The effect of invasive alien plant species richness on the regeneration of threatened endemic woody species on Reunion Island (Indian Ocean)

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Degree project in biology, Master of science (2 years), 2024
Examensarbete i biologi 45 hp till masterexamen, 2024
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ABSTRACT

Despite increasing co-occurrence of invasive alien plant species and increased evidence of their harmful effect on native biodiversity, their cumulative impact remains poorly documented. In this study, I investigated how invasive alien plant species richness influences the regeneration of threatened endemic woody species on the oceanic island of Reunion (Western Indian Ocean).

I used species occurrence data from historical records from 1998 to 2023 combined with new fieldwork data from 2023-2024 to examine whether the proportion of juveniles in 180 records of threatened endemic woody species declined with the number of co-occurring invasive alien plant species. I also investigated whether habitat and life-history traits (maximum height, seed size, dispersal syndrome) of the threatened species influenced their response to invasives, and whether the growth form of invasive alien plants influenced their impact on threatened plants.

Results indicated a negative effect of invasive alien species richness on the regeneration of threatened endemic woody species, but the effect was only statistically significant in threatened species with medium to large-sized seeds. The reduced regeneration with increased invasive richness was primarily attributable to the impact of invasive alien trees and lianas, and not to herbs and shrubs. The presence of a single invasive tree species, *Syzygium jambos*, was associated with a 12.5% reduction in regeneration.

The study stresses that the impact of invasive alien plant species richness on the regeneration of threatened endemic woody species depends both on invasive species identity and life-history traits of the threatened species. Furthermore, I speculate that the threatened species whose regeneration decreased the most with number of invasive species are also typically affected by the extinction of their native seed dispersers. These findings can help devise more effective strategies to control invasive alien species and better preserve threatened native species on oceanic islands.

INTRODUCTION

During the last century, the world's economies, cultures, and populations grew increasingly interdependent (Seebens et al., 2017). This process has brought many benefits through cross-border trade in goods and people, but also led to the intentional and unintentional transfer of organisms among previously separate biogeographical regions (Keller et al., 2011; Simberloff et al., 2013). The number of alien species is increasing rapidly such that they are now recognized as one of the major threats to biodiversity (Kuebbing et al., 2013; Langmaier & Lapin, 2020; Pyšek et al., 2020; Seebens et al., 2017). Indeed, a subset of those alien species contributes to the unprecedented biodiversity crisis in terms of species extinction risk and habitat degradation we are currently experiencing, by causing a number of complex long-term impacts (Butchart et al., 2010; Díaz et al., 2019; Roy et al., 2023). For instance, alien species can affect the richness and abundance of native species (Pyšek et al., 2020; Rojas-Sandoval et al., 2022). Invasive alien species can also modify ecosystem functioning and services by altering, for example, the nutrient cycle, hydrology, or habitat structure (Carboni et al., 2021; Pyšek et al., 2020). Of particular concern is the possibility that invasive alien species might engender an extinction debt, where short-term survival hides deterministic extinction trajectories (Crooks et al., 1999; Sax & Gaines, 2008). Whereas the mechanisms contributing to extinction risk appear relatively clear for animal taxa (e.g., mammalian predators, disease carriers, or competitive exclusion), the ecological processes associated with plant invasion are much more debatable (Downey & Richardson, 2016).

A recent review carried out by Langmaier & Lapin (2020) on the impact of invasive alien plants on native tree species in European temperate forests identified several main mechanisms affecting regeneration, the process by which mature individuals in a plant population are replaced by new individuals of the next generation through seed production, dispersal, germination, seedling emergence, establishment and survival (Jamloki et al., 2023; Langmaier & Lapin, 2020; Larson & Funk, 2016). Competition for resources was found to be the prominent mechanism, as it restricts the allocation of resources to reproduction in adult individuals (Monty et al., 2013), particularly competition for light, which also has the greatest impact on native tree seedling establishment (Caujapé-Castells et al., 2010; Dueñas et al., 2018; Levine et al., 2003). Chemical effects such as the release of allelopathic compounds directly affecting neighboring native plants' growth and survival were also important (Qu et al., 2021). In addition, physical effects, such as changes in soil moisture or structural effects through homogenization of species composition were found to affect species regeneration. Finally, indirect effects also appeared to play a role through interactions with other species, for example by attracting pollinators (Caujapé-Castells et al., 2010; Stout & Tiedeken, 2017; Traveset & Richardson, 2014) or dispersers from native species (Spotswood et al., 2012).

It has also been argued that the outcome of an invasion is not random, but influenced by plant traits that make some native species more vulnerable than others and some invasive species more harmful than others (Hejda et al., 2017; Kueffer et al., 2009). Maximum plant height determines the ability to intercept light in competition with neighboring individuals (Kunstler et al., 2016), and height of the invasive species could therefore be expected to be positively related to the severity of impact of alien species. In addition, smaller invasive species such as herbs or shrubs would be expected to mainly affect the establishment and growth of juveniles of native tree species, whereas trees and lianas would be expected to affect the reproductive rates of adult trees. Furthermore, the persistence of native species in the face of invaders depends on the traits that confer strong competitive capacity (Fried et al., 2019), which could be traits such as large seeds when it comes to regeneration-associated traits. Long-distance dispersal could also improve opportunities to reach non-invaded areas. Indeed, plants with large seeds tend to have larger seedlings and higher survival rates (Moles, 2018). Thus, seed size, dispersal syndrome and maximum height are traits that capture critical dimensions of a species ecology, and that are likely to influence their productivity, competitive ability and survival in the face of biological invasions. This suggests that the impact of invasive species may depend on both native and alien species traits.

The effects of invasive alien plant species on demography and abundance of native species have been investigated in several observational studies. For example, competition for space and light was associated with reduced recruitment of young native tree individuals in dry and moist deciduous forests in India (Rashmitha et al., 2023). This study demonstrated that the invasive alien shrub *Lantana camara* creates dense cover by vertical stratification due to its allelopathic properties, thereby reducing the intensity and duration of light exposure for seedlings present under its canopy. In another study in tropical forests in southeast Brazil, the invasive alien small tree *Leucaena leucocephala* had the same effect, leading to increased competition between native tree and shrub species, and negative effects on their seedling recruitment (Zardetto & Siqueira, 2023). In addition, *L. leucocephala* promoted the establishment of more aggressive invasive alien plant species and subsequently influenced community susceptibility to invasion. Thereby, mechanisms affecting regeneration reported previously by Langmaier & Lapin (2020) in European forests also seem present in tropical forests.

The effect of invasive plants on native species has also been experimentally studied. Thomson (2005) used removal experiments to assess the effect of invasive alien grasses on the demography of a rare endangered endemic perennial plant in California. Removal of the invasive species increased native seedling recruitment but did not affect adult plants. A similar framework was used by Truong et al. (2021), who manipulated plots invaded by the invasive alien grass *Microstegium ciliatum* with the use of herbicide in a secondary forest in Vietnam. By looking at the percentage cover of the invasive alien grass and identifying and counting the number of native tree seedlings with a diameter < 6 cm in each plot, they inferred that in a tropical forest environment, invasive alien grasses inhibited native tree regeneration. This was due to the fact that invasive alien species were creating a physical barrier, trapping seeds before they could reach the ground, and also reducing the duration and intensity of light exposure, thus inhibiting germination. Lower regeneration was also hypothesized to have been caused by competition for soil resources such as water and nitrogen, which are vital resources for native seedling survival. Moreover, the authors concluded that canopy cover was influencing the establishment of alien species as they found a higher number of native tree seedlings and species under medium to high-density canopies. A contributing factor to this effect was a more favorable microclimate under a non-disturbed canopy (Truong et al., 2021). Furthermore, a study conducted by Dann et al. (2023) found that the management of a thick-forming invasive alien small tree *Psidium cattleianum* enhanced plant recruitment and forest regeneration in subtropical forests of Norfolk Island in the South Pacific. In sum, the literature suggests an overall tendency towards a negative effect of invasive alien species on native species, but there have also been a few specific cases where both experimental and observational studies found that invasive alien trees had a positive effect, by acting as ‘nurse plants’ for the regeneration of native species (Feyera et al., 2002; Wilson, 1994). Taken together, existing studies suggest that invasive species affect native species via several mechanisms and that both the direction and magnitude of alien impact on the regeneration of native plants can be species-specific.

This range of positive and negative effects of invasive species on native species could be accentuated by facilitative interactions among multiple alien invaders that accelerate invasion processes and amplify the magnitude of impact on native communities, introduced as the ‘invasional meltdown hypothesis’ by Simberloff and Von Holle (1999). As the level of invasion increases, the combined impacts of co-occurring invaders can decrease, stagnate, or increase, in a linear (additive) or non-linear (non-additive) fashion (Simberloff & Von Holle, 1999). Non-additive effects can be demonstrated experimentally and are endorsed if the resulting effect of multiple alien species is greater than the sum of their individual effects (Braga et al., 2018). To test this hypothesis, Rastogi et al. (2023) examined the effect of co-occurrence of two invasive alien plant species, *Lantana camara* and *Pogostemon benghalensis*, in an Indian dry tropical forest, and found that the additive impacts of multiple invasions on native vegetation structure, composition, soil nutrients, and herbivory were greater than the individual impacts. Moreover, two functionally similar shrub invaders, *Ligustrum sinense* and *Lonicera maackii*, had non-additive impacts on the plant community and soil processes in natural stands in Tennessee (Kuebbing et al., 2014). The 'invasional meltdown hypothesis' was also experimentally supported in a riparian ecosystem in which the co-occurrence of three invasive plant species had a greater harmful impact on soil properties, functioning and native woody plant diversity than occurrence of single invasive species (Vujanović et al., 2022). Overall, a review based on 150 empirical studies showed that the invasional meltdown hypothesis appears to be widely supported, but that only a subset showed an actual link between the positive interactions between invasive species and their synergetic negative impacts on native species (Braga et al., 2018). Therefore, this calls for studying alien species in combination rather than separately. Moreover, only a few studies (e.g., Thomson, 2005) have so far focused on the impact of alien plants on the regeneration of threatened plants, which makes it difficult to identify which mechanisms prevail at driving extinction risk, and should primarily be addressed in conservation actions.

Island ecosystems are exceptionally affected by extinctions mediated by alien species, since island species have evolved for millions of years in isolation, leading to high frequencies of endemism, with few native competitors or predators (Fernández-Palacios et al., 2021; Pyšek et al., 2017; Simberloff, 1995; Veron et al., 2019). As a result, island species can be severely affected by introduced diseases, predators, herbivores, or competitors. As many as 86% of recent extinctions in which alien species have been identified as drivers have concerned island species (Bellard et al., 2016). Within islands, endemic plant species might also be more severely affected by plant invasions than non-endemic native plants (Jäger et al., 2009). In this context, the tropical oceanic island of Reunion provides an interesting case study, because, although it is one of the last places on the planet to have been reached by man, its vegetation is profoundly influenced by anthropogenic impacts, and invasive alien species are among the main threats to native plants (Monnier, 2023; Strasberg et al., 2005). The lowlands of Reunion, which have experienced the most severe conversion of natural habitats to agricultural and urban areas are particularly affected by invasions (Strasberg et al., 2005), with *ca.* 60% of lowland dry and wet forests invaded (Fenouillas et al., 2021). The high level of endemism and variation in habitat types, combined with high degree of invasions, make Reunion a suitable system for exploring the effects of multiple invasive species.

By combining plot inventories with existing data from previous surveys, I examined whether regeneration of threatened endemic woody species declined with increasing invasive alien species richness on Reunion Island because of facilitative interactions between invasive species (Simberloff & Von Holle, 1999). In a second part, I tested whether the effect of invasive alien species richness on native regeneration varies according to habitat or life-history traits of the threatened species. I expected regeneration of threatened endemic plants to decline with invasive species richness in all habitat types, with stronger decline in heavily degraded lowland habitats. When it comes to life-history traits, I expected tall threatened endemic species with large seed sizes to be more resistant to increased invasive species presence due to greater access to resources thus conferring greater competitive abilities. I also speculated that smaller seeds would be able to disperse further away as well as wind-dispersed species, improving opportunities to reach and establish in a less competitive or less-invaded site. I expected all other life-history trait categories to show a reduced regeneration with higher invasive species richness. Furthermore, I tested whether the effects of invasive species richness on native regeneration depend on the growth form of the invasive alien species. I expected invasive herbs and shrubs to reduce regeneration of threatened plants via reduced establishment success and growth of juveniles, caused by physical barriers or resource competition. I expected invasive trees and lianas to reduce the reproductive rates of adult plants via resource competition, leading to a lower regeneration of threatened species.

MATERIAL & METHODS

Study site

The study was conducted on Reunion Island, the largest (2512 km^2) and youngest (2-3 million years old) island within the Mascarene archipelago (Western Indian Ocean), which also comprises Mauritius and Rodrigues Islands. Reunion is a tropical high-elevation volcanic island (maximum elevation of 3070 m a.s.l.) with a complex topography that generates large temperature and precipitation gradients and a diversity of ecosystems, ranging from tropical lowland forest to subalpine vegetation (Cadet, 1977) (*Figure 1 & S1*). More than 28% of native vascular plants are endemic to Reunion, 17% are endemic to the Mascarenes, and 15% are endemic to the West Indian Ocean (Bosser et al., 1990). Because of its high proportion of endemic plant species and severe loss of native habitats, the island has been included in the biodiversity hotspot ‘Madagascar and the Indian Ocean Islands’ (Myers et al., 2000). A total of 474 alien plants have been identified as invasive on Reunion Island, as they pose a threat to native species and their habitat, especially coastal and forest ecosystems (Liebhold et al., 2017; Monnier, 2023; Strasberg et al., 2005).

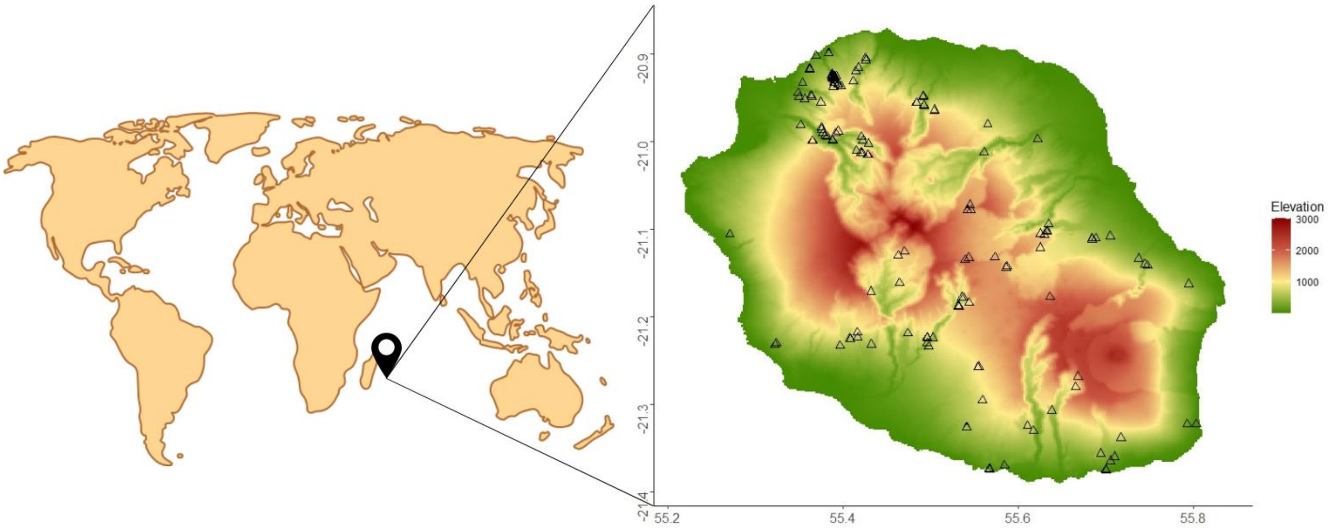

Figure 1: Location of Reunion Island (left) and spatial coverage of the 158 inventories used in this study (right).

Data collection

To examine how regeneration of threatened endemic woody species is related to invasive alien species richness, I used existing data collated on the local information system for biodiversity, Borbonica (https://www.borbonica.re/), combined with data from my own fieldwork as part of the EDENE project, which runs from 2023 to 2026 and examines the interactions between endemic trees threatened with extinction and co-occurring invasive alien plants (https://sites.google.com/view/edene/home). The Borbonica portal is a regional platform initiated by the Ministry for the Environment in 2006 for disseminating naturalist data (flora and fauna), collected mainly by scientific authorities, but to which the public can contribute. Since 1972, a total of 194,737 occurrences of alien or native plant species have been recorded in the Borbonica portal.

Here, I considered 'threatened species' those classified as critically endangered (CR), endangered (EN), or vulnerable (VU) according to the IUCN red list criteria. I defined 'invasive species' as those dominant or co-dominant in natural or semi-natural environments, having a strong direct impact on the composition, structure, and functioning of ecosystems (Boullet & Picot, 2017). I filtered the records to include only those where the number of juveniles and the number of adults of the threatened species were specified along with data on the community composition (presence of other native or alien species). Juvenile individuals refer to the life stage between seedlings and adult plants, such that individuals have overcome critical steps from early life stages, but are still immature. The resulting dataset included 1,138 threatened species occurrences with associated community data occurrence lists, from a total of 1,037 inventories, derived from conservation programs, naturalist inventories, and other surveys from the main local stakeholders in biodiversity management including the Mascarine National

Botanical Conservatory (CBNM), the National Forest Office, and the Reunion National Park. Data were partly collected systematically within a specific area (plot) and partly more opportunistically over observation points or along transects. Depending on the program, inventories consisted of BraunBlanquet abundance-dominance scores or species occurrence lists. The resulting dataset was supplemented by data from my own fieldwork on Reunion Island.

From October 2023, we established 135 additional 10 ×10 m plots where every woody species with a diameter at breast height above 1 cm were identified at the species level. In each of the four corners and in the center of the plot, subplots of 1 m^2 were established to record herbaceous alien species. In a circle of 28 m radius from the center of the 100 m^2 plot, we recorded the number of juveniles and adults of all threatened endemic woody species. Plots were distributed over the whole island.

For data analyses, I combined the datasets derived from the Borbonica species portal and the EDENE project fieldwork. Species were categorized according to the index of the flora of the Mascarene, as invasive alien, alien, native, or endemic (Bosser et al., 1990). To ensure replication, we excluded all threatened endemic woody species with less than five records in total, all threatened species that did not have a single juvenile among the records, and all threatened species for which less than five species (alien or native) other than the focal threatened species were recorded. This resulted in a total of 18 threatened endemic woody species recorded in 158 inventories, of which 120 originated from Borbonica and 38 from EDENE. In some inventories, more than one threatened endemic woody species was found, so the final dataset included a total of 180 records of threatened endemic woody species. In total, 21 invasive alien species were found in the inventories. The maximum number of inventories per year was 28 in 2024 while no inventory met the criteria in 2004, 2009, 2011, and in the period 2017-2022 (*Figure 2*). Elevation of the inventories ranged from 188 to 1816 m above sea level.

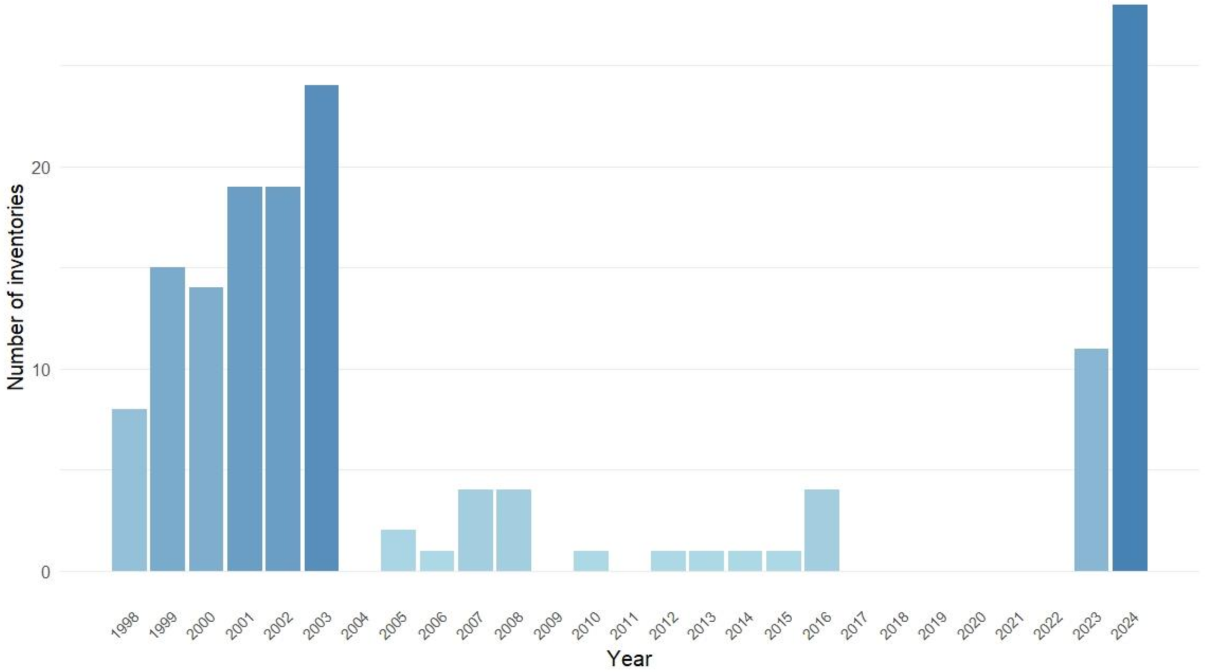

Figure 2: Temporal coverage of the 158 inventories derived from the Borbonica species portal and the EDENE project fieldwork between the years 1998 and 2024.

Data analysis

I quantified regeneration by calculating the proportion of juveniles, defined as the ratio of the number of juveniles to the number of all individuals in the record ($Pj = n_{juveniles} / (n_{juveniles} + n_{adults})$). The proportion of juveniles was used to assess the reproductive health of the population, serving as an indicator of its future trajectory. All threatened endemic woody species were classified according to main habitat type (semi-dry, lowland wet, and mountain wet forest) and to three different life-history traits (*Table 1*): maximum plant height (<5 m, 5-15 m, >15 m), average seed size (<5 mm, 5-15 mm, >15 mm), and dispersal syndrome (biotic, i.e., zoochory versus abiotic, i.e., barochory and anemochory) based on existing literature (*Table S1*). I used upsets plots with the *upset* function in the *'UpsetR'* R package, which creates visualizations of set intersections using a matrix layout and introduces aggregates based on groupings to illustrate the co-occurrence between the life-history traits. This classification revealed that tall species tended to have bigger seeds while smaller species tended to have smaller seeds and that the majority (92%) of medium to large-sized trees were biotically dispersed (*Figure S2*).

Table 1: Characteristics of the 18 threatened woody species endemic to Reunion considered in this study, including number of records, growth form, level of endemism, conservation status, main habitat, and life-history traits (maximum plant height, average seed size and dispersal syndrome). References are given in Table S1.

Threatened species	**Number of records**	**Growth form**	**Level of endemism**	**Conservation status**	**Habitat**	**Maximum height (m)**	**Average seed size (mm)**	**Dispersal syndrome**
Aloe macra Haw.[1 2 3]	8	shrub	Reunion	EN	semi-dry forest	<5	<5	zoochory
Badula fragilis Bosser et Coode[1 4]	8	tree	Reunion	EN	mountain wet forest	5<15	<5	zoochory
Croton mauritianus Lam.[1 2 5]	7	shrub	Reunion	CR	semi-dry forest	<5	<5	barochory
Diospyros borbonica I. Richardson[1 2]	10	tree	Reunion	EN	lowland wet forest	>15	5<15	zoochory
Dombeya acutangula Cav.[1 2]	6	shrub	Reunion, Mauritius & Rodrigues	VU	semi-dry forest	<5	<5	anemochory
Drypetes caustica (Frapp. ex Cordem.) Airy Shaw[1 2 6]	16	tree	Reunion & Mauritius	EN	lowland wet forest	>15	5<15	zoochory
Erythroxylum hypericifolium Lam.[1 2]	11	tree	Reunion & Mauritius	VU	semi-dry forest	5<15	5<15	zoochory
Foetidia mauritiana Lam.[1 2 7]	13	tree	Reunion & Mauritius	CR	semi-dry forest	5<15	5<15	zoochory
Hernandia mascarenensis (Meisn.) Kubitzki[1 2 8]	10	tree	Reunion & Mauritius	CR	lowland wet forest	>15	>15	zoochory
Hibiscus columnaris Cav.[1 2 9]	10	tree	Reunion & Mauritius	CR	semi-dry forest	5<15	5<15	anemochory
Hugonia serrata Lam.[1 2 10]	11	shrub	Reunion & Mauritius	EN	lowland wet forest	5<15	<5	zoochory
Obetia ficifolia (Poir.) Gaudich.[1 2 11]	17	shrub	Reunion, Mauritius & Rodrigues	EN	semi-dry forest	<5	<5	anemochory
Ochrosia borbonica J.F. Gmel.[1 2 12]	15	tree	Reunion & Mauritius	VU	lowland wet forest	5<15	<5	zoochory
Parafaujasia fontinalis (Cordem.) C. Jeffrey[1 13]	5	shrub	Reunion	VU	mountain wet forest	<5	<5	anemochory
Polyscias rivalsii Bernardi[1 14]	6	tree	Reunion	CR	lowland wet forest	5<15	<5	zoochory
Scolopia heterophylla (Lam.) Sleumer[1 2]	8	tree	Reunion, Mauritius & Rodrigues	EN	lowland wet forest	5<15	5<15	zoochory
Sideroxylon majus (C.F. Gaertn.) Baehni[1 2 15]	11	tree	Reunion	EN	lowland wet forest	>15	>15	zoochory
Zanthoxylum heterophyllum (Lam.) Sm.[1 2]	8	tree	Reunion, Mauritius & Rodrigues	EN	semi-dry forest	>15	<5	zoochory

To test whether invasive alien species richness influences the regeneration of threatened endemic woody species, I used a linear mixed-effects model with the proportion of juveniles in each record as response variable, the number of co-occurring invasive alien species as continuous explanatory variable, and threatened endemic species identity as a random factor. Prior to data analysis, outliers were excluded and normality of residuals was checked.

To examine the effect of specific invasive alien species on regeneration, I ran a series of similar linear mixed-effects models with the presence/absence of each specific invasive alien species (one model per invasive alien species) instead of invasive alien species richness as explanatory variable.

Furthermore, to investigate whether the effect of invasive alien species richness on the regeneration of threatened species depends on habitat or life-history traits of the threatened species, I used linear mixed-effects models with the proportion of juveniles as response variable and the interaction between invasive alien richness and each categorical factor (habitat, maximum height, average seed size, and dispersal syndrome) as explanatory variable in four separate models. I included threatened endemic species identity nested within category as a random factor in all models. In case of a significant main effect of the interaction between invasive alien richness and the categorical factor, I used the summary statement in the *lmer* package in R to test for which level of the factor the interaction with invasive alien richness was significant. To control for multiple testing, *P*-values were adjusted with the Holm method, using '*method = Holm'* from the *p-adjust* function in the '*stats*' R package.

Finally, to test whether the effect of invasive alien species richness on the regeneration of threatened endemic woody species varies with the growth form of invasive alien species, I repeated these models while distinguishing invasive alien herbaceous and shrub species versus invasive alien trees and lianas in two separate models (*Table S2*) and adjusted *P*-values with the Holm method. This growth form distinction resulted in 10 invasive alien species belonging to the herb and shrub group versus 11 species in the tree and liana group.

The model including habitat type had 87 records in lowland wet forest, 80 in semi-dry forest and 13 in mountain wet forest. Regarding the maximum height of the threatened species, 43 records belonged to the smaller size class (< 5m), 82 to the intermediate (5 < 15m), and 55 to the high size class (> 15 m). In the model with average seed size, there were 91 records of species with a small seed size (< 5 mm), 21 with an intermediate seed size (5 < 15 mm), and 68 records with a bigger seed size (> 15 mm). There were 135 records of threatened species with biotic dispersal and 45 records of species with abiotic dispersal.

All statistical analyses were performed with the statistical program R version 4.0.3. (R Core Team, 2020). Linear mixed-effects models were built using the *lmer* function in the '*lme4*' package (Bates et al., 2015).

RESULTS

The proportion of native juveniles varied between zero (no juveniles, only adults) and one (only juveniles) with a median of 0.33 (*Figure S3*). The threatened endemic species *Aloe macra*, *Badula fragilis*, *Dombeya acutangula*, *Parafaujasia fontinalis* and *Polyscias rivalsii* always had at least one juvenile in their records, and *Drypetes caustica* and *Hibiscus columnaris* were the only species with a record consisting of only juveniles. The richness of invasive alien species ranged from zero in eight inventories to nine in one inventory, with a median of three species (*Figure S4*). The inventory with nine invasive alien plants was identified as an outlier and excluded from subsequent analyses. The most widespread invasive alien species was *Litsea glutinosa*, which was present in 59% of the inventories, followed by *Psidium cattleianum*, with a proportion of 39%, and *Syzygium jambos* with a proportion of 25% (*Table S2*). The least common invasive alien species, *Fuchsia x exoniensis*, was found in only one inventory.

The proportion of juveniles of threatened endemic woody species tended to decline with invasive alien species richness (estimate = -0.024, *Figure 3*), but the relationship was not statistically significant ($P = 0.091$, $R^2 = 0.10$).

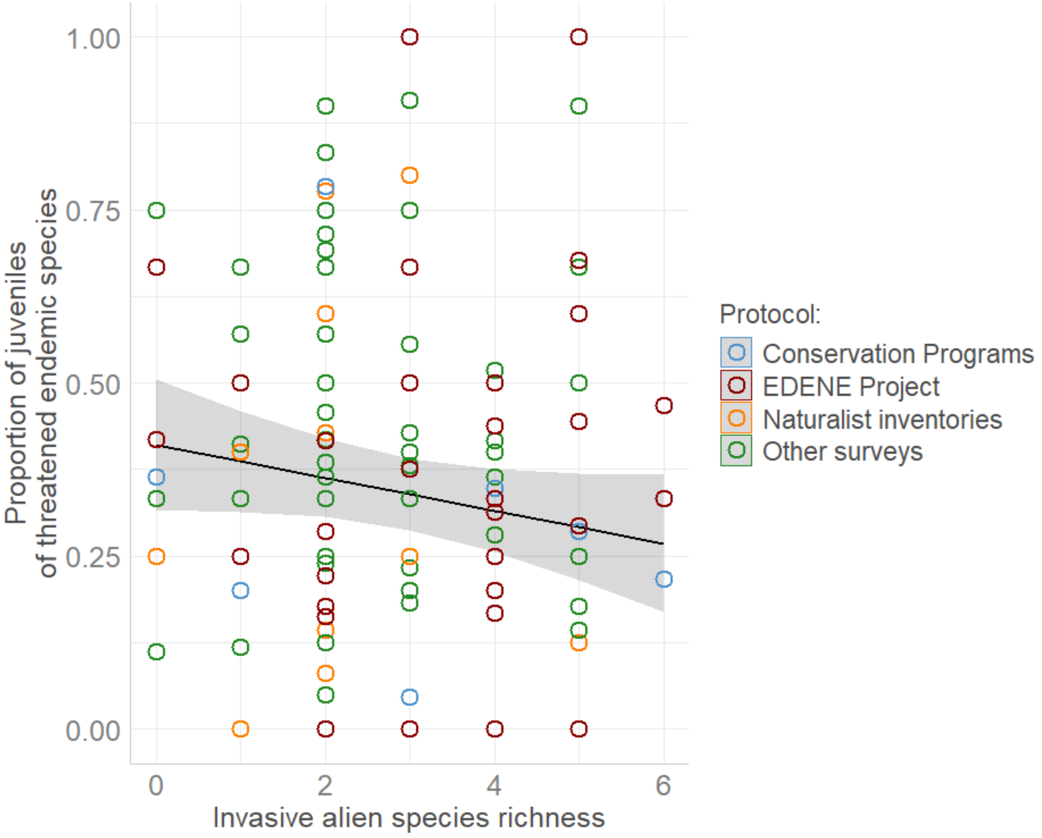

*Figure 3: Proportion of juveniles of threatened woody species endemic to Reunion in relation to invasive alien species richness (*n* = 158 inventories). The color of the symbols indicates the data source (see legend). The black line represents the predicted trend of a linear mixed-effects model with the identity of threatened woody species as random factor, and the grey area indicates the 95% confidence interval.*

In models analyzing the presence of each invasive alien species separately, the effect of a specific invasive alien species on regeneration was statistically significant for only one of the 21 species, *Syzygium jambos* (estimate = -0.125, *P* = 0.005, $R^2 = 0.13$) (*Figure 4*). The model estimate indicates that the proportion of juveniles of the threatened endemic woody species was 12.5% lower when *Syzygium jambos* was present.

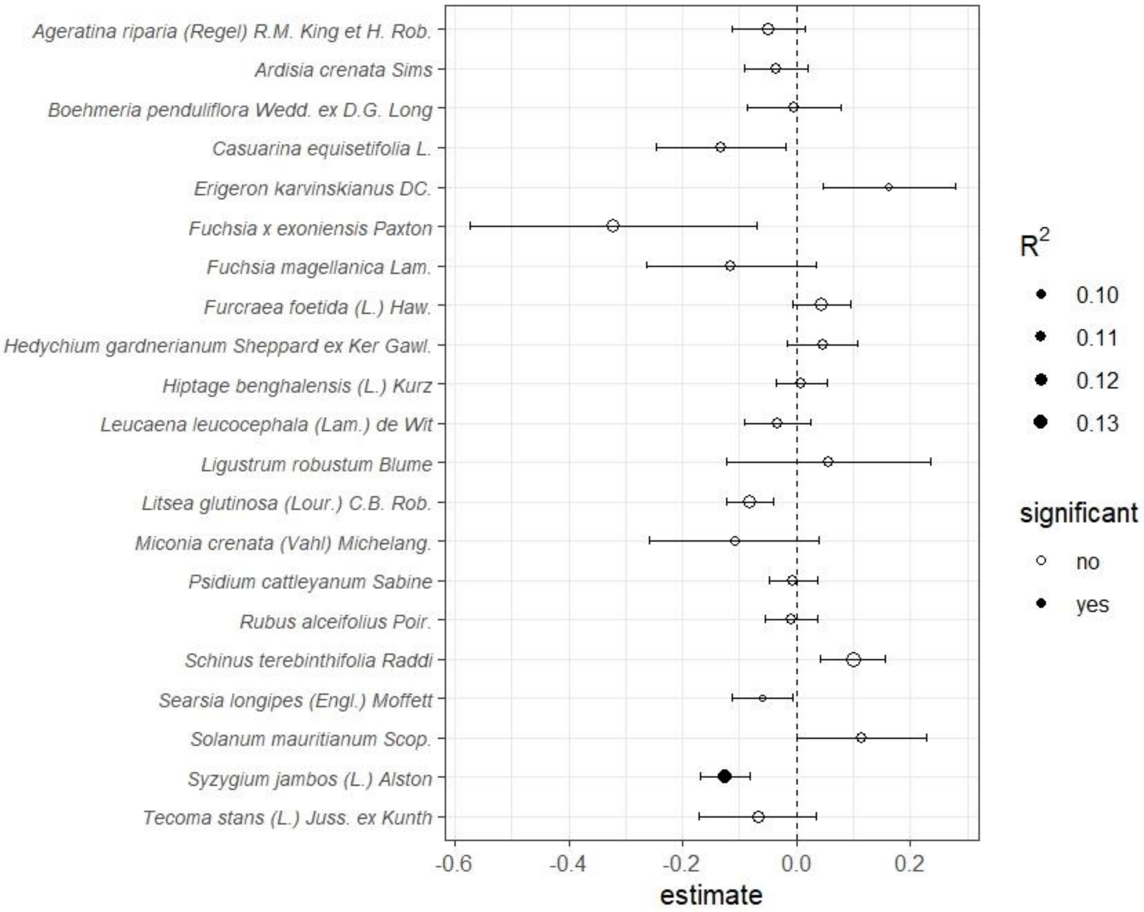

Figure 4: Effect of the presence of specific invasive alien species on regeneration of threatened Reunion-endemic species analyzed with linear mixed-effects models. The x-axis represents the value of the model estimate and the y-axis represents the invasive alien species identity. Filled dots indicate statistical significance (P < 0.05) and dot size indicates the value of the model determination coefficient.

In models examining the effect of habitat and life-history traits of the endemic species, the effect of richness of invasive alien plants on the regeneration of threatened endemic woody plants depended on seed size (*P* = 0.04 with Holm adjustment, $F_{3,36} = 4.2$), but not on habitat (*P* = 0.39, $F_{3,65} = 1.0$, df = 3), maximum height (*P* = 0.31, $F_{3,45} = 1.9$) or dispersal syndrome (*P* = 0.31, $F_{2,54} = 2.$). Increased richness of invasive alien species significantly reduced the regeneration of threatened species with medium-sized seeds (average seed size of 5-15 mm; estimate = -0.038, *P* = 0.03, $R^2 = 0.16$; *Figure 5*). The model estimate suggests a 3.8% decrease in the proportion of juveniles of threatened endemic woody species with a seed size of 5 - 15 mm by the addition of one invasive alien species to the inventory. Increased richness of invasive alien species had a similar negative effect on the regeneration of threatened species with large seeds (average seed size > 15 mm), but this effect was not statistically significant (estimate = -0.05, $P = 0.12$, $R^2 = 0.16$).

In models evaluating the effect of invasive alien growth form, the effect of species richness of trees and lianas depended on seed size of the threatened endemic woody plants ($P = 0.03$, F = 4.4), but not on habitat, maximum height, or dispersal syndrome ($P > 0.23$). Tree and liana invasive alien species richness reduced the regeneration of threatened woody species with medium-sized seeds (estimate = -0.048, $P = 0.02$, $R^2 = 0.14$) (*Figure 5*). The richness of herbaceous and shrubby invasive alien plants did not affect the regeneration of threatened endemic woody plants, whatever their habitat or life history traits ($P = 1.00$).

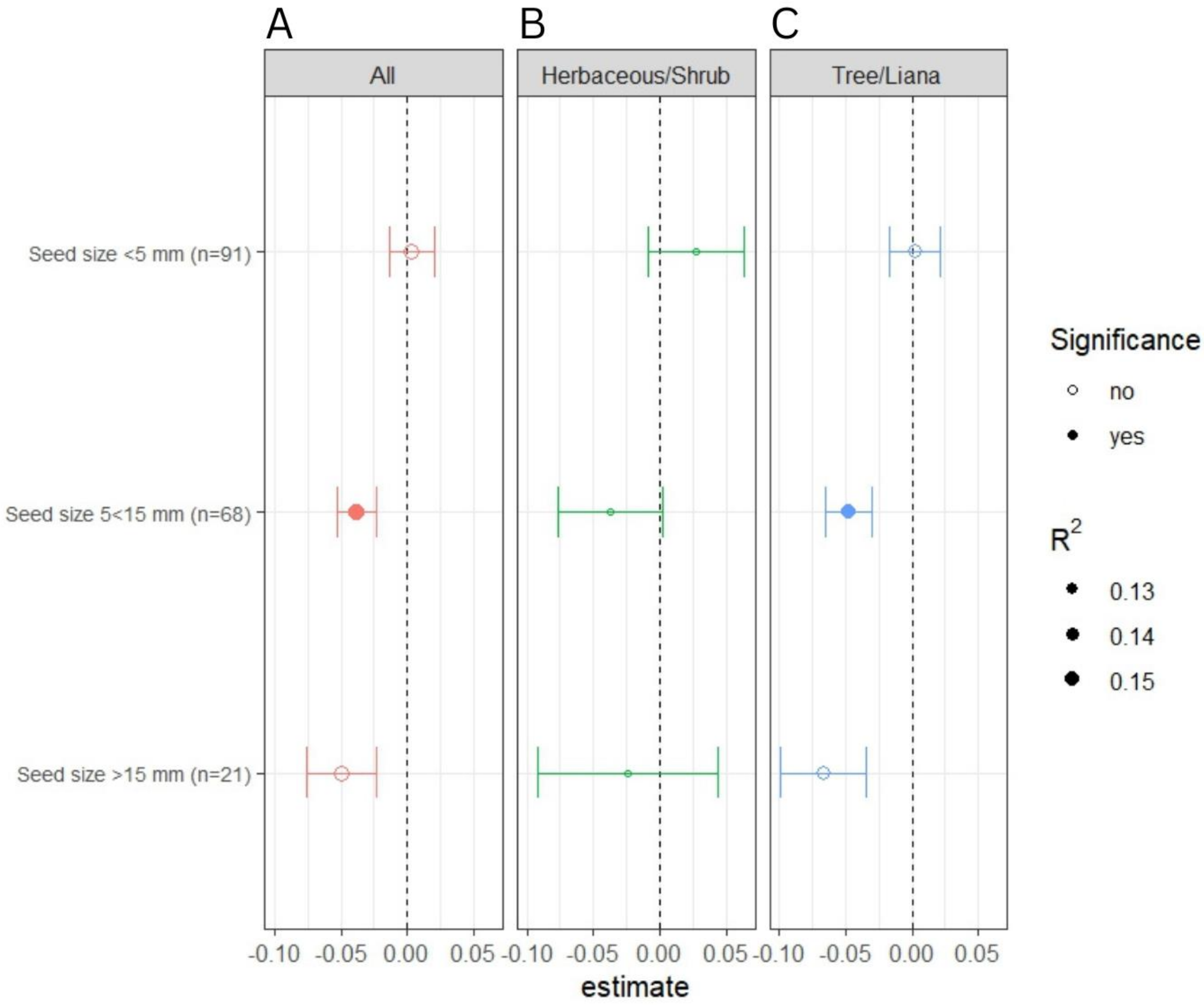

*Figure 5: Effects of invasive species richness of (A) all species, irrespective of growth form (*n *= 21 species), (B) herbs and shrubs (*n *= 10 species), and (C) trees and lianas (*n *= 11 species) on regeneration of threatened Reunion-endemic species with different seed size analyzed with linear mixed-effects models. Model estimates are shown for three seed-sized categories. The number of records for each sub-category (*n*) is indicated on the y-axis. Filled dots indicate statistical significance (P < 0.05) and dot size indicates the value of the model determination coefficient.*

DISCUSSION

Our study highlights that increasing invasive alien plant species richness reduced the regeneration of threatened endemic woody species on Reunion island, but the effect was only statistically significant for endemic species with medium- to large-sized seeds. This tendency was primarily attributable to the impact of invasive alien trees, such as *Syzygium jambos,* and not to herbs and shrubs.

Multiple invasive alien species could be directly responsible for weaker regeneration of threatened endemic woody species by means of additive or non-additive pathways (Simberloff & Von Holle, 1999). Overall, our study did not provide evidence of a reduction in the proportion of juveniles of all threatened woody endemic species in response to increased invasive alien species richness. This finding is similar to that of Pearson et al. (2016), who quantified the community-level impact of multiple plant invaders using data from grasslands across west-central Montana, USA. Their result did not support the invasional meltdown hypothesis or synergistic interactions between the 25 alien species included in the study, but they were able to infer that the local abundance of invaders was positively associated with the likelihood of impact on native species cover. This suggests that abundance might be more informative than species richness when quantifying the potential impact of invasive species.

In a previous study, increased invasive richness significantly increased invasive plant biomass and invasion success, but did not reduce native plant biomass (Wang et al., 2022). These results suggest the presence of partly complementary resource niches between invasive and native species (Wang et al., 2022). Indeed, native species were shown to have a significantly higher extinction risk if threatened by close alien relatives (Pouteau, Van Kleunen, et al., 2023), which could be caused by higher niche overlap compared to unrelated species. Some threatened species considered in our study may have a niche that is partly complementary to co-occurring invasive species, e.g. with a large phylogenetic distance, while other threatened species may experience strong competition by sharing a large part of their niche with the invasive species. Variation in niche overlap between native and invasive species may lead to species-specific effects, and could underlie weak overall effects in the present study.

Furthermore, a study by Florens et al. (2016) on the abundance of invasive alien woody plants in a wet forest in Mauritius showed that invasive alien plant species richness was a poor measure of invasion threat, given that a single problematic invasive species (e.g., known to cause a significant reduction in the reproductive output of native species), in their case *Psidium cattleianum*, could result in a major invasion, showing extreme densities and high growth rate. This suggests that the presence of certain invasive alien species can have a stronger effect than species richness. However, it should be noted that not all systems benefit from control and elimination of a single invasive species because other invasive species may experience competitive release and increase in abundance and dominance after removal of the primary dominant species (D'Antonio et al., 2017; Kuebbing & Nuñez, 2016). It is therefore possible that in our system, invasive alien species had both negative (competitive) and positive (facilitative additive) interactions depending on their identity, leading to weak overall effects that were statistically non-significant.

The generally weak relationship in our study between regeneration of threatened species and richness of invasive species could also have been influenced by variation in the focal scale of the study. A potential discrepancy in responses observed at regional and local scales is debated, with positive or lack of relationships being more common at a larger scale (Fridley et al., 2007). Several protocols on slightly different scales (e.g. transects versus plots) were used in the present study, as inventories were originally seeking different objectives thus causing variation in the study scale. Research on threatened species inherently limits the amount of accessible data, as only a few naturally occurring individuals remain for most species. Particularly in volcanic oceanic island ecosystems, data collection may also be biased in favor of accessible locations as a result of geographical barriers. Such limitations could have influenced the power to detect a negative effect of invasive richness on the regeneration of threatened endemic woody species.

I was able to show an overall decrease in the proportion of juveniles for threatened endemic woody species with a specific life-history trait, namely medium and large seeds, in contrast to species with small seeds. I speculate that small seeds could disperse farther, thus improving opportunities to reach non-invaded areas. Small seeds may also be preferred by small invasive alien birds like the red-whiskered bulbul *Pycnonotus jocosus*. Interestingly, some life-history traits in the Reunion flora appear to be co-occurring, since lowland forest habitats are dominated by large tree species with medium or large fleshy fruits, which were dispersed by now-extinct frugivores such as giant tortoises, flying foxes, parrots, and fruit pigeons (Albert et al. 2021, 2023). Apart from competition with invasive alien plant species, Albert et al. (2023) emphasized the fundamental role of dispersal loss in the disruption of ecological succession. Reunion Island is known to have experienced a mass extinction of its large-bodied frugivores since human colonization in 1665 (Albert et al., 2021). Albert et al. (2021) showed that in tropical forests of Reunion Island, dispersal loss was a primary cause of regeneration failure because of the dependence on frugivores to recover. The co-occurrence of invasive alien plant species could therefore be an additional pressure on already regeneration-deficient threatened endemic woody species rather than being the primary driver. The presence of multiple invasive species would then indirectly act on the regeneration by enhancing this pressure. Indeed, it is challenging to untangle the impact of invasive alien plants on native species from the multitude of other pressures like habitat degradation, or loss of dispersers, given that these threats generally act simultaneously (Stricker et al., 2015). This is a criticism that can be leveled at observational studies, as they allow results to be aggregated because of their large scale, but do not allow cause and effect to be distinguished (Stricker et al., 2015).

Our study also revealed that the regeneration of threatened species was negatively affected by the number of invasive trees and lianas, but not by the number of invasive herbs and shrubs. This finding is comparable with a study on the natural regeneration of European forests by Dyderski & Jagodziński (2020), where invasive trees decreased the regeneration of forest-forming native trees. Similarly, Ni et al (2021) identified maximum height of invaders to be one of the most important variable explaining the severity of invasion impact. In their study, taller plants introduced from the Americas tended to have more severe impacts on the invaded ecosystem of China compared to shorter plants (Ni et al., 2021). I expected invasive herbs and shrubs to affect the establishment success and growth of juveniles through physical barriers, while invasive trees and lianas to affect the reproductive success of adult woody plants through resource competition. Our results suggest that the impact on adults' reproductive success mechanism prevails over the competition with juveniles. Invasive alien plants were shown to reduce adult reproductive success in Mauritius by reducing the production of flowers and fruit in native forest species (Monty et al., 2013). Moreover, another study found that alien woody species more often had positive interactions with their alien neighbor compared to herbaceous alien species, which exhibited mainly negative to neutral interactions (Kuebbing & Nuñez, 2015). Facilitative interactions between alien woody species could explain why trees and lianas had a negative impact on regeneration in our study.

Interestingly, the only invasive alien species' presence associated with a significant reduction in regeneration of threatened endemic woody species was the tree *Syzygium jambos*. This result is consistent with previous studies that found this shade-tolerant tree to reduce understory seedling diversity in secondary forests in Puerto Rico (Brown et al., 2006) and in a premontane tropical forest of Costa Rica (Avalos et al., 2006). In my study, the effect of specific invasive species may have been underestimated, because our dataset was not large enough to perform a habitat-specific analysis. Conducting a habitat-specific analysis would have been a stronger approach to reveal potential effects of other invasive alien species, focusing on their preferred habitat type. Indeed, the presence of *Syzygium jambos* reduced the proportion of juveniles by 12.5% in my study, compared with a 61% reduction in native seedling abundance in the study by Alvaros et al. (2006), which focused on a single habitat type. In addition, I expected a severe effect on the regeneration of native plants of Reunion Island of certain invasive species, such as *Psidium cattleianum* in low- to mid-elevation wet forests, and *Leucaena leucocephala* in semi-dry forests, as reported from other sites (Dann et al., 2023; Florens et al., 2017; Strasberg et al., 2005; Zardetto & Siqueira, 2023).

I demonstrated that the impact of invasive alien plant species richness on the regeneration of threatened endemic woody species depended both on the identity of the invasive species and the life-history traits of the threatened species. Furthermore, I speculate that the threatened species most affected by invasive species are also typically affected by the extinction of their native seed dispersers while the least affected are more likely to be dispersed by invasive alien birds. This study therefore provides a better understanding of how regeneration of native plants at risk of extinction is impacted by the richness of invasive alien plants. It can be used to inform further experimental or modeling studies, and thus develop more effective strategies to control invasive species and preserve the highly vulnerable biodiversity of oceanic islands.

ACKNOWLEDGMENTS

I want to thank Nina Sletvold (Uppsala University) and Robin Pouteau (IRD-AMAP) for their supervision and support of my research. I want to thank Margaux Rojat (IRD-AMAP) for her assistance in reading drafts, and for her advice. I thank the Mascarine National Botanical Conservatory for sharing its inventory data. I also want to thank those who collected data in the field with me including Olivier Flores (University of Reunion), Sarah Roussel (CBNM), Rémi-Paul Grondin (University of Reunion), Arnaud Rhumeur (CBNM), Robin Pouteau (IRD-AMAP), Margaux Rojat (IRD-AMAP), Bastian Laforgue (University of Reunion) and Elise

Adrien (IRD-AMAP). I would like to express my gratitude to Dominique Lamonica (IRD-AMAP), Christophe Lavergne (CBNM) and Dominique Strasberg (University of Reunion) for their comprehensive advices. This research was supported by the French National Research Agency under the framework of the EDENE project (ANR-22-CE32-006) and by the French National Research Institute for Sustainable Development (IRD). Finally, I want to thank my friends Erik Rijnsburger, Vinciane Mossion, Eleftherios Parasyris, Alessandro Nobile, Cara Heldmaier, Ludovica Parra, Tommaso Semprini-Cesari for their moral support throughout the thesis work.

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SUPPLEMENTARY

Table S1: List of references used to characterize the biology of the 18 threatened endemic woody species included in Table 1.

[1] https://www.cbnm.org/wp-content/uploads/2023/06/CBNM_PlantesNativesDeLaReunion_part1.pdf

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[3] RIOU A., RHUMEUR A., LAVERGNE C. & GIGORD L. 2017. – Le mazambron marron, *Aloe macra Haw.* – Plan directeur de conservation: outils d'aide à la conservation des espèces végétales menacées d'extinction. Version 2016. Conservatoire Botanique National – Centre Permanent d'Initiatives pour l'Environnement Mascarin, Saint-Leu, Réunion, 113p.

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[5] ROCHIER T. & LAVERGNE C. 2011. – Le ti bois de senteur, *Croton mauritianus Lam.* – Plan directeur de conservation : outils d'aide à la conservation des espèces végétales menacées d'extinction. Version 2011 (mise à jour du 13 juillet 2011). Conservatoire Botanique National de Mascarin, Saint-Leu (Réunion), 87 p.

[6] PIQUOT C., ROCHIER T. & LAVERGNE C. 2012. – La corce blanc bâtard, *Drypetes caustica (Frapp. ex Cordem.) Airy Shaw* – Plan Directeur de Conservation 2012-2016 : outils d'aide à la conservation des espèces végétales menacées d'extinction. Version 2012 (mise à jour du 13 avril 2012). Conservatoire Botanique National de Mascarin, Saint-Leu, Réunion, 87 p.

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[9] LAVERGNE C. & PICOT F. 2004. – *Hibiscus columnaris Cav.* – Plan directeur de conservation : outils d'aide à la conservation des espèces végétales menacées d'extinction. Version 2012 (mise à jour du 8 octobre 2012). Conservatoire Botanique National de Mascarin, Saint-Leu (Réunion), 58 p.

[10] ROCHIER T. & LAVERGNE C. 2012. – La liane de clé, *Hugonia serrata Lam.*– Plan Directeur de Conservation 2012-2016 : outils d'aide à la conservation des espèces végétales menacées d'extinction. Version 2012 (mise à jour du 28 mars 2012). Conservatoire Botanique National de Mascarin, Saint-Leu, Réunion, 90 p.

[11] EISENBACH J. & LAVERGNE C. 2005. – *Obetia ficifolia (Poir.) Gaudich*. – Plan directeur de conservation : outils d'aide à la conservation des espèces végétales menacées d'extinction. Version 2009 (mise à jour du 20 octobre 2010). Conservatoire Botanique National de Mascarin, Saint-Leu (Réunion), 59 p.

[12] PICOT F., FONTAINE C. & LAVERGNE C. 2003. – *Ochrosia borbonica G.F. Gmel.* – Plan directeur de conservation : outils d'aide à la conservation des espèces végétales menacées d'extinction. Version 2003 (mise à jour du 16 février 2010). Conservatoire Botanique National de Mascarin, Saint-Leu (Réunion), 66 p

[13] PAUSÉ J.-M. & LAVERGNE C. 2007. – *Parafaujasia fontinalis (Cordem.) C. Jeffrey* – Plan directeur de conservation : outils d'aide à la conservation des espèces végétales menacées d'extinction. Version 2007 (mise à jour du 16 mars 2007). Conservatoire Botanique National de Mascarin, Saint-Leu (Réunion), 49 p.

[14] ROCHIER T. & LAVERGNE C. 2011. – Le bois de papaye, *Polyscias rivalsii Bernardi* – Plan national d'actions 2012-2016 : outils d'aide à la conservation des espèces végétales menacées d'extinction. Version 2011 (mise à jour du 27 octobre 2011). Conservatoire Botanique National de Mascarin, Saint-Leu, Réunion, 88 p.

[15] FOLGOAT N. & BARET S. 2011. – Le bois de fer blanc, *Sideroxylon majus (C.F. Gaertn.) Baehni* – Plan Directeur de Conservation : outils d'aide à la conservation des espèces végétales menacées d'extinction. Version 2011 (mise à jour du 18 mai 2011). Conservatoire Botanique National de Mascarin, Saint-Leu (Réunion), 73 p. 5

Table S2: Summary of the 21 invasive alien plant species recorded in the 158 inventories on the island of Reunion, and the proportion of inventories with their presence. Growth form and habitat preference have been extracted from https://www.especesinvasives.re/geir/ .

Invasive species	**Growth form**	**Habitat**	**Proportion of inventories with presence**
Ageratina riparia (Regel) R.M. King et H. Rob.	Herb	Lowland wet forest	11%
Ardisia crenata Sims	Shrub	Lowland wet forest	16%
Boehmeria penduliflora Wedd. ex D.G. Long	Shrub	Semi-dry forest	4%
Casuarina equisetifolia L.	Tree	Semi-dry forest	3%
Erigeron karvinskianus DC.	Herb	Lowland and mountain wet forest	3%
Fuchsia magellanica Lam.	Shrub	Mountain wet forest	2%
Fuchsia x exoniensis Paxton	Shrub	Mountain wet forest	1%
Furcraea foetida (L.) Haw.	Shrub	Semi-dry forest	19%
Hedychium gardnerianum Sheppard ex Ker Gawl.	Herb	Lowland and mountain wet forest	11%
Hiptage benghalensis (L.) Kurz	Liana	Lowland wet and semi-dry forest	22%
Leucaena leucocephala (Lam.) de Wit	Tree	Lowland wet and semi-dry forest	9%
Ligustrum robustum Blume	Tree	Mountain wet forest	1%
Litsea glutinosa (Lour.) C.B. Rob	Tree	Lowland wet forest	59%
Miconia crenata (Vahl) Michelang.	Shrub	Lowland wet forest	2%
Psidium cattleianum Sabine	Tree	Lowland and mountain wet forest	39%
Rubus alceifolius Poir.	Liana	Lowland wet forest	23%
Schinus terebinthifolia Raddi	Tree	Semi-dry forest	15%
Searsia longipes (Engl.) Moffett	Tree	Semi-dry forest	10%
Solanum mauritianum Scop.	Tree	Lowland wet and semi-dry forest	3%
Syzygium jambos (L.) Alston	Tree	Lowland wet forest	25%
Tecoma stans (L.) Juss. ex Kunth	Shrub	Semi-dry forest	4%

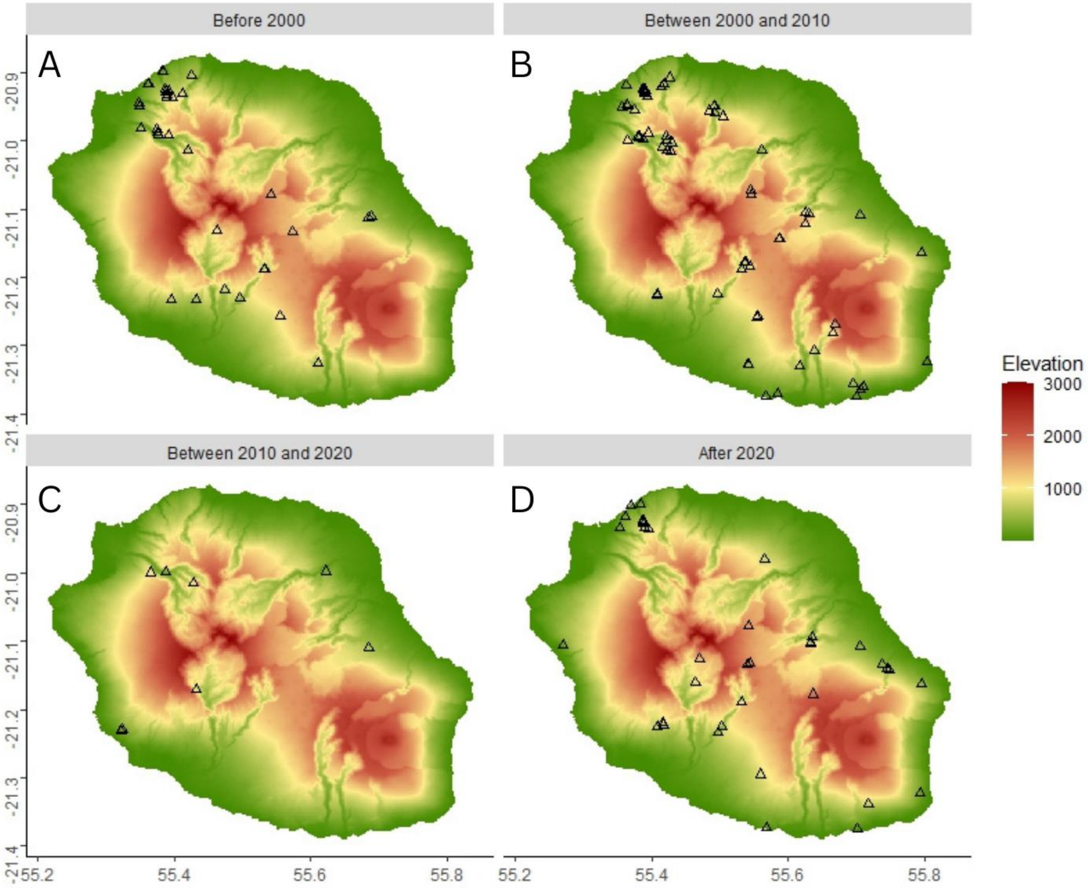

Figure S1: Spatial and temporal coverage of the 158 inventories on the island of Reunion used in this study (A) before 2000, (B) between 2000 and 2010, (C) between 2010 and 2020, and (D) after 2020.

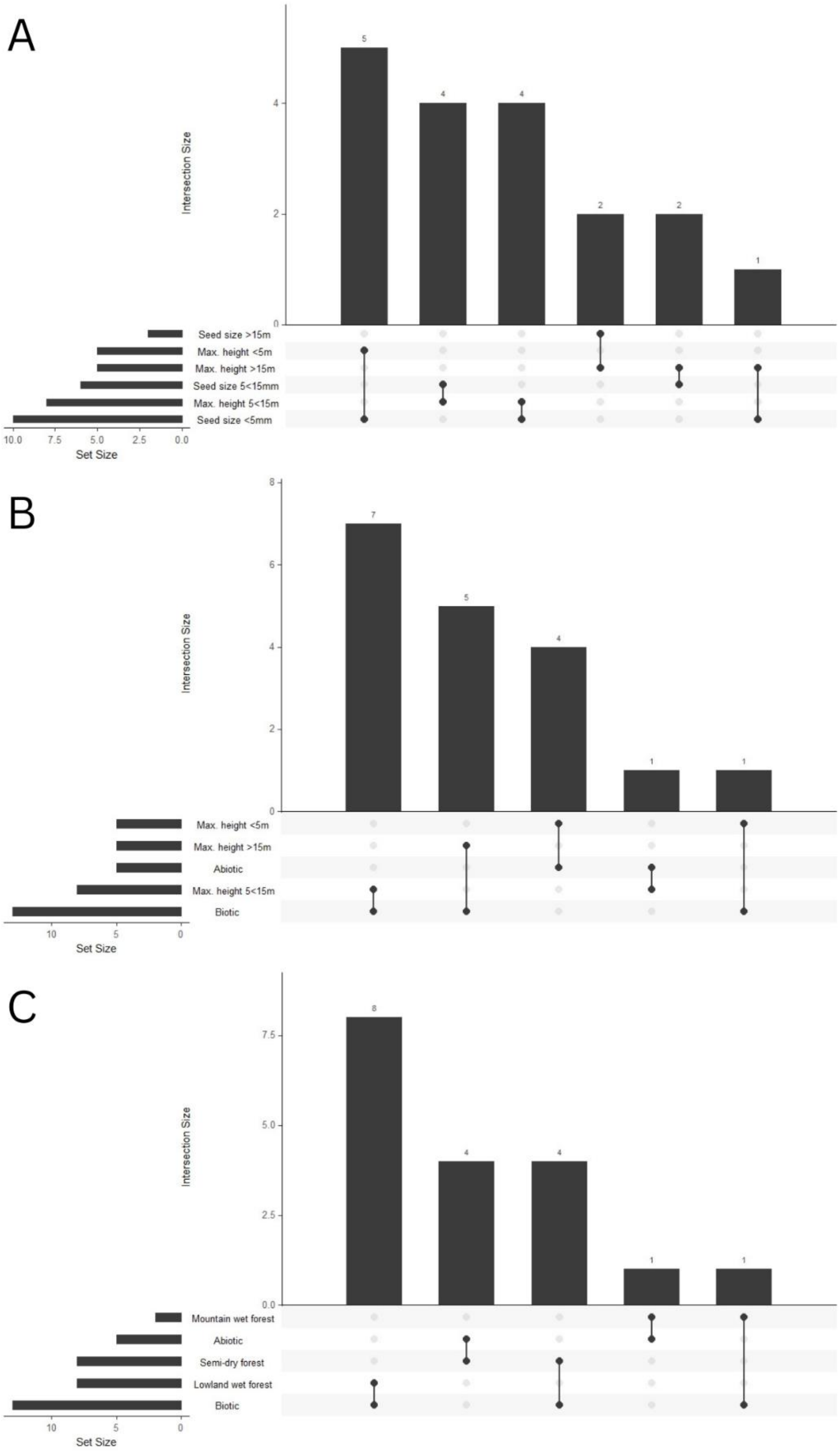

Figure S2: 'Upset plots' representing the intersection between (A) maximum height and seed size (B) maximum height and dispersal syndrome and (C) habitat and dispersal syndrome of the 18 threatened endemic woody species included in this study. The vertical bar charts represent the intersection size between two sub-categories, i.e., the number of species that belongs to both categories. The horizontal bar charts show the number of data points (here *species) belonging to the sub-category. The intersection between the sub-categories is emphasized by a line.*

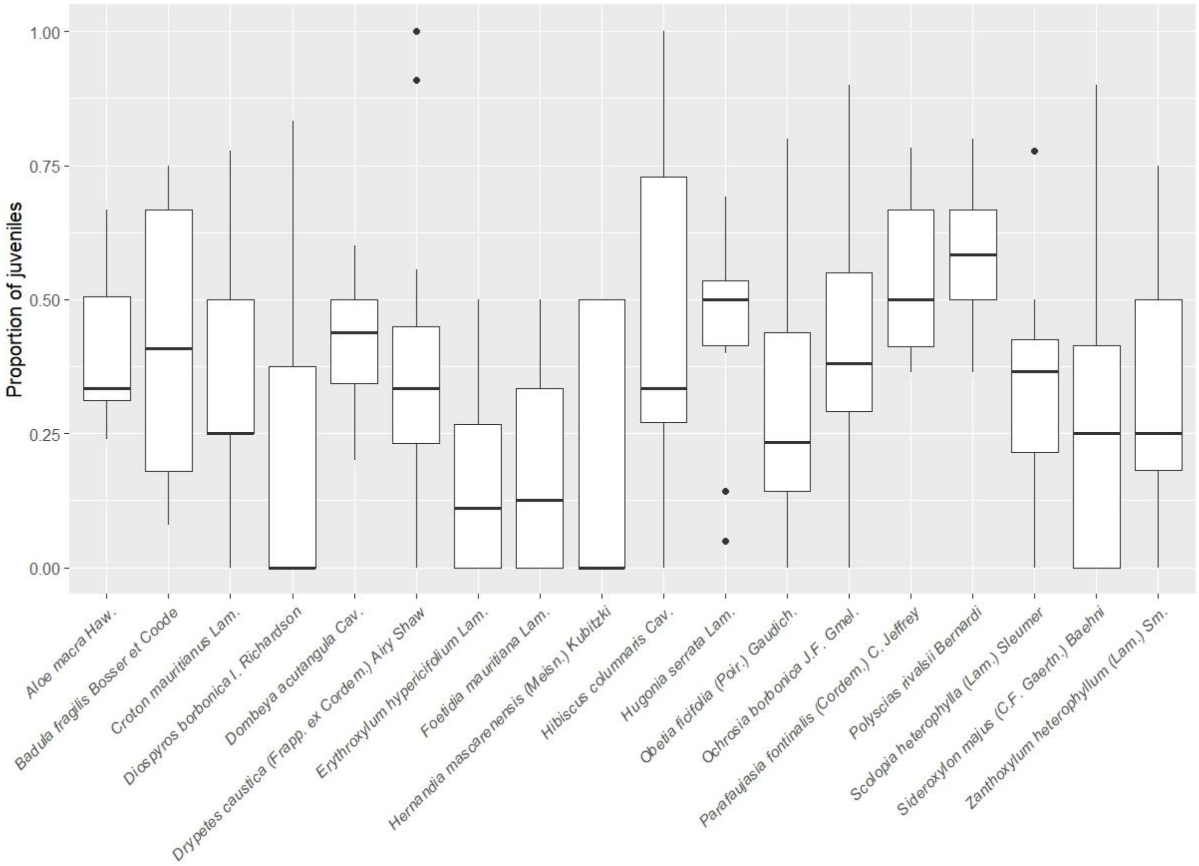

Figure S3: Distribution of the proportion of juveniles of each of the 18 threatened endemic woody species, listed alphabetically. Horizontal bars show median values, the box spans the interquartile range, the whiskers show the minimum and maximum values, and outliers are represented as points beyond the whiskers.

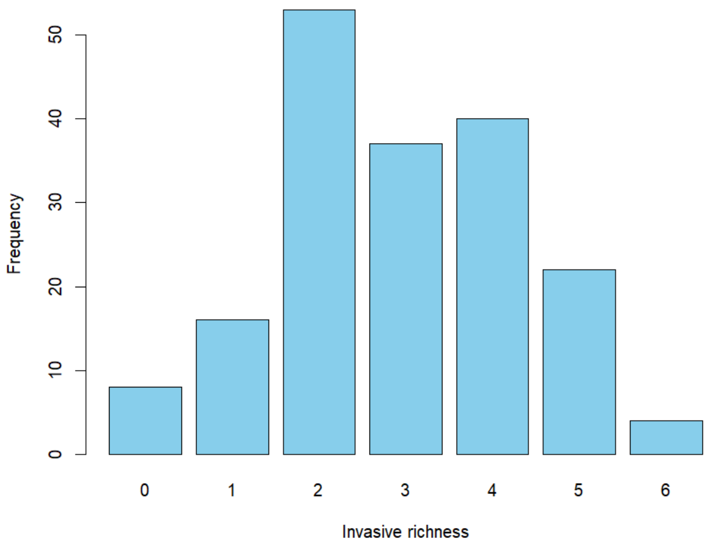

Figure S4: Distribution of invasive alien species richness per inventory. An outlier inventory with nine invasive alien plants was excluded from this figure and all the analysis conducted.