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ORIGINAL PAPER

Biotic and abiotic changes in subtropical seasonal deciduous forest associated with invasion by *Hovenia dulcis* Thunb. (Rhamnaceae)

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Abstract Several tree species are found among the most well-know and impacting invasive plants that produce changes in richness, abundance and composition of native plant species as well as in environmental characteristics and ecosystem functioning. *Hovenia dulcis* Thunb. (Rhamnaceae) is a tree native to East Asia, invasive in southern South America in different forest ecosystems. This study was aimed at assessing the effects of *H. dulcis* on richness, abundance and composition of regenerating species in seasonal deciduous forest (SDF) by comparing invaded and non-invaded areas. The existence of correlations between abundance and richness of regenerating species with age and density of the invasive species, as well as with characteristics of canopy openness, litter thickness, slope, and soil moisture, was investigated in areas invaded by *H. dulcis*. Differences observed in canopy openness and litter tickness between areas invaded by *H. dulcis* and control areas suggest that *H. dulcis* is able to change environmental conditions on a local scale. Although no difference was observed in species richness between areas with and without *H. dulcis*, the differences registered in abundance and composition of regenerating species make the impact by *H. dulcis* on regeneration patterns in SDF fragments evident. The impacts caused by *H. dulcis* on SDF confirmed by this study highlight the need for its control in legally protected areas and their immediate surroundings, as well as for the adoption of public policies to promote the substitution of *H. dulcis* for locally native species.

Keywords Invasive tree · Japanese raisin tree · Light regime · Plant invasion · Forest regeneration · Soil moisture · Species composition

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Introduction

There are several tree species among the most well-known and impacting invasive plants (Richardson and Rejmánek 2011; Rejmánek and Richardson 2013; Richardson et al. 2014). Invasive non-native trees can produce changes in the richness, abundance and composition of native plant species as well as in environmental characteristics and ecosystem functioning (Hughes and Denslow 2005; Bertin et al. 2005; Reinhart et al. 2006; Wardle et al. 2011; Constán-Nava et al. 2014; Aragón et al. 2014; Lorenzo et al. 2016; Enoki and Drake 2017; Bellingham et al. 2018). As a result, the structure of invaded communities, as well as successional trajectories, may be affected (Hughes and Denslow 2005; Vilà et al. 2011; Richardson et al. 2014; Zucaratto and Pires 2014; Potgieter et al. 2014; Lorenzo et al. 2016). Biological invasions, along with the extinction of indigenous species, may result in biotic homogenization due to an increase in genetic, taxonomic and functional similarities between two or more sites in a known period of time (Olden et al. 2018). Biotic homogenization is considered one of the facets of the global biodiversity crisis, with significant ecological, evolutionary and social consequences (Olden et al. 2018).

Invasive trees in forests usually present a combination of traits typical of species in early (large seed crops and fast growth) and late sucessional stages (shade tolerance and high competitive ability) (Martin et al. 2010). Although invasions by tree species tend to develop more slowly than invasion by shrubs or herbs, given the longer juvenile period of trees, their effects on plant communities tend to last a long time, increasing with age and density (Wangen and Webster 2006; Pysek et al. 2009; Staska et al. 2014). Invasive tree species such as *Acer platanoides* (Reinhart et al. 2005, 2006), *Prunus serotina* (Aerts et al. 2017), *Pittosporum undulatum* (Bellingham et al. 2018) and *Psidium cattleianum* (Enoki and Drake 2017) are well known for their impacts on communities and functioning in several invaded forest ecosystems around the world.

Changes in canopy composition and structure generated by invasive non-native species can alter the quality and intensity of light available for regenerating plants (Reinhart et al. 2006; Fajardo and Gundale 2017). Light is a determining factor in plant ecological and physiological processes and may influence the development and establishment of saplings in positive or negative ways (Bianchini et al. 2001; Bartemucci et al. 2006). Variation in light due to the formation of clearings, the structural complexity of the canopy and, in some cases, deciduousness, create a great variety of microhabitats in forests (Bianchini et al. 2001). These variations may explain composition differences in plant communities developing in the forest undergrowth as well as determine regeneration dynamics and recruitment of new regenerating plants (Reinhart et al. 2006; Fajardo and Gundale 2017).

Reinhart et al. (2006), for example, observed that the quantity of light available in the undergrowth of areas densely invaded by *Acer platanoides* was drastically reduced ($< 5\%$) compared with areas comprising indigenous species (20%), and that the quality of the light available [measured in relation to light composition in the red electromagnetic spectrum (656–664 and 726–734 nm)] was 58% inferior to the light available in areas with indigenous species. Additionally, these changes in the quantity and quality of available light induced by the invasive tree *A. platanoides* were an important factor in the suppression of native species and in the success of the invasive species in invaded communities (Reinhart et al. 2005, 2006). In quantitative terms, Reinhart et al. (2005) verified a 69% decrease in species richness in the undergrowth in sites with higher canopy cover by *A. platanoides* (76%) compared with areas with lower canopy cover by the invasive species (0–11%).

Litter can also be altered due to the composition of dominant species in the canopy (Castro-Díez et al. 2012), positively or negatively affecting seed germination and recruitment of regenerating species, regardless of whether they are native or not (Baskin and Baskin 2014; Constán-Nava et al. 2014). Litter generally reduces the range of temperature variation in the soil as well as water evaporation rates, contributing to the maintenance of soil moisture while providing better conditions for seed germination (Eriksson 1995; Scariot 2000). On the other hand, litter may reduce seed germination and sapling establishment due to antagonistic effects associated with allelopathic chemical interactions, by decreasing the amount of light on seeds, or by acting as a physical barrier to the penetration of roots (Eriksson 1995; Scariot 2000; Baskin and Baskin 2014; Zucaratto and Pires 2014; Dechoum et al. 2015b; Lorenzo et al. 2016).

Zucaratto and Pires (2014) observed that the abundance and diversity of saplings found under the invasive palm *Roystonea oleracea* was lower than in an area withouth the species, and associated the fact with the accumulation of litter produced by the palm. This, in turn, led to altered light availability and soil moisture. Similarly, Hata et al. (2010) observed that litter accumulation by the invasive tree *Casuarina equisetifolia* can negatively interfere in the germination and initial growth of the indigenous species *Schima mertensiana* on the Ogasawara Islands, Japan. Additionally, in some cases, rapid degradation of the litter produced by some invasive plants tends to increase nutrient availability, possibly benefitting their own establishment (Schuster and Dukes 2014). This was observed for the invasive tree *Prunus serotina* in temperate dediduous forest (Aerts et al. 2017) and by Aragón et al. (2014) for the invasive tree *Ligustrum lucidum* in mountain forests in northwest Argentina.

Neotropical seasonal forests are marked by different levels of deciduousness. They occur in tropical and subtropical regions in South America and in other parts of the world (Beard 1955). In Brazil, the distribution of these forests is not continuous. They occur in different regions under two distinct climatic conditions: in the tropical zone, characterized by a rainy season followed by a dry season; in the subtropical zone, characterized by the absence of a dry season and a marked winter (monthly average temperatures below or equal to 15 °C) (IBGE 2012). In the subtropical Deciduous Seasonal Forest (DSF), trees typically lose leaves between May and September as a result of restrictive climatic factors associated with lower temperatures and shorter photoperiod in winter (Vibrans et al. 2012a). Deciduality occurs especially in canopy and emerging trees, affecting more than 50% of the tree species (Klein 1972; IBGE 2012; Vibrans et al. 2012a). The DSF originally covered 8% of the state of Santa Catarina (southern Brazil). It was distributed along the Uruguay river and its affluents at altitudes between 200 and 600 m a.s.l. (Klein 1972; IBGE 2012). The remaining forest cover in the region is currently estimated at 16%, 90% of forest remnants being smaller than 50 ha (Vibrans et al. 2012a). Besides fragmentation, other causes of DSF degradation are the selective exploitation of precious woods and invasion by non-native species such as *Hovenia dulcis* Thunb. (Rhamnaceae) (Vibrans et al. 2012a; Dechoum et al. 2015a).

Hovenia dulcis was introduced to rural properties in southern Brazil for wood, shade for agriculture and pasture, energy production and as a wind break (Carvalho 1994). It is able to spread from cultivation areas and alter the structure and composition of plant communities, in time becoming an important species in the tree-shrub component (Schaff et al. 2006; Boeni 2011; Dechoum et al. 2015a; Lazzarin et al. 2015; Padilha et al. 2015). The ability to form dense, dominating stands, with high growth rates, indicates its capacity to generate changes in the regeneration patterns of invaded forests, and potentially to cause changes in ecosystem functions (Dechoum et al. 2015a, b; Lazzarin et al. 2015; Padilha et al. 2015).

The main aim of this study was to assess the effect of the invasive non-native tree *H. dulcis* on forest regeneration in an area of subtropical seasonal deciduous forest in southern Brazil. Our hypotheses were (1) canopy openness, soil moisture and litter thickness differ in areas with and without *H. dulcis*; (2) *H. dulcis* changes patterns in the abundance, richness and composition of regenerating species in SDF; and (3) the combination of abiotic factors (canopy openness, soil moisture, litter thickness, slope) and biotic factors (*H. dulcis* density and age) assessed can explain richness and abundance patterns of indigenous regenerating species. Studies assessing the effect of *H. dulcis* on the regeneration of indigenous species do not exist to date. This approach contributes to the understanding of the mechanisms involved in *H. dulcis* invasion and its effects on invaded plant communities.

Materials and methods

Study system

This study was conducted in the Fritz Plaumann State Park (FPSP) in Santa Catarina state, southern Brazil (27°16′18″ and 27°18′57″ S; 52°04′15″ and 52°10′20″ W). According to the Köppen–Geiger classification, the climate is subtropical, humid mesothermic with hot summers (Cfa) for the region. The total average annual rainfall is 1735 mm, with monthly rainfall varying from 104.4 to 182.7 mm over the year (Santa Catarina 2014).

The FPSP was established in 1998, protecting 735.11 ha of secondary SDF fragments in diverse sucessional stages as well as species on the official list of species threatened with extinction, such as *Ocotea odorifera* (Vell.) Rohwer (Lauraceae) (Brasil 2008). The past uses of the area include agricultural cultivation, grazing and wood exploitation, which explain the use and spread of the non-native tree *Hovenia dulcis* Thunb. (Rhamnaceae) (Vibrans et al. 2012a; Dechoum et al. 2015a).

Hovenia dulcis, the Japanese raisin tree, is a deciduous zoochoric tree (Carvalho 1994). Native to East Asia, it occurs naturally in forest ecosystems in Japan, Korea and eastern China, at altitudes between 165 and 2200 m a.s.l. (Hyun et al. 2010). It is under cultivation in China, Argentina, Paraguay and southern Brazil, was introduced for ornamental purposes to the United States, Australia, New Zealand and East Africa, has become naturalized in Tanzania and invasive in forest ecosystems in South America (Hyun et al. 2010; Zenni and Ziller 2011; Rejmánek and Richardson 2013; Dechoum et al. 2015a).

Adult *H. dulcis* trees grow to 10–15 m height and 20–40 cm diameter at breast height (DBH). Trees up to 25 m in height and 50 cm or more DBH can be observed in southern Brazil (Carvalho 1994; Hyun et al. 2010). Crowns are wide, globose, with pubescent branches while young (Carvalho 1994). Trees reach maturity at 3 or 4 years of age (Carvalho 1994). In southern Brazil, *H. dulcis* trees drop their leaves completely between April and August, while fruits are produced between March and October (Carvalho 1994). Fruits are produced in large quantities, being small, dry, globose capsules containing between two to four seeds. The fruits are linked to a fleshy peduncle (pseudofruit) of cinnamon color and sweet flavor, dispersed mainly by small and medium-sized birds and mammals (Carvalho 1994; Cáceres and Monteiro-Filho 2001; Hendges et al. 2012; Lima et al. 2015).

The cultivation of *H. dulcis* in Brazil was mostly motivated by economic reasons. As a result, the species is widespread in rural properties in the Uruguay river basin (Dechoum et al. 2015a). *Hovenia dulcis* has spread beyond cultivation areas, being found along forest borders and in clearings of secondary forest fragments in SDF (Vibrans et al. 2012b). Although often described as a pioneer species due to its rapid growth, preferring habitats with high incidence of light (Carvalho 1994), it is tolerant to shade and therefore also present in advanced stages of forest succession in SDF (Dechoum et al. 2015b; Padilha et al. 2015).

Data collection

Field data were collected between September 2016 and June 2017. The effects of *H. dulcis* on the regeneration of indigenous species in intermediate stage forests were assessed by comparing regenerating plants underneath 30 *H. dulcis* stands in forest fragments, henceforth referred to as "areas with *H. dulcis*", with 30 paired, adjacent areas of the same size without adult *H. dulcis* trees (DBH > 5 cm), henceforth referred to as "areas without *H. dulcis*" that served the function of control areas (Fig. 1). "Stands" were considered groupings of *H. dulcis* trees with a minimum of three plants with juxtaposed or intertwined crowns and DBH > 10 cm. The minimum distance between stands was set at 20 m. These forest areas were previously used for agriculture and grazing, being therefore relatively open, dominated by pioneer tree species (average height around seven meters). Each pair of areas invaded and non-invaded by *H. dulcis* had the same history of land use which strengthen the idea that the invasion by *H. dulcis* was the main cause for the results observed. The forest has been regenerating in these areas for at least 20 years (Siminski et al. 2011; Dechoum et al. 2015a).

The crown projection and DBH of each *H. dulcis* tree was measured. All adult trees forming each stand were cut down once the study on regenerating species was concluded in order to estimate the age of the trees. This was done by counting growth rings on tree stumps (Dechoum et al. 2015a).

Plots of 0.5 × 0.5 m were established underneath *H. dulcis* stands, with paired control plots in areas without *H. dulcis*, for the assessment of natural regeneration of woody plants 10–100 cm high (Fig. 1). The plots were set up along parallel transects two meters away from one another, beginning from the central point of each *H. dulcis* stand. Equivalent control plots were established in areas without *H. dulcis*. Once a stand was identified, wooden stakes were placed at each vortex and in the central point of the area covered by *H. dulcis* crowns, delimiting a square or rectangle to make replication of control areas easier. The measuring tape was then stretched across the center of the stand along its longest axis, where the 0.5 × 0.5 m regeneration plots were alternatively set up (to the right and to the left) every two meters (Fig. 1). Parallel transects were defined from the central transect, two meters apart, until reaching the limit of the delimited area. The area occupied by *H. dulcis* stands varied between 25 and 483 m^2 (average = 194.73; SD = 103.70) and the number of plots varied between 12 and 84 (average = 42; SD = 17.07). The total area of plots per stand varied

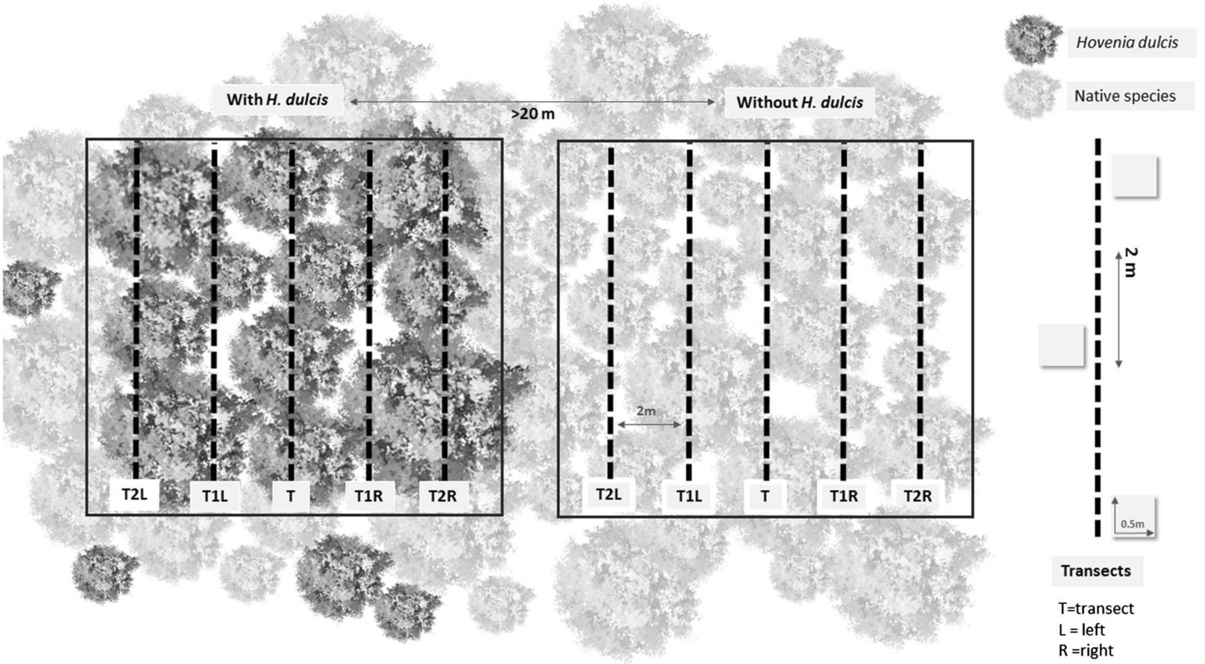

Fig. 1 Sampling design for comparing regenerating plants underneath 30 *H. dulcis* stands (with *H. dulcis*) with 30 paired, adjacent areas of the same size without adult *H. dulcis* trees (without *H. dulcis*) in the Fritz Plaumann State Park (SC, Brazil). "Stands" were considered groupings of *H. dulcis* trees with a minimum of three plants with juxtaposed or intertwined crowns and DBH > 10 cm. The minimum distance between stands was set at 20 m. Plots of 0.5 × 0.5 m were established underneath *H. dulcis* stands for the assessment of natural regeneration of woody plants (10–100 cm high). The plots were set up along parallel transects two meters away from one another, beginning from the central point of each *H. dulcis* stand. The measuring tape was then stretched across the center of the stand along its longest axis, where the 0.5 × 0.5 m regeneration plots were alternatively set up (to the right and to the left) every two meters. Parallel transects were defined from the central transect, two meters apart, until reaching the limit of the delimited area. Equivalent control plots were established in areas without *H. dulcis*

between 3 and 21 m^2 (average = 10.5; SD = 4.27). Equivalent control plots in areas without *H. dulcis* replicated the plots established in areas with *H. dulcis*. The density of regenerating plants was calculated based on the number of saplings in the area surveyed (calculated by dividing the total number of saplings by the total area of plots established for each *H. dulcis* stand or paired control area).

Paired measurements of the variables soil moisture, litter thickness and canopy openness were taken for each *H. dulcis* stand and respective control area in the winter (July 2016) and summer seasons (January 2017), when the crowns of deciduous trees have less and more leaves, respectively. Soil moisture was measured with Falker HidroFarm equipment, model HFM2010. Four measurements were taken in each *H. dulcis* stand and respective control area. Four measurements were also taken of litter thickness, using a ruler, in each *H. dulcis* stand and control area. Canopy openness was estimated using a Lemmon Spherical Concave Densiometer (Lemmon 1957) to the north, south, east and west of the center of each *H. dulcis* stand and control area, 1.2 m above the ground. Measurements were always taken by the same person to ensure consistency. Slope was calculated using an Abney clinometer, two scaled wooden poles, and a measuring tape.

Data analysis

A principal component analysis (PCA) based on Euclidian distance followed by a Permutational Multivariate Analysis of variance (Permanova) were conducted to assess differences between the variables slope, and average litter thickness, average moisture and canopy openness in summer and winter. A *t* test was used to verify differences between the averages of the variables that fit the premises of normality and homoscedasticity, while the Mann–Whitney–Wilcoxon test was used for the variables that did not fit these premises. Resulting p values were corrected using the Bonferroni method.

Generalized linear mixed models (GLMM) with Poisson distribution for the response variable and log link function between the response and explanatory variables were used to test the hypothesis related to differences between total richness and abundance of regenerating indigenous species between areas with and without *H. dulcis*. The total area surveyed was used as an "*offset*" in each model. The models were generated independently for the response variables richness and abundance, with condition (with and without *H. dulcis*) as fixed effect and pairs of plots as random effect. Model validation was determined by graphical analysis of residuals.

A PCA based on the Bray–Curtis dissimilarity index followed by a Permanova were conducted to assess differences in the floristic composition of regenerating species between areas with and without *H. dulcis*. The twenty most abundant species in each condition, including non-native species, were considered for this analysis. These twenty species were selected due to the low abundance of many species (less than 45 plants registered for each species in all plots) and because the species identified only to the genus level were excluded. Abundance data were transformed using the Hellinger method (Legendre and Gallagher 2001).

Generalized linear models (GLM) with Poisson distribution for the response variable and log link function between the response and explanatory variables were used to assess which of the measured variables best explained the abundance and richness of indigenous regenerating species in *H. dulcis* stands. Only data collected from *H. dulcis* stands were considered in both models (one for abundance and one for richness). The explanatory variables considered in both models were: *H. dulcis* average age and density, slope, average litter thickness in summer and winter, average soil moisture in summer and winter, and canopy openness in summer and winter. The total area surveyed (m^2) was used as "*offset*". Colinearities between explanatory variables were assessed using the variance inflation factor (VIF) varied from 1.35 to 3.79, confirming the inexistence of colinearity between the parameters assessed. All parameters were therefore maintained and the relative importance (weight) of the parameters was calculated. Model validation was determined by graphical analysis of residuals. All analyses were conducted using the RStudio software version 1.0.153 (RStudio Team 2017), packages "lme4" (Bates et al. 2015), "MuMIn" (Barton 2016), "vegan" (Oksanen et al. 2013), and "jtools" (Long 2019).

Results

A total of 5575 regenerating plants of 96 species and morphospecies in 38 families were registered in the surveyed areas. Eight of these species were non-native. Among the native species, 77 were identified to the species level and 11 to the genus level. The list with all species and respective abundance in each condition (with and without *H. dulcis*) is available from Online resource.

A total of 856 adult *H. dulcis* trees were registered in areas with stands of the invasive species (DBH > 5 cm), resulting an average of 28.5 plants in each stand (SD = 21.4, min–max = 3–73). The average height of trees was 9.7 m (SD = 4.4, min–max = 1–25). The average area of individual crown was 11 m^2 (SD = 15, min–max = 0.07–189.9). The average basal area was 1.2 m^2 (SD = 1.5, min–max = 0.02–12.9) and the average density, 0.21 plants/m^2 (SD = 0.1, min–max = 0.03–0.37).

The areas with *H. dulcis* were different from areas without *H. dulcis* with regard to the environmental parameters measured (Permanova-F = 5.9, $R^2 = 0.09$, $p < 0.01$) (Fig. 2). These values are available from Online Resource. The PCoA explained 52.5% of the variation in these data [axis 1 (PCoA 1) = 32.7%, axis 2 (PCoA 2) = 19.8%] (Fig. 2). Paired comparisons between areas showed that the litter layer was thinner in summer in areas with *H. dulcis* stands than in areas without the invasive species (t = 4.67. g.l. = 29, $p_{adj} < 0.01$), while canopy openness was higher in winter (w = 26, $p_{adj} < 0.01$) but lower in summer (w = 289.5, $p_{adj} < 0.05$) in areas with *H. dulcis* stands than in areas without the invasive species.

Abundance of regenerating indigenous species was higher in areas without *H. dulcis* than in areas with this species (Fig. 3, Table 1). A total of 2477 plants was found in areas without *H. dulcis*, resulting in an

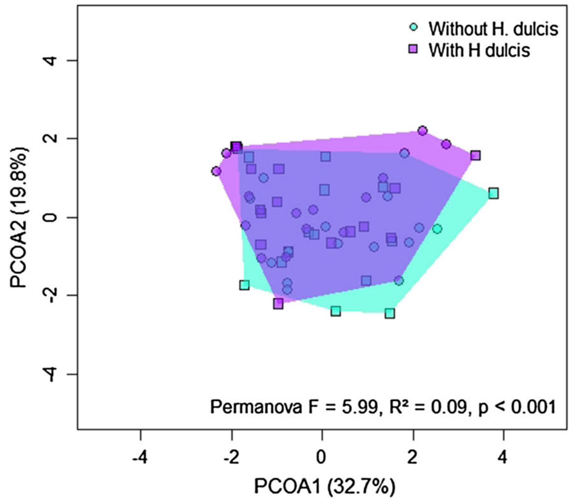

Fig. 2 Graphic representation of permutational multivariate analysis of variance (PCoA) for environmental parameters obtained from areas with and without *Hovenia dulcis* stands in the Fritz Plaumann State Park (SC, Brazil)

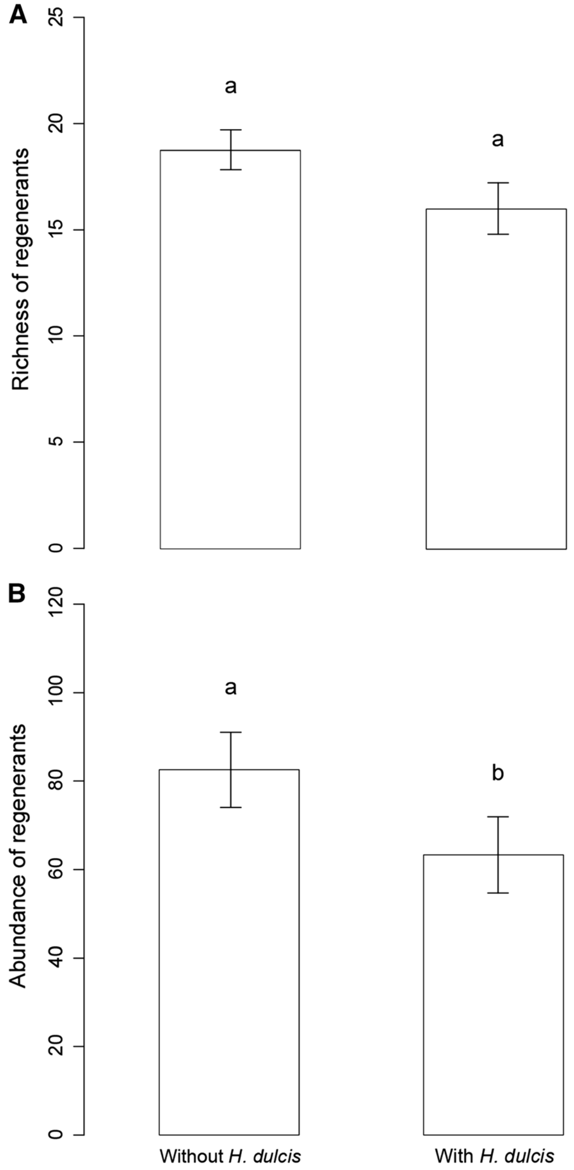

Fig. 3 Abundance and richness of native regenerating species in areas with and without *Hovenia dulcis* stands obtained in the Fritz Plaumann State Park (SC, Brazil). **a**, **b**: Different letters indicate significant differences ($p < 0.01$)

average of 82.57 (SD = 46.46) regenerating plants. In turn, 1900 plants were registered in areas with *H. dulcis*, resulting in an average of 63.33 (SD = 47.28) regenerating plants per stand. Although species richness did not differ significantly between areas with and without *H. dulcis*, there was a tendency for lower richness in areas where *H. dulcis* was present (Fig. 3, Table 1). A total of 82 regenerating indigenous species was registered in areas without *H. dulcis*, while 73 species were found in areas with *H. dulcis*.

Differences in species composition of regenerating plants were observed when considering the twenty most abundant species in areas with and without *H. dulcis*, including non-native species ($F = 5.0$, $R^2 = 0.07$, $p = 0.001$; Fig. 4). Fourteen of these species were present in both conditions. The indigenous species *Nectandra megapotamica*, *Nectandra lancelolata* and *Solanum mauritianum* were more abundant. *Psychotria leiocarpa*, *Strychnos brasiliensis*, *Tabernaemontana catharinensis*, *Matayba elaeagnoides*, *Ilex paraguariensis* and *Parapiptadenia rigida* were more abundant only in areas without *H. dulcis*, while the indigenous *Pavonia sepium*, *Erythroxylum myrsinites*, *Cabralea canjerana* and the non-native *H. dulcis* and *Eriobotrya japonica* were more abundant only in areas with *H. dulcis*. The number of regenerating plants of *H. dulcis* (n = 1126) was about five times higher than the highest number of the most abundant indigenous species (*Nectandra megapotamica*; n = 204) in areas with *H. dulcis* (Table 2).

The model using environmental parameters (*H. dulcis* average age and density, slope, average litter thickness in summer and winter, average moisture in summer and winter and canopy openness in summer and winter) in areas with *H. dulcis* and their correlation with richness of indigenous regenerating species

Table 1 GLMM statistics used in the analysis of native regenerating species abundance in areas with and without *Hovenia dulcis* based on data obtained in the Fritz Plaumann State Park (SC, Brazil)

Parameter	Estimate	Standard error	Z	*p*
Intercept (with *H. dulcis)*	1.999	0.078	25.459	< 0.001
Without *H. dulcis*	– 0.332	0.112	– 2.963	0.003

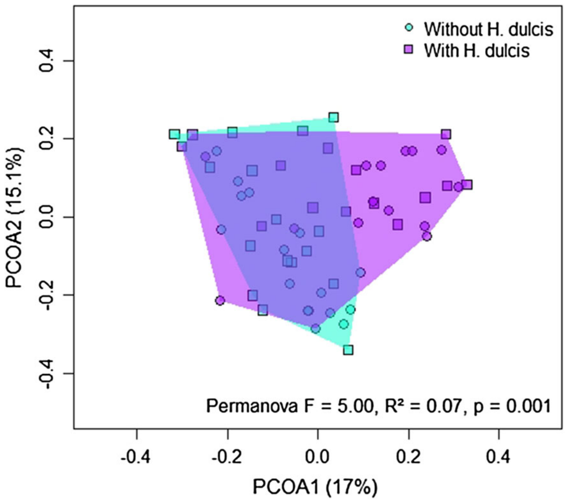

Fig. 4 Graphic representation of permutational multivariate analysis of variance (PCoA) for composition of twenty most abundant regenerating species, including non-native species, registered in areas with and without *Hovenia dulcis* stands in the Fritz Plaumann State Park (SC, Brazil)

Table 2 Generalized linear mixed models (GLMM) statistics used in the analysis of regenerating native species richness in area with and without *Hovenia dulcis* based on data obtained in the Fritz Plaumann State Park (SC, Brazil)

Parameter	Estimate	Standard error	Z	*p*
Intercept (with *H. dulcis*)	0.597	0.064	9.302	< 0.001
Without *H. dulcis*	– 0.165	0.092	– 1.776	0.07

resulted in an AICc value of 179.4. The relative importance of analyzed parameters showed that soil moisture in winter, canopy openness in summer, litter thickness in summer, and density of *H. dulcis* trees, in descending order, were the most important parameters (Fig. 5a). Canopy openness in summer and litter thickness in summer were positively correlated with richness of indigenous regenerating species, while the correlation with soil moisture in winter and *H. dulcis* density were negative (Fig. 5a, Online resource).

The model for abundance of indigenous regenerating species in areas with *H. dulcis* indicated seven of the nine parameters initially considered (Fig. 5b). The model resulted in an AICc value of 517.2. The parameters estimated for the model showed that *H. dulcis* age, *H. dulcis* density, litter thickness in winter, litter thickness in summer, slope, soil moisture in winter and soil moisture in summer were statistically significant (Fig. 5b). The relative importance of the paramenters analyzed suggests that, in descending order, soil moisture in winter, soil moisture in summer, litter thickness in winter, and litter thickness in summer were more important, followed by slope, *H. dulcis* density, and *H. dulcis* age (Fig. 5b). All the significant parameters, with the exception of litter thickness in summer, are negatively correlated with abundance of indigenous regenerating species (Fig. 5b, Online resource).

Discussion

The differences observed in canopy openness and litter thickness between areas with and without *H. dulcis* indicate the capacity of the invasive species to alter environmental conditions on a local scale and confirm the first hypothesis proposed in this study. The results partially confirm the second hypothesis that the invasive species *H. dulcis* alters regeneration patterns in seasonal deciduous forest (SDF) fragments, as significant differences were observed in abundance of indigenous regenerating species, but only marginally significant differences were found in terms of richness. Although no statistical difference was found, the results showed a tendency for decreasing richness in areas invaded by *H. dulcis*. The composition of the twenty most abundant species in each condition was distinct, corroborating the second hypothesis. The combination of the variables *H. dulcis* density, canopy openness, soil moisture and litter thickness influenced the richness of indigenous regenerating species in areas with *H. dulcis*. In the same areas, the variables *H. dulcis* average age, *H. dulcis* density, litter thickness, slope and soil moisture influenced the abundance of

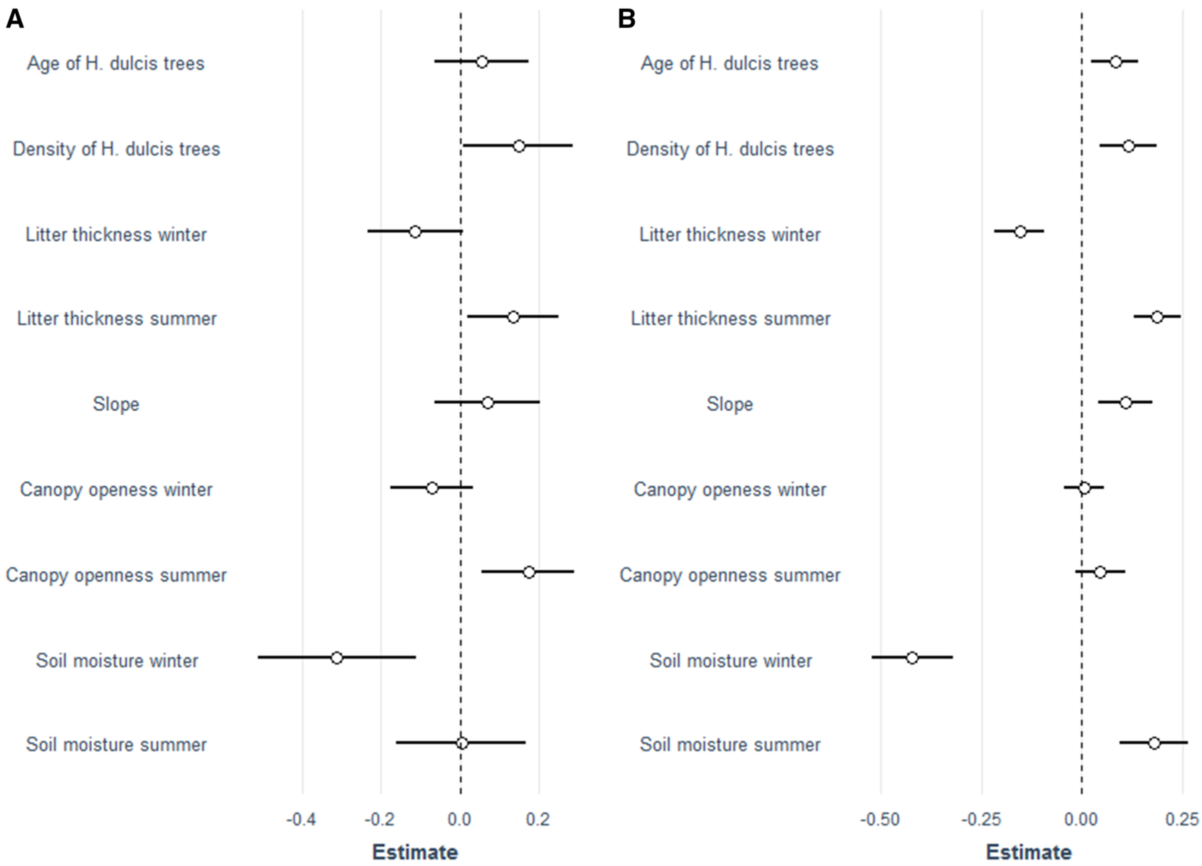

Fig. 5 Standardized coefficients (± IC 95%) of all variables used in our generalized linear model analyses to assess the correlation between regenerating species richness (**a**) and abundance of regenerating species (**b**) and environmental parameters registered in 30 *Hovenia dulcis* stands in the Fritz Plaumann State Park (SC, Brazil). In **a**—the relative importance of analyzed parameters showed that soil moisture in winter, canopy openness in summer, litter thickness in summer, and density of *H. dulcis* trees, in descending order, were the most important parameters. In **b**—the relative importance of analyzed parameters showed that, in descending order, soil moisture in winter, soil moisture in summer, litter thickness in winter, and litter thickness in summer were more important, followed by slope, *H. dulcis* density, and *H. dulcis* age

indigenous regenerating species, corroborating the third hypothesis proposed in this study.

Changes in the canopy as a consequence of the development of dense *H. dulcis* stands can alter the offer of essential resources such as light, nutrients and soil moisture, apart from altering other abiotic factors (for example, extreme temperatures) that are regulated by dominating and emergent trees (Bartemucci et al. 2006; Fajardo and Gundale 2017). Changes in abiotic factors promoted by invasive non-native species result in direct and indirect changes in ecosystem functioning (Cadotte et al. 2011; Constán-Nava et al. 2014; Aragón et al. 2014; Castro-Díez et al. 2016). These changes are determinant in the establishment of different species, affecting patterns of richness and abundance of regenerating species (Bartemucci et al. 2006; Hejda et al. 2009; Fajardo and Gundale 2017).

Deciduousness patterns in SDF in southern Brazil, characterized by the loss of about 50% of leaves of canopy and emergent trees between May and September (Klein 1972; IBGE 2012; Vibrans et al. 2012a) are altered in the presence of *H. dulcis.* Because this species forms dense stands (up to 0.37 ind./m^2 in the areas surveyed), the total loss of leaves in winter produced more open canopies than areas without *H. dulcis*. In the summer, on the other hand, because *H. dulcis* forms dense, ample crowns (Carvalho 1994), canopy openness was drastically reduced, at times being almost zero due to the density and height of *H. dulcis* trees. Profound changes in light regimes as a consequence of invasion by non-native trees have proven to be an important mechanism in producing changes in plant communities and facilitating invasion success (Levine et al. 2003; Reinhart et al. 2006; Constán-Nava et al. 2014). Studies on invasion by *Acer platanoides*, for example, showed that the atypical shading generated by these trees is responsible for its invasion success as well as for the decreased establishment of indigenous species with low or medium tolerance to shade, therefore altering species composition in the forest (Bertin et al. 2005; Reinhart et al. 2005; 2006). As observed by Dechoum et al. (2015b), germination of *H. dulcis* seeds was facilitated in areas with lower canopy openness, survival of seedlings was higher in areas with intermediate canopy openness, and seedling growth was higher in areas with higher canopy openness. The canopy cover generated by *H. dulcis* therefore favors its own germination and survival in the summer, while canopy openness in winter favors its growth. Both consequences of invasion result in the self-benefit of *H. dulcis* in SDF.

Litter accumulation was similar in control areas in summer and winter. In areas with *H. dulcis*, however, a significant decrease in litter was observed in summer. This suggests that, although *H. dulcis* trees drop all their leaves, decomposition occurs at a faster rate than for litter produced by indigenous species, as observed in non-invaded areas (Aragón et al. 2014; Capellesso et al. 2016). Makkonen et al. (2012) showed that the decomposition of litter produced by tropical species occurs at slower rates than that of litter produced by temperate or Mediterranean species. Therefore, the identity of species as well as the physical and chemical structure of tissues are more relevant in the decomposition process than the surrounding micro habitat (Zanne et al. 2015).

Fast-growing species such as *H. dulcis* generally have palatable leaves rich in nutrients with high concentrations of nitrogen and phosphorous (Kazakou et al. 2009; Szefer et al. 2016), higher leaf area, lower tenacity and lower carbon concentration (Aragón et al. 2014; Kazakou et al. 2006), which result in higher decomposition rates (Szefer et al. 2016). As a consequence, there tends to be an increase in the availability of nutrients in the soil in sites with *H. dulcis*, again self-benefitting the invasive species and facilitating its establishment (Davis et al. 2000; Hughes and Denslow 2005). The chemistry of litter may, on the other hand, differently affect seed germination and seedling growth, interfering in plant communities regardless of resource availability and competition post-germination. Allelopathy may therefore represent another important factor in the reduced establishment of indigenous regenerating species (Conway et al. 2002; Gundale et al. 2008; Aragón et al. 2014; Warren et al. 2017). Secondary compounds found in leaves of *H. dulcis* were associated with both defense against herbivores and allelopathic effects (Buono et al. 2008; Wandscheer et al. 2011). Further investigation focused on ecosystem processes such as decomposition rate and nutrient cycling by the comparison of invaded and non-invaded areas and by the comparison of functional traits of plant communities in both conditions could shed light on the effect of *H. dulcis* on the ecosystem level.

Changes in structure and in species composition in the plant community due to the presence of *H. dulcis* have been described for different types of subtropical forests (Schaff et al. 2006; Boeni 2011; Dechoum et al. 2015a; Padilha et al. 2015; Lazzarin et al. 2015). The results from the present study reveal that when the twenty most abundant species were considered in areas with and without *H. dulcis*, a difference is evident in the composition of regenerating species despite the fact that fourteen species are present in both conditions. *Nectandra megapotamica*, *Nectandra lancelolata* and *Solanum mauritianum* were the most abundant indigenous species in areas with *H. dulcis* as well as in areas without this species. In control areas, *Psychotria leiocarpa*, *Ilex paraguariensis* and *Tabernaemontana catharinensis* represent species characteristic of the forest undergrowth, while *Strychnos brasiliensis*, *Matayba elaeagnoides* and *Parapiptadenia rigida* represent the forest canopy. *P. leiocarpa*, *I. paraguariensis and S. brasiliensis* are considered secondary species, while *T. catharinensis*, *M. elaeagnoides* and *P. rigida* are considered pioneer species (Vibrans et al. 2012a; Meyer et al. 2012; Dechoum et al. 2015a). In areas with *H. dulcis*, *Pavonia sepium* and *Erythroxylum myrsinites* were the most abundant species of the forest undergrowth, while *Cabralea canjerana* was the most abundant species of the forest canopy along with the non-native *H. dulcis* and *Eriobotrya japonica*. Of these species, only *E. myrsinites* is considered secondary, while all others are pioneer species, which suggests a simplification of existing functional groups due to invasion by *H. dulcis*

(Dechoum et al. 2015a). The high abundance of *H. dulcis* seedlings registered underneath the stands is noteworthy, as it was up to five times higher than the highest abundance of indigenous species (*Nectandra megapotamica*). Although the seedlings assessed were still in the development phase and would not necessarily reach maturity, the high abundance of *H. dulcis* shows that the invasion is actively expanding, while possibly driving forest structure and composition into a distinct trajectory over space and time when compared to areas that have not been invaded (Martin and Marks 2006; Essl et al. 2011, 2012; Padilha et al. 2015).

The assessment of the effects of biotic and abiotic variables on indigenous regenerating species in areas with and without *H. dulcis* showed that canopy openness in summer and litter thickness in summer were positively correlated with indigenous species richness. As a result, we inferred that in less dense stands with higher light availability in summer as well as higher litter accumulation, a larger number of species were benefitted. Soil moisture in winter, on the other hand, is negatively correlated with richness of indigenous regenerating species, which suggests that the excess of moisture may be detrimental to the regeneration of a larger number of species (Baskin and Baskin 2014).

Litter thickness in summer was the only variable positively correlated with abundance of indigenous regenerating species. Given the high temperatures registered in the study area during the summer, with an absolute maximum of 43.4 °C (Santa Catarina 2014), thicker litter layers in summer provide milder conditions for seedling establishment. On the other hand, litter thickness and soil moisture were negatively correlated with abundance of indigenous regenerating species, which suggests that the excess of moisture and high accumulation of litter are detrimental to seedling establishment in winter. Although slope was negatively correlated with abundance of indigenous regenerating species, this variable must be interpreted with caution, as only 10% of *H. dulcis* stands were located on flat or gentle terrain, while the other 90% were on steep terrain, which may lead to an overestimate of the importance of this variable.

Hovenia dulcis age and density were negatively correlated with richness and abundance of indigenous regenerating species in invaded areas. Although these tendencies can be considered strong evidence of the negative impact of *H. dulcis* on forest regeneration, one must consider that this cause-effect relationship can only be proved by an experiment. Having said that, we strongly recommend that future studies on the impact of *H. dulcis* should be focused on the comparison of areas with similar historical land use, in which non-invaded plots, invaded plots with different densities of *H. dulcis* adult trees, and plots where *H. dulcis* trees were eliminated must be compared (Kumschick et al. 2015). The results using this experimental approach would strengthen the evidence that invasion by *H. dulcis is* the main driver of the observed patterns, and not the “passenger” benefitted by other confounding factors.

To sum up, we present strong evidence that *H. dulcis* is capable of altering environmental conditions on a local scale, and that these changes are detrimental to the recruitment and establishment of indigenous regenerating species, while favoring the invasive species. These effects lead to composition changes in the plant community. The capacity of *H. dulcis* to colonize forest areas regardless of successional stage (Dechoum et al. 2015a; Padilha et al. 2015; Lazzarin et al. 2015) combined with intense seedling recruitment (Cáceres and Monteiro-Filho 2001; Hendges et al. 2012; Lima et al. 2015) emphasize the need for the implementation of prevention and control measures. These should begin with a strong focus on legally protected areas, but, considering the regional extent of *H. dulcis* invasion, develop into a regional control program to protect the scarce remnants of SDF in the state and associated ecosystem services.

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