Title: Pervasive Negative Effects of *Leucaena leucocephala* (White-Popinac) Invasion on Regenerating Areas of the Atlantic Forest

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Abstract

The use of invasive species in ecological restoration is controversial and has raised recent concerns. In Brazil, some ecosystem restoration and agroforestry projects have proposed that white-popinac (*Leucaena leucocephala* (Lam.) de Wit), a broadly distributed invasive species, is a promisor species to be used when the soil is severely altered, based on the premise that it might not necessarily disrupt natural regeneration processes, especially in fragmented forests. To address this uncertainty, we investigated its effects on the functional diversity of naturally regenerating forests dominated by invasive grasses within the Atlantic Forest domain. We conducted floristic surveys on the arboreal and herbaceous strata in 29 regenerating areas invaded by white-popinac, each with a unique time-since-invasion, thereby creating a gradient of invasion duration. We estimated the average seed mass of each regenerating area (CWM), as well as species richness and abundance of trees/shrubs and animal dispersed species, and α and β functional metrics. The progression of invasion led to (i) a major decrease in the average seed mass of native species, contrasted by an increase of this metric for invasive species; (ii) an increase in tree abundance, without increasing tree species richness; and (iii) a reduction in the richness of animal-dispersed species. Collectively, these results indicate that the natural regeneration trajectories of Atlantic Forest fragments can be strongly compromised by the advance of white-popinac invasions.

Practical implication: Our results highlight the need for early control measures and caution against using white-popinac in restoration, emphasizing the value of functional metrics in monitoring.Therefore, management protocols for the prevention and control of white-popinac must be implemented, and its use in restoration projects should not be advised.

Key-words: *leucena*; invasional meltdown; metacommunity ecology; functional traits; restoration

Introduction

The consequences of biological invasions for forest regeneration can be severe and often irreversible (Londe et al. 2017; Chiba De Castro et al. 2019; Dyderski and Jagodziński 2020). Invasive species (IS) can drive native species to local and regional extinctions (Flory and Clay 2010; Chase et al. 2020), resulting in the losses in functional traits (Flory and Clay 2010; Loiola et al. 2018; Guido et al. 2021) and contributing to the homogenization of local communities (Renault et al. 2022). For example, larger-sized seeds may be lost in invaded areas (Gioria and Pyšek 2015), and seed dispersal networks can be severely disrupted (Spotswood et al. 2012). Despite efforts to eradicate or control IS in forests or other vegetation types, legacy effects (Elgersma et al. 2011) and invasional meltdowns (Simberloff and Von Holle 1999) are frequently observed, demonstrating that complete recovery from IS impacts is often unachievable (e.g. Reynolds et al. 2017; Chen and van Kleunen 2022). In some cases, native species richness may not change substantially in invaded areas (Fridley et al. 2007), leading to potential misinterpretations about the real impacts that IS have caused. This highlights the limitations of an exclusive taxonomical approach, which often overlooks the nuanced effects of IS on ecosystem functioning, underscoring the need for functional trait-based frameworks to fully assess these impacts. Despite the growing recognition of functional assessments, a critical gap remains in understanding how IS-driven alterations to functional traits and processes shape forest regeneration dynamics (Langmaier and Lapin 2020; Lázaro-Lobo et al. 2021).

The use of non-native plant species in ecosystem restoration has long been controversial (Schlaepfer et al. 2011; Dunwiddie and Rogers 2017; Pyšek et al. 2020). Some argue that, in severely degraded areas, non-native species may be the only viable option to restore soil quality and ecosystem functions (e.g. D'Antonio and Meyerson 2002; Singh et al. 2022; Silva et al. 2023). In Brazil, one species that has garnered both praise and concern is white-popinac (*Leucaena leucocephala* (Lam.) de Wit; *leucena*, in Portuguese). Once hailed a "miracle plant" for its resilience, rapid growth, and ability to thrive in nutrient-poor soils (Leão et al. 2011; Sharma et al. 2022), it has since become a focal point of ecological debate. Introduced primarily for its economic value as a forage species for cattle during the dry season, white-popinac has become invasive in ecosystems such as savannas, *restingas*, and regenerating forests, causing significant ecological disruption (Zenni and Ziller 2011). Despite its invasiveness, it continues to be recommended for certain forest restoration and agroforestry projects (Drumond and Ribaski 2010; Ishihara et al. 2018; Bageel et al. 2020). Some even argue that white-popinac facilitates forest regeneration, functioning similarly to other pioneer species (Costa and Durigan 2010; Wolfe and Van Bloem 2012).

In Brazil, recent changes in environmental legislation have required landowners in rural areas to allocate portions of their property to native vegetation, typically by abandoning former pasturelands or plantations to facilitate natural forest regeneration (Brasil 2012). White-popinac is a prevalent IS in these areas, often forming large, dense and homogeneous patches (de Melo-Silva et al. 2014; Werema and Wilson 2022). These patches typically surround forest fragments, encroaching upon regenerating areas. Most regenerating areas are dominated by invasive grasses (Zardetto and Siqueira 2024), and the density within white-popinac patches is so high that, over time, grasses and herbaceous species are displaced to the fragment edges (Hata et al. 2010; Osawa et al. 2016). This

displacement results from competitive effects, such as reduced sunlight incidence, as well as known allelopathic effects (Kato-Noguchi and Kurniadie 2022). Recently, Zardetto and Siqueira (2024) demonstrated that white-popinac invasions in naturally regenerating forests lead to biotic homogenization, reduced native species richness, and increased susceptibility to further invasions by other non-native species.

Despite growing concerns about the annual spread of white-popinac and repeated failures in management efforts, the species is still frequently regarded as promising and manageable. For many decision-makers – including local politicians, landowners, agroforestry specialists, and even some ecologists – it remains unclear whether white-popinac functions like other pioneer species (Costa and Durigan 2010; Wolfe and Van Bloem 2012), facilitating the establishment of secondary species, or whether it disrupts the expected trajectory of forest natural regeneration. To address this uncertainty, we investigated the effects of white-popinac invasions on the functional diversity of naturally regenerating forests dominated by invasive grasses within the Atlantic Forest domain.

Using a space-for-time substitution approach, we constructed a chronosequence of white-popinac invasion to assess how the progression of invasion over time influences natural regeneration, with a focus on the functional aspects of these regenerating forests. Specifically, we examined (i) the average seed mass in the regenerating areas, (ii) the balance between animal- and non-animal-dispersed species, (iii) shifts in the dominance of trees versus shrubs, and (iv) the dynamics of functional α-diversity within the regenerating areas and β-diversity among transects. If the impacts of white-popinac are substantial, they could disrupt the expected pathways of natural forest regeneration, with potentially profound consequences for restoration and biodiversity conservation.

Materials and Methods

Sampling design

We conducted fieldwork on 38 private properties located in rural and peri-urban areas in the interior region of the state of São Paulo, southeastern Brazil. Each property contained naturally regenerating forests adjacent to at least one major patch of old-growth native forest (Atlantic Forest domain) and one patch of white-popinac. Of these 38 private properties, we selected 29 to establish a temporal gradient of invasion for analysis. Fieldwork was carried out between March 2020 to September 2022.

All study areas consisted of abandoned pastures or agricultural lands undergoing natural regeneration. These areas were initially dominated by invasive grasses, primarily *Urochloa brizantha* (Hochst. ex A.Rich.) R.D.Webster and *Megathyrsus maximus* (Jacq.) B.K.Simon & S.W.L.Jacobs, shortly after abandonment. In pastures, these grasses, particularly *U. brizantha*, served as the primary forage for cattle, which contributed to their dominance in the region even prior abandonment. In agricultural lands, invasive grasses typically proliferate along roads, firebreaks, and the edges of forest patches. After abandonment, these grasses quickly dominate the regenerating areas within a few years. This grass-dominated landscape creates favorable conditions for the establishment and spread of white-popinac. Although scattered individuals of white-popinac may be present prior to abandonment, population growth and proliferation only occur after invasive grasses became the dominant vegetation, as white-popinac requires more time to reproduce and establish a larger population.

Our sampling design incorporated two hierarchical scales of sampling units: the regenerating area itself (n = 29) and the transects within each regenerating area (n = 131). Both scales were systematically replicated to ensure consistent coverage. Regenerating

areas were defined as abandoned pastures or agricultural lands that surrounded, at least partially, an old-growth forest patch and contained at least one patch of white-popinac. Within each regenerating area, we established four to five transects for sampling. Each transect measured 14 m x 2 m and was positioned at the interface between the forest fragment and its adjacent regenerating area, with 7 m extending into the forest fragment and 7 m into the regenerating area.

At each transect, we estimated the abundance of all species, including both native and IS, in the arboreal and herbaceous strata. The arboreal stratum included all tree and shrub species within the transect area (14 m x 2 m), with all individuals recorded and counted. For the herbaceous stratum, each transect was divided into 28 grids (1 m x 1 m). Seven evenly distributed grids were selected within the transect for sampling. In these grids, we visually estimated the ground cover percentage of each species using the Braun-Blanquet approach (Braun-Blanquet 1964). The ground cover of each species for the entire transect was calculated as the average ground cover across the seven grids.

All recorded species were classified based on the following criteria: (i) dispersal mechanism, as either animal or non-animal-dispersed (Van der Pijl 1972); (ii) growth-habit (JBRJ 2023); and (iii) status as native or invasive in the study region, using information from established invasive species databases, including the Invasive Species Compendium, the Global Invasive Species Database, and the Horus Institute for Environmental Conservation and Development. Further methodological details are provided in the Supplementary Information (SI) file.

Response variables

We estimated species richness for animal- and non-animal-dispersed species as well as for trees and shrubs (Fig. 1) using sample-coverage rarefaction and extrapolation

methods in the iNext R-package (v3.0.0, Chao et al. 2014; Hsieh et al. 2016). This analysis was conducted separately for the arboreal and the herbaceous strata. The observed abundance of each species in both strata, used to estimate species richness, was calculated as the sum of observed abundances across all transects within each regenerating area.

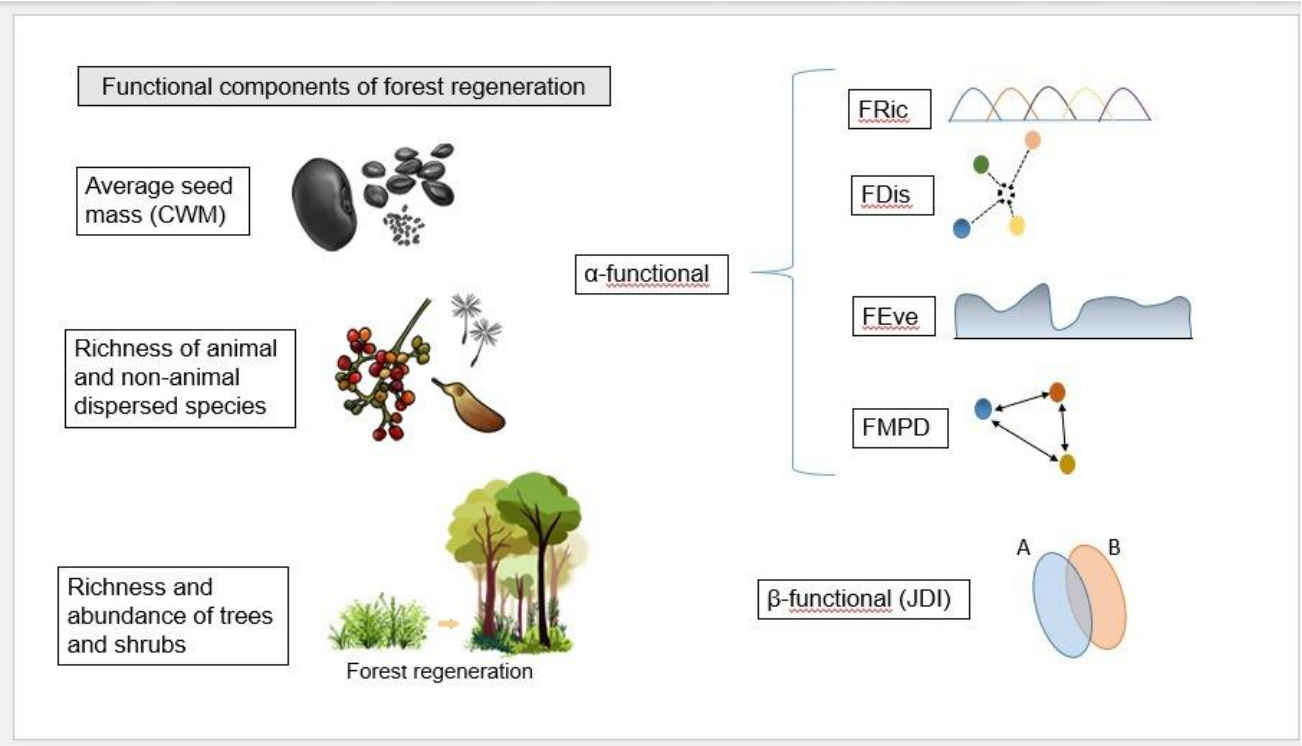

Fig 1. The response variables, representing functional components of forest natural regeneration. CWM: Community weighted mean. FRic: functional richness. FDis: functional dispersion. FEve: functional evenness. FMPD: functional mean pairwise distance. JDI: Jaccard's dissimilarity index.

Seed mass - Community weighted mean (CWM)

For each recorded species, we obtained the average diaspore dry mass (referred to here as seed mass) from trait databases (Bello et al. 2017; Kattge et al. 2020) and bibliography (Lorenzi 2016, 2020, 2021), with some measurements obtained directly from our own samples. Detailed information on the databases and measurement methods used for each species is provided in the SI file. We estimated the community-weighted mean (CWM) seed mass by calculating the average seed mass for each regenerating area, weighted by their respective abundances. Since the abundance metrics differed between the arboreal (individual counts) and herbaceous (ground cover percentage) strata, the CWM was calculated separately for each stratum.

Functional α-diversity

Functional diversity indices were derived from the multidimensional trait space of plant communities, using the R package MFD. Functional α-diversity metrics were estimated with the *alpha.fd.multidim function*, using as input the first three Principal Coordinates Analysis (PCoA) axes previously extracted from the multidimensional trait space (see SI: Trait space). We calculated the following functional α-metrics: functional richness (FRic) representing the functional diversity of traits within a single community (Mouillot et al. 2013); functional dispersion (FDis) defined as the extent to which species in a community functionally deviate from the center of functional space, weighted by the abundance of each species (Mouillot et al. 2013); functional evenness (FEve) quantified as how regularly distributed the species of a community are within the functional space (Mouillot et al. 2013); and functional mean pairwise distance (FMPD) quantified as the degree of functional dissimilarity between species pairs, based on their ecological traits (Webb et al. 2002; Mouillot et al. 2013). We tested Pearson’s correlation among the

observed alpha diversity indices but didn't find any strong correlation (see SI: Functional α-diversity).

Functional β-diversity

We estimated beta functional diversity of each transect using the function *beta.fd.multidim* of the MFD package (Magneville et al. 2022). Metrics were calculated based on species occurrence and the first three PCoA axes extracted previously (see SI: Trait space). We calculated Jaccard's dissimilarity index and its functional turnover and functional nestedness-resultant components (Villéger et al. 2013), (see SI: Functional α-diversity). We estimated the median functional β-diversity among the transects (four of five) within each regenerating area, to obtain a single value of β-diversity for the entire regenerating area.

Predictor variables

We established chronosequences using a space-for-time substitution approach, in which different stages of invasion were represented through spatial replication. To quantify the progression of white-popinac invasion over time, we used three variables related to the white-popinac patch within each regenerating area: basal area (BA), average diameter at breast height of the largest individuals (ADL), and age proxy obtained by satellite imagery (AP). BA, measured in square meters per plot, represents the total area occupied by white-popinac tree trunks in each plot. Higher BA indicate older trees and, therefore, longer established invasions. ADL (centimeters) was calculated as the average diameter at breast height (dbh) of the largest trees within the white-popinac patch, specifically those in the top 25% of the dbh distribution (upper quantile). Larger ADL values reflect older and more mature trees, indicative of extended invasion timelines. AP (years) was estimated using

historical satellite imagery from Google Earth. By identifying the first appearance of each patch, we assigned an approximate age to the invasion event.

Model selection

For each of hypothesis, we built a set of alternative models to represent potential relationships between a response variable and each time-advance predictor variable, which was standardized prior to inclusion in the models. Our models also included a categorical predictor variable to account for strata (herbaceous or arboreal) when diversity metrics were calculated differently for each stratum. Additional categorical predictor variables were included to capture interactions with the time-advance variable: one to describe dispersal mode (animal-dispersed or non-animal-dispersed) and another to differentiate growth habit within the arboreal stratum (tree or shrub).

We employed Generalized Linear Models (GLM) for each response variable, selecting distribution families based on the nature of the data (e.g., continuous, discrete or proportional). For example, for estimated species richness, we compared models using Gamma and Gaussian distributions. Model selection followed an information-theoretic approach (Aho et al. 2014), using the corrected Akaike Information Criterion (AICc) and derived metrics (e.g., Δi, AICc weight) to rank models. Additional details on model structures, distribution families, selection criteria, and the software and R packages used are provided in the SI file.

Results

In total, we recorded 328 plant species across both native and invasive categories, with 178 species identified in the arboreal stratum and 150 in herbaceous stratum (Table 5

– SI). Twenty species could not be identified due to the absence of key taxonomic structures, particularly among deciduous species. The remaining 308 identified species were distributed across 218 genera and 73 families, with Fabaceae, Asteraceae and Malvaceae being the most represented in terms of species richness.

The average observed species richness per regenerating area was 46.5 species (range = 25.4 - 84; SD = 14.2; n = 29). The progression of white-popinac invasions influenced several key aspects of the regenerating areas: (i) the average seed mass; (ii) the proportion of animal-dispersed species; and (iii) the dominance of trees in older invaded areas. In contrast, white-popinac invasions did not affect functional α-diversity (FRic, FDis, FEve, FMPD) or β-diversity metrics.

Our analysis revealed a complex interplay between tree abundance and species richness as the time-advance of invasion progressed. We observed a consistent increase in the total abundance of trees over time (model 1; Figure 2A; Table 1; Nagelkerke's R^2 = 0.84), suggesting that certain tree species (other than white-popinac) are thriving in the invaded areas. However, this increase in abundance was not accompanied by an increase in tree species richness (model 2; Figure 3; Table 1; time-advance coefficient [95% CI] = -6.9 to 1.2; Nagelkerke's R^2 = 0.48). These findings highlight a potential trade-off between abundance and diversity within the tree community. While certain tree species may be benefiting from the altered conditions, the overall diversity of the tree community does not seem to respond in the same way.

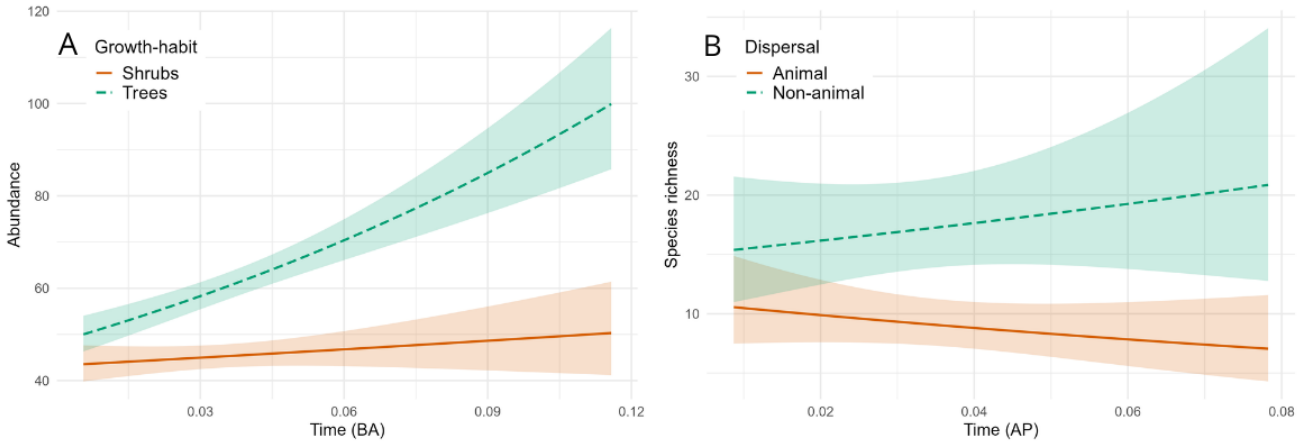

Fig 2. Interaction plots representing the response variable in function of time conditional on categorical variable. Values on x-axis are standardized. A. Predicted total abundance of trees and shrubs in regenerating areas (model 1, Table 1). B. Precited species richness of animal and non-animal dispersed species in the regenerating areas (model 10, Table 1). BA, basal area (m^2), is a time-advance variable that represents the area occupied by white-popinac trunks within a standardized plot. AP, age proxy (years) is a time-advance variable that represents when the white-popinac patch was large enough to be detectable in the satellite imagery.

When considering the average seed mass of all species (calculated as CWM), we found no relationship with any of the time-advance variables. However, when analyzing native and invasive species separately, we observed contrasting trends. For native species, the CWM of seed mass decreased with increasing time since invasion (AP) in both arboreal and herbaceous strata (model 5, Figure 3; Table 1; time-advance coefficient [95% CI] = -15.2 to -0.53; Nagelkerke-R^2 = 0.83). Conversely, for invasive species, the CWM of seed mass increased with increasing time since invasion (BA) also in both arboreal and herbaceous strata (model 6, Figure 3; Table 1; time-advance coefficient [95% CI] = 0.73 to 18.5; Nagelkerke-R^2 = 0.95).

Regarding the proportion of animal and non-animal-dispersed species, two model structures were among the best supported models in the selection process (Δi < 2): a model with an interaction between time-advance of invasion and dispersal mode (animal vs. non-animal) and a simpler additive model without this interaction. The additive model (model 7) indicated a weak decrease in the overall species richness with increasing time since invasion (ADL) (model 7, Figure 3; Table 1; time-advance coefficient [95% CI] = -14.7 to 3.5; Nagelkerke-R^2 = 0.19). The interactive model (model 10) showed a clear decrease in the richness of animal-dispersed species, while the richness of non-animal-dispersed species increased with time since invasion (AP), irrespective of stratum (model 10; Figure 2B; Table 1; Nagelkerke-R^2 = 0.19). Both models were equally plausible (Δi < 2) and provide valuable insights into the potential effects of invasion on plant-animal interactions. Notably, both models suggest a decline in the richness of animal-dispersed species with increasing time since invasion.

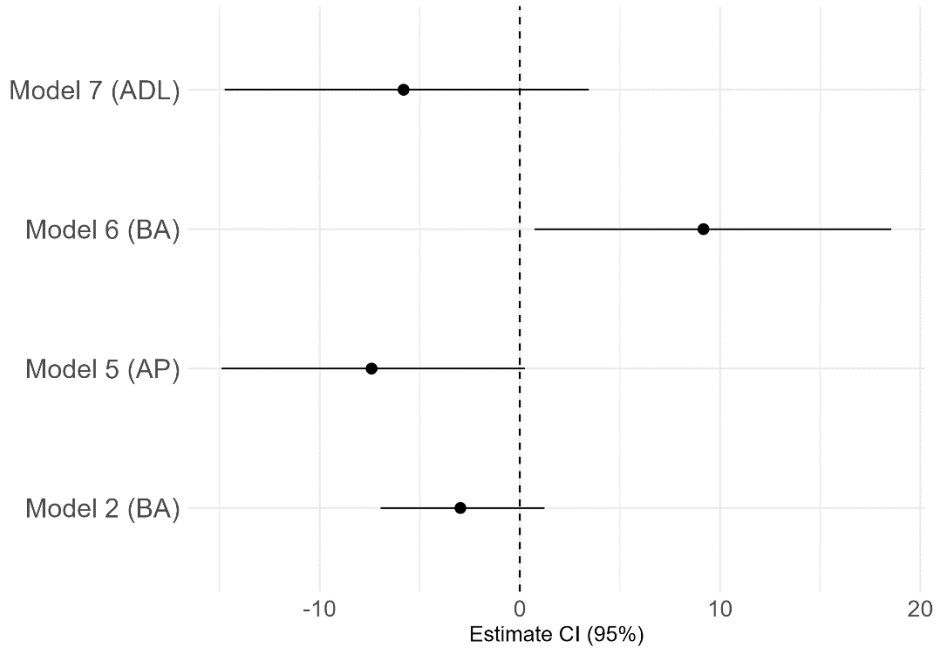

Fig 3. Confidence intervals (95%) from predicted estimates on selected additive models. Once each model has its own distribution family and link function, the values on x-axis are

not standardized and cannot be directly compared among models. This plot only presents if the CI include zero or not. ADL: Average diameter at breast height (dbh) of the largest white-popinac trees within a regenerating area (cm). AP: Age-proxy of the white-popinac patch (years). BA: Basal area of the white-popinac patch (m^2).

Table 1. Model selection statistics for top-ranked models ($\Delta i < 2$). AICc: Corrected Akaike Information Criterion (AIC). Δi: Difference between a given model's AICc and the AICc of the best-ranked model. AICc (W): Akaike weight, representing the relative likelihood of a given model. R^2*: Pseudo-R^2 for Poisson and Beta models; Nagelkerke R^2 for Gamma models. ADL = Average diameter at breast height (dbh) of the largest white-popinac trees within a regenerating area (cm). AP = Age-proxy of the white-popinac patch (years). BA = Basal area of the white-popinac patch (m^2). Strata = Herbaceous or arboreal. Dispersal type = Animal-dispersed or non-animal-dispersed species. Habit = Trees or shrubs.

Model structure	**Distribution family**	**AICc**	**Δi**	**AICc (W)**	**R^2***
Abundance of trees and shrubs					
(1) Time (BA) * habit	Poisson	828.5	0	0.99	0.84
Species richness (trees and shrubs)					
(2) Time (BA) + habit	Gamma	335.5	0	0.35	0.48
(3) Time (AP) + habit	Gamma	336.4	0.94	0.22	0.47
(4) Time (ADL) + habit	Gamma	336.9	1.47	0.17	0.46
Seed Mass (CWM) of native species					
(5) Time (AP) + strata	Gamma	518.6	0	0.79	0.83
Seed Mass (CWM) of invasive species					
(6) Time (BA) + strata	Gamma	388.4	0	0.78	0.95

Species richness (animal and non-animal-dispersed species)					
(7) Time (ADL) + dispersal type + strata	Gamma	722.3	0	0.28	0.19
(8) Time (BA) + dispersal type + strata	Gamma	722.5	0.18	0.26	0.19
(9) Time (AP) + dispersal type + strata	Gamma	723.8	1.48	0.14	0.18
(10) Time (AP) * dispersal type + strata	Gamma	724.0	1.75	0.19	0.19

Discussion

Our findings demonstrate that white-popinac (*Leucaena leucocephala*) invasion exerts pervasive impacts on the functional trajectory of regenerating Atlantic Forest fragments. By linking invasion progression to declines in functional diversity, reduced native species establishment, and shifts in dispersal and growth strategies, our analysis reveals a critical disconnect between white-popinac's perceived role as a facilitator of regeneration (Wolfe and Van Bloem 2012; Bageel et al. 2020) and its actual ecological effects. These results challenge assumptions that the species functions analogously to native pioneer taxa (Wolfe and Van Bloem 2012), as its dominance alters the functional composition of regenerating communities in ways that may hinder long-term forest recovery. This underscores the risks of prioritizing short-term vegetation cover over functional resilience in restoration planning, particularly in systems already compromised by biological invasions.

The reduction in the average seed mass of native species in older invaded regenerating areas indicates an ongoing loss of large-seeded native species. These large-

seeded species play a critical role in forest functioning by providing resources for animals (Galetti et al. 2006), maintaining ecosystem services (Culot et al. 2017), and ensuring the long-term continuity of forest regeneration (Costa et al. 2012). Previous studies demonstrated that native large-seeded species are particularly vulnerable to disturbances such as fragmentation (Melo et al. 2007; Costa et al. 2012) and, potentially, biological invasions (Gioria and Pyšek 2015), often exhibiting higher extinction rates. Most large-seeded species in tropical forests are shade-tolerant and more abundant in late-successional stages and mature forests (Sonkoly et al. 2017; Werden et al. 2020). The conditions that favor these species may be compromised by the presence of by dominant invasive species such as white-popinac, which can significantly alter resource availability and environmental conditions (GISD 2015). Our results indicate that they are increasingly being replaced by invasive species, most notably white-popinac and other less abundant invaders. Interestingly, it is not the functional trait of large seeds that is being lost, as this dynamic was not evident in the general model; rather, there is a shift in species identities from native to invasive. To our knowledge, no previous research has documented an invasive species causing the replacement of large-seeded native species with invasive counterparts that also produce large seeds. This finding underscores a unique aspect of white-popinac invasions and warrants further investigation into the ecological implications of these trait-specific yet identity-driven dynamics.

The decrease in the richness of animal-dispersed species is a concerning effect of white-popinac invasion, with potential cascading consequences, such as local extinctions of dispersers, shifts in species distribution, and disrupted trophic interactions (García and Martínez 2012; Brodie et al. 2024). This decline is partially driven by the exclusion of large-seeded, animal-dispersed species, which are replaced by small-seeded, non-animal-dispersed species, often wind-dispersed. These changes create feedback loop: fewer

353 animal-dispersed plants reduce local resource availability, leading to declines in animal
354 dispersers, especially specialists, which further compromises seed dispersal processes
355 (Wotton and Kelly 2011; Culot et al. 2017). The remaining animal-dispersed species in
356 older invaded areas were either primarily invasive species (e.g. *Psidium guajava* L., *Melia*
357 *azedarach* L. and *Syzygium cumini* (L.) Skeels) or ruderal natives (e.g. *Solanum* spp.,
358 *Celtis iguanaea* (Jacq.) Sarg. and *Piper aduncum* L.). While the long-term consequences of
359 these changes are known, including potential local extinctions of animal dispersers, the
360 extent to which these impacts can be reversed remains uncertain.

361 Our findings reveal that while tree abundance increases in older invaded areas, the
362 richness of both tree and shrub species does not follow this pattern. Under normal forest
363 natural regeneration in the Atlantic Forest, an increase in tree abundance is expected
364 (Campanello et al. 2007), often surpassing the abundance of shrubs. Once richness of
365 trees is not increasing, this pattern underscores that while tree recruitment occurs, it is not
366 accompanied by the establishment of new tree species as white-popinac invasion
367 advances. In older invaded areas, dominant tree species are ruderal, non-animal-
368 dispersed, or have smaller seeds (e.g. *Tabernaemontana catharinensis* A.DC.,
369 *Moquiniastrum polymorphum* (Less.) G. Sancho*,* and *Aloysia virgata* (Ruiz & Pav.) Juss.*,*
370 respectively). This apparent increase in tree abundance may contribute to misconceptions
371 about the ecological impacts of white-popinac. Although tree recruitment may seem to
372 indicate regeneration, the richness and functional diversity of tree species is not increasing,
373 as expected in a naturally regenerating forest (Siminski et al. 2021).

374 Our results indicate strong impacts of white-popinac invasions on naturally
375 regenerating Atlantic Forest patches, although other factors likely contribute to these
376 dynamics. A critical, unaddressed issue is the chronology of grass invasion versus white-

popinac invasion. Invasive grasses (*Megathyrsus maximus* and *Urochloa brizantha*) were present in all the areas before abandonment, but their interactions with white-popinac – whether facilitative, synergistic, or competitive – remain unclear. While competition between these invasive species has been indirectly explored (Zardetto and Siqueira 2024), a field-based study excluding grasses would be unfeasible as abandoned Atlantic Forest areas are invariably dominated by them. Other IS were less abundant, with 16 herbaceous and 12 arboreal species recorded, none approaching the dominance of white-popinac or grasses. The inclusion of the herbaceous stratum in our study was crucial, given its pivotal role in early-stage regeneration. In fact, half of all recorded species were found this stratum, comprising 66 forbs, 16 species of grasses and graminoids, 55 climbing species and 6 other growth forms. These results underscore the importance of prioritizing the herbaceous layer in studies of forest natural regeneration.

Considering the 2-20-year time span encompassed by our chronosequences (via AP), the expected forest regeneration appears to be severely compromised, and potentially inhibited, in both strata. While we cannot predict whether these conditions will persist indefinitely, we found no clear evidence that the disruptive effects of white-popinac invasions diminish over time in naturally regenerating areas of the Atlantic Forest. We suggest that white-popinac invasions deserve greater attention in terms of prevention and control, and that the use of white-popinac in restoration projects should be discouraged. Given that white-popinac is rapidly spreading across several Brazilian biomes, particularly in open areas, urgent implementation of management protocols for its prevention and control is imperative.

Acknowledgments

The authors thank the São Paulo Research Foundation (FAPESP) for financial support (grants 21/00619-7 and 20/14104-6). TS also acknowledges the National Council for Scientific and Technological Development (CNPq) for a research productivity grant (309496/2021-7).

Author contributions

JZ, TS and WS analyzed the data and wrote the paper; JZ and TS conceived the idea and designed fieldwork; WS collected trait data for the species; JZ collected field data and identified the species

Conflict of interest: The authors have no conflict of interest to declare.

Data availability statement: All data and coding will be archived in Zenodo.

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Title: Pervasive Negative Effects of *Leucaena leucocephala* (White-Popinac) Invasion on Regenerating Areas of the Atlantic Forest

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Supplementary Information

Material and methods

Study region

Our study region comprises rural and peri-urban areas in five municipalities within state of São Paulo, southeastern Brazil. Nineteen of the 29 areas were in the city of Porto Feliz. All other ten areas were in neighbor cities, near the division line with Porto Feliz, being: one in Rafard, one in Capivari, two in Itu and six in Boituva (Figure 1A). All five cities are relatively small and share similar climatic, vegetation and geological features.

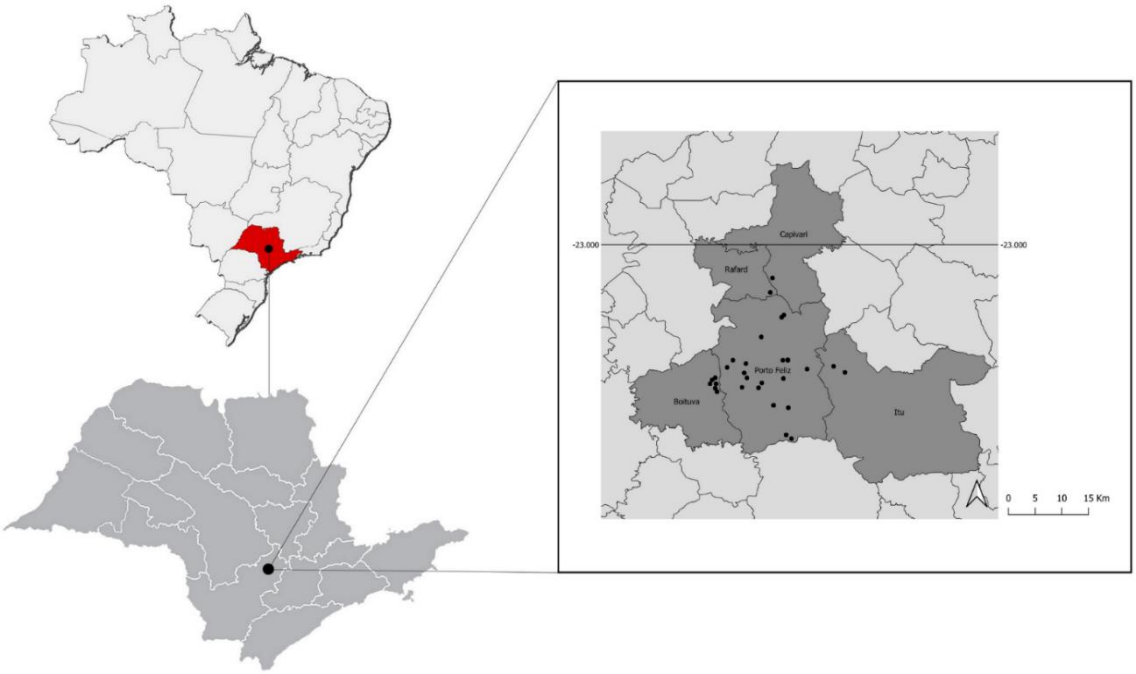


Fig. 1A Location of our study region. State of São Paulo, Brazil. The points on the right side chart are our areas.

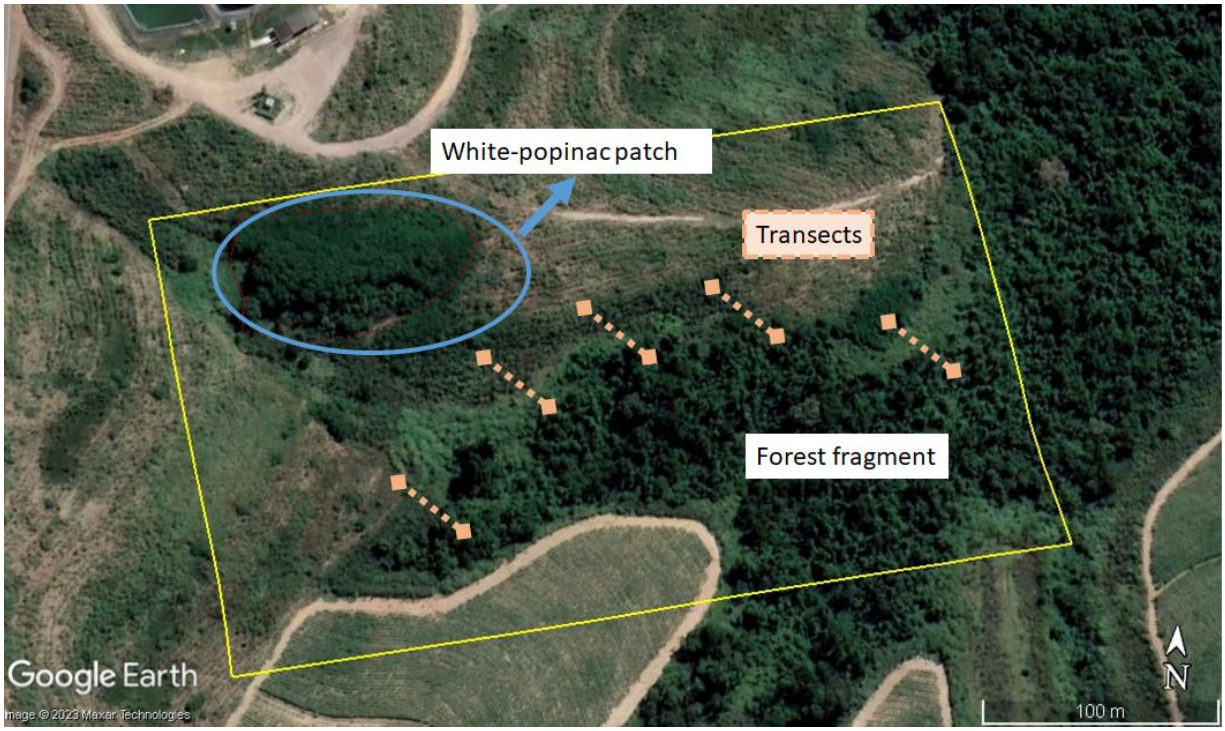


Fig. 1B Representation of our sampling units.

The region is located within Paraná's Sedimentary Basin, and the most abundant soil types are Latosoils and Ultisoils. The climate is classified as CWA by Köppen classification, which is characterized by a warm and rainy summer and a dry winter season. The region is crossed by one of the most important rivers in the state of São Paulo, the Tietê River (Oliver, 2016). The following geographical coordinates delimit the region: North: 23º02'48.64" (S); 47º31'58.92" (W); East: 23º14'59.57" (S); 47º22'23.79" (W); South: 23º21'23.00" (S); 47º29'01.13" (W); West: 23º14'11.83" (S); 47º37'43.70" (W).

Our sampling units were systems composed of a forest fragment and its respective regenerating area, which became invaded by a white-popinac patch (Fig. 1B). All fieldwork was done from March 2020 to September 2022. We divided fieldwork into two phases: the first for sampling and measuring white-popinac (predictor variables) and the second for floristic surveying (response variables). Thus, all sampling units were visited twice. All sampling units were in private lands, with different history of land management and abandonment. However, the last land uses before abandonment were either pasture or sugar cane cropping. We got this information based on properties' owners and neighbor's reports. We discarded potential areas that had recently gone through fires or cattle (re)introduction.

Details on predictor variables

Bellow, we detail the methods involved in estimating our predictor variables. We created three different gradients to express the potential effects of time-advance of invasion because each one of them captures a different component of time-advance (Spearman's correlation coefficients among these variables are displayed in Table 1). Despite the age-proxy being more intuitively related to time-advance, the scale of years may not be enough to describe changes in community dynamics, because white-popinac is an extremely fast-growing tree. Therefore, we understand that other approaches to time-gradients can be useful as well. The use of proxies was necessary because we had an observational design, in which the precise age of a patch is not achievable.

Basal area

Basal area describes the amount of area occupied by tree trunks. The sum of cross-sectional area values of all tree trunks, considering breast height, within a standardized area, gives the basal area value. Usually, it is expressed in square feet per acre, or square meters per hectare (Cancino, 2012). In our design, basal area was chosen because it is easy to obtain, and can represent time-advance of invasion. It is expected that as a white-popinac patch grows and develops, the average basal area also increases. We acknowledge that different soil and climate conditions may influence basal area's growth rate, and that creating gradients with basal area estimates from multiple distinct areas may not be advisable. However, because all of our regional sampling units are considerably near each other, under the same climate conditions and very similar soil types, the use of average basal area as a proxy to time-advance is more reliable.

To estimate basal area (BA) of a white-popinac patch, we followed this sequence of events:

1- Each regenerating area had its own "invader" white-popinac patch.

2- For each small patch (total area < 100 m^2), we stablished one 5m x 5m plot, avoiding patch's edge areas, and placing it on the center of the patch. For larger patches, we stablished two or even three plots, and the patch's basal area was the average among them.

3- Within each plot, all white-popinac trees higher than 1.70 m were measured. The measuring consists in the trunk's perimeter on breast height (pbh), which was measured with a measuring tape (precision = 0.1 cm) at breast height (1.3 m).

4- We calculated the respective diameter at breast height of each individual applying the perimeter as equal to $2\pi R$, being R the circumference radius to be calculated and multiplied by 2, obtaining the diameter.

5- For each patch, the sum of all diameters results in basal area (or average among plots for large patches), which is expressed in square meters (m^2), considering a standardized plot area of 25 m^2.

6- Each basal area value works as a point on the time-gradient proxy. Remind that our approach is based upon a space-for-time substitution method.

Average diameter of the largest white-popinac trees

This variable is also a proxy of time-advance of invasion. We assumed that the largest (largest = greater dbh) white-popinac trees within a patch can be used as models to indirectly express age. The largest trees in a patch are necessarily the oldest ones because (i) the average lifespan of a white-popinac individual is 20-40 years (GISD, 2015) and (ii) all of our patches are younger than 18 years (considering our age-proxy approach with Goggle Earth Imagery). Therefore, we can assume that there was not enough time for a complete cycling of individuals in a patch.

We used the same measurements as the ones for basal area. The same data was used to calculate the average of largest trees, but with a second approach to include older trees. Walking into a white-popinac, we actively looked for the largest (greater dbh) individuals, even if they were not included within the plot, to guarantee that we had a representative sampling of older trees. For each path, we filtered the trees that were larger than the superior quantile (75%) in dbh, and estimated the average value, which we call "average diameter of the largest trees"- ADL.

Age proxy

We previously recorded the geographical coordinates of all patches using a Garmin eTrex®10 GPS, and used Google Earth Imagery to visualize the white-popinac patches (which are usually very distinctive on the landscape). We compared older images (from previous years) to current ones using the historical imagery tool, until we could visualize when the patch started to be seen on the imagery, and attribute a value in years. We were aware that we were not considering the exact period where the first propagules arrived or developed. Instead, the "age" variable actually represents how many years ago the white-popinac population structured itself in the sampling unit to the point it was recognizable on the satellite imagery.

Table 1 Spearman's correlation coefficients among our time-related predictor variables. ADL = Average diameter of the largest white-popinac trees.

	Age	**Basal area**
Basal area	0.53	-
ADL	0.55	0.61

Categorical grouping variables

When arranging the statistical models for selection, there were categorical grouping variables, which reflected distinct categories in the response variables. These categorical grouping variables were put in additive or interactive effect to a given time-advance variable (predictor variable). The categorical grouping variables used in the analysis were: "strata" (arboreal or herbaceous), "origin" (native or invasive), "dispersal" (animal or non-animal dispersed) and "habit" (tree/shrub; we did not have models for different growth habits in herbaceous stratum). We will detail each categorical grouping variable below. We clarify that for each categorical grouping variable related to species richness, we firstly grouped our species into each category and then proceeded to species richness estimation (see "Details on response variables") separately between the two categories.

Strata

We considered both strata separately (arboreal and herbaceous), by creating a categorical variable called “strata”, in additive effect to a given predictor variable. We proposed to consider both arboreal and herbaceous strata because we understand that, even though our region is essentially a forest vegetation (Seasonal Semideciduous Forest), herbaceous stratum can bring interesting and important responses that are often disregarded in this type of phytophysiognomie (Flory & Clay, 2010; Gilliam, 2007).

Origin

We also created a variable called “origin”, which groups the species into native and invasive. In this case, we established models with interaction between the “origin” variable and a time-related variable, once we expected that the effects of time-advance of invasion disrupt different responses between these two groups (native vs. IS). The classification was based upon IS databases (Invasive Species Compendium – CABI; Global Invasive Species Database – GISD; The Horus Institute for Environmental Conservation and Development). All species were checked in terms of native range and localities where they are reported as IS. If at least one of these databases reported the species as IS in our study region, it was considered as IS for our analysis.

Dispersal

Each species was classified as animal or non-animal dispersed, according to the concepts of Van der Pijl (1972). Most of the animal-dispersed species were cited in the Atlantic Frugivory Database (Bello et al., 2017). If some of our recorded species was not present in the database, but has fleshy fruits and relative taxa (i.e. species of the same genus) were present in the database, the species was considered as animal-dispersed as well. We did not consider *Megathyrsus maximus* (Jacq.) B.K. Simon & S.W.L. Jacobs as animal-dispersed because we understand that there is no sufficient evidence that birds feeding on *M. maximus* seed is something other than predation.

Habit (growth habit/form)

156 We only used this variable when analyzing arboreal stratum. We classified each species as tree or
157 shrub. We understand that this type of classification is a challenging task, especially in Atlantic Forest.
158 Therefore, our criteria were:

159 a) Shrub: species where adult individuals with dbh usually < 5 cm; ramification starting bellow
160 1.5 m; total plant height usually < 3 m (except for scandent shrubs, that can grow taller than
161 that, but with small dbh).
162 b) Tree: species where adult individuals with dbh usually > 5 cm; ramification starting above 1.5
163 m; total plant height usually > 3 m.

164

165 ***Floristic survey***

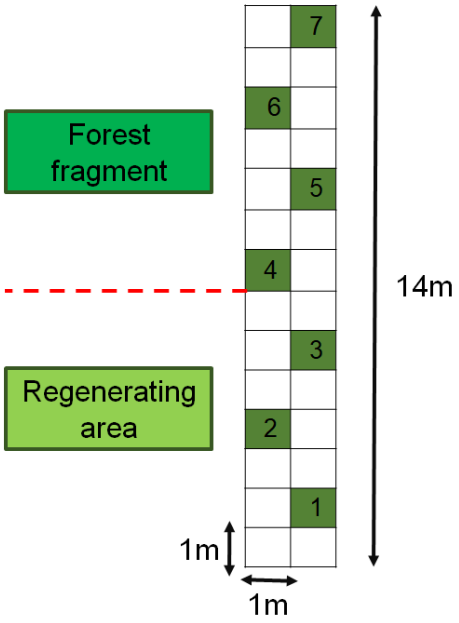
166 The floristic surveys conducted in each transect (Fig. 1B) were the main methodology to obtain
167 our response variables. The collected species were submitted to taxonomic evaluations, and the majority
168 of them were identified at species level. All transects were placed in the contact zone between the forest
169 fragment and its respective regenerating area, with 7 meters advancing towards each area. In some cases,
170 especially older-regenerating areas, the spatial delimitation from forest to regenerating area was not ex-
171 plicit. Inherently, the floristic survey provided material for an herbarium, which has been kept by the au-
172 thors and is available for consultations.

173

174 ***Herbaceous stratum***

175 For the herbaceous stratum, we divided the entire transect into 28 grids (1 m x 1 m). The sam-
176 pling procedure (Figure 2) consisted in choosing seven grids that were always in the same position. On
177 these seven grids, we recorded the ground cover percentage of each species. Notice that the abundance
178 metric is based into a percentage, instead of counting individuals, once it is often difficult to delimit an
179 individual for some species at this stratum. We considered as part of the grid all species that had vegeta-
180 tive parts comprised by the grid, even if they were not rooted there. We made this decision because
181 climbing species are often included by the grid's area, but are rooted somewhere else. We designed a
182 framework that could fit into our scenario of fragmented Seasonal Semideciduous Forest going through
183 natural regeneration, where we can find extensive ground cover by invasive grasses, many liana species

184 growing like herbs or shrubs (due to the low density of arboreal individuals), other invasive species be-
185 sides grasses and white-popinac, and scattered young trees and shrubs.
186



187

188 **Fig. 2** Diagram of transect division into grids. Among the 28 one-meter-square grids, we chose seven, fol-
189 lowing the same spatial arrangement as the figure: grid 1 was always the farthest to the forest fragment.
190 From 14 meters in length, 7 entered the forest fragment and 7 entered the regenerating area.
191

192 All species except moss and parasite species were identified. In other words, we identified herbs,
193 grasses, climbing plants (lianas and vines), and other types such as ferns and epiphytes. Moreover, we in-
194 cluded litter layer, white-popinac seedlings and overall seedlings (not white-popinac) as "species". Here,
195 it is important to stress that we considered all plant species that were growing bellow 1 meter height as
196 part of herbaceous strata. That means that climbing species found only on higher ranges, such as upper
197 canopy, were not included.
198 We visually estimated ground cover percentage of each species we found within a grid, as in
199 *relevé* approach (Braun-Blanquet, 1964). Within a grid, the sum of all species ground cover did not neces-
200 sarily equal to 100, once different plant heights can create "layers" of ground cover that prevent smaller
201 individuals to be recorded if just considering a single-frame vision.
202 Summarizing, we followed the sequence:

1- Delineated a transect;

2- Placed the 1 m^2 grid (made of PVC pipes) within the first sampling spot (grid 1, see figure 2);

3- Visually estimated the ground cover percentage (intervals of 10%) of each species found within the grid, and also litter and two classes of seedlings (overall ones and white-popinac ones);

4- Collected samples of species with uncertain identification or not yet identified on the survey;

5- Followed to grid number 2 (Figure 2) and redoing the previous steps;

6- Once all seven grids were sampled, then we moved to arboreal stratum sampling on the same transect.

Arboreal stratum

We considered as components of arboreal stratum all tree and shrub species within the transect area (14 m x 2 m). Distinctively from herbaceous stratum, we did not divide transects into subsamples. All individuals on the arboreal stratum were recorded and counted (including adult individuals of white-popinac, dbh > 2 cm, height > 1.7 m). In case of saplings - young individuals that are not considered seedlings anymore - they were counted as regular individuals. Abundance in this stratum referred to the number of individuals (absolute abundance) of each species. Individuals that were growing outside of transect but whose branches were entering the transect space were also included (Figure 3).

We surveyed the arboreal stratum after we finished the survey of herbaceous stratum because walking amid transects could potentially disturb the herbaceous stratum. After surveying the first transect, we followed to the second, at least 10 meters distant from the previous one. This distance among transects could be greater in larger areas, but never lower than that. This minimum distance of 10 meters was established because it was sufficient to avoid that the same individual was included in more than one transect, considering the fact that the trees on regenerating forests are small and do not have canopies wider than 10 m. We tried to place the transects in a way we could achieve a distance-gradient (from transect to white-popinac patch) within the regenerating area.

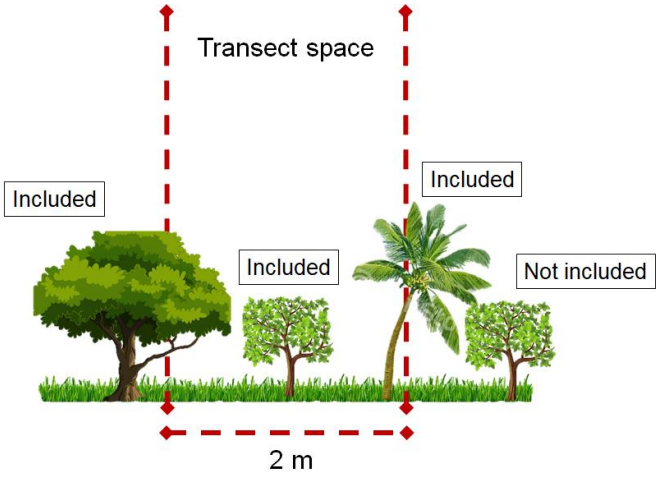


Fig. 3 Diagram representing the inclusion criterion of trees and shrubs regarding the transect area. If an individual was rooted outside but grows branches inside the transect, it was included. If it was totally inside, it was obviously included. In case it was rooted inside, but lens completely towards the outside, it was included as well. Therefore, the condition for not being included is if the individual was fully located outside the transect area.

Details on response variables

In the field, two types of variables were measured: (i) observed species richness, which accounts the total number of species within transects; and (ii) abundance, described by two distinct measures: number of individuals (for arboreal stratum) and ground-cover percentage (for herbaceous stratum). We detail estimation methods and R-packages below, considering the two hierarchical scales of response variables: the regenerating areas diversity and the among-transects (within regenerating area; β-diversity) diversity.

Species richness and abundance

We understand that the observed richness is a variable intrinsically dependent of sample size (total abundance) and number of samples, and may not be the best one to be used for ecological analysis (Chao et al., 2014). Therefore, we used sample-coverage based methodology to estimate species richness that was developed by Chao and Jost (2012). This approach allows standardizing species richness-values

based in community completeness, instead of sample size or sample number. Completeness is described by sample-coverage, a value that ranges from zero to one and refers to the proportion of the total amount of individuals in a community (in our case, regenerating area) that were comprised by the sample.

Firstly, for both arboreal and herbaceous strata, we summed the abundances on the transects within the regenerating area, for each species. Therefore, each value of observed abundance on the regenerating area refers to the sum of the transects within it (Figure 4). For the herbaceous stratum, specifically, we initially calculated the average ground cover percentage for each species (average among the 7 grids within a transect), and then obtained the abundance value for the entire transect.

We estimated species richness by using iNext package (v3.0.0; Hsieh, Ma, and Chao 2016) on R-Studio software (v4.1.2; R Core Team 2022). We estimated species richness separately between arboreal and herbaceous strata, once their abundance was described with different metrics. The output also displays if the estimate was obtained via interpolation (rarefaction), extrapolation, or none (actual observed data) depending on whether the sampled size standardized by sample-coverage is less than, greater than or equal to the reference (observed) sample size.

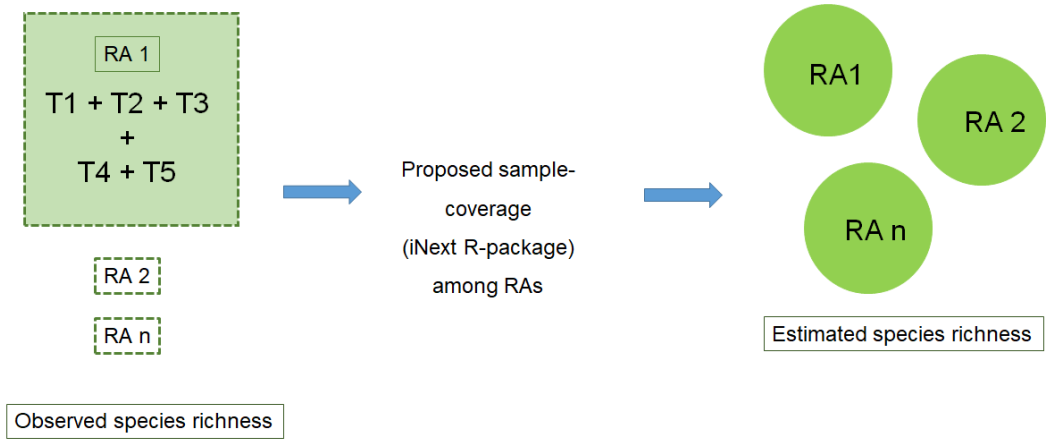


Fig. 4 Conceptual approach to species richness estimation on the regenerating area's scale. T1 to T5 represent transects within a given regenerating area. Using iNext R-package, we could standardize communities (regenerating areas) based on their completeness, instead of size.

Trait space

First, we obtained the Gower's distance matrix (Gower, 1966) between species and their multivariate set of traits using the *funct.dist* function of the MFD package (Magneville et al., 2022) on R-Studio software (v4.1.2; R Core Team 2022). We computed the multidimensional space of traits for plant species and used the function *quality.fspaces* to assess the quality of n-dimensional functional spaces derived from a Principal Coordinate Analysis (PCoA). We identified the optimal number of dimensions by selecting the lowest mean absolute deviation (MAD, Tabel 2, Figure 5), which served as a cutoff for retaining the PCoA axes as new trait variables (Magneville et al., 2022). The MAD index ranges from 0 to 1, with lower values indicating higher-quality functional spaces, where the distances between species pairs are more congruent with the initial functional distances (Maire et al., 2015). The first three PCoA axes (MAD = 0.057, Tabel 2, Figure 5), were retained for all traits and used to calculate both functional alpha and beta diversity indices.

Tab. 2 Quality index of functional spaces for 328 species in 131 communities (transects) assessed using the mean absolute deviation (MAD) and the root of mean squared deviation (RMSD) from one to ten dimensions. For each n-dimensional functional space resulting from a principal coordinates analysis, correlation between pairwise distances computed on species traits (Gower distance) and standardized (Euclidean) distance. Values in bold represent higher-quality functional space.

	MAD	RMSD
PCoA_1d	0.147	0.183
PCoA_2d	0.079	0.122
PCoA_3d	**0.057**	**0.087**
PCoA_4d	0.070	0.095
PCoA_5d	0.071	0.097
PCoA_6d	0.076	0.100
PCoA_7d	0.077	0.101
PCoA_8d	0.078	0.101
PCoA_9d	0.078	0.102
PCoA_10d	0.079	0.102

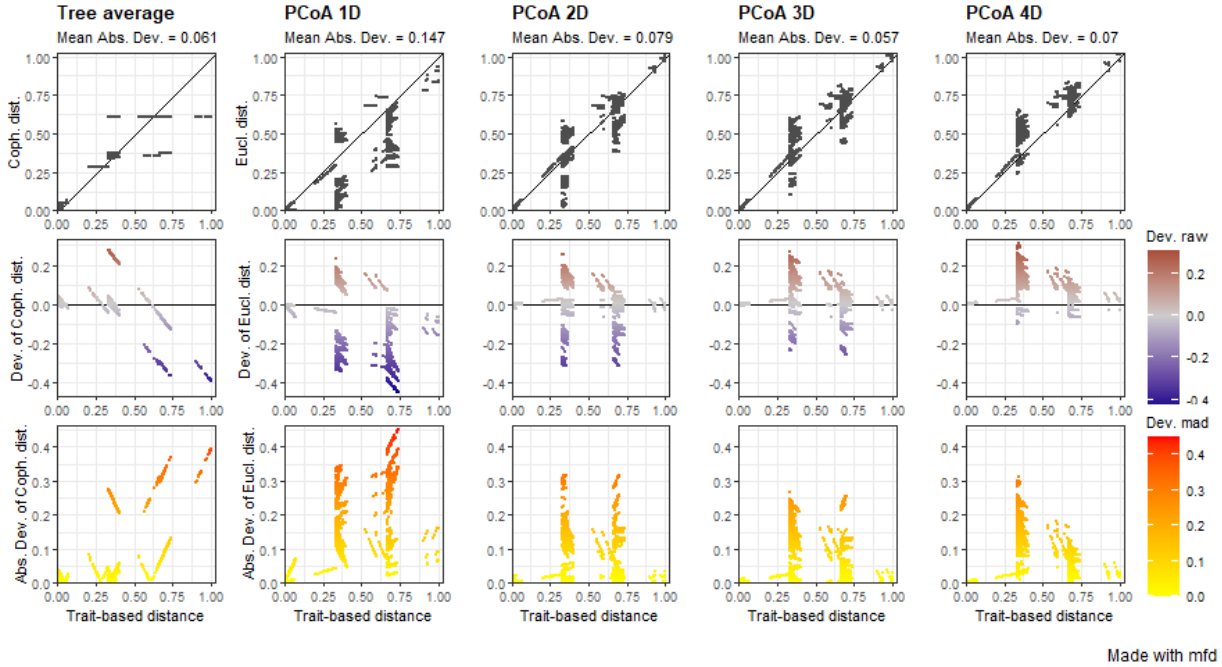


Fig. 5 Quality representation for four functional spaces for 328 species in 131 communities (transects) assessed using the mean absolute deviation (MAD) from one to ten dimensions. For each n-dimensional functional space resulting from a principal coordinates analysis, correlation between pairwise distances computed on species traits (Gower distance) and standardized (Euclidean) distance. The top row panel shows trait-based distance between species vs. space-based distance. The middle row panel shows trait-based distance vs. deviation between space-based and trait-based distances. The bottom row panel shows trait-based distance between species vs. transformed deviation used to compute the quality metric All plots have the same X axis.

Functional α-diversity

Based on the species abundances and the three PCoA axes extracted before, we calculated the functional α-metrics as follows:

1- Functional Richness (FRic): corresponds to the volume of the convex hull occupied by the species in the multidimensional functional space, as proposed by Cornwell et al. (2006) and Villéger et al. (2008). It was calculated as the hypervolume formed by the extreme points of the species on the selected axes of the PCoA, standardized by the maximum richness observed.

2- Functional Dispersion (FDis): measures the weighted average distance of the species to the functional centroid of the community (Laliberte & Legendre, 2010). The calculation considers relative abundances and is given by:

$$FDis = \frac{\sum a_j z_j}{\sum a_j}$$

where a_j is the abundance of species j and z_j is the distance of species j to the weighted centroid.

3- Functional Eveness (FEve): assesses the regularity in the distribution of abundances in the functional space. It is based on the minimum spanning tree (MST), which connects all species with the shortest possible total distance. The index is calculated as:

$$FEve = \frac{\sum_{l=1}^{S-1} min\left(PEW_l, \frac{1}{S-1}\right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}$$

where *PEW* is the partial weighted evenness, *l* is the branch of species involved in the minimum spanning tree, and *S* is the number of species.

4- Functional Mean Pairwise Distance (FMPD): represents the average functional distance between all pairs of species, weighted by their abundances:

$$FMPD = \frac{\sum_{i=1}^{S} \sum_{j>i}^{S} d_{i,j}}{S(S-1)/2}$$

where *S* is the species number, *ai* and *aj* are abundances, and *d* (**x***i*, **x***j*) is the functional distance between species *i and j*.

5- We tested Pearson's correlation among the observed alpha diversity indices setting a cutoff value of 0.70 or higher to identify correlations. No strong correlation between alpha functional diversity indices was found.

Functional β-diversity

Once again, based on three PCoA axes extracted before and the species occurrence (presence-absence), we calculated β-functional diversity through the functional modification of the Jaccard index proposed by Villéger et al. (2013). The method assesses the dissimilarity in functional composition between pairs of communities through the formula:

$$f\beta div = \frac{V(C1) + V(C2) - 2 \times V(C1 \cap C2)}{V(C1) + V(C2) - V(C1 \cap C2)}$$

where V is the volume of the convex hulls of each of the two communities C1 and C2.

We then estimated the median functional β-diversity among the transects (four of five) within each regenerating area, to obtain a single value of β-diversity for the entire regenerating area.

Details on model selection

For each response variable Y, we followed the sequence:

1- Standardized numeric predictor variables: all numeric predictor variables were standardized by using the "decostand" function in the "vegan" R-package (v2.6-4), with method = "total".

2- Chose predictor variables:

3- The number of competing models for a given response variable depended on predictor variables (numerical time-related or categorical-grouping) and distribution families.

4- Chose the distribution family:

(i) If the response variable was continuous (e.g., estimated species richness), we competed models with two different adjustments in terms of distribution: Gaussian (with identity link function) and Gamma (with log link function).

(ii) If it the response variable was discrete (e.g., abundance of trees), we used the Poisson distribution (with log link function).

(iii) In the case of proportions (e.g., α-functional metrics), we used the Beta distribution (logit link function).

5- We employed GLMs (Generalized Linear Models), using "glm" function, in the "stats" R-package (v4.2.2).

6- If our previous hypothesis included an interaction between the time-advance variable and some categorical grouping variable (i.e., strata, habit, origin or dispersal), we competed the interactive models

with additive "simpler" models as well. If the additive models were selected as among the best ones, we considered that maintaining the interaction is not justified. We only maintained the interaction if it was in at least one of the best ones.

7- Competed the models for each response variable:

(i) We used "compare_performance" function in the "performance" R-package (v0.10.1), which provides a series metrics to compare and evaluate models. The ranking was based upon AICc values (corrected Akaike Information Criterion).The lowest the AICc value, the better its predictive power (Aho et al., 2014; Burnham et al., 2011).

(ii) We considered as equally plausible models those which AICc value was less than two unities greater than the lowest one ($\Delta i < 2$). This metric is called Δi, being the difference between a given AICc value and the lowest AICc value found among the competing models (Δi = AICc – [min]AICc).

8- Considered R^2 values: we did not interpret models which R^2 values were too small (< ~ 0.10), i.e., we discarded the hypothesis that they represented.

9- Plotted equally plausible models: this step did not include models with interaction between time-related variables and the categorical grouping variable.

(i) For each response variable, we plotted the respective coefficient confidence intervals from all equally plausible models. We used the function "modelplot" from "modelsummary" R-package (v1.3.0). Each model was plotted separately.

(ii) After plotting, we checked all coefficient confidence intervals regarding its inclusion of zero. In case of including zero, it means that the relationship was not strong, once "no effect" (zero) is also within the probability range.

(iii) Among all equally plausible models, some of them might have variables whose coefficient confidence intervals included zero, whereas the other ones did not. In those cases, once they are considered as equally plausible, we chose the ones not including zero to be plotted at "Results" section. If none of them included zero, we chose the one with highest R^2 (or correlates) value to be plotted.

10- Final plots:

(i) Plots were made with "modelsummary" R-package (v1.3.0). In case of interaction, we used "interactions" R-package (v1.1.5).

Results

Diversity metrics

Tab. 3: Diversity metrics in each regenerating area. SR = Estimated species richness. IS = invasive species. CWM = Community weighted mean. Beta = functional beta diversity via Jaccard's dissimilarity index. FDis = functional dispersion. FEve = functional evenness. FMPD = functional mean pairwise distance. FRic = functional richness. NA values represent absent of that specific category (e.g. NA in IS seed mass means absence of invasive species)

Regenerating area	Stratum	Metric	Value
a	Arboreal	Animal dispersed SR	9.8
a	Arboreal	Non-animal dispersed SR	7.4
a	Herbaceous	Animal dispersed SR	3.5
a	Herbaceous	Non-animal dispersed SR	23.0
a	Arboreal	Shrub abundance	70.0
a	Arboreal	Tree abundance	39.0
a	Arboreal	Tree SR	21.6
a	Arboreal	Shrub SR	4.3
a	Arboreal	IS seed-mass (CWM)	47.2
a	Herbaceous	IS seed-mass (CWM)	8.5
a	Arboreal	Native seed-mass (CWM)	37.0
a	Herbaceous	Native seed-mass (CWM)	15.2
a	Both	Beta	0.414
a	Both	FDis	0.607
a	Both	FMPD	0.562
a	Both	FEve	0.311
a	Both	FRic	0.327
aa	Arboreal	Animal dispersed SR	15.3
aa	Arboreal	Non-animal dispersed SR	10.7
aa	Herbaceous	Animal dispersed SR	5.0

aa	Herbaceous	Non-animal dispersed SR	16.9
aa	Arboreal	Shrub abundance	68.0
aa	Arboreal	Tree abundance	56.0
aa	Arboreal	Tree SR	13.0
aa	Arboreal	Shrub SR	14.5
aa	Arboreal	IS seed-mass (CWM)	154.8
aa	Herbaceous	IS seed-mass (CWM)	2.2
aa	Arboreal	Native seed-mass (CWM)	136.2
aa	Herbaceous	Native seed-mass (CWM)	12.0
aa	Both	Beta	0.508
aa	Both	FDis	0.520
aa	Both	FMPD	0.548
aa	Both	FEve	0.243
aa	Both	FRic	0.332
bb	Arboreal	Animal dispersed SR	7.6
bb	Arboreal	Non-animal dispersed SR	6.2
bb	Herbaceous	Animal dispersed SR	1.1
bb	Herbaceous	Non-animal dispersed SR	8.1
bb	Arboreal	Shrub abundance	26.0
bb	Arboreal	Tree abundance	40.0
bb	Arboreal	Tree SR	7.8
bb	Arboreal	Shrub SR	7.4
bb	Arboreal	IS seed-mass (CWM)	NA
bb	Herbaceous	IS seed-mass (CWM)	NA
bb	Arboreal	Native seed-mass (CWM)	111.3
bb	Herbaceous	Native seed-mass (CWM)	18.6
bb	Both	Beta	0.610
bb	Both	FDis	0.727
bb	Both	FMPD	0.662
bb	Both	FEve	0.502
bb	Both	FRic	0.509

c	Arboreal	Animal dispersed SR	9.5
c	Arboreal	Non-animal dispersed SR	7.7
c	Herbaceous	Animal dispersed SR	1.7
c	Herbaceous	Non-animal dispersed SR	28.0
c	Arboreal	Shrub abundance	41.0
c	Arboreal	Tree abundance	58.0
c	Arboreal	Tree SR	13.6
c	Arboreal	Shrub SR	7.1
c	Arboreal	IS seed-mass (CWM)	53.1
c	Herbaceous	IS seed-mass (CWM)	2.2
c	Arboreal	Native seed-mass (CWM)	54.9
c	Herbaceous	Native seed-mass (CWM)	14.2
c	Both	Beta	0.571
c	Both	FDis	0.393
c	Both	FMPD	0.438
c	Both	FEve	0.210
c	Both	FRic	0.299
cc	Arboreal	Animal dispersed SR	4.2
cc	Arboreal	Non-animal dispersed SR	5.9
cc	Herbaceous	Animal dispersed SR	1.0
cc	Herbaceous	Non-animal dispersed SR	12.8
cc	Arboreal	Shrub abundance	6.0
cc	Arboreal	Tree abundance	49.0
cc	Arboreal	Tree SR	6.1
cc	Arboreal	Shrub SR	5.7
cc	Arboreal	IS seed-mass (CWM)	44.4
cc	Herbaceous	IS seed-mass (CWM)	6.5
cc	Arboreal	Native seed-mass (CWM)	197.1
cc	Herbaceous	Native seed-mass (CWM)	25.7
cc	Both	Beta	0.545
cc	Both	FDis	0.415

cc	Both	FMPD	0.420
cc	Both	FEve	0.319
cc	Both	FRic	0.160
dd	Arboreal	Animal dispersed SR	8.9
dd	Arboreal	Non-animal dispersed SR	2.7
dd	Herbaceous	Animal dispersed SR	1.6
dd	Herbaceous	Non-animal dispersed SR	9.0
dd	Arboreal	Shrub abundance	72.0
dd	Arboreal	Tree abundance	88.0
dd	Arboreal	Tree SR	11.6
dd	Arboreal	Shrub SR	4.6
dd	Arboreal	IS seed-mass (CWM)	69.4
dd	Herbaceous	IS seed-mass (CWM)	2.2
dd	Arboreal	Native seed-mass (CWM)	120.3
dd	Herbaceous	Native seed-mass (CWM)	49.1
dd	Both	Beta	0.736
dd	Both	FDis	0.633
dd	Both	FMPD	0.576
dd	Both	FEve	0.365
dd	Both	FRic	0.143
e	Arboreal	Animal dispersed SR	10.4
e	Arboreal	Non-animal dispersed SR	14.6
e	Herbaceous	Animal dispersed SR	2.5
e	Herbaceous	Non-animal dispersed SR	12.7
e	Arboreal	Shrub abundance	85.0
e	Arboreal	Tree abundance	89.0
e	Arboreal	Tree SR	21.8
e	Arboreal	Shrub SR	6.7
e	Arboreal	IS seed-mass (CWM)	244.7
e	Herbaceous	IS seed-mass (CWM)	1.6
e	Arboreal	Native seed-mass (CWM)	142.8

e	Herbaceous	Native seed-mass (CWM)	18.3
e	Both	Beta	0.643
e	Both	FDis	0.530
e	Both	FMPD	0.551
e	Both	FEve	0.308
e	Both	FRic	0.417
ee	Arboreal	Animal dispersed SR	27.9
ee	Arboreal	Non-animal dispersed SR	4.5
ee	Herbaceous	Animal dispersed SR	1.3
ee	Herbaceous	Non-animal dispersed SR	17.0
ee	Arboreal	Shrub abundance	41.0
ee	Arboreal	Tree abundance	55.0
ee	Arboreal	Tree SR	24.8
ee	Arboreal	Shrub SR	9.7
ee	Arboreal	IS seed-mass (CWM)	93.0
ee	Herbaceous	IS seed-mass (CWM)	1.0
ee	Arboreal	Native seed-mass (CWM)	144.2
ee	Herbaceous	Native seed-mass (CWM)	33.3
ee	Both	Beta	0.603
ee	Both	FDis	0.392
ee	Both	FMPD	0.526
ee	Both	FEve	0.211
ee	Both	FRic	0.200
f	Arboreal	Animal dispersed SR	7.8
f	Arboreal	Non-animal dispersed SR	9.7
f	Herbaceous	Animal dispersed SR	2.2
f	Herbaceous	Non-animal dispersed SR	20.1
f	Arboreal	Shrub abundance	19.0
f	Arboreal	Tree abundance	65.0
f	Arboreal	Tree SR	10.6
f	Arboreal	Shrub SR	8.1

f	Arboreal	IS seed-mass (CWM)	25.6
f	Herbaceous	IS seed-mass (CWM)	2.1
f	Arboreal	Native seed-mass (CWM)	138.8
f	Herbaceous	Native seed-mass (CWM)	6.2
f	Both	Beta	0.575
f	Both	FDis	0.325
f	Both	FMPD	0.462
f	Both	FEve	0.245
f	Both	FRic	0.166
g	Arboreal	Animal dispersed SR	17.9
g	Arboreal	Non-animal dispersed SR	9.9
g	Herbaceous	Animal dispersed SR	9.0
g	Herbaceous	Non-animal dispersed SR	28.1
g	Arboreal	Shrub abundance	58.0
g	Arboreal	Tree abundance	51.0
g	Arboreal	Tree SR	20.6
g	Arboreal	Shrub SR	11.0
g	Arboreal	IS seed-mass (CWM)	43.0
g	Herbaceous	IS seed-mass (CWM)	2.9
g	Arboreal	Native seed-mass (CWM)	87.6
g	Herbaceous	Native seed-mass (CWM)	20.0
g	Both	Beta	0.734
g	Both	FDis	0.464
g	Both	FMPD	0.528
g	Both	FEve	0.298
g	Both	FRic	0.342
gg	Arboreal	Animal dispersed SR	14.8
gg	Arboreal	Non-animal dispersed SR	11.4
gg	Herbaceous	Animal dispersed SR	4.9
gg	Herbaceous	Non-animal dispersed SR	16.2
gg	Arboreal	Shrub abundance	103.0

gg	Arboreal	Tree abundance	73.0
gg	Arboreal	Tree SR	15.0
gg	Arboreal	Shrub SR	13.7
gg	Arboreal	IS seed-mass (CWM)	73.7
gg	Herbaceous	IS seed-mass (CWM)	5.6
gg	Arboreal	Native seed-mass (CWM)	64.8
gg	Herbaceous	Native seed-mass (CWM)	17.5
gg	Both	Beta	0.505
gg	Both	FDis	0.505
gg	Both	FMPD	0.561
gg	Both	FEve	0.276
gg	Both	FRic	0.642
h	Arboreal	Animal dispersed SR	15.0
h	Arboreal	Non-animal dispersed SR	11.2
h	Herbaceous	Animal dispersed SR	2.2
h	Herbaceous	Non-animal dispersed SR	21.7
h	Arboreal	Shrub abundance	45.0
h	Arboreal	Tree abundance	60.0
h	Arboreal	Tree SR	17.8
h	Arboreal	Shrub SR	8.9
h	Arboreal	IS seed-mass (CWM)	64.7
h	Herbaceous	IS seed-mass (CWM)	1.9
h	Arboreal	Native seed-mass (CWM)	101.2
h	Herbaceous	Native seed-mass (CWM)	6.7
h	Both	Beta	0.447
h	Both	FDis	0.391
h	Both	FMPD	0.472
h	Both	FEve	0.239
h	Both	FRic	0.524
ii	Arboreal	Animal dispersed SR	10.0
ii	Arboreal	Non-animal dispersed SR	5.4

ii	Herbaceous	Animal dispersed SR	NA
ii	Herbaceous	Non-animal dispersed SR	5.1
ii	Arboreal	Shrub abundance	27.0
ii	Arboreal	Tree abundance	73.0
ii	Arboreal	Tree SR	10.6
ii	Arboreal	Shrub SR	6.0
ii	Arboreal	IS seed-mass (CWM)	NA
ii	Herbaceous	IS seed-mass (CWM)	1.5
ii	Arboreal	Native seed-mass (CWM)	59.9
ii	Herbaceous	Native seed-mass (CWM)	18.4
ii	Both	Beta	0.649
ii	Both	FDis	0.304
ii	Both	FMPD	0.553
ii	Both	FEve	0.207
ii	Both	FRic	0.160
j	Arboreal	Animal dispersed SR	14.0
j	Arboreal	Non-animal dispersed SR	6.8
j	Herbaceous	Animal dispersed SR	NA
j	Herbaceous	Non-animal dispersed SR	11.8
j	Arboreal	Shrub abundance	40.0
j	Arboreal	Tree abundance	41.0
j	Arboreal	Tree SR	15.3
j	Arboreal	Shrub SR	10.7
j	Arboreal	IS seed-mass (CWM)	37.0
j	Herbaceous	IS seed-mass (CWM)	1.8
j	Arboreal	Native seed-mass (CWM)	33.7
j	Herbaceous	Native seed-mass (CWM)	4.6
j	Both	Beta	0.851
j	Both	FDis	0.317
j	Both	FMPD	0.484
j	Both	FEve	0.231

j	Both	FRic	0.228
jj	Arboreal	Animal dispersed SR	23.4
jj	Arboreal	Non-animal dispersed SR	17.5
jj	Herbaceous	Animal dispersed SR	2.0
jj	Herbaceous	Non-animal dispersed SR	20.0
jj	Arboreal	Shrub abundance	59.0
jj	Arboreal	Tree abundance	65.0
jj	Arboreal	Tree SR	38.1
jj	Arboreal	Shrub SR	13.3
jj	Arboreal	IS seed-mass (CWM)	44.4
jj	Herbaceous	IS seed-mass (CWM)	2.2
jj	Arboreal	Native seed-mass (CWM)	218.9
jj	Herbaceous	Native seed-mass (CWM)	19.8
jj	Both	Beta	0.245
jj	Both	FDis	0.376
jj	Both	FMPD	0.497
jj	Both	FEve	0.281
jj	Both	FRic	0.341
k	Arboreal	Animal dispersed SR	14.7
k	Arboreal	Non-animal dispersed SR	6.0
k	Herbaceous	Animal dispersed SR	1.1
k	Herbaceous	Non-animal dispersed SR	29.7
k	Arboreal	Shrub abundance	20.0
k	Arboreal	Tree abundance	67.0
k	Arboreal	Tree SR	13.2
k	Arboreal	Shrub SR	8.2
k	Arboreal	IS seed-mass (CWM)	45.9
k	Herbaceous	IS seed-mass (CWM)	1.5
k	Arboreal	Native seed-mass (CWM)	107.8
k	Herbaceous	Native seed-mass (CWM)	13.1
k	Both	Beta	0.478

k	Both	FDis	0.290
k	Both	FMPD	0.473
k	Both	FEve	0.289
k	Both	FRic	0.290
kk	Arboreal	Animal dispersed SR	13.4
kk	Arboreal	Non-animal dispersed SR	11.8
kk	Herbaceous	Animal dispersed SR	NA
kk	Herbaceous	Non-animal dispersed SR	15.9
kk	Arboreal	Shrub abundance	23.0
kk	Arboreal	Tree abundance	47.0
kk	Arboreal	Tree SR	21.9
kk	Arboreal	Shrub SR	7.4
kk	Arboreal	IS seed-mass (CWM)	5.2
kk	Herbaceous	IS seed-mass (CWM)	1.5
kk	Arboreal	Native seed-mass (CWM)	81.2
kk	Herbaceous	Native seed-mass (CWM)	7.7
kk	Both	Beta	0.262
kk	Both	FDis	0.406
kk	Both	FMPD	0.510
kk	Both	FEve	0.159
kk	Both	FRic	0.260
mm	Arboreal	Animal dispersed SR	7.7
mm	Arboreal	Non-animal dispersed SR	9.5
mm	Herbaceous	Animal dispersed SR	1.0
mm	Herbaceous	Non-animal dispersed SR	10.9
mm	Arboreal	Shrub abundance	34.0
mm	Arboreal	Tree abundance	51.0
mm	Arboreal	Tree SR	11.5
mm	Arboreal	Shrub SR	6.4
mm	Arboreal	IS seed-mass (CWM)	44.4
mm	Herbaceous	IS seed-mass (CWM)	1.0

mm	Arboreal	Native seed-mass (CWM)	65.4
mm	Herbaceous	Native seed-mass (CWM)	9.1
mm	Both	Beta	0.347
mm	Both	FDis	0.291
mm	Both	FMPD	0.446
mm	Both	FEve	0.248
mm	Both	FRic	0.089
n	Arboreal	Animal dispersed SR	15.1
n	Arboreal	Non-animal dispersed SR	8.2
n	Herbaceous	Animal dispersed SR	1.7
n	Herbaceous	Non-animal dispersed SR	20.0
n	Arboreal	Shrub abundance	59.0
n	Arboreal	Tree abundance	134.0
n	Arboreal	Tree SR	11.6
n	Arboreal	Shrub SR	9.6
n	Arboreal	IS seed-mass (CWM)	42.8
n	Herbaceous	IS seed-mass (CWM)	8.4
n	Arboreal	Native seed-mass (CWM)	152.2
n	Herbaceous	Native seed-mass (CWM)	19.8
n	Both	Beta	0.538
n	Both	FDis	0.535
n	Both	FMPD	0.513
n	Both	FEve	0.296
n	Both	FRic	0.413
nn	Arboreal	Animal dispersed SR	14.6
nn	Arboreal	Non-animal dispersed SR	6.5
nn	Herbaceous	Animal dispersed SR	1.6
nn	Herbaceous	Non-animal dispersed SR	7.9
nn	Arboreal	Shrub abundance	58.0
nn	Arboreal	Tree abundance	62.0
nn	Arboreal	Tree SR	14.7

nn	Arboreal	Shrub SR	7.5
nn	Arboreal	IS seed-mass (CWM)	37.1
nn	Herbaceous	IS seed-mass (CWM)	1.5
nn	Arboreal	Native seed-mass (CWM)	285.0
nn	Herbaceous	Native seed-mass (CWM)	24.7
nn	Both	Beta	0.917
nn	Both	FDis	0.533
nn	Both	FMPD	0.628
nn	Both	FEve	0.224
nn	Both	FRic	0.428
p	Arboreal	Animal dispersed SR	12.5
p	Arboreal	Non-animal dispersed SR	11.5
p	Herbaceous	Animal dispersed SR	4.2
p	Herbaceous	Non-animal dispersed SR	12.2
p	Arboreal	Shrub abundance	23.0
p	Arboreal	Tree abundance	37.0
p	Arboreal	Tree SR	9.4
p	Arboreal	Shrub SR	14.5
p	Arboreal	IS seed-mass (CWM)	22.3
p	Herbaceous	IS seed-mass (CWM)	2.1
p	Arboreal	Native seed-mass (CWM)	42.7
p	Herbaceous	Native seed-mass (CWM)	13.8
p	Both	Beta	0.531
p	Both	FDis	0.309
p	Both	FMPD	0.498
p	Both	FEve	0.291
p	Both	FRic	0.349
q	Arboreal	Animal dispersed SR	12.7
q	Arboreal	Non-animal dispersed SR	7.0
q	Herbaceous	Animal dispersed SR	1.5
q	Herbaceous	Non-animal dispersed SR	11.2

q	Arboreal	Shrub abundance	39.0
q	Arboreal	Tree abundance	84.0
q	Arboreal	Tree SR	14.2
q	Arboreal	Shrub SR	6.8
q	Arboreal	IS seed-mass (CWM)	132.7
q	Herbaceous	IS seed-mass (CWM)	5.2
q	Arboreal	Native seed-mass (CWM)	53.0
q	Herbaceous	Native seed-mass (CWM)	9.2
q	Both	Beta	0.531
q	Both	FDis	0.545
q	Both	FMPD	0.532
q	Both	FEve	0.268
q	Both	FRic	0.311
r	Arboreal	Animal dispersed SR	7.9
r	Arboreal	Non-animal dispersed SR	5.2
r	Herbaceous	Animal dispersed SR	1.8
r	Herbaceous	Non-animal dispersed SR	11.0
r	Arboreal	Shrub abundance	39.0
r	Arboreal	Tree abundance	28.0
r	Arboreal	Tree SR	15.5
r	Arboreal	Shrub SR	3.6
r	Arboreal	IS seed-mass (CWM)	36.6
r	Herbaceous	IS seed-mass (CWM)	3.0
r	Arboreal	Native seed-mass (CWM)	83.4
r	Herbaceous	Native seed-mass (CWM)	33.0
r	Both	Beta	0.470
r	Both	FDis	0.620
r	Both	FMPD	0.599
r	Both	FEve	0.417
r	Both	FRic	0.294
s	Arboreal	Animal dispersed SR	15.1

s	Arboreal	Non-animal dispersed SR	10.0
s	Herbaceous	Animal dispersed SR	2.7
s	Herbaceous	Non-animal dispersed SR	19.5
s	Arboreal	Shrub abundance	25.0
s	Arboreal	Tree abundance	33.0
s	Arboreal	Tree SR	20.1
s	Arboreal	Shrub SR	8.4
s	Arboreal	IS seed-mass (CWM)	252.2
s	Herbaceous	IS seed-mass (CWM)	5.6
s	Arboreal	Native seed-mass (CWM)	54.2
s	Herbaceous	Native seed-mass (CWM)	8.8
s	Both	Beta	0.593
s	Both	FDis	0.374
s	Both	FMPD	0.508
s	Both	FEve	0.204
s	Both	FRic	0.295
t	Arboreal	Animal dispersed SR	17.6
t	Arboreal	Non-animal dispersed SR	11.5
t	Herbaceous	Animal dispersed SR	2.4
t	Herbaceous	Non-animal dispersed SR	21.1
t	Arboreal	Shrub abundance	73.0
t	Arboreal	Tree abundance	49.0
t	Arboreal	Tree SR	19.7
t	Arboreal	Shrub SR	11.1
t	Arboreal	IS seed-mass (CWM)	24.8
t	Herbaceous	IS seed-mass (CWM)	1.9
t	Arboreal	Native seed-mass (CWM)	102.0
t	Herbaceous	Native seed-mass (CWM)	11.4
t	Both	Beta	0.236
t	Both	FDis	0.565
t	Both	FMPD	0.555

t	Both	FEve	0.254
t	Both	FRic	0.588
v	Arboreal	Animal dispersed SR	19.9
v	Arboreal	Non-animal dispersed SR	12.8
v	Herbaceous	Animal dispersed SR	4.1
v	Herbaceous	Non-animal dispersed SR	15.8
v	Arboreal	Shrub abundance	39.0
v	Arboreal	Tree abundance	58.0
v	Arboreal	Tree SR	28.8
v	Arboreal	Shrub SR	9.7
v	Arboreal	IS seed-mass (CWM)	61.2
v	Herbaceous	IS seed-mass (CWM)	1.6
v	Arboreal	Native seed-mass (CWM)	129.2
v	Herbaceous	Native seed-mass (CWM)	31.5
v	Both	Beta	0.492
v	Both	FDis	0.545
v	Both	FMPD	0.555
v	Both	FEve	0.327
v	Both	FRic	0.484
x	Arboreal	Animal dispersed SR	15.5
x	Arboreal	Non-animal dispersed SR	8.8
x	Herbaceous	Animal dispersed SR	3.6
x	Herbaceous	Non-animal dispersed SR	11.5
x	Arboreal	Shrub abundance	71.0
x	Arboreal	Tree abundance	86.0
x	Arboreal	Tree SR	17.4
x	Arboreal	Shrub SR	9.0
x	Arboreal	IS seed-mass (CWM)	168.5
x	Herbaceous	IS seed-mass (CWM)	1.7
x	Arboreal	Native seed-mass (CWM)	101.0
x	Herbaceous	Native seed-mass (CWM)	22.4

x	Both	Beta	0.472
x	Both	FDis	0.534
x	Both	FMPD	0.556
x	Both	FEve	0.275
x	Both	FRic	0.397
y	Arboreal	Animal dispersed SR	11.6
y	Arboreal	Non-animal dispersed SR	9.2
y	Herbaceous	Animal dispersed SR	1.7
y	Herbaceous	Non-animal dispersed SR	11.4
y	Arboreal	Shrub abundance	26.0
y	Arboreal	Tree abundance	66.0
y	Arboreal	Tree SR	18.6
y	Arboreal	Shrub SR	5.5
y	Arboreal	IS seed-mass (CWM)	85.8
y	Herbaceous	IS seed-mass (CWM)	1.6
y	Arboreal	Native seed-mass (CWM)	68.5
y	Herbaceous	Native seed-mass (CWM)	17.8
y	Both	Beta	0.346
y	Both	FDis	0.505
y	Both	FMPD	0.558
y	Both	FEve	0.251
y	Both	FRic	0.308
z	Arboreal	Animal dispersed SR	17.4
z	Arboreal	Non-animal dispersed SR	7.6
z	Herbaceous	Animal dispersed SR	1.3
z	Herbaceous	Non-animal dispersed SR	6.7
z	Arboreal	Shrub abundance	23.0
z	Arboreal	Tree abundance	54.0
z	Arboreal	Tree SR	9.3
z	Arboreal	Shrub SR	8.7
z	Arboreal	IS seed-mass (CWM)	44.4

z	Herbaceous	IS seed-mass (CWM)	1.5
z	Arboreal	Native seed-mass (CWM)	138.7
z	Herbaceous	Native seed-mass (CWM)	10.7
z	Both	Beta	0.975
z	Both	FDis	0.317
z	Both	FMPD	0.496
z	Both	FEve	0.257
z	Both	FRic	0.178

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394 **Model selection**

395 **Tab. 4:** Model selection statistics for all competing models. AICc refers to the corrected Akaike Infor-
396 mation Criterion (AIC). Δi refers to the difference between a given AICc value and the lowest among
397 competing models. AICc (W) refers to AICc "weight", being interpreted as the model's relative likeli-
398 hood. (*) Models fitted with Poisson and Beta distributions are with pseudo-R^2 values, whereas models
399 fitted with Gamma distribution are associated with Nagelkerke R^2, which are mathematically different
400 from a regular R^2, but may be interpreted in a similar way. ADL = Average-diameter (dbh - cm) of largest
401 white-popinac trees within a metacommunity (region); A = white-popinac patch's age-proxy (years); BA
402 = white-popinac patch's basal area (m^2). S = strata (herbaceous and arboreal); Disp = dispersal type (ani-
403 mal and non-animal); Hab = growth habit (tree and shrub). Null models have y ~ 1 structure.

Model structure	Distribution	AICc	AICc (W)	Δi	R^2*
Estimated species richness (animal and non-animal dispersed species)					
ADL + Disp + S	Gamma	722.301	0.285	0	0.191
BA + Disp + S	Gamma	722.477	0.261	0.177	0.189
AP + Disp + S	Gamma	723.777	0.136	1.476	0.178
ADL * Disp + S	Gamma	724.049	0.119	1.749	0.195
BA * Disp + S	Gamma	724.333	0.103	2.032	0.192
AP * Disp + S	Gamma	724.467	0.096	2.166	0.191
Null model 1	Gamma	736.007	0	13.707	0
ADL + Disp + S	Gaussian	746.222	0	23.922	0.119
BA + Disp + S	Gaussian	746.745	0	24.444	0.115
AP + Disp + S	Gaussian	747.932	0	25.631	0.105

ADL * Disp + S	Gaussian	748.13		0	25.83	0.121
BA * Disp + S	Gaussian	748.271		0	25.971	0.12
AP * Disp + S	Gaussian	748.82		0	26.52	0.116
Null model 2	Gaussian	754.075		0	31.775	0
Abundance (trees and shrubs)						
BA * Hab	Poisson	828.51	0.987		0	0.845
BA + Hab	Poisson	837.221	0.013		8.711	0.813
ADL * Hab	Poisson	866.99		0	38.48	0.7
ADL + Hab	Poisson	867.198		0	38.688	0.686
AP * Hab	Poisson	867.933		0	39.423	0.695
AP + Hab	Poisson	868.573		0	40.063	0.679
Null model	Poisson	930.092		0	101.582	0
Estimated species richness (trees and shrubs)						
BA + Hab	Gamma	335.471	0.356		0	0.48
AP + Hab	Gamma	336.409	0.222		0.938	0.471
ADL + Hab	Gamma	336.943	0.17		1.473	0.466
BA * Hab	Gamma	337.679	0.118		2.208	0.481
AP * Hab	Gamma	338.397	0.082		2.926	0.475
ADL * Hab	Gamma	339.335	0.051		3.865	0.466
BA + Hab	Gaussian	361.935		0	26.464	0.378
AP + Hab	Gaussian	362.63		0	27.159	0.371
ADL + Hab	Gaussian	362.699		0	27.229	0.37
BA * Hab	Gaussian	364.334		0	28.863	0.378
AP * Hab	Gaussian	364.983		0	29.512	0.371
ADL * Hab	Gaussian	364.992		0	29.522	0.371
Null model 1	Gamma	366.65		0	31.18	0
Null model 2	Gaussian	384.941		0	49.471	0
Seed mass (CWM) of invasive species						
BA + S	Gamma	388.393	0.78		0	0.948
AP + S	Gamma	391.451	0.169		3.058	0.945
ADL + S	Gamma	393.86	0.051		5.467	0.942
Null model 1	Gamma	494.508		0	106.115	0
BA + S	Gaussian	577.58		0	189.187	0.426
AP + S	Gaussian	579.382		0	190.989	0.407
ADL + S	Gaussian	579.754		0	191.361	0.403
Null model 2	Gaussian	603.575		0	215.182	0
Seed mass (CWM) of native species						

AP + S	Gamma	518.589	0.791		0	0.83
BA + S	Gamma	522.417	0.117		3.827	0.817
ADL + S	Gamma	522.886	0.092		4.297	0.815
Null model 1	Gamma	599.899		0	81.31	0
AP + S	Gaussian	600.145		0	81.555	0.57
BA + S	Gaussian	601.906		0	83.317	0.557
ADL + S	Gaussian	602.095		0	83.506	0.555
Null model 2	Gaussian	644.535		0	125.946	0
Functional beta diversity						
AP	Beta	-11.216	0.461		0	0.106
Null model	Beta	-10.068	0.26		1.148	NA
BA	Beta	-9.041	0.156		2.175	0.044
ADL	Beta	-8.577	0.123		2.639	0.03
FDis						
BA	Beta	-39.81	0.467		0	0.125
Null model	Beta	-38.459	0.238		1.35	NA
ADL	Beta	-38.074	0.196		1.735	0.071
AP	Beta	-36.691	0.098		3.118	0.025
FEve						
Null model	Beta	-72.822	0.451		0	NA
BA	Beta	-71.624	0.248		1.198	0.048
AP	Beta	-70.626	0.151		2.196	0.011
ADL	Beta	-70.62	0.15		2.202	0.011
FRic						
Null model	Beta	-31.515	0.383		0	NA
ADL	Beta	-31.148	0.319		0.367	0.072
AP	Beta	-29.77	0.16		1.745	0.027
BA	Beta	-29.482	0.139		2.033	0.016
FMPD						
Null model	Beta	-82.312	0.449		0	NA
ADL	Beta	-81.403	0.285		0.909	0.053
AP	Beta	-79.888	0.134		2.424	0.003
BA	Beta	-79.875	0.133		2.437	0.002

407 **List of recorded species**

408 **Tab. 5** All species (native and IS) recorded in our floristic survey. Species tagged with (*) are IS.

Species		**Family**
Acalypha velamea	Baill.	Euphorbiaceae
Acanthocladus brasiliensis	(A.St.-Hil. & Moq.) Klotzsch ex Hassk.	Polygalaceae
Actinostemon klotzschii	(Didr.) Pax	Euphorbiaceae
Adenocalymma bracteatum	(Cham.) DC.	Bignoniaceae
Albizia polycephala	(Benth.) Killip ex Record	Fabaceae
Alchornea glandulosa	Poepp. & Endl.	Euphorbiaceae
Alchornea sidifolia	Müll.Arg.	Euphorbiaceae
Allophylus edulis	(A.St.-Hil. et al.) Hieron. ex Niederl.	Sapindaceae
Aloysia virgata	(Ruiz & Pav.) Juss.	Verbenaceae
Alternanthera brasiliana	(L.) Kuntze	Amaranthaceae
Alternanthera philoxeroides	(Mart.) Griseb.	Amaranthaceae
Ambrosia polystachya	DC.	Asteraceae
Anadenanthera colubrina	(Vell.) Brenan	Fabaceae
Anemia phyllitidis	(L.) Sw.	Anemiaceae
Annona dolabripetala	Raddi	Annonaceae
Aristolochia labiata	Willd.	Aristolochiaceae
Aristolochia triangularis	Cham. & Schltdl.	Aristolochiaceae
Asclepias curassavica	L.	Apocynaceae
Aspilia pascalioides	Griseb.	Asteraceae
Astronium graveolens	Jacq.	Anacardiaceae
Baccharis dracunculifolia	DC.	Asteraceae
Baccharis trinervis	Pers.	Asteraceae
Banisteriopsis muricata	(Cav.) Cuatrec.	Malpighiaceae

Banisteriopsis nummifera	(A.Juss.) B.Gates	Malpighiaceae
Banisteriopsis sp	-	Malpighiaceae
Banisteriopsis stellaris	(Griseb.) B.Gates	Malpighiaceae
Bastardiopsis densiflora	(Hook. & Arn.) Hassl.	Malvaceae
Bauhinia forficata	Link	Fabaceae
Bauhinia longifolia	(Bong.) Steud.	Fabaceae
Bauhinia ungulata	L.	Fabaceae
Bernardia pulchella	(Baill.) Müll.Arg.	Euphorbiaceae
Bidens pilosa	L.	Asteraceae
Bidens subalternans	DC.	Asteraceae
Blechnum occidentale	L.	Blechnaceae
Boehmeria caudata	Sw.	Urticaceae
Boehmeria nivea *	(L.) Gaudich.	Urticaceae
Buddleja stachyoides	Cham. & Schltdl.	Scrophulariaceae
Calliandra foliolosa	Benth.	Fabaceae
Callisia monandra	(Sw.) Schult.f.	Commelinaceae
Callisthene fasciculata	Mart.	Vochysiaceae
Campomanesia guaviroba	(DC.) Kiaersk.	Myrtaceae
Campomanesia sp	-	Myrtaceae
Capsicum baccatum	L.	Solanaceae
Cardiospermum grandiflorum	Sw.	Sapindaceae
Cardiospermum halicacabum	L.	Sapindaceae
Casearia decandra	Jacq.	Salicaceae
Casearia gossypiosperma	Briq.	Salicaceae
Casearia sylvestris	Sw.	Salicaceae
Cecropia pachystachya	Trécul	Urticaceae
Cedrela fissilis	Vell.	Meliaceae
Ceiba speciosa	(A.St.-Hil.) Ravenna	Malvaceae

Celtis iguanaea	(Jacq.) Sarg.	Cannabaceae
Cereus hildmannianus	K.Schum.	Cactaceae
Cestrum mariquitense	Kunth	Solanaceae
Chamaecrista nictitans	(L.) Moench	Fabaceae
Chaptalia integerrima	(Vell.) Burkart	Asteraceae
Chaptalia nutans	(L.) Pol.	Asteraceae
Chionanthus filiformis	(Vell.) P.S.Green	Oleaceae
Christella dentata *	(Forssk.) Brownsey & Jermy	Thelypteridaceae
Chromolaena laevigata	(Lam.) R.M.King & H.Rob.	Asteraceae
Chromolaena maximiliani	(Schrad. ex DC.) R.M.King & H.Rob.	Asteraceae
Chromolaena odorata	(L.) R.M.King & H.Rob.	Asteraceae
Chromolaena squalida	(DC.) R.M.King & H.Rob.	Asteraceae
Chrysophyllum marginatum	(Hook. & Arn.) Radlk.	Sapotaceae
Cissampelos glaberrima	A.St.-Hil.	Menispermaceae
Cissus verticillata	(L.) Nicolson & C.E.Jarvis	Vitaceae
Citharexylum myrianthum	Cham.	Verbenaceae
Citrus x limonia *	Osbeck (pro. sp.)	Rutaceae
Commelina benghalensis *	L.	Commelinaceae
Commelina diffusa	Burm.f.	Commelinaceae
Commelina erecta	L.	Commelinaceae
Condylocarpum isthmicum	(Vell.) A.DC.	Apocynaceae
Copaifera langsdorffii	Desf.	Fabaceae
Cordia africana *	Lam.	Boraginaceae
Cordia americana	(L.) Gottschling & J.S.Mill.	Boraginaceae
Cordia superba	Cham.	Boraginaceae
Cordia trichotoma	(Vell.) Arráb. ex Steud.	Boraginaceae
Cordyline spectabilis	Kunth & Bouché	Asparagaceae

Coutarea hexandra	(Jacq.) K.Schum.	Rubiaceae
Critonia megaphylla	(Baker) R.M.King & H.Rob.	Asteraceae
Crotalaria incana	L.	Fabaceae
Croton floribundus	Spreng.	Euphorbiaceae
Croton urucurana	Baill.	Euphorbiaceae
Ctenodon elegans	(Schltdl. & Cham.) D.B.O.S.Cardoso & A.Delgado	Fabaceae
Cupania vernalis	Cambess.	Sapindaceae
Cuphea carthagenensis	(Jacq.) J.F.Macbr.	Lythraceae
Cyperus aggregatus	(Willd.) Endl.	Cyperaceae
Cyperus difformis *	L.	Cyperaceae
Cyperus esculentus *	L.	Cyperaceae
Cyperus lanceolatus	Poir.	Cyperaceae
Cyperus laxus	Lam.	Cyperaceae
Cyperus surinamensis	Rottb.	Cyperaceae
Cyrtocymura scorpioides	(Lam.) H.Rob.	Asteraceae
Dahlstedtia muehlbergiana	(Hassl.) M.J.Silva & A.M.G.Azevedo	Fabaceae
Dalbergia frutescens	(Vell.) Britton	Fabaceae
Dalechampia triphylla	Lam.	Euphorbiaceae
Dasyphyllum vagans	(Gardner) Cabrera	Asteraceae
Dendropanax cuneatus	(DC.) Decne. & Planch.	Araliaceae
Desmodium incanum	(Sw.) DC.	Fabaceae
Desmodium tortuosum	(Sw.) DC.	Fabaceae
Diatenopteryx sorbifolia	Radlk.	Sapindaceae
Dicella bracteosa	(A.Juss.) Griseb.	Malpighiaceae
Dichondra macrocalyx	Meisn.	Convolvulaceae
Dicksonia sellowiana	Hook.	Dicksoniaceae

Dioscorea multiflora	Mart. ex Griseb.	Dioscoreaceae
Dioscorea piperifolia	Humb. & Bonpl. ex Willd.	Dioscoreaceae
Distimake aegyptius	(L.) A.R. Simões & Staples	Convolvulaceae
Distimake dissectus	(Jacq.) A.R. Simões & Staples	Convolvulaceae
Distimake macrocalyx	(Ruiz & Pav.) A.R. Simões & Staples	Convolvulaceae
Dolichandra unguis-cati	(L.) L.G.Lohmann	Bignoniaceae
Elephantopus mollis	Kunth	Asteraceae
Emilia fosbergii *	Nicolson	Asteraceae
Endlicheria paniculata	(Spreng.) J.F.Macbr.	Lauraceae
Enterolobium contortisiliquum	(Vell.) Morong	Fabaceae
Erythrina speciosa	Andrews	Fabaceae
Erythroxylum deciduum	A.St.-Hil.	Erythroxylaceae
Erythroxylum pelleterianum	A.St.-Hil.	Erythroxylaceae
Esenbeckia febrifuga	(A.St.-Hil.) A. Juss. ex Mart.	Rutaceae
Eugenia uniflora	L.	Myrtaceae
Euphorbia comosa	Vell.	Euphorbiaceae
Ficus guaranitica	Chodat	Moraceae
Fimbristylis autumnalis	(L.) Roem. & Schult.	Cyperaceae
Fridericia chica	(Bonpl.) L.G.Lohmann	Bignoniaceae
Fridericia samydoides	(Cham.) L.G.Lohmann	Bignoniaceae
Garcinia gardneriana	(Planch. & Triana) Zappi	Clusiaceae
Gouania sp	-	Rhamnaceae
Gouania ulmifolia	Hook. & Arn.	Rhamnaceae
Guadua angustifolia *	Kunth	Poaceae
Guarea guidonia	(L.) Sleumer	Meliaceae
Guarea macrophylla	Vahl	Meliaceae
Guazuma ulmifolia	Lam.	Malvaceae

Gymnanthes klotzschiana	Müll.Arg.	Euphorbiaceae
Handroanthus impetiginosus	(Mart. ex DC.) Mattos	Bignoniaceae
Handroanthus umbellatus	(Sond.) Mattos	Bignoniaceae
Heliotropium transalpinum	Vell.	Boraginaceae
Heterocondylus alatus	(Vell.) R.M.King & H.Rob.	Asteraceae
Heteropterys argyrophaea	A.Juss.	Malpighiaceae
Heteropterys sp	-	Malpighiaceae
Hildaea pallens	(Sw.) C.Silva & R.P.Oliveira	Poaceae
Hydrocotyle leucocephala	Cham. & Schltdl.	Araliaceae
Hyptis sp	-	Lamiaceae
Inga edulis	Mart.	Fabaceae
Iochroma arborescens	(L.) J.M.H. Shaw	Solanaceae
Ipomoea bonariensis	Hook.	Convolvulaceae
Ipomoea cairica *	(L.) Sweet	Convolvulaceae
Ipomoea nil	(L.) Roth	Convolvulaceae
Ipomoea saopaulista	O'Donell	Convolvulaceae
Iresine diffusa	Humb. & Bonpl. ex Willd.	Amaranthaceae
Jacaranda mimosifolia *	D. Don	Bignoniaceae
Jacquemontia heterantha	(Nees & Mart.) Hallier f.	Convolvulaceae
Justicia carnea	Lindl.	Acanthaceae
Lafoensia pacari	A.St.-Hil.	Lythraceae
Lantana camara	L.	Verbenaceae
Lantana trifolia	L.	Verbenaceae
Laportea aestuans	(L.) Chew	Urticaceae
Lasiacis ligulata	Hitchc. & Chase	Poaceae
Leandra sp	-	Melastomataceae
Leonotis nepetifolia *	(L.) R.Br.	Lamiaceae
Lepismium cruciforme	(Vell.) Miq.	Cactaceae

Lessingianthus glabratus	(Less.) H.Rob.	Asteraceae
Leucaena leucocephala *	(Lam.) de Wit	Fabaceae
Lippia origanoides	Kunth	Verbenaceae
Lithraea molleoides	(Vell.) Engl.	Anacardiaceae
Luehea divaricata	Mart.	Malvaceae
Machaerium brasiliense	Vogel	Fabaceae
Machaerium hirtum	(Vell.) Stellfeld	Fabaceae
Machaerium nyctitans	(Vell.) Benth.	Fabaceae
Machaerium stiptatum	Vogel	Fabaceae
Machaerium villosum	Vogel	Fabaceae
Matayba elaeagnoides	Radlk.	Sapindaceae
Megathyrsus maximus *	(Jacq.) B.K.Simon & S.W.L.Jacobs	Poaceae
Melia azedarach *	L.	Meliaceae
Melochia oyramidata	L.	Malvaceae
Melochia villosa	(Mill.) Fawc. & Rendle	Malvaceae
Mesosphaerum pectinatum *	(L.) Kuntze	Lamiaceae
Mesosphaerum sidifolium	(L'Hér.) Harley & J.F.B.Pastore	Lamiaceae
Miconia ligustroides	(DC.) Naudin	Melastomataceae
Miconia sp	-	Melastomataceae
Mikania cordifolia	(L.f.) Willd.	Asteraceae
Mikania glomerata	Spreng.	Asteraceae
Mimosa bimucronata	(DC.) Kuntze	Fabaceae
Mimosa caesalpiniifolia *	Benth.	Fabaceae
Mollinedia widgrenii	A.DC.	Monimiaceae
Momordica charantia *	L.	Cucurbitaceae
Monteverdia aquifolium	(Mart.) Biral	Celastraceae
Monteverdia gonoclada	(Mart.) Biral	Celastraceae
Moquilea tomentosa	Benth.	Chrysobalanaceae

Moquiniastrum polymorphum	(Less.) G. Sancho	Asteraceae
Muellera campestris	(Mart. ex Benth.) M.J. Silva & A.M.G. Azevedo	Fabaceae
Murraya paniculata *	(L.) Jack	Rutaceae
Myrcia neoclusiifolia	A.R.Lourenço & E.Lucas	Myrtaceae
Myrciaria floribunda	(H.West ex Willd.) O.Berg	Myrtaceae
Myroxylon peruiferum	L.f.	Fabaceae
Myrsine coriacea	(Sw.) R.Br. ex Roem. & Schult.	Primulaceae
Myrsine guianensis	(Aubl.) Kuntze	Primulaceae
Nectandra oppositifolia	Nees & Mart.	Lauraceae
Neonotonia wightii *	(Graham ex Wight & Arn.) J.A.Lackey	Fabaceae
Ocotea puberula	(Rich.) Nees	Lauraceae
Ocotea pulchella	(Nees & Mart.) Mez	Lauraceae
Ocotea velloziana	(Meisn.) Mez	Lauraceae
Oeceoclades maculata	(Lindl.) Lindl.	Orchidaceae
Olyra ciliatifolia	Raddi	Poaceae
Oplismenus hirtellus	(L.) P.Beauv.	Poaceae
Oxalis debilis	Kunth	Oxalidaceae
Oxalis triangularis	A.St.-Hil.	Oxalidaceae
Parapiptadenia rigida	(Benth.) Brenan	Fabaceae
Passiflora edulis	Sims	Passifloraceae
Passiflora suberosa	L.	Passifloraceae
Paullinia elegans	Cambess.	Sapindaceae
Paullinia rhomboidea	Radlk.	Sapindaceae
Pavonia communis	A.St.-Hil.	Malvaceae
Peltophorum dubium	(Spreng.) Taub.	Fabaceae
Pereskia grandifolia	Haw.	Cactaceae

Petrea volubilis	L.	Verbenaceae
Phyllanthus niruri	L.	Phyllanthaceae
Phyllanthus orbiculatus	Rich.	Phyllanthaceae
Piper aduncum	L.	Piperaceae
Piper amalago	L.	Piperaceae
Piper glabratum	Kunth	Piperaceae
Piptadenia gonoacantha	(Mart.) J.F.Macbr.	Fabaceae
Pityrogramma trifoliata	(L.) R.M.Tryon	Pteridaceae
Platypodium elegans	Vogel	Fabaceae
Plinia peruviana	(Poir.) Govaerts	Myrtaceae
Poecilanthe parviflora	Benth.	Fabaceae
Pombalia atropurpurea	(A.St.-Hil.) Paula-Souza	Violaceae
Porophyllum ruderale	(Jacq.) Cass.	Asteraceae
Portulaca oleracea	L.	Portulacaceae
Prunus myrtifolia	(L.) Urb.	Rosaceae
Psidium guajava *	L.	Myrtaceae
Psychotria carthagenensis	Jacq.	Rubiaceae
Pterocaulon lanatum	Kuntze	Asteraceae
Pterocaulon virgatum	(L.) DC.	Asteraceae
Pyrostegia venusta	(Ker Gawl.) Miers	Bignoniaceae
Randia armata	(Sw.) DC.	Rubiaceae
Rhamnidium elaeocarpum	Reissek	Rhamnaceae
Rhipsalis cereuscula	Haw.	Cactaceae
Rhynchosia phaseoloides	(Sw.) DC.	Fabaceae
Richardia brasiliensis	Gomes	Rubiaceae
Ricinus communis *	L.	Euphorbiaceae
Rubus urticifolius	Poir.	Rosaceae
Ruellia jussieuoides	Schltdl. & Cham.	Acanthaceae

Ruellia brevifolia	(Pohl) C.Ezcurra	Acanthaceae
Salvia guaranitica	A.St.-Hil. ex Benth.	Lamiaceae
Sapium glandulosum	(L.) Morong	Euphorbiaceae
Schaefferia argentinensis	Speg.	Celastraceae
Schinus terebinthifolia	Raddi	Anacardiaceae
Schizolobium parahyba	(Vell.) Blake	Fabaceae
Scleria gaertneri	Raddi	Cyperaceae
Sicyos edulis *	Jacq.	Cucurbitaceae
Seguieria langsdorffii	Moq.	Phytolaccaceae
Senegalia polyphylla	(DC.) Britton & Rose	Fabaceae
Senna multijuga	(Rich.) H.S.Irwin & Barneby	Fabaceae
Senna pendula	(Humb.& Bonpl.ex Willd.) H.S.Irwin & Barneby	Fabaceae
Senna pilifera	(Vogel) H.S.Irwin & Barneby	Fabaceae
Senna splendida	(Vogel) H.S.Irwin & Barneby	Fabaceae
Serjania fuscifolia	Radlk.	Sapindaceae
Serjania reticulata	Cambess.	Sapindaceae
Sida planicaulis	Cav.	Malvaceae
Sida rhombifolia	L.	Malvaceae
Sida urens	L.	Malvaceae
Sidastrum micranthum	(A.St.-Hil.) Fryxell	Malvaceae
Sidastrum paniculatum	(L.) Fryxell	Malvaceae
Siparuna guianensis	Aubl.	Siparunaceae
Smilax brasiliensis	Spreng.	Smilacaceae
Smilax elastica	Griseb.	Smilacaceae
Smilax fluminensis	Steud.	Smilacaceae
Solanum americanum	Mill.	Solanaceae
Solanum concinnum	Schott ex Sendtn.	Solanaceae

Solanum granulosoleprosum	Dunal	Solanaceae
Solanum palinacanthum	Dunal	Solanaceae
Solanum paniculatum	L.	Solanaceae
Solanum pseudoquina	A.St.-Hil.	Solanaceae
Solanum robustum	H.L.Wendl	Solanaceae
Solidago chilensis	Meyen	Asteraceae
Spathodea campanulata *	P. Beauv.	Fabaceae
Stizophyllum perforatum	(Cham.) Miers.	Bignoniaceae
Syagrus romanzoffiana	(Cham.) Glassman	Arecaceae
Symplocos pubescens	Klotzsch ex Benth.	Symplocaceae
Syzygium cumini *	(L.) Skeels	Myrtaceae
Tabernaemontana catharinensis	A.DC.	Apocynaceae
Talinum paniculatum	(Jacq.) Gaertn.	Talinaceae
Tapirira guianensis	Aubl.	Anacardiaceae
Tecoma stans *	(L.) Juss. ex Kunth	Bignoniaceae
Teramnus uncinatus	(L.) Sw.	Fabaceae
Terminalia glabrescens	Mart.	Combretaceae
Thalia geniculata	L.	Marantaceae
Thaumatophyllum bipinnatifidum	(Schott ex Endl.) Sakur., Calazans & Mayo	Araceae
Thunbergia alata *	Bojer ex Sims	Acanthaceae
Tilesia baccata	(L.) Pruski	Asteraceae
Tradescantia zebrina *	Heynh. ex Bosse	Commelinaceae
Trema micrantha	(L.) Blume	Cannabaceae
Trichilia catigua	A.Juss.	Meliaceae
Trichilia clausseni	C.DC.	Meliaceae
Trichilia elegans	A.Juss.	Meliaceae
Trichilia pallida	Sw.	Meliaceae

Triumfetta bartramia	L.	Malvaceae
Triumfetta semitriloba	Jacq.	Malvaceae
Urera baccifera	(L.) Gaudich. ex Wedd.	Urticaceae
Urochloa brizantha *	(Hochst. ex A.Rich.) R.D.Webster	Poaceae
Urvillea laevis	Radlk.	Sapindaceae
Varronia guazumifolia	Desv.	Boraginaceae
Vernonanthura polyanthes	(Sprengel) Vega & Dematteis	Asteraceae
Wissadula hernandioides	(L.Hér.) Garcke	Malvaceae
Xylosma venosa	N.E.Br.	Salicaceae
Zanthoxylum caribaeum	Lam.	Rutaceae
Zanthoxylum rhoifolium	Lam.	Rutaceae
Zanthoxylum riedelianum	Engl.	Rutaceae

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