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Monitoring of forest components reveals that exotic tree species are not always invasive in areas under ecological restoration

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Abstract Exotic species are known to become invasive in several ecosystems, including areas undergoing restoration. But does that always happen? We monitored the tree layer, seed rain, and regenerating layer of 10-year and 20-year-old forests under restoration in southeast Brazil to verify if planted exotic trees were behaving as invasive; if they were influencing the species richness and abundance of regenerating native plants; and the probabilities of exotic trees perpetuating over time. Data from the three forest components (trees, seed rain, and regenerating) were collected in 12 permanent plots of 100 m^2 each in each study area. Collected data were analyzed through generalized linear models (GLM) and Markov chains. We verified that exotic species were not behaving as invasive species. Of the five species planted, *Acacia mangium*, *Syzygium cumini*, and *Psidium guajava* were dispersing seeds but recruiting only six new individuals. In general, the species richness and abundance of exotic trees were not related to the richness and abundance of regenerating native plants. In addition, the chances of individuals' transition between forest components were in most cases nil, so that exotic species should continue not to spread in the 10- and 20-year-old forests. We assume that biotic resistance was occurring in the assembled communities and this prevented exotic trees from behaving as invaders. Monitoring of forest components helped to better understand the role of non-native species in the dynamics of these novel ecosystems. Monitoring also indicated that not all recovering forests need management actions against exotic trees after a decade or two of restoration.

Keywords Biological invasion · Biotic resistance · Ecological indicators · Regenerating plants · Seed rain · Tree layer

Introduction

Ecological restoration is now a consolidated practice, and ambitious goals of restoration have been developed aiming to recover degraded ecosystems in many countries (Bonn Challenge 2014). Ecological restoration is understood as an intentional activity which initiates or accelerates the recovery of an ecosystem in relation to its health, integrity, and sustainability (SER 2004). Distinct objectives can be defined when a restoration action is implemented (e.g., to restore functionality and/or diversity), but in general attempts to return the ecosystem to its historic trajectory (SER 2004).

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During the ecological restoration process, which demands time, some events may occur and modify the intended trajectory. The occurrence of fires and invasion by exotic species are circumstances which affect the development of areas under restoration, resulting, for example, in the dominance of one or a few plant species (Lamb and Gilmour 2003). Indeed, a great challenge in ecological restoration is to create plant communities which are resistant to invasion by exotic species (Funk et al. 2008).

Restoration practitioners are mainly concerned with exotic species because these species can alter successional processes and prevent the formation of native communities (D'Antonio and Meyerson 2002). However, there are circumstances in which the use of exotic species can be tolerated and generate some benefits (Ewel and Putz 2004), such as in very degraded sites where native species are not able to survive or perform their functions (D'Antonio and Meyerson 2002). Nevertheless, it is a fact that there is always an inherent risk when using exotic species in restoration projects (Ewel and Putz 2004), but this was a common practice a few years ago when the science of restoration ecology was still developing (Lamb et al. 2005).

The use of exotic species in restoration projects is currently not advisable given the history of problems that many species have caused (Ziller and Zalba 2007). On the other hand, older restoration areas where exotic species were intentionally introduced can serve as a source for testing for biological invasion-related hypotheses, as well as to better understand the invasion process and why some invasive species fail in some areas but do not fail in other areas (Zenni and Nuñez 2013).

Although many studies have reported the implications of exotic plant species for restoration (Funk et al. 2008; Le Maitre et al. 2011; Reid et al. 2009), few case studies actually prove how exotic species behave in areas under restoration, especially trees (an example in Hakim and Miyakawa 2015). Thus, further investigations are needed for a better understanding about the invasiveness of exotic species in areas under restoration. In addition, studies of this nature can contribute to develop more flexible management strategies (Prévot-Julliard et al. 2011) and improve our understanding about the biodiversity capacity of these novel ecosystems (Svenning 2018).

That said, the objective of this study was to investigate whether exotic tree species intentionally planted in forests under restoration in southeast Brazil were behaving as invasive species, meaning if their populations have successfully increased in this new environment (Levine 2008). To do so, we monitored and evaluated the tree layer, seed rain, and regenerating layer in three forests under restoration of 10 and 20 years of age. Then, we tested the following hypotheses: (i) if planted exotic species are behaving as invaders, then they are investing greatly in seeds and recruiting many new individuals; (ii) the exotic trees are negatively affecting the recruitment of native plant species (regenerating layer); and (iii) the probability of perpetuation of exotic species between forest components is high in the forests under restoration.

Materials and methods

Study areas

We studied three forests undergoing restoration around the reservoir of the "Volta Grande" Hydroelectric Power Plant between the states of Minas Gerais and São Paulo, southeast Brazil (Fig. 1). The maximum distance between the forests was about 39 km. Although these forests were near the power plant reservoir, they were not considered riparian zones because forests were planted in these sites after the creation of the reservoir. Riparian zones were not present in these sites before the dam construction. Thus, our results are applicable to a broad of areas not influenced by reservoirs. The areas under restoration were formerly used for agriculture, mainly for sugarcane plantation.

The climate in the region is classified as Köppen's Cwa (Alvares et al. 2013): tropical with hot summers and dry winters. Climatic data obtained from the nearest climatic station (in the city of Uberaba, Minas Gerais) from 1987 to 2017 (INMET 2018) presented an average annual precipitation of 1635.68 mm, average maximum temperature of 29.8 °C, and an average minimum temperature of 16.9 °C. The forests under restoration are about 500 m above sea level.

The study areas are in the process of restoration by the active method, which means weeds were removed leaving the soil bare and saplings of native and exotic tree species were planted, about 35 species in each area, with most of them being native (± 30 species). After planting the saplings, weed control was carried out to prevent reinfestation and increase the saplings' survival chances. The identities of all planted species as well as

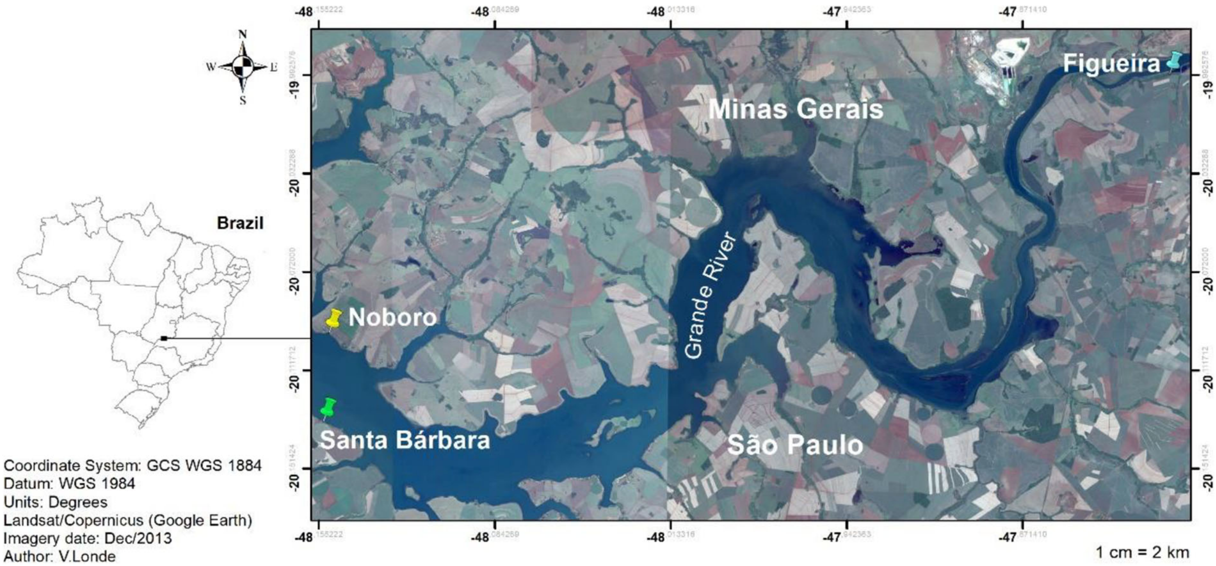

Fig. 1 Location of the forests under restoration of Noboro, Santa Bárbara, and Figueira around the reservoir of the "Volta Grande" hydroelectric power plant between the states of Minas Gerais and São Paulo, southeast Brazil

the planting density are unknown (we did not find any records with these information), but the saplings planted were produced in a nursery of the company responsible for the hydroelectric plant (CEMIG). The exotic species *Acacia mangium* Willd., *Mangifera indica* L., *Morus nigra* L., *Psidium guajava* L., and *Syzygium cumini* L. Skeels were planted in the areas in order to attract fauna (personal communication of a CEMIG's employee). These areas were recovered aiming to protect the reservoir's banks from erosion and comply with environmental legislation.

Two forests under restoration were 20 years of age (called "Noboro" and "Figueira"), and the other was 10-year-old ("Santa Bárbara") (Fig. 1). Noboro is 30 m wide and 1.17 km long, Santa Bárbara is 30 m wide and 1.83 km long, and Figueira is 100 m wide and 2.08 km long. The forests under restoration were in agricultural matrices and surrounded by sugarcane and rubber tree plantations. Thus, the forest cover of the surrounding area was low—about 45% in Noboro (mainly plantation forests) and 10% in Santa Bárbara and Figueira (secondary forest remnants) (Londe et al. 2020). The forests studied were part of a larger project that aimed to assess the effectiveness of some areas recovered by the power production company in partnership with local owners. The study areas were chosen jointly by researchers from the Federal University of Ouro Preto and employees of the power production company.

Experimental design

We installed 12 permanent plots of 100 m^2 each (1200 m^2) in each study area. The plots were systematically distributed, creating four blocks with three parallel plots in each (Fig. 2). These blocks were 100 m apart, and the parallel plots were contiguous in the study areas of Noboro and Santa Bárbara (of 30 m wide) and 20 m apart in the study area of Figueira (100 m wide). Next, all trees with diameter at breast height (DBH at 1.3 m) equal or greater than 3.18 cm were marked using numbered aluminum plates to monitor and assess the tree layer. Botanical materials with reproductive structures were then collected for herborization and identification of species from February 2013 to December 2014. All individuals with DBH (at 1.3 m) equal to or lesser than 1.59 cm were also marked and identified to estimate the regenerating layer, i.e., arboreal plants naturally growing in the understory.

Seed traps of 1 m^2 made of iron bars and 2 mm nylon mesh were installed in the middle of each sample plot to estimate seed rain. The seed traps were about 80 cm high and fixed with PVC bars. We carried out monthly collections of all material deposited inside the seed traps from April 2013 to March 2014. Seed traps damaged by storms or intruders were replaced when damage occurred. The material inside seed traps was packed in identified plastic bags and taken to the laboratory for seed and fruit separation. Seeds/fruits partially eaten by

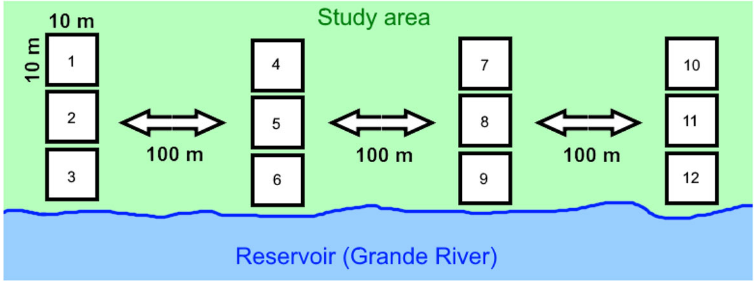

Fig. 2 Diagram of the experimental design used to collect data in forests under restoration around the reservoir of the Volta Grande hydroelectric power plant, southeast Brazil. The numbered squares represent the sampling plots (100 m^2 each), and the arrows represent the distance (100 m) between blocks of sampling plots

animals were only accounted when it was possible to identify the species or genus they belonged. Seeds/fruits were grouped by morphotypes until their identification at the level of genus and/or species.

The specimens sampled in the tree layer, seed rain, and regenerating layer were identified by our own experience, through comparisons with herbarium voucher specimens previously deposited in herbaria and by consulting specialists and literature (IPÊ 2016; IPEF 2016; Lopes 2012; Lorenzi 1998, 2009a, b). The genera and species were named according to World Flora Online (2019) platform and families according to Angiosperm Phylogeny Group IV (2016). The botanical material collected was deposited at the Herbaria "Professor José Badini" (OUPR) of the Federal University of Ouro Preto, Ouro Preto city, Minas Gerais state.

Data analysis

We graphically compared the composition of exotic species and the number of exotic individuals of the three forest components (trees, seed rain, and regenerating) to verify which exotic species were inhabiting the forests under restoration and quantify the investment in seeds/fruits and recruitment of new individuals by adult exotic trees.

Then, regression analyses were performed through generalized linear models (GLM, with normal distribution and identity function) to determine if the adult (flowering) exotic species were negatively affecting the species richness and abundance of the regenerating layer. We used GLM because these models are more appropriate for non-normal and heterogeneous data (Logan 2010). Assumptions of normality and homogeneity of variances were previously checked by Kolmogorov-Smirnov and Levene' tests, respectively (Hammer 2019). The species richness and abundance of adult exotic species were used as independent variables and the species richness and abundance of regenerating native plants as dependent variables in performing the regression analyses. These statistical tests were performed in SPSS 23 software (IBM, Armonk, NY, USA).

The probabilities of perpetuation of the exotic species in the forests under restoration were estimated through Markov chains. A Markov chain is a stochastic model that describes a sequence of possible events in which the probability of each event depends on the state reached in the previous event (Gagniuc 2017). As a stochastic model, the Markov chains have many applications on the processes of the real world. They are useful in the study fields such as meteorology, ecology, and computer science (Powell and Lehe 2014).

The abundance of trees, seeds, and regenerating individuals of the exotic species in each restoration area were used to build the transition matrices necessary for calculating the probabilities. Thus, we had one independent transition matrix for each forest under restoration. Each forest component was considered a state in the matrix. Each matrix had three columns (trees, seed rain, and regenerating) and three rows (abundance of individuals/seeds in each state). Then, the chances of transition between states (i.e., forest components) were calculated, for example, the probability of transition from the tree layer to seed rain and from seed rain to regenerating layer. A chi-square test reported the probability that data were taken from a system with random proportions of transitions (Hammer 2019). The PAST 3.15 software was used to perform Markov chains (Hammer et al. 2001).

Results

We found 27 species represented by 282 individuals in the tree layer of Noboro (a 20-year-old forest). Exotic trees corresponded to 19% of the individuals and belonged to the species *Acacia mangium* and *Psidium guajava* (Fig. 3). A total of 34 species were found in the tree layer of Santa Bárbara (the 10-year-old forest), and they were represented by 263 individuals. Exotic trees corresponded to 12% of the individuals and belonged to four species (*Mangifera indica*, *Morus nigra*, *P. guajava*, and *Syzygium cumini*) (Fig. 3). The study area of Figueira (the other 20-year-old forest) had fewer individuals and species than other study areas, and only one exotic species was found there (*P. guajava*) (Fig. 3).

In total, 6628 seeds/fruits were recorded in the seed rain, and 60% of them were collected in Noboro (other 19% were collected in Santa Bárbara and 21% in Figueira). Seeds of exotic species accounted for 37% of the Noboro's seed rain and 35% of Santa Bárbara. Exotic species were not found in Figueira (Fig. 4). With regard to species richness, we identified 20 species in Noboro (*A. mangium* and *P. guajava* were exotic), 27 in Santa Bárbara (*A. mangium*, *Cenchrus purpureus* (Schumach.) Morrone, *P. guajava*, and *S. cumini* were the exotic ones), and 15 in Figueira (all native species).

Recruitment of new individuals and species was generally low in all areas studied, especially exotic species. Only 4.5% of the regenerating individuals found in Noboro were exotic and belonged to *P. guajava* (Fig. 5). In Santa Bárbara, 11.8% of the regenerating individuals were of exotic species and belonged to *S. cumini* (Fig. 5). As in the seed rain, all regenerating individuals found in Figueira belonged to native species (Fig. 5). We present the list of all species and individuals sampled in the tree layer, seed rain, and regenerating layer in the Supplementary Material.

As seen, three of the five tree exotic species found in the forests under restoration were dispersing seeds but recruiting few new individuals. In addition, only the exotic tree species planted during the execution of the restoration projects were found in the three study areas. We summarize the number of individuals/seeds of exotic species recorded in at least two forest components (*A. mangium*, *S. cumini*, and *P. guajava*) in Fig. 6.

Although the *A. mangium* species had adult individuals in Noboro and Santa Bárbara and was found dispersing a lot of seeds (mainly in Noboro), it was not recruiting new individuals in both areas (Fig. 6a). The exotic species *S. cumini* was recorded only in Santa Bárbara but with few individuals/seeds in the three forest components (Fig. 6b). The only exotic species sampled in the three study areas was *P. guajava* and with greater number of trees than other exotic species (Fig. 6c). However, a few seeds of *P. guajava* were found to be dispersed, and only two new individuals were recruited in Noboro and Santa Bárbara. No seeds or regenerating plants of *P. guajava* were found in Figueira (Fig. 6c).

With regard the effects of exotic trees on regenerating native plants, no significant relation between the richness of exotic species of the tree layer (independent variable) and the richness of regenerating species (dependent variable) was found in the study areas (Table 1). Contrary to expectations, the abundance of regenerating native plants was positively related to the abundance of

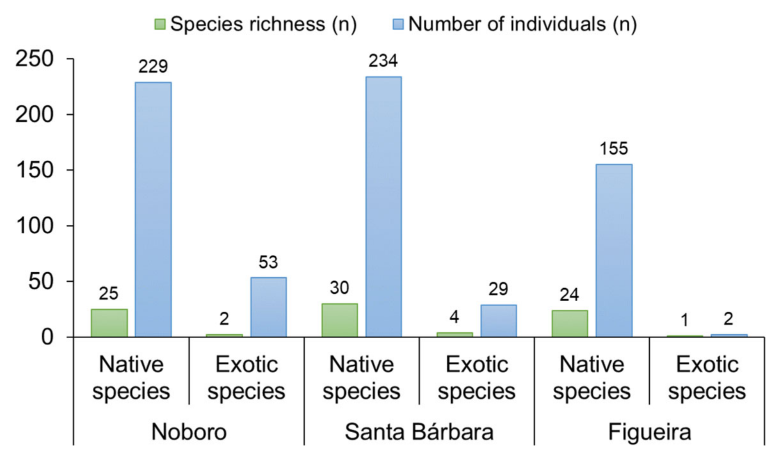

Fig. 3 Species richness and number of individuals of native and exotic trees registered in the forests under restoration of Noboro, Santa Bárbara, and Figueira, southeast Brazil

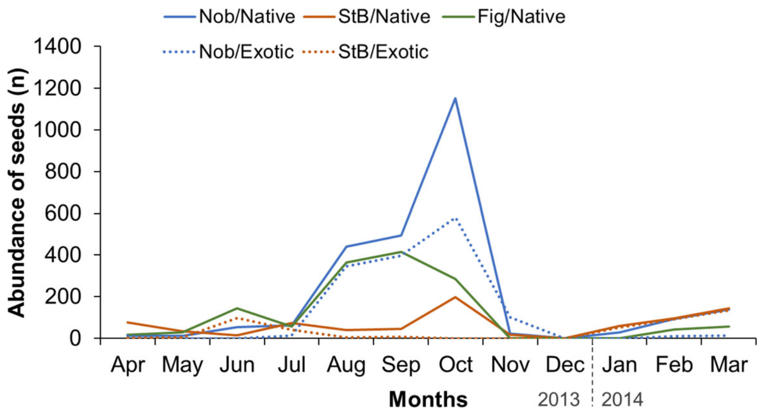

Fig. 4 Seeds of native and exotic species collected over a year in the forests under restoration of Noboro (Nob), Santa Bárbara (StB), and Figueira (Fig) in southeast Brazil

adult exotic trees in the area of Santa Bárbara, but the variables had a very weak correlation (Table 1, Fig. 7).

In analyzing the Markov chains, we verified that there was more chance that the individuals of the exotic species remain in their current components. For example, there was 100% probability of the exotic individuals remaining in the tree layer and in the seed rain in Figueira; therefore, there was no change of recruitment of regenerating individuals. In Noboro and Santa Bárbara, the probability of exotic individuals transitioning from the tree layer to seed rain and regenerating was null. The greatest chance was that the exotic individuals would remain in the tree layer. On the other hand, we found a 100% probability of transitioning from the seed rain to the regenerating layer, along with a 70% chance of regenerating plants ($n = 6$) becoming adults in Noboro and Santa Bárbara. Probability of random proportions of transitions was not found for the study areas ($p > 0.05$).

Discussion

The monitoring and evaluation of the tree layer, seed rain, and regenerating layer were very useful to know the dynamics of exotic species in areas under restoration. In general, species go through the stages of introduction, establishment, propagation, and impact when they become invasive (Levine 2008). The introduction stage occurred intentionally in the forests under restoration studied because the exotic species were planted in the areas with the purpose of attracting the fauna, mainly birds and small mammals. However, contrary to our expectations, the exotic tree species have failed to move into the stages of establishment, propagation, and impact and therefore were not behaving as invasive species.

In effect, of the five tree exotic species found in the forests under restoration, just three were dispersing seeds and two were recruiting (few) new individuals. The abundance of individuals initially introduced into

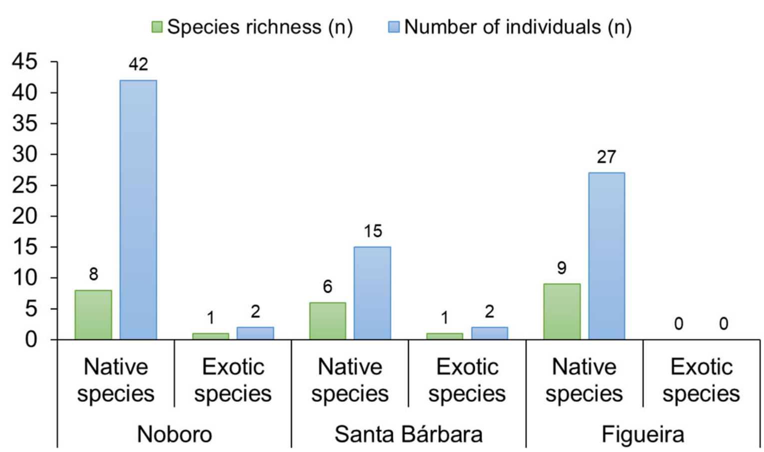

Fig. 5 Species richness and number of individuals of regenerating plants (native and exotics) registered in the forests under restoration of Noboro, Santa Bárbara, and Figueira in southeast Brazil

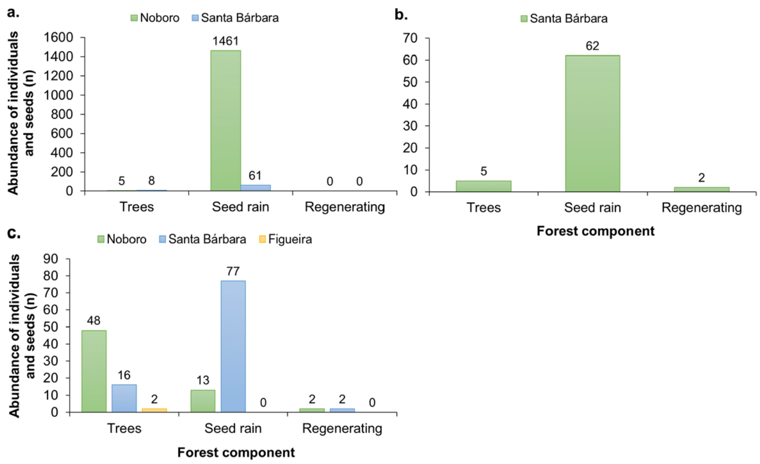

Fig. 6 Abundance of individuals and seeds of exotic species occurring in at least two forest components (tree layer, seed rain, and/or regenerating layer) in the areas under restoration of Noboro, Santa Bárbara, and Figueira, southeast Brazil. (**a**) *Acacia mangium*, (**b**) *Syzygium cumini*, and (**c**) *Psidium guajava*

an ecosystem and the subsequent rate of immigration to it are factors which affect the establishment of invasive species (Drake and Lodge 2006). As few individuals of adult exotic species were found in the areas (except for *P. guajava* in Noboro) and low immigration should occur because the areas are isolated in agricultural matrices, the introduced exotic species are probably being prevented from establishing, propagating, and impacting native species even after 10 and 20 years of recovery.

Contrary to other cases where exotic tree species were propagating out of the planting areas (Aguiar et al. 2014), we did not see individuals of the exotic trees growing out of the forests under restoration during fieldwork. Indeed, it is possible that the highly mechanized agricultural matrices where the areas under restoration were inserted are preventing the dispersion of exotic species outside them (seeds may be dispersed to the adjacent areas, but seedlings do not grow because the soil is plowed for planting new crops). On the other hand, the agricultural matrices must also prevent the arrival of native species in the areas, but further studies are required to test these hypotheses.

Other characteristics related to the successful establishment of invasive plants, which increase the likelihood of invasion, are whether the species have a history of invasion at other ecosystems and whether they have vegetative reproduction (Kolar and Lodge 2001). Invasion by species of the genus *Acacia* as well as *S. cumini* and *P. guajava* have been reported in several countries, including Brazil (Invasive Species Compendium 2019; Le Maitre et al. 2011). Indeed, *A. mangium* and *S. cumini* were deliberately introduced in Brazil for use in the recovery of degraded (logged) areas in the 1990s (Horus Institute for Environmental Conservation and Development 2020). Nowadays it is not advisable to use exotic species with potential for invasion in projects of ecological restoration in the country (Ziller

Table 1 Outputs of the regression analyses performed through generalized linear models (GLM) between the adult exotic trees and regenerating native plants (species richness and abundance) registered in the forests under restoration of Noboro, Santa Bárbara, and Figueira in southeast Brazil

	Study area		
	Noboro Independent variable	Santa Bárbara	Figueira
Dependent variable	Species richness of adult exotic trees		
Species richness of regenerating native plants	$\chi^2 = 10.303$, gl = 6, $p = 0.112$	$\chi^2 = 2.888$, gl = 3, $p = 0.409$	$\chi^2 = 0.471$, gl = 1, $p = 0.493$
	Abundance of adult exotic trees		
Abundance of regenerating native plants	$\chi^2 = 10.303$, gl = 6, $p = 0.112$	$\chi^2 = 21.088$, gl = 5, $p = 0.001$, $r^2 = 0.09$*	$\chi^2 = 0{,}026$, gl = 1, $p = 0.871$

An asterisk (*) indicates a significant relationship between variables ($\alpha = 0.05$)

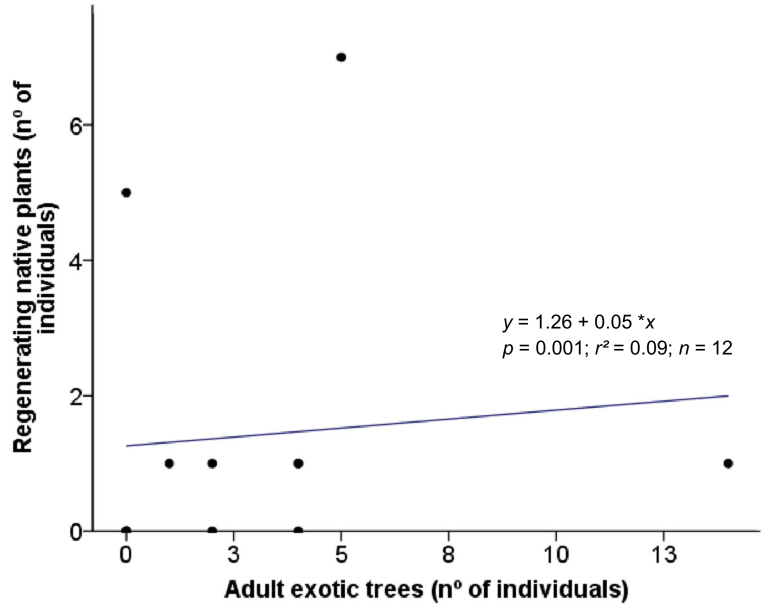

Fig. 7 Relation between the number of adult exotic trees and regenerating native individuals in the study area of Santa Bárbara, São Paulo state, southeast Brazil

and Zalba 2007), and some states even prohibit this practice (e.g., São Paulo) (Secretaria de Estado do Meio Ambiente 2014). Considering the extensive history of invasion by these species in other ecosystems around the world, it is interesting to note that they did not behave as invaders in the forests studied.

Ecologically, the three exotic species recorded have some common characteristics. For example, *A. mangium*, *P. guajava*, and *S. cumini* developed in several types of soil are fast growing species and have zoochoric dispersion (Invasive Species Compendium 2019). *Psidium guajava* is shade-tolerant and *S. cumini* can shade native vegetation with its large canopy (Invasive Species Compendium 2019). Because of these characteristics, species would be expected to be invasive in forests under restoration, as found, for example, in Indonesia (Hakim and Miyakawa 2015). However, we have not found them behaving as invaders, and this is likely to occur in other areas worldwide.

The failure of biological invasion by exotic species suggests that there is some kind of resistance to invasion in the assembled communities. This resistance may be the result of interaction with competing plants and herbivores resident in the communities or even because of the total diversity of resident species (Levine et al. 2004). Other factors that impose strong restrictions on invasion are the number of propagules that arrive at the site and the density of resident plants (Von Holle and Simberloff 2005). We could not statistically test whether the pressure of propagules and density of resident trees exerted resistance to invasion because few regenerating individuals of exotic species were found in the areas. However, this is an interesting hypothesis that can be tested in other areas under restoration with a sufficient number of regenerating plants.

In addition to biotic resistance, stresses imposed by the physical environment can also provide resistance to biological invasion (Levine 2008). Limiting resources such as nitrogen can have a strong effect on biomass and reproduction of invasive trees (Going et al. 2009). However, edaphic analyses carried out for the study areas by another research group have shown that forests under restoration have slightly acidic fertile soils (classified as eutrophic purple latosol), with a high content of bases and without aluminum (Leite et al. unpublished). Eutrophic latosols are soils of high fertility and suitable for good deep root development (EMBRAPA 2019). The good development of exotic species would then be expected in these fertile soils, but perhaps native species are making better use of resources and exotic species are not competitive enough to establish themselves and propagate. Implementing native species that make better use of fertile soils would be a good option against biological invasion.

New assemblages with combinations of native and non-native species are being formed all over the planet, and removal of non-native species may be unfeasible in many regions (Svenning 2018). In this context, it is positive that there was a low probability of the transition of exotic species between forest components, as they can remain in these novel ecosystems without causing disturbances. The exotic trees were recruiting few individuals even producing large amounts of seeds. Thus, it is likely that such exotic species will not become invasive in the forests under restoration avoiding the need for management actions, which is usually required in forests invaded by exotic plants (Rai 2015).

Conclusions

The monitoring of forest components revealed relevant information about the dynamics of exotic species in forests under restoration. The five species of exotic trees intentionally introduced in the forests were not behaving as invasive species, contradicting our initial hypotheses. The exotic species *A. mangium*, *M. indica*, *M. nigra*, *S. cumini*, and *P. guajava* do not always follow an invasive trajectory. They may not become invasive even after 10 or 20 years of forest restoration. However, because these species have not behaved as invaders in the study forests, it does not mean that they should be used indiscriminately to restore other areas. The assembly of the communities with many native species and few exotic ones may be one of the factors that prevented the planted exotic trees from becoming dominant invaders after 10 and 20 years of recovering. More experiments should be conducted comparing forests under restoration where exotic species are invasive with forests under restoration where they are not invasive so we can better elucidate the determinants of biological invasions and how these novel ecosystems contribute to conservation.

Authors' contributions MCTBM and VL conceived the idea; VL, HCS, and MCTBM collected the data; VL analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval Not applicable.

Consent to participate All authors did consent to participate.

Consent for publication All authors contributed with the manuscript and consent its publication.

Code availability Not applicable.

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