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Differential effects of soil waterlogging on herbaceous and woody plant communities in a Neotropical savanna

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R.O. Xavier, M. B. Leite and D.M. Silva-Matos conceived the ideas and designed the methodology; R.O. Xavier and M. B. Leite collected the data; R. O. Xavier and K. Dexter analysed the data; R. O. Xavier and K. Dexter led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication

ABSTRACT

The impacts of soil properties and fire regime on Neotropical savannas are well-known, but the importance of hydrological regime for plant species assembly has received less attention. Here we assessed changes in diversity patterns of herbaceous and woody communities along a water table gradient in a fire-excluded Neotropical savanna. We found that increased waterlogging of soils was associated with declines in both herbaceous and woody species richness. Woody species richness decreased once the water table depth is less than 4 m and no woody species occurred once water table depth was less than 23 cm. Herbaceous communities remained species rich until the shallowest water table depth, where there is flooding at some point in the year, and even there, over a dozen species occurred. Woody species that occurred in areas with shallower water tables were a nested subset of those in areas with deeper water tables. In contrast, herbaceous communities showed turnover over the hydrological gradient, with distinct species specialised for different water table levels. However, we found that those specialists are restricted to few evolutionary lineages, evidenced by increased phylogenetic clustering over the water table gradient in herbaceous communities. We suggest that evolutionarily conserved hydrological niches define the herbaceous layer over the hydrological gradient, whereas only generalist woody species persist under high water tables. Our findings show that the effect of soil waterlogging differs between the herbaceous and woody layer of savannas, indicating that these communities will respond differently to shifts in the hydrological regime under future environmental change.

Keywords: water table depth, hydrological niches, turnover, phylogenetic.

Introduction

The varying patterns of plant community assembly across environmental gradients have inspired important ecological concepts and have been a recurring subject of research since the earliest ecological studies (Clements 1936; Keddy 1992; Laliberté et al. 2014; Whittaker 1956), and there is increasing interest in understanding plant community assembly in light of ongoing global environmental changes (Lewthwaite et al. 2017). The effects of larger-scale geographic gradients in water availability on community composition and species richness have been demonstrated in a wide range of ecosystems, from tropical forests (Esquivel-Muelbert et al. 2017; Pyke et al. 2001) and seasonally dry ecosystems (Scholes et al. 2002) to riparian forests (Garssen et al. 2015) and floodplains (Casanova and Brock 2000; McGinness et al. 2018; Stevenson et al. 2018). In addition, local variation in hydrological regime can shape plant community composition at individual sites (Araya et al. 2011; Kirkman et al. 2001; Silvertown et al. 1999), which has led researchers to define distinct hydrological niches for different species (Silvertown et al. 2015). However, research in this area has been limited by the difficulty of quantifying hydrological regime. Although assessing soil texture, a proxy for how quickly water percolates through the soil (Wakindiki and Ben-Hur 2002), and topography, which generally relates to the water table depth (Desbarats et al. 2002), is relatively easy, actually measuring water table depth over annual cycles requires substantially more time and financial investment (Morgan and Stolt 2004). Spatial and temporal variation in water tables has been quantified in temperate plant communities, where it is consistently found to have strong effects on plant community composition (Allen-Diaz 1991; Dwire et al. 2006; Shafroth et al. 2000; Silvertown et al. 1999). Similar studies are scarce in the tropics (although see Moulatlet et al. 2014; Targhetta et al. 2015), despite the tropics housing the overwhelming majority of plant diversity.

Tropical savannas occur in seasonally dry climates, and typically show a continuous herbaceous layer and a discontinuous woody canopy (Sarmiento 1984). Factors driving the occurrence of savanna *versus* forest have been extensively investigated (de Castro and Kauffman 1998; Sankaran et al. 2005), and recent large-scale studies have highlighted the role of fire regime and herbivory (Hempson et al. 2015; Lehmann et al. 2014; Staver et al. 2011). However, seasonal flooding and soil waterlogging, potentially in conjunction with fire occurrence, are also related to the occurrence of savannas in large areas of South America, including the *llanos* of Venezuela and Colombia (Sarmiento and Pinillos 2001), the Rupupuni savannas of Guyana (Eden 1970) and the Llanos de Moxos of Bolivia (Hamilton et al. 2004). There are also extensive areas of hydrologically determined savannas in Brazil (Batalha et al. 2005; Cianciaruso et al. 2005; Tannus and Assis 2004), yet most studies of the woody cover and composition of Brazilian savanna have focused on fire regime as a driving variable (Cianciaruso et al. 2012; Moreira 2000; Silva and Batalha 2010).

The few studies of hydrological gradients in Brazilian savannas (e.g. Villalobos-Vega et al. 2014, Leite et al 2018) have focused on the woody plant layer, while much of plant species richness of Brazilian savannas lies in the herbaceous layer (Rodrigues Munhoz and Felfili 2007; Tannus and Assis 2004). In fact, herbaceous species can account for over 90% of the plant species richness (Mendonça et al. 1998; Rezende et al. 2008) and most of the primary productivity (Lloyd et al. 2008). In other ecosystems, diversity patterns of herbaceous and woody species are differentially related to environmental variation (Moro et al. 2015; Yan et al. 2013). This is especially expected under distinct hydrological regimes, considering the recurrent differences in water acquisition strategies between herbaceous and woody species (Dodd et al. 1998; Moro et al. 2015; Walter 1979).

In this study, we aimed to assess the effect of water table depth and other abiotic drivers on patterns of species richness and lineage diversity in both woody and herbaceous plant communities along a hydrological gradient in fire-excluded savannas in Southern Brazil, where shallow water tables are thought to be a key driver of open vegetation (Leite et al. 2018). Although both recent fire suppression and past fire regimes are expected to affect current plant community patterns in these savannas, as with any other savanna (Bond and Parr 2010; Brockway and Lewis 1997), the overall study site has experienced little changes in woody cover during the last three decades despite marked variation in woody cover within the site. In other words, the spatial pattern of variation in woody cover has remained relatively static, suggesting that the hydrological regime may be the major force affecting vegetation structure at the site (Leite et al. 2018). Therefore, our study site offers a rare opportunity of investigating the effect of a hydrological gradient on community diversity patterns while controlling for potential additional effects of fire regime.

We specifically aimed to answer the following questions: i) Is the water table depth a major driver of variation in the species richness of plant communities?; ii) Is there turnover in plant species composition along water depth gradients, or are the plant species in more species-poor communities a nested subset of those in more species-rich communities?; iii) Are the plant communities in areas with high water tables comprised of species from few or many evolutionary lineages, i.e. do these plant communities show phylogenetic clustering? iv) Do these patterns differ for herbaceous and woody plant communities? Flooding gradients often lead to high species and phylogenetic turnover in plant communities (Garssen et al. 2015; Silvertown et al. 1999; Tanentzap and Lee 2016), and hence we expect large differences in species and phylogenetic community structure between sites with contrasting hydrological regimes. In addition, recent research at our study site has demonstrated that the density of the woody layer decreases as water tables become shallower (Leite et al. 2018), so we also expect matching decreases in woody plant species richness. In contrast, we hypothesize that changes in diversity patterns at the herbaceous layer will be present, if at all, along a smaller extent of the water depth gradient, considering that poorly drained Neotropical grasslands and savannas are often species-rich ecosystems (Bueno et al. 2014; Munhoz and Felfili 2006; Killeen and Hinz 1992, Tannus and Assis 2004).

Material and methods

Study site

This study was carried out at the Itirapina Ecological Station (IES), a 2,300 ha protected area in southeast Brazil (Fig. 1a). The local climate is Cwa (Köppen) and the average annual rainfall and temperature during the study period were 1,613 mm and 20.6 °C, respectively (IFSP 2018). There is typically a favourable water balance during the rainy season and a short period of water deficit in the dry season (Xavier et al. 2017). The prevalent soil is an entisol with at least 90% sand (Leite et al. 2018). The IES contains a gradient in vegetation physiognomy that is typical of broader savanna vegetation in Brazil, from grasslands with few shrubs and trees (open savanna - *campo sujo*) to a more closed savanna with higher tree density (dense savanna - cerrado *sensu stricto*) and including an intermediate type (savanna - *campo cerrado*) (Coutinho 1978). The IES maintains some of the last remnants of tropical grasslands in southeast Brazil, where open savannas have been affected by degradation and woody encroachment (Durigan et al. 2007; Stevens et al. 2016). There are no detailed data on the disturbance regime before the IES was established (early 1980s), although the lack of past fire management policies suggest that fire used to occur at the reserve prior to this period.

Managers have excluded fire from the IES during the last 25 years. Aerial and satellite imagery taken since the mid-1980s suggest that the distribution of open savannas and grasslands in the IES has changed little during the last 30 years (Leite et al. 2018).

We selected 19 sites along a water table depth gradient (Fig. 1a). Vegetation along this gradient varies from wet and marshy grasslands with no woody species to savannas with variable woody cover (campo sujo, campo cerrado and cerrado *sensu stricto* – *sensu* Coutinho (1978), Electronic Supplemental Material ESM1). Although we initially aimed to sample an equal the number of sites within each of these three savanna categories, we found that woody cover varies widely within each savanna category (Leite et al. 2018). Likewise, we found that grassland types initially categorized based on visual differences in their flooding regime were in effect distributed along a hydrological gradient, including distinct annual periods of soil waterlogging and standing water (Xavier et al. 2017). Considering these limitations on identifying *a priori* physiognomies or vegetation types at our study site and our aim of assessing community responses to water table depth, our study focus on assessing diversity patterns of woody and plant communities occurring along a continuum of woody cover and hydrological regimes. Sites initially classified into the same vegetation type were always at least 500 m from one another. None of the sites have experienced fire during the last two decades.

At each site, we identified and counted all woody individuals with basal diameter greater than 3 cm in six randomly allocated 10 x 10 m plots (Fig. 1b). In order to sample the herbaceous community, in each of these plots we also established six regularly distributed 1 x 1 m subplots spaced 2 m apart, where we identified and counted all individuals of herbaceous species (Fig. 1b, Electronic Supplemental Material ESM2). We assumed that all the stems connected aboveground or at the soil level belonged to the same individual; turfs of caespitose grasses and sedges with no aboveground connections between them were considered distinct individuals. Individuals were identified to the species level in the field or with further support of previous surveys in the study site, plant collections and consultation with taxonomists (Tannus and Assis 2004). We followed the nomenclature of The Plant List (2017). Unidentified species were classified into morphospecies within genera or families. Across all sites, we could not identify 828 herbaceous individuals to the family level (3.8 % of all herbaceous individuals sampled). Although these individuals were not included in the analysis, most of these morphotypes were single occurrences and hence their absence is unlikely to strongly affect inference on patterns of community assembly at our study sites. Based on these identifications and field observations, species were classified as trees, shrubs or herbs; subshrubs and woody species with no permanent aboveground woody stem were included in the herbaceous layer plant community as they interact primarily with the graminoid and forb species that are typically dominant at this layer. Specimens were deposited in the herbarium of the Federal University of São Carlos, Brazil.

Phylogenetic and Environmental Data

We created a phylogeny that included all species across the plots using the online tool Phylomatic (Webb and Donoghue 2005), based on the Angiosperm Phylogeny Group's APGIII consensus tree (R20120829). Node ages were estimated using the *bladj* algorithm in the software Phylocom 4.2. (Webb et al. 2008) with age constraints from Gastauer et al. (2017). This phylogeny was then pruned to a woody plant species phylogeny and an herbaceous plant species phylogeny, in order to generate separate null expectations for woody and herbaceous plant communities when quantifying phylogenetic community structure.

During the peak of the dry season in 2011 (August), we used a manual auger to drill one 40 mm-wide well down to the groundwater just outside five of the six 10 x 10 m vegetation sampling plots at each site (Electronic Supplemental Material ESM2). At sites where initial drilling showed the water table to be deeper than the maximum drilling capacity of our equipment (7 m), we drilled wells in only two of the six surveyed 10 x 10 m plots. We measured the groundwater depth every two weeks from October 2011 to October 2013 using a Solinst Water Level Meter 102 500' measuring tape. We used the minimum water table depth over this period as an explanatory variable because it represents the maximum waterlogging or highest water table that plants at a given site experience (Xavier et al. 2016). We averaged values across the different plots at a given site. The maximum capacity of the drilling equipment (7.5 m) was used as the minimum water table depth estimate for the sites where the groundwater was too deep to be measured.

We collected 15 soil samples from 0 to 30 cm depth at each study site, which were thoroughly mixed to produce a composite sample by site (see Electronic Supplemental Material ESM3 for the abiotic characterization of each site). Soil texture (sand, silt and clay content) and soil chemical composition (P, N, K, Mg, Al, Ca, pH and organic matter) were obtained following Camargo et al. (2013).

Data analysis

Our main response variables in analyses were the species richness, species diversity and lineage diversity of herbaceous and woody plant communities. Given an equal sample effort in terms of area sampled, our species richness values can be directly compared across sites. To quantify species diversity, we used the Simpson Index (1 – D), which is not only a measure of species richness but also reflects how evenly individuals are distributed across species. Phylogenetic diversity, or the total branch length of a phylogeny comprising the species at a given site, is the most basic measure of lineage diversity; however, this measure is strongly correlated with species richness, and high variation in species richness across communities, as we have at our sites, can obscure any patterns in variation of lineage diversity. We therefore used a null model to calculate the standardized effect size of phylogenetic diversity, based on reshuffling the tips of the phylogeny 1000 times. We refer to this standardized effect size as lineage diversity (c.f. Honorio Coronado et al. 2015; Rezende et al. 2017). It is also a measure of phylogenetic community structure, with negative values reflecting phylogenetic clustering and positive values reflecting phylogenetic overdispersion (Webb et al. 2002). We did not use alternative measures of phylogenetic community structure, such as the standardised effect size of the mean phylogenetic distance between species in a community (also referred to as the net relatedness index), because these alternative measures can be highly sensitive to the distribution of species among the three major clades of angiosperms (magnoliids, monocots and eudicots; see Honorio Coronado et al. 2015) and our herbaceous and woody plant communities differ substantially in the distribution of their constituent species across these clades. This would therefore complicate comparison of results for woody and herbaceous plant communities. Phylogenetic diversity and its effect size were calculated separately for tree and herbaceous species based on pruned trees comprising only tree and herbaceous species, respectively. These calculations were performed in the R package "picante" (Kembel et al. 2010).

Many of our soil variables covary strongly with each other and we therefore used biological reasoning to select a subset of the most pertinent explanatory variables. For example, the abundances of individual base cations are positively correlated with each other, so we used the sum of bases as an explanatory variable in analyses. Also, the soil cation exchange capacity, base saturation, organic matter content and pH were strongly correlated with each other (see Electronic Supplementary Material ESM3 for soil properties from each study site). We included the soil base saturation as an explanatory variable as the variable most likely to be mechanistically related to plant community composition. The minimum water table depth and certain soil properties (N, sum of bases, Al) showed strongly right-skewed distributions in preliminary analyses and were therefore log-transformed prior to linear modelling to reduce heteroscedasticity.

We modelled the effect of water table depth and soil properties on species richness, species diversity and lineage diversity using generalized linear models with a negative binomial distribution for species richness (as it represents count data) and a Gaussian distribution for species and lineage diversity. Models were constructed separately for woody and herbaceous plant communities. Explanatory variables were scaled to have the same mean and variance to allow direct comparison of their regression coefficients as a measure of their relative effect on community composition. Given that our overarching aim was to assess the effect of water regime on community composition, we compared the Bayesian Information Criterion (BIC) of models including only water table depth as an explanatory variable with models including water table depth and each of the other soil properties in turn. Limited sample size in terms of study sites (N = 19) prevented us from considering more complex models with more than two explanatory variables, or interactions. However, our approach does serve to test if our results for water table depth are robust to including the major axes of soil variation as covariates. When presenting results, we focus on presenting the best-fitting model for water table depth and one additional soil variable. Semivariograms showed no clear spatial patterns in raw variables or residuals. Further, accounting for spatial autocorrelation did not improve model estimation in generalized linear models (following Zuur et al. 2009), and spatial autocorrelation was therefore not included in the final models presented here.

In order to visualise in greater detail how species richness, species diversity and lineage diversity vary with the original non log-transformed water table depth values, we used additive models with thin plate regression splines as smoothing functions with the R package “mgcv” (Wood 2006), without defining a maximum number of basis dimensions. We used this approach because additive models assume no *a priori* relationship between explanatory and response variables (Zuur et al. 2009). Therefore, they are a flexible alternative for identifying ecological thresholds and different types of biologically meaningful non-linear responses (Francesco Ficetola and Denoël 2009; Zuur et al. 2009), which are often found along extensive hydrological gradients such as at our study site (Dwire et al. 2004; Lite and Stromberg 2005).

We followed the approach of Leibold and Mikkelson (2002) to assess if there is community turnover or nestedness along the water table gradient, separately for herbaceous and woody plant communities. We sorted the community matrix according to increasing water table depth and calculated the number of times a species was replaced by another between sites with adjacent water table depth; the resulting average turnover value was then compared to the values obtained from 1000 random communities created by permuting the original matrix (Leibold and Mikkelson 2002). Significant differences between these values indicate that the community follows a turnover pattern, whereas similar values suggest a nested pattern. We performed these analyses using the function “Turnover” in the R package “metacom” (Dallas 2014). We also quantified the amount of nestedness in woody and herbaceous plant using the

NODF metric, which is based on decreasing fill and paired overlap in the community matrix (Almeida-Neto et al. 2008). Values obtained for each layer were compared to null expectations based on 30000 random communities that preserved the number of species occurrences and row and column totals (Ulrich et al. 2009). These analyses were performed in the R packages “vegan” (Oksanen et al. 2013) and “bipartite” (Dormann et al. 2008).

Herbaceous and woody morphotypes that could not be identified to the genus or family level were included in nestedness analyses. Matrices for the herbaceous layer included the whole water table gradient, whereas for the woody layer, they only included sites where woody species occurred (11 out of 19 sites). All analyses were performed in the R statistical environment (R_Core_Team 2017), with further support of packages cowplot (Wilke 2016) and ggplot2 (Wickham 2010) for graphic presentation of results.

Results

We identified, at least to the family level, 22,652 individuals from 50 families and 210 species and morphospecies, including 154 herbs and 66 trees. The most common families in terms of abundance and species richness were Myrtaceae, Asteraceae and Fabaceae in the woody layer, and Poaceae and Cyperaceae in the herbaceous layer (see Electronic Supplemental Material ESM3 for species composition at each study site).

Species richness and species diversity were strongly correlated and similarly related to environmental variables, and we therefore only present results for species richness here (see Electronic Supplemental Material ESM4 for results based on species diversity). Species richness and lineage diversity of the herbaceous layer were closely related to water table depth. Most of the best models in terms of BIC values also included soil properties, but the effect of these variables was always smaller than that showed by water table depth and did not affect the sign or significance of the water table depth effect (Table 1). Tree species richness was also strongly related to water table depth and weakly related to soil base saturation, whereas lineage diversity of woody plants was largely unrelated to water table depth or soil factors we measured (Table 1).

Generalised additive models (GAMs) showed that the diversity patterns of herbaceous and woody layer had different thresholds of response to water table depth (Fig. 2, Table 2). Although the herbaceous communities on sites subjected to flooding (i.e. negative water table depth) exhibited much lower species richness (points in bottom left of Fig. 2a), additive models only captured a weak linear relationship between water table and species richness. The failure to statistically detect this clearly non-linear relationship is likely related to the very small difference in the measured water table depth values between species-rich grasslands with very shallow water tables and species-poor seasonally flooded grasslands (Fig. 2a). Additive models showed that the lineage diversity of the herbaceous layer increased sharply as water table depth increased until approximately 1 m and remained stable thereafter (Fig. 2c). Woody species richness increased as the water table depth increased to about 4 m, and then showed no clear association with water table depth (Fig. 2b). Woody plant lineage diversity showed no clear relationships with water table depth (Fig. 2d).

The community structure of the herbaceous and woody layer also showed different patterns along the water table gradient (Fig. 3). Although certain generalist herb species occurred from grasslands with shallow water table to savannas with deep water table (Fig. 3a), the number of species replacements in the herbaceous layer between sites with adjacent water table depth was significantly higher than expected according to a null model (z=-4.76 p<0.001), suggesting a turnover pattern. In contrast, the number of replacements in the woody layer did not differ from expected according to a null model (z=0.64, p=0.520), suggesting a nested pattern along the water table gradient (Fig. 3b). Consistent with these findings, the amount of nestedness in the herbaceous layer (NODF=31.10) was significantly lower than expected based on a null model (z=-4.45, p=0.003) and considerably higher than in the woody layer (NODF=49.50), although the amount of nestedness at the woody layer did not differ from the null expectation (z=0.53, p=0.678).

Discussion

Our study shows that seasonally high water tables, which lead to soil waterlogging, have major impacts on both herbaceous and woody plant communities, although the nature of these impacts differs. As shown in previous research at this site (Leite et al. 2018), woody plant species richness declines as water tables become shallower, with no woody plants able to persist as adult trees (> 3 cm diameter at ground level) in areas where the water table comes within 20 cm of the ground surface (see also Fig. 2b). In contrast, many herbaceous species (more than a dozen) can persist at all water table levels, although herbaceous species richness does halve at the shallowest water table depths, where seasonal flooding occurs (Fig. 2a). The herbaceous species that persist at the shallowest water table depths are distinct from those that occur on higher and drier ground (Fig. 3a), and analyses of phylogenetic clustering show that these species come from relatively few evolutionary lineages. In contrast, woody species show a nested pattern of species distributions over hydrological gradients (Fig. 3b), and species occurring at shallower water tables do not seem restricted to particular evolutionary lineages.

Woody communities

As we expected, the richness at the woody layer was severely limited by shallow water table, suggesting intolerance to seasonal waterlogging. The flooding regime often has large effects on riparian woody plant communities (da Paz et al. ; Garssen et al. 2015; Garssen et al. 2017), and recent studies have shown a negative effect of shallow water table on the tree species richness of savannas (Villalobos-Vega et al. 2014). We found no trees on sites where the minimum annual water table level was very close to or above the soil surface (i.e. where flooding occurred). These results are somewhat surprising, because in South America many seasonally flooded savannas have been described (Batalha et al. 2005; Bueno et al. 2014; Sarmiento et al. 2004), although these studies did not measure water table depth directly. Considering the negative effects of flooding on plant survival and performance, which require specific adaptations (Mommer et al. 2006), we hypothesize that extended time periods of shallow water tables and flooding are strong abiotic filters that, at least in some areas, cannot be overcome by woody species. Clearly, most tree species present in the species pool for our study area cannot survive such challenging hydrological conditions. We did find that a few tree species could occur where the water table remained a few centimeters deeper than the soil surface, as has been found for other poorly drained Neotropical savannas (Batalha et al. 2005; Bueno et al. 2014). Once water tables were deeper than 3 m, we found that minimum water table depth had little effect on tree species richness. Shallow water tables may be buffering open savannas in our study site against woody encroachment associated with fire exclusion, which has been occurring in well-drained Neotropical savannas (Durigan and Ratter 2016; Stevens et al. 2016). However, our findings also show that small changes in the water table dynamics of sites with shallow water table could have large effects on the species richness of woody plant communities in hydrologically-determined savannas.

Contrasting with the effects on woody species richness, there was no association between water table depth and the lineage diversity of woody communities. Although we found that certain tree species and families (e.g. Myrtaceae, Bignoniaceae, Fabaceae) only occurred where the water table was deeper than 3 m, a few species from multiple lineages (e.g. *Tibouchina stenocarpa*, *Lippia velutina*, *Moquiniastrum polymorphum*) occurred in savannas with both shallow and deep water tables. This is consistent with the complex interaction of anatomical, morphological and physiological adaptations associated with flood-tolerance (Garssen et al. 2015; Kolb and Joly 2009; Kozlowski 1997), which tend not to be phylogenetically clustered (Mommer et al. 2006). Although it is possible that this flooding tolerance generally occurs at taxonomic levels lower than the resolution in our phylogeny (family and genus-level resolution), phylogenies at the same resolution have been used to associate environmental variation and phylogenetic composition (Fine and Kembel 2011; Kubota et al. 2014). In addition, a study based on a fully-resolved phylogeny also found no evidence of phylogenetic clustering along a soil moisture gradient, suggesting that responses to distinct water regimes may be evolutionarily labile in woody plant lineages (Araya et al. 2012). Although assessing if this is a widespread pattern in tropical savannas subjected to high water tables would require investigations at larger spatial scales, our findings suggest that future changes in the hydrological regime in our study site would affect the woody community lineage diversity less than the species richness.

We found that woody species that do occur in areas with high water tables are simply a subset of species from higher and drier areas that have the necessary physiological adaptations to manage this stressful, water-logged environment. Previous studies also found little turnover of tropical woody species along water availability gradients (Esquivel-Muelbert et al. 2016). In effect, we found that poorly drained savannas were dominated by *Moquiniastrum polymorpha* (Less.) G. Sancho, which also occurs in well-drained areas. This species shows high plasticity in leaf structure, which has been associated with its occurrence in both Neotropical savannas and forests (Rossatto and Kolb 2010). Similarly, certain woody species from the family Melastomataceae, which were common where water tables were high in our study area, are common in Neotropical palm swaps and show leaf anatomy plasticity what seem to favour their occurrence in poorly drained sites (Somavilla and Graciano-Ribeiro 2011). Although plasticity may not be associated with environmental tolerance (Dostál et al. 2016), plasticity on anatomical, physiological and morphological traits, also called low oxygen escape syndrome, allows species without metabolic adaptations to flooding to persist in flood-prone environments (Bailey-Serres and Voesenek 2008). For example, *Sinojackia huangmeiensis* J.W. Ge & X.H. Yao showed distinct seed morphology and composition when subjected to soil waterlogging (Wei et al. 2018). Therefore, phenotypic plasticity, rather than evolutionarily rare adaptations to soil waterlogging, may enable the persistence of these savanna trees species under shallow water tables.

Herbaceous communities

Our data suggest that herbaceous species richness was only reduced over the shallowest water tables, where seasonal flooding occurred. This is expected considering the large negative effect on plant performance and survival of severe soil anoxia and hypoxia associated with flooding, whereas more herbaceous species are expected to occur where there is only seasonal soil waterlogging (Wegner 2010). These findings are consistent with the typically high herbaceous species richness found in other poorly drained Brazilian savannas (Bueno et al. 2014; Munhoz and Felfili 2006; Rodrigues

Munhoz and Felfili 2007; Tannus and Assis 2004). Previous studies in temperate grasslands found similar diversity patterns (Dwire et al. 2006), suggesting that seasonally shallow water tables may not be a constraint on herbaceous species richness in a wide range of ecosystems.

In contrast to effects on species richness, the lineage diversity of the herbaceous layer was reduced under high water tables. Consistent with this effect, the herbaceous layer of savannas with water tables deeper than 3 m included families (e.g Menispermaceae, Bromeliaceae) absent from sites with shallow water tables. In Neotropical savannas, many perennial herbs and subshrubs are found with relatively large underground structures that support both water uptake and rapid post-fire regeneration (de Castro and Kauffman 1998; Sarmiento 1984). These species may be unable to overcome the hypoxic conditions in sites subjected to soil waterlogging (Bailey-Serres and Voesenek 2008; Pezeshki 2001; Wegner 2010). In our study, these lineages seem to be replaced by a few lineages of small perennial and annual herbs on sites with intermediate water table depth (e.g. Onagraceae, Xyridaceae, Eriocaulaceae), which maintained a high species richness; this likely led to the only slightly lower lineage diversity at these sites compared to the better drained savannas. In contrast, continuous waterlogging and periodic flooding require specific mechanisms to overcome severe soil hypoxia (Bailey-Serres and Voesenek 2008; Kozlowski 1984), so that lineage diversity decreases markedly towards more severe flooding (Tanentzap and Lee 2016). Consistent with this expectation, a few graminoid species and taxa typical from ephemeral wetlands (e.g. *Hidrocotyle*, Maiacaceae) (Deil 2005) occurred in sites subjected to flooding.

Differently from the woody layer, we found compositional turnover in the herbaceous layer over the hydrological gradient, possibly because herbaceous and woody plants are differentially affected by high water table. Poor drainage is expected to be a constraint to many cerrado woody species, which often have a deep underground system (Oliveira et al. 2005). Conversely, herbaceous species are often shallow rooted (Rawitscher 1948) and are only expected to be affected by soil waterlogging where the water table is right below the soil surface. In seasonally dry ecosystems, high water tables may even favour the occurrence of herbaceous species with poor tolerance to water deficit, as it may increase the moisture at the superficial soil layer by capillary action (Moore 1939). In effect, there is no annual period of water deficit in most of our study sites subjected to seasonal waterlogging (Xavier et al. 2017). Therefore, we hypothesize that conditions associated with high water tables support specific herbaceous species, and competitive ability is expected to be important for their persistence (Grime 1988). In summary, herbaceous species are most likely to occur where the hydrological regime enables them to perform close to their ecological optima (Silvertown et al. 1999), leading to low niche overlap and species segregation along water table depth gradients (Silvertown et al. 1999). The long-term fire suppression at our study sites has possibly contributed to the emergence of these patterns, as it is expected to favour the most competitive species under different hydrological conditions, to the detriment of generalist and disturbance-prone herbaceous species (Grime 1988; Tilman 1985). Regardless of this possible local effect, our findings highlight the functionally unique composition, and high conservation value, of Neotropical grasslands with high water tables.

We conclude that water table depth is the major abiotic factor affecting savanna plant communities at our study site, but this effect varies between the herbaceous and woody layer. There were no trees under hydrological flooding, and only a few woody species, albeit from multiple lineages, persisted at high water tables. Indeed, shallow water table is a major constraint to the occurrence of tree species in savannas, which may be buffering open savannas in our study site against woody encroachment associated with fire exclusion. Conversely, only actual flooding limited the richness of herbaceous plant communities, whilst high water tables excluded certain lineages and favoured others. For herbaceous plant communities, there was species turnover along the water table depth gradient, consistent with species having distinct hydrological niches. Although further studies should investigate if these diversity patterns are widespread in savanna communities that occur in poorly-drained sites, and how they interact with fire regime, these findings clearly suggest that herbaceous and woody plant communities will respond differently to shifting hydrological regimes under global environmental change.

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Disclosure of potential conflicts of interest

Authors declare no conflict of interest.

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Tables

Table 1. The effect of water table depth and the most significant additional soil property (in terms of model fit) on the local species richness and phylogenetic clustering of the herbaceous and woody layer in savannas in southeast Brazil, using the generalized linear models. Models assumed negative binomial and Gaussian distributions, respectively.* -p<0.05, **p<0.01, ***p<0.001

Model	Fixed effects	Estimate	SE	*t*
Species Richness				
Herbaceous layer	log(water table depth)	0.20	0.06	3.65***
	soil P	-0.10	0.05	-1.90
Woody layer	log(water table depth)	2.09	0.30	6.97***
	soil P	-0.38	0.19	1.98*
Lineage Diversity				
Herbaceous layer	log(water table depth)	0.83	0.21	3.97***
	base saturation	0.37	0.21	1.78
Woody layer	log(water table depth)	-0.26	0.19	-1.39

Table 2. Results of the generalized additive models estimating the effect of groundwater depth on the local species richness and phylogenetic clustering of the herbaceous and woody layer in savannas in southeast Brazil. Models estimating effects on richness and lineage diversity assumed negative binomial distribution and Gaussian distributions, respectively. edf - effective degrees of freedom. * -$p<0.05$, **$p<0.01$, ***$p<0.001$

Model	edf	Chi.sq/F	R^2 adj
Richness			
Herbaceous layer	1.00	5.14*	0.24
Woody layer	3.55	75.8***	0.88
Lineage diversity			
Herbaceous layer	5.32	13.61***	0.82
Woody layer	1.00	0.00	-0.11

Figure legends

Fig 1. Study site and experimental design. a) Satellite image of the Itirapina Ecological Station showing each of the 19 study sites, including marshy grasslands (rhombuses), wet grasslands (crosses) and savannas with low (squares), intermediate (triangles) and high (circles) woody cover. b) Design of a study site with the six 10 x 10 m sample plots (woody layer sampling) and detail of a plot with six the 1 x 1 m subplots (herbaceous layer sampling).

Fig 2. Relationship between species richness and lineage diversity of the herbaceous a,c) and woody layer b,d) and the water table depth in a Neotropical savanna in southeast Brazil. Negative values of lineage diversity indicate phylogeneetic clustering and positive values indicate phylogenetic overdispersion. Lines are predicted values based on the results of generalized additive models and dashed lines indicate 95% confidence intervals

Fig 3. Occurrence of a) herbaceous and b) woody species along a water table depth gradient in Southeast Brazil, highlighting the distinct pattern of changes in species composition shown by herbaceous (turnover) and woody plant communities (nestedness). Species of each layer are ranked by their average water table occurrence ((minimum water table depth occurrence + maximum water table depth occurrence) / 2).

Fig 1.

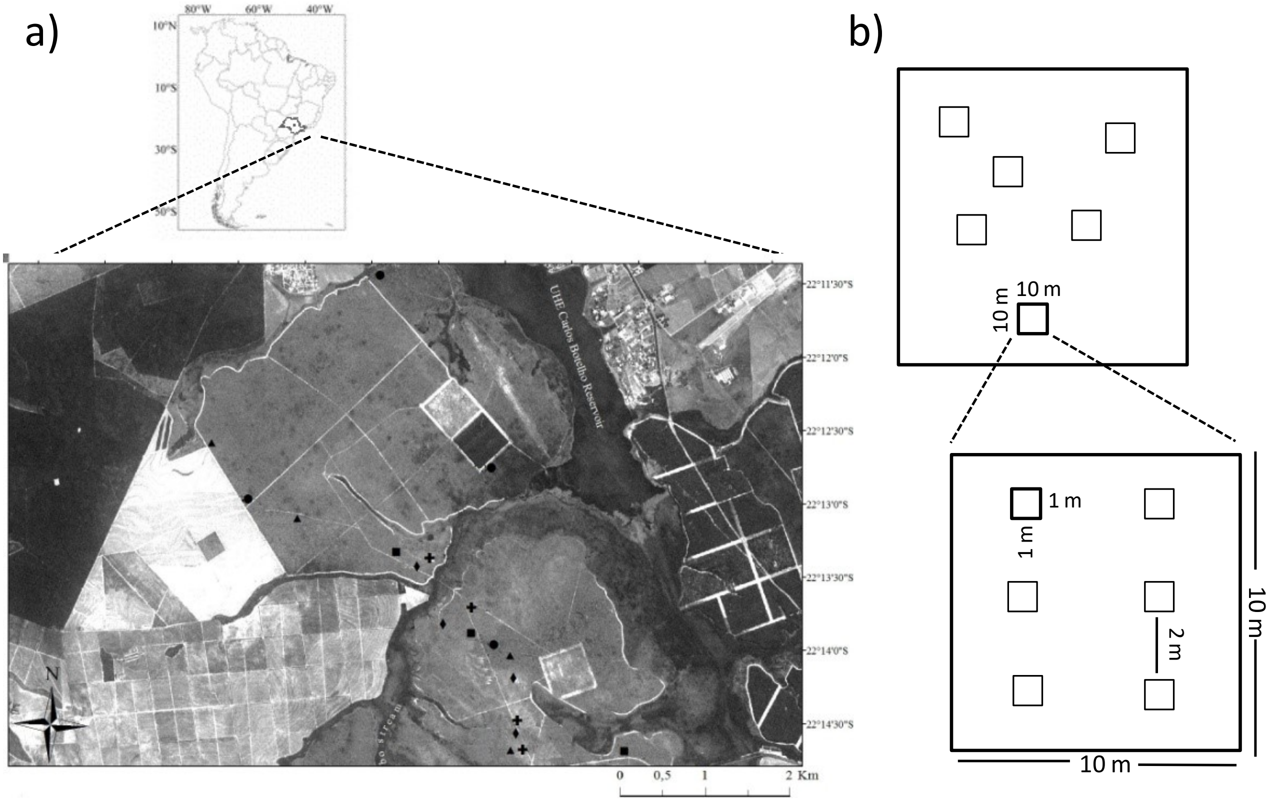

a)
80°W
60°W
40°W
10°N
10°S
30°S
50°S
22°11'30"S
22°12'0"S
22°12'30"S
22°13'0"S
22°13'30"S
22°14'0"S
22°14'30"S
UHE Carlos Botelho Reservoir
N
0
0,5
1
2 Km
b)
10 m
10 m
1 m
1 m
2 m
10 m
10 m

Fig 2.

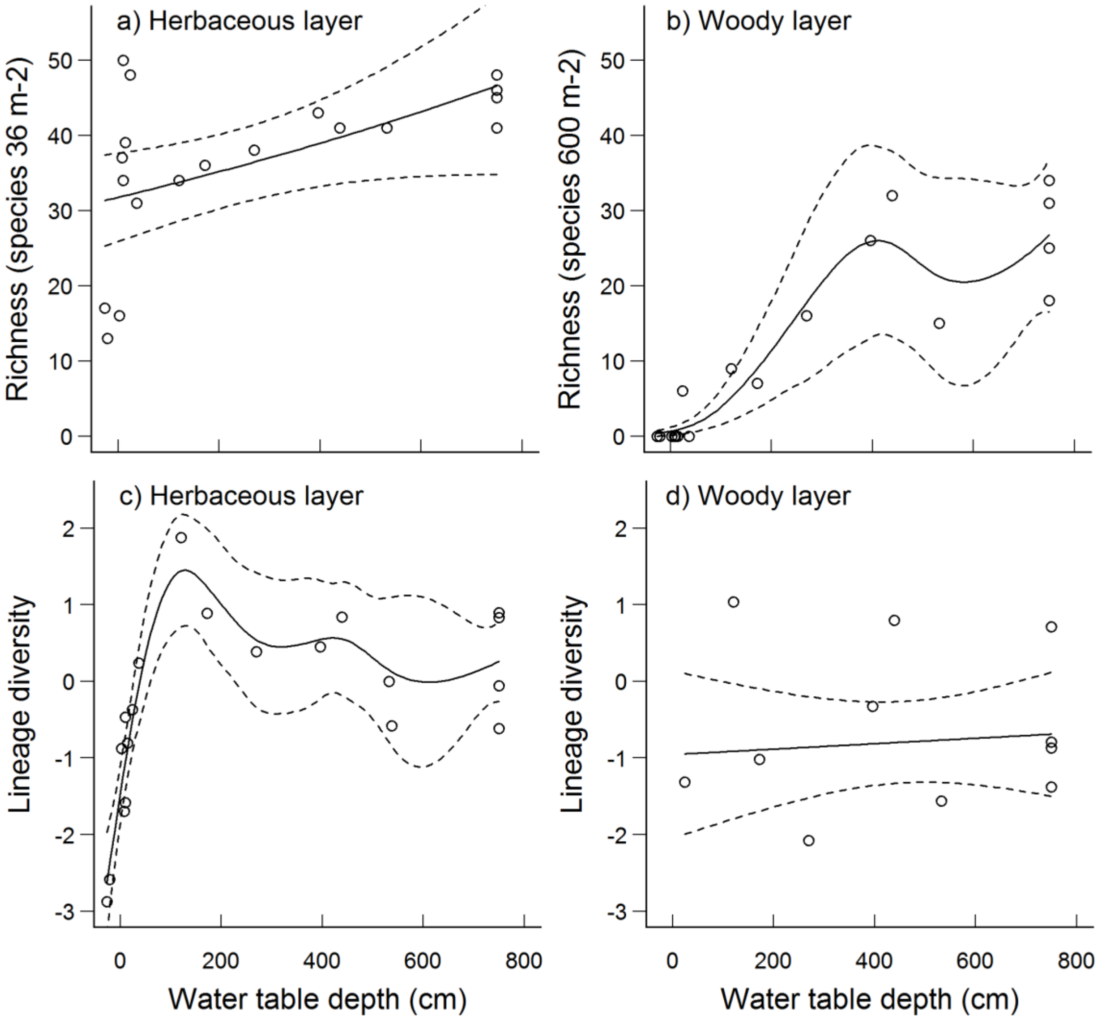
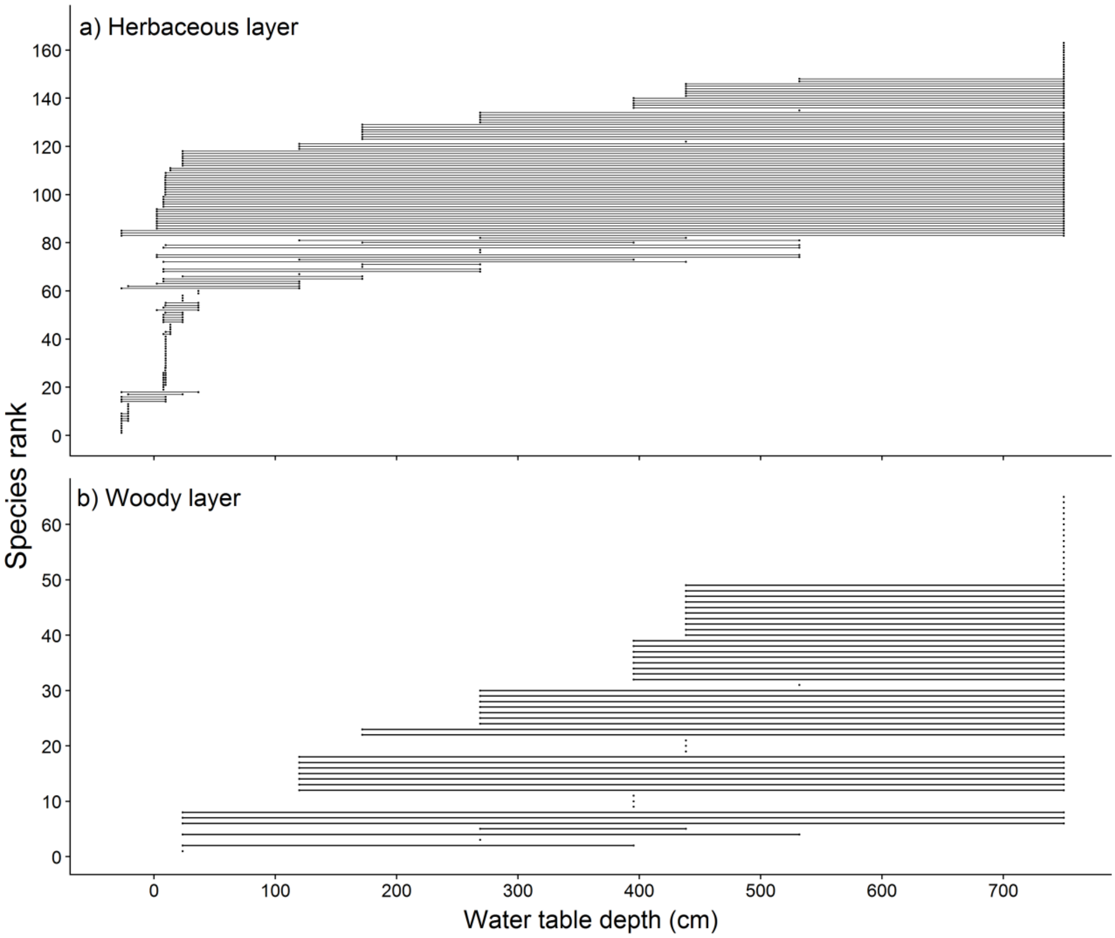

a) Herbaceous layer
b) Woody layer
c) Herbaceous layer
d) Woody layer
Richness (species 36 m-2)
Richness (species 600 m-2)
Lineage diversity
Lineage diversity
0
10
20
30
40
50
-3
-2
-1
0
1
2
0
200
400
600
800
Water table depth (cm)
Water table depth (cm)

Fig 3.


a) Herbaceous layer
160
140
120
100
80
60
40
20
0
b) Woody layer
60
50
40
30
20
10
0
Species rank
0
100
200
300
400
500
600
700
Water table depth (cm)