Core and transient species in an Amazonian savanna bird assemblage

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ABSTRACT: In this paper, we report the number of core and transient bird species in an Amazonian savanna site and assess their ecological differences. We conducted our study at Campo Experimental do Cerrado (CEC) da Embrapa–Amapá, 48 km north of Macapá (0°2'5" N / 51°2'2" W), Amapá, Brazil. Forty points were monitored on a monthly basis over the course of one year, using the unlimited-distance point counts in a plot of 360 hectares of well-preserved and relatively homogeneous upland savanna from September 2006 to August 2007. Species were classified in core (recorded in the area in nine or more months), transient (recorded in the area in four or less months) and intermediate (the ones recorded between five and eight months). Species were also classified according to feeding guilds and habitat preferences. Statistical analyses were made to compare core and transient species. We recorded 72 species in the plot, of which 36 were transients, 12 were intermediates, and 22 were core. Core species have higher abundances than transient species. Core species are found mostly in the savanna while transient species also occur in other habitats within the landscape. Both core and transient groups presented well-marked seasonal variation in abundance. Recruitment explains abundance variation for core species, while differences in the availability of food resources in the site explains variation of the abundance in transient species. We predict that plot-level (not more than 500 hectares) bird assemblages in South American savannas will be composed of a small number of abundant and habitat-restricted species that occupy the site almost year round, combined with a high number of low abundant transient species that are habitat generalists and use the plot only during limited periods of their annual life cycle.

KEY-WORDS: conservation biogeography, landscape dynamics, local assemblages, South America, tropical savannas.

INTRODUCTION

The most common approach to biodiversity conservation is to identify and protect natural features such as ecosystems and threatened species, whose distributions can be mapped and targeted through conservation management activities (Watson *et al.* 2011). While such an approach is important, the conservation of species and ecosystems cannot be achieved unless the ecological and evolutionary processes that sustain them are understood and maintained (Cowling *et al.* 1999, Fuller *et al.* 2001).

One of the most important ecological processes to be documented for any conservation plan is the movement of organisms (Bennett *et al.* 2009). Organisms move at different scales and for many purposes: to find food and shelter, for social interactions, to track resources that vary irregularly over space and time, for seasonal migration, and to disperse and establish in new locations (Bennett *et al.* 2009).

Movements of populations and species link habitat patches within a landscape, landscapes within a region, and entire regions (Wiens 1992). Therefore, a thorough understanding of the major patterns of biological movements from the local to the regional scales is a critical step towards the design of conservation systems that maintain ecological flows and enable the resilience of populations against the effects of global changes (Watson *et al.* 2011).

One concept that has not yet been fully explored in conservation biogeography is the important distinction between core and transient species (Grinnell 1922, Magurran & Henderson 2003). Core species are those that persist in a habitat patch (or site) through time and transient species are those that occur intermittently in a habitat patch (or site) as a result of dispersal from surrounding habitats or regions (Coyle *et al.* 2013).

Core and transient species usually differ in their ecological requirements as well as their abundance patterns (Magurran & Henderson 2003, Magurran 2007). Core species are predicted to be locally abundant,

habitat-restricted, and follow a lognormal abundance distribution, whereas transient species are predicted to be rare, habitat generalist, and follow the log series abundance distribution model (Magurran 2007, Belmaker 2009).

Core and transient species arise in local assemblages through different mechanisms. Core species are influenced mostly by local-scale factors that allow the persistence of the species in a habitat patch, whereas transient species are influenced mostly by regional factors that govern the number of species that potentially could move into the habitat patch from the surrounding landscape (Coyle *et al.* 2013).

Tropical avian assemblages are well known to exhibit temporal and spatial variation in their species' richness and abundance at the site scale (Karr 1976, Loiselle 1988, Poulin *et al.* 2001). These variations are usually correlated with the availability of fruit, flowers, seeds, and insects that are, in turn, impacted by seasonal changes in rainfall and associated soil moisture cycles (Karr 1976). In regions with long dry seasons, resource availability is low during the dry season and high during the wet season (Poulin *et al.* 2001, Blendiger 2005). Resource scarcity during the dry season can create ecological 'crunches' or 'bottlenecks' that limit species' abundances and biotic interactions and processes (Wiens 1977, 1992).

Temporal variance in abundances of tropical birds at the site scale can be caused by population recruitment and mortality (Blake & Loiselle 1991) but short-term (e.g., < 3 months) variations in abundance can be caused by movements of individuals into or out of a site (Martin & Karr 1986). Movements by individuals have been suggested as an important cause of the variance in tropical bird abundances (Martin & Karr 1986, Silva *et al.* 2011), but very few studies have evaluated the contribution of core and transient species on the richness and abundance of local assemblages (Karr & Freemark 1983, Poulin *et al.* 2001).

Here we report for the first time the numbers of core and transient bird species in a 360-ha plot of relatively uniform Amazonian upland savanna. We assessed the variation of the bird assemblages in this plot over a one-year period. Then we identified the core and transient species and evaluated how these two groups of species differ in their species richness, abundance, feeding habitats, and habitat use. In addition, we evaluated how species richness and abundance of the core and transient groups vary over time. We used our findings to propose some general predictions on the contribution of the core and transient species for site-level bird assemblages in South American upland savannas.

STUDY AREA

Our field research was conducted at Campo Experimental do Cerrado (CEC) of Embrapa–Amapá, 48 km north of Macapá (0°2'5" N / 51°2'2" W), Amapá, Brazil. The CEC protects 796 ha of well-managed South American upland savannas.

The CEC landscape has four major habitat types: upland savannas, wet grasslands, gallery forests, and anthropic areas. Upland savannas compose the matrix of the landscape. They occupy nutrient-poor soils, with strong to medium acidity, low in organic matter and with frequent iron concretions. Savanna vegetation is low, with few (usually no more than 100 per hectare) short (up to 4-6 m) trees (Silva *et al.* 2011). The grass *Trachypogon plumosus* and the sedge *Bulbostylis spadicea* dominate the ground (Sanaiotti *et al.* 1997). Wet grasslands are found in narrow valleys where soils are shallow and permanently inundated. Narrow belts of *Mauritia martiniana* palms can be used to identify the position of these wet grasslands. Gallery forests are linear formations (usually 15-25 m tall) that are restricted to wide valleys formed by the permanent streams that cut the landscape. Tree species such as *Jacaranda copaia* and *Symphonia globulifera* as well as palms such as *Euterpe oleracea* are the most common species in these gallery forests. Anthropic areas used for agriculture and agro-forestry experiments are small in size and are located near the CEC's housing and laboratory facilities.

The climate is hot (average temperature of 27°C) and humid (average relative humidity of 81%). Average annual precipitation from 1961 to 1990 is around 2,700 mm with a well-marked dry season from August to November, when total monthly rainfall is below 50 mm.

METHODS

We set 40 sampling points within a plot of 360 hectares of well-protected and relatively homogeneous upland savanna located at 0°2'5" N / 51°2'2" W. We set points at least 300 m apart to maintain sample independence and at least 300 m from any habitat edge. We used this distance because Tubelis *et al.* (2004) found that forest birds do not move more than 200 m within the savannas in central Brazil. Our goal with this approach was to sample the avifauna in the most homogenous savanna area possible, avoiding the influence of other habitats in the landscape as well as edges or transitional vegetation.

To study the bird assemblages within the plot, we used the unlimited-distance point count method (Blondel *et al.* 1970). For 10 min we noted all birds seen or heard in each point. For species that travel in groups, when we heard but did not see the birds, we assumed that the group size was the average from when we did see and count a group of the same species. We noted the species seen while the observer walked between points, but these sightings were not included in the quantitative analyses. The order of point sampling changed every month to eliminate any

bias. RB conducted all monthly censuses from September 2006 to August 2007, always between 06h00 and 08h00. She used a Pentax 8X40 binocular and a Sony TCD5 PRO II tape-recorder with a Sennheiser ME67 microphone.

Following Coyle *et al.* (2013), we classified each species as core if it was present in the plot for at least two-thirds of the period of time that was surveyed (nine months or more) and transient if it was present in no more than one-third of the surveyed period (four months or less), regardless of whether the species was recorded or not breeding in the plot. Intermediate are those species that were neither classified as core nor as transients. We used this pragmatic approach to minimize misclassification at the expense of excluding a small fraction of intermediate species from analyses.

Species were also classified as habitat-restricted if they were recorded in the landscape only in the upland savannas; they were classified as habitat non-restricted when they were also found in other natural habitats within the landscape. Our classification is based on qualitative data collected by RB during our study period in other habitats as well as the information reported by Silva *et al.* (1997) for our study area.

We classified bird species into six major guilds based on their diet. These feeding guilds are: (RS) raptors + scavengers (including families of Cathartidae, Accipitridae and Falconidae); (IN) insectivores; (IF) insectivore-frugivore; (FG) frugivore-granivore; (GR) granivore; and (NE) nectarivore. We used personal field experience and literature (Silva 1995, Silva *et al.* 1997, Sick 1997) to classify species into feeding guilds.

We calculated the monthly richness for core and transient groups as well as for each feeding guild by summing up the number of species of each group recorded monthly in the plot. We calculated the monthly abundance for each species, summing up its number of detections in all 40 points (Maron *et al.* 2005). By summing up monthly abundances of species, we were able to calculate monthly abundances for the entire core and transient species groups as well as the annual abundance for each species.

We used the Kolmogorov-Smirnov test to test if the species abundance distributions of core and transient groups were different. We used the Median Test to determine if species classified as core and transient differed in their annual abundances. We used the G-Test to evaluate if proportions of core and transient species among feeding guilds as well as habitat use categories were different. We used the G-Test for goodness-of-fit to a uniform distribution to determine whether abundances and species richness of core and transient groups showed any variation over time. We used Biostat 5.0 (Ayres *et al.* 2007) for all statistical analyses. Latin and English names of the bird species follow Remsen *et al.* (2014).

RESULTS

We recorded 72 species in the plot, corresponding to 37.2% of all species recorded in the entire site until now (Boss 2009). The presence of species in the plot over the year follows the expected bimodal pattern (Figure 1) with 36 transients, 12 intermediates and 22 core species. Intermediate species were *Colinus cristatus, Columbina passerina, Thalurania furcata, Amazilia fimbriata, Heliactin bilophus, Caracara cheriway, Milvago chimachima, Amazona ochrocephala, Amazona amazonica, Myiarchus ferox, Cyclarhis gujanensis, Piranga flava, Thraupis palmarum, and Sporophila plumbea.*
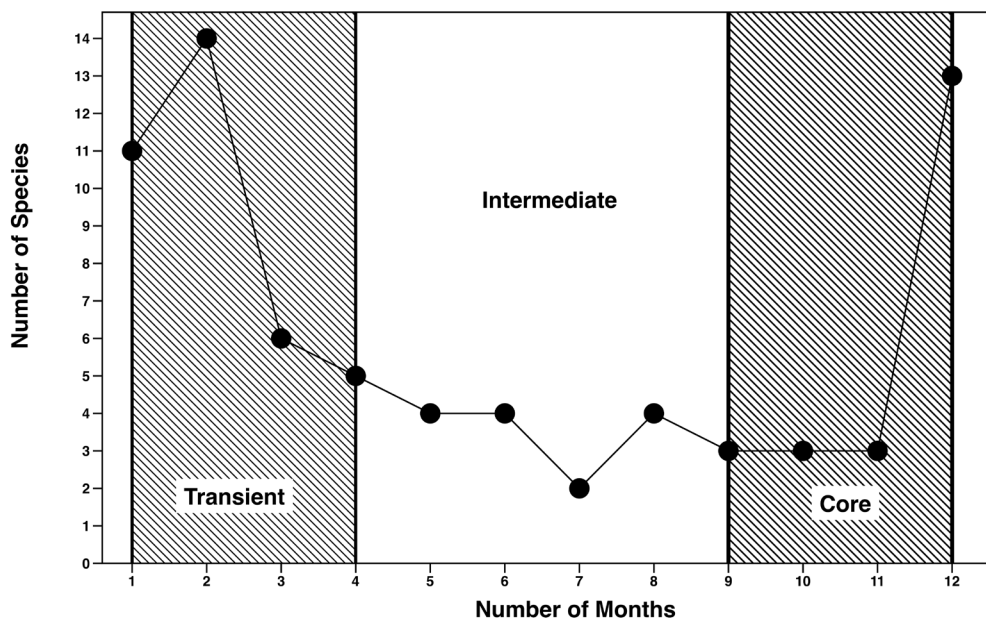

FIGURE 1. Temporal occupancy of bird species in the 360-ha plot of upland savanna in Amapá, Brazil. The temporal occupancy of a species is the number of surveyed months in which the species was recorded as present. Core species were those recorded in nine or more months and transient species were those recorded in four our less months.

The abundance distribution patterns of core and transient groups (Figure 2) are significantly different (KS, Dmax = 0.91, $p < 0.001$). Core species are significantly more abundant than transient species (Median Test, $\chi^2 = 36.6$, $p < 0.001$). The frequencies of core and transient species among the five guild categories (Figure 3) are not different (G = 3.97, $df = 5$, $p < 0.55$). In contrast, core and transient species are very different in their habitat use (G = 27.2, $df = 1$, $p < 0.0001$) because most of the core species (68.2%) are found only in savannas, whereas most of the transient species (94.4%) occur in two or more habitats (Table 1).
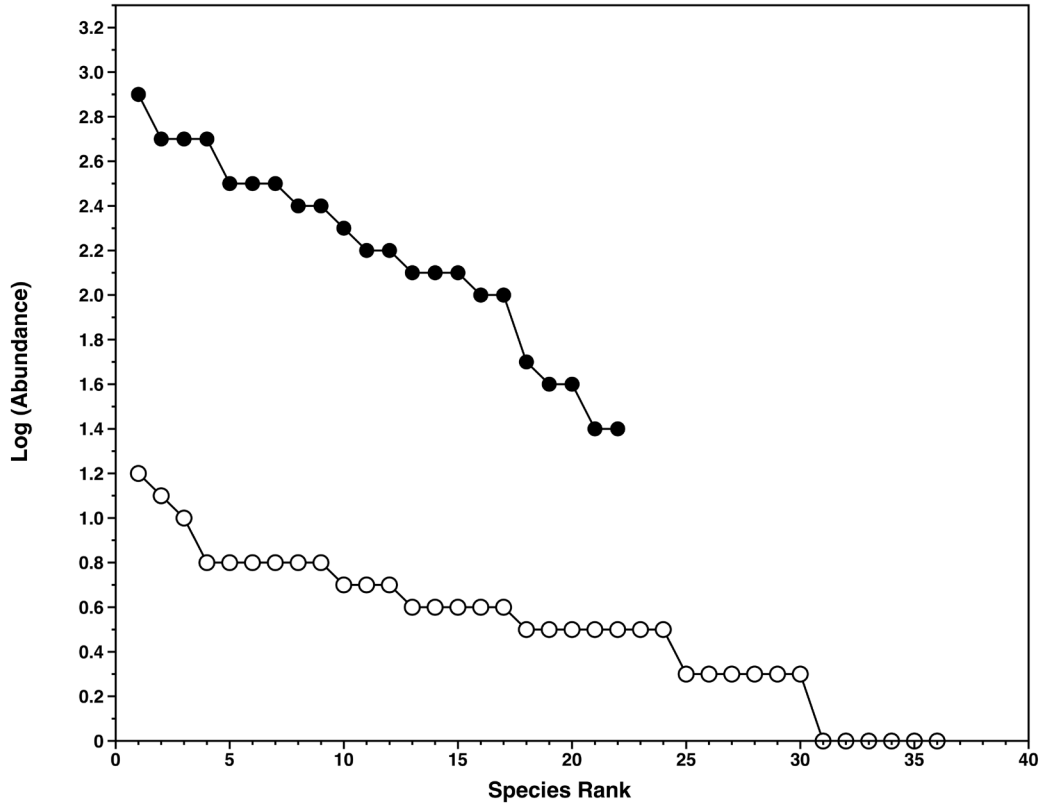

FIGURE 2. Abundance distributions patterns of core (black) and transient (white) bird species recorded in a 360-ha plot of an upland savanna in Amapá, Brazil.
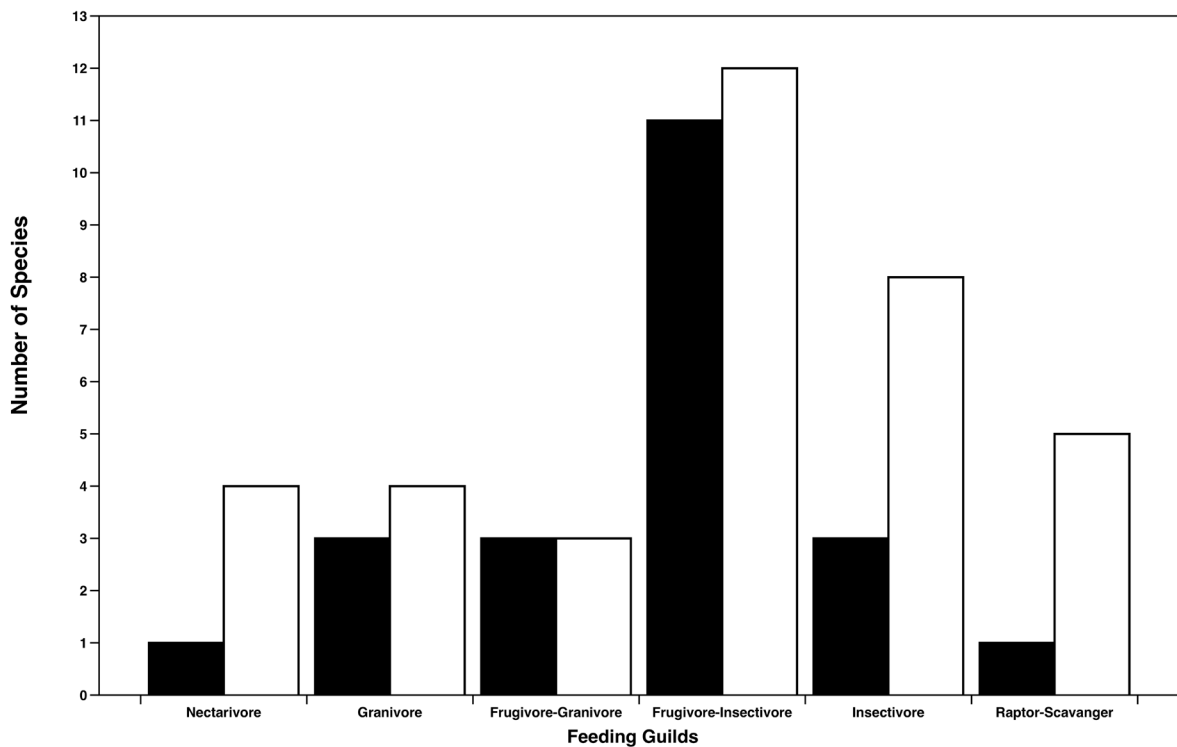

FIGURE 3. Numbers of core (black) and transient (white) species among five feeding guilds recorded in a 360-ha plot of an upland savanna in Amapá, Brazil.

TABLE 1. List of bird species recorded during one year in a 360 hectares of savanna upland at Campo Experimental do Cerrado, Embrapa-Amapá, Amapá, Brazil. Core species are those found during at least nine months while transient species were reported in less than four months. Feeding guilds are: RS (raptors + scavangers), IN (insectivores), IF (insectivore-frugivore), FG (frugivore-granivore), GR (granivore), and NE (nectarivore). Habitat categories are: (1) restricted to upland savanna; (2) recorded in other habitats in the broad landscape. Annual abundance is the total number of detections of the species over one year.

Species	English Name	Feeding Guild	Habitat	Annual Abundance
CORE SPECIES				
Geranoaetus albicaudatus	White-tailed Hawk	RS	2	27
Patagioenas cayennensis	Pale-vented Pigeon	FG	2	129
Zenaida auriculata	Eared Dove	FG	1	103
Aratinga aurea	Peach-fronted Parakeet	FG	1	161
Eupetomena macroura	Swallow-tailed Hummingbird	NE	2	38
Colaptes campestris	Campo Flicker	FI	1	23
Lepidocolaptes angustirostris	Narrow-billed Woodcreeper	IN	1	153
Elaenia flavogaster	Yellow-bellied Elaenia	FI	2	331
Elaenia chiriquensis	Lesser Elaenia	FI	1	185
Suiriri suiriri	Suiriri Flycatcher	FI	1	332
Xolmis cinereus	Gray Monjita	IN	1	327
Tyrannus albogularis	White-throated Kingbird	FI	1	131
Tyrannus melancholicus	Tropical Kingbird	FI	2	102
Tyrannus savana	Fork-tailed Flycatcher	FI	1	816
Myiarchus swainsoni	Swainson's Flycatcher	FI	1	256
Troglodytes aedon	House Wren	IN	2	38
Mimus saturninus	Chalk-browed Mockingbird	FI	2	134
Neothraupis fasciata	White-banded Tanager	FI	1	552
Cypsnagra hirundinacea	White-rumped Tanager	FI	1	486
Emberizoides herbicola	Wedge-tailed Grass-Finch	GR	1	273
Ammodramus humeralis	Grassland Sparrow	GR	1	554
Sturnella magna	Eastern Meadowlark	GR	1	56
TRANSIENT SPECIES				
Theristicus caudatus	Buff-necked Ibis	IN	2	6
Cathartes aura	Turkey Vulture	RS	2	1
Buteogallus meridionalis	Savanna Hawk	RS	2	2
Rupornis magnirostris	Roadside Hawk	RS	2	6
Burhinus bistriatus	Double-striped Thick-knee	IN	2	6
Columbina talpacoti	Ruddy Ground-Dove	GR	2	1
Patagioenas speciosa	Scaled Pigeon	FG	2	1
Leptotila verreauxi	White-tipped Dove	FG	2	6
Guira guira	Guira Cuckoo	IN	2	6
Chordeiles pusillus	Least Nighthawk	IN	2	4
Phaethornis ruber	Reddish Hermit	NE	2	3
Phaethornis superciliosus	Long-tailed Hermit	NE	2	3
Chrysolampis mosquitus	Ruby-topaz Hummingbird	NE	1	12
Anthracothorax nigricollis	Black-throated Mango	NE	2	3
Campephilus melanoleucos	Crimson-crested Woodpecker	FI	2	4
Herpetotheres cachinnans	Laughing Falcon	RS	2	5
Falco femoralis	Aplomado Falcon	RS	2	4
Forpus passerinus	Green-rumped Parrotlet	FG	2	2
Thamnophilus doliatus	Barred Antshrike	IN	2	1

Species	English Name	Feeding Guild	Habitat	Annual Abundance
Formicivora rufa	Rusty-backed Antwren	IN	2	2
Synallaxis albescens	Pale-breasted Spinetail	IN	2	5
Phaeomyias murina	Mouse-colored Tyrannulet	FI	2	4
Euscarthmus rufomarginatus	Rufous-sided Pygmy-Tyrant	IN	1	1
Tolmomyias flaviventris	Yellow-breasted Flycatcher	FI	2	1
Megarynchus pitangua	Boat-billed Flycatcher	FI	2	7
Myiarchus tyrannulus	Brown-crested Flycatcher	FI	2	5
Vireo olivaceus	Red-eyed Vireo	FI	2	2
Hylophilus pectoralis	Ashy-headed Greenlet	FI	2	15
Turdus leucomelas	Pale-breasted Thrush	FI	2	10
Schistochlamys melanopis	Black-faced Tanager	FI	2	2
Ramphocelus carbo	Silver-beaked Tanager	FI	2	3
Volatinia jacarina	Blue-black Grassquit	GR	2	2
Oryzoborus angolensis	Chestnut-bellied Seed-Finch	GR	2	3
Molothrus bonariensis	Shiny Cowbird	FI	2	4
Sturnella militaris	Red-breasted Blackbird	GR	2	3
Euphonia chlorotica	Purple-throated Euphonia	FI	2	3

Core species represented most (90.6%) of all detections over the year (Figure 4b). Monthly species richness of core (G = 6.36, df = 11, p = 0.84) and transient (G = 0.32, df = 11, p = 0.32) groups did not differ from a uniform distribution (Figure 4a). However, significant seasonal variation in abundance was found for both core (G = 309.5, df = 11, p < 0.0001) and transient (G = 26.25, df = 11, p < 0.0001) groups (Figure 4b). Both groups presented their highest abundance values from October to February, with a clear peak in November (Figure 4b).
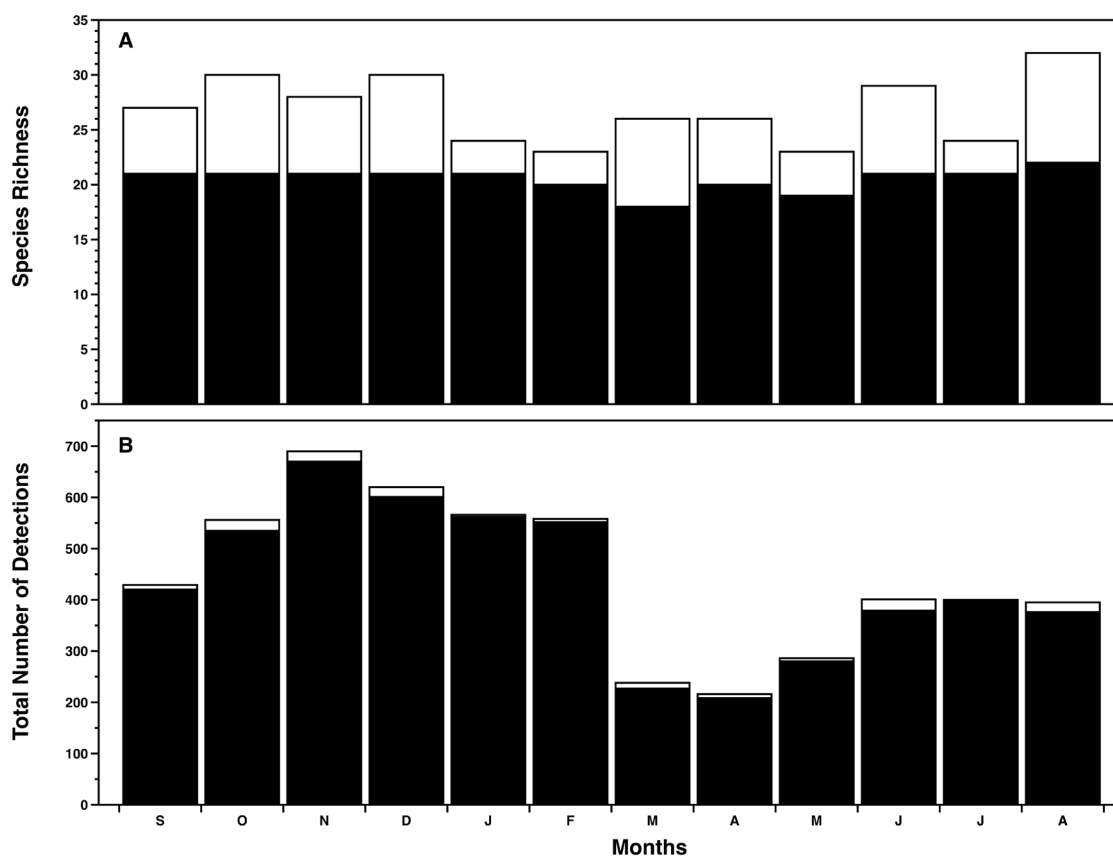

FIGURE 4. Monthly variations in the species richness (a) and total number of detections (b) of core (black) and transient (white) bird species recorded in a 360-ha plot of an upland savanna in Amapá, Brazil.

DISCUSSION

We recorded that only 22 species (30.5%) are core, with most of the species being transients. However, core species represented 90.6% of all detections in one year and are on average more abundant than transient species. Therefore, although species' richness in the site is mostly dominated by transient species, abundance is dominated by core species.

Core species are mostly restricted to savannas, while transient species occupy other habitats in the landscape. This finding is supported by findings in other tropical bird assemblages. For instance, Poulin *et al.* (2001) found that transient birds represented a large portion of the local assemblages of tropical arid and semi-arid habitats in northern Venezuela. Martin and Karr (1986) suggested that transients are an important component of tropical forest bird assemblages, but they did not present their proportions.

The core species recorded in our research site are also found frequently in other savannas in central South America and some of them are amongst the most abundant species (Silva 1995, Sick 1997, Tubelis & Calvacanti 2000, Cintra & Sanaiotti 2005, Aleixo & Poletto 2007). In addition, five core species (*Lepidocolaptes angustirostris*, *Suiriri suiriri*, *Mimus saturninus*, *Neothraupis fasciata*, and *Cypsnagra hirundinacea*) are considered as nuclear species in the mixed-species flocks that are found in most of the South American upland savannas (Tubelis 2007).

Combining our findings with general theories on bird assemblages, we can make some general predictions about the proportions of core and transient species in other South American upland savannas. At the local scale (up to 500 ha), we predict that savanna bird assemblages will be composed of a small number of abundant and habitat-restricted species that occupy the site almost year-round, combined with a high number of low abundant transient species that are habitat generalists and use the site only during some periods of their annual life cycle. Because local diversity is a consequence of regional diversity plus habitat selection (Ricklefs 2004), we can also predict that the number of core species in a given savanna site will increase with the structural complexity of the vegetation (Mac Arthur & Mac Arthur 1961, Karr & Roth 1971). In addition, because the number of transient species in a site is dependent on the pool of species in the landscape (Belmaker 2009) and because the landscape species richness correlates with landscape heterogeneity (Coyle *et al.* 2013), we can also predict that the richness of transient species in a savanna bird assemblage will increase with the heterogeneity of the landscape in which the savanna patch is located (Coyle *et al.* 2013). These predictions can be tested by carefully designed long-term seasonal studies on sites covering an array of landscapes that compose the South American savannas.

Populations of both core and transient species exhibited marked seasonality and followed roughly the same variation pattern. Overall, bird abundance is high from October to February and low from March to September. The five months in which bird abundance is higher coincides with the last two months of the dry season and the first three months of the rainy one. Although fruits and insects are available year-round in tropical savannas (Silvério & Lenza 2010, Silva *et al.* 2011), the availability of these resources peaks during the transition between dry and rainy seasons (Sanaiotti & Cintra 2001). It is also during this period that most of the species breed in the plot (Boss 2009), a pattern that has been observed in other tropical savannas as well (Sanaiotti & Cintra 2001, Silvério & Lenza 2010).

The overlap between breeding period and higher abundance indicates that recruitment is the simplest explanation for the increase of the detections of core species at the local level (Martin & Karr 1986). However, there are six species (*Elaenia flavogaster*, *Elaenia chiriquensis*, *Tyrannus albogularis*, *Tyrannus melancholicus*, *Tyrannus savanna*, and *Myiarchus swainsoni*) that have populations that breed in central South America and are known to migrate northwards during the austral migration (Chesser 1994). Therefore, it is also possible that individuals coming from migratory populations of those species and stopping by the site during some days or weeks may also contribute to the variation in abundance of these core species. Finally, core species might have been more abundant during the breeding period because they were more vocal and consequently their detectability increased. More studies are required to evaluate these hypotheses.

Because transient species are expected to track resources across the landscape more frequently than core species, the variation in the abundance observed for transient species can be explained by the high concentration of insects, fruits, and flowers during some periods of the year in the plot. The abundance of food resources during the end of the dry season and beginning of the rainy season possibly attracts several species from other habitats in the landscape to the study plot, leading to an increment of both richness and abundance of transient species (Martin & Karr 1986).

Our study also indicates that several species from gallery forests and wet grasslands are able to fly more than 300 meters into the upland savannas to use resources, indicating that possibly the intensity of the movements between habitats within landscapes dominated by upland savannas are greater than was originally expected (Tubelis *et al.* 2004). Because South American savannas' landscapes are heterogeneous landscapes subjected to

strong environmental variability (Furley 2006), their local bird assemblages are composed mostly of species that have a generalist feeding habit and a high capacity to exploit resources in the interfaces between open and forest physiognomies (Silva 1995, Tubelis *et al.* 2004). Understanding the dynamics of the avian assemblages over time and space will require focus along the boundaries of the different structural elements of the landscape because inter-habitat movements may have been underestimated in most of the studies so far (Dunning *et al.*1992, Silva *et al.* 1996).

Our results demonstrated that few core species were present in an upland savanna site over the entire year and that a considerable flow of individuals and species existed across the landscape as a consequence of the resource dynamics. The implications of these findings for the design of persistent conservation systems are clear. The conservation of South American savannas requires large protected areas covering representative entire landscapes integrated through large-scale multiple-use corridors designed to maximize the environmental heterogeneity of the region and thus ensure the maintenance of the ecological and evolutionary processes that have shaped their biota (Silva & Bates 2002, Cavalcanti & Joly 2002).

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