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FORESTRY SCIENCE

Climate change effects on marginal savannas from central-north Brazil

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Abstract: This study estimated the potential effects of climate change on peripheral plant diversity by predicting the distribution of species from Cerrado of Northern Brazil. Ecological niche modeling was used to provide present and future projections of responses in terms of occurrence of ten woody species based on four algorithms and four future climate change scenarios for the year 2050. Potential refuge areas for conservation actions were identified, and evidence of the vulnerability of the flora was demonstrated based on the disparity between potential areas of climate stability amid current protected areas. The results suggested a lack of pattern between the scenarios and an idiosyncratic response of the species, indicating different impacts on plant communities and the existence of unequal stable alternative conditions, which could bring consequences to the ecological relationships and functionality of the floras. Even in the most pessimistic scenarios, most species presented an expansion of potential occurrence areas, suppressing or cohabiting with species of adjacent biomes. Typically marginal plants were the most sensitive. Overlapping adequate habitats are concentrated in the NBC. The analysis of habitats in relation to anthropized areas and PAs demonstrate low future effectiveness in the protection of these savannas.

Key words: biodiversity forecasting modeling, ecological niche modeling, refuge, woody distribution.

INTRODUCTION

Changes in climatic conditions are periodic and common in nature in different regions of the planet. They correspond to a natural cyclic process involving warming, cooling and intense geological activities of the earth that promote various phenomena and effects, causing changes in biological systems and ecological interrelations (Oliveira et al. 2017). However, anthropogenic actions of the last 200 years have contributed to harmful conditions, changing particle/gas concentrations in the atmosphere with the intensification of land use and occupation (Oliveira et al. 2017, IPCC 2018), and accelerating the speed of environmental processes to the point of preventing species from adapting or finding more suitable places to live.

The increase in the average global surface temperature is one of the main concerns of the scientific community in view of its immediately noticeable effects and relation with the biosphere in general. During the last century, the increase recorded was of approximately 0.87 °C above pre-industrial levels (IPCC 2018) and if the temperature continues to rise at the current rate, the increase is estimated to reach 1.5 °C between 2030 and 2052 (IPCC 2018). The expected average increase in South America is 4 °C, indicating a higher frequency of extreme events in Brazil, such as floods and heat waves (Marengo 2005). Regional models indicate that by the end of the 21st century, the most intense effects will occur in the tropical region, specifically in the Amazon and Northeast of Brazil (Nobre et al. 2008).

Climate and geological transformations have triggered adaptive processes in biological communities, leading to their evolution, development, diversification, dispersion and extinction throughout the history of lineages (Costa et al. 2012a). It is particularly important to be aware of their effects on biodiversity, because of the associated changes in distribution, phenology, migration calendar, nesting success, and population sizes of species. Thus, the response of biodiversity to climate change has become a very fruitful field for research (Hughes 2000, McCarty 2001, Walther et al. 2002, 2005, De Marco Junior & Siqueira 2009, Bellard et al. 2012), including studies with animal (Crick 2004, Ribeiro et al. 2018, Miranda et al. 2019) and plant assemblages (Siqueira & Durigan 2007, Simões et al. 2019).

Biological interaction with climate is observed in geophysical patterns of vegetation distribution, reflecting different bioclimatic zones (Salazar et al. 2007). Within the South American climate ranges, Amazônia and Cerrado are the predominant biomes. They are also largely deforested, which has led to worsening climate change because the removal of vegetation cover promotes a warmer and drier regional climate (Nobre et al. 2008). However, although some evidence of current extinctions is correlated with climate change, studies suggest that climate phenomena could outweigh habitat destruction as the greatest global threat to biodiversity in the coming decades (Pereira et al. 2010, Bellard et al. 2012).

Studies on Quaternary climate fluctuations and vegetation in Brazil confirm that successive expansions and retractions occurred between forests and savannas (Silva & Bates 2002, Werneck et al. 2012, Bueno et al. 2016), the main habitat typologies in Brazil. Cerrado is the largest forest savanna in South America, covering 21% of the country's land area and extending marginally into Paraguay and Bolivia, behind only the Amazon Forest in terms of extension (CI 2019). Research in tropical South America has shown Brazil as a region where significant amounts of forests are converted into non-forest areas as a result of global warming (Ledru 2002, Sanaiotti et al. 2002, Salazar et al. 2007). Field observations and numerical models also indicate loss of tropical forest cover (Soares-Filho et al. 2006, Vale et al. 2008, Rochedo et al. 2018, Gomes et al. 2019), replaced by savannas (Salazar et al. 2007); this potential reorganization of the distribution of biodiversity can affect the structure, dynamics and functioning of ecosystems and their respective contributions (Gallagher et al. 2013).

Research about spatiotemporal ecological representations of species has increased considerably in recent years with the advancement of geoprocessing and species distribution modeling tools by ecologists and conservation managers, and thus the need to provide efficient assessments of these predictive models (Teles 1996, Allouche et al. 2006). Species Distribution Models (SDMs) allow spatial extrapolation of known occurrence records at different scales and generate potential distribution maps based on the effects of climate change on species distribution (Teles 1996, Costa et al. 2012b, Oliveira & Cassemiro 2013).

Although the assessment of the effects of climate change on Brazilian biodiversity is increasing in all biomes, especially those predominantly forested and with greater species richness and endemism (Amazon and Atlantic Forest) (Aleixo et al. 2010), there are few attempts to predict the impacts on non-forest areas (Siqueira & Peterson 2003, Terribile et al. 2012). High levels of environmental devastation have made Cerrado to be included in the list of biodiversity hotspots (Myers et al. 2000, CI 2019), and yet minimal (scientific and political-social) attention has been given to the marginal and disjunct patches of the Cerrado of the North and Northeast, called the modern Brazilian agricultural frontier. They refer, in large part, to "MATOPIBA", a portion of the North and Northeast savannas with more than 73 million hectares (8.5% of the Brazilian territory), recognized as the portion between the states of Maranhão, Tocantins, Piauí and Bahia (Heck & Menezes 2016) that accounts for much of Brazil's grain and fiber production (https://www.embrapa.br/tema-matopiba).

Despite its importance, there is a growing concern with maintaining biodiversity and understanding the ecological relationships among local species, intensified by projections of climate scenarios. In order to support conservation strategies in this ecological transition region in central-north Brazil (from the Amazon to the Brazilian Sertão), this research applied spatial analysis procedures and modeling tools to predict the potential distribution of a representative set of common species considering the entire Cerrado biome (generalists") and another representative set of species most frequently associated with the marginal and disjunct areas of the biome ("marginals). Our hypothesis is that the "generalists" will be favored by a scenario of increased temperatures, especially in ecotonal areas replacing forest formations, but marginal species may suffer losses from climatically suitable areas.

Based on the physical-environment (thematic maps) and biological (species occurrence) variables of the current times, algorithms were applied in order to model the fundamental niche and the potential area of occurrence of the species. The following questions were investigated in this study: based on the potential current occurrence range of the target species, do the impacts of future climate change on their distribution predict retraction or expansion of the forecasted occurrence of the central-north peripheral Cerrado? Do predictions of future occurrence among species of wide geographical distribution ("generalists") differ from those most frequent in the northern portion of the Biome "marginals')? Are environmentally stable areas of future predicted scenarios located inside Protected Areas (PAs) at present? In this context, this study aimed to estimate the impact of climate change on the future extent of occurrence of peripheral Cerrado of central-north Brazil.

MATERIALS AND METHODS

Focal area

The geographic area investigated belongs to the central-north region of Brazil, focusing on marginal and disjunct savannas in relation to the continuous block of the Cerrado biome. The aim was to investigate the effects of climate change on different vegetation types showing the influence of adjacent phytogeographic domains. Projections and analyses are mainly concentrated in the North and Northeast regions (approximate limits 6°N, 19°S, 74°O and 34°O), covering the Amazon, Cerrado, Caatinga and their ecotonal areas, involving natural climatic boundaries between rainforests, savannas and semi-arid steppes (IBGE 2012). The studied area is one of the Cerrado's biodiversity and endemism supercenters, but lacks information on primary biological data, and therefore represents a preferred target for inventories (Vieira et al. 2019).

Data selection

Species lists were initially obtained from floristic data networks from Cerrado areas (http://savanna.rbge.org.uk, Ratter et al. 2011, Castro et al. 2010, Vieira et al. 2019). In addition, twenty-one areas were sampled in the northern region of Cerrado (in the states of Piauí, Maranhão, Pará and Amapá; data available at https://doi.org/10.5061/dryad.9cnp5hqd4). To test our hypothesis, we divided the species on these lists into two groups that we will refer to here as “generalists” (SpG) and “marginals” (SpM). First, all species on the lists (N=235) were ranked according to their constancy value and the first five were selected as representatives of the generalist group (*Bowdichia virgilioides* [754 occurrences], *Byrsonima crassifolia* [523], *Qualea grandiflora* [858], *Q. parviflora* [727], *Salvertia convallariodora* [561]; Table I). Then, from the lists of the northern region of Cerrado inventories, the species were ranked by importance value and the five were selected (*Curatella americana* [956], *Himatanthus articulatus* [441], *Parkia platycephala* [259], *Plathymenia reticulata* [604], and *Vatairea macrocarpa* [413] (Table I).

Several ecological indexes in taxocenoses of woody plants (constancy, diversity, richness, evenness, and importance value index - IV) ware used as indicators of environmental degradation through the analysis of standardized. IV is an estimator of the ecological importance of taxon within a forest community, calculated as the sum of the relative density, relative dominance and relative frequency of a given species (see Costa-Coutinho et al. 2019, 2021) for more details on the ten species selection criteria.

Finally, in addition to inventory and field survey data, occurrence records of these species were obtained from the Global Biodiversity Information Facility open access platform (http://gbif.org) using the *rgbif* package (Chamberlain et al. 2019) in *R* (R Development Core Team 2019). In addition, three pseudo-absence/background databases were created containing ten times the number of occurrences and arranged outside the minimum convex polygon containing the occurrences.

The total known area occurences of each species in South America was used for the model fitting process (see below), as it represents the complete up-to-date data available from the species. We excluded non-georeferenced records, and those outside the expected distribution for the species (through visual inspection), and we kept only records 1 km apart from each other, to minimize the spatial autocorrelation. Although typical of Cerrado, they are plants also recorded in ecotonal areas under the influence of neighboring domains, and for this reason we double checked the records based on the checklist of the present study, in the revised floristic lists of Castro et al. (2010), Ratter et al. (2011), Vieira et al. (2019) and the Species List of the Brazilian Flora (BFG 2018, http://floradobrasil.jbrj.gov.br). The final database included 6,106 presence records (ranging from 256 to 956) for the ten native species of Brazil, which were significantly represented in Cerrado sites.

WorldClim data on current climate and projections for 2050 (http://worldclim.org, Fick & Hijmans 2017), at a resolution of 30 arcseg (about 1 km²) within the spatial boundaries of South America (12°N, 56°S, 91°O, 34°O) were used for the purpose of creating ecological niche models (ENMs). This extension was used to capture the spectrum of climate variation for the entire known distribution of species. Among the 20 variables (altitude and 19 bioclimatic variables), the least collinear variables were selected using the *remove Collinearity* function (multicollinearity.cutoff = 0.75, nb.points = 10000) from the *virtual species* package (Leroy et al. 2015): altitude, annual mean temperature, max temperature of warmest month, isothermality,

Table I. Species and metrics used in modeling the potential distribution of northern savannahs in the Cerrado Biome. Nocc: number of occurrences; Status: generalist (Gen), disjunct northern savannah (SD) and marginal northern savannah (SM); Model performance parameters: ROC, TSS, Cut-off threshold (limit values maximized by TSS for binarization), Sensitivity, Specificity; Extension, difference, and proportion of the projected area according to the scenarios. Highlight: gain (blue) or loss (red) of environmental suitability area.

	Species	Family	Nocc	Status	ROC	TSS	Cut-off	Sensitivity	Specificity
1	*Bowdichia virgilioides* Kunth	Fabaceae	754	Gen	0.99	0.86	99.601	86.326	242
2	*Byrsonima crassifolia* (L.) Kunth	Malpighiaceae	523	Gen	0.99	0.89	99.025	89.532	263
3	*Curatella americana* L.	Dillenicaceae	956	SM/SD	0.99	0.86	99.787	86.103	253
4	*Himatanthus articulatus* (Vahl) Woodson	Apocynaceae	441	SD	0.98	0.86	92.184	93.520	535
5	*Parkia platycephala* Benth.	Fabaceae	259	SM	0.99	0.90	96.139	94.091	343
6	*Plathymenia reticulata* Benth.	Fabaceae	604	SM	0.99	0.88	92.715	94.789	545
7	*Qualea grandiflora* Mart.	Vochysiaceae	858	Gen	0.99	0.88	99.417	88.367	222
8	*Qualea parviflora* Mart.	Vochysiaceae	727	Gen	0.99	0.89	96.699	92.138	424
9	*Salvertia convallariodora* A. St.-Hil.	Vochysiaceae	561	Gen	0.99	0.89	92.857	95.834	576
10	*Vatairea macrocarpa* (Benth.) Ducke	Fabaceae	413	SM	0.99	0.88	92.010	95.560	586

	Current (km^2)	cc45bi50 (km^2)	Differ (km^2)	Prop (%)	cc85bi50 (km^2)	Differ (km^2)	Prop (%)	hg45bi50 (km^2)	Differ (km^2)	Prop (%)	hg85bi50 (km^2)	Differ (km^2)	Prop (%)
1	5.871.057	6.373.603	502.546	8.6	7.548.132	1.677.075	28.6	7.541.033	1.669.976	28.4	7.966.073	2.095.016	35.7
2	7.069.114	7.736.200	667.086	9.4	7.900.337	831.223	11.8	7.884.514	815.400	11.5	8.042.946	973.832	13.8
3	7.017.382	7.998.670	981.288	13.9	8.282.553	1.265.171	18.0	8.398.079	1.380.697	19.7	8.532.321	1.514.939	21.6
4	7.277.459	7.343.353	65.894	0.9	6.849.047	-428.412	-5.9	6.470.654	-806.805	-11.1	6.261.363	-1.016.096	-13.9
5	2.094.985	3.170.098	1.075.113	51.3	3.529.374	1.434.389	68.5	3.134.034	1.039.049	49.6	3.796.085	1.701.100	81.2
6	3.406.092	3.142.752	-263.340	-7.7	3.315.609	-90.483	-2.7	3.564.197	158.105	4.6	3.949.747	543.655	15.9
7	3.819.096	4.442.998	623.902	16.3	4.942.522	1.123.426	29.4	4.906.591	1.087.495	28.5	5.623.282	1.804.186	47.2
8	3.516.116	3.640.991	124.875	3.55	4.014.350	498.234	14.2	3.852.748	336.632	9.6	4.310.968	794.852	22.6
9	3.517.549	3.230.293	-287.256	-8.2	2.970.391	-547.158	-15.6	3.120.214	-397.335	-11.3	2.959.385	-558.164	-15.9
10	3.408.351	3.503.640	95.289	2.8	3.721.776	313.425	9.2	3.622.850	214.499	6.3	3.958.949	550.598	16.2

mean diurnal range, precipitation of coldest quarter, annual precipitation, precipitation of warmest quarter, precipitation seasonality, and precipitation of driest quarter.

Future climate projections were derived from two global atmosphere-ocean circulation models (AOGCM) - the Community Climate System Model (CCSM4) and the Hadley Center Global Environmental Model (HadGEM2-CC) - in two greenhouse gas concentration pathways (RCPs 4.5 and 8.5) foreseen by the Fifth Assessment ($CMIP_5$) of the Intergovernmental Panel on Climate Change (IPCC 2018), representing an optimistic achievable scenario and a "business-as-usual" scenario.

Modeling runs and analyses

To estimate the potential distribution of species, ENMs were generated in the biomod2 package (Thuiller et al. 2019) by running four different algorithms: Generalized Linear Model (GLM), Artificial Neural Network (ANN), Random Forest (RF), and Maximum Entropy (MAXENT). All parameters for models tuning and selection were left in default mode. Species datasets (presence + pseudo-absence records) were randomly divided into 75% for calibration (training points) and 25% for evaluation (test points) and this procedure was repeated 10 times for each set. To assess the predictive power of the models, the True Skill Statistics (TSS; threshold-dependent) values (Allouche et al. 2006) and the area under the receiver operating characteristic (ROC) curve (Phillips et al. 2006) were measured. Sensitivity (proportion of correctly predicted presences/true positives) and specificity (proportion of correctly predicted absences/true negatives) levels were also reported.

The consensus maps were generated by the committee averaging method to represent the concordances between the different runs. The lower performing models (TSS < 0.5) were eliminated from the consensus building process (ensemble). Thus, five consensus maps were generated per species for each scenario (one current, two RCP 4.5 and two RCP 8.5). Continuous habitat suitability values were transformed into binary data (presence/absence) using a cut-off threshold that maximized TSS (see Cutoff in Table I) and the projected area of occurrence was calculated by multiplying the cell area (considered 1x1km) by the cell count.

We also measured the potential dynamics of change in the range extension (area gain/loss) of the species based on the differences between the projected area for current and each future climate scenario. This analysis was made for each species separately, to recognize ecological functional differences between plant populations. The amount of areas with greater climate stability (referred to as refuges in the present study) was calculated from the amount of pixels considered as presence when overlapping the models of all scenarios – individually, by category (generalist [SpG] and marginal [SpM]), and altogether. Based on these refuge maps, the future effectiveness of present PAs from a climate change perspective was measured, accounting for the size of refuge areas for SpG and SpM and both which overlap with the PAs. The data of the Brazilian PAs were obtained from the website of the Ministry of Environment (http://mapas.mma.gov.br).

The modeling results were visualized through the QGIS Geographic Information System (QGIS 2019) and analyzed using the R Statistical environment and the *raster* library). All the procedures described above were chosen to balance the best practices of the method (Feng et al. 2019) with computational feasibility issues.

RESULTS

The models demonstrated high levels of accuracy according to the TSS (0.86 - 0.90) and ROC (all values 0.99), indicating models with predictive quality (Table I). The area for current projections between SpG and SpM species showed high variation (SpG: from 3.5 to 7.0 million km² and SpM: from 2.0 to 7.2 million km²). Estimates made by AOGCM institutions, in general, maintained consistency, but the highest rates of change with more hostile effects were recorded by CCSM4 (CC) (Figure 1).

Considering the maps with continuous suitability values, the areas with the highest rating (red color) in the future will be reduced, fragmented and/or displaced in relation to the present, regardless of whether they are SpG or SpM. However, considering cut-off thresholds for the presence (i.e., the binary maps), our results pointed to a tendency to increase the suitable areas in the future, which is greater in the worst scenario (i.e., 2050 RCP 8.5). Only two species, *S. convallariodora* and *H. articulatus* showed loss of adequate areas in future projections of different scenarios (Figure 2). Much of the future projections remain in the areas dominated by Brazilian Cerrado, but potentially invasions in the adjacent biomes can occur, especially in the Amazon (Figure 1). This means that the marginal savanna region in central north Brazil would gain adequate areas. And more interestingly, both categories will be affected virtually the same way (i.e., gain of area). Still regarding future projections, it is worth noting a southwestward shift, with increased extensions in the states of Mato Grosso, Rondônia and Acre, and Bolivia.

In general, the results of binary maps showed that most projected species are actually being favored with increased potential suitable area in the future. The average gain was of 18.5% in the most optimistic scenario (2050; RCP 4.5) and 26.9% in the worst (2050; RCP 8.5). Comparing the species, *H. articulatus* had the largest environmentally suitable area predicted in the current scenario, followed by *B. crassifolia*, *C. americana* and *B. virgilioides*. However, three species showed a loss of spatial range: *S. convallariodora* (SpG) showed 11% reduction in the less pessimistic and 16% in the most pessimistic scenarios; *H. articulatus* (SpM), also showed between 6 and 14% loss in three of the five scenarios; and there was a similar prediction for *P. reticulata* (between 3 and 11% loss) in two out the five scenarios.

The distribution of refuge areas varies enormously (Figure 3). For instance, considering the SpGs, virtually the entire Brazilian Cerrado region will continue to be suitable in the future, regardless of the scenario, in addition to the western Mato Grosso, Rondônia, in Brazil and the border areas in Bolivia (Figure 3). In contrast, the SpMs' refuge areas are concentrated in the central-north portion of Brazil (i.e., in the south of Maranhão, in the north of Tocantins and in the west of Piauí), highlighting that despite having projected an increase in the range (except *H. articulatus* and *P. reticulata*), this will occur in non-coincident portions with the current range. Thus, influenced by marginal species, refuge areas considering all species are in this central-north portion of Brazil. In future projections, the 278 protected areas of different categories that overlapped the focal areas will house only 4.6% (5,634 km²) of our projected refuges. Less than 10 current PAs are found specifically in refuge areas that encompass all species, the largest being the Ilha do Bananal/Cantão State Environmental Protection Area in Tocantins and the Chapada das Mesas National Park in southern Maranhão (1.7 million hectares). Only 4.8% (7,822 km²) and 8.1% (142,196 km²) of the marginal and generalist species, respectively, will be protected inside PAs (Figure 3).

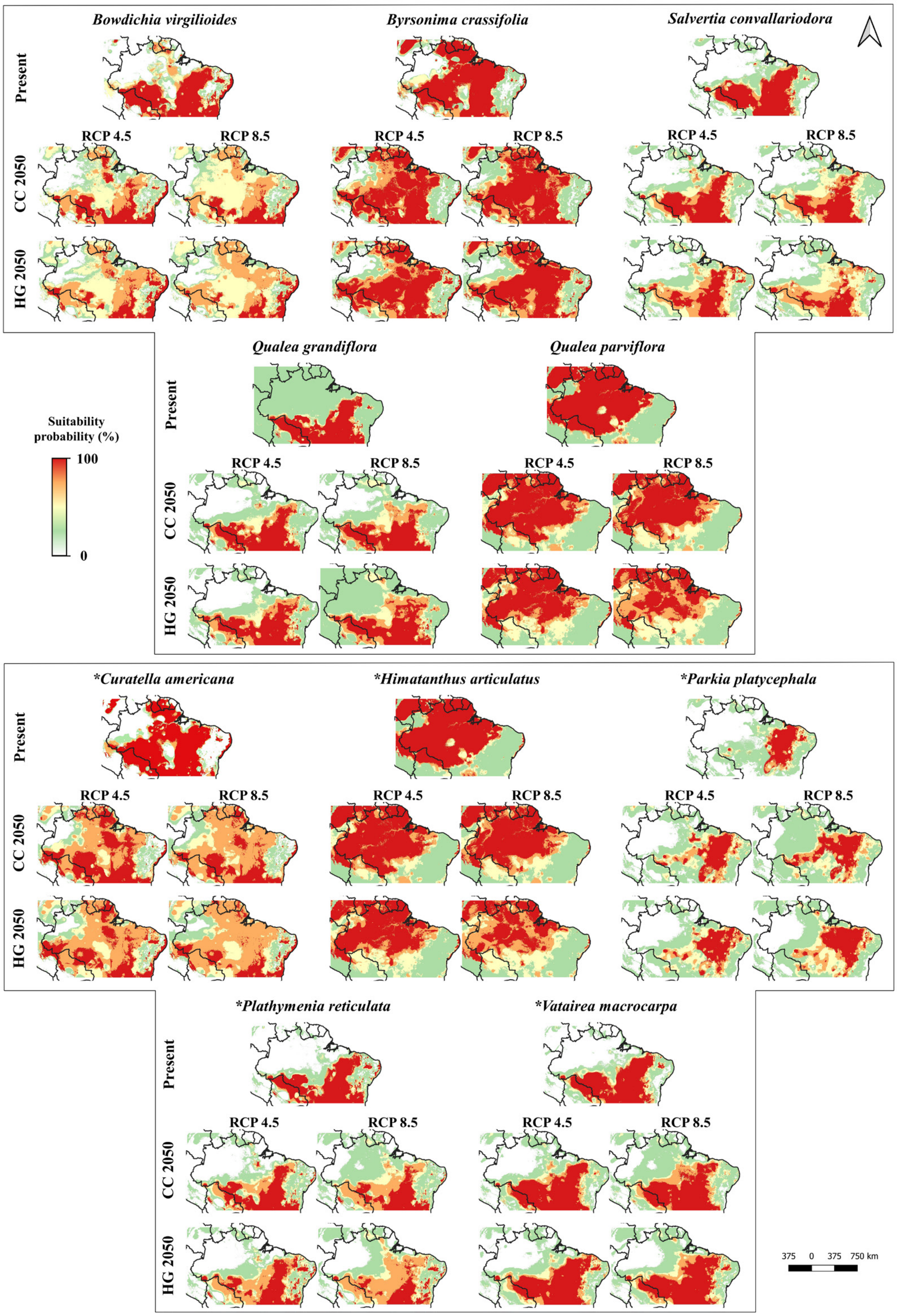


Figure 1. Climate stability models for the 10 woody species of the Cerrado in current and future climate change scenarios (2050) (RCP 4.5 and 8.5), according to the global climate models (GCM) CCSM4 (CC) and HadGEM2-CC (HG). Warmer colors represent greater environmental suitability predicted by species for each scenario.

DISCUSSION

The results of this study demonstrate that, even in the most optimistic climate change scenarios (i.e., RCP 4.5), climate requirements will potentially have a strong effect on woody assemblages of savannas from the central-north portion of Brazil in the near future (2050). The

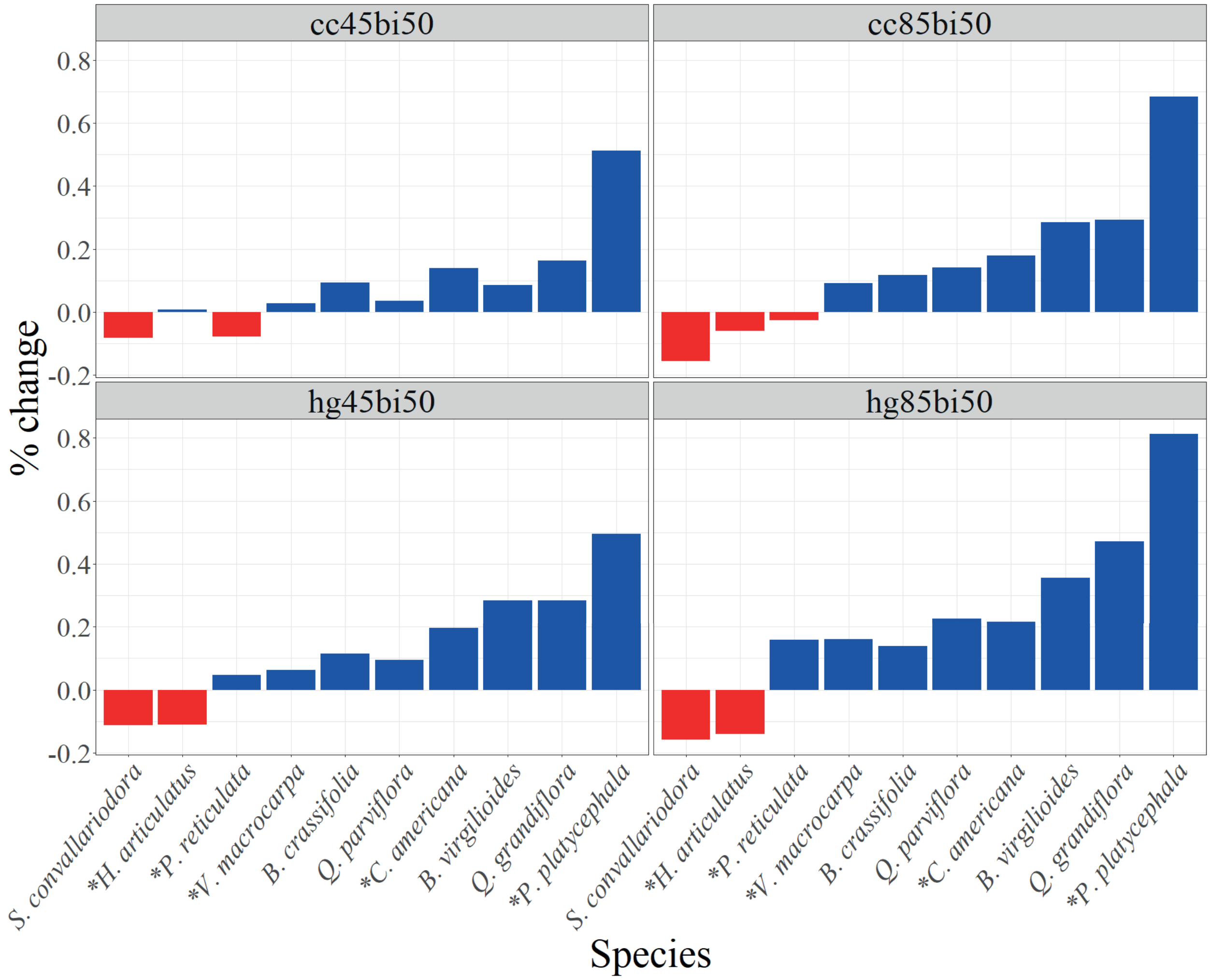
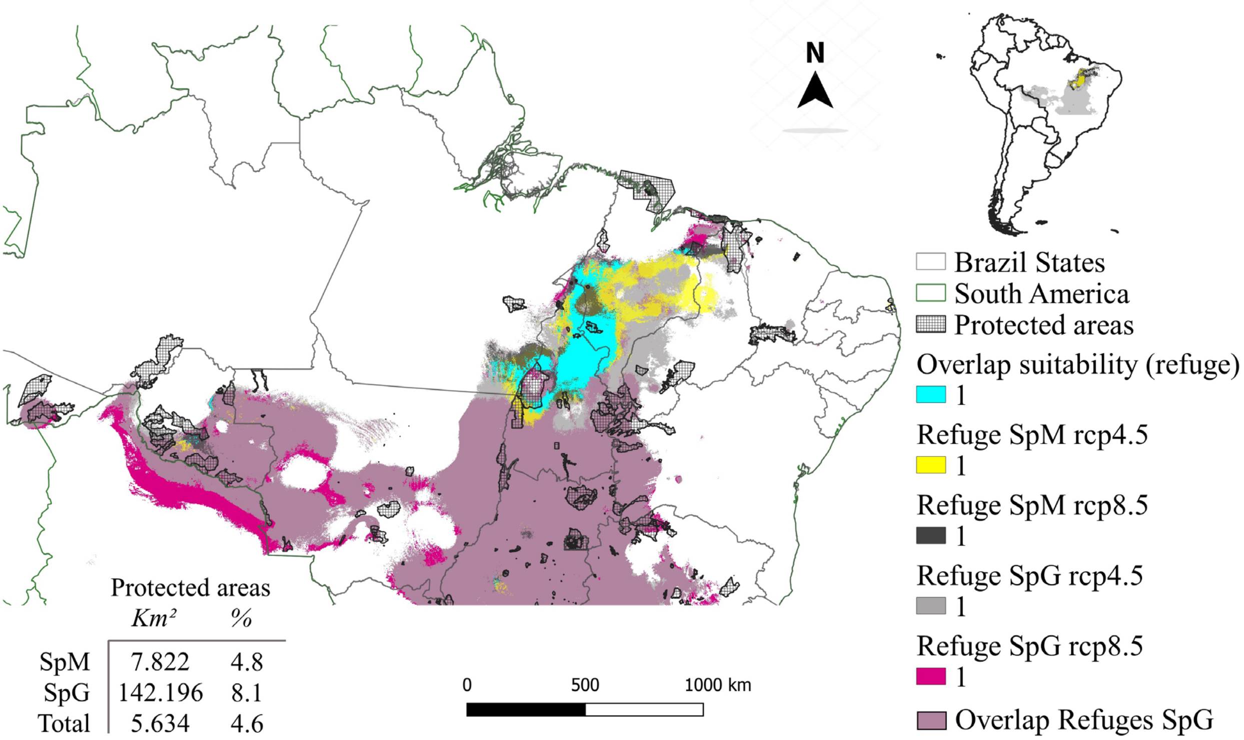


Figure 2. Potential change in the area by species in different scenarios of future climate change (2050; GCMs CC and HG; RCP 4.5 and RCP 8.5). Blue: expansion; red: retraction. * Marginal species typical of the northern savannahs.

ENMs estimated changes in the spatial pattern of habitat suitability for the species and flora composition at macro-regional scale and showed that 70% of the species will occupy new niches and 30% will have smaller ideal ranges. In addition, very few climatically stable areas for the occurrence of these species are under protection.

The understanding of biogeographic processes such as dispersal of organisms, emergence of barriers that promote vicariance, and generation of new lineages and species (cladogenesis), makes it clear that climate change is central to these evolutionary processes, triggering the origin and extinction of organisms within a given historical context (Haffer 2008). Some hypotheses (such as Pleistocene refuges and Disturbance-vicariance) have been proposed to explain the great contemporary Neotropical and Brazilian biodiversity (Haffer 2008, Aleixo et al. 2010). Heating and cooling cycles are thought to have triggered adaptive processes in different biological groups in the numerous paleogeographic phases.

Episodes of retraction and expansion of forest and open formations combined with



Protected areas

	Km²	*%*
SpM	7.822	4.8
SpG	142.196	8.1
Total	5.634	4.6

Figure 3. Potentially stable climatic areas for conservation actions. Map of species overlap in the four scenarios indicating more stable climatic areas (refuges, in blue) for generalist (SpG) and marginal (SpM) species. Color scales represent overlapping models. The areas were plotted with existing protected areas. The values refer exclusively to the northern region. The table represents the absolute (km²) and relative (%) extent of occurrence of species in protected areas based on the current distribution scenario.

isolation and speciation would have affected Cerrado biodiversity (Silva & Bates 2002, Haffer 2008, Werneck et al. 2012, Bueno et al. 2016). Therefore, understanding how species might respond to climate changes predicted to occur in the coming years is pivotal to formulate actions of management and conservation of biodiversity. Greater turnover can be expected in future savanna domains in response to climate change, especially in areas with marked west-east moisture gradient (Davidson et al. 2012), such as in central-north Brazil. In addition, recent works indicate that this area is more sensitive to global climate change due to the current high rates of deforestation and landscape transformation (Salazar et al. 2007, Malhi et al. 2008, IPCC 2018). Although the species are typical of savanna, they are recorded in ecotonal areas under the influence of neighboring domains (BFG 2018) and, as they are heliophilous plants, we had predicted that they will potentially respond by expanding their habitats, possibly increasing competition between floras within and between biomes.

All of our "generalist" species (SpG) demonstrated little change in their ranges according to our models, which can be interpreted as a sign of resilience given the projections of environmental changes mainly in the central-north region of Brazil. For instance, considering only the climate factor, the Climate Observatory/ SEEG (http://www.observatoriodoclima.eco.br) forecasts a 72% increase over the average temperature and a decrease in precipitation, with the most negative trends in the Cerrado and the Amazon (Azevedo et al. 2018, Penereiro et al. 2018). Similar projections were observed for the "marginal" species (SpM), although, *S. convallariodora, H. articulatus* and *P. reticulata* may lose their climate suitability, be restricted to alternative stable states and adopt new environmental equilibrium ranges. Beisner et al. (2003) discussed the perspectives of alternative stable states that suggest that resilience can be achieved either by adaptive changes (i.e., "shifts in variables" according to the authors), which seems to be the case with SpG, or by anticipating changes in the environment through changes in the range (i.e., "shifts in parameters"), as seems to be the case with SpM.

Most species showed spatial range gain in the projections, suggesting that there will be minimal survival conditions for these heliophilous species. This corroborates the assumption of expansion of xeric environments possibly initiated in the Holocene and maintained in the present period (Simões et al. 2019). Although, the idiosyncratic response of some species (three species showed decreased projected area) reflects the lack of a pattern in the scenarios and indicates that climate change will have a variable influence on the varied plant communities of Cerrado.

Actually, the difficulty of native floras to adapt to climate change tends to aggravate the natural habitats degradation in a few decades. Even widely distributed species can have population sizes reduced in some areas and suffer local extinction in others, in long time series with seasonal tendency to aridity (Simões et al. 2019). It can be extrapolated that the structural simplification, increased mortality, and reduced average plant density are indicators of changes caused by the "desertification" of the northeastern savannas and semi-arid steppes, the "savannization" of the Amazon, and the "erosion" of central Cerrado, contributing in all cases to the contemporary reduction of phylogenetic diversity and to new patterns of ecological niches (Costa et al. 2012a, Terribile et al. 2012).

Long-term drought experiments in the Amazon have shown considerable niche resilience to natural climatic variation, but interactions between climate change, deforestation, fire, and potential carbon storage discharge and precipitation lead to an increasingly vulnerable ecosystem (Davidson et al. 2012). Although the climate is a predominant driver of community changes, several current factors operate in the disturbance of habitats, preventing the recovery and/or natural growth of landscapes and interfering with the real environmental suitability. Under the conditions analyzed in this study, all species are expected to find adequate habitats in the central-north Brazil, even in the worst climate scenario. However, it is noteworthy that other environmental and anthropogenic complications were not considered, neither the inherent biological relationships of inter-population nor intra-ecosystem interactions. Research has indicated the importance of soils in the distribution of plant species (Siqueira & Durigan 2007), but edaphic variables were not included in the models of northern Cerrado, because previous analyses pointed to the topographic and climatic attributes as the main predictors of these savannas (Costa-Coutinho et al. 2019, 2021).

In addition, this data also showed less relevance to edaphic aspects, which are subordinated to climate variations, especially the high rainfall regime of Amazonian savannas, drought and sharp thermal amplitude in the northeastern savannas. Similarly, through a modeling study in the Amazon-Cerrado transition, Dionizio et al. (2018) found that the dynamics of environmental effects along the latitude-longitudinal gradient are particularly due to climate, and then due to the frequency of fires and phosphorus limitation in the soil.

The dynamics of environmental suitability are most likely to decrease in the Amazon-Cerrado border, where deforestation is greatest and where climate and plant diversity move between ecosystems (Davidson et al. 2012). In line with these authors, lower precipitation in these ecotones will make the conditions between forest (short drought) and Cerrado (long drought) less limiting, promoting its expansion.

ENMs in Cerrado plant lineages gives an idea of the susceptibility of this Biome to current trends in climate change and, ultimately, about land use changes, since a considerable part of Brazil's greenhouse gas emissions originates from habitat degradation. The present study show that the largest inclusive extent of the projected refuge will potentially be concentrated in the center of the focal area, coinciding with one of the "subhotspots" of the biome (i.e., supercenters of Cerrado biodiversity), and considered by Castro & Martins (1999) as the savanna's peripheral limits with high. The lower and plastic diversity is expected from peripheral floras in fragmented, ecotonal habitats with high structural complexity acting as environmental filters that cause the homogenization of diversity (Kortz & Magurran 2019). But as the models show, for the species analyzed, many of these areas will provide the ideal conditions for some savanna communities.

The prediction of the real influence of environmental changes on the different elements that act on plant diversity is based on conjectures and are conditioned to fluctuations in direct (e.g., temperature, CO_2 emission, solar radiation, precipitation, sea ice extent) and indirect (e.g., food availability, pests, soil moisture, sea level) components that impact biodiversity (IPCC 2018). According to Costa et al. (2012a), the latest diversification cycles of some biological groups were correlated with recent climate changes; for other groups, though, such changes contributed little to today's richness and geographical distribution. Terribile et al. (2012) consider appropriate to examine both the past and the future to map the most likely areas of savanna in the future. In this context, assessing the consequences of variations in phenological and reproductive patterns, ecological interactions, length of annual seasons, and responses linked to adaptability, plasticity, migration or extinction in populations, for example, would be a goal of current research (Azevedo et al. 2018, IPCC 2018).

Finally, combined with climate change, deforestation and fires are the factors with the biggest impacts, stimulated by the growing importance of the northern savannas as a cultivation lands for South America, due to a growing competitive advantage. Agricultural expansion and urbanization, which are not limited to a single phytogeographic region, impose an environmental footprint that furthers the savanna's vulnerability. Contrary to the current environmental policy of the Brazilian government, the identification of these environmental refuges and indication for preservation represent the minimal palliative measures to stop anthropic actions, yearning for greater future effectiveness of PAs, certainly as buffer zones for these events in ecosystem functioning and conservation.

CONCLUSIONS

The predictive power of ENMs showed high reliability and the results provided evidence that climate change will affect the distribution performance of the ten investigated oreadic woody species and alter the potential extent of their fundamental niches. The projected occurrence range coincides with the extension of the savanna biome, but interpenetrations in adjunct biomes are estimated to be greater, especially in the Amazonian border. There was no pattern of displacement of species towards higher elevations and towards climatically milder areas. With the gradual atmospheric warming, plants in the central-north savanna will be affected even in the most optimistic scenario. In both distribution status, the pattern of climatic influence of the species was not the same, which could have consequences on the ecological relationships and functionality of the floras. The main impact for the largest number of species, consistent in most scenarios, was the expansion of potential areas of occurrence, leading to suppression or cohabitation with species of other biomes. Therefore, northern savanna vegetation tends to benefit from the expansion of thermal suitability, although fragmentation and/or displacement of optimal environmental suitability is expected as the scenarios advance, especially for typically marginal plants. The confluence of the most suitable areas is considered a refuge and the largest extension is foreseen in the central-north area of the studied area, mainly involving parts of Maranhão, Tocantins and Pará. Combining data from legal reserves and vegetation suppression, the protected areas as a whole have the potential to protect less than 5% of the identified stable climatic areas. The models generated here show environmental refuges for species of the central-north savannas as the most indicated areas to be focused on conservationist measures. The findings also demonstrate the insufficiency of the PAs for protecting present and future oreadic floras, thus suggesting optimizations of maintenance strategies in the Brazilian Savanna.

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