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ARTICLE

The Biogeographic Network of Birds in the Brazilian Cerrado May Guide Conservation Efforts

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ABSTRACT

The Brazilian Cerrado, characterized by grasslands, savannahs and riverine forests, is a biodiversity hotspot, threatened by the expansion of the agricultural frontier, and therefore, needs effective conservation actions. At the national level, the Cerrado core-region has received more conservation efforts than the marginal (non-core) areas, being considered more biodiverse. However, many marginal areas are also home to high species richness and endemism. Birds represent a highly diverse and widely distributed biological group, whose variety of functions gives them important roles in the maintenance of ecosystem services. In this study the authors analysed the distribution patterns of bird biodiversity in the Brazilian Cerrado and verified whether a separation into core and marginal Cerrado zones would make sense for birds' distribution, as this is an important issue concerning resources allocation for biodiversity conservation. The authors developed a biogeographic network analysis considering 42 sites with savannah vegetation distributed throughout the country and built two presence-absence matrices for birds – with and without species typical of the woodland Cerrado and forest physiognomies – and generated two biogeographic networks. The network without woodland/forest bird species showed no modularity, whereas the complete network produced three modules: Northwest, Centre-South and Centre-North. Network modularity was mainly determined by forest/woodland bird species. The Northwest region was richer and had a greater number of regional species compared to the other two modules; lower richness of bird species was found in the Centre-South region, which had more widespread species. The biogeographic pattern for the Cerrado birds perceived in this study did not evidence a clear dichotomy between core *versus* marginal regions. Therefore, the same conservation effort should be implemented throughout the Cerrado.

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1. Introduction

The conservation of natural ecosystems in times of rapid land use changes requires policy efforts as well as actions that can be costly and/or labour-intensive. Therefore, using good indicators to guide the application of more effective conservation actions is essential. Birds are good indicators of biodiversity [1,2] as they embody high functional diversity and perform important ecological roles in maintaining ecosystem integrity, such as pollination, seed dispersal, and provision of food to fauna [3,4]. Studies on the patterns of biodiversity distribution are crucial to elucidate the diversification processes and biodiversity dispersion as well as threats to biodiversity, which aid in devising more efficient conservation strategies [5]. Thus, understanding bird distribution patterns are essential to support managers of protected areas to plan and implement conservation measures, as well as for the establishment of new protected areas.

Traditionally, studies that compare the ecological structure of communities have used similarity indices and cluster analyses (e.g., see [6]). More recently, a network approach has been adopted to identify patterns of biogeographic distribution [7-11]. By linking a series of sites and species network analysis reveals any biodiversity compartmentalisation and species composition similarities that may reflect spatio-ecological systems [9,12,13].

In the present study we used a comprehensive database of bird species that occur in sites of Brazilian territory covered by Cerrado vegetation to build a biogeographical network, including species present in savannah and grassland physiognomies in both the Cerrado biome (Figure 1) and enclaves in the Amazon. The Cerrado vegetation includes a gradient of grassland and savannah physiognomies (Figure 1A-1E) that cover the vast majority of about 2,000,000 km^2 in the Brazilian central region. Different types of forests (e.g., riverine and dry forests) and other grassland types (e.g., wet and rupestrian fields) also occur in the Cerrado region [14-16]. Cerrado savannahs and grasslands make up the richest savannah in the world, exhibiting extremely high level of endemism [17]. However, half of the Cerrado area has been replaced by agriculture (especially livestock and crop farming) [18], which has adversely affected its natural biodiversity. These conditions have converted the Cerrado into a global biodiversity hotspot [19].

The Cerrado is bordered by the Atlantic and the Amazon rainforests, and the semi-arid Caatinga [14,16] (Figure 1), which influence its flora and fauna composition, and may explain its extremely high biodiversity [20-22]. In previous studies, authors who described the Cerrado vegetation and environment [15,23-25] discriminated a *core* zone (or *central*, *nuclear*) and a *marginal* zone (*non-core*). The *core* Cerrado zone occupies the Brazilian Central Plateau, and the *marginal* zone borders the *core* zone. The *marginal* zone also includes isolated savannah enclaves in other morphoclimatic domains, especially in the Amazonian region. The distinction between *core* and *marginal* zones has been assumed in most references to the Cerrado, although some studies have reported that floristic similarity between such zones does not support such classification [26,27]. Regarding the Cerrado fauna, most studies on birds [28-32] or other biological groups [33] have been carried out in the *core* Cerrado, as the remaining *marginal* areas are usually considered as relatively less representative of the Cerrado bird biodiversity [34-36]. As an example, Silva & Santos [37] proposed the removal of two bird species (*Neothraupis fasciata* and *Cypsnagra hirundinacea*) from the list of

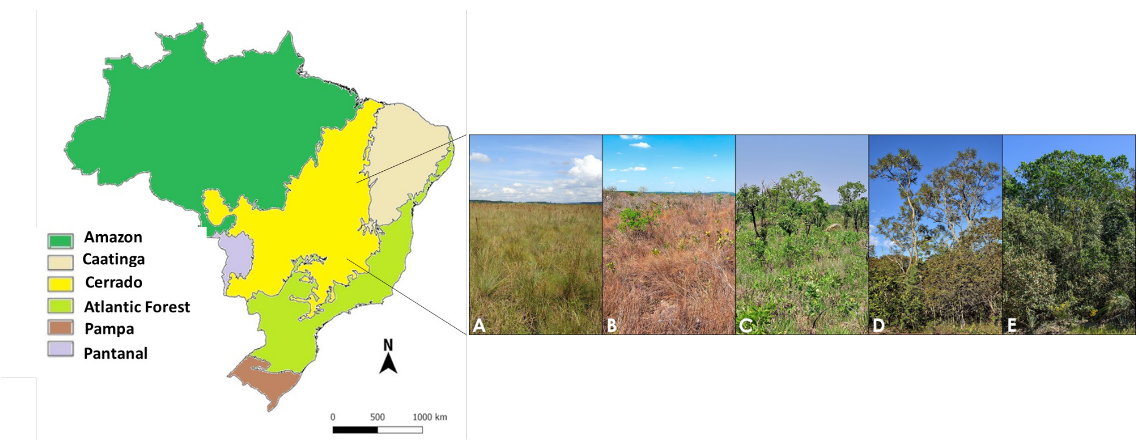

Figure 1. The map shows the Brazilian continental biomes according to IBGE [20], which in fact represent morphoclimatic domains according to Ab'Saber's [15] definition. The photos show the main grassland and savannah physiognomies of the Cerrado: A= *campo limpo*, B= *campo sujo*, C= *campo cerrado*, D= *cerrado sensu stricto*, E= *cerradão*. (Photos: J. C. Motta-Junior).

Cerrado endemic birds because they occur not only in the Cerrado *core* region, but also in Cerrado enclaves at the Amazonian Domain.

As the avifauna in Brazil is highly diverse, widely distributed, and relatively well-known, we selected this group to test the hypothesis of existing differentiated bird assemblages between the *core* and the *marginal* Cerrado zones, using the network approach. We identified biogeographic modules for the Cerrado birds and the patterns that determine them. Our main working questions were: i) Are there distinct biogeographic units of Cerrado sites that share specific avifauna? ii) If so, how are these biogeographic units distributed? iii) Is the traditional division of *core* and *marginal* Cerrado suitable to explain the patterns found? iv) How important are forest/savannah-woodland birds in structuring Cerrado modules? v) Does the *core* Cerrado region deserve greater conservation concern? The answers to these questions may guide planners and managers on devising better conservation actions for the Cerrado biodiversity.

2. Material and Methods

2.1 Database and Study Area

Our data come from an extensive review by Morandini [38], which we expanded and updated with some new published references, and then comprised information from 50 bird surveys in 42 sites covered by Cerrado physiognomies (Table 1). We adopted the following criteria to select the surveys: data collection covering all Cerrado physiognomies present in that area, and studies that combined more than one sampling method in order to minimise errors (e.g., active search, fixed points, transects, mist nets, and data from collections).

The study sites were distributed throughout the Brazilian territory, being some within the *core* Cerrado, while others are in the *marginal* Cerrado (according to Ab'Saber [15]). The sites varied greatly in size, geomorphology, and protection status. Most of them are presumed to be effectively protected (those included in the category of integral protection, according to the Brazilian system of protected areas, SNUC [39]), while others are not protected (Table 1). In addition, the sites were embedded in distinct matrices within natural or agricultural landscapes. The recent remaining land cover types and main land uses in the immediate surroundings of each study area according to Mapbiomas version 7.0 [40] are listed in the Table 1.

2.2 Biogeographical Network Analysis

There are two types of nodes in a biogeographic network: geographic units (sites) and species. A link between a site and a species indicates that the species occurs at that site [7]. A highly linked subgroup of sites and species is defined as a module [10,41]. Thus, sites from the same module share more species than with sites from other modules [7]. In this context, modules may be defined as groups of sites that share specific avifauna in terms of species identity [42]. The network approach provides tools to quantify modularity, that is, the extent to which the network is organised in distinct groups or modules, and also permits the description of the role of each node in the modular network based on their linkage pattern [41,43,44].

For the network analyses we built two presence-absence matrices (site *versus* bird species), which represented two biogeographic networks, both containing the 42 sites. Because not all 50 surveys included aquatic species, we removed them from both matrices. In the second matrix we also removed the species typical of forest/woodland physiognomies (i.e., riverine forests and the woodland savannah, named *cerradão*) to make it contain species exclusively found in open Cerrado physiognomies (*campo limpo*, *campo sujo*, *campo cerrado*, and *cerrado sensu stricto*, following Coutinho [45], Figure 1). The classification of the birds' preferential habitats followed Silva [46] and Bagno & Marinho-Filho [47], besides specifications contained in the original surveys (Table 1) and the authors' own experience. By comparing both matrices, we could verify the influence of forest/woodland birds on the modules structuring.

Using Netcarto software [43] we analysed the network modularity and identified compartments, or modules. To evaluate the modularity significance of each matrix, we compared the observed modularity in our network with the modularity of 100 matrices generated by a null model that considered the number of links of both sites and species: null model 2 [48]. Null models were developed using R software, version 3.4.0 [49].

We also used Netcarto software [43] to compute the number of links (degree) at each site to indicate the number of species (or richness). Using the same software, we also calculated two metrics that indicated the topological role of each site in the modular network: the among-module connectivity (c) and the standardised within-module degree (z). The metric c reflected the connections with other modules, with higher c values indicating the presence of widespread species belonging to different modules, as the site would have bird species evenly from all modules. In contrast, a higher z*-metric* value of a specific site indicates more bird species in common with the other sites of the same module (i.e., the presence of more local species) [7]. In this way, we named sites according to their position in c-z space (cut-off values of 0.62 for c and 2.5 for z) [44].

Table 1. Surveys of bird species in areas covered by savannah and grassland physiognomies throughout the Brazilian territory used in this study.

Study area (State)	Publication	Protected area	LCLU
Chapada dos Guimarães (MT)	Lopes, L.E., Pinho, J.B., Bernardon, B., et al. 2009. Aves da Chapada dos Guimarães, Mato Grosso, Brasil: uma síntese histórica do conhecimento. Papéis Avulsos de Zoologia. 49(2), 9-47.	Yes	F, S, Pa
Rio das Mortes (MT)	Sick, H.,1955. Aspectos fitofisionomicos da paisagem do médio Rio das Mortes, MT, e a avifauna da região. Arquivos do Museu Nacional. 42, 541-576.	No	F, S, Pa
Serra do Lajeado (TO)	Bagno M.A., Abreu, T.L.S., 2001. Avifauna da região da Serra do Lajeado. Humanitas. 3, 51-70.	Yes	F, S, Pa, So, Ur
Parque Nacional das Emas (GO/MS/MT)	Hass, A., 2005. Plano de Manejo do PNE/GO-MS-MT. Relatório de avifauna. unpublished report.	Yes	F, S, W, Pa, So, Co
Estação Ecológica de Águas Emendadas (DF)	Bagno, M.A., 1998. As aves da Estação Ecológica de Águas Emendadas. Vertebrados da ESECAE. SEMATEC, pp. 1-92p.	Yes	S, F, G, So, Pa, Ur
Estação Ecológica de Águas Emendadas (DF)	Lopes,L., Leite, L., Pinho, J.B., et al., 2005. New birds records to the Estação Ecológica de Águas Emendadas, Planaltina, DF. Ararajuba. 13(1), 107-108.	Yes	S, F, G, So, Pa, Ur
Estação Ecológica de Águas Emendadas (DF)	Bagno, M.A., Abreu, T L S., 2008. Avifauna. In: Águas Emendadas. SEDUMA, pp. 233-241.	Yes	S, F, G, So, Pa, Ur
Reserva Ecológica do IBGE (DF)	Tubelis, D.T., 2011. Reserva Ecológica do IBGE. Série Biodiversidade Terrestre. IBGE, 1: 147-158.	Yes	F, S, G, Pa, So, Ur
Parque Nacional de Brasília (DF)	Antas, P.T.Z., 1995. Aves do Parque Nacional de Brasília. Coleção Meio Ambiente. Série Fauna Brasileira. IBAMA, 53p.	Yes	F, S, G, Pa, Ur
Parque Nacional de Brasília (DF)	Braz, V., 2008. Ecologia e Conservação de aves campestres do bioma cerrado. Tese Doutorado UnB, 187p.	Yes	F, S, G, Pa, Ur
Parque Nacional de Brasília (DF)	Oliveira, A.C., Kanegae, M.F., Amaral, M.F., et al., 2011. Guia para observação de aves do Parque Nacional de Brasília ICMBio, 300p.	Yes	F, S, G, Pa, Ur
Fazenda Água Limpa (DF)	Braz, V., Cavalcanti, R.B., 2001. A representatividade de áreas protegidas do DF na conservação da avifauna do Cerrado. Ararajuba. 9(1), 61-69.	Yes	F, S, G, Pa, So, Ur
Parque Nacional da Serra da Canastra (MG)	Silveira, L.F., 1998. The birds of Serra da Canastra National Park and adjacent areas. Cotinga. 10, 55-63.	Yes	F, S, G, Pa, So, Sc
Parque Nacional da Serra do Cipó (MG)	Rodrigues, M., Carrara, L.A., Faria, L.P., et al. 2005. Aves do Parque Nacional da Serra do Cipó: o Vale do Rio Cipó, MG, Brasil. Revista Brasileira de Zoologia. 22(2), 326-338.	Yes	S, G, R, F, Pa
Estação Ecológica de Itirapina (SP)	Motta-Junior, J.C., Grazinolli,, M.A.M., Develey, P.F., 2008. Aves da Estação Ecológica de Itirapina, estado de São Paulo, Brasil. Biota Neotropica. 8(3), 207-227.	Yes	S, G, F, Fp, Pa, Ur
Itirapina (SP)	Telles, M., Dias, M.M., 2010. Bird communities in two fragments of Cerrado in Itirapina, Brazil. Brazilian Journal of Biology. 70(3), 537-550.	Yes	S, G, F, Fp, Pa, Ur
Itirapina (SP)	Willis, E.O., 1995. Algumas aves de habitats especiais da região de Itirapina (São Paulo). Atualidades Ornitológicas 68: 7.	Yes	S, G, F, Fp, Pa, Ur
Itirapina (SP)	Willis, E.O., 2004. Birds of a habitat spectrum in the Itirapina savanna, SP, Brasil (1982-2003). Brazilian Journal of Biology. 64(4), 901-910.	Yes	S, G, F, Fp, Pa, Ur
Cantão (TO)	Pinheiro, R.T., Dornas, T., 2009. Distribuição e conservação das aves na região do Cantão, TO: ecotono Amazonia/Cerrado. Biota Neotropica. 9(1), 188-205.	Yes	F, S, W, G, Pa
Parque Estadual do Jalapão (TO)	Pacheco, J.F., Olmos, F. 2010. As aves do Tocantins, Brasil - 2: Jalapão. Revista Brasileira de Ornitologia. 18(1), 1–18.	Yes	G, S, W, F
Planalto da Bodoquena (MS)	Pivatto, M.A.C., Manço, D.G., Straube, F.C., et al. 2006. Aves do Planalto da Bodoquena, estado do Mato Grosso do Sul (Brasil). Atualidades Ornitológicas. 129, 1-26.	Yes	F, S, W, Pa
Pedro Afonso (TO)	Lopes, L.E., Braz, V.S., 2007. Aves da região de Pedro Afonso, TO, Brasil. Revista Brasileira de Ornitologia. 15(4), 530-537.	No	S, F, Pa, So
Cerrado-Caatinga transition area (PI)	Santos, M.P.D., 2008. Bird community distribution in a Cerrado-Caatinga transition area, PI, Brazil. Revista Brasileira de Ornitologia. 16(4), 323-338.	No	S, F, G

Table 1 continued

Study area (State)	Publication	Protected area	LCLU
Southern Region in Tocantins (TO)	Pacheco, J.F., Olmos, F., 2006. As aves do Tocantins, Brasil - 1: Região Sudeste. Revista Brasileira de Ornitologia. 14(2), 85-100.	No	G, S, W, F
Fazenda Brejão (MG)	Faria, L.C.P., Carrara, L.A, Amaral, F.Q., et al., 2009. The birds of Fazenda Brejão: a conservation priority area of Cerrado in northwestern Minas Gerais, Brazil. Biota Neotropica. 9(3), 223-240.	No	F, Pa, So, Ot
Estação Ecológica Serra das Araras (MT)	Silva, J.M.C., Oniki, Y., 1988. Lista preliminar da avifauna da Estação Ecológica Serra das Araras, MT, Brasil. Boletim do Museu Paranaense Emilio Goeldi, série Zoológica. 4(2), 123-143.	Yes	S, F, Pa, Ot
Reserva Ecológica Panga (MG)	Marçal-Junior, O., Franchin, A.G., Altef, E.F., et al., 2009. Levantamento da avifauna na Reserva Ecológica Panga (Uberlandia, MG, Brasil). Bioscience Journal. 25(6), 149-164.	Yes	F, S, Ur, Pa, Ot
Estação Ecológica Serra Geral (TO)	Rego, M.A., Silveira, L.F., Piacentini, V.Q., et al., 2011. As aves da Estação Ecológica Serra Geral do TO, Centro do Brasil. Biota Neotropica. 11(1), 283-297.	Yes	G, S, W, So.
Complexo Aporé-Sucuriú (MS)	Silva, M.B., Zucca, C.F, Souza, C.R., et al, 2006. Inventário da avifauna no Complexo Aporé-Sucuriú. In: Biodiversidade do Complexo Aporé-Sucuriú: subsídios à conservação e manejo do bioma Cerrado - Área prioritária 316 Jauru. Editora UFMS, pp. 1-308p.	No	F, S, G, Pa, W, So, Ot
Rio Manso (MT)	Vasconcellos, L.A.S., Oliveira, D.M.M., 2000. Avifauna. In: Alho, C.J.R. (Ed.), Fauna silvestre da região do Rio Manso, MT. IBAMA-Eletronorte, pp. 191-216.	No	S, F, Pa, Ot
Paracatu (MT)	Benfica, C.E., n.d. Lista de aves de Paracatu. Unpublished data.	No	F, S, G, Pa, So, Ot
Parque Estadual do Juqueri (SP)	Figueiredo, L.F., Gussoni, C.O.A., Campos, R.P., 2000. Levantamento da avifauna do Parque Estadual do Juquery, Franco da Rocha, SP: uma avaliação autocrítica das técnicas de campo para inventários ornitológicos. Boletim CEO. 14, 36-43.	Yes	F, S, Ur
Campus da USP de Pirassununga (SP)	Gussoni, C.O.A., 2003. Avifauna do campus da USP, Município de Pirassununga, Estado de SP. Boletim CEO. 15, 2-15.	No	F, S, Sc, Pa, Fp, Ur
Parque Estadual de Vassununga, Gleba Pé-de-Gigante (SP)	Develey, P.F., Cavana, D.D., Pivello, V.R., 2005. Aves. In: Pivello, V.R. & Varanda, E.M. (orgs.). O Cerrado Pé-de-Gigante (Parque Estadual de Vassununga, SP) - ecologia e conservação. SMA-SP, pp. 1-312.	Yes	F, S, Sc, Pa, Fp, Ur
Estação Ecológica de Jataí + Estação Experimental de Luiz Antônio (SP)	Dias, M.M., 2000. Avifauna das Estações Ecológicas de Jataí e Experimental de Luiz Antônio, São Paulo, Brasil. In Santos J. E. & Pires, J. S. R. (Eds.). Estação Ecológica de Jataí. Editora Rima, pp. 285-301.	Yes	F, S, Sc, Pa, Fp, Ur
Chapada do Araripe (CE)	Nascimento, J.L.A.S., Nascimento, I.L., Azevedo-Junior, S.M., 2000. Aves da Chapada do Araripe (Brasil): biologia e conservação. Ararajuba. 115-125.	No	S, F, Pa, Ot
Campus da UFSCar, São Carlos (SP)	Motta-Junior, J.C., Vasconcellos, L.A., 1996. Levantamento das aves do campus da UFSCar, SP, Brasil. Anais do VII Seminário Regional de Ecologia. 7, 159-171.	No	F, S, Sc, Pa, Fp, Ur
Alta Floresta Region (MT)	Zimmer, K.J., Parker III, T.A., Isler, M.L., et al., 1997. Survey of a Southern Amazonian Avifauna: The Alta Floresta Region, MT, Brazil. Ornithological Monographs. 48, 887-918.	No	F, Pa, Mi
Área de Proteção Ambiental do Rio Curiaú (AP)	Aguiar, K.M.O., Naiff., R.H., 2010. Composição da avifauna da Área de Proteção Ambiental do Rio Curiaú, Macapá, AP, Brasil. Ornithologia. 4(1), 36-48.	Yes	F, G, Ur
Vila Bela Region, Santíssima Trindade (MT)	Silveira, L.F., D'Horta, F.M., 2002. A avifauna da região de Vila Bela da Santíssima Trindade, MT. Papéis Avulsos de Zoologia. 42(10), 265-286.	No	F, S, G, Pa
Parque Estadual do Cerrado (PR)	Straube, F. C., Urben-Filho, A., Gatto, C., 2005. A avifauna do Parque Estadual do Cerrado (Jaguariaíva, PR) e a conservação do Cerrado em seu limite meridional de ocorrência. Atualidades Ornitológicas. 127, 29-49.	Yes	F, G, Fp, So, Pa, Ur
Savannahs of Amapá (AP)	Silva, J.M.C., Oren, D.C., Roma, J.C., et al., 1997. Composition and distribution patterns of the avifauna of an Amazonian upland savanna, AP, Brazil. Ornithological Monographs. 48, 743-762.	No	G, F, W

Table 1 continued

Study area (State)	Publication	Protected area	LCLU
Savannahs of Amapá (AP)	Boos, R.L., 2009. Variações espaciais e temporais em comunidades de aves de uma savana amazonica no Estado do AP. MSc. Dissertation UNIFAP, 153p.	No	G, F, W
Enclave in Southern Brazilian Amazonia (AM)	Aleixo, A., Poletto, F., 2007. Birds of an open vegetation enclave in Southern Brazilian Amazonia. The Wilson Journal of Ornithology. 119(4), 610-630.	No	F, G, Pa
Serra do Cachimbo (PA)	Santos, M.P.D., Silveira, L.F., Silva, J.M.C., 2011. Birds of Serra do Cachimbo, Pará State, Brazil. Revista Brasileira de Ornitologia. 19(2), 244-259.	No	F, G, S, Pa
Balsas region (MA)	Hass, A., Paula, W.S., Barreto, L., 2007. Caracterização da avifauna da região de Balsas. In: Barreto, L. Cerrado Norte do Brasil. USEB, 378p.	No	S, F, G, Pa So, Ot
Alter de Chão (PA)	Sanaiotti, T.M., Cintra, R., 2001. Breeding and Migrating Birds in an Amazonian Savanna. Studies of Neotropical Fauna and Environment. 1: 23-32.	No	F, G, Pa, Ur, Ot
Roraima Savannas (RR)	Santos, M.P.D., Silva, J.M.C., 2007. As aves das savanas de Roraima. Revista Brasileira de Ornitologia. 15(2): 189-207.	No	G, F, Pa, Ot
Estação Ecológica de Santa Bárbara (SP)	Lucindo, A.S., Antunes, A.Z., Kanashiro, M.M., et al., 2015. Birds at Santa Barbara Ecological Station, one of the last Cerrado remnants in the state of São Paulo, Brasil. Biota Neotropica. 15(4), e0155	Yes	F, S, Sc, Pa, Fp, Ur
Rio do Fogo (RN)	Pichorim, M., Silva, M., França, B.R.A., et al., 2014. A Cerrado Bird Community in the northernmost portion of the northeastern Brasil - recommendations for conservation. Revista Brasileira de Ornitologia. 22(4), 347-362.	No	G, S, Ot

The table highlights the protected areas and main land cover and land uses (LCLU) in the area surroundings (according to [40]): F= Forest natural formation; S= Savanna formation; G= Grassland; W= Wetland; R= Rocky outcrop; Pa= Pasture; So= Soybean culture; Co= Cotton culture; Sc= Sugar cane; Fp= Forest plantation; Ot= Other agriculture uses; Mi= Mining; Ur= Urban Area.

The four possible categories of roles were: Peripheral: few local species and few widespread species; Connector: few local species and many widespread species; Module hub: many local species and few widespread species; and Network hub: many local species and many widespread species [7,44].

We applied the Shapiro-Wilk normality test for the variables *c*, *z*, and degree to assess data normal distribution. To evaluate the differences among the modules concerning the metrics *c* and degree, which presented normal distribution, we used an ANOVA test with Tukey's post-hoc tests. For metric *z*, we used the Kruskal-Wallis's test with Dunn's nonparametric post-hoc tests. We also compared the values of *c, z*, and degree between *core* and *marginal* Cerrado areas using a Student's *t*-test for *c* and degree, and a Mann-Whitney U test for *z*. The critical significance level of 0.05 was adjusted to 0.017 after applying the Bonferroni correction. We performed these statistical tests on R version 3.4.0 [49].

As a final step, the 42 sites were located on a map of Brazil, classified according to their modules following the first presence-absence matrix (all birds recorded in the 50 bird surveys except for aquatic species, and all Cerrado physiognomies) using the software QGiz 2.18.25 [50].

3. Results

The first biogeographic network, comprising species from both woodland and open Cerrado physiognomies, included the 42 sampling sites and 967 bird species (Table A1). Comparing the observed modularity with the 100 matrices generated by a null model, this network showed significant modularity ($M = 0.2061$; $p < 0.01$). The bird species were grouped into three modules: Northwest (red), Centre-South (blue), and Centre-North (green) (Figure 2).

According to the Shapiro-Wilk normality test for *c*, *z* and degree, only the *z*-metric was not normally distributed ($W = 0.824$; $p < 0.001$, at the level of significance = 0.017 after Bonferroni correction). We could not find significant differences between the *core* and *marginal* regions for metrics *c*, *z*, and degree. However, these three metrics differed among the modules (Table 2). The Northwest module comprised five sites (Figure 2, red dots) and contained the three areas with the highest network degrees, containing 423, 417, and 376 species each, as species richness was indicated by the degree value. The Kruskal-Wallis and Dunn's tests revealed significant differences ($p < 0.01$) between the Northwest module relative to the other two modules for both average degree (number of species in each module) and average *z* index (related to the presence of local species) (Table 2). In other words, the Northwest module was the richest and had more local species than the Centre-South and Centre-North modules. The Centre-South module contained 22 sites (Figure 2, blue dots), and its *c* index was significantly lower ($p < 0.01$) compared with that of the other two modules (Table 2),

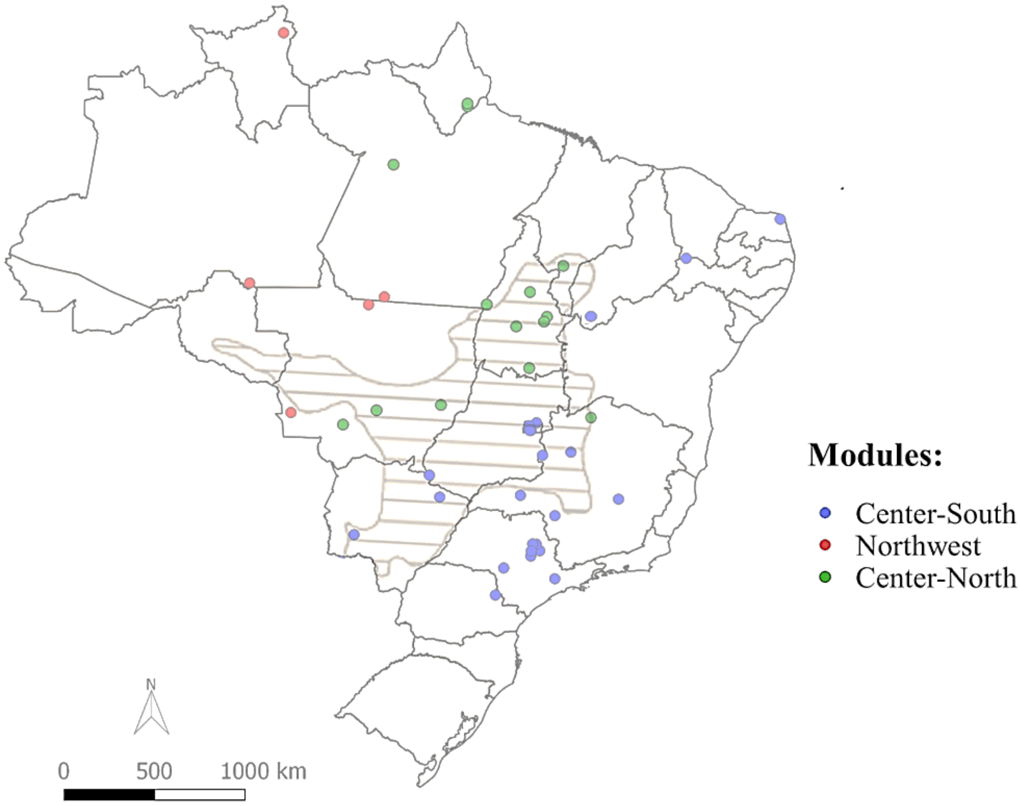

Figure 2. Distribution of the Cerrado bird sampling sites and their corresponding network modules: Centre-South (blue dots), Northwest (red dots), and Centre-North (green dots). The hatched central area represents the *core* Cerrado according to Ab'Saber [15].

indicating fewer widespread species. The Centre-North module comprised 15 sites (Figure 2, green dots).

Classification of sites into topological roles in the biogeographic network indicated that the majority of the 42 sites (86%) could be classified as Module hubs (Figure 3), that is, possessing many local species and a few widespread ones. This pattern was strongly followed by the Centre-South module (with 95% of the sites classified as Module hubs), yet these sites had the lowest among-module connectivity (c) and the Centre-North module (87% of the sites defined as Module hubs). In contrast, only 40% of the Northwest module sites were classified as Module hubs and 60% were defined as Network hubs (many local and many widespread species). Only two sites appeared as Peripheral (few local and few widespread species): one site in the Centre-South module and the other site in the Centre-North module. None of the 42 sites were classified as Connector (few local and many widespread species) (Figure 3).

The second network we built excluding all bird species that preferably use woodland savannah/forest physiognomies (*cerradão*, gallery and dry forests) and it was there-

Table 2. Degree, *c*, and *z* metrics for the tree modules of the Cerrado bird biogeographic network. The level of significance was 0.017 after Bonferroni correction.

Module	No. of areas	Average Degree (std. dev.)	Average *c* index (std. dev.)	Average *z* index (std. dev.)
Northwest	5	378 (43.69) ***	0.61 (0.06)	8.50 (2.06) *
Centre-south	22	224.18 (57.06)	0.40 (0.09) **	3.78 (1.00)
Centre-north	15	248.53 (62.16)	0.56 (0.04)	3.85 (0.95)

*** ANOVA = $p < 0.001$, Tukey's post-hoc test = for Northwest / Centre-North, and Northwest / Centre-South ($p < 0.01$)

** ANOVA = $p < 0.001$, Tukey's post-hoc test = for Centre-South / Centre-North, and Centre-South / Northwest ($p < 0.01$)

* Kruskal-Wallis's test = $p < 0.001$, Dunn's post-hoc test for Northwest / Centre-North ($p = 0.01$), and Northwest / Centre-South ($p < 0.01$)

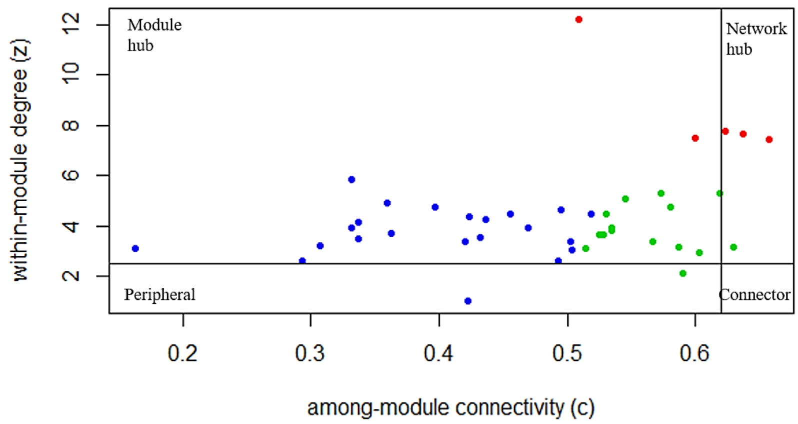

Figure 3. Distribution of sites in the modules Northwest (red), Centre-South (blue), and Centre-North (green) according to their network role: Peripheral, Connector, Module hub, or Network hub.

fore composed only of open Cerrado bird species. This network contained a total of 94 species that occurred at the same 42 sites (Table A2). This second network did not reveal significant modularity (p = 0.09).

4. Discussion

The three distinct biogeographical units found for Cerrado birds indicated an evident sectionalism regarding species distribution. However, bird richness (degree) and the proportion of widespread (*c* index) or local species (*z* index) in the studied sites did not support the Cerrado division between *core* and *marginal* regions. None of the modules corresponded to the *core* Cerrado. Further, the *core* Cerrado encompassed two of the three modules: Centre-North and Centre-South. All sites from the Northwest module would be considered *marginal* Cerrado, as well as 59% (N=13) of the sites from the Centre-South module.

Diverse factors probably influenced the distribution pattern revealed, such as topography and relief, availability of food resources, climatic conditions, geographic position in relation to the coast (continentality), and the presence of riparian forests crossing the savanna or the proximity of other forest patches. In a recent study based on tree species composition of 588 sites distributed across the Cerrado, Françoso et al. [51] identified seven floristic biogeographic districts in the Cerrado and correlated them with climatic variables (temperature, precipitation, solar irradiation, and moisture). The authors clustered these seven districts into two major groups, distinguished mainly by the annual temperature. In the Centre-North and Centre-South modules, we found that birds corresponded well to these two major groups of districts. Such consistency between bird diversity and the woody flora strengthens the idea that the Centre-South module is formed by sites that are strongly influenced by the Atlantic Forest. Moreover, the lowest among-module connectivity (c) obtained for this module highlights its regionality and its importance on keeping the regional bird diversity. Sano et al. [52] proposed a division of the Cerrado into 19 ecoregions based on topography, vegetation, precipitation, and soil data. They used the current delimitation of Brazilian biomes [20], which in fact represent the Brazilian Morphoclimatic Domains according to Ab'Saber's definition [15]. According to the mapped information presented by Sano et al. [51], the Centre-North and Centre-South modules we found in our analysis followed climatic and topographic conditions: the Centre-North module sites correspond to altitudes below 415 m, while part of the Centre-South module overlaps a plateau, with altitudes between 528 m and 1085 m. At first sight, anthropogenic land uses did not show strong influence in the modularity of bird species. For example, land uses in the state of São Paulo (SP) are very peculiar (Table 1), where planted forests (usually of *Eucalyptus* spp. and *Pinus elliottii*), sugarcane plantations and urbanization frequently surround the study areas (which does not happen in the other ones), but this did not prevent the SP bird species from composing the Center-South module, where soybean plantations often surround the other study areas, located in the Federal District (DF) and the states of Goiás (GO), Minas Gerais (MG) and Mato Grosso do Sul (MS). However, we emphasize that the main land uses pointed out here (Table 1) are based on more recent information than the dates of the studies on which we based our analyses (although land uses have not changed significantly around SP areas in the last two decades). Furthermore, the present study did not aim to analyse the influence of land use on the richness and distribution of avifauna, for which an appropriate experimental design would be necessary, focusing on the historical evolution of land cover and land use changes.

The Northwest module is mostly formed by enclaves of savannah vegetation in the Amazon Domain. These sites are distant and isolated from one another (ranging from 03°54′53″N to 15°02′60″S). According to the Refuge Theory [53] these sites correspond to relict areas from the Quaternary period, when climatic fluctuations produced alternating cycles of forest expansion in the warm-humid phases, and savannah expansion in the cold-dry phases. They are also related to specific conditions of very poor and sandy soils [16]. In these patches, strongly influenced by the Amazon Forest, the avifauna represented a mix of species from the Cerrado and the Venezuelan Llanos, as well as other widespread South American species [36]. The highest within-module degree (*z*) for the Northwest module indicated that it contained more regional species not shared with the two other regional modules. Some examples of forest-dependent species that only occurred in the Northwest module and were well distributed within the sites are: *Zimmerius gracilipes* (Tyrannidae), *Tinamus major (*Tinamidae*)*, *Thamnomanes caesius* (Thamnophilinae), *Schiffornis turdina* (Tityridae), *Myrmotherula brachyura* (Thamnophilidae), *Galbula leucogastra* (Galbulidae), *Dendrocolaptes certhia* (Dendrocolaptidae), and *Cercomacra cinerascens* (Thamnophilidae). Therefore, contrary to the idea that *marginal* Cerrado areas are species-impoverished and less important, the Amazonian savannah patches are composed of a large number of regional species and several widespread species, as shown by the high percentage of network hub sites in the Northwest module.

Our results provide strong evidence that the bird species occurring in forests are fundamental for establishing the modular pattern in the Cerrado biogeography. The three clear modules that emerge when all bird species were considered did not appear when bird species from forest physiognomies were excluded. The analysis presented here does not support the idea that the *core* Cerrado is richer than the *marginal* Cerrado, at least considering bird species. In line with this, Aguiar et al. [28] showed that bird species from the Atlantic and the Amazon forests cause considerable increment to the Cerrado avifauna, highlighting the importance of the *marginal* areas.

Given the high level of threat to the Cerrado and the perspective that 31%–34% of its remaining area (which is only 50% of what it was originally) will be replaced by other land uses by the year 2050 [54] efficient conservation actions for the Cerrado – throughout its entire territorial extension, in order to preserve maximum biodiversity – are crucial. Around 48 bird species found in the Cerrado are already threatened with extinction [55], mostly due to habitat loss and land degradation [18,54]. The biogeographic patterns of Cerrado bird distribution revealed by the present study indicate that concentrating environmental protection measures only in the *core* Cerrado is a misleading strategy, as the great biodiversity of the *marginal* areas would be left aside. Furthermore, projections of global climate change effects indicate the possibility of migration of species from the central Cerrado (considered *core*) to the south-eastern Cerrado (areas considered *marginal*) in the near future [56]. Therefore, it is essential to implement conservation efforts in the *marginal* patches of the Cerrado, such as areas in the southeast [57] and the Amazonian savannahs. Other relevant information that reinforces the importance of the *marginal* Cerrado areas is highlighted by Durigan [21], who observed that, despite representing less than 2% of the total Cerrado extension, its southern part constitutes more than 40% of its total floristic richness. In addition, it is important to consider the diverse roles played by each site for bird conservation, by both providing high species richness (Network hubs) and maintaining regional diversity (Module hubs).

5. Conclusions

We found no evidence based on the distribution of bird biodiversity to separate the Cerrado into core and marginal zones. Furthermore, there is also no reason to allocate greater conservation effort to the presumed core region of the Cerrado based on the argument that it has greater biodiversity, at least concerning birds. On the contrary, our results show that the richest module was the Northwest, which would be entirely classified as marginal according to previous thoughts. We emphasize the need of both abandoning the idea of the existence of a richer Cerrado core region and the call for allocating conservation efforts throughout the entire Cerrado, especially considering the trends in land use change and threats of climate change.

Author Contributions

This study was conceived by Lívia P. De Sordi and José C. Motta-Junior. Data was collected by Lívia P. De Sordi and Rochely S. Morandini; data analyses were undertaken by Lívia P. De Sordi and Mariana M. Vidal; manuscript preparation and revision were undertaken by all authors.

Conflict of Interest

There are no conflicts of interest associated to this research.

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