# *Community structure, succession and invasibility in a seasonal deciduous forest in southern Brazil*

**M. S. Dechoum, T. T. Castellani, S. M. Zalba, M. Rejmánek, N. Peroni & J. Y. Tamashiro**

**Biological Invasions**

ISSN 1387-3547

Biol Invasions
DOI 10.1007/s10530-014-0827-6

Springer

Biol Invasions
DOI 10.1007/s10530-014-0827-6

ORIGINAL PAPER

# Community structure, succession and invasibility in a seasonal deciduous forest in southern Brazil

**M. S. Dechoum · T. T. Castellani · S. M. Zalba ·**
**M. Rejmánek · N. Peroni · J. Y. Tamashiro**

Received: 7 February 2014 / Accepted: 9 December 2014

**Abstract** Majority of invasive trees colonize grasslands, shrublands, and temperate forests. *Hovenia dulcis* is an exception, because it is one of the most pervasive invaders in Brazilian subtropical forests where it has changed their structure and composition. This study has aimed to identify the clues for its success by defining the structural and functional characteristics of plant communities in different stages of succession with and without *H. dulcis*. Following the general assumptions of invasion ecology, we expected that *H. dulcis* establishment and invasion success would be significantly higher in early successional communities, with high resource availability and low species richness and diversity, as well as low functional diversity. Contrary to this hypothesis, no differences were found between plant communities invaded and non-invaded by *H. dulcis* at three different succession stages. No relationship was found between species richness and diversity and functional diversity, with respect to invasibility along the successional gradient. *Hovenia dulcis* is strongly associated with semi-open vegetation, where the species was found in higher density. The invasion of open vegetation is more recent, providing evidence of the species's ability to invade plant communities in early successional stages. We concluded that the colonization by *H. dulcis* was associated with forest openness, but the species is also able to colonize semi-

---

**Electronic supplementary material** The online version of this article (doi:10.1007/s10530-014-0827-6) contains supplementary material, which is available to authorized users.

M. S. Dechoum (✉) · T. T. Castellani · N. Peroni
Departamento de Ecologia e Zoologia, Centro de Ciências Biológicas, Universidade Federal de Santa Catarina,
Campus Universitário s/n, Sala 208, Bloco C – Córrego Grande, Florianópolis, SC 88040-900, Brazil
e-mail: mdechoum@gmail.com

T. T. Castellani
e-mail: ttcastel@ccb.ufsc.br

N. Peroni
e-mail: peronin@gmail.com

S. M. Zalba
Departamento de Biología, Bioquímica y Farmacia,
Universidad Nacional del Sur, San Juan 670,
C.P. B8000LMI, Bahía Blanca, Buenos Aires, Argentina
e-mail: szalba@criba.edu.ar

M. Rejmánek
Department of Evolution and Ecology, University of California, One Shields Avenue, Davis, CA 95616, USA
e-mail: mrejmanek@ucdavis.edu

J. Y. Tamashiro
Departamento de Botânica, Instituto de Biologia,
Universidade Estadual de Campinas, Cidade Universitária Zeferino Vaz, Campinas, SP 13083-970, Brazil
e-mail: tamashi@unicamp.br

open vegetation, and persist in the successionally more advanced communities.

**Keywords** Invasive trees · *Hovenia dulcis* · Subtropical forests · Functional diversity · Biotic resistance · Disturbance

## Introduction

Ecosystem invasibility is the result of several factors, including physical environmental characteristics, the competitive ability of resident species, and the disturbance regime of the habitat (Rejmánek 1989; Lonsdale 1999; Huston 2004; Whitfield et al. 2014). The availability of resources such as water, light and nutrients, and the reduction in competitive interactions following disturbance facilitate the establishment of alien plants (Davis et al. 2000; Goldstein and Suding 2013). Indirect effects of disturbance on invasibility may also occur due to changes in community composition that may end with species differing in their resistance to disturbance and post-disturbance rates of recovery (Symstad 2000).

Elton (1958) proposed that susceptibility to invasion is also directly affected by community species richness. According to this hypothesis, rich communities are more resistant to invasions because the competition for resources is also higher than in species poor communities. In the case of plant communities, this mechanism may function through competition with native species (Levine 2000) or through other negative interactions triggered by resident species including predation, herbivory and diseases, upon the arrival of an introduced species (Levine et al. 2004). From a functional perspective, higher species richness results in higher functional diversity as long as the species in the community present different functional traits and therefore different strategies to acquire resources (Byun et al. 2013). Higher functional diversity would reduce susceptibility to invasion through the preemption of available resources (Tilman et al. 1997; Pokorny et al. 2005; Brown and Rice 2010; Ammondt and Litton 2011). Additionally, functional trait similarities between resident species and introduced species result in superimposed resource requirements and, as a consequence, in competition among species and biotic resistance (Funk et al. 2008; Byun et al. 2013).

Intact or undisturbed communities are expected to present low susceptibility to invasion by alien species (Elton 1958). Undisturbed forests in particular are considered highly resistant to invasion, in large part because of low light availability (Rejmánek 1989, 1996; Fine 2002; Von Holle et al. 2003; Whitfield et al. 2014). Forests, however, have been intensely threatened by human activities, which result in habitat loss and fragmentation (Laurance and Peres 2006). Fragmentation promotes rapid and predictable shifts in patterns of biological organization across population to ecosystem levels due to a myriad of processes including habitat loss, sample effect, creation of forest edges, rupture of biological connectivity, subdivision/isolation of populations, and post-isolation proliferation of invasive species (Laurance et al. 2002, 2006; Fahrig 2003). Forest fragmentation may facilitate invasion in forests because resource availability is increased, especially on the edges created between original and transformed areas (Fine 2002; Denslow and DeWalt 2008; Hobbs 2011). Land use changes sometimes involve an increased use of introduced species (Hobbs 2011), which can expose natural habitats to propagule pressure of alien species present in surrounding degraded or managed areas (Denslow and DeWalt 2008). Furthermore, many opportunistic animal dispersers can occupy fragment borders and altered matrices, promoting the spread of plant invaders (Buckey et al. 2006).

Given that many invasive alien species usually present traits associated with early successional stages (high seed production, fast growth, short juvenile period—Rejmánek and Richardson 1996; Pysek and Richardson 2007; Catford et al. 2012), early successional communities often host higher numbers and proportions of invasive alien species than those in advanced stages (Rejmánek 1989). However, some studies have shown evidence that an important group of forest invasive species are neither dependent on disturbance nor restricted to early successional stages of plant communities (Webb et al. 2000; Martin et al. 2009), showing shade tolerance and ability to invade closed-canopy forests (Gilbert and Lechowicz 2005; Martin and Marks 2006; Major et al. 2013).

Neotropical seasonal forests are defined as forest types with different degrees of deciduousness occurring in tropical and subtropical regions of Central and South America (Beard 1955). The seasonal deciduous forest has a disjoint distribution in all Brazilian biomes of the tropical and subtropical regions (IBGE 2012). Originally, this type of forest covered 8 % of the state of Santa Catarina, southern Brazil (Klein 1978), occurring in the Uruguay River basin at elevations ranging from 200 to 600 m, with annual precipitation of ca. 1,800 mm/year (Klein 1972). This forest is characterized by a closed canopy dominated by Lauraceae and emergent deciduous species, mostly Fabaceae, and a subcanopy dominated by *Sorocea bonplandii*, *Gynnanthes concolor* and *Trichilia* spp. (Klein 1972). It is nowadays highly fragmented and restricted to 16 % of its original area in Santa Catarina state (7,670.57 km$^2$), with 90 % of the remnants smaller than 50 ha (Vibrans et al. 2012). Apart from fragmentation, other causes of environmental degradation of these forests include current or historical selective logging and invasion by alien species, such as *Hedychium coronarium* and *Impatiens walleriana* (Dechoum and Ziller 2013). Additionally, the natural deciduousness, alone, may make these forests more susceptible to invasion than tropical ombrophilous forests because it opens a window of opportunity for disturbance-dependent alien species to invade.

The overall objective of this study was to define the composition, structure and functional characteristics of woody plant communities in fragments with and without the presence of *Hovenia dulcis* Thunb. (Rhamnaceae). Our specific objectives were: (1) to compare density, basal area, height and age of *H. dulcis* trees among successional stages; (2) to assess the influence of soil characteristics and canopy openness on abundance and basal area of the native plant species sampled; (3) to compare density, basal area, richness, diversity, evenness and functional diversity among successional stages and among plots with and without *H. dulcis*; (4) to identify functional groups that contributed more significantly to the separation of plots with and without *H. dulcis* for each successional stage; and (5) to identify possible positive or negative associations among native species and *H. dulcis* in the plots. We hypothesized that *H. dulcis* is best able to establish in and invade plant communities in early successional stages with high resource availability and low species richness and diversity, as well as low functional diversity, and that its presence in successionally advanced forests could be explained by colonization following disturbance events in the past. Because *H. dulcis* is widespread in this part of Santa Catalina state, we assumed that propagule pressure of this species was equivalent across the studied area.

## Materials and methods

### Study species

*Hovenia dulcis* is tree species native to east Asia. The species' natural distribution ranges from Japan, Korea and east China to the Himalayas, up to altitudes of 2,000 m. It grows preferably in sunny locations on moist sandy or loamy soils (Yun and Lee 2002; Hyun et al. 2009). It is cultivated in plantations in China (Hyun et al. 2009), invasive in South American forests (Zenni and Ziller 2011) and Tanzania (Rejmánek and Richardson 2013), and has been introduced as a rare ornamental plant in different regions including the USA, Australia, New Zealand, and Central Africa (Hyun et al. 2009). Adult trees reach an average 10–15 m in height and 20–40 cm in diameter, although in southern Brazil they grow up to 25 m in height and 50 cm or more in diameter (Carvalho 1994a). The fruits are small, dry globose capsules carrying 2–4 seeds bound to a cinnamon-colored fleshy peduncule which is sweet and tasty. Seeds are more or less circular, measuring 4–8 mm in diameter, and dispersed by animals. The main dispersers in Brazil are mammals of medium size, such as *Dasypus* and *Euphractus* armadillos (Carvalho 1994a) and *Didelphis aurita* (Mammalia, Marsupialia) (Cáceres and Monteiro-Filho 2001). Infructescence consumption by the monkey species *Sapajus nigritus* was observed in the study area (Hendges et al. 2012), and consumption by the bat species *Platyrrhinus* (*Vampyrops*) *lineatus* was observed in Espirito Santo state, Brazil (Zortéa 1993).

In the second half of the twentieth century, human occupation of the western part of Santa Catarina state led to the introduction of *H. dulcis* (Vibrans et al. 2012). The species has been extensively planted in rural properties for wood since its introduction (Selle 2009), as well as for shade over cultivation areas and pasture, wind-breaks, sawmills, and energy production (Carvalho 1994a). *Hovenia dulcis* can change the structure and composition of plant communities in seasonal, dense, and mixed ombrophilous forests (Bardall et al. 2004; Schaff et al. 2006; Boeni 2011).

## Description of study area

This study took place at the Fritz Plaumann State Park, a 740 ha protected area established in 1998 in Concordia (Santa Catarina state, Brazil) (27°16′18″ and 27°18′57″S; 52°04′15″ and 52°10′20″W) along the Uruguay River, a region of Cfa (subtropical) climate in the Köppen–Geiger classification. The park is located in the Atlantic forest domain, in a transition area between seasonal and mixed ombrophilous forest (IBGE 2012) containing the threatened species *Ocotea odorifera* (Vell.) Rohwer (Lauraceae) (Brasil 2008). All the data for this study were collected in seasonal deciduous forest fragments.

As all data were collected in the field between July 2010 and January 2011, it was assumed that the vegetation in the area has been under regeneration for at least 13 years. Three vegetation types were defined in the sampling areas: open, semi-open and closed forest, according to current physiognomy, time of abandonment, and history of use (aerial photographs from 1978, 2005, 2008 and 2011, and Siminski et al. 2011). Open and semi-open areas were formerly used for agriculture and/or grazing. Open areas had a herbaceous or herb–shrub cover and few isolated small-size trees of pioneer species, while semi-open areas were characterized by open forest with a low layer of trees (average height around 7 m) dominated by native pioneer tree species. Closed areas were under selective logging, which enabled the tree layer not to be totally suppressed and the physiognomy of a closed forest with a higher tree layer to be preserved (average height about 10 m), with a greater vertical stratification compared to the other vegetation types. These vegetation types were considered successional stages, following a sequence from open to semi-open and closed vegetation types.

## Data collection

Twenty 10 m × 20 m plots per vegetation type were set up, 10 with and 10 without *H. dulcis*, making a total of 60 plots. A minimum distance of 100 m was kept between plots. All trees with diameters above 5 cm at breast height (DBH), living or dead, were identified, and had their height visually estimated. For the trees whose identification was not possible in the field, herbarium specimens were collected and sent to experts.

The native species sampled were classified into functional groups (FG) according to dispersal syndrome, regeneration strategy, vertical stratification, and foliar phenology. Species dispersal syndromes were *animal*, *wind* or *self-dispersed* (Van der Pijl 1982). Regeneration strategies refer to *non-pioneer* species as those that regenerate in the undergrowth of mature forests, and *pioneer* species as those that require light to regenerate (Hartshorn 1978; Whitmore 1989). Vertical stratification was divided into *undergrowth* species, represented by small trees and shrubs which flower and bear fruit in the lower forest stratum (<10 m); *canopy* species, which occur in the canopy or sub-canopy); and *emergent* species, which stand out above the forest canopy. Foliar phenology refers to *deciduous* species as those that totally or partially lose their leaves during the cold season, or *evergreen* species as those that do not drop their leaves every year.

The species were classified according to field observations and/or literature (Klein 1972; Reitz 1974; Reitz et al. 1978, 1988; Carvalho 1994b; Ivanauskas and Rodrigues 2000; Mikich and Silva 2001; Budke et al. 2005; Sobral et al. 2006; Giehl et al. 2007; Ruschel et al. 2007; Yamamoto et al. 2007; Franco 2008; Costa et al. 2011; Kilka and Longhi 2011; Loregian et al. 2012). Although the combination of four parameters and ten classes within these parameters results in 36 possible functional groups, the existing species fell into only 19 groups, as some of the combinations did not match the characteristics of the species sampled (Appendix I).

An assessment of the percentage of canopy openness was carried out based on photographs taken with a digital camera (Nikon Coolpix L20) set on a tripod, positioned one meter above the ground at the center of each plot. These photographs were evaluated through the CPCe software (Kohler and Gill 2006), providing canopy openness percentage results based on a matrix of points distributed at random over each of the images. Two categories, “covered” and “uncovered”, were visually identified under each of the random points. Two photographs were taken in each plot, the first one in July 2012, the second one in January 2013, in order to make measurements at the maximum and minimum foliar presence, respectively.

Five sub-samples of approximately 100 g of surface soil (to 10 cm depth) were collected, one in each vertex and one in the center of each plot, then pooled to be used as a single sample per plot. The samples were analyzed in the Physical, Chemical and Biological Laboratory of the Integrated Company for Agricultural Development of Santa Catarina State for texture, pH, phosphorous, available potassium, organic matter, exchangeable aluminum, exchangeable calcium, exchangeable magnesium, sodium, H + Al, cation exchange capacity (CEC) and base saturation (V). Soil samples were analyzed from 51 of the 60 plots.

## Data analysis

Differences in values of canopy openness among vegetation types and among areas with and without *H. dulcis* were tested by permutation tests for two-way analysis of variance test (ANOVA) with Tukey's multiple comparison tests (Wheeler 2010). A histogram of the tree diameters of the populations of *H. dulcis* was completed, and density (number of trees/ha) and basal area ($m^2$/ha) were calculated. Differences in values of density (number of trees/plot), basal area ($cm^2$/ha) and height (m) of *H. dulcis* trees were compared among vegetation types using permutation tests for one-way ANOVA with Tukey's multiple comparison tests (Wheeler 2010). All the variance analysis tests with permutation followed by Tukey's tests were performed using the package 'lmPerm' (5,000 iterations) of the R software (R Core Team 2014). Box-and-whisker plots were constructed for canopy openness and *H. dulcis* trees data using R software (R Core Team 2014).

The age estimates of sampled *H. dulcis* trees were based on regression equations generated from data on 495 trees cut down in October 2012, in a parallel study (Dechoum et al. unpublished data) in which 35 trees originated from open areas, 318 in semi-open areas and 142 in closed areas. We measured the radius of each tree after cutting it and estimated the age by counting annual growth rings of each stump. The radius of each tree was measured from just inside the bark to the center of the trunk. Each year in age is represented by one annual growth ring. An annual ring is comprised of one layer of small vessels and one layer of large vessels, the former corresponding to the winter season and the latter to the summer season. The basal area of each tree was calculated by using the following equation: basal area = $\pi$ (radius)$^2$. Regression models for the relationship between age and basal area were conducted using the Biostat 5.0 software (Ayres et al. 2007). The equations that describe those regressions are: $Y = 0.240 + 2.364 \times \ln X$ for the open vegetation type ($R^2 = 0.63$), $Y = 3.906 \times X$^0.258 for semi-open ($R^2 = 0.60$), and $Y = 5.213 \times X$^0.238 for closed ($R^2 = 0.54$), where Y = age and X = basal area. The age of the sampled trees was estimated through these equations, and histograms were plotted for each vegetation type.

The influence of soil characteristics and canopy openness on abundance and basal area of the native plant species sampled was assessed using canonical correspondence analysis (CCA) using CANOCO 4.5 software (ter Braak and Smilauer 2002; Leps and Smilauer 2003). In order to test the significance of the influence of environmental variables on species composition based on density and basal area, Monte Carlo permutation tests were carried out with 449 iterations. Ordination diagrams of the plots with isoclines of the "basal area" and "diversity" (Simpson Diversity Index) were produced in CANOCO 4.5, based on abundance and basal area (diversity isoclines only) of the sampled species to visualize the variation of these factors in relation to the plots.

Density, basal area, richness, Simpson Diversity Index (D), Shannon–Wiener diversity index (H′), Pielou evenness index (J), functional diversity index (FD) and functional diversity index weighted by abundance (wFD) (Casanoves et al. 2010; Pla et al. 2012) were compared between vegetation types and in plots with and without *H. dulcis*. The comparisons were made by applying permutation tests for two-way ANOVA with Tukey's multiple comparison tests (Wheeler 2010), with vegetation type and presence/absence of *H. dulcis* included as factors. The tests were performed using the package 'lmPerm' (5,000 iterations) of the R software (R Core Team 2014). Rarefaction curves were produced using 100 randomized orders and the Sobs Mau Tao estimators were calculated using EstimateS Software Version 8.2.0 (Colwell 2006). The mean values and confidence intervals (±95 %) obtained were graphically compared among vegetation types in areas with and without *H. dulcis*.

Functional diversity indices were calculated (FD and wFD) from a matrix composed by the absolute abundance of each species and presence/absence of the categories established for the selected parameters (dispersal syndrome, regeneration strategy, vertical stratification, and foliar phenology) per plot. The index value in each plot was estimated using the FDiversity Software (Casanoves et al. 2010). Correlations between FD, wFD and Shannon–Wiener Diversity Index values and the density of *H. dulcis* in each plot were evaluated using the STATISTICA 7.0 software package (Statsoft 2004).

Discriminant analyses were conducted for each vegetation type using the *stepwise* method of addition and removal of functional groups as discriminant variables in order to identify the functional groups that contributed more significantly and to detect differences in plots with and without the invasive species. A canonical correlation analysis was then performed to determine which functional groups were more relevant in forming the groups of the plots defined a priori. These analyses were carried out using the IBM SPSS Statistics 19.0 software (IBM Corp 2010). The Chi Square test of association was performed using StatView 5.0.1 (SAS Institute Inc. 1998), in order to identify possible positive or negative associations among native species and *H. dulcis* in the plots.

## Results

A total of 1976 trees belonging to 125 species and morphospecies and 40 families were recorded in the sampling plots. Nine of the species were not native. Among native species, 94 were identified at the species level and 22 as morphospecies at the genus or family levels. The list of all species, along with their native range, functional groups and number of trees recorded in each vegetation type is presented in Appendix I. The families with the largest numbers of species were Fabaceae, with 20 species (about 17 %); Lauraceae, with 11 species (about 9 %); Solanaceae, with eight species (about 7 %); and Euphorbiaceae, with seven species (about 6 %). There were native and alien species in Rutaceae, Moraceae, Myrtaceae, and Lauraceae, while Oleaceae, Cupressaceae, and Rhamnaceae were represented by alien species only.

### Comparison of canopy openness among vegetation types and in plots with and without *H. dulcis*

"Vegetation type" was the only significant factor that allowed the differentiation of sampling plots with regard to canopy openness ($F_{(5,54)} = 15.41$; $p < 0.001$). As expected, canopy openness was greater in open than in semi-open and closed vegetation types (Fig. 1).

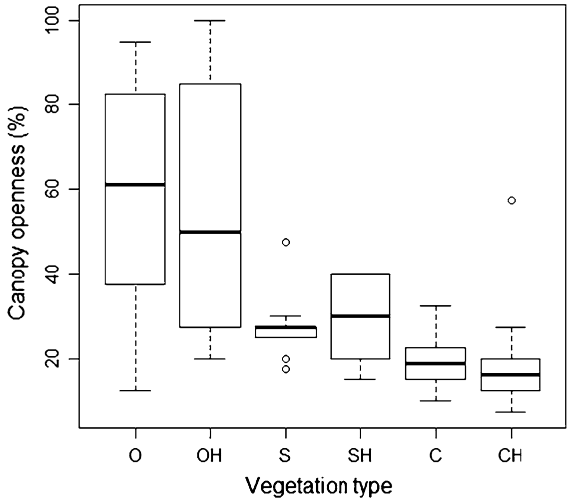


**Fig. 1** *Box-and-whisker plot* for canopy openness (%) compared among seasonal deciduous forest vegetation types in the Fritz Plaumann State Park (Concordia, SC, Brazil). Vegetation types: O—open without *H. dulcis*; OH—open with *H. dulcis*; S—semi-open without *H. dulcis*; SH—semi-open with *H. dulcis*; C—closed without *H. dulcis*; CH—closed with *H. dulcis*. *Circles* are outliers

### Comparison of density, basal area, height and age of *H. dulcis* trees among vegetation types

Of the 113 *H. dulcis* trees recorded, the largest number of individuals was present in the semi-open vegetation type (68; 60 % of the total), with lower numbers in the closed (27; 24 %) and open vegetation types (18; 16 %) ($F_{(2,27)} = 4.3$; $p = 0.02$) (Fig. 2). The numbers of trees did not differ between closed and open vegetation types (Fig. 2). Average height differed among vegetation types ($F_{(2,27)} = 3.7$; $p = 0.04$), with taller trees in closed vegetation (Fig. 2). The mean basal area was larger in closed vegetation than in open or semi-open types ($F_{(2,27)} = 8.9$; $p = 0.001$), not differing between semi-open and open types (Fig. 2).

Overall, *H. dulcis* trees in semi-open and open vegetation types had smaller diameters than those in the closed vegetation type (Fig. 3a). In semi-open vegetation, 96 % (65 of 68) of *H. dulcis* tree diameters were below 20 cm, while all the trees in open

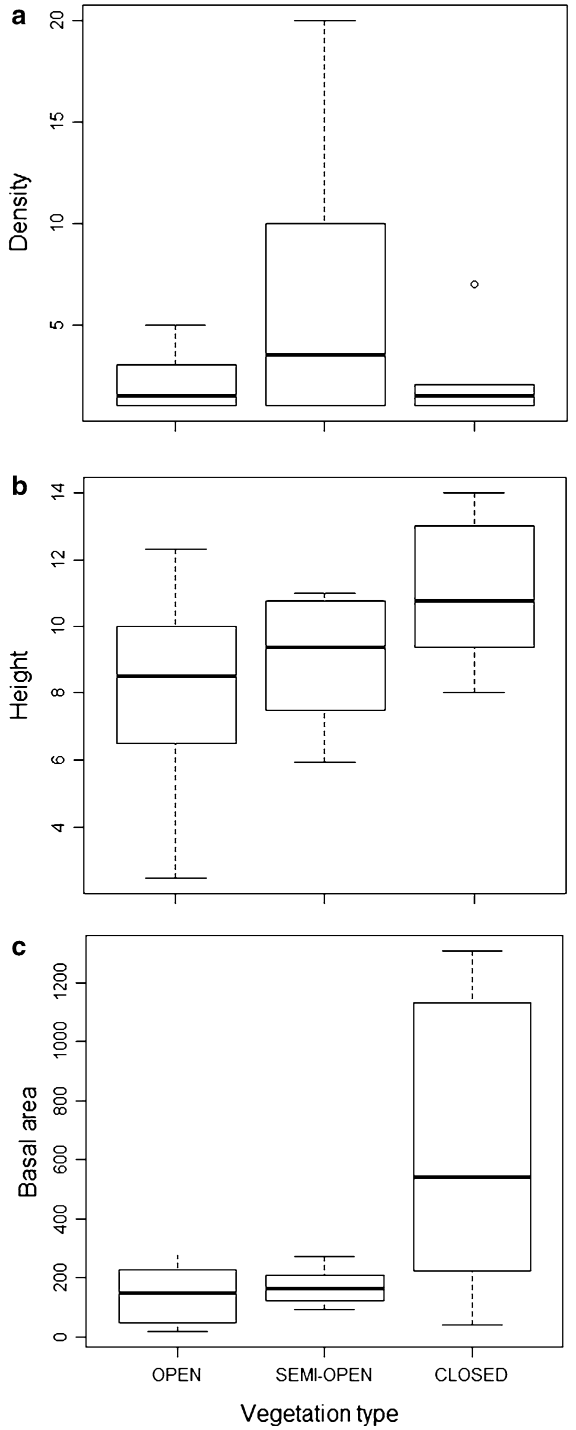


**Fig. 2** *Box-and-whisker plot* for density (**a**), height (**b**) and basal area (**c**) of *Hovenia dulcis* compared among seasonal deciduous forest vegetation types in the Fritz Plaumann State Park (Concordia, SC, Brazil). Vegetation types: OPEN—open; SEMI—semi-open; CLOSED—closed. *Circles* are outliers

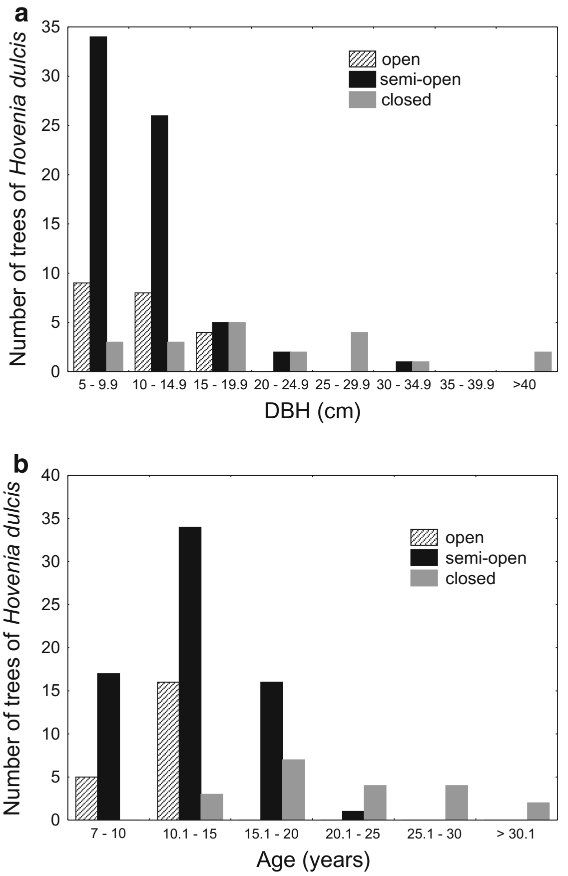
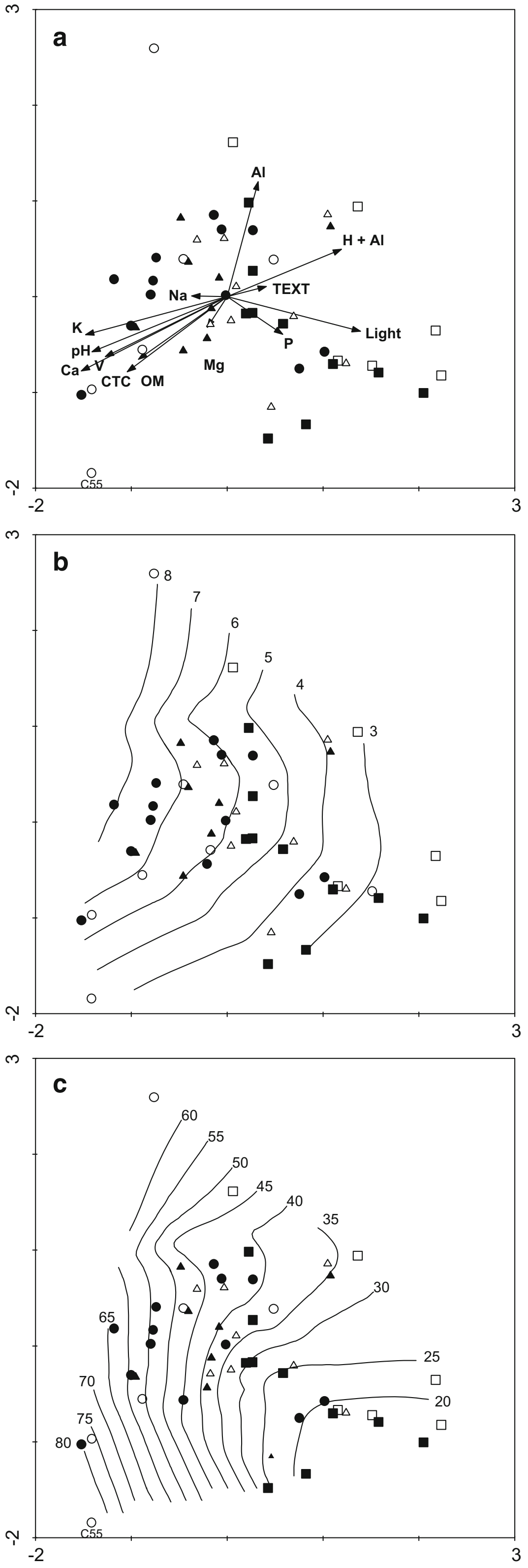


**Fig. 3** Diameter (**a**) and age (**b**) structure of *H. dulcis* populations in open (*slashed bars*), semi-open (*black bars*) and closed (*grey bars*) seasonal deciduous forest vegetation types in the Fritz Plaumann State Park (Concordia, SC, Brazil)

vegetation were below 20 cm in diameter (Fig. 3a). A larger variation in diameter was found in the closed vegetation type, with trees in the largest diameter class (>40 cm) found only in this type (Fig. 3a). A similar pattern was observed in the age histogram of *H. dulcis*, with the majority of trees in the open and semi-open vegetation types belonging to the younger age classes, and greater age variation in the closed vegetation type (Fig. 3b). The average age in the open vegetation type was 12 years (±3.3), varying from 7 to 19 years (95 % CI $10.55 \leq \mu \leq 12.37$). In semi-open vegetation, the average age was 16.3 (±6.3), varying between 9 and 23 years (95 % CI $12.28 \leq \mu \leq 13.72$). In the closed vegetation type, the average age was 21.4 (±6.5), varying from 9 to around 30 years (95 % CI $18.35 \leq \mu \leq 24.44$).



◀**Fig. 4** Canonical correspondence analysis (CCA) ordination biplot with plots and environmental variables (vectors) (**a**), isoclines of Simpson Diversity Index (**b**) and isoclines of basal area (**c**) based on density of the native tree species sampled in different seasonal deciduous forest vegetation types in the Fritz Plaumann State Park (Concordia, SC, Brazil). Environmental variables: Light—% canopy openness; TEXT—soil texture; pH; P—phosphorus; K—potassium; OM—% organic matter; Al—aluminum; Ca—calcium; Mg—magnesium; Na—sodium; CTC—cation exchange capacity; e V—base saturation. Vegetation types—*empty squares*: open without *H. dulcis*; *full squares*: open with *H. dulcis*; *empty triangles*: semi-open without *H. dulcis*, *full triangles*: semi-open with *H. dulcis*; *empty circles*: closed without *H. dulcis*; *full circles*: closed with *H. dulcis*

### Assessment of the influence of soil and canopy openness on native plant species

The cumulative variance of the CCA based on tree species density explained only 7.5 % of the total variance when based on density (F = 1.2; $p = 0.04$). Ca, Mg and canopy openness were the variables that best explained the distribution of plots in the ordination space (Fig. 4a). The Simpson Diversity Index (Fig. 4b) and basal area isoclines (Fig. 4c) showed lower diversity and smaller basal area in open vegetation plots. On the otherhand, there was a gradual increase in both measures in semi-open and closed vegetation types. The accumulated variance of the CCA based on tree species basal areas explained 33 % of the total variance (F = 1.4; $p = 0.004$). Ca, Mg and K best explained the distribution of plots in the ordination (Fig. 5a). The Simpson Diversity Index isoclines (Fig. 5b) showed lower diversity in the open vegetation plots, and a gradual increase in semi-open and closed vegetation.

### Comparison of density, basal area, richness, diversity, evenness and functional diversity among vegetation types and in plots with and without *H. dulcis*

Structural parameters of the plant communities, density, basal area, richness, diversity by Shannon–Wiener diversity index, FD, and wFD varied significantly among habitat categories, while diversity by Simpson Diversity Index and evenness by Pielou Index did not vary significantly among plots (Table 1). Only the "vegetation type" factor was significant

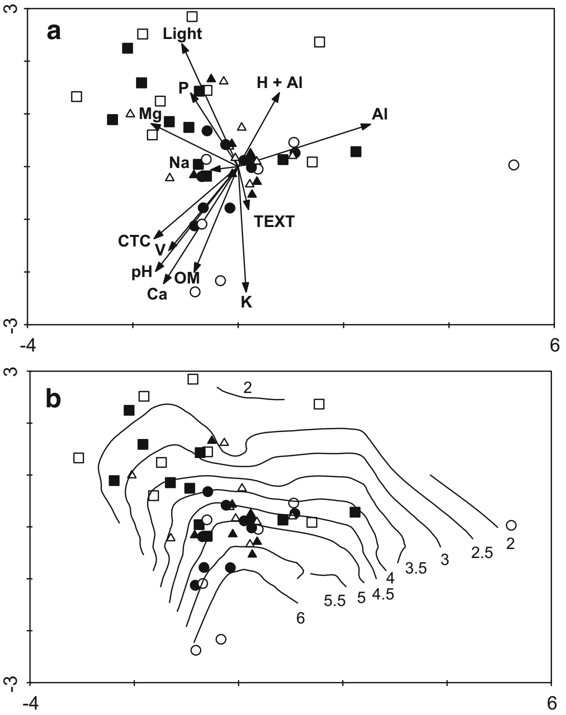


**Fig. 5** CCA ordination biplot with plots and environmental variables (vectors) (**a**) and isoclines of Simpson Diversity Index (**b**) based on the basal area of the native species sampled in different seasonal deciduous forest vegetation types in the Fritz Plaumann State Park (Concordia, SC, Brazil). (B) Environmental variables: Light—% canopy openness; TEXT—soil texture; pH; P—phosphorus; K—potassium; OM—% organic matter; Al—aluminum; Ca—calcium; Mg—magnesium; Na—sodium; CTC—cation exchange capacity; e V—base saturation. Vegetation types—*empty squares*: open without *H. dulcis*; *full squares*: open with *H. dulcis*; *empty triangles*: semi-open without *H. dulcis*, *full triangles*: semi-open with *H. dulcis*; *empty circles*: closed without *H. dulcis*; *full circles*: closed with *H. dulcis*

($p < 0.0001$) among habitat categories for density, basal area, FD, and wFD (Table 1). Density was lower in the open vegetation type than in semi-open and closed vegetation (Table 1). Basal area, richness, Shannon–Wiener diversity index, FD, and wFD showed significantly higher values in the closed vegetation type when compared to semi-open and open vegetation (Table 1). There were no significant correlations between the density of *H. dulcis* and Shannon–Wiener diversity index ($y = 1.9849-0.0063x$; $R^2 = 0.004$; $p = 0.75$); the density of *H. dulcis* and FD ($y = 5.2155-0.0416x$; $R^2 = 0.019$; $p = 0.47$); and the density of *H. dulcis* and wFD ($y = 4.0678-0.0196x$; $R^2 = 0.07$; $p = 0.65$). Plots with and without *H. dulcis* are not significantly different in estimated richness by rarefaction for the three vegetation types (open without *H. dulcis* = 19 ± 8; open with *H. dulcis* = 36 ± 10.3; semi-open without *H. dulcis* = 42 ± 10.7; semi-open with *H. dulcis* = 40 ± 10.4; closed without *H. dulcis* = 63 ± 12; closed with *H. dulcis* = 63 ± 11.9).

### Identification of functional groups that contributed more significantly to the separation of plots with and without *H. dulcis* for each vegetation type

The functional groups containing zoochorous species showed higher abundance in all successional stages, with the group represented by zoochorous, pioneer, understory, evergreen species (FG11) containing the largest number of individuals (331). The group of zoochorous, non-pioneer, understory, and evergreen species (FG15) had the most species (16). A higher number of functional groups was present in the closed vegetation type (17) in comparison to the semi-open (16) and open (15) vegetation types (Appendix 1). *Hovenia dulcis* was the only alien species classified in the functional group composed by zoochorous, pioneer, canopy, deciduous species (FG14) (Carvalho 1994a). FG14 was represented by only four native species and 21 individuals.

The best discriminant analysis for open and semi-open vegetation types selected three of the 19 functional groups: 6, 13, and 17 for the open vegetation type, and 1, 13, and 17 for semi-open vegetation (Tables 2, 3, respectively). The function $DS = 0.436 \times FG17 + 0.345 \times FG6 + 0.168 \times FG13$ discriminated the two open vegetation type groups (with and without *H. dulcis*, $p < 0.001$), while the function $DS = 0.517 \times FG17 + 0.343 \times FG1-0.22 \times FG13$ discriminated the two semi-open vegetation groups ($p < 0.01$). The percentage of correctly allocated plots using the function obtained for the open vegetation type was 80 % for plots with *H. dulcis* and 100 % for plots without the species; the percentages were 70 and 100 %, respectively, for semi-open vegetation with and without *H. dulcis*. The discriminant analysis showed the group composed by zoochorous, non-pioneer, canopy, evergreen species (FG17) was more important in separating plots with and without *H. dulcis* both in open and in semi-open vegetation types (Tables 2, 3). The open vegetation type with *H. dulcis* contained 52 individuals from FG17 and the open vegetation type without *H. dulcis* had 13

**Table 1** Values (means ± 1 S.D.) for density (n of trees/hectare—Dens), basal area ($m^2$/ha—Basal), richness (number of species—Rich), Simpson diversity index (D), Shannon–Wiener diversity index (H'), Pielou evenness index (J), Functional diversity index (FD) and Functional diversity index weighted by abundance (wFD) compared between each single vegetation type in areas with and without *H. dulcis*, in seasonal deciduous forest in the Fritz Plaumann State Park (Concordia, SC, Brazil). Vegetation types—O: open without *H. dulcis*; OH: open with *H. dulcis*; S: semi-open without *H. dulcis*; SH: semi-open with *H. dulcis*; C: closed without *H. dulcis*; CH: closed with *H. dulcis*

| | O | OH | S | SH | C | CH | $F_{(5,54)}$ | *p* |
|---|---|---|---|---|---|---|---|---|
| Dens | $825^{a} \pm 610.2$ | $1100^{a} \pm 467.2$ | $1720^{b} \pm 519.2$ | $1720^{b} \pm 500.6$ | $1580^{b} \pm 415.8$ | $1850^{b} \pm 322.3$ | 7.2 | <0.0001 |
| Basal | $10.9^{a} \pm 7.6$ | $18.8^{a} \pm 5.9$ | $33^{a} \pm 8$ | $40.2^{a} \pm 9.1$ | $70^{b} \pm 16.3$ | $61.2^{b} \pm 21.9$ | 32.6 | <0.0001 |
| Rich | $4.5^{a} \pm 2$ | $7.2^{a} \pm 3.2$ | $10^{a} \pm 3.8$ | $10.8^{a} \pm 3.2$ | $13.6^{b} \pm 3.1$ | $14.9^{b} \pm 2.4$ | 17.2 | <0.0001 |
| D | $4.4^{a} \pm 2.8$ | $5^{a} \pm 3.2$ | $3.7^{a} \pm 2.4$ | $6.1^{a} \pm 2.4$ | $6.8^{a} \pm 3.5$ | $7.5^{a} \pm 3.7$ | 2.3 | 0.06 |
| H′ | $1^{a} \pm 0.5$ | $1.6^{a} \pm 0.4$ | $1.8^{a} \pm 0.6$ | $1.9^{a} \pm 0.4$ | $2.2^{b} \pm 0.3$ | $2.4^{b} \pm 0.2$ | 14.6 | <0.0001 |
| J | $0.6^{a} \pm 0.3$ | $0.7^{a} \pm 0.1$ | $0.6^{a} \pm 0.2$ | $0.7^{a} \pm 0.1$ | $0.7^{a} \pm 0.1$ | $0.8^{a} \pm 0.1$ | 2.2 | 0.07 |
| FD | $2.82^{a} \pm 1.3$ | $4.08^{a} \pm 1.21$ | $4.83^{a} \pm 1.22$ | $5.03^{a} \pm 1.29$ | $5.87^{b} \pm 1.24$ | $6.08^{b} \pm 1.05$ | 9.74 | <0.0001 |
| wFD | $2.13^{a} \pm 1$ | $3.29^{a} \pm 0.73$ | $3.57^{a} \pm 1.17$ | $3.90^{a} \pm 1.04$ | $4.90^{b} \pm 1.17$ | $4.80^{b} \pm 0.89$ | 10.07 | <0.0001 |

[a,b] Different letters in each row indicate significant differences (Tukey test, $p < 0.05$) for a single vegetation type in areas with and without *H. dulcis* and among vegetation types

**Table 2** Discriminant analysis results for functional groups compared between open vegetation plots with and without *H. dulcis*, in a seasonal deciduous forest in the Fritz Plaumann State Park (Concordia, SC, Brazil)

| Variables | Standardized coefficients |
|---|---|
| FG6 (anemochorous, non-pioneer, canopy, evergreen) | 0.999 |
| FG13 (zoochorous, pioneer, canopy, evergreen) | 0.888 |
| FG17 (zoochorous, non-pioneer, canopy, evergreen) | 1.16 |
| Wilk's λ | $0.329^{a}$ |
| Canonical correlation coefficient | 0.819 |

[a] $p < 0.001$

**Table 3** Discriminant analysis results for functional groups compared between semi-open vegetation plots with and without *H. dulcis*, in a seasonal deciduous forest at the Fritz Plaumann State Park (Concordia, SC, Brazil)

| Variables | Standardized coefficients |
|---|---|
| FG1 (zoochorous, pioneer, understory, evergreen) | 0.844 |
| FG13 (zoochorous, pioneer, canopy, evergreen) | −0.696 |
| FG17 (zoochorous, non-pioneer, canopy, evergreen) | 1.101 |
| Wilk's λ | $0.484^{a}$ |
| Canonical correlation coefficient | 0.718 |

[a] $p < 0.001$

individuals, while the semi-open type with *H. dulcis* contained 85 individuals from FG17 and the semi-open type without *H. dulcis* had 39 individuals.

The best model for the closed vegetation type used seven of the 19 functional groups: FG3, FG4, FG6, FG9, FG11, FG15, and FG18 (Table 4). The function $DS = 0.584 \times FG3 + 0.75 \times FG4 + 0.946 \times FG6 + 9.606 \times FG9 + 0.755 \times FG11 + 0.542 \times FG15 - 2.084 \times FG18$ discriminated between the two groups, leading to the correct allocation of 100 % of the plots with and without *H. dulcis* ($p < 0.001$). The discriminant analysis showed that the group composed by zoochorous, non-pioneer, canopy, deciduous species (FG18) was more important in separating the plots with and without *H. dulcis* (Table 4). The closed vegetation type with *H. dulcis* contained six individuals from FG18, while the closed vegetation type without *H. dulcis* had 17 individuals.

## Identification of associations among native species and *H. dulcis* in plots

*Hovenia dulcis* is positively associated with *Casearia sylvestris* ($\chi^2 = 6.67$; df = 1; $p = 0.01$), *Muellera campestris* ($\chi^2 = 5.93$; df = 1; $p = 0.05$), *Nectandra lanceolata* ($\chi^2 = 9.6$; df = 1; $p = 0.01$) and *Randia armata* ($\chi^2 = 5.45$; df = 1; $p = 0.05$), and negatively associated with *Actinostemon concolor* ($\chi^2 = -5.45$;

**Table 4** Discriminant analysis results for functional groups compared between closed vegetation plots with and without *H. dulcis*, in a seasonal deciduous forest at the Fritz Plaumann State Park (Concordia, SC, Brazil)

| Variables | Standardized coefficients |
|---|---|
| FG3 (anemochorous, pioneer, canopy, deciduous) | 2.292 |
| FG4 (anemochorous, pioneer, emergent, deciduous) | 0.989 |
| FG6 (anemochorous, non-pioneer, canopy, evergreen) | 2.443 |
| FG9 (anemochorous, non-pioneer, understory, evergreen) | 2.148 |
| FG11 (zoochorous, pioneer, understory, evergreen) | 1.806 |
| FG15 (zoochorous, non-pioneer, understory, evergreen) | 1.143 |
| FG18 (zoochorous, non-pioneer, canopy, deciduous) | −3.126 |
| Wilk's λ | 0.051[a] |
| Canonical correlation coefficient | 0.974 |

[a] $p < 0.001$

df = 1; $p = 0.05$). Because of multiple comparisons, the significance of these results should be taken with caution. Three of the four species with which *H. dulcis* is positively associated are evergreen. *C. sylvestris* and *M. campestris* are more abundant in the semi-open and closed vegetation types, while *N. lanceolata* is very abundant in all the vegetation types (Appendix 1). On the other hand, *A. concolor* is deciduous and was more abundant in the closed vegetation type in plots without *H. dulcis* (Appendix 1).

## Discussion

*Hovenia dulcis* reached higher densities in intermediate stage, and lower densities in early and advanced stages. The species' colonization process took place 10–15 years ago in the forest now at an intermediate stage of succession, and at least 30 years ago in the forest now in advanced stage. In both cases, however, the forest probably had greater canopy openness when the colonization process occurred due to selective logging (Siminski et al. 2011). The colonization of the open vegetation type is more recent, and consequently, invasive trees are younger in early and older in more advanced successional stages. The estimated ages should be taken with caution because the $R^2$ values for the relationship between basal area and age were not very high. However, the clear pattern of more older-aged trees observed in closed vegetation when compared to semi-open and open vegetation should be considered. Contrary to the initial hypothesis, no differences were observed between plant communities invaded and non-invaded by *H. dulcis* in all successional stages. No negative relationship was found among species richness, diversity, functional diversity, and the species density in the successional stages.

Changes in structure and composition of plant communities due to *H. dulcis* presence were described for different types of subtropical forests (Bardall et al. 2004; Schaff et al. 2006; Boeni 2011). However, the results obtained in these studies should not be compared to our study, considering that Bardall et al. (2004) and Schaff et al. (2006) did not compare areas with and without the species' presence, but instead compared the same areas before and after the species' arrival. In turn, Boeni (2011) compared areas with dense forest in advanced successional stages with and without *H. dulcis*, but did not compare different successional stages. In our study, we did not observe differences in structure and composition between plant communities invaded and non-invaded by *H. dulcis*. The same results were observed for other invasive tree species (Martínez 2010; Siderhurst et al. 2012; Whitfield et al. 2014). One possible explanation for this result is that spatial and temporal variation in extrinsic factors, such as disturbance history and propagule pressure, could have been more important in determining the forest regeneration dynamics than the invasive species presence (Shea and Chesson 2002). Complementary, the low density of *H. dulcis* in most of the plots, especially in the open and closed vegetation types, would not be sufficient to reveal changes on the plant communities due to the species presence. Studies about *H. dulcis* influence on density and/or species richness of tree seedlings and herbaceous species below dense stands compared with non-invaded stands could shed light on identifying *H. dulcis* impacts in fragmented deciduous forest.

*Hovenia dulcis* colonized both disturbed and younger successional forests and may be unable to survive and persist as a forest matures, as described for other alien invasive shrubs and trees in temperate decidual forests (Johnson et al. 2006; Webster et al.

2006; Cunard and Lee 2009; Burnham and Lee 2010; Radtke et al. 2013). Because the species is described in literature as a pioneer (Carvalho et al. 1994a, b), which suggests that it requires high levels of light to regenerate (Hartshorn 1978; Whitmore 1989), the high density of *H. dulcis* observed in the semi-open vegetation type was not expected. Although the forest had a greater canopy openness when the colonization process occurred due to selective logging (Siminski et al. 2011), those areas that presently are semi-open vegetation were not treeless in the past. Instead, aerial photographs from 1978 have provided evidence of the presence of some trees. This indicates that the species' may be tolerant to some shading, as has been observed for other invasive species in temperate, tropical and subtropical regions (Green et al. 2004; Martin and Marks 2006; Flory and Clay 2009; Martin et al. 2009; Godoy et al. 2011; Major et al. 2013).

On the other hand, the lower densities of *H. dulcis* in earlier and later successional stages could be a consequence of limited seed arrival and/or lack of suitable sites for seed germination and seedling establishment (Coutts et al. 2011; Schupp 2011). The low densities may be also due to biotic interactions that limited invasion in these successional stages. A possible biotic resistance mechanism through competition could be attributed to the higher abundance of individuals in the functional group composed by zoochorous, non-pioneer, canopy, deciduous species (FG18) in areas without *H. dulcis* in closed vegetation. This functional group is similar to the *H. dulcis* group (zoochorous, pioneer, canopy, deciduous species), and it is the most important one separating plots with and without *H. dulcis* in the closed vegetation type. Cunard and Lee (2009) showed a clear positive correlation between the invasive shrub *Frangula alnus* mortality, decreased light, decreased nutrients, and abundance in late successional species. According to the authors, this suite of relationships was explained by competition. Besides, reduced light levels promoted by evergreen species may also help explain the low densities of *H. dulcis* in the closed vegetation type (Silva 2012). The density of native trees is lower in open vegetation, when compared to semi-open and closed vegetation, making it less likely that biotic resistance through competition with similar species is a factor that is limiting population growth in these areas. Limitations imposed by abiotic and biotic factors in seed germination and seedling establishment are more prone to be responsible for the low density, besides the possibility of limited seed arrival in open vegetation. Assessments about seed arrival, seed predation, seedling herbivory, and the influence of factors such as herbaceous and shrub species cover, litter thickness and soil moisture on seed germination and seedling survival and growth could help to determine which factors are most important in limiting the species spread in open vegetation.

Colonization by *H. dulcis* in younger successional forests may have been a consequence of landscape fragmentation and forest disturbance, as reported for other invasive plant species (Belote et al. 2008; Burnham and Lee 2010). In a fragmented landscape, disturbance can be a major factor interacting with fragment size to influence species richness and composition in forest fragments (dos Santos et al. 2007). This interaction can be explained by the increasing sensitivity to disturbance as fragments get smaller (increased edge:interior ratio) (dos Santos et al. 2007), and by the assumption that anthropogenic disturbance promotes the invasion of alien species in forest patches (Hobbs 2011). These factors can either impact forest composition regardless of land use history or can disproportionately affect forests with specific land use histories (Katz et al. 2010). Land use history remains a major determinant of forest composition and structure (Flinn and Marks 2007; Martínez 2010), and many studies have indicated that the history of use may increase the abundance of invasive plants in forest landscapes (Von Holle and Motzkin 2007; DeGasperis and Motzkin 2007; Martínez 2010; Siderhurst et al. 2012). The historic component of human occupation in the region was therefore decisive for forest fragmentation as well as essential for the increase of propagule pressure of *H. dulcis*, consequently optimizing the colonization by the species (Siderhurst et al. 2012), with the greatest benefits to the invasive species occurring in low competition, high disturbance sites (Bellingham et al. 2005).

Selective logging and other forest management activities can also favor the establishment of invasive species (Major et al. 2013; Radtke et al. 2013). The intensity of tree harvesting, for example, may influence the degree of invasion success (Rejmánek 1989) as large gaps receive more light and may provide more resources for recruiting plants (Radtke et al. 2013). Besides, selective logging of economically-valued species in fragments currently classified as closed vegetation may have led to the temporary or permanent impoverishment of specific functional groups, both in species richness and abundance. The biotic and abiotic changes caused by fragmentation may also have led to the loss of certain functional groups (Laurance et al. 2000; Michalski et al. 2007; Santos et al. 2008). Such differences in species richness and abundance among functional groups, and in functional diversity, caused by human activities, may change the invasibility of plant communities (Pokorny et al. 2005). The low species richness and low abundance of individuals in the functional group composed by zoochorous, pioneer, canopy, deciduous species (*H. dulcis* functional group) may be the result of fragmentation or logging leading to its rarefaction, or an intrinsic characteristic of the plant community. In the last case, opportunities for occupation of relatively open niches may have facilitated *H. dulcis* establishment (Funk et al. 2008; Byun et al. 2013).

Considering the context of intense forest fragmentation and the high susceptibility of young disturbed secondary forests to invasion by *H. dulcis*, a management strategy at different scales should be implemented, focusing on preventative and control work. At the local scale, control actions need to be conceived prioritizing small satellite or peripheral populations (Moody and Mack 1988) and populations in highly suitable habitat (Higgins et al. 2000), such as small and disturbed native vegetation patches, gaps and edges between closed and open vegetation types. A successful plan for reducing *H. dulcis* should also include management strategies to minimize disturbance (Whitfield et al. 2014) and subsequent reinvasion. One potential mechanism is to introduce native species assemblages that are highly competitive with the invasive species and can increase resistance to future invasion (Pywell et al. 2003). Successful resistance to invasion may be further strengthened if restored native species are functionally similar to and competitive with invading species, preempting available niche space for the invader (Pokorny et al. 2005; Funk et al. 2008; Ammondt and Litton 2011). In our study, *H. dulcis* showed a negative association with deciduous species, which could mean competitive exclusion or different habitat requirement by the native and the alien species. Although we cannot conclude which is the reason for the negative association; however, we can recommend that pioneer, deciduous and fast-growing species should be used in restoration efforts following removal of the invasive species.

Propagule availability is an extremely important determinant of the invasion extent in all habitats (Von Holle and Simberloff 2005; Eschtruth and Battles 2011). Any management strategy at the regional scale should include native species, which may replace *H. dulcis* for different purposes preferred by landowners and result in the reduction of the species' propagule pressure. Zoochorous, pioneer, and fast-growing species should be promoted by the local government in place of *H. dulcis*. Policies to both promote native species and restrict or prohibit the use of *H. dulcis* are essential for a strategy reaching the needed scale and providing opportunities for restoration of remaining forest fragments.

**Acknowledgments** The expert help of Cassio Daltrini Neto, Tiago Barbosa and Daniel Falkenberg. Sílvia Ziller, Clare Aslan, Elaine Chow and Hugh Safford provided important suggestions and helped improve the language. Two anonymous referees whose comments and suggestions substantially improved the manuscript. Financial support came from Tractebel Energia S.A., from the Graduate Program in Ecology of the Federal University of Santa Catarina and from the Fundação de Apoio à Pesquisa Científica e Tecnológica do Estado de Santa Catarina, Brazil. MS Dechoum is supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Brazil. N Peroni is supported by Conselho Nacional de Desenvolvimento Científico e Tecnólogico, Brazil. SM Zalba receives support of Universidad Nacional del Sur and CONICET, Argentina.

## References

Ammondt SA, Litton CM (2011) Competition between native Hawaiian plants and the invasive grass *Megathyrsus maximus*: implications of functional diversity for ecological restoration. Restor Ecol 20(5):638–646

Ayres M, Ayres Junior M, Ayres DL, Santos AA (2007) Biostat 5.0—aplicações estatísticas nas áreas das ciências biomédicas. OnG Mamirauá, Belém

Bardall ML, Roderjan CV, Galvão F, Curcio GR (2004) Caracterização florística e fitossociológica de um trecho sazonalmente inundável de floresta aluvial, em Araucária. PR Ci Fl 14(2):37–50

Beard JS (1955) The classification of tropical American vegetation-types. Ecology 36(1):89–100

Bellingham PJ, Tanner EVJ, Healey JR (2005) Hurricane disturbance accelerates invasion by the alien tree *Pittosporum undulatum* in Jamaican montane rain forests. J Veg Sci 16(6):675–684

Belote RT, Jones RH, Hood SM, Wender BW (2008) Diversity-invasibility across an experimental disturbance gradient in Appalachian forests. Ecology 89:183–192

Boeni BO (2011) Riqueza, estrutura e composição de espécies em floresta secundária invadida por *Hovenia dulcis* Thunb., caracterização do seu nicho de regeneração e efeitos alelopáticos. Thesis, Vale dos Sinos University, Brazil

Brasil (2008) Instrução Normativa 6, de 23 de setembro de 2008. Reconhece as espécies da flora brasileira ameaçadas de extinção. Diário Oficial da República Federativa do Brasil, Poder Executivo, Brasília, 24 Sept 2008

Brown CS, Rice KJ (2010) Effects of belowground resource use complementarity on invasion of constructed grassland plant communities. Biol Invasions 12:1319–1334

Buckey YM et al (2006) Management of plant invasions mediated by frugivore interactions. J Appl Ecol 43:848–857

Budke JC, Athayde EA, Giehk ELH, Záchia RA, Eisinger SM (2005) Composição florística e estratégias de dispersão de espécies lenhosas em uma floresta ribeirinha, arroio Passo das Tropas, Santa Maria, RS, Brasil. Iheringia 60(1):17–24

Burnham KM, Lee TD (2010) Canopy gaps facilitate establishment, growth, and reproduction of invasive *Frangula alnus* in a Tsuga canadensis dominated forest. Biol Invasions 12:1509–1520

Byun C, Blois S, Brisson J (2013) Plant functional group identity and diversity determine biotic resistance to invasion by an exotic grass. J Ecol 101:128–139

Cáceres NC, Monteiro-Filho ELA (2001) Food habits, home range and activity of *Didelphis aurita* (Mammalia, Marsupialia) in a forest fragment of southern Brazil. Stud Neotrop Fauna Environ 36:85–92

Carvalho PER (1994a) Ecologia, silvicultura e usos da uva-do-japão (*Hovenia dulcis* Thunberg). Circular Técnica EMBRAPA Florestas, Colombo

Carvalho PER (1994b) Espécies florestais brasileiras—recomendações silviculturais, potencialidades e uso da madeira. EMBRAPA Florestas, Colombo

Casanoves F, Pla L, Di Rienzo JA, Díaz S (2010) FDiversity: a software package for the integrated analysis of functional diversity. Methods Ecol Evol 2(3):233–237

Catford JA, Daehler CC, Murphy HT, Sheppard AW, Hardesty BD, Westcott DA, Rejmánek M, Bellingham PJ, Pergl J, Horvitz CC, Hulme PE (2012) The intermediate disturbance hypothesis and plant invasions: implications for species richness and management. Perspect Plant Ecol Evol Syst 14:231–241

Colwell RK (2006) Estimates: statistical estimation of species richness and shared species from samples. Version 8. Persistent purl.ock.org/estimates

Costa JT, Estevan DA, Bianchini E, Fonseca ICB (2011) Composição florística das espécies vasculares e caráter sucessional da flora arbórea de um fragmento de Floresta Estacional Semidecidual no Sul do Brasil. Rev Bras Bot 34(3):411–422

Coutts SR, van Klinken RD, Yokomizo H, Buckley YM (2011) What are the key drives of spread in invasive plants: dispersal, demography or landscape: and can we use this knowledge to aid management? Biol Invasions 13:1649–1661

Cunard C, Lee TD (2009) Is patience a virtue? Succession, light, and the death of invasive glossy buckthorn (*Frangula alnus*). Biol Invasions 11:577–586

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88(3):528–534

Dechoum MS, Ziller SR (2013) Métodos para controle de plantas exóticas invasoras. Biotemas 26(1):69–77

DeGasperis BG, Motzkin G (2007) Windows of opportunity: historical and ecological controls on *Berberis thunbergii* invasions. Ecology 88(12):3115–3125

Denslow JS, Dewalt SJ (2008) Exotic plant invasion in tropical forests: patterns and hypothesis. In: Carson W, Schnitzer S (eds) Tropical forest community ecology. Wiley, New York, pp 409–426

dos Santos K, Kinoshita LS, dos Santos FAM (2007) Tree species composition and similarity in semi deciduous forest fragments of southeastern Brazil. Biol Cons 135:268–277

Elton CS (1958) The ecology of invasions by animals and plants. University of Chicago Press, Chicago

Eschtruth AK, Battles JJ (2011) The importance of quantifying propagule pressure to understand invasion: an examination of riparian forest invasibility. Ecology 92:1314–1322

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Ann Rev Ecol Evol Syst 34:487–515

Fine PVA (2002) The invasibility of tropical forests by exotic plants. J Trop Ecol 18:687–705

Flinn KM, Marks PL (2007) Agricultural legacies in forest environments: tree communities, soil properties and light availability. Ecol Appl 17:452–463

Flory SL, Clay K (2009) Effects of roads and forest successional age on experimental plant invasions. Biol Conserv 142(11):2531–2537

Franco AMS (2008) Estrutura, diversidade e aspectos ecológicos do componente arbustivo e arbóreo em uma floresta estacional, Parque Estadual do Turvo, Sul do Brasil. Dissertation, Federal University of Rio Grande do Sul, Brazil

Funk JL, Cleland EE, Suding KN, Zavaleta ES (2008) Restoration through reassembly: plant traits and invasion resistance. Trends Ecol Evol 23(12):695–703

Giehl EL, Athayde EA, Budke JC, Gesing JPA, Einsiger SM, Canto-Dorow TS (2007) Espectro e distribuição vertical das estratégias de dispersão de diásporos do componente arbóreo em uma floresta estacional no sul do Brasil. Acta Bot Bras 21(1):137–145

Gilbert B, Lechowicz MJ (2005) Invasibility and abiotic gradients: the positive correlation between native and exotic plant diversity. Ecology 86:1848–1855

Godoy O, Saldaña A, Fuentes N, Valladares F, Gianoli E (2011) Forests are not immune to plant invasions: phenotypic plasticity and local adaptation allow *Prunella vulgaris* to colonize a temperate evergreen rainforest. Biol Invasions 13:1615–1625

Goldstein LJ, Suding KN (2013) Aplying competition theory to invasion: resource impacts indicate invasion mechanisms in California shrublands. Biol Invasions 16:191–203

Green PT, Lake PS, O'Dowd DJ (2004) Resistance of island rainforest to invasion by alien plants: influence of microhabitat and herbivory on seedling performance. Biol Invasions 6:1–9

Hartshorn GS (1978) Treefalls and tropical forest dynamics. In: Tomlinson PB, Zimmermann MH (eds) Tropical trees as living systems. Cambridge University Press, New York, pp 617–638

Hendges CD, Fortes VB, Dechoum MS (2012) Consumption of the invasive alien species *Hovenia dulcis* thumb.

(Rhamnaceae) by *Sapajus nigritus* Kerr, 1792 in a protected area in southern Brazil. Rev Bras Zoociências 14(1, 2, 3):255–260

Higgins SI, Richardson DM, Cowling RM (2000) Using a dynamic landscape model for planning the management of alien plant invasions. Ecol Appl 10:1833–1848

Hobbs RJ (2011) Land use. In: Simberloff D, Rejmánek R (eds) Encyclopedia of biological invasions. University of California Press, Berkeley, pp 425–427

Huston MA (2004) Management strategies for plant invasions: manipulating productivity, disturbance, and competition. Divers Distrib 10:167–178

Hyun TK, Eom SH, Yu CY, Roitsch T (2009) *Hovenia dulcis*—an Asian traditional herb. Planta Med 76:943–949

IBGE (2012) Technical Manual of Brazilian vegetation, 2nd edn. IBGE, Rio de Janeiro

IBM Corp (2010) IBM SPSS statistics for Windows, version 19.0. IBM Corp, Armonk

Ivanauskas NM, Rodrigues RR (2000) Florística e fitossociologia de remanescentes de floresta estacional Deciduous em Piracicaba, São Paulo, Brasil. Rev Bras Bot 23(3):291–304

Johnson VS, Litvaitis JA, Lee TD, Frey S (2006) The role of spatial and temporal scale in colonization and spread of invasive shrubs in early successional habitats. For Ecol Manag 228(1–3):124–134

Katz DSW, Lovett GM, Canham CD, O'Reilly CM (2010) Legacies of land use history diminish over 22 years in a forest in southeastern New York. J Torrey Bot Soc 137(2):236–251

Kilka RV, Longhi SJ (2011) A regeneração natural e a sucessão condicionada por diferentes tipos de distúrbios: um estudo de caso. In: Schumacher MV, Longhi SJ, Brun E, Kilca RV (eds) A Floresta estacional subtropical—caracterização e ecologia no rebordo do planalto meridional. Santa Maria, pp 121–140

Klein RM (1972) Árvores nativas da floresta subtropical do Alto Uruguai. Sellowia 24:9–62

Klein RM (1978) Mapa fitogeográfico do estado de Santa Catarina. In: Klein RM (ed) Flora Ilustrada Catarinense. Herbário Barbosa Rodrigues, Itajaí

Kohler KE, Gill SM (2006) Coral Point Count with Excel extensions (CPCe): a visual basic program for the determination of coral and substrate coverage using random point count methodology. Comput Geosci 32:1259–1269

Laurance WF, Peres CA (2006) Emerging threats to tropical forests. University of Chicago Press, Chicago

Laurance WF, Delamônica P, Laurance SG, Vasconcelos HL, Lovejoy LE (2000) Rainforest fragmentation kills big trees. Nature 404:836

Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC, Gascon C, Bierregaard RO, Laurance SG, Sampaio E (2002) Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conserv Biol 16:605–618

Laurance WF, Nascimento HEM, Laurance SG, Andrade AC, Fearnside PM, Ribeiro JEL, Capretz RL (2006) Rain forest fragmentation and the proliferation of successional trees. Ecology 87:469–482

Leps J, Smilauer P (2003) Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge

Levine JD (2000) Species diversity and biological invasions: relating process to community pattern. Science 288:852–854

Levine JD, Alder PB, Yelenik SG (2004) A meta-analysis of biotic resistance to exotic plant invasions. Ecol Lett 7:975–989

Lonsdale WM (1999) Global pattern of plant invasions and the concept of invasibility. Ecology 80(5):1522–1536

Loregian AC, Silva BB, Zanin EM, Decian WS, Henke-Oliveira C, Budke JC (2012) Padrões espaciais e ecológicos de espécies arbóreas refletem a estrutura em mosaicos de uma floresta subtropical. Acta Bot Bras 26(3):593–606

Major KC, Nosko P, Kuehne C, Campbell D, Bauhus J (2013) Regeneration dynamics of non-native northern red oak (*Quercus rubra* L.) populations as influenced by environmental factors: a case study in managed hardwood forests of southwestern Germany. For Ecol Manag 291:144–153

Martin PH, Marks PL (2006) Intact forests provide weak resistance to a shade-tolerant invasive Norway maple (*Acer platanoides* L.). J Ecol 94:1070–1079

Martin PH, Canham CD, Marks PL (2009) Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. Front Ecol Environ 7(3):142–149

Martínez OJA (2010) Invasion by native tree species prevents biotic homogenization in novel forests of Puerto Rico. Plant Ecol 211:49–64

Michalski F, Nishi I, Peres CA (2007) Disturbance-mediated drift in tree functional groups in Amazonian forest fragments. Biotropica 36:691–701

Mikich SB, Silva SM (2001) Composição florística e fenologia das espécies zoocóricas de remanescentes de Floresta Estacional SemiDeciduous no centro-oeste do Paraná. Acta Bot Bras 15(1):89–113

Moody ME, Mack RN (1988) Controlling the spread of plant invasions: the importance of nascent foci. J Appl Ecol 25:1009–1021

Pla L, Casanoves F, Di Rienzo J (2012) Quantifying functional biodiversity. Springer, New York

Pokorny ML, Sheley RL, Zabinski CA, Engel RE, Svejcar TJ, Borkowski JJ (2005) Plant functional group diversity as a mechanism for invasion resistance. Restor Ecol 13(3):448–459

Pysek P, Richardson D (2007) Traits associated with invasiveness in alien plants: where do we stand? In: Nentwig W (ed) Biological invasions. Ecological studies, vol 193. Springer, Berlin, pp 97–123

Pywell RF, Bullock JM, Roy DB, Warman L, Walker KJ, Rothery P (2003) Plant traits as predictors of performance in ecological restoration. J Appl Ecol 40:65–77

R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org/

Radtke A, Ambraß S, Zerbe S, Tonon G, Fontana V, Ammer C (2013) Traditional coppice forest management drives the invasion of *Ailanthus altissima* and *Robinia pseudoacacia* into deciduous forests. For Ecol Manag 291:308–317

Reitz R (1974) Palmeiras. Flora Ilustrada Catarinense, Herbário Barbosa Rodrigues

Reitz R, Klein RM, Reis A (1978) Projeto Madeira de Santa Catarina. Revista Sellowia 28–30

Reitz R, Klein RM, Reis A (1988) Projeto madeira do Rio Grande do Sul. Governo do Estado do Rio Grande do Sul, Porto Alegre

Rejmánek M (1989) Invasibility of plant communities. In: Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmanek M, Williamson M (eds) Biological invasions: a global perspective. Wiley, Chichester, pp 369–388

Rejmánek M (1996) Species richness and resistance to invasion. In: Orians G, Dirzo R, Cushman JH (eds) Biodiversity and ecosystem processes in tropical forests. Ecological studies 122. Springer, New York, pp 153–172

Rejmánek M, Richardson DM (1996) What attributes make some plant species more invasive? Ecology 77(6): 1655–1661

Rejmánek M, Richardson DM (2013) Trees and shrubs as invasive species—2013 update on the global database. Divers Distrib 19:1093–1094

Ruschel AR, Nodari RO, Moerschbacher BM (2007) Woody plant species richness in the Turvo State park, a large remnant of deciduous Atlantic forest, Brazil. Biodivers Conserv 16:1699–1714

Santos BA, Peres CA, Oliveira MA, Grillo A, Alves-Costa C, Tabarelli M (2008) Drastic erosion in functional attributes of tree assemblages in Atlantic forest fragments of northeastern Brazil. Biol Conserv 141:249–260

SAS Institute (1998) StatView for Windows: version 5.0.1

Schaff LB, Filho AF, Galvão F, Sanquetta CR, Longhi SJ (2006) Modificações florístico-estruturais de um remanescente de Floresta Ombófila Mista Montana no período de 1979 e 2000. Ci Fl 16(3):271–291

Schupp EW (2011) Dispersal ability, plants. In: Simberloff D, Rejmánek R (eds) Encyclopedia of biological invasions. University of California Press, Berkeley, pp 159–165

Selle GL (2009) Guias de densidade e índices de sítios para *Hovenia dulcis* Thunberg na região central do estado do Rio Grande do Sul, Brasil. Dissertation, Federal University of Santa Maria, Brazil

Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. Trends Ecol Evol 17(4):170–176

Siderhurst LA, Griscom HP, Kyger C, Stutzman J, Trumbo B (2012) Tree species composition and diversity and the abundance of exotics in forest fragments of the Shenandoah Valley, Virginia. Castanea 77(4):348–363

Silva JG (2012) Efeito da arbórea introduzida *Hovenia dulcis* Thunb. (Rhamnaceae) sobre o componente arbóreo-arbustivo regenerante da Floresta Atlântica no sul do Brasil. Thesis, Federal University of Rio Grande do Sul, Brazil

Siminski A, Fantini AC, Guries RP, Ruschel AR, Reis MS (2011) Secondary forest succession in the Mata Atlantica, Brazil: floristic and phytosociological trends. ISRN Ecol. 2011, (Article ID 759893), p 19. doi:10.5402/2011/759893

Sobral M, Jarenkow JA, Brack P, Irgang B, Larocca J, Rodrigues RS (2006) Flora arbórea e arborescente do Rio Grande do Sul. Editora Rima, São Carlos

StatSoft Inc. (2004) STATISTICA (data analysis software system) version 7. www.statsoft.com

Symstad AJ (2000) A test of the effects of functional group richness and composition on grassland invasibility. Ecology 81(1):99–109

ter Braak CJF, Smilauer P (2002) CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca

Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E (1997) The influence of functional diversity and composition on ecosystem processes. Nature 277:1300–1302

Van der Pijl L (1982) Principals of dispersal of higher plants. Springer, Berlin

Vibrans AC, Sevegnani L, Gasper AL, Lingner DV (2012) inventário florístico florestal de Santa Catarina—floresta estacional deciduous, vol 2. Edifurb, Blumenau

Von Holle B, Motzkin G (2007) Historical land use and environmental determinants of nonnative plant distribution in coastal southern New England. Biol Conserv 136(1):33–43

Von Holle B, Simberloff D (2005) Ecological resistance overwhelmed by propagule pressure. Ecology 86(12): 3212–3218

Von Holle B, Delcourt HZ, Simberloff D (2003) The importance of biological inertia in plant community resistance to invasion. J Veg Sci 14:425–432

Webb SL, Dwyer M, Kaunzinger CK, Wyckoff PH (2000) The myth of the resilient forest: case study of the invasive Norway Maple (*Acer platanoides*). Rhodora 102:332–354

Webster CR, Jenkins MA, Jose S (2006) Woody invaders and the challenges they pose to forest ecosystems in the eastern United States. J For 104(7):366–374

Wheeler RE (2010) Permutation tests for linear models in R. http://cran.r-project.org/web/packages/lmPerm/vignettes/lmPerm.pdf. (Accessed 14 Nov 2013)

Whitfield TJS, Lodge AG, Roth AM, Reich PB (2014) Community phylogenetic and abiotic site characteristics influence abundance of the invasive plant *Rhamnus cathartica* L. J Plant Ecol 7(2):202–209

Whitmore TC (1989) Canopy gaps and the two major groups of tropical trees. Ecology 70:536–538

Yamamoto LF, Kinoshita LS, Martins FR (2007) Síndromes de polinização e de dispersão em fragmentos da Floresta Estacional Semidecídua Montana, SP, Brasil. Acta Bot Bras 21(1):137–145

Yun CW, Lee BC (2002) Vegetation structure of *Hovenia dulcis* community in South Korea. Korean J Ecol 25(2):93–99

Zenni RD, Ziller SR (2011) An overview of invasive plants in Brazil. Rev Bras Bot 34(3):431–446