

RESEARCH ARTICLE

Controlling a tree invader for coastal plant communities' restoration affected below-ground dynamics

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Abstract

1. Controlling invasive non-native species is one of the main challenges of ecological restoration, but little is known about what happens below-ground when they are controlled. A better understanding of what happens below-ground when restoring plant communities may be useful to better plan restoration. To fulfil this knowledge gap, we used coastal vegetation on sandy soils in the Brazilian Atlantic Forest (so-called *restinga*) as a model to investigate below-ground dynamics in communities under restoration.
2. We evaluated the effect of controlling an invasive pine tree (*Pinus elliottii*) on fine root biomass, community root length and ectomycorrhizal rate (% of ectomycorrhizae—ECMs in root tips) on *resting* plant communities. We collected root samples in non-invaded and invaded areas, and areas where pine trees have been removed as a control method (hereafter managed areas).
3. The plant community fine root biomass and fine root length density were lower in the invaded area, and similar in non-invaded and managed areas. Effect sizes showed higher ECM rate in the invaded and non-invaded areas, and the lowest ECM rate where *P. elliottii* was controlled, but no significant differences were observed among those values.
4. By showing novel data on fine root biomass, length and ECM rate when invasive non-native trees were controlled, our work fills a knowledge gap exploring how native plant communities respond to invasion control after 6 years of interventions. The decrease in fine roots in the invaded area, and the equivalent values in the managed and non-invaded ones suggest that the removal of pines was sufficient for the recovery of native vegetation.
5. *Synthesis and applications.* Invasive plant species can lead to changes in root structure and affect ecosystem functioning. Root dynamics play a role in the process of natural regeneration and restoration when an invasive plant is controlled, and legacy effects should be considered in planning and monitoring.

KEYWORDS

coastal ecosystem restoration, ectomycorrhizal colonization, *Pinus elliottii*, *restinga*, root biomass, root length, root–root interactions

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1 | INTRODUCTION

Biological invasions are caused by the translocation of species beyond their native range due to human activities. After introduction, non-native species must overcome a survival and a reproduction barrier to establish self-sustained populations, and a dispersal barrier to spread to new locations, being called invasive (Blackburn et al., 2011). Biological invasions are one of the main threats to biodiversity and human wellbeing worldwide (Roy et al., 2024). The structure of native plant communities can be affected by the invasion of non-native species (Vilá et al., 2011), causing impacts on the abundance and diversity of native species (Mesacasa et al., 2022; Pyšek & Richardson, 2010). If not controlled, invasive non-native plants may irreversibly alter the functioning and structure of ecosystems (Blackwood et al., 2010).

The control of invasive non-native species is one of the biggest challenges for ecological restoration (Kettenring & Adams, 2011; Weidlich, Flórido, et al., 2020). However, only the above-ground parts of plants are usually eliminated or removed in restoration initiatives. Possibly, roots from the non-native plants (and its microbiota) remained in the soil, leaving a legacy that may have hindered assembly and the restoration itself (Corbin & D'Antonio, 2012; Dickie et al., 2014; Reynolds et al., 2017). The success of restoration after invasive species control varies depending on the resident plant community identity, seedbank composition, presence of other invasive non-native plants, as well as on how management is done (Machado et al., 2020; Minden et al., 2010; Mostert et al., 2017). In addition, invasive non-native plants can alter soil microbiota and nutrients, and these effects can remain even after these species are removed. This so-called legacy effect (Dickie et al., 2014; Grove et al., 2017) can hinder the restoration success of native communities (Funk et al., 2008; Marchante et al., 2009). The lower the local and landscape resilience is, the greater is the need, intensity and costs of restoration interventions, as well as the need for active methods (Brancalion et al., 2019).

Root traits are important as they are drivers of ecosystem processes, such as productivity, carbon stocks and nutrient cycling (Bardgett & Van Der Putten, 2014; de Kroon et al., 2003; Ravenek et al., 2016), but they are not often measured in comparison with above-ground parameters (Policelli, Horton, García, et al., 2020). Roots are also responsible for allocating resources between roots and shoots (Pérez-Harguindeguy et al., 2013), and if root: shoot allocation changes, this can impact on competitive and facilitative interactions and hence the local plant community performance. Root traits, such as biomass and length, are useful for understanding the changes that occur below-ground (Guo et al., 2007; Lopes et al., 2010). While root biomass is related to ecosystem productivity and carbon storage (Ratuchne et al., 2016), root length describes the ability of roots to exploit a given volume of soil and acquire limited resources, such as water and nutrients (Hecht et al., 2016; Ravenek et al., 2016). More specifically, fine roots (≤ 2 mm) are more dynamic than thicker roots and differ in their ability to acquire nutrients and water, which is their main function (Jackson et al., 1997; Ratuchne et al., 2016; Selle et al., 2010). Fine roots can acquire resources

directly from the soil or through symbionts (Pérez-Harguindeguy et al., 2013). In the latter, fine roots are associated with mycorrhizal fungi (Smith & Read, 2008).

Ectomycorrhizae (ECMs) are associations between plant roots and fungi, where the hyphae do not pierce the hosts' cell wall but occupy the intercellular space of the root cortex or the space among the epidermic cells, forming a so-called *Hartig net* (Smith & Read, 2008). ECM fungi capture nutrients and water from the soil for plants and increase the absorptive area of the root system. In exchange, the fungus receives carbohydrates from plant photosynthesis (Bardgett et al., 2014). These positive below-ground interactions play a key role in plant survival. How control of invasive plants affects root dynamics, including ECM below-ground, has barely been assessed in a restoration context. Thus, evaluating root development patterns and their symbiotic interactions can help to understand what interactions may change when an invasive plant is controlled for restoration.

Invasive non-native trees in coastal ecosystems can reduce the abundance of native species and the functional diversity of local plant communities (Fischer et al., 2014; Mesacasa et al., 2022). In coastal ecosystems in southern Brazil, invasive trees of the genus *Pinus* (usually from North America) are responsible for changing the composition of native communities by reducing the availability of light for native plant communities and producing a thick layer of litter that decomposes very slowly (Fischer et al., 2014; Mesacasa et al., 2022). Pine trees are highly invasive in the Atlantic Forest coastal zones (Bechara et al., 2013) and are known to have symbiotic ectomycorrhizal fungi (Yokomizo & Rodrigues, 1998) that positively impact the establishment of these species in the new environment (Policelli et al., 2018). A recent study suggests that ECM may play an important role in restoring coastal communities in Neotropical regions (Weidlich, Mioto, et al., 2020).

Below-ground studies related to biological invasion are scarce, and even more so in coastal ecosystems. In addition, few studies have evaluated below-ground attributes in the field of restoration ecology (Dickie et al., 2014; Mendes et al., 2018). There are even fewer studies that assess what happens in the soil when invasive non-native species are controlled. The success of restoration and control of invasive non-native species is usually measured by above-ground parameters (e.g. height and basal area), while below-ground parameters are less explored (e.g. biomass and of fine root length and microbiota). To fill these knowledge gaps, we used the Brazilian Atlantic coastal vegetation (so-called *restinga*) as a model to investigate below-ground dynamics in plant communities under restoration. These areas are commonly invaded by pine trees, and controlling them is a major component of interventions in *restinga* restoration.

Our goal was to evaluate the effect of controlling an invasive non-native tree on fine root dynamics of plant communities. We took advantage of a volunteering programme, where citizens have been eliminating invasive pine trees in a protected area on a southern Brazil island (Dechoum et al., 2018), to collect root samples in three different conditions: non-invaded and invaded areas, and areas where pine trees had been removed due to the volunteer actions. We used the same sampling points where above-ground data were collected to evaluate

the success of the control interventions (Mesacasa et al., 2022). A better understanding of what happens underground when controlling invasive species to restore coastal vegetation may be useful to better plan and implement restoration settings. More specifically, this study addressed the following question: What is the effect of controlling invasive non-native pine trees (*Pinus* spp.) on community fine root biomass, length and ECM rate (% of ECM in root tips) of *restinga* plant communities? We answered it by collecting root samples in areas not invaded and invaded, as well as in areas where pine trees have been controlled for 15 years by cutting down the trees at the basal trunk.

2 | METHODS

2.1 | Study area

We collected root samples in a protected area (*Dunas da Lagoa da Conceição Municipal Natural Park*, 27°38'11.69" S and 48°27'45.09" W), which covers an area of 706.76 hectares in Florianópolis, an island in Southern Brazil (Figure 1). The climate is humid mesothermal with hot summers (Alvares et al., 2013) and well-distributed rain, with an annual

average of 1500 mm and greater precipitation in the summer months from December to February. The mean annual temperature is 21°C, with a mean of 25°C in summer and 17°C in winter (INMET, 2021). The Park protects different vegetation types within the larger *restinga* (plant coastal communities on sandy soils in Brazil) remnants that cover fixed, semi-fixed and mobile dunes, in dry, wet and flooded lowland areas (Guimarães, 2006). The vegetation is a mosaic of herb, shrub and tree species (Falkenberg, 1999; Guimarães, 2006). A volunteer programme focused on the control of invasive pine trees has been developed in the protected area since 2010 (Dechoum et al., 2018), summing a total area of 211 ha of control interventions. Therefore, we were able to sample roots in a region still invaded by pine trees, another not invaded, and a third region where pine trees were controlled by the volunteer programme. Each of these regions had around 0.075 hectares, and we name them as our treatment areas.

Pine trees were first planted in the region in 1963, and after 10 years several smaller plantations had already been established across the island, generating additional sources of seeds that could naturally disperse into the different *restinga* vegetation types (Dechoum et al., 2018). Subsequently, new plantings of *Pinus* spp. took place for ornamental purposes and for stabilizing dunes in existing private

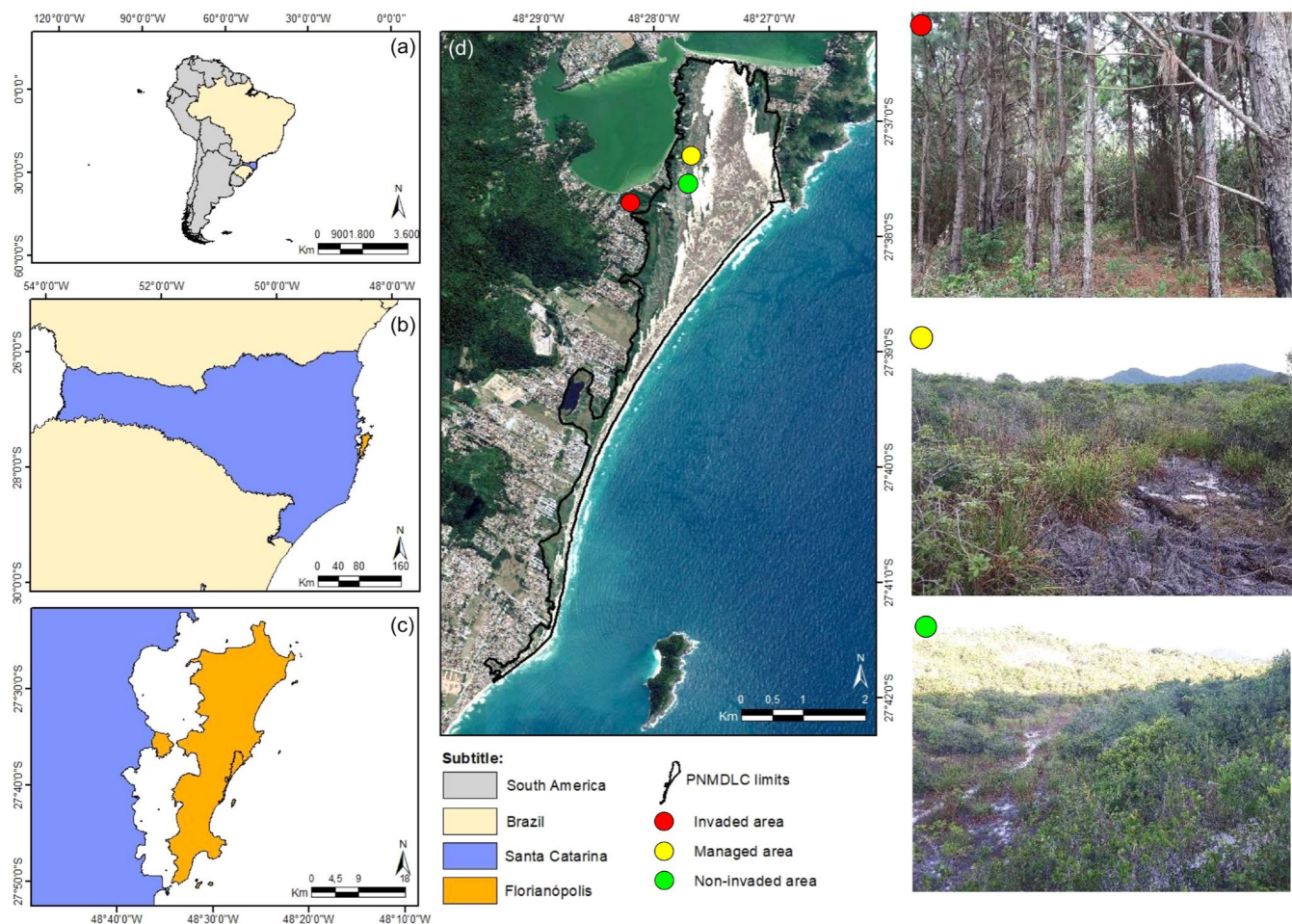


FIGURE 1 Location of the study area showing (a) the State of Santa Catarina in Southern Brazil; (b) Florianópolis island, in State of Santa Catarina; (c) location of the study area in Florianópolis; (d) aerial view of the study area. Orange dot: Location and photograph of the managed area; yellow dot: Location and photograph of the invaded area; blue dot: Location and photograph of the non-invaded area.

properties around the area (Dechoum et al., 2018). *Pinus elliottii*, native to North America, is the most common pine species planted on the island and can exceed 20m in height and has a very deep root system. Individuals of *P. elliottii* reach reproductive age in 5 years and have continuous seed rain throughout the year, dispersing approximately 204 seeds/m² per year (Bechara et al., 2013). Since 2010, a volunteer programme started to remove the pines, aiming to restore areas invaded by *Pinus* spp. by controlling populations (Dechoum et al., 2018). In 10 years, nearly 372,000 individuals of *Pinus* spp. have been eliminated (by cutting and/or uprooting) in the studied area, favouring the regeneration of native vegetation (Hórus, 2020).

2.2 | Data collection

Soil samples were collected to obtain roots in three areas (Figure 1), named hereafter as invaded, managed and non-invaded areas. These are the same areas sampled by Mesacasa et al. (2022) that reported the regeneration of native vegetation. The invaded area was mainly covered by adult pine trees (*Pinus elliottii*, with an estimated density of 1920 individuals per hectare), some shrub species and a few herbaceous species (Mesacasa et al., 2022). The managed area was located where pine trees were controlled by cutting or hand pulling in 2013 (Dechoum et al., 2018). When the roots were sampled in this area, the native vegetation was regenerating, and there were no individuals of *P. elliottii* (Mesacasa et al., 2022). The non-invaded area was a dry lowland composed exclusively of native herbaceous-shrubby and woody vegetation and no individuals of *P. elliottii*, representing what the other two areas would have been if there had not been an invasion (Mesacasa et al., 2022). All plots were set up in areas between sand dunes where the original vegetation was characterized by herbs and shrubs (Guimarães, 2006) and nutrient-poor soils with high sand content and organic matter in depressions between dunes (Mesacasa et al., 2022). Data collection took place in October and December 2019 (authorized by FLORAM, Licence number: 058/2019).

Thirty soil cores were collected with 30cm long soil cores (4cm diameter) in each of the three sampling areas, summing to 90 samples. In the invaded area, soil samples were collected at a maximum distance of 1.5m from *P. elliottii* individuals (minimum height of 5m). We chose sampling soil 1.5m away from a pine tree in order to standardize the sampling method. As the non-invaded area had no pine tree, we sampled it randomly. Samples in the managed area were collected in places with evidence of clear-cutting of pine trees (presence of stumps), at a maximum distance of 1.5m from the base of a stump and with the presence of shrubby vegetation.

2.3 | Community fine root biomass and length

For large root samples, a subsample was taken by randomly selecting half of the root material sorted with sieves in trays with water. The result was extrapolated for the entire sample collected from the field. Roots were washed, scanned, and the images were saved in high

resolution. Fine roots with diameter ≤ 2 mm were selected, and roots with more than 2mm diameter were excluded from this study. The fine root length density was calculated as the ratio between the total length of roots obtained from the image analysis (total of 347 images) and the volume of soil collected. The fine root length density was estimated with RhizoVision Explorer ver. 2.0.3, using the batch-processing mode (thresholding level of 200; filter non-root objects larger than 2mm²; edge smoothing threshold of 1; root pruning threshold of 5, Seethepalli et al., 2021), which allows the measurement of several root fragments. To obtain fine root biomass, the roots were dried in an oven at 60°C for 72h and weighed on an analytical scale. The root biomass was calculated as the ratio between weight (g) and cylinder volume (cm³).

2.4 | Ectomycorrhizal colonization rate

To evaluate the effects of controlling an invasive species on ECM colonization rate, soil cores were collected from January to February 2020, in 10 sampling points per area (30 samples). The samples were collected and processed in the same local and way as for root biomass and length. For each sample collected, 20 fragments of fine roots were randomly selected (subsamples), summing 600 fragments. When selecting the roots to count the tips, we selected the roots that had more than one branch to be able to differentiate whether these were primary, secondary or tertiary root tips. Thus, we were sure that we did not quantify the beginning and end points of the central axis of the root. The ECM rate was calculated using (Equation 1), where TMT represents the total ectomycorrhizal rate; PM is the number of root tips with ECMs, and PT is the total number of root tips (Gehring & Whitham, 1994).

$$TMT = \frac{PM}{PT} \quad (1)$$

2.5 | Statistical analyses

We performed one-way ANOVAs to test the effects of controlling an invasive species treatment (fixed factor, three levels) on total root dry weight and ECM rate. When the null hypothesis was rejected ($p < 0.05$), the mean values were compared using the Newman and Keuls test using the R package agricolae (from de Mendiburu, 2015). The fine root length density data were compared among the three conditions using the non-parametric Kruskal-Wallis test, followed by Dunn's tests for pairwise comparisons. All data were analysed using the statistical software R 1.2.5033 (R Core Team, 2020).

3 | RESULTS

The plant community fine root biomass and fine root length density were lower in the invaded area and similar in non-invaded and managed areas (Figure 2a,b). Fine root biomass in the invaded area

was 35% lower than in the non-invaded area and 72% lower than in the managed area. Fine root length density in the invaded area was 22% lower than in the non-invaded and 26% lower than in the managed area. Effect sizes showed a higher ECM rate in the invaded and non-invaded areas and the lowest ECM rate where *P. elliotii* was controlled (Figure 2c), but no significant differences were observed among those values.

4 | DISCUSSION

By showing novel data on fine root biomass, length and ECM rate when invasive non-native trees were controlled, our work fills a knowledge gap on below-ground patterns exploring how roots respond to invasion control after 6 years of control interventions. Overall, our results show that invasive non-native pine trees altered root patterns, which is an important information for ecological restoration. The decrease in fine roots in the invaded area and the equivalent values in the managed and non-invaded ones suggest that the removal of pines was an adequate method for allowing the roots of native vegetation to recover. In addition, the time since invasion can be related to invasive species density in different stages of the invasion process. A stronger increase in pine density was observed in the establishment stage when the recruitment of many pine seedlings and juveniles was followed by mortality due to high density effects (Mesacasa et al., 2022).

Studies on pine species have shown that the production and biomass of fine roots are higher in younger than in older individuals, emphasizing that the community age structure is relevant (Andersen et al., 2008; Chen et al., 2016). The results found in the invaded area suggest that since the pine trees were adults, they

have few fine roots and consequently thicker roots. The observed decrease in fine roots in the invaded area is possibly due to the characteristics of adult pines, which typically have fewer fine roots. In addition, the lower fine root biomass and length in the invaded area may be explained by the fact that the invasive non-native tree is dominant, with sparse individuals of native shrub and herbaceous species in this area (Mesacasa et al., 2022). Thus, there was less fine root in the invaded area because of the dominance of pine trees (larger roots) and fewer smaller plants from the native community. Another factor that may explain the low values of fine root biomass and length in the invaded area is the presence of a thick layer of litter on the soil. Litter decomposition of pine species is slow and not very sensitive to climatic variations (de Carvalho et al., 2019). This decomposition can release allelopathic exudates into the soil, which can increase acidity and lead to nutrient deficiency, affecting root growth and seed germination of other plants (Lopes et al., 2010; Sartor et al., 2009).

The managed and non-invaded areas showed higher fine root biomass and length when compared to the invaded area. Root biomass and root length indicate soil exploitation to access water and the ability to compete for soil nutrients (Pérez-Harguindeguy et al., 2013). For example, to avoid competition for resources in poor soils, plants can increase the surface area and length of fine roots (Li et al., 2017) or increase the allocation of biomass to below-ground organs (Liao et al., 2019). The increase in fine root biomass can often be related to scarcity of soil resources (Weemstra et al., 2017)—for instance, when available nutrients are low, fine root biomass is high. Thus, high root biomass allocation and fine root density suggest a competitive advantage (de Kroon et al., 2012). Allocation of carbon to fine roots can also increase in soils that lack in humidity, water and nutrients (Bloom et al., 1985), causing plants to invest

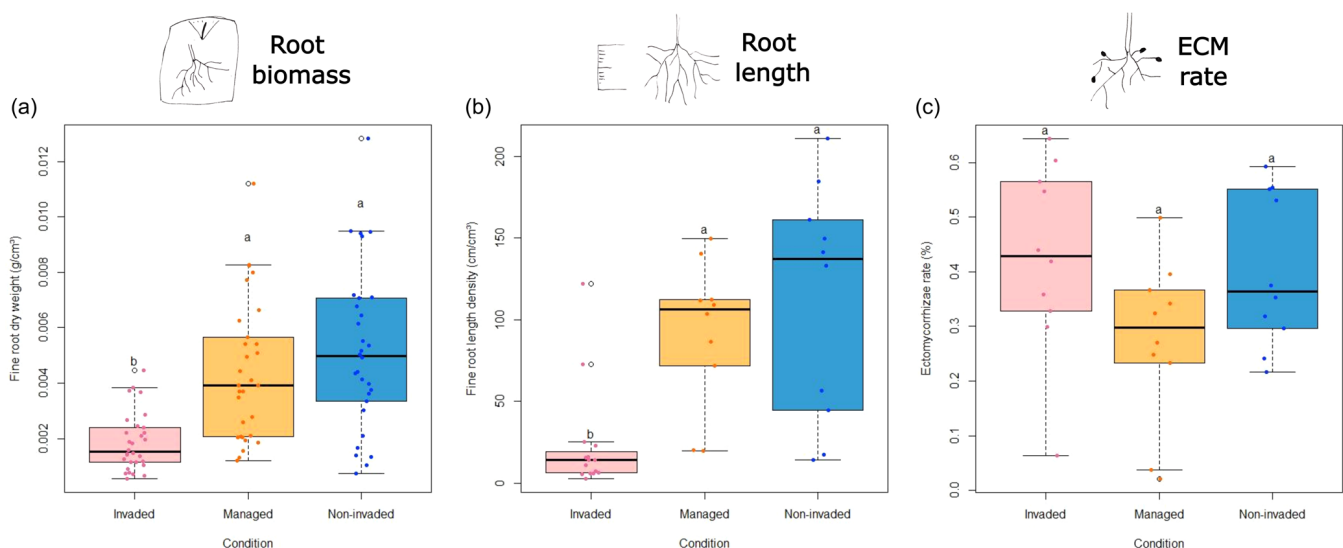


FIGURE 2 Effect of controlling an invasive tree species on fine root dry weight (a), root length density (b) and ectomycorrhizal colonization rate (%) (c). Different letters show statistical differences between treatments (ANOVA followed by Newman-Keuls, $p < 0.05$; in a and c and Kruskal-Wallis followed by Dunn's Tests, $p < 0.05$ in c). Line dividing the bar in half indicates the median, dots represent the samples.

more resources to access and acquire water from the soil (Antunes et al., 2019). Considering that *restinga* soils are predominantly sandy, poor in nutrients and organic matter, rich in salinity and with great permeability to water (Bresolin, 1979; Falkenberg, 1999), a large investment in fine roots can be expected by the native species as a way of adapting to harsh conditions. Thus, a reduction in investment in fine roots may lead to a reduction in fitness and ability to obtain resources for native plants, and this may be one of the mechanisms by which the pines suppress native vegetation.

The higher values on fine root length and biomass in the managed and non-invaded areas (as opposed to the invaded area) suggest that the removal of the invasive species increased the fine root biomass and length of the regenerating native plant community. Our findings can be supported by the fact that roots rely on interactions between biotic and abiotic factors in the soil (McMichael & Quisenberry, 1993; Weemstra et al., 2016) and respond to changes in the environment (Bardgett et al., 2014). Thus, factors such as moisture, nutrient supply and soil properties can change their density and, consequently, the adaptation of the plant community at the site (Sainju & Good, 1993).

The fact that we found similar ECM rates between the three areas may indicate that the ECM fungi associated with the invasive non-native tree are able to successfully colonize the areas to where they were introduced. We observed that the roots collected in the invaded area presented many ECM with a morphology typical of the association of *Pinus* spp. with *Suillus*, which are easily recognized by its short and clustered branches of root tips (Yokomizo & Rodrigues, 1998). In a study conducted in South America, pine trees established novel interactions with native ECM, adopting different strategies to keep symbiotic interactions in the introduced range (Vlk et al., 2020). Moeller et al. (2015) observed that the invasive tree *Pseudotsuga menziesii* (Pinaceae) in New Zealand can associate with several native fungi. Schulz et al. (2012) found that the total ECM colonization rate in plants varied according to the heterogeneity of fungal partners colonizing them and the type of substrate where the plants were growing, which may help to explain the high ECM rate that we observed in the invaded area.

The non-invaded area was predominantly composed of herbaceous-shrubby vegetation and represents what the areas would be without the invasion by *P. elliotii* (Mesacasa et al., 2022). Thus, the absence of the invasive non-native tree allows us to infer that the ECM collected is commonly associated with the native plants growing there (or at least with some of them). *Guapira opposita* (Nyctaginaceae) is a common shrub found in the non-invaded area, which is considered a nurse plant as it facilitates the growth of other plant species in the *restinga* (Dalotto et al., 2018), and is, therefore, important in the processes of ecological succession in *restinga* plant communities. Several ECM fungi associated with *Guapira opposita* have been identified in the *restinga* (Furtado et al., 2022; Genebra, 2021; Roy et al., 2017; Słodkowski, 2020; Vanegas-León et al., 2019). Since invasive trees can establish and grow in places that have not yet been invaded, where native tree species predominate (Policelli, Horton, García, et al., 2020), we highlight the

importance of controlling these invaders so that they do not spread to natural environments.

Our study brings novel results, suggesting that the native vegetation is recovering well and that the potential legacy effect of pine tree invasion did not compromise the recovery of below-ground structure of the native vegetation. Further studies that endeavour to partition which portion of the roots belong to the pine and which to the native species would help confirm this finding. Our results allowed us to answer our research question by showing that restoration intervention (invasive tree elimination) affected below-ground dynamics. We conclude that controlling invasive non-native pine trees affected community fine root biomass and length of *restinga* plant communities. The similar ECM rates found between the three areas suggest that the ECM fungi associated with the pine trees can successfully colonize the areas invaded by this non-native species.

AUTHOR CONTRIBUTIONS

Emanuela W.A. Weidlich, Indiani Conti Della Vechia, Mariana Adami Borgert, Maria Alice Neves, João Paulo Ernzen, Rafael Trevisan and Michele de S. Dechoum conceived the ideas and designed the methodology. Emanuela W.A. Weidlich, Indiani Conti Della Vechia, Mariana Adami Borgert and João Paulo Ernzen performed the experiment and collected the data. Emanuela W.A. Weidlich, Indiani Conti Della Vechia, Mariana Adami Borgert and Michele de S. Dechoum analysed the data. Emanuela W.A. Weidlich led the writing. All authors contributed to the revisions and approved the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests. Emanuela W. A. Weidlich is an Associate Editor of Journal of Applied Ecology but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

The data used in this paper are available in the following link: <https://doi.org/10.6084/m9.figshare.29976325.v1> (Della Vechia, 2025).

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SUPPORTING INFORMATION

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

Supporting Information S1. Results of normality tests showing how the data meets the assumptions of the tests performed.

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