TREE SPECIES OF ATLANTIC FOREST AND PAMPA ALLUVIAL FORESTS IN THE CONTEXT OF CLIMATE CHANGE

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ABSTRACT – Although species are continually exposed to variations in climate over time, there is growing concern about the accelerated pace of climate change to which they are currently exposed, as climate is determinant in the geographic distribution of animals and plants. This study evaluated the climatic niche and impact of climate change in the 2061-2080 period on areas of occurrence of indicator tree species of alluvial forests in the south-central portion of the Atlantic Forest and Brazilian Pampa. Nineteen climatic variables were considered for the contemporary and future climates. The species' climatic niches were modeled using the Maxent algorithm. Climatic adequacy for species in the Parana-Uruguay group was strongly influenced by variables related to temperature, while adequacy for species in the Atlantic group was related to rainfall and temperature. A decrease in the area of climatic adequacy is estimated for most species considered, with similar behavior in the two groups assessed. The species tend to occupy a more southern position, using areas of higher altitude, latitude and proximity to the Brazilian coast as climate refuges, highlighting these areas as strategic for environmental conservation.

Keywords: Climatic niche; Modeling; Climate refuge.

ESPÉCIES ARBÓREAS DE FLORESTAS ALUVIAIS DA MATA ATLÂNTICA E PAMPA NO CONTEXTO DE MUDANÇA CLIMÁTICA

RESUMO – Embora as espécies estejam continuamente expostas a variações do clima ao longo do tempo, há uma preocupação crescente em relação ao ritmo acelerado de mudança climática a que estão expostas atualmente, pois o clima é determinante na distribuição geográfica de animais e plantas. O presente trabalho avaliou o nicho climático e o impacto da mudança climática para o período de 2061-2080 sobre as áreas de ocorrência geográfica das espécies indicadoras dos agrupamentos de florestas aluviais da porção centro-sul da Mata Atlântica e do Pampa brasileiro. Foram consideradas 19 variáveis climáticas para o clima contemporâneo e futuro. Os nichos climáticos das espécies foram modelados por meio do algoritmo Maxent. A adequabilidade das espécies do grupo Paraná-Uruguai foi influenciada fortemente por variáveis relacionadas à temperatura, enquanto a adequabilidade das espécies do grupo Atlântico relacionou-se com precipitação e temperatura. Estima-se redução na área de adequabilidade climática para a maioria das espécies consideradas, com comportamento semelhante para os dois grupos abordados. As espécies tenderão a ocupar uma posição mais austral, utilizando as áreas de maior altitude, latitude e próximas ao litoral do Brasil como refúgios climáticos, destacando essas áreas como estratégicas para a conservação.

Palavras-Chave: Nicho climático; Modelagem; Refúgio climático.

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1. INTRODUCTION

Considering that climate is determinant in the geographic distribution of species, the expansion and contraction of plant and animal populations in their native ranges have been strongly associated with climate change (Guitérrez and Trejo, 2014). Changes in patterns of species occurrences have been highlighted in several studies (e.g. Thuiller, 2007; Marchioro et at., 2019; Siqueira et al., 2019) as one of the main consequences expected in the global warming scenario. Although species have been continually exposed to variations in the climate throughout their evolutionary history, there is increasing concern about the accelerated rate of recent changes in global climate patterns (Melo et al., 2015; Pecl et al., 2017). Despite several sources of threat to biodiversity, the effects of climate change tend to become more prominent than others in the long term (Thuiller, 2007). A better understanding of how species will respond to climate change and the identification of areas of high conservation value based on vulnerability to climate change are therefore highly relevant for impact mitigation (Feeley et al., 2012; Thorne et al., 2018) and the conservation of biodiversity (Costa et al., 2018).

Predictive modeling is an alternative for simulating species distribution in future climate scenarios and assessing the impacts of climate change (Thomas et al., 2004; Costa et al., 2018). The use of appropriate modeling techniques in order to reduce uncertainty by adopting more specific criteria in the use of models and carefully selecting geographic and climate data (Medeiros et al., 2013), as well as the use of current knowledge in several fields of science (e.g. ecology, paleontology and evolution), can potentially transform the way the vulnerability of species to climate change has been evaluated (Dawnson et al., 2011).

An evaluation of climatic niche and impacts of climate change for the 2061-2080 period in areas of geographic occurrence of tree species that are indicators (indicator species hereafter) of alluvial forests in the central-southern region of the Atlantic Forest and Brazilian Pampa biomes is presented in this paper. Four main questions are answered: i) Will climate change alter the potential distribution range of tree species indicators of alluvial forests? ii) Which floristic group of alluvial forests will be potentially more impacted by climate change? iii) Which tree species will undergo more changes in their climatic suitability area? iv) Which climate variables are related to the climatic adequacy of these tree species indicators of alluvial forests?

2. MATERIAL AND METHODS

The indicator species of alluvial forests identified by Silva et al. (2020) were selected for an impact assessment of climate change on the central-southern region of the Atlantic Forest and Brazilian Pampa biomes. As clarified by Hill et al. (1975), indicator species are those with ecological preferences that identify specific environmental conditions. Therefore, indicator species of each group of alluvial forests were used to characterize distinct environmental conditions ($p < 0,001$): *Gymnanthes klotzschiana* Müll.Arg., *Allophylus edulis* (A.St.-Hil. et al.) Hieron. ex Niederl., *Vitex megapotamica* (Spreng.) Moldenke, *Campomanesia xanthocarpa* (Mart.) O.Berg, and *Eugenia uniflora* L. were used as indicators of alluvial forests in the Parana-Uruguay basin; *Andira fraxinifolia* Benth, *Pera glabrata* (Schott) Baill., *Aniba firmula* (Nees & Mart.) Mez, *Cecropia glaziovii* Snethl., *Hyeronima alchorneoides* Allemão, *Inga edulis* Mart., *Nectandra oppositifolia* Nees, *Tapirira guianensis* Aubl., *Calophyllum brasiliense* Cambess., *Guatteria australis* A.St.-Hil., *Inga thibaudiana* DC., *Lecythis pisonis* Cambess., *Myrcia racemosa* (O.Berg) Kiaersk., *Pseudopiptadenia contorta* (DC.) G.P.Lewis & M.P.Lima, *Simarouba amara* Aubl., *Tabebuia cassinoides* (Lam.) DC., *Alchornea triplinervia* (Spreng.) Mull.Arg., *Annona dolabripetala* Raddi, *Coussapoa microcarpa* (Schott) Rizzini, *Euterpe edulis* Mart., *Garcinia gardneriana* (Planch. & Triana) Zappi, *Pseudobombax grandiflorum* (Cav.) A.Robyns, and *Pterocarpus rohrii* Vahl were used as indicators of alluvial forests in the Atlantic basin. Silva et al. (2020) observed that the group of alluvial forests in the Parana-Uruguay basin was strongly associated with subtropical (temperate) characteristics, while the group of alluvial forests in the Atlantic basin was strongly associated with areas in tropical conditions, characteristic of the Atlantic basin domain.

Species occurrences were extracted from the Botanical Information and Ecology Network (BIEN) (Enquist and Boyle, 2012; Fegraus, 2012; SpeciesLink, 2012; Anderson-Teixeira et al., 2015;

Enquist et al., 2016, GBIF.org, 2018). Data for *E. uniflora* were extracted from the Global Biodiversity Information Facility (GBIF.org 2019) because there were no data available from BIEN. All data were spatially filtered considering a resolution of 10 minutes to avoid sampling bias (Aiello-Lammens et al., 2015). The geographic occurrence data of the species were rigorously verified and only native range areas were used. Distribution references were obtained from the Flora do Brasil 2020 Database (2017).

Nineteen climate variables taken from the WorldClim database (Hijmans et al., 2005) were used for modeling the climatic niche at 10 minute resolution (about 18.5 km at the equator) for contemporary and future climates (2061-2080 period): bio1 (mean annual temperature), bio2 (mean diurnal thermal range), bio3 (isothermality), bio4 (thermal seasonality), bio5 (maximum temperature in hottest month), bio6 (minimum temperature in coldest month), bio7 (annual thermal range), bio8 (mean temperature in wettest quarter), bio9 (mean temperature in driest quarter), bio10 (mean temperature in hottest quarter), bio11 (mean temperature in coldest quarter), bio12 annual rainfall), bio13 (rainfall in wettest month), bio14 (rainfall in driest month), bio15 (rainfall seasonality), bio16 (rainfall in wettest quarter), bio17 (rainfall in driest quarter), bio18 (rainfall in hottest quarter) and bio19 (rainfall in coldest quarter). Variance inflation factors (VIF) were determined to eliminate the problem of multicollinearity of explanatory climate variables (Graham, 2003), and highly correlated variables were eliminated (VIF > 10) (Dormann et al., 2013; James et al., 2014) for each indicator species considered.

Two assumptions usually considered in climate modeling studies on species geographic distribution were adopted to apply the models: i) species are in balance; ii) species do not adapt. The species climatic niches were modeled using the Maximum Entropy algorithm (Maxent) (Philips et al., 2017), using 10,000 pseudo-absences (Lobo and Tognelli, 2011) distributed at random in a 500 km radius around each occurrence (VanDerWal et al., 2009). Five rounds of calibration (70% of data) and test adjustments (30% of data) were conducted. The adequacy of adjustments was verified by TSS statistics (True Skills Statistics), which varies between -1 and 1 (Allouche et al., 2006), where 1 represents the value of the perfect adjustment. The projection of potential spatial occurrence areas was based on the consensus between adjustments to reduce predictive uncertainties inherent to each adjustment,. The mean of different adjustments of climate adequacy estimations was calculated (TSS > 0.4) (Landis and Koch, 1977). Bioclimate variables with the strongest influence on the area of climatic adequacy were determined from adjustments with TSS > 0.4. Response curves between the estimate of climatic adequacy and the best explanatory variables were built for each species.

The most pessimistic climate change scenario for the 2061-2080 period (RCP 8.5 - Representative Concentration Pathways), in which humanity will not adopt mitigation strategies, was considered to quantify the impacts of climate change on the area of potential species occurrence using future predictions. These predictions were based on data from the Intergovernmental Panel on Climate Change report (IPCC, 2014) and on the atmospheric circulation model HADGEM2-ES of the MET OFFICE in the United Kingdom.

Consensual projections were produced for indicator species of the two forest groups with TSS adjustments > 0.4 and more than 100 spatially filtered occurrences. Five species were considered for the Parana-Uruguay group and 16 species for the Atlantic group. Present and future binary maps (presence/absence) were produced for these species. Areas were considered adequate for species occurrence when adequacy estimations were higher than 50%. The maps were then superposed to quantify lost pixels, gained pixels, and stable pixels for all species, representing the climatic adequacy area for each one. Possible differences in the impact of changes on the groups (Parana-Uruguay and Atlantic basins) were verified through a boxplot and Mann-Whitney test, as the data set did not follow a normal distribution.

The analyses were conducted in R programming language version 3.4.1 (R Development Core Team, 2017) using the usdm (Naimi et al., 2014), raster (Hijmans, 2015), biomod2 (Thuiller et al., 2014), spThin (Aiello-Lammens et al., 2019), BIEN (Maitner, 2018) and rgbif (Chamberlain et al., 2019) packages. R Scripts are available at https://github.com/higuchip/jessica_oneda_paper.

3. RESULTS

After spatial filtering, the number of geographic occurrences of tree species in alluvial forests varied from 59 (*T. cassinoides*) to 984 (*A. triplinervia*). The analysis of occurrence data showed that the Parana-Uruguay basin (A-E) indicator species were predominantly concentrated in the southern region of Brazil, both in the coastal region and in the continental area.The indicator species of the Atlantic basin (F-U) were generally more distributed regionally but expressively concentrated along the Atlantic coast (Figure 1).

Isothermality (bio 3) and mean temperature in the wettest quarter (bio 8) stood out for species of the Parana-Uruguay group (A-E). While the likelihood of occurrence of *A. edulis* and *E. uniflora* was higher in areas with intermediate isothermal values, *G. klotzschiana* and *C. xanthocarpa* were intolerant to areas with high temperatures in the period of the year with the highest rainfall (Figure 2). On the other hand, rainfall in the driest quarter (bio 14) was the most frequent variable among species in the Atlantic group (F-U), as most species were gradually more intolerant to the month with minimum rainfall under approximately 50mm.

A decrease in area of climatic adequacy for most indicator species in both groups is predicted for the 2061-2080 period (Figure 3). In the Parana-Uruguay group, *V. megapotamica* (-57.5%) and *C. xanthocarpa* (-52.4%) were marked by a decrease in the potential area of occurrence. In the Atlantic group, the most relevant losses in area were estimated for *C. glaziovii* (-86.6%) and *G. australis* (-83.4%). The species less sensitive to climate change in the Parana-Uruguay and the Atlantic basin were, respectively, *E. uniflora* (-34.8%) and *M. racemosa* (-2.1%). The only species for which the area of climatic adequacy should increase is *A. fraxinifolia* (+85.2%), in the Atlantic basin, with significant expansion in Central Brazil.

Despite the great difference in behavior between the indicator species of the groups of alluvial forests in the Parana-Uruguay and Atlantic basins, their behavior towards climate change in the 2061-2080 period is similar (p=0.398) (Figure 4).

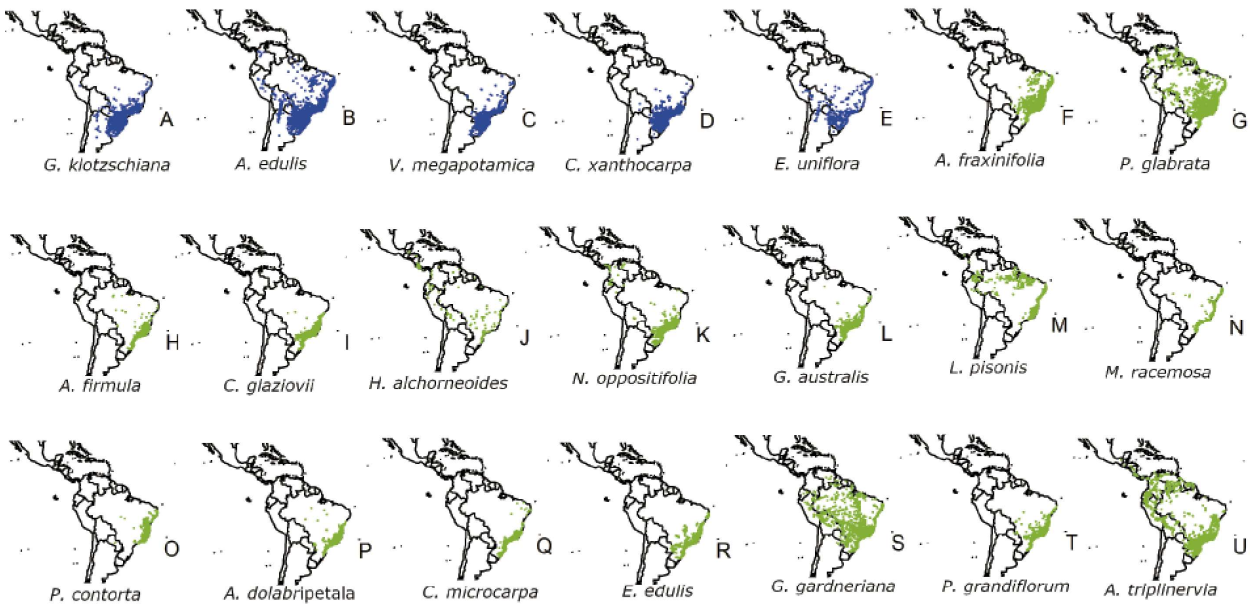

Figure 1 – Areas of geographic occurrence of indicator species of the group of alluvial forests in the Parana-Uruguay basin (A-E) and indicator species of the group of alluvial forests in the Atlantic basin (F-U) used to produce contemporary and future (2061-2080 period) climate adequacy projections considering the RCP 8.5 scenario.

Figura 1 *– Áreas de ocorrência geográficas das espécies indicadoras do grupo de florestas aluviais da bacia Paraná-Uruguai (A-E) e indicadoras do grupo de florestas aluvias da bacia do Atlântico (F-U), que foram utilizadas para as projeções de adequabilidade climática contemporânea e futura (período de 2061-2080), considerando o cenário RCP 8.5.*

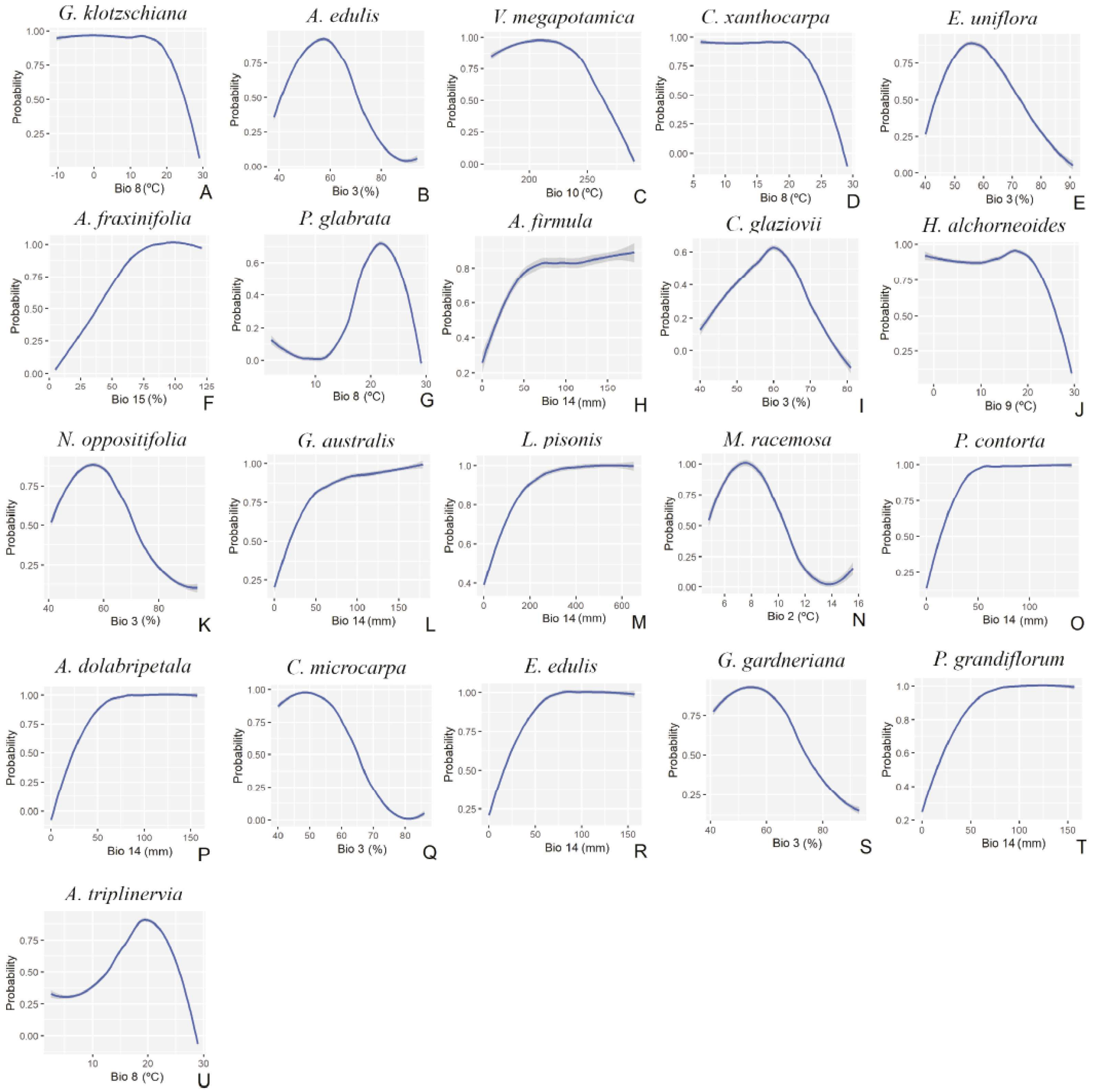

Figure 2 – Estimate of climate adequacy according to Maxent adjustments with TSS > 0.4 in relation to the best explanatory variables for indicator species of the group of alluvial forests in the Parana-Uruguay basin (A-E) and indicator species of the group of alluvial forests in the Atlantic basin (F-U) used for projections of contemporary and future (2061-2080 period) climate adequacy considering the RCP 8.5 scenario (bio2: mean diurnal thermal range; bio3: isothermality; bio8: mean temperature in wettest quarter; bio9: mean temperature in driest quarter; bio10: mean temperature in hottest quarter; bio14: rainfall in driest month; bio15 rainfall seasonality).

Figura 2 *– Estimava de adequabilidade climática, de acordo com os ajustes do Maxent com TSS > 0,4, em função das variáveis de maior poder explicativo, para as espécies indicadoras do grupo de florestas aluviais da bacia Paraná-Uruguai (A-E) e espécies indicadoras do grupo de florestas aluvias da bacia do Atlântico (F-U), que foram utilizadas para as projeções de adequabilidade climática contemporânea e futura (período de 2061-2080) considerando o cenário RCP 8.5 (bio2: amplitude térmica diária média; bio3: isotermalidade; bio8: temperatura média no trimestre mais úmido; bio9; temperatura média no trimestre mais seco; bio10: temperatura média no trimestre mais quente; bio14: precipitação no mês mais seco; bio15 sazonalidade da precipitação).*

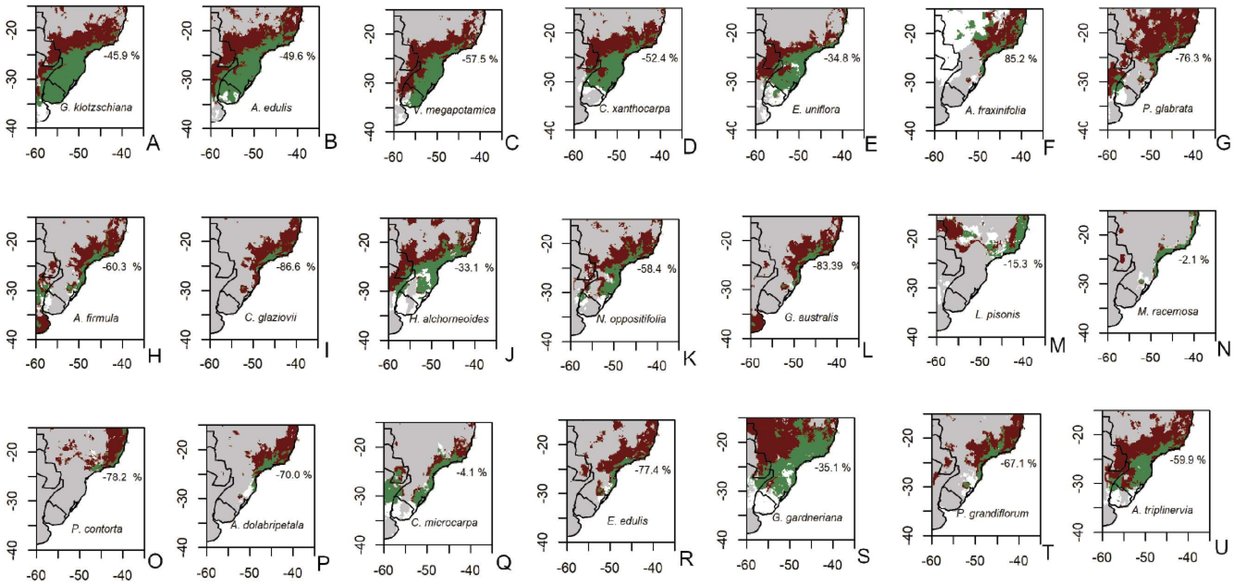

Figure 3 – Impact of climate change (RCP 8.5) for the 2061-2080 period on the area of climate adequacy of indicator species in the Parana-Uruguay basin (A-E) and indicator species in the Atlantic basin (F-U) (Green: stable areas with favorable climate to continue in the future; Grey: stable areas where the climate is not favorable and will continue not to be favorable in the future; Red: unstable areas where the climate will stop being favorable for the occurrence of the species; White: unstable areas that will become favorable in the future).

Figura 3 *– Impacto de mudança climática (RCP 8.5), para o período de 2061-2080 sobre a área de adequabilidade climática para espécies aluviais indicadoras da Bacia do Paraná-Uruguai (A-E) e indicadoras da Bacia do Atlântico (F-U) (Verde: áreas estáveis, que apresentam o clima favorável e continuarão apresentando no futuro; Cinza: áreas estáveis, que não apresentam o clima favorável e continuarão não apresentando no futuro; Vermelho: áreas instáveis, que deixarão de apresentar condições favoráveis para a ocorrência da espécie; Branco: áreas instáveis, que passarão a apresentar condições climáticas favoráveis).*

4. DISCUSSION

Distinct geographic distribution patterns were identified for tree species based on the groups of alluvial forests considered in this study. Occurrence in subtropical regions predominates in the Parana-Uruguay group, as in the south of Brazil, while in the Atlantic basin species are more distributed near the coast and are more related to higher tropicality.

When bioclimate variables that influence these distribution standards were observed, temperature variables were more influential in the Parana-Uruguay group. Analysis of climatic adequacy estimation curves showed that the geographic distribution of the species in the group is associated with milder summer temperatures (subtropical conditions) and medium variations between diurnal and annual thermal ranges (medium isothermality). Estimation of adequacy for the species with the highest indicator value in the Parana-Uruguay group, *G. klotzschiana*, and for *C. xanthocarpa*, is favorable up to the approximate mean temperature of 20ºC in the wettest quarter (usually in the summer). With the increase of temperature beyond this value, the estimation of adequacy for these species is dramatically reduced. The behavior of *V. megapotamica*, more influenced by temperature in the hottest quarter (also usually in the summer), is similar, but the optimum mean temperature is around 21ºC. Only *A. edulis* and *E. uniflora* in the Parana-Uruguay basin are more influenced by isothermality, with climate adequacy optimums between 50 and 60%. Isothermality, which refers to the difference between diurnal thermal range and annual thermal range, is related to the tropicality effect. These species are therefore less tolerant to higher tropicality conditions.

In the Atlantic group, rainfall influences climatic adequacy patterns besides temperature variables. This may be related to the physiological tolerance of species in each group, a determinant of spatial distribution (Lou et al., 2018). Species more tolerant to flooding or drought tend to have a wider niche amplitude. The most influential variables are rainfall in

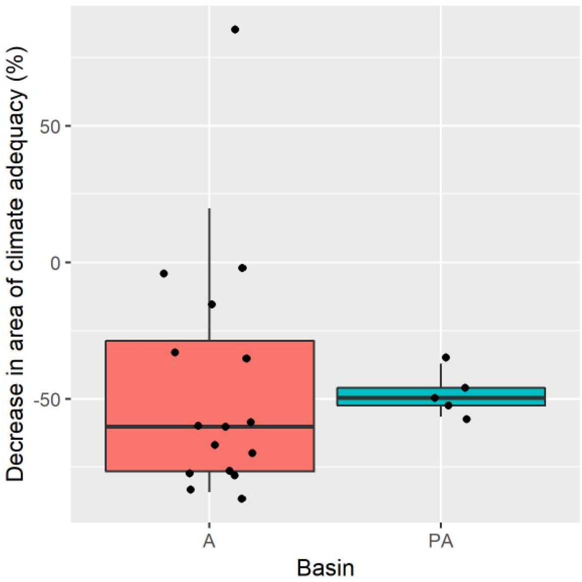

Figure 4 – Estimate of the impact of climate change on area of climate adequacy of groups of alluvial forests in the Parana-Uruguay (PA) and Atlantic (A) basins.
Figura 4 – *Estimativa do impacto da mudança climática sobre a área de adequabilidade climática dos grupos de florestas aluviais da bacia Paraná-Uruguai (PA) e da bacia do Atlântico (A).*

the driest month, strongly related to the occurrence of seven species, and isothermality, which significantly influences climatic adequacy for four species.

The rainfall seasonality variable is, in turn, strongly associated with the species of highest indicator value in the group, *A. fraxinifolia*. The interpretation of the response curve may suggest that the regular distribution of rain throughout the year is a limiting factor. On the other hand, the seasonality of high annual rainfall favors its occurrence, with maximum expression under circumstances of high inequality in which the variation of the period with the highest rainfall in relation to the period with less rainfall is comprehended in the interval between 75 to 115%. The majority of species in the group - *A. firmula*, *G. australis*, *L. pisonis*, *P. contorta*, *A. dolabripetala*, *E. edulis* and *P. grandiflorum* - are strongly related to rainfall in the driest month. It is possible to note that the estimation of climatic adequacy for these species is reduced under situations of low rainfall in the driest month (< 50 mm), with an optimum range beyond approximately 75 mm. The sensitivity of the rainfall regime highlighted by modeling suggests that these species are intolerant to extreme drought events.

As stated by Caron et al. (2014), the seasonality of climate elements may change plant physiological behavior. Therefore, climate change, especially high temperatures and low rainfall, may increase water and nutritional stress. High temperatures beyond optimum values is harmful to plant growth and may damage photosynthetic capacity (Kluge et al., 2015; Martinez et al., 2015). Extreme temperatures and water stress may cause stomata closure and reduce carbon intake, reducing photosynthesis and chlorophyll concentration while impacting net carbon gain. Wheeler et al. (2000) stated that increased temperatures may affect the most sensitive development phases of plants, such as flowering, thus reducing seed production due to interrupted pollination or loss of pollen viability, in turn affecting other plant patterns and interspecific relations (Wheeler and Reynolds, 2013).

The isothermality variable strongly influences the climate adequacy of *C. glaziovii*, *N. oppositifolia*, *C. microcarpa* and *G. gardneriana*, which basically repeat the behavior pattern related to the existence of variations between diurnal and annual thermal ranges observed for species in the Parana-Uruguay group. In addition to tropicality factors related to latitude, isothermality may be related to altitude. Therefore, the species strongly related to this variable are associated with lower altitudes, subject to smaller ranges of diurnal temperature, and intolerant to higher altitudes, in turn related to higher thermal ranges. In like manner, the probability of occurrence of *M. racemosa* is strongly related to mean diurnal thermal range, with a higher probability of occurrence in lower thermal ranges. Low altitude areas in the absence of extreme droughts are therefore adequate for a large portion of Atlantic species. However, other factors related to temperature also influence species in the Atlantic group. *P. glabrata* and *A. triplinervia* are more related to mean temperature in the wettest quarter, with temperature optimums around 22ºC and 20ºC, respectively. *H. alchorneoides* is strongly associated with mean temperature in the driest quarter. Climatic adequacy for this species is higher under mild temperatures, with a climate optimum around 20ºC. The likelihood of occurrence of this species is significantly reduced with an increase in temperature beyond this value.

Estimations for nearly all species assessed in the present study indicate a loss of area of climatic adequacy, with values varying from -2.1% (*M. racemosa*) to -86.6% (*C. glaziovii*). The only exception is *A. fraxinifolia*, as the potential area of occurrence increased. Among 21 species considered, only eight are predicted to lose less than 50% of adequate area, while 13 should incur in area losses higher than 50%. This trend of area loss was also observed by Velazco et al. (2019) upon an evaluation of the vulnerability of Brazilian Savanna (Cerrado) species to climate change which culminated in changes in species distribution patterns.

Stable areas in the Parana-Uruguay group were mostly concentrated in southern Brazil, from the coast to the highest altitudes. The unstable areas where climatic adequacy will decrease occur in different regions in Brazil above the Tropic of Capricorn, with higher expression in the southeastern and part of the Central-Western regions, where temperature increase tends to be more severe. Warming was also estimated in projections of future climate scenarios for the state of Parana (Melo et al., 2015). The authors expressed concern as temperature increase is expected to prompt a reorganization of natural systems. The loss of areas of adequate climate is partially a result of an increase in tropicality, which will generate changes in the rainfall regime and in temperature (Salviano et al., 2016), factors that influence species occurrence (Gotelli et al., 2009; Carvalho et al., 2019). Medeiros et al. (2013) corroborated this observation by predicting an increase in annual and seasonal maximum and minimum temperatures for the Southern region. In a study on the Atlantic Forest, Colombo and Joly (2010) identified a pattern of reduction in areas of occurrence of the species considered that varied between 25% and 50%, with migration to more meridional areas in Brazil. Several studies (Thomas et al., 2004; Parmesan, 2006; Lemes and Loyola, 2014) have pointed out that climate change may deeply affect environmental dynamics, even leading to species extinctions, overall at local levels.

The areas that tend to remain stable under favorable climate conditions in the Atlantic group are mainly located near the coast in the Northeastern, Southeastern and Southern regions. A reduction in climatic adequacy will occur in unstable areas, mainly concentrated in the Northeast and in the Southeast, both along the coast and in continental regions. Some currently unstable areas will develop an adequate climate for Atlantic species (especially *A. fraxinifolia*, *L. pisonis*, *H. alchorneoides* and *G. gardneriana*), mostly in Central and Southern Brazil. The displacement geographic occurrence limits to higher altitudes and latitudes in response to temperature increase is a tendency that has been observed for several species (Colombo and Joly, 2010; Chen et al., 2011; Feeley et al., 2012; Moritz and Agudo, 2013) as a consequence of higher tropicality in the future. Besides, the decrease in more continental areas of adequate climate may be explained by a decrease in rainfall in these areas.

The groups assessed include pioneer species such as *G. klotzschiana*, *E. uniflora*, *A. fraxinifolia*, and *C. glaziovii* (Aidar et al., 2003; Meyer et al., 2013), usually associated with higher environmental plasticity and higher adaptation capacity to environmental variation than non-pioneers (Valladares and Niinemets, 2008). Pioneer species may thus have better chances of survival from changes in rainfall and temperature. This is in line with Noss (2001), who stated that improved knowledge of functional groups could contribute to the understanding species resistance mechanisms against climate change.

Areas of climatic adequacy are expected to decrease between 30 and 77% for most species in the Atlantic group. However, some species are outside this range and may be less (between 2 and 15%) or more (between 78 and 87%) affected. Counteracting the pattern of area loss for species in the group, the area of occurrence of *A. fraxinifolia* is estimated to increase by more than half, with an expectation of increase in area of climatic adequacy of 85.2%. As mentioned earlier, the occurrence of this species is limited by the homogeneous distribution of rainfall throughout the year. Therefore, as more drought events are expected in the future, the species will benefit from higher rainfall seasonality and increase its distribution range. A decrease in climate adequacy in the order of 45 to 55% is expected for the majority of the indicator species in the Parana-Uruguay basin, with the exception of *E. uniflora* and *V. megapotamica*, as the values for these species are beyond the limits established for the group. The estimations of reduced climate adequacy for both groups are therefore variable, with relatively similar mean values, but result in no difference between groups in terms of decrease in climate adequacy.

Considering that the Atlantic group is subject to higher tropicality, higher adaptation capacity to climate change was expected, with a less significant decrease in areas of climatic adequacy for the indicator species. However, as climate change does not only result in global warming, but also in changes in rainfall patterns, species not adapted to extreme droughts will also undergo a decrease in area of adequate climate. Besides, it is important to note the high variation of the values of decrease in climate adequacy in both groups, which shows that, in both cases, species have different patterns of behavior. This indicates the complexity of forest ecosystems and the difficulty of establishing patterns for such heterogeneous groups.

The climate in areas of higher altitude and latitude as well as areas nearer the coast are more suitable for the alluvial tree species considered in the present study and may be considered strategic for conservation, as they may function as climate refuges. In a scenario of global warming and altered rainfall patterns, the potential occupation of these climate refuges by different species highlights the need to implement protection measures such as the establishment of protected areas (Pecl et al., 2017).

Although geographic distribution modeling is being widely used, its limitations must be acknowledged. They include the lack of capacity to model biotic interactions, dispersal patterns, and evolutionary changes (Soberón and Peterson, 2005; Torres and Vercillo, 2012). Species adaptation capacity is therefore not considered, as other factors beyond climatic niche (biological, pedological) may create more selective habitats that limit the occurrence of certain species (Pacifici et al., 2015).

5. CONCLUSION

The potential distribution range of species that function as indicators of alluvial forests will be altered due to changes in climate expected in the period 2061-2080. The majority of species considered in the present study tend to undergo significant changes in area of climatic adequacy, with losses above the order of 50%. However, no differences were observed between the Parana-Uruguay and Atlantic groups in terms of decrease in area of climatic adequacy. In a global warming scenario, the species assessed will tend to occupy a more southern distribution, occurring in higher altitudes and latitudes, as well as near the coast. These areas will constitute climate refuges, which highlights the relevance of their conservation.

AUTHOR CONTRIBUTIONS

Conceptualization: Silva, J.O.; Silva, A.C.; Galvão, F. Formal analysis: Silva, J.O. Investigation: Silva, J.O.; Writing - Original Draft: Silva, J.O. Writing - Review & Editing: Silva, J.O; Galvão, F.; Silva, A.C.; Higuchi, P. Visualization: Silva, J.O; Silva, A.C.; Galvão, F.; Higuchi, P. Supervision: Galvão, F.; Methodology: Higuchi, P. Software: Higuchi, P. Data Curation: Silva, J.O.

6.REFERENCES

Aidar MPM, Schmidt S, Moss G, Stewart GR, Joly CA. Nitrogen use strategies of neotropical rainforest trees in threatened Atlantic Forest. Plant, Cell and Environment. 2003;26(3):389-399. doi: doi.org/10.1046/j.1365-3040.2003.00970.x

Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, Anderson RP. SpThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography. 2015;38:541-545. doi: 10.1111/ecog.01132

Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, Anderson RP. spThing: Functions for Spatial Thinning of Species Occurrence Records for Use in Ecological Models. R package version 0.1.0.1. 2019 [cited 2019 Apr 08]. Avaliable from: https://cran.r-project.org/web/packages/spThin/index.html

Allouche O, Tsoar A, Kadmon R. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology. 2006;43(6):1223-1232. doi: 10.1111/j.1365-2664.2006.01214.x

Anderson-Teixeira KJ, Davies SJ, Bennett AC, Gonzalez-Akre EB, Muller-Landau HC, Joseph Wright S, et al. CTFS-Forest GEO: a worldwide network monitoring forests in an era of global change. Global Change Biology. 2015;21(2):528-549. doi: 10.1111/gcb.12712

Caron BO, Perrando ER, Schmidt D, Manfron PA, Behling A, Elli EF, et al. Physiologic relationships in Brazilian Orchid Tree (*Bauhinia forficata* Link) seedlings. Revista Brasileira de Plantas Medicinais. 2014;16(2):196-201. doi: 10.1590/S1516-05722014000200005

Carvalho MC, França LCJ, Lopes IL, Araújo LA, Mello JM, Gomide LR. Machine learning algorithms for modeling the potential distribution habitat of tree species. Nativa. 2019;7(5):600-606. doi: 10.31413/nativa.v7i5.7214

Chamberlain S, Barve V, Desmet P, Geffert L, Mcglinn D, Oldoni D, et al. rgbif: Interface to the Global Biodiversity Information Facility API. R package version 1.2.0. 2019 [cited 2019 Apr 08]. Avaliable from: https://cran.r-project.org/web/packages/rgbif/index.html

Chen IC, Hill JK, Ohlemuller R, Roy DB, Thomas CD. Rapid Range Shifts of Species Associated with High Levels of Climate Warming. Science. 2011;333(6045):1024-1026. doi: 10.1126/science.1206432

Colombo AF, Joly CA. Brazilian Atlantic Forest *lato sensu*: the most ancient Brazilian forest, and a biodiversity hotspot, is highly threatened by climate change. Brazilian Journal of Biology. 2010;70(3):697-708. doi: 10.1590/S1519-69842010000400002

Costa TR, Moura CC, Machado ELM, Bueno ML. Predictive modeling of the species *Lychnophora pohlii* SCH. BIP., in the state of Minas Gerais. Nativa. 2018;6(1):100-106. doi: 10.31413/nativa.v6i1.4696

Dawnson T, Jacksin ST, House J, Colin I, Mace GM. Beyond predictions: Biodiversity conservation in a changing climate. Science. 2011;332(6025):53-58. doi: 10.1126/science.1200303

Dormann CF, Elith J, Bacher S. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography. 2013;36(1):27-46. doi: 10.1111/j.1600-0587.2012.07348.x

Enquist B, Boyle B. SALVIAS - The SALVIAS vegetation inventory database. Biodiversity & Ecology. 2012;4:288-288. doi: 10.7809/b-e.00086

Enquist BJ, Condit R, Peet RK, Schildhauer M, Thiers BM. Cyberinfrastructure for an integrated botanical information network to investigate the ecological impacts of global climate change on plant biodiversity. PeerJ Preprints. 2016;4:e2615v2. doi: 10.7287/peerj.preprints.2615v2

Feeley KJ, Malhi Y, Zelazowski P, Silman MR. The relative importance of deforestation, precipitation change, and temperature sensitivity in determining the future distributions and diversity of Amazonian plant species. Global Change Biology. 2012;18(8):2636-2647. doi: 10.1111/j.1365-2486.2012.02719.x

Fegraus, E. Tropical Ecology Assessment and Monitoring Network (TEAM Network). In: Dengler J, Oldeland J, Jansen F, Chytrý M, Ewald J, Finckh M, et al., editors. Vegetation databases for the 21st century. Biodiversity & Ecology. 2012;4:287-287. doi: 10.7809/b-e.00085

Flora do Brasil 2020 em construção. Jardim Botânico do Rio de Janeiro. 2017 [cited 2017 Aug 22]. Available from: http://floradobrasil.jbrj.gov.br/

GBIF.org. GBIF Occurrence. 2018 [cited 2018 Aug 14]. Available from: https://doi.org/10.15468/dl.fpwlzt

GBIF.org. GBIF Occurrence. 2019 [cited 2019 Jun 10]. Available from: https://doi.org/10.15468/dl.mh1fy8

Gotelli NJ, Anderon MJ, Arita HT, Chao A, Colwell RK, Connolly SR, et al. Patterns and causes of species richness: a general simulation model for macroecology. Ecology Letters. 2009;12:873-886. doi: 10.1111/j.1461-0248.2009.01353.x

Graham MH. Confronting multicollinearity in ecological multiple regression. Ecology. 2003;84 (11):2809-2815. doi: 10.1890/02-3114

Guitérrez E, Trejo I. Effect of climatic change on the potential distribution of five species of temperature forest trees in Mexico. Revista Mexicana de Biodiversidad. 2014;85(1):179-188. doi: 10.7550/rmb.37737

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvins A. Very high resolution interpolated climate surfaces for global land areas. Internacional Journal of Climatology. 2005;25(15):196-1978. doi: 10.1002/joc.1276

Hijmans RJ. Raster: geographic data analysis and modeling. R package version 2.6-7. 2015 [cited 2018 Jun 04]. Available from: https://cran.r-project.org/web/packages/raster/

Hill MO, Bunce RGH, Shaw MW. Indicator species analysis, a divisive polythetic method of classification, and its application to a survey of native pinewoods in Scotland. Journal of Ecology. 1975;63(2):597-613. doi: 10.2307/2258738

Intergovernmental Panel of Climate Change - IPCC. Climate Change 2014: Mitigation of Climate Change - Contribution of Working Group III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge: Cambridge University Press.

James G, Witten D, Hastie T, Tibshirani R. An Introduction to Statistical Learning: With Applications in R. New York: Springer Publishing Company; 2014. ISBN 978-1-4614-7138-7

Kluge RA, Tezotto-Uliana JV, Silva PPM. Physiological and Environmental Aspects of Photosynthesis. Revista Virtual de Química. 2015;7(1):56-73. doi: 10.5935/1984-6835.20150004

Landis JR, Koch GC. The measurement of observer agreement for categorical data. Biometrics. 1977;33(1):159-174. doi: 10.2307/2529310

Lemes P, Loyola RD. Climate change and priorities for the biodiversity conservation. Revista de Biologia Neotropical. 2014;11(1):47-57. doi: 10.5216/rbn.v11i1.30699

Lobo JM, Tognelli MF. Exploring the effects of quantify and location of pseudo-absences and sampling biases on the performance of distribution models with limited point occurrence data. Journal for Nature Conservation. 2011;19(1):1-7. doi: 10.1016/j.jnc.2010.03.002

Lou Y, Gao C, Pan Y, Xue Z, Liu Y, Tang Z, et al. Niche modelling of marsh plants based on occurrence and abundance data. Science of the Total Envinronment. 2018;616-617:198-207. doi: 10.1016/j.scitotenv.2017.10.300

Maitner B. BIEN: Tools for Accessing the Botanical Information and Ecology Network Database. R package version 1.2.3. 2018 [cited 2019 Apr 08]. Available from: https://cran.r-project.org/web/packages/BIEN/index.html

Marchioro CA, Santos KL, Siminski A. Present and future of the critically endangered *Araucaria angustifolia* due to climate change and habitat loss. Forestry. 2019;93(3):401-410. doi: 10.1093/forestry/cpz066

Martinez CA, Oliveira EAD, Mello TRP, Alzate-Marin AL. Plants responses to increase in atmospheric carbon dioxide and temperature. Revista Brasileira de Geografia Física. 2015;8:635-650. doi: 10.26848/rbgf.v8.0.p635-650

Medeiros MB, Cardoso MS, Albuquerque RW, Noronha SE. Climate change vulnerability and uncertainty reduction in projections for *Dicksonia sellowiana* (Pres.) Hook. Pesquisa Florestal Brasileira. 2013;33(75):299-308. doi: 10.4336/2013.pfb.33.75.372

Melo LC, Sanquetta CR, Corte APD, Virgens Filho JS. Future climate scenarios for Parana: opportunities for the forest sector. Revista Brasileira de Climatologia. 2015;16:120-131. doi: 10.5380/abclima.v16i0.41149

Meyer L, Sevegnani L, Gasper AL, Schorn LA, Vibrans AC, Lingner DV, et al. Phytosociology of the tree/shurb component of the Mixed Ombrophylous Forest in Santa Catarina. In: Vibrans AC, Sevegnani L, Gasper AL, Lingnet DV, editors. Inventário Florístico Florestal de Santa Catarina, V. III, Floresta Ombrófila Mista. Blumenau: Edifurb; 2013. p. 157-189. ISBN 9788571143326.

Moritz C, Agudo R. The future of species under climate change: Resilience or decline? Science. 2013;341(6145):504-508. doi: 10.1126/science.1237190

Naimi B, Hamm NAS, Groen TA, Skidmore AK, Toxopeus AG. Where is positional uncertainty a problem for species distribution modelling? Ecography. 2014;37(2):191-203. doi: 10.1111/j.1600-0587.2013.00205.x

Noss RF. Beyond Kyoto: Forest management in a time of rapid climate change. Conservation Biology. 2001;15(3):578-590. doi: 10.1046/j.1523-1739.2001.015003578.x

Pacifici M, Foden WB, Visconti P, Watson JEM, Butchart SHM, Kovacs KM, et al. Assessing species vulnerability to climate change. Nature Climate Change. 2015;5(3):215-224. doi: 10.1038/nclimate2448

Parmesan C. Ecological and Evolutionary Responses to Recent Climate Change. Annual Review of Ecology, Evolution and Systematics. 2006;37:637-669. doi: 10.1146/annurev.ecolsys.37.091305.110100

Pecl GT, Araujo MB, Bell JD, Blanchard J, Bonebrake TC, Chen IC, et al. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. Science. 2017;355(6332):1-9. doi: 10.1126/science.aai9214

Philips SJ, Robert P, Anderson RP, Dudik M, Schapire RE, Blair M. Opening the black box: an open-source release of Maxent. Ecography. 2017;40(7):887-893. doi: 10.1111/ecog.03049

R Development Core Team. R: A language and environment for statistical computing. Viena, Austria: R Foundation for Statistical Computing; 2017. Available from: http://www.r-project.org

Salviano MF, Groppo JD, Pellegrino GQ. Trends Analysis of Precipitation and Temperature Data in Brazil. Revista Brasileira de Meteorologia. 2016;31(1):64-73. doi: 10.1590/0102-778620150003

Silva JO, Galvão F, Silva AC, Higuchi P. Floristic patterns of alluvial forests in Atlantic Forest and Pampa: climate and geographic insertion as determining factors. Anais da Academia Brasileira de Ciências. 2020;92(3):e20180803. doi: 10.1590/0001-3765202020180803

Siqueira SF, Higuchi P, Silva AC. Contemporary and future potential geographic distribution of *Cedrela fissilis* Vell. under climate change scenarios. Revista Árvore. 2019;43(3): e430306. doi: 10.1590/1806-90882019000300006

Soberón J, Peterson AT. Interpretation of models of fundamental ecological niches and species' distributional areas. Biodiversity Informatics. 2005;2(10):1-10. doi: 10.17161/bi.v2i0.4

SpeciesLink. 2012 [cited 2012 Mar 29]. Available from: http://www.splink.org.br/

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, et al. Extinction risk from climate change. Nature. 2004;427:145-148. doi: 10.1038/nature02121

Thorne JH, Choe H, Stine PA, Chambers JC, Holguin A, Kerr AC, Schwartz MW. Climate change vulnerability assessment of forests in the Southwest USA. Climatic Change. 2018;148: 387-402. doi: 10.1007/s10584-017-2010-4

Thuiller W. Climate change and the ecologist. Nature. 2007;448:550-552. doi: 10.1038/448550a

Thuiller W, Georges D, Engler R. Biomod2: ensemble platform for species distribution modeling. R package v.3.3-7. 2014 [cited 2018 Jun 04]. Available from: https://cran.r-project.org/web/packages/biomod2/

Torres NM, Vercillo UE. How Can Species Distribution Modeling Tools Support Government Actions? Natureza & Conservação. 2012;10(2):228-230. doi: 10.4322/natcon.2012.023

Valladares F, Niinemets U. Shade tolerance, a key plant feature of complex nature and consequences. Annual Review of Ecology, Evolution and Systematics. 2008;39:237-257. doi:10.1146/annurev.ecolsys.39.110707.173506

VanDerWal J, Shoo LP, Graham C, Williams SE. Selecting pseudo-absence data for presence-only distribution modeling: How far should you stray from what you know? Ecological Modelling. 2009;220(4):589-594. doi: 10.1016/j.ecolmodel.2008.11.010

Velazco SJE, Villalobos F, Galvão F, De Marco Júnior P. A dark scenario for Cerrado plant species: Effects of future climate, land use and protected areas ineffectiveness. Diversity and Distributions. 2019;25(4):1-14. doi: 10.1111/ddi.12886

Wheeler T, Reynolds, C. Predicting the risks from climate change to forage and crop production for animal feed. Animal Frontiers. 2013;3(1):36-41. doi: 10.2527/af.2013-0006

Wheeler TR, Craufurd PQ, Ellis RH, Porter JR, Prasar PVV. Temperature variability and the yield of annual crops. Agriculture, Ecosystems and Environment. 2000;82:159-167. doi: 10.1016/S0167-8809(00)00224-3