



RESEARCH ARTICLE

Sampling methods affect observed response of bird species richness to vegetation structure in Brazilian savannas

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ABSTRACT

Vegetation structure is a potentially important ecological factor structuring bird communities, but can also affect bird detectability, which can complicate the resolution of ecological patterns. We addressed how vegetation structure may bias the efficiency of the 3 methods most commonly used to sample bird species richness in the Brazilian savanna (Cerrado), which features a gradient of vegetation structure from grasslands to woodlands. We compiled secondary data on Cerrado bird species richness from the scientific literature, master's theses, doctoral dissertations, and regionally important biological publications. We used generalized linear mixed models (GLMM) to analyze the effects of habitat type and sampling method on Cerrado bird species richness estimates, controlling for variation among publications, researchers, and study sites. The data provided strong support for interactive effects between habitat type and sampling method on observed bird species richness. Point count surveys had a greater average number of species sampled per unit time in all habitats, especially in shrublands and grasslands. The number of species sampled per unit time by transect surveys did not vary across the vegetation gradient. Mist net surveys showed a slight decrease in species numbers sampled with increasing vegetation complexity. Random effects accounted for 40% of data variation, mainly because of methodological differences among studies. Despite the amount of work that has been done in the Cerrado, it is not currently possible to ascertain the relationship between bird species richness and vegetation structure because of the interaction between sampling method and vegetation complexity, as well other factors leading to variation among studies. We suggest that estimating detectability is a feasible solution for studies in which the ecological effect of interest also strongly affects sampling, as is the case in the Cerrado.

Keywords: field methods, habitat structure, point count, transect count, mist net, species diversity, biodiversity hotspot, detectability

Los métodos de muestreo afectan la respuesta observada de la riqueza de especies de aves a la estructura de la vegetación en las sabanas brasileiras

RESUMEN

La estructura de la vegetación es un factor ecológico potencialmente importante para estructurar las comunidades de aves, pero puede afectar también la detectabilidad de las aves, lo que puede complicar la resolución de los patrones ecológicos. Analizamos como la estructura de la vegetación sesga la eficiencia de los tres métodos más comúnmente usados para muestrear la riqueza de especies de aves en la sabana brasileña (Cerrado), que presenta un gradiente de estructura de vegetación desde pastizales a bosques. Compilamos información secundaria sobre la riqueza de especies de aves del Cerrado a partir de literatura científica, tesis de maestría y disertaciones de doctorado, y publicaciones biológicas importantes para la región. Usamos modelos mixtos lineales generalizados para analizar los efectos del tipo de hábitat y del método de muestreo en las estimaciones de riqueza de especies de aves en el Cerrado, controlando por la variación entre publicaciones, investigadores y sitios de estudio. Los datos brindan un fuerte apoyo a los efectos interactivos entre el tipo de hábitat y el método de muestreo que afectan la riqueza observada de especies de aves. Los muestreos de puntos de conteo tuvieron un mayor número promedio de especies muestreadas por unidad de tiempo en todos los hábitats, especialmente en sabanas y pastizales. El número de especies muestreadas por unidad de tiempo en censos de transecta no varió a lo largo del gradiente de vegetación. Los muestreos con redes de niebla mostraron una ligera disminución en el número de especies muestreadas a medida que aumenta la complejidad de la vegetación. Los efectos aleatorios representaron 40% de la variación de los datos, principalmente debido a las diferencias metodológicas entre estudios. A pesar de la cantidad de trabajos que se ha realizado en el Cerrado, no es posible actualmente determinar la relación entre la riqueza de especies de aves y la estructura de la vegetación debido a la interacción entre el método de muestreo y la complejidad de la vegetación, así como otros factores que llevan a variación entre los estudios. La estimación de la detectabilidad puede ser una solución factible para los estudios donde

el efecto ecológico de interés también afecta fuertemente el muestreo, como en el caso del *Cerrado*.

Palabras clave: detectabilidad, diversidad de especies, estructura del hábitat, métodos de campo, punto caliente de biodiversidad, punto de conteo, redes de niebla, sesgo de muestreo, transecta de conteo

INTRODUCTION

Despite their wide variety, all current bird sampling methods have biases toward some species groups and are affected by habitat characteristics (Bibby et al. 1992, Blake and Loiselle 2001, Bonter et al. 2008, Taulman 2013, Golding and Dreitz 2016, Yip et al. 2017). For example, using point counts, birds are recorded from a fixed location (Ralph et al. 1993), thus detectability decreases in habitats with dense vegetation (e.g., forests) as this impairs bird sightings and sound propagation (Allredge et al. 2007, Yip et al. 2017). In contrast, with transect methods, the observer walks along a path during the sampling period, which may increase detectability (Bibby et al. 1992). However, an observer moving through dense vegetation may become distracted or scare away birds (Verner and Ritter 1985, Golding and Dreitz 2016). Capture methods by interception, such as mist nets, do not rely on field skills to detect birds, but have been criticized for being dependent on bird movement and behavior (Remsen and Good 1996) and also for under-sampling the bird assemblages in unsampled habitat strata (Bonter et al. 2008).

Nevertheless, point and transect counts and mist-netting are among the main sources of information currently available for the abundance and distribution of birds in most ecosystems (Bibby et al. 1992, Sutherland et al. 2004). If the effectiveness of these methods for recording birds is related to habitat variables, then many observed patterns of responses of bird populations and communities to habitat variables might be compromised (Gu and Swihart 2004, Ruiz-Gutiérrez and Zipkin 2011). In this paper, we investigate whether sampling method can affect one of the most important patterns of avian ecology, the relationship of bird species richness with vegetation complexity and habitat heterogeneity (MacArthur and MacArthur 1961, MacArthur et al. 1962, Willson 1974, Cody 1985, Tews et al. 2004). Vertical structure, or stratification of vegetation, is one of the most obvious aspects of vegetation complexity and can be defined as the vertical physical structure and arrangement of vegetation (MacArthur and MacArthur 1961, Pearson 1971, Barton et al. 2014). Stratification is widely used to define vegetation physiognomies or habitat types, and many studies have found a positive correlation between vegetation stratification and bird assemblage diversity (Rotenberry 1985, Poulsen 2002, Hurlbert 2004, Díaz 2006). Nevertheless, some recent studies have shown that increases in vegetation complexity can also affect the detectability of

bird species and thus estimates of diversity, population density, species occupancy, and turnover rates (Zipkin et al. 2010, Ruiz-Gutiérrez and Zipkin 2011, Anderson et al. 2015, McNew and Handel 2015).

Tropical savannas offer a unique opportunity to test the effects of vegetation stratification on the efficiency of various bird sampling methods. This biome (sensu Olson et al. 2001) is formed by a complex mosaic of grasslands, shrublands, and forests, and so harbors a high diversity of habitat types differing markedly in vegetation stratification (Bond and Parr 2010). Various sampling methods have been used to compare bird diversity among habitat types in the Brazilian savanna (Cerrado), but a general pattern for the relationship of bird diversity to vegetation structure in this region remains elusive. There are indications of both higher bird species richness in more stratified habitat types (e.g., shrublands compared with grasslands; Tubelis and Cavalcanti 2001, Motta et al. 2008, Fieker 2012) and the reverse (Silva 2004, Piratelli and Blake 2006, Rodrigues and Faria 2007). Other studies have not found significant relationships between these variables (Valadão 2012, Posso et al. 2013).

In this paper, we test whether the efficiency of bird sampling methods varies across a gradient of vertical vegetation structure in Cerrado tropical savanna. The main habitat types found in the Brazilian savanna (i.e. grasslands, shrublands, and woodlands) vary markedly in vertical vegetation stratification. Besides directly affecting bird diversity, such variation could potentially affect bird sampling efficiency and, consequently, species richness estimates. To test whether this occurs, we amassed published data from surveys of bird communities in these 3 Cerrado habitat types and which used one or more of the 3 most common bird census methods, point counts, transects, and mist-netting. We then tested whether the efficiency of each census method (i.e. number of species sampled per unit effort) used in these surveys was affected by habitat type. By using mixed-effects linear models, we also accounted for any correlation between surveys performed in the same area, by the same researchers, or that used the same study sampling protocol. By using a measure of efficiency (species recorded by time), we accounted for the wide variation in sampling effort among surveys. As a result of statistically controlling for methodological effects, we could compare bird sampling methods in the main habitat types of the Cerrado tropical savanna. Such estimates can shed light on the behavior of the species accumulation curves obtained with each method and in each habitat type, allowing us to evaluate



FIGURE 1. Brazilian savanna (Cerrado) vegetation complexity gradient analyzed in our study testing whether the efficiency of bird sampling methods varied across a gradient of vertical vegetation structure: (A) Grasslands; (B) Shrublands; and (C) Forests.

the relationship between vegetation structure and bird species richness.

METHODS

Study Region

The Cerrado ecoregion is a savanna that originally covered most of the central portion of South America, mostly in Brazil (Olson et al. 2001). It occurs mainly in areas of old, dystrophic, aluminum-rich, and well drained soils (Oliveira-Filho and Ratter 2002). Many classifications have been proposed to encompass the great diversity of habitat types found in the Cerrado (see Goodland 1971 and Ribeiro and Walter 1998 for detailed descriptions), but they can be grouped into 4 broad classes (Ratter et al. 1997, Ribeiro and Walter 1998): (1) grasslands, which are dominated by the herbaceous stratum (mainly grasses but also forbs), with few shrubs and small trees; (2) shrublands, or savannas *sensu stricto*, where shrubs and trees 3–8 m high form a distinct stratum in addition to the herbaceous layer; (3) savanna forests or woodlands, which have a continuous and dense tree canopy 8–15 m high but sparse grasses and forbs and low shrub density; and (4) forest enclaves, such as semideciduous, deciduous, evergreen, and riverine forests, which include plant species from other ecoregions. Classes 1–3 (Figure 1) are typical savanna and occupy $\sim 3/4$ of the region (da Silva and Bates 2002). These different habitat types usually occur in patches within a single area or landscape because local differences in soil properties and fire occurrence (Ratter et al. 1997). Thus, vegetation structure in the Cerrado may transition from grassland to forest at the landscape scale.

The Cerrado is also one of the most threatened global biodiversity hotspots (Myers et al. 2000). It harbors a great diversity of plants and animals (da Silva and Bates 2002, Simon et al. 2009, Nogueira et al. 2011). About 840 bird species have been recorded in the Cerrado region (Marini and Garcia 2005), which is almost 50% of the Brazilian avifauna. Of these species, $\sim 4\%$ are endemic to the region (da Silva and Bates 2002), and almost 12% are classified as

globally threatened (Marini and Garcia 2005). At least 40–60% of the total area of the Cerrado has already been converted to human uses (Carvalho et al. 2009), and its high land conversion rates could lead to a massive extinction event in coming decades (Strassburg et al. 2017).

Data Selection

We amassed published data on the numbers of species recorded in different Cerrado habitat types using a systematic search protocol (Supplemental Material A.1 and Figure S1). The first step was to gather publications with or without a keyword search using 4 main data sources: indexed journals, nonindexed journals, M.S. theses and Ph.D. dissertations, and technical governmental reports.

We searched for papers published in indexed journals using Web of Science, Scopus, and Scielo databases. We consulted these databases using their search tools and retained the studies containing the keywords defined by us (see details in Supplemental Material A.1 and Table S1). We also reviewed regional nonindexed publications in avian, ecological, and biological research from Brazil and South America from 1971 to 2016 (Supplemental Material Table S2). Additionally, we searched for M.S. theses and Ph.D. dissertations in the Brazilian graduation studies agency (CAPES) database (<http://bancodeteses.capes.gov.br/>), and also in biology, zoology, and ecology graduate course databases from universities in the Cerrado region (Supplemental Material Table S3). Finally, we searched for bird inventories in technical reports and/or management plans for federal- and state-protected Cerrado areas. These governmental reports were located by visiting the websites of governmental agencies responsible for protected areas within the Cerrado region. We completed our search by adding studies found by previous reviews (Accordi et al. 2003, 2005a, 2005b, Borges 2008, Morandini 2013), and with an Internet search using Google and Google Scholar search tools using “Cerrado”, “bird”, and “vegetation” as keywords. We then asked 20 researchers working on

TABLE 1. Number of areas (Figure 2), sites within these areas by habitat type, and sampling effort per survey method in the data gathered for our analyses testing whether the efficiency of bird sampling methods varied across a gradient of vertical vegetation structure in the Brazilian savanna (Cerrado). Data are from Motta (1990), Lins (1994), Antas (1999), Abreu (2000), Tubelis and Cavalcanti (2001), Almeida (2002), Silva (2004), Pacheco and Olmos (2006), Piratelli and Blake (2006), Curcino et al. (2007), Martins (2007), Olmos and Brito (2007), Rodrigues and Faria (2007), Braz (2008), Motta et al. (2008), Sendoda (2009), Costa and Rodrigues (2012), Fieker (2012), Valadão (2012), Cavarzere (2013), Pascoal et al. (2013), and Posso et al. (2013).

Habitat type	Survey method	Number of sites	Number of areas	Sampling effort (range, hr)	Total effort (hr)
Grassland	Point count	8	2	9–20	91.66
	Mist net	2	2	36–242	277.86
	Transect	4	4	7–82	186.00
Shrubland	Point count	19	6	20–20	181.66
	Mist net	19	12	36–601	1,358.10
	Transect	12	8	14–80	518.21
Forest	Point count	3	1	2–36	60.00
	Mist net	3	3	14–375	737.80
	Transect	4	4	8–80	227.50
Total		74	26	2–601	3,638.79

Cerrado birds to check the resulting list and suggest any additional data sources that we might have missed (none of them added new data to our analyses). We checked the summaries of all studies to filter those not concerned with Cerrado birds and the Cerrado region. We retained only those studies performed inside the Brazilian Cerrado ecoregion, excluding studies from other tropical savanna vegetation types lying outside Brazil (e.g., African, Australian, Venezuelan, Bolivian, and Paraguayan savannas) or other Brazilian ecoregions (e.g., *Pantanal* wetlands or *Campinarana* savannas in Amazonia), resulting in 175 studies, of which 123 surveyed the entire diurnal avifauna (Supplemental Material Figure S1).

From these 123 studies, we selected a subset of 99 studies that presented data from surveys in areas greater than 30 ha and that included at least one of the main habitat types of the Cerrado: grassland, shrubland (savanna) or woodland. We excluded surveys conducted in areas with intense human land use (usually crops), deciduous or semideciduous forests, riparian vegetation, or areas subject to flooding or waterlogging during most of the year (e.g., seasonally flooded grasslands). To evaluate the effects of sampling method, and to control for the well-established effect of sampling effort, we only included studies that provided precise data on each sampling method used, along with the sampling effort employed at each sampled site for each method, resulting in 70 studies.

We considered sampling units in a single habitat type within a study to be independent. We then retained the publications that reported, for each site, the number of species recorded, habitat type sampled, sampling method(s), and sampling effort.

After applying the above criteria, we also excluded 6 studies that shared data with other more complete ones. Additionally, we were not able to recover data from 14 potentially interesting studies, even after directly contacting their authors and institutions. Ideally, all studies should

have sampled all habitat types using the 3 different methods, but we also considered those that sampled only 1 Cerrado sensu lato habitat type using just 1 sampling method, resulting in 22 studies across 74 sites that we could analyze (Table 1; Motta 1990, Lins 1994, Antas 1999, Abreu 2000, Tubelis and Cavalcanti 2001, Almeida 2002, Silva 2004, Pacheco and Olmos 2006, Piratelli and Blake 2006, Curcino et al. 2007, Martins 2007, Olmos and Brito 2007, Rodrigues and Faria 2007, Braz 2008, Motta et al. 2008, Sendoda 2009, Costa and Rodrigues 2012, Fieker 2012, Valadão 2012, Cavarzere 2013, Pascoal et al. 2013, Posso et al. 2013).

Response and Predictor Variables

To compare the species richness recorded in each survey, we standardized the number of species recorded by the sampling effort spent in each site using each method (see details in the next subsection). The numbers of species per site were sometimes reported in the manuscript's results section, but most authors also reported a list of species sampled by site (59 of 74 sites, ~80% of cases). In these latter cases, we checked the number of species found and recalculated the number of species excluding nocturnal species (owls, nightjars, and potoos). We only included species identified to genus level (e.g., *Elaenia* sp.) when no other congeneric species was recorded at the site. We included boreal and austral migratory species as part of the site species pool.

We calculated sampling effort for each site and each sampling technique (Supplemental Material Table S4). Point counts lasted 10, 15, or 20 min, and sites were sampled with 3 to 30 points. Transect census durations also varied (from 45 min to 2 hr), as did transect lengths (from 0.5 to 1.5 km), often reported as just total distance and total time. Mist net sampling effort varied from 2 to 25 standard nets (12 m length, between 2.0 and 3.0 m in height, and 36 mm mesh size), which we converted to mist

net hours based on the time that nets were open (Supplemental Material B.1). We compared species richness considering 10 mist-net hr, 1 hr of point counts, and 1 hr of transects to be equivalent.

We used habitat type and sampling method as categorical predictors in our analysis. For the habitat type variable, we grouped habitat types reported by study authors into grasslands, shrublands, and forests, following Goodland (1971), Ribeiro and Walter (1998), and da Silva and Bates (2002; Supplemental Material Table S5).

As many surveyed sites were aggregated in study areas and in publications, these surveys could not be considered as completely independent replicates. Accordingly, we considered as independent random variables the study areas where the data were collected, the author of each study, and the study in which the data were published (author name and publication year). These variables summarized the uncontrolled effects of the sampled study area, the researchers' biases, and uncontrolled aspects of each publication.

Model Fitting and Model Selection

We used generalized linear mixed models (GLMMs; Bolker et al. 2009, Zuur et al. 2009) to examine the effects of all combinations of the predictor variables on species richness of birds recorded at each site. We followed the protocol of Zuur et al. (2009) to construct and test GLMMs fitted to nested and hierarchical data (i.e. replicates of habitats and sampling methods distributed over study areas and publications). First, we built 12 GLMMs using combinations of random variables and selected the model with the best random effects structure (using all fixed effects). We then used this selected random effects structure to identify the best set of fixed effects predictors (Supplemental Material B.2). In all models, the response variable was the number of species recorded per effort unit, which was modeled as a Poisson variate with the logarithm of the number of sampling hours as an offset. As we included in all fitted models the log of sampling hours in each survey as an offset, our response variable, species richness, can be interpreted as the number of species added in each log(hr) of sampling. This response variable corresponds to an important aspect of diversity, the initial slope of species accumulation curves (Gotelli and Colwell 2001). Habitat type, sampling method, and their additive and interactive effects were tested as fixed effect predictors. The additive effects hypothesis assumes that both variables could influence species richness, but that these effects are independent. The interactive effects hypothesis assumes that vegetation structure and sampling method interact to affect species richness. Study area, author, and publication identities were included in models as random effects.

Competing models were compared using Akaike's information criterion corrected for small samples (AIC_c), which identifies the model that is best supported by the data (Burnham and Anderson 2002). We also calculated Akaike evidence weights (w_i). AIC_c and w_i were calculated using the AICcTab function of the bbmle package (Bolker 2017) in R (R Core Team 2015). All analyses were completed using R software (R Core Team 2015), with models fitted using the glmer function in the lme4 package (Bates et al. 2015). The best-supported models ($\Delta AIC_c \leq 2$) were inspected and validated by residuals analysis, which did not reveal any significant departure from model assumptions (Supplemental Material Figure S2 and Figure S3).

To gauge the precision of the model predictions, we calculated bootstrap confidence intervals based on 10,000 randomizations of bird species richness values predicted by the selected model, with and without the variance caused by random effects. For these calculations, we used the bootmer function in the lme4 package (Bates et al. 2015). To evaluate the magnitude of variance explained by the fixed and total effects of the model, we also calculated marginal and conditional coefficients of determination for mixed models with the r.squaredGLMM function in the MuMIn package (Bartoń 2016) in R.

RESULTS

We identified 22 studies across 74 sites distributed over 26 study areas (Figure 2, Table 1, Supplemental Material Table S4). Shrubland, the most prevalent of the Cerrado habitat types (Goodland 1971), was the best represented habitat, with 50 sites. Grassland was represented by 14 sites, and forest by 10 sites. By comparison, the distribution of survey methods across sites and study areas was more balanced. The 3 survey methods were each used in $\sim 1/3$ of the study sites and in 27% to 53% of the study areas (values for point counts and mist nets, respectively). The spatial distribution of study areas was also representative, covering both the core and peripheral areas of the Brazilian Cerrado. Sampling effort differed substantially between methods and between habitat types within each method.

We used model selection to determine the most informative random effects structure and then to compare fixed effects (Table 2). Two top random effects structures were identified using our model selection criterion ($\Delta AIC_c \leq 2$): one that included the random intercept effects of study area and study author, and a second that had study area and publication as random intercept effects (Table 2A). As both models were considered equally plausible using ΔAIC_c , we chose the latter as the best random effects structure. We made this choice because we believe that we did not have enough study author replicates ($n = 2$) to support a strong author random effect, and because we

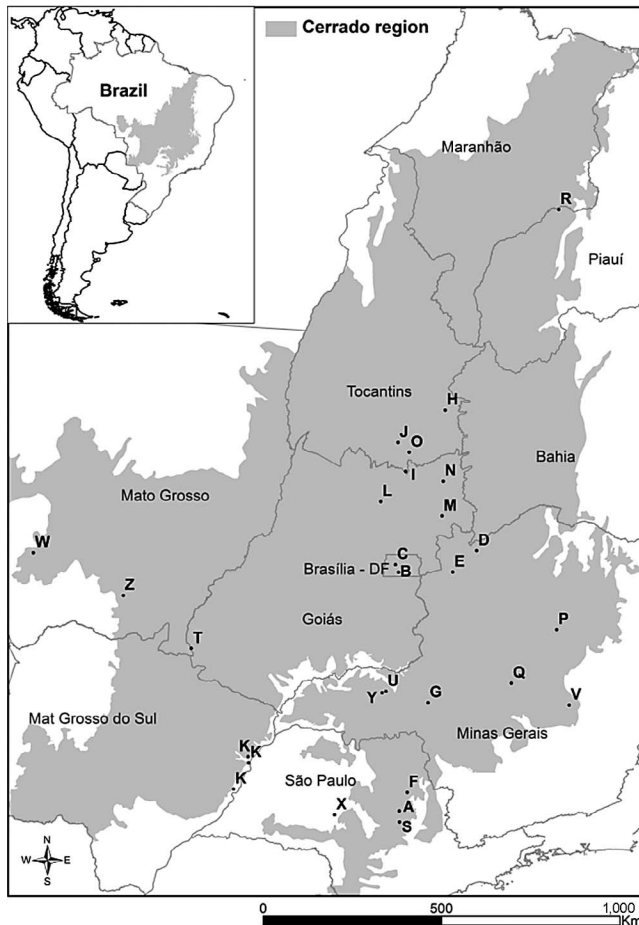


FIGURE 2. Map of South America and Brazil, showing the area in Brazil occupied by the Cerrado ecoregion (shaded in gray). In the amplified view, Brazilian states are shown and letters indicate the 26 sampled study areas for which we gathered the data used in our analyses testing whether the efficiency of bird sampling methods varied across a gradient of vertical vegetation structure. Studies and sampled sites are described in Supplemental Material Table S4.

believe that the effects of study author or bird observer are captured in the publication variable.

Next, we compared models with different sets of fixed effects. The model that was best supported by the data included the interactive effects of habitat type and sampling method (Table 2B). All other models, including the null model, had high ΔAIC_c values, and thus very low evidence weights. Hence, the data gathered provide support for an interaction effect between vegetation structure and census method used on species richness estimates for the Cerrado.

Model predictions and the observed data indicated that the differences in bird species richness among habitat types were strongly affected by the survey method used (Figure 3). For instance, the model predicted that point counts would record 40% more species per log(hr) in

shrublands (10.5 species per log[hr]) than in grasslands (7.5 species per log[hr]), and that this method would record close to 5 times more species per log(hr) in shrublands than in forests (2.1 species per log[hr]). On the other hand, the model predicted that censuses with mist nets would record the greatest species richness in grasslands (0.7 species per log[hr]), intermediate species richness in shrublands (0.6 species per log[hr]), and the lowest species richness in forests (0.4 species per log[hr]), although the differences were much smaller. Finally, the model predicted that transect counts would record essentially the same species richness in the 3 habitat types (1.44, 1.41, and 1.53 species per log[hr] in grasslands, shrublands, and forests, respectively). Despite the interaction between method and habitat type, the model predicted that, within each habitat type, point counts would record the highest values of species per log(hr) (specially in shrublands and grasslands), followed by transects and then by mist nets, although this comparison hinges on the arbitrary decision to equate 10 mist-net hr with 1 hr of point count or transect survey.

The model also estimated that the random effects of study area and publication accounted for a standard deviation of 1.3 and 2.4 in the expected number of species per log(hr), respectively (Supplemental Material Table S6). This means that the species richness initially expected to be sampled in each habitat type using a specific method can vary by ~ 3.7 species per hour, simply due to the sum of the variation between study site and publication. Such a large effect is evident in the wide confidence intervals of the predicted values when random effects were taken into account (light gray bars in Figure 3). Nevertheless, the variance explained by the fixed effects was $\sim 63\%$ of the total variance explained by all effects included in the model (ratio of the marginal coefficient of determination, $R^2_m = 0.55$, to the conditional coefficient of determination, $R^2_c = 0.87$).

DISCUSSION

The efficiency of each bird census method was affected in a different way by vegetation complexity in the Cerrado ecoregion. Surveys using point counts recorded a greater number of species sampled per hour in relation to other methods, but still recorded fewer species in woodlands than in shrublands and grasslands. Mist net censuses showed a decreasing trend of species recorded per effort unit with increasing vegetation complexity. Conversely, transect-based surveys did not show any relationship between recorded bird species richness and vegetation complexity. These results were obtained by controlling for different sources of heterogeneity among samples, such as study area sampled and individual study particularities. Also, we used as a response variable the number of species

TABLE 2. Comparison of generalized linear mixed effect models (GLMMs) used to identify the most informative random effects structure and compare fixed effects of sampling methods on species richness of birds recorded in sites across a gradient of vertical vegetation structure in the Brazilian savanna (Cerrado). **(A)** Model selection results for the best random effects structure (with all fixed effects included in the model). **(B)** Model selection results for fixed effects of habitat (Hab), method (Met), and their interaction (Hab*Met) based on the random effect structure identified in **A**. Random effects: 1|Area = random intercept effect of study area; 1|Aut = random intercept effect of study author; 1|Pub = random intercept effect of publication; Hab|Aut = random slope effect of author in the relation of species richness and habitat; Hab|Pub = random slope effect of publication in the relation of species richness and habitat; NULL = no random effect used. Models were ranked based on differences in Akaike's information criterion corrected for small sample size (ΔAIC_c). K is the number of parameters in the model, w_i is the Akaike weight, and $-2\ln L$ is the negative maximum likelihood.

Fixed effects	Random effects	ΔAIC_c	K	w_i	$-2\ln L$
(A) Random effects structure					
Hab + Met + Hab*Met	1 Area + 1 Aut	0.0	11	0.490	683.8
Hab + Met + Hab*Met	1 Area + 1 Pub	0.4	11	0.390	684.2
Hab + Met + Hab*Met	1 Area + 1 Pub + 1 Aut	2.8	12	0.120	686.6
Hab + Met + Hab*Met	1 Area	19.5	10	<0.001	703.3
Hab + Met + Hab*Met	Hab Aut	23.9	15	<0.001	707.1
Hab + Met + Hab*Met	Hab Pub	25.7	15	<0.001	708.9
Hab + Met + Hab*Met	1 Pub	40.5	10	<0.001	723.7
Hab + Met + Hab*Met	1 Pub + 1 Aut	42.8	11	<0.001	726.0
Hab + Met + Hab*Met	1 Aut	43.0	10	<0.001	726.2
Hab + Met + Hab*Met	Met Aut	45.2	15	<0.001	728.2
Hab + Met + Hab*Met	Met Pub	46.1	15	<0.001	729.1
Hab + Met + Hab*Met	NULL	1,756.5	9	<0.001	2,439.7
(B) Fixed effects					
Hab + Met + Hab*Met	1 Area + 1 Pub	0.0	11	1.000	684.2
Hab + Met	1 Area + 1 Pub	17.6	7	<0.001	701.8
Met	1 Area + 1 Pub	25.1	5	<0.001	709.3
Hab	1 Area + 1 Pub	1,043.0	5	<0.001	1,727.1
NULL	1 Area + 1 Pub	1,050.6	3	<0.001	1,734.8

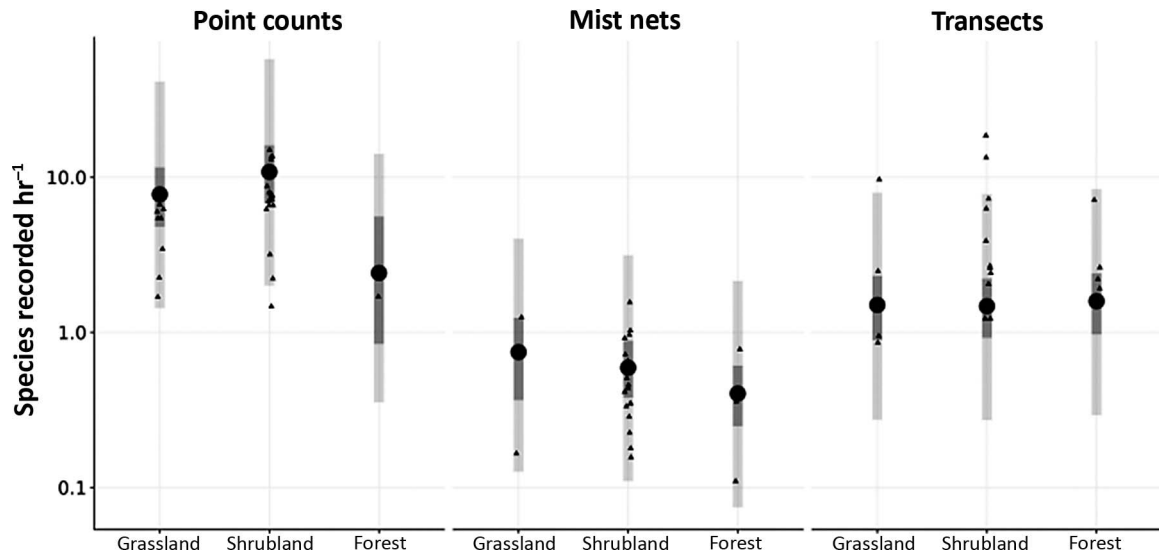


FIGURE 3. Observed and predicted numbers of species recorded per log(hr) of census and for combinations of each habitat type and census method at 74 recorded sites in 22 published bird surveys conducted in the Cerrado ecoregion in Brazil. Small black triangles are observed values; the larger black dot is the value predicted by the selected model (Table 2), taking into account the effects of both method and habitat type (fixed effects), and the effects of publication and study area (random effects). Gray bars show the confidence intervals for the predicted values including both fixed and random effects (light gray) and fixed effects alone (dark gray).

per sampling hour, which enabled us to control the great variation in sampling effort among studies and its clear impacts on diversity estimates (Gotelli and Colwell 2001). This metric is not appropriate to estimate the total number of species in each habitat, as it is a linear approximation of the initial part of the species–effort curve (that is, when an asymptote is not yet evident). It also requires arbitrary scaling of mist net effort to the time used for point counts or transects. Even so, our results allowed us to fully compare the accumulation of species records among these 3 bird sampling methods, highlighting how well they each performed in different habitat types.

Eight of the 22 studies that we collated compared the diversity of birds among habitat types in the Cerrado ecoregion (Supplemental Material Table S7). Half of these studies used different sampling effort in each habitat, 7 studies compared only 2 of the 3 broad habitat types, and just 1 study used 2 sampling methods to compare habitats. Only 3 studies provided statistical tests of differences in diversity indices between habitats. Nevertheless, the patterns found by these studies were generally in accordance with what we found for the whole set of studies. The only exception was a higher species richness found by Silva (2004) in shrublands than in grasslands and forests using transect censuses.

Our results showed that point counts were far more efficient than transects and mist nets in grasslands, shrublands, and woodlands. Indeed, point counts in general are the most commonly used method to sample bird communities (Rosenstock et al. 2002), as they are considered the most efficient and least selective method (Bibby et al. 1992). However, point counts are greatly dependent on only auditory contacts in more complex habitats (Alldredge et al. 2007), whereas in open habitats visual contacts are more frequent. We thus propose that the negative effect of vegetation complexity on bird detection caused by a decrease in bird sightings explains the decrease of point count efficiency in forests. Transect sampling has been considered less efficient than point counts because of the noise and distraction produced during observer movement (Verner and Ritter 1985, Taulman 2013). However, Golding and Dreitz (2016) noted that bird flushing by observer movement during transect sampling increased the rate of visual detection (93% of total records) compared with point counts (67% of total records). Because the efficiency of transect surveys was lower than the efficiency of point counts in the Cerrado, we hypothesize that the increase in visual detections by flushing came at the cost of not detecting many of the individuals that were scared away, were not heard or kept silent. On the other hand, the efficiency of transects did not decrease in forests, suggesting that this flushing effect provided the same rate of visual contact in the 3 vegetation types, or

compensated for the differences in species richness among vegetation types.

Additionally, we found that 1 hr of 10 standard nets opened produced less than one-tenth of the number of species sampled per hour than the point count method. The low efficiency of mist nets has been attributed to their limited spatial coverage compared with the range that visual and aural censuses can have (Bibby et al. 1992, Blake and Loiselle 2001, Bonter et al. 2008). An obvious outcome of this limitation is a decrease in efficiency in more complex, multilayered vegetation types (as we found), probably because mist nets tend to be set at the same height range in all habitats. However, mist net censuses provided the most precise estimates of species richness per hour in all 3 habitat types, because this method substantially reduced the need for visual or auditory observer identification skills (Karr 1981). The advantages that nets have over the 2 visually and aurally based detection methods lie in their providing a better control of heterogeneity in detection. This makes mist nets more appropriate for studies that rely on strict sampling standardization, such as long-term monitoring and replicated surveys at the landscape level (Stouffer et al. 2006, Ferraz et al. 2007, Banks-Leite et al. 2010).

We also showed that the variance explained by singularities in publication methodologies was almost twice as high as the estimated variance among study areas, which points to a greater relative importance of methodology over local aspects in the estimation of community species richness. This prevalence of methodological effects over site attributes is impressive, as the study areas encompassed a wide range of environmental conditions that strongly affect bird diversity in the Cerrado, such as variations in climate (da Silva 1996, Blamires et al. 2008), as well as important predictors of avian diversity such as land cover and land use (Boulinier et al. 2001, Hill and Hamer 2004, Radford et al. 2005, Ferraz et al. 2007, Banks-Leite et al. 2010). However, the great variation between publications observed by us could have been due other details, such as number and experience of observers, number of points, number and extension of transects, census radius, and size and mesh of mist nets, all of which could have been included in the statistical models had they been reported. Going further, the lack of key information on sampling designs (e.g., geographical coordinates of sites surveyed, and sampling effort for each habitat type and method) precluded the use of more than two-thirds of the surveys of bird communities that we found (Supplemental Material Figure S1). In consequence, we recommend that future bird inventories in the Cerrado, and in other less explored and threatened regions, should provide full sampling methods and effort information.

In summary, our analysis suggests that it is not possible to ascertain the relationship between bird species richness

and vegetation structure in the Cerrado, partly because of the interaction between sampling method and vegetation complexity, and partly because of the extensive variation in observed bird species richness among studies. Both issues are instances of detection heterogeneity (e.g., Otis et al. 1978, Burnham and Overton 1979). An extensive toolbox to deal with variable species detection has been developed (e.g., Boulinier et al. 1998, MacKenzie et al. 2002). Distance sampling methods can be particularly useful to compare habitats that have different distance detectability functions (Buckland et al. 2001, Rosenstock et al. 2002). Alternatively, multispecies occupancy models can be used to disentangle the effects of vegetation structure on bird communities from its effects on species detectability (Zipkin et al. 2010, Kéry and Royle 2015). For example, in both eastern U.S. forests (Zipkin et al. 2010) and Alaskan alpine shrublands (McNew and Handel 2015), understory vegetation cover, tree basal area, and shrub density can decrease species detections and then bias the observed relationship of vegetation structure with bird species richness. We therefore suggest that future studies of the effects of habitat structure on bird diversity should evaluate potential sampling biases linked to habitat structure itself. This can be properly achieved with statistical models that estimate species detectability, although at the cost of considerable increments in sampling effort. Nonetheless, we believe that the use of these models is the best alternative, because controlling detection biases in the sampling design (Banks-Leite et al. 2014) is hardly feasible when the putative ecological effect also strongly affects species detection, as was the case in this study.

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Author contributions: R.C.R. collected the data; and R.C.R. and P.I.P. conceived the idea, designed methods, analyzed the data, and wrote the paper.

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