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Research Article

Limited seed dispersal may explain differences in forest colonization by the Japanese raisin tree (*Hovenia dulcis* Thunb.), an invasive alien tree in Southern Brazil

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Abstract

In South American forests, the Japanese raisin tree (*Hovenia dulcis* Thunb.) is an invasive tree that produces capsuled fruits attached to peduncles that grow thick and fleshy when ripe. Several frugivorous birds are reported to be dispersal agents of *H. dulcis*. The spread of *H. dulcis* propagules to non-invaded sites was evaluated at a local spatial scale in deciduous forests in Southern Brazil, in order to propose management strategies to prevent the arrival of propagules of such species in non-invaded sites. Seed arrival via birds was assessed by five 0.6 x 0.6 m seed traps in each of the 10 x 10 m plots in non-invaded sites at different distances from invaded sites. Seed arrival was also compared between control plots and plots where all *H. dulcis* trees were felled within a 30m radius from the center of plots. A limitation in short distance seed dispersal by birds was observed in the study area. There was a negative exponential relationship between number of seeds and distance from *H. dulcis* trees to non-invaded sites, and a positive exponential dependence of the number of seeds found in seed traps on the basal area of *H. dulcis*. Felling *H. dulcis* trees was effective in reducing the arrival of seeds in non-invaded sites, resulting in significantly fewer seeds in managed plots than in control plots.

Keywords: colonization, propagule pressure, bird dispersal, management, control.

Resumo

A uva-do-Japão (*Hovenia dulcis* Thunb.) é uma espécie exótica invasora em florestas na América do Sul que produz infrutescências compostas por frutos secos aos quais estão presos pedúnculos que se tornam doces e carnosos quando maduros. Espécies de aves frugívoras são citadas como agentes dispersores de *H. dulcis*. A chegada de sementes de *H. dulcis* em sítios não-invadidos foi avaliada em escala espacial local em área de Floresta Estacional Decidual no sul do Brasil, com o intuito de propor estratégias de manejo para conter a colonização por *H. dulcis* nesses sítios. A chegada de sementes foi avaliada por meio de coletores de sementes instalados em sítios não-invadidos, localizados a diferentes distâncias de sítios invadidos. A chegada de sementes também foi comparada entre parcelas controle e parcelas submetidas ao corte de árvores de *H. dulcis* em um raio de 30 metros ao redor das mesmas. Detectou-se uma limitação na dispersão de sementes de *H. dulcis* por aves a curtas distâncias na área de estudo. Foi observada uma relação exponencial negativa entre o número de sementes e a distância de árvores de *H. dulcis* em sítios não-invadidos, enquanto uma relação exponencial positiva foi encontrada entre o número de sementes e a área basal das árvores amostradas. A eliminação de árvores de *H. dulcis* foi efetiva para reduzir a chegada de sementes em sítios não colonizados pela espécie, havendo um menor número de sementes em parcelas submetidas ao corte do que em parcelas controle.

Palavras-chave: colonização, pressão de propágulos, dispersão por aves, manejo, controle.

Introduction

Successful plant invasions involve appropriate biological traits of introduced species, characteristics of the communities where they arrive, local abiotic environments, and propagule pressure [1, 2]. Propagule pressure is an essential condition for the success of invasions at different scales [3, 4] and has two major components: the number of individuals released in each introduction effort, and the number of introduction events [4]. There is also a genetic component called propagule diversity, which refers to the number of genetically different source populations in a certain area [3]. The more intense the propagule pressure and the larger the genetic diversity of source populations, the larger the chance of establishment success of alien species [5].

Once a species has naturalized at a local scale, i.e., is capable of surviving and producing reproductive descendants in the new habitat [6], dispersal mechanisms will determine the magnitude and speed of propagule arrival onto new sites, which may influence invasion success [7]. Species with fleshy fruits, attractive to animal seed dispersers, are often considered potentially highly invasive [8-10] because vertebrate dispersal leads to rapid spread at different spatial scales, often increasing seed germination and seed deposition in sites favorable for seedling establishment [11-13].

Attracting frugivores to patches of invasive plants requires the local abundance of fruit, which may primarily depend upon density, size, age structure, and spatial distribution of invasive plants [14-16]. Characteristics such as fruit color, fruit or infructescence size, nutritional content, and pulp/seed ratio are also important determinants of frugivore attraction [17-20]. Different groups of animals may act as long- or short-distance dispersers of invasive species [7, 21]. While short-distance dispersal determines local population dynamics, long-distance dispersal induces the establishment of new populations and their connection in metapopulations [7]. In general, local dispersal fills the gaps left by the advance of new invasions (but also see Cousens et al. [22]). Understanding the growth patterns of existing patches and the distance and intensity of propagule arrival in different habitats is necessary to constrain the spread of invasive plants.

The Japanese raisin tree (*Hovenia dulcis* Thunb. - Rhamnaceae) is a deciduous tree species native to East Asia [23] and invasive in forests in South America and in Tanzania [24-26]. It is a fast growing pioneer species that reaches 10 to 25 meters in height and reproduces sexually by seeds [27]. It bears fruits between March and October in Brazil [27], with more intense fruiting in winter, between June and July. It produces dark brown, dry globular fruits measuring 6-7mm in diameter containing two to four seeds connected to brown peduncles rich in carbohydrates that become thick and fleshy when ripe [27, 28] (Fig. 1). Intact seeds are consumed both in its native range and in South American forests and dispersed over short and long distances in mammal feces [28-30]. In both regions, birds feed on the fleshy peduncles but do not swallow or carry the seeds long distances. The infructescences are in general carried short distances by the peduncles, so their transport and seed droppings are incidental [28, 30]. Forest dwelling birds *Trogon surrucura* (Southern surucua trogon), *Penelope obscura* (Dusky-legged guan), and *Pyroderus scutatus* (Red-ruffed fruitcrow) have been observed feeding on *H. dulcis* infructescences in tree crowns in the study area [30, 31]. The first of these bird species is quite common in forests in Southern Brazil and is adapted to anthropogenic disturbance; the other two species occur in more protected forests with higher density vegetation, their populations reduced due to hunting and deforestation [31, 32]. Ants can serve as secondary dispersers of *H. dulcis* [30].

Hovenia dulcis occurs in patches of different sizes in the study area, in a vegetation mosaic resulting from fragmentation caused by logging until the first half of the 20th century [33] (Fig. 1). While habitat fragmentation may create barriers to animal dispersal in some situations at a landscape scale [34], it may increase invasion rates in others [35]. Vegetation fragments may serve as stepping stones for frugivorous birds and, consequently, function as seed dispersal foci for invasive plants (sensu nascent foci [36]). In this study, our assumption was that the local spread of *H. dulcis* from invaded patches is mediated by frugivore birds that use the infructescences as a food source. The main objective of this study was to characterize the arrival of *H. dulcis* propagules in non-invaded sites from invaded patches at a local spatial scale. The specific objectives were to (1) compare the arrival of *H. dulcis* propagules by local bird seed dispersal in non-invaded sites with different vegetation types, establishing the relation of propagule pressure to age, distance, and abundance of potential seed sources; and (2) assess the effect of felling adult *H. dulcis* trees on propagule arrival in different vegetation types.
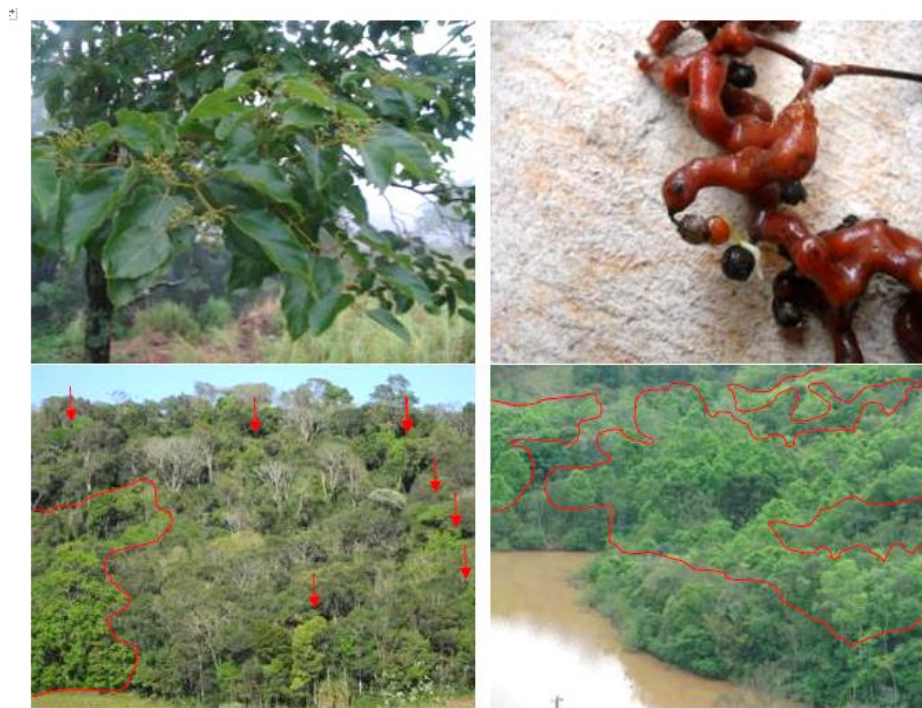

Fig. 1 Leaves, fruits and seeds of *Hovenia dulcis* populations in forest fragments in the Fritz Plaumann State Park, Brazil. The invasive species can be distinguished by the light green color of the crowns indicated by red arrows and by areas delimited by red lines (Credit: Michele de Sá Dechoum).

Methods

Study area

This study was carried out in remnants of seasonal deciduous forest in the Fritz Plaumann State Park, Santa Catarina, Brazil (27° 16'18" and 27° 18' 57" S, and 52° 04' 15" and 52° 10' 20" W) (Fig. 2), in Cfa (subtropical) climate according to the Köppen-Geiger classification system. The seasonal deciduous forest is now highly fragmented and reduced to 16% of its original area in Santa Catarina state, with 90% of the remnants smaller than 50 ha [37]. The park was established in 1998 and covers 740 hectares in the Atlantic forest domain, containing the threatened species *Ocotea odorifera* (Vell.) Rohwer (Lauraceae) (canela-sassafrás) [38]. The vegetation is currently composed of forest fragments in different successional stages, herein defined as "closed vegetation," interspersed with herbaceous-shrubby vegetation in early regeneration stages, herein defined as "open vegetation." The area was formerly occupied by rural properties used for agriculture, cattle ranching, and wood exploitation [33]. The vegetation has been regenerating since the park was established.

Fig. 2 Location of the Fritz Plaumann State Park, Santa Catarina state, southern Brazil [Source: 29].

Hovenia dulcis was introduced in the study region in the second half of the 20th Century [37], and intensively cultivated after the 1980s, when agroindustries in the region promoted its use in pig and chicken farms [39]. Since its introduction, *H. dulcis* has been extensively planted in rural properties for wood [39], shade for cultivation and pasture areas, hedges, and energy production [27].

Data collection
Sixty 10 x 10 m plots were set up in sites without *H. dulcis*, forty of them in closed vegetation, and twenty in open vegetation. A minimum distance of 100 meters was kept between plots. The number of plots set up in open and closed vegetation was different because the closed vegetation forest fragments are the main vegetation types in the area, covering about 65% of the park surface [31]. All *H. dulcis* trees with diameter at breast height (DBH) over 5 cm located outside the plots in a 30 meter radius from the central points of each plot were marked, measured, and their heights estimated. These trees were considered potentially reproductive adults [27]. The distance from each tree to the center of the plot was measured, and the surrounding vegetation was classified as open or closed.

Five 0.6 x 0.6 m seed traps were set up in each plot 0.5 m above the ground, one in the center and the other four 2.5m from each corner towards the center. The number of trees functioning as perch poles was counted inside each plot. All trees higher than four meters with at least one branch were considered potential perch poles for birds. The material accumulated in the seed traps was collected every fortnight during the species fruiting period (May to September, 2012), and the *H. dulcis* seeds were counted.

In October 2012 the adult *H. dulcis* trees located within a 30 meter radius of 50% of the plots in each vegetation type were felled. These plots were selected at random. Between May and September 2013 the collection of seeds was repeated in all the plots (managed and not managed). The age of the felled trees was determined from the growth rings, generating data that were used to estimate the age of the remaining trees in the plots.

Data analysis
In order to relate propagule arrival to *H. dulcis* tree abundance, distance and age, the age of trees had to be estimated. Regression equations generated from the data from the 506 trees felled in October 2012 were used to estimate the age of the remaining *H. dulcis* trees using Biostat 5.0 software [40]. The equations that best described the correlations were: $y = 0.24 + 2.36\ln(x)$ ($R^2 = 58.4$) for trees growing in open vegetation, and $y = 4.01x^{0.26}$ ($R^2 = 62.5$) for trees in closed vegetation, where y equals age and x is basal area. Propagule arrival was estimated by the potential seed rain index (PSRI), which is a single parameter calculated in order to estimate propagule production and arrival in non-invaded sites. The formula $\sum(BA/d^2)$ was used to estimate PSRI, in which BA stands for basal area, and d is the distance in meters from the plot center to each mature tree in a 30 meter radius (modified from Rejmánek et al. [41]). This calculation was made for the years 2012 and 2013 for each vegetation type (open and closed).

Differences in the mean number of *H. dulcis* trees in 2012, as well as the mean basal area, age and height of plants sampled in the 30 meter radius around open and closed vegetation sites were compared via t tests with permutation (5000 iterations; [42]) because the distribution of data was not normal and did not result in homogeneity of variance. The mean distance between each tree and the center of the respective plot, the mean PSRI values and the number of perch trees in 2012 were compared between closed and open vegetation sites using the same test. Frequency histograms were constructed using the age data from sampled trees for comparison between those growing in open and closed vegetation. These histograms were based on five 8-year interval age classes, where the first

class was comprised of trees that started to grow after the Park was established (between six and 14 years) when logging was no long occurring in the forest .

The numbers of seeds collected in the five seed traps in each plot were added up for all the field visits made in each year, resulting in the total number of seeds per plot per year (2012 and 2013). One plot where branches of an *H. dulcis* tree were found hanging over the seed trap was excluded from the analysis. The number of seeds found in closed vegetation in 2012 was used to assess the relation between propagule arrival in sites where *H. dulcis* was not present (response variable) and three explanatory variables: PSRI in each plot, total number of perch poles in each plot, and mean age of *H. dulcis* trees sampled in a 30 meter radius around the plots. The analysis was carried out only for closed vegetation, as no seeds were found in the traps set up in the open vegetation plots (see Results). A collinearity analysis among the variables was performed *a priori* using variance inflation factors (VIF). However, no variable was excluded, as all VIF values were lower than three, indicating no collinearity among variables [43]. A generalized linear model (GLM) was used assuming the Poisson distribution for the number of seeds and the log link function for the relationship between seed number and explanatory variables. The inclusion or exclusion of variables was based on AIC (Akaike´s Information Criterion) values calculated using maximum likelihood. As data overdispersion was detected (overdispersion = variance > mean in response variable), a correction of standard errors was made using a quasi-GLM model in which variance is the result of $f \times \mu$, where f is the dispersion parameter, and μ the mean [44]. The estimate of the dispersion parameter f was 9.59, which led to all standard errors being multiplied by 3.1 (the square root of 9.59).

To assess the effect of *H. dulcis* felling, we compared the total number of collected seeds between managed and unmanaged plots in closed vegetation. The analysis used generalized linear mixed modeling (GLMM) assuming the Poisson distribution for the number of seeds and the log link function for the relationship between seed number and explanatory variables. The variables year (2012 or 2013), treatment (control or felling), and the interaction between year and treatment were considered fixed effects, while the plots were repeatedly measured replicates and therefore considered random effects. All statistical analyses and figures were produced with R software [45], using the lmPerm package for parametric tests with permutation, the lme4 package for GLM and GLMM, and the Sciplot package for the bar plots.

Results

A total of 1,169 *H. dulcis* trees was recorded around the plots, 383 in closed vegetation, and 786 in open vegetation. *Hovenia dulcis* was absent in the 30 m radius area of eight plots, six of them in closed vegetation, and two in open vegetation. The age range in closed vegetation varied from six to 44 years, with about 39% (n=306) of the plants in the first age class (6 to 14 years), and 40% (n=320) in the second age class (> 14 to 22 years) (Fig. 3a). In open vegetation, 78% (n=299) of the trees were in the first age class, while the age range varied between six and 37 years (Fig. 3b). Of all sampled trees, 43.3% (506) were felled near plots selected for management, with 422 (83.4%) near plots in closed vegetation, and 84 (17.6%) near plots in open vegetation.

In 2012, average height (t=3.6, df=32.6, p=0.001), average basal area (t=3, df=42.3, p=0.004), and average age (t=6.1, df=47.1, p<0.0001) of *H. dulcis* trees were higher around closed vegetation plots than in open vegetation (Fig. 4).The number of perch poles (t=2.4, df=43.5, p=0.01) and PSRI (t=2.8, df=40.8, p=0.007) were also higher in closed vegetation (Fig. 4). Only average distance (t=-0.9, df=35.4, p=0.4) and average density (t=0.3, df=44.6, p=0.8) of *H. dulcis* trees did not differ between vegetation types (Fig. 4). A reduction in value of the parameters evaluated in 2013 was observed due to the felling of *H. dulcis* trees in 50% of the plots in each vegetation type (Fig. 4).
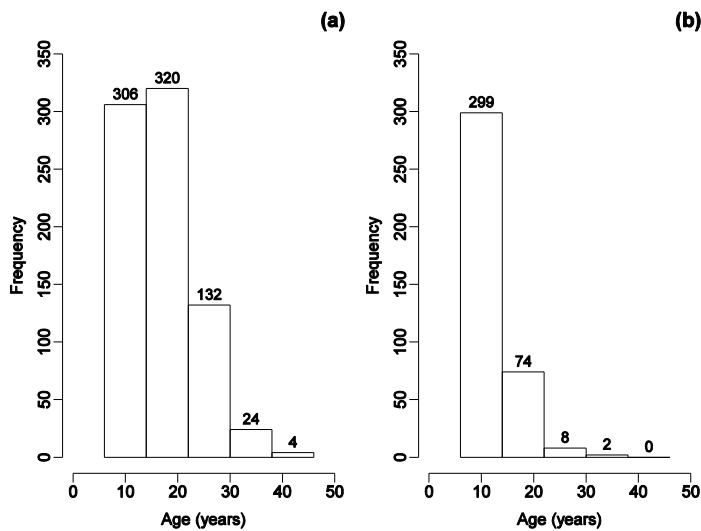
Fig. 3 Age frequency histograms of *Hovenia dulcis* trees sampled within a 30 meter radius around plots in closed vegetation (a) (n=985) and in open vegetation (b) (n=184) in the Fritz Plaumann State Park, Brazil. The numbers above the bars refer to the number of plants in each age class. Age classes (years): (1) 6 - 14; (2) >14 - 22; (3) >22 - 30; (4) >30 - 38; (5) >38 - 46.
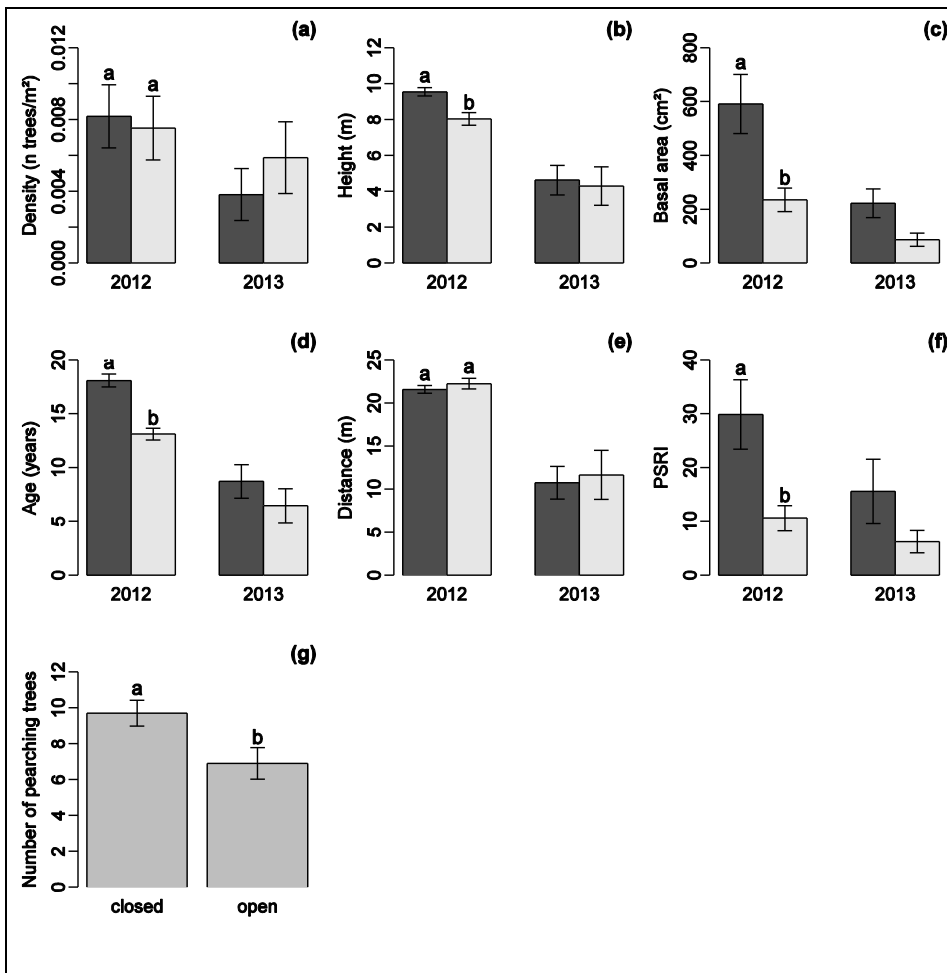

Fig. 4 Parameters evaluated in plots (n=60) set up in closed vegetation (dark bars) and open vegetation sites (light bars) in the Fritz Plaumann State Park, Brazil, in 2012 and in 2013. Average density (a), height (b), basal area (c), and age (d) (± standard deviation) refer to *Hovenia dulcis* trees present in a 30 m radius around plots. Distance (e) = average distance of *H. dulcis* trees around plots. PSRI (f) - *potential seed rain index* = $\sum (BA/d^2)$, where BA stands for basal area, and d stands for distance from the center of a plot to a mature tree, in meters, within a 30 m radius. Perch poles (g) indicate the average number of woody plants with a minimum height of four meters and at least one stem bifurcation. The 2013 data refer to the same plots after the felling of *H. dulcis* trees around 50% of the plots (n=30 plots). The number of perch poles (g) was compared between closed and open vegetation in 2012 only. Parameters represented by bars with different symbols differed between closed and open vegetation types in 2012.

No seeds accumulated in the seed traps in open vegetation in 2012 or in 2013. The numbers of seeds collected in closed vegetation did not differ between control and (pre) felling plots in 2012 (Z=0.97, p=0.33), but were different between seed collection years (Z=21.2, p<0.0001) and between control and felling plots in 2013 (Z=-7.5, p<0.0001) (Tables 1 and 2).

Table 1. Numbers of seeds found in plots (n=40) in closed vegetation sites in the Fritz Plaumann State Park, Brazil, in 2012 and in 2013. Seeds were collected before and after felling *Hovenia dulcis* trees in a 30 meter radius around half the plots. Felling = plots where *H. dulcis* trees were cut down in a 30 meter radius after seed trap monitoring in 2012; No felling = plots in which *H. dulcis* trees were not cut down after seed trap monitoring in 2012.

	2012		2013	
	Felling	No felling	Felling	No felling
Number of plots with seeds	2	6	1	7
Number of traps with seeds	4	9	2	18
Number of seeds	11	44	2	1268

Table 2. Statistics for the models analyzed for differences in number of seeds of *Hovenia dulcis* between 2012 and 2013, and between control and felling plots in closed vegetation sites in the Fritz Plaumann State Park, Brazil.

Fixed effects	Estimate	Standard error	Z value	df	p
Intercept	-9.211	1.8871	-4.881		<0.0001
Control x felling 2012	2.0059	2.067	0.97	1	0.332
2012 x 2013	3.5327	0.1668	21.181	1	<0.0001
Control x felling 2013	-5.7299	0.7638	-7.502	1	<0.0001

PSRI showed a significant effect of the number of seeds collected in closed vegetation sites in 2012 (*Explained deviance*=19.86, p<0.0001) (Fig. 5, Table 3). The variables "perch poles" and "age" were stepwise excluded as they were not significant (p>0.05). The distribution of the number of seeds is best represented by the exponential function in relation to PSRI, which minimizes variance dispersion (Fig. 5).

Table 3. Statistics of the model analyzed for number of seeds of *Hovenia dulcis* in seed traps (response) and potential seed rain index (PSRI) (factor) in closed vegetation in the Fritz Plaumann State Park, Brazil. PSRI - *potential seed rain index* = $\sum (BA/d^2)$, where **BA** stands for basal area, and **d** stands for distance from the center of a plot to a mature tree, in meters, within a 30 m radius.

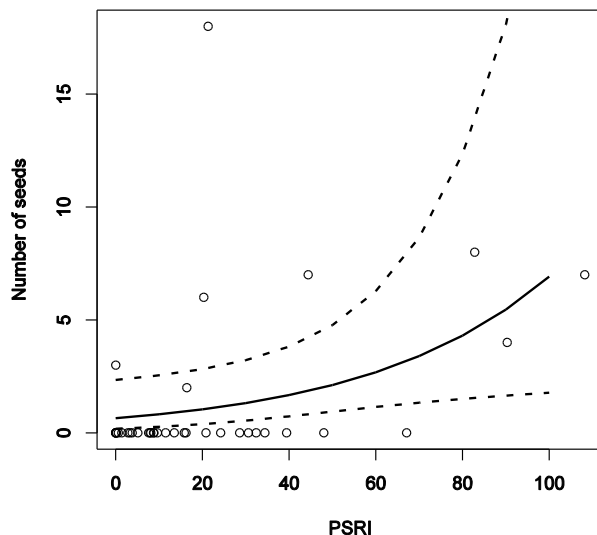| Parameter	Estimate	Standard error	t value	df	p
Intercept	-0.43514	0.65648	-0.0663	38	0.51
PSRI	0.02369	0.0165	2.223	37	0.0324

Fig. 5 Relationship between seed number and potential seed rain index (PSRI) of *Hovenia dulcis* in closed vegetation sites in the Fritz Plaumann State Park, Brazil, in 2012. PSRI - *potential seed rain index*=∑ (BA/d²), where BA stands for basal area, and d stands for the distance from the center of each plot to a mature tree, in meters, in a 30 meter radius around plots. Full line = model prediction; dotted lines = confidence intervals (±1.96 standard error).

Discussion

Dispersal of *H. dulcis* seems to be relatively rare at the local scale in the study area. This limitation seems to occur both in open vegetation, where no seeds accumulated in the seed traps, and in closed vegetation, where the numbers of seed traps with seeds as well as the numbers of seeds found in the traps were low in relation to the sampling effort (the maximum number of seed traps with seeds was 18, equivalent to 6% of the 300 seed traps set up in the area) and to the number of fruits produced per plant in the study site (which varied between 22.2 and 40.2 fruits/tree/month/m² crown projection - [30]). Limited seed dispersal of exotic woody plants at similar scales was observed in several other studies [46-49].

A lower frequency of bird visitation in the open vegetation type may be one cause of limited seed dispersal in this habitat. Patches of *H. dulcis* trees in the open vegetation were formed by smaller (smaller basal area and height) and younger plants than in the sites with closed vegetation. Considering the positive relationship between basal area and age found in this study (age = f[basal area] function presented in Material and Methods), and positive correlation between fecundity and basal area, height, and age, it is certain that younger and smaller plants produce fewer fruits than older and larger trees [50-52]. Lower fruit yield likely leads to lower bird attraction for foraging, reducing the amount of consumed fruit and seed dispersal, as demonstrated by Amodeo and Zalba [16].

According to Deckers and collaborators [53], landscape structures acting as perches seem to especially promote dispersal by frugivorous birds. The perch pole effect may be defined as the increase of seed deposition under perch trees or under structures serving as perches for birds [12, 54], which are of fundamental importance for invasive species dispersal [55]. A smaller number of perch poles in open vegetation plots may cause birds to use these areas less than closed vegetation sites [49, 53], reducing seed arrival. However, in our study, perch poles did not seem to be an important predictor variable of seed numbers arriving in closed vegetation sites.

It is important that our study considered the primary short distance dispersal of *H. dulcis* seeds by frugivorous birds in order to explain spread from already established patches. However, we stress that apart from birds, *H. dulcis* is also dispersed by terrestrial mammals such as *Cerdocyon thous* [30]. *Cerdocyon thous* (Crab-eating fox) is generally recognized as an efficient seed dispersal agent as it feeds on large quantities of seed and is capable of covering long distances even in heterogeneous landscapes [56]. Seeds of *H. dulcis* were also observed in *Atta sexdens* ant nests [30]. Although frequently ignored, secondary dispersal of seeds may greatly affect seed shadow and dispersal distances [14]. Secondary

dispersal by ants, for example, may result in seeds displaced to sites with higher light intensity, rich in nutrients and protected from predators [57], expanding existing foci. Understanding the relevance of secondary dispersal to invasion is essential, therefore, to selection of management strategies for the invasive species under study.

The presence of plants younger than ten years old in closed vegetation is evidence that the species is regenerating in the study area [58]. This result was unexpected, given that the species is considered a pioneer [27] and may be an indicator of shade tolerance in the seedling stage [58], as already demonstrated for other invasive plants [59-60]. Seed germination may occur in winter, when more light reaches the forest floor due to leaf loss by deciduous trees and *H. dulcis* reaches the peak of fruit production. Studies on seed viability in the soil and shade tolerance in the seedling establishment phase can provide complementary information about possible invasion opportunity associated with deciduous forests, and consequently, for prioritizing control efforts.

In closed vegetation areas the variable that best explained the numbers of *H. dulcis* seeds was PSRI, with a positive exponential relation between variables. The graphic representation of this relationship (Fig. 5) is very similar to the exponential curve proposed in the theoretical model describing the dose-response relationship between propagule pressure and establishment probability of introduced species [61]. In this theoretical model, the exponential relationship means that the saturation value of propagule pressure that would result in maximum establishment success for the species has not yet been reached, so management efforts to reduce the arrival of the species propagules may be beneficial [3]. Following a logic similar to the dose-response model [61], management strategies may be directed at keeping PSRI lower than 60 before the dramatic increase in propagule production following this value. This could be achieved by removing the trees with largest basal area from the borders of invaded patches. Outlying isolated trees or low density patches of invasive trees must be a primary target of management [36, 62, 63], because isolated trees are usually more fertile than trees in patches [52]. In this management strategy for reducing or containing invasion [64], habitat heterogeneity must also be considered for defining priority sites for control, and control efforts must primarily target higher invasion-prone sites [63], such as those characterized by semi-open vegetation.

Implications for conservation

Even at a small scale, short distance bird dispersal may facilitate the establishment of *H. dulcis* in closed vegetation sites. Felling adult *H. dulcis* trees in a 30-meter radius around non-invaded closed vegetation sites was sufficient to substantially reduce the arrival of seed in these areas. Therefore, we recommend that a minimum distance of 30 meters from forest fragment borders should be considered a priority for elimination of *H. dulcis* individuals, as well as continuous monitoring and control activities to reduce the intensity of seed arrival in protected areas and in other sites of high conservation value. This should prevent, or at least slow, the establishment of new invasion foci or the aggravation of already existing invasions (Fig. 1). We recommend that pioneer, deciduous and fast-growing native species should be used in restoration efforts following removal of the invasive species, in order to outcompete *H. dulcis* [58].

Acknowledgements

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