CELLULAR AND MOLECULAR BIOLOGY

Impact of climate change on the current and future distribution of threatened species of the genus *Lessingianthus* (Vernonieae: Asteraceae) from the Brazilian Cerrado

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Abstract: Climate change has already altered global biodiversity, causing the migration of species and changes in habitat distribution. To implement a sustainable conservation strategy, it is necessary to understand the impacts of climate change on species. *Lessingianthus* is a South American genus that includes numerous endangered species, some of which grow in the Brazilian Cerrado, a Neotropical savanna considered a world's biodiversity hotspot. However, the impact of global climate change on these species has still not been estimated. We evaluate the effect of climate change on the habitat of 10 threatened *Lessingianthus* species and on their potential distribution, and assess the effectiveness of current protected areas (PAs) using ecological niche models. Based on the maximum entropy algorithm (Maxent), we first modeled the potential distribution of these species under current climatic conditions and then projected the distribution for two future scenarios of climate change (RCP 4.5 and RCP 8.5) and two time periods (2050 and 2070). We predicted current habitat suitability and identified suitable bioclimatic variables for these species. Our findings suggest that the area comprising the south and southeast of Cerrado is irreplaceable and the most biotically stable region for these endangered species; therefore, it should be considered a conservation priority area.

Key words: Climate, conservation, endangered species, Neotropical savanna, niche modeling.

INTRODUCTION

Red lists are an important tool for the conservation of biodiversity. The Brazilian flora includes more than 40,000 plant species (Flora do Brasil 2020), of which 2,953 are threatened according to CNCFlora (Centro Nacional de Conservação da Flora, National Center for Plant Conservation). Most of those threatened species are included in The Red Book of Brazilian Flora (Martinelli & Moraes 2013), as well as in the Red book of the Flora do Brasil-Rare Plants of the Cerrado (Martinelli et al. 2014), which includes a list of rare and endangered plants growing in this biome. Both works are based on the IUCN (The International Union for the Conservation of Nature) methodology, which establishes the category of threat for these species. All species of the red lists are highly vulnerable to natural and human disturbances, such as overexploitation, habitat loss, invasion of alien species, and global environmental changes (Sekercioglu et al. 2008), showing different levels of extinction risk (Harnik et al. 2012). Endangered species remain a priority for conservation biology; there is a wide range of reasons to conserve them (Nakajima et al. 2012, Martinelli et al. 2014), since their extinction would represent an imbalance in the ecosystems where they occur.

Protected areas (PAs) are established to protect biodiversity and safeguard part of species geographical distribution from disturbances (Thomas & Gillingham 2015), and threatened species may have a part of their distribution within in PAs. On the other hand, the remaining unprotected distribution of these species may suffer loss of natural cover and climate change (Swift & Hannon 2010). Therefore, the vulnerability of a species is related to its degree of representativeness inside and outside the PAs. According to Velazco et al. (2019), the dark scenario occurs when a species loses territory within PAs due to climate change, while they also lose range outside PAs due anthropogenic land use (crops, urban areas, managed pastures and rangelands). The Cerrado is an example of an ecoregion that, despite being one of the world's biodiversity hotspots, faces intense habitat loss, resulting in anthropized and fragmented ecosystems (Klink & Machado 2005, Strassburg et al. 2017). Many of the threatened Brazilian species belong to this floristically rich savanna (>7,000 species), located in the central region of Brazil (Klink & Machado 2005, Strassburg et al. 2017). Despite its importance, the Brazilian Cerrado is poorly protected, with only 7.7% of its surface area being under protection (Oliveira et al. 2017). Proper management and conservation of biodiversity should take into account the impact of climate change, which is considered one of the most serious threats to the conservation and sustainable use of biodiversity. Therefore, there is a real need to look into the future for the establishment of more effective conservation actions. One of the possible ways to define and evaluate regions for the long-term conservation of biodiversity in a biome is to predict the responses of this biome to global change. Several studies have extensively used ecological niche models (ENMs) to understand the impact of future climate change on biodiversity (Araújo

et al. 2004, Bitencourt et al. 2016, Velazco et al. 2019). This tool provides climate scenarios, and therefore simulations of future conditions on a global and regional scale, which are provided by the General Circulation Models (GCMs). These simulations can help us to understand the current species distribution and estimate biological responses to improve conservation strategies in a changing world.

The Asteraceae family comprises almost 10% of the flowering plants of the Cerrado biome, with 1074 taxa being listed (Sano et al. 2008). It is probably the richest family in the Cerrado; it is also by far the largest plant family in the herbaceous layer, especially in open Cerrado physiognomies (Filgueiras 2002). Within the family, the Vernonieae tribe is one of the best represented groups in this biome, with approximately 317 species (Flora do Brasil 2020). The Vernonieae is a very diverse and complex group in biological and taxonomic terms (Funk et al. 2009), which has received much attention from diverse disciplines and different approaches (Angulo & Dematteis 2010, 2012, Angulo et al. 2015, Via do Pico et al. 2019). One of the largest genus of this tribe is *Lessingianthus* H. Rob., an exclusively South American group that comprises about 133 species distributed from Venezuela to Argentina (Angulo & Dematteis 2010). It includes widely distributed species, as well as endemic and rare species, many of which are under threat. Of the 114 species that occur in Brazil, 97 are present in the Brazilian Cerrado (Flora do Brasil 2020). Although it is a widely studied group, the contributions to the geographical distribution and conservation of the species are very scarce. The very important phytogeographic study of Lopes Rivera (2010) was the first contribution to the conservation of species of the genus *Vernonia* s.l. in the Brazilian Cerrado. However, the works conducted so far have not included ecological niche modeling.

In this study, we assessed the impact of climate change on the distribution of 10 *Lessingianthus* species at extinction risk that occur in the Brazilian Cerrado. According to the IUCN (2016), these species are considered vulnerable (VU) or endangered (EN); some are endemic to and/or "rare" in this biome. Therefore, the present study compares the consequences of climate change on species with different degrees of distribution and categories of threat, and assesses their conservation status in the future. Target 7 of the Global Strategy for Plant Conservation (GSPC) for 2020 indicates that at least 75% of known threatened plant species should be conserved in situ from 2011 to 2020. However, the data available for endangered *Lessingianthus* species indicate that only part of their geographical distribution is within protected areas (Martinelli & Moraes 2013, Martinelli et al. 2014). Therefore, it is probable that current protection measures do not adequately support their conservation, and additional conservation efforts are urgently required.

In this context, we modeled the current and future suitable habitat distribution of *Lessingianthus* species from the Brazilian Cerrado. Our main objectives were to (1) understand the effect of climatic change on the potential distribution of *Lessingianthus* species and (2) assess the effectiveness of current protected areas. The generated knowledge could be potentially useful to plan monitoring and conservation strategies in Brazilian Cerrado.

MATERIALS AND METHODS

Study area and its ecological significance

The Brazilian Cerrado is the second largest biome in South America after the Amazon (Bitencourt et al. 2016). The biome has a great diversity of climates and habitats due to its vast latitudinal and altitudinal extent (Oliveira & Marquis 2002). The Cerrado is considered a biodiversity hotspot, i.e., an area of priority at the global scale due to its species richness and endemism, and to the high degree of threat those species are subjected (Myers et al. 2000, Ceballos & Ortega-Baes 2011). The biome includes much of central Brazil and parts of north-eastern Paraguay and eastern Bolivia, and borders the Amazon and Atlantic Forest and the arid regions of Caatinga, Pantanal and Chaco. In this study we considered the official boundaries of the Brazilian Cerrado (Brasil 2004), which covers an area of 2.03 million km^2 and includes the state of Goiás, the Federal District, most of Mato Grosso, Mato Grosso do Sul, the state of Tocantins, the western part of Minas Gerais and Bahia, the southern part of Maranhão and Piauí, and small areas of São Paulo and Paraná. The area is located between 24°58' and 2°47'S, and 42°1' and 59°55'W, with an altitude ranging from sea level to 2000 m.

The prevailing climate in the Cerrado Domain is seasonal tropical, with a dry winter. The average annual temperature is about 22-23ºC, with monthly averages exhibiting little seasonality. The absolute monthly maximums do not vary considerably throughout the year, and can exceed 40ºC. On the other hand, the monthly absolute lows vary greatly, reaching values close to or even below zero in winter. Frost usually occurs in the southern region. In general, the average annual rainfall is between 1200 and 1800 mm. The average monthly rainfall is highly seasonal, concentrated in the rainy season (spring and summer months). In the middle of this season there may be short periods of drought, called summers. Between May and September, monthly rainfall is considerably reduced and there can be months with no rainfall (Bustamante et al. 2012).

Study species

We analyzed 10 threatened species of *Lessingianthus* from the Brazilian Cerrado, which are vulnerable (VU) or endangered (EN) according to the red list (2013, 2014) and, therefore, supposed to be facing a very high or high risk of extinction in the wild, respectively (Table I). Three species are endemic to the Cerrado: *L. eitenii*, *L. irwini*, and *L. venosissimus*, whereas one species, *L. arachniolepis*, is considered rare in this biome because it has few records, with a range of geographical distribution mainly restricted to Paraná state. The remaining six species also occur outside the Cerrado, mainly in the transition zone between the south and southeast portions of the Atlantic Forest. Because of these differences among species, their abundance within the biome, and the different threat categories, each species was modeled separately. However, consensus models were obtained for all species.

Environmental data and ecological niche modeling (ENM)

We modeled the present and future potential geographic distribution of 10 species of *Lessingianthus* of the Brazilian Cerrado using point locality information and environmental data in QGis 3.4.2-Madeira (QGIS Development Team, 2018) and Maxent 3.4.1 (Phillips et al. 2017). This model uses presence only machine learning algorithm to predict the probability of species occurrence in areas with unknown occurrence based on species data and different environmental constraints (Phillips et al. 2006).

The localities of occurrence of the *Lessingianthus* species were obtained from geographic coordinates extracted from the labels of herbarium specimens of the Institute of Botany of the Northeast (CTES), or derived from localities with the help of Google Earth (http://www.google.com/earth/index.html) and species occurrence georeferencing points from the SpeciesLink database (http://splink.cria.org.

Table I. Species, IUCN category: VU: vulnerable, EN: endangered (according to Martinelli & Moraes 2013, Martinelli et al. 2014) and number of data records of *Lessingianthus* species studied.

Species	IUCN category	No. of data records used for the analysis
NON-ENDEMIC AND RARE		
L. arachniolepis (Mart. ex DC.) H. Rob.	VU	8
NON-ENDEMIC		
L. adenophyllus (Mart. ex DC.) H.Rob.	EN	15
L. asteriflorus (Mart. ex DC.) H.Rob.	VU	13
L. exiguus (Cabrera) H.Rob.	VU	8
L. pumillus (Vell.) H.Rob.	VU	13
L. stoechas (Mart. ex Baker)	VU	17
L. zuccarinianus (Mart. ex DC.) H.Rob.	VU	26
ENDEMIC		
L. eitenii (H.Rob.) H.Rob.	EN	12
L. irwinii (G.M. Barroso) H.Rob.	VU	9
L. venosissimus (Sch. Bip. ex Baker) H.Rob.	EN	15

br/), from Centro de Referência em Informação Ambiental (CRIA 2005). The data used are in the public domain. We considered only species with at least five records, therefore, only 10 species were analyzed (Table I). Species distribution data were rigorously checked to verify the existence of duplicate geographic coordinates or those falling outside the study area. A total of 136 georeferenced points were used for the study (Table SI - Supplementary Material).

For the current and future modeling of the species, the 19 bioclimatic variables were used at a resolution of 2.5 minutes. To model the current potential distribution, the environmental variables were extracted from the WorldClim database (http://www.worldclim.org/) (Hijmans et al. 2005). To avoid overestimation of climatic data that can lead to misleading results (Phillips et al. 2006, Peterson & Nakazawa 2008), we calculated Pearson's correlation coefficients (r≥0.80) in QGis 3.4.2-Madeira (QGIS Development Team 2018). We identified highly correlated variables and selected six that we considered more biologically meaningful and directly relevant. These were: Annual mean temperature (Bio1), Mean Diurnal Range (Mean of monthly (max temp-min temp)) (Bio2), Isothermality (Bio2/Bio7) (*100) (Bio3), Max Temperature of Warmest Month (Bio5), Precipitation of Driest Month (Bio14) and Precipitation of Wettest Quarter (Bio16). Temperature variables in °Celsius and precipitation variables in millimeters. For the assessment of future distributional potential in years 2050 and 2070, we downloaded the same set of six bioclimatic variables at 2.5 min resolution from the CCAFS (Climate Change, Agriculture and Food Security) downscaled general circulation model (GCM) data portal (http://www.ccafs-climate.org/), in the form of data for two emissions scenarios (RCP 4.5 and RCP 8.5) and two GCMs (MIROC-ESM and CSIRO-Mk3.6.0). These RCPs were assumed

as optimistic (RCP 4.5) and pessimistic (RCP 8.5) scenarios. A buffer zone was created to cover the transition zone between the Cerrado and the Atlantic Forest. The bioclimatic layers were trimmed to the surrounding areas of the geographic distribution of Brazilian Cerrado and then projected over a wider region (200 km) from latitude 1°47'S to 27°24'S and from longitude 61°58'W to 39°45'W, covering an area of 4.22 km² million. Outputs from the future models were averaged to give a single consensus model for each species in each time period (2050-2070) and each scenario (RCP 4.5 and RCP 8.5). We used the Multivariate Environmental Similarity Surface (MESS) analysis in Maxent to determine areas that contained novel environmental conditions for all species. The MESS index was estimated following the procedure described by Elith et al. (2010).

As the final result of the analysis, five potential distribution maps for each of the 10 species and five consensus maps of all species were obtained: one for the present, two for each time (2050 and 2070), and two RCPs: 4.5 and 8.5.

Maxent was run using the following settings for current and future models: ten replicates with linear, quadratic and hinge features, response curves, jackknife tests, logistic output format, random seed, random test percentage=0% (due to the few locations per species), replicate run type=cross-validate, regularization multiplier=1, maximum iterations=500, convergence threshold=0.00001, maximum number of background points=10,000, Extrapolate, and Do Clamping. For the consensus modeling, the same parameters were used, but the "Auto features" option was chosen due to the greater number of locations. To determine the threshold value for each prediction, web used the value of the 10 percentile training presence. Variable importance was determined comparing percent contribution values and jackknife plots.

To statistically evaluate model performance, we used the area under the curve (AUC) of the receiver operating characteristic (ROC) plot (Phillips et al. 2006), and we estimated True Skill Statistic (TSS) (Allouche et al. 2006) with RStudio Version 1.1.453 (RStudio, Inc., Boston, MA). The AUC is a threshold-independent measure of model performance and varies from 0 to 1; 0.5 means no predictive ability or randomness and 1.0 shows perfect predictive ability (Fielding & Bell 1997). We used only models that presented an AUC greater than 0.7. TSS is defined as sensitivity (correctly classified presences) + specificity (correctly classified absences) −1. TSS values range from −1 to 1; when the values are negative or close to zero, the models are not different of a randomly generated model; models with values close to 1 are considered excellent. Acceptable models present TSS values over 0.5 (Allouche et al. 2006).

The Predicted Suitability (PS) was classified using four probability classes based on Khafaga et al. (2011): Very low (<0.1); Low (0.1-0.4); Medium (0.4-0.6); High (0.6-1.0) (see Habitat suitability classes in Fig. 4a).

The current consensus model was assembled on a map with the federal, state, and municipal PAs of Brazil (National System of Conservation Units-SNUC, updated January 2019, http://www.mma.gov.br/), to compare and evaluate whether the PAs cover the current and potential range of the species. Names, categories, dependency, biome to which it belongs, and area (km^2) of the PAs that fall within the favorable area predicted (Medium (0.4-0.6) to High (0.6-1.0) for the *Lessingianthus* species studied were detailed in Table SII of Supplementary Material.

RESULTS

Current and future ecological niche models generated for *Lessingianthus* species were highly accurate, as indicated by AUC and the TSS.

Models presented AUC and TSS values ranging from 0.888 to 0.992 and from 0.581 to 0.886, respectively (Table II).

Current distribution of *Lessingianthus* species in the Cerrado

The ENMs under current climatic conditions predict suitable localities for the 10 *Lessingianthus* species that mostly match their known distributions. Nevertheless, other suitable localities identified by the models are outside the present known ranges of these species (Fig. 1-2). According to the species distribution maps, the largest distribution area corresponds to *L. venosissimus*, *L. exiguus*, *L. pumillus*, and *L. zuccarinianus* (17.38-35.79% of the 4.22 km^2 of the study area); this area is recognized as highly potential habitat under current conditions (PS: Medium to High class: 0.4-1.0) (Table III). Contrarily, the smallest area of occurrence corresponds to *L. irwini*, *L. arachniolepis*, *L. eitenii*, *L. adenophyllus*, *L. asteriflorus*, and *L. stoechas* (between 3.83-8.40%) (Table III, Fig. 1-3). The Maxent model predicts the south-southeast region of the Cerrado and the transition zone with the Atlantic Forest as habitats with greater prediction for *L. arachniolepis* (rare), *L. asteriflorus*, *L. exiguss*

Table II. AUC and TSS validation values of current modeling of *Lessingianthus* species.

	AUC	TSS
L. arachniolepis	0.981	0.850
L. adenophyllus	0.944	0.593
L. asteriflorus	0.987	0.858
L. exiguus	0.917	0.581
L. pumillus	0.942	0.663
L. stoechas	0.974	0.861
L. zuccarinianus	0.888	0.613
L. eitenii	0.992	0.886
L. irwinii	0.982	0.720
L. venosissimus	0.955	0.703
Consensus	0.926	0.7293

and *L. pumillus* (all non-endemics). The three endemic species (*L. eitenii*, *L. irwinii* and *L. venosissimus*) have a potential discontinuous distribution mainly in the center and east of the modeled area. For *L. venosissimus*, there is also a favorable area in the west of the Cerrado. For the non-endemics, *L. adenophyllus*, *L. stoechas*, and *L. zuccarinianus*, the favorable region is the center and east of the modeled area (Fig.

1-2); the two former species (*L. stoechas* and *L. adenophyllus*) have a potential discontinuous patchy distribution.

Distribution of *Lessingianthus* species in future climate scenarios

The current habitat features of the 10 species are likely to change in the future. The model projection for 2050 as well as for 2070, in both
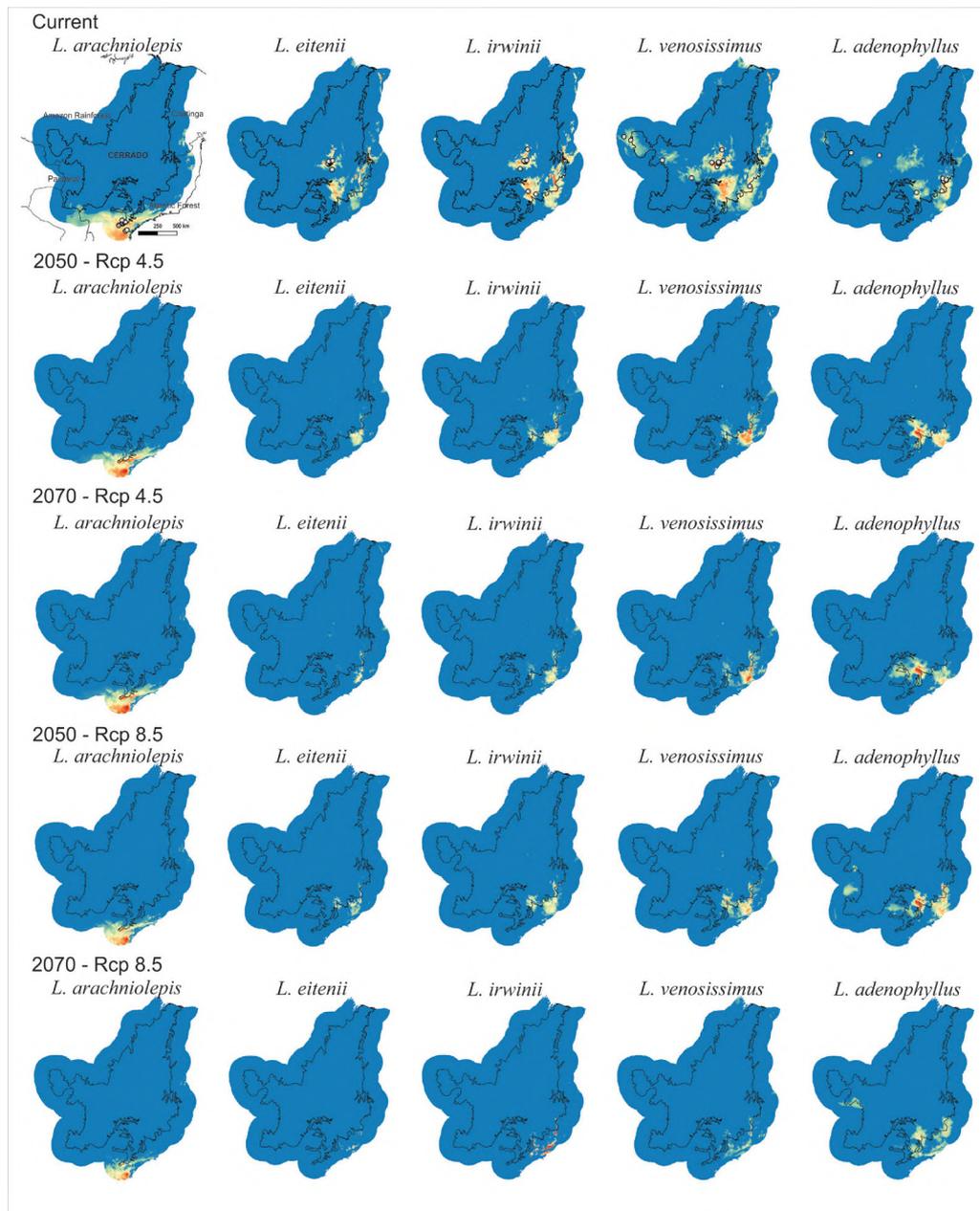

Figure 1. Current and future ecological niche models under optimistic (RCP4.5) and pessimistic (RCP8.5) scenarios forecasted for 2050 and 2070 for the studied *Lessingianthus* species. The points represent the occurrence data of the species. Low to high suitability is indicated with colours ranging from blue to red, respectively (see Fig. 4a).

scenarios (optimistic and pessimistic), revealed that the habitat suitable for *Lessingianthus* species will be drastically reduced compared with the current distribution (Table III, Fig. 1-3). Under the optimistic scenario (RCP 4.5) for 2050 and 2070 (Fig. 3a), the most affected species are likely to be the three endemics and *L. zuccarinianus*, with a reduction of the potential habitats of 64-80% (2050) and 72-84% (2070) concerning to the current suitable area.

However, for the endemic species *L. eitenii* there is a small difference between 2050 and 2070. For other species, a reduction of between 18-53% (2050) and 34-83% (2070) is predicted. For the non-endemic *L. adenophyllus*, the model predicts a reduction is for 2050, with an increase of the favorable habitat likely to occur in 2070. For *L. stoechas* a minimum reduction of the area (18%) is predicted for 2050, but a drastic reduction by 83% is likely to occur in 2070. The
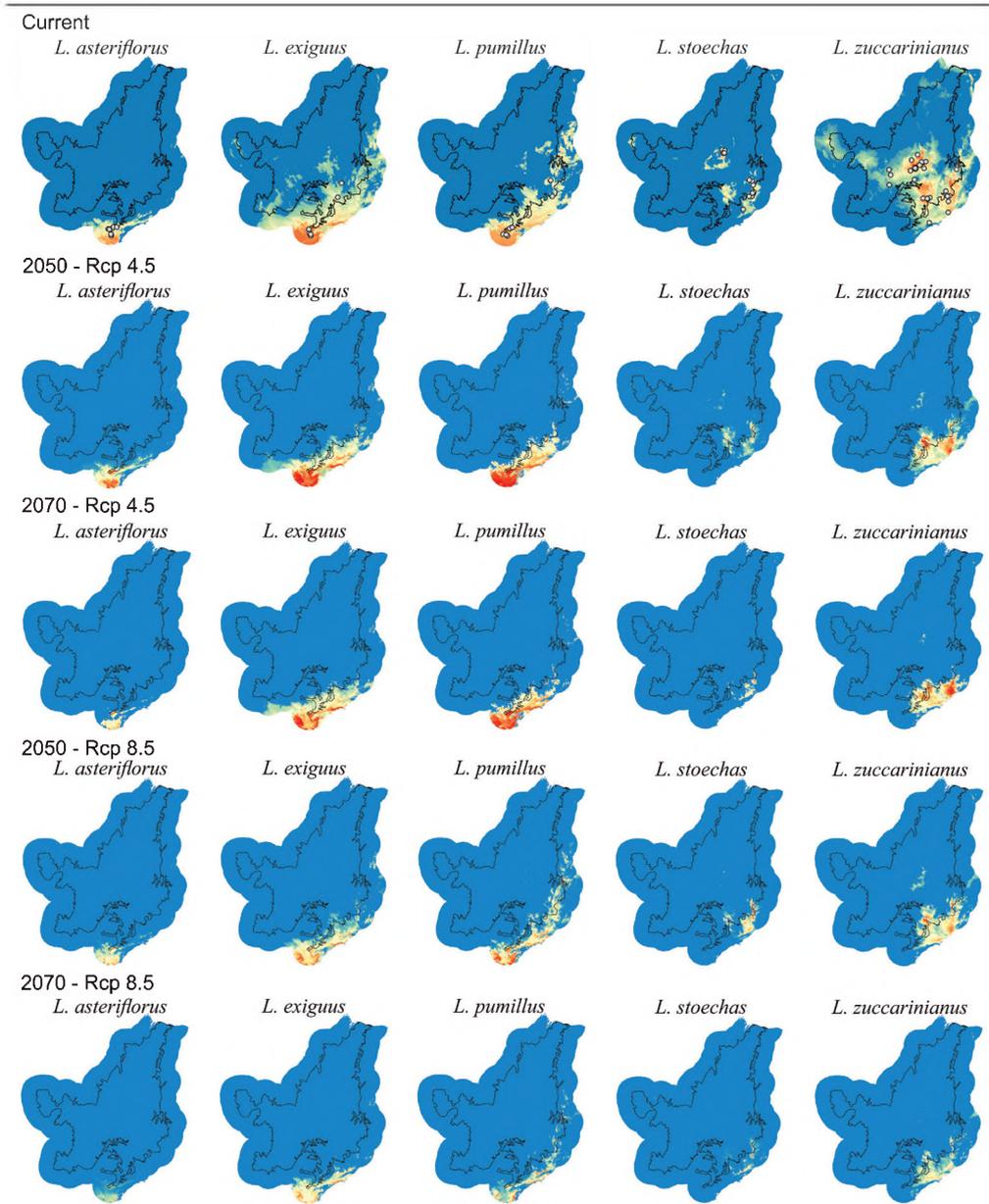

Figure 2. Current and future ecological niche models under optimistic (RCP 4.5) and pessimistic (RCP 8.5) scenarios forecasted for 2050 and 2070 for species of *Lessingianthus* studied. The points represent the occurrence data of the species. Colour blue to red indicates the suitability from low to high (see Fig. 4a).

same situation is predicted for *L. asteriflorus* for 2050 and 2070, with a reduction of 20% and 70 %, respectively. Under the pessimistic scenario (RCP 8.5), the situation is even more unfavorable (Fig. 3b). The three endemic species and *L. zuccarinianus* will undergo a 71-86% reduction of their suitable area in 2050 and will almost disappear by 2070 (88-97%). For the other species, the greatest reduction of the favorable area is predicted in 2070 (77-93%). Only for *L. adenohyllus* a minimum reduction of the area is predicted for both 2050 and 2070, with 31% and 39%, respectively. The favorable area for *L. eitenii* will almost disappear. In all future models, in addition to the reduction of the favorable habitat area and habitat suitability concerning to the current situation, a tendency for the more favorable areas to be located in the transition zone between the Cerrado and the Atlantic Forest is observed.

The MESS analysis identifies areas with highly similar environmental conditions between current and future climate scenarios. The areas of future potential distribution projected for 2050-2070 and RCPs 4.5 and 8.5 (Fig. 4b-c) of all *Lessingianthus* species are associated with positive MESS values, which indicates that the Maxent models outputs has high reliability. The modelled area that was associated with novel environmental conditions (negative MESS values) was the north and northwest (see Appendix SI for MESS analysis).

Importance of climatic variables

The percent contribution and permutation importance values of the six variables used in the current models were evaluated (Fig. S1 – Supplementary Material, Table SIII). Figure SI shows the response curves of the variables used in the current distribution model for each species. Species response curves represent the relationships between environmental factors and species occurrence probability (PS).

Two to three of the six bioclimatic variables had more than 85% contribution to each Maxent model (Table SIII). The most significant variables affecting the current and future distribution of most *Lessingianthus* species were Bio5 (Max

Table III. Area (in Km^2) and percent of the total studied area considered as optimal potential habitat of *Lessingianthus* species fo current and future models. %HPH: percent of high potential habitat. Total area studied: 4.22 km^2.

Species	Current		Rcp 4.5				Rcp 8.5			
	Area	% HPH	2050 Area	2050 %HPH	2070 Area	2070 %HPH	2050 Area	2050 %HPH	2070 Area	2070 %HPH
L. arachniolepis	354694.33	8.40	200769.56	4.75	169022.22	4.00	148944.3	3.52	80270.54	2.00
L. adenophyllus	302755.97	7.20	142036.84	3.36	199711.49	4.73	207073.82	4.90	184578.67	4.37
L. asteriflorus	161954.38	3.83	130008.51	3.07	48067.3	1.13	86822.84	2.05	29538.51	0.69
L. exiguus	988790	23.41	464505.27	11.00	384734.65	9.11	342445.29	8.11	157154.75	3.72
L. pumillus	625970.18	14.82	317988.89	7.53	247550.34	5.86	279119.81	6.61	116572.76	2.76
L. stoechas	181949.41	4.30	148295.64	3.51	29585.31	0.70	70065.03	1.65	16458.53	0.38
L. zuccarinianus	1499754.84	35.52	289269.3	6.85	235101.22	5.56	265402.6	6.28	179916.86	4.26
L. eitenii	276600.78	6.60	45960.6	1.08	42910.35	1.01	37158.65	0.88	6275.66	0.14
L. irwinii	322786.34	7.70	114963.76	2.72	88097.31	2.08	91793.81	2.17	25353.42	0.60
L. venosissimus	728498.27	17.25	143110.22	3.38	126268.85	3.00	109583.22	2.59	46698.63	1.11

Temperature of Warmest Month) and Bio14 (Precipitation of Driest Month). The curves of all species for Bio5 had a sigmoid shape, except the *L. eitenii* curve, which showed a Gaussian-like shape. The species prefer habitats with temperatures ranging between 18 and 30°C in the warmest months (PS > 0.55). For most species, the Bio14 showed a Gaussian shape. Favorable conditions reached a maximum of 0.7 of PS in a very narrow range of precipitation in the driest month (between 0-40 mm), except for *L. zuccarinianus*, which extends up to 90 mm. The curves of four species (*L. arachniolepis,L. asteriflorus, L. exiguus,* and *L. pumillus*) for Bio14 had a sigmoid shape. For these species, the favorable conditions (PS> 0.60) occur between 50-160 mm. The variables that least contributed to the modeling, in decreasing order, were Bio1 (Annual mean temperature), Bio16 (Precipitation of Wettest Quarter), Bio2 (Mean Diurnal Range), and the Bio3 (isothermality) (Fig. S1). The contribution of each of these variables to the modeling of each species also varied. The shape of the response curves varied considerably among species. Overall, Bio2 and Bio3 were the least contributing variables. An overall negative nonlinear response was detected for all temperature-related climatic predictors (Bio5, Bio1, Bio2, and Bio3).

Habitat stability and loss in protected areas

In the current scenario, the consensus map shows three areas with a high probability of occurrence (>0.6): center, south and southeast of the Cerrado (Fig. 4a). The protection degree shows that species are poorly represented within the PAs. While some of the occurrence data of the species fall within PAs and modeling under current conditions shows potential areas of habitability within PAs, this model also estimates large potential regions of habitability outside these areas. This is mainly observed in

the south of Cerrado, where there are few and small PAs.

The potential habitat areas predicted for the central region of the Cerrado include federal and state PAs (Table SII); in terms of their surface area (about 700-8700 km²) the most important are the following: The Environmental Protection Areas do Planalto Central (EPAPC), João Leite (EPAJL), Pouso Alto (EPAPA), Bacia do Rio São Bartolomeu (EPABRSB), and the National Parks Brasília (BNP), and Chapada do Veadeiros (CVNP). In the southeast, the predicted potential habitat falls within federal, state and municipal protected areas; some of the areas are in the transition zone and belong to the Atlantic Forest. Those with the largest surface area (about 800 - 1760 km²): Environmental Protection Area Morro da Pedreira (EPAMP), Sul-RMBH (EPAS-R), Aguas Vertentes (EPAAV), the Sempre Vivas National Park (SVNP). In the south, the most important PA is the Serra da Canastra National Park (SCNP) (2122 km²). There are also some smaller areas, mainly privately-owned national patrimonial reserves and ecological stations.

Under future conditions (both optimistic and pessimistic scenarios), most of the PAs where these species grow will become unsuitable and will be lost as a result of climate warming (Fig. 4b-c). In the future scenario, the PAs of the central region show a total absence of suitable climatic conditions for *Lessingianthus* species. The PAs located in the south and southeast are also vulnerable, but maintain some areas with probability of occurrence in the transition zone with the Atlantic Forest. As the models for each species, the consensus model also showed a reduction of the favorable area and habitat suitability concerning to the current model, and a tendency for the favorable areas to be located in the transition zone between the Cerrado and the Atlantic Forest.
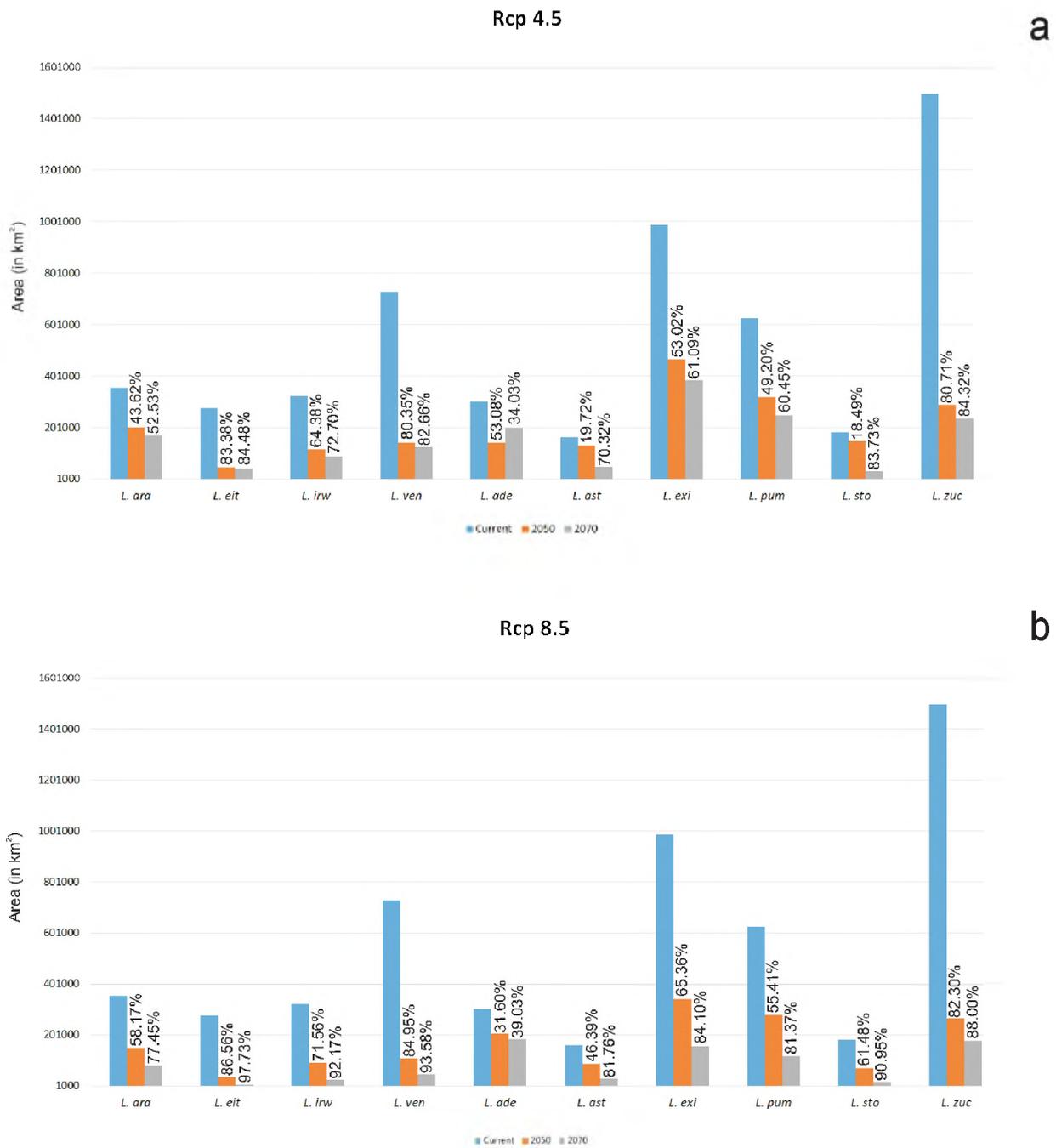
Figure 3. Area (km^2) occupied by *Lessingianthus* species in the present and future (2050 and 2070). (a) Under optimistic scenario (RCP 4.5). (b) Under pessimistic scenario (RCP 8.5). Percent of loss of optimum habitat area with respect to the estimated optimum area for the present.

DISCUSSION

Our findings show a drastic loss of the current suitable habitat for *Lessingianthus* in both optimistic and pessimistic scenarios for 2050

and 2070. Currently, the Cerrado biome plays an important role in the protection of these species because part of their distribution is within PAs; however, this biome will not be suitable for all of these species in the future. Therefore, climate

change will pose a serious threat to the future survival of these endangered *Lessingianthus* species and conservation efforts are urgently required.

The results of this study show that only six of the 19 bioclimatic variables were useful to predict current and future suitable distribution of the species. Therefore, the suitable current distribution of *Lessingianthus* species are mostly controlled by four variables related to temperature (Bio1, Bio2, Bio3 and Bio5), and only

two precipitation variables (Bio14 and Bio16). Temperature plays a key role in determining the distribution of potential habitats for these species, which prefer temperatures between 17-30ºC in the warmest months. This fact becomes a concern if we consider that the Earth is approximately 0.3-0.7ºC warmer than 100 years ago and is projected to be likely more than 2ºC warmer by 2100 as a consequence of global warming (IPCC 2014). Although precipitation variables had less influence in determining
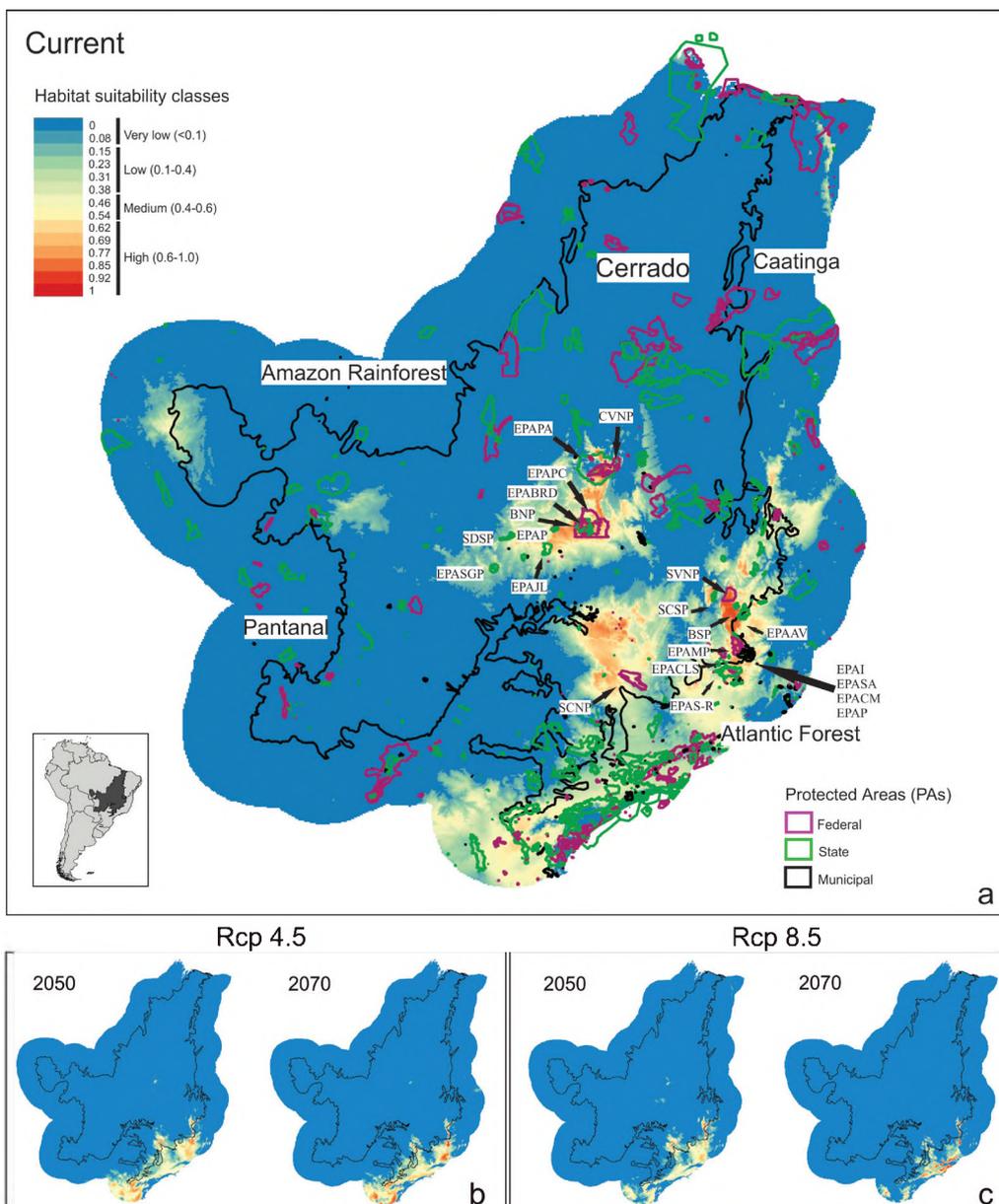

Figure 4. Consensus maps of all *Lessingianthus* species analysed under current and future conditions. **(a)** Consensus maps under current conditions in federal, state, and municipal protected areas of Brazil. The arrows indicate the PAs most vulnerable to climate change in future scenarios. **(b)** Future models under RCP 4.5 scenario in 2050 and 2070. **(c)** Future models under RCP 8.5 scenario in 2050 and 2070.

the distribution of potential habitats for the study taxa than temperature, in our current model, some species (*L. asteriflorus*, *L. exiguus* and *L. pumillus*) that also occur in the Atlantic Forest show favorable conditions when rainfall increases in the driest month. These species may be better adapted to conditions of regular and well-distributed rainfall throughout the year, as occurs in the Atlantic Forest. Therefore, the increase in temperature combined with the increase in the frequency of extreme rainfall events and the longer dry seasons will pose the greatest risk for those endangered species in the future.

Several studies using ENMs demonstrated the negative effects of climate change on numerous flora and fauna species of the Brazilian Cerrado (Siqueira & Peterson 2003, de Oliveira et al. 2015, Aguiar et al. 2016). The mechanisms underlying climate change are very complex and affect species in several physiological processes (Cahill et al. 2012). Vilela et al. (2017) suggested that climate change may influence the synchronization of phenological events that affect the interactions and reproductive success of some Cerrado plants. However, natural resilience and adaptive capacity of biodiversity in response to the several natural climatic fluctuations over time were observed in numerous cases and the few documented species extinctions can be attributed solely to climatic change (Dawson et al. 2011). In the last decades, human activities boosted the rate of climate change, contributing to the loss of biodiversity (Dawson et al. 2011), with anthropogenic land use being one of the main threats in the current and future scenarios of the Brazilian Cerrado. Accordingly, Velazco et al. (2019) suggested that land use and climate change will cause great damage to Cerrado flora by 2050 and 2080. Many of the species here analyzed are partially distributed outside PAs

and occur in zones under the anthropogenic pressure for deforestation, burning, monoculture plantations, subsistence agriculture, and even tourism (Loyola et al. 2014), which further increases their vulnerability.

According to several studies, species endemic to small areas are expected to be more sensitive to climate change, and therefore likely to be the first ones to become extinct, than species with broad distribution (Bitencourt et al. 2016). Our results partly support this assumption because all the species here studied would undergo reductions in their current distributions in the future, but the loss of habitat will be more drastic for endemic species than for non-endemic taxa.

Habitat stability and loss in protected areas

Niche modeling is the best-adapted method to address uncertain scenarios such as future climate change in the prioritization of conservation and the reserve selection process (Tulloch et al. 2016). For example, in the Cerrado, ENMs were used successfully to identify critical habitats and understand the effect of climate change on the distribution of threatened species of bats (Mendes & Marco 2018) and other endangered mammal species (Hidasi-Neto et al. 2019) in future climate warming scenarios. On the other hand, a recent study on the degree of protection of the biodiversity of Brazilian PAs carried out in groups of vertebrates, arthropods and angiosperms showed that, although Brazil is a megadiverse country with conservation priorities, the degree of protection of these areas is deficient. Brazilian PAs are apparently not protecting most endemic species and lineages. Moreover, only 7.7% of the Brazilian PAs are in the Cerrado cover, which is one of the Brazilian biomes with the lowest percentage of species and lineages, along with the Pantanal and the Pampa (Oliveira et al. 2017). All

these studies have shed light on the need to preserve the areas that are most suitable for the persistence of these threatened species in future scenarios. The present study predicts that the PAs located to the southeast of the Cerrado and in the transition zone between the Cerrado and the Atlantic Forest are likely to have some stable areas in different climate change scenarios; however, the other PAs will undergo severe habitat loss in the future. Our results show a tendency for favorable habitat areas to be located in the transition zone between the Cerrado and the Atlantic Forest, and are in agreement with several studies also suggesting that the south and southeast regions of the Brazilian Cerrado will be the most climatically stable areas or the areas where the species will tend to move (Siqueira & Paterson 2003, de Oliveira et al. 2015, Aguiar et al. 2016). However, these regions, besides having a low number of PAs, have already been subjected to serious levels of degradation, being highly fragmented and impacted by pastures and croplands (Klink & Machado 2005, Sano et al. 2008). Therefore, the need to conserve these areas with greater biotic stability becomes even more evident, since they could act as important refuges that ensure the long-term persistence of biodiversity.

Knowledge of the biodiversity of the Cerrado and its degree of conservation is still scarce, despite some contributions (Oliveira et al. 2017, Velazco et al. 2019). Since the genus *Lessingianthus* is a key and representative group of the Brazilian Cerrado, the current and predicted maps of habitat suitability and identification of suitable bioclimatic variables obtained in this study may serve as a guide for the management and conservation of threatened plants of the Cerrado. Our analysis shows that in the future the risks for the species will increase with the loss of the current climatically adequate zones for the species and their resulting movement to

transitional areas between the Cerrado and the Atlantic Forest, which are even more threatened by habitat destruction. Therefore, we strongly suggest that the most irreplaceable areas on the edges of the south and southeastern Cerrado region should be given priority for conservation actions (e.g., the implementation of PAs, sustainable management, and restoration) to ensure the long-term persistence of these species.

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SUPPLEMENTARY MATERIAL

Figure S1.
Table SI.
Table SII.
Table SIII.
Appendix SI.

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MB Angulo and G Via do Pico contributed equally to this work: identified the specimens, analyzed the data, prepared figures and/or tables and wrote the manuscript; prepared, wrote the manuscript and discussed the results. M Dematteis reviewed and corrected the manuscript. All authors critically revised the manuscript and approved the final version.