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NATURAL REGENERATION AND SOIL FERTILITY IN FRAGMENTS OF BRAZILIAN ATLANTIC FOREST WITH DIFFERENT HISTORY OF DISTURBANCE

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NATURAL REGENERATION AND SOIL FERTILITY IN FRAGMENTS OF BRAZILIAN ATLANTIC FOREST WITH DIFFERENT HISTORY OF DISTURBANCE

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Botucatu, 17 de agosto de 2022

To my beloved family,

Marineide, José, Nayara, and Nicholas

I dedicate

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To God, for the gift of life, for always guiding my steps and for showing me the right path.

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“Alle volte uno si crede incompleto ed è soltanto giovane”.

CALVINO, I. **Il visconte dimezzato**. 1. ed. Milano: Mondadori, 2016. p. 84.

ABSTRACT

Brazilian Atlantic Forest (BAF) is a tropical forest biome that have been dramatically devastated in the past and is still under anthropic action, specially by deforestation and soil degradation, which causes fragmentation processes, implying in severe consequences for biome's sustainability. This study investigated the natural regeneration and soil fertility in fragments of BAF, characterized by increasing human disturbance histories as: secondary (SF) > disturbed (DF) > late forest (LF). The aim was to understand how and the degree to which BAF fragmentation and human disturbance affected vegetation, soils, and the whole soil-plant relationships and feedbacks. It was investigated the natural regeneration vegetation and soil chemistry 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 "ancient" formation (LF) *vs* more "recent" 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 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. It was 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: tropical forests; plant; soil; soil-plant feedbacks.

RESUMO

A Mata Atlântica (MA) é um bioma de floresta tropical que foi drasticamente devastado no passado e ainda está sob ação antrópica, principalmente pelo desmatamento e degradação do solo, que provocam processos de fragmentação, implicando em graves consequências para a sustentabilidade do mesmo. Este estudo investigou a regeneração natural e a fertilidade do solo em fragmentos de MA, caracterizados por históricos crescentes de perturbação antrópica como: floresta secundária (SF) > perturbada (DF) > tardia (LF). O objetivo era compreender como e até que ponto a fragmentação da MA e a perturbação humana afetaram a vegetação, o solo e todas as relações e *feedbacks* solo-planta. Foram investigadas a regeneração natural e a química do solo em doze parcelas permanentes de 2000 m^2, distribuídas nas formações florestais LF, DF e SF. Diferenças significativas foram determinadas por ANOVA. Matriz de correlação (CM) e análise fatorial (AF) foram utilizadas para a compreensão das correlações e *feedbacks*/variabilidade entre os parâmetros investigados, respectivamente. A maioria dos parâmetros da vegetação e do solo investigados apresentaram diferenças significativas ($p < 0,05$) entre as formações com histórico de perturbação mais "antigo" (LF) *vs* mais "recente" (SF), com diferenças principalmente devido ao estágio de desenvolvimento do solo. Todas as formações florestais investigadas são caracterizadas por uma grande influência das relações solo-planta e *feedbacks*, com magnitude decrescente LF → DF → SF. Assim, há um impacto direto, estatisticamente reconhecível, tanto da perturbação humana "recente" quanto da "antiga" nas formações investigadas. A influência antrópica afetou claramente não apenas a planta e o solo como sistemas "separados", mas todo o complexo de interações e *feedbacks* entre os componentes do ecossistema. Uma qualidade decrescente nos parâmetros do solo e da vegetação foi observada à medida que a perturbação humana aumentava. Foi demonstrado que a planta e o solo requerem décadas para sua recuperação após perturbações humanas, com mecanismos e comportamentos complexos nas relações entre os componentes do ecossistema. Os resultados podem ser úteis para a recuperação de um ecossistema de importância mundial, a MA.

Palavras-chave: florestas tropicais; plantas; solo; *feedbacks* solo-planta.

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1 INTRODUCTION

The Brazilian Atlantic Forest (BAF, hereafter) is considered one of the main biodiversity hotspots in the world (MYERS et al., 2000). It is a tropical forest biome, that in its original extension covered the Atlantic coast of South America, allowing exceptional levels of endemism and species richness (RIBEIRO et al., 2011) and providing major ecosystem services, such as high biodiversity (MURRAY-SMITH et al., 2009), soil and vegetation carbon stock (SPRACKLEN; RIGHELATO, 2014), and rain and fog water storage (MARTINS et al., 2015). Consequently, the degradation of the biome implies local, regional, and global issues (OLIVEIRA et al., 2014).

The BAF has experienced extensive historical harvesting and continues to face significant human-induced impacts, with deforestation activities and soil degradation being the primary concerns. Originally, the BAF occupied about 150 million ha (RIBEIRO et al., 2009). At present, it consists of an almost continuous cover, at different stages of ecological succession; remaining just 12,4% of the native vegetation with more than 3 ha in the entire biome (FUNDAÇÃO SOS MATA ATLÂNTICA; INPE, 2021). Circa around 69% of the biome is covered by human-dominated areas (PROJETO MAPBIOMAS, 2021), hosting approximately 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 originated in the BAF region (FUNDAÇÃO SOS MATA ATLÂNTICA; INPE, 2021).

The biome, nowadays, is characterized by the presence of regenerating and degraded forest areas, often found in small fragments arrangements, presenting risk of species extinction and collapse of populations at local and regional scales (RIBEIRO et al., 2011). Despite their fragmentation, these forest areas are a valuable renewable natural resource for the present and future generations (SOUZA et al., 2002).

Insufficient and wrong management in the biome can lead to soil degradation, degrading soil quality due to losses of soil organic matter (SOM), essential nutrients, and decreased biological activity. The natural conditions of the BAF are already relatively nutrient-poor due to high rainfall and long residence times, which promotes intensive leaching processes. Despite this, the BAF pedosystems are strongly connected with vegetation in a complex equilibrium influencing soil-vegetation behavior and feedback, and protecting from degradation (MARTINS et al., 2015).

Therefore, a better understanding of the complex and interactive relationships between biodiversity and the supporting ecosystem 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 (LECINA-DIAZ et al., 2018).

The "Edgardia and Lageado" (EL) experimental farms are situated in Botucatu, São Paulo State University (UNESP), south-east Brazil, covering a total area of 2,139.28 ha, including fragments of seasonal semideciduous Atlantic Forest (total cover: 938.2 ha) (*vide infra*). The continuity of the primeval forest has been disrupted by human activities, such as the establishment of pastures and cultivation of crops. Additionally, these fragments have different histories and magnitude of human disturbance due to selective deforestation activities, livestock influence, fire events, and other disturbances, all occurring since the 1960s (NASCIMENTO et al., 2011).

Currently, the EL Atlantic Forest fragments are protected by Brazilian laws and is under passive ecological restoration. They are located in the "Corumbataí – Botucatu - Tejupá Environmental Protection Area", created in 1983, aiming at protecting: *i*) the Basaltic *cuesta* geological formation (*vide infra*); *ii*) formations composed by volcanic rocks; *iii*) the inselbergs; *iv*) the flat-topped hills of the *cuesta*; *iv*) regional flora and fauna; *v*) the Guarani Aquifer; and others (SÃO PAULO, 2022). These features make the EL fragments an important ecosystem to implement knowledge about BAF biodiversity under the influence of different types and magnitude of human interventions. Knowing the history of BAF disturbance can allow understanding the current situation better, and outline future actions for conservation purposes.

Moreover, it is essential to monitor both the vegetation and soil fertility in the BAF, while also comprehending the intricate relationships and feedback that exist between them, particularly under different stages of degradation and vegetation recovery, and especially during "natural regeneration" phase. Unfortunately, historically, these relationships and feedbacks have received limited investigation and understanding.

This study aimed to investigate the structure and successional dynamics in BAF natural regeneration in fragments with different human disturbance histories, underwent passive ecological restoration. Furthermore, to understand and investigate how and the extension to which BAF fragmentation and human disturbance affected plant, soil, and soil-plant relationships and feedbacks.

2 LITERATURE REVIEW

2.1 Brazilian Atlantic Forest and fragmentation

The BAF biome is considered one of the main biodiversity hotspots in the world (MYERS et al., 2000). In its original extension, the forest was spread along the Atlantic coast of South America for more than 1.5 million km², covering tropical and subtropical climates in highly diversified conditions, which allowed exceptional levels of endemism and species richness (RIBEIRO et al., 2011).

It is home to *c.a.* 2200 species of vertebrates (birds (990 species), amphibians (370), reptiles (200), mammals (295) and fishes (350)), representing more than 5% of the world's vertebrate species. Regarding the flora, the estimation is that the biome has over 15,700 species, representing 5% of the world's flora and which *c.a.* 50% are endemic (PAGLIA; PINTO, 2010). The BAF biome is a set of different forest formations, including natural fields, sandbanks, mangroves and others (MMA, 2010). The two major forest formations/vegetation types are the coastal forest or Atlantic Rain Forest and the tropical seasonal forest or Atlantic Semi-deciduous forest (MORELLATO; HADDAD, 2000).

According to Paglia and Pinto (2010), more than 70% of the Brazilian population lives in the BAF; with more than 145 million people in 3,429 municipalities, corresponding to 61% of the municipalities in Brazil (FUNDAÇÃO SOS MATA ATLÂNTICA, 2022). It is in this biome that industrial production and the country's gross domestic product are concentrated (PAGLIA; PINTO, 2010).

During history, the BAF has suffered by anthropic actions and disturbances, causing severe habitat loss (RIBEIRO et al., 2011) and fragmentation. Disturbances are considered, in case of forest ecosystem, as any event that opens a clearing in the canopy, which can be by natural or anthropic origin (UHL et al., 1990).

The BAF was the first biome to be human-affected by deforestation and forest degradation (RODRIGUES et al., 2009). Due to the economic activity, the biome has lost between 84 and 88% of its natural/original vegetation cover since the Europeans' arrival in the 16th century (PAGLIA; PINTO, 2010), resulting in a forest cover reduced to around 12% of its original extension (RIBEIRO et al., 2009; RIBEIRO et al., 2011; FUNDAÇÃO SOS MATA ATLÂNTICA; INPE, 2021).

As a consequence of the human influence, the BAF landscape has been turned into agromosaics in different dynamic successional stages, being characterized especially by: *i)* small patches of old growth forest and assisted regenerating; *ii)* patches of early to late secondary forest on abandoned cropland/pasture; *iii)* agroforestry; and *iv)* exotic trees plantations (RIBEIRO et al., 2011). If compared with their original floristic composition, in general, the BAF present a fragmented, altered and impoverished situation (SOUZA et al., 2002).

The EL fragments are among few well-preserved remnants of BAF formations in the central-south region of the São Paulo state, having an important ecological and taxonomic value, and also, give information regarding the structure and functioning of this type of ecosystem, even if they were human-altered (ORTEGA; ENGEL, 1992).

Fragmentation processes put at risk the long-term sustainability of the BAF biome, implying severe consequences (SIVISACA, 2020). It reduces the whole area while increasing forest fragment isolation, making the ecosystem less permeable and attractive for native flora and fauna, thus reducing biodiversity; consequently, their local extinction increased, which can result in: *i*) a reduction of gene flow; *ii*) increased pressure from nonnative, often invasive, species coming from the edge; thus, *iii*) dramatically changing most of BAF's ecosystem processes and functions (CASSOLA, 2008).

In terms of number and sizes of fragments, the BAF is distributed in over 245,000 fragments, being most of them (*c.a.* 83%) characterized by patches smaller than 50 ha and only *c.a.* 0.03% are larger than 10,000 ha, underlying the critical conservation condition of the BAF biome (RIBEIRO et al., 2011); a scenario that present severe implications to the maintenance of the BAF (RIBEIRO et al., 2009).

Ribeiro et al. (2009) suggested general guidelines to improve or stimulate BAF forest-species conservation, being the following: *i)* to sign large mature forest fragments as high conservation priority; *ii)* to use small fragments to form functionally linked mosaics; *iii)* to manage adequately the matrix surrounding the fragments, in order to minimize edge effects; *iv)* to practice restoration actions.

2.2 Ecological restoration

The restoration is one of the key actions to guarantee the conservation of the BAF biome and reverse the fragmentation trend (RIBEIRO et al., 2009). The Society

for Ecological Restoration (SER) define ecological restoration “as the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed”. Therefore, it aims to recreate viable communities in an ecological point of view, allowing the natural ability to change, thus promoting a healthy relationship between man and nature (ENGEL; PARROTTA, 2008).

Degraded ecosystem is considered by Carpanezzi et al. (1992) as an ecosystem that, after the disturbance, had the biotic regeneration forms (i.e., seed bank, seedling bank, seed rains and regrowth) eliminated together with the vegetation, which implies in a low resilience, and the capacity to return to the previous state may be not occur, or occur slowly; instead, disturbed ecosystem is defined by an ecosystem that suffered with disturbance but maintained the biotic regeneration forms.

The human intervention/action, in case of degraded ecosystems, is necessary to stabilize and reverse the degradation processes, in order to accelerate and orientate the succession, which can be done under different approaches, objectives and results (ENGEL; PARROTTA, 2008). For disturbed ecosystems, human action is not mandatory, but can be used to assist the recovery (CARPANEZZI et al., 1992).

As previously reported, the ecological restoration can be done through passive or active approaches/initiatives. The passive ecological restoration, that is also referred as natural regeneration, aim to the recovery without active human intervention (ZAHAWI; REID; HOLL, 2014), including also stopping further human interference, i.e., destructive logging, road construction, cattle grazing, mining, dam and water diversions construction, use of off-road vehicles and alteration of fire regime (DELLASALA et al., 2003). This approach is the most cost-effective when the potential for the natural recovery is high (GANN et al., 2019). The areas (EL fragments) used for the present study are product of years of passive restoration, after different history human disturbances (*vide infra*) (SIVISACA, 2020).

On the other hand, the active restoration has the necessity of the human intervention, and should be used when the potential of the natural recovery it is absent or low (GANN et al., 2019).

In forest restoration, the main objective is to recovery the forest ecosystem, making it capable to self-perpetuation and do not depend on constant human interventions (BRANCALION et al., 2010). Ecological restoration projects/programs should allow to the ecosystem arrive at a high level of ecological integrity by restoring natural processes and resiliency (DELLASALA et al., 2003); nevertheless, it is

impossible to restore natural ecosystem in their integrity and in their original stage, due to their own dynamic features (ENGEL; PARROTTA, 2008).

When well-implemented and in a sustainable way, ecological restoration contributes to: *i)* protect the biodiversity; *ii)* improve human health and well-being; *iii)* increase food and water security; *iv)* produce goods, services and economic profit; *v)* mitigate climate change, supporting resilience and adaptation (GANN et al., 2019).

2.3 Natural regeneration

According to Marangon et al. (2008), the natural regeneration (NR, hereafter) is part of the forest ecosystem growth cycle, representing the initial stages of its development and establishment. Generally, tropical forests present a high capacity for NR, especially when closer to a source of propagules and in areas not intense-used (GUARIGUATA; OSTERTAG, 2002).

In order to ensure the rational and sustainable use of forest resources, it is essential to know about the NR potential stock, as well the successional dynamics processes, the growth and production of the forests (SOUZA et al., 2002). Studies about structural analysis of the NR provide information regarding: *i)* the relationship and the number of the species in regeneration; *ii)* the dimension and distribution of the plants; making possible predictions about the socio-ecological characteristics and the development of the forest ecosystem, as well helping in the correct elaboration of silvicultural management (CARVALHO, 1984).

Furthermore, assessing the dynamics of NR by considering entry, mortality, and growth provides valuable information into which species will assume significant roles in the future and which ones are likely to diminish their presence within the NR structure (SCHORN; GALVÃO, 2006). The survival and growth during the juvenile stage are important to allow to arboreal individuals reaching the adult tree community, and the differences in this stage influences forest dynamics, species composition and diversity (KOBE; COATES, 1997).

The term NR (referring to the NR stratum, the object of this study) is very broad and varies in its definition among different authors based on the investigated ecosystem, and consequently, it influences in the methodologies that are used. Finol (1971) considered as NR all existing plants between 10 cm in height and 10 cm in diameter at breast high (DBH). Rollet (1978) referred, generally, to the juvenile stages

of the species, for example, individuals with DBH less than 5 cm. Lamprecht (1990) considered all individuals with height equal to or greater than 30 cm and with DBH up to 10 cm. For Volpato (1994), the NR is all individuals with DBH less than 5 cm.

Ecosystems are composed of both living (biotic) and non-living (abiotic) components. The abiotic term is considered as non-living materials and conditions present in the ecosystem, which includes soil, rock, dead wood, litter or aqueous substrate, the atmosphere, weather and climate, topography, nutrient, hydrological regime, fire and salinity regime (GANN et al., 2019).

The NR is a multidimensional space, where the action of many abiotic and biotic factors happens contemporaneously and interactively (BORJA, 2014); however, understanding how these factors affect the structure and composition of NR is still not fully understood (WEISKITTEL et al., 2011).

Plants affect directly the properties of the soil, i.e., chemical, physical and biological, and these properties affects the type of plants that grow in the ecosystem (GANN et al., 2019). The plants and soils are connected through a bioregulation system.

The BAF vegetation and soil properties/quality need to be monitored, as well is important to understand the relationships and feedbacks among them under different stages of degradation and vegetation recovery, especially during NR; relationships and feedbacks have been poorly investigated.

Soil conditions present a close relationship with the succession (VIERECK, 1970). Studies have been presenting a potential role of plant-soil feedbacks in succession (BAUER, MACK, BEVER, 2015).

3 MATERIAL AND METHODS

3.1 Study area

The “Edgardia and Lageado" (EL) experimental farms (Botucatu, south-east Brazil), belongs to the Capivara River basin (3,432.23 km^2). The climate of the area is classified as hot and humid subtropical (Cfa) according to Köppen criteria (ALVARES et al., 2013). 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 and February, respectively (NOGUEIRA JR. et al., 2011).

Geology is mainly composed of igneous rocks of the Paraná basin, such as the basaltic *cuesta* formation of the São Bento Group (Serra Geral formation). *Cuesta* (from Spanish “slope”) is a vulgar 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.

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).

3.2 Experimental design

Due to differences in past and present management and historical vicissitudes that affected the whole area over the last few centuries, vegetation has been fragmented in different patches characterized by differences in physiology and flora composition, as well as species and floristic associations (ORTEGA; ENGEL, 1992). For the purposes of this study, it was investigated three different patches (formations, hereafter), covering 938 ha (Fig. 1a), that were selected due to their clear differences in terms of increasing human disturbance.

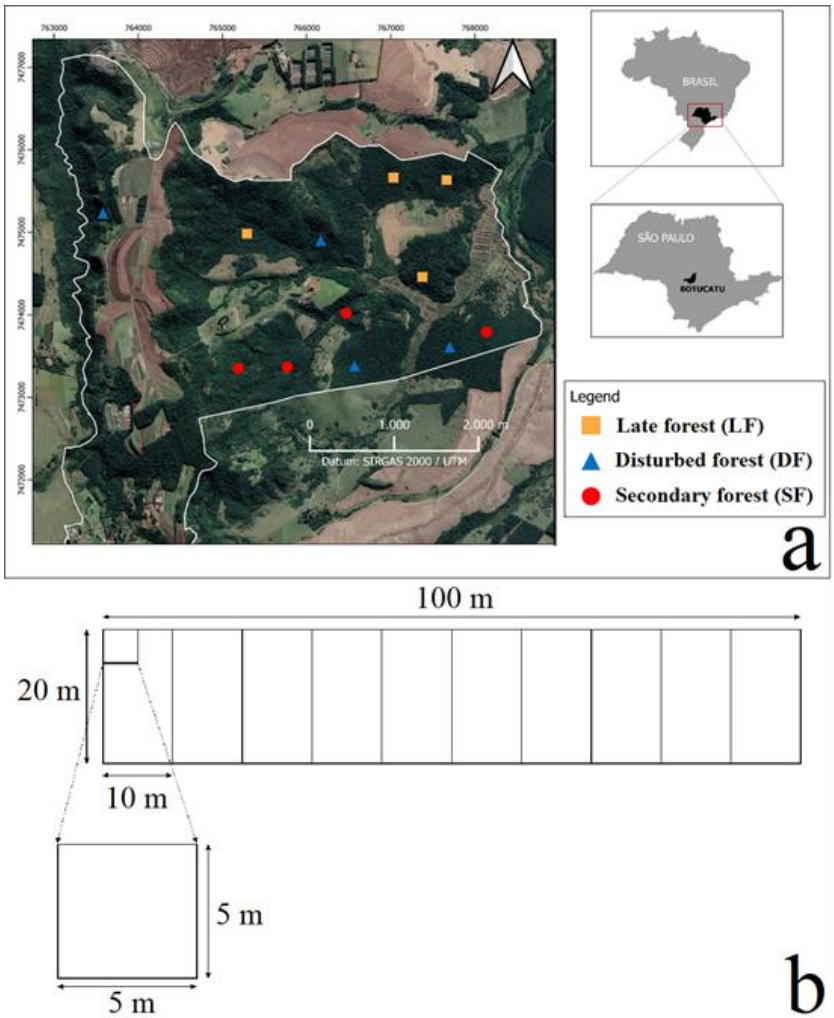
The three investigated BAF formations, presented according to an increasing human disturbance (or decreasing naturality) gradient, are the following:

- Late Forest (LF, hereafter): characterized by 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 (JORGE; SARTORI, 2002);

- 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 extraction of tree species (JORGE; SARTORI, 2002);
- 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 (JORGE; SARTORI, 2002).

Figure 1 - Study area (a) and experimental plot design (b)



Source: Adapted from Sivisaca (2020).

The sampling methodology for flora investigation was conducted according to a non-destructive standard procedure. Twelve permanent plots of 2000 m^2 (20 × 100 m)

were randomly distributed in LF, DF, and SF (four plots for each investigated formation), with a distance between plots of 500 m. To avoid any edge effect, each plot was far from the border at least 200 m. Replications consist of five randomly distributed subplots of 25 m² (5 × 5 m), inside in the twelve permanent plots (Fig. 1b). In total, 60 subplots were studied.

3.3 Vegetation and soil analysis

3.3.1 Vegetation

In each plot, plants with a diameter at breast height ($DBH_{1.30m}$) lower than 5 cm and at least 1.50 m tall were identified, measured and labelled, i.e., those fully considered as NR as proposed by Volpato (1994), that defined NR as a set of individuals with DBH lower than 5 cm (*vide supra*).

The species identification was primarily done in the field and then, when necessary, in the laboratory according to Angiosperm Phylogeny Group (SOUZA; LORENZI, 2005) and the taxonomic nomenclature of the species was revised on the "Flora do Brasil" website (<http://floradobrasil.jbrj.gov.br/>).

Tree development was assessed by measuring the height (H) and the DBH. For the DBH, the circumference at the breast height was measured with a diametric tape in the field and converted for DBH.

In order to better understand ecological behaviour and soil-plant relationships and feedback, general plant parameters were calculated for each formation, including: the total number of individuals (TI), species (TS), and families (TF), diversity indexes of the vegetal community (such as Shannon-Wiener diversity index (H') and Equability index/Pielou's evennes (J')), total density (TDe), basal area (G), number of plants (NP), number of different families (NDF), number of different species (NDS), and number of seedling species (NS). The seed dispersal way/syndrome (DW) was assessed and classified (dispersal by wind (anemochory), animals (zoochory), self-dispersal (autochory)), as well the successional class (SC; pioneers *vs* not pioneer species).

For the most abundant species in each formation, the following parameters were calculated: total number of individuals (N), basal area (G), relative density (Dr); relative dominance (Dor), relative frequency (Fr), and importance value index (IV).

3.3.2 Soil

Surface soil horizons (A; 0-20 cm) were sampled in each of the five previously reported subplots (*vide supra*; Fig. 1b). In particular, for each subplot, five different soil subsamples were collected in random locations within each subplot. Twenty-five (5 soil sample × 5 subplots) different soil samples were collected for each plot, resulting in 100 (25 soil samples in each plot × 4 LF, DF or SF) for each investigated area. Overall, 300 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 (Perkin Elmer). For the resin-extractable P, it was used the Amer et al. (1955) methodology. Iron, Cu, Mn and Zn concentrations were determined using the extractor Mehlich 1, while for K, Ca and Mg concentrations were used the Mehlich 3.

3.4 Statistical analysis

Statistics (univariate and multivariate) were carried out using the software program R (R Core Team, 2021).

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, the formations were graphically compared using 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.

4 RESULTS AND DISCUSSION

4.1 Floristic survey of the natural regeneration

Overall, 1,957 individuals under natural regeneration were sampled, belonging to 114 different species and 41 botanical families, being only 12 morphospecies identified until the genus level (Table 1).

Table 1 – Floristic list of the natural regeneration

Family	Species	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	

Family	Species	LF	DF	SF
	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
	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	

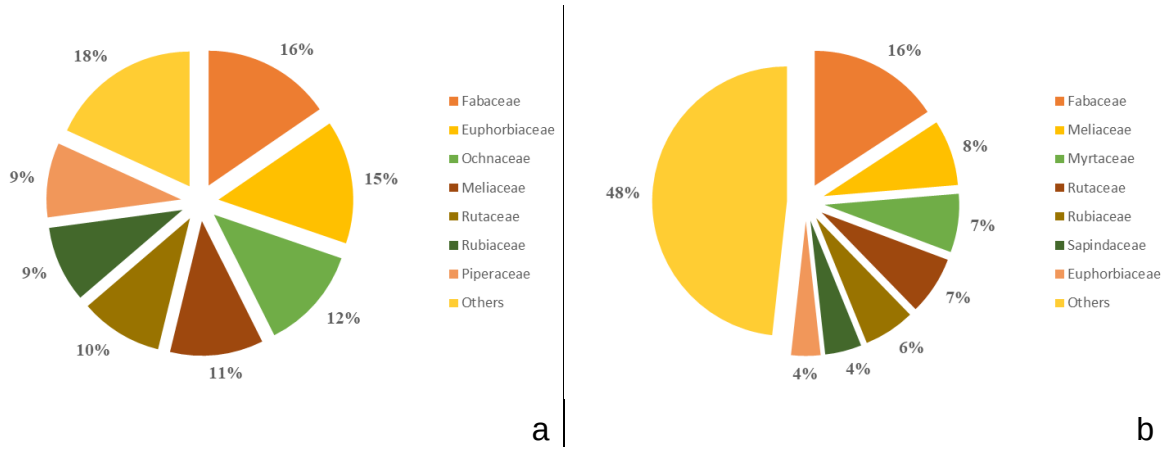
Family	Species	LF	DF	LF
	Myrcia guianensis (Aubl.) DC.		x	x
	Myrciaria floribunda (H.West ex Willd.) O.Berg	x	x	x
Nyctaginaceae	*Guapira opposita* (Vell.) Reitz.	x		x
Ochnaceae	*Ouratea castaneifolia* (DC.) Engl.	x	x	
Phytolaccaceae	*Gallesia integrifolia* (Spreng.) Harms	x	x	x
	Phytolacca dioica L.		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
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

Family	Species	LF	DF	LF
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	

Where: LF = Late forest; DF = Disturbed forest; SF = Secondary forest.

The five most numerous 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 (Fig. 2a). The Fabaceae family had the highest richness, accounting approximately 16% of the total, followed by Meliaceae (8%), Myrtaceae (7%), Rutaceae (7%), Rubiaceae (6%), Sapindaceae (4%), Euphorbiaceae (4%) and others (48%) (Fig. 2b).

Figure 2 – Most numerous (a) and richness (b) families in all the investigated formations



In terms of floristic composition in all investigated forest formations, the Fabaceae family is predominant in terms of richness as well (Fig.3), being 11% for LF (Fig. 3a), 18% for DF (Fig. 3b) and 13% for SF (Fig. 3c). Fabaceae is the family with the greatest diversity and number of species in the Brazilian flora (IRRJBG, 2018).

Figure 3 – Families with the highest richness in late (a), disturbed (b) and secondary (c) forests

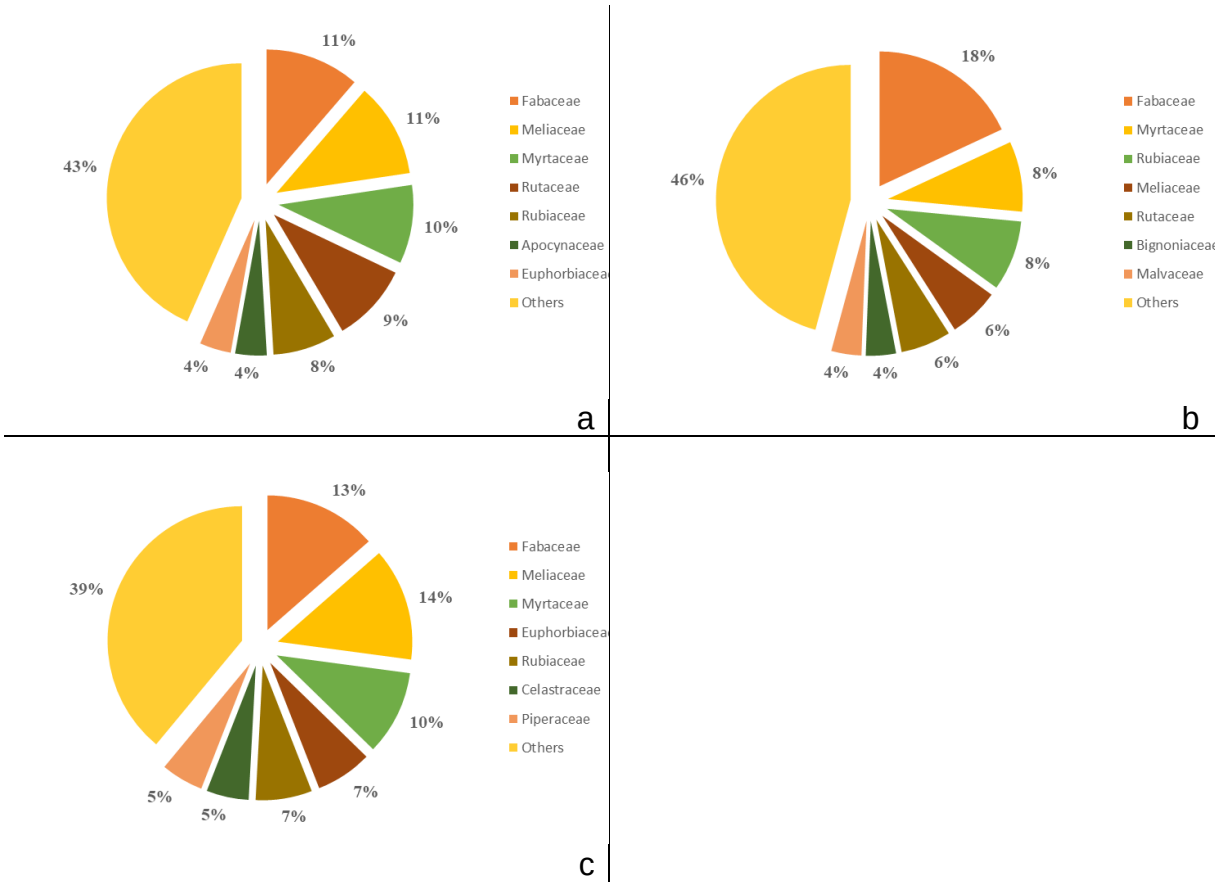


Table 2 shows several indexes for each investigated forest formation. Results showed DF > LF > SF in terms of total individuals, families, and basal area. In terms of species and, consequently, Shannon-Wiener diversity index (H'), it was noted DF > SF > LF. The Equability index (J') ranked as DF = SF > LF, while for total density was SF > LF > DF.

Table 2 – Vegetation indexes by formations

	LF	DF	SF
Total number of individuals (TI)	630	768	559
Total number of species (TS)	53	83	59
Total number of families (TF)	27	32	24
Shannon-Wiener 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})	0.243719	0.30886	0.20729

Where: LF = Late Forest; DF = Disturbed Forest; SF = Secondary Forest.

Overall, results showed that more human-impacted forest formations (SF) contain fewer plant individuals, families, and smaller basal areas. 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; STORCH, 2018). One of the strategies is increasing space invasion; thus, density and even diversity index 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.

Table 3 shows the most abundant species in each studied formation. The most abundant species were *Ouratea castaneifolia*, *Metrodorea nigra* and *Actinostemon concepcionis* in LF, DF and SF formations, respectively.

Table 3 – The most abundant species for each studied formation

	Species	**N** (ind ha^{-1})	**G** (m² ha^{-1})	**Dr** (%)	**Dor** (%)	**Fr** (%)	**IV** (%)
LF	*Ouratea castaneifolia* (DC.) Engl.	174	0.058890	27.62	24.16	7.04	19.61
	Metrodorea nigra A.St.-Hil.	67	0.033144	10.63	13.60	8.45	10.89
	Actinostemon concepcionis (Chodat & Hassl.) Hochr.	54	0.024163	8.57	9.91	5.63	8.04
	Piper amalago L.	41	0.023302	6.51	9.56	4.23	6.76
	Trichilia catigua A.Juss.	26	0.012274	4.13	5.04	7.98	5.71
	Trichilia elegans A.Juss.	36	0.012044	5.71	4.94	5.16	5.27
	Trichilia casaretti C. DC.	28	0.011587	4.44	4.75	6.57	5.26
	Others	204	0.068315	32.38	28.03	54.93	38.45
	Total	630	0.243719	100.00	100.00	100.00	100.00
DF	*Metrodorea nigra* A.St.-Hil.	105	0.039996	13.67	12.95	8.17	11.60
	Actinostemon concepcionis (Chodat & Hassl.) Hochr.	88	0.041883	11.46	13.56	5.84	10.29
	Piper amalago L.	75	0.026410	9.77	8.55	4.67	7.66

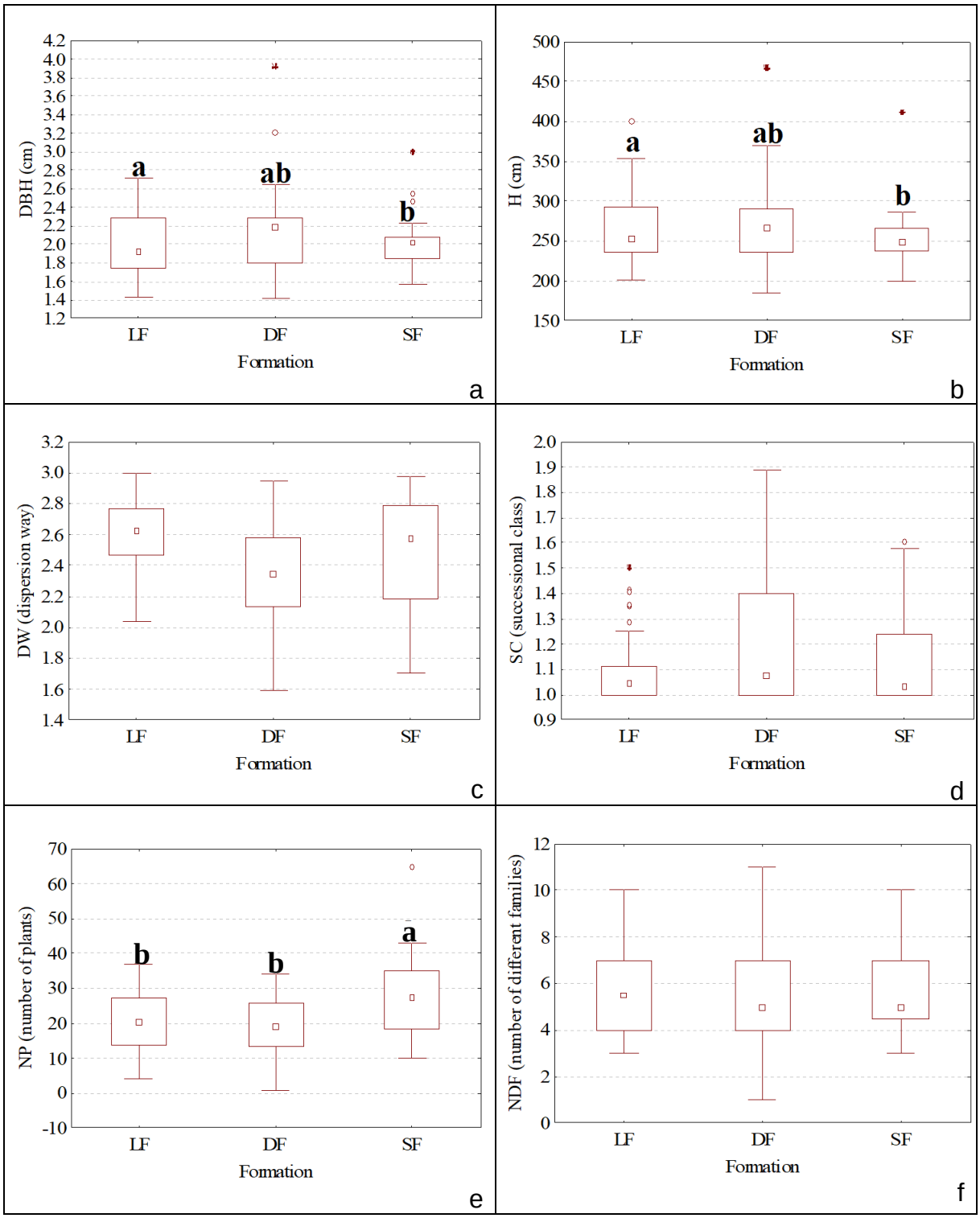
	Species	N (ind ha^{-1})	G (m² ha^{-1})	Dr (%)	Dor (%)	Fr (%)	IV (%)
	Ouratea castaneifolia (DC.) Engl.	68	0.021535	8.85	6.97	4.28	6.70
	Trichilia elegans A.Juss.	23	0.006149	2.99	1.99	6.23	3.74
	Calliandra sp.	28	0.011580	3.65	3.75	1.95	3.11
	Others	307	0.132958	39.97	43.05	64.98	49.33
	Total	768	0.308859	100.00	100.00	100.00	100.00
SF	*Actinostemon concepcionis* (Chodat & Hassl.) Hochr.	142	0.046539	25.40	22.45	4.49	17.45
	Parapiptadenia rigida (Benth.) Brenan	38	0.014161	6.80	6.83	7.69	7.11
	Trichilia casaretti C. DC.	32	0.018589	5.72	8.97	5.13	6.61
	Machaerium scleroxylon Tul.	41	0.018659	7.33	9.00	2.56	6.30
	Duroia sp.	45	0.013179	8.05	6.36	3.21	5.87
	Piper amalago L.	34	0.009088	6.08	4.38	2.56	4.34
	Randia ferox (Cham. & Schltdl.) DC.	20	0.005502	3.58	2.65	5.77	4.00
	Others	207	0.081573	37.03	39.35	68.59	48.32
	Total	559	0.207290	100.00	100.00	100.00	100.00

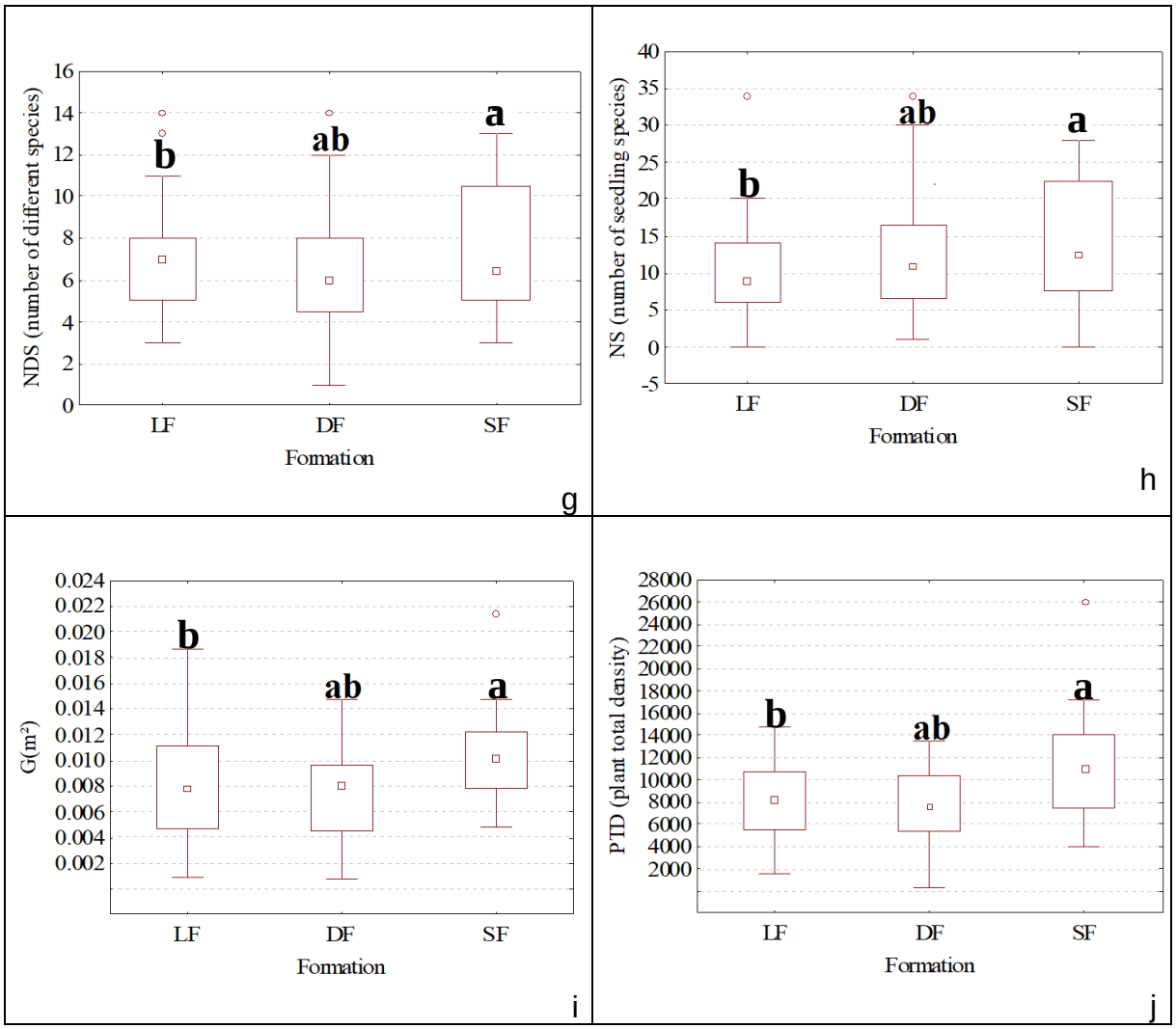
Where: LF = Late Forest; DF = Disturbed Forest; SF = Secondary Forest; N = number of individuals per hectare; G = basal area; Dr = relative density; Dor = relative dominance; Fr = relative frequency; IV = importance value index.

4.2 Vegetation parameters

Fig. 4 shows the distributions and differences between forest formations for all investigated vegetation parameters.

Figure 4 – Box-plots showing differences in plant parameters among investigated forest formations





Where: LF = late forest; DF = disturbed forest; SF = secondary forest; DBH = diameter at breast height (DBH); H = height; DW = dispersal way; SC = successional class, NP = number of plants; NDF = number of different families; NDS = number of different species; NS = number of seedlings species (NS); G = basal area; PTD = plant total density. Different lowercase letters are for significant differences ($p < 0.05$) based on Tukey honestly significant difference post-hoc comparisons.

Both plant DBH (Fig. 4a) and H (Fig. 4b) 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 maturation's stage. Pearson correlation coefficients from the correlation matrix (Table 4, *vide infra*) showed a positive correlation between DBH and H (r = 0.66**), which confirms the generally understood relationship that as plant height increases, the diameter increases as well.

The dispersal way (DW; Fig. 4c) and the successional classes (SC; Fig. 4d) did not show significant differences ($p < 0.05$) among the investigated forest formations. Pearson correlation coefficients (Table 4) showed that the DW was influenced by several soil parameters such as pH (r = 0.22*), Al (r = -0.24*), H+Al (r = -0.25*), Mn (r

= 0.21*), and finally with DBH (r = -0.23*) within plant parameters. These multiple correlations showed that in more developed pedosystems (LF), animal-driven dispersion is more frequent compared to others (wind, gravity, etc.); the opposite is true in more degraded environments (SF). In more developed LF formations, where the soil is less acidic, animals play a pivotal rule for mature plants reproduction. In the more degraded SF formations, in contrast, where the plant canopy had a decreasing cover of trees relative to shrubs and herbaceous species, animal-driven dispersion played a less important role compared to wind and gravity.

The number of plants (NP; Fig. 4e) was significantly higher in the most disturbed environments, even though the number of families was not significantly different (Fig. 4f). The higher number of species in more disturbed environments follows the theory of ecological succession, where in early colonizing species decline over time giving way to a smaller number of species (mainly trees) that dominate the canopy once they become established (MALHI et al., 2010). In the first stages of ecological succession (case of 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 H + Al (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 more degraded 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. It was 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.

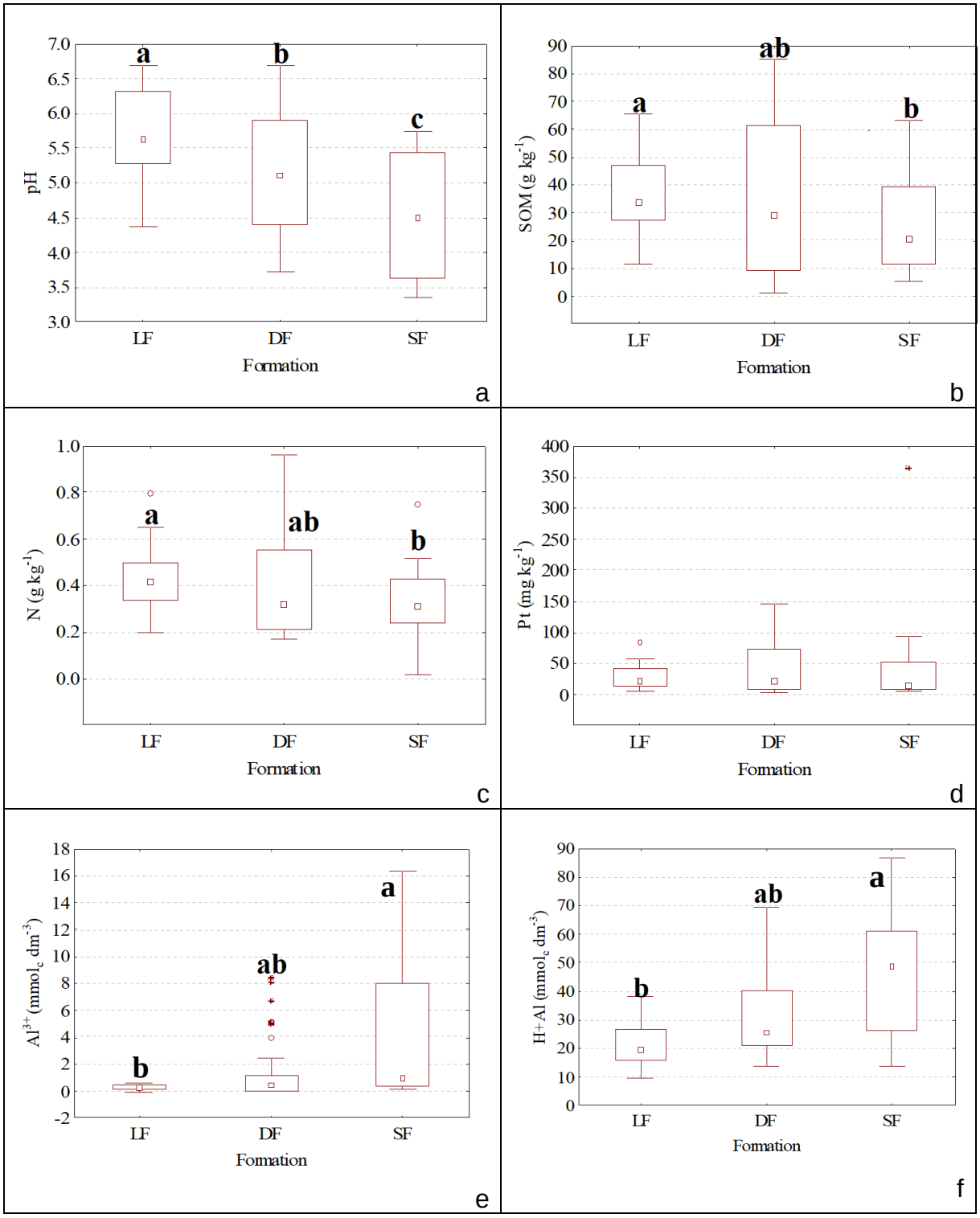
The number of different species (Fig. 4g), the number of seedlings (Fig. 4h), the basal area (Fig. 4i) and plant total density (Fig. 4j) all increased in more disturbed formation (SF) compared to more mature ones (LF). Also, observed Pearson product moments coefficients in the CM (Table 4), completely corroborates this hypothesis, being results affected by soil's development stage.

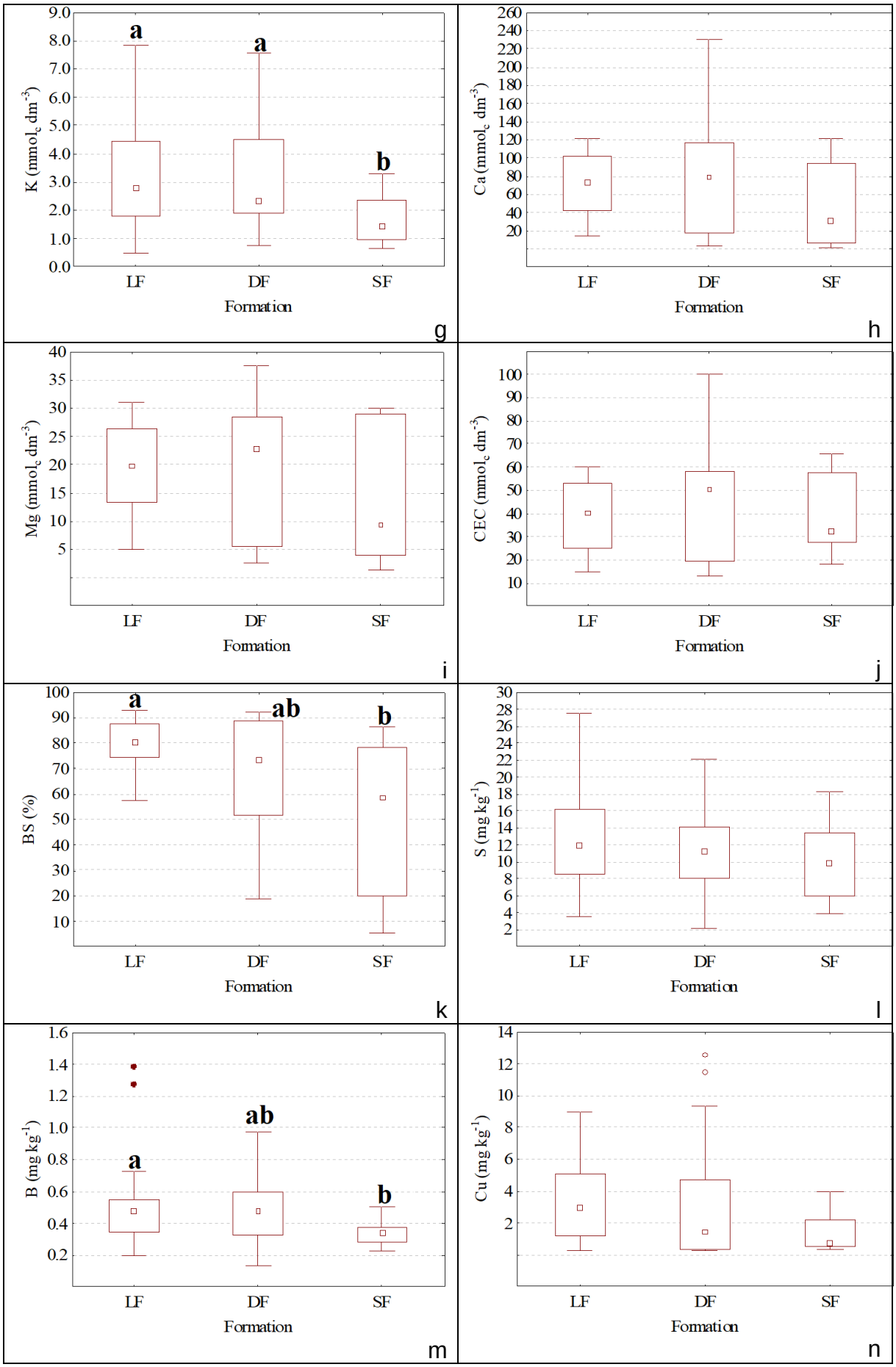
Overall, most of the investigated plant parameters showed statistically significant differences between less degraded plant formations (LF) *vs* more degraded ones (SF), and these differences were also due to the soil's development stage.

4.3 Soil features

Fig. 5 shows the distributions and differences between forest formations for all investigated soil physical-chemical parameters.

Figure 5 – Box-plots showing differences in soil physical-chemical parameters among investigated forest formations




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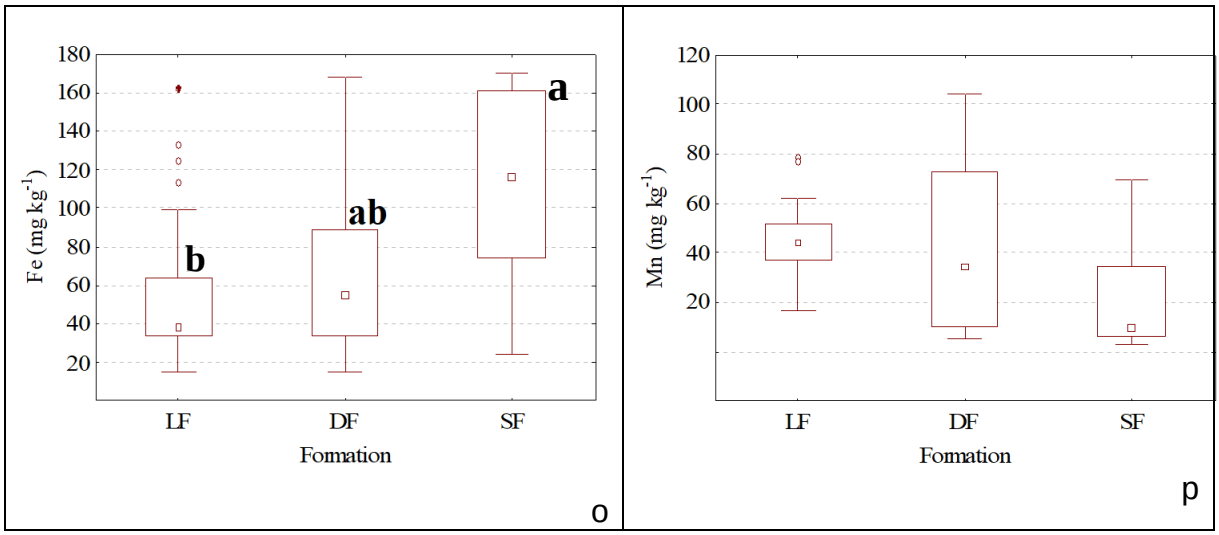

Where: LF = late forest; DF = disturbed forest; SF = secondary forest; SOM = soil organic matter; N = total nitrogen; P = resin-phosphorus; Al^{3+} = exchangeable aluminum; H+Al = exchangeable acidity K^{+} = exchangeable potassium; Ca^{2+} = exchangeable calcium; Mg^{2+} = exchangeable magnesium; CEC = cation exchange capacity; BS = base saturation; S = sulfur; B = boron; Cu = copper; Fe = iron, and Mn = manganese. Different lowercase letters indicate significant differences ($p < 0.05$) based on Tukey honestly significant difference post-hoc comparisons.

Soil pH-$CaCl_2$ (Fig. 5a) showed a clear significant difference among investigated formations, decreasing from 5.7 ± 0.1, to 5.2 ± 0.1, and to 4.5 ± 0.2 in LF, DF and SF, 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 (PINHEIRO 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., 2020). In more degraded environments (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 (Table 4) confirmed all of these hypotheses, showing a 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**).

Table 4 – 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

	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	PTD
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
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***
PTD										1.00

Where: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; SOM = soil organic matter; N = total nitrogen; Pt = resin-phosphorus; Al^{3+} = exchangeable aluminum; H+Al = exchangeable acidity; K = exchangeable potassium; Ca = exchangeable calcium; Mg = exchangeable magnesium; CEC = cation exchange capacity; BS = base saturation; S = sulfur; B = boron; Cu = copper; Fe = iron; Mn = manganese; Zn =

zinc; DBH = diameter at breast height; H = height; DW = dispersal way/syndrome; SC = successional class; NP = number of plants; NDF = number of different families; NDS = number of different species; NS = number of seedlings; G = basal area; PTD = plant total density.

Soil organic matter (SOM; Fig. 5b) and N (Fig. 5c) showed a clear significant ($p < 0.05$) decreasing trend with increasing human disturbance. In LF, SOM had a mean value of 35 ± 3 g kg^{-1} *vs* 25 ± 4 g kg^{-1} in SF, meaning a decrease of around 30% in SOM in SF. 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. Phosphorous (Fig. 5d) did not show any statistical differences among investigated forest formations. As expected for these type of soils, which are acidic and nutrient poor, SOM was the main source of soil nutrition and had positive correlations with macro- (N: r = 0.66**; P: r = 0.39*; K: r = 0.44*; Ca: r = 0.69**; S: r = 0.56**) and micro-nutrients (B: r = 0.52**; Cu: r = 0.65**; Mn: r = 0.67**; Zn: r = 0.32*) (Table 4).

Acidic exchangeable cations (Figs. 5e, f) confirmed what was previously observed for pH. They increased in more degraded, more leached (thus more acidic) pedosystems. 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. In contrast, LF formations had more robust cation cycling (Figs. 5g-i) and higher base saturation (Figs. 5k).

Exchangeable-cations (Figs. 5g-i) and CEC (Fig. 5j) did not show a specific difference among investigated formations, with the exception of K, which increased significantly in less disturbed formations. However, BS significantly decreased with increased human disturbance. In more developed forests an increase in forest canopy brings to more enriched surface organic horizons, thus increasing basic cations (SILVA et al., 2020) and less leached soils (SILVA et al., 2021). Cation-exchange capacity was significantly correlated to SOM, indicating that pH dependent charges on organic molecules were an important source of CEC.

Regarding the investigated micronutrients (Figs. 5l-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 more degraded (SF). Boron had a significant, positive correlation with SOM (r = 0.52**; Table 4), which corresponds with SOM being one of the principal B sources for plant nutrition (DAS; PURKAIT, 2020).

4.4 Multivariate statistics

Principal factor analysis was performed for each of the forest formations separately. For all investigated formations, the eigenvalues of the first three extracted factors (Table 5) 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 formation.

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 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 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 (NDS), families (NDF), and higher plant total density (PTD). In the less 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 reported soil and plant conditions and feedbacks seem to be more favorable for animal rather than abiotic (gravity, wind, ballistic, water) seeds dispersal way. 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. 5e), thus being less acidic (Fig. 5a), 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” (BOLANOS; BREWIN; BONILLA, 1996) since higher B in LF formations (Fig. 5m) 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”.

Table 5 – 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
PTD	**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; PTD = 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 5). 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 more degraded (SF) and the most developed (LF) forest formations. For all of these reasons, F1 was interpreted 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. Indeed, even if soil features were more favorable compared to SF, showing higher soil pH (Fig. 5a), N (Fig. 5c), K (Fig. 5g), and B (Fig. 5m), 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” (BOLANOS; BREWIN; BONILLA, 1996). 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; 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, factor F1 (72% of the variance), extracted several soil parameters (N, B, S, Cu, Fe, Mn excluded) and plant measurements (DW, SC, G, PTD 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 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. 5b). Overall, by considering this factor as well as by comparing all F1 extracted factors, it can be underlined that: *i*) SF formations were characterized 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.

5 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.

The investigation of natural regeneration in BAF fragmented formations provided novel outcomes for improving future management of the natural regeneration layer. 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 Brazilian Atlantic Forest, as a biome of worldwide interest, must be preserved from further human disturbance with appropriate management actions. Analyzing the natural regeneration and soil parameters, it was demonstrated that after almost 40 years in the absence of human disturbance, an almost complete vegetation (in terms of natural regeneration layer) and soil recovery was observed, with increasing complexity in plant-soil relationships and increase in ecosystem services (such as micro and macronutrients stocks, improved general ecosystem fertility and complexity). After almost 30 years without human disturbance (DF), the natural regeneration 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 is a highly fragile ecosystem, requiring protection against further human disturbance.

Knowing that the present study serves as a complementary investigation to the previous studies of Silva (2018) and Sivisaca (2020), it is essential to encourage new studies to complement the existing findings and enhance our understanding of the investigated processes. For instance, conducting studies on light and water availability,

as well as exploring other aspects of the soil that remain unexplored, will contribute significantly to advancing our knowledge of the BAF and its ecological dynamics. The main study about of the interested area is that conducted by Sivisaca (2020), which had as its general objective to investigate how the fragmentation of the BAF affected the biomass, carbon, and biodiversity, focusing on the tree layer (i.e., plants with more than 5 cm), not the natural regeneration. In addition, Silva (2018) delved into the investigation of deeper soil horizons and litter, aiming to estimate the stock of carbon and nutrients in litter and soil.

This study strongly advocates for the engagement of all relevant stakeholders to implement necessary measures for the protection of the BAF biome. This entails meticulous management of human activities, including the outright prohibition of highly impactful practices like agriculture. Instead, the focus should shift towards utilizing the area for tourist-recreational and scientific purposes.

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