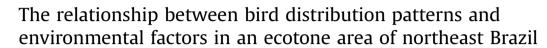
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ABSTRACT

Determining the processes that contribute to the establishment and maintenance of species diversity has been one of the great challenges for biologists. Of the many mechanisms and factors that affect diversity, environmental condition (i.e. the biophysical characteristics of habitats) is one of the main drivers structuring biological communities. In the present study, we assessed bird diversity patterns in a Cerrado-Caatinga ecotone area in the northeast of Brazil and investigated which environmental variables determined variation in species richness and composition among habitats. Cerrado areas had the highest richness of bird species among sampled sites, with ecotone areas presenting an intermediate richness, and Caatinga sites containing the lowest richness. There was a higher occurrence of generalist species from the two surrounding biomes in the ecotone region. However, some endemic species to the Caatinga were also found in the ecotone region, but only within habitat patches typical of the Caatinga. Temperature and humidity were the two most important environmental variables in explaining variation in species composition among study sites. Therefore, our results suggest climatic differences between habitat types underpin changes in local species composition and, thus, can be used to inform predictions about the potential impacts of future environmental changes on bird communities in this region.

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1. Introduction

Identifying the processes that contribute to the origin and maintenance of species diversity has been one of the great challenges for biologists (Hubbell, 2003; Hutchinson, 1959; Pimm et al., 1995; Püttker et al., 2015). For a long time, studies have focused on species assemblages in ecologically-distinct habitat types to investigate the processes that underpin the structure of biological communities (Holland, 1991; Risser, 1995). However, transitional areas (ecotones) between distinct habitats, particularly in dry regions, have received less attention from researchers. Thus, there is pressing need to study biological communities in ecotones to

* Corresponding author. E-mail address: gabrielasrgoncalves@gmail.com (G.R. Gonçalves). understand the ecological processes that determine species composition and community structure in these areas.

The definition of an ecotone, and diversity patterns within these areas, are extremely variable, and depend largely on the physical and biological characteristics of the surrounding environment. Based on the existing scientific literature, there are three possible patterns of species richness in ecotones. Firstly, that ecotones contain a mixture of species from communities in adjacent habitats, which, consequently, makes species richness of ecotones higher than in adjacent areas. Therefore, high richness in ecotones is a result of extensive overlap in the geographical distributions of species from surrounding habitats (Risser, 1995). Secondly, that communities in ecotones contain specialist species exclusive to these areas (not found in adjacent areas), and therefore restricted to the unique environmental conditions of the ecotone (Jose et al., 1996). And thirdly, that ecotones contain a low diversity of







species, as proposed by Van der Maarel (1990), who suggests richness is lower in ecotones as environmental fluctuations make these regions unfavorable for adaptation of specialist species, leading to a lower overall species richness and with communities composed mainly of generalist species from adjacent habitats.

There are many mechanisms and factors that can determine diversity in ecotones, such as environmental heterogeneity, historical stability, competition, predation rates, density and ecotone type (Risser, 1995). However, variables relating to environmental condition, i.e. biophysical characteristics of habitats, have been identified as the main factors responsible for structuring communities in these transitional habitats (Samuels and Drake, 1997). Environmental characteristics, such as habitat structure and microclimate, directly influence bird distribution patterns, expanding or restricting their distribution throughout the landscape, and thus play a key role in determining species composition found in different habitats (Weiher and Keddy, 1999). Accordingly, areas with high environmental heterogeneity support a larger number of species than areas where environmental heterogeneity is low (Conner and Dickson, 1997; Paglia et al., 1995; Roth, 1976; Simberloff and Abele, 1982). In relation to habitats, this means vegetation that is more stratified and structurally-complex provides a greater number of potential niches than structurally-simple habitats. High environmental heterogeneity facilitates greater habitat sharing and colonization by species with distinct environmental requirements and/or preferred microhabitats, in turn leading to a higher local diversity of species (Aleixo, 1999; August, 1983; Conner and Dickson, 1997; Macarthur et al., 1966).

Environmental structure is closely related with Hutchinson (1957) niche concept, where the niche of any given species comprises their response to multiple environmental variables (i.e. multidimensional niche space). Knowledge on the environmental factors determining community composition is particularly important for studies on the distribution and conservation of birds in ecotones, where the unique environmental and structural characteristics present in these habitats may influence species diversity.

All characteristics of ecotones, including species richness, are a consequence of the ecological conditions and processes found in these areas, as well as of traits of the surrounding landscape. Thus, the main objective of this study was to identify bird diversity patterns in the ecotone between the Caatinga and Cerrado biomes, in Northeastern Brazil and environmental factors that determine species composition in these areas. We expect to answer the following questions: (1) What are the richness and species composition patterns of bird communities in the ecotone between Caatinga and Cerrado? (2) Are endemic bird species of the Cerrado and Caatinga biomes found syntopically in ecotone areas, or are they segregated in different habitats? (3) Which environmental factors explain variation in richness and species composition observed among the Cerrado, Caatinga and ecotone areas?

2. Methods

2.1. Study area and sampling design

A wide ecotone area occurs between the Caatinga and Cerrado biome, ranging from the north-central portion of the state of Piauí, North Bahia until northeastern Minas Gerais (Eiten, 1972). These two distinct biomes remain in close proximity over a large area, especially in the state of Piauí, where the ecotone band occurs longitudinally, across the state, with large areas still well conserved but no under legal protection. Such conditions, where large tracts of each biome are present within the same landscape, make it an excellent area to study bird distribution patterns between the two biomes and its contact zone (ecotone). The region is composed of two zones and three climate types: tropical zone (A), which has a dry winter (Aw), occurring mainly in the Cerrado biome, and a dry summer (As) occurring mainly between Aw and BSh climates (Alvares et al., 2013); and a semi-arid zone (B), which has a semi-arid climate with low latitude and altitude (BSh), where annual rainfall is on average less than 800 mm, as in the Caatinga biome (Alvares et al., 2013). The study area comprises several climate types, and is very heterogeneous concerning to annual rainfall, soils and vegetation types.

The structure and composition of vegetation in the Cerrado biome is very heterogeneous, ranging from dense grassland with sparse shrubs and small trees to mature forest. Commonly, five types of vegetation structure are recognized in Cerrado: (1) forest formation with a canopy height of 8–15 m, frequently with a dense canopy, called 'cerradão'; (2) sparse trees and large shrubs with 2-8 m height and a well-developed grassy layer, called 'cerrado sensu stricto'; (3) an open vegetation with 3–6 m height with fewer trees than previous vegetation types, called 'campo cerrado'; (4) large grassy fields with sparsely distributed shrubs, 2–3 m height, called 'campo sujo'; and (5) grassy fields with few or no shrubs and trees, called 'campo limpo' (Eiten, 1972). The Caatinga biome also has a heterogeneous vegetation, which can be differentiated into two main types: (1) arboreal caatinga - a forest formation with a dense canopy in the wet season, and leaf shedding in the dry season; and (2) shrubby caatinga - characterized by uniform shrubby layer with thorny plants, such as cacti and bromeliads (Fernandes and Bezerra, 1990).

The study was conducted in the northern portion of the ecotone located between the Caatinga and Cerrado biomes, within the Piauí state limits. The habitats studied included: Cerrado, ecotone and Caatinga; with a total of 24 sampling sites across the Cerrado/ ecotone/Caatinga gradient, with 8 sites in each habitat type. For logistical reasons, we divided the study area into four sub-regions and selected two sites of each habitat type within these subdivisions (Fig. 1, Table 1). All the sites within the same habitat type included the same type of vegetation, for example, all sites in the Cerrado region focused on the cerrado *sensu stricto* vegetation type; in the Caatinga region, arboreal vegetation, and in the ecotone, where vegetation is a mosaic of the other two habitat types, i.e., where vegetation typical of the Caatinga and Cerrado occur together in the same area.

2.2. Data sampling

Bird surveys were carried out from April 12 to May 5, 2014. We conducted 15 fixed width (75 m) 10-min point counts per sampling site, located at 200 m-intervals to obtain the abundance, richness and composition of bird species (Blondel et al., 1970; Vielliard et al., 2010). All point counts were conducted by P. V. C. an experienced ornithologist. The surveys were started always from early morning, near to sunrise, until the last point count and were not carried out on days with persistent rain and/or strong winds.

We used an adapted protocol for the study area to measure vegetation structure parameters of each site (based on Peck et al., 2006). This protocol aims to quantify the largest possible number of environmental variables to evaluate their effect on species composition and diversity (see Supplementary Material Appendix A). Vegetation data were collected in three plots established in each sampling site (3×3 m plots and spaced 500 m from each other). These plots were set in the same tracks used for the point counts carried out for bird surveys. The quantitative variables measured were litter height (cm, measured using a ruler from the soil until the top of the leaf litter), temperature (°C) and humidity (%), both measured using a digital thermo-hygrometer. Three measures were taken in each plot and we used the mean of this

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