ORIGINAL RESEARCH ARTICLE

Climate change shifts the distribution of vegetation types in South Brazilian hotspots

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Abstract
Research on the dynamics of vegetation distribution in relation to past climate can provide valuable insights into terrestrial ecosystems' response to climate change. However, paleoenvironmental data sources are often scarce. The integration of ecological niche modeling and paleoecological data can fill in this knowledge gap. In order to elucidate the potential impacts of past and future climate change on the distribution of multiple vegetation types, we used 433 occurrence points of 100 species to build distribution models of five vegetation types occurring in southern Brazil, based on past, current, and future scenarios. Past models indicated the existence of a steppe domain during the Last Glacial Maximum, with forest expansion during the Mid-Holocene, which is consistent with paleoenvironmental data. The current distribution model identified a large area that was climatically suitable for ecotones in an important protection area threatened by agribusiness. The optimistic projections for 2070 predicted an expansion of mixed ombrophilous and seasonal semi-deciduous forests to a higher altitude and latitude, respectively. The pessimistic projections predicted a catastrophic scenario, with the extinction of the steppe and the savanna and a major increase of areas unsuitable for all vegetation types. The ombrophilous dense forest remained stable in all time scenarios, even in the pessimistic future projection. The results of the present study reinforce the need for the implementation of policies that will reduce greenhouse gas emissions that drive global climate change, which may lead to the extinction not only of species but also of landscapes as we know them today.

Keywords Atlantic Forest · Cerrado · Ecological niche modeling · Global warming · Maxent · Paleodistribution

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Introduction

Climatic fluctuations during the Quaternary, mainly the glacial and interglacial cycles in Pleistocene (Barnola et al. 1987), have driven many changes in the distribution range of organisms globally (Hewitt 2000; Bueno et al. 2017). Paleoenvironmental studies have shown that the vegetation mosaic that covers Southern Brazil and consists of forests, grasslands (steppes), and savannas was the result of climatic fluctuations, which alternated between hot/wet and cold/dry periods (Behling 1997, 1998; Ledru et al. 1998; Behling and Negrelle 2001; Behling et al. 2004). With the exception of the Pampas, which cover the southernmost portion of Brazil, these different vegetation types in Southern Brazil are mainly found in two global biodiversity hotspots: the Atlantic Forest and the Cerrado (Myers et al. 2000). This distribution suggests that this vegetation mosaic features exceptional concentrations of endemic species, and also experiences excessive habitat loss.

In terrestrial ecosystems, deforestation is the major cause of extinctions (Sala et al. 2000; Newbold et al. 2015; WWF

2018); however, climate change may have an equal or even greater impact on biodiversity loss (Selwood et al. 2014), especially in biodiversity hotspots (Malcolm et al. 2006; Jantz et al. 2015). According to the Intergovernmental Panel on Climate Change (IPCC), the global temperature is likely to increase by up to 4.8 °C by the end of the century (IPCC 2014). South America is the continent with the highest extinction risks caused by climate change (Urban 2015) and the Atlantic Forest is a hotspot particularly vulnerable to global warming (Bellard et al. 2014).

Research on the dynamics of vegetation distribution in relation to past climate can provide valuable information on terrestrial ecosystems' response to future climate change (Blois et al. 2013; Nolan et al. 2018). However, there are still many gaps in terms of knowledge on the identity and distribution of species (Cardoso et al. 2011; Diniz-Filho et al. 2013; Hortal et al. 2014). The existing knowledge on the structure of the Atlantic Forest is based on only 0.01% of the forest that remains (de Lima et al. 2015). A strategy that can fill in these biodiversity knowledge gaps, while also generating information on the effects of the climate on vegetation distribution, is ecological niche modeling (ENM).

ENM is a computational method that can estimate the potential distribution of species by associating occurrence points with environmental variables, characterizing environmental conditions that are appropriate for the species, and identifying where and how these suitable environments are distributed in space, time, and geographic scenarios (Pearson 2007; Peterson and Soberón 2012). The integration of ENM results and paleoecological data provides a detailed geographic framework for addressing many biogeographic questions of great value to ecology and conservation, such as identifying factors that determine the limits of species' distribution and assessing the impacts of climate change on this distribution (Peterson et al. 2004; Svenning et al. 2011).

Although ENM tools are most commonly used in species distribution analysis, they also provide valuable information on ecosystems and biomes (Sobral-Souza et al. 2015, 2018; Manish et al. 2016; Wang et al. 2017). The State of Paraná (Southern Brazil) is situated in an interesting phytogeographic location, in which tropical and subtropical floral elements are mixed, and multiple disjunct and relictual vegetation types occur, which make Paraná a vast field on which to conduct biogeographic studies (Kaehler et al. 2014). The vegetation mosaic of Paraná is formed by distinct forest intervals with herbaceous and shrub formations, resulting from different environmental conditions (Roderjan et al. 2002; Marques et al. 2011). Furthermore, in Paraná State exist areas where two Brazilian hotspots, the Atlantic Forest and the southernmost portion of the Cerrado, meet (Myers et al. 2000), which is a rare occurrence; these areas are characterized by high endemism (Ritter et al. 2010; Maia and Goldenberg 2014; Pereira and Labiak 2018) and ecotone formations (Bianchi et al.

2012; Moro et al. 2012; Batista and Bastos 2014; Caxambú et al. 2015).

In this study, we used the vegetation types of Paraná as models to elucidate the potential impact of past and future climate change on the distribution and conservation of the multiple vegetation types in a rare contact zone of the two aforementioned Brazilian hotspots. More specifically, our goals were (1) to demonstrate the power of ENM in studying the distribution of different vegetation types in relation to climate, (2) to reconstruct the vegetation distribution during the Last Glacial Maximum (LGM) and Mid-Holocene (MID) and compare these results with paleoenvironmental data, (3) to identify suitable areas for ecotone occurrences, and (4) to estimate the changes in each vegetation type from the LGM to 2070, with the use of both optimistic and pessimistic future projections for the latter.

Material and methods

Occurrence points of vegetation types

As a guide, we used the distribution of vegetation types in Paraná that we obtained from Maack (1948), who described the original vegetation cover before it was replaced by farmland and pasture land (Da Silva and Passos 2010). Maack identified five major vegetation types (Fig. 1): ombrophilous dense forest (ODF), which covers the eastern portion of the State and is characterized by a high canopy, where trees reach heights of up to 40 m; mixed ombrophilous forest (MOF), which covers plateau portions of the State and is characterized by the presence of Araucarias, the Paraná pine (*Araucaria angustifolia*); seasonal semi-deciduous forest (SSF), localized in western and northern regions, which also has a high canopy, but the trees partially lose their leaves in the driest months; steppe (STE), which is situated at higher altitudes and is formed by grasslands and shrubs; savanna (SAV), which is located in the southernmost portion of the Cerrado and formed by arboreal and shrubby woody plants.

We selected a set of species to represent each vegetation type, prioritizing endemic species and species with concentrated distributions in regions around Paraná, including the States of São Paulo, Mato Grosso do Sul, Santa Catarina, and Rio Grande do Sul (Online Resource 1.1). The species set was selected based on information from Brazilian Flora 2020 (floradobrasil.jbrj.gov.br/), a project that includes descriptions, identification keys, and illustrations of all plants, algae, and fungi species known in Brazil.

Occurrence records were obtained from the GBIF and SpeciesLink databases. We removed duplicate records, or those from which data were missing or were unreliable. We filtered the records so that no pair of points was closer than 10 km, a treatment suggested by Boria et al. (2014) in order to
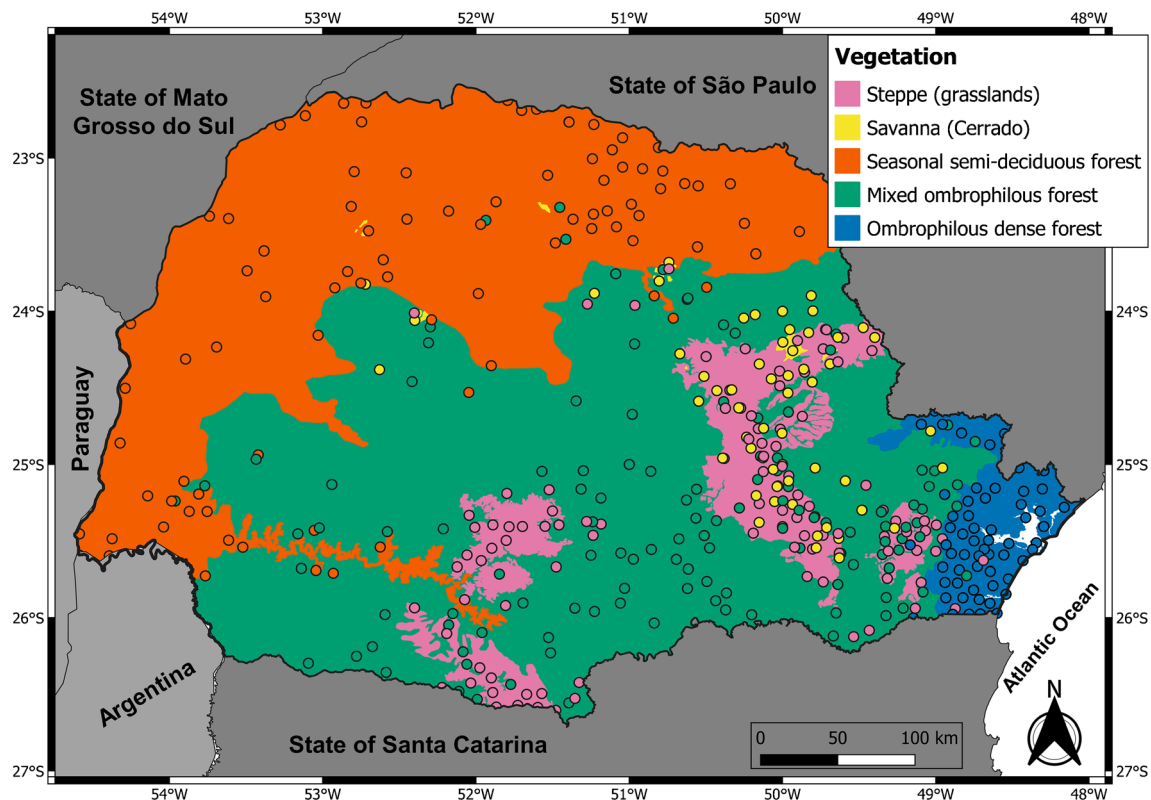
Fig. 1 Distribution of vegetation types in the State of Paraná (Southern Brazil) according to Maack (1948), and occurrence points (dots) used to build distributions models in Maxent

reduce the effects of sampling bias and spatial autocorrelation on model performance. In sum, we used 433 occurrence records of 100 species (Fig. 1, Online Resource 1.2), which consisted of 101 STE (39 species), 63 SAV (15 species), 89 SSF (10 species), 120 MOF (12 species), and 60 ODF (24 species) records.

Environmental variables and climate change scenarios

We obtained environmental variables for the current climatic conditions as well as for past and future climate projections from the WorldClim database at a spatial resolution of 30 arcsec, except for the LGM layer, for which data were available only at 2.5 arcmin. In order to reduce the dimensionality and collinearity of the environmental layers, we used Pearson's correlation coefficient to remove variables with high cross-correlation values ($> \pm 0.6$; Online Resource 1.3 and Online Resource 2), thereby reducing the set of 19 variables to four variables, which were temperature annual range (Bio07), mean temperature of warmest quarter (Bio10), precipitation of wettest quarter (Bio16), and precipitation of driest quarter (Bio17). This set of variables condensed the climate conditions in Paraná, including seasonal variations, and may have had an impact on vegetation distribution.

The same bioclimatic variables were obtained for past climatic conditions during the LGM (22 ka) and MID (6 ka) and for future projections, for which we formulated an optimistic (RCP 2.6) and a pessimistic (RCP 8.5) scenario for 2070. We used the bioclimatic variables derived from two global climate models (GCMs), CCSM4 and MIROC-ESM, because they are available in WorldClim for both past and future scenarios. The use of a range of GCMs and future emission scenarios is more appropriate for ecological studies because climatic predictions can vary greatly among GCMs, and considering both optimistic and pessimistic scenarios may be important in conservation management and political negotiations (Harris et al. 2013, 2014; Porfirio et al. 2014; Varela et al. 2015). Online Resource 2 provides a more detailed description of each bioclimatic variable projected in each time scenario by these GCMs.

Ecological niche models

We used Maxent 3.4.1 to identify environmentally suitable sites for the persistence of each vegetation type in past, current, and future climate scenarios. We chose Maxent over other available modeling methods because of its superior performance and suitability for presence-only data (Phillips et al. 2006) and for vegetation types (Wang et al. 2017); additionally, Maxent has been cited in more than 1000 published

papers since 2006 (Merow et al. 2013); it is free to use and became open source in 2017 (Phillips et al. 2017).

Seventy percent of the occurrence data of each vegetation type were randomly allocated to model calibration and the remaining 30% to model evaluation, with 100 bootstrap replications. We used the following validation metrics: area under the receiver operating characteristic curve function (AUC) (Fielding and Bell 1997), calculated by Maxent; true skill statistics (TSS) (Allouche et al. 2006), corresponding to the maximum training sensitivity plus specificity threshold; and the Boyce Index (Boyce et al. 2002), calculated using the "ROCR" and "ecospat" R packages. We created response curves showing how the variation of each variable affected the probability of the presence of each vegetation type using the DAT outputs (*_only.dat) generated by Maxent.

Vegetation shifts and paleoenvironmental data

The vegetation type with the highest suitability for a given grid cell was assigned as the most likely vegetation type of that grid cell, based on the methodology proposed by Wang et al. (2017). Grid cells below the threshold corresponding to the maximum sensitivity plus specificity (Liu et al. 2013) for all vegetation types were classified as undefined. We estimated the percentage of persistence and changing areas of each vegetation type relatively to their distributions between each time scenario. We also compiled paleoenvironmental records published by other authors and compared these with models built for the LGM and MID scenarios. In sum, we used seven LGM and 12 MID records (Online Resource 1.4).

Climatically suitable areas for ecotones

We converted suitability models from continuous to binary values (presence or absence) using as a threshold the tau value corresponding to the Cloglog output in Maxent (tau = 0.632). Tau is the minimum value given to a grid cell considered a typical location of a specie (Phillips et al. 2017). We defined as climatically suitable areas for ecotones the grid cells in which the suitability values of 2 or more vegetation types reached values above the threshold. The climatically suitable areas for ecotones identified in this study were close to the ecotone concept defined by the Brazilian Vegetation Technical Manual (IBGE 2012); in this, ecotones are described as areas of tension between two or more vegetation types, which is similar to one of the first definitions given by Clements (1905). Thus, we considered as climatically suitable areas for ecotones not only simple transition areas but also regions where there was a high probability of different vegetation types coexisting.

More details about the analysis are provided in the Online Resource 3, which includes a fully reproducible, dynamic document that combines code, rendered results (figures and tables), and explanations.

Results

The statistical validation measures suggested that the models of all vegetation types performed well (Table 1). Vegetation types with narrow distribution (STE, SAV, and ODF) performed better than those with broader distribution (SSF and MOF).

According to the response curves (Fig. 2), the areas with the lowest temperature variation were more suitable for ODF and the areas with the highest temperature variation were more suitable for SSF. The coolest areas were more suitable for STE, while the warmest areas were more suitable for ODF and SSF. SAV and MOF have highly suitability in areas with intermediate temperatures. The driest areas were more suitable for SSF, while the wettest areas were more suitable for ODF. STE, SAV, and MOF have highly suitability in areas with intermediate precipitation.

The current vegetation distribution predicted by Maxent (Fig. 3) is similar to the phytogeographical map created by Maack (1948; Fig. 1). This distribution made possible the identification of a large area that was climatically suitable for ecotones and consisted of STE, SAV, and MOF in the central eastern region of Paraná, which coincides with the Devonian Scarp, an important protection area in Paraná State.

In general, the projections showed the same patterns in the GCMs derived from CCSM4 (Fig. 4) and MIROC-ESM (Fig. 5). Both models predicted a domain consisting of STE and MOF during the LGM, with SAV and ODF stretches in the north and on the coast, respectively. During the MID, both models indicated an expansion of certain forest types, mainly MOF over STE and SSF over MOF. The paleoenvironmental profiles with which a vegetation type was associated were located within or in very close proximity to the modeled distribution range of the vegetation type in both past scenarios (Fig. 3, Online Resource 1.4). Between the MID and the current scenario, both models showed a further expansion of MOF over STE and a southward expansion of SSF.

The optimistic projections for 2070 (RCP 2.6) predicted a major expansion of MOF over STE in high-elevation areas and a southward expansion of SSF over MOF and SAV.

Table 1   Statistical validation measures of vegetation type models

Vegetation type	AUC	TSS	Boyce Index
Steppe	0.91	0.74	0.80
Savanna	0.90	0.74	0.70
Mixed ombrophilous forest	0.83	0.58	0.74
Seasonal semi-deciduous forest	0.79	0.54	0.79
Ombrophilous dense forest	0.96	0.87	0.63

Means of 100 replications. *AUC*, area under the curve; *TSS*, true skill statistic

Fig. 2 Response curves of each vegetation type to bioclimatic variables. The dashed line marks the tau value (0.632), which corresponds to the minimum value determined for grid cells with environmental conditions considered by Maxent as typical of the location in which each vegetation type occurs
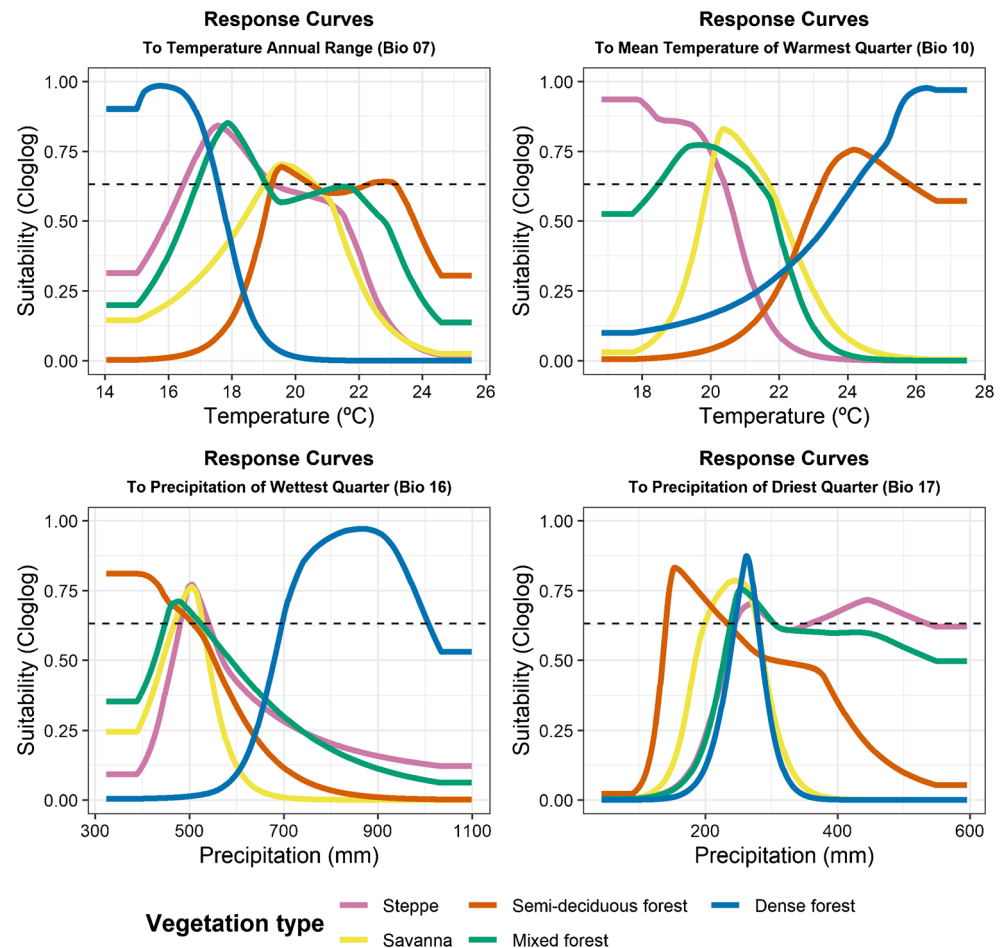
The suitable ecotone areas were reduced by 66% and 82% in the optimistic scenarios derived from CCSM4 and MIROC-ESM, respectively. The pessimistic projection for 2070 (RCP 8.5) predicted a catastrophic scenario, in which STE and SAV are expected to be virtually extinct, MOF is restricted to small patches, SSF expands to the southernmost portion of Paraná, and large areas become unsuitable for all vegetation types. The only exception is ODF, which remained stable even in the pessimistic projections. In neither of the pessimistic scenarios there were suitable ecotone areas.

Discussion

The characterization of vegetation responses to climate is important for assessing the potential impact of climate change on terrestrial ecosystems (Seddon et al. 2016). In this study, we utilized for the first time data generated by ENM to describe the responses of different vegetation types to bioclimatic variables. The response curves of vegetation types to bioclimatic variables were consistent with the general descriptions of Roderjan et al. (2002) and of others who conducted studies in Paraná and reported the presence of ODF in regions with

high temperature and rainfall (Marques et al. 2011), MOF in wet and cold regions (Fritzsons et al. 2018), SAV in areas that were colder compared with its core region further north (Bustamante et al. 2012; Oliveira et al. 2014), STE in the coldest regions usually associated with the highest altitudes (Iganci et al. 2011), and SSF in regions with high temperatures and with a defined dry and warm period (Higuchi et al. 2013).

In addition to the response curves, the good predictive ability of the models was reaffirmed by the congruence between the paleoenvironmental data and the projections to past periods. In general, paleoenvironmental studies in Paraná report a STE domain during the LGM, with a few records of MOF, and a forest expansion over STE and SAV caused by temperature or precipitation increases. Continental (Behling 1998; Behling and Negrelle 2001; Cruz et al. 2006) and marine (Gu et al. 2017) records from adjacent regions in São Paulo and Santa Catarina also indicate the existence of a grassland domain in the highlands and a forest and grassland mosaic in the lowlands during the LGM, with a marked expansion of forests over grasslands during the MID. Although there is no direct evidence of the presence of ODF during the LGM in Paraná, there is evidence of an expansion of this vegetation type in São Paulo owing to high precipitation levels in tropical

Fig. 3 Distribution models of Paraná vegetation types during the Last Glacial Maximum (LGM) (22 ka), Mid-Holocene (MID) (6 ka), and current period as well as in 2070 (RCP 2.6 and RCP 8.5); these scenarios were derived from CCSM4 and MIROC-ESM. Stripped areas indicate climatically suitable areas for ecotones and grid cells indicate two or more vegetation types with suitability values above the tau value (0.632). In the LGM and MID models, points indicate paleoenvironmental records (Online Resource 1.4)
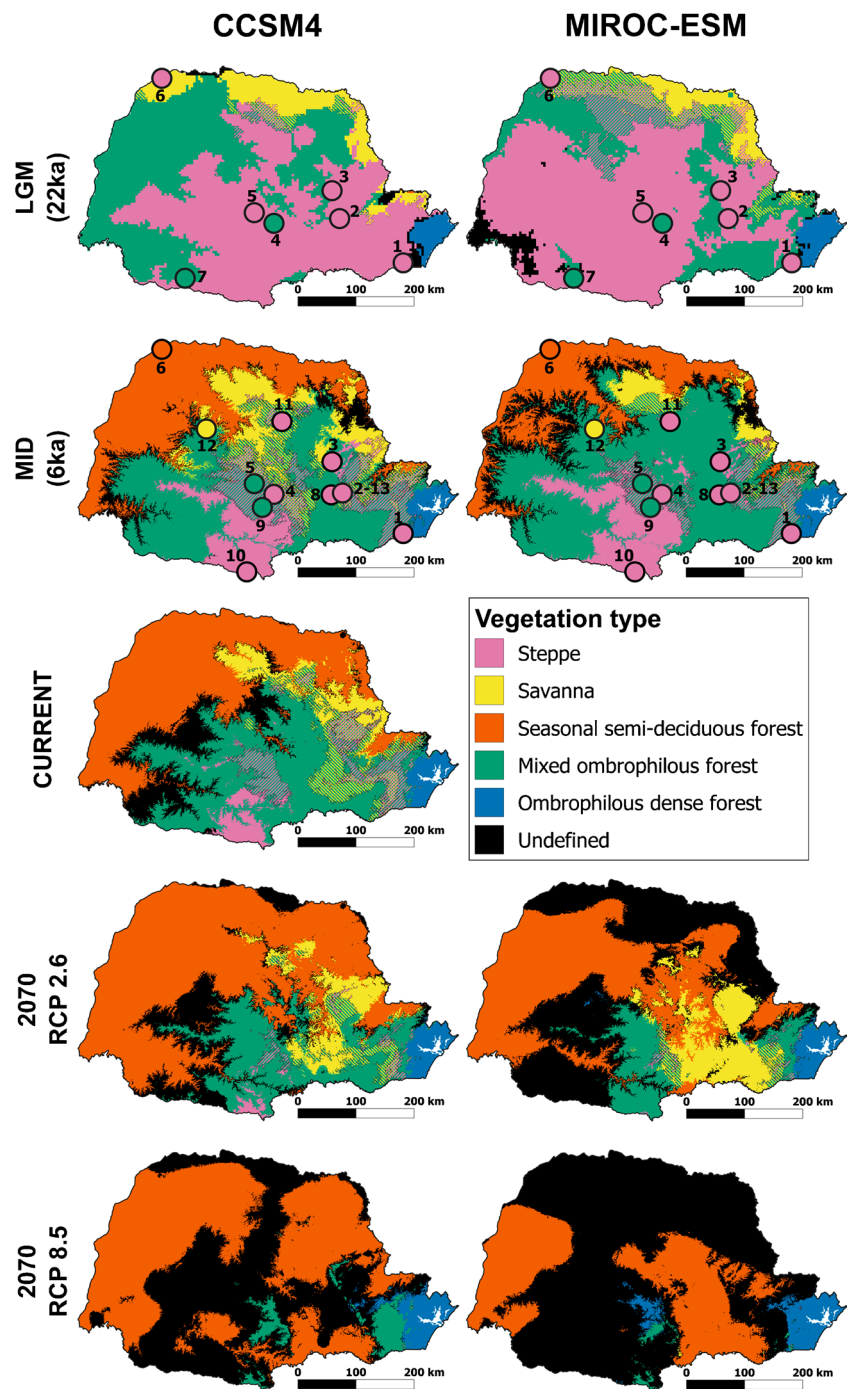

and subtropical latitudes between 24 ka and 21 ka ago (Ledru et al. 2005). The integration of the ENM results with paleoenvironmental data offers the potential for an enhanced contribution of paleobiology to ecology and conservation biology, thereby offering a quantitative ecological perspective that may inform conservation management decisions by estimating future climate change impacts (Svenning et al. 2011).

The current vegetation distribution predicted by Maxent (Fig. 3) also evidenced the predictive power of the models, as it was similar to the phytogeographical map created by

Maack (1984; Fig. 1), which is considered the most important Paraná vegetation record because it was described before original vegetation was replaced by farmland and pasture land (Da Silva and Passos 2010). In this study, ENM results were used for the first time to identify climatically suitable areas for ecotones, which are places of great importance in terms of conservation and the study of evolutionary and ecological processes (Smith et al. 1997; Kark et al. 2007; Kark 2017). Also worth mentioning is the conservation unit called Devonian Scarp, a topographic step with peaks rising up to

Fig. 4 Percentage of persistence and change of the dominant vegetation types among the time scenarios produced by CCSM4. The values above the bars indicate the area (%) covered by each vegetation type before a change occurred. (a) Changes between the Last Glacial Maximum and Mid-Holocene, (b) changes between the Mid-Holocene and the current period, (c) changes between the current period and 2070 (RCP 2.6), and (d) changes between the current period and 2070 (RCP 8.5). The Y-axis takes into account only one vegetation type per grid cell (the dominant vegetation type with the highest suitability), and does not take into account the presence of more than one vegetation type in areas classified as ecotones
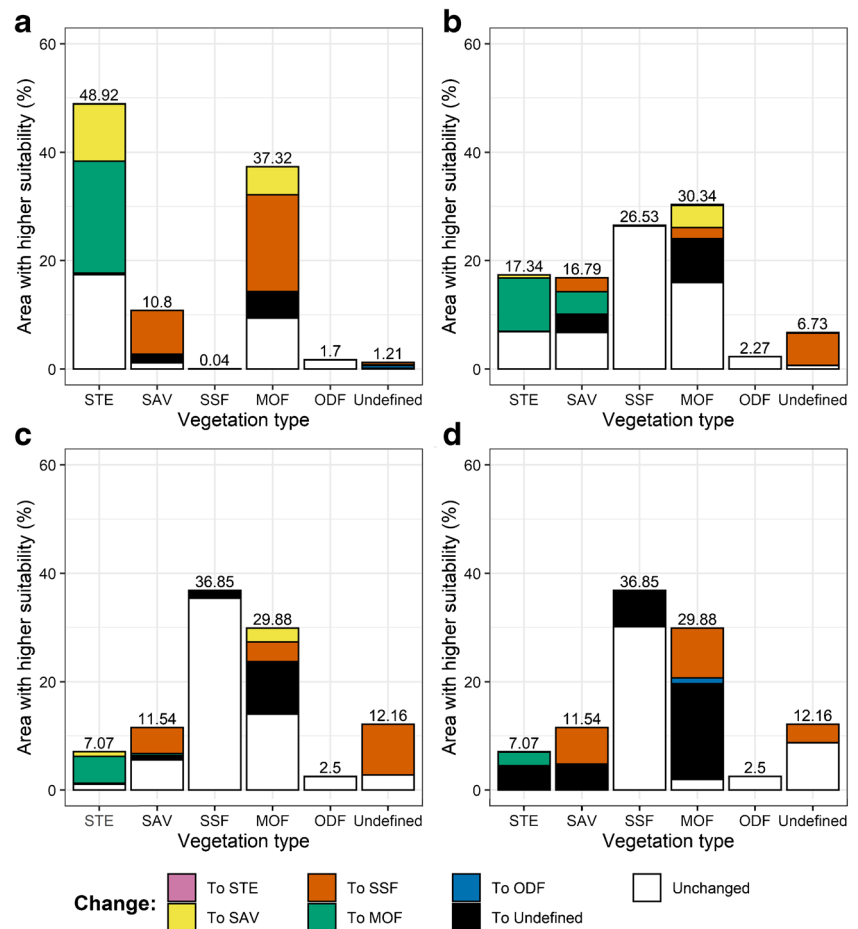

1290 m and slopes up to 450 m (Maack 2002), which, according to the current predicted distribution, had a high probability of coexisting with STE, SAV, and MOF. Floristic surveys in Devonian Scarp confirm the existence of STE with SAV and MOF patches (Takeda et al. 1996; Carmo et al. 2010; Da Silva and Passos 2010; Moro and Carmo 2010; Ritter et al. 2010; Carmo and Assis 2012).

Recently, a bill (PL 527/2016) was proposed to reduce the Devonian Scarp area by 68%, on the premise that its current borders are overly restricting land use by farmers (Paraná 2016). The bill was shelved in 2018, but it can be raised for discussion any time. The results of the present study reinforce the importance of the Devonian Scarp as a conservation unit. This area offers protection to a vegetation mosaic formed by the oldest vegetation in Paraná (STE), which is the result of the encounter of two Brazilian hotspots (the Atlantic Forest and the southern border of the Cerrado SAV), and by the vegetation type that is the symbol of Paraná State (MOF), where the Paraná pine and mate tea (*Ilex paraguariensis*) are found, which are species of economic and medicinal importance that are represented in the Paraná State flag (Martins-Ramos et al. 2010).

Both GCM scenarios indicate that the ODF has remained fairly stable throughout the past 22 ka and should remain stable in the future, even in the pessimistic projection. Climatically stable areas are related to centers of high diversity and endemism (Harrison and Noss 2017), play an important role in understanding the evolutionary history of biodiversity, and can contribute to protecting it against climate change (Keppel et al. 2012, 2015). Other studies have identified the coast of Paraná as a climatically stable area (Carnaval and Moritz 2008; Ferro et al. 2014; Carvalho and Del Lama 2015; Costa et al. 2018) and a center of endemism (Murray-Smith et al. 2009) and high diversity (Zwiener et al. 2017a), which highlights the importance of conserving this forest.

The models suggest that climate change is a threat to biodiversity. In the optimistic projections for 2070 (RCP 2.6), the models predicted a major expansion of MOF over STE in high-elevation areas, and a southward expansion of SSF over MOF and SAV. Indeed, species distributions have recently shifted to higher altitudes and higher latitudes (Chen et al. 2011) and they are likely to affect ecosystem functioning and human well-being (Pecl et al. 2017). The MOF in Paraná harbors species of economic and medicinal importance

Fig. 5 Percentage of persistence and change of the dominant vegetation types among the time scenarios produced by MIROC-ESM. The values above the bars indicate the area (%) covered by each vegetation type before a change occurred. (a) Changes between the Last Glacial Maximum and Mid-Holocene, (b) changes between the Mid-Holocene and the current period, (c) changes between the current period and 2070 (RCP 2.6), and (d) changes between the current period and 2070 (RCP 8.5). The Y-axis takes into account only one vegetation type per grid cell (the dominant vegetation type with the highest suitability), and does not take into account the presence of more than one vegetation type in areas classified as ecotones
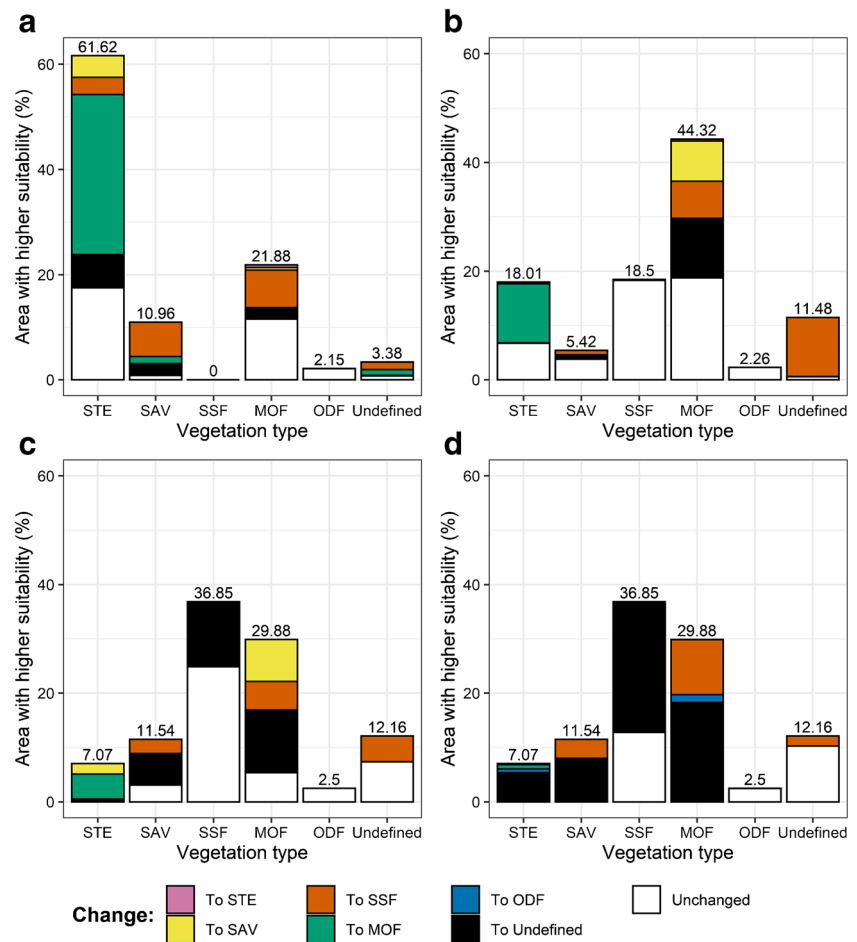
(Martins-Ramos et al. 2010). STE areas are often used as forage resources by livestock, play an important role in greenhouse gas mitigation (O'Mara 2012; Andrade et al. 2015), and are more reliable carbon sinks than forests (Dass et al. 2018). A notable reduction of suitable areas was observed for both vegetation types, even in the optimistic scenario, which coincides with the UNFCCC Paris Agreement that aims to limit global warming well below 2 °C and as close to 1.5 °C as possible (UNFCCC 2015).

In the pessimistic projection for 2070 (RCP 8.5), the models produced an even more worrying scenario, which predicted the extinction of STE, SAV, and the ecotones. The SSF is unlikely to expand to the southernmost portion of Paraná. The extent to which populations will migrate and adapt will depend upon several factors, such as the effective population size and dispersal ability (Aitken et al. 2008). The SSF is currently restricted to small fragments, mostly in agricultural areas (Dettke et al. 2008), and it may stop the movement of species (Heller and Zavaleta 2009). The immense increase of areas identified as unsuitable for all vegetation types in the pessimistic projections is also worthy of concern. Under a pessimistic scenario, the synergistic effects of future land use changes and global warming are projected to reduce the

natural vegetation cover by up to 58% in hotspots (Jantz et al. 2015), with an accompanying disruption of ecosystem services and impact on biodiversity (Nolan et al. 2018). The unsuitable areas identified in this study may be covered by either widespread native species (Zwiener et al. 2017b), species from other vegetation types not included in this study (e.g., from seasonal deciduous forests), or invasive species (Walther et al. 2009; Bradley et al. 2010; Gallardo et al. 2017; Lamsal et al. 2018). Therefore, climate change may enhance biotic homogenization by facilitating the invasions of widespread native species and alien species.

In addition to validation metrics, other indirect inferences such as response curves and paleoenvironmental data reinforce the predictive power of the models. However, the model results should be interpreted with caution. Vegetation distribution also depends upon complex ecological relationships involving predictors not included in model calibration and predictions, such as the soil, microclimate, dispersal capacity, biotic interactions, time-lag effects, and human activities (Pearson 2006; Wisz et al. 2013; Wu et al. 2015; Wang et al. 2017). For example, combining bioclimatic and soil properties may prevent an overestimation of the current vegetation cover and allow us to better predict the transitions

between biomes (Arruda et al. 2017). However, incorporating soil variables in past and future projections can be problematic owing to a lack of information on past pedoenvironments. Keeping soil variables constant in the past or future projections may result in unlikely scenarios because some pedogenic processes occur over short time periods (Targulian and Krasilnikov 2007) and soil properties change along with climate and vegetation by means of complex feedbacks (Stärz et al. 2016). There are significant gaps in our understanding of the migratory capacity of plants in a rapid climate change scenario (Corlett and Westcott 2013) and the inclusion of these variables in ENM is an important challenge to improve the robustness of models in projecting the distribution of vegetation under future conditions.

Conclusions

In this study, we estimated the current, past, and future distribution of multiple vegetation types in a contact zone of two Brazilian hotspots, by using a niche modeling approach. The Atlantic Forest and the Cerrado are highly threatened by fragmentation and land use changes, and here we showed that climate change may further intensify biodiversity loss. Future projections reinforce the need for policies to reduce greenhouse gas emissions that drive global climate change, which may lead to the extinction not just of species but also of landscapes as we know them today.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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