

Distribution dynamics of South American savanna birds in response to Quaternary climate change

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Abstract Several lines of evidence suggest that savannas currently distributed disjointedly in the southern and northern portions of South America might have been connected and disconnected many times during the Quaternary climatic fluctuations. Here, we investigated how climate change since the Last Interglacial may have modified the distribution of bird species associated with South American savannas. We evaluated the connections between South America's savannas using 10 broadly distributed species and the impact of climate changes in community composition using 18 species endemic to Cerrado. We fit ecological niche models to each of the 28 bird species to compare the potential distribution patterns for the Last Interglacial (120 kyr BP), the Last Glacial Maximum (21 kyr BP) and the present. Our results corroborated hypotheses of past connections between northern and southern blocks of savannas through three hypothetical corridors that existed along the Andes, Atlantic Coast and through central Amazonia. In addition, our results also suggested the existence of a fourth plausible corridor located along the Madeira River, crossing Amazonia from the southwest to the northeast. Finally, our analysis showed significant changes in the community composition dynamics of endemic Cerrado species. Our results further reinforce the notion that climate change has major impacts on the distribution of savanna species.

Key words: birds, Cerrado, climatic fluctuation, ENM, neotropical, turnover.

INTRODUCTION

Biogeography is the study of the dynamics of species distribution patterns across space and time. While some observed patterns likely reflect the ecological factors unfolding in recent times, patterns across large spatial and temporal scales tend to be related to geophysical events (Crisci *et al.* 2006). Climatic fluctuations represent a major influence that can occur at both large and small time scales and may affect species distributions at multiple spatial scales.

An important tool to estimate fundamental niches and predict potential distributions under climate change scenarios is the ecological (or environmental) niche model (ENM; Peterson & Soberón 2012). ENMs are widely used in paleoclimate studies because they are relatively robust for predicting suitable areas in geographic regions when little is known about the species distribution. Additionally, ENMs are able to identify suitable areas over multiple time periods (Warren & Seifert 2011).

Palaeodistribution modelling provides information regarding the temporal dynamics of landscapes and species distributions in the recent past (Franklin *et al.* 2015; Martínez-Méndez *et al.* 2015). The emphasis of palaeodistribution models ranges from the study of spe-

cies (Dantas *et al.* 2013) to the distribution of biomes (Carnaval & Moritz 2008; Werneck 2011; Werneck *et al.* 2012b), and they are suitable to propose testable biogeographic and evolutionary scenarios (Poelchau & Hamrick 2013; Werneck *et al.* 2012a). The contribution of ENMs to palaeobiology was recently reviewed, and some drawbacks were discussed, including the assumption of niche stability across space and time (Svenning *et al.* 2011). Careful consideration of data compilation, model generation, calibration, validation and projection in ecological models can guarantee their utility for a variety of ecological, evolutionary and conservation questions (Svenning *et al.* 2011; Araújo & Peterson 2012; Merow *et al.* 2013).

Several biogeographic hypotheses associate biota diversification with climate fluctuations (Batalha-Filho *et al.* 2013), and it has been suggested that the dynamics of forest/savanna expansion and contraction during the Quaternary period promoted speciation in South America (Haffer 1969; Prance 1982). Successive vegetation cycles in South America in response to Pleistocene climatic fluctuations caused profound changes in the geographical distribution of fauna and flora, ultimately affecting speciation, diversity patterns and community composition (Silva 1995; Silva 1997; Werneck *et al.* 2012b). In that scenario, high temperatures and humidity during the Last Interglacial (LIG) period approximately 120 000 years ago (kyr BP) could have favoured the expansion of forests in South America at the expense of

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savannas (Otto-Bliesner *et al.* 2006), while temperature and humidity decreases during the Last Glacial Maximum (LGM; 21 kyr BP) may have inverted the balance of vegetation types and connected the South American savannas located north and south of Amazonia by large corridors with high climatic suitability (Haffer 1974).

Sarmiento (1983) was the first to propose the existence of such Pleistocene savanna corridors based on the occurrence of biotic similarities among savannas. Silva and Bates (2002) elaborated further on three possible climate corridors that could have made these connections possible: (i) an Andean corridor connecting southern South America savannas directly to the Llanos and Roraima through the Andean slopes; (ii) a central corridor connecting the savanna blocks through fragments occurring in Monte Alegre and Paru; and (iii) a coastal corridor connecting the savannas of Amapá and Marajó via a pathway along the Atlantic coastline. However, evidence from palaeoecological data, dynamic vegetation modelling and biome distribution modelling challenge the notion of corridors by suggesting that savannas did not replace major portions of the forested Amazon Basin and that the Cerrado savannas might have even shown a narrower distribution during the LGM (Colinvaux & Oliveira 2000; Werneck *et al.* 2011; Werneck *et al.* 2012b).

Bird community studies in the savannas located in northern South America reveal high species composition similarity to those of Suriname and Amapá (Brazil) and the communities from the core of the Cerrado in central Brazil, whereas the bird communities of Roraima are highly similar to those found in Llanos de Moxos (Bolivia) (Santos & Silva 2007). This similarity in species composition supports the idea that corridors might have connected these bird communities recently (Silva 1995).

Information about the effects of climate fluctuations on endemism and distribution patterns of taxonomic groups in South American savannas remains scarce (Werneck *et al.* 2012a). However, birds have long been used as a model system to investigate the diversification and biogeographic patterns of South American savannas, pioneered by the seminal biogeographical analysis of the Cerrado avifauna conducted by Silva (1995). Since then, several studies have helped to further clarify the biogeographic patterns of the South American savanna avifauna (Robbins *et al.* 2004; Santos & Silva 2007; Silva 1995; Silva 1997; Vasconcelos *et al.* 2011).

Although Cerrado has a rich avifauna (approximately 850 species), the low endemism (3.7%) within this group (Silva & Bates 2002) may be related to frequent cycles of climate change that might have fragmented populations and eventually caused local extinctions, leading to a decrease in the number of endemic species in some communities (Pauls *et al.* 2013). To date, no study has verified the impact that climate changes since

the LIG may have had on the distribution of endemic birds of the savanna and on their community composition. Therefore, such investigation may help us in understanding the impact of climate change on biodiversity.

To date, no ecological niche modelling study has explicitly integrated the role of Quaternary climatic fluctuations into the potential distribution of the South American savanna avifauna. Here, we used ENM to evaluate the role of past climate changes on the potential distribution patterns of South American savanna bird species. We assumed that if natural corridors connected southern and northern savannas in South America, these corridors should have been located in areas that were climatically similar to both regions. More specifically, we conducted analyses to (i) identify potential Quaternary corridors that might have facilitated connections between bird populations within the major South American savanna disjunctions located north and south of the Amazon Basin; (ii) explore the distribution of Cerrado endemic birds during recent fluctuations of the Quaternary; and (iii) characterize the compositional shifts of Cerrado-restricted bird communities during the recent climatic fluctuations.

MATERIAL AND METHODS

Study area

The South American savannas originally occupied approximately 250 million hectares (Mha), mostly distributed within Brazil (203 Mha or 81%) (Fisher *et al.* 1994) and have a disjointed distribution that is divided into two main portions: the savannas of northern South America, formed by the Llanos (Venezuela), Roraima, Pará in the Paru – Monte Alegre and Marajó regions, and Amapá (Brazil); and the savannas of southern South America, consisting of the Cerrado (woodland savanna) and Pantanal (seasonally flooded savanna) (Brazil) and Llanos de Moxos (Bolivia) (Silva & Bates 2002). The savanna vegetation is characterized by an extensive herbaceous stratum dominated by a large number of perennial grass species (Sarmiento 1983). Savannas occur in a dry and humid tropical climate in which the annual rainfall varies from 1500 to 2000 mm and mean temperatures range from 20 to 26 °C, with strong seasonality (Sarmiento 1983; Silva & Bates 2002).

Occurrence data collection

We identified potential Quaternary savanna corridors for bird species, which were selected according to their degree of dependency on open vegetation habitats, assuming that any movement between areas should occur through savanna corridors. Accordingly, we selected 28 species (representing 15 families) that are restricted to the open vegetation ecosystems within the South American savannas, according to the classification proposed by Silva (1995).

Subsequently, we classified the selected species into two groups according to their distribution patterns. The first group (hereafter referred to as broadly distributed) was composed of 10 species that are widely distributed throughout the South American savannas, while the second group (restricted range) was composed of 18 species restricted in their distribution to the core of the Cerrado biome in central Brazil (Silva & Bates 2002) (Appendix S1).

We obtained occurrence data across the distribution range of the previously mentioned species using the following tools: (i) the open access platform Global Biodiversity Information Facility (<http://gbif.org/>), which provides georeferenced data on biodiversity; (ii) the SpeciesLink platform (<http://splink.cria.org.br/>), which compiles information about the data from Brazilian scientific collections; (iii) the Xeno-Canto platform, which compiles bird sounds data (<http://xeno-canto.org/>); and (iv) a literature review. We used only georeferenced data or information that provided a specific description of the locality (e.g. cities or protected areas). In cases where the occurrences were not georeferenced but the information adequately described the location of a point, we used maps from Google Earth to detect the most likely occurrence of the species (i.e. vegetation types and distance to urban centres). Because this type of database may have inaccurate coordinates, we compared all occurrence points for a particular species and filtered according to specialists' maps obtained from the Birdlife platform (<http://birdlife.org.br/>; Appendix S1).

Ecological niche modelling

Potential distribution maps were estimated individually for each species and analysed according to the breadth of the species distribution. All species were modelled in three different time projections: Present – PRES (0 kyr BP) obtained through the Worldclim database (<http://worldclim.org/>), LGM (21 kyr BP) obtained from Paleoclimate Modelling Intercomparison Project Phase II using the CCSM general circulation model and the LIG (120 kyr BP) obtained from Otto-Bliesner *et al.* (2006) through the same general circulation model. We selected seven Worldclim bioclimatic variables and cropped them to span most of South America, considering the spatial limits of 58° Lat S to 12°30' Lat N – 32° to 83° Long W. The bioclimatic variables selected were annual mean temperature (Bio 1), mean diurnal range (Bio 2), maximum temperature of the warmest month (Bio 5), minimum temperature of the coldest month (Bio 6), annual precipitation (Bio 12), precipitation of the wettest month (Bio 13) and precipitation of the driest month (Bio 14), which are the same variables used by Hosner *et al.* (2014) to characterize the diversification of birds during the Pleistocene period (Appendix S2). All variables were represented in a spatial resolution of 2.5 arc min or approximately 5 × 5 km for each cell.

We used the maximum entropy algorithm through the software MAXENT (version 3.3.3; Phillips *et al.* 2006) to characterize the distribution of the climatic variables based on

presence-only data for each species. We implemented 10 bootstrap replicates using 90% of all occurrences obtained for each species to train the model. The remaining 10% of points were taken prior to the analysis to perform model evaluation with Partial ROC implemented in a Partial ROC programme (Barve 2008). The ENM maps presented for each species represent the mean of the 10 replicated runs. We used the 'multivariate environmental similarity surface' (MESS) across the models to evaluate how similar the projections were in comparison with the training of the model in the present, allowing us to establish 'Novel Climate Conditions'. The MESS analysis was conducted using the package *dismo* (Hijmans *et al.* 2015) in R (R Core Team 2013).

To identify the corridors, we used circuit theory, which takes into account all possible pathways to determine, in our case, the conductance between two points. To define the two points and calculate the conductance, we first defined the centre of mass inside the Cerrado using the suitability values for each species. The second point remained the centre of the Gran Savanna (in Venezuela) for all of the species, as the source and destination points. Analyses were performed using the package *gdistance* (van Etten 2011) in R (R Core Team 2013) and the open source software *CIRCUITSCAPE* (version 4; McRae *et al.* 2013).

Impacts of climate change in the community richness and composition

To analyse the temporal variation in community composition, we built maps for each time period that depicted the richness of all restricted-range Cerrado bird species by summing their individual ENMs. To this end, we converted the estimated distribution maps into binary values (1 for potential presence and 0 for absence) using the 10th percentile training presence value, which relies only on presence data and generally behaves better than other thresholds (Vale *et al.* 2014). To verify the tendency to decrease or increase the distribution over time, we compared the mean distribution size between present and LGM and between LGM and LIG using a paired *T*-test. This analysis was performed by using R software (R Core Team 2013).

We calculated the turnover of Cerrado endemic species for each pixel to evaluate how community composition changes through the time. Calculations were performed by using the equation proposed by Buisson *et al.* (2008):

$$\text{turnover} = 100 \times \frac{SG + SL}{SR + SG}$$

where SG is the number of restricted-species gain, SL is the number of restricted-species loss and SR is the total of restricted-species richness. The turnover values ranged from 0 to 100, with 0 indicating no turnover or change in community composition between temporal projections and 100 indicating complete change in the composition of the community in the area analysed (Buisson *et al.* 2008).

RESULTS

Environmental niche models and climatic suitability connections

According to partial ROC analysis, all models except that of *Suiriri islerorum* were capable of predicting the ecological niche during the present better than the random spectating (Appendix S3). Another two models (those for *Columbina cyanopis*, *Phyllomyias reiseri*) were also omitted from our analysis because they did not satisfactorily characterize the distribution of species, which could generate some uncertainty in the LGM/LIG projections. For the restricted-range species, we decided to analyse only the Cerrado region because this region was more reliable for the projections according to the MESS analysis (Appendix S4). The contributions of the variables did not differ greatly between the individual species models; however, the variable maximum temperature of warmest month (Bio 5) was more important to the restricted-range species than to the broadly distributed species, while the precipitation of the driest month (Bio 14) was more important to the restricted-range species (Appendix S2).

Twenty-one species showed greater similarity between present and LIG models than between any of these periods and the LGM, a pattern easily observed for *Machetornis rixosa* (Fig. 1). However, for eight species, there was more similarity between the present and LGM projections, as observed for *Polytmus guainumbi* (Fig. 1).

Models for broadly distributed species revealed overall high climatic suitability in the regions proposed by other authors as corridors between the savanna blocks in northern and southern South America (Silva 1997; figure in Silva & Bates 2002), showing larger areas with high environmental suitability during the LGM. This projection more frequently included high climatic suitability areas that could have formed corridors. This was the case for *Ammodramus hummeralis* and *Machetornis rixosa* (Appendix S5), although some exceptions were also noted, such as for *Polytmus guainumbi* and *Cypsnagra hirundinacea*. Both of those species presented a larger suitable area during the LIG than during the LGM (Appendix S5).

The high climatic suitability for *Cypsnagra hirundinacea* and *Neothraupis fasciata* suggested an Andean corridor occurring during LGM, which was the most consistent connection found between the savannas located in the southern and northern vegetation blocks (Appendices S5 and S6). The existence of this corridor was supported by 10 of 10 broadly distributed species (Fig. 2; Appendix S6), even though this corridor does not show the greatest conductance in all of the species.

Six of the 10 broadly distributed species had a significant increase in suitability along a potential Atlantic corridor connecting northeastern Brazilian populations

with those from the Amapá savannas (Appendix S5). Most of these corridors also connect to the savannas of Venezuela through the central corridors (Appendix S6). The discontinuous and continuous regions of high climatic suitability (0.6–0.8) recovered for nine of the 10 species suggest that a central Amazon stepping stone corridor of climatic suitability is a feasible scenario for the LIG and LGM (Appendices S5 and S6). This corridor is consistently the corridor with the highest conductance when all species are evaluated (Fig. 2). Finally, based on a visual inspection of our models, we suggest a new potential climate connection following the Madeira River. This corridor, although not shown by the conductance analysis, is observable in eight of the 10 broadly distributed species during LGM. Therefore, the Madeira corridor may have facilitated the movement of birds between the northern and southern South American savanna blocks (Appendix S5).

Impacts of climate change on community richness and composition

For restricted-range species, we observed a dynamic of grant sponsorions and expansions of the distribution area over time (Fig. 3). In 11 of the 15 analysed species, we observed a significant grant sponsorion of the area during the present in comparison with the LGM ($t = -3.77$, d.f. = 14, $P = 0.002$), followed by a expansion of the distribution for 12 of the 15 species during the LGM in comparison with LIG ($t = 4.2171$, d.f. = 14, $P < 0.001$) (Fig. 3). This expansion and grant sponsorion has also been observed for some species occurring in areas with low environmental suitability values (< 0.4), although they have higher suitability values in the same fields (> 0.6) for the LGM. One example of species following this pattern is *Alipiopsitta xanthops* (Fig. 4).

The richness map produced by the sum of the binary distribution maps showed a significant increase in appropriate areas in the peripheral region of the Brazilian Cerrado during the LGM, followed by a grant sponsorion of these areas in the present, and a similar grant sponsorion was shown by LIG projection (Fig. 5). However, even though both the LIG and the present show reduced species richness when compared with the LGM, an increase in the areas of environmental suitability in the southeastern portion of Brazil during the present can be noted (Fig. 5).

The turnover analysis showed strong compositional turnover values from the LIG to the LGM (69.5% SD = 26.63) and from the LGM to the present (61.2% SD = 23.71; Fig. 6), indicating a strong replacement of restricted-range species throughout the Quaternary climatic fluctuations.

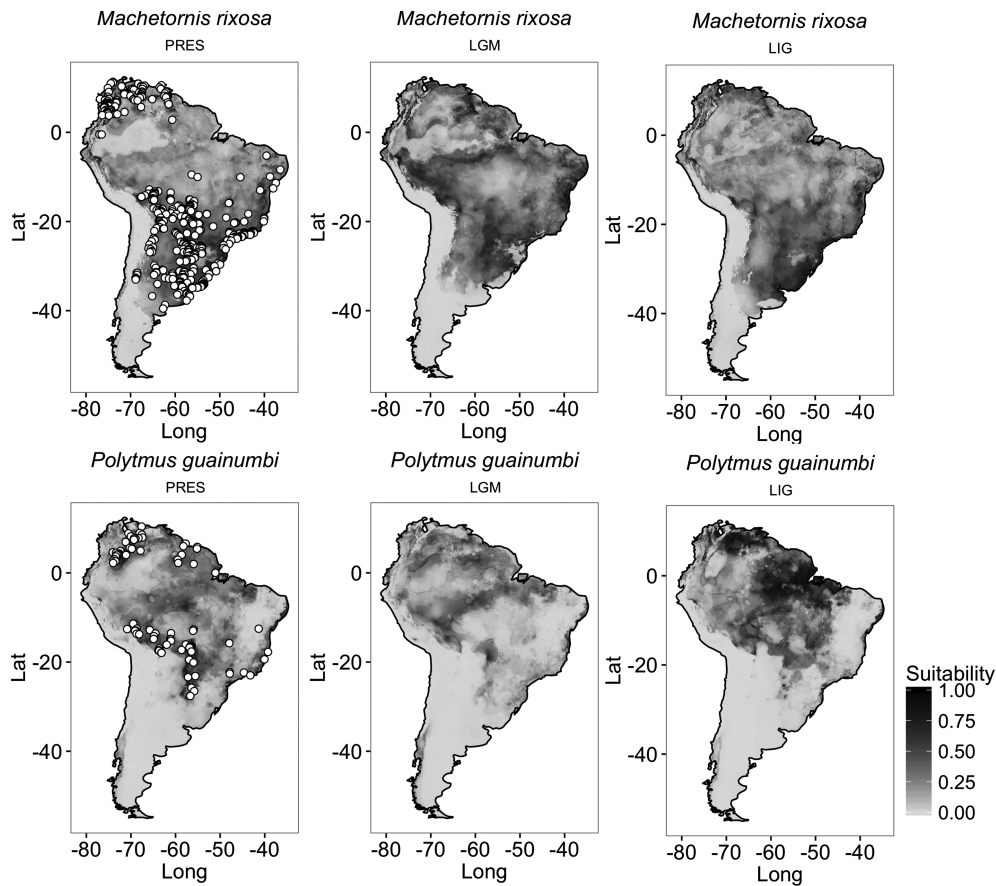


Fig. 1. Historic climatic suitability for *Machetornis rixosa* and *Polytmus guainumbi* across three time periods. Dots represent the occurrence data of the species. The light and dark gray indicate low and high environmental suitability, respectively.

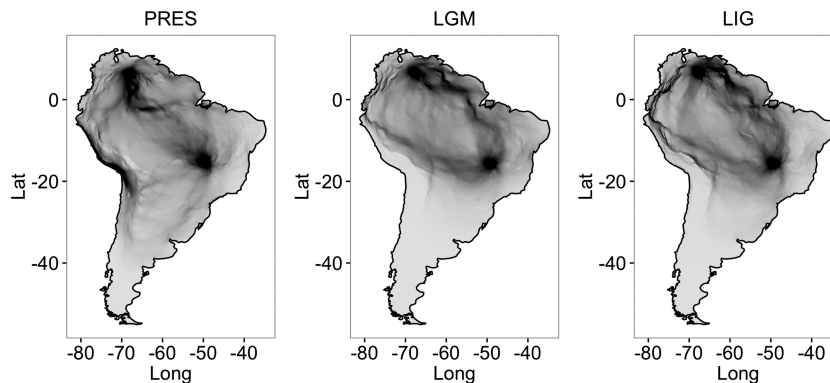


Fig. 2. Cumulative conductance between northern and southern South American savannas based on the sum of individual conductances for each broadly distributed species during the present and for two projections (present (PRES) – 0 ka, Last Glacial Maximum – 21 ka and Last Interglacial – 120 ka).

DISCUSSION

Climatic suitability connections between South American savannas

Ecological niche models and associated palaeoprojections offer high-resolution predictions about the potential past

distribution of organisms, allowing tests of evolutionary and biogeographic scenarios (Svenning *et al.* 2011). Using a niche modelling approach, we found indications of four possible regions of high habitat suitability for birds that could have allowed population connectivity between the savannas of northern and southern South America during the Quaternary climatic fluctuations. Three of

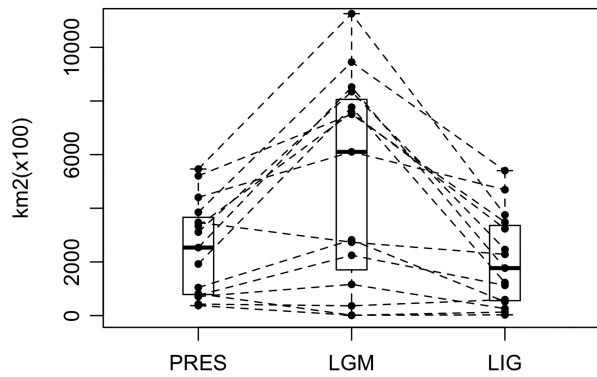


Fig. 3. Changes in distribution size in km² (×100) from present (PRES) to the Last Glacial Maximum (LGM) and from the LGM to the Last Interglacial (LIG).

them (Andean region, central Amazon and Atlantic coast) were proposed by previous work (Silva & Bates 2002), and we also suggest a novel connection route through the Madeira River.

The existence of such savanna connections is still controversial. The results obtained with different methodologies by other research groups indicate different scenarios during the LGM. There is a

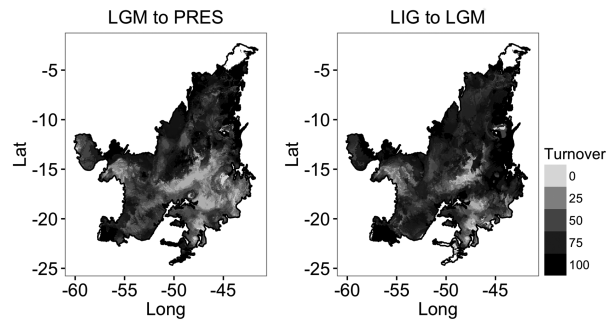


Fig. 6. Cerrado endemic species turnover as modelled in different periods. Turnover values (%) for the modelled restricted-range bird species in the Cerrado between temporal projections (Last Glacial Maximum (LGM) – 21 ka/Last Interglacial (LIG) – 120 ka; LGM – 21 ka/Present (PRES) – 0 ka). Dark colours indicate greater species turnover than light colours.

discussion about the potential expansion of open areas during the LGM, mainly contesting the existence of a connection in the Amazon central region (Silva & Bates 2002; Werneck *et al.* 2012b). In contrast, our work reinforces the existence of a central Amazon connection, which is also supported by studies that attribute this corridor to the presence of a belt

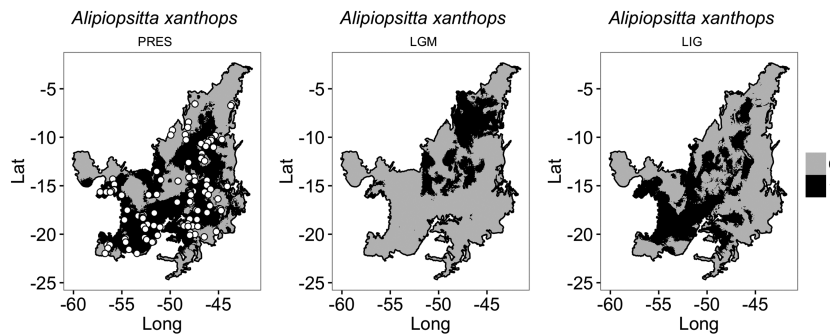


Fig. 4. Realized niche dynamics of *Alipiopsitta xanthops* across Quaternary climatic fluctuations. The gray and black colours indicate absence and presence of the species, respectively. Dots represent the occurrence data of the species. PRES, present; LGM, Last Glacial Maximum; LIG, Last Interglacial.

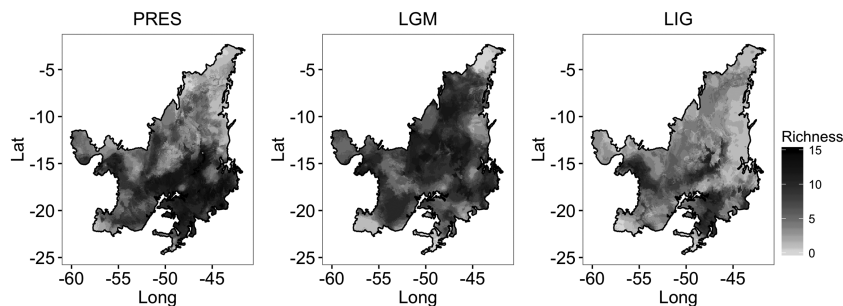


Fig. 5. Cerrado restricted-range species richness across three Quaternary projections (present (PRES) – 0 ka, Last Glacial Maximum (LGM) – 21 ka and Last Interglacial (LIG) – 120 ka) based on the sum of 18 individual restricted-range species distribution models. Dark colours indicate greater richness value than light colours.

of low precipitation in the central portion of the Amazon (Bonaccorso *et al.* 2006). Thus, forest retractions during the LGM may have left space for the persistence of open area species.

One commonly cited piece of evidence to support the hypothesis of a connection in the Amazon central region is the occurrence of disjunctive populations between savannah blocks (de Vivo & Carmignotto 2004). Nevertheless, our results show that during the last Quaternary fluctuation, since the LIG, some areas in this region were suitable for the existence of savanna bird species, such as *Neothraupis fasciata* and *Cypsnagra hirundinacea*.

For the first time, we present evidence that additional regions of suitable climate outside the previously proposed corridors (Silva 1995; Werneck *et al.* 2012b) could have acted as connections for some species. Our analysis revealed that climatically suitable areas for bird species associated with open areas might have occurred in association with open vegetation habitats along the Madeira River. Evidence from pollen records in the Katira region, located in Rondônia state (Brazil), shows that during the LGM, there was a rainfall reduction of approximately 60% compared with the present conditions (van der Hammen & Hooghiemstra 2000). This increased dryness coupled with the region's sedimentary geomorphology suggests the existence of typical components of the savannas in this location, supporting the occurrence of suitable areas for species associated with open areas (van der Hammen & Hooghiemstra 2000). Given the known importance of riparian areas in providing connectivity that supports biodiversity (Lees & Peres 2008), such a corridor may have had fundamental importance in the exchange of individuals between populations.

Therefore, we suggest that species likely explored various sets of corridors during the Quaternary climatic fluctuations and that routes outside the projection periods presented herein have existed. Our results support previous studies suggesting that some connections are not mutually exclusive in space and time but might have co-occurred (Werneck *et al.* 2012b). In some instances, a single species could potentially use more than one route at the same time, especially when considering that bird species associated with Cerrado vegetation have relatively large distribution ranges (Silva 1995), which would allow different geographical sources of dispersion.

Unlike the palaeomodelling proposed for the Cerrado (Werneck *et al.* 2012b), individual bird species maps suggest areas of increased environmental suitability during the LGM (e.g. *Synallaxis albescens*, *Sporophila nigricollis* and *Machetormis rixosa*). Population establishment, area occupation and somewhat free connections between northern and southern savannas were likely facilitated during this period. Conversely, a strong reduction in climatic suitability was observed during the

LIG, limiting the geographical distributions of restricted-range species. As the projections advanced towards the present, a clear delimitation between the savanna blocks (south and north) was established, resulting in the current disjunctive distribution pattern for some species.

Current occurrence in areas with low climatic suitability is relatively common and could be explained by the high environmental suitability in the recent past. This observation reinforces the need to study population genetics because climate change is known to impact historical demography, eventually leading to reductions in effective population sizes and causing local/regional extinctions (Dawson *et al.* 2011).

Impacts of climate change on the community richness and composition

Climate has been considered a major factor in bird distribution, metabolism and behaviour (Crick 2004). Recent climatic fluctuations greatly influenced the size and distribution of populations (Peterson *et al.* 2002), with major impacts on biodiversity patterns. In this work, we report a strong variation in the potential niche of birds restricted to the Cerrado since the LIG period to the present.

The open areas of South America had a complex temporal and spatial distribution pattern during the Quaternary climatic fluctuation. In general, evidence points to warmer and wet periods during interglacial times and cooler and drier periods during the glacial intervals (Werneck 2011). This climatic dynamism greatly influenced the distribution and diversity of Cerrado birds over time, potentially resulting in reduced richness during the LIG and a subsequent expansion of ranges and increased richness levels during the LGM, followed by a shift of richness to the southeast during the present.

Although such views are not supported by models constructed for the Cerrado biome (Werneck *et al.* 2012b), most of the species studied in this work have populations outside the current biome distribution. Populations found outside the optimum area of environmental suitability may be remnants of an expansion of the realized niche during the LGM, now maintaining their populations in a sub-optimal climate (Reed *et al.* 2010).

Even if certain populations can persist in a sub-optimum climate, it is expected that at some point, decreasing environmental suitability would lead the population to extinction (Thomas *et al.* 2004). Accordingly, profound changes in community composition during the climatic fluctuations can be seen in certain locations (Peterson *et al.* 2002). We found a high species turnover in the northern and northeastern Cerrado, which highlights how significant climate change can be a source of ecological disturbance (Peterson *et al.* 2002).

The richness map of restricted-range species indicates that during the LIG, some areas of the Cerrado potentially experienced a significant drop in the number of endemic bird species when compared with the present and especially the LGM. Additionally, higher turnover rates were found towards the LGM, especially in transitional areas (for instance, on the ecotone between the Cerrado and Amazonia). This pattern identifies a role for the influence of climate on the species finally established in the Cerrado and its transitional/ecotonal areas and deserves further study.

Given how climate change created constraints and barriers for species movements during the LIG (Gugger *et al.* 2013), we can assume that the same situation can occur again in the future. Reductions in environmental suitability can cause many consequences, such as population fragmentation and decreased genetic diversity.

Restricted-range species might be more strongly affected by climate change than more broadly distributed ones, either because they have smaller effective population sizes or lower overall genetic diversity (Morueta-Holme *et al.* 2010; Pauls *et al.* 2013). The maintenance of climatic refuges (Ashcroft 2010) and corridors between isolated populations could then represent a valid conservation strategy to maintain evolutionary processes within the South American savannas. Important areas for the conservation of birds of the Cerrado have already been suggested (Marini *et al.* 2009) in studies of the impact of climate change on birds. Suggestions include more proactive steps from the government and creation of new conservation areas, essential steps to minimizing the threats to species of the region.

In addition to the pressures arising from climate fluctuations, land use has intensified in the Cerrado region, especially with respect to agriculture, beef cattle and biofuel production (Klink & Machado 2005). These uses contribute to the decrease in natural areas, making the persistence of natural populations dubious (Pimm & Raven 2000). Intense conversion of natural areas into pastures, farm fields and other types of land use removes natural areas that serve as options to host species as they attempt to keep pace with climate change (Loarie *et al.* 2009) and may leave these species with nowhere to go. Such conditions impose huge challenges to planning conservation actions that would maintain the Cerrado biodiversity (Faleiro *et al.* 2013).

Understanding the effects of recent climate change on biogeographic scenarios and species distributions can help predict future distribution patterns in response to changing climates, supporting measures for conservation. Composite and individual maps of potential richness and species distribution across the Quaternary climatic fluctuations provided here can serve as a guideline for developing biogeographical and demographic hypotheses that can be tested with independent data, such as genetic approaches. Such studies will be

particularly important to understand the historical diversification of Cerrado endemic bird species (both broadly distributed and restricted range) and provide a further basis for their conservation.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web site:

Appendix S1. Bird species used in this study and the respective number of training and test points implemented in the ecological niche modeling analyses.

Appendix S2. Average relative contributions of each environmental variable for the groups of broadly distributed and restricted-range species. Values were obtained by averaging the relative contributions of each individual model.

Appendix S3. Values obtained from model performance test. AUC Ratio greater than 1 indicates that the model was better than expected for chance.

Appendix S4. Result of MESS analysis to a) Broadly-distributed species during Last Glacial Maximum-LGM, b) Last Interglacial-LIG, c) restricted-range species during LGM and, d) LIG.

Appendix S5. Species distribution models estimated for broadly distributed species during a) present, b) Last Glacial Maximum and c) Last Interglacial. Maps represent the pointwise means of the 10 output grids. White points in the models for the present represent the occurrence of the specie. The dotted line indicates the Madeira River corridor.

Appendix S6. Result of corridor analysis using CIRCUITSCAPE to broadly-distributed species during a) Present-PRES, b) Last Glacial Maximum-LGM and c) Last Interglacial-LIG.

Appendix S7. Species distribution models estimated for restricted-range distributed species during a) present, b) Last Glacial Maximum and c) Last Interglacial. Maps represent the pointwise means of the 10 output grids. White points in the models for the present represent the occurrence of the specie.