Title: Regenerating tropical forests are consistently affected by biological invasions across spatial scales

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Abstract. Biological invasions are complex scale-dependent processes. Metacommunity ecology provides the means to understand the effects of invasive non-native species (INNS) because it explicitly considers how local and regional processes interact to drive the three main components of biodiversity: alpha, beta, and gamma. White-popinac (*Leucaena leucocephala* (Lam.) de Wit) is a widely distributed INNS in regenerating forests in the Atlantic Forest (Brazil). White-popinac invasions results in a particular spatial structure as the species forms dense and homogeneous patches, instead of spreading individuals throughout invaded areas. Here we took advantage of this unique spatial configuration formed by patches of native forest, regenerating areas, and patches of white-popinac to investigate how local and regional dynamics of plant (meta-)communities under natural regeneration are affected by white-popinac. We conducted replicated multi-strata surveys in 131 communities distributed among 29 metacommunities of regenerating forests that had different ages of white-popinac invasion. We found (i) mirrored responses among local and regional scales: at both scales, native species richness decreased with the increase of invasion age, whereas INNS richness increased; and (ii) β-diversity of native species decreased with the increase of invasion age, showing that time-advance of invasion led to a homogenizing effect. We also found evidence that the advance of white-popinac patches towards regenerating forests increases with time and proximity to the forest fragment, which likely had indirect effects on regenerating communities by reducing the size of the regenerating area. Our results indicate that the effects of white-popinac invasions on regenerating forests can be so vigorous that they propagate from the local to the regional scale, via a decrease in β-diversity. We reinforce the importance of considering multiscale approaches on assessing effects of white-popinac invasions.

Key words: alien species, metacommunities, natural regeneration, upscaling, biotic indirect effects, White-popinac.

Introduction

Biological invasions are the result of multiple processes operating at various spatial and temporal scales, from inter-continental (e.g., species introductions) to local (e.g., species establishment), and from diel (e.g., species interactions) to decennial (e.g., homogenization of landscapes) (Cadotte et al. 2006). Despite this being widely accepted and the emergence of conceptual frameworks that explicitly incorporate ecological processes at multiple scales (Patrick et al. 2021; Brown and Barney 2021), invasion biology is still predominantly focused on the role of local processes and effects (Powell, Chase, and Knight 2011). Understanding the local effects of biological invasions is still crucial, but this is only part of a more complicated puzzle – we must understand if and how local effects propagate to the regional scale. For example, do invasive non-native species (INNS) reduce the alpha, beta, and gamma facets of biodiversity? Investigating this is particularly important in the context of fragmented landscapes, where local and regional dynamics of invasion are determined by historical land use and species introductions, which comprise broad temporal and spatial scales (Didham et al. 2007; Gibson et al. 2013; Waddell et al. 2020).

Disentangling the effects of biological invasions on biodiversity in fragmented landscapes is a challenging task. For example, while in some contexts increasing the spatial connectivity among communities enhances INNS establishment (Chapman et al. 2020), in others it may also enhance community resistance to invasion (Cadotte 2006; Grainger and Gilbert 2016; Howeth 2017). Also, whereas β-diversity patterns explain why some fragmented plant communities go through an increase in species richness after invasion events (O'Sullivan et al. 2023), the opposite can also occur (see also Peng et al. 2019; Jauni and Hyvönen 2012; Fridley et al. 2007). To address these challenges, studies need to be based on hypotheses, sampling designs and variables that explicitly consider multiscale phenomena (Schiesari et al. 2019; Patrick et al. 2021). The propagation of effects across spatial scales due to biological invasions has rarely been reported, perhaps by an underuse of scale-explicit approaches, but also due to an apparent diminishment - or even inversion - of INNS effects at broader spatial scales, which has been cited as one of the components of the "invasion paradox" (Fridley et al. 2007).

The deforestation and fragmentation of the Atlantic Forest has historically been one of the most intense changes in landscape structure and biodiversity in Brazil (Rezende et al. 2018). Recent public policies have defined that private lands in Brazil must have a percentage of their area covered by natural vegetation (Brasil 2012; Rezende et al. 2018). As a consequence, portions of private lands that once were used as pasture and for agriculture have been abandoned so that natural regeneration could occur (César et al. 2018; Crouzeilles et al. 2020). However, regenerating forests in historically fragmented forested landscapes are highly susceptible to biological invasions (With 2004; Aguirre-Acosta et al. 2014; Zhang et al. 2021). For example, invasive grasses have invaded the majority of those areas in Brazil, where they occur abundantly at early regeneration stages (Zenni and Ziller 2011; Sobanski and Marques 2014; Zwiener et al. 2014). Although invasive grasses typically predominate, many other INNS are also often found in regenerating areas, from herbs (Dubbern et al. 2013; Chiba De Castro et al. 2019) to trees (Londe et al. 2017; CABI 2023).

Most INNS in regenerating forests can spread themselves across native communities. For example, the INNS *Melia azedarach* L. (China berry) has long-distance dispersal, and therefore is able to spread across invaded communities, with low-density but broad local distribution (Voigt et al. 2011; Bhatt et al. 2021). On the other hand, some INNS form dense and homogeneous agglomerations, with high-density of individuals and limited local distribution, usually due to distance-limited dispersal mechanisms (Portela et al. 2009; Chiba De Castro et al. 2019). One interesting example of species that forms dense monospecific patches is white-popinac (*Leucaena leucocephala* (Lam.) de Wit). White-popinac is a small tree native to Central America, that is broadly distributed in the Brazilian territory, occurring in open ecosystems like savannas and regenerating forest areas (Zenni and Ziller 2011).

In regenerating forests dominated by invasive grasses, the density of white-popinac patches can be so high that grasses and herbaceous species are forced towards the edges of the regenerating area (Hata, Suzuki, and Kachi 2010; Osawa, Hata, and Kachi 2016), due to reduction in sunlight incidence and known allelopathic effects (Kato-Noguchi and Kurniadie 2022). White-popinac can alter soil-nitrogen fixation and has been cited as a potential habitat transformer (Henderson 2001; CABI 2019), especially in regenerating forests (Yoshida and Oka 2000). White-popinac invasions are associated with a decrease in diversity of native species (GISD 2015; Machado 2018; CABI 2019), and an enhancement in community susceptibility to invasion by other INNS (Yoshida and Oka 2004).

Because of its short-distance seed dispersal, white-popinac usually forms dense and homogeneous patches, with larger individuals at the center (de Melo-Silva et al. 2014; Werema and Wilson 2022). Patches of white-popinac frequently occur in the surrounding of forest fragments, occupying part of the respective regenerating area (Marod et al. 2012; Wolfe and Van Bloem 2012). Here, we took advantage of this unique spatial configuration formed by patches of native forest, regenerating areas, and patches of white-popinac (Figure 1) to investigate how local and regional dynamics of plant (meta-)communities under natural regeneration are affected by white-popinac. More specifically, we analyzed the relationship between various aspects of white-popinac invasions and the local (alpha), regional (gamma) and among-sites (beta) diversity of naturally regenerating areas in the Brazilian Atlantic Forest. To do that, we set up a replicated sampling design that explicitly considered a local (131 communities) and regional scale (29 metacommunities). We expected that the temporal and spatial advance of white-popinac invasion would be associated with (i) a decrease in alpha and gamma diversity; (ii) an increase in the similarity of species composition within metacommunities (reduced beta-diversity); and (iii) an increase of white-popinac abundance in metacommunities and communities, dependent on the spatial distance between the regenerating forest and the white-popinac patch.

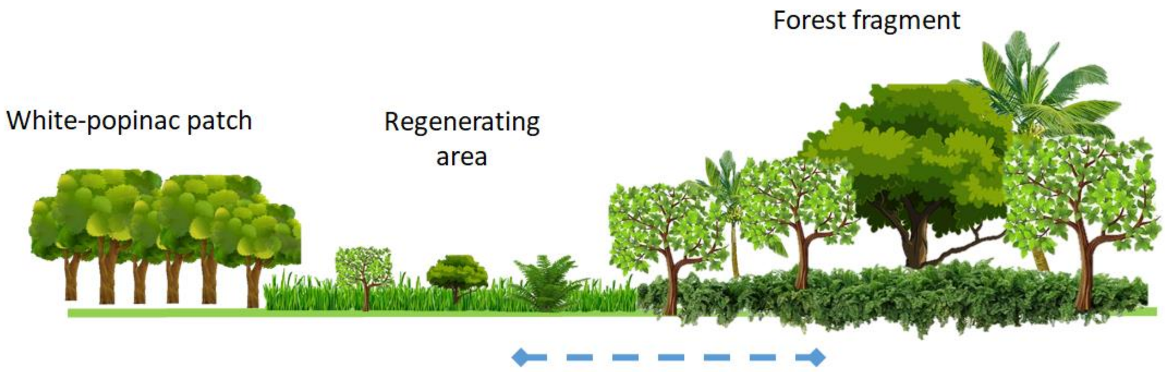

Fig. 1 Horizontal perspective of our regional sampling unit (n = 29). As time of invasion advances, the white-popinac patch is assumed to expand towards the regenerating area, and therefore affect (meta-) community dynamics.

Methods

Sampling design

We conducted this study in the interior region of the state of São Paulo, southeast Brazil. We visited 38 rural and peri-urban private lands whose owners have destined portions of the property to forest natural regeneration and that were surrounded by at least one major patch of native Seasonal Semideciduous Forest and one patch of white-popinac. We actively chose areas that had different ages of invasions, to create a temporal gradient of white-popinac invasion. From 38 areas, we chose 29 that evenly filled the temporal gradient. All fieldwork was done from March 2020 to September 2022. Detailed information about the region can be found in the Supplementary Information section.

Our sampling design explicitly considers two spatial scales – local (131 communities) and regional (29 metacommunities). A metacommunity represented a system composed of a native forest fragment, partially surrounded by a regenerating area, which had at least one patch of white-popinac (Figure 2). Within each metacommunity, communities were defined as transects (14m x 2m) established at the edge between the forest fragment and its respective regenerating area (7m towards the forest fragment and 7m towards the regenerating area). Each metacommunity included four or five communities with varying distances from the white-popinac patch (Figure 2).

At each transect, we estimated the abundance of all species (native and INNS) on the arboreal (trees and shrubs) and herbaceous strata (climbing plants, herbs, ferns, epiphytes and grasses; below 1 m high), as well as of all seedlings. The abundance on the arboreal stratum was estimated via counting individuals, whereas on the herbaceous stratum it was done by visually estimating relative (percentage) ground cover (all methodological procedures and details are presented in Supplementary Information).

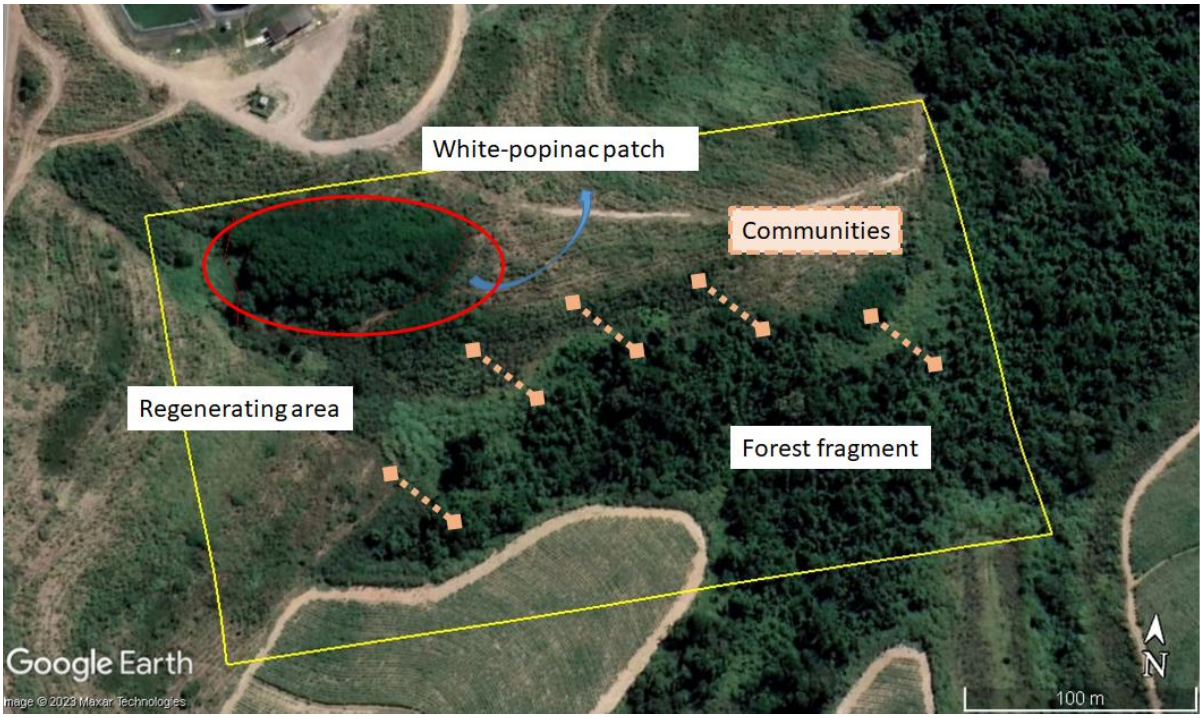

Fig. 2 Representation of our sampling design. The yellow rectangle delimits the sampling unit at the regional scale (metacommunity). The patch within the red ellipse is the white-popinac patch. Dotted lines are communities. A metacommunity (n = 29) was defined as a spatial unit composed of a forest fragment, a regenerating area and a white-popinac patch. Within each metacommunity, a community (n = 131) was defined as a transect (four or five per metacommunity) placed on the edge between the forest fragment and the regenerating area. Within each metacommunity, local communities were unequally distant from the white-popinac patch.

Response variables

We estimated species richness for each local community (n = 131 transects) using sample coverage rarefaction/extrapolation methods in iNext R-package (v3.0.0, Chao et al. 2014; Hsieh, Ma, and

Chao 2016). Each region (n = 29 metacommunities) had its own sample coverage, considering the maximum sample coverage possible among communities within a metacommunity. This process was made separately for the arboreal and the herbaceous strata. Sample-coverage-based estimation was also applied separately for INNS (excluding white-popinac) and native species. We defined regional (gamma) diversity as the summed richness estimates of all communities within a metacommunity. For the local and regional scales, we also calculated the abundance of white-popinac, with two different metrics: number of white-popinac adult individuals (dbh > 2 cm) and relative ground cover by white-popinac seedlings (%).

We estimated variation in species composition among communities within a metacommunity (i.e., β-diversity) using a metric that applies coverage-based rarefaction/extrapolation to infer changes in non-random intraspecific aggregation (β-c; Engel et al. 2021). β-c is not affected by gamma diversity and allows more adequate comparisons of β-diversity among regions with different species pools. We estimated β-diversity separately for the arboreal and herbaceous strata once abundance metrics were different among strata. We used the “betaC” R-package (v0.1.0) to estimate β-c.

Predictor variables

We divide our numeric predictor variables into two groups: (i) time-advance and (ii) space-related variables.

Time-advance variables: we created three different gradients that could work as proxies to describe the temporal progression of invasion in each metacommunity. We used proxies because it is an observational design; thereby we did not know exactly when the invasion took place initially. Our approach is essentially a time-for-space substitution framework, where the replicates in space comprise different invasion stages, creating a temporal gradient. We detail measuring and standardization methods in Supplementary Information section.

a. Basal area (square meters/plot): basal area was the total area on a given plot that was occupied by tree trunks of white-popinac. We measured diameter at breast height (dbh; breast height = 1.5 m) and calculated trunk area of all white-popinac trees in a standardized plot (25 m^2) to estimate the basal area of each patch. We assumed that higher values of basal area should represent older trees and, therefore, older invasion events.

b. Average dbh of the largest trees (centimeters): we calculated the average dbh of trees larger than the superior quantile (75%) for each white-popinac patch. The larger individuals are the most important to provide time-since-invasion estimates. Higher values should also represent older trees.

c. Patch age proxy by satellite imagery (years): white-popinac populations usually occur as large and homogeneous agglomerations that are easily visualized with satellite imagery tools. Because they grow fast, the growth of the patch can be seen through time, using older images provided by Google Earth Software. Because we were able to detect when the patch firstly appeared on the imagery, we could attribute an estimated age (years) to each patch.

Space-related variable: we measured the distance (meters) between the center of each community to the nearest edge of the white-popinac patch. We expected that longer distances would mean a weaker effect of white-popinac, considering that white-popinac dispersal is distance-limited by its autochory (Hata et al. 2010). This was the only predictor variable applied to each community, instead of one value for the entire metacommunity.

Finally, our models also included a categorical predictor variable to describe strata (herbaceous or arboreal, when the diversity metric was calculated differently between strata, such as β-diversity) and one to describe origin (native or INNS for interaction with time-advance variable).

Model selection

For each of our hypotheses, we built a set of alternative models that represented a potential relationship between one of the response variables and a specific combination of predictor variables (Tables 1 and 2, Supplementary Information). Depending on the spatial scale, alternative models included a combination of predictor variables that had one time-advance variable (basal area, average dbh of the largest trees, or age-proxy by satellite imagery), the space-related variable, and two-level categorical variables (stratum and origin). All numeric predictor variables were standardized before being applied to the models.

For response variables measured at the local community level, we competed Generalized Linear Mixed-Effect Models (GLMM), considering metacommunity identity as a random component. For variables measured at the regional scale, we competed Generalized Linear Models (GLM) for each response variable. In some cases, the same model was fitted (and competed) with different distribution families.

When a model included the categorical variable "origin" (native or INNS), we included it as a potential interaction with the time-advance variable, as we expected that the effects of white-popinac invasion age would be different between native and other INNS. In these cases, we also used interaction-plots to visualize the relationships.

Model selection was based upon an Information-theory approach (Aho et al. 2014), using the corrected Akaike Information Criterion (AICc) ranking, and derived metrics (e.g., Δi , AICc weight). The selection and post selection routines followed these steps:

(i) Model ranking considering AICc values: models with $\Delta i < 2$ were considered as equally plausible (Δi is the subtraction between a model's AICc value and the lowest AICc value among all competitor models [Burnham, Anderson, and Huyvaert 2011]);

(ii) If the best model had an R^2 (or another equivalent metric of explained variance) lower than 0.05, we discarded that hypothesis and did not interpret the model;

(iii) We examined the coefficients and their respective confidence intervals (95% CI) for equally plausible models to evaluate their magnitude and direction. Coefficients which CIs included zero were considered to have no effect on the response variable.

For GLMs, we used the "stats" R-package (v.4.2.2), and for GLMMs we used the "glmmTMB" R-package (v1.1.5). For model selection we used the "performance" R-package (v.0.10.0). More details about model structure, distribution families, decisions in selection, software and packages are included in Supplementary Information.

Results

We sampled 328 species: 178 in the arboreal stratum and 150 in herbaceous stratum. We could not identify 21 species due to the absence of taxonomically important structures, especially in case of deciduous species. The 307 identified species were distributed among 218 genus and 73 families, being

Fabaceae, Asteraceae and Malvaceae the most representative ones in terms of number of species. The average number of species per metacommunity was 46.5 (minimum [min.] = 25.4; maximum [max.] = 84; standard deviation [s.d.] = 14.2; n = 29). For communities, the average number of species was 22.3 (min. = 3.6; max. = 44.1; s.d. = 8.9; n = 131). The list of recorded species can be found in Supplementary Information section (Table 5 - SI).

Selected models

For the local (community) scale, we found no evidence that either invasion age or community-patch distance were related to species richness. However, when we split the data per stratum, the most plausible model indicated that variation in herbaceous species richness was explained by an interaction between time and origin (Table 1). Whereas herbaceous native species richness decreased with time, herbaceous INNS richness increased (Figure 3a). We also found that the number of adults of white-popinac in the regenerating community was negatively related to the distance from the patch of white-popinac (Table 1; Figure 4a).

Table 1 Model selection statistics for equally plausible models at local scale. AICc refers to the corrected Akaike Information Criterion (AIC). Δi refers to the difference between a given AICc value and the lowest among competing models. AICc (W) refers to AICc "weight", being interpreted as the model's relative likelihood. R^2c refers to amount of variation explained by the entire model, both fixed and random components, whereas R^2m refers only to the fixed component. ADL = Average-diameter (dbh - cm) of largest white-popinac trees within a metacommunity (region); A = white-popinac patch's age-proxy (years); BA = white-popinac patch's basal area (m^2). RE = random effects.

Model structure	**Distribution**	**AICc**	**Δi**	**AICc (W)**	**R^2c**	**R^2m**
Species richness of the herbaceous stratum						
Time (ADL) * origin + RE	Gamma	1035.79	0	0.221	0.58	0.45

Time (ADL) * origin + distance + RE	Gamma	1035.89	0.091	0.211	0.57	0.47
Time (A) + origin + distance + RE	Gamma	1037.16	1.361	0.112	0.56	0.47
Time (A) + origin + RE	Gamma	1037.67	1.876	0.086	0.56	0.46
White-popinac abundance						
Time (BA) + distance + RE	Poisson	520.32	0	0.392	0.88	0.68
Time (A) + distance + RE	Poisson	520.82	0.503	0.305	0.88	0.68
Time (ADL) + distance + RE	Poisson	520.84	0.52	0.303	0.88	0.68

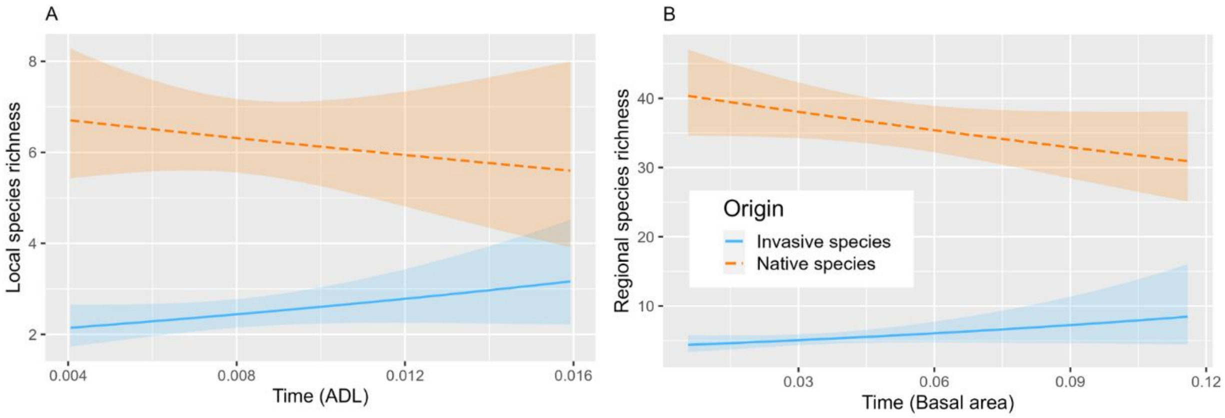

Fig. 3 Interaction plots representing the relationship between species richness and time conditional on origin (native species of INNS). **a.** Predicted relationship between local-scale species richness on herbaceous stratum and time conditional on origin. **b.** Predicted relationship between regional-scale species richness and time conditional on origin. ADL is a time-advance variable: average diameter (cm) of the largest white-popinac trees within a patch. Basal area (m^2) is a time-advance variable that represents the area occupied by white-popinac trunks within a standardized plot.

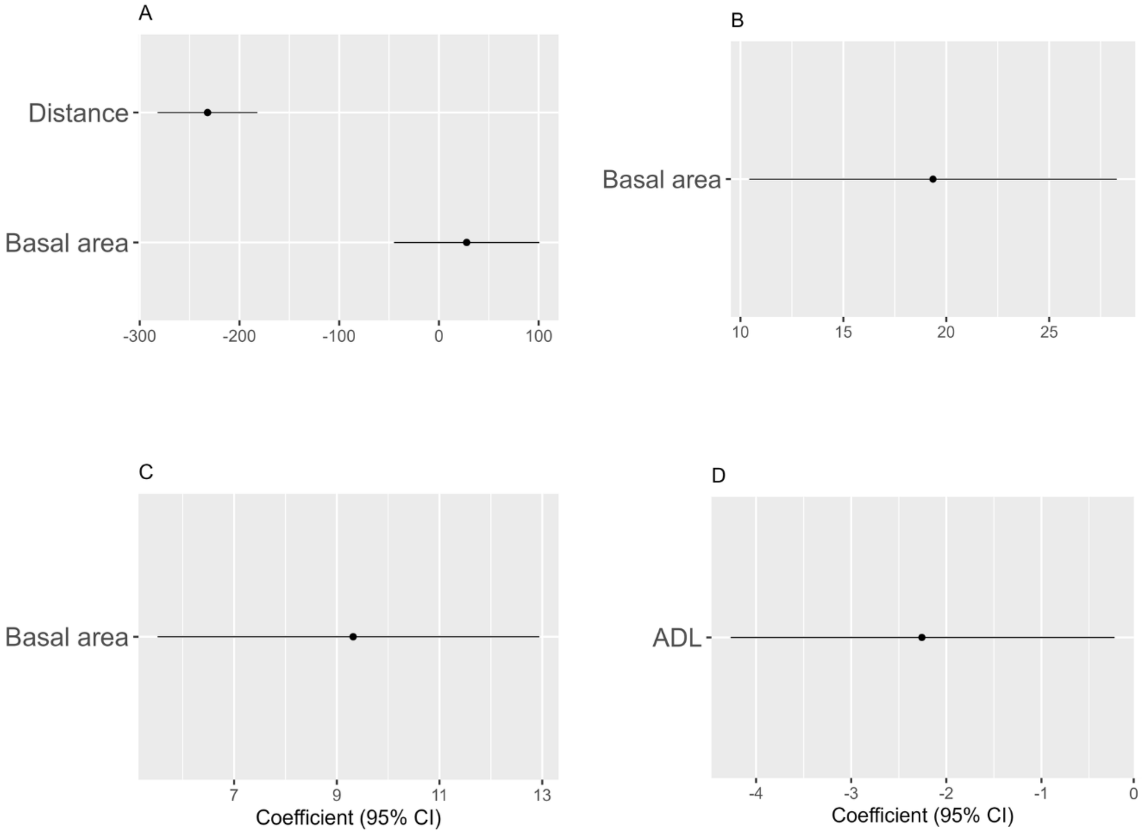

Fig. 4 Confidence interval (95%) plot describing parameter estimates of predictor variables related to: **a.** The abundance of white-popinac trees at regenerating communities (local scale). **b.** Relative (%) ground coverage by white-popinac seedlings on metacommunities (regional scale). **c.** Number of adult individuals of white-popinac on metacommunities. **d.** For β-diversity modeling; here, the response variable is β-c, which is a β-diversity metric (see Methods section and Supplementary Information for details). The higher the β-c value, the less homogenous are the communities within a metacommunity in terms of species composition. Basal area (m^2) is the time-advance variable that represents the area occupied by white-popinac trunks within a standardized plot. Distance (m) is a space-related variable that express how far the community is from the main white-popinac patch. ADL is a time-advance variable: average diameter (cm) of the largest white-popinac trees within a patch.

The most plausible models describing variation at the regional scale (metacommunity; Table 2) agreed with those at the local scale (Table 1). We found no strong evidence of white-popinac affecting overall metacommunity species richness without discriminating species origin. When we did so, a model including an interaction between time and species origin indicated that native regional species richness decreased with invasion age, whereas the opposite happened with INNS, irrespective of stratum (Table 2; Figure 3b). Regarding white-popinac abundance, we found that both relative (%) ground cover by white-popinac seedlings and number of adult individuals were positively related to invasion age (Figure 4b, c). Finally, we found strong evidence that β-diversity decreased with invasion age, irrespective of stratum (Table 2; Figure 4d).

Table 2 Model selection statistics of equally plausible models describing variation at the metacommunity regional scale and β-diversity. Models fitted with Poisson and Beta distributions are associated with pseudo-R^2 values, whereas models fitted with Gamma distribution are associated with Nagelkerke R^2, which are mathematically different from a regular R^2, but may be interpreted in a similar way. Abbreviations as in Table 1.

Model structure	Distribution family	AICc	Δi	AICc (W)	R^2 (Nagelkerke)
Species richness					
Time (A) * origin	Gamma	375.40	0	0.235	0.89
Time (A) + origin	Gamma	375.47	0.063	0.228	0.88
Time (BA) * origin	Gamma	375.61	0.202	0.212	0.88
Time (BA) + origin	Gamma	376.27	0.867	0.152	0.88
Time (ADL) + origin	Gamma	377.04	1.640	0.104	0.88
White-popinac seedlings’ relative (%) ground cover					
Time (BA)	Beta	-120.6	0	0.924	0.18
Response variable = Number of white-popinac adult individuals (γ scale)					

Time (BA)	Poisson	472.25	0	0.99	0.52
Response variable = β-c (β-diversity metric)					
Time (ADL) + strata	Gamma	-60.93	0	0.667	0.63
Time (BA) + strata	Gamma	-59.10	1.836	0.266	0.62

Discussion

Our study provides evidence that the effects of white-popinac on regenerating forests are consistently manifested across different spatial scales in the Brazilian Atlantic Forest. Native species richness in regenerating forests decreased with time since invasion, whereas the species richness of INNS increased, both at the community and metacommunity levels. This mirrored local-regional negative relationship was due to a clear decrease of β-diversity in function of time since invasion. That is, communities within invaded metacommunities became more homogeneous in terms of species composition as time of invasion advanced. Together, these results indicate that white-popinac effects on invaded landscapes are so vigorous that they propagate across spatial scales, negatively affecting the three main components of biodiversity.

At the local scale, as time since invasion advanced, the herbaceous stratum became more invaded by other INSS and less species rich of natives. Because the regenerating communities did not contain the main white-popinac patch (only some sparsely distributed individuals), the mechanism that drives this decrease in native species richness is likely to be related to spatial distance. Our results support this view as we found that the farther the regenerating community was from the main white-popinac patch, the lower the abundance of white-popinac adult individuals in the regenerating community (see Hata, Suzuki, and Kachi 2010 for similar results). The advance of white-popinac towards regenerating communities may reduce space available for the regenerating forest, which is already invaded by grass species. This reduction in space availability may enhance competition among native species on the herbaceous stratum and invasive grasses (Wilsey et al. 2011; Martin et al. 2014), and affect trees and shrubs seedlings recruitment (Flory and Clay 2010; Aronson and Handel 2011). Ultimately, an increase in white-popinac abundance in the regenerating community could indirectly lead to the exclusion of less competitive native species by increasing the community's susceptibility to invasion (i.e. invasibility, Lonsdale 1999) by other INNS (simliar results were found by Yoshida and Oka (2004)).

The upscaling of the negative relationship between native and INNS richness from local to regional scale is a result rarely seen in invasion studies. A plethora of studies regarding plant invasions has found discrepancy on responses between regional and local scales, which has become a highly debated topic, under the name of "invasion paradox" (Pyšek and Hulme 2005; Fridley et al. 2007; Pyšek et al. 2008; Powell et al. 2011; Peng et al. 2019; Brown and Barney 2021). It is common to find no relationship or even a positive one between native and INNS richness at broader scales (e.g. metacommunities), often due to an increase in β-diversity across communities (e.g. Davies et al. 2005; Chen et al. 2010). As it should be expected, the rare examples of analogous mirrored local-regional effects similarly found a decrease in β-diversity (e.g. Jauni and Hyvönen 2012). Our results show that the effects of white-popinac invasion on regenerating forests can be so strong that the local response dynamics propagate to the regional scale, even though the invasion is considerably recent (< 20y).

The β-diversity of both the arboreal and herbaceous strata decreased with the increase of invasion age. This means that communities within invaded metacommunities become more similar to each other as invasion advances in time. Unless demographic stochasticity plays a major role in community assembly (Siqueira et al. 2020; Jacobi and Siqueira 2023), competition is likely enhanced in a regenerating forest that is dwindling in size (Amarasekare 2003; Cadotte 2007; Bowker and Maestre 2012). If this process is replicated across various regenerating forest patches, the same set of species may thrive in different communities, which leads to a homogenizing effect (Smart et al. 2006; Solar et al. 2015; McKinney and Lockwood 1999; Arroyo-Rodríguez et al. 2013). For example, all communities within our oldest invaded metacommunity had the same six dominant species, which represented more than 50% of total abundance on each community. Contrastingly, in none of the communities within one of the most recent invaded metacommunities (smallest ADL) there was a clear dominant species – the most abundant species were just slightly more abundant than the others. This decrease in β-diversity along the temporal gradient of invasion explains the propagation of effects from the local to the regional scale (Legendre et al. 2005; Anderson et al. 2011; Chao and Jost 2012).

The responses alpha, beta and gamma diversity to white-popinac invasion were essentially temporal. However, we identified indirect spatial effects that likely underlined temporal dynamics. As time of invasion advances, patches of white-popinac tend to grow in area and reduce their distance from regenerating communities (Hata et al. 2010; Osawa et al. 2016). We found that white-popinac abundance was also affected at regional scale; however, it was not related to distance (as it was for local scale), but to invasion age. We propose that this process describes biotic indirect effects hypothesis (Strauss 1991; Marler et al. 1999; White et al. 2006; Catford et al. 2009). The spatiotemporal advance of white-popinac patches may generate indirect effects on regenerating communities by reducing the size of the regenerating area. We suggest that biotic indirect effects provide a likely explanation on how white-popinac invasions disrupt the dynamics of regenerating plant (meta-)communities. In an explicit metacommunity framework, such biotic indirect effects can be seen as analogous to spatial spillover effects (Kuschnig et al. 2021; Wang et al. 2021).

We recognize that other factors than the ones we addressed here can affect how (meta-)communities respond to invasion, such as landscape configuration (Vilà and Ibáñez 2011; Zhang et al. 2021), historical land use (Colón and Lugo 2006; Didham et al. 2007), fire events (Portela et al. 2009; Flory et al. 2015), and even cattle sporadically sneaking into the regenerating area (Reisner et al. 2015; Osawa et al. 2016). Also, propagule pressure is as pivotal as time-advance (Lockwood et al. 2005; King and Howeth 2019), but it was not addressed here. Observational field-based studies on biological invasions have major limitations, especially regarding temporal gradients. The use of time-advance proxies and space-for-time substitutions are very common and, despite being useful, these methods may reduce result precision and predictive power. Despite these limitations, our models were associated with reasonably high explanatory power – e.g., R^2 values varied from 0.18 to 0.89. Because the models we compared were all based on sounding hypotheses, we are confident that the relationships and high explanatory of some models we found here are not the result of chance or unaccounted hidden sources of variation.

Investigating how alpha, beta and gamma diversity of regenerating communities are affected by invasive species was only possible because our sampling design explicitly incorporated two aspects that are not frequently considered in other studies: (i) we meticulously surveyed the herbaceous stratum, even though our study region is originally dominated by Seasonal Semideciduous Forests. Had we not included the herbaceous stratum, we would not have found any relationship between species richness and invasion age at the local scale. (ii) We included spatial replication at both the local and regional scales, which allowed us to understand how changes in the local structure of communities upscaled to the metacommunity level. Thus, we reinforce the need to adopting a metacommunity approach that explicitly considers multi-scale consequences of biological invasions (Brown and Barney 2021; Patrick et al. 2021). We suggest that future studies on white-popinac invasions consider both local and regional scales, and explicitly address how β-diversity responds to invasion. Despite white-popinac being considered an arboreal species in Brazil, we recognize that non-arboreal native species should be comprised by floristic surveys on scenarios of forest regeneration (Gilliam 2007; Flory and Clay 2010). Finally, the effects of spatial spillover seem to be crucial for understanding the effects of invasive species that do not spread into communities but establish as isolated patches.

We aimed to understand how various aspects of white-popinac invasions affect communities and metacommunities undergoing through natural regeneration, in a tropical Seasonal Semideciduous Forest system. We found that both communities and metacommunities are negatively affected by white-popinac age of invasion. At both scales, we found that the number of native species decreases as time of invasion advances, concurrently as the regenerating communities become more invaded by other INNS. We also found that communities within invaded metacommunities become more homogeneous regarding species composition with invasion age. The mechanism that underlies these consequences is probably based upon biotic indirect effects. We suggest that future studies on white-popinac invasion address the effects of other facets of biological invasions, especially propagule and source-population dynamics. We also stress that the effects of white-popinac invasions should not be underestimated in terms of management, once the relatively recent invasions that we studied have caused severe diversity declines.

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Statements & Declarations

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Competing interests

JZ and TS declare that they do not have any conflict of interests that may have influenced this work.

Author contributions

JZ and TS conceived the idea, designed fieldwork, analyzed the data and wrote the paper. JZ collected field data and identified the species.

Data availability

The datasets generated during and/or analyzed during the current study are available in the Zenodo repository, on the link https://doi.org/10.5281/zenodo.8111724.

Title: Regenerating tropical forests are consistently affected by biological invasions across spatial scales

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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 metacommunities were in the city of Porto Feliz. All other ten metacommunities 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 1). All five cities are relatively small and share similar climatic, vegetation and geological features.

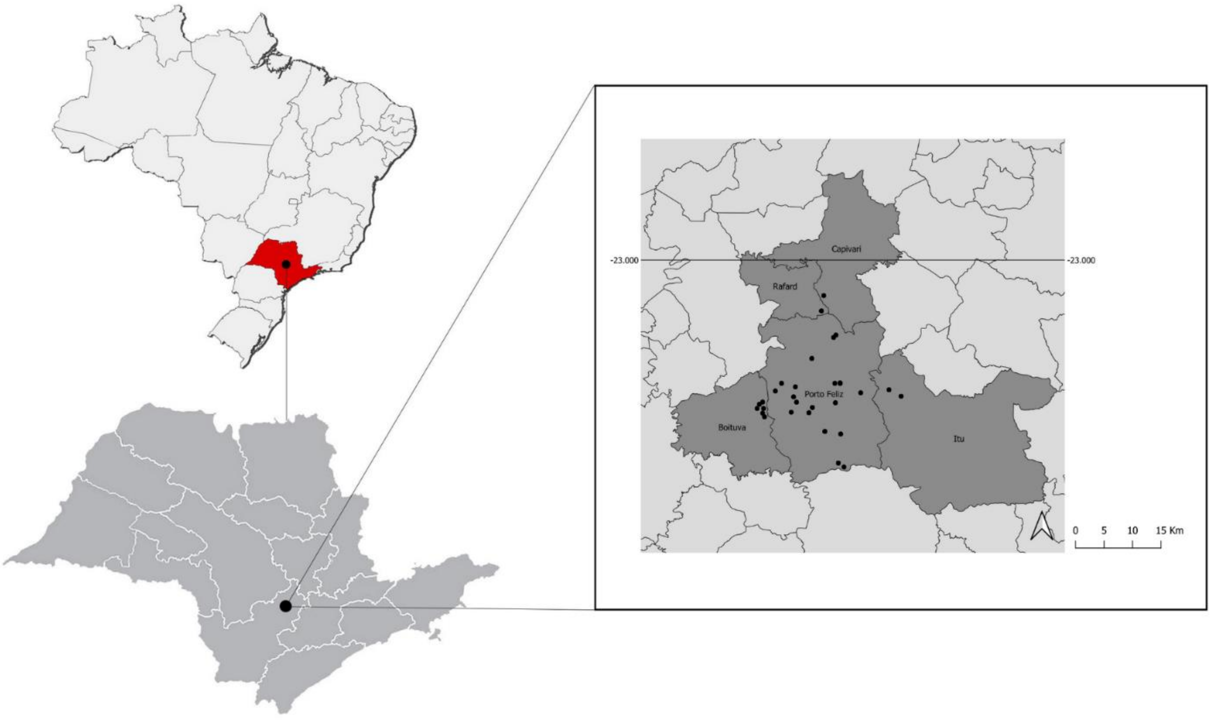

Fig. 1 Location of our study region. State of São Paulo, Brazil. The points on the right side chart are our metacommunities.

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 regional sampling units (metacommunities) were systems composed of a forest fragment and its respective regenerating area, which became invaded by a white-popinac patch. 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 regional 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. Despite the age-proxy being more intuitively related to time-advance, the scale of years may not be enough to describe changes in meta(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 metacommunity had its own "invader" white-popinac patch. Therefore, the measures that come from that patch were applied for the entire metacommunity and its respective communities.

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 (1.5 m).

4- We calculated the respective diameter at breast height of each individual applying the perimeter as equal to 2πR, 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.

Community-patch distance

This was our space-related variable, which described the distance, in meters, between each local community within a metacommunity and the white-popinac patch. All communities (14 m x 2 m transects) had geographical coordinates recorded, so we managed to estimate the distance from them to the patch using line-measurement tool from Google Earth. We considered the coordinates from communities' "center", being the medium point where 7m of transect leaned towards the forest and the other 7m leaned towards the regenerating area. Moreover, the patch's point for reference was not the center, but the edge that was closest to the forest. We decided to consider the edge as reference point because white-popinac has a distance-limited dispersal, and it is plausible to consider that the most "influent" white-popinac individuals are the ones that are closer to the community, and not the central ones (Hata, Suzuki, and Kachi 2010). The overall distance range was 2 – 183 m, highly different throughout metacommunities.

Grouping variables

When arranging the statistical models for selection, we considered both strata separately (arboreal and herbaceous), by creating a categorical variable called "strata", in additive effect to a given time-related 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 (Gilliam 2007; Flory and Clay 2010).

We also created a variable called "origin", which groups the species into native and invasive non-native (INNS). 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. INNS).

We clarify that we obtained the "origin" variable towards species richness estimation (detailed on "Details on response variables" section). We firstly grouped our species into "native" and "INNS" categories and then proceeded to species richness estimation separately between these two categories, for both local and regional scales. The classification was based upon INNS 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 INNS. If at least one of these databases reported the species as INNS in our study region, it was considered as INNS for our analysis.

Floristic survey

The floristic surveys conducted in each community were the main methodology to obtain our response variables. The collected species were submitted to taxonomic evaluations, and the majority of them were identified at species level. Consider that "transect" and "community", in our framework, are spatially equivalent concepts. All transects were placed in the contact zone between the forest fragment and its respective regenerating area, with 7 meters advancing towards each area. In some cases, especially older-regenerating areas, the spatial delimitation from forest to regenerating area was not explicit. Inherently, the floristic survey provided material for a herbarium, which has been kept by the authors and is available for consultations.

Herbaceous stratum

For the herbaceous stratum, we divided the entire transect into 28 grids (1 m x 1 m). The sampling procedure (Figure 2) consisted in choosing seven grids that were always in the same position. On these seven grids, we recorded the ground cover percentage of each species. Notice that the abundance metric is based into a percentage, instead of counting individuals, once it is often difficult to delimit an individual for some species at this stratum. We considered as part of the grid all species that had vegetative parts comprised by the grid, even if they were not rooted there. We made this decision because climbing species are often included by the grid's area, but are rooted somewhere else. We designed a framework that could fit into our scenario of fragmented Seasonal Semideciduous Forest going through natural regeneration, where we can find extensive ground cover by invasive grasses, many liana species growing like herbs or shrubs (due to the low density of arboreal individuals), other invasive species besides grasses and white-popinac, and scattered young trees and shrubs.

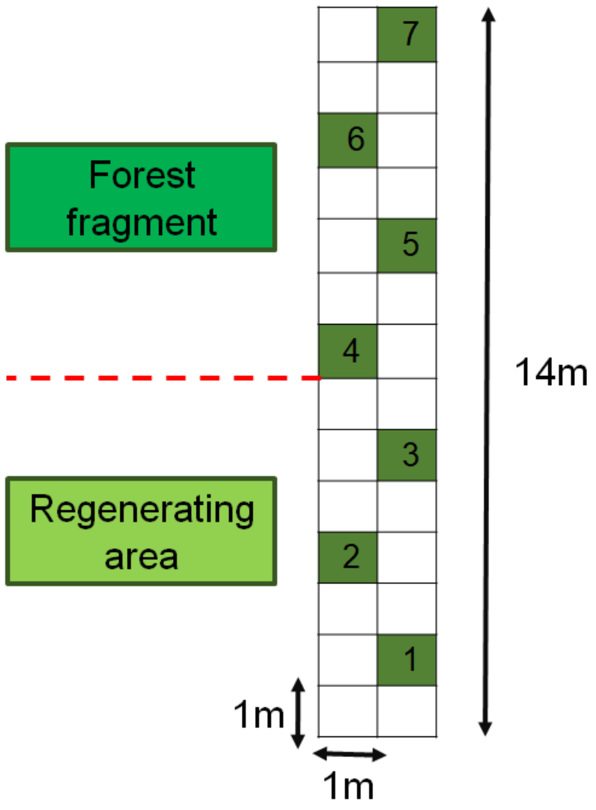

Fig. 2 Diagram of transect division into grids. Among the 28 one-meter-square grids, we chose seven, following the same spatial arrangement as the figure: grid 1 was always the farthest to the forest fragment. From 14 meters in length, 7 entered the forest fragment and 7 entered the regenerating area.

All species except moss and parasite species were identified. In other words, we identified herbs, grasses, climbing plants (lianas and vines), and other types such as ferns and epiphytes. Moreover, we included litter layer, white-popinac seedlings and overall seedlings (not white-popinac) as “species”. Here, it is important to stress that we considered all plant species that were growing bellow 1 meter height as part of herbaceous strata. That means that climbing species found only on higher ranges, such as upper canopy, were not included.

We visually estimated ground cover percentage of each species we found within a grid, as in *relevé* approach (Braun-Blanquet 1964). Within a grid, the sum of all species ground cover did not necessarily equal to 100, once different plant heights can create “layers” of ground cover that prevent smaller individuals to be recorded if just considering a single-frame vision.

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 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. 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 brunches were entering the transect space were also included (Figure 3).

The survey of the arboreal stratum was proceed after the herbaceous one, once the walking amid transect area potentially disturbs herbaceous stratum. After accomplishing the first transect, we followed to the second, at least 10 meters of distant from the previous one. This distance among transects could be greater in larger areas, but never lower than that. We tried to place the transects in a way we could achieve a distance-gradient (from transect to white-popinac patch) within the meta-community.

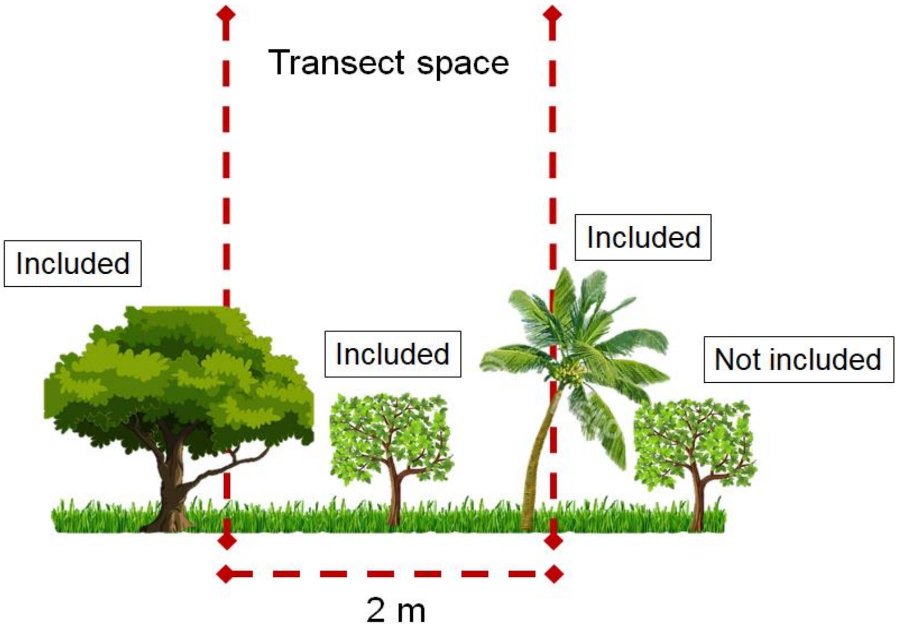

Fig. 3 Diagram representing the inclusion criterion of trees and shrubs regarding the transect area. If an individual was rooted outside but grows brunches inside the transect, it was included. If it was totally inside, it was obviously included. In case it was rooted inside, but lens completely towards 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 (meta-)communities; 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 three levels of response variables: local scale (alpha – community), regional scale (gamma– metacommunity) and among-sites diversity (β-diversity).

Local scale

This scale refers to the community level. 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 that were comprised by the sample.

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 package itself proposes the best sample-coverage that is possible among communities within a particular metacommunity, and displays if the estimation for each community was obtained via extrapolation or rarefaction (Figure 4).

For the herbaceous stratum, we initially calculated the average ground cover percentage for each species (average among the 7 grids within a transect). Then, we applied sample-coverage based estimation considering the suggested sample-coverage value for each metacommunity. The average sample-coverage for herbaceous stratum among our 29 metacommunities was 0.98 (sd = 0.03, min = 0.81, max = 1.0). For the arboreal stratum, no averaging was needed once there were not subsamples within transects. The average sample-coverage for this stratum among all metacommunities was 0.74 (sd = 0.13, min = 0.30, max = 0.94).

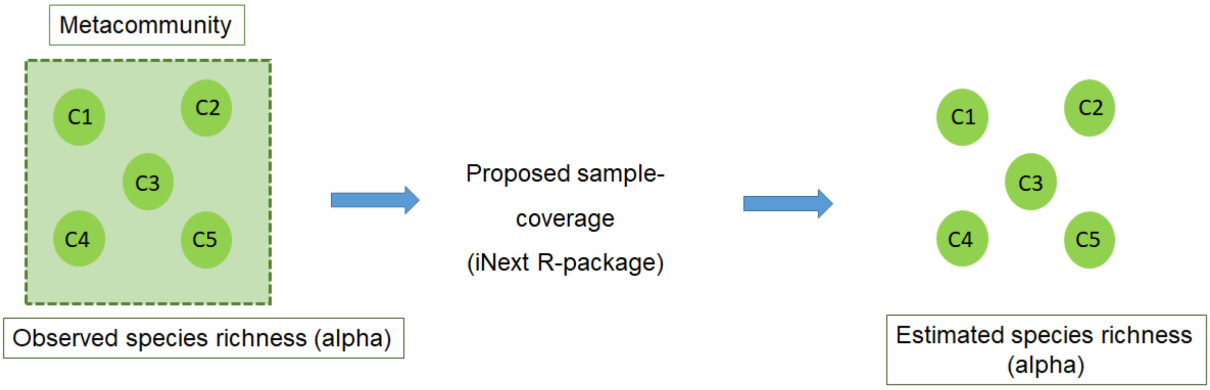

Fig. 4 Conceptual approach to species richness estimation on α-scale (community). C1 to C5 represent communities within a given metacommunity. Each metacommunity has its own proposed sample-coverage, obtained from iNext. This value allows communities to be standardize by their completeness, instead of size.

Regional scale

This scale refers to metacommunity level. We used iNext package (v3.0.0; Hsieh, Ma, and Chao 2016) to estimate species richness considering the same sample coverage among all metacommunities (for the arboreal stratum: 0.88; for the herbaceous stratum: 0.96). Finally, we obtained species richness estimations for this scale, as seen in Figure 5.

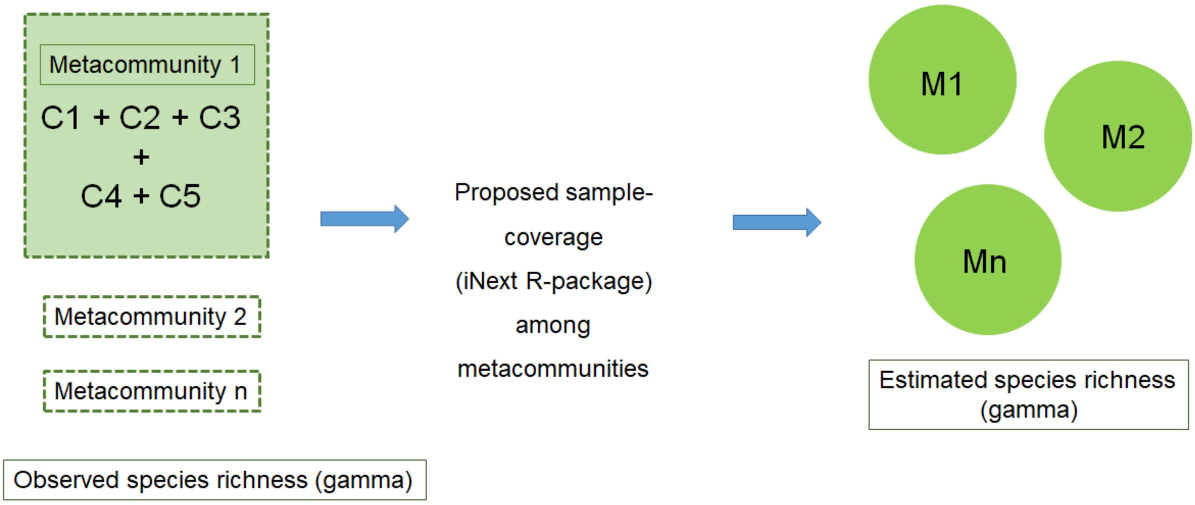

Fig. 5 Conceptual approach to species richness estimation on regional scale (metacommunity). C1 to C5 represent communities within a given metacommunity. Using iNext R-package, we could standardize metacommunities based on their completeness, instead of size.

β-diversity

Comparing differences in species composition among communities among regions is considered challenging as most β-diversity metrics are influenced by γ-diversity. Engel and collaborators (2021) developed a new metric called β-c, which employs the approach of coverage-based estimation to infer changes in non-random intraspecific aggregation, without being affected by γ-diversity (Engel et al. 2021). The new metric considers species composition based in equally complete communities, instead of standardizing them by total abundance. We used the "betaC" R-package (v0.1.0), which provides sample-coverage values for each metacommunity (Figure 6). The standard procedure is to use the smallest provided value (named "C-target") to estimate β-c metric. The C-target for arboreal stratum was 0.48, which is close to what is considered the minimum for unbiased estimation (Chao and Jost 2012), whereas for herbaceous it was 0.94.

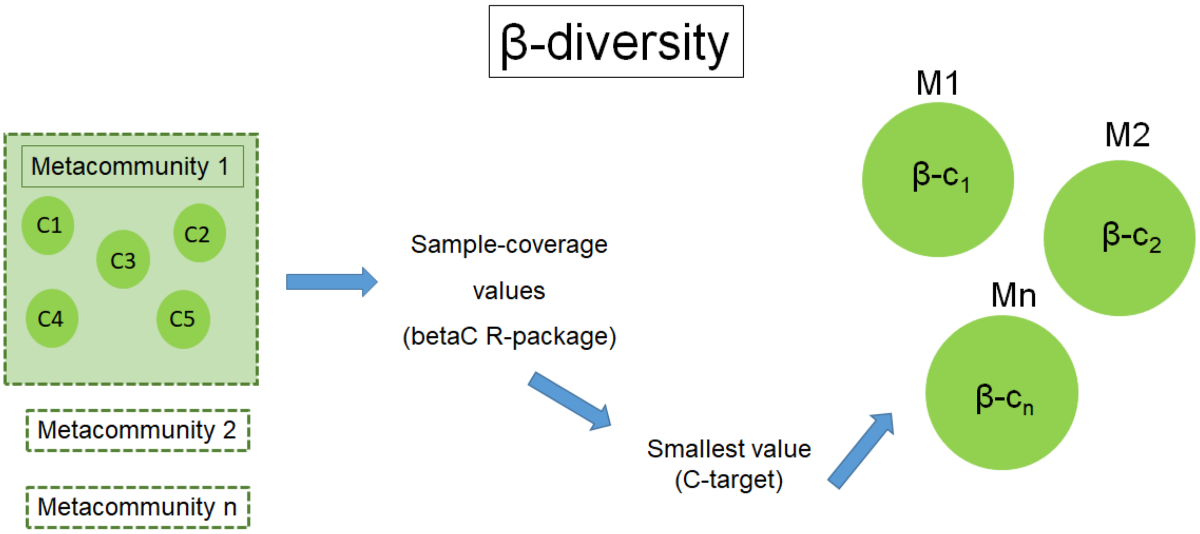

Fig. 6 Conceptual representation of β-diversity estimation (β-c metric). R-package betaC proposes sample-coverage values among metacommunities, and the smallest one (C-target) is chosen to estimate β-c, expressing differences in species composition among communities within a given metacommunity.

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: the number of competing models for a given response variable depended on predictor variables and distribution families:

(i) Because we had three different time-related variables, each one was used on an individual model. For the regional scale and β-diversity, the first step stops here and goes to item 2. For the local scale, we followed to sub-items ii and iii before continuing to item 2.

(ii) There was a space-related variable at local scale (community-patch distance), so we created models with time and space and with only time.

(iii) All models at local scale had a random component, once our replicas were spatially dependent (communities within a metacommunity are not independent, they are spatially aggregated).

3- 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., number of white-popinac adult individuals), we used the Poisson distribution (with log link function).

(iii) In the case of proportions (e.g., relative groundcover), we used the Beta distribution (logit link function).

4- Chose model type:

(i) For the regional scale and β-diversity, we employed GLMs (Generalized Linear Models), using "glm" function, in the "stats" R-package (v4.2.2).

(ii) For the local scale, we employed GLMMs (Generalized Linear Mixed-Effect Models), using "glmmTMB" function, in the "glmmTMB" R-package (v1.1.5).

5- 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, Derryberry, and Peterson 2014; Burnham, Anderson, and Huyvaert 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 ($\Delta i = AICc - [min]AICc$).

6- Considered R^2 values:

(i) For the regional scale and β-diversity, we did not interpret models which R^2 values were too small (< ~ 0.05), i.e., we discarded the hypothesis that they represented.

(ii) For the local scale, R^2 values were divided into two components: conditional R^2 (R^2c), which comprises the entire GLMM model, both fixed and random components; and marginal R^2 (R^2m), which comprises only the fixed component (that were the predictor variables such as time or distance). If R^2c was high but R^2m was too low, it means that most of the variation in the response variable was associated with the random component, i.e., local effects that were not represented by our predictor variables. In cases where R^2m was lower than approximately 0.05, the models were not interpreted as well (discarded hypothesis).

7- Plotted equally plausible models: this step did not include models with interaction between time-related variables and the categorical variable "origin" (native/INNS).

(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.

8- 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

Local scale

Table S1 Diversity metrics at local scale. ESR = Estimated Species Richness**.**

Metacommunity	**Community**	**ESR – Arboreal stratum**	**ESR – Herbaceous stratum**
a	1	5.64	10.77
a	2	4.85	15.51
a	3	9.76	8.04
a	4	9.82	10.02
a	5	7.35	13.73
aa	1	11	8.15

aa	2	15.1	15.14
aa	3	15.41	11.62
aa	4	12.3	10.22
aa	5	14.52	13
bb	1	19.89	5.99
bb	2	2.86	9.42
bb	3	8.61	5.96
bb	4	9.63	5
c	1	6.52	9.96
c	2	14.66	18.89
c	3	13.69	6.92
c	4	12.95	13.97
c	5	7.44	25.06
cc	1	5.7	6.99
cc	2	9.01	10.99
cc	3	3.78	11.62
cc	4	5.67	11
cc	5	4.12	13
dd	1	25.03	8.82
dd	2	13.38	10.79
dd	3	18.05	10.58
dd	4	8.14	11.85
dd	5	10.76	7.34
e	1	9.65	8
e	2	19.84	12.41
e	3	10.47	8
e	4	22.23	16.06

e	5	13.58	9.43
ee	1	24.13	11
ee	2	11.21	15
ee	3	7.49	10
ee	4	4.41	6
f	1	7.1	6.75
f	2	10.57	10.85
f	3	17.11	13.18
f	4	5.91	6.87
f	5	4.33	14.84
g	1	13.09	16.54
g	2	8.27	11.64
g	3	4.87	10.86
g	4	17.87	10.84
g	5	13.95	8.86
gg	1	27.1	14
gg	2	14.46	12
gg	3	14.03	12
gg	4	17.35	13.63
gg	5	3.34	7
h	1	14.2	26.04
h	2	10.77	11.14
h	3	24.17	13.08
h	4	19.19	13.42
ii	1	10.2	4.99
ii	2	4.25	5.43
ii	3	12.35	6

ii	4	19.37	3.99
j	1	6.52	11.18
j	2	9.05	5.81
j	4	21.07	4.86
j	5	7.05	5.96
jj	1	6.31	9.98
jj	2	8.38	13.98
jj	3	32.99	11.18
jj	4	18.06	11.98
jj	5	3.96	9.85
k	1	9.19	9.95
k	2	10.56	11.44
k	3	9.43	12.79
k	4	12.14	14.9
k	5	3.09	8.96
kk	2	9.89	8
kk	3	8.94	13
kk	4	5.06	11.24
kk	5	4.89	6
mm	1	9.89	10.24
mm	2	5.31	6
mm	3	9.89	6
mm	4	3.38	4
mm	5	5.19	6
n	1	21.05	18.86
n	2	18.08	12.99
n	3	16.96	18.7

n	4	21.34	14.46
n	5	12.24	13
nn	1	18.04	7
nn	2	20.08	8
nn	3	23.38	8
nn	4	7.13	9.16
p	1	11.89	8.43
p	2	6.56	19.03
p	3	2.88	2.49
p	4	8.46	1.38
p	5	5.71	3.71
q	1	10.42	6.31
q	2	9.92	3.93
q	3	3.36	11.85
q	4	16.83	11
r	1	1.74	4.98
r	2	15.98	9.85
r	3	5.82	5.95
r	4	4.31	10.84
s	1	4.55	24.63
s	2	2.49	13.88
s	3	4.39	6.96
s	4	14.71	8.97
t	1	11.68	21.86
t	2	17.92	21.04
t	3	28.13	14.99
t	4	18.51	14.08

v	1	16.87	11.69
v	2	15.97	15.76
v	3	23.4	10.16
v	4	21.53	12.9
x	1	12.63	11.64
x	2	12.34	1.53
x	3	15.79	12.11
x	4	32.14	9.51
y	1	14.15	5.84
y	2	9.1	10.98
y	3	23.02	12.73
y	4	8.49	11.07
z	1	6.82	7.99
z	2	19	7.85
z	3	7.73	6.33
z	4	1.62	1.96
z	5	6.71	4.12

Regional scale and β-diversity

Table S1 Diversity metrics at regional scale. ESR = Estimated Species Richness**.** β-c = among-sites diversity metric (β-diversity).

Metacommunity	ESR – Arboreal stratum	ESR – Herbaceous stratum	βc - Arboreal stratum	βc – Herbaceous stratum
a	18.01	19.56	1.11	1.43
aa	29.45	20.13	1.16	1.49

bb	17	11.57	1.1	1.4
c	21.21	30.9	1.17	1.83
cc	10.33	15.17	1.15	1.29
dd	16.63	13.07	1.01	1.2
e	28.68	17.37	1.24	1.39
ee	35.18	20.37	1.39	1.61
f	19.8	22.49	1.12	1.73
g	37.1	42.17	1.36	1.65
gg	30.83	23.85	1.17	1.78
h	28.48	28.34	1.09	1.6
ii	19.44	6.02	1.17	1.28
j	28.17	13.05	1.13	1.6
jj	60.4	23.64	1.21	1.74
k	27.79	30.85	1.17	1.88
kk	30.47	16.56	1.09	1.52
mm	19.36	13.55	1.08	1.74
n	22.8	22.89	1.09	1.37
nn	26.9	11.04	1.13	1.25
p	27.75	19.18	1.2	1.28
q	22.98	13.88	1.15	1.16
r	18.4	14.97	1.1	1.56
s	25.1	25.38	1.13	1.71
t	35.94	26.99	1.14	1.36
v	39.79	22.47	1.07	1.53
x	30.16	17.27	1.27	1.55
y	30.55	14.75	1.15	1.31
z	26.33	9.26	1.31	1.41

Model selection

Local scale

Table S3 Model selection statistics for all competing models at local scale (community). AICc refers to the corrected Akaike Information Criterion (AIC). Δi refers to the difference between a given AICc value and the lowest among competing models. AICc (W) refers to AICc "weight", being interpreted as the model's relative likelihood. R^2c refers to amount of variation explained by the entire model, both fixed and random components, whereas R^2m refers only to the fixed component. ADL = Average-diameter (dbh - cm) of largest white-popinac trees within a metacommunity (region); A = white-popinac patch's age-proxy (years); BA = white-popinac patch's basal area (m^2). S = strata (herbaceous and arboreal); D = community/patch distance (m); O = Origin (native/INNS); RE = random effects. Null models have y ~ 1 structure.

Model structure	**Distribution**	**AICc**	**AICc(wt)**	**Δi**	**R^2c**	**R^2m**
Species richness						
Null model 1	Gamma	1544.33	0.33	0	0.18	0
A + S + RE	Gamma	1545.71	0.17	1.37	0.18	0.01
BA + S + RE	Gamma	1545.81	0.16	1.47	0.18	0.01
ADL + S + RE	Gamma	1545.96	0.15	1.62	0.18	0.01
A + D + S + RE	Gamma	1547.73	0.06	3.39	0.19	0.01
BA + D + S + RE	Gamma	1547.77	0.06	3.43	0.19	0.01
ADL + D + S + RE	Gamma	1547.95	0.05	3.61	0.19	0.01
Null model 2	Gaussian	1583.31	0	38.97	0.19	0
ADL + S + RE	Gaussian	1583.70	0	39.36	0.20	0.01

BA + S + RE	Gaussian	1583.74	0	39.40	0.20	0.01
A + S + RE	Gaussian	1583.77	0	39.43	0.20	0.01
ADL + D + S + RE	Gaussian	1585.63	0	41.29	0.22	0.01
BA + D + S + RE	Gaussian	1585.67	0	41.33	0.22	0.01
A + D + S + RE	Gaussian	1585.76	0	41.43	0.22	0.01
Species richness - herbaceous stratum (native/INNS)						
ADL * O + RE	Gamma	1035.79	0.22	0	0.57	0.45
ADL * O + D + RE	Gamma	1035.88	0.21	0.09	0.57	0.46
A + O + D + RE	Gamma	1037.15	0.11	1.36	0.55	0.47
A + O + RE	Gamma	1037.67	0.08	1.87	0.56	0.45
BA + O + RE	Gamma	1038.26	0.06	2.46	0.56	0.45
BA + O + D + RE	Gamma	1038.27	0.06	2.48	0.56	0.46
BA * O + RE	Gamma	1038.99	0.04	3.20	0.56	0.45
ADL * O + D + RE	Gamma	1039.02	0.04	3.23	0.5	0.46
BA * O + D + RE	Gamma	1039.05	0.04	3.26	0.56	0.46
A * O + D + RE	Gamma	1039.22	0.03	3.42	0.55	0.47
ADL + O + RE	Gamma	1039.26	0.03	3.47	0.56	0.44
A * O + RE	Gamma	1039.73	0.03	3.93	0.56	0.45
A + O + RE	Gamma	1199.21	0	163.42	0.48	0.37
A * O + RE	Gaussian	1199.58	0	163.79	0.48	0.38
BA + O + RE	Gaussian	1200.31	0	164.52	0.48	0.37
ADL * O + RE	Gaussian	1200.68	0	164.89	0.49	0.37
ADL + O + RE	Gaussian	1200.69	0	164.90	0.48	0.36
A + O + D + RE	Gaussian	1200.91	0	165.11	0.47	0.37
A * O + D + RE	Gaussian	1201.30	0	165.51	0.48	0.38
BA + O + D + RE	Gaussian	1202.12	0	166.32	0.48	0.37

ADL + O + D + RE	Gaussian	1202.37	0	166.58	0.48	0.37
BA * O + RE	Gaussian	1202.39	0	166.59	0.48	0.37
ADL * O + D + RE	Gaussian	1202.39	0	166.60	0.48	0.37
Null model 1	Gaussian	1202.43	0	166.64	0.08	0
BA * O + D + RE	Gaussian	1204.21	0	168.41	0.48	0.37
Null model 2	Gaussian	1326.72	0	290.93	0.06	0
Relative tree/shrub abundance						
Null model	Beta	-70.15	0.34	0	0.64	0
BA + RE	Beta	-69.16	0.21	0.98	0.64	0.05
A + RE	Beta	-68.47	0.15	1.67	0.64	0.02
ADL + RE	Beta	-68.01	0.12	2.13	0.64	0
BA + D + RE	Beta	-67.03	0.07	3.11	0.64	0.05
A + D + RE	Beta	-66.29	0.05	3.85	0.64	0.02
ADL + D + RE	Beta	-65.84	0.04	4.30	0.64	0
Relative ground cover - native/INNS						
Null model	Beta	-26.26	0.35	0	0.99	0
ADL + RE	Beta	-25.39	0.23	0.87	0.99	0.05
A + RE	Beta	-24.14	0.12	2.11	0.99	0
BA + RE	Beta	-24.12	0.12	2.13	0.99	0
ADL + D + RE	Beta	-23.32	0.08	2.94	0.99	0.05
A + D + RE	Beta	-22.20	0.04	4.05	0.99	0
BA + D + RE	Beta	-22.18	0.04	4.07	0.99	0
White-popinac abundance (adult)						
BA + D + RE	Poisson	520.31	0.39	0	0.87	0.68

A + D + RE	Poisson	520.82	0.30	0.50	0.87	0.67
ADL + D + RE	Poisson	520.83	0.30	0.51	0.87	0.68
BA + RE	Poisson	654.79	0	134.47	0.79	0.08
Null model	Poisson	655.86	0	135.54	0.79	0
ADL + RE	Poisson	657.14	0	136.82	0.79	0.02
A + RE	Poisson	657.95	0	137.63	0.79	0
White-popinac's seedlings relative ground cover						
Null model	Beta	-292.32	0.33	0	0.09	0
BA + RE	Beta	-291.23	0.19	1.09	0.11	0.02
A + RE	Beta	-290.35	0.12	1.97	0.09	0
ADL + RE	Beta	-290.12	0.11	2.19	0.10	0
BA + D + RE	Beta	-289.85	0.09	2.47	0.20	0.04
A + D + RE	Beta	-289.03	0.06	3.29	0.19	0.02
ADL + D + RE	Beta	-289.00	0.06	3.32	0.19	0.02

Regional scale and β-diversity

Table S4 Model selection statistics for all competing models describing variation at regional scale (metacommunity) and β-diversity. (*) Models fitted with Poisson and Gamma distributions are with pseudo-R^2 values, whereas models fitted with Gamma distribution are associated with Nagelkerke R^2, which are mathematically different from a regular R^2, but may be interpreted in a similar way. Abbreviations as in Table S3.

Model structure	**Distribution**	**AICc**	**AICc(wt)**	**Δi**	**R^2 (*)**

Species richness					
BA + S	Gamma	411.02	0.44	0	0.20
ADL + S	Gamma	411.52	0.34	0.49	0.19
A + S	Gamma	412.69	0.19	1.67	0.17
BA + S	Gaussian	419.08	0	8.05	0.18
Null model 1	Gamma	419.12	0	8.10	0
ADL + S	Gaussian	419.77	0	8.74	0.17
A + S	Gaussian	420.73	0	9.71	0.16
Null model 2	Gaussian	426.72	0	15.70	0
Species richness (native/INNS)					
A * O	Gamma	375.40	0.23	0	0.88
A + O	Gamma	375.46	0.22	0.06	0.88
BA * O	Gamma	375.60	0.21	0.20	0.88
BA + O	Gamma	376.27	0.15	0.86	0.88
ADL + O	Gamma	377.04	0.10	1.64	0.88
ADL * O	Gamma	377.87	0.06	2.46	0.88
ADL + O	Gaussian	421.69	0	46.28	0.7
BA + O	Gaussian	421.82	0	46.41	0.78
A + O	Gaussian	422.03	0	46.6	0.78
BA * O	Gaussian	422.39	0	46.99	0.79
ADL * O	Gaussian	422.83	0	47.43	0.78
A * O	Gaussian	424.12	0	48.72	0.78
Null model 1	Gamma	476.33	0	100.93	0
Null model 2	Gaussian	506.18	0	130.78	0
Relative tree/shrub abundance					

Null model	Beta	-34.83	0.42	0	NA
BA	Beta	-34.03	0.28	0.80	0.05
ADL	Beta	-32.82	0.15	2.01	0.01
A	Beta	-32.53	0.13	2.29	0
White-popinac abundance (adult)					
BA	Poisson	472.24	0.99	0	0.52
Null model	Poisson	491.38	0	19.13	0
A	Poisson	493.32	0	21.07	0.01
ADL	Poisson	493.44	0	21.19	0.01
White-popinac's seedlings relative ground cover					
BA	Beta	-120.59	0.92	0	0.18
ADL	Beta	-114.30	0.04	6.29	0.1
Null model	Beta	-113.64	0.03	6.95	NA
A	Beta	-111.01	0.01	9.57	0
β-c					
ADL + S	Gamma	-60.17	0.66	0	0.63
BA + S	Gamma	-58.34	0.26	1.83	0.62
A + S	Gamma	-55.34	0.06	4.83	0.60
ADL + S	Gaussian	-50.26	0	9.91	0.60
BA + S	Gaussian	-48.11	0	12.06	0.58
A + S	Gaussian	-45.21	0	14.95	0.56
Null model 1	Gamma	-6.51	0	53.66	0
Null model 2	Gaussian	-1.83	0	58.34	0

List of recorded species

Table S5 All species (native and INNS) recorded in our floristic survey. Species tagged with (*) are INNS.

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 decubens *	(Stapf) 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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