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ORIGINAL ARTICLE

Climatic stability in the Brazilian Cerrado: implications for biogeographical connections of South American savannas, species richness and conservation in a biodiversity hotspot

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ABSTRACT

Aim To investigate the historical distribution of the Cerrado across Quaternary climatic fluctuations and to generate historical stability maps to test: (1) whether the 'historical climate' stability hypothesis explains squamate reptile richness in the Cerrado; and (2) the hypothesis of Pleistocene connections between savannas located north and south of Amazonia.

Location The Cerrado, a savanna biome and a global biodiversity hotspot distributed mainly in central Brazil.

Methods We generated occurrence datasets from 1000 presence points randomly selected from the entire distribution of the Cerrado, as determined by two spatial definitions. We modelled the potential Cerrado distribution by implementing a maximum-entropy machine-learning algorithm across four time projections: current, mid-Holocene (6 ka), Last Glacial Maximum (LGM, 21 ka) and Last Interglacial (LIG, 120 ka). We generated historical stability maps (refugial areas) by overlapping presence/absence projections of all scenarios, and checked consistencies with qualitative comparisons with available fossil pollen records. We built a spatially explicit simultaneous autoregressive model to explore the relationship between current climate, climatic stability, and squamate species richness.

Results Models predicted the LGM and LIG as the periods of narrowest and widest Cerrado distributions, respectively, and were largely corroborated by palynological evidence. We found evidence for two savanna corridors (eastern coastal during the LIG, and Andean during the LGM) and predicted a large refugial area in the north-eastern Cerrado (Serra Geral de Goiás refugium). Variables related to climatic stability predicted squamate richness better than present climatic variables did.

Main conclusions Our results indicate that Bolivian savannas should be included within the Cerrado range and that the Cerrado's biogeographical counterparts are not Chaco and Caatinga but rather the disjunct savannas of the Guyana shield plateaus. Climatic stability is a good predictor of Cerrado squamate richness, and our stability maps could be used in future studies to test diversity patterns and genetic signatures of different taxonomic groups and as a higher-order landscape biodiversity surrogate for conservation planning.

Keywords

Cerrado, conservation biogeography, historical stability, Neotropical savanna connection, palaeodistribution modelling, Quaternary climatic fluctuations, South America, species richness, squamate reptiles.

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INTRODUCTION

Understanding biodiversity gradients across multiple spatial and temporal scales has been a major research focus of macroecology and biogeography, with several hypotheses proposed to explain species richness patterns and their implications (Wiens & Donoghue, 2004; Mittelbach *et al.*, 2007). Climate is often claimed to be a driver of evolutionary change and biodiversity (Erwin, 2009), and two contrasting hypotheses explicitly consider climate within a temporal context (Araújo *et al.*, 2008). The 'contemporary climate' hypothesis argues that the immediate availability of food resources limits population densities and, accordingly, the numbers of species that can coexist in a given region (Hawkins *et al.*, 2003). In contrast, the 'historical climate' stability hypothesis asserts that species are differentially excluded from areas that experience severe climate fluctuations, while persistence and speciation are favoured by climate stability over geological time-scales (Jablonski *et al.*, 2006). Under the latter hypothesis, historically stable areas are predicted to enclose higher species diversity and endemism (Graham *et al.*, 2006), and also higher intraspecific genetic diversity (Hewitt, 2004) when compared to unstable regions. Despite these predictions, few studies have provided a direct link between historical climate change and species richness, endemism or genetic diversity (Araújo *et al.*, 2008; Carnaval & Moritz, 2008).

Palaeodistribution modelling provides a method to produce spatially explicit models of landscape dynamics over recent time-scales (e.g. late Pleistocene). Habitat stability has been demonstrated to be more important than current habitat in shaping spatial species richness for low-dispersal taxa of the Australian Wet Tropics (Graham *et al.*, 2006). In the Neotropics, palaeomodelling of the Atlantic Forest (Carnaval & Moritz, 2008) and of Seasonally Dry Tropical Forests (SDTFs) (Werneck *et al.*, 2011) has predicted areas of historical stability for these biomes.

The high species richness and taxonomic resolution of the Brazilian Cerrado palynological record provides a unique opportunity to investigate areas of climatic stability and their implications for biogeography and biodiversity. Knowledge of diversity patterns for selected faunal groups has accumulated quickly in the last decade, but comprehensive species-richness data have never been analysed under past climate scenarios. Here we test whether climatic stability is a good predictor of squamate reptile (Squamata) species richness in the Brazilian Cerrado by utilizing a large database on Cerrado squamate species distributions (Costa *et al.*, 2007; Nogueira *et al.*, 2011); this database is updated via constant study of voucher specimens and ongoing field surveys.

The Cerrado

The Cerrado is the second largest Neotropical biome and is an important biodiversity hotspot (Myers *et al.*, 2000). It is part of a 'diagonal of open formations' (Vanzolini, 1963) that divides two major rain forests: the Amazon to the north and Atlantic Forest to the south-east. Along this 'open diagonal', the Cerrado is bordered by Caatinga (one nuclear region of SDTFs) to the north-east and by Chaco to the south-west, and on a larger biogeographical scale it is part of a major South American savanna disjunction located north (Llanos, Gran Sabana, Roraima, Paru, Monte Alegre, Amapá and Marajó) and south (Cerrado) of the Amazon Forest.

Diversification times of Cerrado woody lineages span the late Miocene to Pliocene (9.8–0.4 million years ago, Ma), with most lineages being less than 4 Myr old (Simon *et al.*, 2009), a timing largely coincident with the worldwide expansion of C_4 grass-dominated savannas that took place from 8 to 3 Ma (Edwards *et al.*, 2010; Ratnam *et al.*, 2011). Following a large information gap (i.e. a lack of palaeorecords and Pleistocene reconstructions), palaeoenvironmental data resembling present-day Cerrado vegetation occurs only around seven thousand years ago (ka) in central Brazil and 10 ka in northern Brazil, suggesting a dynamic history for the biome (Ledru, 2002; Ledru *et al.*, 2006). A summary of Cerrado geomorphology, climatic and vegetation cycles, and biogeography can be found in Werneck (2011).

In the last few decades, over 50% of original Cerrado vegetation has been converted, and only 2.2% is strictly protected (Klink & Machado, 2005). Improved knowledge of the patterns of biodiversity distribution across the Cerrado biome is essential to identify critical areas for protection. If climatically stable areas are congruent with areas of high diversity, then an explicit spatial model can be used to aid Cerrado conservation strategies, and also to serve as a methodological example for other Neotropical biomes.

South American climatic fluctuations and savanna vegetation cycles

South American Quaternary climates have been spatially and temporally complex, with heterogeneous variation in temperature and precipitation. The Last Interglacial (LIG, *c.* 120 ka) was characterized by the warmest global surface temperatures in the past 250 kyr (*c.* 2 °C warmer globally and up to 5 °C warmer in the Arctic), higher summer insolation, prominent deglaciation, elevated sea levels, and forest expansion (Otto-Bliesner *et al.*, 2006). More recently, Late Glacial sedimentation records show marked asynchrony at various sites, particularly at the Last Glacial Maximum (LGM; *c.* 21 ka), probably caused by regional responses to global climate changes (Sifeddine *et al.*, 2003; Burbridge *et al.*, 2004), while mid-Holocene (*c.* 6 ka) evidence is more consistent across studies. Although the magnitude of cooling remains controversial (1° to *c.* 6 °C), surface temperatures in the LGM were globally cooler than they are today, while precipitation varied across South America (Bush & Silman, 2004).

The controversial 'Pleistocene refugia' hypothesis credited the Quaternary fluctuations as the driving force for speciation in the Neotropics, through successive cycles of vegetation expansion and contraction (Haffer, 1969). This hypothesis suggests that South American savannas reached their maximum extension into the Amazon Basin during the LGM, with major connections between northern and southern savanna blocks attributed to one of the following corridors: (1) along the eastern Andean slopes; (2) tracking a belt of lower precipitation across central Amazon; or (3) along the eastern Atlantic coast (Sarmiento, 1983; Webb, 1991; da Silva & Bates, 2002). However, the magnitude of the influence of Quaternary cycles on the diversification of the Neotropical biota is contested (Moritz *et al.*, 2000; Edwards *et al.*, 2010; Hoorn *et al.*, 2010).

Herein we model the potential distribution of the Cerrado biome and obtain historical stability maps (refugia) across Quaternary climatic fluctuations. This is the first time that climate modelling has been applied to South American biomes for dates as far back as the LIG. We check model consistency with vegetation types inferred from available palaeorecords and investigate Pleistocene connections between northern and southern savannas. Finally, we use a richness database for Cerrado squamates to test whether climatic stability is a good predictor of biodiversity in the Brazilian Cerrado, and discuss the implications of our results for conservation.

MATERIALS AND METHODS

Climatic modelling

We modelled the historical spatial range of the Cerrado based on two geographical definitions (Fig. 1). We used Brazil's official vegetation map, which estimates the distribution of vegetation types prior to recent human-driven deforestation (IBGE, 1998) to characterize our narrow spatial definition. This represents a conservative estimate of the Cerrado distribution, including its core continuous area, which is confined mainly to the central Brazilian Plateau and is dominated by typical Cerrado formations. The alternative broad spatial definition is especially relevant to the investigation of potential Pleistocene savanna connections and includes the core area, transition zones (ecotones) that border adjacent biomes, and disjunct savannas in the Guiana shield, the Amazon, the Llanos of Colombia and Venezuela, and the Bolivian Beni savannas, as geographically defined by Olson *et al.* (2001).

For each definition we modelled Cerrado distribution under four time projections: present (0 ka), mid-Holocene (6 ka), LGM (21 ka) and LIG (120 ka). Current climatic variables were downloaded from the WorldClim database at a 30″ spatial resolution (Hijmans *et al.*, 2005). Past climate data for the LIG were obtained from Otto-Bliesner *et al.* (2006), while for the LGM and mid-Holocene we used the ECHAM3 atmospheric General Circulation Model (GCM; DKRZ, 1992). No study has explicitly tested the influence of GCMs on palaeodistribution estimates. However, based on GCM variation described for other regions (Jiang *et al.*, 2011) we expect palaeodistribution outputs to be affected, especially in South America, where LGM aridity patterns were extremely heterogeneous (e.g. wetter Andean versus drier lowlands) and models tend to perform weakly (Vizy & Cook, 2007). Here we used ECHAM3, which has high resolution and general high-quality performances for the LGM and mid-Holocene (Lorenz *et al.*, 1996), to ensure comparability of our results with palaeomod-

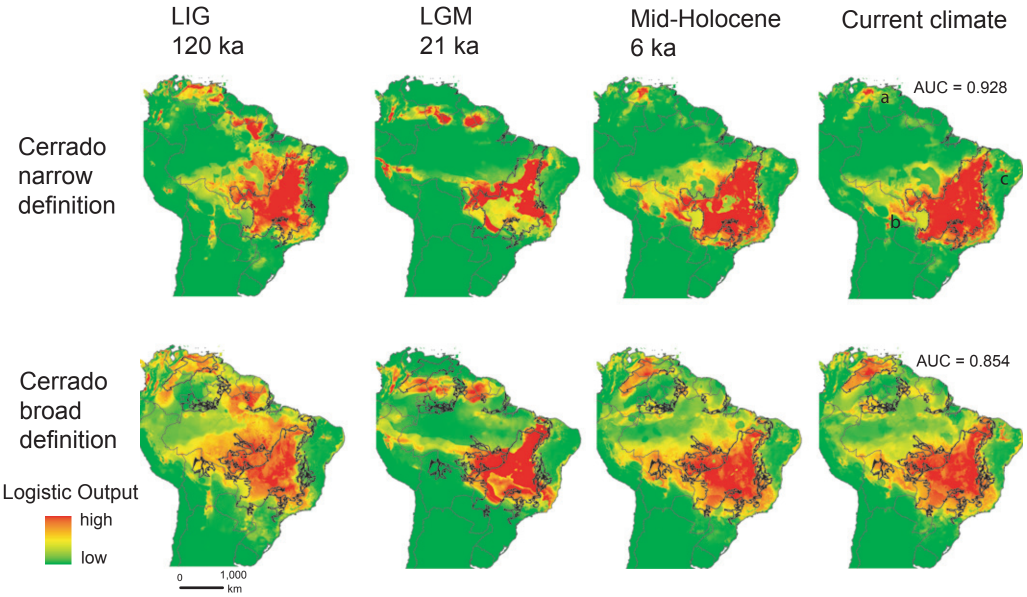

Figure 1 Modelled ranges of the Cerrado under narrow and broad definitions for the Last Interglacial (LIG, 120 ka), the Last Glacial Maximum (LGM, 21 ka), the mid-Holocene (6 ka), and current climatic scenarios. Warmer colours (red/yellow) of the logistic output correspond to regions with a higher probability of Cerrado occurrence, and the darker lines represent the limits of each spatial definition. AUC gives values for the area under the receiver operating characteristic curve, an indicator of model performance. Letters denote: a, Venezuelan savannas; b, Bolivian Beni savannas; and c, Chapada do Araripe region.

elling studies for other Neotropical biomes (Carnaval & Moritz, 2008; Werneck *et al.*, 2011).

Bioclimatic layers were cropped to span from 12°47′ N to 34°46′ S and from 78°31′ W to 35°00′ W, a larger spatial range than the estimated Cerrado distribution. To avoid use of redundant variables, we built a correlation matrix using ArcGIS 9.3 (ESRI, Redlands, CA), and retained only strongly correlated variables ($r > 0.9$) based on their biological relevance (Rissler & Apodaca, 2007). Ultimately, we selected nine environmental variables from the original 19 (WorldClim database), plus elevation (see Table S1, Appendix S1, in Supporting Information).

To visualize how the GCMs simulated South American palaeoclimates we used ArcGIS to subtract values of two representative climatic variables for temperature and precipitation/humidity [the mean temperature of the warmest quarter (Bio10) and the precipitation of the driest month (Bio14)] for each cell in each palaeomodel, against present climate values. This subtraction gives a new raster grid where positive values indicate a past climate that was hotter/wetter, and negative values indicate a past climate that was colder/drier than present climate (Fig. 2). Overall, the LIG was modelled as 0.5–2 °C warmer in the Cerrado region and slightly drier than present; the LGM was modelled as 1–3.5 °C colder (but with some slightly warmer Andean regions) and drier than present; and the mid-Holocene climate within the Cerrado range was modelled as overall close to present-day conditions (Fig. 2). Note that these differences refer to two representative variables (Bio10 and Bio14) and that the magnitude of cooling or drying was possibly higher for other variables [e.g. mean temperature of coldest quarter (Bio11) and precipitation of driest quarter (Bio17), Table S1].

To model potential distributions, we used the maximum-entropy machine-learning algorithm implemented in Maxent 3.3.2 (Phillips & Dudík, 2008) and adopted protocols similar to those used in recent studies for other Neotropical biomes (Carnaval & Moritz, 2008; Werneck *et al.*, 2011). The occurrence datasets were generated from 1000 presence points randomly selected from the entire distribution of the Cerrado, as determined by the two spatial definitions. We trained models based on the set of current selected bioclimatic variables (750 training and 250 testing records), and projected

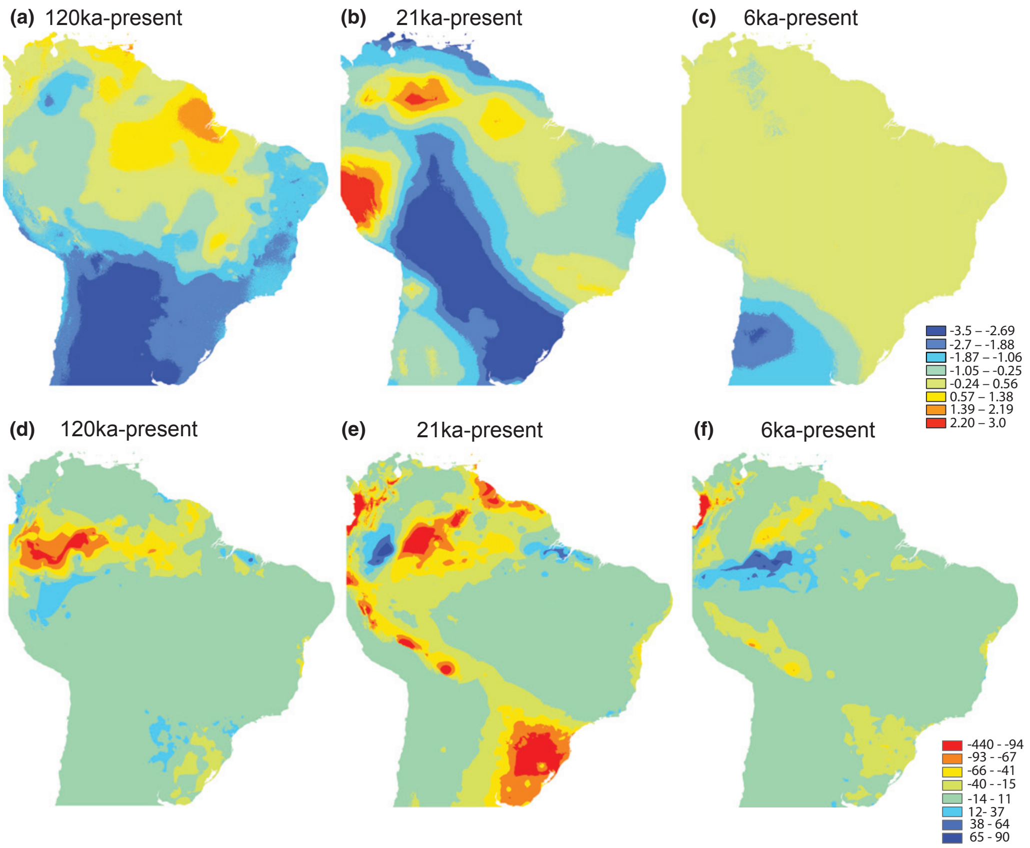

Figure 2 Spatial distributions of the differences between current temperatures and (a) Last Interglacial (LIG, 120 ka); (b) Last Glacial Maximum (LGM, 21 ka); and (c) mid-Holocene (6 ka) temperatures (in °C), as represented by the variable Bio10 (mean temperature of the warmest quarter); and between current precipitation levels and (d) LIG; (e) LGM; and (f) mid-Holocene precipitation (in mm), as represented by the variable Bio14 (precipitation of the driest month). Positive values indicate regions where the past climate was hotter or had higher precipitation (wetter) than the present climate, while negative values represent areas where the past climate was colder or had lower precipitation (drier) than the present climate.

these onto various time periods. To identify refugia (historically stable areas where the Cerrado has potentially occurred since the LIG), we converted the continuous outputs into presence/absence maps by selecting threshold values at which sensitivity (proportion of true positive predictions versus number of actual positives) is equal to specificity (proportion of true negative predictions versus number of actual negatives), and then overlapped the four presence/absence projections for each spatial definition.

Model evaluation and test

To statistically evaluate model performance, we used the area under the curve (AUC) of the receiver operating characteristic (ROC) plot, which is designed to evaluate the specificity (absence of commission error) and sensitivity (absence of omission error) of a diagnostic test (Fielding & Bell, 1997). The AUC provides a threshold-independent measure of model performance as compared to null expectations: an AUC of 0.50 indicates model performance no better than random, while higher AUC values indicate better models (Hanley & McNeil, 1982).

We also independently validated our models by qualitatively comparing the predictions under the more conservative (narrow) definition with vegetation types inferred from available palaeoenvironmental records (fossil pollen and sedimentology) located within the current Cerrado, predicted ranges, and sites near its distributional boundaries, but excluded sites located at the core of other biomes.

Comparisons with patterns of squamate species richness: statistical analyses

We used the historical stability surface to test whether predicted areas of stability have higher squamate species richness. To describe the explanatory power of current climate and climatic stability on squamate species richness, we built a spatially explicit simultaneous autoregressive (SAR) model, which allows for estimation of P-values after the contribution of spatial autocorrelation is removed.

We used Cerrado squamate richness data (Costa *et al.*, 2007), and from the same locality points we extracted values of current and past climate variables (Table S1). To characterize climatic stability at sample localities, we computed the coefficient of variation (CV) for each bioclimatic variable through various climate scenarios (0, 6, 21 and 120 ka), and then used a principal components analysis (PCA) to reduce the number of variables. Scores on the first three components (80% of total variation) mostly represented negative correlations and were used as a measure of climate stability in the SAR model (Appendix S2, Table S2). We performed a PCA on current variables for the same reason, and used scores on the first three components (85% of total variation) as a measure of current climate in the SAR model (Table S2). We also created a new variable (*Refugia*), using the average of MAXENT logistic output (which varies between 0 and 1 and represents the conditional probability of occurrence) for all scenarios. Therefore, higher values of the *Refugia* variable represent areas with a high probability of Cerrado occurrence across the timescale considered.

To account for spatial autocorrelation in the partial regression approach we used spatial filters obtained by principal coordinates neighbour matrices (PCNM), a method that partitions variation explained by the full model between spatial structure and environmental components (present climate and climatic stability), and that works well at different spatial scales (Borcard *et al.*, 2004). The best set of available filters was automatically selected based on their correlation with the response variable. To investigate whether our regression models successfully handled spatial autocorrelation, we built spatial correlograms to examine the residual distribution of Moran's I index (Diniz-Filho *et al.*, 2003). We also performed an ANOVA to test for significant differences of mean squamate richness between refugia and non-refugia.

Extraction of bioclimatic variable values for the regression points was performed in ARCGIS. PCA and ANOVA analyses were performed in R 2.11.1 (R Development Core Team, 2010). The SAR model and partial regression approaches were implemented using SAM – Spatial Analysis in Macroecology 3.1 (Rangel *et al.*, 2010).

RESULTS

Current and Quaternary distribution modelling

Predicted Cerrado distributions under current climatic conditions differed slightly between the two spatial definitions, especially at transition zones and in Amazonian savannas (Fig. 1). A few regions covered by Cerrado vegetation but not considered part of its core area, such as the Venezuelan and Bolivian Beni savannas and Chapada do Araripe (a plateau within Caatinga), were predicted as high-probability Cerrado areas even in the narrow definition (Fig. 1, letters a, b and c on current climate map). Based on AUC values, the narrow-definition model achieved better performance (Fig. 1), which may reflect a known bias in the AUC approach of a tendency to achieve higher values for more restricted-range models (McPherson *et al.*, 2004). Alternatively, operational difficulties in adequately mapping transition areas and contact zones on continental-scale vegetation maps could lead to uncertainty in Cerrado delimitation (Lopes, 2008; Nogueira *et al.*, 2011). In all models, very few areas of predicted Cerrado occurrence were mapped within the Caatinga and Chaco biomes, despite the geographic proximity of the Cerrado to these biomes.

The mid-Holocene and current predictions did not differ substantially, under both spatial definitions. The narrow-definition mid-Holocene model predicted a large portion of the central-western Cerrado core area to be unsuitable (Fig. 1). The LGM predictions under both spatial definitions showed a restricted distribution of favourable climates in the east of the Cerrado core region, while most of the southern portion was predicted to have less suitable climates. LGM models predicted favourable climates in northern Amazonia, where savannas are more widespread (especially in southern Venezuela and at the Guyana–Suriname border, Fig. 1). LIG models were similar in both spatial definitions and suggest widely distributed favourable climates in the Cerrado core, Amazon savannas, and northern transition zones. Both definitions also showed evidence for eastern coastal LIG connections between southern and northern open areas (Fig. 1).

Palaeoecological validation

Palaeoenvironmental data were available from 17 localities for the mid-Holocene and from seven localities for the LGM (Appendix S3, Table S4, Fig. S1), but no records were available for the LIG. Sedimentation gaps at several sites during the LGM indicate severe drying of core sites (Appendix S3, Table S4). Cerrado palaeomodels were mostly congruent with palynological records, either by total validation (palaeomodels and records suggest the occurrence of Cerrado in a given area) or by partial support (palynological record suggest a non-Cerrado vegetation type in an area located out of the predicted occurrence, e.g. LCH and LBV for mid-Holocene predictions; Appendix S3, Table S5). However, in a few cases the pollen record indicated Cerrado occurrence but palaeomodels indicated the area to be unsuitable (sites CAL and Colombian Llanos Orientales during the mid-Holocene and site LCH during the LGM). Alternatively, palaeomodels indicated Cerrado occurrence at some sites where palaeorecords indicated a different vegetation, for example at SAL during the mid-Holocene (Appendix S3, Fig. S1, Tables S5 & S6).

Historical climatic stability

Different Cerrado definitions provided different estimations of stable regions (i.e. refugia; dark colours in Fig. 3). The broad definition identified relatively widespread refugia mostly in the central Cerrado, characterized by a large continuous portion of stable climate with modest internal variation (Fig. 3). However, there was a narrow north–south disjunction, and there were scattered smaller refugia near the western and eastern limits of the Cerrado, at the Beni savannas and in the Espinhaço range. Stable areas were also predicted to occur in the north-eastern part of the biome and in the Cerrado/Amazonia transition areas in the state of Mato Grosso, while the south-western portion of the biome was predicted to be historically unstable, except for scattered areas coincident with the Maracaju and Roncador plateaus (Fig. 3). Some areas north of the Amazon were predicted to be relatively stable, but not across all four models (Fig. 3).

The narrow-definition models predicted much more spatial variation in refugia and different levels of stability (Fig. 3). A single large predicted refugium was predicted where all four

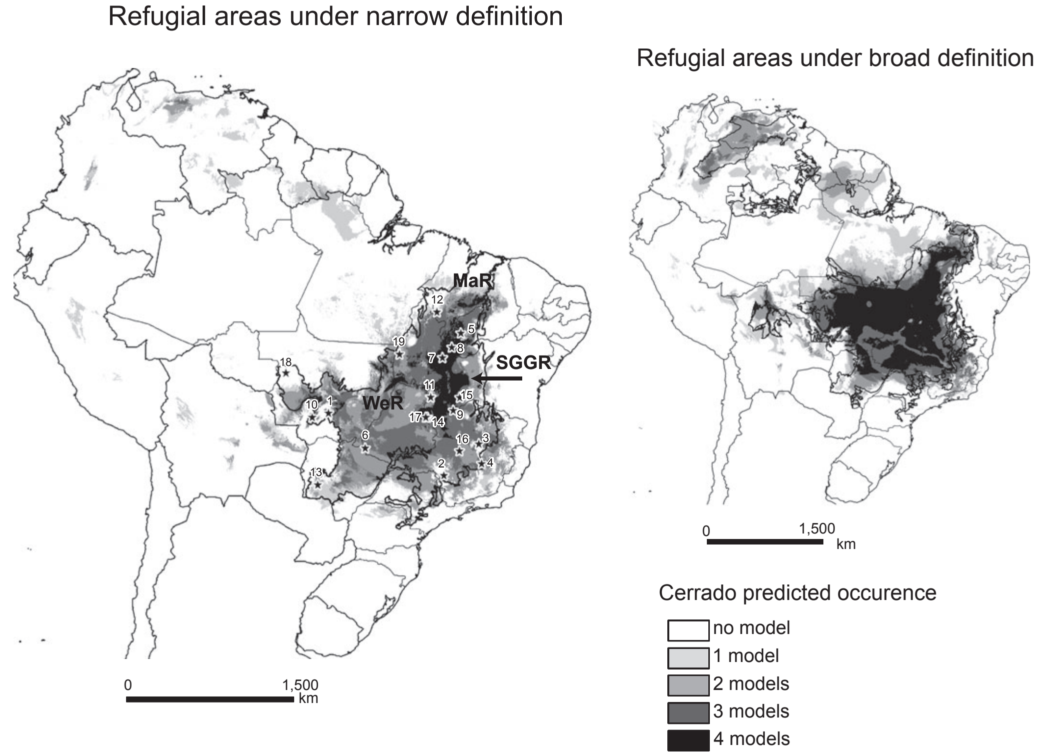

Figure 3 Cerrado historical stability surfaces obtained by overlapping across predicted logistic outputs under current, 6 ka, 21 ka and 120 ka climatic scenarios, and under narrow and broad geographical definitions. Numbers correspond to the established Brazilian protected areas (integral category) as detailed in Table 1, and the large black area identified by the arrow is the Serra Geral de Goiás refugium (SGGR); smaller refugia are identified as the Maranhão (MaR) and West (WeR) refugia.

models overlap, extending south–north in the north-eastern portion of the Cerrado (the Serra Geral de Goiás refugium, SGGR). This is largely coincident with the Serra Geral de Goiás Plateau, an arenitic (sandstone) tableland located in a geologically complex region that is both a natural and a political boundary between Goiás, Tocantins and Bahia states, where several headwaters originate (Cole, 1986). Some other scattered refugia were predicted in the extreme north-eastern distribution of the biome, in the state of Maranhão (Maranhão refugium, MaR) and to the west at the junction of the states of Goiás, Tocantins and Mato Grosso (West refugia, WeR; Fig. 3).

Refugia and species richness

The SAR model showed that both current climate and climatic stability variables contribute to the explanation of present-day patterns of squamate richness in the Cerrado, after successful removal of most of the spatial autocorrelation in regression residuals. The full model explained 68% of the variation ($F = 34.68$; $P < 0.001$; $r^2 = 0.68$). Of the total variation, 57% was explained by environmental variables alone, with the remainder being explained by spatial structure. All variables except PC3 for climate stability have significant standardized regression slopes (Appendix S2, Table S3). The variable *Refugia* has the largest standardized regression coefficient (Appendix S2, Table S3).

The partial regression approach using PCNM filters to account for spatial structure achieved similar results to the SAR model, with 67% of the total variation explained by the full model ($F = 33.27$; $P < 0.001$; $r^2 = 0.67$). Current climate alone explained 19% of the total variation, spatial structure alone explained 22%, and climate stability (refugia) alone explained the greatest partition of the total variation, 47%. The spatial correlogram based on Moran's I coefficient showed that the regression model with PCNM filters successfully removed most of the spatial autocorrelation in regression residuals (not shown). Localities from refugial areas (stable across all four models) had significantly higher squamate richness than non-refugial localities (ANOVA, refugial richness = 51.56, SD = 17.89, $n = 65$; non-refugial richness = 44.66, SD = 22.04, $n = 96$; $F = 4.47$, $P = 0.03$).

DISCUSSION

Distribution modelling and palaeoecological validation

Cerrado distribution models showed good fit (high AUC values), and general concordance with other Neotropical biome Quaternary models and with palynological records. Indeed, our models complement Atlantic Forest (Carnaval & Moritz, 2008) and SDTF (Werneck *et al.*, 2011) palaeomodels in not predicting Cerrado occurrence in areas covered by these biomes. Our models extrapolated potential distributions beyond presence-data surfaces by predicting occurrence in areas outside the current Cerrado core but that in fact harbour Cerrado vegetation (e.g. Venezuelan and Bolivian savannas, Fig. 1). This result reflects the well-known reality that the true extent of Bolivian savannas has been poorly mapped (Larrea-Alcázar *et al.*, 2010). Our models could direct on-site mapping efforts to overcome this limitation and eventually incorporate Bolivian savannas into Cerrado limits.

Despite our confidence in the models' consistency, we acknowledge some limitations. Climate can only partially explain distribution patterns, and on its own does not explain vegetation composition. For example, several Cerrado vegetation types may occur side-by-side under the same climatic conditions but differ widely in floristic composition and structure. At these local scales other variables (edaphic factors, microtopography, drainage, fire dynamics, etc.) may be important, while geomorphological and topographical features are likely to dominate at broader scales, and to interact synergistically with climate. However, there are no available georeferenced palaeolayers for these variables, and some (e.g. soils and geomorphic surfaces) experienced only minor changes during the Quaternary (Motta *et al.*, 2002). Despite these drawbacks, at a large scale we are confident in the broad outline of our models.

Five of the 24 palaeoecological records compiled were inconsistent with our palaeomodels. Marked differences in the climate evolution timing within Cerrado geographical zones (central Brazil versus northern and central-western sites) proposed by Ratter *et al.* (1996) could explain the differences between our predictions and CAL and LCH records (Ledru *et al.*, 2006), which are located at the northern and western limits of the Cerrado, respectively. The use of the narrow definition for validation explains the disagreement for the Colombian Llanos Orientales records; with the broad definition they are consistent. Conversely, SAL is located within an area of predicted Cerrado occurrence at 6 ka, but pollen records indicate the presence of *Araucaria* forest (Ledru, 1993; Ledru *et al.*, 1996). However, Salgado-Labouriau (1997) argue that data from SAL are not sufficient to support the occurrence of *Araucaria* forest in central Brazil; instead, they suggest the presence of a mixed forest if the temperature was 2–3 °C lower, which is likely considering the high elevation and the current mixed vegetation (Table S4). Palynological data may be limited by the use of localized sampling points and the depiction of the vegetation of a relatively small area, representing an example of the common mismatch between local and regional scales in biogeography (de Candolle, 1820). In other words, the local dominance of forest pollen in riparian areas does not preclude the occurrence of dominant savannas at broader scales.

At each period, predicted Cerrado distributions under the two geographical definitions were generally similar. Looking back in time, the warmer and slightly drier LIG probably favoured a more widely distributed Cerrado, including areas in northern Amazonia and potential eastern coastal connection routes. From the LIG to the LGM the Cerrado retracted, reaching its minimum extent in this period, which is consistent with the lack of Cerrado-indicator taxa at some palynological sites (Ledru, 2002). However, savanna regions located north of

Amazonia remained suitable under both scenarios (Fig. 1), with Cerrado probably prevalent but isolated from the core region. At the LGM, a potential connection through a narrow Andean corridor was also predicted under the broad definition. From the LGM to the mid-Holocene the Cerrado expanded following an increase of moisture, and then experienced only minor changes until reaching its current distribution. This scenario is in accord with studies that often describe the mid-Holocene as a period of high sedimentation of Cerrado taxa pollen. The biome finally became established in this period, and its present-day distribution stabilized around 6 ka (Ledru, 2002).

A similar LGM retraction followed by a mid-Holocene expansion phase was also described for the SDTFs (Werneck *et al.*, 2011), possibly because LGM conditions were too dry and too cold to maintain larger areas of either biome established earlier at southern latitudes (Behling & Lichte, 1997; Ledru *et al.*, 1998). Consequently, Cerrado extension was restricted to the north-eastern part of the core region, back to the area of long-term stability (SGGR), and to the northern Amazonian isolates. Peripheral depressions were probably dominated by xeric-adapted vegetation, derived either from SDTF expansions or from colder/drier southern biomes, such as Pampa and Monte (Werneck *et al.*, 2011). This scenario matches with current squamate distribution patterns in the Cerrado, where interchange is more evident along peripheral depressions, while endemism is concentrated on plateaus (Nogueira *et al.*, 2011).

Biogeography and Neotropical savanna connections

Our results do not support the occurrence of significant portions of Cerrado in central Amazonia or large corridors during the LGM, contradicting the Pleistocene refugia hypothesis. However, we found evidence for two of the three previously proposed savanna corridors. Individual corridors are not mutually exclusive, and may have prevailed under different climatic conditions and periods. Suitable areas, possibly transitory and discontinuous (given low logistic probabilities), may have tenuously connected central Brazil to the central Andes during the LGM. Examples of shared fauna include lizards of the genus *Stenocercus*, widespread in the Andes but with disjunct and rare populations at high elevations in central Brazil, including the SGGR (Nogueira & Rodrigues, 2006). Andean connections were not evident in other time frames though, which support the existence of coastal connections, especially during the LIG (Fig. 1). da Silva & Bates (2002) found evidence for the same two corridors based on current ranges of savanna birds. A central Amazonian corridor is thus unlikely, and the most recent biotic connections between northern Amazon savannas and the Cerrado probably occurred along the Atlantic coast (Ávila-Pires, 1995; da Silva & Bates, 2002).

Despite their adjacent distributions, Caatinga and Chaco areas were predicted as being unsuitable for Cerrado occurrence in all models (Chapada do Araripe is an exception within Caatinga), contradicting studies that treat the open diagonal biomes as a single biogeographical unit or area of endemism (Porzecanski & Cracraft, 2005; Morrone, 2006). This sharp delimitation between biomes on the basis of climatic and geomorphological grounds indicates that these classifications are artificial and that the open diagonal is a composite area, defined by superficial affinities (e.g. shared species as a result of dispersal). Particular geomorphological events that differentially shaped the origin and diversification of the open diagonal biomes and associated biota (e.g. global savanna expansion affecting the Cerrado, stronger effects of marine introgressions in the Chaco, regional geological surface influences in the Caatinga) probably account for their biogeographical distinctiveness (Werneck, 2011). It is, therefore, plausible that the biogeographical counterparts to the Cerrado are not the Chaco and Caatinga, but isolated and disjunct savannas located on the Guyana shield (Llanos and Gran Sabana).

Historical climatic stability and species richness

The predicted areas of historical stability (SGGR, MaR, WeR) were probably important refugia for regional biotas during Quaternary climatic and vegetation fluctuations. Ab' Sáber (1983) postulated that the higher plateaus in central and north-eastern Cerrado (e.g. Serra Geral de Goiás, Mesa Plateaus) were probably disturbed by Caatinga expansions and, in contrast, the southern and western plateaus (e.g. Upper Paraná basin, Brasília region, Chapada dos Veadeiros) probably remained stable and formed a single large Cerrado refugium during the late Pleistocene. Our results suggest that Ab' Sáber's (1983) prediction was approximately accurate in associating stability with plateaus, but inaccurate in considering one of the most extensive plateaus and our largest refugium (SGGR) as having been invaded by Caatinga. Caatinga floristic elements currently found in the SGGR probably result from recent dispersal. Furthermore, Ab' Sáber (1983) focused only on the late Pleistocene/early Holocene transition, while our results indicate longer-term stability.

Climatic stability is a better predictor of squamate species richness in the Brazilian Cerrado than current climate, as anticipated by the historical climate stability hypothesis, recently invoked to explain the biodiversity patterns of multiple taxa in temperate regions (Araújo *et al.*, 2008), the Australian Wet Tropics (Graham *et al.*, 2006), and also at global scales (Jansson, 2003). Narrow-range and/or low-vagility species were potentially more affected by Quaternary climatic fluctuations than wide-range and/or high-vagility species, given the limited ability of the former to track climate change (Jansson, 2003; Graham *et al.*, 2006).

Phylogeographical studies can provide independent tests of our historical stability maps because stable refugia and recently colonized non-stable areas are expected to have very distinct genetic signatures (Carnaval & Moritz, 2008). Owing to the greater variation and smaller predictions of refugia, the narrow-definition map seems more appropriate for these purposes. Despite not explicitly testing our stability model, some studies support it. A higher genetic diversity for the 'vinhático' tree (*Plathymenia reticulata*) was detected in the central region of Cerrado near our proposed SGGR, while southern populations showed low diversity and signals of recent range expansion from central sources (Novaes *et al.*, 2010). Ramos *et al.* (2007) also reported a similar pattern for the 'jatobá-do-cerrado' tree (*Hymenaea stigonocarpa*). Such congruence does not imply that most diversification of the Cerrado biota took place exclusively during the Quaternary, as several groups have older divergence times (Almeida *et al.*, 2007; Werneck *et al.*, 2009), but provides evidence that Quaternary climatic fluctuations could have been strong enough to affect genetic diversification and community dynamics at shallow time-scales (Jansson, 2003).

Conservation implications

Our data imply that refugia can potentially function as surrogates ('indicator areas') to predict biodiversity patterns at different scales relevant for conservation. However, the use and choice of biodiversity surrogates is not free of controversy (Lewandowski *et al.*, 2010), and the inclusion of other variables (e.g. taxonomy, vegetational and environmental heterogeneity) is preferred (Margules & Pressey, 2000). Here we propose that environmental stability (refugia) be considered as a higher-order landscape biodiversity surrogate, which should be incorporated into systematic conservation planning, together with high-quality, detailed data on species endemism and diversity.

Climatic models for the LIG are typically used as proxies to anticipate the consequences of future climate change (Otto-Bliesner *et al.*, 2006). If LIG conditions mimic future global warming scenarios, the Cerrado could experience an expansion phase, considering that it reached its maximum potential extent during the LIG. Explicit vegetation dynamic models considering future global warming confirm this pattern, with the Cerrado predicted to expand over tropical forests, especially along the south-eastern margins of the Amazon Basin (Salazar *et al.*, 2007; Hirota *et al.*, 2010). However, no potential expansion could compensate for the extremely high current conversion rates for the Cerrado (Machado *et al.*, 2004). The patterns modelled herein span geological time-scales, allowing gradual evolution and range shifts, whereas scenarios of anthropogenic climate change are framed within decades, an extremely short time frame to accommodate evolutionary changes meaning that taxa that fail to adapt rapidly may risk extinction (Davis & Shaw, 2001).

The SGGR, which should receive high priority for conservation, largely overlaps with a region that is extremely threatened by ongoing massive deforestation. Fortunately, the two largest strictly protected Cerrado areas lie within the SGGR (nos. seven and eight; Fig. 3; Table 1). However, both were created very recently and are still poorly established, and the MaR and WeR refugia do not contain any protected areas. Additional efforts are crucial to achieve a satisfactory conservation network for the Cerrado, preferably including stable and unstable areas, and connections between them, and our maps constitute a useful aid for area selection and conservation strategies.

Table 1 Table showing protected areas from the strictest categories (IUCN categories I to III; or the 'integral protection' category from the Brazilian system, including PARNA, Parque Nacional; and EE, Estação Ecológica) that lie within the limits of the Cerrado narrow distribution as defined by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), last updated in October 2010. For geographical locations see Fig. 3.

ID	Name	Area (ha)	Creation year
1	PARNA da Chapada dos Guimarães	33,000	1989
2	PARNA da Serra da Canastra	200,000	1972
3	PARNA das Sempre Vivas	124,000	2002
4	PARNA da Serra do Cipó	31,639	1984
5	EE de Uruçuí-Una	135,000	1981
6	PARNA das Emas	132,642	1972
7	EE Serra Geral do Tocantins	716,306	2001
8	PARNA das Nascentes do Rio Parnaiba	729,814	2002
9	PARNA Grande Sertão Veredas	230,853	2004
10	EE Serra das Araras	28,700	1982
11	PARNA da Chapada dos Veadeiros	64,795	1981
12	PARNA da Chapada das Mesas	159,952	2005
13	PARNA da Serra da Bodoquena	76,481	2000
14	Reserva Biológica da Contagem	3460	2002
15	Refúgio da Vida Silvestre Veredas do Oeste Baiano	128,521	2002
16	EE de Pirapitinga	1090	1987
17	PARNA de Brasília	30,000	1961
18	EE de Iquê	200,000	1981
19	PARNA do Araguaia	555,518	1980

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix S1 Environmental variables used in the distribution modelling and relative contributions to the MAXENT model (Table S1).

Appendix S2 Principal components analysis results (Table S2) and simultaneous autoregressive (SAR) model results (Table S3).

Appendix S3 Comparisons between published palaeoenvironmental and sedimentology records (Table S4) and model predictions for Cerrado occurrence at 6 ka (Fig. S1, Table S5) and at 21 ka (Fig. S1, Table S6).

BIOSKETCH

Fernanda P. Werneck is a Brazilian PhD student at Brigham Young University with major interests in the evolutionary biology, biogeography, phylogeography and conservation genetics of the South American dry biomes, with an emphasis on associated reptiles. Approaches used include multi-locus statistical phylogeographic and coalescent-based methods coupled with distribution modelling for species delimitation and phylogenetic inference.

Author contributions: F.P.W., G.C.C. and C. N. conceived the ideas; F.P.W. and G. C.C. gathered and analysed the data; and F.P.W. prepared the figures and led the writing, with help from the other authors.

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