



Modeling climatic and hydrological suitability for an encroaching tree species in a Neotropical flooded savanna

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ABSTRACT

Woody encroachment converts savanna systems to forests, altering the composition and productivity of native forage species and the supply of several ecosystem services. In this study, correlative species distribution models were applied to predict the chances of proliferation of a flood-tolerant encroaching tree (*Vochysia divergens*, Vochysiaceae) over the large Pantanal savanna floodplain and to provide a management tool with the aim of defining strategies for invasion control and containment over natural pastures. BIOCLIM and DOMAIN, two correlative models based on presence data, were used, accurately defining areas with a higher risk of invasion based on abiotic limits for the species distribution. The results of the models indicate that areas with high precipitation in the warmest period of the year and high annual mean temperature increase the chances of occurrence of this species, thus increasing the risk of invasion. Maintaining the integrity of natural pastures in climatic zones that are favorable to invasion requires management strategies such as low livestock density and maintenance of the hydrological regime, which prevent the degradation of natural pastures. Therefore, the management of encroaching trees must consider the socioeconomic and ecological benefits of removing populations of such trees, while seeking a balance in the conservation of ecosystem services and human livelihoods.

1. Introduction

Grasslands and other savanna systems occur worldwide and are regarded as multifunctional because they provide several ecosystem functions and services for humanity, especially the production of forage species for livestock farming (Andrade et al., 2015). The occupation of these pastures by native or exotic woody plants, a phenomenon known as woody encroachment (Devine et al., 2017), suppresses grasses and other herbaceous plants, resulting in a strong impact on the ecological integrity of natural grass-dominated savanna worldwide (Guido et al., 2016) and on the sustainability of these production systems. These impacts occur because woody encroachment converts open savannas to forest or woodland savanna systems, altering the composition and productivity of native forage species and the supply of several ecosystem services, e.g., nutrient cycling or water supply and regulation (Hobbs and Huenneke, 1992; Seidl and Moraes, 2000; Zedler and

Kercher, 2004; Archer et al., 2011). From a socioeconomic perspective, the occupation of natural pasture by woody plants leads to the (re) direction of part of the financial capital applied to invasion problems, often unsuccessfully (Archer et al., 2011; Santos et al., 2011, 2014; Devine et al., 2017).

Woody encroachment describes a biogeographic phenomenon of establishment, local spread, and increase of local populations of new species over new areas (Colautti and MacIsaac, 2004). Due to its socioeconomic and ecological impacts, encroachment has been debated in the context of invasive species control with the aim to design sustainable management guidelines for natural open savannas used as pastures (Santos et al., 2006). Investigation of the environmental forces that guide the large-scale proliferation of woody plants, such as temperature and precipitation, determines the success of initiatives to contain the advance of these plants because management responses can vary across bioclimatic zones (Archer et al., 2011).

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Wetlands are particularly susceptible to encroachment by herbaceous, woody, or shrub species that are tolerant to hydric stress by flooding because of the frequent lateral flux of floodwater that carries organisms and organic and inorganic matter to the flood area. This water movement favors the colonization and rapid growth of these traveling species (Zedler and Kercher, 2004). This is the case of *Vochysia divergens* Pohl, a native tree species that has rapidly dispersed since the last century over the Pantanal, a huge c. 150,502 thousand km² seasonally inundated savanna wetland in South America. The annual increase in the duration and level of flooding in wetter years, which results in the flooding of large areas of the landscape, is considered a trigger for the proliferation of opportunistic, flood-tolerant, woody species such as *Vochysia divergens* (Nunes da Cunha and Junk, 2004; Zedler and Kercher, 2004). This native species shares characteristics with some exotic wetland invasive species (e.g., *Polygonum cuspidatum* Sieb. and Zucc., *Mimosa pigra* L., *Spartina alterniflora* Loisel., and *Schinus terebinthifolius* Raddi) (Zedler and Kercher, 2004), including a wide ecological niche, fast colonization and growth over exposed soil, high regeneration rates, tolerance to frequent fluctuations in environmental conditions, and efficiency in nutrient use (Nunes da Cunha and Junk, 2004; Arieira and Nunes da Cunha, 2012; Dalmagro et al., 2016). These characteristics contribute to invasion success, enabling the conversion of floodable grass-dominated savannas with a high diversity of forage plants into monospecific forests (Zedler and Kercher, 2004; Pott et al., 2011; Santos et al., 2014; da Silva et al., 2016).

The potential causes of the proliferation of woody plants on grasslands and savannas are widely debated and are associated with both natural and anthropic factors, such as changes in climate (e.g., an increase in precipitation), grazing regime, fire, or hydrology, which individually or collectively increase the chances of invasion (Bren, 1992; Hobbs and Huenneke, 1992; Fensham et al. 2005; Overbeck et al., 2005; Santos et al., 2006; Archer et al., 2011; Rebellato et al., 2012; Devine et al., 2017). Disturbances such as fire, grazing, and flooding, for example, are part of the natural dynamics of several savanna ecosystems and are often associated with the maintenance of grassland communities that are rich in herbaceous species (Overbeck et al., 2005; Junk et al., 2006; Pott et al., 2011; Rebellato et al., 2012). However, alterations in the intensity and frequency of these disturbances, in addition to landscape fragmentation, may result in environmental degradation by the proliferation of woody species, as occurs in tropical savannas subjected to seasonal flooding (Bren, 1992; Briggs et al., 2005; Rebellato and Nunes da Cunha, 2005; Archer et al., 2011).

In the Pantanal, multiannual climatic variations, with periods of extreme drought and extreme humidity, affect the frequency and intensity of rains, flooding and fire, and is assigned as the main driver of *V. divergens* population expansion and retraction (Junk et al., 1989; Nunes da Cunha and Junk, 2004; Archer et al., 2011).

Species distribution modeling (SDM), has been widely used to predict the distribution of animals and plants. SDM enables quantifying the potential distribution of the species; testing biogeographic, ecologic and evolutionary hypotheses; evaluating species proliferation and invasion; and evaluating the impact of changes in climate, land use, and other environmental factors on species distribution (Peterson et al., 2007; Booth et al., 2014; Kriticos and Brunel, 2016). In this study, two correlative species distribution models (SDMs)—BIOCLIM and DOMAIN—were used to predict the chances of proliferation of a flood-tolerant encroaching tree, *Vochysia divergens*, over the floodplains in the Pantanal, especially over grass-dominated savannas. In addition, this study also examines how these bioclimatic models may support the establishment of management strategies for encroaching trees. Farmers in the region consider *V. divergens* an invasive species because of its rapid proliferation over natural savanna systems used as natural pasture, especially since approximately 1970.

Based on these models, this study addresses the following questions: What are the species-specific habitat requirements with respect to the climate and inundation conditions? Are predictions on the importance of inundation and precipitation on the distribution of *V. divergens* populations in accordance with previous scientific knowledge (Nunes da Cunha and Junk, 2004; Arieira and Nunes da Cunha, 2006; Dalmolin et al., 2015; Machado et al., 2015; Sallo et al., 2017)? What is the likelihood of *V. divergens* to spread to suitable habitats in regions with varying bioclimatic conditions?

2. Material and methods

2.1. Mapped area

The model of the potential distribution of *V. divergens* was applied to the extension of the Brazilian Pantanal, that occupies an area of 138,183 km² within the Upper Paraguay Basin (Padovani, 2010). Located in the central part of South America, the Pantanal is an active sedimentary basin filled with quaternary sediments forming a fluvial megafan (Assine and Soares, 2004). In Brazil, the Pantanal includes part of the territories of the states of Mato Grosso and Mato Grosso do Sul, and to the east, it extends over a small fraction of Paraguay and Bolivia between latitudes 14°S and 23°S and longitudes 53°W and 61°W (Padovani, 2010).

The predominant climate in the Pantanal and surrounding areas is characterized by a succession of dry winters and rainy summers (Aw) (Alvares et al., 2013). The Austral summer (from November to April) is marked by high temperatures (average day temperature is 34 °C), and it is the season with the highest precipitation. The precipitation decreases in the Austral winter, hence this season is very dry (de Musis et al., 1997). The soils are generally hydromorphic, with a texture varying from clayey in the lowest parts of the alluvial fan, which fall under the direct influence of floodwaters when the rivers overflow their banks or enter through secondary channels, to sandier in the highest parts of the alluvial fan (RadamBrasil, 1982).

On average, 42% of the Pantanal is flooded annually (Padovani, 2010). The rivers discharge and the flood peak of the northern Pantanal follow the seasonal trend of the precipitation, with long-term climate trends (20–50 years) reflecting in the strength of precipitation and river discharge (Barros et al., 2000; Camilloni and Barros, 2003). In the southern Pantanal flood peaks achieves its maximum four months later than rainfall peaks in the riverheads, as a result of the drainage delay in the region (Hamilton et al., 1996). In contrast to other grass-dominated systems in Brazil, the Pantanal has a predictable monomodal annual flooding pulse with a low amplitude (water depth < 4 m) which, in association with the geomorphological and edaphic variations of the landscape, generates a mosaic of permanently aquatic zones, periodically aquatic or terrestrial zones, swamp zones, zones permanently flooded by shallow water, and permanently terrestrial zones (Nunes da Cunha et al., 2015). In these zones, several types of forest and savanna vegetation occur with spatio-temporal variation (Pott et al., 2011). *Vochysia divergens*, called locally “Cambará” (Fig. 1), belongs to the family *Vochysiaceae*, and its phylogeographic origin is associated with the Amazonian flora, which is rich in species adapted to flooding (Pott et al., 2011). This species occupies areas subjected to seasonal flooding in the Pantanal such as Landi forests (forest dominated by *Calophyllum brasiliense* Cambess.), riverine forests, and savanna systems, such as vegetated earth mounds, and grasslands, where it becomes extremely abundant (Nascimento and Nunes da Cunha, 1989; Nunes da Cunha and Junk, 2004; Arieira and Nunes da Cunha, 2006).

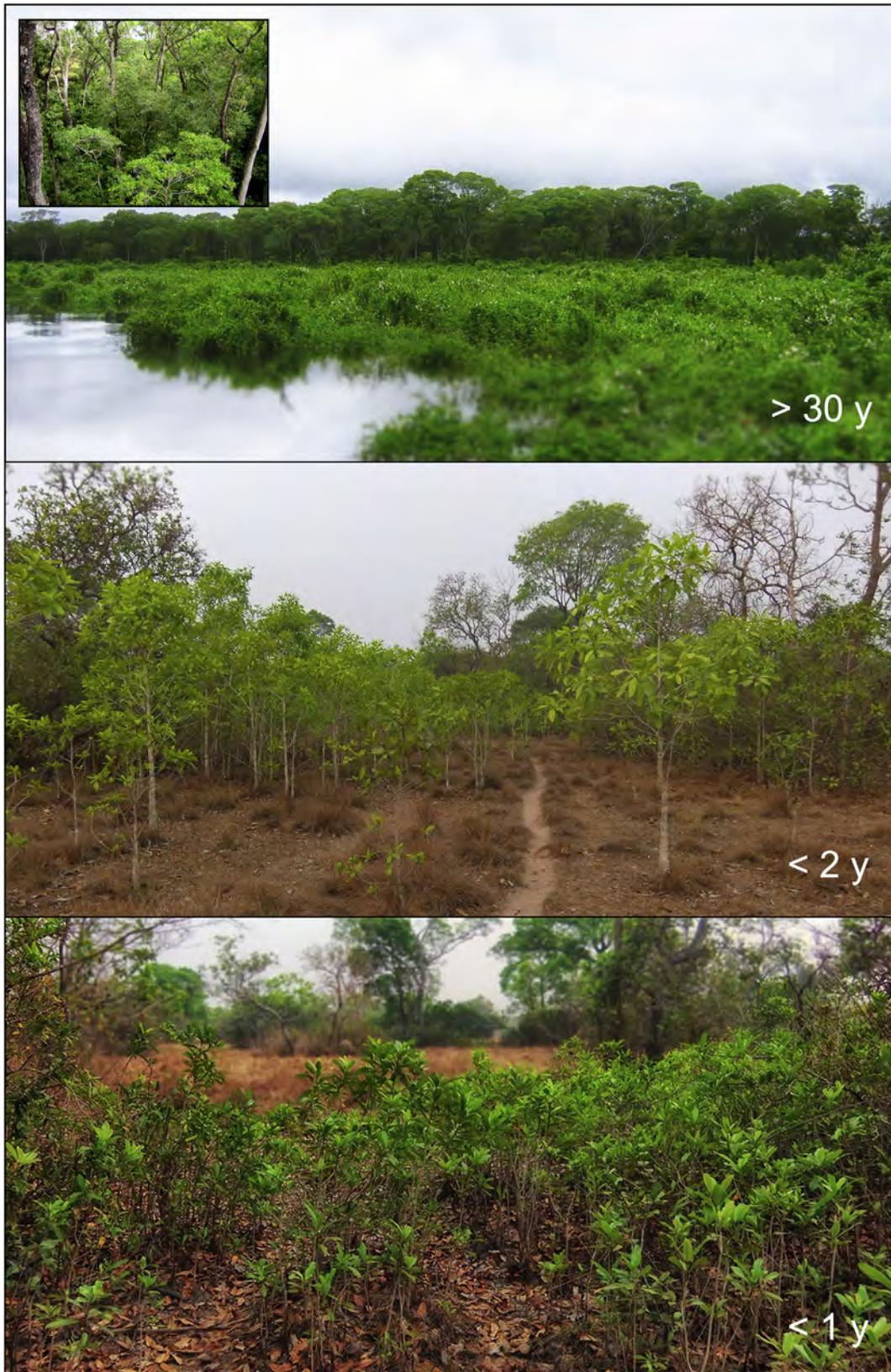


Fig. 1. Invasive stages of *Vochysia divergens* in the Pantanal wetlands (bottom under one year, center over two years, above over 30 years), with different succession layers of monodominant *V. divergens* trees.

2.2. Data set

2.2.1. Occurrence of *Vochysia divergens*

To obtain a representative sample of the entire Pantanal landscape, 148 points of *V. divergens* occurrence were acquired from different information sources such as online herbaria (<http://splink.cria.org.br/>), phytosociological and floristic studies, as well as from expert identification of individuals from high-spatial resolution remote-sensing images (5 m to 30 m), such as from *QuickBird* and *WorldView*, which are available from Google Earth. The 148 points of *V. divergens* occurrence were randomly subdivided into two parts: 75% of the points were used to calibrate the models (training data) and 25% were used as test data to evaluate the models (Smith, 1994; Miller and Franklin, 2002).

2.2.2. Scenopoetic environmental variables

The environmental predictors used in the SDMs represented factors that - according to current literature - may affect the establishment and development of *V. divergens* (Arieira and Nunes da Cunha, 2006; Dalmolin et al., 2015; Machado et al., 2015; Sallo et al., 2017). The models considered 23 scenopoetic environmental variables available in geographic information systems (GIS): 19 climatic variables (e.g., temperature and precipitation) and four hydrological variables (flooding frequency). Flooding data are represented by the mean and maximum frequency, standard deviation, and sum of years of flooding in the Pantanal (2000–2009), as modeled by Padovani (2010) at a spatial scale of 250 m. Climatic variables were obtained from WorldClim, version 1.4 (<http://www.worldclim.org>), at a spatial resolution of 1 km via the website AMBDATA (<http://www.dpi.inpe.br/Ambdata/>). These 19 climatic variables represent average data for the 1960–1990 period (Hijmans et al., 2005) and were resampled to the 250 m flood spatial resolution applying the interpolation algorithm “nearest-neighbor” in the program ArcMap version 10.3. Spatial downscaling is a common procedure when dealing with spatially coarse-grained climate data, since fine spatial scale of predictors are required to better understand regional systems (Flint and Flint, 2012; Jaberansar et al., 2018). Because the elevation gradient (c. 25 cm km⁻¹ from east to west) found in the Pantanal is not a determinant climate-forcing factor (Franco and Pinheiro, 1982), less bias and errors in spatial climate data sets are expected after image downscaling (Daly, 2006). Nevertheless, to ensure higher model confidences, we compared model outcomes (ROC-AUC statistic and predicted habitat areas) with coarse (1 km) and fine-scale (250 m) climate data (Khosravi et al., 2016); moreover, we compared spatial variation in climate trends of 1 km WorldClim layers with other sources of precipitation mapping detecting a high match between both data sets (coefficients of correlation (r) = 0.90) (Appendix A).

Principal components analysis (PCA) (Legendre and Legendre, 1998) was applied to a correlation matrix with data for the 23 environmental variables at the points of occurrence of the species to select the most important environmental gradients and exclude redundant environmental variables. Variables showing correlation above 0.8 in the two primary axes of the PCA were selected. Next, collinear variables were grouped, and the variable with the highest data interpretability in terms of biological importance for the focal species, was chosen to represent each group or environmental gradient. PCA was performed using the function *prcomp* from the R package *stats* (R Core Team, 2017).

2.3. Modeling procedures

In this study, the correlative models BIOCLIM and DOMAIN, were used to predict abiotically suitable areas for the establishment and development of *V. divergens*. Both models are widely applied when (a)

there is no information on locations where the species is absent, and (b) when the modeling goal is to predict potential areas with suitable environmental conditions for the species spreading (Busby, 1991; Jiménez-Valverde et al., 2011; Peterson et al., 2011). Based on the niche concept of Hutchinson (1957), these models relate occurrence data with environmental variables, e.g., climate (Kearney et al., 2010), generating continuous probabilities of habitat suitability for the species (Jackson and Overpeck, 2000; Kearney et al., 2010), varying from 0 (low probability) to 1 (high probability). BIOCLIM (Nix, 1986) is a model that interpolates locations that are abiotically suitable for a species based on its limits of environmental distribution, thus describing the environmental or “climatic envelope” of the species (Beaumont et al., 2005; Booth et al., 2014). In contrast to the BIOCLIM model, which measures the distance to a mean point of the occurrence data in the climatic space, the DOMAIN model estimates abiotically suitable locations for the species based on the environmental similarity between each point of occurrence and the non-visited points, using the Gower metric. The ranges of the environmental variables are standardized to match their contribution in the model (Carpenter et al., 1993).

The models were fitted using 75% of the records of species occurrence and using the variables selected as predictive by the PCA. The models were run using the R environment (R Core Team, 2017) with the function *bioclim* and the function *domain* of the library *dismo* (Hijmans et al., 2011).

The performance of the two models was evaluated using two threshold-independent accuracy measures: Pearson’s point-biserial correlation (COR) and area under the receiving operating characteristic curve (AUC) (Hanley and McNeil, 1982). COR evaluates the existence of a linear relation between the predictions and the test data as cross-validation (25% of the observations) (Elith et al., 2006; Phillips et al., 2009). AUC quantifies the predictive success of the model by rates of true positives (sensitivity) and false positives (specificity) taking values of predicted habitat suitability in the range of 0–1, and uses background data as pseudo-absences to build a confusion matrix. There is no consensus with regard on how many pseudo-absences should be applied to accurately predict and evaluate species distribution models (Barbet-Massin et al., 2012). Here, the same number of pseudo-absence (i.e., background) as available presences were randomly selected throughout the study area. In models based only on presence data, such as the ones used in this study, the AUC must be understood as the model’s capacity to scores presence at sites higher than random sites from the study area (i.e. background data) (Phillips et al., 2009).

Because knowledge is lacking on species prevalence, that is, the quantity of locations with species presence that are predicted as absences in the model, the AUC results of the models based on recorded occurrences were tested against a null model, where the species is considered indifferent to its environment (Raes and ter Steege, 2007). The null model was built using 1000 groups of 111 data points of pseudo-presence, generated randomly and without replacement over the mapped area, and by running the BIOCLIM and DOMAIN models with the same environmental parameters of the calibration model. Frequency histograms of the AUC and COR values expected under the null model were generated and compared to the AUC and COR values from the model evaluation based on the recorded occurrence of *V. divergens*. Significant differences between these results were used to conclude whether the species occurrence predictions of the SDMs differ significantly from what is expected by chance.

The predictive capacity of SDMs is strongly affected by the choice and number of predictors used in the models (Rödder and Lötters, 2010). The importance of each of the n environmental variables on the predictive power of the two models was evaluated using a method of resampling similar to *Jackknife* (Peterson et al., 2011), consisting of running the models while excluding the predictive variables according

to the following sequence: (1) using all preselected climatic and hydrological variables, (2) using all variables except one, and (3) using only one predictor in each turn. This procedure provided the gains and losses in AUC values for the different subgroup variables, indicating those that contributed most to improve model distribution predictions of *V. divergens*.

Different models result in different projections of predicted habitat suitability for the species because of the differences in their assumptions, algorithms, and parametrizations (Anderson et al., 2003; Peterson et al., 2011). One approach to the uncertainties associated with the predictions of a single model has been to create a map of environmental suitability that combines different models with high consensus in their predictions but also shows the differences in the projection ranges of the models, thus reducing the mean error (Araujo and New, 2007). The consensus between the BIOCLIM and DOMAIN models was evaluated based on the proportion of areas predicted as environmentally suitable (binary map = presence) for the species. The models were then combined by averaging the forecasted distribution of the single models, weighted by the pre-evaluated AUC (Marmion et al., 2009). The resulting habitat suitability map (i.e. the consensus map) was transformed into a binary map of presence (1) and absence (0) of *V. divergens* considering as cut-off point the average of threshold values for the single models obtained at the apex of the ROC curve, where the sum of sensitivity (true positive rate) and specificity (true negative rate) values are maximized (Manel et al., 2001). The improvement in accuracy of the consensus map was evaluated through the AUC and the elements of confusion matrix, using the functions *roc* from the R package *pROC* (Robin et al., 2011) and *confusion.matrix* from the package *SDMTools*.

2.4. Chances of *Vochysia divergens* spreading over grass-dominated savannas

The 2014 map of vegetation and land use produced by the Socio-environmental Institute of the Upper Paraguay Watershed (Instituto Sócio-Ambiental da Bacia do Alto Paraguai (BAP) – SOS Pantanal, <http://www.sospantanal.org.br>) was applied to extract the areas of current distribution of *V. divergens*, represented by the category “vegetation with fluvial influence,” and the grass-dominated savanna systems in the Pantanal, corresponding to the category *Savana Gramínea* described as “natural vegetation with predominantly grassy aspect but with sparse presence of tree-shrub species” (Instituto SOS Pantanal, WWF-Brasil, 2015).

The current distribution area of *V. divergens* was compared to its potential distribution area produced by the model used in this study to calculate the area of possible expansion of this species in the Brazilian Pantanal (Padovani, 2010). The *Savana Gramínea* areas were overlapped with the map of habitat suitability for *V. divergens* encroachment produced by the model used in this study (i.e. the map of environmental suitability), enabling the visualization of the grass-dominated savannas with the highest risk of invasion. The polygons of *Savana Gramínea* and of current *V. divergens* occurrence were extracted from the map of land use in the program ArcMap (ESRI, 2003) using the function *clip*.

3. Results

3.1. Model comparison

The BIOCLIM and DOMAIN models were run using the factors that represented the most important climatic-hydrological gradients for this study as covariables: mean annual temperature (Bio 1), mean temperature of the wettest quarter (Bio 8), precipitation in the wettest month (Bio 13), precipitation of warmest quarter (Bio 18), precipitation in the coldest quarter (Bio 19), and sum of 10 years of flooding

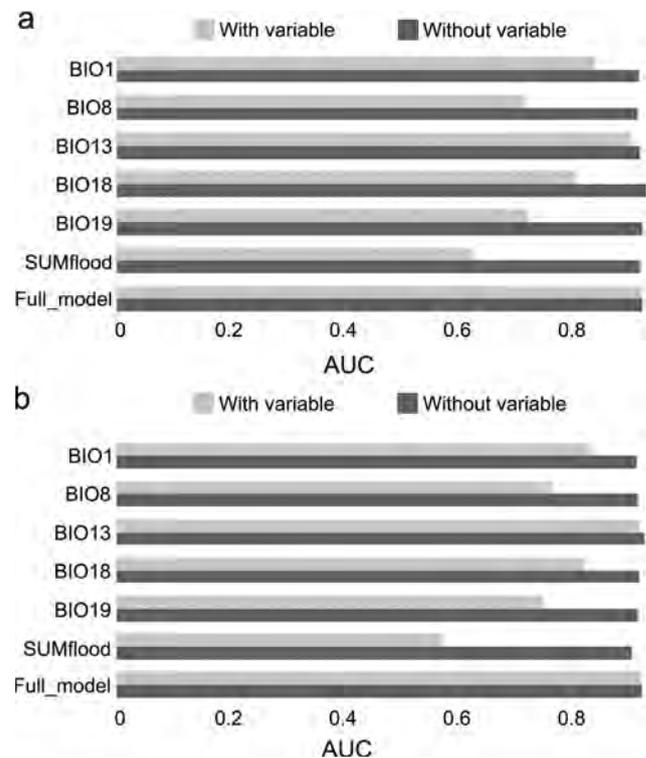


Fig. 2. Jackknife test of AUC in (a) BIOCLIM and (b) DOMAIN models for environmental variables. Bio1 = annual mean temperature, Bio8 = mean temperature of wettest quarter, Bio13 = mean precipitation of wettest month, Bio18 = mean precipitation of warmest quarter, Bio19 = mean precipitation of coldest quarter, SUMflood = sum of 10 years of flooding.

(SUMflood).

Both models, BIOCLIM and DOMAIN, produced highly accurate individual maps, with high values of AUC (Bioclim = 0.90, and Domain = 0.86) and correlation COR (Bioclim = 0.64, and Domain = 0.62). Because the values of the two accuracy measures, AUC and COR, produced by 1000 runs of the null model, were lower than the values produced with the BIOCLIM and DOMAIN models based on species occurrence records, the predictions were concluded to be not random, indicating that the species has requirements that are niche-specific and found in its recorded occurrence locations.

Although the BIOCLIM model predicted a more restricted-range of *V. divergens* to the hydrological and climatic gradients than the DOMAIN model, and because the cut-off thresholds for suitability were lower in BIOCLIM (0.10) than in DOMAIN (0.68), high consensus (86%) existed between both models regarding the areas with the highest chance of species occurrence. In both models, the most important variables in explaining the distribution of *V. divergens* were precipitation in the wettest month (Bio 13), mean annual temperature (Bio 1), and precipitation in the warmest quarter (Bio 18) (Fig. 2a and b).

The integration of both models (Fig. 3a) produced a more robust estimate of the areas of potential distribution of *V. divergens*, as indicated by higher AUC (0.91) and a superior rate of correctly identified presence/absence records (82%), compared to BIOCLIM (79%) and DOMAIN (81%) models. The probability of finding suitable habitats for the species varied from 0 to 0.81 in consensus map (Fig. 3a).

3.2. Potential and current distribution of *Vochysia divergens*

Climatic gradients appeared to limit the potential distribution of *V. divergens* in the Pantanal. The map of environmental suitability

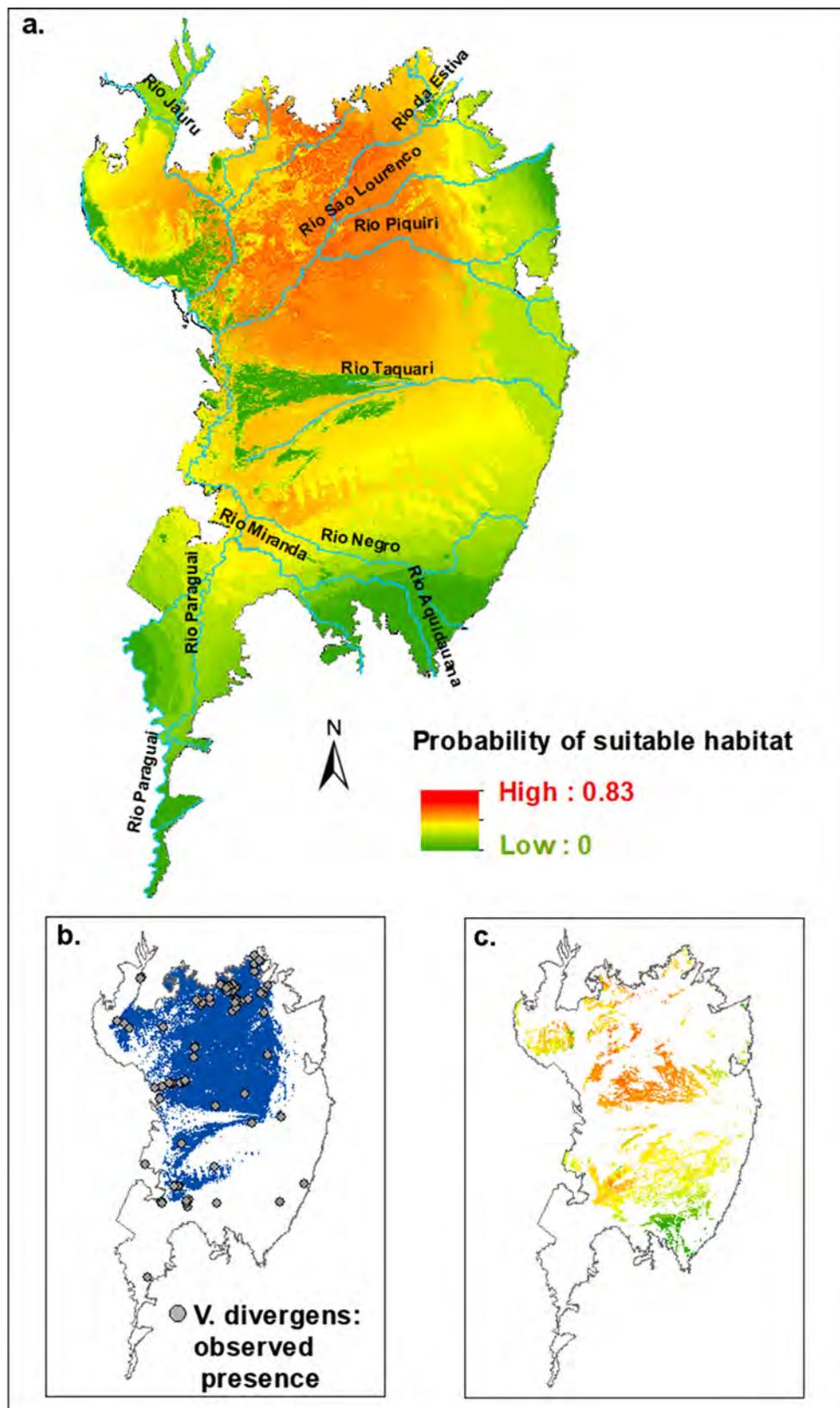


Fig. 3. (a) Map of environmental suitability for *Vochysia divergens* in the Pantanal, resulting from the weighed mean between the probabilities generated by the models BIOCLIM and DOMAIN. Inserted maps: (b) predicted habitats suitable for *V. divergens* occurrence (blue) and observed presence (dots), and (c) probability of suitable habitats for *Vochysia divergens* in grass-dominated savanna.

indicated that 67% of the territory of the Brazilian Pantanal, corresponding to 130,546 km², does not have suitable environmental conditions for occupation by *V. divergens* (Fig. 3b). Considering the current

distribution of this species (Fig. 4), derived from remote sensing data provided by Instituto SOS Pantanal, WWF-Brazil (2015), *V. divergens* occupies approximately 17% of the Pantanal. Comparing this current

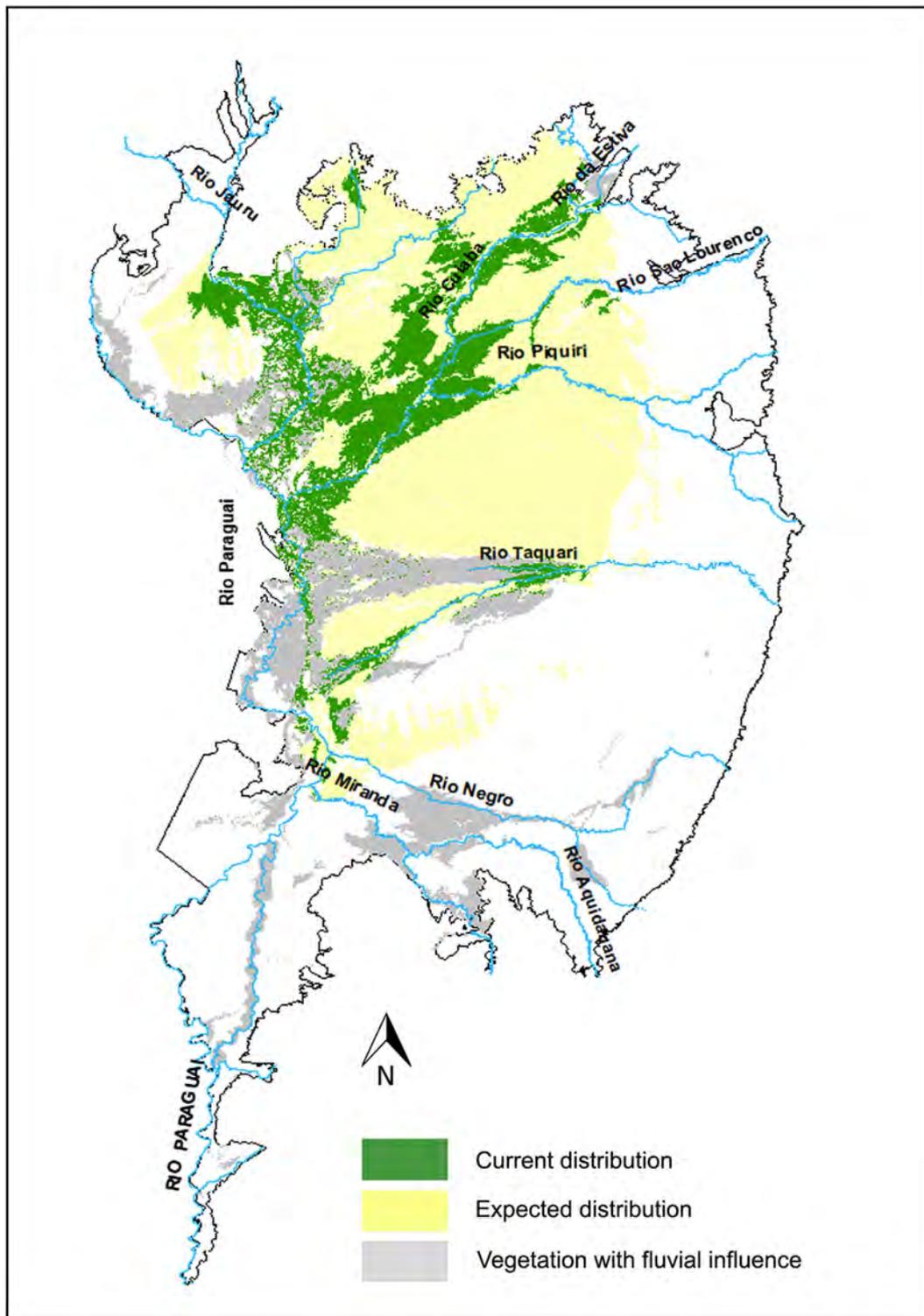


Fig. 4. Current distribution (according to SOS Pantanal) and areas of possible invasion (according to the species distribution models) for *Vochysia divergens* in the Pantanal.

distribution with the potential distribution produced by the SDM, the possible area of expansion of this species corresponds to 26,208 km², a gain of 16%. Considering only the *Savana Gramínea*, which correspond to 19% (24,179 km²) of the Pantanal, only 23% (5579 km²) have

suitable environmental conditions for occupation by *V. divergens*.

Suitable locations for the development of *V. divergens* must have high mean annual temperature, high climatic seasonality regarding precipitation, hydric deficit during the dry season (winter), high

Table 1
Climatic and hydrological limits for the distribution of *Vochysia divergens* in the Pantanal.

Variables	Mean	Range
Bio1 = annual mean temperature (°C)	25.9	24.9–26.3
Bio8 = mean temperature of wettest quarter (°C)	27.6	26.7–28.5
Bio13 = precipitation of wettest month (mm)	216.6	138–244
Bio18 = precipitation of warmest quarter (mm)	529.8	326–638
Bio19 = precipitation of coldest quarter (mm)	114.9	83–198
SUMflood (day * year ⁻¹)	79	0–329

precipitation during the wet season (summer), and a mean flooding frequency of three months per year under intermediate flooding regimes. These conditions occur mainly in the floodplains of the rivers found in the north-central region of the Pantanal, indicating that grass-dominated savannas in these areas have the highest risk of invasion by *V. divergens*.

In general, the most favorable locations for the establishment of the species are those where the precipitation is high in the wettest month and warmest quarters, means of 217 mm and 530 mm, respectively (Table 1), and is reduced in the coldest and driest quarter (i.e., June to August), with a minimum of 83 mm in the quarter. These patterns indicate the association of this species with locations of high climatic seasonality in the west-central region of the state of Mato Grosso, Brazil. Regarding the flooding regime, *V. divergens* may occur in locations where flooding duration varies widely but is more likely to occupy areas in the plain where flooding lasts on average 79 days per year.

Although the southern region of the Pantanal shows the highest coverage by grass-dominated savannas (Fig. 3c), the transition to a wet subtropical climate to the south, associated with milder mean annual temperatures and more balanced rainfall distribution, seems to reduce the chances of *V. divergens* spreading in this area. The highest probability of encroachment of this species over open savanna occurs in locations where flooding lasts more than one month. In grass-dominated savannas flooded for less than one month, such as some those close to the Aquidauana River, the probability of finding suitable habitats for *V. divergens* is reduced, emphasizing the association of this species with wetlands.

4. Discussion

Grass-dominated savannas cover more than 24,000 km² of the Pantanal and are represented by different types of habitats which are dominated by distinct groups of species, such as *Elionurus muticus* (Spreng.) Kuntze (called “caronal” locally), *Axonopus purpusii* (Mez) Chase and *Reimarochloa brasiliensis* (Spreng.) Hitchc. (called “capim mimoso” locally), *Andropogon hypogynus* Hack. and *Axonopus leptotachyus* (Flüggé) Hitchc. (called “capim-vermelho” locally) (Santos et al., 2005; Nunes da Cunha et al., 2015). These ecosystems provide a varied menu of forage plants, making livestock farming over natural pastures the main economic activity in the Pantanal for more than two centuries (Santos et al., 2002; Pott and Pott, 2004; Santos et al., 2009).

The different types of natural pastures are sustainable when they can maintain their structure, diversity, and resilience in the face of natural and anthropic disturbances (Santos et al., 2006). The conversion of natural grass-dominated savannas to monodominant *V. divergens* forests is considered a threat to the sustainability of these natural pastures in the Pantanal, reducing the area available to grazing and the quantity and quality of native forage plants (Santos et al., 2014). Conservation of these open savannas requires knowledge of the relation between the life traits of invasive species (encroaching trees) and the environmental conditions that represent decades of climatic and

hydrological variations, to further understand the dynamics of these ecosystems as well as to design more efficient strategies for the control of invasive species (Monaco and Sheley, 2012).

The SDMs used in this study advance the understanding of the dynamics of *V. divergens* populations in the Pantanal, resulting in an approximation of the potential of species invasion. As expected, model results showed that habitat suitability related to climatic and hydrologic limits for species distribution, varies among bioclimatic regions, affecting the probability of encroachment of *V. divergens* in grass-dominated savannas. The consensus map of environmental suitability showed a high predictive power of the areas of possible occurrence of *V. divergens*, including 88% of the occurrence records for the species and showing a large overlap with the species occurrence areas mapped by remote sensing (Conservação Internacional, 2015). This map is therefore a useful tool for defining decision-making strategies to prevent invasions in new areas or to control dissemination in areas already invaded (Jiménez-Valverde et al., 2011).

In introduction, we asked what were the hydro-climatic limits for *V. divergens* advance, and if model predictions were in accordance with previous scientific knowledge (Nunes da Cunha and Junk 2004; Arieira and Nunes da Cunha, 2006; Dalmolin et al., 2015; Machado et al., 2015; Sallo et al., 2017). In agreement with former studies, both models, BIOCLIM and DOMAIN, indicated that climate, especially precipitation, is the strongest limiting factor of the distribution of *V. divergens* in the Pantanal. This result indicates that higher precipitation enables the development and expansion of woody species over savanna areas (Fensham et al., 2005; Schöngart et al., 2011; Machado et al., 2015; Fortes et al., 2018). Oscillations in the precipitation regime controlled by cyclical climatic events result in multiannual variations in the frequency of rains and flooding, which, individually or combined, affect the dynamics of this flood-tolerant tree species. Extreme droughts for example, such as those associated with the sea surface temperature (SST) cold anomalies in the region Niño 1 + 2 (i.e., La Niña condition), reduce the growth rates of *V. divergens* and may increase plant mortality and decrease seed production, indicating a possible reduction of the populations of the species when precipitation is reduced (Nunes da Cunha et al., 2000; Fortes et al., 2018). In contrast, the decrease in natural fires and annual increase in flooding during wet years, mainly in areas that are currently seldom or rarely flooded, corroborates the proliferation of opportunistic flood-tolerant woody species such as *V. divergens* (Nunes da Cunha and Junk, 2004; Zedler and Kercher, 2004). Even if greater precipitation in the rainy season increased the chances of the encroachment of *V. divergens*, it might also increase the regeneration rates of herbaceous forage species, thus assisting in grassland recovery after removal of the invasive species (Archer et al., 2011). Therefore, climatic projections should precede management decisions because they alter the response of the invasive species and of the invaded plant communities to favorable, normal, and unfavorable rainfall and flooding conditions (Archer et al., 2011).

Although considered here for their secondary roles in shaping the distribution of *V. divergens*, the dynamics of floods and droughts experienced in the floodplain landscape is important for the spread of this opportunistic species (Nunes da Cunha and Junk, 2004). This importance is due to the lateral water flow from rivers, responsible for flooding the plain, which functions as a diaspora propagator, conductor of materials and nutrients, and gap formation (Zedler and Kercher, 2004; Junk and Nunes da Cunha, 2012; Alho and Silva, 2012). Grass-dominated savannas in the north-central region of the Pantanal, subjected to intermediate flooding for one to two months, are more favorable to occupation by this species. Some of these savannas have a high probability of species establishment, such as the floodplain of the São Lourenço and Piquiri rivers. These open savannas, which can be located in subtly higher zones in the landscape, are important

management units of natural pastures in the Pantanal. Farmers in the region consider *V. divergens* over these higher zones as more problematic for the management and sustainability of pastures because although most of these savanna systems have forage plants with a low protein value (e.g., *Elyonurus muticus* and *Andropogon hypogynus*), invasion by woody species reduces the locations available for cattle during periods of extreme flooding (Allem and Valls, 1987; Santos et al., 2014). However, in these areas, *V. divergens* is generally found at low density or with a predominance of juvenile individuals (Nunes da Cunha and Junk, 2004; Damasceno-Junior et al., 2005). The absence or sparse occurrence of this species must be associated with two processes: the higher incidence of fires in these drier areas, where mean precipitation may be below 25 mm per month in the dry season, and higher interspecific competition in areas subjected to short-term flooding (Nunes da Cunha and Junk, 2004; Santos et al., 2006; Arieira et al., 2016). These forces result in an increase in the mortality rates of juvenile life stages, even though abiotic conditions (e.g., flooding and climate) are favorable to its establishment (Arieira et al., 2016), demonstrating the importance of fine-scale ecological processes on the invasion susceptibility of plant communities and the invasiveness of the species (Williamson, 1999, 2001). Additionally, the reduction or lack of flooding must reduce seed dispersal by hydrochory, thus reducing the rates of colonization in these parts of the landscape (Nunes da Cunha and Junk, 2004).

In contrast, open savannas located in more favorable climatic regions (i.e., north-central and northwestern Pantanal) and in lower parts of the plain also have a high risk of invasion. These ecosystems, subjected to long flooding periods (\geq three months), represent important sources of forage plants with high protein content for herbivores. Therefore, their invasion could strongly impact the main economic activity of the region, which is extensive livestock farming (Santos et al., 2006). Monodominant stands of *V. divergens* have been found in these zones, indicating the high risk of invasion and establishment of this tree (Nunes da Cunha and Junk, 2004; Arieira and Nunes da Cunha, 2006, 2012). The presence of forest stands of *V. divergens* in parts of the plain subjected to long flooding periods, such as the floodplain of the Cuiabá river (Arieira and Nunes da Cunha, 2006), may be associated with the occurrence of wetter climatic periods, like those followed by the year of 1973 in the Pantanal, which enabled the colonization by this species in the interior zones of the plain (Arieira et al., 2016), reinforcing the importance of climatic windows for the establishment of opportunistic species such as *V. divergens*.

Addressing the climatic and hydrological effects on the dynamics of invasive populations requires innovative management approaches, focused on multiple spatio-temporal scales (Monaco and Sheley, 2012). Grass-dominated savannas invaded by woody species in the Pantanal is supported by the Pantanal State Law (Lei Estadual do Pantanal N° 8.830 - art. 11 de 2008, SEMA, 2008) and by municipal decrees N° 8.150/06 and 8.188/06 - Seção II, which instruct farmers to clear natural pastures according to the duration of the invasion and the minimum trunk diameter of adult individuals (Santos et al., 2006). However, success in containing the proliferation after establishment is considerably reduced, which decreases the chances of public economic investment in the management of invaded savanna systems (Epanchin-Niell, 2017). In general, in climatic zones that are less favorable for the establishment of invasive species, management strategies such as fire and selective cutting of *V. divergens* tend to be more efficient in containing encroachment (Lurgi et al., 2016). Conversely, in areas already occupied or with a high risk of invasion the definition of control or eradication strategies may benefit from knowledge of the effect of climatic variables on the chances of establishment of the species (Lurgi et al., 2016). Maintaining the integrity of natural grass-dominated savanna wetlands

through low livestock density and maintenance of the hydrological regime is important in reducing the chances of invasion in more environmentally suitable zones (Santos et al., 2009; Lurgi et al., 2016). Additionally, maintaining the forest and savanna vegetation mosaic, which determines the interconnectivity among populations of invasive species (Fahrig and Merriam, 1994), should reduce the chances of the spread of this tree in wetter years because it reduces the capacity of long-distance dispersal by floodwater and thus prevents propagules from reaching new locations.

5. Conclusions

Bioclimatic models have been widely used to define areas with a higher risk of invasion, thus providing advantages for the containment and control of invasive species (Peterson, 2003; Rödder and Lötters, 2010; Kriticos, 2012; McClure et al., 2015). The spatial predictions generated by the models used here demonstrate the relation between climatic seasonality, particularly high precipitation in the warmest period of the year, and a high chance of the spread of this species. In contrast to the approach used for invasive exotic species, the management of grass-dominated savannas invaded by native woody species in environmentally suitable areas should consider not only economic interests, such as the loss of pasture areas, but also the effects of species removal on biodiversity and ecosystem services (Archer et al., 2011), such as habitat for a large diversity of animals, reserves of carbon and other nutrients like phosphorus in the woody biomass and soil, control of local temperature and precipitation, and regulation of the hydrological cycle. Finally, managers should interpret the results of the SDMs with caution because species distribution is affected by complex interactions among several factors such as dispersal, climate, and biological interactions (Pearson and Dawson, 2003). Controlling the expansion of *Vochysia divergens* Pohl into savanna wetlands with a high risk of encroachment depends on multiple-scale approaches that consider the integrity of the natural pastures at the local level and the maintenance of their ecosystem functions on a wider scale. As a consequence, future encroachment studies should focus on the effects of fine-spatial scale ecological drivers, such as cattle grazing intensity, seed dispersal, flood dynamics, and soil conditions on *V. divergens* population dynamics in hydroclimatic zones of high probabilities of establishment. With this approach, predictive modeling is a useful tool helping to understand the impact of management scenarios of encroaching trees under different local conditions.

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Appendix A

See Fig. A1.

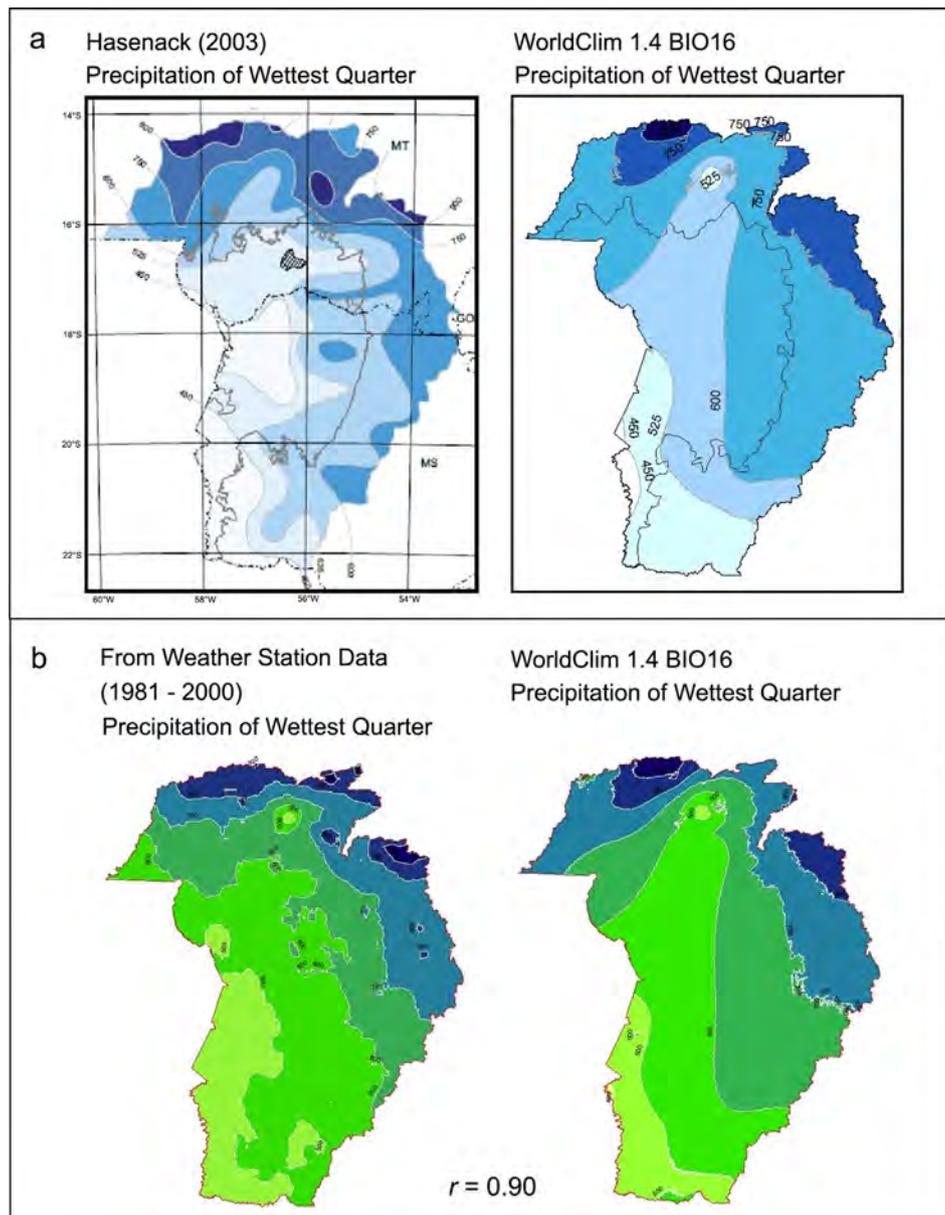


Fig. A1. Precipitation trend comparisons of wettest quarters (December, January, February) in the Upper Paraguay Basin and the Pantanal (contours in gray). Comparing (a) Hasenack et al. (2003) and (b) IDW interpolation of 1981–2000 time series of weather station data (NOAA/ESRL Physical Sciences Division) with Worldclim 1.4 BIO16 models. Coefficient of correlation (r) was 0.90, indicating a high match between data sets.

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