Received: 21 March 2017 | Revised: 9 August 2017 | Accepted: 16 August 2017

DOI: 10.1111/geb.12646

RESEARCH PAPER

WILEY Global Ecology and Biogeography A Journal of Macroecology

Vegetation cover of Brazil in the last 21 ka: New insights into the Amazonian refugia and Pleistocenic arc hypotheses

Daniel M. Arruda[1] | Carlos E. G. R. Schaefer[2] | Rúbia S. Fonseca[1] | Ricardo R. C. Solar[3] | Elpídio I. Fernandes-Filho[2]

[1]Departamento de Biologia Vegetal, Universidade Federal de Viçosa, Viçosa, Brazil

[2]Departamento de Solos, Universidade Federal de Viçosa, Viçosa, Brazil

[3]Departamento de Biologia Geral, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil

Correspondence
Daniel M. Arruda, Instituto de Ciências Agrárias, Universidade Federal de Minas Gerais, CEP: 39, 404-547 Montes Claros, Brazil.
Email: arruda.dm@hotmail.com

Funding information
CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior)

Editor: John Pandolfi

Abstract

Aim: The two main hypotheses about the Neotropical palaeovegetation, namely that of Amazonian refugia by Haffer and of the Pleistocene arc by Prado and Gibbs, are still constantly debated. We offer new insights on this debate using ecological niche modelling with combined climate–soil predictors to test both hypotheses, reconstruct the palaeovegetation of the Last Glacial Maximum (LGM; 21 ka) and Mid-Holocene (Mid-H; 6 ka) and indicate the configuration of refugia areas.

Location: Brazil.

Time period: Last 21 ka.

Major taxa studied: Biomes.

Methods: We modelled the environmental space of the 10 most representative biomes with the RandomForest classifier, using climate predictors from three atmospheric general circulation models (CCSM4, MPI-ESM-P and MIROC-ESM) and soil predictors, the same for the different situations. Based on the consensus among the models, we reconstructed the palaeovegetation cover for LGM and Mid-H and used fossil pollen sites to validate the reconstructions in a direct comparison.

Results: The climate in the past was cooler and wetter throughout most of the territory. The Amazon basin region was the most affected by climate change in the last 21 ka, with equatorial rain forest retracting to refugia areas, while the tropical rain forest (with climatic preferences similar to the Atlantic forest) expanded in the basin. In southern Brazil, the mixed forest (*Araucaria* forest) shifted to lower latitudes, while the grasslands expanded. In most biomes, the greatest changes occurred in the ecotonal zones, supported by pollen fossils.

Main conclusions: With regard to Haffer's hypothesis, the forests of the Amazonian lowlands retreated to refugia areas, while the colder and wetter climate of the basin created a favourable niche for another type of forest, instead of savanna. The advance of dry vegetation was restricted to ecotonal conditions, preventing the formation of a continuous Pleistocene arc, predicted by Prado and Gibbs's hypothesis.

KEYWORDS

Amazon forest, Atlantic forest, biogeography, cerrado savanna, climate change, ecological niche models, macroecology, palaeovegetation, refuge theory, vegetation dynamics

1 | INTRODUCTION

Studies focused on the cover of neotropical palaeovegetation have increased considerably over the past 50 years (Bueno et al., 2016; Colinvaux, De Oliveira, & Bush, 2000; Haffer, 1969; Prado & Gibbs, 1993). There is a consensus that cold and dry periods are favourable for seasonal biomes (e.g., deciduous forests, caatingas and savannas), whereas humid and warm periods favour moist forests. However, there is an intense debate about the Neotropical paleovegetation cover in the Last Glacial Maximum (LGM; 21–18 ka) and Mid-Holocene (Mid-H; 6 ka). This discussion is based on different methods, such as endemic species distribution (Haffer, 1969; Pennington, Prado, & Pendry, 2000; Prado & Gibbs, 1993), palynology (Colinvaux, De Oliveira, Moreno, Miller, & Bush, 1996; Haberle & Maslin, 1999; Ledru, Mourguiart, & Riccomini, 2009; Marchant et al., 2009), ecological niche models (Bueno et al., 2016; Carnaval & Moritz, 2008; Collevatti et al., 2013; Werneck, Costa, Colli, Prado, & Sites, 2011; Werneck, Nogueira, Colli, Sites, & Costa, 2012) and the dynamic global vegetation model (Harrison et al., 2010; Prentice, Harrison, & Bartlein, 2011), resulting in considerable controversy.

Based on the premise of a predominantly arid climate history of the LGM, Haffer (1969) proposed that Amazonian forest habitats remained as isolated enclaves, sufficiently warm and moist, embedded within a savanna matrix, which might have caused reproductive isolation and consequent speciation. This proposal triggered what is called the 'Amazonian refugia hypothesis', inspiring other assumptions on the vegetation dynamics with regard to climate change. Considering exclusively the same climatic premise for LGM, but focusing on connectivity of the seasonal biomes rather than speciation, Prado and Gibbs (1993) proposed the 'Pleistocenic arc hypothesis', which suggests the existence of a continuous arc of seasonal vegetation formations in the Neotropical region. According to this hypothesis, the current scattered distribution of populations in different seasonal habitats in Neotropics is the outcome of a past expansion of seasonal biomes during the dry and cold climate of the glacial past (see Pennington, Lavin, & Oliveira-Filho, 2009).

Several authors have supported one of these hypotheses and used the geographical distribution assumptions of Haffer (1969) or Prado and Gibbs (1993) as the most parsimonious explanation for their results (e.g., Carnaval & Moritz, 2008; Collevatti et al., 2013; Van der Hammen & Hooghiemstra, 2000). However, there is substantial disagreement, which has led many authors to question both hypotheses. The alternative argument is that the climate of the Amazon region prevented the expansion of seasonal biomes during the LGM and that moist forest was always predominant (Bush & De Oliveira, 2006; Colinvaux et al., 1996, 2000; Haberle & Maslin, 1999; Leite et al., 2016; Mayle & Power, 2008). Additionally, these authors assumed that the distribution of seasonal biomes was greatest in the Holocene, triggered by more recent climate conditions, rather than during the LGM (Werneck et al., 2011; Whitney et al., 2011).

Although there is a consensus on the cooler climate in the LGM, the rainfall pattern is still being discussed (Cheng et al., 2013; Sylvestre, 2009). Different proxies and climate models confirmed that the Amazon climate in the LGM was indeed complex throughout the basin, although generally wetter than today, in response to orbital forcings and the position of the Intertropical Convergence Zone (Baker et al., 2001; Sylvestre, 2009; Van Breukelen, Vonhof, Hellstrom, Wester, & Kroon, 2008). The complexity of rainfall in the Amazon basin has been associated with a quasi-dipole (seesaw effect) between the western Amazon and the eastern Amazon/northeast of Brazil during the austral summer (Cheng et al., 2013; Cruz et al., 2009). Therefore, the wetter condition may be decisive for the re-creation of a palaeovegetation cover distinct from the pioneer proposals.

The climate, the main underlying predictor, is important to determine standards for vegetation distribution on large scales (Harrison et al., 2010). Additionally, soil predictors have proved highly efficient in determining biomes or even communities (Arruda, Fernandes-Filho, Solar, & Schaefer, 2017). However, it is noteworthy that few models used soil properties for modelling frameworks (e.g., Arruda et al., 2017; Coudun & Gégout, 2007; Coudun, Gégout, Piedallu, & Rameau, 2006). The use of combined climate–soil predictors can improve the model accuracy and allow a more precise reconstruction of the spaces occupied by vegetation (Arruda et al., 2017).

Considering the recent proposals of a generally cooler and humid climate of the past, as well as the climate and soil preferences of the biomes, our main aim was to propose new insights into this debate, by testing the geographical distribution assumptions underlying the Amazonian refugia and Pleistocenic arc hypotheses from the perspective of ecological niche modelling. We expect that the configuration of the Brazilian palaeovegetation in the last 21 ka was not favourable for the expansion of seasonal biomes within or outside the Amazon basin. Along this line, we propose the reconstruction of the vegetation cover of Brazil during the LGM and Mid-H, and the identification of the potential refugia areas, defined as a multidimensional domain of environmental variables stable over time and space (Keppel et al., 2012).

2 | METHODS

2.1 | Climate–soil model

The data for constructing the model were obtained from a grid with 100-km^2 cells (approximate resolution of 0.1°) overlaid on the Vegetation Map of Brazil (1:5,000,000). In this way, independent sampling units (500 randomly sampled cells) were obtained for the 10 most representative biomes in Brazil. The following biomes were taken into account: equatorial rain forest, tropical rain forest, caatinga, white-sand vegetation, southern grasslands, deciduous forest, semi-deciduous forest, open ombrophilous forest, mixed subtropical forest and savanna. All transitional vegetation types were not considered. A description of the biomes is presented in Table 1, and more details about the environmental space of each biome were described by Arruda et al. (2017).

The soil variables were obtained from horizon A of 5,380 soil profiles analysed in different exploratory soil surveys in Brazil (Arruda et al., 2017), and the climate variables were extracted from Worldclim version 1.4 (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). The model predictors were selected on the basis of a previous training model,

TABLE 1 Description of Brazilian biomes used in the model, adapted from Arruda et al. (2017)

Biome	Description
Equatorial/tropical rain forest	Typically, high canopy (25–30 m) when in lowlands, rather stratified, abundant in epiphyte lianas; temperatures and rainfall are high, without a biologically dry period. The equatorial biome differs from the tropical in higher values of temperature seasonality, temperature of the coolest quarter and annual precipitation
Caatinga	Bush/woodland physiognomy, generally without grassy stratum; shallow and rocky substrate; biologically dry period > 8 months
White-sand vegetation	Varied physiognomy (from grassland to forests), with fine trees; restricted to the Amazon basin, occurrence on plain reliefs and wetlands; associated with sandy soils with high eluviation rates (Spodosols)
Southern grasslands	Grassland physiognomy, on plain and gently undulating topography, with typically high temperature ranges, with frosts in the winter and very hot summers
Deciduous forest	Forest physiognomy, little stratified; with a biologically dry period of 5–7 months; leaf deciduousness of the canopy of > 50%
Semi-deciduous forest	Forest physiognomy, stratified; biologically dry period of 3–4 months; leaf deciduousness of the canopy of 25–50%
Open ombrophilous forest	Forest physiognomy, clearly stratified; with many lianas, epiphytes, and bamboo and palm trees; biologically dry period of 2–3 months; low leaf deciduousness
Mixed forest	Forest physiognomy; stratified; with no biologically dry period; marked presence of *Araucaria angustifolia* prevailing in the canopy
Savanna	Predominantly savanna physiognomy (although also grassland and forest); dense grassy stratum; with dry periods of 4–7 months and frequent fires

where any autocorrelated or irrelevant variables for the model were excluded (Arruda et al., 2017). Thus, for the final model, we defined four bioclimatic variables (temperature seasonality, minimal temperature of the coldest quarterly period of the year, annual rainfall and rainfall of the driest quarter) and six soil properties (organic matter content, exchangeable aluminum, clay, pH, base saturation and terrain slope), all at a resolution of 1 km. Although we understand that soil is a product of the weathering process of the rock matrix over time, the exact behaviour of the physical and chemical properties under climate change is still unknown for most tropical soils. Thus, based on the stability of the rock matrix, we assume that the time spam considered here to run these models is insufficient to induce major alterations in the soil physical and chemical properties.

For calibration of the model, we used the RandomForest method (Breiman, 2001) and the function 'train' of the caret package (200 calibration and 300 testing samples). Details on the establishment of soil predictors, selection of model predictors and model calibration and validation were described by Arruda et al. (2017). The prediction model for the present ($\kappa = .82$) is represented in Figure 1.

2.2 | Projections for the past scenarios

It is well known that the reconstruction of past climate by different general circulation models (GCMs) produces different hydrological patterns (Buytaert et al., 2010). This discrepancy tends to be a result of differences in spatial scales of GCMs, which are biased towards underestimating the orographic effect embedded in the regional scale (Buytaert et al., 2010), especially flattening the strong influence of the Andean mountain chains on the climate of South America (Sepulchre, Sloan, & Fluteau, 2010). Thus, with the underestimation of the Andes, the reconstructed environments would be much drier along the path of influence of the South American Low-Level Jet (M.B. Bush, 2017, personal communication). Other parameters, such as atmospheric CO_2 concentration, temperature of the Earth and sea surface, hydrological cycles, external forcings and feedback interactions can vary slightly in the initial conditions of each model, resulting in differences in the projections, particularly in relationship to tropical rainfall (Collevatti et al., 2013; Flato et al., 2013; Sylvestre, 2009; Varela, Lima-Ribeiro, & Terribile, 2015). To reduce this bias, we used the following three different GCMs (see Supporting Information Appendix S1) to project the scenarios of the LGM (21 ka) and Mid-H (6 ka): CCSM4 (resolution 0.9° × 1.25°), MPI- ESM-P (1.9° × 1.9°) and MIROC-ESM (2.8° × 2.8°). By doing so, we expect that the combined use of the three models will contribute to reduce the above-mentioned bias in results. These GCMs are derived from the Coupled Model Intercomparison Project Phase 5 (available at http://www.worldclim.org/).

For the reconstruction of the different scenarios, we replaced the climatic parameters of the current prediction model by the estimated parameters of the different GCMs. To minimize the above issue, the projections were combined (e.g., Collevatti et al., 2013). Thus, we reconstructed the vegetation cover of each GCM and considered the consensus among them for each scenario.

Stability areas for the different biomes were estimated by overlaying prediction maps of different scenarios on the current map. We validated our models by a direct comparison with 40 fossil pollen sites compiled in the literature (Supporting Information Appendix S2).

3 | RESULTS

The differences between the averages of the GCMs and of the current climate are highlighted in Figure 2.

3.1 | Projection for the Last Glacial Maximum

In general, the Amazon was the region most affected by climate change in the LGM. In this phase, the temperature of the coldest quarter was between 3.5 and 4.5 °C lower than today throughout almost all of Brazil. The temperatures in the northern region (Amazon basin) were even lower, up to 5.5 °C colder than today (Figure 2a). In the

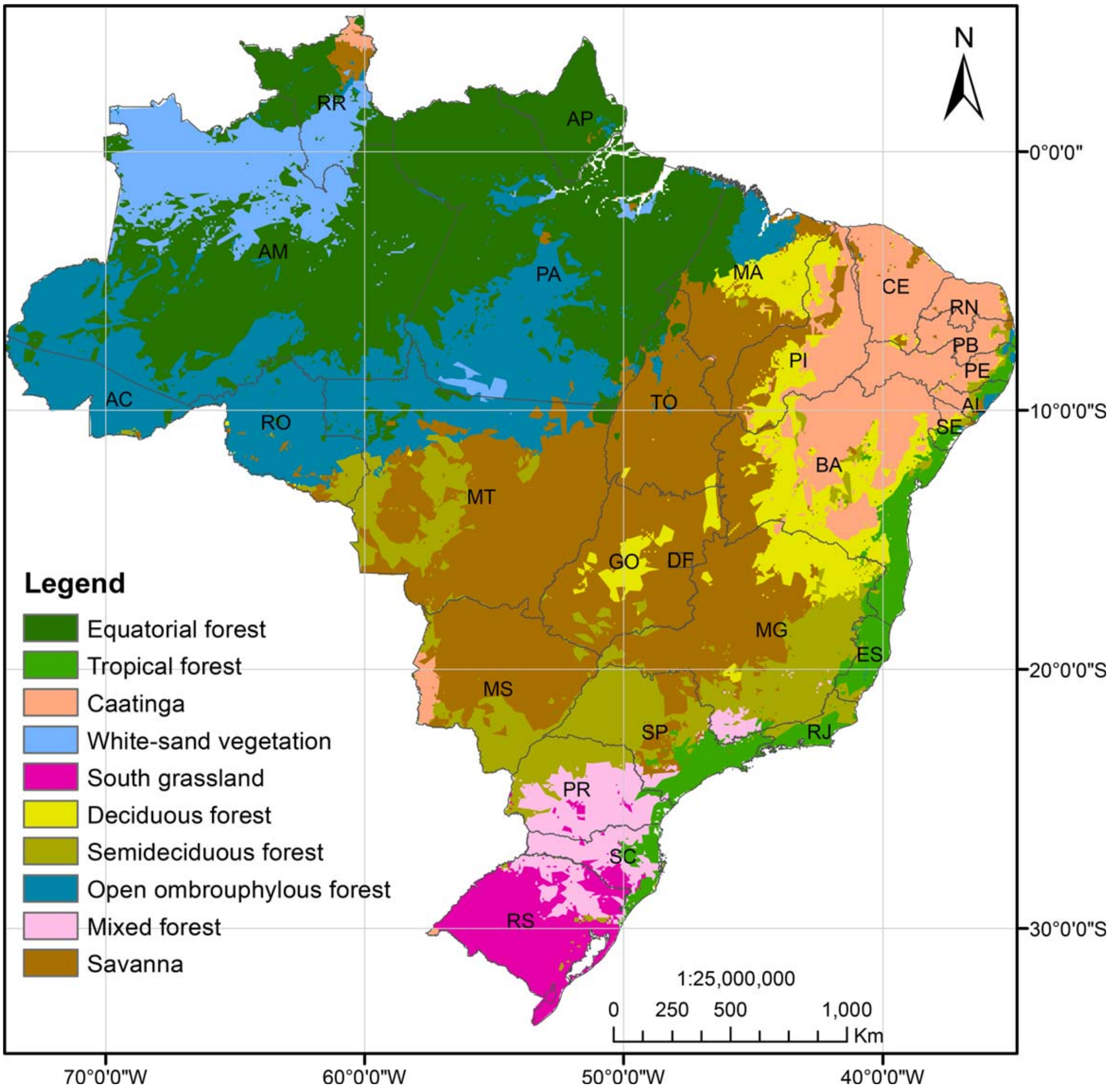

FIGURE 1 Current distribution of Brazilian biomes, according to the prediction of the soil–climate model proposed by Arruda et al. (2017). The two-letter codes represent the official abbreviations of the Brazilian states and are specified in the text

northeastern region, the temperature variation was lower than in the rest of the country (Figure 2b). Rainfall increased by 350–750 mm compared with the present in the eastern and south-central Amazon basin (Figure 2c), and the length of the dry season was reduced (Figure 2d). Conversely, in the upper Rio Negro region of the northwestern Amazon, rainfall was clearly lower than at present, particularly in the dry season. A significant decrease in rainfall was also observed in the northeastern part [i.e., state of Maranhão (MA)]. However, it is possible that the lower precipitation observed in these regions might be attributable to a bias, resulting from the underestimation of the Andes mountains by the GCMs.

The decrease in temperature and increase in rainfall in the Amazon induced a profound reconfiguration of the vegetation cover. Part of the equatorial rain forest and almost all open ombrophilous forest, which currently represents the contact between equatorial rain forest and savanna, was dominated by tropical rain forest (similar to Atlantic forest; Figure 3a). In other words, the creation of this new niche in the basin was more conducive to the establishment of tropical forest than of other vegetation types, maintaining the forest physiognomy in the basin. However, reduced rainfall in the far north of the country, especially in the dry season, led to an expansion of the isolated savanna fragment. This climate change also led to the nearly complete substitution of the white-sand vegetation by tropical forest in the Upper Rio Negro region. The core savanna also expanded to the Amazon region, but was restricted to the south of the state of Pará (PA). Regarding the expansion of the coastal tropical forest, the cooler climate in the southern portion also promoted a decline at latitudes $> 25°$.

As a result of a general increase in rainfall in the LGM, the seasonal forests (deciduous and semi-deciduous) decreased slightly (by 28 and 22%, respectively, in that period, compared with the present cover; Figure 4). The caatinga was also slightly contracted, although the climate stability was greater in the northeastern region of Brazil. Conversely, the southern grasslands expanded *c.* 250 km to the north, into the subtropical forest, which in turn shifted northwards into the

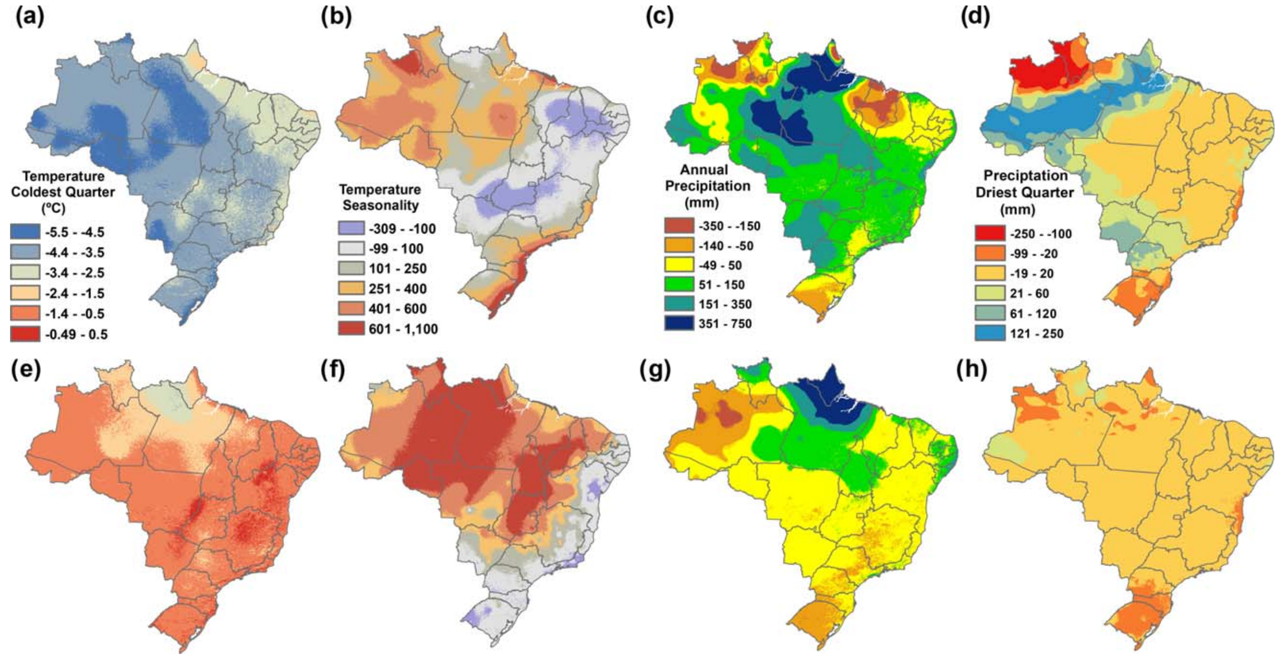

FIGURE 2 Spatial distribution of the difference between the average of the general circulation models and the present climate (past minus present) in the scenarios Last Glacial Maximum (a–d) and mid-Holocene (e–h)

semi-deciduous forest, occupying part of Central Brazil, the state of Mato Grosso do Sul (MS), and reaching lower latitudes in the region of Alto Paranaíba, in the West of the state of Minas Gerais (MG).

3.2 | Projection for the mid-Holocene

During the Mid-H, the temperature of the coldest quarter was slightly lower than nowadays in almost the entire country, with a reduction from 0.5 to 1.5 °C (Figure 2e). The greatest temperature difference was observed in the eastern Amazon, with decreases of up to 3.5 °C, compared with the present. Significantly warmer regions than at present were not indicated by the consensus of GCMs. In terms of rainfall, the eastern Amazon was more humid, especially in Amapá (AP) and northern Pará, with up to 350 mm more rain than at present (Figure 2g). However, the western portion of the Amazon and southern Brazil were slightly drier and more seasonal (Figure 2h), indicating a decrease in rainfall since the LGM. For the other regions of Brazil, no significant changes in the amount of rainfall were observed.

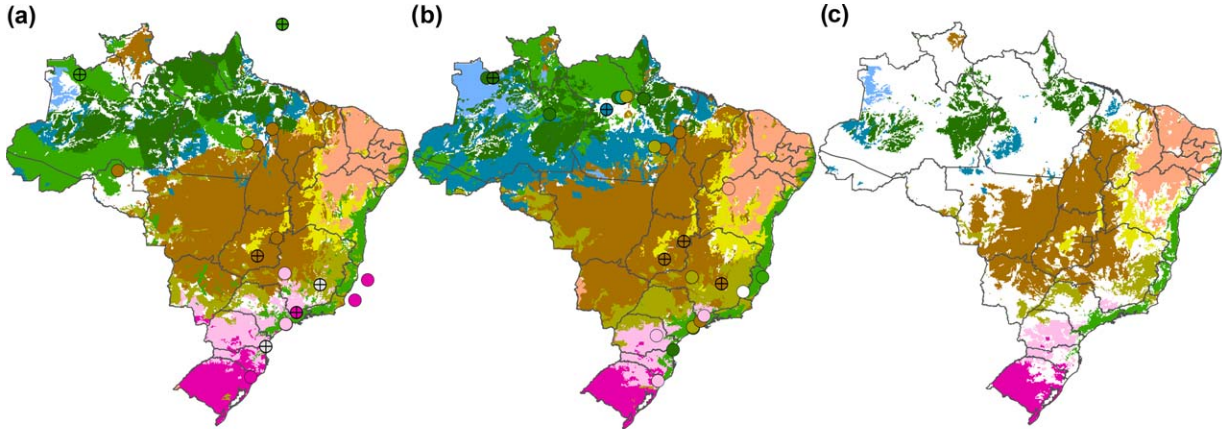

FIGURE 3 Spatial distribution of biomes at different moments in the past. Biome distribution in (a) the Last Glacial Maximum and (b) the Mid-Holocene. (c) Stability/refugia areas of the biomes based on the consensus between the two distribution scenarios and the present distribution (Figure 1). White areas on the maps indicate areas of conflict between the different general circulation models. Circles on the maps (a and b) are pollen records, whose colours represent the biome in the corresponding period. Circles marked with a cross indicate important observations at the sites. Green circle = rain forest pollen with presence of Andean species in the Last Glacial Maximum (Colinvaux et al., 1996; Haberle & Maslin, 1999) and pollen grains of herbs in the forest interior during the mid-Holocene (Mayle & Power, 2008). Brown circle = savanna pollen with evidence of flooding, similar to veredas (swamp forests; Salgado-Labouriau, Barberi, Vicentini, & Parizzi, 1998). White circle = grassland surrounded by forest in the southeast (Behling & Lichte, 1997) and grassland without Araucaria in the south (Behling & Negrelle, 2001). Blue circle = open ombrophilous or semi-deciduous forest (Irion et al., 2006). A list of the data sources is found in Supporting Information Appendix S2

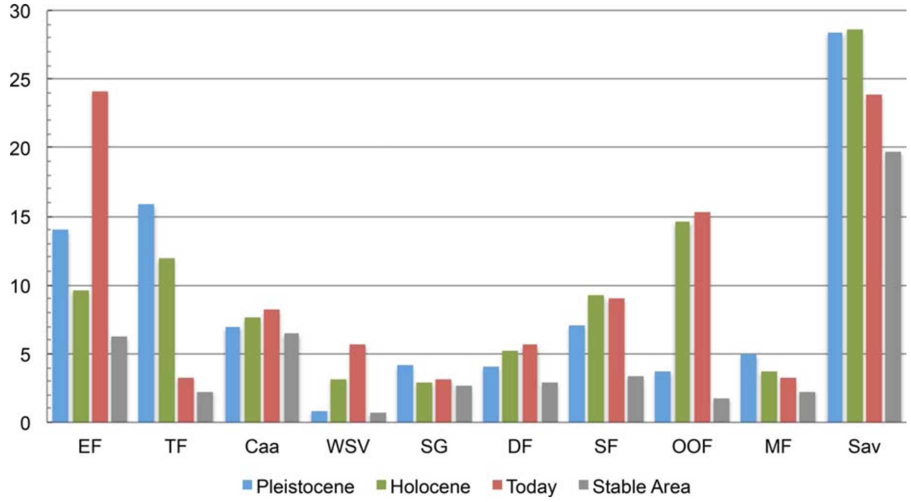

FIGURE 4 Area of Brazilian biomes (× 10^5 km^2) for the different prediction scenarios and area of climate stability over the last 21 ka (Caa = caatinga; DF = deciduous forest; EF = equatorial forest; MF = mixed forest; OOF = open ombrophilous forest; Sav = savanna; SF = semideciduous forest; SG = south grassland; TF = tropical forest; WSF = white-sand vegetation)

As in the LGM scenario, the Amazon basin was most affected by the climate alterations in the Mid-H (Figure 3b). As a result of lower rainfall levels, the white-sand vegetation cover was reduced by half (Figure 4), in comparison with the present period, and the open ombrophilous forest retracted in the southern Amazon region, where it was replaced by savanna, mainly in the north of Mato Grosso (MT). In contrast, the climate change in the northern part of the Amazon resulted in the substitution of equatorial by tropical forest. Conversely, the Mid-H climate changes in southern Brazil were not significant to influence the spatial configuration of the biomes.

3.3 | Areas of stability/vegetation refugia

As the establishment of biomes depends heavily on soil, soil-related predictors act as ‘constraints’ for vegetation dynamics under severe climate change. Thus, refugia environments could be characterized as areas with greater climate stability on a pedological basis unaltered over the last 21 ka.

The past climate change allowed the expansion or contraction of the vegetation types, with major dynamics observed in the transition areas of biomes in most of Brazil. However, in the Amazon basin the changes exceeded the borders of the biomes. This caused the scattering of the refugia of equatorial and open rain forest in patches throughout the basin (Figure 3c).

4 | DISCUSSION

We found here that the climate changes of the LGM were more likely to have remodelled the vegetation cover of Brazil than those of Mid-H. However, the dynamics of biome shrinkage and expansion were restricted to the ecotonal areas in most of the country, and the conditions of the core areas represented potential refugia zones. An exception to this pattern occurred in the Amazon region, an area with great climatic instability in both LGM and Mid-H, resulting in strong vegetation dynamics.

The temperature reduction of up to 5 °C in the Amazon basin is consistent with several estimates for the LGM (Colinvaux et al., 2000; Pennington et al., 2000; Van der Hammen & Hooghiemstra, 2000). These colder conditions, associated with increased rainfall (annual and dry season) in most of the basin, triggered major changes in the vegetation cover of the Amazon region. However, with regard to the debate on the validity of the assumptions of geographical distribution of the refugia hypothesis, we found that the most likely scenario of the basin in the LGM was in between the opposing arguments. In other words, the climate established during this period caused the retraction of the equatorial forests to refugia; however, instead of giving way to savanna, other forests could be established.

As previously advocated by several authors (Haffer, 1969; Van der Hammen & Hooghiemstra, 2000), the establishment of the new environmental space in a large part of the Amazon basin in the last 21 ka caused a retraction of the current superhumid equatorial rain forest to environmentally more suitable regions (between the basins of the rivers Madeira and Tapajos, and scattered patches in the basin of River Juruá and northeastern Pará, as proposed by Haffer, 1969). Conversely, climate changes in the basin would not allow a change of the forest character, as originally proposed by Haffer (1969), or a replacement by seasonal forests (e.g., Pennington et al., 2000). Thus, the rain forests were continuously maintained in this space, but with different environmental preferences from equatorial rain forest. Possibly, the taxa occupying these different rain forests were also different. According to palynological records (Colinvaux et al., 1996; Haberle & Maslin, 1999; Mayle, Burn, Power, & Urrego, 2009), the climate changes in the Amazon basin allowed the colonization by Andean forest taxa during the LGM. For Oliveira-Filho and Ratter (1995), the extensive network of alluvial forests of Central Brazil also allowed the colonization by Atlantic tropical forest taxa [while conversely, Amazonian taxa migrated to the Atlantic forest, as suggested by Costa (2003) and Santos, Cavalcanti, Silva, and Tabarelli (2007)].

According to Van der Hammen and Hooghiemstra (2000), a rainfall reduction of 35–55% would have led to an occupation by savannas in the Amazon basin. However, these estimates are inconsistent with the different circulation models analysed here (Supporting Information Appendix S1). In addition, the authors proposed that the presence of large dune grasslands in central Amazonia supported the premise of drought in the Amazon. However, the dune grasslands of the Upper Rio Negro region are consistent with the white-sand vegetation, the location of highest rainfall in Brazil, where the soil is massively leached, resulting in large areas of Spodosol (Mendonça et al., 2014).

Based on our results, we postulate that the establishment of a non-forest vegetation or even of a seasonal forest would not be possible, not even in the portion of greatest rainfall reduction [western Amazonia; Figure 2c; a trend described by Mayle, Burbridge, and Killeen (2000) and Bush (2005)], because the rainfall indices were still high, exceeding the tolerance levels of seasonal formations (see table 2 of Arruda et al., 2017). The reduction of 350 mm in the region where the current rainfall is close to 3,000 mm would still be insufficient to alter the vegetation cover significantly, although it could have been the case if the decrease occurred in other biomes (e.g., caatinga, savanna or seasonal forests). Moreover, if the forest–climate interactions were taken into consideration (e.g., water recycling by the forest during the dry season; Nobre, Sellers, & Shukla, 1991), such a change in vegetation cover in the basin would be even less likely. Thus, the advance of the savanna into the Amazon basin in the LGM was more likely to have been restricted to the southern ecotonal regions (Burbridge, Mayle, & Killeen, 2004; Mayle et al., 2000, 2009), for instance, of Carajás (Pará), Katira, Porto Velho [Rondônia (RO)], Bella Vista (Bolivia) and, as shown here, from the upper Rio Xingu to the south of Pará.

For the tropical forest of the Atlantic coast, in disagreement with the consensus of the models proposed by Carnaval and Moritz (2008) (although similar to the results of Maxent models in their paper), the cover was not reduced in either scenario. In contrast, our results agree with those of Leite et al. (2016) in refuting the hypothesis of refugia for the Atlantic coast forest. This biome retreated to regions with latitudes > 25° only in the LGM, and may have remained virtually unchanged throughout the Holocene (Behling & Negrelle, 2001; Pessenda et al., 2009). We postulate that the main driving factor of this biome, the orographic forcing of the East of Brazil, was not significantly affected by past climate changes. However, as the sea level may have been up to 120 m lower than currently (Fairbanks, 1989), the area of the tropical Atlantic forest for the LGM was possibly underestimated (see Leite et al., 2016). With the advance of the coastline in the Mid-H, part of this forest may have been replaced by vegetation under marine influence (e.g., Buso-Junior et al., 2013), with a slightly smaller area.

The wet and cold LGM climate was also conducive to shift the mixed forest *c*. 400 km northwards from its present distribution into the semi-deciduous forest. The lowest latitude reached by this biome was 19° S, in the region of Salitre (Minas Gerais), where Ledru et al. (1996) sampled *Araucaria* pollen (typical gymnosperms of this biome) for periods before the LGM (32 ka) and the early Holocene (12–8 ka; a gap of sedimentation between 28 and 16 ka impaired conclusions on the vegetation composition for the LGM). As shown in our model, this biome probably occupied the region in the LGM as well.

When the mixed forest shifted north, the southern grassland cover expanded in the south [as demonstrated by Behling, Pillar, Orlóci, & Bauermann (2004)]; however, driven by the increasing drought in the far south of the country [as registered by Cruz, et al. (2006) and Wang et al. (2006)]. This situation was reversed in the Mid-H. The post-glacial warming caused the mixed forest to move south, replaced by semi-deciduous forest, as pointed out by Ledru et al. (1996) in the region of Salitre and Colônia [São Paulo (SP); Ledru et al., 2009]. The new climate created in southern Brazil, in the state of Santa Catarina (SC), allowed the reinstallation of mixed forest on the southern grasslands (as stated by Behling et al., 2004), until the configuration was similar to the present. In general, the wetter climate today is still favourable for the continuity of this natural process, although the anthropogenic influence on the grasslands prevents it (Behling & Pillar, 2007).

The distribution of the seasonal biomes caatinga and deciduous and semi-deciduous forest (considered the Brazilian portion of the biome *sensu lato* Neotropical Seasonally Dry Forests; Pennington et al., 2000), in disagreement with previous proposals (Collevatti et al., 2013; Pennington et al., 2000; Prado & Gibbs, 1993), was lower in the LGM because of higher rainfall and lower temperatures in this period. With decreasing rainfall and post-glacial warming, the cover of these biomes expanded (e.g., Werneck et al., 2011; Whitney et al., 2011). However, the dynamics of caatinga and deciduous forest were restricted to ecotonal conditions on small scales (e.g., De Oliveira, Barreto, & Suguio, 1999). Their clear soil preferences, for high-pH and nutrient-rich soils (Arruda, et al., 2017), restrict their establishment to the few favourable areas of a geologically ancient and pedologically leached country. The semi-deciduous forest, however, less demanding in terms of soils, expanded its territory during the Mid-H, following the drought increase at latitudes > 20° S. In short, the increase (not decrease) in temperature and water stress caused the expansion of these seasonal biomes, where the soil was favourable. The savanna, however, had a greater extent in the LGM (in disagreement with Bueno et al., 2016) and Mid-H than nowadays. The higher temperature range in the basin and the compatibility with the leached landscape favoured its expansion, essentially into the open ombrophilous forest, an ecotonal biome of the Amazon border. However, after post-glacial warming, the savanna began to lose space to the open ombrophilous forest (e.g., Mayle et al., 2000).

Thus, we postulate that if major climate changes reconfigured the Neotropical landscape, they occurred in periods before 21 ka (e.g., Bueno et al., 2016; Leite et al., 2016; Werneck, et al., 2012). Other short-term climate changes after this period were not evaluated here, but we assume that they were sufficient for impacts only on small spatial scales, restricted to the edges of biomes or peculiar landscape conditions (e.g., De Oliveira et al., 1999; Whitney et al., 2011). We suggest that specific approaches targeting these periods could be made to understand climatic variations of short periods and test these assumptions.

Finally, the term 'biome' used here is based on the phenology and dominant life-forms in certain abiotic conditions, recorded by remote sensing (Arruda et al., 2017; Woodward, Lomas, & Kelly, 2004). We are aware and agree that the biotic component is not always restricted to the environmental space of a single biome and that the adaptive response to climate change may allow a species to remain in the newly altered environment or favour its migration (Davis & Shaw, 2001; Hill, Griffiths, & Thomas, 2011; Urrego et al., 2009). Thus, the addition or extinction of a species will not induce a shift of the biome (Pennington, Cronk, & Richardson, 2004). Likewise, there is no guarantee that the change in vegetation cover in response to climate change will result in a change across all biotic components, but validation by fossil pollen may allow extrapolations. Future fossil pollen sampling in the core of the biomes may add relevant contributions to our model, because the currently exploited areas are mostly located in ecotonal regions (see Flantua et al., 2015). However, the findings at the available sites were consistent with the models proposed here, which enabled us to contribute to the discussion on biogeographical hypotheses, for example on the hypothesis of Amazonian refugia, which, unlike the statements by Colinvaux et al. (2000) and Bush and De Oliveira (2006), is not yet concluded.

5 | FINAL CONSIDERATIONS

Regarding geographical distribution assumptions of Amazonian refugia, the replacement of the equatorial forest by seasonal vegetations was impossible because of soil constraints and the climate of the past. However, the colder conditions of the Amazon basin paved the way for the establishment of another type of rain forest, causing the equatorial rain forest to retreat to more stable climate areas. With regard to the geographical distribution assumptions of the Pleistocenic arc, the seasonal (deciduous and semidecidual) forests and caatinga began to expand only after warming and reduction of water availability in the post-glacial period, but limited to environments with favourable soils and never forming a continuous arc during these periods.

ACKNOWLEDGMENTS

This paper is based on a thesis submitted by D.M.A. in partial fulfilment of the requirements for the PhD degree at Universidade Federal de Viçosa. D.M.A. was supported by research grants of CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior). The authors are grateful to Marcelo Bueno and Markus Gastauer for insightful suggestions on the early version of the manuscript. The authors also thank Mark Bush and an anonymous referee for the valuable comments, which contributed significantly to the final version of the manuscript.

DATA ACCESSIBILITY

The data used to generate the model in the current state are accessible in the electronic supplementary material of Arruda et al., 2017 (DOI: 10.1007/s00114-017-1456-6). The climate data of the past were extracted from the Worldclim platform (http://www.worldclim.org/paleo-climate1).

ORCID

Daniel M. Arruda http://orcid.org/0000-0002-3541-4786

REFERENCES

Arruda, D. M., Fernandes-Filho, E. I., Solar, R. R. C., & Schaefer, C. E. G. R. (2017). Combining climatic and soil attributes better predicts cover of Brazilian biomes. *Naturwissenschaften*, *104*, 32. https://doi.org/10.1007/s00114-017-1456-6

Baker, P. A., Seltzer, G. O., Fritz, S. C., Dunbar, R. B., Grove, M. J., Tapia, P. M., . . . Broda, J. P. (2001). The history of South American tropical precipitation for the past 25,000 years. *Science*, *291*, 640–643.

Behling, H., & Lichte, M. (1997). Evidence of dry and cold climatic conditions at glacial times in tropical Southeastern Brazil. *Quaternary Research*, *48*, 348–358.

Behling, H., & Negrelle, R. R. B. (2001). Tropical rain forest and climate dynamics of the Atlantic lowland, southern Brazil, during the late quaternary. *Quaternary Research*, *56*, 383–389.

Behling, H., & Pillar, V. D. (2007). Late Quaternary vegetation, biodiversity and fire dynamics on the southern Brazilian highland and their implication for conservation and management of modern Araucaria forest and grassland ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*, 243–251.

Behling, H., Pillar, V. P., Orlóci, L., & Bauermann, S. G. (2004). Late Quaternary *Araucaria* forest, grassland (Campos), fire and climate dynamics, studied by high-resolution pollen, charcoal and multivariate analysis of the Cambará do Sul core in southern Brazil. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, *203*, 277–297.

Breiman, L. (2001). Random forests. *Machine Learning*, *45*, 5–32.

Bueno, M., Pennington, R. T., Dexter, K. G., Kamino, L. H. Y., Pontara, L., Neves, D. R. M., . . . Oliveira-Filho, A. T. (2016). Effects of quaternary climatic fluctuations on the distribution of Neotropical savanna tree species. *Ecography*, *40*, 403–414.40. https://doi.org/10.1111/ecog.01860

Burbridge, R. E., Mayle, F. E., & Killeen, T. J. (2004). Fifty-thousand-year vegetation and climate history of Noel Kempff Mercado National Park, Bolivian Amazon. *Quaternary Research*, *61*, 215–230.

Bush, M. B. (2005). Holocene climates of the lowland tropical forests. In A. Mackay, R. Battarbee, J. Birks & F. Oldfield (Eds.), *Global change in the Holocene* (pp. 293–306). New York, NY: Academic Press.

Bush, M. B., & De Oliveira, P. E. (2006). The rise and fall of the Refugial Hypothesis of Amazonian speciation: A paleoecological perspective. *Biota Neotropica*, *6*, 1–17. Retrieved from http://www.biotaneotropica.org.br/v6n1/pt/abstract?point-of-view+bn00106012006

Buso-Junior, A. A., Pessenda, L. C. R., De Oliveira, P. E., Giannini, P. C. F., Cohen, M. C. L., Volkmer-Ribeiro, C., . . . Siqueira, G. S. (2013). Late Pleistocene and Holocene vegetation, climate dynamics, and Amazonian taxa in the Atlantic Forest, Linhares, SE Brazil. *Radiocarbon*, *55*, 1747–1762.

Buytaert, W., Vuille, M., Dewulf, A., Urrutia, R., Karmalkar, A., & Célleri, R. (2010). Uncertainties in climate change projections and regional downscaling: Implications for water resources management. *Hydrology and Earth System Sciences*, *14*, 1247–1258.

Carnaval, A. C., & Moritz, C. (2008). Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. *Journal of Biogeography*, *35*, 1187–1201.

Cheng, H., Sinha, A., Cruz, F. W., Wang, X., Edwards, R. L., D'horta, F. M., . . . Auler, A. S. (2013). Climate change patterns in Amazonia and biodiversity. *Nature Communications*, *4*, 1411.

Colinvaux, P. A., De Oliveira, P. E., & Bush, M. B. (2000). Amazonian and neotropical plant communities on glacial time-scales: The failure of the aridity and refuge hypotheses. *Quaternary Science Reviews*, *19*, 141–169.

Colinvaux, P. A., De Oliveira, P. E., Moreno, J. E., Miller, M. C., & Bush, M. B. (1996). A long pollen record from lowland Amazonia: Forest and cooling in glacial times. *Science*, *274*, 85–88.

Collevatti, R. G., Terribile, L. C., Oliveira, G., Lima-Ribeiro, M. S., Nabout, J. C., Rangel, T. F., & Filho, J. A. F. (2013). Drawbacks to palaeodistribution modelling: The case of South American seasonally dry forests. *Journal of Biogeography*, *40*, 345–358.

Costa, L. P. (2003). The historical bridge between the Amazon and the Atlantic Forest of Brazil: A study of molecular phylogeography with small mammals. *Journal of Biogeography*, *30*, 71–86.

Coudun, C., & Gégout, J. C. (2007). Quantitative prediction of the distribution and abundance of *Vaccinium myrtillus* with climatic and edaphic factors. *Journal of Vegetation Science*, *18*, 517–524.

Coudun, C., Gégout, J. C., Piedallu, C., & Rameau, J. C. (2006). Soil nutritional factors improve models of plant species distribution: An illustration with *Acer campestre* (L.) in France. *Journal of Biogeography*, *33*, 1750–1763.

Cruz, F. W., Burns, S. J., Karmann, I., Sharp, W. D., Vuille, M., & Ferrari, J. A. (2006). A stalagmite record of changes in atmospheric circulation and soil processes in the Brazilian subtropics during the Late Pleistocene. *Quaternary Science Review*, *25*, 2749–2761.

Cruz, F. W., Vuille, M., Burns, S. J., Wang, X., Cheng, H., Werner, M., . . . Nguyen, H. (2009). Orbitally driven east–west antiphasing of South American precipitation. *Nature Geoscience*, *2*, 210–214.

Davis, M. B., & Shaw, R. G. (2001). Range shifts and adaptive responses to Quaternary climate change. *Science*, *292*, 673–679.

De Oliveira, P. E., Barreto, A. M. F., & Suguio, K. (1999). Late Pleistocene/Holocene climatic and vegetational history of the Brazilian caatinga: The fossil dunes of the middle Sao Francisco River. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, *152*, 319–337.

Fairbanks, R. G. (1989). A 17,000-year glacio-eustatic sea level record: Influence of glacial melting rates on the Younger Dryas event and deep-ocean circulation. *Nature*, *342*, 637–642.

Flantua, S. G., Hooghiemstra, H., Grimm, E. C., Behling, H., Bush, M. B., González-Arango, C., . . . Van Boxel, J. H. (2015). Updated site compilation of the Latin American Pollen Database. *Review of Palaeobotany and Palynology*, *223*, 104–115.

Flato, G., Marotzke, J., Abiodun, B., Braconnot, P., Chou, S. C., Collins, W., . . . Rummukainen, M. (2013). Evaluation of climate models. Climate change 2013: The physical science basis. In T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. . . . P. M. Midgley (Eds.), *Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 741–866). Cambridge, U.K. and New York, NY: Cambridge University Press.

Haberle, S. G., & Maslin, M. A. (1999). Late Quaternary vegetation and climate change in the Amazon Basin based on a 50,000 year pollen record from the Amazon Fan, ODP Site 932. *Quaternary Research*, *51*, 27–38.

Haffer, J. (1969). Speciation in Amazonian forest birds. *Science*, *165*, 131–137.

Harrison, S. P., Prentice, I. C., Barboni, D., Kohfeld, K. E., Ni, J., & Sutra, J. P. (2010). Ecophysiological and bioclimatic foundations for a global plant functional classification. *Journal of Vegetation Science*, *21*, 300–317.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*, 1965–1978.

Hill, J. K., Griffiths, H. M., & Thomas, C. D. (2011). Climate change and evolutionary adaptations at species' range margins. *Annual Review of Entomology*, *56*, 143–159.

Irion, G., Bush, M. B., Mello, J. A. N., Stüben, D., Neumann, T., Müller, G., . . . Junk, J. W. (2006). A multiproxy palaeoecological record of Holocene lake sediments from the Rio Tapajós, eastern Amazonia. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, *240*, 523–535.

Keppel, G., Van Niel, K. P., Wardell-Johnson, G. W., Yates, C. J., Byrne, M., Mucina, L., . . . Franklin, S. E. (2012). Refugia: Identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography*, *21*, 393–404.

Ledru, M. P., Braga, P. I. S., Soubiès, F., Fournier, M., Martin, L., Suguio, K., & Turcq, B. (1996). The last 50,000 years in the Neotropics (Southern Brazil): Evolution of vegetation and climate. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, *123*, 239–257.

Ledru, M. P., Mourguiart, P., & Riccomini, C. (2009). Related changes in biodiversity, insolation and climate in the Atlantic rainforest since the last interglacial. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, *271*, 140–152.

Leite, Y. L., Costa, L. P., Loss, A. C., Rocha, R. G., Batalha-Filho, H., Bastos, A. C., . . . Pardini, R. (2016). Neotropical forest expansion during the last glacial period challenges refuge hypothesis. *Proceedings of the National Academy of Sciences USA*, *113*, 1008–1013.

Marchant, R., Cleef, A., Harrison, S. P., Hooghiemstra, H., Markgraf, V., van Boxel, J., . . . Wille, M. (2009). Pollen-based biome reconstructions for Latin America at 0, 6000 and 18 000 radiocarbon years ago. *Climate of the Past Discussions*, *5*, 725–767.

Mayle, F. E., & Power, M. J. (2008). Impact of a drier Early–Mid-Holocene climate upon Amazonian forests. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*, 1829–1838.

Mayle, F. E., Burbridge, R., & Killeen, T. J. (2000). Millennial-scale dynamics of southern Amazonian rain forests. *Science*, *290*, 2291–2294.

Mayle, F. E., Burn, M. J., Power, M., & Urrego, D. H. (2009). Vegetation and fire at the Last Glacial Maximum in tropical South America. In F. Vimeux, F. Sylvestre & M. Khodri (Eds.), *Past climate variability in South America and surrounding regions* (pp. 89–112). Springer Netherlands: Springer Science & Business Media B.V., Berlin.

Mendonça, B. A. F., Simas, F. N. B., Schaefer, C. E. G. R., Fernandes-Filho, E. I., Vale-Júnior, J. F., & Mendonça, J. G. F. (2014). Podzolized soils and paleoenvironmental implications of white-sand vegetation (*Campinarana*) in the Viruá National Park, Brazil. *Geoderma Regional*, *2–3*, 9–20.

Nobre, C. A., Sellers, P. J., & Shukla, J. (1991). Amazonian deforestation and regional climate change. *Journal of Climate*, *4*, 957–988.

Oliveira-Filho, A. T., & Ratter, J. A. (1995). A study of the origin of central Brazilian forests by the analysis of plant species distribution patterns. *Edinburgh Journal of Botany*, *52*, 141–194.

Pennington, R. T., Cronk, Q. C., & Richardson, J. A. (2004). Introduction and synthesis: Plant phylogeny and the origin of major biomes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *359*, 1455–1464.

Pennington, R. T., Lavin, M., & Oliveira-Filho, A. (2009). Woody plant diversity, evolution, and ecology in the tropics: Perspectives from seasonally dry tropical forests. *Annual Review of Ecology*, *Evolution*, *and Systematics*, *40*, 437–457.

Pennington, R. T., Prado, D. E., & Pendry, C. A. (2000). Neotropical seasonally dry forests and Quaternary vegetation changes. *Journal of Biogeography*, *27*, 261–273.

Pessenda, L. C. R., De Oliveira, P. E., Mofatto, M., Medeiros, V. B., Garcia, R. J. F., Aravena, R., . . . Etchebehere, M. L. (2009). The evolution of a tropical rainforest/grassland mosaic in southeastern Brazil since 28,000 14C yr BP based on carbon isotopes and pollen records. *Quaternary Research*, *71*, 437–452.

Prado, D. E., & Gibbs, P. E. (1993). Patterns of species distributions in the dry seasonal forests of South America. *Annals of the Missouri Botanical Garden*, *80*, 902–927.

Prentice, I. C., Harrison, S. P., & Bartlein, P. J. (2011). Global vegetation and terrestrial carbon cycle changes after the last ice age. *New Phytologist*, *189*, 988–998.

Salgado-Labouriau, M. L., Barberi, M., Vicentini, K. R. F., & Parizzi, M. G. (1998). A dry climatic event during the late Quaternary of tropical Brazil. *Review of Palaeobotany and Palynology*, *99*, 115–129.

Santos, A. M. M., Cavalcanti, D. R., Silva, J. M. C. D., & Tabarelli, M. (2007). Biogeographical relationships among tropical forests in northeastern Brazil. *Journal of Biogeography*, *34*, 437–446.

Sepulchre, P., Sloan, L. C., & Fluteau, F. (2010). Modelling the response of Amazonian climate to the uplift of the Andean mountain range. In C. Hoorn & F. Weeslingh (Eds.), *Amazonia: Landscape and species evolution: A look into the past* (pp. 211–222). Chichester, U.K.: Wiley-Blackwell.

Sylvestre, F. (2009). Moisture pattern during the last glacial maximum in South America. In F. Vimeux, F. Sylvestre & M. Khodri (Eds.), *Past climate variability in South America and surrounding regions* (pp. 3–27). Springer Netherlands.

Urrego, D. H., Bush, M. B., Silman, M. R., Correa-Metrio, A., Ledru, M. P., Mayle, F. E., ... Valencia, B. G. (2009). Millennial-scale ecological changes in tropical South America since the last glacial maximum. In F. Vimeux, F. Sylvestre and M. Khodri (Eds.), *Past climate variability in South America and surrounding regions* (pp. 283–300). Springer Netherlands: Springer Science & Business Media B.V., Berlin.

Van Breukelen, M. R., Vonhof, H. B., Hellstrom, J. C., Wester, W. C. G., & Kroon, D. (2008). Fossil dripwater in stalagmites reveals Holocene temperature and rainfall variation in Amazonia. *Earth and Planetary Science Letters*, *275*, 54–60.

Van der Hammen, T., & Hooghiemstra, H. (2000). Neogene and Quaternary history of vegetation, climate, and plant diversity in Amazonia. *Quaternary Science Review*, *19*, 725–742.

Varela, S., Lima-Ribeiro, M. S., & Terribile, L. C. (2015). A short guide to the climatic variables of the Last Glacial Maximum for biogeographers. *PLoS One*, *10*, e0129037.

Wang, X., Auler, A. S., Edwards, R., Cheng, H., Ito, E., Solheid, M. (2006). Interhemispheric anti-phasing of rainfall during 690 the last glacial period. *Quaternary Science Reviews*, *25*, 3391–3403.

Werneck, F. P., Costa, G. C., Colli, G. R., Prado, D. E., & Sites, J. W., Jr. (2011). Revisiting the historical distribution of Seasonally Dry Tropical Forests: New insights based on palaeodistribution modelling and palynological evidence. *Global Ecology and Biogeography*, *20*, 272–288.

Werneck, F. P., Nogueira, C., Colli, G. R., Sites, J. W., Jr., & Costa, G. C. (2012). Climatic stability in the Brazilian Cerrado: Implications for biogeographical connections of South American savannas, species richness and conservation in a biodiversity hotspot. *Journal of Biogeography*, *39*, 1695–1706.

Whitney, B. S., Mayle, F. E., Punyasena, S. W., Fitzpatrick, K. A., Burn, M. J., Guillen, R., . . . Metcalfe, S. E. (2011). A 45 ka palaeoclimate record from the lowland interior of tropical South America. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *307*, 177–192.

Woodward, F. I., Lomas, M. R., & Kelly, C. K. (2004). Global climate and the distribution of plant biomes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *359*, 1465–1476.

BIOSKETCH

Daniel M. Arruda is a recent PhD graduate in botany, interested in understanding what and how abiotic factors influence the establishment of plant communities and biomes in space and time. Most of his studies are focused on the phytogeography of Brazil.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Arruda DM, Schaefer CEGR, Fonseca RS, Solar RRC, Fernandes-Filho EI. Vegetation cover of Brazil in the last 21 ka: New insights into the Amazonian refugia and Pleistocenic arc hypotheses. *Global Ecol Biogeogr*. 2018;27:47–56. https://doi.org/10.1111/geb.12646