Effects of fire regime on birds' community in an Amazonian savanna

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ABSTRACT

Savannas are ecosystems maintained by fires, characterized by a fire-adapted biota, and savanna patches occur in Amazonia in patches surrounded by tropical forest. Different fire regimes can generate structurally diverse vegetation, and savanna birds are known to be closely related to vegetation structure. However, long-term approaches and interaction of fire with other environmental factors need to be explored for the better understanding of the effects of habitat fire on birds. In an Amazonian landscape composed by savanna and forest, we investigate the effects of different fire regimes in a 12-ha area in three periods through 23 years. We also examined the effects of frequency and extent of fires, tree cover, and distance to forest on bird composition in twelve 3.7-ha savannas plots. Birds were surveyed with mist-nets and species were classified as to their habitat use by comparison of registers in forest and savanna plots through visual/acoustical surveys. After 13 years of fire suppression, many forest species colonized the area and some savanna species were lost. Fire frequency and tree coverage affect avifauna communities. The avifauna was sensitive to the occurrence of fires, independent of fire extent. After one fire event in a plot that had been protected from fire for 12 years, some savanna species returned. These results highlight the effects of the fire regime on birds species composition and indicate that many savanna bird species depend on the occurrence of regular fires.

Key-words: Alter do Chão; bird community; fire extent; fire frequency; forest-savanna boundary, Neotropics.

Background

Savanna is a vegetation type characterized by the occurrence of grasses, shrubs, and trees, where the density of woody vegetation varies and its canopy is discontinuous (Ferreira et al. 2015, Silva et al. 2019, Azevedo et al. 2020). In the Neotropics, there are three main domains of the savanna biome: the Llanos and the Guianan domains in northern South America, and the Cerrado domain in central South America (da Silva and Bates 2002, Furley 2006, Azevedo et al. 2020). Beyond these domains, there are also several smaller areas of savanna scattered across the Neotropics, such as in the Atlantic Forest, in Central America, on Caribbean islands, and within lowland Amazonia (de Carvalho and Mustin 2017, Pennington et al. 2018). In the Amazonia, savannas are estimated to cover between cover between 1.8% (de Carvalho and Mustin 2017, Mustin et al. 2017) and 3-4% (Pires and Prance 1985) of the region and occur isolated in patches of different sizes, surrounded by a matrix of humid tropical forest (Huber 1982, de Carvalho and Mustin 2017). A factor that differentiates savannas from other open vegetation types is that savannas burn regularly and naturally (Ramos-Neto and Pivello 2000).

Savannas of tropical humid regions are maintained mainly by the incidence of fires (Moreira 2000, Bond and Keeley 2005). Fire regimes differ in the combination of several factors, such as frequency, intensity, the extent of fires, and the period of year in which they occur (Bond and Keeley 2005), and some plant species show adaptations to this disturbance (Fidelis and Zirondi 2021). Savanna organisms are resilient to milder fires, similar to natural fire regimes, and are more impacted by fires that are more frequent or that occur in seasons different from natural regimes (Griffiths and Christian 1996, Ramos-Neto and Pivello 2000, Medeiros and Miranda 2008, Smit et al. 2010, Fidelis and Zirondi 2021). However, savannas are threatened by changes to their natural fire regimes; while in some areas fires have become more frequent, other savannas undergo a process of densification of woody vegetation, possibly due to fire suppression (Sanaiotti and Magnusson 1995, Medeiros and Miranda 2008, Moustakas et al. 2010, Lima et al. 2020).

The effects of the alteration in natural fire regimes could threaten the Amazonian savanna biota. However, studies on the effect of fires on the savanna biota are generally incomplete and fragmented, frequently based on controlled experiments that do not reflect the real variation of the effects of non-experimental fire regimes (Parr and Chown 2003, Russell-Smith et al. 2010). Despite their limited distribution and pressure from the rapid expansion of agriculture and livestock, the Amazonian savannas are underrepresented in Conservation Units (Sanaiotti and Magnusson 1995, Santos and Silva 2007). In this context, studies on well-known taxonomic groups can offer critical insights for the savanna dynamics under different level of disturbance.

Birds are one of the most studied Neotropical groups, and their geographic and morphological variability is better characterized than for other taxa. The composition of the savanna avifauna is associated with the severity of the fires and varies along the gradient of disturbance (Barlow and Peres 2004, Clavero et al. 2011, Davis and Miller 2018). However, evidence of diversified responses to fire regimes led to “pyro-diverse” management techniques in savannas, without regard to the ecological significance of some fire patterns (Parr and Andersen 2006). The investigation of the responses of birds to different intensities and frequency of fires in areas of contact between savanna and forest is important in order to understand the effects of forest expansion or of the use of fire for the restoration of savanna avifauna (Artman et al. 2005, Moura et al. 2016, Davis and Miller 2018). In addition, long-term approaches and those that consider the spatial variation of fires and their interaction with other environmental factors need to be incorporated for a better understanding of the relationship between fire and fauna (Parr and Andersen 2006, Driscoll et al. 2010).

We analysed the variation of the bird community in an eastern Amazonian savanna in response to different spatial and temporal scales of fires. We evaluated the dynamics of the avifauna over 23 years, in which 10 were under regular fire regime and the last 13 years under fire suppression. We also used 12 widely dispersed plots to evaluate the effects of the frequency and extent of fires, tree cover, and distance to forest on bird assemblages. We hypothesised that (i) avifauna composition would be significantly different after 13 years of fires suppression, with colonization by some forest species; (ii) fire frequency and extent would affect avifauna composition, with a higher abundance of savanna species in plots with higher occurrence and extent of fires.

Material and Methods

Study area – The study was conducted in a savanna region in the state of Pará, Brazil, in the municipality of Santarém, near the village of Alter do Chão (2 ° 31 'S, 55 ° 00' W) on the right bank of the Tapajós River (Figure 1). The area covers about 10,000 ha distributed in four non-contiguous enclaves, with a larger portion of the area being composed of sandy soil covered by a herbaceous layer of varying height and density, a shrub layer of 60-80 cm, and a tree layer up to 10 m (Cintra and Sanaiotti 2005, Magnusson et al. 2008). The savanna contains differentsized patches of semi-deciduous forest and is surrounded by the same vegetation (Miranda 1993, Cintra and Sanaiotti 2005). The climate has two well defined seasons: the dry season from July to December, and the rainy season from January to June, with 75% of rainfall occurring from

December to June. Fires in the study area are mainly of anthropogenic origin and usually occur during the dry season.

Bird sampling – We captured birds with mist-nets (mesh size 36 mm). We identified the birds based on identification guides (Mata et al. 2006, Ridgely and Tudor 2009) and consultation with specialists. The nomenclature of birds follows the "List of Brazilian Birds" of the Brazilian Committee of Ornithological Records (CBRO 2011). Birds captured in this study were marked with metal bands provided by CEMAVE-ICMBio (authorization number 1177 / 4, ICMBIO / SNA) or coloured plastic bands.

Temporal analysis – We captured birds in three sampling periods over 23 years: five samples from September 1987 through August 1988, three samples from September 1996 through February 1997 and five samples from August 2009 through June 2010. The sampling site was a savanna area of about 12 ha (250 x 450 m) located on a peninsula (Figure 1A, dotted red rectangle). From at least 1985 until 1997 the area was under a regular fire regime (Sanaiotti and Cintra 2001). From 1998 until 2010 there were no fires in the study site. The sampling protocol was standardized throughout the whole study period, in which we used 20 mist-nets of 12 x 2.5 m (36 mm mesh size). The nets were positioned consecutively, forming a single straight mist-net line. Every second day, the location of the mist-net lines was changed to a perpendicular position distant up to 100 m from the previous net line (Figure 1B). The net-line positions varied between samples, so as to cover the maximum possible area of the 12-ha site (Fig. 1B). Nets were opened from 6 to 9 am and from 15:30 to 17:30 pm. Each sample consisted of four positions of net lines, in which we considered the four morning samples of each net-line position and the two first sampled afternoon periods, accruing a total of 320 net-hours per sample.

Spatial analysis – To assess the spatial variation in bird assemblages, we sampled twelve 3.75 ha plots that were separated by at least 1 km. Each plot had four parallel 250 m transects spaced 50 m apart (Fig. 1C). The birds were captured with 30 mist-nets (36 mm mesh size), arranged consecutively in two lines of 15 mist-nets (nine 9 x 2.5 m mist-nets and six 12 x 2.5 m mist-nets per transect). The mist-nets were opened in the same time interval described previously for one day in each plot. Sampling occurred in the dry season from August to October 2010. Plot 9, which had been under fire suppression since 1997, had an unexpected fire on 23 October 2010. This plot was sampled again in November 2010, immediately following the fire event, with the same protocol used in the 12 plots.

Bird classification – We classified bird species regarding the habitat in which they were most common in the savanna-forest mosaic of the study area. In 1999 and 2000, RC undertook visual and acoustic sampling of birds in 22 savanna plots and 22 forest plots (distributed in isolated forest fragments in savanna matrix and in the adjacent continuous forest) for a posterior classification of species as to their habitat use. The 22 savanna plots had the same characteristics as the 12 plots sampled with mist-nets in this study. RC sampled two 2

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50 m transects from 6 to 9 am and from 4 to 6 pm in the afternoon, stopping for two minutes every 50 m and registering every bird heard or seen within a 10 m radius

(Cintra and Sanaiotti, 2005; Cintra, Magnusson and Albernaz, 2013) . The abundance of the species in the 44 savanna and forest plots were compared through a Wilcoxon test. The species that were more abundant in forest plots ($p<0.05$) were classified as forest species (F), those that were more abundant in savannas were classified as savanna species (S), and species whose abundances did not differ significantly between the two habitats were classified as indifferent (I). Six species (Table 1) were classified based on the literature because they were not recorded in point-count surveys in any of the 44 plots.

Environmental variables – The fire history data from each plot was collected from 1997 to 2009, except for 1998. The four 250 m transects in the plots were sampled annually after the burning period (usually from August to December). To estimate the burn extent in a plot, we checked for burnt vegetation at 2 m intervals, and the annual burn extent value was the percentage of burnt points per plot (number of points with burnt vegetation / total plot points). The fire history of the plots was calculated by summing all of the annual burn extent for each plot (ranged from 0 to 1,200). Another fire history variable that we considered was the occurrence of fires regardless of their extent. This variable was calculated by summing the number of years throughout the 12 sampling years in which the plot was burned. Therefore, this value ranged from 0 to 12 and will hereafter be referred to as fire frequency (Table 2).

Data on tree cover were collected from July to August 2007. We used tree cover measured 3 years prior to bird sampling because tree cover did not change significantly in a four year interval in the study region (Vasconcelos et al. 2008). At 2-m intervals along the four transects in each plot, a cylindrical metal stick 1-m long with a 2 mm diameter was positioned perpendicularly to the ground and it was noted whether it touched a tree or was under a tree canopy (height > 2m). We considered tree cover as the proportion of points that met this criterion (Table 2). For more information about the method, see Magnusson et al. (2008).

The composition of the bands 1, 2, 3, 4, 5, and 7 of a Landsat TM 5 image (orbit 227, point 62) of 29 June 2010 was georeferenced to a geographic information system (ESRI ® ArcMap ™ 3.9) using paths and points collected with GPS in the study area. The resulting image composition underwent a process of supervised classification by maximum likelihood with the program ENVI 4.5 © 2008. This resulted in a thematic map of the study area containing the following classes of land cover: 1) savanna, 2) forest, 3) water bodies, and 4) other. We obtained the forest distance of each plot from this composition, considered as the shortest distance measured from the centroid of each plot and the edge of the closest forest.

Data analyses – We did not include nightjars or hummingbirds in the analyses because our mist-net sampling was not appropriate for capturing these groups. Four species (*Myiarchus swainsoni, Myiarchus ferox, Phaeomyias murina,* and *Camptostoma obsoletum*) were not included in the analysis of temporal variation because irregularities in their identification were detected. These species were included in the analysis of spatial variation given that, during the sampling of this data, birds were photographed allowing posterior certification. Recaptures within each temporal or spatial sample were not included in the analysis. We used the number of captures of each species as an index of relative abundance for each sampling unit for all analysis. All statistical analyses were performed in R software (R Core Team 2021).

To test the first hypothesis (i), we used a one dimensional non-metric multidimensional scaling (NMDS) ordinations as implemented in the metaMDS function in the R package vegan 2.5-7 (Oksanen et al. 2010), with the data from the peninsula over the 23 years. Compositional dissimilarity was quantified with the Bray-

Curtis dissimilarity index. We tested the significance of the NMDS axis for the year of sampling through the envfit function. Next, we used Permutational Analysis of Variance (PERMANOVA) to assess whether sampling occasion affected bird community composition. To visualize the change in bird community composition, we used a direct ordination of samples (McCune et al. 2002) in chronological order to view changes in the community throughout sampling history in a compound graph in which the relative abundance of all species is shown (DOI: 10.5281/zenodo.3784397).

To test the second hypothesis (ii), we used the relative abundance dissimilarity measured through Bray-Curtis distance and the environmental variables (except for plot 9 after fire since the variables were collected before the fire event) that were standardized with mean = 0 and variance = 1. We did a PERMANOVA with the community dissimilarity as the response variable and the fire frequency, percentage of burnt points per plot, tree coverage and the distance to forest as the explanatory variables. We also used multiple regressions on dissimilarity matrices (MRM), as implemented in the function “MRM” of the R package ecodist v.2.0.7 (Goslee and Urban 2007) with the same variables. Statistical significance of the regression coefficients was determined with 10,000 permutations. To visualize the change in the bird composition in plot 9, we plotted the inverse of abundance pre-fire and total abundance post-fire of each species in a lollipop graph with ggplo2 v. 3.3.5 (Wickham 2016).

Additional R packages used for data curation and visualization were tidyverse v.1.3.1 (Wickham 2017), iNEXT v.2.0.20 (Hsieh et al. 2016), and plotly v.4.10.0 (Sievert 2020). Scripts for all analyses are provided in the supplementary material.

Results

Temporal analysis – A total of 620 individuals of 46 species were caught in 723 captures in 13 samples of the peninsula. Our first hypothesis (i) was supported. The samples collected after 13 years of fire suppression did not overlap with the samples collected under the frequent fire regime in the space defined by the two NMDS axes (Figure 2; envfit: $r^2 = 0.59$, $p = 0.001$). The first NMDS axis split samples from the fire-suppression period (green circles) from the two sampling periods under fire regime (87-88 [red triangles] and 96-97 [orange squares]) which overlapped along the NMDS axis (Figure 2). The PERMANOVA analysis also indicated that the bird assemblage composition varied significantly among the three sampling periods in the 12-ha study site of the peninsula ($F = 2.73$, $P = 0.003$).

In the periods with fires, there were more species classified as savanna species in relation to forest species (Figure 3). Some species, such as *Ammodramus humeralis*, *Columbina passerina* and *Suiriri suiriri*, with high occurrence in samples from periods when the plots were burnt, were not captured after fire suppression (Figure 3). *Elaenia chiriquensis* was captured in almost every sample undergoing burns, while only one individual was captured in the post-fire suppression sampling period. There was a predominance of forest species in relation to savanna species in the samples after fire suppression. In the period without fires, the area was colonized by some species that were not registered in previous samples, such as *Pachyramphus polychopterus, Pachyramphus rufus, Ramphocelus carbo,* and *Hylophilus semicinereus* (Figure 3).

Spatial analysis – In the 12 plots sampled, excluding the resampling of plot 9, we caught 666 individuals belonging to 44 species in 744 captures. There were no recaptures between different plots. Plot 9 was located in the area under a 12-year fire suppression (the last fire was in 1997), while the fire frequency among the other plots ranged from 6 to 10 fires in the last 12 years (Table 2). Ten plots (except for 4 and 9) were burned in 2009, one year before the bird sampling took place. Our second hypothesis (ii) was partially supported. The PERMANOVA analysis was significant for fire frequency (F = 3.83, p = 0.001; Table 2), while in the multiple regression analysis tree coverage was significant (coeff. = 0.07, p = 0.01; Table 2).

Some savanna species were not present in low fire frequencies, while forest species occurred mainly on the lowest extreme of the fire frequency gradient (Figure 4). Some forest species occurred only in plots 4 and 9, which were the plots with the lowest fire frequencies in the last 12 years. However, some savanna species, such as *Phaomya murina* and *Volatina jaccarina,* that were absent in plot 9 but were present in the rest of the fire-frequency gradient also occurred in plot 4.

The bird species composition in plot 9 a month after the 2010 fire was different from the composition observed previously (Figure 5). Species such as *Schistoclamys melanopis*, *Myiarchus ferox, M. tyrannulus,* and *Dendroplex picus* were not captured after the fire, while *Claravis pretiosa* and *Ammodramus humeralis* were captured exclusively in the post-fire census. In the long-term study, in which the study site overlaps plot 9, these species were not captured in any of the samples collected after fire suppression. However, these species occurred in samples from periods with a frequent-fire regime, and *A. humeralis* was one of the most frequent species in these samples (Figure 3).

Discussion

We evaluated the temporal and spatial change in bird assemblages under distinct fire regimes in an Amazonian savanna. After 13 years of fire suppression, the avifauna composition included more forest species. Similarly, in the spatial analysis, the fire frequency and tree coverage had affected the avifauna, with some savanna species appearing soon after a fire in a plot under fire suppression. Changes in the frequency of fire, including the fire suppression management are changing the biotic communities in Cerrado savanna (Moreira 2000, Durigan and Ratter 2006, Geiger et al. 2011, Davis and Miller 2018). Summed with other factors, such as climate change, increased CO2, and land-use change, this will certainly impact species composition (Khavhagali and Bond 2008), ecosystem structural dynamics, aboveground woody biomass (Phillips et al. 2009, Marimon et al. 2014, Morandi et al. 2016), occurrence of fire-tolerant plants (Miranda et al. 2002, Henriques 2005, Fidelis and Zirondi 2021) and vegetation encroachment (Khavhagali and Bond 2008).

The dynamics of local bird assemblages changed over time in in accordance with changes in the fire regime. Regular fires maintained the area suitable for an avifauna comprising typical savanna species, and fire suppression lead to influx and consequent predominance of forest species in the bird assemblages. Changes in predominance of species was also found for birds and other vertebrates in an Australian savanna under fire suppression for 23 years (Woinarski et al. 2004). During fire suppression, there was a marked increase in woody-vegetation cover, mainly due to an increase in density of tree species associated with forests in the study region (Lima et al. 2020). Forest birds foraging in adjacent savannas potentially disperse forest seeds into the savanna (Tubelis 2004). Therefore, it is likely that the influx of forest birds has intensified the process of forest-tree recruitment by seed dispersal in the savanna area. The main factor that restricts the establishment of forest tree seeds in savannas is fire, in spite of seed morphological constraints, and fire suppression favours the expansion of forest species into the savanna (Hoffmann et al. 2004, de Souza Campos and Jardim

2020, Lima et al. 2020).

Shrub encroachment (*i.e.* woody-cover increase) has been indicated as a driver of changes in bird assemblages in African savannas, especially due to the loss of species associated with open savannas (Krook et al. 2007, Sirami et al. 2009, Sirami and Monadjem 2012). In our samples, two species that were amongst the most frequent species from 1987 to 1997, *A. humeralis* and *C. passerine*, were not recorded in the study site after fire suppression. These species are ground dwellers and probably associated with grass cover, a characteristic ubiquitous in African savanna birds that are undergoing habitat loss due to shrub encroachment (Sirami and Monadjem 2012, Abreu et al. 2017). Savannas protected from fire have less grass cover and denser woody vegetation in relation to savannas undergoing frequent burning (Moreira 2000, Woinarski et al. 2004, Passos et al. 2018). The passage of fire reduces the density of the middle stratum of the vegetation and reduces shrub-cover extent (Sanaiotti and Magnusson 1995), and favours the expansion of grasses (Moreira 2000, Fidelis and Zirondi 2021). *Ammodramus humeralis* re-colonized the area within the first month after the 2010 fire, together with *Claravis pretiosa,* another ground-dwelling species that was only captured prior to fire suppression. An influx of ground-dwelling bird species after a fire was also observed in an Australian savanna (Crawford 1979). The passage of fire reduced the cover of the middle stratum that was impairing the access of birds to the soil (Crawford 1979), and it is likely that a similar process occurred in our study site.

Typical savanna species favoured by fire were not exclusively associated with the herbaceous stratum: *e.g. E. chiriquensis,* an understory omnivore species that had a response pattern to fire history similar to *A. humeralis.* Therefore, even after prolonged fire suppression, a single fire restored environmental characteristics favourable for some typical savanna species.

Fire frequency and tree cover drove variations in assemblage structure between plots due to differences in the relative abundance of species. The bird assemblages were more affected by the accrual of fire occurrence than by the extent of the fires. This result can be expected if the extent of burning does not reflect its severity in the study area, or if the severity of the burn does not have a significant effect on birds. The flora and fauna of an Australian savanna were in general resistant and resilient to fire in the medium-term, but the occurrence of fire regardless of its intensity was the main factor that influenced the species sensitive to this disturbance (Andersen et al. 2005), which is a pattern similar to our result. However, a fire severity index that combined fire extension, shrub cover loss and branch diameter (a proxy value for fire intensity) affected birds in European mountain rangelands (Pons and Clavero 2010). Since fire regime is a multifactorial disturbance, which probably has a multitude of synergistic direct and indirect effects on the biota, it is challenging to assign organism responses to particular aspects of a fire regime. Nevertheless, in our study we observed an effect when we simplified our fire history measure, which highlights the sensitivity of the avifauna structure to fire history and shows the value of studies of fire impact, even when based solely on fire occurrence.

The effects of tree cover and fire frequency were not distinguishable due to their high covariance. Fire inhibits the establishment of young trees and sprouts, while adult trees in savannas survive burns (Prior et al. 2010). We expected that plots under a regular fire regime would have little variation in tree cover over time because of the inhibition of tree recruitment by fire, and consequently it would be the vegetation strata least correlated to fire history. Therefore, we chose tree cover as the main vegetation variable. However, tree cover was highly correlated with fire history, impairing the distinction between the effects of these two variables (Camill et al. 2009). Fire affected the beetle community in the study area when associated to vegetation cover, but it had no direct effect when it was considered regardless of its interactions with vegetation (Louzada et al. 2010).

The interaction between the direct and indirect effects of fires on the biota makes it difficult to consider them separately. For instance, despite the death of some individuals due to direct effects of fire, the abundance of frill-neck lizards in an Australian savanna was higher post fire in relation to prior to the fire, due to a post-fire enhancement of food availability (Griffiths and Christian 1996). We did not detect direct short-term effects of fire on birds. In contrast, many individuals were recaptured after fires in the short and long-term, a result also observed previously in the same region (Cintra and Sanaiotti 2005) and in the Cerrado of Central Brazil (Piratelli and Blake 2006). As savanna birds have high specificity in terms of vegetation structure (Tubelis and Cavalcanti 2001, Krook et al. 2007, Sirami et al. 2009) the direct effects of fire on birds should be less pronounced and noticeable than the strong response of birds to changes in the environment. Therefore, the effect of fire on birds is probably mainly indirect, through the vegetation.

Some species occurred almost exclusively in the extreme of the fire and tree cover gradient gradient. Plot 4 and plot 9 had a similar and extensive tree cover, but the fire frequency in plot 4 was pronouncedly higher. The effect of the interaction between these variables is illustrated by the occurrence pattern of some species in plot 4. Even though plot 4 shared some forest species exclusively with plot 9 (e.g. *Hemitriccus striaticollis* and *Pathyramphus poluchopterus*), some savanna species (*e.g. A. humeralis* and *E. chiriquensis*) that occurred in plot 4 were only captured in plot 9 after fire occasion. In spite of its extensive woody vegetation, its fire frequency also favoured the occurrence of some typical savanna species.

The spatial variation in the fire regime, as observed here, may contribute for the diversity in the landscape level. In some ecosystems, such as Cerrado savanna and forest areas, variation in the biota can be explained by the climax-gradient model (Whittaker 1953). This model suggests that there is no single, absolute biotic community climax state across large areas. Hence, according this model, the assemblages change dynamically over time in response to continuous variations in availability of different resources and frequency of disturbances, such as fires. Indeed, tropical forests and savannas seem to represent alternative states in certain areas, and their transition may be associated with thresholds or tipping points in environmental variables (Hirota et al. 2011, Lehmann et al. 2014). Furthermore, in another Amazonian savanna landscape, most birds' species crossed the boundaries between forests and savannas, and just rare species were restrict to a habitat or another (de Sousa *et al.*, 2022) .

Implications for conservation – Amazonian savannas share species in common with the Cerrado, allowing the expansion of the Central South America savanna biota to the region (Aleixo and Poletto 2007, Ritter et al. 2020), including some threatened species , such as *Cercomacra carbonaria* and *Synallaxis kollari* (Santos and Silva 2007). Amazonian savannas are important for conservation at both local and regional levels, since they occur surrounded by the tropical forest, forming mosaics of complex vegetation (Adeney et al. 2016), which increase the beta diversity. Furthermore, Amazonian savannas shelter several species from Cerrado with distinct evolutionary and biogeographic characteristics (Garzón-Orduña et al. 2014, Resende-Moreira et al. 2019, Ritter et al. 2020).

Savannas are generally distributed in areas with low annual precipitation and high precipitation seasonality (Lehmann et al. 2011). However, many tropical savannas currently occur in areas that are predicted to support forests (Bond and Keeley 2005) (Bond and Keeley 2005, Murphy and Bowman 2012). In these areas, disturbances, such as fires help to keep the vegetation open (Fidelis and Zirondi 2021). Fire histories that favoured forest species and culminated in a higher richness were in general detrimental for savanna species (Durigan 2020). However, a frequent-fire regime may lead to species loss and ecological disequilibrium (Medeiros and Miranda 2005, Fidelis and Pivello 2011). In ecosystems, such as the Cerrado, where patches of forest harbour a great portion of the diversity (da Silva 1995), it is advantageous to apply comprehensive conservation strategies considering less frequent fire regimes. However, Amazonian savannas have a limited extension and are under-protected and threatened, and efforts to conserve their diversity should be concentrated on the savanna species strongly associated with this habitat. Indeed, a study focusing forest habitats in the same area of this study showed that forest fragments keep a large portion of bird communities (80%) of the forest continuous area (Cintra, Magnusson and Albernaz, 2013) , highlighting the higher vulnerability of savanna species birds on the region.

The savannas of Alter do Chão are all in private property, resulting in an idiosyncratic and unplanned fire regime. This allowed the existence of a dynamic community over time and space. Regrettably, areas of tropical savannas are particularly under pressure for agriculture and livestock, undergoing an alarming rate of degradation. Recent changes in Brazilian environmental policy have resulted in an alarming increase in the rate of deforestation in Amazonia (Pereira et al. 2019, Rapozo 2021), many times associated with wildfires (Silva et al. 2021). Although fire is a key factor for the maintenance of typical savanna species, the increase of anthropogenic fires associated with climatic change may lead to the loss of bird diversity. Hence, avoiding the largest unauthorized fires is important, but keeping small-scale fires may be a better strategy than trying to avoid fires altogether or manage complex and costly fire regimes (Andersen and Hoffmann 2011).

Conclusion

Fire affected bird assemblage composition at several temporal and spatial scales, and the effects were congruent. Areas under frequent fire disturbance had a predominance of savanna species in relation to forest species, while some forest species were more frequent in areas with lower fire frequency. The congruence of the results highlights validity of space for time substitution when temporal data are unavailable. However, the use of these two scales provides complementary information and allows a more complete comprehension of the effects of fire on the fauna. Fires are a key element in maintaining the eastern-Amazonian savanna-bird communities, but, climate change and increased frequency and intensity of anthropogenic fires may threaten bird diversity if the subtle effects are not understood.

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Table 1. Species captured by mist-net sampling in the savana of Alter do Chão - PA. Species marked with • had not been registered before in the study area (Sanaiotti & Cintra, 2001). Habitat use refers to the habitat where species was most frequent in the region (Savanna, Forest or Indifferent, * are species classified based on literature, for which we did not have enough data for analyses).

Family	Species	Habitat Use
Columbidae	*Crypturellus parvirostris*	S
	Columbina passerina	S
	Claravis pretiosa	I
	Zenaida auriculata	S*
	Leptotila rufaxilla	F*
Bucconidae	*Nystalus maculatus*	S
Dendrocolaptidae	*Dendroplex picus*	F
	Lepidocolaptes angustirostris	S
Thamnophilidae	*Formicivora grisea*	F
	Formicivora rufa	S
	Thamnophilus stictocephalus	F
Pipridae	*Neopelma pallescens*	F
	Manacus manacus	F
Tityridae	*Pachyramphus polychopterus*	F
	Pachyramphus rufus•	F*
Tyrannidae	*Tolmomyias flaviventris*	F
	Todirostrum cinereum	F
	Camptostoma obsoletus	S*
	Hemitriccus striaticollis	F
	Elaenia flavogaster	S
	Elaenia cristata	S

	Elaenia chiriquensis	S
	Elaenia parvirostris	S*
	Phaeomyias murina	S*
	Suiriri suiri	S
	Myiopagis viridicata•	F*
	Myiarchus swainsoni	I
	Myiarchus ferox	S
	Myiarchus tyrannulus	S
	Sirystes sibilator	F
	Megarynchus pitangua	F
	Tyrannus albogularis	I
	Tyrannus melancholicus	I
	Griseotyrannus aurantioatrocristatus•	S*
	Empidonomus varius	I
Vireonidae	*Cyclarhis gujanensis*	S
	Vireo olivaceus	F
	Hylophilus semicinereus•	F*
	Hylophilus pectoralis	F
Hirundinidae	*Stelgidopteryx ruficollis*	I
Troglodytidae	*Troglodytes musculus*	S
	Cantorchilus leucotis	F
Turdidae	*Turdus leucomelas*	F
Thraupidae	*Saltator maximus*	I
	Tachyphonus rufus	F
	Ramphocelus carbo	F
	Tangara cayana	S
	Thraupis episcopus	I
	Thraupis palmarum	F

	Schistochlamys melanopis	I
	Cyanerpes cyaneus	F
Emberizidae	*Ammodramus humeralis*	S
	Volatinia jacarina	S
Cardinalidae	*Piranga flava*	S
Fringilidae	*Euphonia chlorotica*	I

Table 2. Fire frequency for the twelve years (Freq), the sum of fire extension percentage per year (Ext), tree cover percentage (Cov), the distance of plot centroid for the forest (For), the results of F model and their respective p-value in the PERMANOVA analysis, and the coefficientes (coeff.) and their p-values for the multiple regressions (MRM) analysis.

	P9	**P9**	**P4**	**P6**	**P8**	**P16**	**P21**	**P25**	**P26**	**P29**	**P34**	**P33**	**P36**	**PERMANOVA**		**MRM**	
	pre	**post**												**F**	**p**	**Coeff.**	**p**
Freq	**1**	2	6	8	7	9	7	8	8	10	10	8	9	**3.83**	**0.001**	0.11	0.074
Ext	**96**	-	534	679	558	864	576	744	682	834	950	557	729	1.38	0.207	-0.05	0.32
Cov	39	-	38	19	15.2	9.2	24	23.2	15	7.6	15.8	27.7	16	1.19	0.306	**0.07**	**0.012**
For	56	-	55	220	280	187	280	127	127	180	198	120	383	1.85	0.066	-0.02	0.421

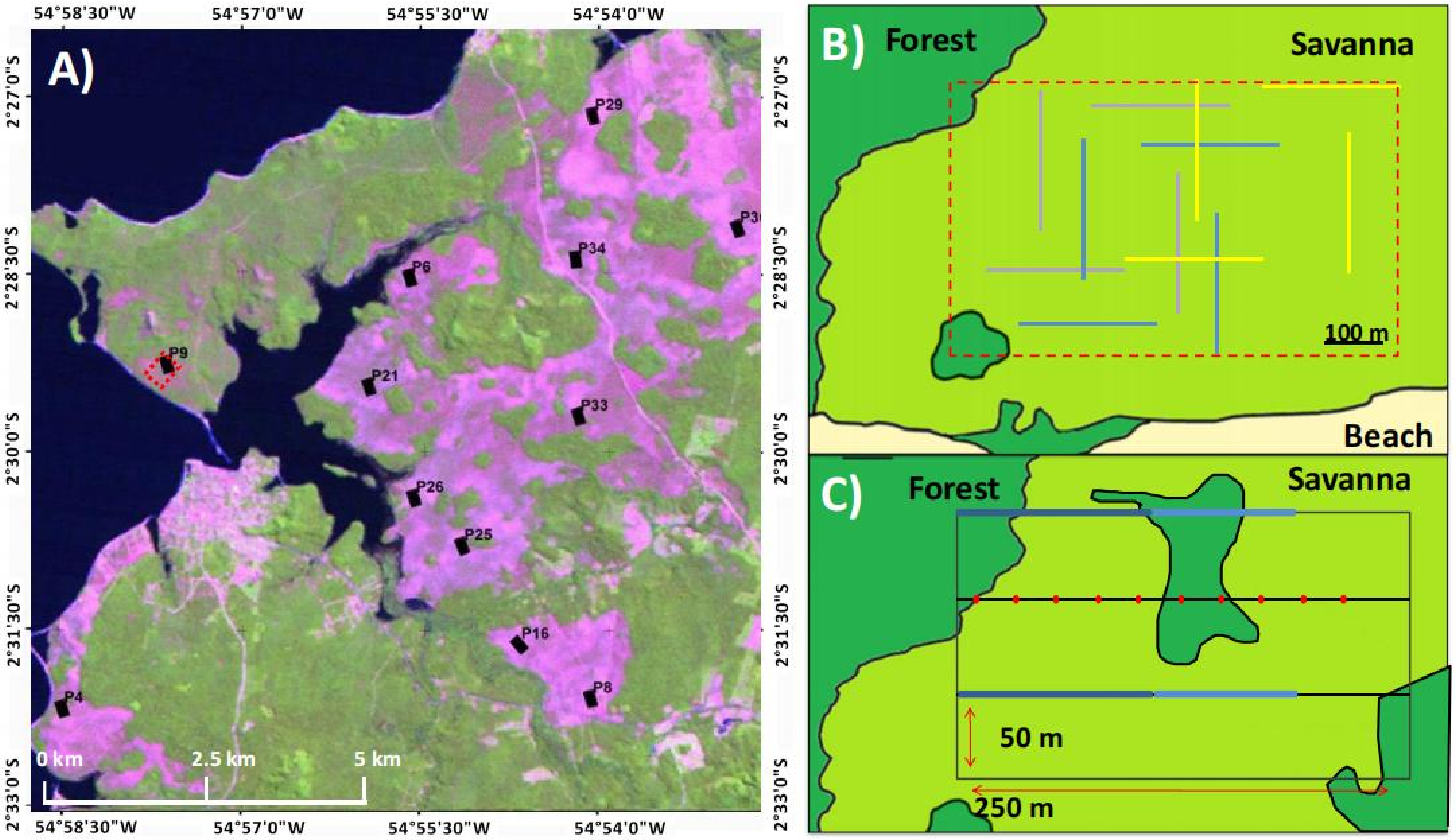

Figure 1. A) Landsat image of the study area from June 2010. The purple portion represents the savanna area; the green corresponds to forest vegetation; and the black colour is the Tapajos River. The black rectangles represent the 12 sampling plots (150 x 250m), while the single red

and dotted rectangle indicates the area where the long-term avifauna dynamics study was undertaken (12ha, "peninsula"); B) Sampling design of the temporal analysis of variation in bird community study. The outer red dashed rectangle represents the sampling site. The solid lines represent net-lines, and each set of 4 lines in the same color represents net-line positions in one sample period (in this case, the sampling schemes of three samples are represented). The overlap of the positions of net-lines throughout the study formed a grid of 12 ha (outer red dashed rectangle); C) Sampling design of the spatial analysis of bird assemblages. Four parallel transects of 250 m, distant 50 m from each other, were placed in each plot. In the all four transects, for each 2 m the fire extension and vegetation cover percentage were measured (sum of points with burnt vegetation or wood vegetation or canopy coverage / total points), represented by the red dots. Birds were sampled in two net-lines placed in the first and third transects represented by blue lines (dark blue represents the six mist-nets of 12 m and light blue the nine mist-nets of 12 m).

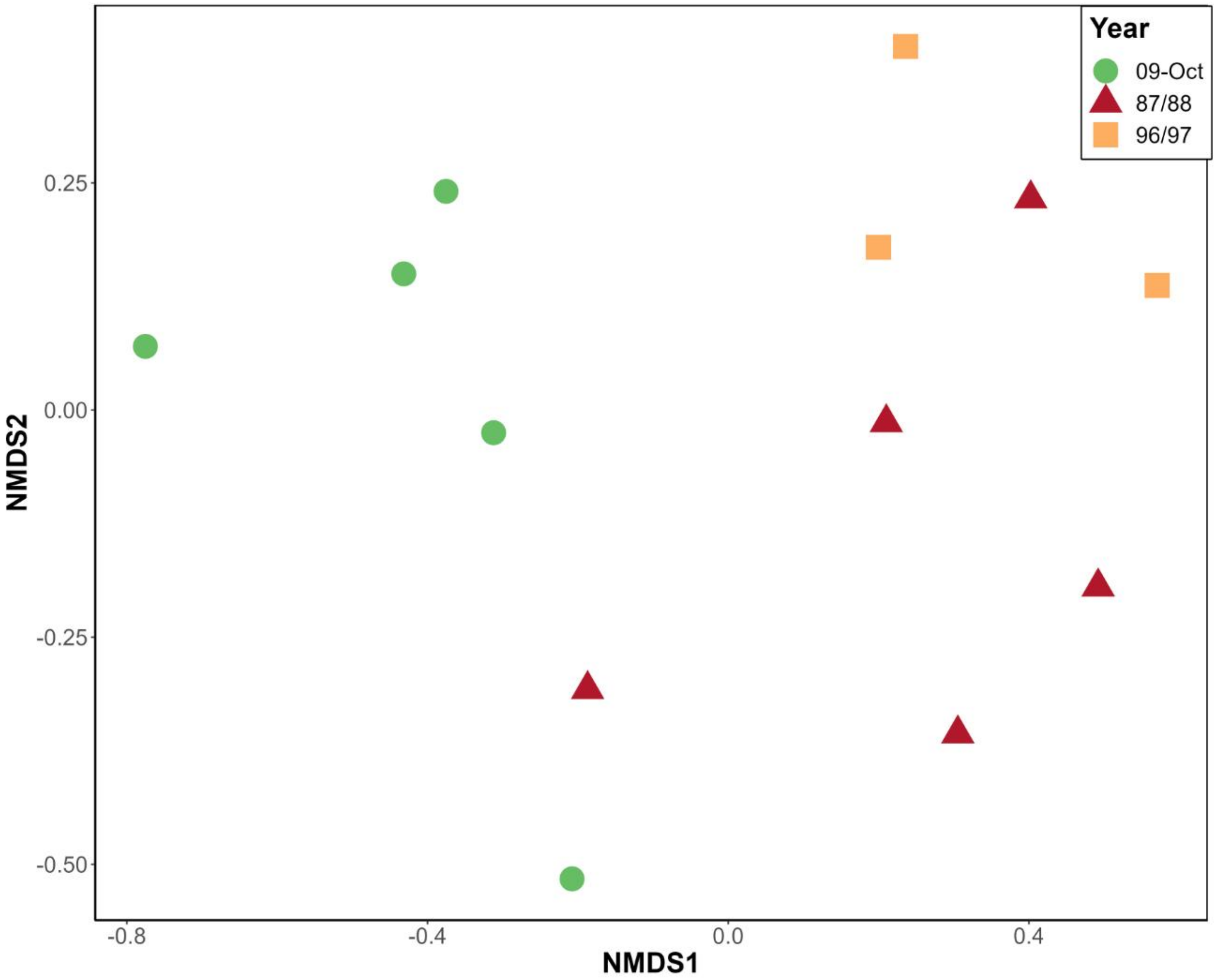

Figure 2. Non-metric Multidimensional Scaling (NMDS) with long-term samples. The red triangles and orange squares represent samples from periods where the 12 ha study site in the peninsula was under a regular fire regime. The green circles represent samples collected after 12 years of fire suppression. The first NMDS axis split without overlap the samples under regular fire regime period from the samples after fire suppression.

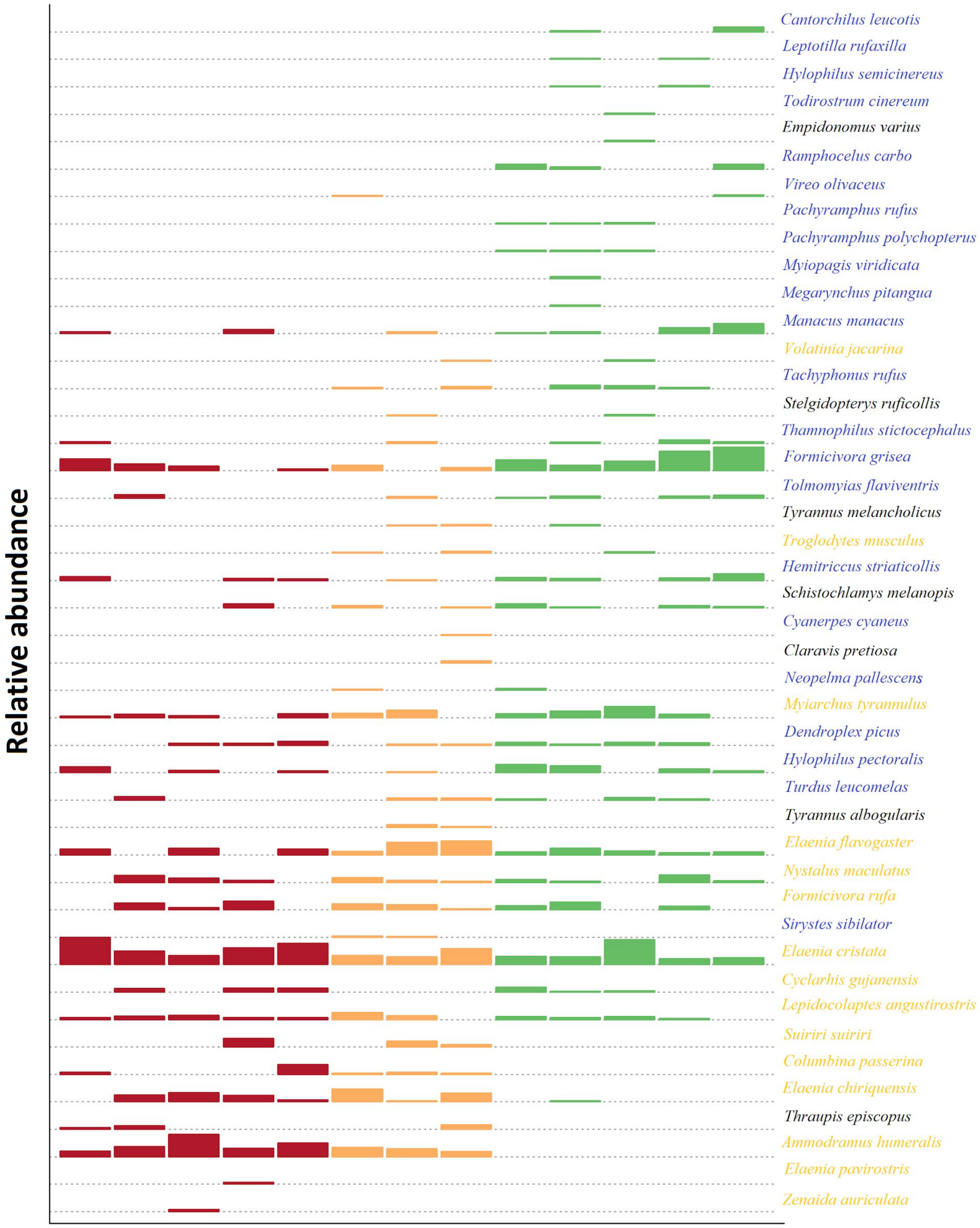

Figure 3. Species relative abundance in the 12 ha area of the peninsula. Each row represents a species and the bars represent the relative abundance of the species in the sample. The bar colors represent the sampling period (red = 87/88, orange = 96/97, and green = 09/10). Each column represent a sampling occasion. The samples are ordered chronologically (oldest to

most recent) on the horizontal axis. The color of species name indicates that it occurred mainly in savanna (yellow), forest (blue) or the data did not show a trend regarding habitat use (black). After 13 year of fire suppression some savanna species disappeared of the area.

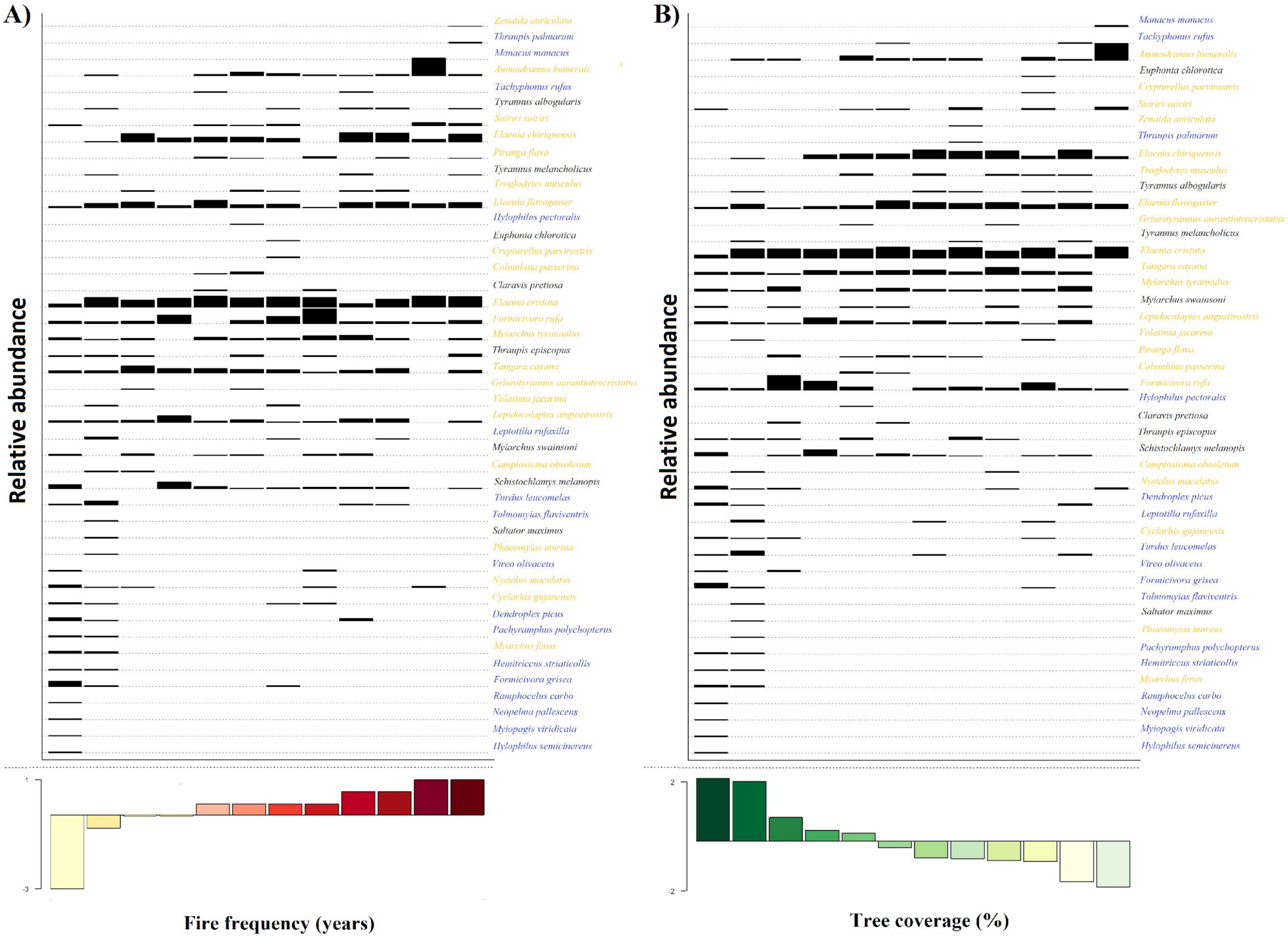
A)
Relative abundance
Zenaida auriculata
Thraupis palmarum
Manacus manacus
Ammodramus humerali
Tachyphonus rufus
Tyrannus albogularis
Suiriri suiriri
Elaenia chiriquensis
Piranga flava
Tyrannus melancholicus
Troglodytes musculus
Elaenia flavogaster
Hylophilus pectoralis
Euphonia chlorotica
Crypturellus parvirostris
Columbina passerina
Claravis pretiosa
Elaenia cristata
Formicivora rufa
Myiarchus tyrannulus
Thraupis episcopus
Tangara cayana
Griseotyrannus aurantiotrocristatus
Volatinia jacarina
Lepidocolaptes angustirostris
Leptotilla rufaxilla
Myiarchus swainsoni
Camptostoma obsoletum
Schistochlamys melanopis
Turdus leucomelas
Tolmomyias flaviventris
Saltator maximus
Phaeomyias murina
Vireo olivaceus
Nystalus maculatus
Cyclarhis gujanensis
Dendroplex picus
Pachyramphus polychopterus
Myarchus ferox
Hemitriccus striaticollis
Formicivora grisea
Ramphocelus carbo
Neopelma pallescens
Myiopagis viridicata
Hylophilus semicinereus
1
-3
Fire frequency (years)
B)
Relative abundance
Manacus manacus
Tachyphonus rufus
Ammodramus humeralis
Euphonia chlorotica
Crypturellus parvirostris
Suiriri suiriri
Zenaida auriculata
Thraupis palmarum
Elaenia chiriquensis
Troglodytes musculus
Tyrannus albogularis
Elaenia flavogaster
Griseotyrannus aurantiotrocristatus
Tyrannus melancholicus
Elaenia cristata
Tangara cayana
Myiarchus tyrannulus
Myiarchus swainsoni
Lepidocolaptes angustirostris
Volatinia jacarina
Piranga flava
Columbina passerina
Formicivora rufa
Hylophilus pectoralis
Claravis pretiosa
Thraupis episcopus
Schistochlamys melanopis
Camptostoma obsoletum
Nystalus maculatus
Dendroplex picus
Leptotilla rufaxilla
Cyclarhis gujanensis
Turdus leucomelas
Vireo olivaceus
Formicivora grisea
Tolmomyias flaviventris
Saltator maximus
Phaeomyias murina
Pachyramphus polychopterus
Hemitriccus striaticollis
Myarchus ferox
Ramphocelus carbo
Neopelma pallescens
Myiopagis viridicata
Hylophilus semicinereus
2
-2
Tree coverage (%)

Figure 4. Species occurrence in the 12 savanna plots. A) The plots are ordered by fire frequency per year in the last 12 years and B) the plots are ordered by percentage of tree cover. Each row represents a species and the bars represent the relative abundance of the species in the plot. Color of species name indicates that it occurred mainly in savanna (yellow), forest (blue) or the data did not show a trend regarding habitat use (black). Some species, mostly forest species, are only present with lower fire frequency and higher tree coverage.

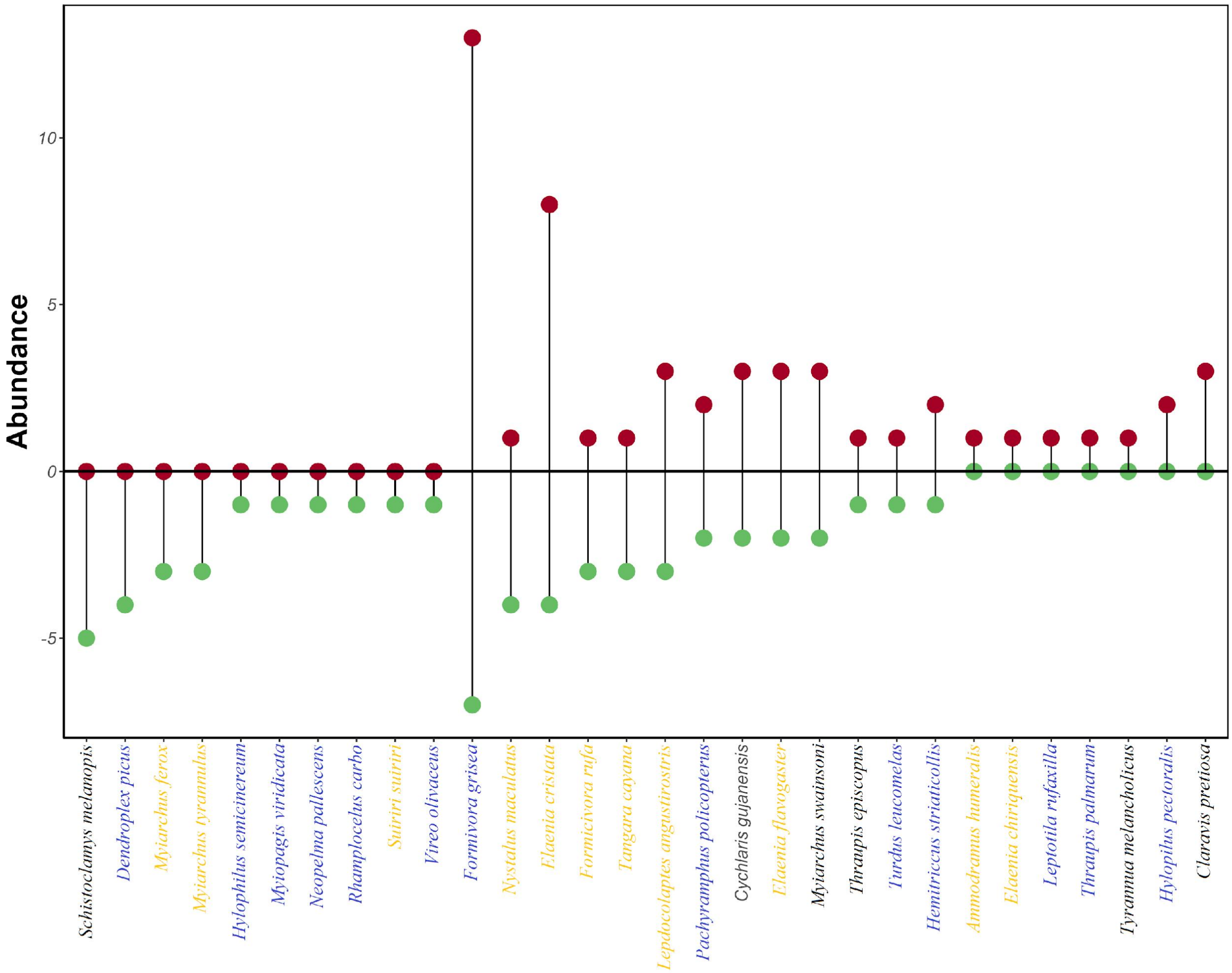

Figure 5. Changes in the bird community in plot 9 before (12 years of fire suppression) and after the fire in 2010. The y-axis represents the difference abundance of each species captured pre-fire (green dots) and post-fire (red dots). Color of species name indicates that it occurred mainly in savanna (yellow), forest (blue) or the data did not show a trend regarding habitat use (black). Ten species were just captured in pre-fire, while seven were just captured post-fire, bot including savanna preference and forest preference species.