


Biome stability in South America over the last 30 kyr: Inferences from long-term vegetation dynamics and habitat modelling

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Abstract

Aim: The aim was to examine the links between past biome stability, vegetation dynamics and biodiversity patterns.

Location: South America.

Time period: Last 30,000 years.

Major taxa studied: Plants.

Methods: We classified South America into major biomes according to their dominant plant functional groups (grasses, trees and shrubs) and ran a random forest (RF) classification with data on current climate. We then fitted the algorithm to predict biome distributions for every 1,000 years back to 21,000 yr BP and estimated biome stability by counting how many times a change in climate was predicted to shift a grid cell from one biome to another. We compared our model-based stability map with empirical estimates from selected pollen records covering the past 30 kyr in terms of vegetation shifts, changes in species composition and time-lag of vegetation responses.

Results: We found a strong correlation between our habitat stability map and regional vegetation dynamics. Four scenarios emerged according to the way forest distribution shifted during a climate change. Each scenario related to specific regional features of biome stability and diversity, allowing us to formulate specific predictions on how taxonomic, genetic and functional components of biodiversity might be impacted by modern climate change.

Main conclusions: Our validated map of biome stability provides important baseline information for studying the impacts of past climate on biodiversity in South America. By focusing exclusively on climatic changes of manifested relevance (i.e., those resulting in significant habitat changes), it provides a novel perspective that complements previous datasets and allows scientists to explore new questions and hypotheses at the local, regional and continental scales.

KEYWORDS

climate change, diversity, habitat stability, landscape dynamics, pollen records, refugia

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1 | INTRODUCTION

Distinct biological communities and sets of organismal traits often form in response to different abiotic environments (Whittaker, 1962, 1975). Changes in temperature and precipitation alter the spatial distribution of suitable climates for organisms and their habitats and may result in local to landscape-scale transitions from one biome to another (Donoghue & Edwards, 2014). Such biome shifts cause massive population fluctuations and community reshuffling (Pavelkova Ricankova, Robovsky, & Riegert, 2014), catalyse speciation and extinction, and thus ultimately, influence net diversification rates (Mittelbach et al., 2007; Weir & Schluter, 2007). Biome shifts have been a common phenomenon during past periods of intense climate change (Willis & MacDonald, 2011) and are predicted to increase in frequency as a consequence of recent global warming (Scholze, Knorr, Arnell, & Prentice, 2006). A better understanding of how patterns of past biome stability have shaped the geographical distribution of extant biodiversity can thus strengthen predictions of future diversity trends under human-induced environmental change (Moritz & Agudo, 2013).

Previous attempts to model past biome shifts in the Neotropics have to date mostly relied on correlative models of habitat distribution (e.g., Carnaval et al., 2014; Werneck, Costa, Colli, Prado, & Sites, 2011). In the Atlantic Forest, the models identified stable areas that seem to be important drivers of biodiversity in the northern portion of the biome (Carnaval, Hickerson, Haddad, Rodrigues, & Moritz, 2009; Carnaval et al., 2014), whereas different processes may have had greater influence in the southern portion of the biome (Carnaval et al., 2014; Martins, 2011; Porto, Carnaval, & da Rocha, 2013). In the Amazon, recent models supported the hypothesis of multiple connections with the Atlantic Forest, especially via a southeast-to-northwest route (Ledo & Colli, 2017). For the Cerrado, climate stability models predicted squamate species richness (Werneck, Nogueira, Colli, Sites, & Costa, 2012), but did not predict genetic diversity in two species of lizards (Santos, Nogueira, Giugliano, & Colli, 2014) and an orchid species (Pinheiro et al., 2013). Although not tested explicitly, genetic data from some Cerrado plant species seem to conform to spatial predictions of climate stability (Ramos, De Lemos-Filho, & Lovato, 2008; Ramos, Lemos-Filho, Ribeiro, Santos, & Lovato, 2007). In Seasonally Dry Tropical Forests (SDTFs), genetic predictions were supported for a tree species (Collevatti et al., 2012), but not for lizards (Werneck, Gamble, Colli, Rodrigues, & Sites, 2012). Clearly, the correlative approach has proved useful but not universal, and more palaeoenvironmental studies and comparisons are needed to gain a better understanding of how, when,

why and which type of stability predicts the different aspects of biodiversity. Previous models are somewhat limited in their scope because they produce climatic suitability hypotheses for each biome separately, often in the shape of continuous values per pixel, without integration across the landscape and not considering threshold responses that might be linked to physiological responses of plant functional types (Hirota, Nobre, Oyama, & Bustamante, 2010; Oyama & Nobre, 2004). Moreover, many of the available models have not been subjected to validation with independent data, such as fossil pollen records. A deeper integration between regional-scale modelling and data from palaeoproxies is an important next step to advance studies of biological responses to past climate change.

Here, we apply and test a new threshold-based framework that models past shifts in biome types (e.g., forest to grassland, and vice versa) as a function of past climate change. Combining elements of correlative and mechanistic habitat modelling approaches, we draw a direct link between climatic variation and biome configuration, considering different biome types simultaneously rather than separately. In a first step, we train our model to recognize those boundary conditions that define present-day biomes and to identify situations where climate change catalyses transitions from one biome to another. We thus focus not on the absolute but on the 'biologically relevant' magnitude of climate change, that is, the amount that triggers real changes in the dominance of different plant functional types. In a second step, we model past biome stability across South America using millennium-scale climate data for the past 21,000 years (21 kyr). We also derive a grid-based stability measure representing the extent to which climatic change has potentially shifted major vegetation types in South America. In a third step, we compile palynological records to validate and interpret our model output, inferring former vegetation dynamics in response to climate change. Finally, we propose a conceptual framework that describes how each of four major scenarios of biome stability could influence patterns of species richness, endemism and phylogenetic, functional and genetic diversity. This framework provides several readily testable hypotheses concerning the geographical distribution of extant biodiversity across levels of biotic organization in South America.

2 | METHODS

2.1 | Modelling biome stability

We first divided South America into seven major biomes according to their dominant plant functional group types (grasses, trees and shrubs)

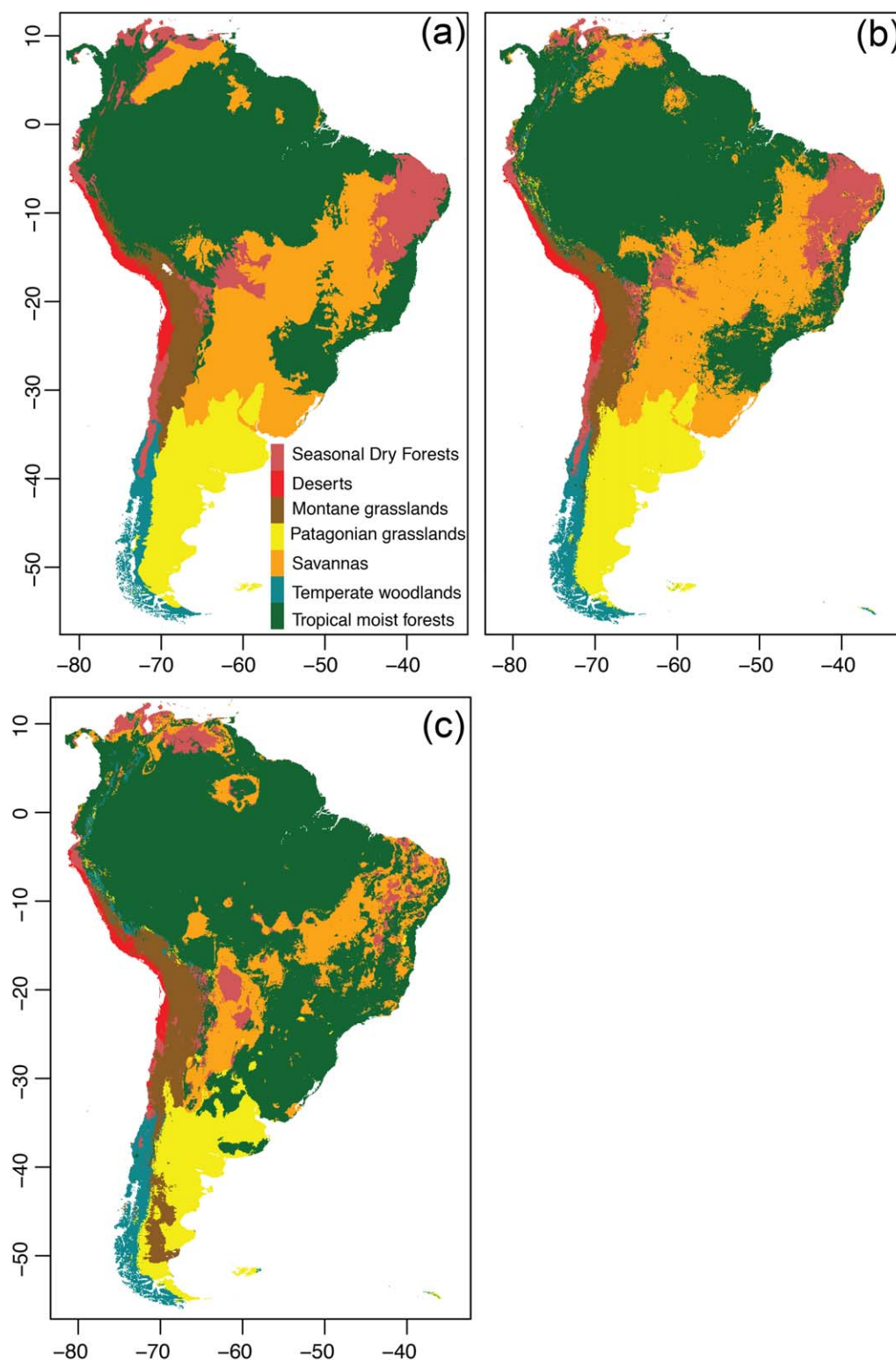


FIGURE 1 (a) Biome classification for South America according to Olson et al. (2001). (b) Results of random forest classification procedure using data on mean annual temperature, mean annual precipitation and precipitation seasonality. (c) Random forest model projected to the Last Glacial Maximum (LGM, 21,000 yr BP)

and climate (rainfall, seasonality and temperature), as follows: (a) tropical moist forests, (b) temperate woodlands, (c) savannas, (d) Patagonian grasslands, (e) montane grasslands, (f) seasonal dry forests, and (g) deserts (Figure 1a and Table 1). Our classification largely corresponds

to that by Olson et al. (2001) except for some modifications that we introduced, as follows: (a) we grouped the Pantanal (a seasonally flooded savanna) with other savanna types (i.e., the Cerrado) because their differences are mainly attributable to geomorphology and not

TABLE 1 Biome types and their upper and lower climatic ranges estimated by the random forest model

Biome	Temperature (°C)	Precipitation (mm)	Seasonality	<i>n</i>	Error
Tropical moist forests	27.3–15.2	3,505–919	9–1.4	405,415	0.07
Temperate woodlands	12.5–2.3	4,439–427	9.4–0.9	25,902	0.11
Savannas	27.6–17.1	2,065–483	9.5–1	209,865	0.12
Patagonian grasslands	19.1–5.4	1,080–145	7.2–1.7	98,586	0.02
Montane grasslands	17.7 to –1.2	915–29	19.8–4.3	44,159	0.12
Seasonal dry forests	28.1–16.2	1,607–284	14–3.9	9,381	0.28
Deserts	22.6–6.2	747–1	34.6–8.6	13,241	0.15

Note. The most extreme values (2.5% of each side of the distribution) were not considered to calculate climatic ranges because they are located at areas of low accuracy in the random forest model prediction. Also, these extreme values considerably increase range sizes. Columns indicate mean annual temperature (in degrees Celsius), mean annual precipitation (in millimetres) and precipitation seasonality (coefficient of variation), the number of observations and biome classification error rates for all climatic data.

climate or functional group dominance; (b) for the same reasons, we also grouped the dry broadleaf forests of central South America, the xeric shrublands in northeastern Brazil (Caatinga) and the Chilean Matorral into the seasonally dry forests; (c) we treated the Atacama and Sechura deserts as a unique vegetation type (deserts); and (d) mangroves were not considered because of their low representation. We obtained the geographical distributions of our seven biomes by directly editing the map of Olson et al. (2001).

Next, we ran a random forest (RF) classification model on the climate data for each biome. For this purpose, we used mean annual precipitation, precipitation seasonality and mean annual temperature, with a spatial resolution of 0.042° (c. 5 km²), that were drawn from WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). RF is a machine-learning algorithm that classifies objects by combining the predictions of many classification trees generated by random samples of the data. The approach outperforms most other methods used for classification in ecology (Cutler et al., 2007). RF is particularly useful for making projections because it combines predictions of many classification trees fitted to random samples of the data, with replacement, to prevent overfitting (Prasad, Iverson, & Liaw, 2006). Each tree identifies range values that determine and characterize each biome (Table 1). To help interpret our results, we built a decision tree using the predicted classification of the RF model. This decision tree illustrates threshold values that characterize biome transitions (Figure 2). We constructed 500 trees using present-day climate information extracted from 20% of the pixels of each biome, totalling 88,226 observations. The predicted class for each pixel is the one that most occurred in the 500 trees generated in our RF model. Values in Table 1 were based on the range of the three climatic variables used to calibrate the RF model (excluding extreme values). The decision tree was constructed using recursive partitioning (Breiman, Friedman, Stone, & Olshen, 1984).

We used the Kappa statistic to evaluate model performance because it can take into account how chance may affect the agreement between model prediction and the reference map. Kappa ranges from –1 to +1, where +1 indicates perfect agreement, and values of zero or less indicate a performance no better than random (Cohen, 1960).

We also calculated the overall disagreement rate, separating it into quantity and allocation disagreement components (Pontius & Millones, 2011). High quantity disagreement means that the total predicted areas of the biomes are different from the reference map. High allocation disagreement means that the positions of the predicted biomes are different from the reference map. In addition, to evaluate the impact of sampling on the downstream biome stability analyses, we repeated the procedure 100 times, each time randomly resampling 20% of the pixels. Accuracy was measured as the proportion of times that each pixel was consistently classified; we used this map to interpret our results in the face of biome assignment uncertainty.

Once all biomes were classified in present-day climatic conditions, we used the fitted algorithm to hindcast their geographical distributions for time slices of 1,000 years through the past 21 kyr. Past climate scenarios were based on simulations using the Hadley Centre Climate model (HadCM3; Singarayer & Valdes, 2010). Monthly temperature and precipitation anomalies were downscaled with a bilinear spline to 0.2°, then with a bicubic spline to 0.042°, and the final resolution of all maps in the analyses was 0.042°. Mean annual temperature, mean annual precipitation and precipitation seasonality were recreated for each 1,000-year time slice. The palaeoclimate dataset, used by Carnaval et al. (2014), is available for download at Dryad (<http://data-dryad.org/resource/doi:10.5061/dryad.8kc1v>). Biome stability was quantified by counting how many times a change in climate was predicted to push a raster grid cell from one biome to a different one through the past 21 kyr. Biome classifications for each time slice, stability and accuracy raster files are available as Supporting Information (Appendices S1–S24).

2.2 | Long-term vegetation dynamics in South America

We assessed long-term vegetation dynamics across the continent by compiling pollen records from the past 30 kyr for eight reasonably well-studied and diverse target regions in South America: north, west, east and south Amazonia, central and north Cerrado

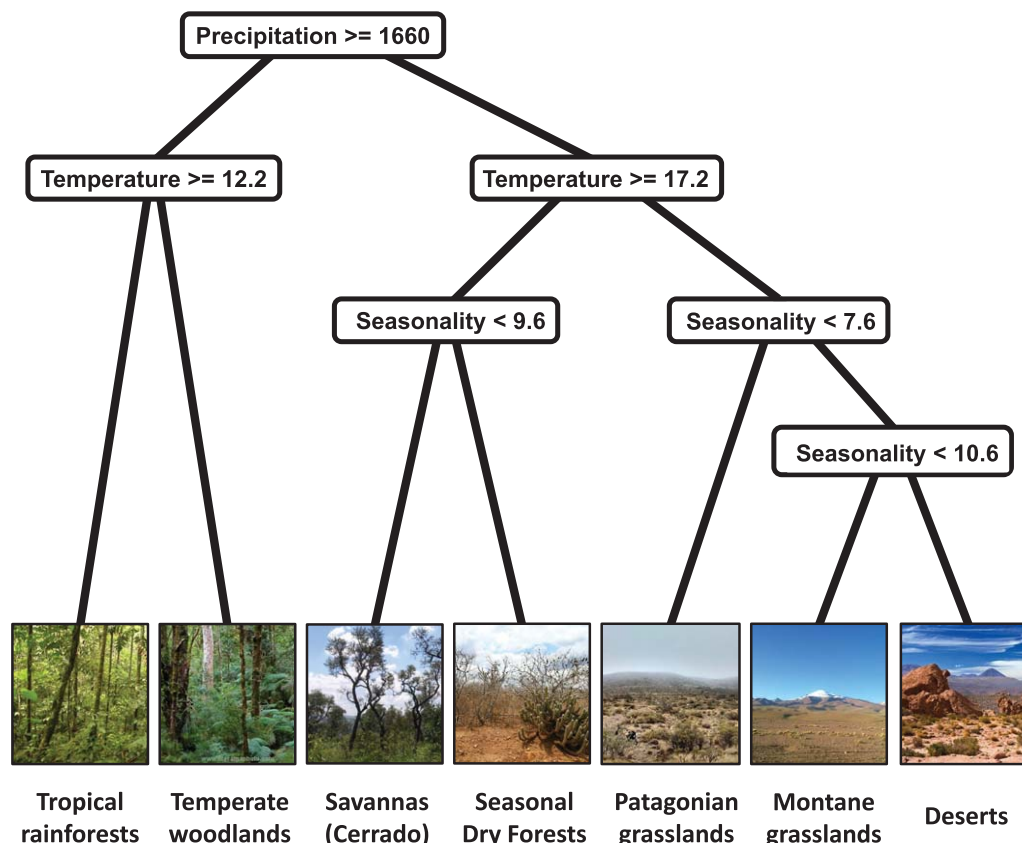


FIGURE 2 Decision tree showing relationships between predicted vegetation types of the random forest model with mean annual temperature (in degrees Celsius), mean annual precipitation (in millimetres per year) and precipitation seasonality (no units). The tree was pruned to a size of seven terminal nodes (leaves) that represent the seven vegetation types used to calibrate the random forest model. Non-terminal nodes indicate the splitting criteria. Branches to the left of non-terminal nodes contain predicted vegetation types for which the splitting criteria are true

and southeast and south Atlantic Forest. To be included in this verification analysis, pollen records had to fulfil two criteria: (a) include a robust chronology that allowed plausible linear interpolations between dates, and (b) encompass a sufficiently large number of samples to ensure appropriate temporal resolution. Underlying assumptions are that sedimentation has been continuous between time slices and that observed ecological change was continuous between sequential fossil samples.

For each region, we used the available pollen records to measure the time-lag of local biome transitions (e.g., forest to grassland). Based on available data, we assigned the time-lag in a given pixel to one of three classes: ≤ 1 kyr, 1–8 kyr or ≥ 8 kyr. We did this because the speed of biome change provides insights into the spatial configuration of the vegetation before the occurrence of a biome change (e.g., a change from grassland to forest). For instance, a rapid expansion of forest in response to increased precipitation points to the previous existence of forested areas (microrefugia) in the area, whereas a slow expansion suggests previous widespread tree extinction.

We also compiled the number of times each region underwent changes in floristic composition (i.e., beyond the functional plant types that define biomes). Based on the number of pollen taxa identified in the record, we estimated trends in species richness during biome changes.

To estimate the number of vegetation shifts per time unit, plant compositional changes were derived from fossil pollen analysed at discrete points in time (i.e., time slices). We calculated rates of change (RoC) as the dissimilarity between pollen assemblages from two adjacent time slices divided by the time interval between them (Urrego, Bush, & Silman, 2010), and transformed them as $(RoC_{\max} - RoC_{\min})/RoC_{\min}$. Underlying assumptions of our calculation were that sedimentation was continuous between time slices and that observed ecological change was continuous between two fossil samples. When these assumptions could not be met, we did not make the calculation (no data).

3 | RESULTS

3.1 | A model of biome stability for South America

Our RF model for the distribution of biomes in South America (Figure 1b), based on present-day climate conditions, produces a map (Figure 1a) remarkably similar to that of Olson et al. (2001). The RF model performs well, with a Kappa value of .87 and an overall disagreement rate of 11% (Table 1). Most (83%) of the overall disagreement is attributable to allocation disagreement, which is mainly because of misassignment between tropical forests and savannas, tropical forests and seasonally

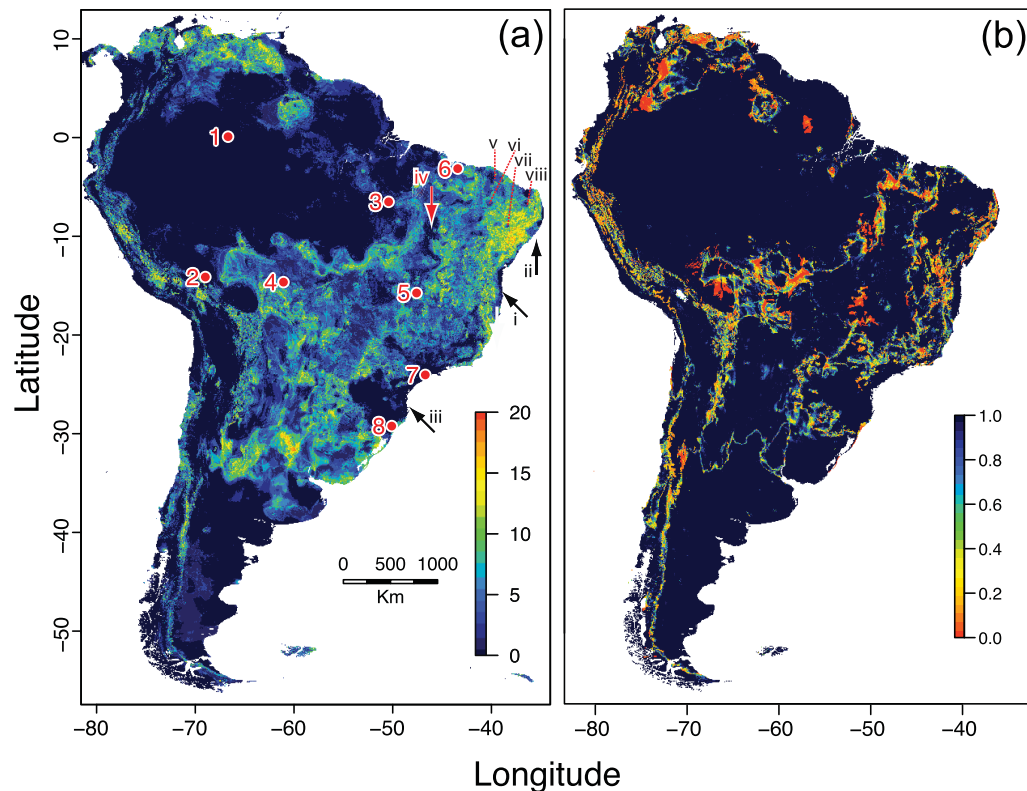


FIGURE 3 (a) Biome stability map based on the random forest classification model shown in Figure 1a, applied in 1,000-year climatic intervals until the Last Glacial Maximum (LGM, 21 kyr BP). Higher values indicate pixels with more potential vegetation shifts. Numbered localities correspond to the pollen localities given in Table 2. (b) Map of cell-by-cell model accuracy in the classification of biomes. Accuracy is measured as the proportion of times that each cell was classified correctly in 100 runs with 20% of climate data resampled in each run. Lower accuracy is shown in red and higher accuracy in blue. Arrows indicate climate refugia mentioned in the text, as follows: (i) Bahia refugium, (ii) Pernambuco refugium, (iii) Southern Atlantic Forest refugium, (iv) Serra Geral de Goiás refugium, and (v–viii) locations of some isolated patches Atlantic Forest patches known as ‘brejos de altitude’: (v) Serra do Baturité, (vi) Serra da Ibiapaba, (vii) Serra Negra, and (viii) Planalto da Borborema

dry forests, and to a lesser extent, savannas and seasonally dry forests. Figure 2 shows a decision tree illustrating the most important variables and their thresholds for biome transitions. Annual precipitation $> 1,660$ mm separates forested biomes from the non-forested biomes. Within the forested biomes, mean annual temperature $> 12.2^{\circ}\text{C}$ results in tropical rain forests, whereas lower temperatures result in temperate woodlands. Within the non-forested biomes, temperatures $> 17.2^{\circ}\text{C}$ result in savannas or seasonal dry forests, with the distinction between these two biomes occurring because of higher precipitation seasonality values in seasonal dry forests. The other non-forested biomes (Patagonian grasslands, montane grasslands and deserts) are also distinguished by precipitation seasonality, which is highest in deserts and lowest in Patagonian grasslands.

Projecting the RF model to the Last Glacial Maximum (LGM; 21 kyr) results in overall considerable expansion of tropical forests, and a contraction and fragmentation of seasonal dry forests and savannas (Figure 1c). A biome stability map built from palaeoprojections of the RF model is shown in Figure 3a, and the accuracy of predictions (with pixels having lower accuracy tending to cluster in ecotones) is in Figure 3b. The RF model indicates that tropical forest has remained fairly stable throughout the past 21 kyr in most of the

Amazon basin. Regions of lower relative stability are mostly restricted to east Amazonia. In the Atlantic Forest, biome stability is inferred to be high in the Pernambuco and Bahia coastal regions as well as in the largely montane southern parts of the biome (Figure 3a). The Caatinga, a seasonally dry forest located in northeast Brazil, is largely unstable, especially near its border with the Atlantic Forest, but also in contact zones with the Cerrado; several of these unstable areas coincide with pixels where the model has lower classification accuracy (Figure 3b). Montane grasslands, Patagonian grasslands and temperate forests are generally stable. Inferred levels of stability in the Cerrado region of central Brazil are geographically heterogeneous, with values showing a tendency to decrease from the core of the biome towards its periphery.

3.2 | Long-term vegetation dynamics in South America

The pollen fossil data indicate different levels of biome stability, ranging from areas experiencing no change at all to others with multiple changes (Table 2). The former occurs in north and west Amazonia, although pollen records show gradual floristic changes, with a

TABLE 2 Features of representative high-quality pollen records from different regions in South America (see Figure 3a for locations) representing different biomes

Region	Locality	Vegetation	Rate	Pollen taxa richness	Time-lag	Number	Scenario	Reference
1. Northern Amazon	Pata, 0°16' N 66°41' W, 300 m	Cool to warm rain forest	1	No data	8,000	0	4a	Colinvaux, De Oliveira, Moreno, Miller, and Bush (1996)
2. Western Amazon	Consuelo, 13°57' S 68°59' W, 1,360 m	Cool to warm rain forest	1	No data	8,000	0	4a	Bush, Silman, and Urrego (2004); Urrego et al. (2010)
3. Eastern Amazon	Carajás, 6°20' S 50°25' W, 700 m	Grassland to rain forest	No data	No data	3,000	6	4b	Absy et al. (1991)
4. Southern Amazon	Laguna Chaplin, 14°28' S 61°04' W, 175 m	Grassland to rain forest	1	No data	1,700	1	4d	Burbridge, Mayle, and Killeen (2004)
5. Central Cerrado	Águas Emendadas, 15°34' S 47°35' W, 1,040 m	Cool/moist forest (pre-LGM) to warm/dry forest (post-LGM)	No data	No data	14,000	1 (2)	4c	Barberi, Salgado-Labouriau, and Suguio (2000)
6. Northern Cerrado	Caço, 2°58' S 43°25' W, 120 m	Grassland to rain forest	4.89	30–40 post-LGM 50–60 Forest development 3.5 Forest 2.5 Cerrado	500	3	4b	Ledru et al. (2006)
7. Southeastern Atlantic Forest	Colônia, 23°52' S 46°42' W, 900 m	Grassland to rain forest	12.57	10 to 40 1.75 to 4 (Atlantic Forest development)	500	4	4b	Ledru et al. (2009)
8. Southern Atlantic Forest	Cambará do Sul, 29°03' S 50°06' W, 1,040 m	Grassland to rain forest	7	40 to 15 2 to 3.5 (atl for devpt)	9,500	1	4c	Behling and Pillar (2007)

LGM = Last Glacial Maximum; Locality = coordinates and elevation a.s.l.; Number = number of extreme vegetation change events that occurred in the past 30 kyr; Pollen taxa richness = richness and/or biodiversity index for the most extreme event of the record; Rate (RoC) = rate of changes for the most extreme event of the record; Scenario = inferred biodiversity scenario as illustrated in Figure 4; Time-lag = time-lag (in years) needed for total forest recovery from the most extreme event of the record; Vegetation = vegetation shift registered for the most extreme event of the record.

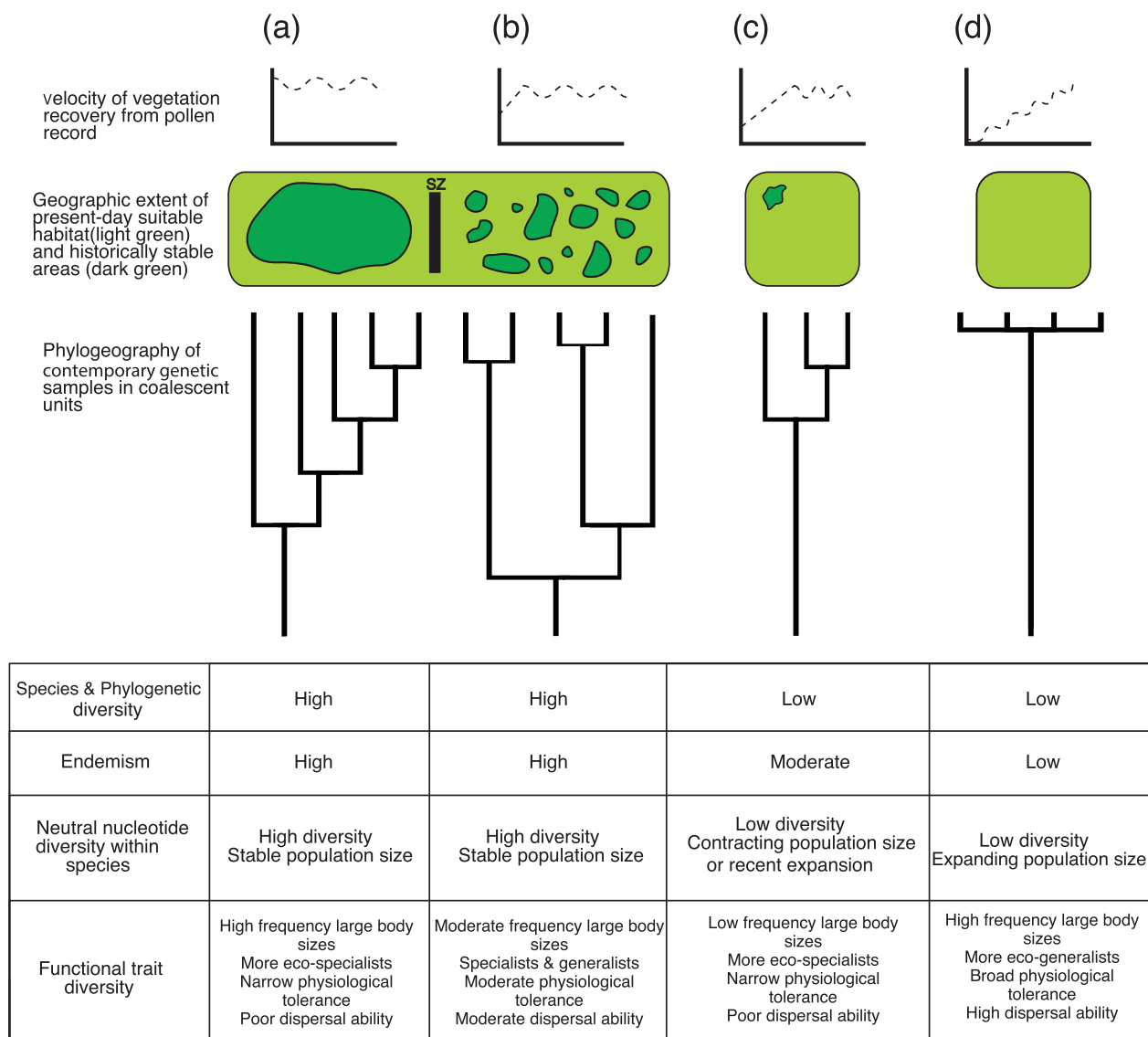


FIGURE 4 Conceptual model of different scenarios of climate-driven vegetation dynamics and their effects on different components of biodiversity: (a) a large area that was climatically stable through time, (b) mosaic of stable and unstable habitats in space and time, (c) small area of stable habitat (dark green) inside a large unstable area (light green) where all lineages remain geographically or environmentally isolated, and (d) completely unstable areas with present vegetation being established only recently. Summaries of predicted biodiversity patterns under different scenarios are given in the box (see text for details on each scenario). SZ = suture zone

successive disappearance of Andean species from the lowlands after the LGM. One biome transition event is reported in south Amazonia and the south Atlantic Forest, when grasslands were replaced by forest vegetation. In contrast, three or more biome transitions have occurred in the east Amazon, the southeast Atlantic Forest and in northeast Brazil, particularly in ecotone regions.

There is also significant geographical variation in the rate of habitat change and the time-lag for habitat recovery after the most extreme climatic event (Table 2). High rates of change are reported, for instance, for the southeast Atlantic Forest and, to some extent, the south Atlantic Forest and north Cerrado. Consistent with the models, the pollen fossil records from the southeast Atlantic Forest and the north Cerrado also show the smallest time-lags in biome

recovery, whereas the records from central Cerrado, north and west Amazonia and south Atlantic Forest show longer transition times.

4 | DISCUSSION

Our biome model, when fitted to present-day climate, was statistically robust and a very close match to commonly used South America biome maps (Figure 1a). Assignment accuracy is slightly lower in pixels located within seasonally dry forests. Our decision tree shows that threshold values determining biome transitions are similar to values reported previously (e.g., Hirota, Holmgren, Van Nes, & Scheffer, 2011; Oyama & Nobre, 2004; Staver, Archibald, & Levin, 2011). These results suggest

that our RF model successfully captures how the South American biomes respond to broad-scale climatic drivers.

4.1 | Amazon basin

Interestingly, our model projection for the LGM shows a conspicuous expansion of tropical moist forests. This result seems to contradict the widespread traditional assumption of drier conditions in the region during the LGM (Farquhar, 1997). However, it is in line with recent studies based on speleotherm data (e.g., Cheng et al., 2013) that proposed an expansion of forest vegetation in the western Amazon and the southern Atlantic Forest during the LGM, with a concurrent retraction in the Eastern Amazon and Northern Atlantic Forest. Our results corroborate the forest expansion in the Western Amazon and Southern Atlantic Forest, whereas they do not detect the hypothesized retractions in the Eastern Amazon and Northern Atlantic Forest. As a consequence of this expansion, our results highlight the importance of ancient connections between the Atlantic Forest and the Amazon. Specifically, our results corroborate that the southeast-to-northwest connection has a stronger relative importance than a connection through the northeast. This hypothesis was proposed by Por (1992) and was recently supported by correlative distribution models (Ledo & Colli, 2017).

Our analysis of biome stability indicates that most of the Amazon basin remained relatively stable during the past 21 kyr, which is in agreement with vegetation simulations (e.g., Cowling et al., 2004). However, we also detected a longitudinal gradient, with consistently higher biome stability in the western portion relative to the east. This trend is supported by the fossil data, which indicated considerably fewer habitat shifts, lower rates of change and lengthier time-lags for vegetation turnover in the western and northern part of the biome than in the eastern and southern Amazon. These results clearly point to higher forest stability in the former parts.

4.2 | Atlantic Forest

Our RF model shows climatically stable areas known as the Pernambuco and Bahia refugia (Carnaval & Moritz, 2008). Interestingly, we also identified stable areas in the southern portion of the Atlantic Forest, a result that also emerges when this climatically distinct region is modelled separately (Carnaval et al., 2014). These southern forests have recently been described as historically stable refugia for different taxa in the Atlantic Forest (Porto et al., 2013; Thomé et al., 2010) and hold one of the world's most irreplaceable protected areas (Le Saout et al., 2013), with high levels of genetic diversity (Raposo do Amaral, Albers, Edwards, & Miyaki, 2013) and endemism (Carnaval et al., 2014). Our fossil vegetation record for this region shows high rates of inferred biome shifts and short time-lags for forest recovery (Table 2). In this region, grasslands were predominant 2,000 yr BP, before being progressively replaced by forest. This highly dynamic history inferred in the pollen record, combined with our model stability in coarse scale, suggests that the biome configuration may not have been homogeneous in the region and that multiple small forest refugia may have existed during the grassland phase, allowing for a rapid forest

expansion when the climate shifted to conditions more favourable to a tropical forest biome.

4.3 | Savannas

High biome stability is inferred for the core portion of the Brazilian Cerrado. Our model was able to identify the well-established Serra Geral de Goiás refugium and other previously identified stable areas scattered across central Brazil (Werneck, Nogueira et al., 2012). Pollen records also show the persistent occurrence of Cerrado vegetation in the region through the last 30 kyr, despite minor changes in the density of trees relative to grasses (Ledru, 2002). Near the border of the Cerrado, however, at present covered by a transitional seasonal rain forest, both our model and the pollen record suggest markedly higher biome instability over time. However, as mentioned above, the transition zones are more difficult to model and tend to have lower accuracy levels for our model.

4.4 | Other biomes

Deserts, montane grasslands, Patagonian grasslands and temperate forests do not show signs of multiple transitions (Figure 3a). However, some substantial changes in biome configuration are shown in the LGM projection of our RF model (Figure 1c). Regions of high instability are also shown in northern and central Andes (Figure 3a). However, predictions on these regions must be interpreted with caution because it also shows lower levels of accuracy, which is expected in a region of such complex topography (Figure 3b). The fossil pollen record for southern Chile indicates a similar environmental history and behaviour to the southern portion of the Atlantic Forest (e.g., Bennett, Haberle, & Lumley, 2000). Another interesting pattern is the high instability observed in seasonal dry forest, both in northeast Brazil (i.e., the Caatinga) and in northern Argentina and Paraguay (i.e., the Chaco region). This result may be explained by the fact that a large part of seasonal dry forest occurs near transitions with other biomes. Also, seasonal dry forest occupies a similar environmental space to other biomes (e.g., savannas), and their presence might be driven by other variables, such as geomorphology and edaphic conditions (Mayle, 2004; Werneck et al., 2011).

4.5 | Effects of habitat stability on biodiversity: four scenarios

The trends that we observed, although by nature continuous, can be classified in four major scenarios of past biome changes according to the relative importance of different mechanisms by which climate change has affected the distribution of biomes in South America since the LGM. As we expect that these scenarios might be observed in other regions of the world, with similar biological effects, we describe them here under a broader conceptual framework (see also Hampe & Jump, 2011).

4.5.1 | Scenario 1. Long-term persistence of continuous habitat

Both the models and the fossil pollen data indicate high biome stability (albeit with shifts in floristic composition) over the past 30 kyr in north

and southwest Amazonia, the south Atlantic Forest and parts of the Cerrado (Figure 3a and Table 2); these regions fit the scenario illustrated in Figure 4a. We propose that, owing to low extinction rates, these areas of continuous, stable habitat are expected to harbour very high levels of both taxonomic and phylogenetic diversity, including high levels of endemism (Graham, Moritz, & Williams, 2006; Sandel et al., 2011). At the within-species level, these regions are expected to harbour populations of high and stable effective sizes (Excoffier, Foll, & Petit, 2009) and high genetic diversity (Carnaval et al., 2009). From the viewpoint of functional diversity, even species with specialized ecological requirements, narrow physiological tolerances and poor dispersal abilities should have had enough time to colonize the region. Finally, its long-term stability would imply the predominance of stable communities that provide opportunities to generate complex biotic interaction networks and, eventually, co-evolutionary processes (e.g., Dalsgaard et al., 2011; Jansson & Dynesius, 2002).

4.5.2 | Scenario 2. Rapid retraction–expansion dynamics favoured by the existence of multiple microrefugia

Our maps of regions such as the northern Cerrado and the southeast Atlantic Forest show a mosaic of stable and unstable biomes. In line with this spatial heterogeneity, the fossil pollen records from these areas show very rapid biome changes, with three to four major vegetation shifts and a time-lag ≤ 1 kyr, respectively (Table 2). Such intense vegetation dynamics can best be explained by recurrent climate-driven local extinction events followed by rapid recolonization processes, which are catalysed by the existence of multiple source populations that persist through climatically unfavourable periods in regionally widespread microrefugia (i.e., multiple microrefugia; Rull, 2009). Such a multirefugia situation corresponds to our second scenario, shown in Figure 4b. We expect regions with such a configuration to harbour high taxonomic richness owing to the long-term persistence of many (yet not all) species in multiple microrefugia. Depending on the time-scale of isolation, vicariance might result in speciation events (Bell et al., 2011; Ledru, Mourguiart, & Riccomini, 2009; Médail & Diadema, 2009). However, phylogeographical diversity should be dominated by genealogies with shorter terminal branches and longer internal branches than under scenario 1 (Gattepaille, Jakobsson, & Blum, 2013; Nei, Maruyama, & Chakraborty, 1975) because recurrent biome fragmentation should lead to lower historical connectivity among populations (especially in organisms with low dispersal ability) and thus, deeper coalescence of lineages. At the within-species level, recurrent colonizations from long-term refugia might result in a mosaic of highly divergent and admixed populations, with strong differences arising from species' dispersal behaviour. This process would result in a regional-scale mix of areas with high proportions of endemic lineages (i.e., putative refugia; Sandel et al., 2011) intermingled with suture zones where different lineages come into secondary contact (Moritz et al., 2009; fig. 4 of Remington, 1968). Species distributed across such regions are predicted to have generally high yet unequally distributed levels of genetic diversity (Ledru et al., 2009). Finally, patterns of functional diversity should be characterized by a mixture of communities with a high proportion of specialists (in microrefugia) and other, more

widespread communities with a stronger dominance of generalists and good dispersers (in areas of colonization; Jansson & Dynesius, 2002).

4.5.3 | Scenario 3. Moderate extinction–colonization dynamics constrained by a low abundance of microrefugia

Our models and inferred vegetation dynamics of the '*brejos de altitude*' in the northern Atlantic Forest (Figure 3a, areas v–viii) indicate that current and past climate restricted this biome to a small portion of the geographical space, whereas most of its surroundings shifted to another biome configuration (in that case, seasonally dry forests). Under such spatial configuration of habitat shifts, a stability map of the biome would show only a small portion of the habitat as stable through time ('microrefugia'; dark green area in Figure 4c) within a larger unstable region (light green area in Figure 4c; in the case of the '*brejos de altitude*', this area is occupied by Atlantic Forest today). Once climatic conditions again become favourable for biome expansion, one would expect the pollen record to show slow biome restoration in the unstable area, mainly because recolonization by the vegetation is now prompted by propagules coming from a small refugium. When all of the unstable area is occupied by the new biome, pollen levels stabilize.

The described situation corresponds to the scenario illustrated in Figure 4c. Both taxonomic and phylogenetic diversity should be moderate, with clear-cut peaks in scattered enclaves (the putative microrefugia). Endemics are likely to be rare. The diversity of low-dispersal, specialist species is expected to decrease rapidly as one moves away from refugial areas, whereas the high-dispersal generalist species dominating newly colonized areas are expected to be widespread geographically across the biome. At the within-species level, marked historical bottlenecks should have reduced effective population sizes, and hence genetic diversity (Clegg et al., 2002; Hewitt, 2004). Genetic signals of demographic expansion should generally be strong, although they may have been overridden in the most dispersive species. And even species widespread today will still tend to show low effective population sizes (as measured with molecular markers) compared with species inhabiting historically more stable areas (Charlesworth, 2009). From the viewpoint of functional diversity, scenario 3 is characterized by an elevated risk of local to regional scale species extinctions during periods of unfavourable environmental conditions. Hence, species that are not well adapted to persist over long periods of time at small population size and low carrying capacity (e.g., large-sized herbivores, top predators or highly specialized parasites) should be underrepresented in such environments. Accordingly, communities should be characterized by relatively simple networks of biotic interactions.

4.5.4 | Scenario 4. Recent biome formation

The seasonally dry forest of northeastern Brazil, termed Caatinga, is the most historically unstable region in South America. The fossil pollen record underpins the young age of the present-day biome itself, which appears to result from changes in vegetation structure and floristic composition at a variable pace. The Caatinga falls within the fourth scenario of biome stability (Figure 4d), for which we expect generally low taxonomic and phylogenetic diversity, with lower levels of endemism (Graham et al., 2006; Sandel et al., 2011). The region is likely to be

dominated strongly by generalist species with high dispersal capacity. Populations of such species are likely to show evidence of recent and rapid growth, such as low nucleotide diversity, haplotypes coalescing to a very recent common ancestor and overall low among-population differentiation (Carnaval et al., 2009; Gehara et al., 2017; Hewitt, 2000). Likewise, biotic communities should be characterized by low alpha, beta and gamma diversity compared with other tropical seasonally dry forest biomes.

5 | CONCLUSION

Understanding how climatic fluctuations shape biodiversity is a fundamental goal of macroecology and biogeography. Many studies dealing with biodiversity patterns at different levels of organization have used conceptual and empirical approaches to understand the relationships among climatic predictors and biodiversity, and different methods have been used to generate spatially explicit estimates of stability. Our study approach differs from previous ones in that it does not simply link the magnitude or velocity of climatic trends with patterns of biodiversity but instead focuses on the relationship between long-term temporal variation in climate and its effect on habitat stability. The new approach allowed us to develop a map of biome stability for South America, whose validity was tested, and largely corroborated, using high-quality fossil evidence. Our models can be applied easily to different climatic scenarios, including future projections of climate change. Using our models, we would be able to predict regions that are at increased risk of a biome shift, which when coupled with anthropogenic land changes could imperil biodiversity more severely. Naturally, our models and their interpretations are contingent upon the quality of the climatic data used to build the model, and as newer and better datasets become available the models can be revised accordingly. Finally, our derived conceptual scenarios provide a priori hypotheses that can be tested in specific study systems. We thus hope that our study will be a baseline resource to stimulate discussion and spur new research among those in the scientific community interested in the past and future of biodiversity in South America.

DATA ACCESSIBILITY

The palaeoclimate dataset used here is available for download at Dryad (<http://datadryad.org/resource/doi:10.5061/dryad.8kc1v>). Our biome classifications for each time slice, stability and accuracy raster files are available as Supporting Information (Appendices S1–S24).

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BIOSKETCH

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SUPPORTING INFORMATION

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

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