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Atlantic rainforest natural regeneration in fragmented formations affected by increasing human disturbance

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Abstract

Forests provides major ecosystem services worldwide. The Brazilian Atlantic Forest (BAF) has been dramatically devastated, with fragmentation processes jeopardizing its long-term sustainability. This study investigated the structure and successional dynamics in BAF natural regeneration along an anthroposequence characterized by increasing human disturbance histories

as: secondary (SF) > disturbed (DF) > late forest (LF). We aimed to understand how and the degree to which BAF fragmentation and human disturbance affected plants, soils, and the whole soil-plant relationships and feedbacks. We investigated the natural regeneration conditions of plants (using plant classification and quali-quantitative analyses) and soil chemistry (including pH-$CaCl_2$, H+Al, C, N, Pt, cation-exchange capacity (CEC), exchangeable cations, Al, B, Cu, Fe, K, Mn, and Zn) at twelve permanent, 2000 m^2 plots, distributed across LF, DF, and SF forests. Significant differences were determined by ANOVA. Correlation matrix (CM) and factor analysis (FA) were used for understanding correlations and feedbacks/variability among investigated parameters, respectively. Most of investigated plant and soil parameters showed significant differences ($p < 0.05$) between more developed plant formations (LF) *vs* less developed ones (SF), with differences mainly due to soil's development stage. All investigated forest formations are featured by a great influence of the soil-plant relationships and feedbacks, with a decreasing magnitude as LF → DF → SF. Thus, there is a direct, statistically recognizable impact of both "recent" as well as "ancient" human disturbance on investigated soil-plant formations. The anthropogenic influence clearly affected not only plant and soil as "separate" systems but the whole complex of interactions and feedbacks among ecosystem components. A decreasing quality in soil and plant parameters was observed as human disturbance increased. We demonstrated that BAF plant and soil require decades for their recovery after human disturbances, with complex mechanisms and behaviors in the relationships among ecosystem components. The results can be useful for managing future recovery in an ecosystem of worldwide strategic importance.

Keywords: Anthroposequence; Plant; Soil; Soil-plant feedbacks; Tropical forests.

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1. Introduction

The tropics alone host 45% of all forests on Earth (FAO, 2020). Tropical forests (TF), which mainly occur in Central Africa, Brazil, Indonesia, and Papua New Guinea, are considered a pivotal ecosystem worldwide due to their great influence on global biodiversity patterns (c.a. 80% of the world's discovered species), the ecosystem's ecological complexity, overall productivity, and biogeochemical cycles (Malhi et al., 2010). The State of the World's Forests (FAO and UNEP, 2020) reported that among the five major climatic domains (boreal, polar, temperate, subtropical, and tropical) the largest decrease in forest cover was observed for TF (13 million hectares per year).

Despite international agreements and national laws increasing the number of protected TF in the last several decades, they are still affected by a wide range of human disturbances (FAO and UNEP. 2020). Conversion of TF to agricultural croplands including corn (*Zea mays* L.), soybean (*Glycine* sp.), coffee (*Coffea* sp.), cacao (*Theobroma cacao* L.), sugarcane (*Saccharum officinarum* L.) for sugar and ethanol production, and meat (from beef, chicken, etc.), timber, etc.) represent the most dangerous threat for TF worldwide (Nogueira et al., 2018). The Brazilian Atlantic Forest (BAF, hereafter), a tropical forest biome that covers the country's east, southeast, and south coast, represents a paradigmatic example of the effects of land use change. It provides major ecosystem services, such as high biodiversity (Murray-Smith et al., 2009), soil and vegetation carbon stock (Spracklen and Righelato, 2014), and rain and fog water storage (Martins et al., 2015). Consequently, its degradation/destruction implies local, regional, and global issues (Oliveira et al., 2014).

The BAF has been dramatically harvested and developed in the past and is still under intense human pressure, including deforestation and soil degradation threats. Before the

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Portuguese colonization (1500 AD), the BAF occupied about 130 million hectares (Campanili and Schaffer, 2010). Currently, it consists of an almost continuous cover, at different stages of regeneration, of just 26% of the original area, with an additional 9% of the original area in scattered fragments (about 100 hectares each) (MMA, 2012). The remaining 65% is covered by human-dominated areas (Rezende et al., 2018), hosting c.a. 70% of Brazil's population, including two of the largest urban areas in the world, i.e., São Paulo and Rio de Janeiro. About 80% of the Brazilian Gross Domestic Product comes from the BAF region, home to Brazil's largest industrial and agroforestry centers (IBGE, 2017). Therefore, the safety of BAF ecosystems is of worldwide strategic importance (Nogueira et al., 2018).

Fragmentation processes jeopardize the long-term sustainability of the BAF biome, implying severe consequences on the ability to provide ecosystem and socio-economic services to society. Increases in forest fragment isolation due to anthropogenic disturbance make the BAF ecosystem less permeable and attractive for native flora and fauna, thus reducing biodiversity. Fragmentation increases local extinction rates, which can result in (Cassola, 2008): *i*) a reduction of gene flow; *ii*) increased pressure from nonnative, often invasive, species coming from the edge; thus, *iii*) changes to most of BAF's ecosystem processes and functions. In severe cases, what remains of an extensive BAF becomes a tangle of lianas, broken trunks, and/or dead trees often associated with extensive monoculture plantations (Cassola, 2008).

If not adequately managed, forest clearing and cultivation may degrade soil quality due to losses of soil organic matter (SOM), nutrients, and biological activity. Indeed, under natural Atlantic Forest conditions, even if such pedosystems are naturally poor in nutrients due to the high rainfall and long residence times promoting intensive leaching processes, they are (Martins et al.,

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2015): *i*) strongly connected with vegetation in a complex equilibrium influencing soil-vegetation behavior and feedbacks; and *ii*) protected from degradation.

Therefore, a better understanding of the complex and interactive relationships between biodiversity and the supporting pedosystem is needed. Investigating the complex behaviors and relationships in the BAF is crucial to improving the sustainable management of natural resources, as these areas can simultaneously support conservation and climate change mitigation (Diaz et al., 2018).

The "Edgardia and Lageado" (EL) experimental farms (Botucatu, University of Sao Paolo (UNESP), south-east Brazil), covering a total area of 2,139.28 ha, includes fragments of seasonal semideciduous Atlantic Forest (total cover: 938.2 ha). Humans have broken the continuity of primeval forest through pastures, crops, and ecotone with the *Cerrado* biome. Additionally, these fragments have different histories and magnitude of human disturbance due to selective deforestation activities, livestock influence, fire events, and other disturbances, mainly occurring since the 1960s (Nascimento et al., 2011).

Currently, the EL Atlantic Forest fragments are protected by Brazilian laws. They are located in the "Botucatu Environmental Protection Area", which aims to protect (da Silva et al., 2013): *i*) the last and only one BAF fragments characterizing a *cuesta* geological formation (*vide infra*); *ii*) the natural ecological corridors featuring the *cuesta*'s front; and *iii*) the Guarani aquifer's recharge areas under EL BAF fragments. All of these features make the EL fragments a unique ecosystem to implement knowledge about BAF biodiversity under the influence of different types and magnitude of human interventions. Indeed, knowing the history of BAF disturbance can allow us to better understand the current situation while outlining future actions for conservation purposes. Additionally, the BAF vegetation and soil quality needs to be monitored as well as

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understanding relationships and feedbacks among them under different stages of degradation and vegetation recovery, especially during the "natural regeneration" phase. Historically, these relationships and feedbacks have been poorly investigated; despite many studies referencing the importance of natural regeneration (Shimamoto et al., 2018; Bordin and Müller, 2019; Guerra et al., 2020; Gavito et al., 2021), the effects of forest recovery in the fragmented BAF remain under-studied. Several conditions can affect the forest ecosystem responses to natural regeneration processes (Romanelli et al., 2020) and consequently paired assessments at the same site produce more reliable comparisons (Reid et al., 2018). However, these studies are scarce due to the intrinsic complexities of conducting research comparing natural regeneration processes affected by different human disturbance at the same site, i.e., under comparable environmental conditions. Indeed, the novelty of the present research falls in investigating an anthroposequence by combining, for the first time, both soil and plant qualitative/quantitative relationships and feedbacks in a worldwide strategic and threatened forest environment, belonging to the same unique environmental area. This will furnish pivotal information about how human disturbance can be a driving force in BAF ecosystems, thus helping foresters, environmental managers, and decision-makers by providing new information for improving landscape management (Cetin, 2013).

This study aimed to investigate the structure and successional dynamics in BAF natural regeneration in fragments/patches with different human disturbance histories. In particular, we aimed to understand and investigate how and the extent to which BAF fragmentation and human disturbance affected plant, soil, and soil-plant relationships and feedbacks.

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2. Materials and methods

2.1. Study area

The "Edgardia and Lageado" (EL) experimental farms (Botucatu, south-east Brazil; 22°47'30" – 22°50' S and 48°26'15" to 48°22'30" W), belongs to the Capivara River basin (3,432.23 km^2) within the Paranapanema Valley region in the western São Paulo Plateau.

The climate is classified as hot and humid subtropical (Cfa) (Koeppen criteria; Cunha and Martins, 2009). Mean annual rainfall is 1,495 mm, distributed mainly between October and March. The mean annual temperature is 20.5 ºC, with coolest and warmest periods recorded in July (17.5 ºC) and February (23 ºC), respectively.

Geology beneath EL is mainly composed of igneous rocks of the Paraná basin, such as the basaltic *cuesta* formation of the São Bento Group (Serra Geral formation), which makes this landscape unique and famous worldwide. *Cuesta* (from Spanish "slope") is a term to indicate the so-called "homoclinal ridge," i.e., a geological structure with a cliff or escarpment on one side and a gentle dip or backslope on the other. These characteristic landforms occur in areas of tilted strata with a harder capping layer underlying a softer, cliff making layer; this last layer erodes more rapidly than the capping layer, thus making differential erosion and weathering phenomena key processes in the whole *cuesta*'s formation (Machado et al., 2015).

Soils predominantly belong to Oxisols and Ultisols Order (Soil Taxonomy, 2014). They feature either an oxic (B_o) or argillic (B_t) deep mineral horizon, respectively, with the whole depth profile varying according to morphology. Soils are extremely leached, thus being acidic and poor in nutrients (Nogueira et al., 2018).

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2.2. Experimental design

Due to differences in past and present management and historical vicissitudes that affected the whole area over the last few centuries (starting from Portuguese colonization, *vide supra*), vegetation has been fragmented in different patches characterized by differences in physiology and flora composition, as well as species and floristic associations. Jorge and Sartori (2002) grouped these fragments in seven different formations. For the purposes of this study, we investigated three of them, covering 938 ha (Fig. 1a). They were selected because of their clear differences in terms of increasing human disturbance (*vide infra*). In particular, the three investigated BAF fragments, presented according to an increasing human disturbance (or decreasing naturality) gradient, are the following (Jorge and Sartori, 2002): ***Late Forest (LF, hereafter):*** characterized by almost-native vegetation cover of more than 40 years old. Human disturbance can be considered almost absent since the fragment located in not easily accessible areas (orange squares in Fig. 1a); ***Disturbed Forest (DF):*** the vegetation has been strongly affected by human disturbance until 30-40 years ago. In particular, it underwent intense anthropogenic intervention with selective exploitation of tree species (blue triangles in Fig. 1a); ***Secondary Forest (SF):*** the vegetation was disturbed by intensive human activities until 20 years ago, when it was finally abandoned. The primary intensive use was as pasture (red circles in Fig. 1a).

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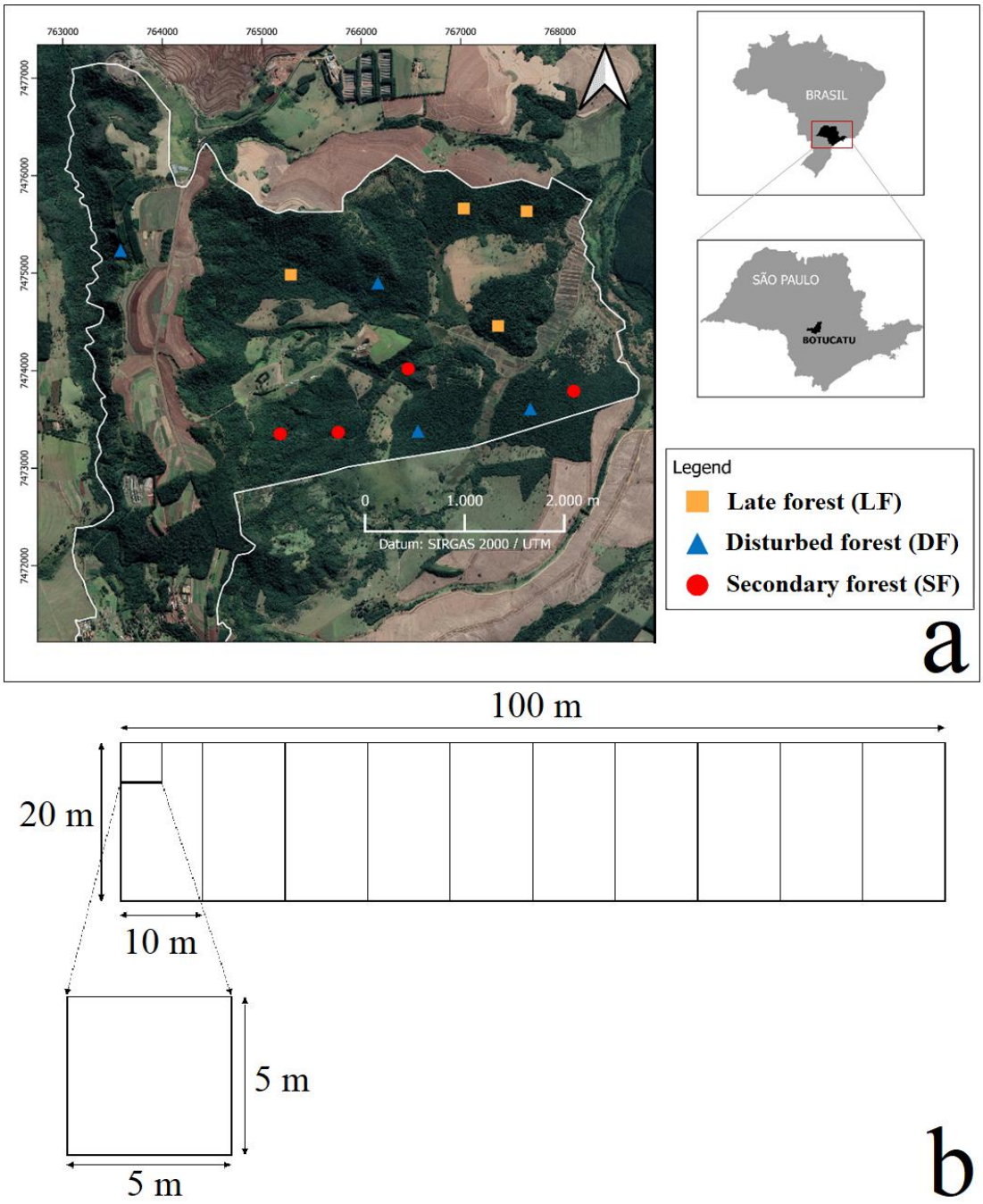

Fig. 1. Study area (a) and experimental plot design (b).

2.3. Sampling methodology

Twelve permanent plots of 2000 m^2 (20 × 100 m; Fig. 1b) were randomly distributed in LF, DF, and SF (four plots for each investigated area). To avoid any edge effect, each plot was far

from the others with a border of at least 500 m. Replications consisted of five randomly distributed subplots of 25 m² (5 × 5 m) (Fig. 1b). Overall, 60 subplots were investigated, i.e., 5 replications × 4 plots × 3 different BAF fragments (LF, DF, SF). Then the following measurements were done in each of them.

2.4. Plant investigation

To better understand ecological behaviour, forest development, and soil-plant relationships and feedbacks, several plant parameters were measured or calculated, including: height (H), diameter at the breast height (DBH), total density (TDe), relative density (RDe), species dominance (G), Shannon-Wiener diversity index (H´), Pielou's evenness/equitability index (J'), seed dispersion pathway (DW), successional class (SC), total number of plants (NP), number of different families (NDF), number of different species (NDS), and number of seedling species (NS) (formulas are reported in Supplementary Material 1).

Supplementary Material 1

Investigated plant parameters.

$$Total\ density = TDe = \frac{ni}{ha} \quad (1)$$

where *TDe* is the number of individuals of a given species per unit area. In forest formations, the corresponding unit of area is one hectare (ha); *ni* the number of individuals per sampled species in the area; *ha* the hectares.

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$$Relative\ density = RDe = \frac{ni/_{ha}}{N/_{ha}} \times 100 \quad (2)$$

where *RDe* is the relationship (expressed in %) between the number of individuals of a given species (*ni*) and the total number of individuals (*N*) sampled in the same area (measured in *ha*).

$$Species\ dominance = G = \frac{\pi \times DBH^2}{4} \quad (3)$$

where *G* is the area of environment occupation by individuals of a given species. Indeed, in forest communities, dominance is obtained through the basal area (*BA*), i.e., the square meters occupied by a given species per unit area (1 ha); *DBH* is the diameter at the breast height.

$$Shannon - Wiener\ diversity\ index = H' = \frac{[N * \ln(N) - \sum_{i-1}^{S} ni\ ln(ni)]}{N} \quad (4)$$

where *N* is the total number of individuals for all species, *ni* the total number of individuals for the species-i, and *S* the total number of species

$$Pielou's\ \frac{evenness}{equitability}\ index = J' = \frac{H\prime}{\ln S} \quad (5)$$

where *S* is the total number of species.

Tree development was assessed by measuring the DBH and the height (H). The seed dispersion pathway (DW) was assessed, classified (gravity, wind, ballistic, water, or animals)

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and quantified for each species, as was the successional class (SC; pioneers *vs* not pioneer species).

$$DW, SC = \frac{Ndw, sc}{N} \quad (6)$$

where *DW, SC* are the relationship between the number of individuals (N) of a given species dispersion pathway (*dw*, sc) or successional class (*dw*, sc) and the total number of individuals (*N*) sampled in the same area.

For each forest formation, the number of plants (NP), number of different families (NDF), number of different species (NDS), and number of seedling species (NS), were also assessed.

2.5. Soil sampling and analysis

Surface soil horizons (A; 0–20 cm) were sampled in each of the five previously reported subplots (Fig. 1b). In particular, for each subplot, five different soil subsamples were collected in random locations within each subplot. Twenty-five (5 soil samples × 5 subplots) different soil samples were collected for each plot, resulting in one-hundred (25 soil samples in each plot × 4 LF, DF or SF) for each investigated area. Overall, three-hundred soil samples were gathered.

Physical-chemical analyses were conducted on soil air-dried Ø < 2 mm, according to Brazilian official procedures (Raij et al., 2001). Soil pH-$CaCl_2$ and potential acidity (H+Al) were measured potentiometrically with a glass electrode in a soil/solution mixture of 1:2.5 1 N $CaCl_2$. Total C and N were determined by dry combustion using a CHN analyzer. Total P was measured through the NH_4Cl and HCl acid digestion method. Cation-exchange capacity (CEC) was determined via saturation with $BaCl_2$ at pH 8.2. Calcium and Mg content was measured through

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extraction in 1M KCl. Al, B, Cu, Fe, K, Mn, and Zn concentrations were determined by the Olsen extraction procedure at pH 8.5.

2.6. Statistical analysis

Statistics (univariate and multivariate) were carried out using the software program R (R Core Team, 2021). Open-source software is advantageous because it provides free data processing, analysis, and presentation of data (Kaya et al. 2018).

Data were compared using ANOVA. Significant differences between mean values, for both soil physical-chemical and plant parameters, were determined using Tukey's post-hoc honest significant difference test with $p < 0.05$. From this point of view, LF, DF, and SF formations were graphically compared by the use of box-plots. The procedure proposed by Capra et al. (2014) was applied for dataset treatment before correlation matrix (CM; *0.05, **0.01, ***0.001) and factor analysis (FA) application: *i*) normal distribution of variables in dataset was tested; *ii*) the raw datasets were Box–Cox transformed to approach normality; *iii*) a CM was performed based on the Box–Cox transformed data; and, *iv*) FA was carried out based on the CM. For a more robust statistical approach and to facilitate interpretation of the results, varimax rotation was used.

Reported values indicate the mean ± standard error of the mean.

3. Results and discussion

3.1 Floristic survey

Overall, 1,957 individuals under natural regeneration conditions were sampled (Supplementary Material 2). They belong to 114 different species and 41 botanical families. In terms of origin, only one was naturalized and all others were natives from Brazil.

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Supplementary Material 2

Floristic list of the species in natural regeneration conditions.

Families	Scientific Name	LF	DF	SF
Acanthaceae	*Anisacanthus trilobus* Lindau		x	
Anacardiaceae	*Astronium graveolens* Jacq.	x	x	x
Annonaceae	*Annona* sp.		x	
	Guatteria latifolia R.E.Fr.		x	
Apocynaceae	*Aspidosperma parvifolium* A. DC.	x		
	Aspidosperma polyneuron Müll. Arg.	x	x	
	Tabernaemontana hystrix Steud.		x	x
Arecaceae	*Syagrus romanzoffiana* (Cham.) Glassman		x	
Asteraceae	*Vernonanthura discolor* (Spreng.) H.Rob.			x
Bignoniaceae	*Handroanthus impetiginosus* (Mart. ex DC.) Mattos		x	
	Tecoma stans (L.) Juss. ex Kunth		x	
	Zeyheria tuberculosa (Vell.) Bureau ex Verl.		x	x
Boraginaceae	*Cordia americana* (L.) Gottschling & J.S.Mill.		x	x
	Cordia sellowiana Cham.			x
Cactaceae	*Cereus jamacaru* DC.		x	
Cannabaceae	*Celtis fluminensis* Carauta		x	
	Celtis iguanea (Jacq.) Sarg.		x	
Celastraceae	*Monteverdia aquifolia* (Mart.) Biral	x	x	x
	Monteverdia gonoclada (Mart.) Biral		x	x
	Monteverdia truncata (Nees) Biral			x
Ebenaceae	*Diospyros inconstans* Jacq.	x		
Euphorbiaceae	*Actinostemon concepcionis* (Chodat & Hassl.) Hochr.	x	x	x
	Alchornea sidifolia Müll. Arg.			x
	Alchornea triplinervia (Spreng.) Müll.Arg.		x	x
	Croton floribundus Spreng.	x		x
Fabaceae	*Anadenanthera colubrina* (Vell.) Brenan		x	
	Anadenanthera colubrina var. cebil (Griseb.) Altschul		x	
	Bauhinia longifolia (Bong.) Steud.		x	
	Calliandra foliolosa Benth.	x		
	Calliandra sp.		x	x
	Cenostigma pluviosum (DC.) Gagnon & G.P.Lewis var. *pluviosum*		x	
	Centrolobium tomentosum Guillem. ex Benth.	x	x	
	Holocalyx balansae Micheli	x	x	
	Inga striata Benth.	x		
	Machaerium aculeatum Raddi			x
	Machaerium brasiliense Vogel		x	x
	Machaerium scleroxylon Tul.		x	x

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	Machaerium stipitatum Vogel		x	
	Parapiptadenia rigida (Benth.) Brenan		x	x
	Poecilanthe parviflora Benth.		x	
	Pterocarpus violaceus Vogel		x	x
	Senegalia polyphylla (DC.) Britton & Rose	x	x	x
	Senna multijuga (Rich.) H.S.Irwin & Barneby	x	x	x
Lauraceae	*Nectandra grandiflora* Nees & Mart			x
	Nectandra megapotamica (Spreng.) Mez	x	x	x
	Nectandra sp.		x	
Lecythidaceae	*Cariniana estrellensis* (Raddi) Kuntze	x	x	
Lythraceae	*Lafoensia pacari* A.St.-Hil.	x		
Malvaceae	*Ceiba speciosa* (A.St.-Hil.) Ravenna		x	x
	Guazuma ulmifolia Lam.		x	
	Luehea divaricata Mart.		x	x
Meliaceae	*Cabralea canjerana* (Vell.) Mart.			x
	Cedrela odorata L.			x
	Guarea macrophylla Vahl	x		x
	Trichilia casaretti C.DC.	x	x	x
	Trichilia catigua A.Juss.	x	x	x
	Trichilia clausseni C.DC.	x	x	x
	Trichilia elegans A.Juss.	x	x	x
	Trichilia pallida Sw.		x	x
	Trichilia sp.	x		
Monimiaceae	*Mollinedia oligantha* Perkins			x
Moraceae	*Maclura tinctoria* (L.) D.Don ex Steud.		x	
	Sorocea bonplandii (Baill.) W.C.Burger et al.	x		
Myrtaceae	*Campomanesia guazumifolia* (Cambess.) O.Berg			x
	Campomanesia xanthocarpa (Mart.) O.Berg	x	x	x
	Eugenia longipedunculata Nied.	x	x	x
	Eugenia ramboi D.Legrand	x	x	x
	Eugenia uniflora L.	x	x	
	Myrcia brasiliensis Kiaersk.		x	
	Myrcia guianensis (Aubl.) DC.		x	x
	Myrciaria floribunda (H.West ex Willd.) O.Berg	x	x	x
Nyctaginaceae	*Guapira opposita* (Vell.) Reitz.	x		x
Ochnaceae	*Ouratea castaneifolia* (DC.) Engl.	x	x	
Phytolaccaceae	*Gallesia integrifolia* (Spreng.) Harms	x	x	x
	Phytolacca dioica L.		x	
Picramniaceae	*Picramnia ramiflora* Planch.	x	x	
Piperaceae	*Piper aduncum* L.			x
	Piper amalago L.	x	x	x
	Piper arboreum Aubl.		x	x
Poaceae	Criciuma sp.	x		
Polygonaceae	*Coccoloba mollis* Casar.	x	x	x

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Primulaceae	*Myrsine umbellata* Mart.	x		x
Rhamnaceae	*Rhamnidium elaeocarpum* Reissek	x		
Rosaceae	*Prunus myrtifolia* (L.) Urb.		x	x
	Prunus sp.		x	
Rubiaceae	*Coutarea hexandra* (Jacq.) K.Schum.	x	x	
	Coutarea sp.		x	
	Duroia sp.	x	x	x
	Palicourea sp.		x	x
	Psychotria sp.		x	
	Randia ferox (Cham. & Schltdl.) DC.	x	x	x
	Rudgea jasminoides (Cham.) Müll. Arg.	x	x	x
Rutaceae	*Balfourodendron riedelianum* (Engl.) Engl.	x		
	Esenbeckia febrifuga (A.St.-Hil.) A. Juss. ex Mart.	x	x	
	Metrodorea flavida K.Krause	x		
	Metrodorea nigra A.St.-Hil.	x	x	
	Pilocarpus spicatus A.St.-Hil. subsp. *Spicatus*		x	
	Pilocarpus pauciflorus A.St.-Hil.	x		
	Zanthoxylum fagara (L.) Sarg.		x	
	Zanthoxylum rhoifolium Lam.		x	
Salicaceae	*Casearia gossypiosperma* Briq.	x	x	x
	Casearia sylvestris Sw.	x	x	x
Sapindaceae	*Allophylus edulis* (A.St.-Hil. et al.) Hieron. ex Niederl.		x	x
	Cupania tenuivalvis Radlk.		x	x
	Cupania vernalis Cambess.			x
	Diatenopteryx sorbifolia Radlk.	x	x	
	Dilodendron bipinnatum Radlk.	x		
Sapotaceae	*Chrysophyllum gonocarpum* (Mart. & Eichler ex Miq.) Engl.	x	x	
Siparunaceae	*Siparuna guianensis* Aubl.			x
Solanaceae	*Cestrum* sp.	x		
	Solanum pseudoquina A.St.-Hil.	x	x	
	Solanum sp.		x	x
Urticaceae	*Urera baccifera* (L.) Gaudich. ex Wedd.		x	
Verbenaceae	*Aloysia virgata* (Ruiz & Pav.) Juss.		x	

The five most abundant families were Fabaceae (16%), Euphorbiaceae (15%), Ochnaceae (12%), Meliaceae (11%), Rutaceae (10%), Rubiaceae (9%), and Piperaceae (9%), accounting alone for up to 82% of the total number of individuals (Supplementary Material 3a). The Fabaceae family had the highest richness (*H'*, Shannon-Wiener diversity index) too (16%), followed by

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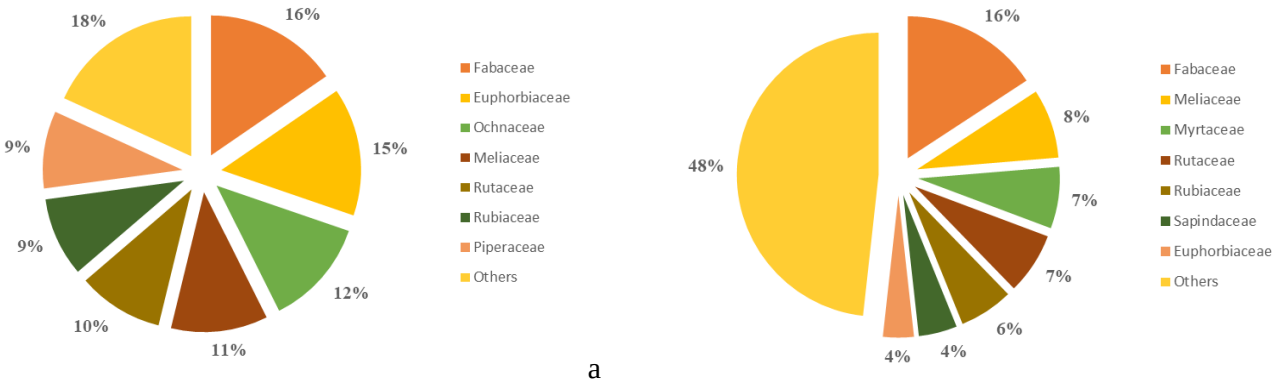
Meliaceae (8%), Myrtaceae (7%), Rutaceae (7%), Rubiaceae (6%), Sapindaceae (4%), and Euphorbiaceae (4%) (Supplementary Material 3b).

Supplementary Material 3

Families' relative abundance (a) and richness (b) in the investigated formations.



a b

In terms of floristic composition in all investigated forest formations, the Fabaceae family is predominant in terms of richness as well (Supplementary Material 4a-c), being 11% for LF (Supplementary Material 4a), 18% for DF (Supplementary Material 4b), and 13% for SF (Supplementary Material 4c). Fabaceae is the family with the greatest diversity and number of species in all the Brazilian flora (IRRJBG, 2018).

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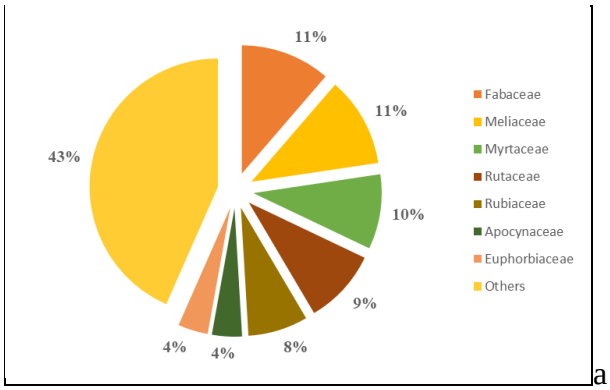
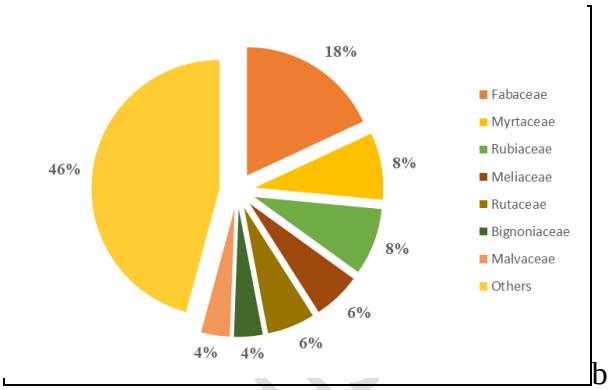
Supplementary Material 4

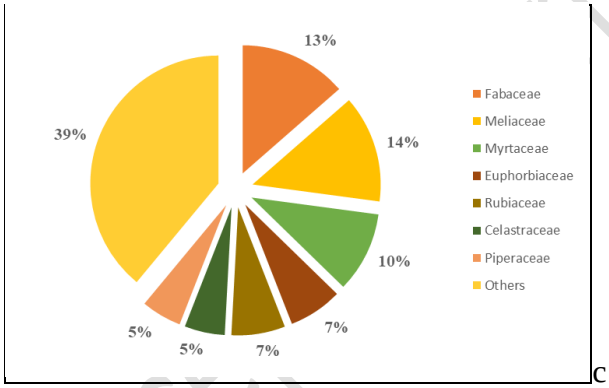
Families' richness in late (a), disturbed (b), and secondary (c) forests.



a



b



c

Table 1 shows several diversity indexes for each investigated forest formation. Results showed DF > LF > SF in terms of total individuals, families, and basal area. In terms of species and, consequently, H' (Shannon-Wiener diversity index), we noted DF > SF > LF. The Pielou's evenness/equitability index (J') ranked as DF = SF > LF, while total density was SF > LF > DF. This could represent a first clue of the fact that the SF → DF → LF sequence represent a trend towards a more advanced successional stage.

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Table 1

Vegetation indexes by formations (LF = late forest; DF = disturbed forest; SF = secondary forest).

	LF	**DF**	**SF**
Individuals	630	768	559
Species	53	83	59
Families	27	32	24
Diversity index (H')	2.81	3.29	3.00
Equability index (J')	0.71	0.74	0.74
Total density (ind ha^{-1})	8400	7680	11180
Basal area (m^2 ha^{-1})	0.244	0.309	0.207

Overall, results showed that more human-impacted forest formations (SF) contain fewer plant individuals, families, and smaller basal area. However, the opposite was true for plant total density. In disturbed environments, plant species tend to occupy several ecological niches since competition among them is higher (Polechová and Storch, 2018). One of the strategies is increasing space invasion (McMahon et al., 2021); thus, density and even diversity index (*H'* and *J', vide supra*), can show higher values when compared with more natural plant formations (LF). Indeed, in this case, the presence of natural potential vegetation results in a soil-vegetation equilibrium with fewer dominating plants (Aparecido et al., 2018). In more developed plant formations (LF), we observed fewer species than DF and SF formations.

3.2. Soil features

Fig. 2 shows the distributions and differences between forest formations for all investigated soil physical-chemical parameters.

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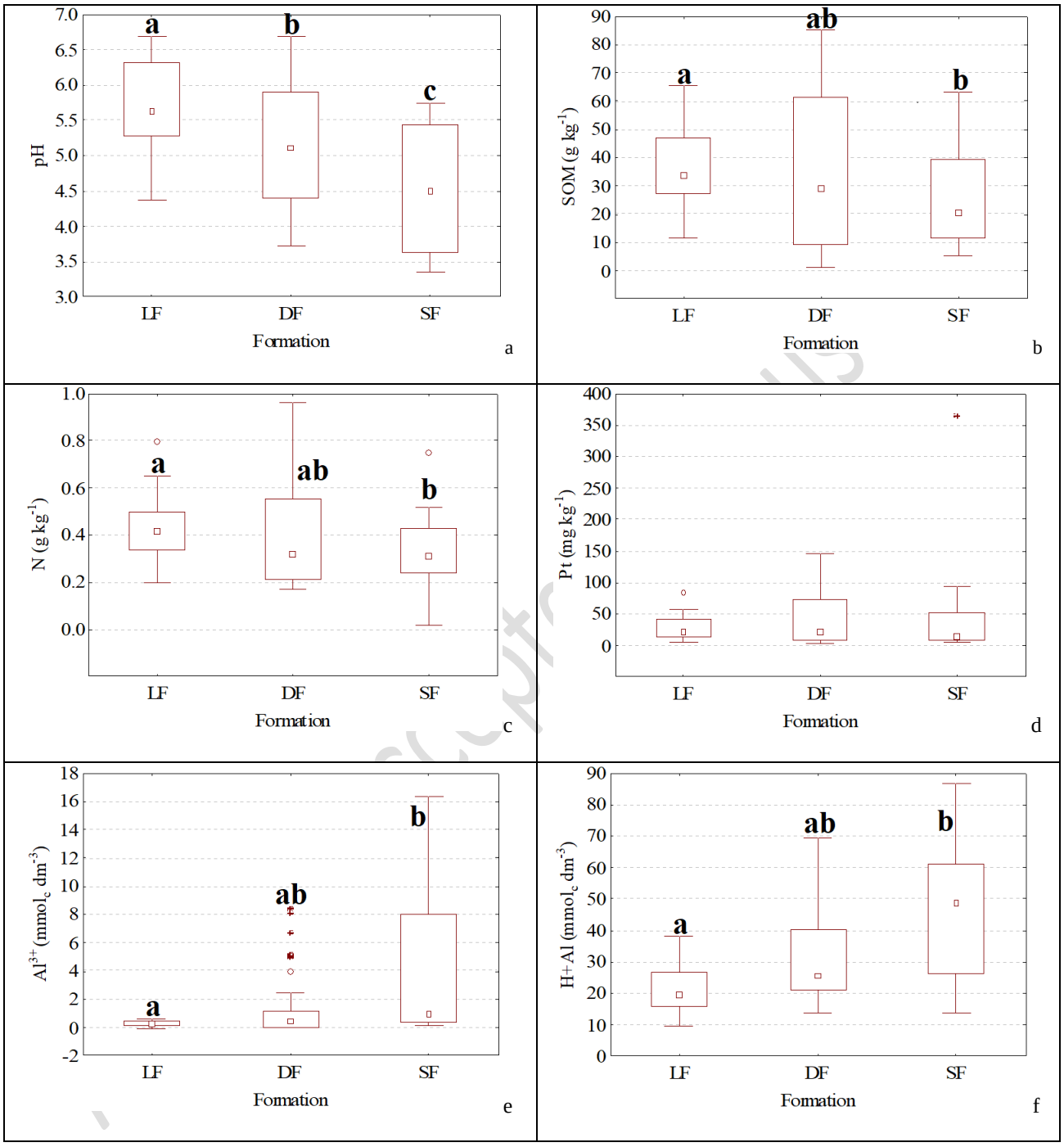
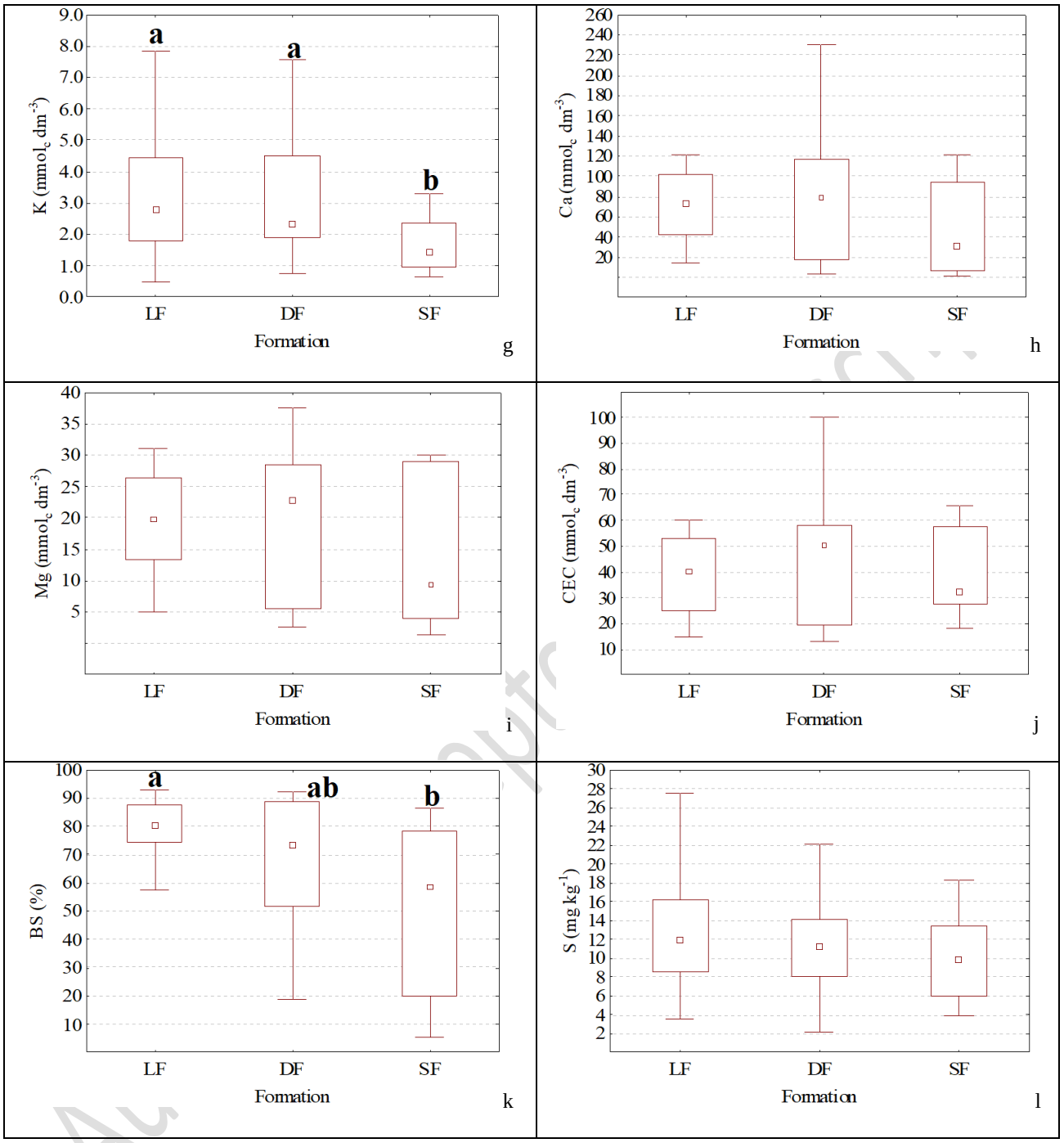

pH
7.0
6.5
6.0
5.5
5.0
4.5
4.0
3.5
3.0
a
b
c
LF
DF
SF
Formation
a
SOM (g kg-1)
90
80
70
60
50
40
30
20
10
0
a
ab
b
LF
DF
SF
Formation
b
N (g kg-1)
1.0
0.8
0.6
0.4
0.2
0.0
a
ab
b
LF
DF
SF
Formation
c
Pt (mg kg-1)
400
350
300
250
200
150
100
50
0
LF
DF
SF
Formation
d
Al3+ (mmolc dm-3)
18
16
14
12
10
8
6
4
2
0
-2
a
ab
b
LF
DF
SF
Formation
e
H+Al (mmolc dm-3)
90
80
70
60
50
40
30
20
10
0
a
ab
b
LF
DF
SF
Formation
f


K (mmol$_c$ dm^{-3})
a
a
b
LF
DF
SF
Formation
g
Ca (mmol$_c$ dm^{-3})
Formation
h
Mg (mmol$_c$ dm^{-3})
Formation
i
CEC (mmol$_c$ dm^{-3})
Formation
j
BS (%)
a
ab
b
Formation
k
S (mg kg^{-1})
Formation
l

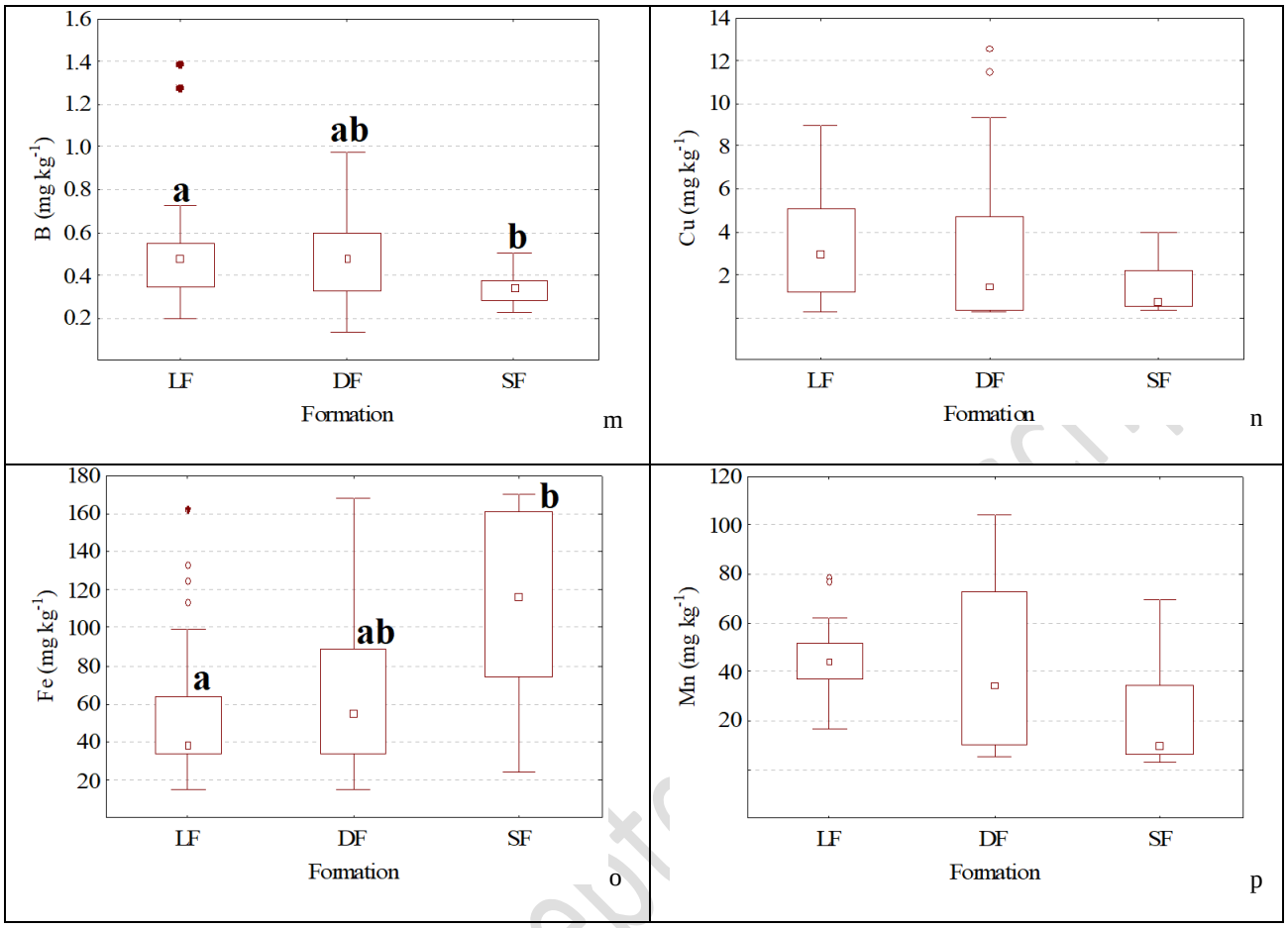


Fig. 2. Box-plots showing differences in soil physical-chemical parameters among investigated plant formations (LF = late forest; DF = disturbed forest; SF = secondary forest) for a) pH, b) soil organic matter (SOM), c) nitrogen (N), d) phosphorus (P), e) exchangeable aluminum (Al^{3+}), f) exchangeable acidity ($H^{+}+Al^{3+}$), g) exchangeable potassium (K^{+}), h) exchangeable calcium (Ca^{2+}), i) exchangeable magnesium (Mg^{2+}), j) cation exchange capacity (CEC), k) base saturation (BS), l) sulfur (S), m) boron (B), n) copper (Cu), o) iron (Fe), and p) manganese (Mn). Different capital letters indicate significant differences ($p < 0.05$) based on Tukey honestly significant difference post-hoc comparisons.

Soil pH-$CaCl_2$ (Fig. 2a) showed a clear significant difference among investigated forest formations, decreasing from 5.7±0.1, to 5.2±0.1, and to 4.5±0.2 in late (LF), disturbed (DF) and

secondary (SF) forests, respectively, which correspond to increasing human disturbance. In undisturbed forest (LF), soils develop under mature vegetation cover able to create conditions for: *i*) the presence of a mature organic surface horizon (O) able to release a greater amount of basic cations, thus increasing soil pH (Junior et al., 2021); and *ii*) a decreasing influence of leaching processes from intense rainfall due to canopy interception, thus avoiding loss of most soluble elements, i.e., basic cations (Silva et al., 2000). In more disturbed environments such as SF, where soil cover by forest canopy dramatically decreased, the processes discussed above are enhanced, resulting in a decrease in soil pH. Pearson correlation coefficients (Supplementary Material 5) confirmed all of these hypotheses, showing a strong positive correlation between pH *vs* SOM (r = 0.62**) and basic cations (K, r = 0.62**; Ca, r = 0.72**; Mg, r = 0.72**), while negative with acidic one (Al^{3+}, r = -0.73**, H+Al, r = -0.71**).

Supplementary Material 5

Pearson correlation coefficients of soil physical-chemical properties and plant parameters.

	pH	**SOM**	**N**	**Pt**	**Al^{3+}**	**H+Al**	**K**	**Ca**	**Mg**
pH	1.00	0.62**	0.66**	0.37*	-0.73**	-0.71**	0.62**	0.72**	0.72**
SOM		1.00	0.66**	0.39*	-0.36*	ns	0.44*	0.69**	0.75**
N			1.00	0.38*	-0.45*	-0.34*	0.59**	0.76**	0.71**
Pt				1.00	-0.29*	ns	0.25*	0.65**	0.59**
Al^{3+}					1.00	0.72***	-0.41*	-0.54**	-0.59**
H+Al						1.00	-0.36*	-0.32*	-0.24*
K							1.00	0.55**	0.54**
Ca								1.00	0.90***
Mg									1.00

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	CEC	BS	S	B	Cu	Fe	Mn	Zn
pH	0.58**	0.92***	0.43**	0.41**	0.61**	-0.59**	0.63**	0.32*
SOM	0.72***	0.57**	0.56**	0.52**	0.65**	ns	0.67**	0.32*
N	0.72***	0.64**	0.42*	0.58**	0.49*	ns	0.44*	ns
Pt	0.65**	0.45*	0.24*	0.24*	0.36*	ns	ns	ns
Al^{3+}	-0.38*	-0.87***	-0.31*	-0.28*	-0.36*	0.56**	-0.49*	-0.25*
H+Al	ns	-0.72**	ns	ns	ns	0.81**	-0.31*	ns
K	0.51**	0.54**	ns	0.48*	0.54**	-0.42*	0.36*	ns
Ca	0.96***	0.78**	0.41*	0.52**	0.55**	ns	0.46*	ns
Mg	0.91***	0.77**	0.51**	0.43*	0.62**	ns	0.60**	ns
CEC	1.00	0.63**	0.42*	0.48*	0.55**	ns	0.43*	ns
BS		1.00	0.38*	0.44*	0.50*	-0.53**	0.59**	0.30*
S			1.00	0.40*	0.31*	ns	0.47*	ns
B				1.00	0.34*	ns	ns	ns
Cu					1.00	ns	0.63**	0.31*
Fe						1.00	-0.32*	ns
Mn							1.00	0.30*
Zn								1.00

	DBH	H	DW	SC	NP	NDF	NDS	NS	G	TDe
pH	ns	ns	0.22*	0.34*	ns	ns	ns	-0.24*	-0.22*	ns
SOM	ns	ns	ns	0.34*	ns	ns	ns	ns	ns	ns
N	ns	ns	ns	0.27*	ns	ns	ns	-0.25*	ns	ns
Pt	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

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Al^{3+}	ns	ns	-0.24*	-0.30*	0.40*	ns	ns	0.29*	0.32*	0.40*
H+Al	ns	ns	-0.25*	ns	0.27*	ns	ns	Ns	0.22*	0.27*
K	ns	ns	ns	ns	ns	ns	ns	Ns	ns	ns
Ca	ns	ns	ns	ns	-0.22*	ns	ns	Ns	ns	-0.22*
Mg	ns	ns	ns	ns	ns	ns	ns	-0.30*	ns	ns
CEC	ns	ns	ns	ns	ns	ns	ns	-0.25*	-0.14*	-0.15*
BS	ns	ns	ns	ns	-0.26*	ns	ns	-0.31*	-0.25*	-0.26*
S	ns	ns	ns	ns	ns	ns	ns	Ns	ns	ns
B	ns	ns	ns	ns	ns	ns	ns	Ns	Ns	ns
Cu	ns	ns	ns	ns	ns	0.23*	ns	Ns	Ns	ns
Fe	ns	ns	ns	ns	ns	-0.22*	-0.22*	Ns	Ns	ns
Mn	ns	ns	0.21*	0.49*	ns	0.22*	ns	Ns	Ns	ns
Zn	ns	ns	ns	ns	ns	ns	ns	Ns	Ns	ns
DBH	1.00	0.66**	-0.23*	ns	-0.24*	ns	ns	Ns	0.24*	-0.24*
H		1.00	ns	ns	ns	ns	ns	Ns	Ns	ns
DW			1.00	0.25*	ns	0.37*	0.28*	Ns	Ns	ns
SC				1.00	ns	0.45*	0.37*	Ns	Ns	ns
NP					1.00	0.36*	0.41*	0.32*	0.82***	1.00***
NDF						1.00	0.90***	Ns	0.29*	0.36*
NDS							1.00	Ns	0.35*	0.41*
NS								1.00	0.22*	0.32*
G									1.00	0.82***
TDe										1.00

*p < 0.05; **p < 0.01; ***p < 0.001

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Soil organic matter (SOM; Fig. 2b) and N (Fig. 2c) showed a clear significant ($p<0.05$) decreasing trend with increasing human disturbance. SOM had a mean value of 35±3 g kg^{-1} in LF *vs* 25±4 g kg^{-1} in SF, meaning a decrease of around 30%. Nitrogen decreased from 0.4±0.0 g kg^{-1} to 0.3±0.0 g kg^{-1}, in LF and SF, respectively, which is a 25% decrease in concentration. These results agree with Souza et al. (2021) which investigated the recovery trends of a fragmented secondary BAF after the absence of human-disturbance for more than 30 years and observed a clear increase in soil carbon storage with increasing forest age. Phosphorous (Fig. 2d) did not show any statistical differences among investigated forest formations. As usual for these pedosystems, which are acidic and nutrient poor, SOM was the main source of soil nutrition (Silva et al., 2021) and had positive correlations with macro- (N: r = 0.66**; P: r = 0.39*; K: r = 0.44*; S: r = 0.56**) and micro-nutrients (B: r = 0.52**; Cu: r = 0.65**; Mn: r = 0.67**; Zn: r = 0.32*) (Supplementary Material 5).

Acidic exchangeable cations (Figs. 2e, f) confirmed what was previously observed for pH (*vide supra*). They increased in less developed, more leached (thus more acidic) pedosystems, and we observed a significant increasing trend from LF to SF. In SF formations, the decreasing tree cover corresponded with greater leaching of base cations and greater presence of Al^{3+} and H^{+} on cation exchange sites (Souza et al., 2021). In contrast, LF formations had more robust cation cycling (Figs. 2g-i) and higher base saturation (Figs. 2k).

Exchangeable-cations (Figs. 2g-i) and CEC (Fig. 2j) did not show a specific difference among investigated formation, with the exception of K, which increased significantly in less disturbed environments. However, BS significantly decreased with increased human disturbance. In more developed forests an increase in forest canopy brings to: *i*) more enriched surface organic horizons, thus increasing basic cations (Silva et al., 2020), and *ii*) less leached soils (Silva et al.

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2021). Cation-exchange capacity was significantly correlated to SOM, indicating that pH dependent charges on organic molecules were an important source of CEC.

Among investigated micronutrients (Figs. 2l-p), only B and Fe showed significant differences, though they had opposite trends with respect to disturbance. Boron increased in more developed formations (LF) while Fe increased in less developed forests (SF). Boron had a significant, positive correlation with SOM (r = 0.52**; Supplemental Material 4), which corresponds with SOM being one of the principal B sources for plant nutrition (Das and Purkait, 2020).

These first outcomes about soil parameters confirm that the pedoenvironment plays a pivotal role in providing edaphic conditions that significantly affect forest dynamics (Bordin and Müller, 2019; Santiago-García et al., 2019). Additionally, soils seem to be moderately resilient with most of the investigated attributes improving within (SF to DF) or over (SF to LF) 4 decades after human disturbance. This observation suggests slower recovery compared with the results from Poorter et al. (2021), who observed a recovery in soil attributes within one decade after low- to moderate-intensity land use. The difference between our results and Poorter et al. (2021) can be attributed to the fact that these authors investigated very few soil parameters (namely bulk density, soil C and N content) that are usually not sufficient for a complete soil resilience assessment (McBratney et al., 2019) and that may have overestimated the real soil resilience capacity.

3.3. Plant measurements

Fig. 3 shows the distributions and differences between forest formations for all investigated plant parameters.

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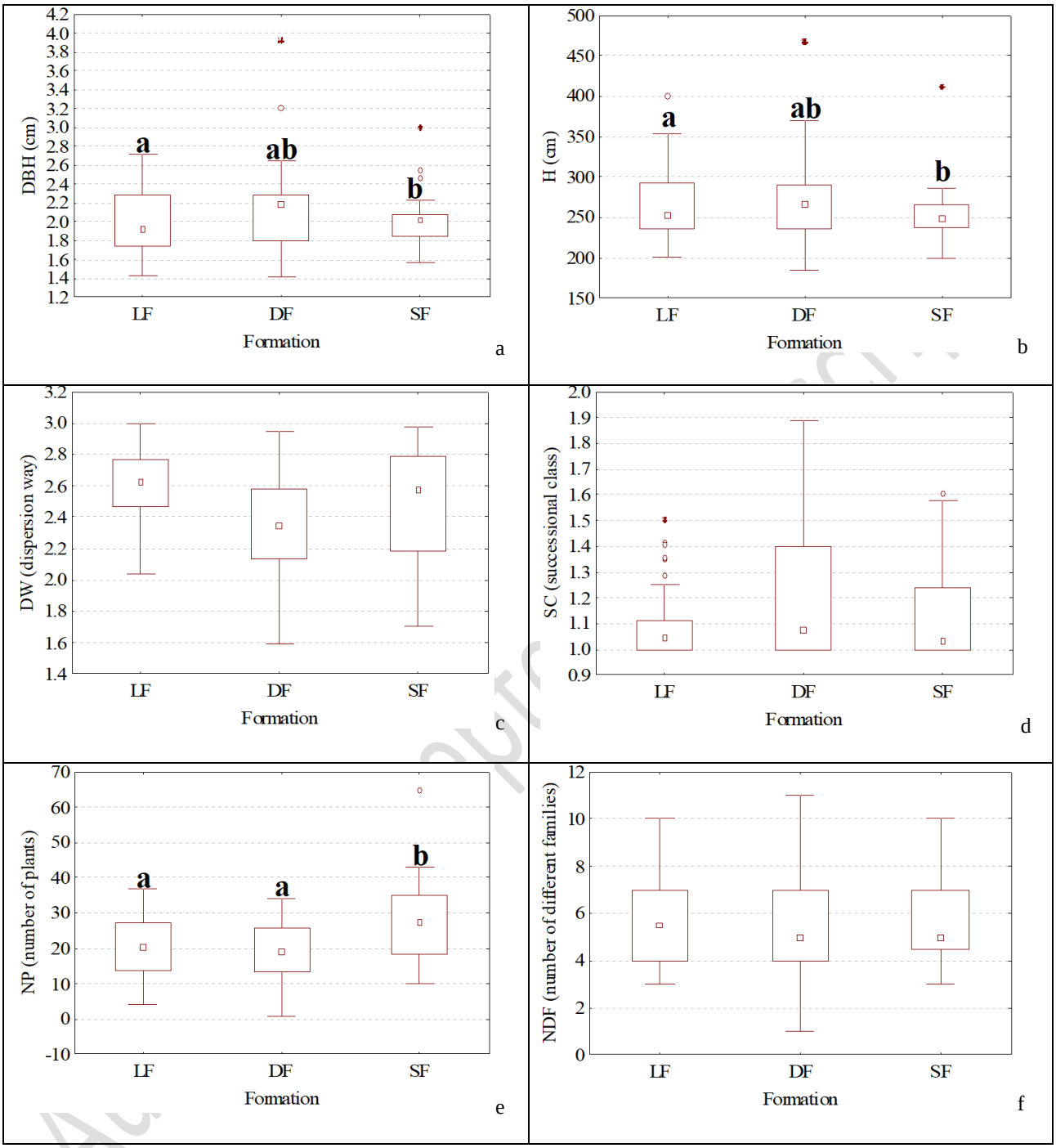
DBH (cm)
4.2
4.0
3.8
3.6
3.4
3.2
3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
a
ab
b
LF
DF
SF
Formation
a
H (cm)
500
450
400
350
300
250
200
150
a
ab
b
LF
DF
SF
Formation
b
DW (dispersion way)
3.2
3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
LF
DF
SF
Formation
c
SC (successional class)
2.0
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1.0
0.9
LF
DF
SF
Formation
d
NP (number of plants)
70
60
50
40
30
20
10
0
-10
a
a
b
LF
DF
SF
Formation
e
NDF (number of different families)
12
10
8
6
4
2
0
LF
DF
SF
Formation
f

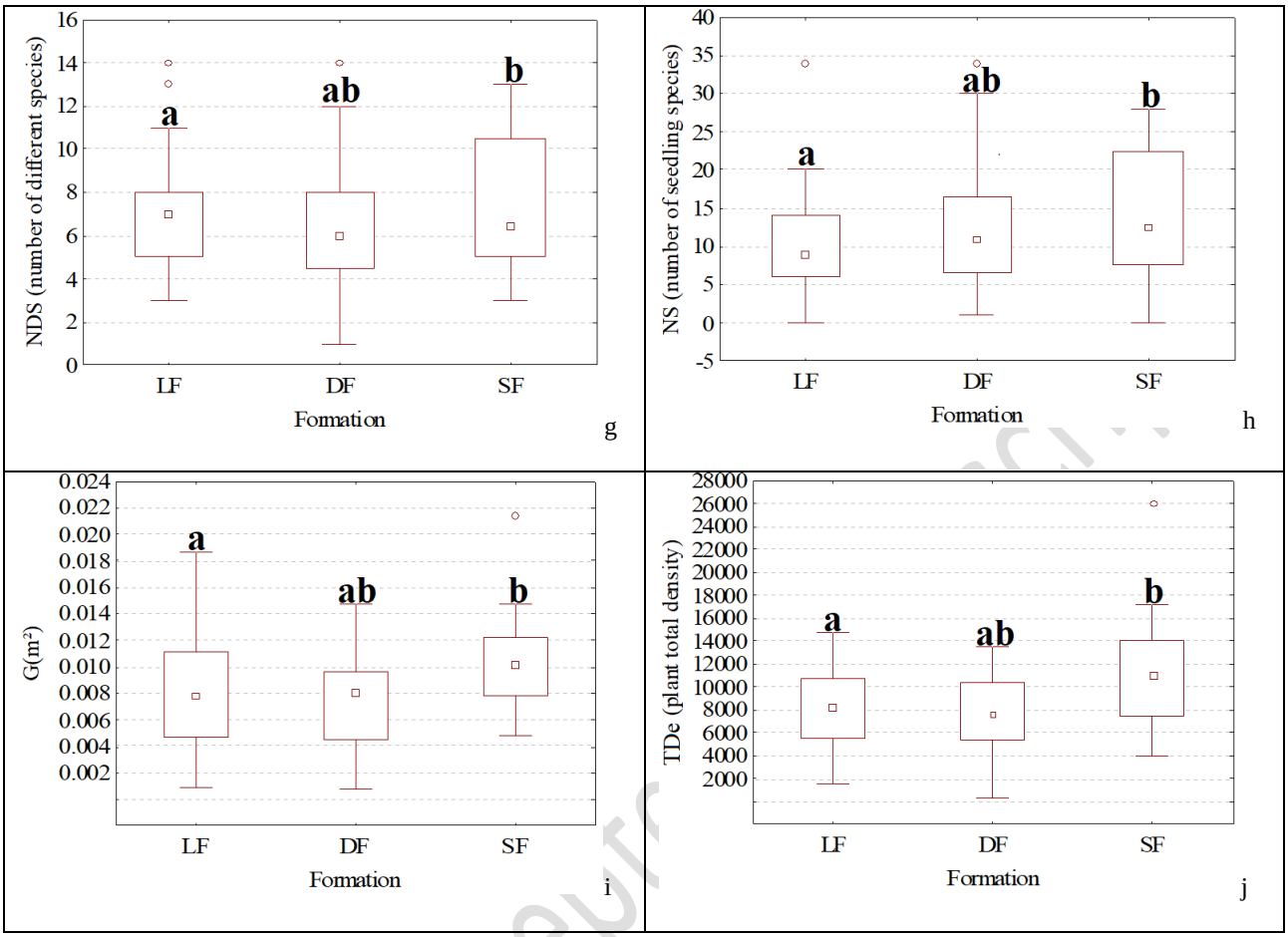

Fig. 3. Box-plots showing distributions and differences in plant parameters among investigated forest formations (LF = late forest; DF = disturbed forest; SF = secondary forest) for a) diameter at breast height, b) height, c) dispersion way, d) successional class, e) number of plants, f) number of different families, g) number of different species, h) number of seedling species, i) species dominance, and j) plant total density. Different capital letters are for significant differences ($p < 0.05$) based on Tukey honestly significant difference post-hoc comparisons.

Both plant DBH (Fig. 3a) and H (Fig. 3b) had statistically higher values in LF *vs* SF formations, while no differences were observed between these two and DF. This was expected since LF plants are characterized for a more developed stage of maturation. Pearson correlation coefficients from the correlation matrix (Supplementary Material 5) showed a positive correlation

between DBH and H (r = 0.66**), which confirms the generally understood relationship that as plant height increases, so too does its diameter. The observed highest DBH and H in a more advanced successional stage, i.e., LF, can be attributed by the longer absence of human disturbance (e.g., forest exploitation) thanks to the full protection granted by the law (*vide supra*). The longer absence of human disturbances (40 years) allowed an advance in forest development stage, thus explaining the observed increase in biomass and SOM stocks (McDowell et al., 2020; Souza et al., 2021). The dispersion way (DW; Fig. 3c) and the successional classes (SC; Fig. 3d) did not show significant differences ($p<0.05$) among the investigated forest formations. Pearson correlation coefficients (Supplementary Material 5) showed that the DW was influenced by several soil parameters such as pH (r = 0.22*), Al (r = -0.24*), Al+H (r = -0.25*), Mn (r = 0.21*), and finally with DBH (r = -0.23*) within plant parameters. These multiple correlations showed that in less acidic pedosystems, i.e., in more developed ones (LF; *vide supra*), animal-driven dispersion is more frequent compared to others (wind, gravity, etc.); the opposite is true in less developed environments (SF). In more developed LF formations, where the soil is less acidic (*vide supra*), animals play a pivotal rule for mature plants reproduction. In the less developed SF formations, in contrast, where the plant canopy had a decreasing cover of trees relative to shrubs and herbaceous species (thus, a more "open" environment) animal-driven dispersion played a less important role compared to (a) wind and (b) gravity.

The number of plants (NP; Fig. 3e) was significantly higher in the most disturbed environments, even though the number of families was not significantly different (Fig. 3f). The higher number of species in more disturbed environments follows the theory of ecological succession, wherein early colonizing species decline over time giving way to a smaller number of species (mainly trees) that dominate the canopy once they become established (Mancini Texeira

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et al., 2018). In the first stages of ecological succession (SF) there were more herbaceous and shrub species and fewer trees (in comparison to the LF formation). A significant, positive correlation between NP *vs* Al^{3+} (r = 0.40*) and Al+H (r = 0.27*) was also observed, while there were significant, negative correlations between NP *vs* Ca^{2+} (r = -0.22*) and base saturation (BS) (r = -0.26*). Thus, in less developed pedosystems, i.e., the more leached one (SF), the number of species was related to soil conditions, specifically chemical parameters that are tied to soil age and development. We also observed a negative correlation with DBH (-0.24*). As the number of species increases, the average diameter decreased accordingly, which corresponds to more disturbed environments where herbaceous species are more prevalent than shrubs and trees.

The number of different species (Fig. 3g), the number of seedlings (Fig. 3h), the basal area (Fig. 3i) and plant total density (Fig. 3j) all increased in more disturbed forests (SF) compared to more mature formations (LF). Also, observed Pearson product moments coefficients in the CM (Supplementary Material 5), completely corroborates this hypothesis, being results affected, again, by soil's development stage.

Overall: *i*) most of the investigated plant parameters showed statistically significant differences between more developed plant formations (LF) *vs* less developed ones (SF), and *ii*) these differences were also due to the soil's development stage. Another important research outcome is that the strategic field of BAF restoration needs to fully include soil due to the number of significant and biologically important relationships we observed between soil and plant parameters. As demonstrated by Mendes et al. (2019) in their literature review, soil parameters are, in most of cases, not investigated prior to BAF restoration activities. this is even true for basic parameters (such as soil pH), showing a general lack of consideration for the soil environment. The importance of soil features cannot be neglected, since changes in soil variables represent a

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central issue in BAF management and conservation (Lourenço et al., 2021). Our research clearly demonstrates the importance of including soil parameters in BAF investigation by also analyzing their relationships with plants. Without inclusion of soil information and analysis, BAF restoration activities may be less successful (Gavito et al., 2021), resulting in losses of environmental and socio-economic resources.

3.3. Multivariate statistics

3.3.1. Principal factor analysis

Principal factor analysis was performed for each of the forest formations separately. For all investigated plant formations, the eigenvalues of the first three extracted factors (Table 2) after matrix rotation were greater than 1. These factors can thus be grouped into a three-component model accounting for 91% (LF), 93% (DF), and 92% (SF) of data variation for each forest type.

For the LF formation, F1, representing 76% of the variance, extracted most of the soil parameters (with the relevant exclusion of N, Al^{3+}, and B) and plant measurements (SC and G apart) as all positively concordant. This showed that, in less disturbed forests, increasing soil quality (higher SOM and pH) corresponded to increased macro- and micro-nutrient cycling. This had a positive effect on whole soil fertility, including improvements in CEC and BS. In such favorable pedosystem conditions, several positive soil-plant feedbacks are observed, such as: *i*) higher average plant diameter (DBH); *ii*) increased average height (H); and, *iii*) the whole forest formation and structure improved with an increased number of individuals (NP), species (NS), families (NDF), and higher plant total density (TDe). In the least disturbed forest (LF) favorable soil conditions seem to drive pivotal ecological aspects. Indeed, a positive highly significant correlation with the dispersion way (DW) was observed. In particular, all of the previously

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reported soil and plant conditions and feedbacks seem to be more favorable for animal rather than abiotic (gravity, wind, ballistic, water) seeds dispersion systems (*vide supra*). This can be explained by thinking about forest structure in these well-structured formations, which are characterized by a denser plant population with few, small open spaces. In such conditions, animal-driven seed dispersal is favored by: *i*) the easy access to plant seeds by animals rather than by abiotic factors; *ii*) a greater animal diversity, with particular reference for birds (Sivisaca, 2020). For all of the previously reported outcomes, factor F1 can be interpreted as the "pivotal role of soil-plant feedbacks in LF formations". F2 (proportional variance = 8%; eigenvalue = 2.097) and F3 (7%; 1.793) are of lower statistical importance in terms of both variance and eigenvalues. F2 extracted Al^{3+} as negatively correlated with successional class (SC). This showed that in LF soils, featured by lower Al^{3+} contents (Fig. 2e), thus being less acidic (Fig. 2a), the prevalent SC is those belonging to not pioneer species; another important outcome showing that soil-plant feedbacks in LF formations play a pivotal rule in driving ecological aspects too. F3 showed a well-known positive correlation between N and B in well-structured forests. Indeed, in such conditions we have the so-called "B effect" (Lannes et al., 2020) since higher B in LF formations (Fig. 2m) strongly favor N_2 fixation by increasing Rhizobium-plant cell-surface interactions. Thus, factor F3 can be interpreted as the "B effect in LF formations".

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Table 2

Factor loadings of a factor analysis (n = 30); Extraction Method: principal factor analysis (PFA); Rotation Method: Varimax; bold loadings > 0.5.

	Late forest (LF)			Disturbed forest (DF)			Secondary forest (SF)		
	F1	**F2**	**F3**	**F1**	**F2**	**F3**	**F1**	**F2**	**F3**
pH	**0.883**	0.030	0.335	**0.623**	**0.779**	0.187	**0.562**	**0.537**	0.196
SOM	**0.992**	0.077	0.089	**0.670**	0.087	-0.015	**0.590**	0.209	0.102
N	0.007	-0.185	**0.955**	-0.114	**0.939**	-0.284	-0.036	**0.594**	**0.749**
Pt	**0.968**	0.063	0.045	**0.777**	0.058	-0.070	**0.680**	0.028	0.061
Al^{3+}	0.011	**0.640**	0.323	**0.645**	-0.583	-0.133	**0.664**	-0.240	-0.103
H+Al	**0.987**	0.098	0.052	**0.677**	0.069	0.117	**0.584**	0.162	0.055
K^{+}	**0.900**	-0.160	0.297	**0.525**	**0.629**	0.010	**0.513**	**0.513**	0.461
Ca^{2+}	**0.992**	0.097	0.065	**0.763**	0.069	-0.020	**0.692**	0.148	0.082
Mg^{2+}	**0.991**	0.050	0.115	**0.643**	0.175	0.021	**0.584**	0.250	0.133
CEC	**0.989**	0.112	0.073	**0.662**	0.100	0.070	**0.592**	0.229	0.074
BS	**0.945**	0.140	0.118	**0.671**	0.161	0.167	**0.559**	0.220	0.082
S	**0.989**	0.080	0.091	**0.522**	0.196	0.102	0.468	0.325	0.161
B	0.132	0.294	**0.755**	-0.025	**0.901**	-0.122	0.007	0.141	0.424
Cu	**0.924**	-0.004	0.100	**0.558**	0.377	-0.088	0.449	**0.641**	0.412
Fe	**0.976**	0.071	0.013	**0.567**	0.062	0.044	0.497	0.203	0.065
Mn	**0.989**	0.100	0.055	**0.544**	0.079	-0.013	0.490	0.167	0.053
Zn	**0.922**	0.010	-0.053	**0.796**	0.094	-0.060	**0.667**	0.347	0.074
DBH	**0.650**	**-0.649**	-0.077	**0.593**	-0.113	-0.111	**0.582**	0.286	**0.546**
H	**0.966**	0.140	0.085	**0.589**	0.154	0.240	**0.519**	0.273	0.062
DW	**0.845**	-0.061	0.240	0.488	0.074	**0.662**	0.405	**0.797**	0.225
SC	0.218	**-0.522**	0.156	0.180	**0.728**	0.384	0.377	**0.907**	-0.057
NP	**0.985**	0.161	0.036	**0.677**	0.099	0.189	**0.574**	0.167	0.023

NDF	**0.927**	0.348	-0.054	**0.536**	0.089	0.381	**0.510**	**0.506**	0.038
NDS	**0.950**	0.288	-0.068	**0.583**	0.096	0.303	**0.542**	0.437	0.048
NS	**0.981**	0.047	-0.061	**0.592**	0.029	0.126	**0.588**	0.100	0.016
G	-0.170	**0.850**	-0.226	0.164	-0.407	**0.626**	-0.182	**-0.769**	-0.322
TDe	**0.992**	0.112	0.048	**0.568**	0.107	0.125	0.482	0.214	0.064
Proportional variance (%)	76	8	7	76	12	5	72	15	5
Cumulative variance (%)	76	84	91	76	88	93	72	87	92
Eigenvalues	20.456	2.097	1.793	15.394	3.308	1.332	19.434	4.171	1.170

In orange soil parameters; in green plant measurements. DW: dispersion way; SC: successional class; NP: number of plants; NDF: number of different families; NDS: number of different species; NS: number of seedling species; G: basal area; TDe: plant total density.

For disturbed forest (DF) formations, F1 (76% of the variance), extracted most of the soil parameters (N and B apart) and plant measurements (DW, SC and G apart) as all positively concordant. While this is similar to F1 in the LF formation, the factor loads extracted for DF formations were substantially smaller (Table 2). Thus, even if previously reported outcomes for LF can be still outlined for DF formation too, these are of less statistical importance; likewise, the eigenvalue of the F1 factor for DF formations was smaller than for LF formations. Thus, it seems that even if showing a similar behavior to LF, DF are quite representative of a "transitional stage" between the less developed (SF) and the most developed (LF) forest formations. For all of these reasons, we interpreted F1 as the "role of soil-plant feedbacks in DF transitional stage". F2 (12% of variance) showed multiple positive relationships among pH, N, K^+, B and, for plant parameters, SC. This factor completely differs from F2 extracted for the LF formation (*vide supra*), and is closer to F2 in SF formation (*vide infra*). This observation provides another line of evidence that the DF formation could represent a transitional stage between the two end-member formations.

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Indeed, even if soil features were more favorable compared to SF, showing higher soil pH (Fig. 2a), N (Fig. 2c), K (Fig. 2g), and B (Fig. 2m), they are lower than LF formation. Factor F2 also showed that in DF formations, these soil parameters are those playing the most important role in determining the prevalence of pioneer species. Nitrogen and B had particularly large factor loadings (> 0.9), which, like for LF formations, confirm the presence of a "B effect" (Lannes et al., 2020). This effect may be more important for DF formations than LF formations since it appears as the second, rather than third, factor and represents a greater proportion of variance. This further confirm the DF "transitional stage" hypothesis, since B increased its impact on soil-plant feedbacks at decreasing development stage (Barker and Pilbeam, 2015). Factor F3 (5%) completely differed from both F3 extracted in LF and SF formations. It showed that at increasing basal area (G) the seeds' dispersion way is mainly conditioned by animals; a fact that can be easily explained considering that in more wood denser forest formation animals tends to play a pivotal role in seed dispersion (Muller-Landau et al., 2008). Thus, it can be interpreted as "the role of animals in seeds transport in DF formation".

For secondary forest (SF) formation, i.e., the most human-disturbed ecosystem, factor F1 (72% of the variance), extracted several soil parameters (N, B, S, Cu, Fe, Mn excluded) and plant measurements (DW, SC, G, TEe excluded) as all positively concordant, similar to LF and DF formations. However, the loadings of soil and plant factors for F1 were lowest in the SF formation. This factor further confirms that as we passed from LF → DF → SF the soil-plant feedbacks become of less magnitude. Several important soil macro- and micronutrients (N, B, S, Cu, Fe, Mn excluded) were either not or less influenced by SOM within SF formations, which had significantly lower SOM to LF and DF formations (Fig. 2b). Overall, by considering this factor as well as by comparing all F1 extracted factors, it can be underlined that: *i*) SF formations were characterized

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as less fertile pedosystems; and *ii*) soil-plant feedbacks are weaker compared with more developed LF and DF formations. Consequently, multivariate statistics confirmed that SF represented the least developed stage among the investigated forest formations, underlining the role of human disturbance in strongly affecting soil and plant development as well as their complex relationships and feedbacks. Factor F2 (15% of variance) shows pH, N, K^+, Cu and, for plants, DW, SC, and NDF as all positively concordant, while as all negatively correlated with the basal area (G). This factor was similar to F2 in the DF formation and dissimilar to the F2 from the LF formation. Compared to the LF and DF formations, the "B effect" totally disappeared. Additionally, there was a decrease in basal area as whole soil fertility increased; thus, outlining that at increasing human disturbance soil fertility decreased accordingly and soil-plant feedbacks shows less interactions and a decreased complexity. F3 (5% of variance) showed that in such primaeval highly human-affected ecosystems, soil macronutrients (N) exerted a great influence on soil plant development (DBH). During the early stage of plant development in human disturbed pedosystems, N can represent the most important macronutrient, especially in terms of competition among species.

Overall, the factor analysis showed several important outcomes. All investigated forest formations featured a great influence of the soil-plant relationships and feedbacks, but there was a decreasing magnitude in the factor F1 loadings from LF → DF → SF. Thus, there is a direct, statistically recognizable consequence of "recent" and "ancient" human disturbance on soil-plant relationships. Such an influence clearly affects not only plant and soil as "separate" systems but the whole complex of interactions and feedbacks among them. The investigated forest formations showed a decreasing quality in soil and forest investigated parameters as human disturbance increased. In terms of the BAF "recovery gap"—i.e., the rate of recovery to a pre-disturbance state occurring during a natural regeneration process—our results fully agree with Romanelli et al.

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(2022) showing that the rate of recovery is strongly influenced by past land use, with vegetation responding more sensitively to the time elapsed since regeneration started. Consequently, even if natural regeneration rarely results in identical conditions to those observed in undisturbed BAF (Guerra et al., 2020), we show that after almost 40 years in the absence of human disturbance: *i*) almost complete vegetation and soil recovery was observed, which resulted in *ii*) an increase in the complexity of plant-soil relationships and delivery of ecosystem services. We observed an increase in soil carbon and micro and macronutrients stocks, improved general ecosystem fertility and complexity, etc. Our investigation showed that forest structure and function as well as soil development trend toward a more advanced successional stage following the cessation of human disturbance in the BAF. This finding confirms previous similar observations for forest vegetation (McDowell et al., 2020; Souza et al., 2021), but is the first to show a successional relationship with soil development. These time-dependent variations indicate the need to understand soil-plant relationships/feedbacks processes for effective environmental management and, consequently, the provision of ecosystem services (Souza et al., 2021).

4. Conclusions

Biodiversity studies represent an essential step in assessing environments at different stages of naturality, as they provide primary data on the diversity, structure, composition, and species distribution. When related to soil features, pivotal information on the investigated environment can be obtained, such as soil-vegetation relationships and feedbacks, and, consequently, how humans influence the environment and how such a disturbance should be managed and/or mitigated. These investigations also represent one of the main challenges decision-makers face for biodiversity, ecosystem conservation and management. Indeed, with provided outcomes, they can

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establish concrete actions and priorities. Our investigation of Atlantic rainforest natural regeneration in fragmented formations of the rare *cuesta* landscape provided novel outcomes for improving future management. In such an ecosystem, humans act as a primary driving force in disturbing plant and soil development and feedback, thus creating an anthroposequence. A clear influence of human activities and disturbance was observed, increasing as LF → DF → SF. The Brazil Atlantic Forest, as a biome of worldwide interest, must be preserved from further human disturbance with appropriate management actions. Indeed, we demonstrated that after almost 40 years in the absence of human disturbance, an almost complete vegetation and soil recovery was observed, with increasing complexity in plant-soil relationships and increase in ecosystem services (such as soil carbon and micro and macronutrients stocks, improved general ecosystem fertility and complexity). After almost 30 years without human disturbance (DF), a clear vegetation and soil recovery were observed too; however, DF represented a transitional stage rather than a complete recovery, featuring less complexity in terms of plant, soil, and plant-soil relationships. After almost 20 years of human disturbance (SF), plant and soil still present several signs of previous human disturbance; a primeval lower complexity characterizes soil-plant relationships. All of these reported outcomes demonstrate that the BAF requires protection against further human disturbance. Our study should further encourage involved stakeholders in taking adequate measures for its protection by carefully managing allowed human activities including wholly prohibiting the most impacting ones (such as agriculture), in favor of its use for tourist-recreational and scientific purposes. Finally, to further investigate the interactions between plants and soil in the BAF, new studies aim to extend our results by looking at the whole soil profile in these very deep tropical soils. Due to strong leaching processes in tropical soils such as those found in the BAF, changes in plant growth and rooting depth during regeneration may have considerable effects

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on soil processes and functions extending deep into the soil profile. From this viewpoint, new studies are under realization aiming at investigating soil to plant interactions, and *vice versa*, along the whole soil profile in very deep Tropical soils by even considering species over their regenerative stage.

CRediT authorship contribution statement

L.R. Roder: Data curation, Formal analysis, Software, Validation, Visualization, Writing - original draft; **I.A: Guerrini:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Validation; **D.C. Lozano Sivisaca:** Data curation, Formal analysis, Investigation, Methodology, Writing - original draft; **C.A.Y. Puglla:** Investigation, Methodology; **F. Góes de Moraes:** Conceptualization, Investigation, Methodology; **J.P. da Silva:** Data curation, Formal analysis, Investigation; **R.C.B. Fonseca:** Data curation; Formal analysis; **M.T. Umbelino:** Data curation, Formal analysis, Investigation; **J.N. James:** Validation; Writing - original draft; Writing - review & editing; **G.F. Capra:** Data curation, Formal analysis, Software, Validation, Visualization, Writing - original draft, Writing - review & editing; **A. Ganga:** Conceptualization, Data curation, Formal analysis, Methodology, Software, Visualization, Writing - original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

The authors do not have permission to share data.

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