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ASSESSMENT OF STAND CHARACTERISTICS AND SOIL OF UPPER PARANA ATLANTIC FORESTS (PARAGUAY) REVEALS HIGH HABITAT HETEROGENEITY

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The Upper Parana Atlantic Forest (UPAF) harbours some of the most endangered ecosystems in the world. However, little data are available on UPAF ecosystems, constraining effective protection and restoration efforts. The objective of this study was to classify UPAF forests, focusing on the stand structure, tree species diversity, tree species composition, and soil properties and their relationships with stand characteristics. We established 71 plots (50 m × 20 m) distributed across eight protected areas in the Paraguayan UPAF and evaluated trees with diameter at breast height ≥ 10 cm and composite soil samples from 0–20 cm in depth. We identified four forest types with their corresponding indicator species. Among these forest types, we observed significant differences between stand structure and tree species diversity. We separated the soil properties into two axes, with essential elements and pH on one axis, and the balance of clay and sand contents on the other. We found significant relationships between essential elements and pH and individual density, and between the balance of clay and sand contents and tree species diversity. Our findings explain the heterogeneity of the tree community and contribute to our understanding of the UPAF, enabling science-based and better-focused forest conservation and restoration programmes.

Keywords: Stand structure, species diversity, stand characteristics, forest types, indicator species, restoration, savanna forest

INTRODUCTION

The Atlantic Forest ecoregion complex is distributed across Paraguay, Brazil, and Argentina and encompasses high species diversity, including 20,000 species of plants, of which 8000 are endemic (Myers et al. 2000, Mittermeier et al. 2011). Based on this high diversity of species, the CEPF (2019) identified the complex as one of the 36 most important biodiversity hotspots in the world, and the World Wildlife Fund (Olson & Dinerstein 2002) listed it as one of 200 priority ecoregions for global conservation.

The Upper Parana Atlantic Forest (UPAF) is one of the 15 terrestrial ecoregions that comprise the Atlantic Forest complex, and it constitutes the south-western portion of this biome, extending from eastern Paraguay and Misiones Province in Argentina to the western slopes of the Serra do Mar in Brazil (Di Bitetti et al. 2003). Historically, the UPAF has always been considered a mosaic of savannas and various forest types (Cartes 2003), with semi-deciduous subtropical forest being the most dominant vegetation type (Hueck 1978).

The spatial continuity of UPAF habitats has been disrupted in recent centuries by human activity, and it currently harbours some of the most endangered ecosystems in the world. In Paraguay, the primary threat to habitats continues to be human-induced landuse change particularly the transformation to agricultural land for soybean, beef and cotton production, and forest degradation due to selective logging (Anonymous 2017). As a result, only slightly over 16% of the original vegetation remains in the Atlantic Forest (Anonymous 2017), and the current extent of the UPAF in Paraguay is estimated to have only 10–15% of the original cover (Di Bitetti et al. 2003, Da Ponte et al. 2017). Therefore, forest conservation and restoration are urgently needed to improve the ecological connectivity of the remaining UPAF fragments. There have been many projects in the UPAF focused on forest conservation at local and regional levels. However, many initiatives are still hampered by a lack of precise knowledge about the characteristics of these forest ecosystems. To make restoration initiatives effective in the face of human impact, understanding the heterogeneity of forest ecosystems is of utmost importance in advancing conservation efforts in the UPAF.

Defining the composition of tree species and the connection with soil properties may give us more insight into the formation of each forest type in the UPAF, and this, in turn, may illustrate the process of forest restoration. Species richness of the UPAF flora is attributable to the high beta diversity across this ecoregion, which can be explained by rainfall gradients, soil heterogeneity, and the influence of other adjacent ecosystem types such as savanna (Spichiger et al. 1995, Nascimento et al. 2022). At the local scale, for instance, soil chemical and physical proprieties have been found to be related to tree diversity and structure of the tropical forest and UPAF habitats (Spichiger et al. 1992, Sollins 1998, Nascimento et al. 2022). Considering that the UPAF in Paraguay was originally composed of vegetation mosaics on several types of soils (oxisols, ultisols, alfosols, etc.), the spatial heterogeneity of the habitats should be considered an intrinsic feature in management and conservation (Spichiger et al. 1992, Cartes 2003). For the Paraguayan UPAF, Spichiger et al. (1992) grouped tree communities into (1) tall semi-evergreen forests with Lauraceae, (2) other less extended tall semi-evergreen forest, and (3) low deciduous forests with Myrtaceae, based on tree composition and some soil properties (pH, colour, and sand and clay proportions). However, available data for the UPAF that could enhance protection and restoration efforts are still scarce. Thus, research evaluating stand characteristics and their relationship with soil properties is an important contribution for these efforts.

The present study aims to contribute to a deeper understanding of the characteristics of UPAF habitats focusing on the relationship between soil properties and stand characteristics, i.e. stand structure, tree species diversity, and tree species composition. To achieve this objective, we evaluated tree communities, including palms, cacti and tree ferns, along with soil chemical and physical properties, and analysed relationships among them across 71 plots in eight protected areas in the UPAF managed by ITAIPU Binacional, Paraguay.

MATERIALS AND METHODS

Study site

ITAIPU Binacional is a hydroelectric entity on the Parana River managed by the governments of Brazil and Paraguay. ITAIPU Paraguay acquired the land to establish the following eight UPAF habitat protected areas between 1984 and 2014: Tati Yupi Natural Reserve, Pikyry Natural Reserve, Itabo Natural Reserve, Yvyty Rokái Natural Reserve, Limoy Natural Reserve, Pozuelo Natural Reserve, Carapã Natural Reserve, and Mbaracayú Biological Refuge (Figure 1). This study was conducted in the forests of these eight protected areas (total 38,407 ha).

The topography of these protected areas is flat to slightly undulating, with the elevation ranging from 220 to 330 m asl. Mean annual precipitation was 1665 mm in the northern protected areas and 1855 mm in the southern ones between 1990 and 2020. Mean annual temperature was about 22.0 °C.

Establishment of survey plots

The protected areas contain four different forest physiognomies: high forest (most commercially important forest with canopy above 30 m), low forest (canopy below 8 m), gallery forest, and savanna forest (adjacent to forests). Savanna forest is only found in the Tati Yupi and Yvyty Rokái Natural Reserves. For a representative sampling of each physiognomy, we applied a stratified semi-random sampling approach in which we established 50 m × 20 m plots distributed across the study area.

The initial minimum sample size was calculated using data from 11 permanent plots established previously in the protected areas using the procedures recommended by Kangas and Maltamo (2006). Estimations based on the number of species, individual density, and basal area suggested minimum sample sizes of 52, 57 and 49 plots respectively. Subsequently, to stratify the study area, we carried out a supervised classification using bands 2, 3, and

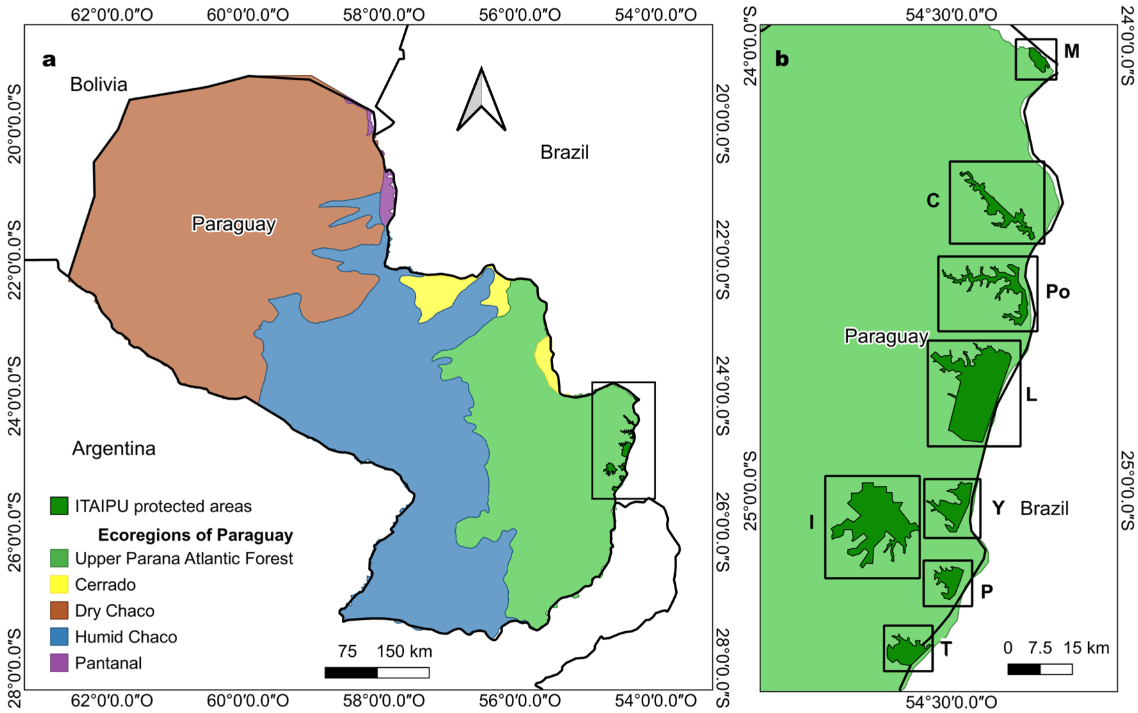

Figure 1 (a) Ecoregions of Paraguay, inset shows location of study site and (b) location of the eight ITAIPU Binacional protected areas in the Upper Parana Atlantic Forest; Tati Yupi Natural Reserve (T), Pikyry Natural Reserve (P), Itabo Natural Reserve (I), Yvyty Rokái Natural Reserve (Y), Limoy Natural Reserve (L), Pozuelo Natural Reserve (Po), Carapã Natural Reserve (C), and Mbaracayú Biological Refuge (M)

4 of Sentinel-2 satellite imagery (RGB colour composite), applying the maximum likelihood classification method of ArcMap 10.3. In this process, we identified high forest, which was the most dominant vegetation type, and grouped the remining low, gallery, and savanna forests and labelled them "other forests". In order to avoid spatial autocorrelation, we divided our study area into 400 m × 400 m cells. We opted to establish 14 more than the calculated 57 plots to enhance sampling representation of the forest types. As a result, we established 71 plots of 1000 m^2 (50 m × 20 m): 57 plots in high forest and 14 plots in other forests, randomly selecting 400 m × 400 m cells for their placement and avoiding spatial autocorrelation. The number of plots designated to each protected area corresponded to their proportion of the total area of the eight protected areas, as did the number of plots per forest type. Each plot was identified with the abbreviation of the protected areas and an identification number (e.g. M1, M2). The plots were installed on the south-western corner of the selected 400 m × 400 m cell unless impediments were found in that corner, in which case the plot was shifted according to a pre-established protocol. The mean elevation of the plots was 255 ± 19 m asl (range: 227–299 m).

Some parts of the study areas were affected by anthropogenic disturbances, including selective logging, agriculture, and human settlements that occurred before the creation of the protected areas. Orthophotos from 1979 showed that 17 plots (24% of all plots) did not have forest cover at that time. However, we did not find a significant relationship between presence/absence of forest cover in 1979 and the two forest categories (high forest and other forests), and we confirmed continuous forest cover for all 71 plots since 1994 using the orthophotos.

Stand structure, tree species diversity and tree species composition

Tree census

The field work was conducted between 2018 and 2019. Species, diameter at breast height (DBH), and height (H) were recorded for all trees, palms, cacti, and tree ferns with DBH ≥ 10 cm

(Condit 1998, TEAM Network 2010). We chose to target individuals with DBH ≥ 10 cm because it was the standard for the area, facilitating the interpretation and application of results from the study by key local actors. Tree heights were estimated visually and we identified species to the highest possible level, but individuals that could not be identified accurately were treated as independent morphospecies.

Estimation of aboveground biomass

The aboveground biomass (AGB, Mg) of each individual tree was estimated using the allometric equation developed for the UPAF (equation 1, Sato et al. 2015).

$$AGB = 0.0613\ (DBH^2 \times H \times WD)^{0.9801} \qquad (1)$$

where, the variables used were DBH (cm), H (m), and wood density (WD, g cm^{-3}). The AGB of forked trees was estimated using the square root of the sum of all squared stem DBHs (Magarik et al. 2020). Data on wood density were incorporated into equation 1 using the BIOMASS package (Réjou-Méchain et al. 2017), which assigns a wood density value to each taxon using the global wood density database as reference (Chave et al. 2009, Zanne et al. 2009). We used wood density values for the species (55.19% of the inventoried individuals), genus (28.58%) and stand mean (16.23%) levels.

Palms, cacti and tree ferns have been found in some cases to contribute significantly to the AGB of tropical forests and can be comparable to the structural variability observed among sites (Sarmiento et al. 2005, Vieira et al. 2008). The AGB of these components was estimated separately using equations 2, 3 and 4 respectively, and incorporated into stand AGB (Sampaio & Silva 2005, Goodman et al. 2013).

$$AGB = 0.094961 \times dmf \times DBH^2 \times H_{stem} \qquad (2)$$

$$AGB = 0.0010\ (DBH)^{3.2327} \qquad (3)$$

$$AGB = 1423.4 \times \exp(0.3233 \times H) \qquad (4)$$

where, dmf is the dry mass fraction (the ratio of dry mass to volume: 0.463) and H_{stem} is stem height (m). We did not have data for H_{stem}, therefore, we used H instead of H_{stem} for equation 2. To estimate the AGB at the plot level, we summed the AGB of all individual trees, palms, cacti, and tree ferns recorded within each plot. This estimation was done using R, version 4.0.3.

Determination of stand characteristics

We quantified stand characteristics, i.e. stand structure, tree species diversity, and tree species composition using the tree census data. All variables were calculated per 0.1 ha plot. We calculated the stand structure variables (individual density, basal area (BA) and AGB), as well as tree species diversity variables (number of families, number of species, Simpson's biodiversity index (D), and Shannon-Wiener biodiversity index (H')) for each of the 71 plots. We determined tree species composition in each plot using relative dominance, which was calculated as relative number of individuals across tree species. We counted forked trees as single individuals to calculate (1) individual density, (2) the variables of tree species diversity, and (3) relative dominance of each species. We calculated BA using the DBH of each stem of the forked trees separately.

Assessment of soil properties

We extracted a composite soil sample in each plot. After the vegetation and litter on the forest floor were removed, we took five subsamples of the topsoil (0–20 cm depth) using a shovel: one in each corner and one in the centre of the plot. We then combined the soil into one composite sample. The composite sample was oven dried at 60 °C until constant weight and then ground and sieved with a 2-mm mesh screen to remove plant tissue and gravel.

The chemical properties analysed were total N (g dm^{-3}), available P, exchangeable K, Ca, and Mg, micronutrients (Cu, Fe, Mn, Zn), S, B, Al, (mg dm^{-3} for all), and pH while the physical properties were contents of clay, silt, and sand (% for all) (Table 1). Total N was assumed to be 5% of organic matter due to the limited equipment available at the local laboratory.

Data analysis

To determine the forest type, we classified the tree species composition using the two-way indicator species analysis (TWINSPAN). Then we conducted an indicator species analysis using r.g.

Table 1 Methodological details of soil chemical and physical properties analyses in the laboratory

Variable	Extraction and measurement method	References
Organic matter	Modified Walkley-Black method	Embrapa (2009)
P	Mehlich-1 extracting solutions and UV/VIS spectrophotometer	
K, Fe, Mn, Cu, and Zn	Mehlich-1 extracting solutions and atomic absorption EAA spectrophotometer	
Ca and Mg	KCl 1.0 mol L^{-1} extraction method and atomic absorption EAA spectrophotometer	
S	Calcium phosphate extraction method and UV/VIS spectrophotometer	
B	Hydrochloric acid extraction method and UV/VIS spectrophotometer	
Al	KCl 1.0 mol L^{-1} extraction method and titration	
pH	Air-dried soil mixed with distilled water (1:2.5) and pH meter	
Clay, silt and sand	Pipette method	Embrapa (2017)
Total N	Assumed to be 5% of organic matter	Julca-Otiniano et al. (2006)

mode to determine the representative tree species for each forest type. We further performed an ordination of tree species composition of all plots using detrended correspondence analysis (DCA) to analyse the relationship between tree species composition and environmental gradients.

We identified the comprehensive soil characteristics for each plot using principal component analysis (PCA). Here we transformed values of soil properties prior to the PCA, applying $\ln(\chi)$ for N, P, K, S, Ca, Mg, B, Cu, Fe, Mn, Zn, pH, silt, and sand contents, $\ln(\chi + 1)$ for Al content, and χ^2 for clay content to meet the requirements of data normality and to standardise the variables. Additionally, we excluded data for plots I20 and Po3 (in Itabo and Pozuelo Natural Reserves respectively) due to the atypical values observed in one of the soil properties (P and S respectively).

Spearman's rank correlation was used to analyse the relationship between soil properties and stand structure, tree species diversity, and tree species composition. Additionally, we compared stand characteristic variables among forest types using a Kruskal-Wallis, and we checked the difference between each pair of forest types using pairwise Wilcoxon rank sum tests.

TWINSPAN and DCA were performed using PC-ORD version 5.31, while the indicator species, PCA, Spearman's rank correlation, the Kruskal-Wallis, and pairwise Wilcoxon rank sum tests were conducted using R version 4.0.3.

RESULTS

Stand structure, tree species diversity and tree species composition

We registered 4286 individuals, 93.54, 2.29 and 3.03% of which were identified to species, genus and family levels respectively. We could not identify the remaining 1.14%. Individuals identified to genus and family levels as well as those that were unidentified were morphotyped. With this, a total of 218 morphotypes were recorded, 60.01, 7.80 and 11.93% to the species, genus, and family levels respectively.

Mean individual density per plot was 60 ± 32 individuals while mean BA was 2.17 ± 0.72 m^2. The mean AGB was 14.64 ± 7.74 Mg. The mean family and species numbers were 14 ± 3 and 21 ± 5 respectively. The mean Simpson's and Shannon-Wiener index values were 0.89 ± 0.12 and 3.81 ± 0.70 respectively (data not shown).

The TWINSPAN analysis identified four forest types which were characterised by distinct indicator species (Figure 2). Forest type I included 34 plots with 10 indicator species, while forest type II included 24 plots with eight indicator species. Three indicator species were shared between forest types I and II. Forest types III and IV included nine and four plots respectively and had similar numbers of indicator species (eight and nine respectively). No shared indicator species were found between types

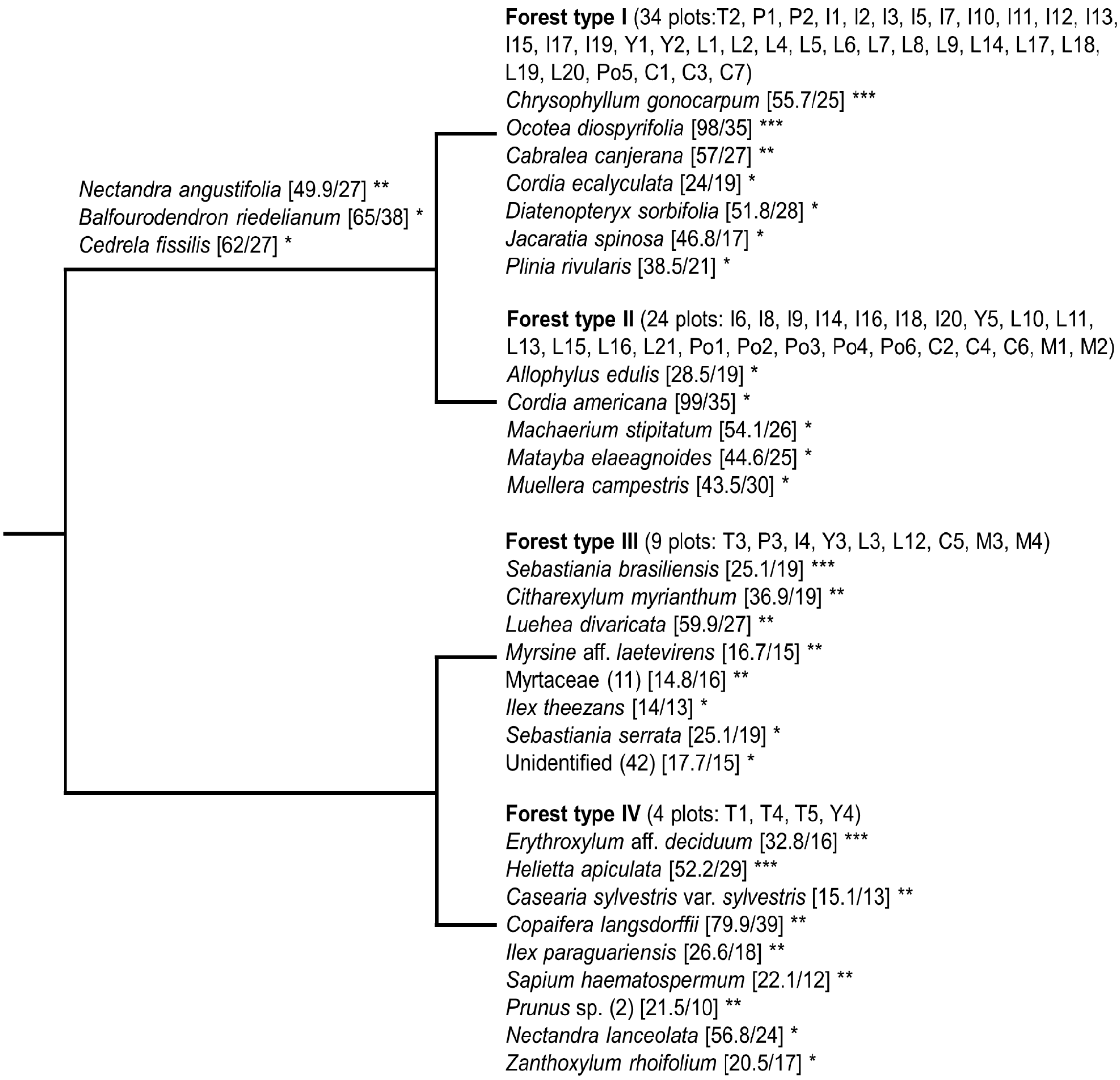

Figure 2 TWINSPAN classification of the four forest types and indicator species for each type; numbers in parentheses indicate the number of morphospecies, and numbers in square brackets are maximum diameter at breast height (cm)/maximum height (m) for each indicator species; * $p \leq 0.05$, ** $p \leq 0.01$ and *** $p \leq 0.001$

III and IV or any other plot pairs. All plots corresponding to forest types I and III belonged to "high forests" and "other forest" respectively. The plots classified as forest type IV were those established in Tati Yupi and Yvyty Rokái Natural Reserves which were close to the savanna, even though in our supervised classification using Sentinel-2 satellite imagery, three of the four plots classified as forest types IV were grouped as high forest. The maximum DBH and H of indicator species of forest types I and II were higher than those of types III and IV.

Forest types were also distinguished in the first and the second axes of the DCA (Figure 3). Plots of forest types I and II showed lower scores on the first axis than plots of types III and IV. The plots of forest types I and II were separated along the second axis, with low scores for forest type I and high scores for forest type II. Additionally, plots in the northernmost protected area (Mbaracayú Biological Refuge) presented very high scores along the second ordination axis. These plots showed singular tree species composition with presence of unique species (e.g. *Cariniana estrellensis*, *Anadenanthera colubrina* var. *cebil*, and *Cinnamomum* cf. *triplinerve*). The four plots in Mbaracayú Biological Refuge formed two groups, namely, M1 and M2 of forest type II with low scores along the first axis and M3 and M4 of forest type III with high scores along the first axis.

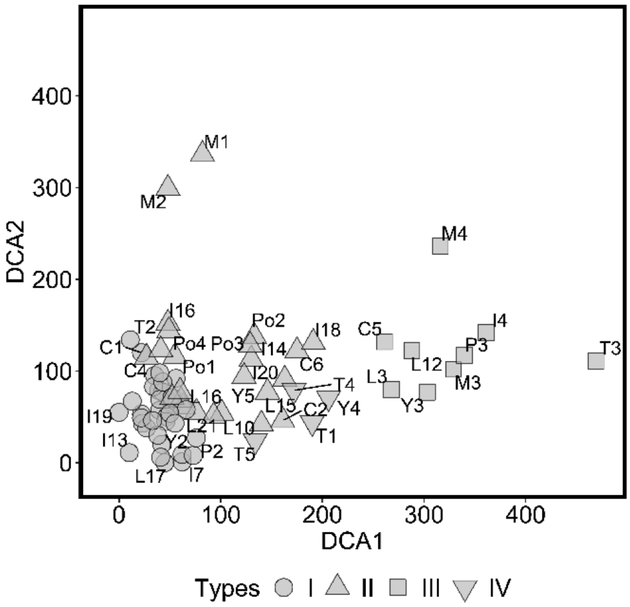

Figure 3 Detrended correspondence analysis (DCA) based on relative dominance of tree species in 0.1 ha plots in the Upper Parana Atlantic Forest; the four forest types (I–IV, indicated by the four shapes) follow the TWINSPAN analysis results

Forest type was significantly linked with the variables of stand structure, except for BA, and the variables of tree species diversity ($p < 0.05$, Table 2). In terms of stand structure, forest type III displayed higher individual density than forest types I, and lower AGB than forest types I and II ($p < 0.05$). As for tree species diversity, forest type I showed higher species diversity, except for Simpson's index values, than the rest of the forest types ($p < 0.05$). Forest type II showed higher variables of species diversity, except for the number of families, than forest type III ($p < 0.05$), while the difference between forest types II and IV was observed only in the Shannon-Wiener index. There were no differences in stand structure and diversity variables between forest types III and IV.

The 17 plots that did not have forest cover in 1979 were distributed across all forest types: 1, 11, 3 and 2 plots in forest types I, II, III and IV respectively. Forest type II showed higher AGB and higher tree species diversity after forest type I (Table 2), despite the 11 plots in forest type II having no forest cover in 1979.

Soil properties

There were high coefficients of variation in the contents of Cu, Fe and Al, while S, Mg and B presented much lower values (Table 3). Clay content was half of soil weight (55.91%), followed by silt and sand contents. The coefficient of variation was highest in the percentage of sand and lowest in clay.

Analysis of the principal components (PCs) of the soil properties showed that the first three principal components (PC1, PC2, PC3) explained 31, 19 and 14% of the total variance, respectively (Table 3). PC1 was associated with soil chemical properties (Table 3). The score of PC1 was positively related to Fe and Al contents and negatively to soil pH and K, Ca, Mg and Mn contents (essential elements). PC2 strongly reflected soil physical properties (particle size composition). The scores of PC2 were positively related to the percentage of sand and negatively with the percentage of clay, S and B contents. PC3 was associated with both soil chemical and physical properties. The scores of PC3 were positively related to N and S contents and the percentage of silt.

Plot ordination by soil properties showed that plots in protected area Mbaracayú Biological Refuge had very different characteristics than those in the other protected areas (Figure 4), with high scores for PC2 and low scores for PC3. These plots had high sand content (78.83%), with 14.71% clay and 6.46% silt. These four plots fell into two groups: M1 and M2 with higher scores for PC3, and M3 and M4 with lower scores.

Table 2 Variables of stand structure and tree species diversity in each plot of 0.1 ha between the forest types I–IV identified by the TWINSPAN analysis

Variable	Type I		Type II		Type III		Type IV		p
Density (individual)	51.44 ± 9.44	b	57.67 ± 20.65	ab	98.67 ± 69.25	a	66.25 ± 10.66	ab	**
BA (m^2)	2.22 ± 0.62		2.11 ± 0.54		2.27 ± 1.29		1.83 ± 0.50		
AGB (Mg)	17.08 ± 8.62	a	14.45 ± 5.63	a	7.70 ± 3.76	b	10.56 ± 4.36	ab	**
No. families	14.94 ± 1.83	a	12.92 ± 3.38	b	11.78 ± 3.36	b	10.50 ± 1.80	b	**
No. species	23.94 ± 3.02	a	20.46 ± 5.05	b	15.00 ± 4.71	c	14.25 ± 3.11	bc	**
Simpson's index (D)	0.93 ± 0.02	a	0.90 ± 0.07	ab	0.75 ± 0.24	c	0.77 ± 0.13	bc	**
Shannon–Wiener index (H')	4.18 ± 0.26	a	3.83 ± 0.53	b	2.86 ± 0.95	c	2.89 ± 0.62	c	**

BA = basal area, AGB = aboveground biomass; letters a, b and c indicate statistically significant differences between forest type pairs in variable values, where * $p \leq 0.05$ and ** $p \leq 0.01$

Table 3 Means, standard deviations (SD), and coefficients of variation (CV) of soil properties, and principal components (eigenvectors values), and contribution ratios (proportions of the variance) of the principal components (PCs) for soil properties

Soil property		Mean ± SD	CV	PC1	PC2	PC3
pH		5.26 ± 0.55	10.46	-0.40	0.17	0.02
N	g dm^{-3}	2.50 ± 1.09	44.02	0.00	-0.11	0.55
P	mg dm^{-3}	3.49 ± 1.96	56.16	0.01	-0.10	0.18
K	mg dm^{-3}	93.39 ± 51.96	55.64	-0.29	-0.23	0.13
S	mg dm^{-3}	10.77 ± 3.66	33.98	0.02	-0.29	0.35
Ca	mg dm^{-3}	871.45 ± 562.49	64.55	-0.42	-0.02	0.07
Mg	mg dm^{-3}	111.69 ± 47.26	42.31	-0.36	-0.04	0.14
B	mg dm^{-3}	0.69 ± 0.25	36.23	-0.14	-0.30	-0.05
Cu	mg dm^{-3}	12.88 ± 16.33	126.79	0.21	0.11	0.11
Fe	mg dm^{-3}	59.94 ± 119.69	199.68	0.28	0.22	0.12
Mn	mg dm^{-3}	54.93 ± 26.96	49.08	-0.28	-0.19	-0.22
Zn	mg dm^{-3}	4.91 ± 4.04	82.28	-0.26	0.27	0.19
Al	mg dm^{-3}	75.20 ± 85.08	113.14	0.39	-0.13	0.16
Clay	%	55.91 ± 19.10	34.16	0.06	-0.52	-0.18
Silt	%	25.78 ± 10.77	41.78	-0.02	0.01	0.57
Sand	%	18.31 ± 17.30	94.48	-0.08	0.51	-0.02
SD		-	-	2.22	1.74	1.50
Proportion of variance		-	-	0.31	0.19	0.14

SD = standard deviation

The relationship between soil properties and stand characteristics

Soil properties were statistically associated with stand structure and tree species diversity (Table 4). Scores of PC1 showed a positive relationship with individual density ($p \leq 0.05$) and a negative one with AGB, Simpson's index, and Shannon–Wiener index ($p \leq 0.05$). Soil pH and elements K, Ca, Mg and Mn, which were associated with PC1, also showed significant negative relationships with individual density, whereas Fe and Al showed positive relationships ($p \leq 0.05$). In relation to nutrients associated with PC1, Simpson's and Shannon–Wiener indices were positively related to K, Ca and Mn and negatively related to Fe content, while AGB was positively related to Mn and negatively related to Fe content ($p \leq 0.05$). Scores of PC2 were negatively related to tree species diversity and AGB ($p \leq 0.05$). Tree species diversity was significantly related to the percentages of clay and sand ($p \leq 0.05$), which were in turn associated with PC2, although it was also related to Mn content, which was associated with PC1. Additionally, the number of families and species and the Shannon–Wiener index values showed positive relationship with S, and both diversity indices showed positive relationship with B content, which was associated with PC2 ($p \leq 0.05$).

Scores of PC1 were positively related to DC1 ($p \leq 0.05$) (Table 4). Soil pH and K, Ca, Mg, Fe, Mn and Al contents, which were associated with PC1 (Table 3), also showed significant relationships with DC1 ($p \leq 0.05$). Scores of PC2 were positively related to both DC1 and DC2 ($p \leq 0.05$). The DC1 and DC2 scores were significantly related to S and B contents and percentages of clay and sand ($p \leq 0.05$), which were associated with PC2 (Table 3), although they were related to soil pH and Al content, which in turn were associated with PC1.

Scores of PC1 and PC2 were statistically different between forest types ($p \leq 0.05$, Table 5). Scores of PC1 showed a difference between forest type III and types I and II, while the difference between type I and types II and III was detected in scores of PC2 ($p \leq 0.05$). Scores of PC2 also

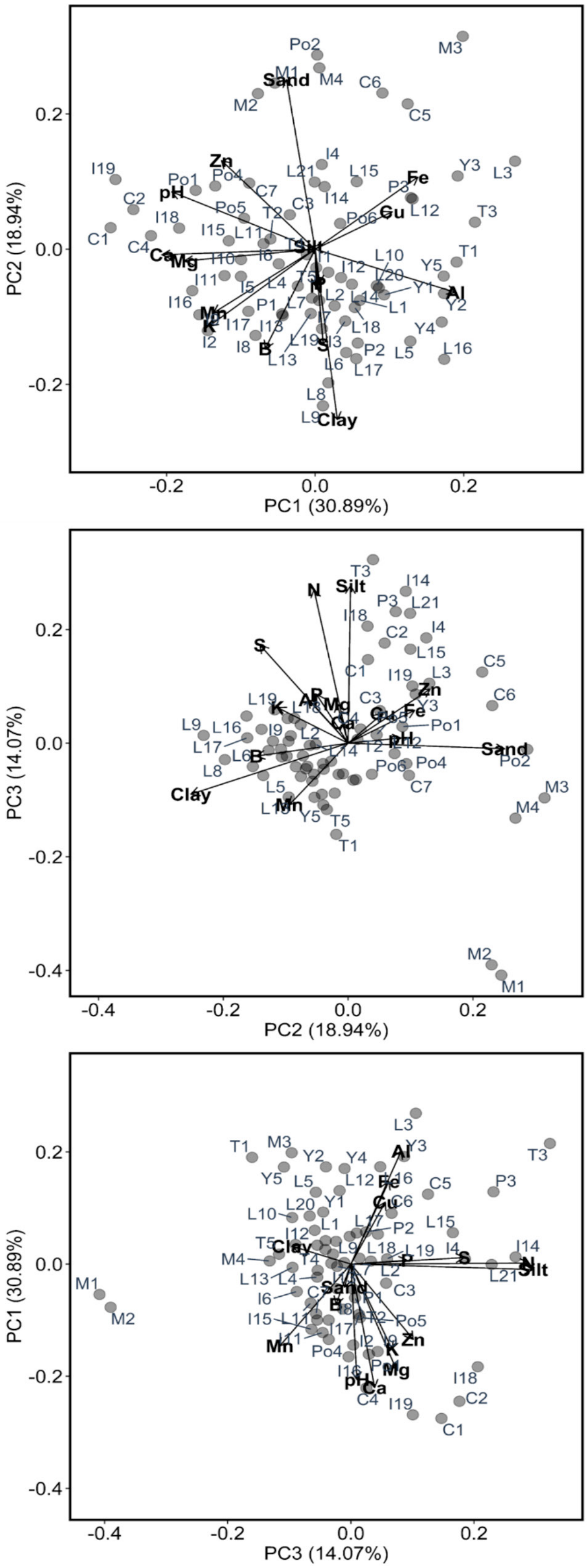

Figure 4 Principal component analysis (PCA) of soil properties in 0.1 ha plots in the Upper Parana Atlantic Forest

Table 4 Spearman's rank correlation coefficients between soil properties (columns) and stand structure variables (density, BA, AGB), tree species diversity (no. families, no. species, Simpsons's index, Shannon-Wiener index), and species composition (detrended correspondence analysis, DC1 and DC2) for the 0.1 ha plots

	Soil property																	
	PC1	PC2	PC3	pH	N	P	K	S	Ca	Mg	B	Cu	Fe	Mn	Zn	Al	Clay	Silt	Sand
Density (individual)	0.53*	0.15	0.00	-0.43**	-0.09	0.04	-0.46**	-0.09	-0.48**	-0.31**	-0.30*	0.23	0.48**	-0.34**	-0.21	0.39**	-0.11	0.03	0.05
BA (m^2)	-0.08	-0.07	0.14	0.03	0.19	-0.04	-0.09	0.17	0.06	0.02	0.03	-0.08	-0.12	0.15	0.08	-0.07	-0.05	0.08	0.02
AGB (Mg)	-0.24*	-0.25*	-0.05	0.09	0.02	-0.05	0.02	0.14	0.21	0.07	0.14	-0.18	-0.29*	0.29*	0.07	-0.20	0.17	-0.13	-0.16
No. familie	-0.03	-0.40**	-0.04	-0.07	-0.03	0.13	0.13	0.30*	0.04	0.08	0.13	0.11	-0.02	0.26*	-0.25*	0.03	0.38**	-0.10	-0.35**
No. species	-0.13	-0.42**	-0.14	-0.01	-0.08	0.02	0.14	0.27*	0.12	0.10	0.17	0.00	-0.16	0.32**	-0.24	-0.08	0.37**	-0.19	-0.34**
Simpson's index (D)	-0.34**	-0.37**	-0.19	0.20	-0.07	-0.06	0.26*	0.19	0.28*	0.17	0.26*	-0.07	-0.29*	0.42**	-0.12	-0.24*	0.31*	-0.22	-0.27*
Shannon–Wiener index (H')	-0.29*	-0.43**	-0.19	0.14	-0.06	-0.03	0.25*	0.24*	0.26*	0.15	0.27*	-0.08	-0.29*	0.42**	-0.18	-0.20	0.36**	-0.22	-0.33**
DC1	0.48**	0.44**	0.10	-0.28*	0.00	0.01	-0.46**	-0.26*	-0.45**	-0.27*	-0.34**	0.27*	0.45**	-0.62**	-0.02	0.40**	-0.36**	0.16	0.31**
DC2	-0.18	0.60**	0.08	0.35**	-0.22	-0.29*	-0.01	-0.36**	0.12	0.09	-0.20	0.11	0.01	-0.14	0.41**	-0.32**	-0.58**	0.27*	0.50**

BA = basal area, AGB = aboveground biomass; * $p \leq 0.05$ and ** $p \leq 0.01$

showed a difference between types III and IV ($p \leq 0.05$). These tendencies were observed for each soil property. The contents of Ca, Mg, Fe, Mn and Al (associated with PC1) of type III were different from those of types I or II ($p \leq 0.05$), but no difference was detected between types I and II. The percentages of clay and sand and S contents (which were associated with PC2) of Type I were different from those of types II and III ($p \leq 0.05$), although no difference was detected between types II and III. The percentage of clay was also different between types III and IV.

DISCUSSION

Tree species diversity in the UPAF

The number of tree species registered in this study (218 morphotypes with 131 confirmed species) reaffirms the high tree species diversity of the UPAF. The greater number of sample plots than previous studies distributed over an extensive area and through heterogeneous tree communities allowed us to better describe the species diversity of this ecoregion. The number of species was higher than that reported by Vera Monges (2009), Degen de Arrúa et al. (2017), and Peralta Kulik et al. (2018), who registered 127, 49, and 72 tree species in remnant forests of UPAF, Paraguay respectively. Our species richness numbers are also higher than those recorded in other parts of the UPAF, e.g. 57 tree species in Misiones, Argentina (Holz et al. 2009) and 86 tree species in Iguaçu National Park, Brazil (Souza et al. 2019). On the other hand, similar species diversity was found in Mbaracayú Forest Nature Reserve, Paraguay, where 204 tree species were reported in various types of vegetation, including forests (Peña-Chocarro et al. 2010).

Soil properties relationships in UPAF forests

Willis and Whittaker (2002) noted that species diversity depends on geographic or time scales and that the processes that best account for patterns of biodiversity at a given scale are not necessarily the same at another smaller or greater scale. At a local scale, soil properties (such as Al toxicity, drainage, water holding capacity, and availability of P, K, Ca and Mg) are known to influence the diversity of tropical forests (Sollins 1998). Studies in Amazonia and Brazilian Atlantic Forests also partially support this observed pattern (Ferreira-Júnior et al. 2007, Laurance et al. 2010).

In our evaluation of the relationship between soil properties and stand characteristics (Table 4), we found that the content of essential elements and soil pH was related to the density of individuals, while the balance of clay and sand was linked to the variables of species diversity (Tables 3 and 4). Similarly, the two axes of soil properties were separately related to the forest types (Table 5); this is also supported by our DCA ordination based on tree community abundances (Figure 3, Table 4).

Low pH and high Al contents, which are typical features of savanna (Haridasan 2008), were observed in forest type IV (Table 5). This suggests that these forests are an ecotone between other types of forests and the savanna that are adjacent to forest type IV. Study plots in Mbaracayú Biological Refuge show high sand content (78.83%), which was derived from sedimentary rock and geologically corresponds to Tertiary sandstone. This geological feature is different from those in the other protected areas, in which the soil is derived from basalt and corresponds to the Upper Parana magmatic suite (Acevedo et al. 1990, Vice Ministry of Mines and Energy Paraguay 2014). However, all plots in Mbaracayú Biological Refuge were divided into forest types II and III and did not form an independent forest type (Figure 3).

Forest types in the UPAF

Our results agree with previous studies that indicate that the UPAF is a spatially heterogeneous ecoregion composed of diverse types of forests, whose development originally took place according to local soil properties and influences of other types of nearby vegetation such as savanna (Spichiger et al. 1992, Cartes 2003). This spatial heterogeneity generated diverse habitats for plant and animal species and contributed to increased gamma diversity at the landscape level. Our study identified four forest types characterised by their soil properties and proximity to savanna formations. The stand characteristics of each forest type provide information that serves as a reference for advancing conservation and restoration efforts in the UPAF.

Forest type I was the most dominant forest type in our study area. This forest type presents similar

Table 5 Comparison of the three principal component scores (PC1–PC3) and soil properties between the forest types I–IV identified by the TWINSPAN analysis

		Type I		Type II		Type III		Type IV		*p*
PC1		-0.36 ± 1.80	b	-0.82 ± 2.14	b	2.61 ± 1.56	a	1.70 ± 1.65	ab	**
PC2		-0.91 ± 1.09	c	0.63 ± 1.77	ab	2.17 ± 1.29	a	-0.61 ± 0.56	bc	**
PC3		-0.13 ± 0.63		-0.06 ± 2.06		1.12 ± 1.77		-1.06 ± 0.72		
pH		5.24 ± 0.52		5.48 ± 0.61		5.01 ± 0.30		4.83 ± 0.22		*
N	g dm^{-3}	2.33± 0.41		2.30 ± 1.34		3.20 ± 2.11		2.24 ± 0.27		
P	mg dm^{-3}	3.56 ± 1.74		3.76 ± 2.55		2.64 ± 1.03		3.32 ± 0.70		
K	mg dm^{-3}	100.97 ± 49.57		100.06 ± 58.57		57.78 ± 32.86		72.34 ± 18.85		
S	mg dm^{-3}	12.32 ± 3.35	a	9.25 ± 3.01	b	10.59 ± 3.35	ab	6.30 ± 2.87	ab	**
Ca	mg dm^{-3}	911.84 ± 506.04	a	1067.49 ± 636.92	a	374.97 ± 198.38	b	566.13 ± 297.31	ab	**
Mg	mg dm^{-3}	110.08 ± 34.23	ab	127.64 ± 55.50	a	75.37 ± 38.02	b	119.43 ± 62.66	ab	*
B	mg dm^{-3}	0.73 ± 0.24		0.70 ± 0.26		0.55 ± 0.27		0.55 ± 0.05		*
Cu	mg dm^{-3}	8.70 ± 6.35	b	10.92 ± 8.29	ab	36.56 ± 32.63	a	6.00 ± 2.36	ab	*
Fe	mg dm^{-3}	21.10 ± 8.06	b	44.95 ± 77.59	b	255.96 ± 223.02	a	31.56 ± 15.16	ab	**
Mn	mg dm^{-3}	66.81 ± 18.28	a	50.43 ± 26.35	ab	32.66 ± 34.84	b	28.94 ± 6.67	b	**
Zn	mg dm^{-3}	4.68 ± 4.73		6.00 ± 3.38		4.42 ± 2.12		1.90 ± 1.33		*
Al	mg dm^{-3}	62.32 ± 58.98	ab	50.65 ± 78.19	b	154.19 ± 123.84	a	141.88 ± 62.87	ab	**
Clay	%	65.55 ± 11.06	a	49.27 ± 19.71	bc	29.32 ± 10.92	c	70.43 ± 3.54	ab	**
Silt	%	22.96 ± 5.15		26.25 ± 10.33		38.06 ± 18.13		19.54 ± 1.39		*
Sand	%	11.49 ± 6.50	b	24.48 ± 20.80	a	32.62 ± 23.85	a	10.04 ± 3.56	ab	**

Letters a, b, and c indicate statistically significant differences between forest type pairs in variable values, where * $p \leq 0.05$ and ** $p \leq 0.01$

characteristics to the "Lauraceae–*Cedrela fissilis*–*Chrysophyllum gonocarpum* well-drained forest: typical facies with *Balfourodendron riedelianum*" described by Spichiger et al. (1992). Many tree species belonging to this forest type were able to reach high DBH and H, raising the stand AGB value (Table 2, López et al. 2002).

Forest type II presents some similarities with type I. Both forest types have tree species considered to be "paranean elements" as suggested by Spichiger et al. (1995) or characteristics of "Alto Parana Forest" (i.e. Upper Parana Forest) as mentioned by Tortorelli (1967). Some indicator species of this forest type, e.g. *Matayba elaeagnoides*, showed some characteristics related to hygrophytic conditions (Lorenzi 2014).

Forest type III is a poorly developed forest on flooded soil. Its high individual density, low AGB, and low tree species diversity (Table 2), and the dominance of hygrophilous indicator species with lower canopy height (Figure 2) could be related to historic flooding events (Marques et al. 2009).

Forest type IV is likely to correspond to the forest–savanna ecotone. This forest type is occupied by indicator species observed in forest–savanna mosaic areas (Figure 2) and presents typical features of savanna soil (Haridasan 2008).

Implications of spatial heterogeneity for UPAF conservation

In this study, we present relevant findings to improve conservation and restoration practices in the UPAF. In particular, our findings indicate that soil properties and the proximity to savanna vegetation influence the heterogeneity of the tree communities, determining the intrinsic tree species diversity at a landscape level. Thus, we recommend that UPAF restoration approaches consider the spatial heterogeneity in vegetation types and the compositional variability of tree species when designing and implementing reforestation and conservation projects. These will increase the chances of maintaining adequate beta and gamma diversity levels, increase chances of reconnecting currently isolated forest patches, and even provide connectivity for wildlife. Ultimately, maintenance and conservation of natural habitat heterogeneity in the UPAF will define the sustainability of this ecoregion.

It is necessary to actively manage and protect the remnants of each forest type on both private and public lands and to promote conservation actions and policies for the sustainable use of the UPAF for effective conservation. At the same time, it is important to have a diverse bank of seeds and seedlings of the indicator and associated species of each forest type to restore the heterogeneous UPAF landscape. Identifying appropriate restoration methods for each forest type will also maximise the effectiveness of restoration efforts.

We propose that restoration processes evaluate the proximity of local savanna areas as an initial step, as it may influence the formation of nearby forests. An assessment of the soil properties using the two axes described here could then be used to define the forests to be restored at the site. By this process, we can determine the appropriate tree species to be planted and thus improve the forest restoration efforts.

Although subcanopy plant species (trees with DBH < 10 cm, shrubs and herbs) are not included in this study, they are an important component of the UPAF floral biodiversity (Cartes 2003). Thus, their conservation and their inclusion in restoration programmes are necessary to maintain UPAF heterogeneity. A next challenge will be to study the spatial heterogeneity of these groups and their relationship with environmental factors such as soil properties. We suggest replication of our study in other public and private areas in the region. The heterogeneous forest types identified in this study suggest heterogeneity on a broad scale, and many forest types are likely to be described.

CONCLUSION

Four forest types with different stand characteristics (in particular, individual density, AGB, and tree species diversity) were classified in this study. The differentiation of forest types I–III was strongly related to soil chemical characteristics and physical properties, and forest type IV had characteristics that seemed to be influenced by the presence of nearby savanna. Building on Spichiger's et al. (1992) results, we found that the effect of soil properties could be divided into two axes. The contents of essential elements with soil pH were related to the difference in stand structure between forest types I and II vs. forest type III. On the other hand, the balance of clay and sand contents was related to tree species diversity, with clayey soil being capable of harbouring higher tree diversity in forest type I compared with forest type II. Forest type IV is likely to be influenced by nearby savanna rather than the contents of essential elements and soil pH, and the balance of clay and sand contents. These relationships between the two dimensions of soil properties and the formation of different forest types and the characteristics of each forest type give important insights into improving the effectiveness of conservation and restoration practices for the remaining UPAF habitats.

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