Spatial Variations in Soil Chemistry and Organic Matter Content across a *Vochysia divergens* Invasion Front in the Brazilian Pantanal

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The Pantanal is a large and diverse wetland that spans three South American countries including parts of Brazil, Paraguay, and Bolivia. An invasive tree, *Vochysia divergens* Pohl (commonly known as Cambara), has been expanding throughout the Pantanal for more than four decades forming monospecific stands. Given the rapid and extensive spread of Cambara, and the potential for woody plant invasion to alter soil organic matter and nutrient stocks, we hypothesized that Cambara invasion would significantly increase soil organic matter and nutrient content. To test this hypothesis we sampled the soil, litter, and vegetation of a monospecific Cambara stand, a grassland (campo) stand in the process of Cambara invasion (transitional), and a campo stand free of Cambara during the dry season in July and August of 2009 and 2010 when stands were free from seasonal flooding. Surface (0–10 cm) soil in sites dominated by Cambara had significantly higher soil organic matter (SOM), P, and cation content, and higher cation exchange capacity (CEC), but soil pH and K^+ concentration were less coincident with Cambara presence. The variation of soil characteristics was also significantly higher in the transitional site, indicating that the transition from a grassland- to a Cambara-dominated system significantly increased the spatial variability of soil chemistry. These results indicate that Cambara invasion fundamentally alters the C and nutrient storage of Panatanal soils. Future research will investigate if these results are general for Cambara invasion and address mechanisms of how Cambara invasion affects the nutrient cycling and storage of Pantanal soils.

Abbreviations: CEC, cation exchange capacity; LAI, leaf area index.

The Pantanal is a 150,000 km^2 wetland that spans three countries (Brazil, Paraguay, and Bolivia), with the majority (71%) located in the Brazilian states of Mato Grosso and Mato Grosso do Sul (Haase, 1999). As the largest wetland in the world, the Pantanal is considered to be extremely diverse, with approximately 144 families of higher plants and more than 1000 plant species (Junk and da Cunha, 2005).

But this diversity is vulnerable because of external land use practices, changes in hydrology and climate, and invasive species (Junk et al., 2006). In terms of invasive species, the spread of *Vochysia divergens* Pohl (commonly known as Cambara) in the Pantanal is a well-documented example. *Vochysia divergens* is a native tree of the Brazilian savanna (*cerrado*) and riparian forest (*mata ciliar*) (Lorenzi, 2002), and is a flood-adapted pioneer species that has been vigorously spreading into seasonally flooded cerrado (locally referred to as *campo cerrado*) for more than four decades (Nunes da Cunha and Junk, 2004). *Vochysia divergens* can grow to heights of 28 to 30 m and has a dense leafy crown that effectively shades-out grasses, forbs, and trees, forming dense, species-poor monocultures known as *Cambarazais* (Nunes da Cunha and Junk, 2004). The reason for the invasion is still poorly understood; however, interactions between inundation, soil physical properties, and fire appear to be critical for invasion success (Zeilhofer and Schessl, 1999; Nunes da Cunha and Junk, 2004). During high rainfall years prolonged flooding allows seedling

recruitment to occur before the dry season when the probability of tree mortality increases, while during dry years, fire is an important agent for limiting the distribution of Cambara outside the riparian zone (Nunes da Cunha and Junk, 2004).

Woody plant invasion has the capacity to alter a variety of ecosystem properties including microclimate, soil C storage and chemistry, water and nutrient availability, plant growth and productivity, plant and animal abundance, and biodiversity (Zeilhofer and Schessl, 1999; Mack et al., 2000; Nunes da Cunha and Junk, 2004; Ashton et al., 2005; Lite and Stromberg, 2005; Liao et al., 2008; Liu et al., 2011). In particular, woody plant invasion has been found to significantly increase the root, litter, and soil C content and plant and litter N concentration because more extensive root systems of woody invaders explore a larger soil volume and return more N-rich litter (Liao et al., 2008). As areas become invaded the spatial variability of soil pools reportedly increases (Liu et al., 2011) because trees concentrate nutrients below the forest canopy. The concentration of nutrients can cause the development of "islands of fertility," which increase in the special patchiness of soil resources (Feldpausch et al., 2004; Troxler Gann et al., 2005; Wetzel et al., 2005; Hanan and Ross, 2010). In grasslands, an increase in the spatial patchiness of soil resources can limit the distribution of native grasses and further promote the persistence of trees (Schlesinger et al., 1996).

Given the potential effects of woody invasion on soil organic matter and nutrient stocks, and the rapid and extensive spread of Cambara, our goal was to quantify soil chemistry and organic matter content along an established *V. divergens* invasion front in the Pantanal of southern Mato Grosso, Brazil. We hypothesized that soil organic matter and nutrient concentration would be significantly higher in areas invaded by Cambara. Furthermore, we hypothesized that the soil organic matter and nutrient concentration would be significantly more variable in areas that are currently being invaded by Cambara. To test these hypotheses we identified three sites along a Cambara invasion front, including a mono-specific Cambarazal, a site in the process of Cambara invasion, and a campo-cerrado stand free of Cambara, and sampled surface soil and litter pools during the dry season of 2009 and 2010.

MATERIALS AND METHODS
Site Description

The field study was conducted in the northern Brazilian Pantanal (16°39'50" S; 56°47'50" W), approximately 160 km south southwest from Cuiabá and 60 km southeast from Poconé, Mato Grosso, Brazil (Fig. 1). Study sites were located within a protected nature reserve, the Reserva Particular do Patrimônio Natural (RPPN) of the Serviço Social do Comércio (SESC)-Pantanal. Annual rainfall of the region is on average 1400 mm with a pronounced dry season extending from May through September (Nunes da Cunha and Junk, 2001). The topography of the floodplain is virtually flat, causing extensive flooding during the wet season (Nunes da Cunha and Junk, 2001). Wet-season floods are 1 to 2 m in depth, but during the dry season many of the floodplain lakes become disconnected from the river channel as the floodwater recedes

(Nunes da Cunha and Junk, 2004). The soil type of the study site is classified as a Gleyic Solonetz (Zeilhofer, 2006).

Three sites that varied in the density of *V. divergens* were identified along a Cambara invasion front (Fig. 1). According to park rangers and satellite imagery, Cambara has been spreading into the adjacent campo stands for at least one to two decades. All three study sites are within 3 km of each other and are seasonally flooded with up to 1 m of surface water during the November to May wet season (Biudes, 2008). The first site was a monospecific stand of *V. divergens* (hereafter referred to as the *Cambarazal*) with a mean canopy height of 25 m and an elevation of 122 m above sea level (asl). The study site was approximately 0.5 ha; however, the spatial distribution of the Cambarazal is more than 2 km wide and 10 km long. Surface soil texture was a mix of clay-loam and clay (Table 1). The second site was a mixed forest-grassland that is in the process of being invaded by *V. divergens* (hereafter referred to as the transitional site). Common tree species of the transitional site include *V. divergens* and *Curatella americana* L. (Dilleniaceae), while the understory is composed of the grass *Gymnopogon spicatus* (Spreng.) Kuntze and the herbaceous perennial *Mimosa pellita* H. et B. (Mimosaceae). The study site was approximately 0.5 ha and 111 m asl, and the soil texture was primarily a sandy-clay loam (Table 1). The final location was a grass-dominated campo-cerrado (hereafter referred to as *campo*) with *G. spicatus* and *M. pellita* as the primary species. Campo cerrado is the major land cover type of the Pantanal (Nunes da Cunha and Junk, 2004). The site studied here was 0.5 ha in area and 107 m asl. Soil texture varied between clay and sandy-clay loam (Table 1).

Field Sampling and Laboratory Analysis

Field sampling occurred on 12–15 July 2009 and 10–13 Aug. 2010, which is during the climatological dry season (Nunes da Cunha and Junk, 2004). Sample points at each site were selected using a stratified random design. First, a random point was selected every 10 m along a 100 m long baseline transect. At each point, a direction perpendicular to the baseline was randomly selected. Finally, in the randomly determined direction, a 1m^2 circular plot was randomly established within 20 m of the baseline. In each plot, vegetation attributes (leaf area index and Cambara density and basal area) were measured and soil and litter samples were collected. In 2009, a total of nine plots per site were sampled in the Cambarazal and transitional stands and five plots were sampled in campo, while in 2010, five plots were sampled in each site.

The density and basal area of *V. divergens* was measured in 2009 at each site using the point-quarter method (Goldsmith and Harrison, 1976). Each plot was divided into four-quadrants based on the cardinal compass directions. Within each quadrant the distance to the nearest *V. divergens* individual and the trunk circumference at breast height (1.3 m) was measured. Density was calculated as a function of the mean distance (Goldsmith and Harrison, 1976) and the basal area was calculated by converting the circumference into trunk area (m^2/individual) and multiplying by the density (individuals/m^2). At the transitional and campo sites, leaf area index (LAI) was measured in each plot using a photosynthetically active radiation (PAR)-ceptometer (AccuPAR LP-80, Decagon Devices, Inc., Pullman, WA). The LAI was calculated from the ceptometer software assuming a spherical leaf angle distribution. For the Carambazal, LAI was calculated from PAR
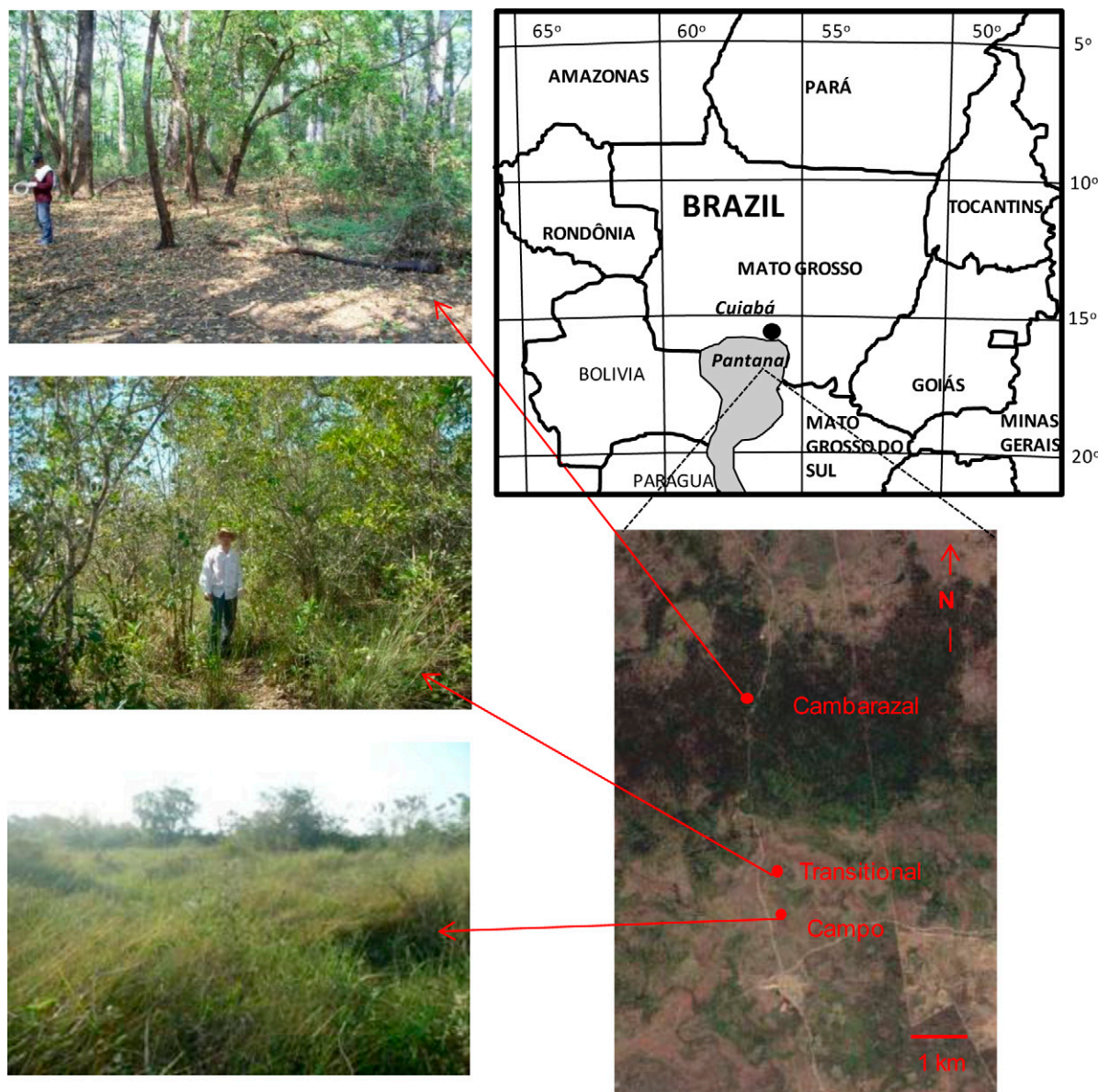
Fig. 1. Map of Mato Grosso, Brazil and the location of the study sites in the Particular Reserve of Patrimônio Natural (RPPN) of the Serviço Social do Comércio (SESC)-Pantanal. Shown is the site with the monospecific stand of mature *Vochysia divergens* (Cambarazal), the site being invaded by *V. divergens* (Transitional), and the site free from *V. divergens* invasion (campo). The image is from the IKONOS satellite (http://www.cartographic.com) accessed on 6 May 2009. Photos were taken by M. Biudes (Cambarazal), G. Vourlitis (Transitional), and H. Dalmagro (Campo).

measurements made above (32 m) and below the canopy (2 m) using quantum sensors (LI-190SB, LI-COR, Inc., Lincoln, NE) attached to a meteorological tower. Forest floor PAR measurements were made at 2 m because this is the maximum depth of standing water during the wet-season flood (Biudes, 2008) and because there was a sparse plant understory below this height. The LAI was estimated from solar elevation data (Beer, 1990) assuming a spherical leaf-angle distribution (Goudriaan, 1988).

The surface litter pool mass was measured at each site in 2010 by collecting all of the surface litter within 25 by 25 cm quadrats that were randomly arrayed within each plot. Litter was defined as dead plant matter that was recognizable and >1 mm in size. Litter samples were lightly rinsed with distilled water to remove mineral debris, dried at 70°C for 1 wk, and weighed to the nearest 0.01 g using a digital balance.

Soil core samples approximately 5 cm in diameter (120 cm^3 in volume) were obtained from each plot from the upper 10 cm soil layer using a hammer core. Samples were analyzed for pH, extractable P, and cation (K$^+$, Ca^{2+}, Mg^{2+}, Al^{3+}, and H$^+$) content, and soil organic matter (SOM) content using a commercial soil analysis laboratory (ArgoAnalise, Inc., Cuiaba, Mato Grosso, Brazil). Briefly, soil pH was analyzed in distilled water extracts from 1:2.5 soil/extract proportions using a standard pH meter (PMPH-1, Digimed, São Paulo, Brazil). Soil extractable P and K$^+$ was analyzed colorimeterically from Mehlich (0.05 M HCl + 0.025 M H$_2$SO$_4$) extracts using a spectrophotometer (Q1–108D, Quimis, São Paulo, Brazil) and a flame photometer (DN-61, Digimed, São Paulo, Brazil), respectively. Soil extractable Ca^{2+} and Mg^{2+} were analyzed from 1 M KCl extracts using a flame-Atomic Absorption spectrometer (AA-275; Varian, Inc., Palo Alto, CA). Soil extractable Al^{3+} and H$^+$ were analyzed by titration using a digital

burette (Model 236–080, Jencons, Leicestershire, UK) from 1 M KCl extracts. Soil organic matter was analyzed colorimeterically using the Walkley–Black method (Nelson and Sommers, 1996). Soil CEC was calculated as the sum of all measured cations (Robertson et al., 1999).

Statistical Analysis

The ANCOVA was used to test whether soil physical and chemical properties varied between the sites arrayed along the Cambara invasion front. Soil clay content was used as a covariate to limit the potential for varying clay content to confound the effects of Cambara invasion status on the soil chemistry (Sokal and Rohlf, 1995). Site and time (year) treated as fixed effects, and although our main objective was to test the hypothesis that soil properties varied along the invasion front, we also analyzed whether there were any significant temporal variations in soil chemical properties and whether the effect of site varied as a function of time. While repeated-measures ANOVA may be more appropriate for analyzing time series, a repeated-measures ANOVA assumes that each subject (plot) is sequentially sampled over time (Sokal and Rohlf, 1995). This was not the case, as plots were randomly located within each site during each sampling event. Differences between means were determined by assessing whether 95% confidence intervals overlapped (Sokal and Rohlf, 1995). To test whether the variation in soil physical and chemical properties were higher in the transitional site we first calculated the coefficient of variation [(standard deviation/mean) × 100] of soil organic matter, and extractable P, K, and cation content for each site and then used bootstrapping over 1000 iterations to calculate the mean (±95% confidence interval) CV for each site (Efron and Tibshirani, 1993). The CV is an effective measure for quantifying the relative variation of response variables at each site (Schlesinger et al., 1996), and because it is dimensionless it can be used to statistically test whether the variability of soil chemical properties differs among sites (Sokal and Rohlf, 1995). Statistical analyses were conducted using SPSS 18 statistical software.

RESULTS
Stand Characteristics

The density and basal area of *Vocyhsia divergens* (Cambara) varied markedly among the study sites (Table 1). Cambara density was significantly higher in the transitional site (student's $t_{16} = 2.31$; $p < 0.05$) than in the Cambarazal, and no Cambara individuals were recorded in the campo stand. The Cambara individuals that were invading the transitional site had low basal area, indicating a high density of small, colonizing trees, while individuals in the Cambarazal had a basal area that was on average 50.2 m^2/ha (Table 1), indicating a well-developed stand of large individuals. Leaf area index and the surface litter pool; however, were similar at each site (Table 1).

Soil Organic Matter and Chemical Properties along the Cambara Invasion Front

The pH of surface (0–10 cm) soil was not significantly different among the study sites; however, surface soil pH varied significantly over time and there was a significant site × time interaction (Fig. 2a). In contrast, differences in soil organic matter varied significantly between sites, and the Cambarazal had the highest soil organic matter content followed by the campo and the transitional sites (Fig. 2b).

The largest difference in soil chemistry observed between the sites was with soil extractable P, and the Cambarazal had more than 10-times higher extractable P than the transitional and campo sites (Fig. 3a). Spatial variations in extractable K$^+$ were not significantly different between sites but there was a significant site × time interaction (Fig. 3b).

The Cambarazal had the highest concentration of exchangeable cations and cation exchange capacity followed by the campo and transitional sites (Fig. 4). For Ca^{2+} and Mg^{2+} the Cambarazal had threefold higher exchangeable cation concentration in 2009, but smaller differences were observed in 2010 (Fig. 4). However, for Al^{3+}, H$^+$, and CEC, differences between sites were more consistent for 2009 and 2010 and indicate a three to fivefold higher cation content and exchange capacity for the Cambarazal (Fig. 4).

The relative variation in the soil properties within a given site, quantified as the coefficient of variation (CV = [standard deviation/mean] × 100), was significantly different for the Cambarazal, transitional, and campo sites. For example, the mean (± 95% confidence interval) CV for the Cambarazal and campo sites was 18.8 ± 4.7 and 18.3 ± 3.6, respectively while the mean value for the transitional site was 36.8 ± 12 (Fig. 5). These data indicate that the relative spatial variation in the exchangeable cations was significantly higher at the transitional site.

DISCUSSION

We hypothesized that soil organic matter and nutrient concentration would be significantly higher in areas invaded by Cambara. While the spatial and temporal extent of the field study was limited, ANCOVA results indicated that soil organic matter (SOM), extractable P, Al^{3+}, and H$^+$, and CEC was significantly higher in the monospecific Cambara stand. Other cations, such as Ca^{2+} and Mg^{2+}

Table 1. Site characteristics, mean (± se) density and basal area of *Vochysia divergens*, and canopy leaf area index for the cambarazal, transitional, and campo vegetation types arrayed along a *V. divergens* invasion front in the Brazilian Pantanal. Numbers in parentheses refer to the sample size used to obtain the displayed data (see text for a detailed description of sampling design and protocol).

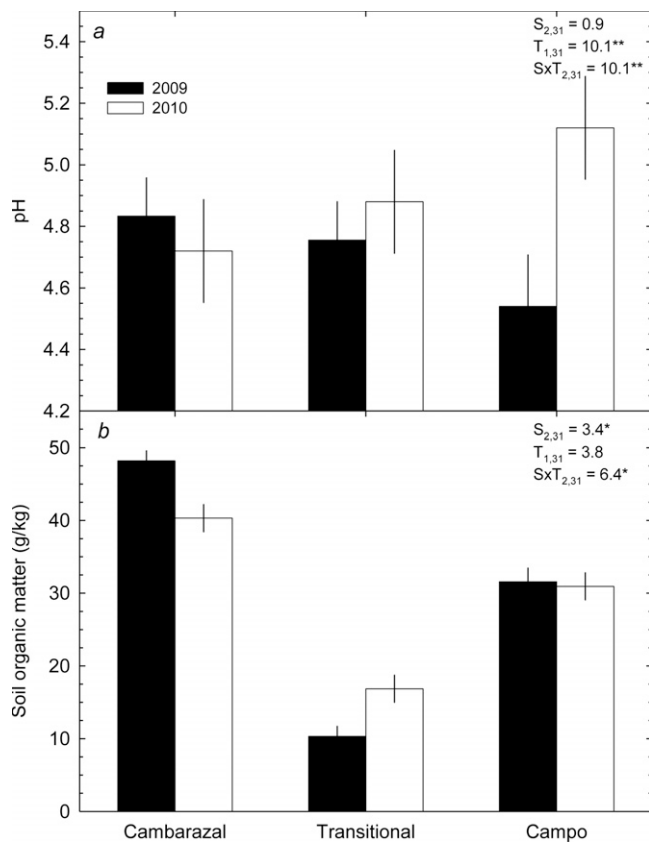| Variable	Site		
	Cambarazal	Transitional	Campo
Dominant plant species	*Vochysia divergens*	*Vochysia divergens, Curatella americana, Gymnopogon spicatus, Mimosa pellita*	*Gymnopogon spicatus, Mimosa pellita*
Density, trees ha^{-1}	210 ± 82 (9)	1134 ± 639 (9)	0 ± 0 (5)
Basal area, m^2 ha^{-1}	50.2 ± 14.7 (9)	0.2 ± 0.2 (9)	0.0 ± 0.0 (5)
Leaf area index, m^2 m^{-2}	3.3 (1)	3.5 ± 0.4 (9)	3.9 ± 0.8 (9)
Soil texture class	clay	sandy clay loam	sandy loam-clay
Surface litter content, kg m^{-2}	1.30 ± 0.12 (5)	1.25 ± 0.14 (5)	1.41 ± 0.19 (5)

Fig. 2. Mean (± 95% confidence interval) (a) pH and (b) organic matter content of surface (0–10 cm) soil in the Cambarazal, transitional, and campo stands in 2009 (solid-bars) and 2010 (open-bars). Also shown are the results (*F* statistics and degrees of freedom) from ANCOVA for differences between site (S), time (T), and the site × time interaction (S×T). For ANCOVA soil clay content was treated as the covariate and site and time were treated as fixed effects. *, *p* < 0.05; **, *p* < 0.01; *, *p* < 0.001.**

Fig. 3. Mean (± 95% confidence interval) extractable (a) P and (b) K concentration of surface (0–10 cm) soil in the Cambarazal, transitional, and campo stands in 2009 (solid-bars) and 2010 (open-bars). Also shown are the results (F statistics and degrees of freedom) from ANCOVA for differences between site (S), time (T), and the site × time interaction (S×T). For ANCOVA soil clay content was treated as the covariate and site and time were treated as fixed effects. *, *p* < 0.05; **, *p* < 0.01; *, *p* < 0.001.**

were also on average higher in the Cambara stand; however, the significant site × time interaction indicates that the spatial differences were dependent on time. Such interactions may arise from interannual variations in the magnitude and/or duration of seasonal flooding (Troxler-Gann et al., 2005). These results indicate the development of monospecific Cambara stands significantly alters soil chemistry in the Brazilian Pantanal.

Cambara establishment may lead to the concentration of nutrients below the forest canopy and the development of "islands of fertility" (Feldpausch et al., 2004; Troxler Gann et al., 2005; Wetzel et al., 2005; Hanan and Ross, 2010). For example, in wetlands such as the Florida Everglades, nutrients accumulate under stands of large trees that are distributed throughout a grass-dominated wetland mosaic (Troxler Gann et al., 2005; Wetzel et al., 2009). In these patterned ecosystems, total and available nutrients such as P can be 10 to 100 times higher under established tree canopies than in grassland (Troxler Gann et al., 2005; Wetzel et al., 2005; Hanan and Ross, 2010), which is qualitatively similar to what was found in the Cambarazal.

Nutrient accumulation in tree islands has been explained by numerous mechanisms, including the evapotranspiration (ET) pumping of leached nutrients from groundwater,
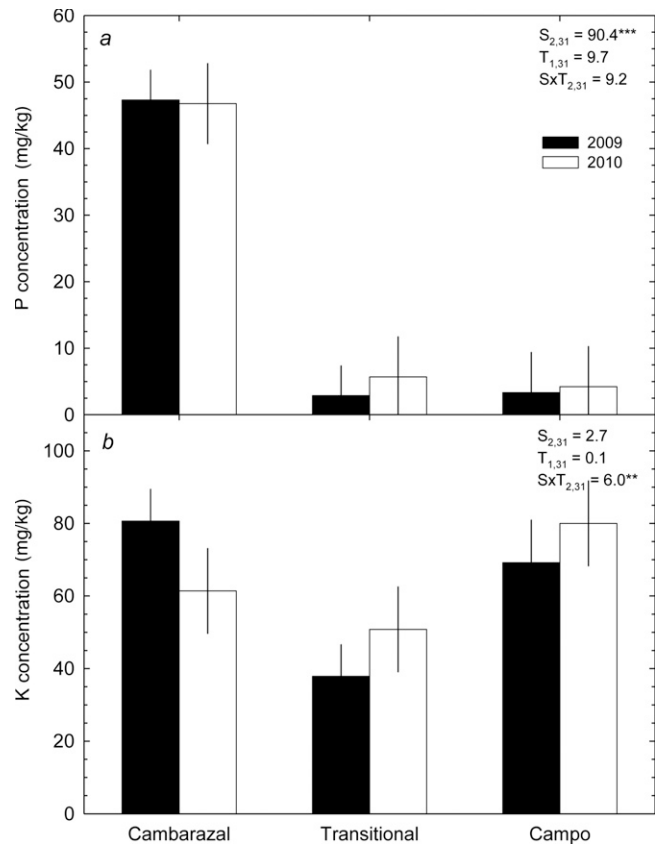
hydraulic redistribution (also known as hydraulic lift), larger inputs of nutrient-rich litter, and/or an increase in throughfall nutrient inputs in the high LAI tree islands (Wetzel et al., 2005; Saha et al., 2010). The similar LAI between the campo and Cambarazal stands suggests that the rates of throughfall are likely to be similar as well. Rather, the increase in nutrient concentration in the Cambarazal is presumably due to the redistribution of leached nutrients by Cambara. Rates of ET are higher in forests than in grass-dominated ecosystems such as pasture (Priante Filho et al., 2004; Biudes, 2008) and campo cerrado (Santos et al., 2003; Oliveira et al., 2005), especially during the dry season. Higher rates of ET are possible in forested areas because tree roots have access to deep water while grass-dominated campo cerrado and pasture have a shallower root system and a greater reliance on surface water (Vourlitis and da Rocha, 2010). In this forest most of the dry-season ET is from transpiration rather than evaporation (Vourlitis et al., 2008) because the soil surface in forested ecosystems receives less radiation and is typically cooler than in grass-dominated ecosystems (Hodnett et al., 1995; Culf et al., 1996). Trees can redistribute deep water to the soil surface through hydraulic redistribution (also known as
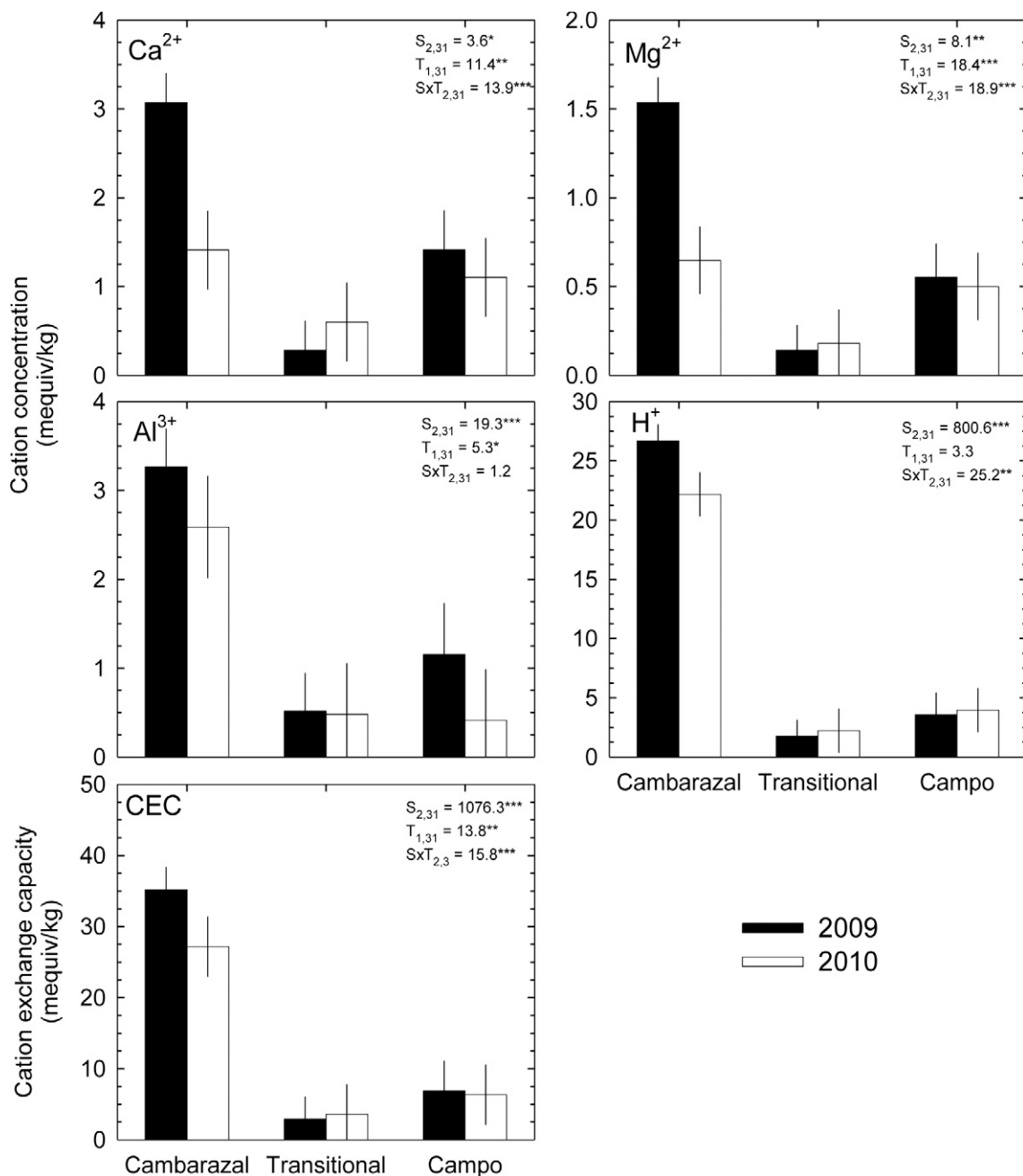
Fig. 4. Mean (± 95% confidence interval) extractable (a) Ca, (b) Mg, (c) Al, and (d) H concentration and (e) the CEC of surface (0–10 cm) soil in the Cambarazal, transitional, and campo stands in 2009 (solid-bars) and 2010 (open-bars). Also shown are the results (F statistics and degrees of freedom) from ANCOVA for differences between site (S), time (T), and the site × time interaction (S×T). For ANCOVA soil clay content was treated as the covariate and site and time were treated as fixed effects. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

hydraulic lift), where water taken up by deeply rooted trees is transferred from wetter to drier soil layers at night (Oliveira et al., 2005). Soil collected during the height of the dry season was saturated with water in the Cambaraza, but in the campo and transitional sites soil water content was <10% by weight. These differences were not because the Cambarazal was at a lower elevation (Table 1), and thus, exposed to higher and/or a longer duration of flooding than the other sites. Rather, reduced rates of soil water loss from evaporation, and the redistribution of deep water discussed above, would presumably keep the soil moist throughout the dry season (Oliveira et al., 2005). These mechanisms of soil water redistribution are undoubtedly

important mechanisms for dissolved nutrients as well (Wetzel et al., 2005; Saha et al., 2010).

The potential for the Cambarazal to produce more nutrient-rich litter is less clear because comparative studies of litter production between Cambarazais and campo stands are lacking. Nutrient storage is thought to be greater in woody than herbaceous tissue (Delitti et al., 2006), and soil and litter nutrient stocks have been found to significantly increase in grasslands invaded by woody trees and shrubs (Liu et al., 2011). In particular, Cambara has been found to accumulate Al^{3+} in leaf litter and P in stem wood (Haase, 1999), which is consistent with the large increase in soil extractable Al^{3+} and P

in the cambarazal. However, surface litter pools were statistically similar among the sites, suggesting that rates of litter input were similar as well. In addition, studies from cerrado, Amazonian forest, and pasture indicate a wide variation in tree and grass foliage and litter nutrient content depending on soil type and fertility, stand age, and past land-use history (Batmanian and Haridasan, 1985; Numata et al., 2003; Feldpausch et al., 2004). Thus, it is currently unclear whether Cambara produces litter with a higher nutrient concentration than the campo it replaces.

Soil organic matter content in the Cambarazal was higher than in the campo and transitional sites even though the differences in LAI and the surface litter pool were negligible. An increase in woody root and litter biomass in grasslands invaded by trees has been shown to significantly increase soil C stocks in a variety of studies (Liu et al., 2011). In addition, the higher SOM content in the Cambarazal may also result from differences in the surface soil environment, especially water content as mentioned above. The SOM decomposition is substantially slower in cooler, wetter soils (Sotta et al., 2004; Valentini et al., 2008) that were likely typical of the Cambarazal.

The transitional stand had a significantly higher density of small (low basal area) trees, which presumably reflects recent Cambara invasion. The Cambarazal and campo stands represent end-points of a grass-tree continuum, and grasslands in the process of being invaded by woody trees and shrubs typically exhibit an increase in the spatial variation of soil resources (Archer, 1990; Schlesinger et al., 1996; Liao et al., 2008). In turn, the development of a highly variable distribution of soil resources may lead to the development of islands of fertility, which can positively feed-back and promote the establishment and persistence of a Cambarazal (Ponce and da Cunha, 1993) or tree island (Troxler-Gann et al., 2005; Hanan and Ross, 2010).

In conclusion, a monospecific stand of *V. divergens* (Cambara) in the Brazilian Pantanal was found to have higher SOM, extractable P, cation content, and CEC than uninvaded campo and a site in the process of Cambara invasion. These results are qualitatively similar to those reported for other forested stands within grassland and wetland matrices, and indicate fundamental changes in soil nutrient cycling and storage by the invasion of Cambara. Presumably, the higher SOM content of the Cambarazal is due to environmental limitations to SOM decomposition, while the higher P and cation content in the Cambarazal is due to the redistribution of leached P and cations from evapotranspiration and/or an increase in input of nutrient-rich litter. Future research will investigate whether these results are general in response to Cambara invasion and address mechanisms of how Cambara invasion affects the nutrient cycling and storage of Pantanal soils.
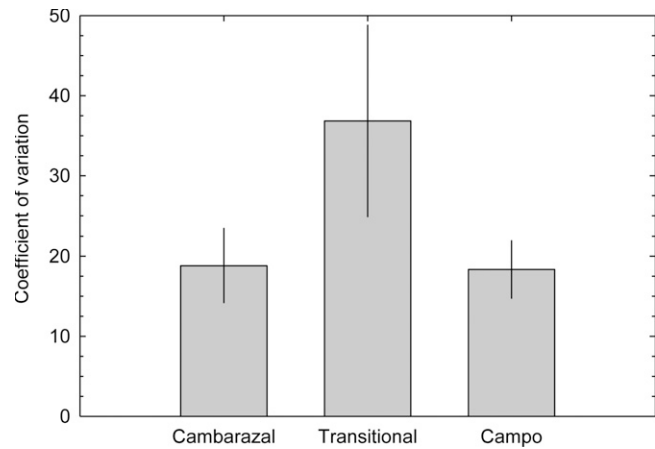
ACKNOWLEDGMENTS

Fig. 5. Mean (±95% confidence interval) coefficient of variation (CV = [standard deviation/mean] × 100) for the soil organic matter and extractable P and cation concentrations of surface (0–10 cm) soil in the Cambarazal, transitional, and campo stands. The mean (± 95% confidence interval) was calculated for each site by calculating the average CV from all of the individual CVs of each soil response variable and bootstrapping the average CV over 1000 iterations.

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