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ADAPTA

Modeling of regional- and local-scale distribution of the genus *Montrichardia* Crueg. (Araceae)

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Abstract Knowledge of the environmental correlates of species' distributions is essential for understanding population dynamics, responses to environmental changes, biodiversity patterns, and the impacts of conservation plans. Here we examine how environment controls the distribution of the neotropical genus *Montrichardia* at regional and local spatial scales using species distribution models (SDMs) and logistic regression, respectively. *Montrichardia* is a genus of aquatic macrophytes with two species, *Montrichardia linifera* and *Montrichardia arborescens*, and is often an important component of flooded habitats. We find that for each species, altitude, precipitation and temperature of the driest month figure in the best performing SDMs as the most important factors controlling large-scale distributions, suggesting that the range limits of both species are climatically constrained by plant water-energy balance and cold intolerance. At small spatial scales, logistic regression models indicate the species partition types of aquatic habitat along local gradients of water pH, conductivity, and water transparency. In summary, a hierarchy of factors may control *Montrichardia* distribution from large to small spatial scales. While at large spatial scales, evolutionarily conserved climatic niches may control the range limits of the genus, at small spatial scales niche differentiation allows individual species to grow in environmentally distinct aquatic habitats.

Keywords Wetlands · Aquatic macrophytes · Species distribution modeling · Maxent · Amazon

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Introduction

Observed species distribution is biologically rooted in local demographic processes—survival, growth, reproduction and dispersal—that can vary widely on an environmentally heterogeneous landscape (Merow et al., 2014). As such, an understanding of the factors that control species distributions from local to regional spatial scales is of key importance in predicting species response to global climate change, local habitat restoration, and conservation programs (Chambers et al., 2008; Lopes et al., 2015, 2016). At regional scales, the spatial distribution of plants is often understood to be limited by climatic factors and geographical barriers that prevent migration (Sculthorpe, 1985; Santamaría, 2002). At local spatial scales, both abiotic (e.g., environmental constraints) and biotic processes (e.g., competition) have been shown to determine species distribution (Silvertown et al., 1999; Ferreira et al., 2015). In general, however, a mechanistic understanding of species distributions across scales is still lacking for most species (Wiens, 2011).

Improved understanding of the factors controlling the spatial distribution of freshwater aquatic macrophytes may be particularly enigmatic, largely because of their restriction to wetlands. For example, because of the patchy distribution of wetlands, the effects of dispersal limitation on the distribution of aquatic macrophytes might be expected to be greater relative to terrestrial plants, leading to more restricted distributions (Lopes et al., 2016). On the other hand, wetland habitats may facilitate dispersal, by both serving as migration corridors and buffering species from adverse climates by generating more favorable microclimates at local scales (Meave et al., 1991; Householder et al., 2015). In light of this, some researchers have tended to emphasize large range sizes and wide environmental tolerance of aquatic macrophytes (e.g., Candolle, 1855; Darwin, 1859; Good, 1953; Santamaría, 2002; Lopes & Piedade, 2014), while others have focused on patterns of rarity, endemicity, and ecological specificity (e.g., Weddell, 1872; Guppy, 1906; Chambers et al., 2008; Figueroa et al., 2013). The need to more precisely understand the environmental drivers of macrophyte distribution across spatial scales has been increasingly recognized, especially in light of potentially large economic and ecological repercussions of changes in macrophyte distribution, either as a result of climate change or human-mediated introduction (Piedade et al., 2010; Lopes et al., 2015).

The distribution and growth of aquatic vegetation have traditionally been understood in terms of plant ecophysiological response to local environmental conditions (such as light, temperature, nutrient availability, pH, salinity, water velocity, and water-level variation) (Barendregt & Bio, 2003; Neiff & Poi de Neiff, 2003; Piedade et al., 2010; Figueroa et al., 2013). While such studies have increased our understanding of ecological function and physiology of aquatic plants, a local-scale perspective is often not adequate to understand distribution pattern on regional scales. Consequently, species distribution modeling is increasingly employed to investigate the factors that control the broader range limits of aquatic macrophytes, especially with regard to regional scale applications, such as in the prediction of the invasive expansion of aquatic plants (Lehtonen, 2009; Loo et al., 2009). Because different factors may control species distribution at different spatial scales, a combined approach aimed at elucidating environmental determinants of species distribution from local to regional spatial scales can arguably lead to novel insight.

In this study, we apply distribution models—using both species distribution modeling and logistic regression—to identify the environmental factors controlling the spatial distribution of the genus *Montrichardia* (Araceae) at regional and local spatial scales, respectively. The genus *Montrichardia* occurs exclusively in the Neotropics (Mayo et al., 1997) and contains two species of emergent aquatic macrophytes, *M. linifera* and *M. arborescens*, both known popularly as Aroid Marsh or as “Aninga” in Brazil. The distributions of the two *Montrichardia* species overlap in the Amazon Basin, where they often form monospecific stands along floodplain lakes and rivers. In this study, we aim to determine (1) what environmental factors constrain the range limits of *Montrichardia* species and how these environmental associations compare among species and (2) what environmental factors are associated with the local distribution patterns of the genus *Montrichardia* and how these associations compare among species. We expect that while climatic factors similarly control the range limits of *Montrichardia* species at continental scales, at local scales, individual species distribution may be strongly differentiated by non-climatic factors.

Materials and methods

Focal region

Our field sampling was restricted to the Amazon basin, where the distributions of both *Montrichardia* species overlap. The Amazon provides a potentially interesting focal region because of the high environmental diversity of wetland habitat types (Junk et al., 2011). Indeed, some aquatic organisms in the Amazon Basin have their distribution restricted to specific wetland habitat types (Piedade et al., 2010; Lopes et al., 2011, 2014). The most important of these include black-, white-, and clear-water habitats, differentiated according to the geology of the drainage basin (Sioli, 1968). This simple categorization of water types is possible, because water color reflects physical and chemical water characteristics (Sioli, 1968; Furch, 2000; Junk et al, 2011). White-water rivers are rich in dissolved minerals and are characterized by intense erosional and depositional processes resulting in high loads of suspended matter and muddy-colored water (várzea) (Furch & Junk, 1997). In contrast, clear and black-water rivers (igapó) drain geologically old formations of the Brazilian and Guiana Shields and carry little suspended sediment (Furch & Junk, 1997). Black-water rivers are further characterized by high levels of dissolved humic substances and low pH (acidic waters) (Junk et al., 2015). Clear-water rivers are characterized by intermediate pH and a high phytoplankton production, comparable to várzea lakes (Richey et al., 1990; Junk, 1997). Both white- and clear-water wetlands show higher abundance of aquatic plants and floating meadows than black-water wetlands (Piedade et al., 2010). Relatively few species of aquatic macrophytes occur in black-water floodplains, mostly belonging to the families Cyperaceae, Poaceae, Maranthaceae, and Araceae (Piedade et al., 2010; Lopes et al., 2014). Because differences among Amazonian wetland habitat types covary, relatively few and easily measured variables can be used as broad surrogates of environmental variation in Amazonian wetland habitats, including pH, conductivity, water transparency, and even botanical criteria (Junk et al., 2011, 2012, 2015).

Field sampling and analysis

To examine the distributions of species along local physiochemical water gradients field sampling in 45 sites distributed over an area of approximately 3.8 million km^2 within the Amazon Basin was undertaken during the period of 2009–2012 in the Brazilian states of Roraima, Amazonas, Rondônia, Pará, and Amapá (Fig. 1). The study sites included the three major Amazonian water types, white, black, and clear waters (Table 1). Field sampling was performed in local populations of isolated *Montrichardia* stands that were located at least 500 meters from a neighboring *Montrichardia* population. Each population was georeferenced with aid of a GPS Garmin using UTM coordinates. Water pH (WTW, model pH 315i, Germany), conductivity (WTW, model cond 315i, Germany), Secchi disk depth (water transparency), and water column depth were measured with standard portable devices. Conductivity, water transparency, and pH are strong indicators of different Amazonian water types (Sioli, 1968). The degree of water-level fluctuation experienced by each population was estimated by measuring the height above ground level of the most recent annual high-water event, as determined by watermarks on woody trees near the sampling area (see more details in Wittmann et al., 2004; Schöngart et al., 2005).

We used logistical regression to examine how pH, conductivity, water transparency, and water column depth influence species occurrence at local spatial scales. Statistical analyses were performed using R 3.0.1 software. In addition, direct ordination of presence/absence data along environmental gradients was analyzed using the software Comunidata 1.6 (Dias, 2009).

Distribution modeling

To examine the neotropical spatial distributions of *Montrichardia* species, we gathered georeferenced data available in online herbaria (Appendix 1 in Supplementary Material; Fig. 2), totaling 284 records for *Montrichardia arborescens* and 114 records for *M. linifera*. We used Maximum Entropy Method (MAXENT version 3.3.3 k) to model the potential distribution of *Montrichardia* species within the neotropics. MaxEnt has been identified as one of the most accurate methods for species niche modeling for

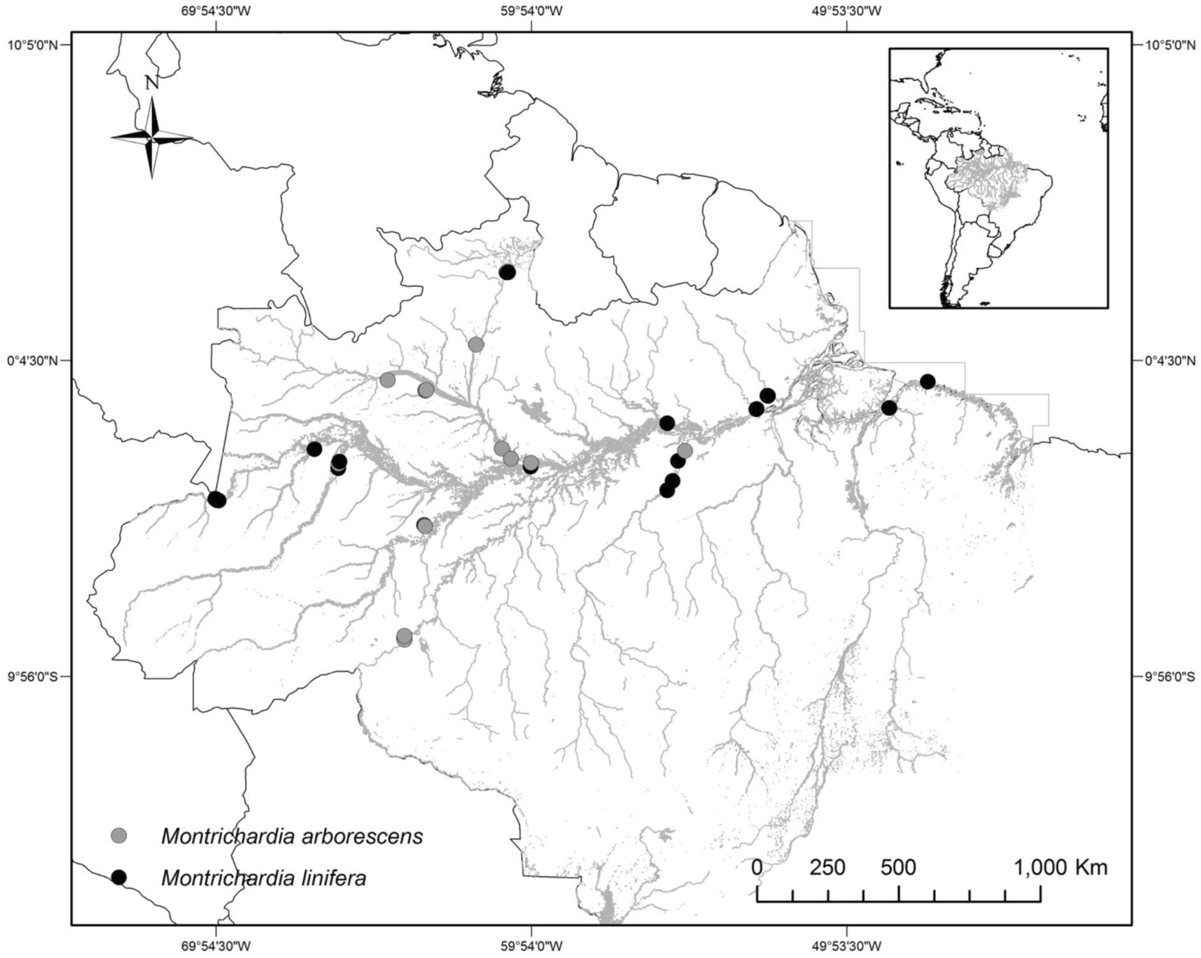


Fig. 1 Sample areas of *Montrichardia linifera* and *Montrichardia arborescens* in the Brazilian Amazon (*gray* colored area)

Table 1 Occurrence of *Montrichardia* species in the different sampled water bodies and water types

Water bodies	Water type	Species	
		M. arborescens	*M. linifera*
Rivers	Clear	4	8
	Black	10	0
	White	1	7
Lakes	Clear	1	4
	Black	4	0
	White	1	6
Total		20	25

geographically sparse occurrence records (Elith et al., 2006; Pearson et al. 2007). The method combines biological data of species occurrence (presence-only data) with environmental grid data to estimate the probability of distribution, subjected to the set of constraints provided by environmental characteristics of grid cells where the species has been recorded (Phillips et al., 2006). For each species, plant records were split into a 70% "training set" and a 30% model "test set," for model validation. Duplicate records were excluded. All other settings were set to default values.

Fifteen environmental variables were used (aspect, elevation, annual accumulation flux, direct flux, inclination, digital soil map, wetlands, global vegetation index-EVI, temperature of hottest month, temperature of coldest month, temperature of driest month, average annual temperature, total annual rainfall, rainfall of hottest, and coolest months) with a resolution of 1 km^2, extracted from public data bases (Appendix 2 in

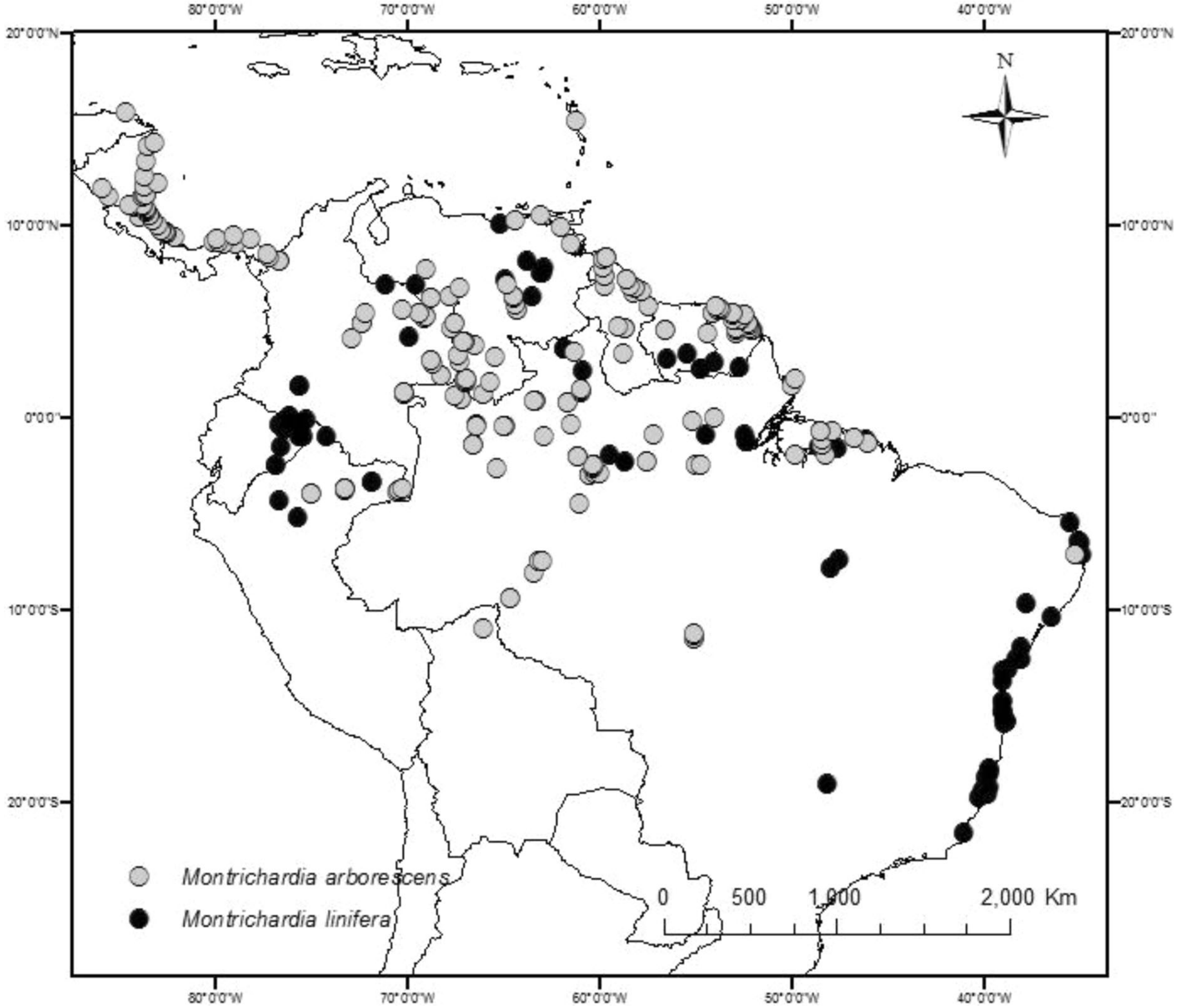


Fig. 2 Distribution of *Montrichardia* genus according to the records of consulted herbarium (list at the Appendix 1 in Supplementary Material)

Supplementary Material). Variables were used individually and in several combinations in the search for the best MAXENT model with the lowest number of variables for each species. All models were performed using 1000 permutations. Model performance was assessed using two methods: (i) the area under the curve (AUC) of the receiver-operating characteristic (ROC) and (ii) the jackknife validation method. The AUC of ROC is obtained by plotting sensitivity (proportion of correct prediction true positive, or absence of omission) and 1-specificity (proportion of false predicted presence—false-positive or commission error) for all possible thresholds of probability (threshold independent evaluation). In presence-only models, the AUC value represents the probability that the model scores a presence site (test locality) higher than a random background site (Phillips et al., 2006). The value ranges from 0.5 to $1 - a/2$, where a is the fraction of pixels covered by the species' distribution that remains unknown (Phillips et al., 2006). An AUC value closer to 1 indicates that the model predicts better than a random model, while a value of 0.5 indicates that the prediction is worse than random (Phillips et al., 2006). AUC values below 0.8 indicates poor model performance, 0.8–0.9 moderate model performance, 0.90–0.95 good model performance, and above 0.95 excellent model performance (Guisan & Thuiller, 2005).

Jackknife tests were used to estimate which of the variables contributed more to the model (Efron, 1981). The percent contribution of each variable was calculated on the basis of how much the variable contributed to an increase in the regularized model gain as averaged over each model run. Individual variable contribution is determined by randomly permuting the values of that variable among the training points (both presence and background) and measuring the resulting decrease in training AUC. A large decrease indicates that the model depends heavily on that variable. Values are normalized to give percentages (MaxEnt Tutorial; http://www.cs.princeton.edu/~schapire/MaxEnt/).

Results

Logistic regressions indicate that physiochemical properties of water are important determinants of the local distribution of both species. The occurrence of *M. arborescens* is significantly associated with low pH (AUC = 0.87; $P < 0.0001$), low conductivity (AUC = 0.87; $P < 0.0001$), and high water transparency (AUC = 0.77; $P = 0.003$). In contrast, the occurrence of *M. linifera* is significantly associated with higher pH values (AUC = 0.87; $P < 0.0001$), high conductivity (AUC = 0.80; $P < 0.0001$), and low water transparency (AUC = 0.70; $P = 0.04$) (Fig. 3). Occurrence of neither species was related to water column depth or maximum flood level ($P > 0.05$, Fig. 3d).

MAXENT models demonstrated low rates of omissions and high statistical significance (Table 2). The same combination of factors resulted in the highest values of AUC in both species (Table 2, model 1; presented in Fig. 4). The Jackknife test for model 1 revealed that the variables altitude (alt) and total precipitation (rain_tot) were the most important variables for modeling the distribution of the two species (Table 2; Fig. 5). While altitude was the most important variable influencing the distribution of *M. arborescens*, total precipitation was the most important variable influencing the distribution of *M. linifera* (Fig. 5). The variables "soil" and "veg 2002" (compost by EVI = Global vegetation index) commonly used to predict the distribution of species (Brown, 1994) had only little importance in model performance (Fig. 5) but remained in the final models to refine the forecast area of species occurrence.

Generated distribution maps based on the averages of the MAXENT models showed that *M. arborescens* has a Neotropical distribution, with the central part of the Amazon and the North of Amazonas State being the areas with highest probability of species occurrence (Fig. 4a). On the other hand, *M. linifera* has a fairly wide distribution in Central and South America and along the coastal region of Brazil. The Maxent models demonstrated a good (AUC > 0.9) and excellent (AUC > 0.95) forecast of species occurrence, confirmed by observations made in the field (Fig. 6a, b).

Discussion

At a regional spatial scale, both *Montrichardia* species were restricted to neotropical lowlands, with preference for hot and per humid tropical climates. Altitude and precipitation were important variables influencing the distribution of both species in all ten best models, while temperature of the driest months was an important variable for the distribution of both species in six of the ten best models. Temperature, and its strong effect on plant water-energy balance, is known to be one of the most important climate factors affecting the distribution range of many aquatic and wetland plant species (Sculthorpe, 1985; Santamaría, 2002; Bornette & Puijalon, 2011). It affects plant physiology, including germination and the periodicity and rate of seasonal growth (Short & Neckles, 1999). In addition, both *Montrichardia* species were detected to occur in regions where high annual precipitation (usually >1800 mm/year) is coupled with the absence of a distinct dry season. This becomes especially evident in extra-Amazonian regions, such as in Northeastern Brazil and the Gulf of Mexico, where the genus *Montrichardia* is restricted to per humid climates of coastal regions and absent in adjacent semi-arid or arid continental climates toward the interior (Fig. 4).

At local scales, our results are consistent with the idea that aquatic macrophytes are, in general, sensitive to the physical and chemical attributes of water (Ferreira et al., 2015). In the Amazon, *Montrichardia* species demonstrate the ability to colonize environments with distinct water characteristics, including wetlands with low amounts of nutrients, such as clear- and black-water river floodplains, as well as wetlands with high nutrient levels, such as white-water river

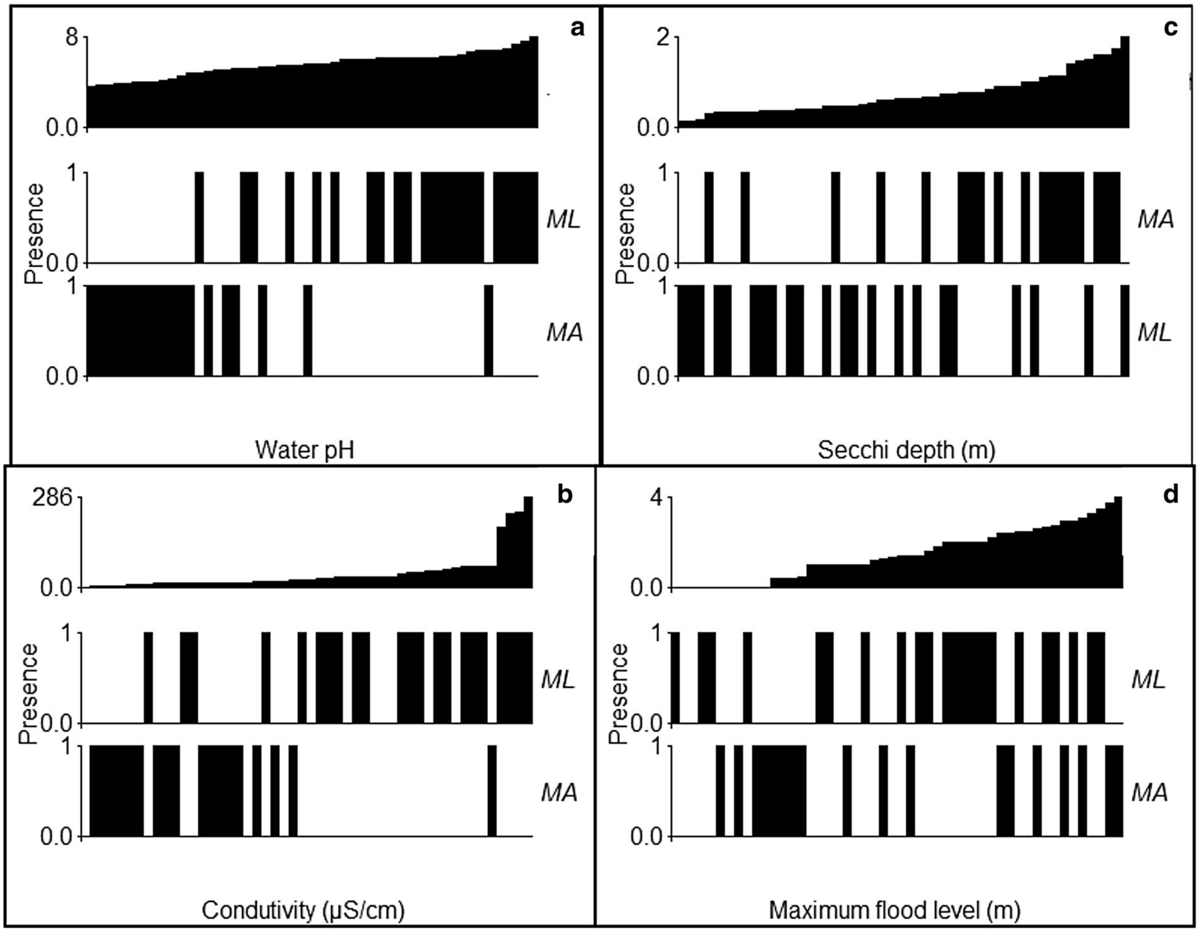


Fig. 3 Distribution of species in gradients: **a** pH, **b** conductivity, **c** water transparency (Secchi depth), **d** maximum flood level of plot. ML = *Montrichardia linifera*, MA = *Montrichardia arborescens*

floodplains. The occurrence of *M. arborescens* in the Brazilian part of the Amazon seems to be related to black- and clear-water rivers, although some records for white-water rivers are available in herbaria. *M. linifera* does not occur along black-water rivers and is likely to be limited to environments with high nutrient availability and neutral pH. *M. linifera* individuals are located in open, non-shaded areas along rivers and lakes and were more aggregated than those of *M. arborescens*, the latter being more sparsely distributed on the floodplain (Lopes et al., 2016). *M. linifera* can be observed on mineral substrates of floodplains as well as on organic substrates of floating islands, called "Matupás" in the várzeas of the Amazon basin (Junk & Piedade, 1997; Freitas et al., 2015). In sum, our results are consistent with the notion that local habitat variation along strong environmental gradients can lead to phenotypic differentiation and diversification in the Amazon basin and thus ultimately could lead to niche differentiation among closely related, co-existing species (i.e., Gentry, 1988; Fine et al., 2005).

Although the model predicted a potential overlap in the distribution of both *Montrichardia* species, both field observations and field data indicated that local habitat variation strongly segregates *Montrichardia* species along physical and chemical water gradients in the Amazon basin. While species segregation by physical and chemical water characteristics within the Amazon basin is evident, the species distribution model was not able to predict the segregation of local niche differences adequately. For example, soil variables that are commonly of high importance for the prediction of species distributions (Brown, 1994) had only little importance for the prediction of the

Table 2 Ten best models for each tested species and their AUC (area under the curve)

Mode	Variables	AUC (median)	
		M. arborescens	*M. linifera*
1	alt, rain_tot, soil, veg2002	0.961[a]	0.878 [a]
2	alt, temp_dry, rain_tot, soil, veg2002	0.922[a]	0.842[a]
3	alt, rain_coolest, soil, veg2002	0.917[a]	0.862[a]
4	alt, rain_tot, slope, temp_avg	0.908[a]	0.860[a]
5	alt, rain_coolest, temp_dry, veg2002	0.906[a]	0.807[a]
6	alt, rain_coolest, temp_dry	0.903[a]	0.816[a]
7	alt, temp_dry, soil, veg2002	0.886[a]	0.816[a]
8	alt, dem, rain_tot, temp_dry	0.882[a]	0.820[a]
9	alt, rain_coolest, soil, veg2002, wet	0.869[a]	0.741[a]
10	All variables[b] (15)	0.904[a]	0.863[a]

[a] $P < 0.0001$. Permutation = 1000. Here, alt (altitude), rain_tot (rain total), soil (map of soil), veg2002 (Global Vegetation Index, 2002), temp_dry (temperature of the driest month), temp_coolest (temperature of coolest month), wet (wetlands map)

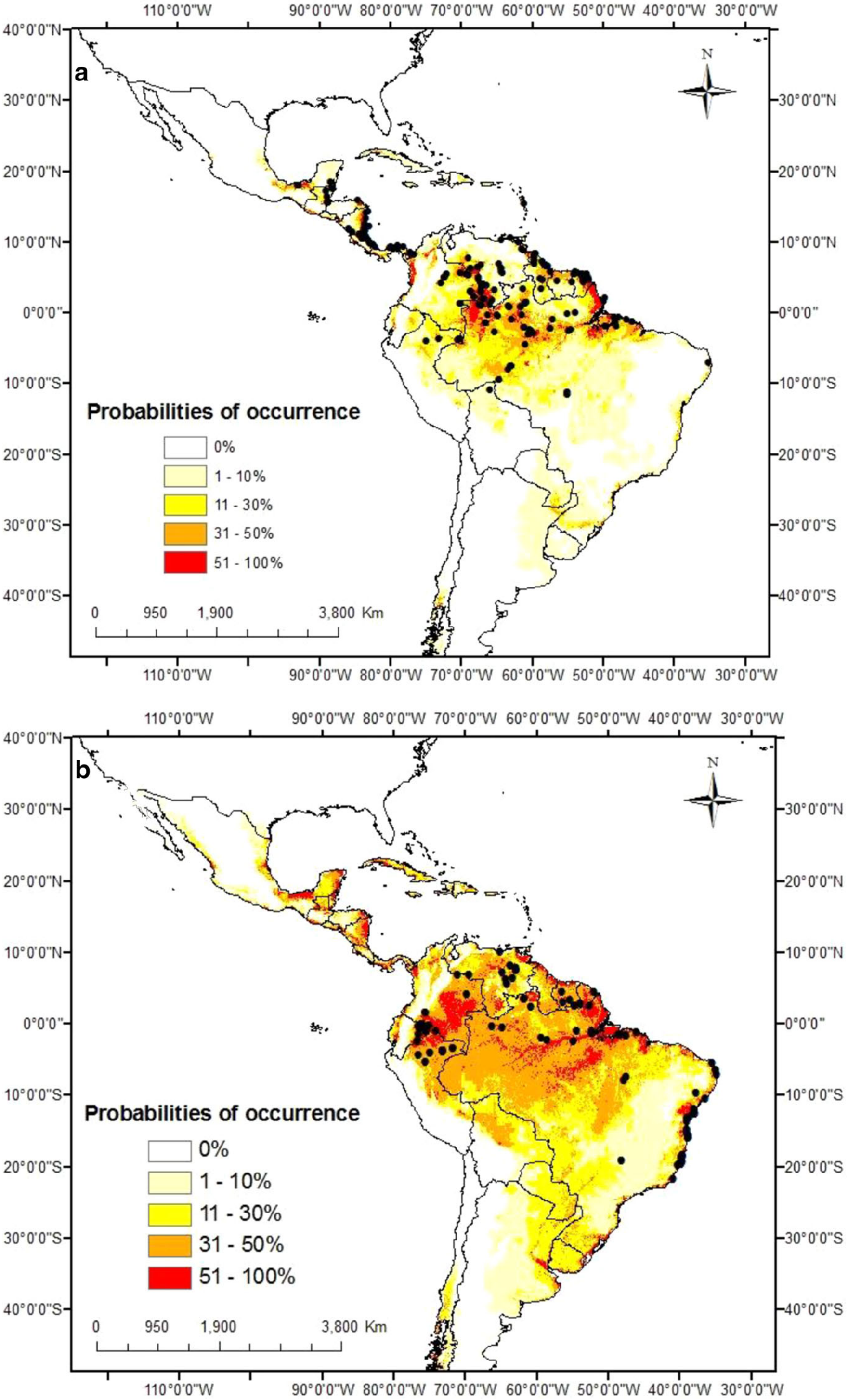
[b] See Table 2

distribution of both *Montrichardia* species. While it might be argued that in aquatic habitats plants might not be expected to respond strongly to soil attributes, the physical and chemical attributes of their aquatic habitat often reflect basin-wide soil properties, especially in the Amazon region. Also, *Montrichardia* is firmly rooted in the soil. Likely, the resolution of the soil layer in the present model is not sufficient to detect the contrasting differences in nutrient conditions between nutrient-rich and nutrient-poor alluvial substrates. We thus call attention to the fact that variations in physical and chemical soil variables may influence species distributions in the Amazon basin at very small spatial scales (<1 km), which are yet not detectable with the available resolution. Very likely, this is also the case for the global vegetation index (EVI), which had only little influence in our models.

IPCC (2013) predicts a 1.5–5.5°C increase of mean annual temperatures in most parts of the Amazon basin by 2100, coupled with a continuous increase in atmospheric CO_2 concentrations. In our models, both *Montrichardia* species showed potentially wider spatial distribution under moderately increased temperature scenarios (average 33–35°C). However, contracting distributions would be indicated in the case of reduced annual precipitation, as predicted by IPCC (2013) for most regions of Northeastern South America for the dry season (April-September). In another approach, a recent experimental study by Lopes et al. (2015) subjected *M. arborescens* to elevated temperature and atmospheric CO_2 concentrations in microcosms. Results indicated that primary productivity of *M. arborescens* was negatively affected when temperature and CO_2 surpassed 33°C 800 ppm respectively, indicating the presence of physiological stress and the sensitivity of this species to climate change (Lopes et al., 2015). Such findings, and how they translate to determine species distributions at large scales are not clear, but they do indicate that a stronger mechanistic basis for understanding species distributions is essential if we are to accurately model the future ranges of species under different climate scenarios.

As inventories of aquatic macrophytes are still poor and sparse in the Amazon Basin (Piedade et al., 2010), the possibility of species niche modeling with few occurrence data opens a large potential for the interpretation of biogeographic patterns. Moreover, with just three or four independent variables, it was possible to develop reliable distribution models, which may be of advantage in remote areas such as the Amazon basin, where environmental data are still scarce. For example, one possible use of potential species distribution maps could be their use in sustainable management plans, in order to discover new populations and to select priority areas for conservation (Kumar & Stohlgren, 2009; Adams et al., 2015).

Fig. 4 Actual distribution by herbarium data (*black dots*) and potential distribution (*colored* area) calculated by average of Model 1 (Table 2) of: **a** *Montrichardia arborescens* and **b** *Montrichardia linifera*



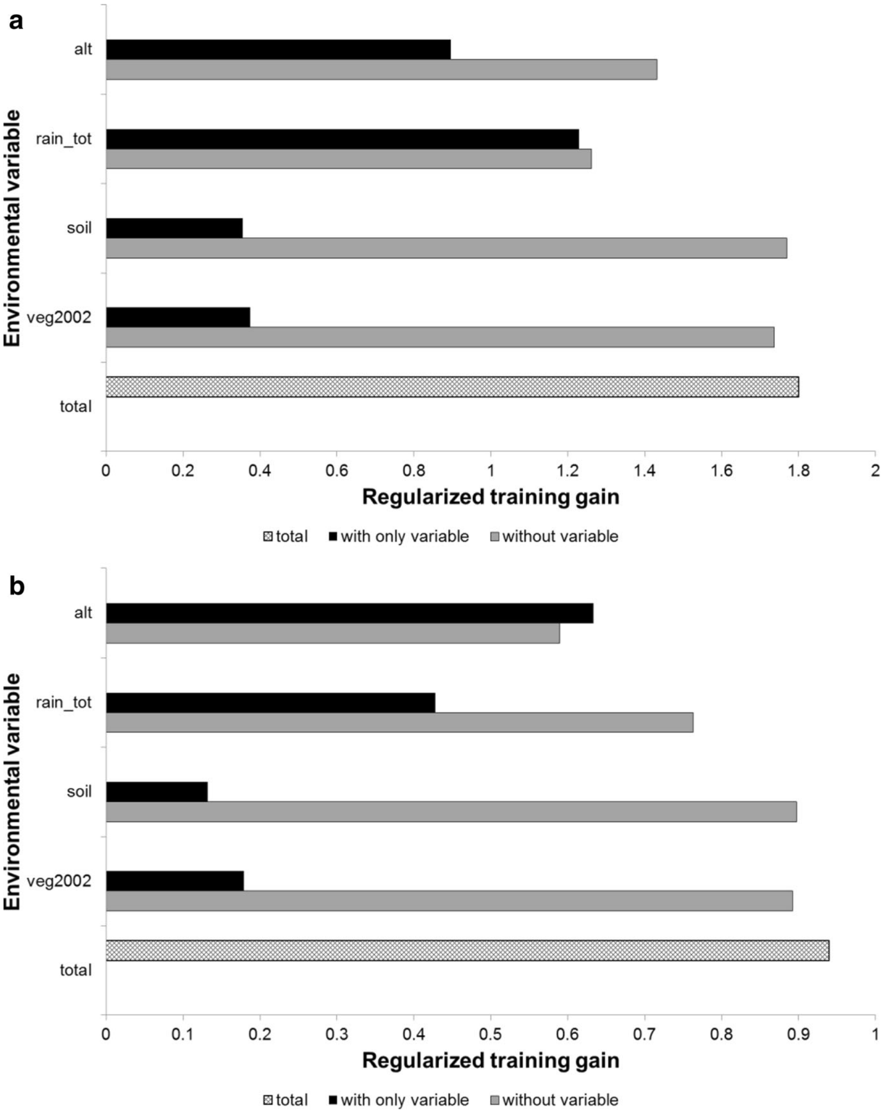


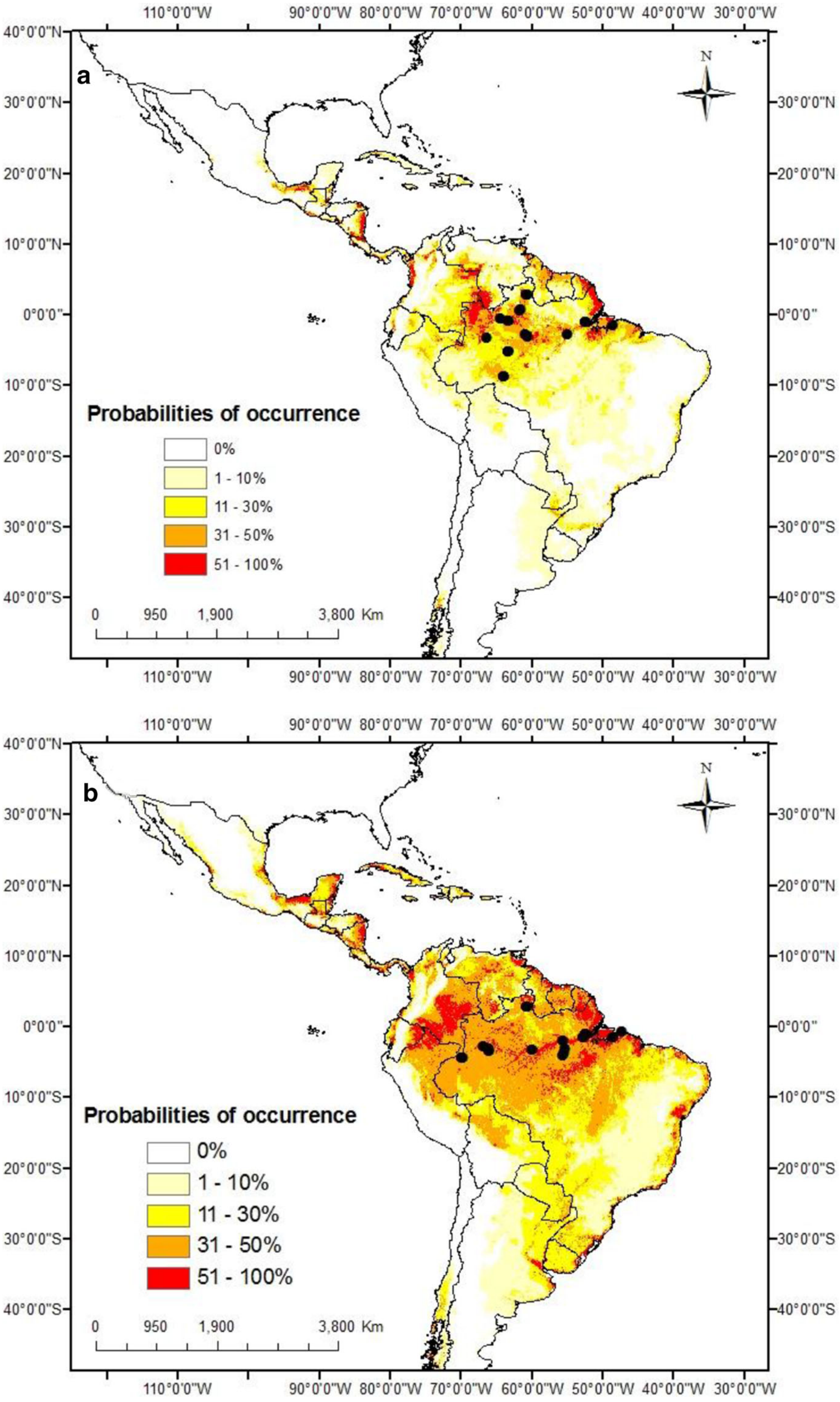
Fig. 5 Jackknife analyses of individual predictor variables important in the development of the full model for *Montrichardia* spp. in relation to the overall model quality or the “regularized training gain.” *Black bars* indicate the gain achieved when including only that variable and excluding the remaining variables; *gray bars* show how much the gain is diminished without the given predictor variable. *Alt* altitude, *rain_tot* rain total, *soil* map of soil, *veg2002* global vegetation index, 2002. **a** *Montrichardia arborescens*; **b** *Montrichardia linifera*

Conclusions

Our results suggest that a hierarchy of environmental factors may control *Montrichardia* species distribution from large to small spatial scales. While at large spatial scales climatic factors may similarly control the range limits of the genus, at small spatial scales individual species may colonize very different aquatic habitats. Both species of *Montrichardia* prefer environments with tropical climates with comparatively high temperature and elevated precipitation. Water chemistry influences the distribution of *Montrichardia* species at local scales where species distributions overlap in the Amazon basin. While *M. linifera* occurs mostly in white-water rivers, *M. arborescens* preferentially occurs in black-water rivers and upland streams. These findings indicate that in *Montrichardia*, an evolutionarily conserved climatic niche co-occurs with a strong capacity for niche differentiation among types of wetland habitats.

Distribution models were able to predict the large-scale distributions of species and their probable climatic determinants. However, they were not able to predict the segregation of the two species across different types of aquatic habitat types in the Amazon. We thus call attention to the need of environmental

Fig. 6 Model 1 results (Table 2) overlaid with field data of **a** *Montrichardia arborescens* and **b** *Montrichardia linifera*



data at small scale resolution in vast areas such as the Amazon basin.

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