

Invasions across secondary forest successional stages: effects of local plant community, soil, litter, and herbivory on *Hovenia dulcis* seed germination and seedling establishment

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Abstract Species abilities for seed germination and seedling survival under different situations are good predictors of their capacity to colonize a broad range of habitats. Biotic conditions related to understory cover, and abiotic factors such as litter thickness and soil moisture can be determinants of plant establishment. We evaluated seed germination, seedling survival, and growth of the invasive tree *Hovenia dulcis*

under experimental field conditions in three successional stages (open, semi-open, and closed vegetation) of a fragmented seasonal deciduous forest in southern Brazil. Our hypotheses were that *H. dulcis* seed germination, seedling survival, and seedling growth decrease along the successional gradient, that these factors are positively affected by soil moisture and percentage of bare soil, and negatively affected by understory cover and litter thickness. We also tested the hypothesis that herbivory on *H. dulcis* would decrease along the successional gradient. Our main finding was that *H. dulcis* can germinate and establish along all forest successional stages because it is shade-tolerant. Abiotic factors were more important than biotic factors for seed germination. Soil moisture positively affected seed germination while litter thickness negatively influenced seed germination. Percentage of bare soil negatively influenced seedling survival. Germination rates were higher in closed vegetation, whereas seedling survival was higher in semi-open vegetation, and growth rates were higher in open vegetation. There was no difference in herbivory among successional stages. The results of our study show that intermediate forest succession stages congregate the most favorable conditions for *H. dulcis* establishment, likely making them more susceptible to invasion.

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Introduction

One fundamental but difficult question to answer over the last decades of biological invasion studies has been which biological attributes make some plants more invasive than others. Within a wide range of woody plant taxa, populations invading disturbed landscapes tend to have short juvenile periods (<10 years), short intervals between large seed crops, small seed masses (<50 mg), and wide native ranges (Rejmánek and Richardson 1996; Pyšek et al. 2009; Hui et al. 2011). Invasiveness, however, is not equal among all invasive plant populations, but determined by different biological attributes depending on where a species is introduced (Rejmánek et al. 2013), on the features of the invaded habitat (Natale et al. 2010), and on the characteristics of the introduction events. Propagule pressure, genetic pool, the amount of time a species has been in the introduced range (residence time), and human assistance can be determinants for success (Rejmánek et al. 2013; Zenni and Simberloff 2013; Zenni et al. 2014), whereas different traits may be important in each stage of invasion (Dawson et al. 2009; Bufford and Daehler 2011; Moodley et al. 2013). For instance, for Proteaceae species, large seeds favor establishment and hold greater nutrient reserves, whereas small seeds facilitate long-distance dispersal and therefore favor spread (Moodley et al. 2013). Among woody plants, biological attributes correlated with invasiveness also vary with taxa (Richardson et al. 2011; Moodley et al. 2013).

Traits related to reproduction and dispersal are crucial for the naturalization and invasion of species in new environments (Richardson et al. 2011). However, no matter how prolific a species, or how efficient its dispersal, it will not invade unless the seeds reach suitable habitat, germinate and plants establish (Coutts et al. 2011). Understanding the factors that limit or promote seed germination and seedling establishment is critical in determining if and where a plant species can invade (McAlpine and Jesson 2008). Consequently, the local abundance of an invasive population may be defined by the magnitude of local seed supplies with seedling requirements acting as a subsequent filter (Levine 2000; Mazia et al. 2001). Reaching high rates of germination, seedling survival, and growth can be challenging for many introduced plants because

seeds and seedlings are exposed to numerous risks during establishment, including resource limitation, loss of viability in the soil, predation, herbivory, pathogens, and competition (Moles and Westoby 2004; Boulant et al. 2009).

Biotic and abiotic factors can act in isolated or aggregated ways, which can be extremely relevant for invasion success. Abiotic factors, such as litter thickness, may have positive or negative effects on seed germination and seedling recruitment (Baskin and Baskin 2014). Litter usually reduces soil temperature amplitude and water evaporation, thereby increasing soil moisture and promoting better conditions for seed germination (Eriksson 1995; Scariot 2000). On the other hand, litter can reduce seed germination and seedling establishment by the antagonistic chemical interaction of allelopathy, by reducing light incidence on seeds, or by acting as a physical barrier to seedling root penetration (Eriksson 1995; Scariot 2000; Baskin and Baskin 2014). There is a general positive relationship between soil moisture and the establishment of invasive plant seedlings (Warren et al. 2013; Rejmánek et al. 2013). Regarding biotic factors, lower understory cover (often due to disturbance), and consequently a higher percentage of bare soil, often facilitates the establishment of invasive alien plants (Fridley 2011). Although herbivory might not always be lethal to seedlings, it is one of the most common seedling mortality causes among species (Moles and Westoby 2004).

Regeneration dynamics in neotropical forests are largely determined by natural disturbance (Hubbel et al. 1999). When human disturbance generates forest fragmentation, significant changes in the natural disturbance regime occur, which may favor invasive species (Hyatt 2008; Moles et al. 2012). Forest fragmentation may facilitate invasion because of increased resource availability, especially in clearings and along the edges between original and converted areas (Fine 2002; Hobbs 2011). Consequentially, invasions are more frequent in small fragments and along edges (Vilà and Ibáñez 2011; Radtke et al. 2013; González-Muñoz et al. 2014). Furthermore, given that invasive alien species are often good colonizers, early stages of secondary forest succession should be more susceptible to invasion (Catford et al. 2012). However, fragmentation can also indirectly influence the success

of invasive species through changes in abundance of native species that can potentially establish interactions with introduced species. In a recent meta-analysis of the effect of fragmentation on herbivorous insects, Guimarães et al. (2014) showed that edge formation had a positive effect on herbivore abundance and richness, and that edge plants exhibited 70 % more damage than interior plants. The effects of environmental heterogeneity may, however, increase or decrease invasion success, depending on the capacity of species establishment under different environmental conditions (Melbourne et al. 2007). Seed germination and seedling survival under a broad range of conditions are good predictors of a species capacity to colonize novel habitats and to spread in a heterogeneous landscape.

Seasonal deciduous forests originally covered 8 % (7671 km²) of Santa Catarina state in southern Brazil (Klein 1978), but are now highly fragmented and restricted to 1.2 % of the original area. About 90 % of forest fragments are smaller than 50 ha (Vibrans et al. 2012). *Hovenia dulcis* Thunb. (Rhamnaceae) was introduced to southern Brazil in the second half of the 20th century (Vibrans et al. 2012). Although described in the literature as a pioneer species (Carvalho 1994), it is currently present in fragments in different successional stages. *H. 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). Determining patterns of invasion and the causes for the observed patterns across fragmented habitats is necessary for effective invasive species management and conservation of native species (Flory and Clay 2009).

The main objective of this study was to evaluate seed germination, seedling survival, and growth of *H. dulcis* under experimental field conditions in three successional stages in a seasonal deciduous forest. Our hypotheses were that *H. dulcis* seed germination, seedling survival, and seedling growth decrease along a successional gradient from initial to advanced secondary forest succession and would be positively affected by soil moisture and percentage of bare soil, and negatively affected by understory cover and litter thickness. We also tested the hypothesis that frequency of herbivory on *H. dulcis* would decrease along the successional gradient.

Materials and methods

The study system

This study took place in seasonal deciduous forest remnants in the Fritz Plaumann State Park, Santa Catarina, Brazil (coordinates 27°16'18"–27°18'57"S, and 52°04'15"–52°10'20"W), in subtropical climate, Cfa type in the Köppen–Geiger classification system. The 740 hectares of the Park comprises secondary forest fragments in different successional stages that have been regenerating since the Park was established in 1998. The area was formerly used for agriculture, cattle breeding, and logging (Silva 2008).

Hovenia dulcis is a deciduous tree native to East Asia, invasive in forests in South America and Tanzania (Kopachon et al. 1996; Hyun et al. 2010; Zenni and Ziller 2011; Rejmánek and Richardson 2013). It is described as a fast growing, pioneer plant commonly regenerating in clearings, disturbed forests, and open areas (Carvalho 1994). It reproduces sexually by seed (Carvalho 1994) and bears fruit between March and October in Brazil (Carvalho 1994). Intact seeds are consumed and dispersed by birds and mammals both in its native range and in South American forests (Zhou et al. 2013; Hedges et al. 2012; Lima 2014). Although there is no consensus about seed dormancy, freshly harvested seeds are successfully germinated in nurseries, suggesting no dormancy (Carvalho 1994; Blakesley et al. 2002). Moderate levels of shade (8–40 % of sunlight) are the most suitable conditions for the germination of *H. dulcis* seeds, whereas deep shade and full sunlight are less favorable under experimental conditions (Kopachon et al. 1996). *H. dulcis* plants have food bodies which attract insectivorous ants, and secondary compounds in its leaves that most likely serve as protection against herbivory (Kimura et al. 1981; Buono et al. 2008).

Experimental design

The forest fragments in the Park were classified as open, semi-open, or closed vegetation based on the physiology at the time of the study, time since abandonment, and history of use (aerial photographs from 1978, 2005, 2008 and 2011, and Siminski et al. 2011). Open areas were colonized by herbaceous or herb-shrub cover as

well as few isolated small-sized trees, whereas semi-open areas were characterized by open forest with a denser layer of trees. Open and semi-open areas were formerly used for agriculture and/or grazing. Closed areas were subjected to selective logging, which maintained the tree layer and the physiognomy of a closed forest with greater vertical stratification compared to the other vegetation types (Dechoum et al. 2014). The three vegetation types were considered distinct successional stages. Ten 10×10 m plots without *H. dulcis* were established for each vegetation type in different fragments, with plots of different vegetation types mixed in each fragment. A minimum distance of 100 m was kept between plots. Five 1×1 m subplots were delimited inside each plot, one in the center and four at 2.5 m from the four corners toward the center (seedling subplots, hereafter).

Hovenia dulcis seeds were collected in the area between June and August 2012 from fallen infructescences under the canopy trees in all vegetation types. The seeds were mixed and kept in plastic bags under refrigeration until March 2013, then taken to a greenhouse for germination. After immersion in water at room temperature for 12 h (following Carvalho 1994), the seeds were sowed into pots on vermiculite substrate. The pots were irrigated once a day. After 73 days, 900 seedlings were transplanted to the field. Six seedlings were planted in each seedling subplot, totaling 30 seedlings per plot and 300 per forest type. Each seedling subplot was divided into two rows and three columns, with distances of 25 cm between columns and 50 cm between rows; the seedlings were planted at the intersections. All seedlings were labeled on the day of planting and the number of leaves and height were recorded (time 0 = day 0 = 04-Jun-2013). Average height was 4 cm (SD = 0.9 cm), and 90 % of the seedlings had at least one leaf besides the cotyledons. We monitored the seedlings monthly for a year (time 12 = day 400 = 02-Jul-2014).

For the germination experiment, four 0.5×0.5 m subplots were delimited inside each plot (seed subplots, hereafter). Fifty *H. dulcis* seeds were sowed in each seed subplot, which was paired with a control seed subplot. The control seed subplots were necessary to verify the seed bank contribution to germination. We monitored seed subplots monthly during 9 months until March 2014, when a new seed crop was ripe. Seed germination was defined by the protrusion of the radicle through the seed coat.

Data collection

Litter thickness, soil moisture, percentage of bare soil, percentage of grass cover, and percentage of non-grass cover were measured in each plot at the beginning of the experiment. Measurements were taken in five quadrats per plot, which were set next to the seed and seedling subplots. Litter thickness was measured with a tape from the litter surface to the top of the mineral soil. Soil moisture was determined with an electronic soil moisture meter (HidroFarm HFM2010/HFM2030, Falker S.A., Brazil) that calculates the percentage of volumetric soil moisture from zero to 10-cm depth with a 3 % error. Understory cover was measured as ground cover by woody and non-woody plants up to 1 m of height. Spaces not occupied by plants were recorded as bare soil. Percentages of cover and bare soil were visually estimated to fit the following classes: 0, 1 (1–5 %), 2 (5–25 %), 3 (25–50 %), 4 (50–75 %), 5 (75–95 %), and 6 (95–100 %). The mean values of each class were used for the analysis.

During the monthly monitoring efforts for seed germination, each emerging *H. dulcis* seedling was labeled, and the number of new seedlings was recorded. The same counting procedure was applied to control seed subplots. Life status (alive or dead) and evidence of herbivory on leaves (presence or absence) were recorded for each seedling. Plant height and number of leaves were recorded again at the end of the experiment (time = 12), when all seedlings and seeds were removed from the plots to prevent further invasion.

Data analysis

Survival functions were estimated for each vegetation type using the Kaplan–Meyer method for censored data, a discrete stepped survivorship curve that adds information as each death occurs. The Mantel–Haenszel test was used to test differences between vegetation types. A Cox proportional hazards regression model considering vegetation type, percentages of grass and non-grass cover, percentage of bare soil, litter thickness, and soil moisture was used in order to verify which variables were determinant for seedling survival. A likelihood ratio test was used to quantify the relation of the group of covariates with survival. Vegetation type was considered a strata variable, which means that each stratum is allowed to have a different baseline hazard function, while the

coefficients of the remaining covariates are assumed to be constant across strata.

Generalized linear mixed-effects models (GLMM) for nested data were used to test the hypotheses related to seed germination, seedling growth, and herbivory. For seed germination, the Poisson distribution was assumed for the response variable and the log link function for the relationship between the response and explanatory variables. The response variable was the sum of germinated seeds in each subplot from time 0 to 12. The explanatory variables (vegetation type, litter thickness, soil moisture, percentage of grass cover, percentage of non-grass cover, and percentage of bare soil), as well as the interactions between all variables, were initially considered fixed effects. As many of the variables were highly correlated, the inclusion or exclusion of variables was based on Akaike's information criterion (AIC) values calculated using maximum likelihood. A less complex model was obtained considering vegetation type, litter thickness, soil moisture, and the interaction between them as fixed effects. Seed subplots were spatially dependent, while plots were considered replicates of each vegetation type and inserted into the model as a random effect. A GLMM was fitted using maximum likelihood and adaptive Gauss–Hermite quadrature to the deviance. Data from 17 subplots were excluded, where the number of germinated seeds in paired control seed subplots was larger than zero, in order to neutralize the effect of the seed bank in the analysis.

Seedling height and number of leaves were correlated (Spearman $r = 0.56$, $p < 0.0001$). Thus, only the height measurement data were used to test the hypothesis that seedling growth varied between vegetation types. The response variable for each seedling was the difference between height at the end and at the beginning of the experiment ($\Delta\text{height} = \text{height in time 12} - \text{height in time 0}$). Three seedlings were excluded from the analysis because their Δheight was negative, probably as a consequence of herbivory. A GLMM was fitted using maximum likelihood and Laplacian approximation to the deviance, and gamma distribution for the response variable. Vegetation type was inserted into the model as a fixed effect. Plots and seedling subplots were considered repeatedly measured replicates, therefore random effects.

To test the hypothesis that herbivory varied between successional stages, the response variable

was defined as the sum of herbivory records along the experiment period for each seedling with a minimum of zero for no herbivory and a maximum of 12 (the total number of observations) for monthly occurring herbivory. Vegetation type was considered a fixed effect and plots and seedling subplots, random effects. Data from all seedlings were considered in the model, including those that died before the end of the experiment. As a consequence, a new random effect was included in the model, which was a binomial variable related to seedling condition at the end of the experiment (alive or dead). A GLMM was fitted using maximum likelihood and Laplacian approximation to the deviance, assuming the Poisson distribution for the response variable and the log link function for the relationship between the response and explanatory variables. All statistical analyses and figures were done with R version 3.0.3 (R Development Core Team 2014), using the 'lme4' package for GLMM, and the 'survival' package for survival analysis.

Results

Seedling survival curves differed between vegetation types ($\chi^2 = 40.7$, $df = 2$, $p < 0.0001$; Fig. 1). Survival rate was higher in semi-open vegetation during

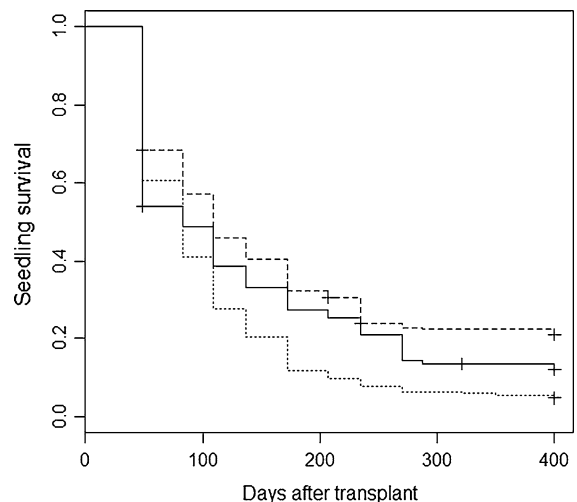


Fig. 1 Survival rates for *Hovenia dulcis* seedlings transplanted to open (full line), semi-open (dashed line), and closed (dotted line) vegetation types for a period of 400 days in seasonal deciduous forest in the Fritz Plaumann State Park (Brazil). Crosses represent censored data

the whole experiment compared to open and closed vegetation. Survival rate was higher for closed vegetation compared to open vegetation in the first month, but after the second month until the end of the experiment, survival in open vegetation overcame survival in closed vegetation (Fig. 1). The mean age at death for *H. dulcis* seedlings was 133 days (SE = 6.9) in open, 170 days (SE = 7.7) in semi-open, and 112 days (SE = 5.1) in closed vegetation. The numbers of transplanted seedlings still alive at the end of the experiment (time 12 = day 400) were 50 in open vegetation (16.7 %), 64 in semi-open (21.3 %), and 14 in closed vegetation (4.7 %). Higher percentages of bare soil lead to lower seedling survival in all vegetation types (Table 1).

A total of 1014 seeds germinated in the three vegetation types (16.9 %). The total numbers of germinated seeds were 127 in open, 253 in semi-open, and 634 in closed vegetation. Seed germination varied among vegetation types (Table 2; Fig. 2a). Soil moisture, litter thickness, and the interaction between these factors were relevant for seed germination (Table 2). Higher numbers of germinated seeds were observed in subplots with thinner litter layers and wetter soils.

Seedling Δ height average was 13.1 cm (SE = 2.1) in open, 7.99 cm (SE = 0.7) in semi-open, and 6.9 cm (SE = 1.1) in closed vegetation (Fig. 2b). The difference in seedling Δ height between vegetation types was significant according to the GLMM (Table 3).

The percentage of alive seedlings with evidence of herbivory at the end of the experiment was 64 % ($n = 32$) in open, 93.75 % ($n = 60$) in semi-open, and 85.7 % ($n = 12$) in closed vegetation. There was a higher variation in herbivory frequency in semi-open vegetation compared with open and closed vegetation

(Fig. 2c), but herbivory frequency did not differ significantly between vegetation types (Table 4).

Discussion

Our results partially support the hypothesis that *H. dulcis* seed germination, seedling survival, and seedling growth would decrease along a successional gradient from initial to advanced secondary forest succession. Higher germination rates were observed in closed vegetation, seedling survival was higher in semi-open vegetation, and growth rates were higher in open vegetation. Once seeds germinate, seedling survival and growth do not limit the species establishment in semi-open and closed vegetation types, confirming its tolerance to different environmental conditions. Our main finding that *H. dulcis* is relatively shade-tolerant and thus able to germinate and establish seedlings along a gradient of forest succession suggests that it can establish and invade all successional stages of secondary forests. This pattern has been observed for other shade-tolerant invasive species in temperate, tropical, and subtropical regions (Green et al. 2004; Martin and Marks 2006; Martin et al. 2009; Major et al. 2013).

Different environmental conditions influenced seed germination, seedling survival, and seedling growth. Abiotic conditions such as soil moisture and litter thickness were more important for seed germination than biotic factors, whereas percentage of bare soil was determinant for seedling survival. In tropical and subtropical forests, litter may play a significant role in preventing seed germination due to effects on light quality or as a physical barrier that prevents root growth into the soil (Baskin and Baskin 2014). The

Table 1 Cox proportional hazards regression model for *Hovenia dulcis* seedling survival in three vegetation types in the Fritz Plaumann State Park, Brazil

Variable	Coefficient	SE (coefficient)	Z value	<i>p</i>
Grass cover	0.003949	0.003819	1.03	0.3
Non-grass cover	0.001	0.00429	0.326	0.7
Bare soil	0.00995	0.003578	2.78	0.005
Litter thickness	0.01125	0.029	0.385	0.7
Soil moisture	0.00958	0.006856	1.398	0.16

Significant *p* values are in bold

$R^2 = 0.126$. Likelihood ratio test = 121.6 on 4 *df*, $p < 0.0001$

Table 2 Statistics for fixed effects of a generalized linear mixed model for seed germination in three vegetation types in the Fritz Plaumann State Park, Brazil

Variable	Estimate	SE	Z value	<i>p</i>
Intercept (open vegetation type)	2.988956	0.46829	6.38	<0.0001
Semi-open vegetation type	0.697767	0.22267	3.1	0.002
Closed vegetation type	1.318778	0.261659	5.0	<0.0001
Litter	-0.635125	0.126425	-5.0	<0.0001
Moisture	-0.1055	0.02287	-4.6	<0.0001
Litter × moisture	0.03466	0.00639	5.4	<0.0001

Significant *p* values are in bold

AIC 262.2

litter layer also influences soil moisture, which in turn can influence seed germination. Small-seeded species are especially responsive to soil moisture, as water stress greatly reduces germination in small-seeded species, but it is not so important for large-seeded species (Baskin and Baskin 2014). Thin litter layers and high soil moisture favor the germination of *H. dulcis* seeds, suggesting that reduced physical barriers and water stress are important for establishment success. Thin litter layers are usually observed in early successional stages, and high soil moisture is more commonly observed in late successional stages as a consequence of denser vegetation cover and thicker litter layers (Baskin and Baskin 2014). Therefore, appropriate conditions for *H. dulcis* seed germination were observed in both successional stages, corroborating what was observed in previous work by Dechoum et al. (2014), who showed that *H. dulcis* is able to colonize plant communities both in early and in advanced successional stages. On the other hand, smaller proportion of bare soil led to higher seedling survival, suggesting that ground cover by non-woody plants is beneficial. These results contradict our initial expectations that disturbed sites would be invisable by *H. dulcis*. Disturbance usually generates prevalence of bare ground and open spaces, and is often considered the best invasibility predictor in vegetation studies (Fridley 2011). However, the positive relationship between disturbance and forest invasibility is not straightforward for all invasive species, as some forest invaders are shade-tolerant. It seems clear that some ground cover is beneficial for *H. dulcis* because it helps maintain adequate soil moisture and light intensity while offering low levels of competition for these resources.

Higher percentages of germination were observed in closed vegetation, where canopy openness varied from 5 to 32.5 %, a range similar to the best light conditions for seed germination and seedling growth under controlled conditions (Kopachon et al. 1996). Conversely, in our experiment the closed vegetation type combined the worst conditions for *H. dulcis* seedling survival and growth, whereas semi-open and open vegetation, respectively, conferred the best overall conditions for seedlings. The disparate patterns between successional stages are evidence of a growth-survival trade-off resulting from *H. dulcis* physiological plasticity (Martin et al. 2010). *Hovenia dulcis* combines rapid growth at high-light with intermediate survivorship at low-light conditions, traits that are typical of early and mid-successional species (Bazzaz 1979). Similar evidence for such trade-off plasticity has been reported for other invasive trees and shrubs (Reinhart et al. 2006; Ridenour et al. 2006; Martin et al. 2010).

Herbivory frequency on *H. dulcis* seedlings did not differ between successional stages. Herbivory is highly context-dependent in natural landscapes, with a variety of biotic and abiotic factors modulating its incidence and intensity, including host plant density and life stages, existence and density of understory vegetation, and canopy openness (Lewis et al. 2006; Cipollini and Lieurance 2012; Giffard et al. 2012; Dostál et al. 2013; Biswas et al. 2014). However, the effects of environmental conditions on herbivory may be masked by spatial and temporal heterogeneity (Biswas et al. 2014). Further studies on herbivory and its importance for *H. dulcis* seedlings should include spatial and temporal heterogeneity to explain the observed patterns.

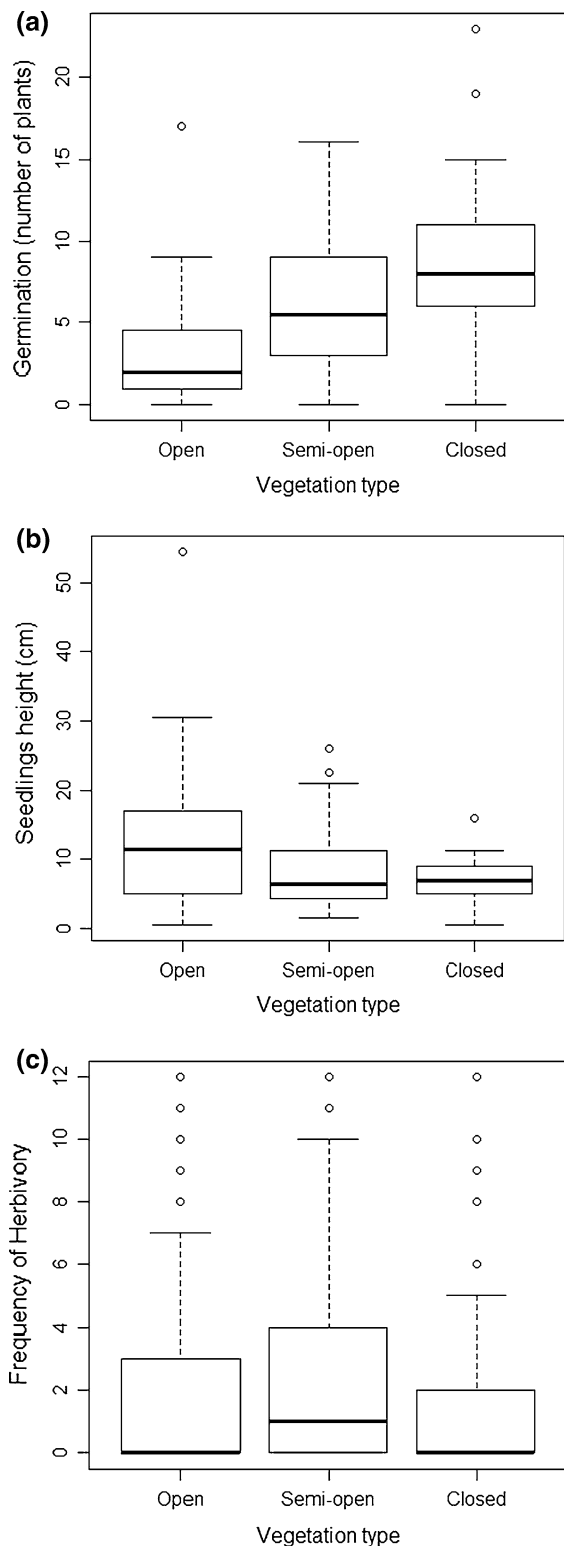


Fig. 2 Box-and-whisker plot for **a** seed germination, **b** seedling Δ height (cm), and **c** frequency of herbivory on *Hovenia dulcis* seedlings compared among seasonal deciduous forest vegetation types in the Fritz Plaumann State Park (Brazil). **Bold central lines** represent the median, **box line** limits the 25 and 75 % quartiles, whisker the quartiles ± 1.5 interquartile range. **Circles** are outliers

Herbivory was high considering the number of plants with herbivory vestiges during the experiment, especially in semi-open and closed vegetation. In our case, even though this highly invasive species escaped its native range herbivores, the enemy release hypothesis (identified by the absence of herbivory damage) seems to be inconsistent (Biswas et al. 2014). Conversely, *H. dulcis* has special structures and chemical defenses in the form of food bodies and secondary compounds likely to help repel herbivores (Kimura et al. 1981; Buono et al. 2008). Additionally, its seedlings resprout vigorously after injury by herbivores, which may reduce the relevance of any damage (Biswas et al. 2014). Further studies on interactions between ant species, herbivores, and *H. dulcis* plants will clarify the role of biotic interactions in invasion failure or success.

The results of this study show that both biotic and abiotic factors are important for explaining *H. dulcis* invasion. Whereas there is some degree of biotic resistance hindering the naturalization process, the abiotic conditions of the site facilitate the invasion. The intermediate forest succession stage, or semi-open vegetation type, combines the most favorable conditions for *H. dulcis* establishment, deeming it more invasible. Initial and advanced successional stages, however, should not be assumed resistant to invasion. Given that alien plant populations growth and propagule pressure increases outside or within such areas, invasions may well start or increase in any of the successional stages (Foster 2001; Duncan 2011). The prevalence of a natural disturbance regime in deciduous forests in southern Brazil can also directly influence *H. dulcis* invasion dynamics (Dechoum et al. 2014). Seasonal canopy openness forms small temporary gaps that may benefit *H. dulcis* regeneration and spread to non-invaded areas. Our results suggest that the most effective means of controlling *H. dulcis* in the study area would be to fell individual *H. dulcis* trees in closed and semi-open vegetation types, which would reduce propagule pressure, and persist with follow-ups

Table 3 Fixed effects of a generalized linear mixed model statistics for *Hovenia dulcis* seedling height in three vegetation types in the Fritz Plaumann State Park, Brazil

Variable	Estimate	SE	<i>t</i> value	<i>p</i>
Intercept (open vegetation type)	0.08964	0.01948	4.601	<0.0001
Semi-open vegetation type	0.04703	0.01559	3.017	0.002
Closed vegetation type	0.0742	0.0303	2.449	0.01

Significant *p* values are in bold

AIC 681.3

Table 4 Statistics for fixed effects of generalized linear mixed model for herbivory frequency on *Hovenia dulcis* seedlings transplanted to three vegetation types in the Fritz Plaumann State Park, Brazil

Variable	Estimate	SE	Z value	<i>p</i>
Intercept (open vegetation type)	0.6759	0.68215	0.99	0.3
Semi-open vegetation type	0.2295	0.40765	0.56	0.57
Closed vegetation type	0.0367	0.408	0.09	0.9

AIC 3439.9

to eliminate regeneration until the seed bank is exhausted. If *H. dulcis* invasions in seasonal deciduous forests are left unattended they will increase in area and severity, potentially causing negative impacts on the regional biodiversity.

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