Received: 13 May 2025 | Accepted: 24 October 2025

DOI: 10.1002/2688-8319.70156

Ecological Solutions and Evidence

RESEARCH ARTICLE

Widespread negative effects of *Leucaena leucocephala* (white-popinac) invasion on regenerating areas of the Atlantic Forest

Juliano Zardetto[1] | **Willian Simioni**[1] | **Tadeu Siqueira**[1,2]

[1]Institute of Biosciences, São Paulo State University (UNESP), Rio Claro, São Paulo, Brazil

[2]School of Biological Sciences, University of Canterbury, Christchurch, New Zealand

Correspondence
Juliano Zardetto
Email: juliano.zardetto@unesp.br

Funding information
Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: 309496/2021-7; Fundação de Amparo à Pesquisa do Estado de São Paulo, Grant/Award Number: 20/14104-6 and 21/00619-7

Handling Editor: Lutendo Mugwedi

Abstract

1. The use of invasive species in ecological restoration is controversial and has raised recent concerns. In Brazil, some ecosystem restoration and agroforestry projects have proposed using white-popinac (*Leucaena leucocephala* (Lam.) de Wit), a broadly distributed invasive species, as a promising option for areas where the soil is severely degraded. This recommendation is based on the premise that it may not necessarily disrupt natural regeneration processes, particularly in fragmented forests.
2. To address this uncertainty, we investigated its effects on the functional diversity of naturally regenerating forests dominated by invasive grasses within the Atlantic Forest domain. We conducted floristic surveys on the arboreal and herbaceous strata in 29 regenerating areas invaded by white-popinac, each with a unique time since invasion, thereby creating a gradient of invasion duration. We estimated the average seed mass of each regenerating area (CWM), as well as species richness and abundance of trees/shrubs and animal-dispersed species, and α and β functional metrics.
3. The progression of invasion led to (i) a major decrease in the average seed mass of native species, contrasted by an increase of this metric for invasive species; (ii) an increase in tree abundance, without increasing tree species richness; and (iii) a reduction in the richness of animal-dispersed species. Collectively, these results indicate that the natural regeneration trajectories of Atlantic Forest fragments can be strongly compromised by the advance of white-popinac invasions.
4. *Practical implication*. Our results highlight the need for early control measures and caution against using white-popinac in restoration, emphasizing the value of functional metrics in monitoring. Therefore, management protocols for the prevention and control of white-popinac must be implemented, and its use in restoration projects should not be advised.

KEYWORDS
functional traits, invasional meltdown, *leucena*, metacommunity ecology, restoration

1 | INTRODUCTION

The consequences of biological invasions for forest regeneration can be severe and often irreversible (Chiba De Castro et al., 2019; Dyderski & Jagodziński, 2020; Londe et al., 2017). Invasive species can drive native species to local and regional extinctions (Chase et al., 2020; Flory & Clay, 2010), resulting in the loss of functional traits (Flory & Clay, 2010; Guido et al., 2021; Loiola et al., 2018) and contributing to the homogenization of local communities (Renault et al., 2022). For example, larger-sized seeds may be lost in invaded areas (Gioria & Pyšek, 2015), and seed dispersal networks can be severely disrupted (Spotswood et al., 2012). Despite efforts to eradicate or control invasive species in forests or other vegetation types, legacy effects (Elgersma et al., 2011) and invasional meltdowns (Simberloff & Von Holle, 1999) are frequently observed, demonstrating that complete recovery from invasive species impacts is often unachievable (e.g. Chen & van Kleunen, 2022; Reynolds et al., 2017). In some cases, native species richness may not change substantially in invaded areas (Hejda et al., 2017; Krieger et al., 2022; Peng et al., 2019), leading to potential misinterpretations about the real impacts that invasive species have caused. This highlights the limitations of an exclusive taxonomical approach, which often overlooks the nuanced effects of invasive species on ecosystem functioning, underscoring the need for functional trait-based frameworks to fully assess these impacts (e.g. Hewitt et al., 2016). Despite the growing recognition of functional assessments, a critical gap remains in understanding how invasive species-driven alterations to functional traits and processes shape forest regeneration dynamics (Langmaier & Lapin, 2020; Lázaro-Lobo et al., 2021).

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

In Brazil, recent changes in environmental legislation have required landowners in rural areas to allocate portions of their property to native vegetation, typically by abandoning former pasturelands or plantations to facilitate natural forest regeneration (Brasil, 2012). White-popinac is a prevalent invasive species in these areas, often forming large, dense and homogeneous patches (de Melo-Silva et al., 2014; Werema & Wilson, 2022). These patches typically surround forest fragments, encroaching upon regenerating areas. Most regenerating areas are dominated by invasive grasses (Zardetto & Siqueira, 2024) and the density within white-popinac patches is so high that, over time, grasses and herbaceous species are displaced to the fragment edges (Hata et al., 2010; Osawa et al., 2016). This displacement results from competitive effects, such as reduced sunlight incidence, as well as known allelopathic effects (Kato-Noguchi & Kurniadie, 2022). Recently, Zardetto and Siqueira (2024) demonstrated that white-popinac invasions in naturally regenerating forests lead to biotic homogenization, reduced native species richness and increased susceptibility to further invasions by other non-native species.

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

Using a space-for-time substitution approach, we constructed a chronosequence of white-popinac invasion to assess how the progression of invasion over time influences natural regeneration, with a focus on the functional aspects of these regenerating forests. Specifically, we examined (i) the average seed mass in the regenerating areas, (ii) the balance between animal- and non-animal-dispersed species, (iii) shifts in the dominance of trees versus shrubs and (iv) the dynamics of functional α-diversity within the regenerating areas and β-diversity among transects. We hypothesized that as white-popinac invasion progresses, its impacts would increasingly disrupt the expected pathways of natural forest regeneration. In particular, we predicted that invaded sites would show a decline in large-seeded and animal-dispersed species, a shift towards shrub dominance and reduced functional α- and β-diversity; patterns that together would indicate impaired recovery processes and potential losses in ecosystem resilience.

2 | MATERIALS AND METHODS

2.1 | Sampling design

We conducted fieldwork on 38 private properties located in rural and peri-urban areas in the interior region of the state of São Paulo, southeastern Brazil. Each property contained naturally regenerating forests adjacent to at least one major patch of old-growth native

forest (Atlantic Forest domain) and one patch of white-popinac. Of these 38 private properties, we selected 29 to establish a temporal gradient of invasion for analysis. The other properties were not selected due to cattle access, recent wildfires or land management activities occurring during the surveys. Fieldwork was carried out between March 2020 and September 2022. Fieldwork was permitted via registration for collection of botanical, fungal or microbiological material (permit number 82299-1; legal context in ICMBio (2014)), and individual authorizations from owners of each private property.

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

Our sampling design incorporated two hierarchical scales of sampling units: the regenerating area itself ($n = 29$) and the transects within each regenerating area ($n = 131$). Both scales were systematically replicated to ensure consistent coverage. Regenerating areas were defined as abandoned pastures or agricultural lands that surrounded, at least partially, an old-growth forest patch and contained at least one patch of white-popinac. Within each regenerating area, we established four to five transects for sampling. Each transect measured 14 m × 2 m and was positioned at the interface between the forest fragment and its adjacent regenerating area, with 7 m extending into the forest fragment and 7 m into the regenerating area.

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

All recorded species were classified based on the following criteria: (i) dispersal mechanism, as either animal or non-animal dispersed (Van der Pijl, 1972); (ii) growth habit (JBRJ, 2025); and (iii) status as native or invasive in the study region, using information from established invasive species databases, including the Invasive Species Compendium, the Global Invasive Species Database and the Horus Institute for Environmental Conservation and Development. Further methodological details are provided in the Supplementary Information (SI) file.

2.2 | Response variables

We estimated species richness for animal- and non-animal-dispersed species as well as for trees and shrubs (Figure 1) using sample-coverage rarefaction and extrapolation methods in the iNext R package (v3.0.0; Chao et al., 2014; Hsieh et al., 2016). This analysis was conducted separately for the arboreal and the herbaceous strata. The observed abundance of each species in both strata, used to estimate species richness, was calculated as the sum of observed abundances across all transects within each regenerating area.

2.3 | Seed mass—Community-weighted mean

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

2.4 | Functional α-diversity

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

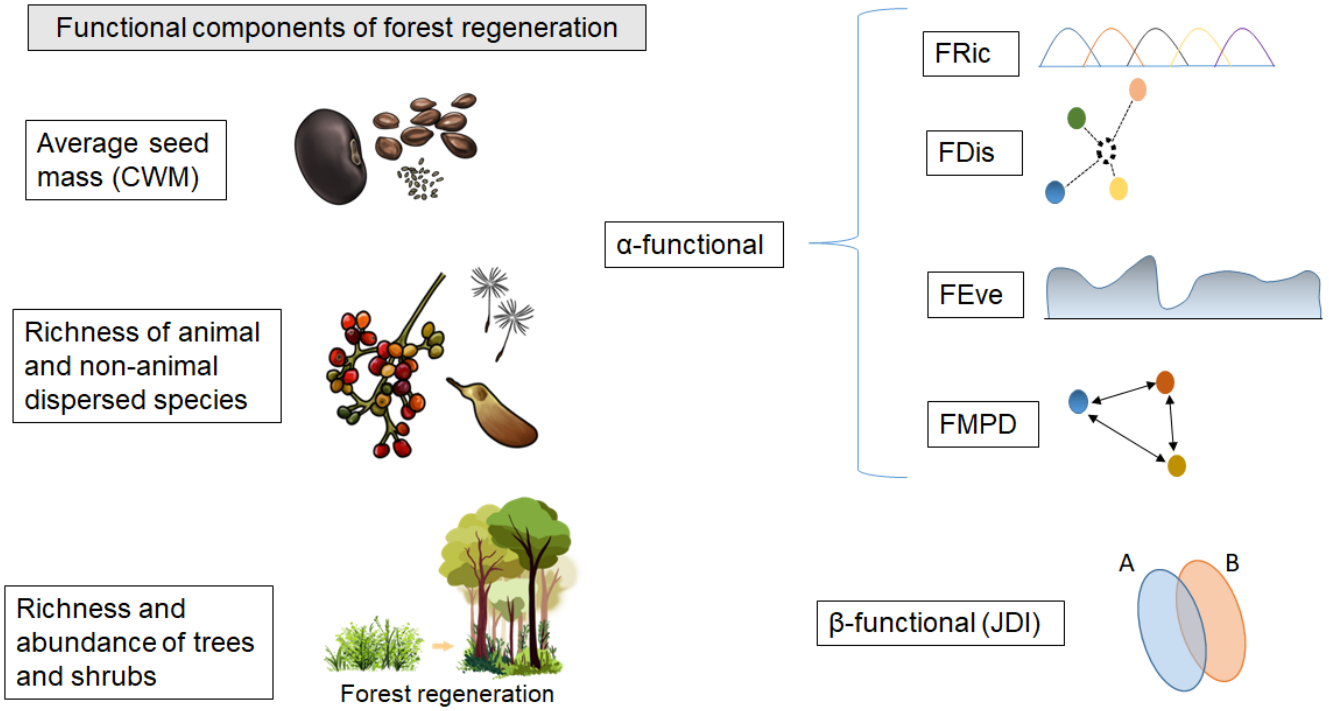

FIGURE 1 The response variables, representing functional components of forest natural regeneration. CWM, community-weighted mean; FDis, functional dispersion; FEve, functional evenness; FMPD, functional mean pairwise distance; FRic, functional richness; JDI, Jaccard's dissimilarity index.

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

2.5 | Functional β-diversity

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

2.6 | Predictor variables

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

2.7 | Data analysis

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

We employed generalized linear models (GLM) for each response variable, selecting distribution families based on the nature of the data (e.g. continuous, discrete or proportional). For example, for estimated species richness, we compared models using Gamma and

Gaussian distributions. Model selection followed an information-theoretic approach (Aho et al., 2014), using the corrected Akaike information criterion (AICc) and derived metrics (e.g. Δi, AICc weight) to rank models. Additional details on model structures, distribution families, selection criteria and the software and R packages used are provided in the SI file.

3 | RESULTS

In total, we recorded 328 plant species across both native and invasive categories, with 178 species identified in the arboreal stratum and 150 in the herbaceous stratum (Table S5). Twenty species could not be identified due to the absence of key taxonomic structures, particularly among deciduous species. The remaining 308 identified species were distributed across 218 genera and 73 families, with Fabaceae, Asteraceae and Malvaceae being the most represented in terms of species richness.

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

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

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

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

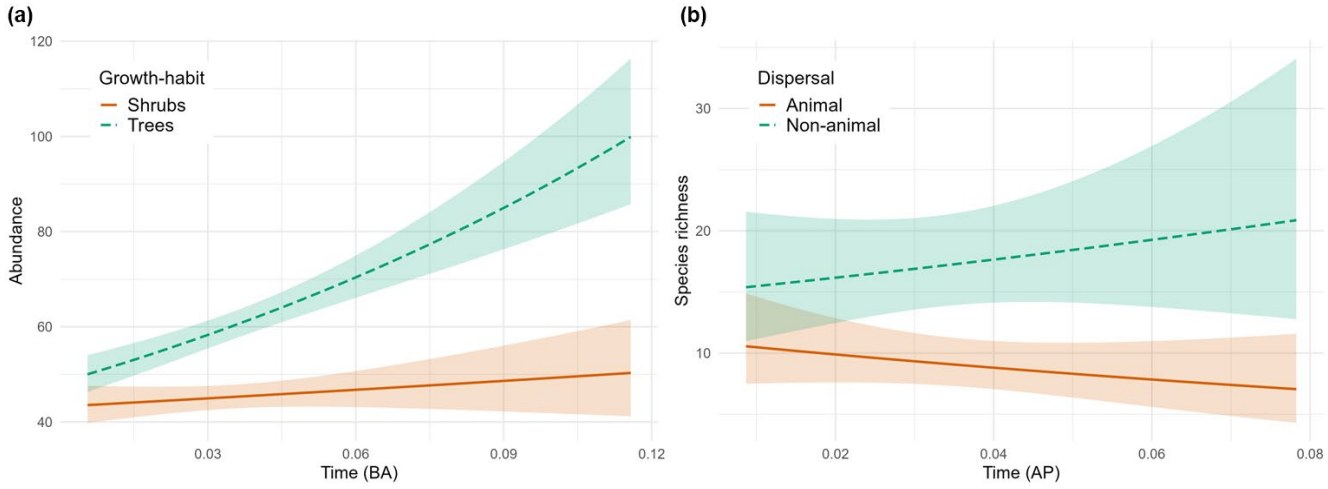

FIGURE 2 Interaction plots representing the response variable in function of time conditional on categorical variable. Values on *x*-axis are standardized. (a) Predicted total abundance of trees and shrubs in regenerating areas (model 1, Table 1). (b) Predicted species richness of animal and non-animal-dispersed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

TABLE 1 Model selection statistics for top-ranked models ($\Delta i < 2$).

Model structure	Distribution family	AICc	Δi	AICc (W)	R^{2*}
Abundance of trees and shrubs					
(1) Time (BA) × habit	Poisson	828.5	0	0.99	0.84
Species richness (trees and shrubs)					
(2) Time (BA) + habit	Gamma	335.5	0	0.35	0.48
(3) Time (AP) + habit	Gamma	336.4	0.94	0.22	0.47
(4) Time (ADL) + habit	Gamma	336.9	1.47	0.17	0.46
Seed mass (CWM) of native species					
(5) Time (AP) + strata	Gamma	518.6	0	0.79	0.83
Seed mass (CWM) of invasive species					
(6) Time (BA) + strata	Gamma	388.4	0	0.78	0.95
Species richness (animal and non-animal-dispersed species)					
(7) Time (ADL) + dispersal type + strata	Gamma	722.3	0	0.28	0.19
(8) Time (BA) + dispersal type + strata	Gamma	722.5	0.18	0.26	0.19
(9) Time (AP) + dispersal type + strata	Gamma	723.8	1.48	0.14	0.18
(10) Time (AP) × dispersal type + strata	Gamma	724.0	1.75	0.19	0.19

Note: AICc: corrected Akaike information criterion (AIC). Δi: difference between a given model's AICc and the AICc of the best-ranked model. AICc (W): Akaike weight, representing the relative likelihood of a given model. R^{2*}: pseudo-R^2 for Poisson and Beta models; Nagelkerke R^2 for Gamma models. ADL = average diameter at breast height (dbh) of the largest white-popinac trees within a regenerating area (cm). AP = age proxy of the white-popinac patch (years). BA = basal area of the white-popinac patch (m^2). Strata = herbaceous or arboreal. Dispersal type = animal-dispersed or non-animal-dispersed species. Habit = trees or shrubs.

and provided valuable insights into the potential effects of invasion on plant–animal interactions. Notably, both models suggest a decline in the richness of animal-dispersed species with increasing time since invasion.

4 | DISCUSSION

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

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

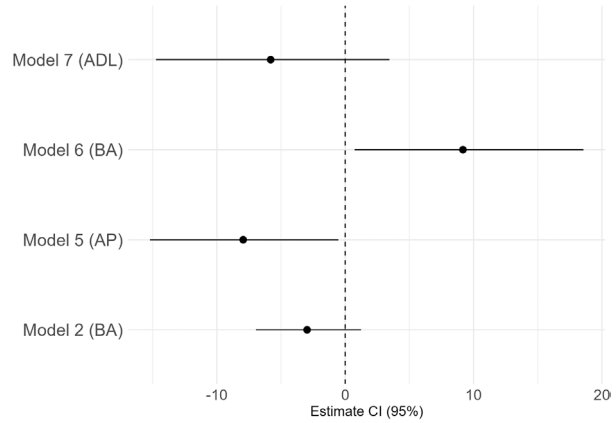

FIGURE 3 Confidence intervals (95%) from predicted estimates on selected additive models. Once each model has its own distribution family and link function, the values on x-axis are not standardized and cannot be directly compared among models. The plot shows whether the confidence intervals (CIs) include zero. The dashed vertical line represents zero; predictor effects whose CIs overlap this line are considered not statistically consistent. ADL, average diameter at breast height (dbh) of the largest white-popinac trees within a regenerating area (cm); AP, age proxy of the white-popinac patch (years); BA, basal area of the white-popinac patch (m^2).

This finding underscores a unique aspect of white-popinac invasions and warrants further investigation into the ecological implications of these trait-specific yet identity-driven dynamics.

The decrease in the richness of animal-dispersed species is a concerning effect of white popinac invasion, with potential cascading consequences, such as local extinctions of dispersers, shifts in species distribution and disrupted trophic interactions (Brodie et al., 2024; García & Martínez, 2012). This decline is partially driven by the exclusion of large-seeded, animal-dispersed species, which are replaced by small-seeded, non-animal-dispersed species, often wind-dispersed. These changes create a feedback loop: fewer animal-dispersed plants reduce local resource availability, leading to declines in animal dispersers, especially specialists, which further compromises seed dispersal processes (Culot et al., 2017; Wotton & Kelly, 2011). The remaining animal-dispersed species in older invaded areas were either primarily invasive species (e.g. *Psidium guajava* L., *Melia azedarach* L. and *Syzygium cumini* (L.) Skeels) or ruderal natives (e.g. *Solanum* spp., *Celtis iguanaea* (Jacq.) Sarg. and *Piper aduncum* L.). While the long-term consequences of these changes are known, including potential local extinctions of animal dispersers, the extent to which these impacts can be reversed remains uncertain.

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

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

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

AUTHOR CONTRIBUTIONS

Juliano Zardetto, Tadeu Siqueira and Willian Simioni analysed the data and wrote the paper; Juliano Zardetto and Tadeu Siqueira conceived the idea and designed fieldwork; Willian Simioni collected trait data for the species; Juliano Zardetto collected field data and identified the species.

ACKNOWLEDGEMENTS

The authors thank the São Paulo Research Foundation (FAPESP) for financial support (grants 21/00619-7 and 20/14104-6).

TS also acknowledges the National Council for Scientific and Technological Development (CNPq) for a research productivity grant (309496/2021-7).

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/2688-8319.70156.

DATA AVAILABILITY STATEMENT

All data and coding are available in https://doi.org/10.5281/zenodo.15392794 (Zardetto et al., 2025).

ORCID

Juliano Zardetto https://orcid.org/0000-0002-0258-4105
Willian Simioni https://orcid.org/0000-0001-8581-6655
Tadeu Siqueira https://orcid.org/0000-0001-5069-2904

REFERENCES

Aho, K., Derryberry, D., & Peterson, T. (2014). Model selection for ecologists: The worldviews of AIC and BIC. *Ecology*, *95*(3), 631–636.

Bageel, A., Honda, M. D. H., Carrillo, J. T., & Borthakur, D. (2020). Giant leucaena (*Leucaena leucocephala* subsp. *glabrata*): A versatile tree-legume for sustainable agroforestry. *Agroforestry Systems*, *94*(1), 251–268. https://doi.org/10.1007/s10457-019-00392-6

Bello, C., Galetti, M., Montan, D., Pizo, M. A., Mariguela, T. C., Culot, L., Bufalo, F., Labecca, F., Pedrosa, F., Constantini, R., Emer, C., Silva, W. R., da Silva, F. R., Ovaskainen, O., & Jordano, P. (2017). Atlantic frugivory: A plant–frugivore interaction data set for the Atlantic forest. *Ecology*, *98*(6), 1729. https://doi.org/10.1002/ecy.1818

Brasil. (2012). *Lei n. 12.651, de 25 de maio de 2012*.

Braun-Blanquet, J. (1964). *Pflanzensoziologie, Grundzüge der Vegetationskunde*. Springer-Verlag. https://doi.org/10.1007/978-3-7091-8110-2

Brodie, J. F., Bello, C., Emer, C., Galetti, M., Luskin, M. S., Osuri, A., Peres, C. A., Stoll, A., Villar, N., & López, A. B. (2024). Defaunation impacts on the carbon balance of tropical forests. *Conservation Biology*, *39*, 1–16. https://doi.org/10.1111/cobi.14414

Campanello, P. I., Genoveva Gatti, M., Ares, A., Montti, L., & Goldstein, G. (2007). Tree regeneration and microclimate in a liana and bamboo-dominated semideciduous Atlantic Forest. *Forest Ecology and Management*, *252*(1–3), 108–117. https://doi.org/10.1016/j.foreco.2007.06.032

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs*, *84*(1), 45–67. https://doi.org/10.1890/13-0133.1

Chase, J. M., Jeliazkov, A., Ladouceur, E., & Viana, D. S. (2020). Biodiversity conservation through the lens of metacommunity ecology. *Annals of the New York Academy of Sciences*, *1469*(1), 86–104. https://doi.org/10.1111/nyas.14378

Chen, D., & van Kleunen, M. (2022). Invasional meltdown mediated by plant–soil feedbacks may depend on community diversity. *New Phytologist*, *235*(4), 1589–1598. https://doi.org/10.1111/nph.18218

Chiba De Castro, W. A., Xavier, R. O., Garrido, F. H. L., Romero, J. H. C., Peres, C. K., & Da Luz, R. C. (2019). Fraying around the edges: Negative effects of the invasive *Tradescantia zebrina* Hort. ex Bosse (Commelinaceae) on tree regeneration in the Atlantic Forest under different competitive and environmental conditions. *Journal of Plant Ecology*, *12*(4), 713–721. https://doi.org/10.1093/jpe/rtz009

Costa, J. B. P., Melo, F. P. L., Santos, B. A., & Tabarelli, M. (2012). Reduced availability of large seeds constrains Atlantic forest regeneration. *Acta Oecologica*, *39*, 61–66. https://doi.org/10.1016/j.actao.2011.12.002

Costa, J. N. M. N., & Durigan, G. (2010). *Leucaena leucocephala* (Lam.) de Wit (Fabaceae): Invasora ou Ruderal? *Revista Árvore*, *34*(5), 825–833. https://doi.org/10.1590/S0100-67622010000500008

Culot, L., Bello, C., Batista, J. L. F., Do Couto, H. T. Z., & Galetti, M. (2017). Synergistic effects of seed disperser and predator loss on recruitment success and long-term consequences for carbon stocks in tropical rainforests. *Scientific Reports*, *7*(1), 1–8. https://doi.org/10.1038/s41598-017-08222-4

D'Antonio, C., & Meyerson, L. A. (2002). Exotic plant species as problems and solutions in ecological restoration: A synthesis. *Restoration Ecology*, *10*(4), 703–713. https://doi.org/10.1046/j.1526-100X.2002.01051.x

de Melo-Silva, C., Peres, M. P., Neto, J. N. M., Gonçalves, B. B., & Leal, I. A. B. (2014). Biologia reprodutiva de *L. leucocephala* (Lam.) R. de Wit (Fabaceae: Mimosoideae): Sucesso de uma espécie invasora. *Neotropical Biology & Conservation*, *9*(2), 91–97. https://doi.org/10.4013/nbc.2014.92.03

Drumond, M. A., & Ribaski, J. (2010). *Leucena (Leucaena leucocephala): Leguminosa de uso múltiplo para o semiárido brasileiro*. Embrapa Semiárido.

Dunwiddie, P. W., & Rogers, D. L. (2017). Rare species and aliens: Reconsidering non-native plants in the management of natural areas. *Restoration Ecology*, *25*, S164–S169. https://doi.org/10.1111/rec.12437

Dyderski, M. K., & Jagodziński, A. M. (2020). Impact of invasive tree species on natural regeneration species composition, diversity, and density. *Forests*, *11*(4), 456. https://doi.org/10.3390/F11040456

Elgersma, K. J., Ehrenfeld, J. G., Yu, S., & Vor, T. (2011). Legacy effects overwhelm the short-term effects of exotic plant invasion and restoration on soil microbial community structure, enzyme activities, and nitrogen cycling. *Oecologia*, *167*(3), 733–745. https://doi.org/10.1007/s00442-011-2022-0

Flory, S. L., & Clay, K. (2010). Non-native grass invasion suppresses forest succession. *Oecologia*, *164*(4), 1029–1038. https://doi.org/10.1007/s00442-010-1697-y

Galetti, M., Donatti, C. I., Pires, A. S., Guimarães, P. R., & Jordano, P. (2006). Seed survival and dispersal of an endemic Atlantic forest palm: The combined effects of defaunation and forest fragmentation. *Botanical Journal of the Linnean Society*, *151*(1), 141–149. https://doi.org/10.1111/j.1095-8339.2006.00529.x

García, D., & Martínez, D. (2012). Species richness matters for the quality of ecosystem services: A test using seed dispersal by frugivorous birds. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1740), 3106–3113. https://doi.org/10.1098/rspb.2012.0175

Gioria, M., & Pyšek, P. (2015). The legacy of plant invasions: Changes in the soil seed bank of invaded plant communities. *BioScience*, *66*(1), 40–53. https://doi.org/10.1093/biosci/biv165

GISD. (2015). Species profile *Leucaena leucocephala*. http://www.iucngisd.org/gisd/species.php?sc=23

Guido, A., Blanco, C. C., & Pillar, V. D. (2021). Disentangling by additive partitioning the effects of invasive species on the functional structure of communities. *Journal of Vegetation Science*, *32*(2), e13004. https://doi.org/10.1111/jvs.13004

Hata, K., Suzuki, J. I., & Kachi, N. (2010). Fine-scale spatial distribution of seedling establishment of the invasive plant, *Leucaena leucocephala*, on an oceanic Island after feral goat extermination. *Weed Research*, *50*(5), 472–480. https://doi.org/10.1111/j.1365-3180.2010.00795.x

Hejda, M., Hanzelka, J., Kadlec, T., Štrobl, M., Pyšek, P., & Reif, J. (2017). Impacts of an invasive tree across trophic levels: Species richness, community composition and resident species' traits. *Diversity and Distributions*, *23*(9), 997–1007. https://doi.org/10.1111/ddi.12596

Hewitt, J. E., Norkko, J., Kauppi, L., Villnäs, A., Norkko, A., & Al, H. E. T. (2016). Scale change and an invasive species. *Ecosphere*, *7*, 1–11.

Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, *7*(12), 1451–1456. https://doi.org/10.1111/2041-210X.12613

ICMBio. (2014). *Instrução Normativa nO. 03, de 12 de setembro de 2014*.

Ishihara, K. L., Honda, M. D. H., Bageel, A., & Borthakur, D. (2018). *Leucaena leucocephala: A leguminous tree suitable for eroded habitats of Hawaiian islands*. https://doi.org/10.1007/978-981-10-8043-2_18

JBRJ. (2025). *Flora e Funga do Brasil*. http://floradobrasil.jbrj.gov.br

Kato-Noguchi, H., & Kurniadie, D. (2022). Allelopathy and allelochemicals of *Leucaena leucocephala* as an invasive plant species. *Plants*, *11*(19), 1–15. https://doi.org/10.3390/plants11192551

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., Abedi, M., Acosta, A. T. R., Adamidis, G. C., Adamson, K., Aiba, M., Albert, C. H., Alcántara, J. M., Alcázar C, C., Aleixo, I., Ali, H., … Wirth, C. (2020). TRY plant trait database—Enhanced coverage and open access. *Global Change Biology*, *26*(1), 119–188. https://doi.org/10.1111/gcb.14904

Krieger, M. T., Ditton, J., Albrecht, H., Baaij, B. M., Kollmann, J., & Teixeira, L. H. (2022). Controlling the abundance of a native invasive plant does not affect species richness or functional diversity of wet grasslands. *Applied Vegetation Science*, *25*(3), 1–13. https://doi.org/10.1111/avsc.12676

Langmaier, M., & Lapin, K. (2020). A systematic review of the impact of invasive alien plants on forest regeneration in European temperate forests. *Frontiers in Plant Science*, *11*(September), 1–15. https://doi.org/10.3389/fpls.2020.524969

Lázaro-Lobo, A., Lucardi, R. D., Ramirez-Reyes, C., & Ervin, G. N. (2021). Region-wide assessment of fine-scale associations between invasive plants and forest regeneration. *Forest Ecology and Management*, *483*(August 2020), 118930. https://doi.org/10.1016/j.foreco.2021.118930

Leão, T. C. C., Almeida, W. R., Dechoum, M., & Ziller, S. R. (2011). *Espécies Exóticas Invasoras no Nordeste do Brasil*.

Loiola, P. P., de Bello, F., Chytrý, M., Götzenberger, L., Carmona, C. P., Pyšek, P., & Lososová, Z. (2018). Invaders among locals: Alien species decrease phylogenetic and functional diversity while increasing dissimilarity among native community members. *Journal of Ecology*, *106*(6), 2230–2241. https://doi.org/10.1111/1365-2745.12986

Londe, V., de Sousa, H. C., & Kozovits, A. R. (2017). Exotic and invasive species compromise the seed bank and seed rain dynamics in forests undergoing restoration at urban regions. *Journal of Forestry Research*, *28*(5), 1019–1026. https://doi.org/10.1007/s11676-017-0370-2

Lorenzi, H. (2016). *Árvores brasileiras: Manual de identificação e cultivo de plantas arbóreas nativas do Brasil*. Instituto Plantarum de Estudos da Flora.

Lorenzi, H. (2020). *Árvores brasileiras: Manual de identificação e cultivo de plantas arbóreas nativas do Brasil*. Instituto Plantarum de Estudos da Flora.

Lorenzi, H. (2021). *Árvores brasileiras: Manual de identificação e cultivo de plantas arbóreas nativas do Brasil*. Instituto Plantarum de Estudos da Flora.

Magneville, C., Loiseau, N., Albouy, C., Casajus, N., Claverie, T., Escalas, A., Leprieur, F., Maire, E., Mouillot, D., & Villéger, S. (2022). mFD: An R package to compute and illustrate the multiple facets of functional diversity. *Ecography*, *2022*(1), 1–15. https://doi.org/10.1111/ecog.05904

Melo, F. P. L., Lemire, D., & Tabarelli, M. (2007). Extirpation of large-seeded seedlings from the edge of a large Brazilian Atlantic forest fragment. *Ecoscience*, *14*(1), 124–129. https://doi.org/10.2980/1195-6860(2007)14[124:EOLSFT]2.0.CO;2

Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H., & Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, *28*(3), 167–177. https://doi.org/10.1016/j.tree.2012.10.004

Osawa, T., Hata, K., & Kachi, N. (2016). Eradication of feral goats enhances expansion of the invasive shrub *Leucaena leucocephala* on Nakoudo-jima, an oceanic Island. *Weed Research*, *56*(2), 168–178. https://doi.org/10.1111/wre.12198

Peng, S., Kinlock, N. L., Gurevitch, J., & Peng, S. (2019). Correlation of native and exotic species richness: A global meta-analysis finds no invasion paradox across scales. *Ecology*, *100*(1), 1–10. https://doi.org/10.1002/ecy.2552

Pyšek, P., Hulme, P. E., Simberloff, D., Bacher, S., Blackburn, T. M., Carlton, J. T., Dawson, W., Essl, F., Foxcroft, L. C., Genovesi, P., Jeschke, J. M., Kühn, I., Liebhold, A. M., Mandrak, N. E., Meyerson, L. A., Pauchard, A., Pergl, J., Roy, H. E., Seebens, H., … Richardson, D. M. (2020). Scientists' warning on invasive alien species. *Biological Reviews*, *95*(6), 1511–1534. https://doi.org/10.1111/brv.12627

Renault, D., Hess, M. C. M., Braschi, J., Cuthbert, R. N., Sperandii, M. G., Bazzichetto, M., Chabrerie, O., Thiébaut, G., Buisson, E., Grandjean, F., Bittebiere, A. K., Mouchet, M., & Massol, F. (2022). Advancing biological invasion hypothesis testing using functional diversity indices. *Science of the Total Environment*, *834*, 155102. https://doi.org/10.1016/j.scitotenv.2022.155102

Reynolds, P. L., Glanz, J., Yang, S., Hann, C., Couture, J., & Grosholz, E. (2017). Ghost of invasion past: Legacy effects on community disassembly following eradication of an invasive ecosystem engineer. *Ecosphere*, *8*(3), e01711. https://doi.org/10.1002/ecs2.1711

Schlaepfer, M. A., Sax, D. F., & Olden, J. D. (2011). The potential conservation value of non-native species. *Conservation Biology*, *25*, 428–437. https://doi.org/10.1111/j.1523-1739.2010.01646.x

Sharma, P., Kaur, A., Batish, D. R., Kaur, S., & Chauhan, B. S. (2022). Critical insights into the ecological and invasive attributes of *Leucaena leucocephala*, a tropical agroforestry species. *Frontiers in Agronomy*, *4*(May), 1–15. https://doi.org/10.3389/fagro.2022.890992

Silva, S. C., Valadao, M. B. X., Inkotte, J., Ribeiro, F. P., Miguel, E. P., & Gatto, A. (2023). Legal provision on the use of exotic species in forest restoration: Eucalyptus leaf decomposition in different Brazilian savannah formations. *Australian Journal of Crop Science*, *17*(1), 14–19.

Simberloff, D., & Von Holle, B. (1999). Positive interactions of nonindigenous species: Invasional meltdown? *Biological Invasions*, *1*(1), 21–32. https://doi.org/10.1023/A:1010086329619

Siminski, A., Zambiazi, D. C., dos Santos, K. L., & Fantini, A. C. (2021). Dynamics of natural regeneration: Implications for landscape restoration in the Atlantic Forest, Brazil. *Frontiers in Forests and Global Change*, *4*(March), 1–15. https://doi.org/10.3389/ffgc.2021.576908

Singh, K., Byun, C., & Bux, F. (2022). Ecological restoration of degraded ecosystems in India: Science and practices. *Ecological Engineering*, *182*(109), 106708. https://doi.org/10.1016/j.ecoleng.2022.106708

Sonkoly, J., Deák, B., Valkó, O., Molnár, V. A., Tóthmérész, B., & Török, P. (2017). Do large-seeded herbs have a small range size? The seed mass–distribution range trade-off hypothesis. *Ecology and Evolution*, *7*(24), 11204–11212. https://doi.org/10.1002/ece3.3568

Spotswood, E. N., Meyer, J. Y., & Bartolome, J. W. (2012). An invasive tree alters the structure of seed dispersal networks between birds and plants in French Polynesia. *Journal of Biogeography*, *39*(11), 2007–2020. https://doi.org/10.1111/j.1365-2699.2012.02688.x

Van der Pijl, L. (1972). *Principles of dispersal in higher plants*. Springer-Verlang. https://doi.org/10.1093/forestscience/16.4.499

Villéger, S., Grenouillet, G., & Brosse, S. (2013). Decomposing functional β-diversity reveals that low functional β-diversity is driven by low functional turnover in European fish assemblages. *Global Ecology and Biogeography*, *22*(6), 671–681. https://doi.org/10.1111/geb.12021

Webb, C. O., Ackerly, D. D., McPeek, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, *33*, 475–505. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448

Werden, L. K., Holl, K. D., Rosales, J. A., Sylvester, J. M., & Zahawi, R. A. (2020). Effects of dispersal- and niche-based factors on tree recruitment in tropical wet forest restoration. *Ecological Applications*, *30*, e02139. https://doi.org/10.1002/eap.2139

Werema, C., & Wilson, C. (2022). Avian use of habitat patches dominated by exotic *Leucaena leucocephala* or native tree species in urban Dar es Salaam, Tanzania. *Tanzania Journal of Science*, *48*(2), 402–413. https://doi.org/10.4314/tjs.v48i2.15

Wolfe, B. T., & Van Bloem, S. J. (2012). Subtropical dry forest regeneration in grass-invaded areas of Puerto Rico: Understanding why *Leucaena leucocephala* dominates and native species fail. *Forest Ecology and Management*, *267*, 253–261. https://doi.org/10.1016/j.foreco.2011.12.015

Wotton, D. M., & Kelly, D. (2011). Frugivore loss limits recruitment of large-seeded trees. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1723), 3345–3354. https://doi.org/10.1098/rspb.2011.0185

Zardetto, J., Simioni, W., & Siqueira, T. (2025). Pervasive negative effects of *Leucaena leucocephala* (white-popinac) invasion on regenerating areas of the Atlantic Forest. *Zenodo*, https://doi.org/10.5281/zenodo.15392794

Zardetto, J., & Siqueira, T. (2024). The effects of white-popinac on regenerating seasonal semideciduous forests propagate across spatial scales. *Biological Invasions*, *26*(5), 1457–1470. https://doi.org/10.1007/s10530-024-03257-x

Zenni, R. D., & Ziller, S. R. (2011). An overview of invasive plants in Brazil. *Revista Brasileira de Botânica*, *34*(3), 431–446. https://doi.org/10.1590/S0100-84042011000300016

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Spearman's correlation coefficients among our time-related predictor variables.

Table S2: Quality index of functional spaces for 328 species in 131 communities (transects) assessed using the mean absolute deviation (MAD) and the root of mean squared deviation (RMSD) from one to ten dimensions.

Table S3: Diversity metrics in each regenerating area.

Table S4: Model selection statistics for all competing models.

Table S5: All species (native and IS) recorded in our floristic survey.

Figure S1: Location of our study region.

Figure S2: Representation of our sampling units.

Figure S3: Diagram of transect division into grids.

Figure S4: Diagram representing the inclusion criterion of trees and shrubs regarding the transect area.

Figure S5: Conceptual approach to species richness estimation on the regenerating area's scale.

Figure S6: Quality representation for four functional spaces for 328 species in 131 communities (transects) assessed using the mean absolute deviation (MAD) from one to ten dimensions.

How to cite this article: Zardetto, J., Simioni, W., & Siqueira, T. (2025). Widespread negative effects of *Leucaena leucocephala* (white-popinac) invasion on regenerating areas of the Atlantic Forest. *Ecological Solutions and Evidence*, *6*, e70156. https://doi.org/10.1002/2688-8319.70156