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Woody plant assemblages in restoration sites and remnants of Seasonal Atlantic Forest in Southern Brazil

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Abstract

The Brazilian Atlantic Forest is one of the world's most threatened forests. In some regions, there is a huge restoration deficit and few, scattered remnants are available to function as reference ecosystems. In this context, this study aims to describe the vegetation of woody plant assemblages in six remnant Seasonal Semideciduous Atlantic Forest fragments (FF) and five restoration sites (RF) in northern Paraná State, in order to address the following questions: 1- How similar are woody plant assemblages from different remnant forests? and 2- Are reforestations converging with remnants in terms of vegetation structure and woody plant diversity? All sites belong to a Long-Term Ecological Research program, being monitored using permanent plots. FF sites (34–690 ha) show varying disturbance histories, with five having prior selective logging. The RF sites are reforestations with native, ranging from 22 to 25 years after establishment. Species richness (diameter at 1,30 m ≥ 2.5 cm) in each FF site ranged from 46 to 70 species. Species composition of previously logged fragments were similar to each other but distinct from undisturbed areas. In RF sites 93 species were sampled, ranging from 34 to 44 species per site; floristic composition was strongly influenced by planted species and with high inter-site similarity. The structural and floristic differences associated with FF site history should be considered when selecting reference sites for ecological restoration. The differences between FF and RF sites reinforces that restoration is a long-term process and depends on historical land use and landscape heterogeneity.

1. Introduction

The Atlantic Forest, which is one of the world's most threatened forests and is considered a biodiversity conservation hotspot (Myers et al. 2000; SOS Mata Atlântica 2021). It comprises different forest formations, with Semidecidual Seasonal Forests (SSF), characterized by semideciduousness during unfavorable periods, predominating in the interior lands (Ribeiro et al. 2009). Once representing the largest area of Atlantic forests, the SSFs are currently one of the most threatened Atlantic Forest ecosystems (Vicente et al. 2009; Carlucci et al. 2021), reduced to fragments with varying degrees of conservation and secondary forests (Ribeiro et al. 2009; Wagner et al. 2020). Nevertheless, these fragments show significant variations in vegetation structure and floristic composition, reinforcing the ecological relevance of even the smallest areas for biodiversity conservation (Ribeiro et al. 2009; Santos and Kinoshita 2003), including its use as seed sources and reference ecosystems for ecological restoration. In the state of Paraná the SSFs originally represented 47% of the native vegetation cover (IPARDES 2017), although it is currently reduced to 4% (IPARDES 2017).

In the Paraná state colonization by European settlers began later than the neighboring states of São Paulo and Minas Gerais. However, the intense agricultural expansion, especially in the north of the state, during the early 20th century, resulted in the reduction and fragmentation of the SSFs, which is now restricted to isolated fragments. In some regions, less than 2% of the original cover remains (Medeiros et al. 2010; Viani et al. 2011). Forest fragmentation intensifies the effects of the surrounding matrix, causing changes in microclimate, species abundance and distribution, and can lead to the extinction of

species and even habitats (Liebsch et al. 2008; Tilman et al. 1994). Furthermore, selective logging, especially after 1975, and the occurrence of fires in forests surrounded by sugarcane fields have contributed to the “secondarization” of these forests (Joly et al. 2014). Thus, it is worth asking whether those small forest remnants are divergent, random samples of a former heterogeneous but continuous forest cover (Santos and Kinoshita 2003), or are convergent, secondarized forests dominated by the same set of generalist species (Joly et al. 2014), with deep implications both for its long term biodiversity conservation and its use as reference ecosystems for ecological restoration.

In addition to fragmented remnants, part of the current forest cover consists of secondary vegetation resulting from the abandonment of lands unsuitable for agriculture, especially after 1980, with the advancement of mechanization and intensive agriculture, especially soybeans. After these agrarian changes, rocky and steep areas were abandoned, allowing natural regeneration in some sites. Over the past 25 years, these naturally regenerated forests have been complemented by active restoration efforts through native species plantations in legally enforced areas, moderately increasing forest cover to just over 10%, on average, in northern Paraná state (MapBiomas 2025). While different in origin, naturally regenerated forests and active restoration sites (reforestation with native species) are expected to converge in terms of structure and species composition with neighboring remnants (Suganuma et al. 2014); this convergence, however, should not occur in a short time scale (Manhães et al. 2022).

In this context, this study aims to describe the vegetation structure and diversity of woody plant assemblages in six remnant Seasonal Semideciduous Atlantic Forest fragments and five active restoration sites, in order to address the following questions: 1- How similar are woody plant assemblages from different remnant forests in the same region? and 2- Are reforestations converging with neighboring fragments in terms of vegetation structure and woody plant diversity?

2. Methods

2.1 General information

The areas comprising the Long-Term Ecological Research site "Atlantic Forest of Northern Paraná" (PELD-MANP) are located within the Seasonal Semideciduous Forest (SSF) domain. The mean annual temperature for the region ranges from 20.6°C to 21.4°C and the mean annual precipitation ranges from 1529 to 1637 mm (IAPAR 2019). The climate is classified as humid subtropical (Cfa according to the Köppen climate classification), characterized by hot summers and infrequent frosts, with no defined dry season (Nitsche et al. 2019). The soils in the region are predominantly Eutroferric Red Latosol and Eutroferric Red Nitosol (Bhering et al. 2007).

2.2 Study sites

The study was conducted in six forest fragments (FFs) and five restoration sites (reforestation with native species; RFs), which are part of the PELD-MANP monitoring network (Fig. 1). All selected sites, which include mandatory reserves on private property, state-owned Conservation Units, and public areas

under concession to a hydroelectric plant, are embedded within an agricultural matrix predominantly composed of soybean and corn crops, with occurrence of sugarcane in some areas.

2.2.1 Forest fragments

The forest fragments (FFs) vary in size, logging history, location, and altitude (Table 1). Information on logging history was obtained through field observations and interviews with local residents. On the Alvorada (ALV), Congonhas (CGH), and Santo Antônio (SAN) farms, the sampled fragments underwent selective logging between 1975 and the early 1980s. The CGH farm fragment recently experienced another wood removal event in 2017. In the fragment located on the Bule (BUL) farm, there are records of wood removal in the northern and eastern edges, in addition to evidence of recent illegal harvesting of *Euterpe edulis* Mart. (Arecaceae) at different points within the area. Ibicatu State Park (IBI) underwent selective logging processes and also at least one fire event in the 1970s, limited to the western portion of the area. In contrast, Mata dos Godoy State Park (PMG) shows no evidence of selective logging within the formally protected area. This Conservation Unit comprises 690 ha, of which approximately 675 ha consist of mature forest, secondary forest, and restoration sites (Instituto Água e Terra 2015). However, following the growth of secondary forests since the 1980s, PMG is now embedded within a forest fragment of approximately 2800 ha.

Table 1
Characterization of the six Seasonal Atlantic Forest fragments comprising the Long-Term Ecological Research Program "Atlantic Forest of Northern Paraná" (PELD-MANP). The six forest fragments are located in the northern region of Paraná State, Brazil.

Site name	Code	Coordinates	Area (ha)	Elevation (m)	Logging history
Alvorada	ALV	22°49’04”S 51°11’25”W	128	360	Yes
Bule	BUL	23°24’19”S 51°19’31”W	288	670	No[a]
Congonhas	CGH	22°59’52”S 50°56’30”W	108	360	Yes[b]
Ibicatu	IBI	22°46'59"S 51°29'17"W	302[c]	370	Yes
Mata dos Godoy	PMG	23°26’46”S 51°14’46”W	675	600	No
Santo Antônio	SAN	22°56’26”S 50°57’10”W	34	350	Yes

[a]Moderate logging occurred in northern and western edges, limited to 80 m from forest boundaries, according to field observations.

[b]Most recent extraction event occurred in 2017, after sampling.

[c]Including secondary forest.

2.2.2 Restoration sites

Five RFs are part of the PELD-MANP core monitoring network (Table 2). The "Projeto Primavera" (PMG RF), established in 2003, is contained within the protected area of Mata dos Godoy State Park. At the State University of Londrina's "Fazenda Escola" (FZE RF), sampling plots are installed in a plantation established in 1996. The remaining RFs were implemented between 2002 and 2003 along the margins of the Capivara Hydroelectric Plant reservoir on the Paranapanema River, adjacent to the FFs located on the Congonhas, Alvorada, and Santo Antônio farms. All sites have a previous history of agricultural cultivation, predominantly soybean and corn for at least two decades, with the exception of Projeto Primavera, where coffee was cultivated until 1990, followed by spontaneous grass cover until 2002.

Table 2
Characterization of the five restoration sites (reforestation with native species; RF) comprising the Long-Term Ecological Research Program "Atlantic Forest of Northern Paraná" (PELD-MANP). The five restoration sites are located in the northern region of Paraná State, Brazil.

Site name	Code	Coordinates	Area (ha)	Elevation (m)	Forest distance (m)	Planted
Alvorada	ALV RF	22°48’47”S 51°11’50”W	11	340	5[a]	may/2004
Congonhas	CGH RF	22°59’46”S 50°56’37”W	15	340	5[a]	jun/2003
Projeto Primavera	PMG RF	23°26’34”S 51°14’44”W	3	630	0	apr/2002
Santo Antônio	SAN RF	22°56’10”S 50°56’57”W	15	330	5[a]	sep/2003
Fazenda Escola	FZE RF	23°20’13”S 51°12’36”W	4	520	500[b]	1996

[a]Only a dirt road separates the restoration plantation from the nearest forest fragment.

[b]The nearest forest fragment, connected by a corridor, is a secondary forest at least 50 years old.

The sampled RFs are similar in age and composition of planted species, except for the RF located at the Fazenda Escola, where planting involved a greater number of species. In the others, approximately 45 native species from the SSF were used, mostly pioneers. Soil preparation consisted of mechanical tilling restricted to planting lines in previously mowed areas. Seedlings were planted at a spacing of 2 x 3 meters. Control of ruderal species was performed mechanically between rows and manually around seedlings during the first two years. Leaf-cutting ants were controlled using insecticide baits (Fipronil®). Other pesticides and fertilizers were not used.

2.3 Data collection

In all sampled areas, two 500 m transects or one 1km transect were established, depending on the size and shape limitations of the forested area. At each site (FF or RF), ten permanent plot clusters were allocated (five on each of the 500 m transects or ten plots along the 1 km transects). Plots were spaced 100 m apart and at least 100 m from edges in the case of FFs. For RFs, given their elongated shape, plots were centered within the restoration strip, equidistant from the nearest edges and spaced 100 m from each other.

Each plot cluster consists of a main 10 x 20 m plot with two nested subplots of 10 x 10 m and 5 x 5 m. This study presents results only from the larger plots (10 x 10 m and 10 x 20 m). In the 10 x 10 m plots, all individuals of shrub and tree species with diameter at breast height (DBH, measured at 1.3 m above ground) between 2.5 and 19.9 cm were sampled. In the 10 x 20 m plots, all tree individuals with DBH ≥ 20 cm were sampled.

Individuals sampled in the plots were tagged with sequentially numbered aluminum labels and measured for circumference at breast height (CBH), obtained using a measuring tape and subsequently converted to diameter at breast height ($DBH = CBH/\pi$). Tree height was estimated using a pole of known length and an electronic laser tape measure.

Identification was conducted in the field when possible, and samples were collected for laboratory confirmation using material from the State University of Londrina Herbarium (FUEL). Botanical names followed the convention of the Flora e Funga do Brasil database (2024).

Sampling in the FFs of ALV, BUL, IBI, PMG, and SAN was conducted in 2023, while the CGH fragment was sampled earlier, in 2017, just before the last timber extraction event. In the RFs, although monitoring began at planting, permanent plots were installed in different years. For this study, the most recent sampling data were used: 2015 for CGH RF, 2023 for PMG RF, and 2024 for ALV RF, SAN RF, and FZE RF. Thus, all RF age references were drawn from the site age at the sampling time.

2.4 Data analysis

Sampled and identified individuals were compiled into tables to calculate species richness and abundance per site, as well as to visualize shared species among sites. Due to the different sizes of the nested plots, individual density per hectare was calculated using the total number of individuals from

each site divided by the plot area (100 or 200 m^2), and tested with permutational Analysis of Variance (ANOVA) using the *vegan* package (Oksanen et al. 2024). Basal area was also calculated and compared among sites with permutational ANOVA for each plot size/size class. Additionally, to evaluate sampling effort sufficiency and compare sampling completeness among forest fragments (FFs) and among restoration plantations (RFs), rarefaction and extrapolation curves based on abundance (q = 0) were generated using the sample coverage method (type = 2) with the iNEXT package (Hsieh et al. 2024). Graphs showing the number of individuals and species by size class at each site were also produced.

To assess composition, Non-metric Multidimensional Scaling (NMDS) was performed based on the Chao dissimilarity index using the vegan package; to visualize the clustering of plots from each site and the proximity between areas, a graph was created using the ggplot2 package (Chao et al. 2005; Oksanen et al. 2024). Also using the vegan package, a Permutational Multivariate Analysis of Variance (PERMANOVA) was conducted to verify how sites differ from each other.

All analyses were performed in the R Studio environment, version 4.4.3 (R Core Team 2025).

3. Results

3.1 Forest fragments

A total of 1,788 individuals were recorded, belonging to 149 species and 42 families (Table 3). Comparison among FFs revealed similar numbers of individuals (ANOVA: p = 0.910; Fig. 2). Sites differed in basal area (BA) of larger trees (DBH ≥ 20 cm; ANOVA: p = 0.002), with unlogged FFs showing higher values, while BA of smaller trees (2.5–19.9 cm DBH) did not differ (ANOVA: p = 0.897). (Table 3).

Table 3
Features of the tree community in six Seasonal Atlantic Forest fragments comprising the Long-Term Ecological Research Program "Atlantic Forest of Northern Paraná" (PELD-MANP), located in the northern Paraná State, Brazil. ALV = Fazenda Alvorada; BUL = Fazenda Bule; CGH = Fazenda Congonhas; IBI = Parque Estadual de Ibicatu; PMG = Parque Estadual Mata dos Godoy. In 10x10 plots all woody plants with DBH between 2.5 and 19.9 cm were sampled; in 10x20 plots all plants with DBH equal or greater than 20cm. Letters following 10x20 plots basal area indicates differences @ p≤0.05

Site code	Families	Species	Basal area (m^2/ha)[a]	Density (ind/ha)
ALV	23	46	10x10–9.44	10x10–2,310
			10x20–17.1 c	10x20–190
BUL	30	70	10x10–9.52	10x10–2,160
			10x20–54.3 a	10x20–250
CGH	29	61	10x10–10.8	10x10–2,530
			10x20–22.1 bc	10x20–210
IBI	24	55	10x10–8.67	10x10–3,030
			10x20–37.7 ab	10x20–210
PMG	24	61	10x10–8.92	10x10–2,760
			10x20–46.6 a	10x20–265
SAN	22	61	10x10–10.4	10x10–2,490
			10x20–24.7 bc	10x20–180
Total	42	149	-	-

[a]Basal area values followed by the same letter in the 10x20 were not significantly different from each other according to the permutational ANOVA ($p > 0.05$).

The families with the highest number of species in the FFs were Myrtaceae (21), Fabaceae (20), Lauraceae (10), and Meliaceae (10), partially reflecting the typical pattern for seasonal semideciduous forests as described by Vale et al. (2009). The most abundant species were: *Astronium graveolens* Jacq. (Anacardiaceae) in ALV, *Trichilia clausseni* C.DC. (Meliaceae) in BUL, *Metrodorea nigra* A.St.-Hill. (Rutaceae) in CGH, and *Actinostemon concolor* (Spreng.) Müll.Arg. (Euphorbiaceae) in IBI, PMG, and SAN (Table S1).

The rarefaction and extrapolation curves (Fig. 3) suggest similar patterns of species abundance. Despite similar rarefied species richness, FFs showed variation in species sharing (Table 4). Located in the northern portion of the study area, ALV, CGH, IBI, and SAN presented overlapping polygons in the NMDS ordination (Fig. 4). The FFs located near Londrina, BUL and PMG, formed a separate cluster, suggesting

a different compositional pattern from the northern group. Furthermore, despite similarity in tree species richness among all FFs, compositional differences are evidenced by the formation of polygons of different sizes and distances in the ordination (see also Table 4). Indeed, PERMANOVA results indicate that FFs differ significantly from each other in terms of species composition ($p < 0.001$) (Table S3).

Table 4
Species richness (S) and shared species across six Seasonal Atlantic Forest fragments selected for vegetation studies within the Long-Term Ecological Research Program "Atlantic Forest of Northern Paraná" (PELD-MANP). Forest fragments are located in the northern region of Paraná State, Brazil. ALV = Fazenda Alvorada; BUL = Fazenda Bule; CGH = Fazenda Congonhas; IBI = Parque Estadual de Ibicatu; PMG = Parque Estadual Mata dos Godoy.

	S	ALV	BUL	CGH	IBI	PMG
ALV	**45**	-				
BUL	**70**	26	-			
CGH	**61**	34	32	-		
IBI	**55**	34	29	36	-	
PMG	**61**	25	40	30	33	-
SAN	**61**	31	28	33	44	29

3.2 Restoration sites

A total of 1,334 individuals were recorded in restoration sites (RFs), distributed across 93 species and 34 families (Table 5). The number of individuals was similar among RFs (ANOVA: $p = 0.665$). Species distribution patterns and the abundance of smaller trees (2.5–19.9 cm DBH) resembled those found in FFs (Fig. 5), as did the basal area in this size class (ANOVA: $p = 0.265$). However, the basal area of larger trees (DBH ≥ 20 cm) was notably lower in RFs compared to FFs (ANOVA: $p < 0.001$). Among the different RFs, basal area did not differ significantly for either size class (smaller trees: $p = 0.661$; larger trees: $p = 0.137$).

Table 5
Characterization of the tree community in five Seasonal Atlantic Forest restoration sites (reforestation with native species) comprising the Long-Term Ecological Research Program "Atlantic Forest of Northern Paraná" (PELD-MANP). Restoration sites are located in the northern region of Paraná State, Brazil. RF = Reforestation; ALV = Fazenda Alvorada; CGH = Fazenda Congonhas; FZE = Fazenda Escola; PMG = Parque Estadual Mata dos Godoy; SAN = Fazenda Santo Antônio. In 10x10 plots all woody plants with DBH between 2.5 and 19.9 cm were sampled; in 10x20 plots all plants with DBH equal or greater than 20cm.

Site code	Families	Species	Basal area (m^2/ha)	Density (ind/ha)
ALV RF	26	41	10x10–8.5	10x10–1,820
			10x20–12.1	10x20–180
CGH RF	23	42	10x10–11.0	10x10–2,250
			10x20–15.8	10x20–335
FZE RF	21	44	10x10–13.1	10x10–2,880
			10x20–14.8	10x20–210
PMG RF	19	34	10x10–9.85	10x10–1,990
			10x20–6.17	10x20–110
SAN RF	21	39	10x10–11.8	10x10–2,380
			10x20–14.8	10x20–175
TOTAL	34	93	-	-

The families with the highest number of species were Fabaceae (18), Meliaceae (8), Malvaceae (7), and Lauraceae (6). The most abundant species in the RFs in the present sample were *Schinus terebinthifolia* Raddi (Anacardiaceae) for ALV RF, *Heliocarpus popayanensis* Kunth (Malvaceae) in CGH RF, *Cabralea canjerana* in FZE RF, *Parapiptadenia rigida* (Benth.) Brenan (Fabaceae) in PMG RF, and *Cecropia pachystachya* Trécul (Urticaceae) in SAN RF (Table S2).

The rarefaction curves showed the same pattern as the FF curves, with rapid growth followed by a plateau and sample coverage ranging from 80 to 90% (Fig. 6). In addition to similar numbers of species, families, and individuals, the sampling also revealed high species sharing among RFs (Table 6).

Table 6
Species richness (S) and shared species across five Seasonal Atlantic Forest restoration sites (reforestations with native species) selected for vegetation studies within the Long-Term Ecological Research Program "Atlantic Forest of Northern Paraná" (PELD-MANP). Restoration sites are located in the northern region of Paraná State, Brazil. ALV = Fazenda Alvorada; CGH = Fazenda Congonhas; FZE = Fazenda Escola; PMG = Parque Estadual Mata dos Godoy.

	S	**ALV**	**CGH**	**FZE**	**PMG**
ALV	**41**	-			
CGH	**42**	22	-		
FZE	**44**	16	19	-	
PMG	**34**	16	19	17	-
SAN	**39**	24	26	16	16

The NMDS plot suggests some proximity among all areas (Fig. 7); however, PERMANOVA indicated significant differences between areas ($p < 0.001$) (Table S3). FZE RF and PMG RF are more distant and show little or no overlap with the other restoration plantations. The polygon size, which reflects internal heterogeneity of the site, did not show as much variation as in the FFs, but FZE RF and CGH RF notably have smaller polygons.

4. Discussion

4.1 Forest fragments

While overall tree abundance and species richness was similar among forest remnants, logged forests exhibited lower basal area, even decades after logging. Differences in dominant species and species composition are also evident, corroborating the formation of two groups, one northern, more disturbed group and another at south, containing two larger and less disturbed fragments (Arroyo-Rodríguez et al. 2013). The existence of these two distinct species composition forest remnant groups could be also partially attributed to some minor environmental differences among areas (elevation, rainfall).

The biotic homogenization hypothesis, though, is not fully supported by taxonomic diversity data, given the significant differences in species composition among all sites. Research on the community´s plant functional diversity and composition, however, can shed some light into the fate of those highly disturbed forests. The lack of landscape connectivity and the quality of the matrix in the landscape surrounding fragments may also explain part of the observed variability in species composition (Martínez-Ramos et al. 2016). Fragments isolated within agricultural matrices tend to exhibit greater

floristic impoverishment over time, and the distance from other remnants directly influences seed dispersal (Chada et al. 2004; Pereira et al. 2013), leading to the recruitment of a subset of the species present in a given fragment.

It is noteworthy that the smallest polygon in the NMDS plot corresponds to PMG, suggesting high similarity among sampled plots. In spite of this internal homogeneity, there was consistently high diversity across all plots, reflecting the lower level of anthropogenic disturbance. PMG is the largest fragment in the sampling, exhibiting greater structural complexity and less edge influence compared to smaller fragments, which are often subject to anthropogenic disturbances that alter their structural characteristics (Harper et al. 2005; Murcia 1995). In this context, environmental dynamics in conserved areas are predominantly driven by small-scale natural disturbances, such as gap formation resulting from tree breakage or death (White and Jentsch 2001).

Smaller fragments may be subjected to progressive changes in species composition (Laurance et al. 2002), and the synergy between fragmentation and selective logging can lead to species homogenization (Joly et al. 2014). However, in the sampled forest fragments, while there is no obvious pattern of species homogenization, functional convergence is a possibility that should be investigated. In all logged fragments, except ALV, the most abundant species are small, slow-growth, shade-tolerant understory trees. The presence of dense liana tangles create favorable conditions for maintaining understory species while negatively affecting the health and survival of large trees (Vieira et al. 2025).

Increased mortality of large trees, which comprise the upper forest stratum, can alter the structure of forest fragments (Arcanjo et al. 2020). Gap formation resulting from tree death alters light regimes and microclimatic conditions (Zhu et al. 2014). Subsequently, these modifications in fragment structure and abiotic conditions can alter species composition, with literature suggesting this would benefit opportunistic or shade-intolerant, fast-growing species at the expense of shade-tolerant, slow-growing ones (Harper et al. 2005), with consequent decrease in functional diversity in these fragments (Holl et al. 2022; Tabarelli et al. 2008).

However, in areas with high disturbance levels, field observations and the data described here suggest that smaller, shade-tolerant species survive under liana tangles at the expense of "pioneer" species, since light levels at ground level in these locations may be comparable to those under intact canopy. These patterns suggest that lianas are an important plant group in the dynamics of these remnants, and may be driving a functional homogenization, rather than a species homogenization among forest fragments.

These findings suggest that, when selecting a reference ecosystem for ecological restoration, the use of a single forest fragment, usually found nearby restoration site, is not advisable. Instead, the use of a set of fragments, especially when assessing species composition, should be a better option (Suganuma and Durigan 2015).

4.2 Restoration sites

Although they share several Fabaceae, Meliaceae, and Lauraceae species with FFs, few Myrtaceae species were observed in RFs. Considering that Myrtaceae is one of the most representative families in Southern Brazilian Atlantic Forests (Soares-Silva 2000), the low occurrence of species belonging to this family in the sampled restoration plantations may be related to dispersal limitations (less likely in this case, since restoration sites are adjacent to seed sources), or to physical environmental limitations, such as soil water availability and microclimate (Tabarelli and Peres 2002), which may indicate limitations of these plantations in providing favorable conditions for regeneration and recruitment of some species (Barbosa et al. 2007).

With the exception of FZE RF, all other sites had planted species as the most abundant. This pattern is common in restoration plantations, since planted individuals, when reaching reproductive maturity, begin contributing to increased density of regenerants through locally produced seeds (Rodrigues et al. 2011).

However, the density of individuals in the 10 x 10 m plots, as well as basal area, are notably similar to FFs. As highlighted by Holl, Luong, and Brancalion (2022), tree density in areas undergoing restoration can become similar to reference areas before other indicators, such as diversity, which may take longer to reach values close to references. It is also notable that although the 10 x 10 m plots in RFs have a basal area similar to FFs, the 10 x 20 m plots still show lower values.

Furthermore, in all RFs the most abundant species among larger trees are on the list of planted species - *Guazuma ulmifolia* Lam. (Malvaceae) in ALV RF, FZE RF and SAN RF, *H. popayanensis* in CGH RF and *Alchornea glandulosa* Poepp. & Endl. (Euphorbiaceae) in PMG RF. This suggests that the restoration plantations will likely undergo intense compositional transformations, as many non-planted species already observed as regenerants have not yet reached the canopy. Thus, the lower strata may indicate future changes in species composition (Chada et al. 2004; Norden et al. 2009).

The proximity between all RF polygons in the NMDS can be partially explained by the common set of species used in planting. All RFs used seedlings from the same set of nurseries, with the exception of FZE RF, which showed the greatest difference in species composition.

Invasive plant species capable of hindering regeneration or colonization by new individuals, such as the C4 grass *Megathyrsus maximus*, were detected in all RFs, in different abundance levels. In PMG RF, unlike other RFs, wild boars was also observed within the sampled plots, which may have caused results similar to those described by Pereira et al. (2013), where a larger area of remnant habitat in the vicinity does not necessarily mean more species colonizing the RFs.

ALV RF, SAN RF and CGH RF, although having adjacent remnants much smaller than PMG RF, show similar richness among themselves. FZE RF, an older area without nearby mature forest fragments, also does not differ in richness from the others. These results corroborate studies indicating that restoration plantations do not always follow predictable successional trajectories toward references (Manhães et al. 2022; Suganuma et al. 2004). Ecological succession may not be unidirectional and predictable, as it

depends on various biotic and abiotic factors, and colonization, for example, is a random process (Barbosa et al. 2007; Hobbs and Norton 2004; Pereira et al. 2013).

Nonetheless, the absence of well-conserved fragments near restoration sites reduces the likelihood of the presence of vertebrate dispersers, leading to lower seed dispersal and less establishment of non-planted species (Barbosa et al. 2007; Palmer et al. 1997).

5. Conclusions

Our findings indicate that Seasonal Semideciduous Forest fragments in northern Paraná exhibit similar patterns of species richness and abundance, but differ in composition and structure, reflecting variations in size, disturbance history, and local environmental conditions. Larger, less disturbed fragments display greater structural complexity and higher species diversity. Therefore, the structural and floristic differences associated with FF site history should be considered when selecting reference sites for ecological restoration.

In restoration plantations, we observed that although tree density approaches levels recorded in forest fragments, floristic composition remains strongly dominated by planted species, with low representation of characteristic mature-forest taxa. The homogeneity among plantations and the absence of consistent signs of convergence with reference areas suggest that even after two decades, these areas remain in early successional stages.

These results highlight the importance of conservation strategies that preserve remaining forest fragments, as well as the critical role of landscape heterogeneity and proximity to conserved areas in ecological restoration. Furthermore, long-term monitoring through temporal series is essential for understanding successional trajectories and guiding management policies and practices that enhance regional resilience and biodiversity.

Declarations

Competing Interests: Authors declare none.

Author contributions: JOA performed field and laboratory work, analyzed data and wrote the first draft; GSG performed laboratory work, analyzed data and edited the manuscript; JDV performed field and laboratory work and edited the manuscript; ALC performed laboratory work and edited the manuscript; JMDT designed and supervised the research, performed field and laboratory work and edited the manuscript

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Figures

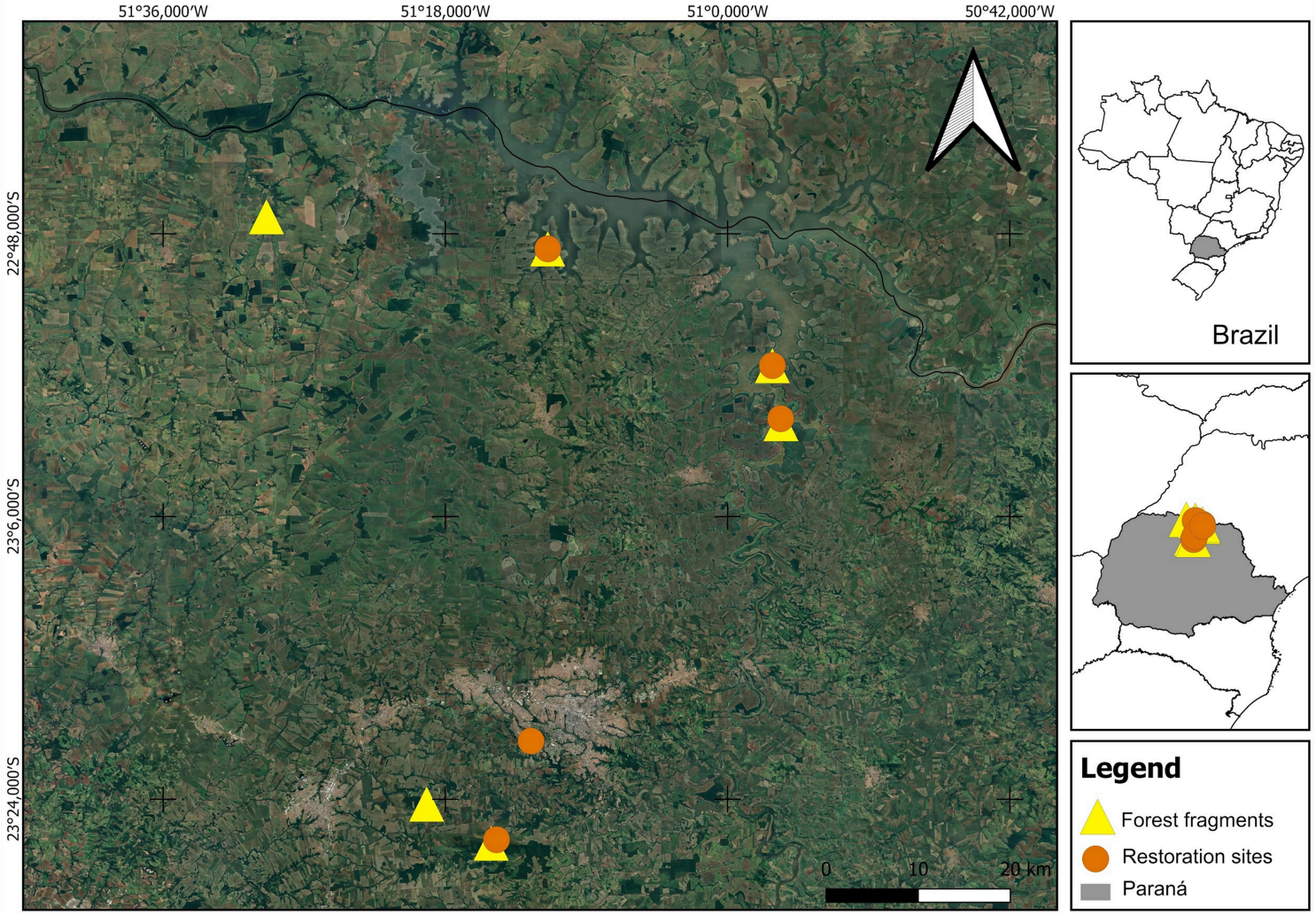


Figure 1

Location of Seasonal Atlantic Forest fragments and restoration sites (reforestations with native species) sampled by the Long-Term Ecological Research Program "Atlantic Forest of Northern Paraná" (PELD-MANP). Study areas are situated in the northern region of Paraná State, Brazil.

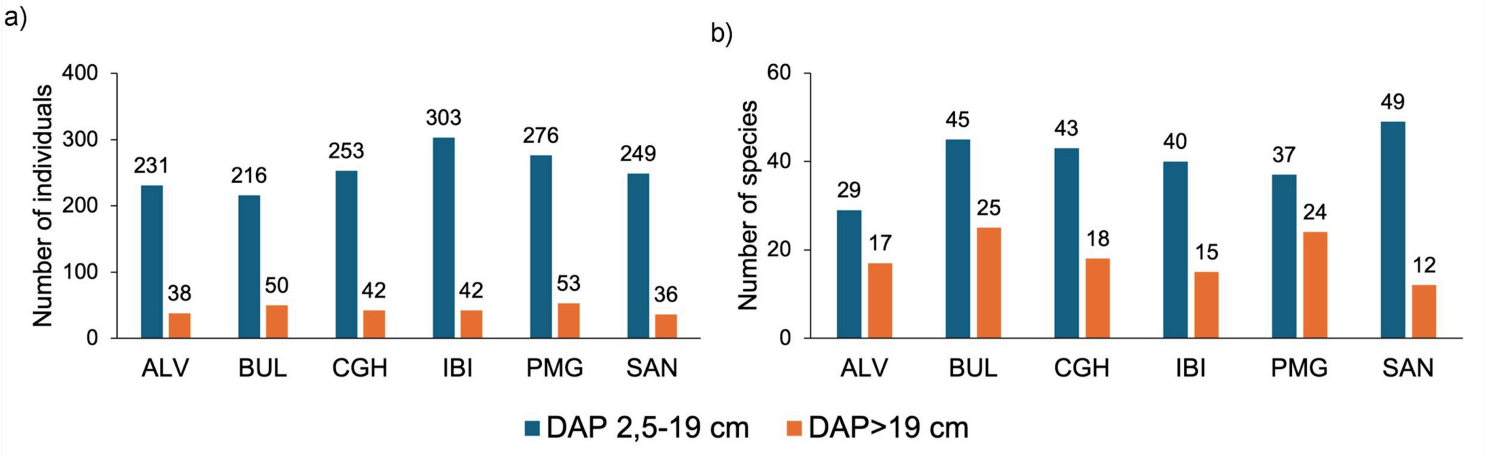


Figure 2

Number of individuals (a) and species (b) distributed by size classes based on diameter at breast height (DBH; 1.30 m) in six Seasonal Atlantic Forest fragments selected for vegetation studies within the Long-Term Ecological Research Program "Atlantic Forest of Northern Paraná" (PELD-MANP), located in northern Paraná State.

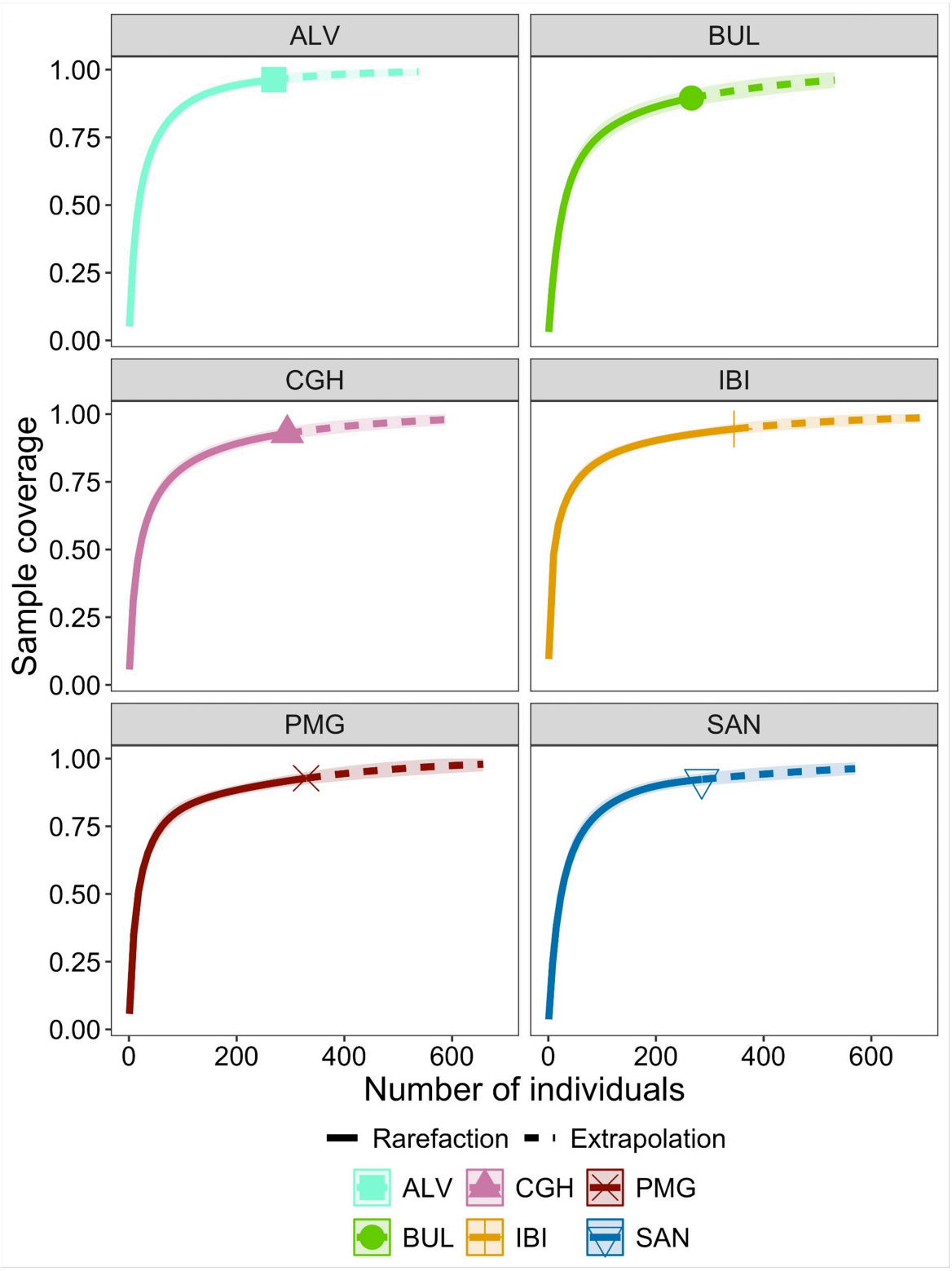


Figure 3

Rarefaction and extrapolation curves (q = 0, species richness) for the six Seasonal Atlantic Forest fragments selected for vegetation studies within the Long-Term Ecological Research Program "Atlantic Forest of Northern Paraná" (PELD-MANP). The forest fragments are located in the northern region of Paraná State, Brazil. Curves were standardized by sample coverage (type = 2).

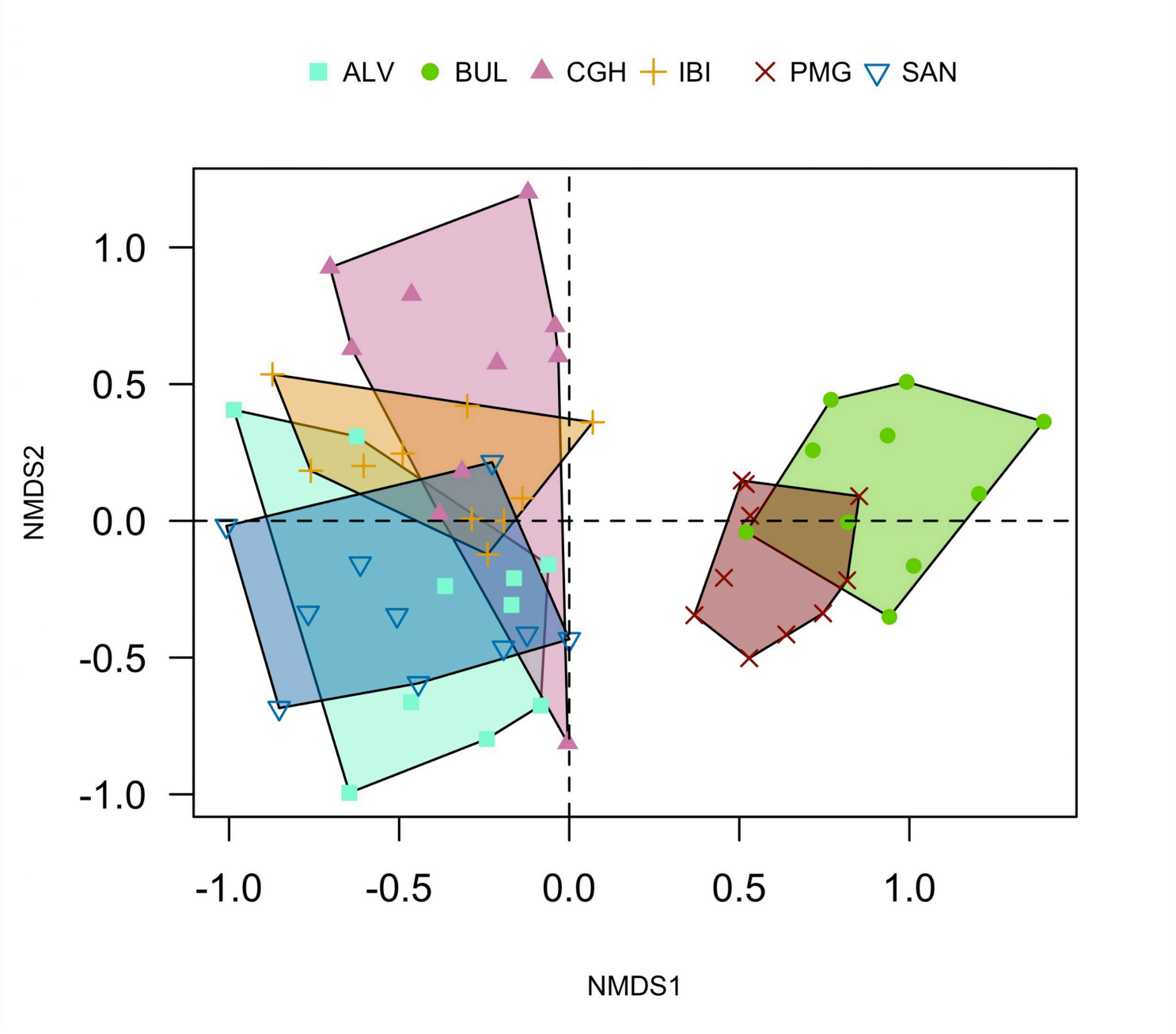


Figure 4

Non-metric multidimensional scaling based on the Chao index using an abundance matrix. Clustering of six Seasonal Atlantic Forest fragments selected for vegetation studies within the Long-Term Ecological Research Program "Atlantic Forest of Northern Paraná" (PELD-MANP). Forest fragments are located in the northern region of Paraná State, Brazil.

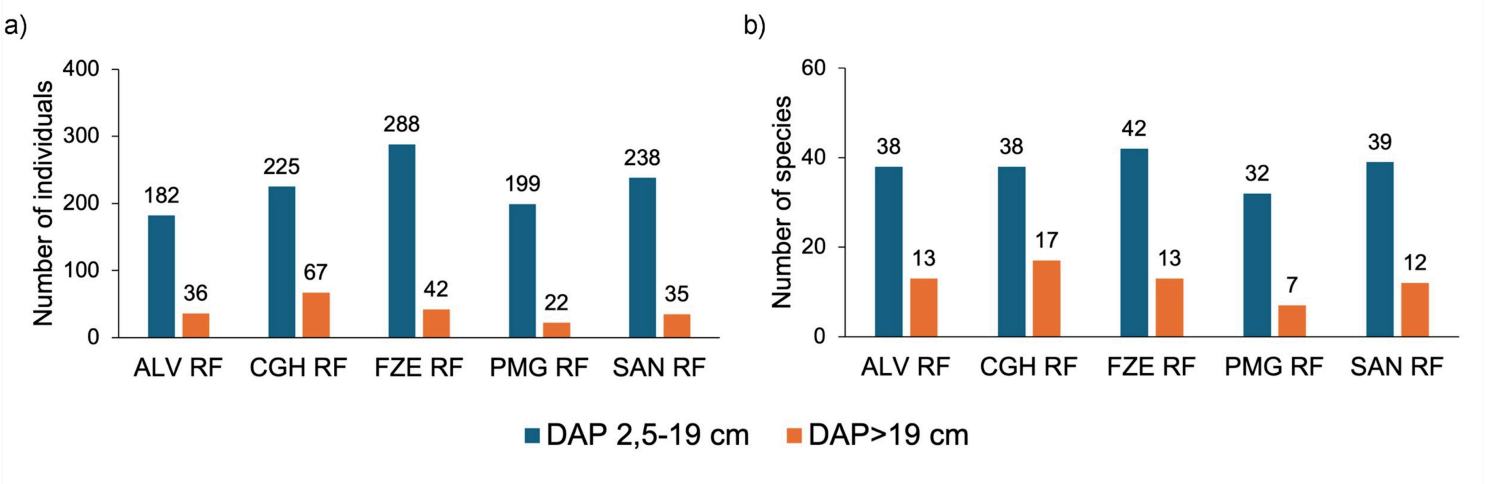


Figure 5

Number of individuals (a) and species (b) distributed by size classes based on diameter at breast height (DBH; 1.30 m) in five Seasonal Atlantic Forest restoration sites selected for vegetation studies within the Long-Term Ecological Research Program "Atlantic Forest of Northern Paraná" (PELD-MANP), located in northern Paraná State.

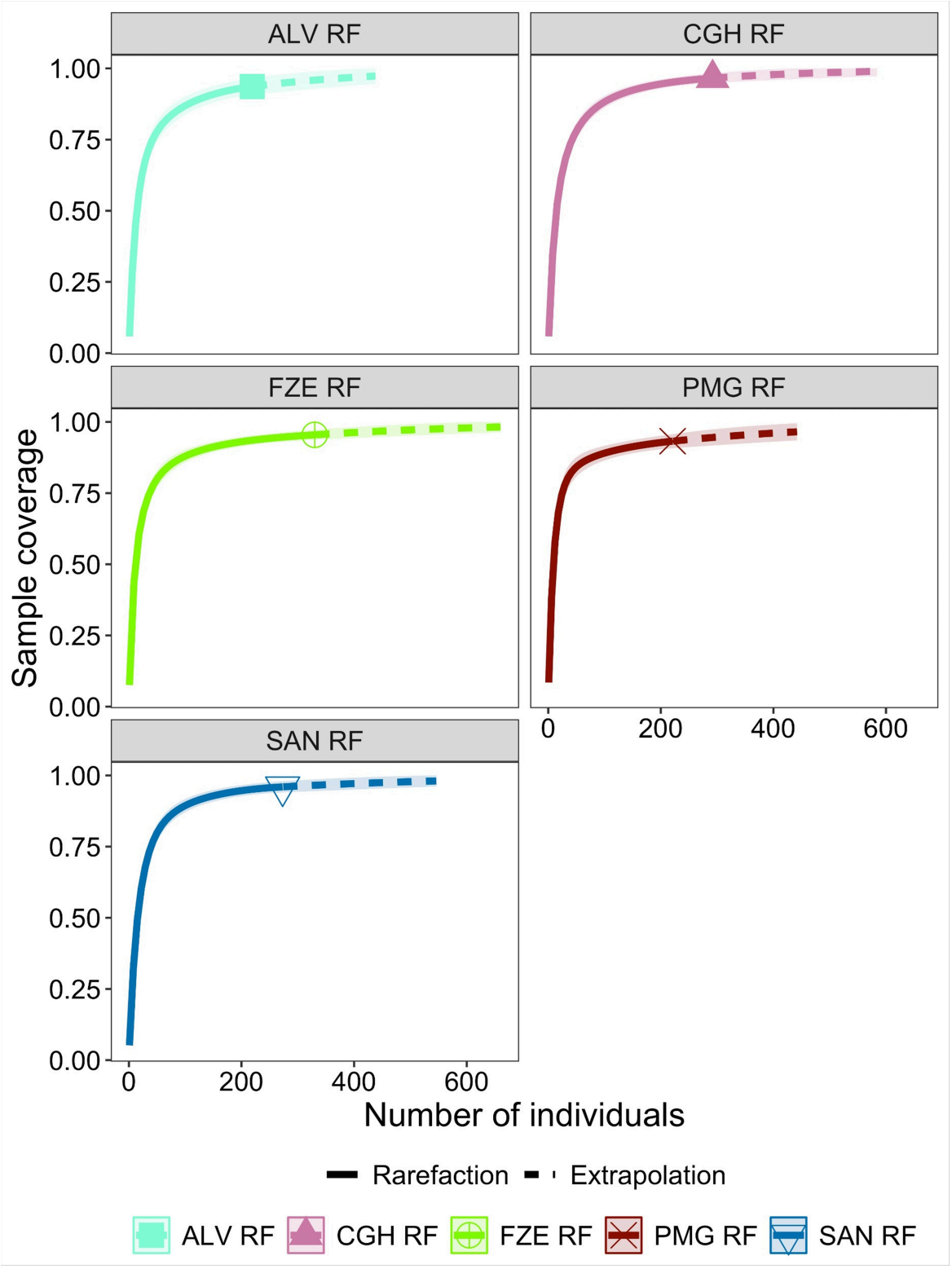


Figure 6

Rarefaction and extrapolation curves (q = 0, equivalent to species richness) for the five Seasonal Atlantic Forest restoration sites selected for vegetation studies within the Long-Term Ecological Research Program "Atlantic Forest of Northern Paraná" (PELD-MANP), located in the northern region of Paraná State, Brazil. Curves were generated using the iNext package and standardized by sample coverage (type = 2).

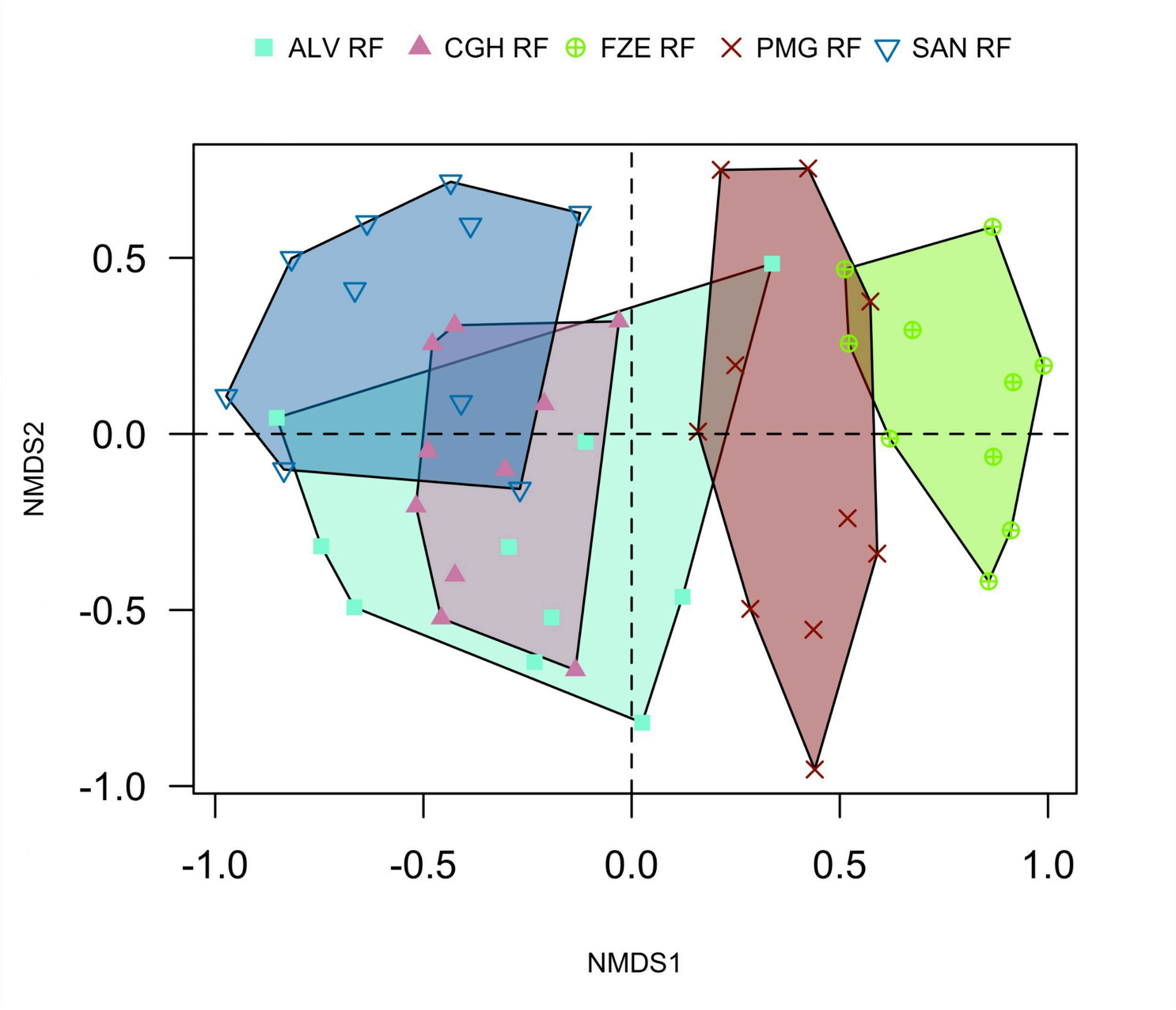


Figure 7

Non-metric multidimensional scaling based on the Chao index using an abundance matrix. Clustering of five Seasonal Atlantic Forest restoration sites selected for vegetation studies within the Long-Term Ecological Research Program "Atlantic Forest of Northern Paraná" (PELD-MANP). Forest fragments are located in the northern region of Paraná State, Brazil.

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