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Lack of protected areas and future habitat loss threaten the Hyacinth Macaw (*Anodorhynchus hyacinthinus*) and its main food and nesting resources

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Habitat loss is a major reason for population declines and thus increases extinction risk, particularly for endemic or specialist species. Protected areas are an important biodiversity conservation strategy in the face of native vegetation conversion, but local and regional factors such as anthropogenic pressure can jeopardize their effectiveness. The Pantanal biome is one of the largest inland wetlands in the world. Currently, only 11% of the Pantanal is protected, 7% with full protection and 4% under sustainable use. However, 14% of the natural vegetation of the biome was lost between 2002 and 2014, negatively affecting its biodiversity. Here, we analyse how the availability of protected areas and habitat loss affects the conservation of the Hyacinth Macaw *Anodorhynchus hyacinthinus*, as well as the Acuri Palm *Attalea phalerata* and the Manduvi Tree *Sterculia apetala*, its two main resources for food and nesting, respectively. We modelled potential distributions to assess the spatio-temporal patterns of habitat loss due to the conversion of native vegetation and to evaluate to what degree currently protected areas contribute to the conservation of these three species in the Pantanal. We found that, on average, 11.8% of the suitable habitat had been converted and that 10.6% of habitat predicted as suitable is currently protected. In addition, our results indicated important areas for the three species, which are of high priority for conservation and restoration. We also identified priorities for protection and restoration to maintain native vegetation, such as the creation of corridors. We believe that the high conversion rate and the low protection of suitable areas are related to the fact that these species are associated with areas that are rarely or never flooded. In the Pantanal, these areas are more prone to the conversion of native vegetation and are poorly protected given their higher economic value compared with areas with a high frequency of flooding. These facts, and the inadequate

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management of these areas, such as inappropriate fire regimens, threaten the persistence of these iconic species in the Pantanal.

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Although establishing and managing protected areas form part of an important biodiversity conservation strategy (Laurance *et al.* 2012), the effectiveness of protected areas can be jeopardized by anthropogenic threats (Spracklen *et al.* 2015). The performance of protected areas in counteracting native vegetation loss and associated effects is known to vary (Clark *et al.* 2013, Leberger *et al.* 2020). Protected areas can also fail to protect highly mobile species and those with distributions outside protected areas (Barlow *et al.* 2016, da Silva *et al.* 2018, Geldmann *et al.* 2018). For instance, in Brazil, angiosperm, invertebrate and vertebrate species have less than 30% of their geographical distribution protected by conservation units (Oliveira *et al.* 2017).

By 2014, about 70% of the world's wetlands had been lost (Davidson 2014), mainly as a result of agricultural expansion and economic and population growth (Van Asselen *et al.* 2013). Inland wetlands have experienced both higher absolute loss and higher loss rates than coastal wetlands (Davidson 2014). Habitat loss is a main reason for population declines, increasing the risk of extinction (Betts *et al.* 2017), in particular for endemic or specialist species, due to their restricted distribution and strong habitat specificity (Deane *et al.* 2017, Symes *et al.* 2018).

The Pantanal, located in central South America, is shared by Brazil, Bolivia and Paraguay. Covering 150 000 km^2, it is one of the largest inland wetlands in the world (Padovani 2010). It has a characteristic annual flood pulse, consisting of flooding and drought (Junk *et al.* 1989, Pott 1995, Padovani 2010). There is interannual variation, with years when up to 40% of the Pantanal is flooded and other years when there is extreme drought (Junk *et al.* 1989, 2011, Moraes *et al.* 2013). There is also spatial variation at a finer scale, with areas permanently, seasonally and never flooded depending on relief (Hamilton *et al.* 1996, Padovani 2010). These patterns lead to a highly heterogeneous biome, with changes from grassland to forest within a few metres of each other (Pott 1995, Pott & Pott 2009).

By 2014, the Pantanal had lost 14.9% of its native vegetation, mainly as a result of pasture cultivation (Roque *et al.* 2016). Recently, an accelerated rate of native vegetation loss has been detected at the eastern edge of the Pantanal, in the 'arc of conversion' (Guerra *et al.* 2020a). Despite the high biodiversity value and the increasing threats, only 11% of the Pantanal is currently protected, with approximately 7% under full protection and 4% with sustainable use permitted (Brazil 2010, Tomas *et al.* 2019). Indigenous lands represent another 1% (Tomas *et al.* 2019). The total of 12% falls short of the 17% representation recommended in the Aichi goals (CBD 2010). The situation is even more dire considering the 15% goal for restoring degraded areas (CBD 2010). Modified areas with low potential for natural regeneration have already been identified in the Pantanal (Pott *et al.* 2018), where active restoration actions will be necessary. Nevertheless, restoration actions are scarce in spite of increasing habitat degradation (Guerra *et al.* 2020a, 2020b, 2020c).

The Hyacinth Macaw *Anodorhynchus hyacinthinus* (henceforth Macaw) is a flagship species for conservation in the Pantanal. This parrot has a disjunct distribution, with one subpopulation in the north of Brazil, one in the northeast and the third in the central-west, in the Pantanal biome, which is its main area of occurrence, with about 70% of the population (Guedes 2002, Guedes *et al.* 2008, Presti *et al.* 2015). Between 2000 and 2013, the species was classified as Endangered, but it was downlisted to Vulnerable in 2014 due to updated population decline rates (BirdLife International 2020). Its current status is justified by an over 80% population decline in the last decade, mainly due to the decrease in the area of occurrence and habitat quality, as well as illegal trade and hunting (BirdLife International 2020).

The species was not included in the Red Data Book of threatened Brazilian fauna in 2014 due to a genuine change in conservation situation (ICMBio 2018). Macaws have benefitted from conservation actions in the Pantanal, including the installation of artificial nests (Guedes *et al.* 2006) and the reduction of the number of individuals captured for trafficking (ICMBio 2018). Nevertheless, some biological traits, such as monogamy and low recruitment rate, make the species prone to extinction (Guedes 1993, 2002). In addition, periodically occurring large fires, such as those in 2020, can significantly affect the biodiversity of the Pantanal (Libonati *et al.* 2020). Fires can affect Macaws by causing habitat loss and diminishing food resources (Libonati *et al.* 2020).

A major factor that contributes to the Macaw's vulnerability is its high level of specialization. In the Pantanal, the Macaw feed mainly on the nuts of the Acuri Palm *Atallea phallerata*, which has been recorded in about 94% of all feeding observations (Guedes 1993, Antas *et al.* 2010, Tella *et al.* 2020). Similarly, the species is highly dependent on the hollows of the Manduvi Tree *Sterculia apetala* for nesting, which is selected *c.* 90% of the time for nest construction (Guedes 1993). However, the population decline of Manduvi Trees, resulting from the conversion of native vegetation to pasture, with subsequent high cattle densities, can have negative effects on the Macaw (Júnior 2010). The nearly exclusive use of these plant species for feeding and nest building demonstrates their importance in the life cycle of the Macaw.

Besides the Macaw, 20 additional invertebrate, mammal and bird species have been described as depending on the Acuri Palm and the Manduvi Tree for food or shelter (Quiroga-Castro & Roldán 2001, Galetti & Guimarães 2004, Ragusa-Netto 2004, Keuroghlian *et al.* 2009). The Acuri Palm is a medium-sized palm species, occurring in non-flooded forested areas of the Pantanal, on fertile clay soil (Pott & Pott 1994). The Manduvi Tree is larger and is also associated with forests in low-lying areas with well-drained soils, and shows a low tolerance to waterlogging (Dvorak *et al.* 1998). Similar to the two plant species, the Hyacinth Macaw is also associated with forest formations in the Pantanal, frequenting both forest edge and interior (Guedes 1993, Antas *et al.* 2010). However, it can also be seen in open habitats, particularly near fruiting Acuri Palms (Guedes 1993, Antas *et al.* 2010).

Through models of potential distribution of these three species within the Pantanal, we sought to identify priority areas for conservation and restoration, based on the areas subject to conversion of native vegetation, the location of currently protected areas and biological information on these species. We also recommend changes in public policy with regard to conservation and restoration at the landscape scale.

METHODS

Subregions of the Pantanal

Our study area was the entire Pantanal, including territories in Brazil, Bolivia and Paraguay (Fig. 1). The spatio-temporal variability of biotic and abiotic factors creates different landscapes in the Pantanal. Based on differences in flooding patterns, the distribution and composition of plant communities and other features of landscape heterogeneity, the biome can be divided into different subregions, each with unique characteristics (Pott 1995, Padovani 2010). This subdivision can help us understand the functioning of the biome as a whole and is used in conservation decision-making. As flooding is one of the main factors that shape species distributions in this biome (Pott 1995), we adopted the subdivisions developed by Padovani (2010), which are based on the flooding patterns of the Pantanal (Fig. 1).

Sources of occurrence data

Occurrence data for the Macaw were acquired from the Embrapa Pantanal database, collected during surveys in 2008–2016, and from the Arara-azul Institute, based on surveys in 1995–2018. For plant species, we used the speciesLink database (www.splink.org.br), as it contains information only from scientific collections, thus reducing taxonomic error (Sousa-Baena *et al.* 2014). After joining all the databases, we removed duplicates and records with errors in geographical position, for example, points located in bodies of water. At the end of this process, we obtained 87 locations for the Acuri Palm, 185 for the Hyacinth Macaw and 384 for the Manduvi Tree (Fig. 2), which were further refined by removing sampling bias (see below).

Variable selection

For the two plant species, we obtained 13 edaphic variables at a 250-m spatial resolution (Hengl *et al.* 2017) from the Soilgrids database (www.isric.org). Using three of these variables – percentage of silt,

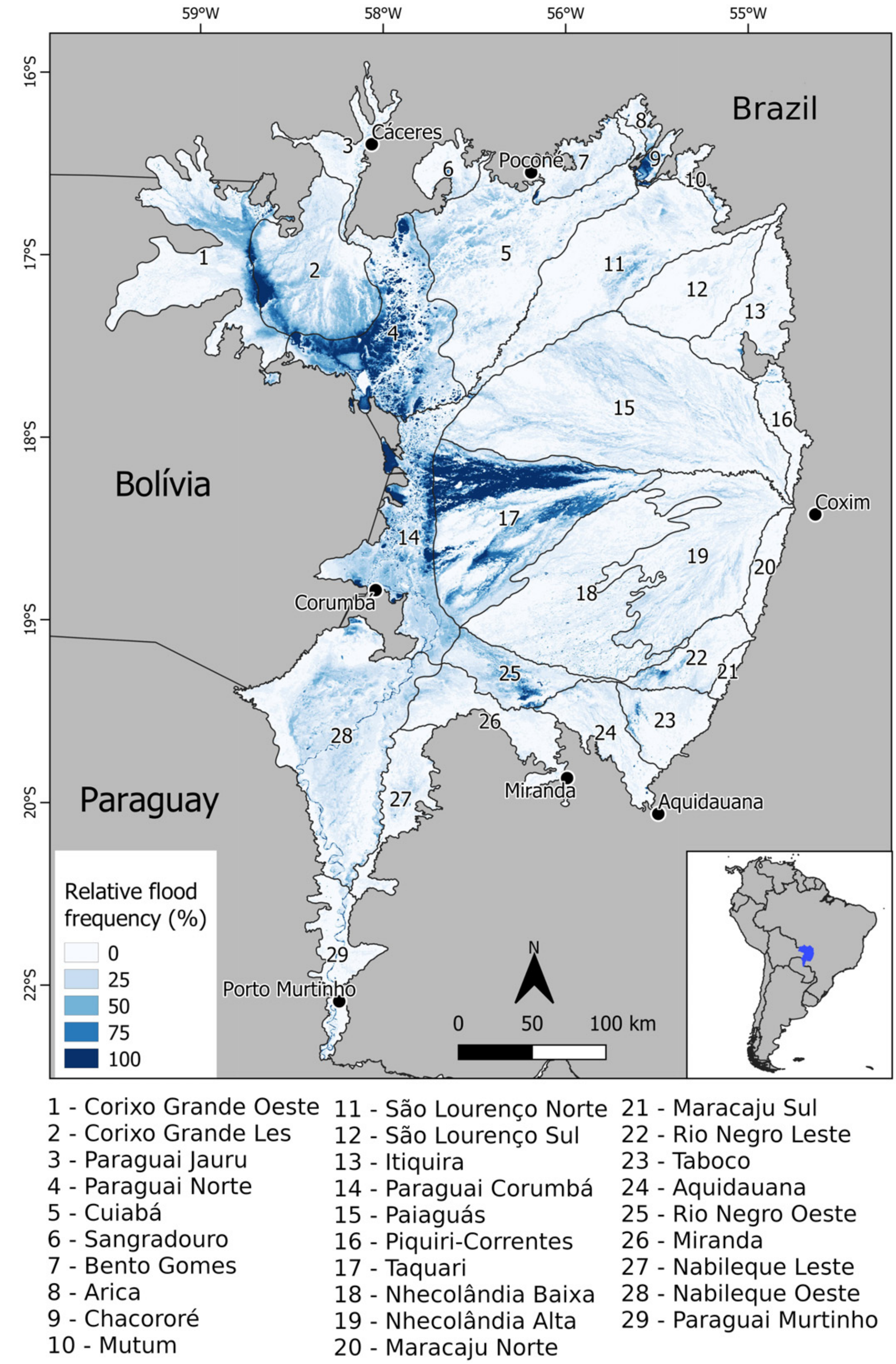

Figure 1. Relative frequency of flooding with the average flood coverage (%) calculated for 2000–2009, the main municipalities, and the limits and subdivisions of the Pantanal biome based on Padovani (2010). [Colour figure can be viewed at wileyonlinelibrary.com]

clay and sand – we constructed a soil texture layer, using the *Soil Texture Classification* tool in the SAGA GIS program (Conrad *et al.* 2015). Thus, we obtained 11 soil variables, comprising 10 variables of Soilgrids and soil texture. These 11 variables were soil depth as far as the underlying rock layer, probability of expected occurrence of the rock layer, absolute depth to rock, apparent density of fine soil, volume of thick fragments, soil organic carbon content, soil pH in H_2O, soil pH in KCl (measurement performed using a diluted solution of potassium chloride), organic carbon stock and soil capacity to exchange cations, and soil texture.

We also used the flood frequency layer created by Padovani (2010) from monthly flooding over the entire Pantanal for 2000–2009, based on MODIS satellite images, at 250-m spatial resolution (for more details see Padovani 2010). We subjected the resulting 12 variables (11 edaphic and the flood frequency; for the full list of variables see Table S1) to Pearson's correlation analysis using the function chart.Correlation in the PerformanceAnalytics package (Peterson & Carl 2020) in R version 3.5 (R Core Development Team 2019). Using $r = 0.7$ as a threshold value for Pearson's correlation (Guisan *et al.* 2017), we found two pairs of variables highly correlated and removed organic carbon stock and soil capacity to exchange cations.

For the Hyacinth Macaw species distribution model, we used the output of the best distribution models for the two plant species. The decision to include biotic variables for species distribution modelling (SDM) for the Hyacinth Macaw was due to two factors: biotic variables, if selected correctly, can significantly improve model performance (Heikkinen *et al.* 2007, Atauchi *et al.* 2018); and the strong interactions between Hyacinth Macaw and the two plant species (Guedes 1993, Antas *et al.* 2010, Júnior 2010).

Reducing sampling bias

An important step in the construction of the models was to reduce sampling bias in the occurrence data, using an appropriate method and parameters. Ignoring bias can lead to problems, resulting in models with high omission rates, low accuracy and reduced predictive strength (Elith *et al.* 2011, Kramer-Schadt *et al.* 2013, Boria *et al.* 2014). To reduce sampling bias, we used a method based on environmental distance, where the occurrence points are presented in a two-dimensional space, created from the values of the predictor variables (Varela *et al.* 2014). Then, the two-dimensional space is divided by user-defined values, creating different compartments, and the points within the same compartment are removed at random, leaving only one point per compartment (Varela *et al.* 2014).

For the two plant species, we conducted a principal component analysis (PCA) for the predictor variables (edaphic variables and flood frequency) using the *prcomp* function in R, and we used the first two axes to build the two-dimensional space (Castellanos *et al.* 2019). As the Macaw had only two predictive variables based on the distribution of the two plant species, we used these to construct a two-dimensional space with no previous analysis. For the compartmentalization of these spaces, we used three different values (30, 50 and 100) applying the *envsampling* function of the *pb-db* R package (Varela *et al.* 2014). The analysis of different removal thresholds was necessary because they affect model performance considerably (Castellanos *et al.* 2019). After reducing sampling bias, we obtained 219 occurrence records for Manduvi Trees for the resolution of 30 compartments, 300 records for 50 compartments, and 362 records for 100 compartments. For Acuri Palms, we had 69, 79 and 82 records, and for Hyacinth Macaw 125, 149 and 160 records for 30, 50 and 100 compartments, respectively.

Models of potential distribution and definition of the area of occurrence

To build these models, we used the Maximum Entropy approach within the MaxEnt version 3.4 program (Phillips *et al.* 2006). This approach creates rules for the occurrence of species based on the relationship between a set of predictor variables and occurrence data (Phillips *et al.* 2006). Based on these rules, the algorithm calculates habitat suitability for the study area, seeking maximum entropy (Phillips *et al.* 2006). The selection of inadequate values in parameters, such as complexity and regularization multipliers, has been found to affect model performance, reducing accuracy and causing overfitting (Warren & Seifert 2011, Radosavljevic & Anderson 2014, Warren *et al.* 2014). To avoid these problems caused by the selection of inadequate parameter values, we

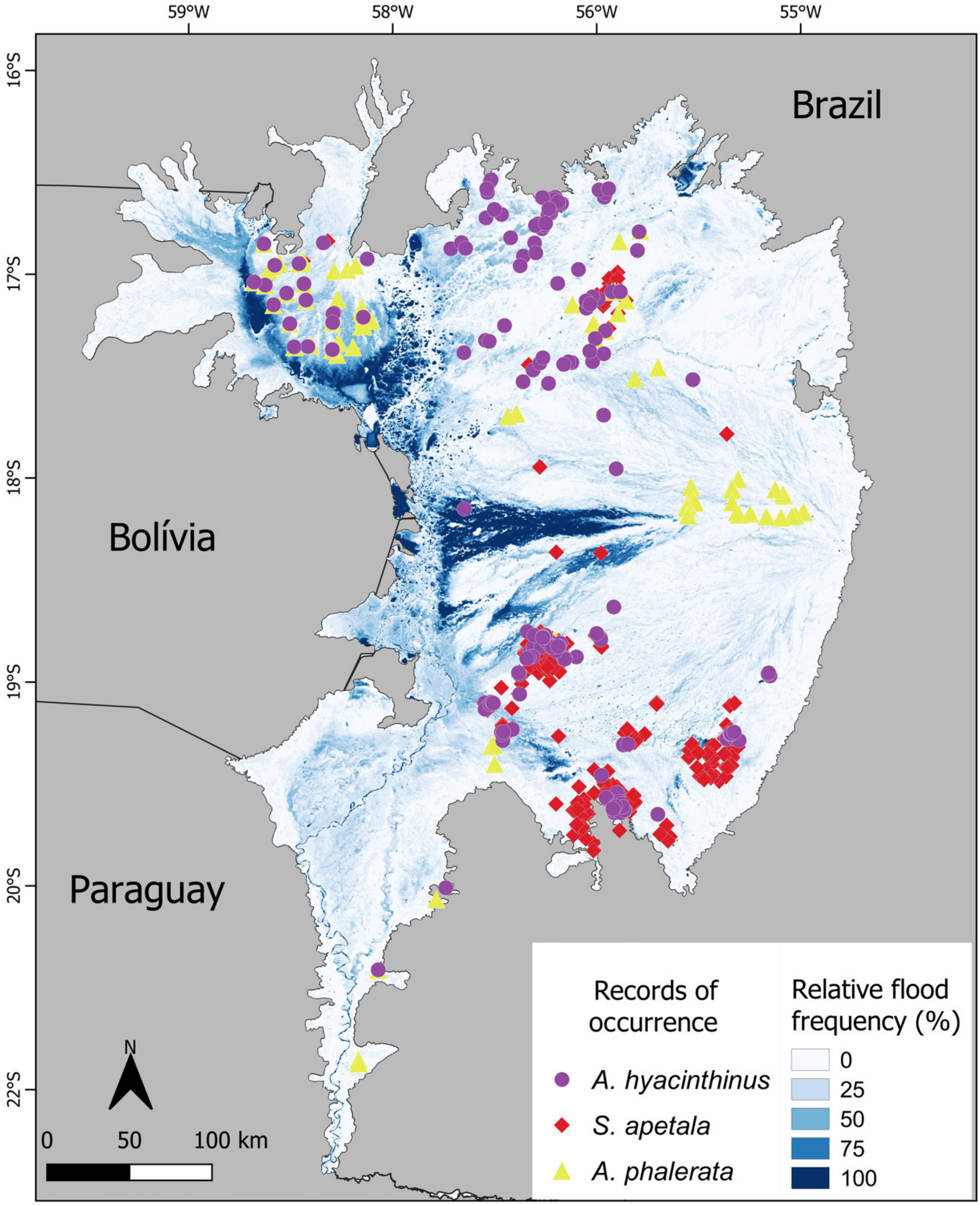

Figure 2. Relative frequency of flooding with the average flood coverage (%) calculated for 2000–2009 and records of occurrence considered in the species distribution models for Acuri Palm, Hyacinth Macaw and Manduvi Tree in the Pantanal. [Colour figure can be viewed at wileyonlinelibrary.com]

generated models combining all five response types (linear, quadratic, product, threshold and hinge) with 17 different regularization multiplier values (from 0 to 1 with intervals of 0.1, and the values 2, 3, 4, 5, 6, 8 and 10). In total, we obtained 493 candidate models for each species. Subsequently, all candidate models were statistically evaluated to select the best models.

We selected the best models based on three criteria, in the following hierarchical order: (1) model significance, (2) omission rates and (3) Akaike information criterion corrected for small sample sizes (AICc; Warren *et al.* 2014). We used this order of importance, as models with lower AICc values do not necessarily have lower omission rates (Cobos *et al.* 2019). Thus, we defined the best models as those that had low omission rates as well as low AICc values. We evaluated the significance and omission rates using the partial receiver operation characteristic (partial ROC) method. Unlike conventional ROC analysis, partial ROC uses only a portion of the curve and the cut-off limit is defined by the user (Peterson *et al.* 2008). We set a 5% cut-off limit and used 1000 replications, so a model was considered significant if more than 95% of the replications were larger than 1 (Peterson *et al.* 2008). One of the metrics of this analysis is the ratio of the area under the curve value that indicates model performance – the higher the value (ratioAUC > 1), the better the performance of the model (Peterson *et al.* 2008, Atauchi *et al.* 2018). We did not use conventional ROC analysis because this analysis has been found to be unsuitable for evaluating potential distribution models (Lobo *et al.* 2008, Shabani *et al.* 2018).

To elaborate the models, we divided the points of occurrence into groups for calibration and validation, with 70% and 30% of the records, respectively. We used bootstrapping with 15 replicates to create the final models. We used the *Kuenm* package (Cobos *et al.* 2019) for all model calibration, selection and creation steps. As a complementary analysis for the final models, we visually assessed model outputs for signs of overadjustment, including the concentration of high-suitability areas and inconsistencies with the ecological characteristics of the species (Radosavljevic & Anderson 2014).

To define the area of occurrence of the three species, we used the results from the best potential distribution models. We transformed the logistic model output into a binary map of suitable and unsuitable habitats for each species using the 'maximum training sensitivity plus specificity logistic threshold'. This threshold prioritizes sensitivity, i.e. the probability of the model to predict correctly an absence (Cantor *et al.* 1999, Vale *et al.* 2014). Therefore, it finds the cut-off point with the most suitable areas for the species (Liu *et al.* 2011, Jorge *et al.* 2013). We overlaid the binary maps of suitable and unsuitable environments for the three species, and the areas considered adequate for the occurrence of the three species were considered a priority for conservation purposes.

Habitat loss and the protection of suitable habitat

Unlike species distribution models, to calculate habitat loss and population size of the Hyacinth Macaw, we only considered the Brazilian Pantanal, as we could not locate a native vegetation loss database for Bolivia and Paraguay. For Brazil, we used land use and land cover data with information on native vegetation conversion between 2002 and 2017, all made available by the SOS-Pantanal Institute (SOS-Pantanal *et al.* 2017). We defined areas of adequate habitat as those that were predicted as suitable for the Macaw by our models with the native vegetation converted (as above). To calculate this, we overlaid land use and land cover data with our binary maps of suitable and unsuitable habitats for each of the three species and compared these with the extent of suitable areas.

We calculated the level of protection of suitable habitats for the entire Pantanal. For the Brazilian part, we overlaid the calculated binary suitability maps with state and federal conservation units, as well as Indigenous Land registered with the Ministry of the Environment (www.mma.gov.br/), Instituto Chico Mendes de Conservação da Biodiversidade (www.icmbio.gov.br/), Fundação Nacional do Índio (www.funai.gov.br/), Environment Institute of Mato Grosso do Sul (www.imasul.ms.gov.br/) and State Secretariat for the Environment of Mato Grosso (www.mt.gov.br/). For Paraguay and Bolivia, we used the Protected Planet website (www.protectedplanet.net). To calculate the ratio protected within the biome, we considered protected areas only within the limits of the Pantanal.

To calculate the amount of suitable habitat protected by conservation units, we also considered the categories of protected areas. Although the Brazilian system is somewhat different from other countries, the categories fit into the IUCN hierarchy. It was important to consider different categories separately, as some of them do not enjoy full protection. These areas of sustainable use have more permissive protection legislation regarding the use and management of the area (Brasil 2011). This class contains Environmental Protection Area (similar to IUCN categories V and VI), Private Natural Heritage Reserve (IUCN categories Ia and II), and Indigenous Land (IUCN category VI). On the other hand, areas under full protection have stricter legislation and only allow a few activities (www.icmbio.gov.br). This class includes National and State Parks (IUCN category II) and Ecological Stations (IUCN category Ia) (Dudley 2008, Brasil 2011).

RESULTS

Best models for the Hyacinth Macaw, Manduvi and Acuri

For the Manduvi Tree and Hyacinth Macaw, the best models used the sample bias reduction threshold of 30 compartments. The best model for the Manduvi Tree had an AUC ratio of 1.70, an omission rate equal to zero and low AICc values compared with the other candidate models. Hyacinth Macaw presented similar results with an AUC ratio of 1.71, zero omission rate and low AICc values in comparison with other candidate models. Both models showed consistency in the visual analysis. For Acuri Palm, the models that used the sample bias reduction threshold of 30 and 100 compartments had similar AUC ratio values (1.70 and 1.65, respectively) and both had zero omission rate. However, these models differed based on the visual comparison, with the 100-compartment model better distinguishing adequate and inadequate habitats (Fig. 3), whereas the 30-compartment threshold model erroneously classified some habitats, indicating environments with a high frequency of flooding as suitable for the species. The high AUC ratio (values > 1) and the low omission rate indicated good model performance for all three species (for model details see Table S2). Although the Hyacinth Macaw model can be subject to cascading errors, as it uses the results of the plant models as predictor variables, the high performance of the models of the three species based on evaluation metrics indicates that this effect may have been small or non-existent in our results.

In the case of the Acuri Palm distribution model, the most important predictor variables were apparent density of fine soil (contribution value of 38.3%), soil texture (22.2%) and flood frequency (15.0%; for model details see Fig. S3). For the Manduvi Tree, the three most important variables were soil organic carbon content (contribution value of 58.9%), flood frequency (25.3%) and soil water pH (13.8%; Fig. S4). The two variables used in the Macaw model differed slightly in their contribution value, with 58.8% for the logistic output of Acuri Palm and 41.2% for Manduvi Tree (for contribution values and response curve of all variables, see Table S3 and Figs S1 and S2). As expected, the response curve showed a positive relationship between the areas predicted as suitable for the two plant species (logistic output) and the areas suitable for the Macaw. Manduvi Tree had the smallest area predicted as suitable habitat, with only 27.3% of the total area of the Pantanal, whereas Acuri Palm and Hyacinth Macaw had 40.2% and 39.1%, respectively (Fig. 3). Frequently flooded areas, for instance in the western edge of the Pantanal, were classified as unsuitable for all three species. We found low suitability in the central part of the study area, whereas the models predicted the highest concentration of suitable areas in the north and the south.

Protected and lost suitable areas

Of the total area predicted as suitable for the particular species, conservation areas only protected 8.6% of the habitat suitable for Acuri Palm, 11.8% for Manduvi Tree and 11.3% for Hyacinth Macaw (Fig. 4). Environmental Conservation Areas represented the highest amount of protected land, covering 4.3% of suitable habitat for Manduvi Tree and Hyacinth Macaw, and 2.9% for Acuri Palm (Fig. 4). For the Macaw and Acuri Palm, the second most important category was Private Natural Heritage Reserve, containing 2.3% and 1.8% of suitable habitat, respectively, while 2% of potential Manduvi Tree habitat was contained in State Park and National Park each (Fig. 4).

We calculated that Acuri Palm had lost 12 983 km^2 (12.4%) of predicted suitable habitat in 15 years; for Manduvi Tree, habitat loss amounted to 8349 km^2 (11.8%; Fig. 5). The Macaw lost 11 470 km^2 (11.3%) of suitable habitat due to

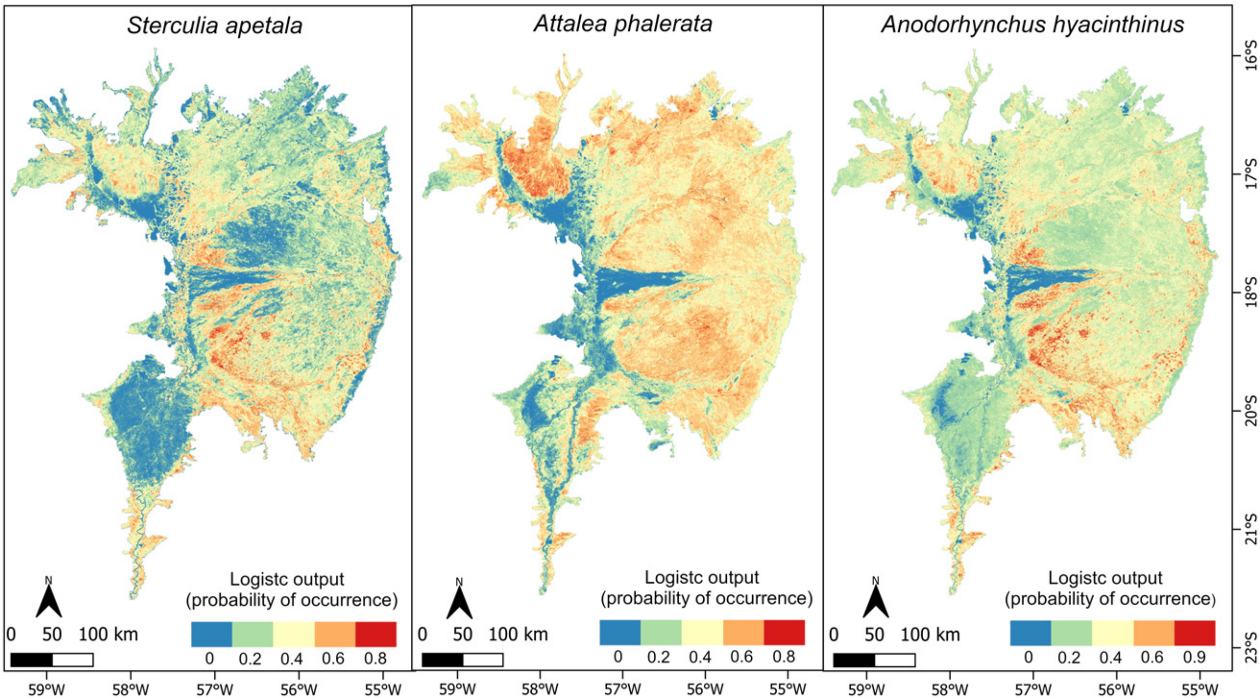

Figure 3. Results of the best species distribution models for Acuri Palm, Hyacinth Macaw and Manduvi Tree in the Pantanal. [Colour figure can be viewed at wileyonlinelibrary.com]

the conversion of native vegetation (Fig. 5). On average, these losses represent a 0.5% annual loss for each species. The rate of loss was highest in 2014–2016, with 1675, 856 and 1421 km^2 of suitable habitat lost in these 2 years for Acuri Palm, Manduvi Tree and Hyacinth Macaw, respectively.

Overlapping the individual binary maps of suitable habitats resulted in a large number of areas suitable for the occurrence of all three species, covering 54 910 km^2, or about 30% of the Pantanal (Fig. 6). These areas are concentrated in the northern and southern parts of the study area and are associated with a low frequency of flooding. Of these areas, 8.8% are within the limits of conservation units, with Environmental Conservation Area and State Park covering 3.9% and 1.8%, respectively (Fig. 6). Considering the suitable habitat for all three species, 7206.1 km^2, or about 13%, were lost up to 2017, with the eastern part of the biome showing the highest rates of conversion.

DISCUSSION

According to our results, suitable habitat for Acuri Palm and Manduvi Tree is unevenly distributed and is concentrated in areas with low frequency or no flooding. Both plants are known to have low tolerance to flooding (Pott & Pott 1994, Pott 1995, Dvorak *et al.* 1998). In the Pantanal, these rarely flooded areas are associated with forest formations, indicating a concordance between our results and the existing literature (Pott & Pott 2009, Padovani 2010). Our models indicated that suitable habitat for the three species is concentrated in the northern and southern regions of the Pantanal (Fig. 5a, c). In the south, suitable habitat is mainly concentrated in the sub-regions of Nhecolândia, Aquidauana, Miranda and Abobral (Rio Negro Oeste and Aquidauana), while in the north, it is concentrated in the subregions of Corixo Grande, Cuiabá and São Lourenço (Figs 1 and 5a, c).

Few conservation areas preserve suitable habitat for Acuri Palms and Manduvi Trees in the Pantanal. Furthermore, the areas predicted as suitable for the two plants were found to be particularly susceptible to habitat loss, as they are also valuable for livestock production and are frequently converted to cultivated pastures with African grasses (Pott *et al.* 2011, Guerra *et al.* 2020a). A decrease in Acuri Palm and Manduvi Tree populations will

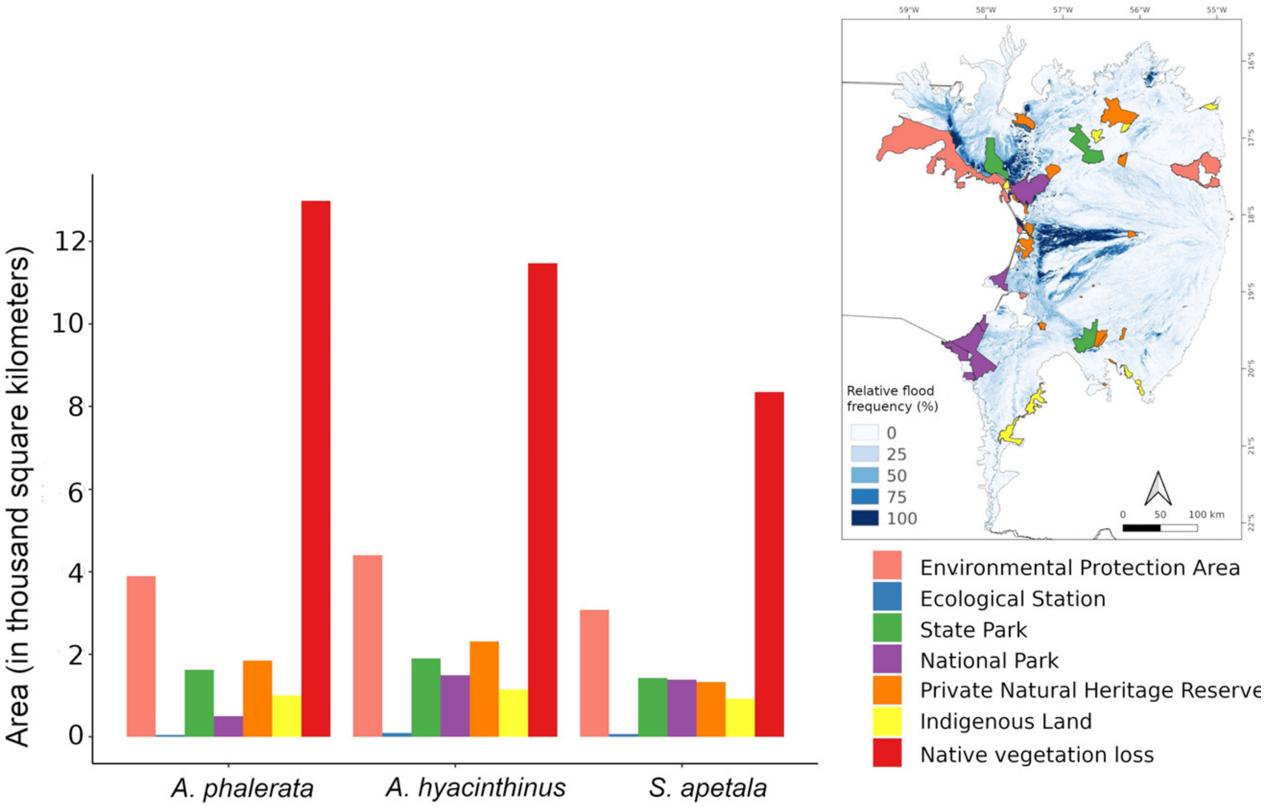

Figure 4. Suitable habitat (km^2) within different conservation units for Acuri Palm, Hyacinth Macaw and Manduvi Tree in the Pantanal. The map insert shows the location of these protected areas in the Pantanal as well as the category of conservation units used and the frequency of flooding (% of time in 10 years). Environmental Protection Area and Private Natural Heritage Reserve units are under sustainable use, while the other categories are fully protected. [Colour figure can be viewed at wileyonlinelibrary.com]

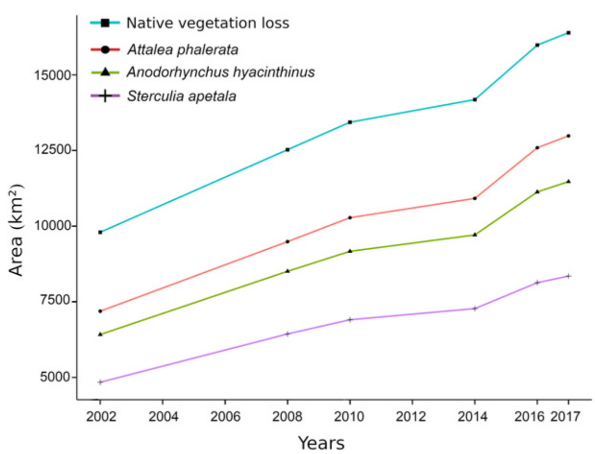

Figure 5. Cumulative native vegetation loss and loss of suitable habitat (km^2) for Acuri Palm, Hyacinth Macaw and Manduvi Tree in the Pantanal. [Colour figure can be viewed at wileyonlinelibrary.com]

affect the Hyacinth Macaw negatively, as it depends on these plants as a source of food and nesting sites. Conversion of native vegetation has also been reported as a main concern for other Neotropical parrots (Berkunsky *et al.* 2017). Hyacinth Macaws sometimes form groups of over 100 individuals that generally establish their home-ranges close to food resources, with a particular preference for Acuri Palms (Guedes 1993, Antas *et al.* 2010). Furthermore, the reproductive period of the Macaw can last up to 1 year, as in addition to the period of egg-laying and caring for the chicks, the pair spends time before laying, choosing and preparing the nest by widening the entrance and the interior of the hollow (Guedes 1993, Antas *et al.* 2010). They also defend the nest from conspecifics and other hollow-nesting species (Guedes 1993, Antas *et al.* 2010). These

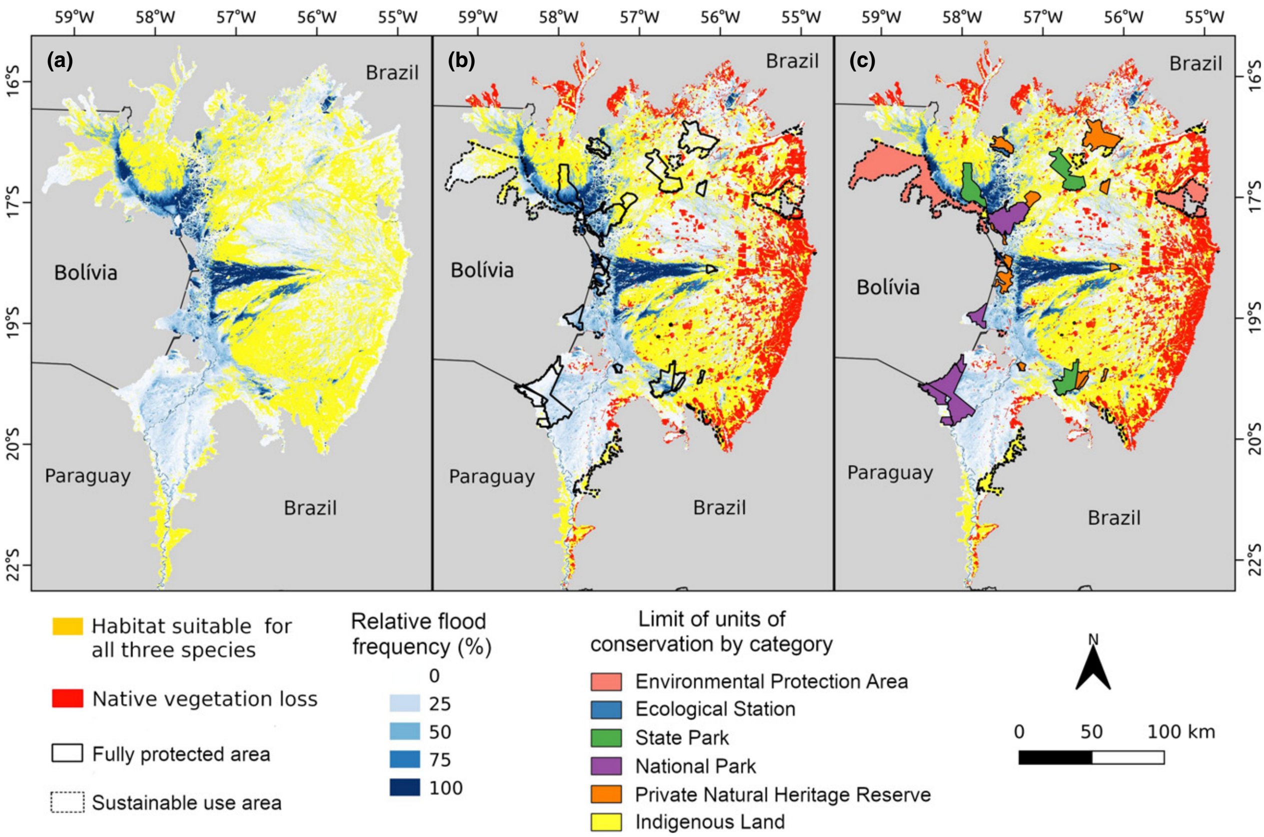

Figure 6. Potential distribution models, habitat loss and habitat protected for Acuri Palm, Manduvi Tree and Hyacinth Macaw in the Pantanal. (a) Flood frequency and habitat predicted suitable for all three species (Acuri, Manduvi and Hyacinth Macaw). (b) Flood frequency, predicted suitable habitat for the three species, native vegetation loss in 2002–2017, habitats protected in units for strict conservation (black border) and units of sustainable use (dashed border). (c) Flood frequency, predicted suitable habitat for the three species, native vegetation loss and conservation units by categories. [Colour figure can be viewed at wileyonlinelibrary.com]

time-consuming behaviours make it necessary for the Macaws to stay close to the nest, thereby preferring areas with Manduvi Trees.

The lack of suitable habitat based on unsuitable environmental conditions (i.e. flooding and soil type) for Manduvi Tree and the prevalence of low-suitability areas for Acuri Palm predicted for the central Pantanal, especially in central Paiaguás, may be limiting factors for the distribution of Hyacinth Macaw (Figs 1 and 5b). Even though adult Macaws can cover over 35 km daily (Seixas *et al.* 2002, Antas *et al.* 2010), this region may present a geographical barrier between the north and the south (Presti *et al.* 2015). This extensive, low-suitability central region serving as a barrier can explain the genetic differences between Hyacinth Macaw populations in the north and south of the Pantanal (Presti *et al.* 2015).

Our models predicted highly suitable areas just north and south of the central region of low-suitability regions in Paiaguas (Figs 6 and 7). Because they are suitable for both plant species, these areas may be able to supply the necessary food and nesting resources for the Macaw, thereby enabling the establishment of a central subpopulation. They can also facilitate the movement of Macaws between the northern and southern regions, serving as a natural corridor. However, a substantial amount of suitable habitat has already been lost through conversion of native vegetation in the east that must be prioritized for restoration (Fig. 5b).

In our study area, the conversion of native vegetation predominantly occurs in the 'arc of deforestation', being most intense at the eastern border of the Pantanal, where the lowland and highland areas meet in the basin of the Upper Paraguay River (Guerra *et al.* 2020a). There is also a difference in the conversion rates of native vegetation with regard to plant communities, with savannahs

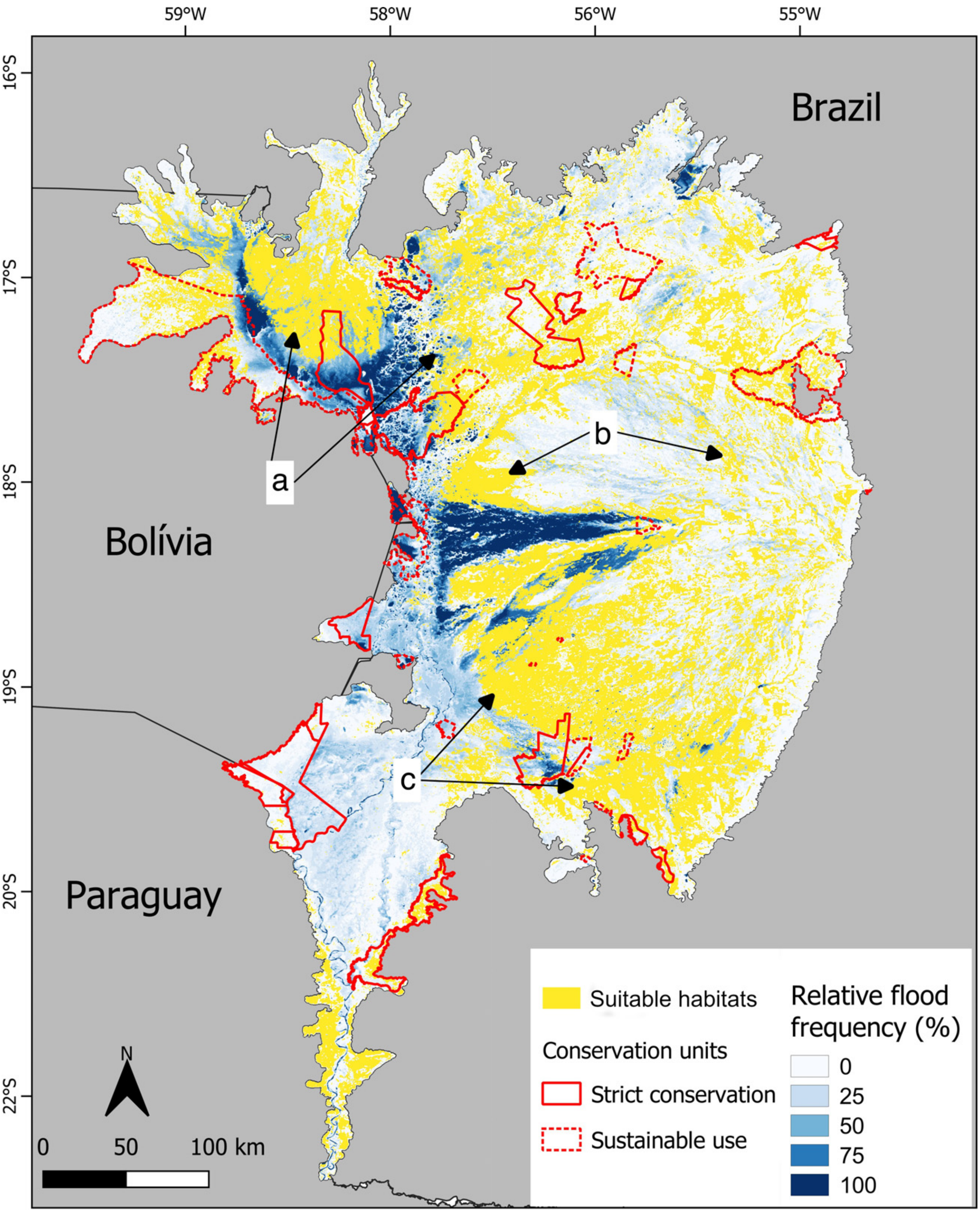

Figure 7. Remnants of suitable habitat predicted for all three species (Acuri Palm, Manduvi Tree and Hyacinth Macaw), with flood frequency, and conservation units (solid border for strict conservation and dashed border for areas of sustainable use) for the Pantanal biome. (a) Cluster of suitable areas in the north. (b) Suitable areas that could potentially connect northern and southern Hyacinth Macaw subpopulations. (c) Cluster of suitable areas in the south. [Colour figure can be viewed at wileyonlinelibrary.com]

and forests having the highest conversion rates (SOS-Pantanal *et al.* 2014, 2017). As these plant communities occur outside frequently flooded areas, they are at a higher risk of being converted to pastures. As our three study species also depend on these areas, they have experienced disproportionately high habitat loss. These factors explain why habitat loss for the two plants and the Macaw follows patterns of native vegetation loss in the Pantanal. Nevertheless, the differences in predicted habitat loss for the two plants arise from the somewhat different distribution of the two species. Acuri Palm had the largest area of suitable habitat predicted and also the highest habitat loss, whereas Manduvi Tree had more restricted potential occurrence and lower habitat loss. The overall loss of suitable habitat during 2002–2017 has already exceeded the amount of habitat currently protected by conservation units. This is an alarming fact, as continuing habitat conversion at current rates (a conservative estimate) will lead to a loss of more than a quarter of the current habitat for each of the three species in 30 years (Figs 6 and 7). Habitat loss might be even higher, as the rate of conversion of native vegetation is expected to increase in the region (Roque *et al.* 2016, Padovani 2017, Guerra *et al.* 2020a, 2020b).

The low amount of area predicted to be suitable for the three species that is currently within conservation units is related to the placement of protected areas. Protected areas are generally located in areas that are flooded permanently or with a high frequency. According to the 'worthless land' theory, conservation units tend to be allocated to areas of low economic value or low suitability for agriculture (Pressey *et al.* 2002). This selective allocation for protection can also be seen in the Pantanal. Due to the length of flooding (up to 8 months), frequently flooded areas do not allow managed pastures or other forms of agriculture, or the mechanization of the production process. They also incur high management costs for livestock grazing, as entire herds need to be removed during the flood season (de Abreu *et al.* 2010). Flooded areas are difficult to access for maintenance of infrastructure. Both accessibility (proximity to roads and rivers) and increased elevation have been identified as drivers of native vegetation conversion (Guerra *et al.* 2020a). All of these factors reduce the economic value of frequently flooded areas compared with rarely flooded ones, explaining the skewed distribution of conservation units (Pressey *et al.* 2002). Therefore, protected areas in the Pantanal are less efficient for species that preferentially or exclusively occur in areas with low flood frequency. Many conservation units are in fact Environmental Protection Areas, a less restrictive conservation category allowing sustainable use (Fig. 4).

Due to their higher suitability for economic activities, particularly livestock grazing, areas with low flood frequency have the highest cattle densities (Tomas *et al.* 2019), which present other risks to our study species, for instance associated with inadequate fire management (Tomas *et al.* 2019). High cattle density and the associated trampling decrease recruitment in Manduvi Tree, which along with other factors associated with inadequate management can change the population structure of this species (Johnson *et al.* 1997, Júnior 2007, 2010). Conversion of native vegetation in non-flooded areas also affects the Manduvi Tree (Júnior 2007, 2010). These effects can lead to the local extinction, which by causing a shortage of nesting hollows will affect Macaw reproduction (Johnson *et al.* 1997, Manning *et al.* 2004, Júnior *et al.* 2007). The hollows Macaws use as nests only appear naturally in > 70-year-old individuals or when the tree suffers damage, for example from termites or the loss of branches (Guedes *et al.* 2006, Júnior 2007, 2010). When natural vegetation is converted to pasture, even if young Manduvi Tree individuals are left as paddock trees, they tend to fall over when they are about 4 years old because they are isolated and have tabular roots. As a consequence, Manduvi Trees have become rare in modified environments (Guedes *et al.* 2006, Júnior 2007, 2010). This demonstrates the need to preserve and restore Manduvi Trees, especially in areas we have identified as priority. So far, no studies have been conducted on the effects of cattle or fire on Acuri Palm.

A large proportion of the adequate habitat for all three species is outside protected areas on private properties, which offers new possibilities for prioritizing areas for conservation. Nevertheless, certain aspects need to be taken into account during conservation planning. Considering the genetic difference between the northern and southern subpopulations of the Macaw (Presti *et al.* 2015) and the geographical barrier that we identified in the central Pantanal, we suggest that new protected areas should be designated in different regions of the Pantanal to maintain the genetic diversity of the Macaw. The possible stepping stones present in the Paiaguás region must be considered as a priority for conservation to create habitat corridors. A western corridor is important, given the lack of suitable habitat in that region, and an eastern corridor is crucial due to the high native vegetation conversion rate. Remnant vegetation should be protected and suitable areas lacking native vegetation should be restored with a view to connecting patches in particular in the 'arc of deforestation' identified by Guerra *et al.* (2020a).

In addition to the creation of new protected areas in these priority regions, public policies should be aimed at protecting low-frequency or non-flooding environments in the Pantanal, such as the Permanently Terrestrial Areas (Tomas *et al.* 2019). For instance, we suggest allocating Environmental Reserve Quotas or Payments for Environmental Services as legal incentive instruments, particularly in priority areas that can connect fragmented subpopulations. The Pantanal biome is not yet subject to specific national legislation, unlike the Atlantic Forest (Brasil 2006). Thus, possible legal changes (e.g. Pantanal Law Project) and adjustments to national and state laws should be assessed to consider their effect on the Hyacinth Macaw and other threatened species in order to safeguard or restore their habitat, especially in places subject to the greatest pressure of conversion of native vegetation, as identified in this study.

Our results proved to be consistent with the literature and the species' biology, in addition to presenting good values in evaluation metrics, thus demonstrating that the approach is robust and of biological significance. The plant and bird occurrence records used in our study come from scientific databases with their inherent spatio-temporal biases. For instance, data tend to be collected near research stations (Newbold 2010). In spite of the possibility of sample bias in the occurrence data, by employing methods used to reduce sample bias and modelling errors, we were able to minimize the effects of biases and generate models with high accuracy based on evaluation metrics (partial AUC, omission rate and AICc values).

Another important factor in the model construction is the selection of predictor variables, which can improve model accuracy (Fourcade *et al.* 2017, El-Gabbas & Dormann 2018, Oliveira *et al.* 2021). Given the characteristics of our study area, the number of possible variables was reduced. Variables such as climate, which commonly shape distributions at global or continental scales, were incompatible with the scale of our study (Oliveira *et al.* 2021). Other variables were unsuitable due to the characteristics of the Pantanal. For example, topography is largely irrelevant, as the biome is a plain and has a low slope. Variables associated with vegetation, such as NDVI (normalized difference vegetation index), or phytophysiognomical distribution, are also inadequate, because they are strongly correlated with flood patterns, a variable already included in the model (Padovani 2010). Considering the Hyacinth Macaw, the use of geographical barriers such as rivers is also impracticable due to the high mobility of the species. Nevertheless, despite the limited number of predictive variables used in the modelling, based on the evaluation metrics our models presented accurate results.

CONCLUSIONS

The Hyacinth Macaw model predicted an uneven distribution within the biome, with preference for areas with low flood frequency. Paiaguás proved to be an important subregion to understand Macaw distribution. This geographical barrier contains areas that can function as a corridor to connect northern and southern subpopulations, which are the two priorities for the conservation of the species. Conservation actions, such as habitat restoration and habitat protection in the case of remnants, are particularly important in the eastern part of Paiaguás, which has experienced higher vegetation conversion rates. We found that for the Macaw, the amount of suitable area that is currently protected is less than the amount lost due vegetation conversion, due to the preference of the species for areas with no or low frequency of flooding. In the Pantanal biome, these habitats are more susceptible to the conversion of native vegetation and are poorly protected, as they have a higher economic value compared with areas with a high frequency of flooding. These facts, associated with other risks such as the inadequate management of these regions, threaten the persistence of these species in the Pantanal biome and their conservation must be spatially prioritized.

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AUTHOR CONTRIBUTION

Judit K. Szabo: Conceptualization (supporting); Supervision (lead); Writing-review & editing (equal). **Walfrido M. Tomas:** Conceptualization (equal); Data curation (lead); Funding acquisition (lead); Methodology (equal); Writing-review & editing (lead). **Neiva Maria R. Guedes:** Data curation (lead); Funding acquisition (lead); Writing-review & editing (lead). **Antônio dos S. Júnior:** Data curation (lead); Writing-review & editing (lead). **Carlos Roberto Padovani:** Data curation (lead); Writing-review & editing (lead). **André R. Camilo:** Data curation (lead). **Andrew T. Peterson:** Conceptualization (supporting); Formal analysis (supporting); Methodology (lead); Visualization (lead); Writing-review & editing (lead). **Letícia C. Garcia:** Conceptualization (lead); Methodology (lead); Supervision (lead); Writing-review & editing (equal).

Data Availability Statement

Hyacinth Macaw is globally vulnerable and to protect the species from its main threat, trafficking of wild animals, we do not make location data available in a public repository. However, the corresponding author will make the data used in this article available upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1 Response curve of the variables used in distribution prediction models of *Attalea phalerata* in the Pantanal.

Figure S2 Response curve of the variables used in distribution prediction models of *Sterculia apetala* in the Pantanal.

Figure S3 Apparent density of fine soil in cg/cm3, indicated as the variable of greatest contribution in species distribution model of *S. apetala*.

Figure S4 Soil organic carbon content in t/ha, indicated as the variable of greatest contribution in the species distribution model of *A. phalerata*.

Table S1 Short description and abbreviation of the variables considered to the distribution prediction models of *Sterculia apetala* and *Attalea phalerata*, the two plant species (abiotic predictors) and for the Hyacinth Macaw *Anodorhynchus hyacinthinus* (biotic predictors) in the Pantanal.

Table S2 Accuracy parameters of the models of potential distribution for *Anodorhynchus hyacinthinus*, *Attalea phalerata* and *Sterculia apetala*, in the Pantanal, considering three parameter of reducing sampling bias.

Table S3 Contribution values of the variables used in distribution prediction models of *Sterculia apetala* and *Attalea phalerata*, the two plant species (abiotic predictors) and for the Hyacinth Macaw *Anodorhynchus hyacinthinus* (biotic predictors) in the Pantanal.