



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 phytogeographic 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).

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