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RESEARCH ARTICLE

# Effects of time since invasion and control actions on a coastal ecosystem invaded by non-native pine trees

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## Abstract

1. Invasive non-native trees cause structural and functional changes in plant communities, which tend to increase over time since invasion. Native vegetation responses after control operations provide important information for restoration.
2. We evaluated the effects of time since invasion and of pine control on plant community structure and on functional traits in a coastal open ecosystem in southern Brazil. We compared richness, diversity, abundance and cover of woody and non-woody native plant species, as well as species composition and community-weighted means (CWM) based on functional traits (dispersal syndrome, fruit type, maximum height and shade tolerance) of plant communities, in four conditions: a non-invaded area, an area where pines were controlled (managed area), an area of recent invasion and an area invaded longer ago.
3. Woody species abundance, richness and diversity declined over time since invasion. However, while abundance recovered to the point of not differing from the non-invaded condition in areas where pines were controlled, species diversity and richness were lower in the managed area than in the area that was never invaded. The effects of pine invasion on richness and diversity of non-woody plants did not increase over time, but plant cover progressively diminished.
4. Woody and non-woody species composition varied between the four conditions. Species composition similarity was lower between conditions for non-woody than for woody species. CWM differed between the older invasion and the other conditions, determined especially by native plant height and shade tolerance. Taller plants and more shade tolerant native species were exclusively sampled in the older invasion.
5. Synthesis and application: Pine invasion reduced species abundance, plant cover, richness and diversity, altering the composition of plant community. The escalation of negative temporal effects of pine invasion was observed on the composition of woody and non-woody species and on functional traits. Although pine control favoured the natural regeneration of non-woody species, diversity of woody species

in the area submitted to pine control was lower than in the non-invaded condition. Restoration activities are therefore required to increase woody species diversity. These results provide relevant guidance for the restoration of coastal ecosystems following invasive pine control.

**KEYWORDS**
community-weighted mean (CWM), functional traits, invasive species, *Pinus*, plant communities, *restinga*, species composition, species diversity, species richness

## 1 | INTRODUCTION

Marine and coastal ecosystems are among the most productive on the planet, providing many ecosystem services for human populations (UNEP, 2006). Approximately 41% of the global population lives on a strip of land not farther than 100 km from the shoreline, including 21 of 33 megacities (CBD, 2012; Katsanevakis et al., 2014). The density of human occupation in these areas leads to a high rate of species introductions and to the degradation of coastal ecosystems, gradually intensified by an increased frequency of extreme weather events generated by the climate crisis (Burgiel & Muir, 2010; Gallego-Fernández et al., 2019; Hulme, 2009; Katsanevakis et al., 2013).

The negative impacts of invasive non-native species compromise the structure and functioning of coastal ecosystems, as well as ecosystem services (Katsanevakis et al., 2014; UNEP, 2006). The effects of increased competition with and displacement of native vegetation, biochemical degradation of water resources and soil destabilization are highlighted among many negative impacts of invasive non-native plants (Makowski & Finkl, 2019). For instance, *Casuarina equisetifolia* and *Cryptostegia madagascariensis* compete for resources and reduce local plant species richness in coastal ecosystems in South America (Gracia et al., 2019; Makowski & Finkl, 2019), generating cumulative negative impacts over time (Wootton et al., 2009).

Studies on *Acacia longifolia* in Portugal show that the effects of reduction in richness, diversity and cover of native plants increased over time of invasion on coastal dunes (Marchante et al., 2015). As time since invasion increased, the number of species shared between invaded and non-invaded areas decreased (Marchante et al., 2015). Other studies demonstrated that the impacts of invasion by *Pinus* spp. in temperate open ecosystems and coastal sand dunes also increased with time since invasion, generating native species richness and diversity losses and functional changes in the native plant community (Bravo-Monasterio et al., 2016; Cuevas & Zalba, 2010; Fischer et al., 2014). On coastal sand dunes in southern Brazil, the presence of thorns in native species was linearly and positively related to the age of invasive *P. taeda* trees, while the potential height of native species had the highest values on intermediate ages (Fischer et al., 2014). On treeless steppe communities in Chile, *P. contorta* promoted the development of traits related to shade tolerance and conservative reproductive strategies (Bravo-Monastério et al., 2016).

Considering the relevance of coastal ecosystems and the potential of invasive non-native species to cause ecosystem changes, control measures are required (Gaertner et al., 2014; Holmes et al., 2020). In some cases, control actions may be sufficient to restore ecosystems, but at times, it may also be necessary to implement complementary restoration actions (Holmes et al., 2020). For example, when control measures lead to exposed soil, the area is subject to reinvasion by the same or other non-native species (D'Antonio et al., 2017; Nsikani et al., 2019, 2020; Pearson et al., 2016). Moreover, the effects of non-native invasive species can be profound, generating changes in structural and functional components of plant communities and creating positive feedback cycles in which invasive non-native species change ecosystems in their favour (Gaertner et al., 2014). In these cases, control measures may not suffice for regeneration to occur naturally or for the ecosystem to resume functioning. Therefore, understanding the magnitude of effects caused by invasive non-native species is key for defining solutions to minimize or revert ecosystem damage after invasion (Lodge et al., 2006; Prior et al., 2017).

The genus *Pinus* contains species considered invasive in different parts of the world, with more records in different ecosystems in the southern hemisphere (i.e. tropical to sub-Antarctic forests, grasslands, savannas and shrublands) (Pauchard et al., 2015; Simberloff et al., 2010). The negative impacts of *Pinus* species vary from declines in native species richness and abundance to changes in native species composition and functional traits, while the intensity of such impacts varies with the type of ecosystem invaded (Andreu & Vilà, 2011; Bravo-Monasterio et al., 2016; Brewer et al., 2018).

In this study, we evaluated the effects of invasion by *Pinus elliottii* over time on structural and functional parameters of plant communities in a subtropical coastal ecosystem. Structural parameters (abundance, plant cover, richness, diversity and composition of woody and non-woody native species) and functional traits (dispersal syndrome, fruit type, maximum height and shade tolerance) of woody native species were compared between a non-invaded area, an invaded area where pines were controlled, an area of recent pine invasion and an area of older pine invasion. The following hypotheses were tested: (1) time since invasion affects the plant community structural and functional parameters evaluated in this study, with more severe effects in areas invaded over longer periods of time; and (2) the control of *P. elliottii* populations is sufficient for plant communities to regain structure and functional traits similar to non-invaded communities.

## 2 | MATERIALS AND METHODS

### 2.1 | Study system

This study was developed in the Dunas da Lagoa da Conceição Natural Municipal Park (PNMDLC, defined as 'Park' hereafter). The Park is located on the island of Santa Catarina (Santa Catarina, Brazil), between coordinates 27°36′38″–27°41′54″ S and 48°26′42″–48°29′25″ W. It was established in 1988 and expanded in 2018, currently covering approximately 707 ha (Florianópolis, 2018). The regional climate is mesothermal (Cfa), with warm summers and average annual rainfall of 1500 mm, with rain well distributed throughout the year (INMET, 2018; Kottek et al., 2006). The average temperature in summer is 26°C, and in winter, 16°C, with an average annual temperature of 20°C (INMET, 2018). The development of this study was authorized by the local environmental agency, FLORAM (Permit 023/2018).

The Park protects a coastal ecosystem named as *restinga* in Brazil, an assemblage of coastal sand dune ecosystems with floristically and physiognomically distinct communities. These plant communities colonize sediments of very diverse origins (marine, fluvial, lagoonal, aeolian or combinations of these), forming an edaphic vegetational complex that occupies a narrow belt along the coast and gives origin to distinct formations such as beaches, dunes and associated depressions, sand ridges, terraces and plains (Falkenberg, 1999). The vegetation in the park is a mosaic of herbaceous and shrub, scrub and forest phytophysiognomies (Guimarães, 2006). Soils are nutrient poor, characterized by high sand content and organic matter in depression between dunes (Mioto, personal communication). These low areas dominated by herbs and shrubs are more susceptible to invasion by pines (Dechoum et al., 2019).

While the introduction of *Pinus* species on the island of Santa Catarina for forestry purposes took place in 1963, it was in the 1970s that spread became visible (Caruso, 1990; Dechoum et al., 2019). In addition, pines were later planted for ornamental purposes and for dune stabilization in private properties. A series of aerial photographs taken in 1937, 1957 and 1978 show that as private properties were developed in the Park surroundings, the first pine trees were planted in the early 1970s. These planted pines are believed to have been and still be the main sources of seeds that caused the park to be invaded (Dechoum et al., 2019).

Volunteering efforts for the control of *P. elliottii* have been ongoing in the park since 2010 (Dechoum et al., 2019). The management of invasive pines basically consists in pulling out seedlings (up to 0.5 m height) and cutting down juveniles and adults with hand saws or chainsaws, depending on the size (more details about the volunteering program in Dechoum et al., 2019).

### 2.2 | Sampling design and data collection

Data collection was conducted between August and October, 2018, in four areas between sand dunes with similar environmental characteristics. Four conditions were evaluated: (A) area not invaded by *P. elliottii*, defined as non-invaded (NI; 0.075 ha); (B) area previously invaded, where pines were managed in 2013, defined as managed area (MA; 0.075 ha); (C) area invaded more recently, defined as recent invasion (RI; 0.025 ha); and (D) area invaded for a longer time, defined as older invasion (OI; 0.050 ha) (Figure 1). The total area of plots was 0.225 ha. All plots and subplots were set up in areas between sand dunes where the original vegetation was characterized by herbs and shrubs (Guimarães, 2006).

The NI condition represents the control area—that is what the other areas would look like if pines had not invaded (Figure 1a). In the MA condition, seedlings were pulled out (<50 cm height) and juveniles (>50 cm height) and adults cut down in 2013—in other words, every pine tree or seedling was removed (Dechoum et al., 2019). All residue of control was left in the area to degrade (Figure 1b). The estimated number of pines eliminated, including adults, juveniles and seedlings in the area, was 16,000 (ca. 114 pines/ha) (Dechoum et al., 2019). In the RI condition, the herb–shrub physiognomy is still dominant, and the majority of pines consist of seedlings and small to medium size juveniles, as well as some scattered adults (Figure 1c). The forest physiognomy in the OI condition is dominated by adult pines, with scattered native shrubs and low herb cover (Figure 1d). There were no pine seedlings, only a few juvenile trees. None of the invaded areas (RI and OI) had been subjected to previous conversion and/or other management intervention. We postulate that the difference in time since invasion is a consequence of density and age of adult pines planted in private properties in the park surroundings (see Section 2.1). In other words, there was a higher density of larger/older adult trees in private areas closer to the OI condition compared with the RI condition.

Ninety 5 × 5 m plots were set up in the four conditions. Conditions NI and MA comprised 30 plots each, 10 plots were set up in RI and 20 in OI. The minimum distance between plots was 20 m. The number of plots varied due to the size of the areas in each of the four conditions.

All native woody plants above 1 m in height were identified and had their height measured in each plot. Four subplots measuring 1 × 1 m were set up at the vertices of each plot, totalling 360 subplots. All plants between 0.1 and 1 m in height were identified at the species level (whenever possible) and categorized as 'woody' or 'non-woody'. Plants not identified in the field were collected for later identification with identification keys and taxonomic references, or with support from experts. Among the specimens not identified at the genus or species level, most are in family Poaceae (grasses), which are very hard to distinguish if not fertile, or in families Myrtaceae and Lauraceae, which are two of the richest woody species families along the Brazilian coast, therefore often hard to identify from sterile material (see Appendix S1).

Percentage of plant cover by woody and non-woody species and class of soil exposure were also measured in the subplots. The proportion of soil without live plant cover in the subplots was classified as exposed soil. Percentage of cover was divided in the following classes: Class 1, 0%–5% (2.5%); Class 2, 5%–15% (10%); Class 3, 15%–25% (20%); Class 4, 25%–50% (37.5%); Class 5, 50%–75% (62.5%); and

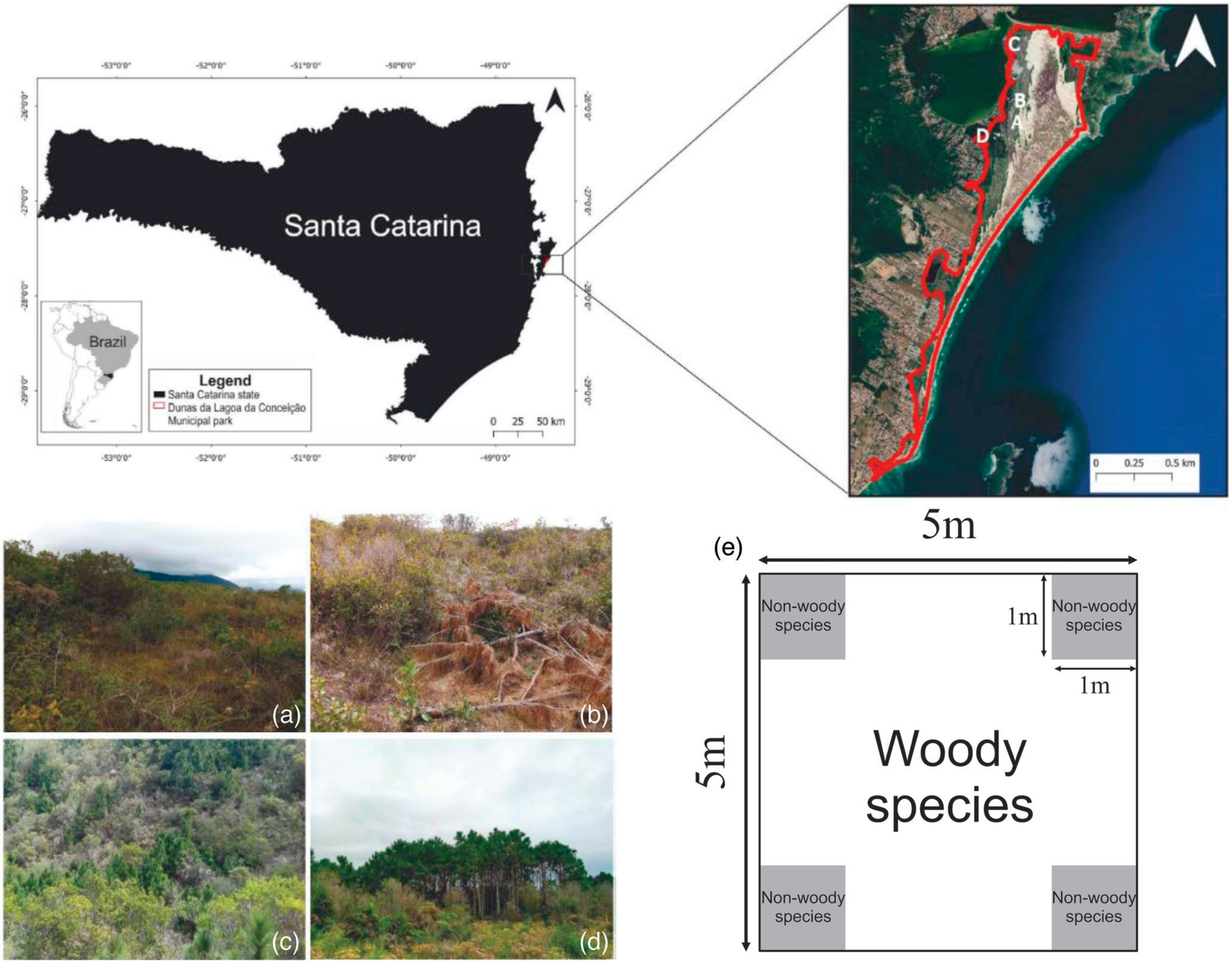


**FIGURE 1** Location and limits of the Dunas da Lagoa da Conceição Natural Municipal Park (Florianópolis, SC, Brazil) and sampling areas: (a) area not invaded by *P. elliottii* (NI); (b) area previously invaded by *P. elliottii* where pines were managed/eliminated in 2013 (MA); (c) area of recent invasion (RI); and (d) area of older invasion (OI). The figure in the lower right (e) illustrates the sampling design in each plot for each condition (NI, MA, RI and OI): woody species were sampled in 5 × 5 m plots, whereas non-woody species were sampled in four subplots established at the corners of each plot. The number of plots per condition was NI: 30, MA: 30, RI: 10 and OI: 20

Class 6, 75%–100% (87.5%) (Assumpção & Nascimento, 2000). Median values were used in statistical analyses.

All pines in the RI and OI plots were counted and the perimeter at ground level (PGL) of all trees with PGL ≥ 25 cm was measured. All the stumps remaining after pine control in MA were counted and classified in two size classes: trees with PGL ≥ 25 cm (adults) and trees with PGL < 25 cm (juveniles).

All woody species taller than 1 m in the plots were classified according to four functional traits: (1) dispersal syndrome: anemochory (wind), zoochory (animals) or autochory (self-dispersed); (2) fruit type: dry dehiscent or indehiscent, fleshy dehiscent or indehiscent; (3) maximum height of woody plants measured in the plots; and (4) shade tolerance: tolerant or intolerant. These four functional traits were selected from scientific literature (Reitz, 1965; van der Pijl, 1982; Carvalho, 2003, 2008, 2010; Lorenzi, 2009; Pires et al., 2009; Seubert et al., 2017; Flora do Brasil, 2020).

## 2.3 | Statistical analyses

Rarefaction curves were built and compared between the four sampling conditions, using abundance of native woody species in plots and cover of non-woody species in subplots (Chao et al., 2014).

A Generalized Linear Model (GLM) was built to compare the abundance of woody native species between the four conditions assessed (NI, MA, RI and OI). In this model, we used the negative binomial distribution for the response variable, and condition as fixed effect. Contrast analyses were then run for pairwise comparison (Russell, 2019). Cover of native woody and non-woody species and percentage of exposed soil were compared between the four conditions evaluated (NI, MA, RI and OI) using Generalized Linear Mixed Models (GLMM). As in each model the beta distribution was used for the response variables, the condition was considered as fixed effect and the subplots as random effect. Model validation was based on graphical analysis of the residuals.

Non-metric multidimensional scaling (nMDS) was used to compare species composition in the four conditions analysed. The Bray–Curtis index was used as distance measure for woody species in the plots and subplots, and the Jaccard index was used for non-woody native species in subplots in the four conditions analysed. The Bray–Curtis and the Jaccard indexes were used to assess the dis(similarity) in species composition between the four conditions. The Bray–Curtis index was calculated based on the abundance of woody species sampled in each plot, whereas the Jaccard index was calculated based on the presence/absence of non-woody species in each subplot. Permutational Multivariate Analyses of Variance (PERMANOVA) were used to compare the statistical difference between the four conditions (Oksanen et al., 2019).

Community-weighted means (CWM) were calculated for the four functional traits selected in one of the four conditions based on the abundance of woody native species. CWM is a useful way to calculate community trait values weighted by species abundance to investigate trait patterns for entire communities rather than just individual species. Once calculated, CWMs were used in a GLM to compare the relationship between the conditions assessed (response variable) and each functional trait (explanatory variable), followed by contrast analyses for pairwise comparison (Russell, 2019). Finally, a Principal Component Analysis (PCA) was conducted to determine the functional structure and similarity between the four conditions analysed.

All analyses were conducted using the RStudio interface (RStudio Team, 2018). The iNEXT package (Hsieh et al., 2019) was used to build the rarefaction curves. The GLM, GLMM and contrast analyses were conducted with packages lme4, MASS, emmeans and lsmeans (Bates et al., 2015; Russell, 2019; Russell et al., 2019); the Vegan package was used for the nMDS analysis (Oksanen et al., 2019); the tidyverse package was used for the CWM analysis (Wickham et al., 2019); and the PCA used the FactoMineR package (Lê et al., 2008). Only native plants identified to the species level were used in all analyses.

## 3 | RESULTS

The sampling efforts revealed 115 native morphospecies and one non-native species (*Holcus lanatus* L.) in 45 families. Of these, 89 (47 woody and 42 non-woody) were identified to the species level, while 27 (8 woody and 19 non-woody) were not (Supporting Information). The numbers of woody plants and the number of species recorded, as well as the estimated density of pine trees (ha) in each condition, are presented in Table 1.

### 3.1 | Species richness, diversity, abundance and cover

Richness of woody and non-woody species did not differ between conditions NI and MA, where it was higher than in conditions RI and OI (Figure 2a,d). A decreasing pattern was observed for woody species diversity: NI > MA > OI > RI (Figure 2b,c), whereas the following pattern was observed for non-woody species: NI = MA > OI > RI (Figure 2e,f). All curves tended to stabilization in the interpolation (Figure 2a–f).

Native woody species abundance did not differ between NI, MA and RI, and was higher in these conditions than in OI (Figure 3a), while native woody plant cover was higher in NI than in RI, OI and MA (Figure 3b). Native non-woody plant cover was higher in NI and MA than in OI and RI, between which no difference was observed (Figure 3c). Exposed soil was higher in OI than in the other conditions but did not differ between MA and NI (Figure 3d). The results of all GLM and GLMM are available in the Supporting Information.

### 3.2 | Species composition

Woody plant composition similarity in plots and subplots differed between the four conditions evaluated (PERMANOVA $p = 0.001$; $r = 0.30$) (Figure 4a). A separation of the OI condition was observed due to higher variation in species similarity than in the other conditions, with lowest variation in NI. The composition of native non-woody species (PERMANOVA $p = 0.001$; $r = 0.29$) varied more between subplots in the OI condition, while similarity was higher between subplots in NI (Figure 4b).

### 3.3 | Functional structure

The CWM values for functional traits of native woody species showed that maximum height was higher in OI ($p = 0.0001$) than in the other three conditions. The other functional traits evaluated did not differ between conditions (Table 2).

The first two PCA axes explained 76.8% of CWM data variation, with the maximum height trait explaining 48.91% of axis 1, and the trait shade tolerance explaining 27.94% of axis 2. Dispersal syndrome explained 22.2% of axis 3, while fruit type explained only 0.93% of axis 4. These results highlight the separation of the OI condition from the others. The functional structure differs in OI, determined especially by taller individuals of native species that are more shade tolerant. In conditions NI, MA and RI, functional structures were superposed, and functional traits were similar (Figure 5).

## 4 | DISCUSSION

In this study, we have disentangled structural and functional effects over time since invasion of plant communities by *Pinus elliottii*, which generally affected the structural and functional parameters evaluated. However, as such effects were not increasingly severe over time since invasion, our first hypothesis was rejected. In short, different results were observed both due to time since invasion and to the parameter evaluated. The second hypothesis of the study was not corroborated, as the diversity of native woody species was lower in managed areas than in non-invaded areas. The combination of results over time and

**TABLE 1** Parameters evaluated in plant communities in the Dunas da Lagoa da Conceição Natural Municipal Park (Florianópolis, SC) in four different conditions: (NI) non-invaded area by *P. elliottii*; (MA) previously invaded area where *P. elliottii* was managed/eliminated in 2013; (RI) area of recent invasion; and (OI) area of older invasion. PGL, perimeter at ground level

| Parameter evaluated | NI | MA | RI | OI |
|---|---|---|---|---|
| Number of woody plants | 2077 | 1689 | 521 | 382 |
| Number of woody plant species | 24 | 20 | 15 | 43 |
| Number of *P. elliottii* plants (PGL < 25 cm) | – | 127 | 146 | 97 |
| Estimated density of young *P. elliottii* trees (ha) | – | 1693 | 5840 | 1940 |
| Number of *P. elliottii* adult trees (PGL ≥ 25 cm) | – | 64 | 32 | 91 |
| Estimated density of adult *P. elliottii* trees (ha) | – | 853 | 1280 | 1920 |
| Total estimated density of adult *P. elliottii* individuals (ha) | – | 2546 | 7120 | 3760 |

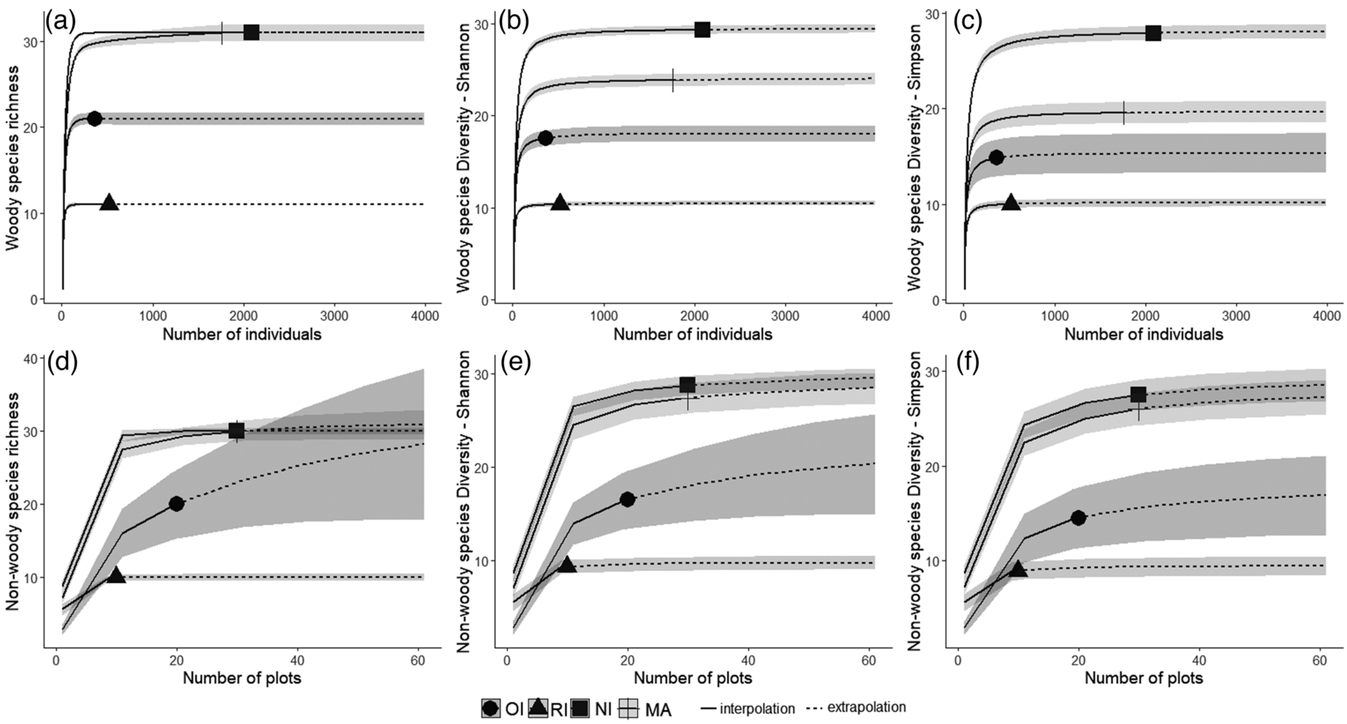


**FIGURE 2** Rarefaction curves for woody and non-woody species in plots and subplots in the Dunas da Lagoa da Conceição Natural Municipal Park (Brazil), comparing four conditions (NI: non-invaded, MA: managed area, RI: recent invasion, OI: older invasion). Rarefaction was estimated from individual plants for woody species and from subplots for non-woody species (*x*-axis). (a) Estimate of woody species richness, (b) diversity of woody species (Shannon Index), (c) diversity of woody species (Simpson Index), (d) richness of non-woody species, (e) diversity of non-woody species (Shannon Index) and (f) diversity of non-woody species (Simpson Index). The solid line represents the interpolation, and the dotted line, the extrapolation to twice the number of sampling units. Shaded area: CI = 95%

the response of plant communities to pine control provide a scientific basis for developing restoration guidelines for invaded areas after control in similar situations where additional actions are required to complement natural regeneration.

Changes in richness, diversity and abundance/cover of woody and non-woody native species in invaded areas have been observed in many studies, as on grasslands in Chile invaded by *P. contorta* (Bravo-Monasterio et al., 2016) and in savannas in central Brazil invaded by *P. elliottii*, *P. caribaea* and *P. oocarpa* (Abreu & Durigan, 2011; Brewer et al., 2018; Cazetta & Zenni, 2020). In this study, we verified that native non-woody plant cover decreased even in an area of recent invasion in coastal scrub, and that this effect was not aggravated over time. For native woody plants, both cover and abundance were higher in areas more recently invaded. Both richness and diversity of native woody and non-woody plants were higher in areas more recently invaded, a result that was expected, as such negative impacts become more severe with invasion density (Bravo-Monasterio et al., 2016; but see Brewer et al., 2018). Conversely, the

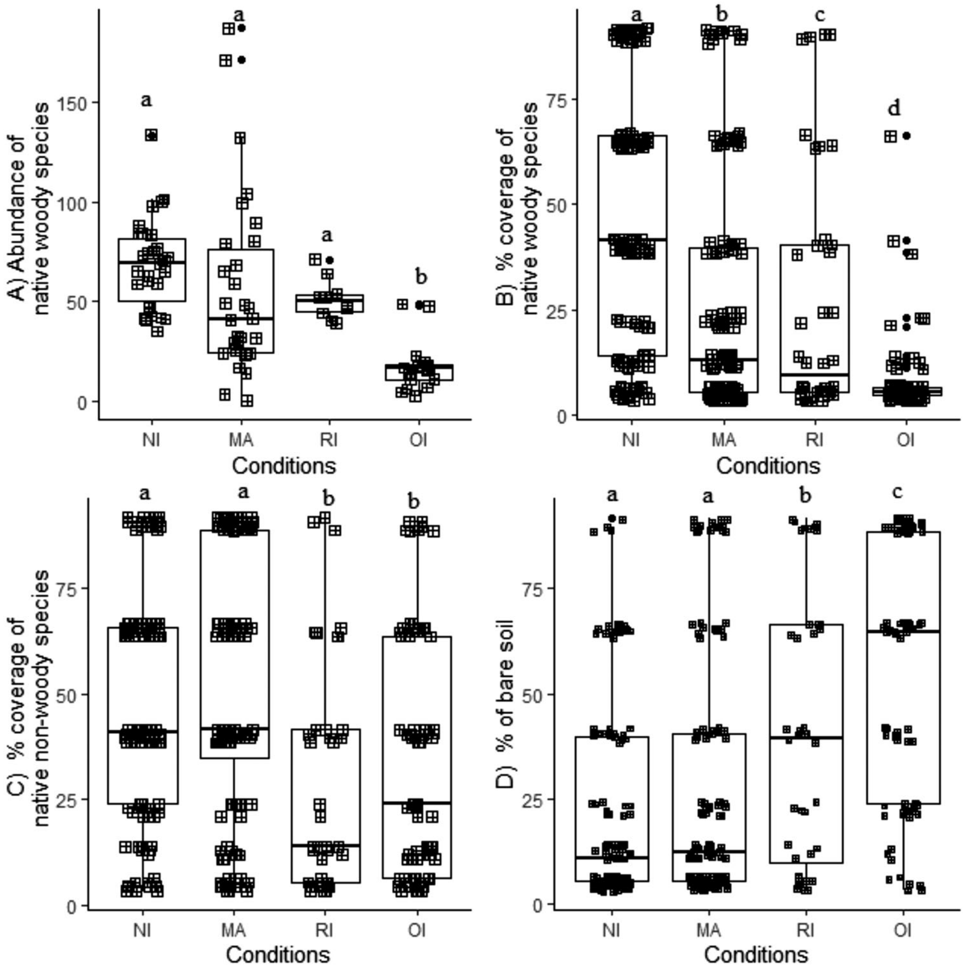


**FIGURE 3** Parameters evaluated in plots and subplots in the Dunas da Lagoa da Conceição Natural Municipal Park (Brazil) comparing four conditions (NI: non-invaded, MA: managed area, RI: recent invasion, OI: older invasion). (a) Abundance of woody native species, (b) % of cover of woody native species, (c) % of cover of non-woody native species and (d) % of exposed soil. Symbols represent the sampling units. Boxplots represent the median (central horizontal line) and the first and third quartiles (lower and higher horizontal lines, respectively). Different letters denote significant differences ($p < 0.05$)

**TABLE 2** Pairwise contrast analyses comparing functional traits of woody species in sampling plots in the Dunas da Lagoa da Conceição Natural Municipal Park (Brazil) in conditions of non-invaded area (NI), managed area (MA), recent invasion (RI) and older invasion (OI)

| Conditions | Height ($p < 0.05$) | Shade tolerance ($p < 0.05$) | Fruit type ($p < 0.05$) | Dispersal syndrome ($p < 0.05$) |
|---|---|---|---|---|
| OI – RI | 0.0001* | 0.74 | 0.85 | 0.98 |
| OI – NI | 0.0001* | 0.82 | 0.91 | 0.84 |
| OI – MA | 0.0001* | 0.95 | 0.99 | 0.79 |
| RI – MA | 0.05 | 0.86 | 0.91 | 0.89 |
| RI – NI | 0.52 | 0.77 | 0.84 | 0.84 |
| NI – MA | 0.07 | 0.85 | 0.89 | 0.93 |

*Significant values ($p < 0.05$).

intensification of the effects of time since invasion was observed on woody species abundance, as well as in increased dissimilarity in species composition, and on the functional structure of the plant communities studied. Percentage of exposed soil was also higher in the area of older invasion, an indicator of degradation (Bravo-Monastério et al., 2016).

The results obtained on the effects of 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 a large number of seedlings and juveniles may be followed by a population drop by mortality due to high density effects, then stabilization while plants grow in height and diameter (Dechoum, personal observation). Density effects are not expected to be linear, and vary over time, which shows that impacts of invasive non-native species may be context dependent and occur either at low or high density (Catford et al., 2019; Sapsford et al., 2020).

Several native woody and non-woody species abundant in adjacent forest communities colonized the area of older invasion and began to change the composition of the plant community. More shade

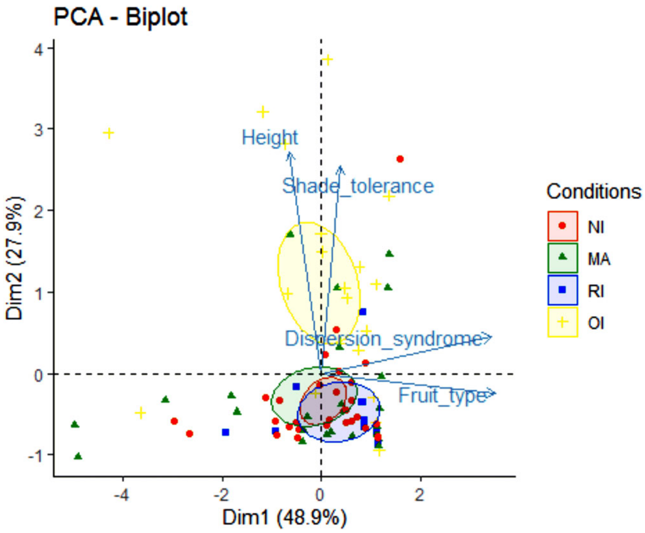


**FIGURE 4** Non-metric multidimensional scaling (nMDS) using the Bray–Curtis index to evaluate similarity in the composition of woody species, and the Jaccard index for non-woody species, in the Dunas da Lagoa da Conceição Natural Municipal Park (Brazil), comparing four conditions (NI: non-invaded, MA: managed area, RI: recent invasion, OI: older invasion). (a) Woody species (stress: 0.12). (b) Non-woody species (stress: 0.12)

tolerant native species were exclusively sampled in the OI condition (Supporting information). These results agree with Cazetta and Zenni (2020), who detected changes in native species composition in savanna (Cerrado) invaded by *Pinus* spp. Fischer et al. (2014) verified that changes by *P. taeda* invasion caused dune species to be replaced by species with different traits more prone to survive in the invaded habitat. Other studies also report that changes in areas invaded by *Pinus* spp. have led to changes in native species composition (Simberloff et al., 2010; Martyniuk et al., 2015).

Invasive plants may also alter the functional structure of communities and ecosystems (Mouillot et al., 2013). Our results show that invasion by *P. elliottii* affected the height of native woody species. A possible explanation is that, as invasion progresses, the canopy grows higher, reducing light availability on the ground—a functional change (Abreu et al., 2011; Lemos-Filho et al., 2010; Fischer et al., 2014; Zanzarini et al., 2019). As a result, plants in the OI condition reacted by developing long stems and petioles in search of light, while the development of leaves and roots was reduced (Li et al., 2012). We also observed that the functional space in condition OI differed from the other conditions, providing evidence of community structural and functional changes over time since invasion. Additionally, changes in vegetation patterns might also be due to changes in soil properties, as observed in different open ecosystems invaded by woody plants (Boscutti et al., 2020; Vitti et al., 2020).

Our results show that *P. elliottii* control was insufficient to allow managed (MA) native plant communities to develop a structure similar to non-invaded communities (NI) after 6 years of management, as the diversity of woody native species was lower in MA than in NI. In these cases, pine control efforts might need to be combined with active restoration efforts such as seeding, planting native species or

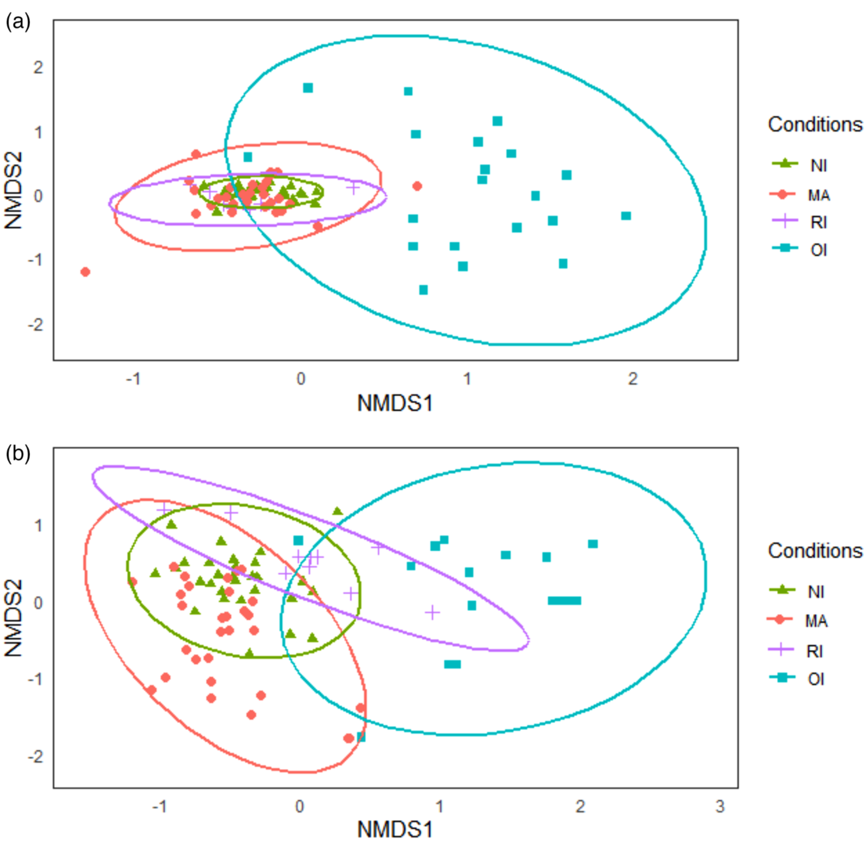


**FIGURE 5** Principal Component Analysis (PCA) comparing the functional structure of plant communities in four conditions (NI: non-invaded, MA: managed area, RI: recent invasion, OI: older invasion) evaluated in the Dunas da Lagoa da Conceição Natural Municipal Park (Brazil) based on CWM values calculated from the abundance of native woody species

promoting germination of the native seed bank in the soil (Warren et al., 2002; McAlpine et al., 2016).

Managed areas may be susceptible to invasion by other species, as in the case of non-native grasses invading the Craigieburn Forest Park in New Zealand after control of *P. contorta* (Dickie et al., 2014). In our study, the non-native grass *Holcus lanatus* (Poaceae), native to Europe, was found in low density in the managed area. It occurs in southern and south-eastern Brazil (Flora do Brasil, 2020), tolerates a wide range of soil conditions and may become invasive (Muller et al., 2017), as it has a history of invasion in coastal ecosystems in Chile (Arroyo et al., 2000). This grass should therefore be controlled, especially in pine control areas, to prevent secondary invasion after control (Dickie et al., 2014; Pearson et al., 2016).

We acknowledge that not knowing the exact amount of time passed since invasion by pines in each study area (RI and OI) created uncertainty. However, the presence of a higher number of large trees and a lower density of small trees/regenerants are proxies for older invasion; the opposite is valid for more recent invasion (see Table 1). In other words, although we do not know how long ago each pine population was established in each condition (RI and OI), it was feasible to separate older and younger populations based on the density of adult and young pines. Future studies focused on the dendrochronology of pine trees could shed light on the temporal relationship between impacts of pine invasions on plant communities as well as on the recovery of plant communities after control.

Our study provides information on how *restinga* communities respond to invasion by *P. elliottii* over time. Impacts caused by invasive pines on the structure of plant communities, even in cases of relatively recent invasion, stress the need for control of invasive non-native trees in coastal ecosystems. The areas in our study where pines have been managed require complementary restoration measures. Although herb species were impacted even in a recently invaded area, herb cover naturally recovered after pine control to a high degree of similarity with an area that was never invaded. Therefore, complementary restoration measures should focus mainly on planting or seeding local native woody species occurring in areas free of invasion that are no longer found in invaded areas, such a *Lithraea brasiliensis*, *Ilex dumosa* and *Davilla rugosa*.

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## CONFLICT OF INTERESTS

No conflict of interest to declare. Michele de Sá Dechoum is an Associate Editor of Ecological Solutions and Evidence, but took no part in the peer review and decision-making processes for this paper.

## AUTHOR CONTRIBUTION

MSD and PF conceived the ideas and designed methodology. LM collected the data. LM and LBM analysed the data. LM and MSD led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## PEER REVIEW

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## DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.63xsj3v43 (Mesacasa et al., 2022).

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