	0	15	4	0	0
<i>Coryphospingus cucullatus</i> (Statius Muller, 1776)	R	14	4	46	X	X	X	3	13	20	2	8	0
<i>Paroaria capitata</i> (d'Orbigny & Lafresnaye, 1837)	R	10	3	38	X	X	X	6	0	8	19	0	5
Cardinalidae													
<i>Saltator coerulescens</i> Vieillot, 1817	R	1	1	3	X	X		0	0	0	3	0	0
<i>Saltator similis</i> d'Orbigny & Lafresnaye, 1837	M	1	1	1	X	X		0	0	1	0	0	0
<i>Saltator atricollis</i> Vieillot, 1817	M	5	3	12	X		X	1	0	5	5	1	0
Parulidae													
<i>Parula pitayumi</i> (Vieillot, 1817)	R	5	3	9	X	X	X	6	0	2	1	0	0
<i>Basileuterus flaveolus</i> (Baird, 1865)	R	4	2	19	X	X	X	16	0	3	0	0	0
Icteridae													
<i>Psarocolius decumanus</i> (Pallas, 1769)	R	20	4	52	X	X	X	8	3	28	1	10	2
<i>Procacicus solitarius</i> (Vieillot, 1816)	R	3	2	5	X	X		2	0	3	0	0	0
<i>Cacicus cela</i> (Linnaeus, 1758)	R	4	3	12	X		X	1	5	6	0	0	0
<i>Icterus cayanensis</i> (Linnaeus, 1766)	R	12	4	27	X	X	X	2	1	17	5	2	0
<i>Icterus croconotus</i> (Wagler, 1829)	R	4	4	8	X	X	X	2	2	3	1	0	0
<i>Gnorimopsar chopi</i> (Vieillot, 1819)	R	9	2	35	X	X	X	0	0	19	12	4	0
<i>Agelaioides badius</i> (Vieillot, 1819)	M	2	2	7		X	X	0	0	6	1	0	0
<i>Molothrus oryzivorus</i> (Gmelin, 1788)	M	1	1	1	X			0	0	1	0	0	0
<i>Sturnella superciliaris</i> (Bonaparte, 1850)	M	1	1	1			X	0	0	0	1	0	0
Fringillidae													
<i>Euphonia chlorotica</i> (Linnaeus, 1766)	R	8	3	14	X	X	X	2	1	7	0	4	0
Total Abundance								611	411	1525	555	302	147
Total Abundance/N parcels								122.2	137	108.93	111	151	147
Species richness								92	66	137	92	58	46
Average species richness								41	34.3	38.1	33.8	41.5	46
N parcels								5	3	14	5	2	1