

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.

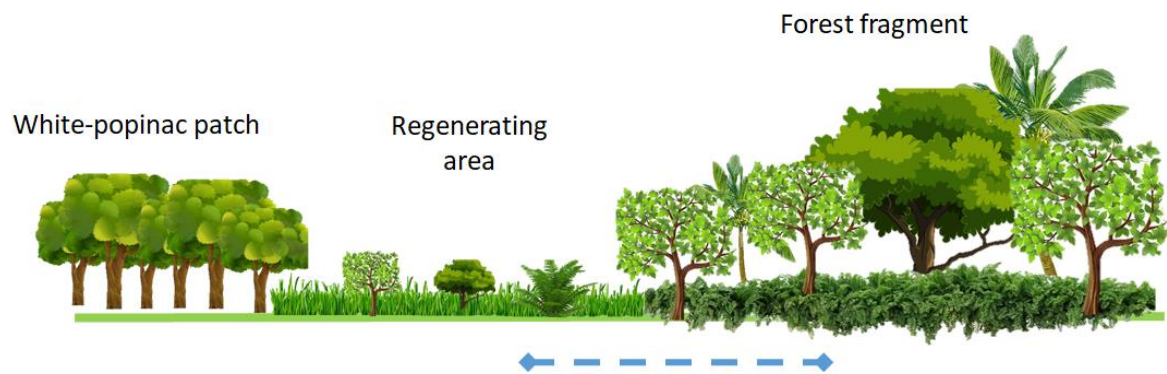


Fig. 1 Horizontal perspective of our regional sampling unit ($n = 29$). As time of invasion advances, the white-popinac patch is assumed to expand towards the regenerating area, and therefore affect (meta-) community dynamics.

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).

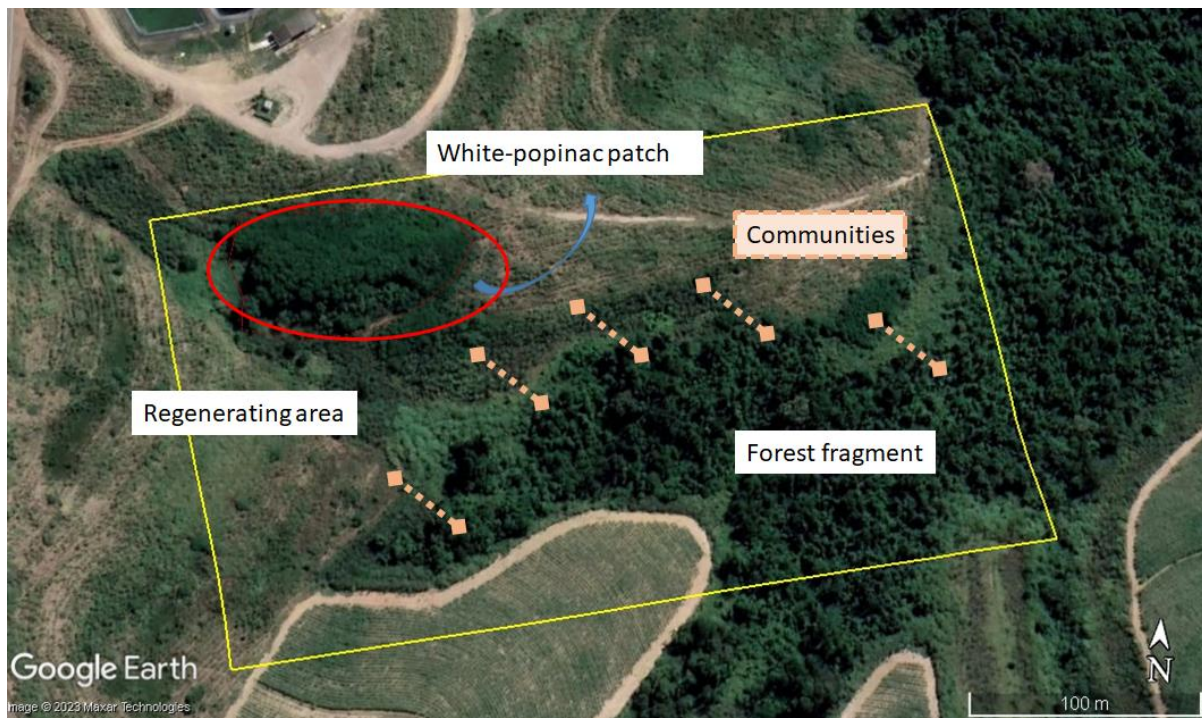


Fig. 2 Representation of our sampling design. The yellow rectangle delimits the sampling unit at the regional scale (metacommunity). The patch within the red ellipse is the white-popinac patch. Dotted lines are communities. A metacommunity ($n = 29$) was defined as a spatial unit composed of a forest 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 ($\text{dbh} > 2 \text{ cm}$) 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-poplinac 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., Δ_i , 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 (Δ_i 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

Model structure	Distri- bution	AICc	Δ i	AICc (W)	R ² c	R ² m
Species richness of the herbaceous stratum						
Time (ADL) * origin + RE	Gamma	1035.79	0	0.221	0.58	0.45

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

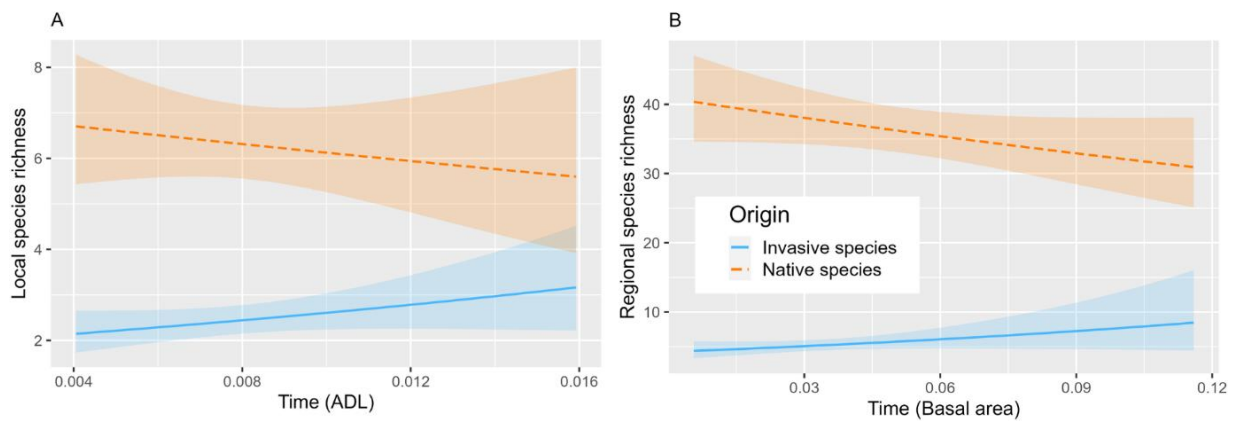


Fig. 3 Interaction plots representing the relationship between species richness and time conditional on origin (native species of INNS). **a.** Predicted relationship between local-scale species richness on herbaceous stratum and time conditional on origin. **b.** Predicted relationship between regional-scale 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.

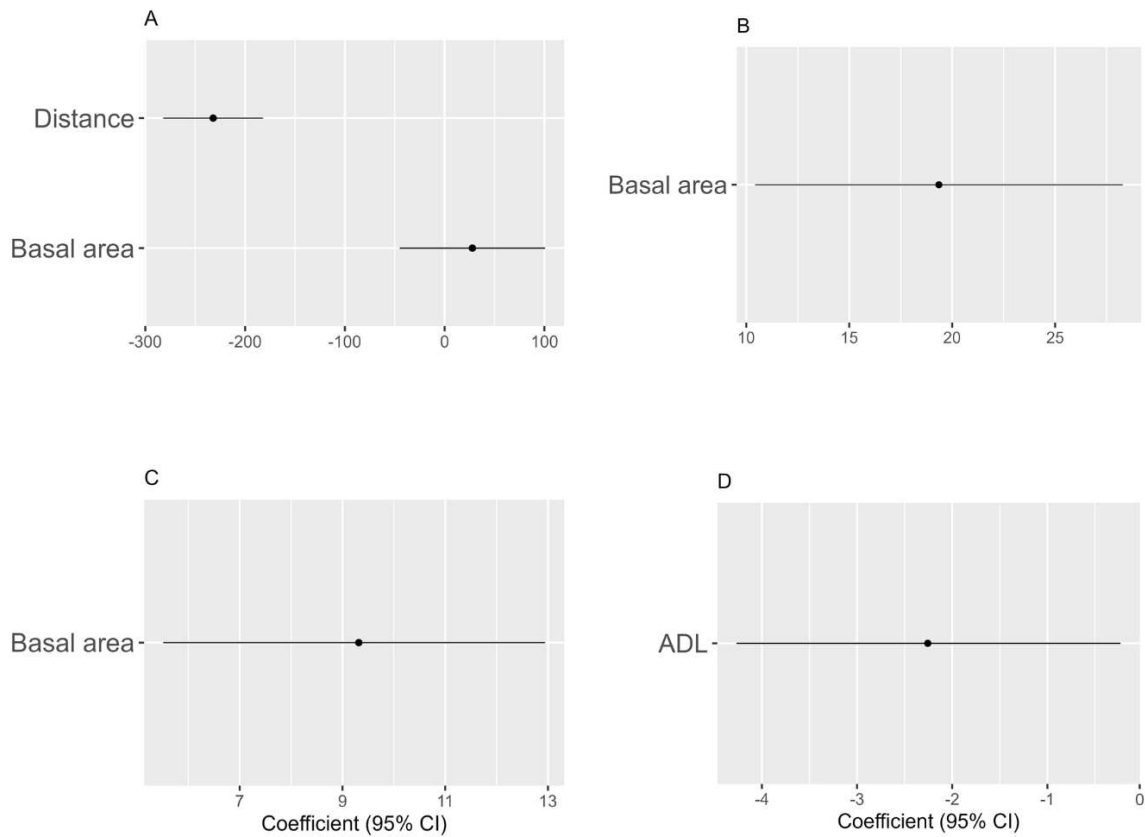


Fig. 4 Confidence interval (95%) plot describing parameter estimates of predictor variables related to: **a.** The abundance of white-popinac trees at regenerating communities (local scale). **b.** Relative (%) ground coverage by white-popinac seedlings on metacommunities (regional scale). **c.** Number 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 (similar 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. meta-communities), 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>.

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