Predicting the potential distribution of aquatic herbaceous plants in oligotrophic Central Amazonian wetland ecosystems

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ABSTRACT

Aquatic herbaceous plants are especially suitable for mapping environmental variability in wetlands, as they respond quickly to environmental gradients and are good indicators of habitat preference. We describe the composition of herbaceous species in two oligotrophic wetland ecosystems, floodplains along black-water rivers (*igapó*) and wetlands upon hydromorphic sand soils (*campinarana*) in the Parque Nacional do Jaú and the Reserva de Desenvolvimento Sustentável Uatumã in Central Amazonia, both protected areas. We tested for the potential distribution range (PDR) of the most frequent species of these ecosystems, which are the ones that occurred in at least two of the sampled wetlands, using species distribution models (SDMs). In total, 98 aquatic herbaceous species were recorded, of which 63 occurred in *igapós* and 44 in *campinaranas*. Most *igapó* species had ample PDRs across the Neotropics, while most *campinaranas* species were restricted to the Amazon Basin. These results are congruent with studies that described similar distribution patterns for tree and bird species, which emphasizes a high degree of endemism in Amazonian *campinarana*. However, we also found differences in the potential distribution of species between the two protected areas, indicating high environmental variability of oligotrophic ecosystems that deserve further investigation to develop effective measures for their conservation and protection.

Keywords: aquatic macrophytes, black-water floodplain, *campinarana, igapó*, SDMs, white-sand savannas

Introduction

Aquatic macrophytes are defined as "aquatic photosynthetic organisms, large enough to see with the naked eye, that actively grow permanently or periodically submerged below, floating on, or up through the water surface of inland freshwater or brackish waterbodies" (Chambers *et al.* 2008). In Amazonian river wetlands, where flood pulses are high (Junk *et al.* 1989), many herbaceous species have short life cycles and occur only during the low water (terrestrial phase). Their diaspores are well adapted to survive the subsequent inundation (aquatic phase). Therefore, these seemingly terrestrial plants are included in the group of aquatic herbaceous plants (Piedade *et al.* 2019). Aquatic herbaceous plants are highly diverse in terms of growth

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forms (*i.e.*, immersed, submerged floating plants, with floating leaves, epiphytic, among others), which are closely associated to differences in resource capture, allocation, stress tolerance and survival strategies (Piedade *et al.* 2019). This ensures rapid population recovery from disturbance and successfull colonization of highly dynamic environments that are subjected to seasonal oscillations of the water level and abrupt transitions in the environmental conditions along the topographic gradient (Murphy *et al.* 2019; Piedade *et al.* 2019). Aquatic herbaceous plants are also especially suitable for mapping environmental variability in wetlands, being sensitive to both long- and short-term changes in environmental conditions (Lacoul & Freedman 2006).

According to international criteria of wetland definition, wetlands in the Amazon Basin cover an area of more than two million square kilometers, including areas that are seasonally flooded by lateral river overflows and those that are episodically waterlogged by oscillating groundwater levels (Junk *et al.* 2014). Floodplains along large rivers in Amazon Basin cover an area of approximately 750,000 km² and are divided in environments with fertile conditions (white-water floodplains, called *várzea* with about 450,000 km² extension) and floodplains of low to intermediate fertility (black- and clear-water floodplains, called *igapó,* with approximately 300,000 km² extension) (Melack & Hess 2010; Wittmann & Junk 2016). *Igapó* and *várzea* floodplains are influenced by a monomodal flood-pulse with amplitudes averaging about 10 m in the Central Amazon region, inducing a distinct seasonality (aquatic and terrestrial phases) in the floodplains (Junk *et al.* 1989). Besides nutrient contents of waters and soils, the floodplains are influenced by the duration of the aquatic phase, resulting in a distinct flora of herbaceous (Piedade *et al.* 2010) and tree communities (Wittmann *et al.* 2012) that can be inundated for periods of more than six months per year. The herbaceous communities in *várzea* and *igapó* are distinct with low floristic similarity (Lopes *et al.* 2019). Because environmental conditions such as water transparency and nutrient contents may vary significantly between rivers, floristic inventories also show a low similarity between the *igapó* of clear- and black-water rivers (Crema 2017). In contrast, the *campinaranas* cover an area of 334,879 km² in the Amazon region (Adeney *et al.* 2016) and occur on nutrient-poor sandy soils. The presence of impermeable soil layers near the surface, in hydromorphic *campinaranas,* results in low drainage and saturation of the soil during the rainy seasons. However, only in some areas the water column rises a few centimeters above the soil surface, and the effects of flooding or waterlogging are mostly restricted to the plant root system (Anderson 1981; Franco & Dezzeo, 1994; Coomes 1997; Junk *et al.* 2011; Damasco *et al.* 2013; Adeney *et al.* 2016). In many regions, as along the lower Negro river, the distribution of these ecosystems is fragmented within the forest matrix (Prance 1996).

Studies on species composition and distribution of Amazonian aquatic plants are still scarce considering that wetlands occupy about 30 % of the region (Junk *et*

al. 2011). Near the city of Manaus (State of Amazonas, Brazil) Junk & Piedade (1993; 1994) conducted studies with a large sample effort and recorded 388 species of aquatic, terrestrial and semiaquatic herbaceous species for the *várzea*. Herbaceous species in black-water *igapós* of different regions in the Central Amazon were less numerous and so far a total number of 178 species has been recorded (Lopes *et al.* 2019), while only 52 species were recorded in clear-water *igapós* in Colombian Guiana (Atuesta-Ibargüen 2019), and 49 species in clear-water *igapós* of the Tapajós river (Pará, Brazil) (Crema 2017). Inventories of herbaceous species in white-sand ecosystems (*campinarana*) at the Parque Nacional do Viruá (Northern Amazon) and Acre State (Southwestern Amazon) reported 196 (Costa *et al.* 2016) and 110 species (Daly *et al.* 2016), respectively. Both nutrient-poor *campinarana* and black-water *igapó* are thought to harbor several endemic species adapted to these harsh and extreme environments (Kubitzki 1989; Wittmann *et al.* 2010). More knowledge on the composition of aquatic herbaceous species and the factors that influence their distribution in these oligotrophic environments is needed to understand the functioning of these ecosystems and in order to contribute to the development of effective conservation and management strategies.

Historical climatic factors could influence the current distribution pattern of aquatic plants but are rarely considered in studies of aquatic vegetation distribution (Lopes *et al.* 2017; Murphy *et al.* 2019). Although each species has its own distribution range, repetitive patterns of distribution are common (Marchioretto *et al.* 2004); while some distribution ranges reflect connections to past climates, others indicate limits imposed by the present environment (Gomes *et al.* 2020). The use of modeling to predict species distribution allows to evaluate both, the current characteristics of the environment and to simulate the distribution in paleo-, present, and future climates. It also allows gaining insights on how species would respond to physiological stressors and to changing environments under rising CO_2 and global warming (Pecchi *et al.* 2019; Santana Jr. *et al.* 219; Zhang *et al.* 2019).

The objectives of this study were: (1) to determine the composition of aquatic herbaceous plants in black-water *igapó* floodplains and hydromorphic *campinarana* ecosystems of two PELD-MAUA sites (Brazilian Long-term Ecological Research Network - Ecology, monitoring and sustainable use of wetlands) located in the protect areas Parque Nacional do Jaú (JNP) and Reserva de Desenvolvimento Sustentável Uatumã (USDR), (2) to compare them with the flora of other Brazilian wetland ecosystems and (3) by using species distribution models (SDMs), to estimate the potential distribution range (PDR) within the Neotropical region for the 10 most frequent species in each ecosystem, as well as for the five shared species between ecosystems. We hypothesized that the potential distribution ranges of black-water *igapó* species are much wider (*i.e.*, Neotropical) than

those of *campinarana* species (*i.e.*, restricted to the Amazon basin), because the latter occur in insular and fragmented habitats interspersed within the Amazonian rainforest. On the other hand, in the black-water *igapó* floodplain the water connectivity would allow a more effective and widespread dispersion. In this regard, we also expected that the *campinarana* would share fewer species with other Brazilian wetlands than the *igapó*.

Materials and methods

The PELD-MAUA sites are established in the Parque Nacional do Jaú (JNP) and the Reserva de Desenvolvimento Sustentável Uatumã (USDR) in the Central Amazon basin, with focus on the oligotrophic wetland vegetation of black-water *igapó* (from now on, when referring to the study areas, called just *igapó*) and *campinarana*. The main objective of the PELD-MAUA project is to monitor changes in vegetation in the background of ongoing climate and land-use changes. The distance between both PELD-sites is approximately 300 km.

Reserva de Desenvolvimento Sustentável Uatumã - USDR

The USDR is located 150 km northeast of Manaus city, shared by the municipalities of Itapiranga and São Sebastião do Uatumã (State of Amazonas). The USDR covers an area of

4,244 km^2 of *terra-firme* forests, *igapós*, and *campinaranas*. The PELD site is located at 02°10'30"-02°11'30" S and 59°00'30"-59°01'30" W (Fig. 1). The USDR is cut by the Uatumã river through its entire extension. The climate is tropical humid, with a pronounced rainy season from November to May and a dry season from June to October, with mean annual temperature of 27 °C and mean annual precipitation of 2,376 mm (IDESAM 2009). The flood pulse is monomodal; however, after the construction of the Balbina dam, flooding is regulated by the opening and closing of the floodgates (Assahira *et al.* 2017), depending on the level of the water reservoir and the demand for power generation.

The USDR consists of different forested ecosystems. The largest part of the territory is covered by dense, non-flooded upland forests (*terra-firme*) on plateaus at a maximum altitude of approximately 130 m a.s.l.. The white-sand vegetation (*campinarana*) of USDR occurs as "islands" in terrain depressions (at approximately 40 m a.s.l.) scattered throughout the *terra-firme* forest, and show great heterogeneity in the vegetation physiognomy due to the variations of the soil nutrients and flooding (Targhetta *et al.* 2015). The open *campinarana* physiognomies are dominated by shrubs, small trees, and a conspicuous herbaceous component. The orchid *Sobralia granitica* G.A.Romero & Carnevali, the fern *Actinostachys pennula* (Sw.) Hook. and several species of Eriocaulaceae, Cyperaceae and Xyridaceae characterize the herbaceous vegetation. In *campinaranas*
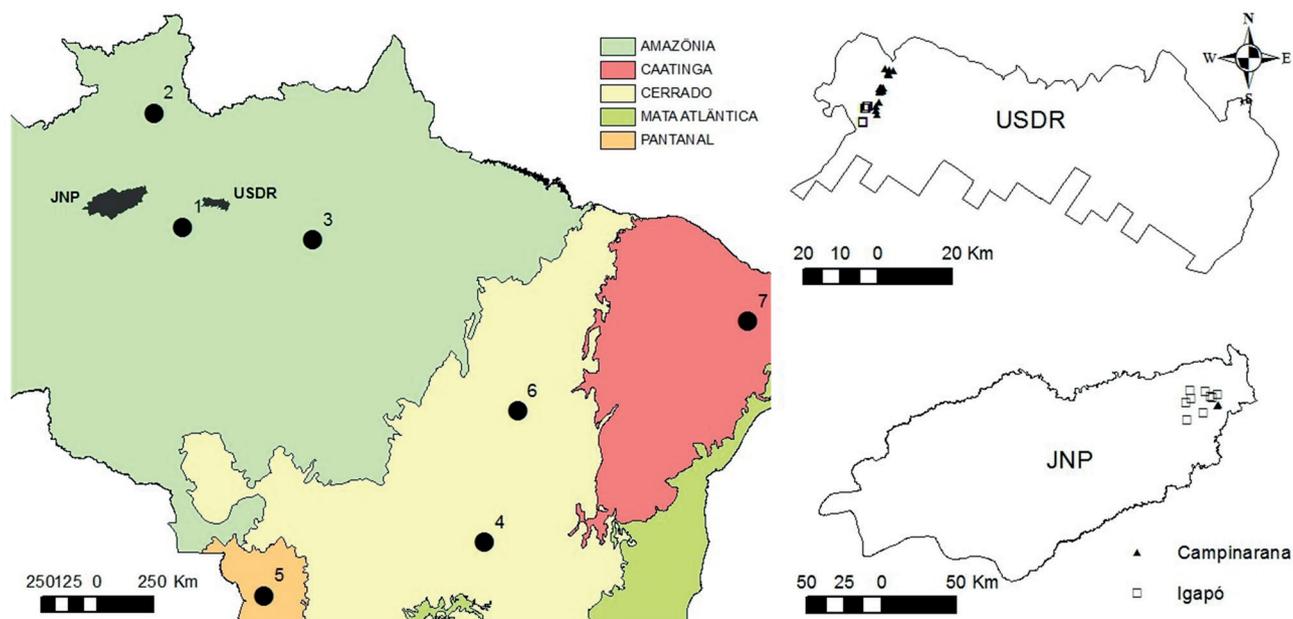
Figure 1. Wetlands (*campinarana* and *igapó*) inventoried in Parque Nacional do Jaú (JNP) and Reserva de Desenvolvimento Sustentável Uatumã (USDR) and location of data from Brazilian wetland inventories: 1) Amazonian *várzea* floodplains, 257 spp. (Junk & Piedade 1993); 2) *campinaranas* of Parque Nacional do Viruá (VNP) in Roraima State, 193 species (Costa *et al.* 2016); 3) clear-water *igapó* of Tapajós River of Pará State, 49 spp. (Crema 2017); 4) wetlands in the savanna biome, gallery forest (516 spp.), *campo limpo úmido* (42 spp.), *campo úmido* (108 spp.), *campo sujo com murundus* (16 spp.), *campo limpo de murundus* (40 spp.), *campo com murundus* (59 spp.), *vereda* (65 spp.) of the Distrito Federal (Chacon *et al.* 2015); 5) several wetlands in the Pantanal of Mato Grosso and Mato Grosso do Sul States, 214 spp. (Pott & Pott 1997); 6) wetlands in the savanna biome, *vereda*, 201 ssp. (Silva *et al.* 2018) and 7) water bodies of semi-arid Caatinga biome of Paraiba State, 121 spp. (Torres *et al.* 2016).

where the arboreal component dominates species richness increases, and the canopy becomes stratified (Fig. 2A).

Black-water floodplain forests (*igapó*) with a distinct zonation of tree species along the flood-level gradient dominate along the main-river channel and oxbow lakes of the Uatumã river (approximately 25 m a.s.l; Targhetta *et al.* 2015). The low *igapó* is flooded by up to 265 days per year on average and the alternation between the terrestrial and aquatic phase determines the dynamics of the annual herbaceous plants. With increasing topography, *igapó* forests

become more complex and the herbaceous component becomes predominantly composed of perennial species restricted to the forest understory. At intermediate and high topographies flooding duration ranges from about 100 to 150 days and less than 50 days per year, respectively (Fig. 2B). The vegetation of the black-water *igapó* of the Uatumã river was subject to several disturbances due to the construction of the Balbina dam, whose consequences are summarized in Assahira *et al.* 2017; Lobo *et al.* 2019 and Rocha *et al.* 2019.
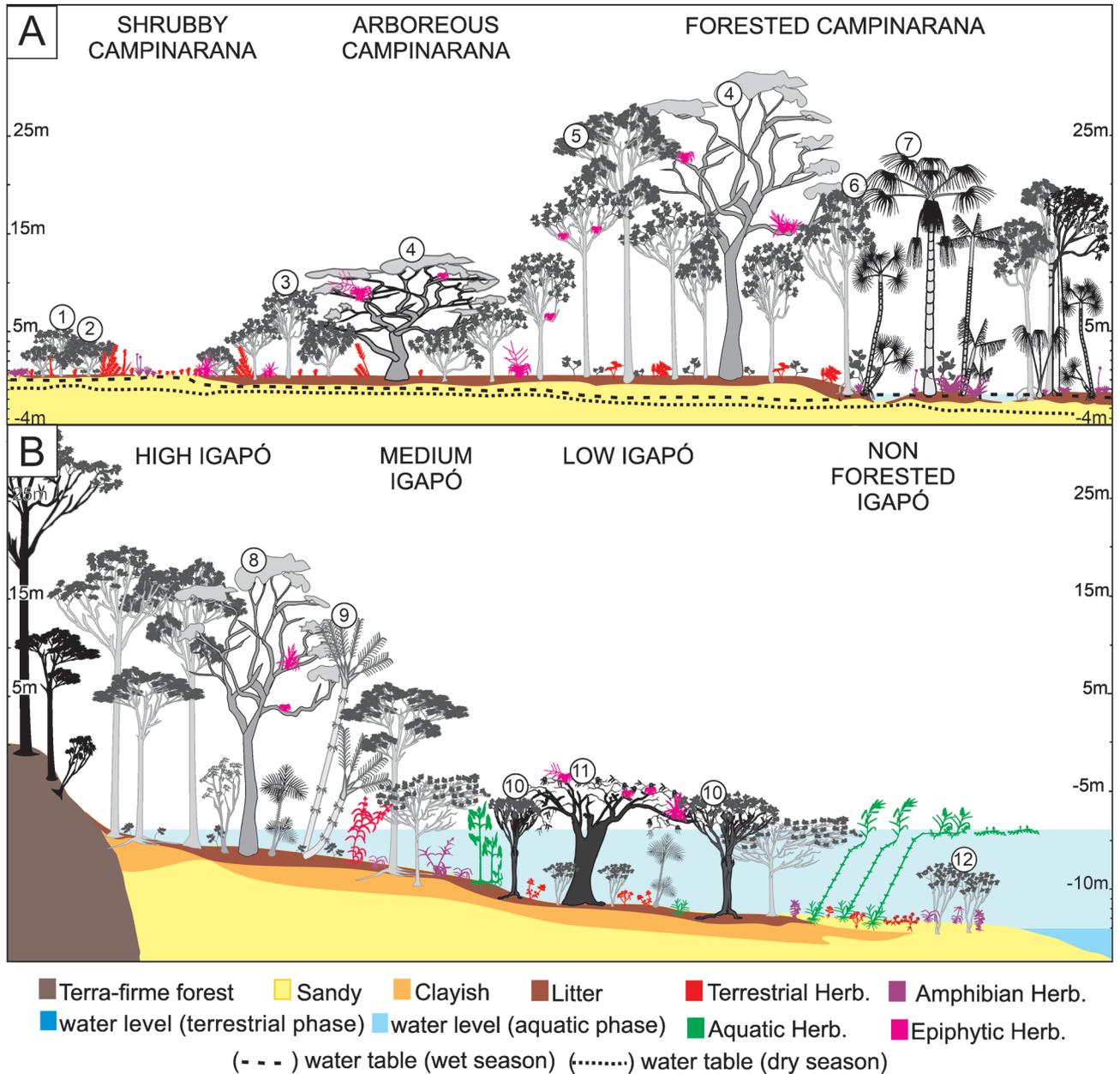
Figure 2. Generic schematic profiles of vegetation structure and some examples of herbaceous life forms in the collection areas. **A**) *Campinaranas* and **B**) *Igapós*. The length and sequence of the physiognomies, as well as the distance from the water table in the dry / rainy season (in the *campinaranas*) and the water levels in the terrestrial / aquatic phase vary from area to area both in the USDR and in JNP. Characteristic woody species: 1. *Humiria balsamifera*; 2. *Ilex divaricata*; 3. *Pradosia schomburgkiana*; 4. *Aldina heterophylla*; 5. *Sterigmapetalum plumbeum*; 6. *Tovomita calophyllophylla*; 7. *Mauritia carana*; 8. *Aldina latifolia*; 9. *Astrocaryum jauari*; 10. *Eschweilera tenuifolia*; 11. *Macrolobium acaciifolium*; 12. *Eugenia inundata*.

Both black-water *igapó* and *campinarana* ecosystems are characterized by nutrient-poor soils of comparatively high acidity. Soil texture in the *campinarana* plots is homogeneously sandy, whereas the *igapó* plots had more variable textures, with predominance of silt and clay soils (Targhetta *et al.* 2015). Despite both *campinarana* and *igapó* soils being poor in nutrients, exchangeable bases, C, N, P, K in the *igapó* were two to three-fold higher than those in the *campinarana* and 10-fold for Fe (Targhetta *et al.* 2015).

Parque Nacional do Jaú - JNP

The JNP is located 220 km northwest of the city of Manaus in the municipalities of Barcelos and Novo Airão of the Amazonas State, and covers an area of approximately 22,720 km^2. The PELD site is established at the coordinates 01°54'-01°57' S and 61°27'-61°28' W (Fig. 1). Mean annual temperature is 26.7 °C, and mean annual precipitation amounts to 2,300 mm. The rainy season occurs from December to May and the dry season from June to September. The flooding cycle is monomodal, with a mean annual amplitude of 8.17 m; highest water levels occur in June and July, and lowest in October and November (Ferreira 2000). The soil is derived from ancient tertiary sediments, with high levels of kaolinitic clay and large areas covered by white sands (podzols) (Junk *et al.* 2015).

The JNP is also mostly covered by *terra-firme* forest with some isolated *campinaranas*. As in the USDR, *campinaranas* present a heterogeneous vegetation mosaic. In open areas, shrubs and herbs predominate, particularly *Everardia montana* Ridl., *Duckea squarrosa* (Willd. ex Link) Maguire and many species of Eriocaulaceae, Xyridaceae, Lentibulariaceae, among others. The forest physiognomies alternate between stratified forests with emergent trees of approximately 20 m height to very dense forests with trees reaching heights of 5-8 m (Fig. 2A).

Igapó forests dominate along the Jaú river and show the typical zonation of tree species along the flood-level gradient. The lowest levels of the flood-level gradient are covered with monodominant formations of the tree *Eschweilera tenuifolia* (O.Berg) Miers. With increasing topography, tree diversity increases to up to 70 species per hectare (> 10 cm diameter at breast height) (Fig. 2B). The herbaceous component predominates at the lower topographies, being restricted to the forest understory at higher topographic positions. When compared to the *igapó* of the USDR, it presents higher richness of tree species, however during the last decades it has been suffering from large-scale anthropogenic fires (PELD MAUA data unpublished).

Field sampling design

In the *igapó* plots have been established in both forested and non-forested areas. In forested areas, three 1-ha plots were installed along the flood-level gradient on: (1) high (<50 days of inundation year^{-1}), (2) intermediate (100-150 days of inundation year^{-1}), and (3) low topographies (>265 days of inundation year^{-1}) (Lobo *et al.* 2019). Within each plot three transects of 25 x 2 m (50 m^2) were established to inventory all herbaceous plants in densely forested areas. For the inventory of herbaceous vegetation in non-forested areas, nine transects of 25 x 2 m (50 m^2) were installed. To inventory herbaceous plants of the hydromorphic *campinaranas* in the USDR (Targhetta *et al.* 2015), nine plots of 5 x 5 m (25 m^2) were installed. Distances between plots in the same ecosystem ranged from 0.5–3.5 km, while average distance of plots between *igapó* and *campinarana* was approximately 6 km. Herbaceous plants were identified to the lowest taxonomic level possible. The scientific names were verified according to Flora do Brasil 2020 (Forzza *et al.* 2020) following the APG IV (Angiosperm Phylogeny Group, 2009) system by the R 3.6.1 program (R Development Core Team, 2020) and the *flora* package (https://CRAN.R-project.org/package=flora). Fertile specimens were deposited at the INPA Herbarium, and sterile specimens were archived at the herbarium of the INPA-MAUA Group. For the analysis of species composition, we used the presence of species per plot, ecosystem (*igapó* and *campinarana*) and site (JNP and USDR).

Potential Distribution Range - PDR

For the analysis of species distribution, we selected the five most frequent species on plot level in each inventoried *igapó* and *campinarana* at each site and five species that were found in at least two of the four inventoried sites (total of 25 herbaceous species). Georeferenced data gathered from the examination of specimens from CRIA herbaria (CRIA 2020) and GBIF (Global Biodiversity Information Facility, 2020) were used. The data were standardized, and duplicates excluded.

To estimate and map the potential distribution of these species we started with gridded data sets at 10 km × 10 km resolution of 41 variables, including bioclimatic variables, vegetation cover, and soil nutrients as predictors (Tab. S1 in supplementary material). A principal component analysis (PCA) was performed with these variables to eliminate collinearity between predictor variables and for controlling the overfitting of models (Guisan & Zimmermann 2000; Dormann *et al.* 2013). The PCA axes that added up 90 % of the variation within the Neotropical region were used as predictor variables. We utilized the rasterPCA function of the RStoolbox package (Leutner *et al.* 2017) in R 4.2.0 (R Development Core Team 2020).

We used eight algorithms offered in the BIOMOD2 package (Thuiller *et al.* 2019) to generate SDMs, categorized as 1) one regression method (Generalized Linear Models - GLM (McCullagh & Nelder 1989)); 2) four machine-learning or complex methods (Artificial Neural Networks – ANN (Hopfield 1982), Generalized Boosted Models - GBM (Friedman *et al.* 2000), Maximum Entropy - MaxEnt (Phillips *et al.* 2006) and Random Forests – RF (Breiman 1999)); 3) two classification methods (Classification Tree Analysis - CTA (Breiman *et al.* 1984), Flexible Discriminant Analysis - FDA (Hastie *et al.* 1994)); 4) Surface Range Envelope – SRE

model, very similar to Bioclim (Jiguet *et al.* 2011). The R script was prepared by Pedro V. Eisenlohr (https://github.com/pedroeisenlohr/niche_modelling).

Because our data consisted of species presence records only, we generated pseudo-absence (background) points, sampled across the study area. When fitting models CTA, RF, and GBM we generated as many pseudo-absence points as our species distribution records, whereas for models ANN, SRE, FDA, GLM, and MAXENT we used 1,000 pseudo-absence points (Barbet-Massin *et al.* 2012). In both cases, we produced 10 replicates of pseudoabsence data and used 70 % of the species presence data to fit models and 30 % to assess model accuracy, repeating this process 10 times.

As suggested by Brown & Yoder (2015) the true skill statistic (TSS) (Allouche *et al.* 2006) was used as a filter for algorithms with number of occurrences above nine. TSS values range from –1 to 1, where 0 indicates no predictive power. The algorithms with TSS ≤ 0.4 were excluded from the final consensus model, because of their low accuracy (Allouche *et al.* 2006; Zhang *et al.* 2015). The remaining algorithms were used to produce a combined projection or consensus map (Araújo & New 2007). This technique consists in generating a consensus model, based on binary maps of each algorithm chosen, where areas of high suitability will be those that most models have indicated as being prone to the occurrence of the species (Giannini *et al.* 2012).

To quantify the uncertainty among the eight different models and the consensus models we calculated the mean, standard deviation and coefficient of the uncertainty measures that BIOMOD2 provides: sensitivity–probability that a test result will be positive when the species is present (true positive rate, expressed as a percentage); specificity– probability that a test result will be negative when the species is not present (true negative rate, expressed as a percentage); and the cutoff point (Thuiller *et al.* 2019). We classified the consensus model generated for each species based on the values of mean sensitivity and sensitivity standard deviation (SD). Better-performing methods have sensitivities close to one hundred. We assigned an overall category of robustness or reliability adapted from Ochoa-Ochoa *et al.* (2016): poor (sensitivity ≤50 or SD ≥ 50), medium (sensitivity ≥50 with SD ≤ 45), good (sensitivity ≥70 with SD ≤ 30) and optimum (sensitivity ≥90 with SD ≤ 30).

We used the consensus map to generate the final potential distribution range (PDR) map. The PDR had a range of values from 0 to 100 which were regrouped into four classes of potential habitats: "high potential" (>60), "good potential" (40-60), "moderate potential" (20-40) and "least potential" (<20). Potential distribution maps were created by ArcGIS Software 9.0 (Esri 2013) for the Neotropical region, Amazon basin, JNP, and USDR. We used the data collected in JNP and USDR (which did not enter the model) to verify that the consensus model was also able to predict the occurrence of the selected species in these protected areas.

Species Similarity to other Brazilian Wetlands

To test the hypothesis that *campinaranas* share fewer species with the black-water *igapó* surveyed (JNP and USDR) and other Brazilian wetland ecosystems, we compared our floristic data with herbaceous species inventories (Junk & Piedade 1993; Silva *et al.* 2018; Chacon *et al.* 2015; Pott & Pott 1997; Costa *et al.* 2016; Torres *et al.* 2016; Crema 2017) from other locations (Fig. 1, Tab. 1), after updating the synonyms by Flora do Brasil 2020 (Forzza *et al.* 2020). We calculated the level of similarity using Jaccard's index $J = c/(a + b - c)$, where a is the number of species in region 1, b is the number of species in region 2, and c is the number of shared species between both regions. J-index ranges between zero and one, indicating complete dissimilarity and similarity, respectively. To recognize characteristic floristic groups, we constructed a phenogram using an unweighted pair-group procedure (UPGMA) from the similarity matrix. UPGMA uses arithmetical averaging between the similarity indices of different groups. For cluster recognition in the phenogram, we conducted bootstrapping on the species-area matrix, using 5000 interactions and recomputing Jaccard's index among different sites in each calculation.

Results

A total of 98 aquatic herbaceous species were found belonging to 32 families (Tab. S2 in supplementary material). At JNP we recorded 33 species in the *igapó* and 10 species in the *campinarana*, being four of them present in *campinarana* and *igapó* (*Everardia montana*, *Miconia subsimplex*, *Ischnosiphon cannoideus* and *Trichomanes martiusii*. In the USDR we recorded 30 species in the *igapó* and 34 species in the *campinarana*, with no species found in the two ecosystems. The *igapós* of JNP and USDR shared four species (*Utricularia foliosa*, *Oryza grandiglumis*, *Montrichardia arborescens* and *Tassadia trailiana*). Only *Trichomanes martiusii* occurred in the *campinaranas* of both study regions and in the *igapó* of JNP (Tab. S2 in supplementary material). Thus, we selected the species *E. montana*, *M. subsimplex*, *U. foliosa*, *O. grandiglumis* and *T. martiusii* for the elaboration of PDRs.

Overall, the families with the highest number of species were Cyperaceae (17 spp.), Poaceae (14 spp.), Orchidaceae (seven spp.), Marantaceae (six spp.) and Eriocaulaceae (five spp.). In the *campinaranas* of JNP, Xiridaceae was the most speciose family with 3 spp. and the Orchidaceae (seven spp.) in the USDR. Cyperaceae (eight spp.) and Poaceae (eight spp.) were the most species-rich families at JNP and USDR, respectively. Four species were listed in the IUCN Red List of Threatened Species (IUCN 2020), three being classified as LC (least-concern), *Alternanthera paronychioides*, *Utricularia foliosa*, *Schizaea elegans*, and *Voyria aphylla* as DD (data deficient). Our inventory includes the first record of *Evolvulus genistoides* in the Amazon region, which, according

to Flora do Brasil 2020 (Forzza *et al.* 2020), occurs in the States of Espírito Santo, Minas Gerais and Rio de Janeiro. No species is considered invasive according to the Brazil National Invasive Alien Species Database (Instituto Hórus, institutohorus.org.br). *Oryza rufipogon* with origin from Asia and *Digitaria ciliaris*, originally from Asia and Africa are considered naturalized according to the Brazilian Flora.

Few species were shared among JNP and USDR and other Brazilian herbaceous wetland inventories (Pott & Pott 1997; Junk & Piedade 1993; Chacon *et al.* 2015; Costa *et al.* 2016;

Silva *et al.* 2018). The *igapó* of JNP showed flora composition closely related with the Central Amazonian *várzea* and the *campinarana* of the Parque Nacional do Viruá (VNP) with eight and seven species in common, respectively. However, the *campinarana* of the JNP only shared three species with the same ecosystem at the VNP. The *igapó* at USDR had 19 species found in the *várzea* and eight in the *campinarana* of the VNP, while the *campinarana* of the USDR shared only two species with the same ecosystem at the VNP (Tab. 1).

Table 1. Presence of herbaceous species in the wetlands (campinarana and igapó) inventoried in Parque Nacional d Jaú (JC= Jaú *campinarana*, JI= Jaú *igapó*) and Reserva de Desenvolvimento Sustentável Uatumã (UC= *Uatumã campinarana*, UI= *Uatumã igapó*) and other Brazilian wetland inventories: 1) Amazonian *várzea* floodplains (Junk & Piedade 1993); 2) *campinaranas* of Parque Nacional do Viruá (Costa *et al.* 2016); 3) clear-water *igapó* of Tapajos River (Crema 2017); 4) wetlands in the savanna biome, gallery forests (4A), *campo limpo úmido* (4B), *campo úmido* (4C), *campo sujo com murundus* (4D), *campo limpo de murundus* (4E), *campo com murundus* (4F) and *vereda* (4G) (Chacon *et al.* 2015); 5) Pantanal (Pott & Pott 1997); 6) wetlands in the savanna biome (Cerrado), *vereda* (Silva *et al.* 2018); 7) semi-arid Caatinga (Torres *et al.* 2016).

Species	JI	JC	UI	UC	1	2	3	4A	4B	4C	4D	4E	4F	4G	5	6	7
Abolboda grandis Griseb.		X															
Aciotis ornata (Miq.) Gleason	X																
Acroceras zizanioides (Kunth) Dandy			X		X										X		
Actinostachys pennula (Sw.) Hook.				X													
Aechmea huebneri Harms				X													
Alternanthera paronychioides A.St.-Hil.			X		X												
Bacopa egensis (Poepp.) Pennell			X			X									X		
Bifrenaria longicornis Lindl.				X													
Brassavola martiana Lindl.				X													
Bromelia tubulosa L.B.Sm.				X													
Bulbostylis junciformis (Kunth) C.B.Clarke				X		X										X	
Catasetum ciliatum Barb.Rodr.				X													
Comanthera kegeliana (Körn.) Moldenke				X													
Croton dissectistipulatus Secco				X													
Cuphea annulata Koehne				X													
Cyperus aggregatus (Willd.) Endl.			X		X	X											
Cyperus distans L.			X		X												X
Digitaria ciliaris (Retz.) Koeler			X		X												
Diplasia karatifolia Rich. ex Pers.	X																
Duckea squarrosa (Willd. ex Link) Maguire		X				X											
Echinochloa polystachya (Kunth) Hitchc.			X		X	X									X		X
Eleocharis minima Kunth	X					X	X								X		
Encyclia mapuerae (Huber) Brade & Pabst				X													
Epidendrum orchidiflorum (Salzm.) Lindl.				X		X											
Erechtites hieracifolius (L.) Raf. ex DC.			X		X											X	X
Euploca filiformis (Lehm.) J.I.M.Melo & Semir			X		X												
Everardia montana Ridl.	X	X															
Evolvulus genistoides Oosstr.				X													
Fimbristylis aestivalis Vahl			X														
Fimbristylis miliacea (L.) Vahl			X		X												
Fimbristylis vahlii (Lam.) Link			X			X											X
Goeppertia acuminata (Steyerm.) Borchs. & S. Suárez				X													
Guadua ciliata Londoño & Davidse	X																
Hymenachne amplexicaulis (Rudge) Nees	X				X	X									X		X
Hypolytrum longifolium (Rich.) Nees	X																
Hyptis atrorubens Poit.	X																
Hyptis parkeri Benth.			X		X												
Ipomoea rubens Choisy	X														X		

Table 1. Cont.

Species	JI	JC	UI	UC	1	2	3	4A	4B	4C	4D	4E	4F	4G	5	6	7
Irlbachia poeppigii (Griseb.) L.Cobb & Maas	X																
Ischnosiphon cannoideus L.Andersson	X	X															
Ischnosiphon leucophaeus (Poepp. & Endl.) Körn.				X													
Ischnosiphon polyphyllus (Poepp. & Endl.) Körn.	X				X												
Justicia comata (L.) Lam.			X		X												
Lagenocarpus rigidus Nees			X			X				X	X			X		X	
Lepidaploa arenaria (Mart. ex DC.) H.Rob.				X													
Lindsaea schomburgkii Klotzsch				X													
Ludwigia erecta (L.) H.Hara			X														X
Ludwigia hyssopifolia (G.Don) Exell	X					X											
Miconia calvescens DC.	X							X									
Miconia subsimplex Pilg.	X	X															
Montrichardia arborescens (L.) Schott	X		X		X	X	X										
Neoregelia eleutheropetala (Ule) L.B.Sm.				X													
Olyra longifolia Kunth	X																
Oryza glumaepatula Steud.	X					X									X		
Oryza grandiglumis (Döll) Prod.	X		X		X												
Oryza rufipogon Griff.	X				X	X											
Oserya perpusilla (Went) P.Royen	X																
Paepalanthus fasciculatus (Rottb.) Kunth				X													
Pariana radiciflora Sagot ex Döll				X													
Paspalum multicaule Poir.			X					X								X	
Paspalum pulchellum Kunth			X														
Paspalum repens P.J.Bergius			X		X	X	X								X		
Piriqueta cistoides (L.) Griseb.			X		X												
Pleurostachys sparsiflora Kunth				X													
Prosthechea fragrans (Sw.) W.E.Higgins				X													
Psychotria stipulosa Müll.Arg.	X																
Reimarochloa brasiliensis (Spreng.) Hitchc.			X		X												
Rhynchospora amazonica Poepp. & Kunth	X																
Rhynchospora divaricata (Ham.) M.T.Strong	X																
Sagittaria guayanensis Kunth			X			X									X		
Saxofridericia aculeata Körn.				X													
Schizaea elegans (Vahl) Sw.				X													
Scleria gaertneri Raddi	X				X	X									X		
Scleria microcarpa Nees ex Kunth			X		X												
Scleria secans (L.) Urb.	X				X												
Sobralia granitica G.A.Romero & Carnevali				X													
Syngonanthus longipes Gleason	X					X											
Syngonanthus setifolius Hensold		X															
Syngonanthus williamsii (Moldenke) Hensold		X															
Tassadia berteroana (Spreng.) W.D.Stevens			X			X											
Tassadia trailiana (Benth.) Fontella	X	X															
Tillandsia adpressiflora Mez				X													
Tococa subciliata (DC.) Triana	X																
Trichomanes martiusii C.Presl	X	X			X												
Trichomanes pinnatum Hedw.					X												
Utricularia foliosa L.	X		X		X	X	X								X		
Utricularia gibba L.	X				X	X									X		
Utricularia olivacea C.Wright ex Griseb.	X				X												
Voyria aphylla (Jacq.) Pers.					X			X									
Voyria caerulea Aubl.					X												
Wedelia calycina Rich.			X		X												
Xyris involucrata Nees		X				X											
Xyris subuniflora Malme		X				X											

The floristic similarity (100 × *J*) between wetland sites distributed throughout Brazil ranged from 0 to 10.8 % (Tab. 2) indicating low proportion of shared species. The highest *J*-values were obtained between *vereda* and *campo com murundus* of the Distrito Federal. In the UPGMA analysis, *campinaranas* of VNJ and phytophysiognomies of Cerrado (Distrito Federal, Brazil) grouped into one cluster, while others Amazonian ecosystems, Pantanal and Caatinga grouped into the second cluster. The *campinarana* of USDR appeared separated from these groups (Fig. S1 in supplementary material).

For the 25 species chosen to PDRs at JNP and USDR the data available in digital herbaria (Specieslink and GBIF) showed few previous records of collection in these two sites and surroundings (Figs. 3, 4, 5). Based on the record data, distribution of the species that occurred in the *campinaranas* of JNP was restricted to the Amazon Basin, while the species of the *igapó* from this site showed a much wider Neotropical distribution. On the other hand, species from the *campinarana* and *igapó* of the USDR showed a wide geographic distribution across the Neotropics (Figs. 3-5).

The sum of 11 axes of the PCA captured 90.4 % of the data variation (Tab. S3 in supplementary material). The number of records varied between 13 and 829 per species and all consensus models were considered good or optimum (Tab. S4 in supplementary material). The algorithm with best values of TSS were ANN and GBM, whilst the SRE showed the worst values. The algorithms used for the consensus model of each species can be consulted in Table S4 in supplementary material.

The PDRs for the Neotropical region were consistent with the patterns shown from data records, just expanding the probability of occurrence around these data records. At the regional level, the SDMs projected contrasting patterns of distribution for *igapó* and *campinarana* herbaceous species. The potential distribution range of the USDR *igapó* species in the Amazon Basin was larger mainly along the major rivers, such as the Amazon and Branco (Fig. 4A), while those from *campinarana* showed a wide distribution pattern. Two species of the *igapó* from JNP were widely distributed in the Amazon Basin, while the other three were mostly restricted to the large rivers (Fig. 4B). In contrast, the *campinarana* species had a wider distributional range in the Northern part of the Amazon Basin (Fig. 3A, B). *Miconia subsimplex* and *Alternanthera paronychioides* had a much broader potential distributional range across the Amazon Basin than the area with currently collected occurrences, while the other *campinarana* species had their potential distribution only narrowly expanded around the current collection areas.

The potential distribution of the selected species in the protected areas was quite variable. Eight of the 10 species at the USDR had a potential distribution of more than 60 %, while the other two species had a limited occurrence around 20 % for the reserve (Figs. 3A and 4A). On the other hand, the species that occurred at JNP had a high potential distribution in small areas within the protected area (Fig. 4B). For the species that occurred in more than one ecosystem and/or study site, the potential distributional range in the reserves was over 40 % and quite variable (Fig. 5). The consensus models predicted well the occurrence of 88 % (22 out of 25) of the species in the inventoried protected areas.

Table 2. Jaccard Similarity Index (J*100) between the wetlands (*campinarana* and *igapó*) inventoried in Parque Nacional do Jaú (JC= Jaú *campinarana*, JI= Jaú *igapó*) and Reserva de Desenvolvimento Sustentável Uatumã (UC= Uatumã *campinarana*, UI= Uatumã *igapó*) and other Brazilian wetland inventories: 1) Amazonian *várzea* floodplains (Junk & Piedade 1993); 2) *campinaranas* of Parque Nacional do Viruá (Costa *et al.* 2016); 3) clear-water *igapó* of Tapajos River (Crema 2017); 4) wetlands in the savanna biome, gallery forests (4A), *campo limpo úmido* (4B), *campo úmido* (4C), *campo sujo com murundus* (4D), *campo limpo de murundus* (4E), *campo com murundus* (4F) and *vereda* (4G) (Chacon *et al.* 2015); 5) Pantanal (Pott & Pott 1997); 6) wetlands in the savanna biome (Cerrado), *vereda* (Silva *et al.* 2018); 7) semi-arid Caatinga (Torres *et al.* 2016).

	JI	JC	UI	UC	1	2	3	4A	4B	4C	4D	4E	4F	4G	5	6	7
JI		10.26	6.90	1.61	3.20	3.20	8.11	0.37	0.00	0.00	0.00	0.00	0.00	0.00	2.92	0.00	0.65
JC	10.26		0.00	2.56	0.00	1.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
UI	6.90	0.00		0.00	7.12	3.74	7.04	0.18	0.00	0.74	2.27	0.00	0.00	1.08	2.53	1.32	3.45
UC	1.61	2.56	0.00		0.00	0.90	0.00	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.43	0.00
1	3.20	0.00	7.12	0.00		3.69	5.92	0.65	0.00	0.55	0.00	0.34	0.32	0.31	10.82	1.10	9.57
2	3.20	1.50	3.74	0.90	3.69		9.09	0.85	0.43	2.03	0.48	0.87	1.61	4.88	7.67	10.06	2.28
3	8.11	0.00	7.04	0.00	5.92	9.09		0.36	0.00	0.65	0.00	0.00	0.00	0.90	12.02	0.81	3.07
4A	0.37	0.00	0.18	0.18	0.65	0.85	0.36		2.57	3.65	0.76	1.65	1.59	4.31	0.69	3.17	0.31
4B	0.00	0.00	0.00	0.00	0.00	0.43	0.00	2.57		1.35	3.57	5.13	5.21	5.94	0.00	4.29	0.00
4C	0.00	0.00	0.74	0.00	0.55	2.03	0.65	3.65	1.35		2.48	4.96	8.44	12.34	0.00	5.82	0.00
4D	0.00	0.00	2.27	0.00	0.00	0.48	0.00	0.76	3.57	2.48		0.00	1.35	3.85	0.00	1.40	0.00
4E	0.00	0.00	0.00	0.00	0.34	0.87	0.00	1.65	5.13	4.96	0.00		2.06	3.96	0.40	2.55	0.00
4F	0.00	0.00	0.00	0.00	0.32	1.61	0.00	1.59	5.21	8.44	1.35	2.06		10.71	0.00	5.69	0.56
4G	0.00	0.00	1.08	0.00	0.31	4.88	0.90	4.31	5.94	12.34	3.85	3.96	10.71		1.09	8.13	0.00
5	2.92	0.00	2.53	0.00	10.82	7.67	12.02	0.69	0.00	0.00	0.00	0.40	0.00	1.09		1.47	4.69
6	0.00	0.00	1.32	0.43	1.10	10.06	0.81	3.17	4.29	5.82	1.40	2.55	5.69	8.13	1.47		0.63
7	0.65	0.00	3.45	0.00	9.57	2.28	3.07	0.31	0.00	0.00	0.00	0.00	0.56	0.00	4.69	0.63	
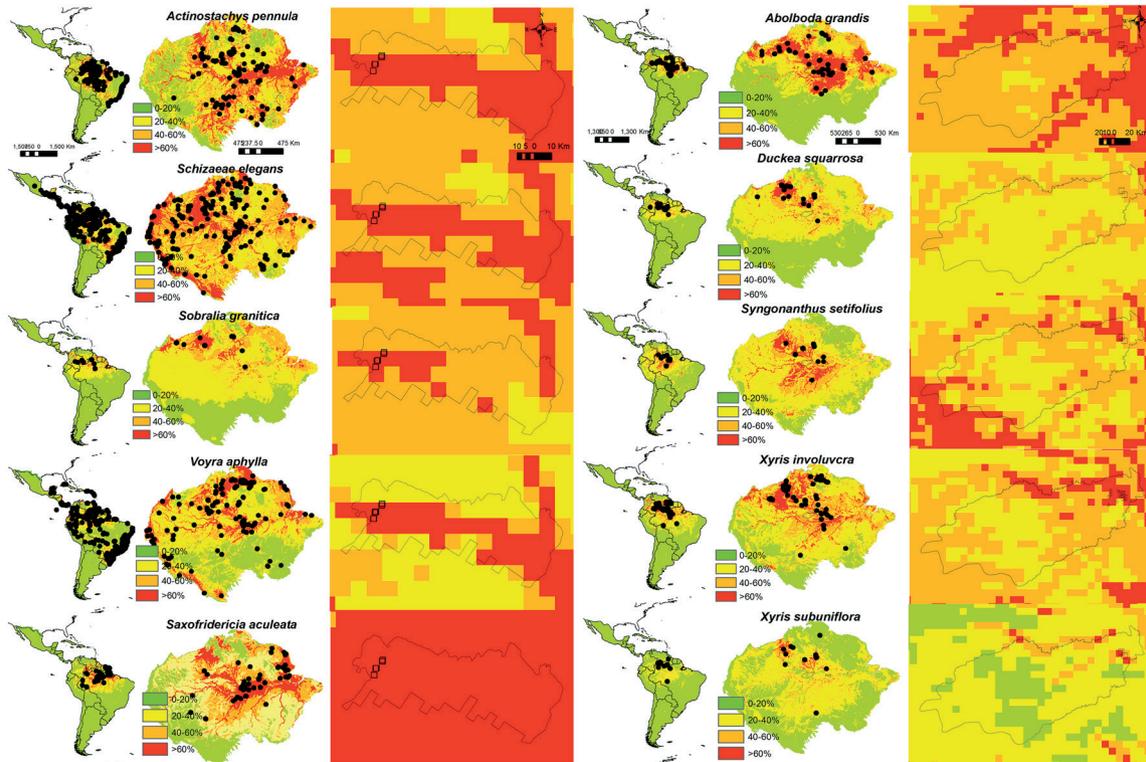
Figure 3. Current (black dots) and potential (colored area) distribution of the most frequent herbaceous plants of the *campinarana* ecosystem in **A**) the Reserva de Desenvolvimento Sustentável Uatumã (indicated by the shape in the high-resolution maps). **B**) the Parque Nacional do Jaú (indicated by the shape in the high-resolution maps).
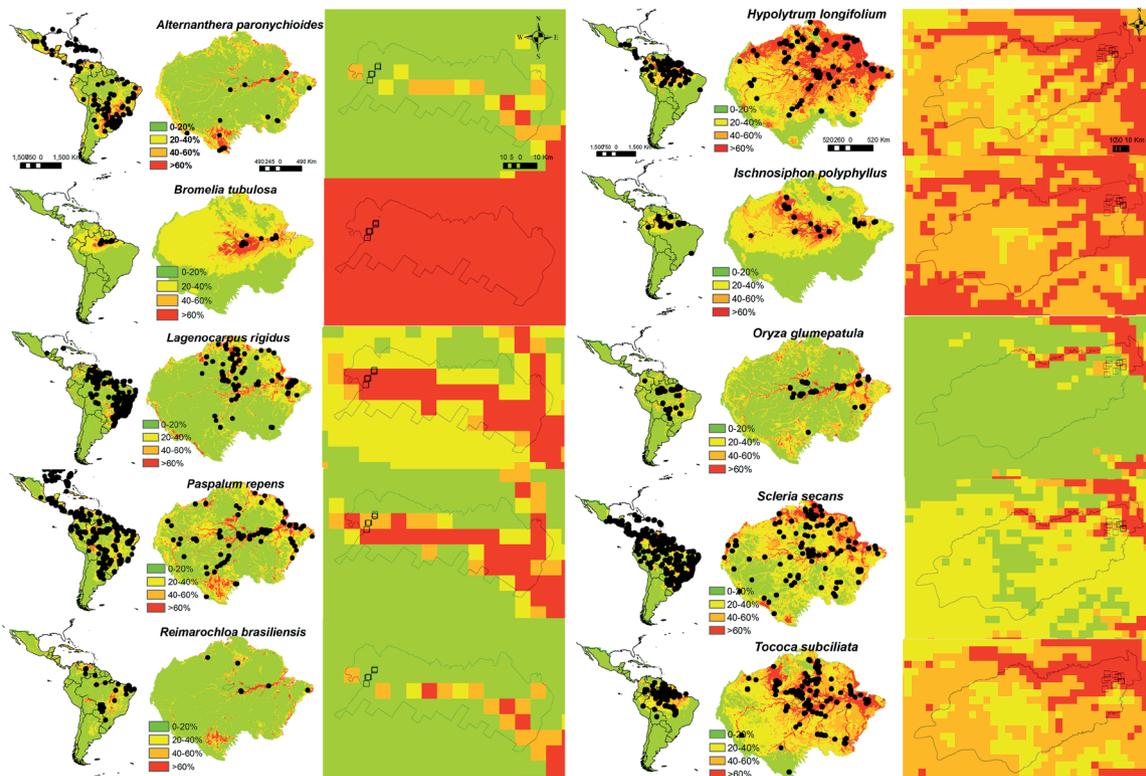
Figure 4. Current (black dots) and potential (colored area) distribution of the most frequent herbaceous plants of the *igapó* ecosystem in: **A**) the Reserva de Desenvolvimento Sustentável Uatumã (indicated by the shape in the high-resolution maps); **B**) the Parque Nacional do Jaú (indicated by the shape in the high-resolution maps).
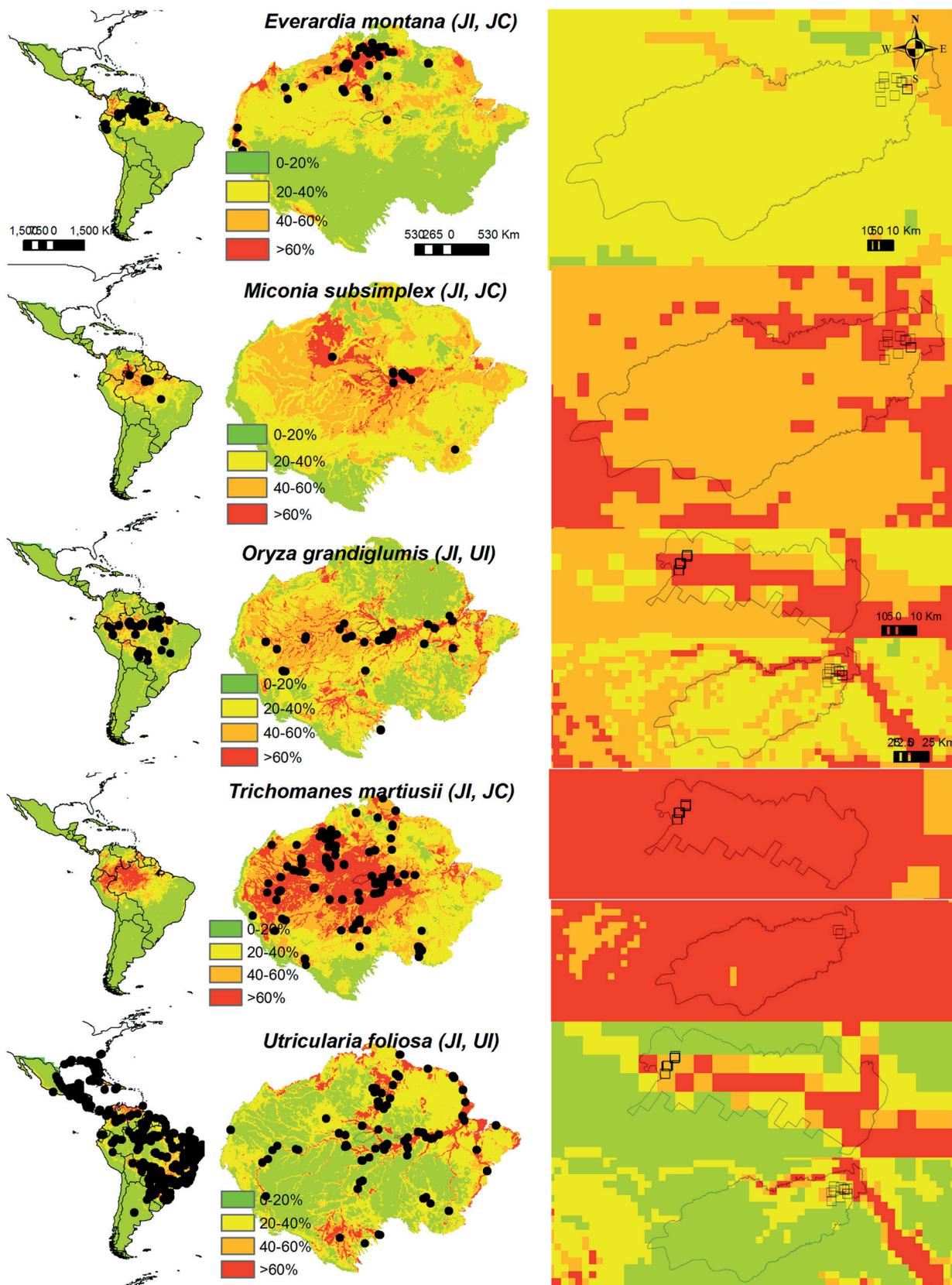
Figure 5. Current (black dots) and potential (colored area) distribution of the most frequent herbaceous that occurred in more than one sample in the *campinarana* and *igapó* wetlands of the JNP and USDR (shapes indicated in the high-resolution maps); JC= Jaú *campinarana*, JI= Jaú *igapó*, UI= Uatumã *igapó*.

Discussion

The comparison of our species list with those of other Brazilian wetlands revealed a very low floristic similarity. With 29 species, Amazonian *várzea* (Junk & Piedade 1993) presented the highest number of species in common with our inventories, being most similar to the *igapó* floodplains of both study sites. This might be related to mutual adaptation of species to monomodal flood pulses of high amplitudes. *Campinaranas* of the VNP (Costa *et al.* 2016) had 18 species in shared with the PELD-MAUA *campinarana* sites, showing a higher similarity with the same ecosystem at both sites. In general, the *várzea* floodplain of Central Amazonia has a higher richness and diversity of herbaceous aquatic plants compared to the *igapó* (Lopes *et al.* 2014; 2019) and *campinaranas* (Costa *et al.* 2016). Both the *igapós* and *campinaranas* have other stressors such as low nutritional quality of soils and anoxic or hypoxic conditions induced by flooding or waterlogging (Anderson 1981; Wittmann *et al.* 2010; Junk *et al.* 2015; Targhetta *et al.* 2015), likely contributing to the low observed species richness. Although many species of the *campinaranas* are not resistant to prolonged flooding (Targhetta *et al.* 2015), the oligotrophic conditions make aquatic herbaceous species richness of *igapó* and *campinarana* comparable to those of other extreme environments, such as those found in arid and semiarid ecosystems of the dry forest (Caatinga) of Northeastern Brazil (Henry-Silva *et al.* 2010).

In the upper Negro river basin, several studies indicated high floristic similarity between the arboreal flora of the *igapós* and *campinaranas* (Kubitzki 1989; Daly & Prance 1989; Damasco *et al.* 2013). This similarity may be linked to the fact that the vegetation upon nutrient-poor soils is strongly floristically related (Guillaumet 1987; Tuomisto *et al.* 1995). This is not what we found. Despite occurring in extremely nutrient-poor and acidic soils (Adeney *et al.* 2016), the studied *igapós* and *campinaranas* showed an extremely low floristic similarity of herbaceous plants even at the family level. Similar results were described by Targhetta *et al.* (2015) for the arboreal vegetation, which observed an extremely low floristic similarity between the *campinarana* and *igapó* forests in the USDR. Sand content and other physiochemical soil properties might vary at macro- and microscales and likely have a strong effect on vegetation structure of white-sand ecosystems (Demarchi *et al.* 2018). Because of the geographic isolation in a *terra-firme* matrix, *campinaranas* hardly recover species that have once lost (Álvarez-Alonso *et al.* 2013).

The performance of the eight tested models varied, however results in terms of ROC sensitivity were similar, except for the SRE and GBM, which performed lower than the other tested algorithms. The Maxent is often reported as performing well with low sample sizes (Pearson 2007; Wisz *et al.* 2013). Besides Maxent, ANN, FDA and RF also provided good accuracy for all species with small numbers of samples (9-24). As a result, reliability of the consensus models was rated "good" and "optimum" by ROC sensitivity for all species. So far there is no single PDR model that perform well in all cases (Araújo & New 2007; Li & Wang 2013) and the use of consensus models encompassing different kinds of algorithms has been proved to be a successful strategy (Araújo & New, 2007; Loyola *et al.* 2012; Ochoa-Ochoa *et al.* 2016). This was also the case here, where the use of multi algorithms models were efficient in predicting the occurrence of aquatic herbaceous plants in the Neotropics and at regional (Amazon basin) level. On a more local scale, we were able to predict the distribution of 22 out of the 25 species when data point locations collected for each of these species in JNP and USDR were overlaid on the generated PDR maps.

The more restricted PDR of *campinarana* species compared to *igapó* species corroborates findings from other studies that investigated the distribution of different *campinarana* taxa. Amazonian white-sand areas are known for their elevated degree of both endemic tree (Fine *et al.* 2004; Guevara *et al.* 2016) and birds' species (Borges *et al.* 2001; Guilherme & Borges 2011). In the central Amazon, *campinaranas* are fragmented, small-sized, and insulated areas that are interspersed in dense Amazon rainforest (Adeney *et al.* 2016). In *campinaranas,* small variations in soil grain size and nutrient contents can influence species composition and distribution at local scales (Damasco *et al.* 2013; Demarchi *et al.* 2018); soils consist of almost pure quartz sands and concentration of important nutrients in the topsoil, such as K, Ca and Mg, is even lower than in *igapó* substrates (Targhetta *et al.* 2015). Due to the low water retention capacity of sandy soils, *campinarana* plant species undergo severe drought stress during the dry seasons (Junk *et al.* 2011), while soils turn into hydromorphic or even superficially inundated during the rainy seasons.

For *campinarana* trees species richness and forest stature, the water-saturation gradient is an important determinant, with the lowest richness and lowest stature occurring in areas of the longest saturation (Junk *et al.* 1989; Worbes 1997; Wittmann & Junk 2016). As arboreal competition is low and areas are relatively unshaded upon these waterlogged soils, they are the habitat where herbaceous species are most competitive (Junk *et al.* 2011). These areas, however, are mostly small and isolated and have reduced connectivity to other wetlands. Propagules from herbaceous species as such originate from the surrounding *terra-firme* forest, where their occurrence is rare or in very low population density or, more likely, have to be brought in by animals from distant areas (Macedo & Prance 1978). Like trees in the surrounding *campinarana* forest, it is thus most likely that most herbaceous species developed high degrees of endemism under these conditions, which is expressed in their narrow PDR within the Amazon basin.

Conversely, herbaceous species of *igapós* are widely distributed over the Neotropical region. River floodplains in the Amazon cover an area of more than 750,000 km^2 (Wittmann & Junk 2016). Although white-water and black-water river floodplains are known for their diverging flora for both, arboreal and herb communities (*i.e.*, Junk *et al.* 2012; 2015), most trees and herbaceous species from one ecosystem are known to occur with low population densities in the other. The river floodplains thus form highly connected corridors for plant dispersal, which is promoted through water currents, fish and/or other aquatic animals (Parolin *et al.* 2013; Geremew & Triest 2019). Some Amazonian rivers also originate from outside the Amazon basin, such as the Xingu and Tocantins rivers, come from the southern Brazilian Shield and Cerrado biome. For trees, rivers are important migration corridors that connect the Amazon, Orinoco, Cerrado and Atlantic rainforest domains (Wittmann *et al.* 2017). Herbaceous floodplain species often have very effective dispersal mechanisms through hydrochory and/or vegetative propagation (Piedade *et al.* 2019), and it is therefore not surprising that most of them had wide PDR across the entire Neotropical region.

The narrow PDR of many *campinarana* herbs provides one more argument for the urgent need of more inventories and the establishment of efficient conservation strategies in the unique Amazonian white-sand ecosystems. Some of the studied species are listed in the IUCN Red List (IUCN 2020) with DD, because do not have enough data to be even categorized. An urgent increase in areas of floristic inventories and sampling effort is necessary to generate information that subsidizes the risk assessment of many species, since several of them may be threatened due to anthropogenic disturbance in this vulnerable environment (Ferreira *et al.* 2013; Adeney *et al.* 2016).

Conclusion

The environmental variables were able to calculate the potential distribution with adequate ROC sensitivity percentage, efficiently predicting the occurrence of all analyzed species at the PELD-MAUA sites. The herbaceous species found in the *igapó* are widely distributed in the Neotropics, indicating an absence of barriers for their dispersal. Most *campinarana* species had their potential distribution more restricted to the Amazon Basin, probably due to the distribution of these ecosystems in isolated patches in the Amazonia rainforest matrix. There was a low floristic similarity of less than 11 % between the *campinarana* and *igapós* areas of the two PELD-MAUA sites, indicating that local environmental factors linked to hydrology, soils and disturbance events need to be better investigated to understand these local characteristics and to establish adequate management plans at local and regional levels.

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