

Forest fragmentation does not matter to invasions by *Hovenia dulcis*

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Abstract Testing whether biological invasions can be facilitated by habitat fragmentation can provide important insights for the study of invasion ecology. *Hovenia dulcis* is considered an aggressive non-native species in subtropical Atlantic forest ecosystems and following the assumptions of invasion ecology we hypothesized it would occur mainly in smaller forest remnants, which are more susceptible to edge effects compared to larger ones. In this study, we verified the relationships between *H. dulcis* invasion on forest remnants and the current habitat fragmentation and tested whether both occurrence and abundance of this species are driven by landscape and habitat variables. We selected 30 forest fragments in initial, middle or late successional stages and verified the occurrence and abundance of trees and saplings of *H. dulcis*. We evaluated spatial autocorrelation and the influence of landscape and habitat metrics on occurrence and abundance of such species and the influence of fruiting trees (adults) on the abundance of non-adult individuals. We found that *H. dulcis* distribution was not related to geographic distance among remnants. The occurrence of adult *H. dulcis* was directly associated to closed-canopy areas and remnant shape and, contrary our initial hypothesis, not related to remnant size. The occurrence of adult trees increased *H. dulcis* regeneration leading to higher sapling abundance. High abundance of *H. dulcis* saplings close to adult trees pointed out the successful colonization of recently invaded Atlantic forest remnants. We showed that this invasive tree species successfully invades closed-canopy forest fragments, which highlight

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undisturbed subtropical Atlantic forest habitats are as susceptible to biological invasions as disturbed ones.

Keywords Biological invasions · Canopy coverage · Habitat fragmentation · Landscape ecology

Introduction

Forest fragmentation is frequently associated with pervasive changes in natural assemblages (Fischer and Lindenmayer 2007) mainly by creating edges exposed to non-forested habitats that lead to changes on microclimate, forest structure, biotic composition and ecological functions that, at landscape scale, achieves to reduction of forest cover and subsequent isolation of forest remnants (Kupfer et al. 2006). Species response to such changes, including the invasion by alien plants, are a function of the edge effect, amount of lost area, size of remaining forest and the synergisms among remaining forest patches (Arroyo-Rodríguez et al. 2013).

By intentional or accidental transport of organisms to areas outside their potential ranges, human activity promotes biological invasions (Richardson 2011) and, notwithstanding, the potential of alien species in becoming invasive ones directly links their ability to survive, establish, reproduce, disperse, spread, proliferate and interact with resident biota (Richardson and Pyšek 2012). In a synergic perspective, habitat fragmentation may generate clear opportunities to facilitate the invasiveness of alien species by allowing them to assume the functions of locally extinct native species on ecological processes (Fuentes-Ramírez et al. 2011).

Invasion by alien species may also be enhanced by traits as the ability to thrive under abundant light conditions, prolific seed production and efficient seed dispersal, resulting in initial establishment along edges and a following expansion toward fragment cores (Decker et al. 2012). This process may culminate in dramatic outcomes where non-native species alter entire landscape structures and ecosystem functioning by completely dominating local communities (With 2002). As most of invasive plants originate from intentional introductions and show early-successional life-history traits that achieve them to colonize areas following disturbance, their capability to colonize only disturbed areas may be overstated (Martin et al. 2009).

By reviewing the role of mutualisms that potentially increase or decrease invasion, Richardson et al. (2000) pointed out that interactions involving animal-mediated pollination and seed dispersal are often non-specific, reflecting the diffuse nature of many mutualisms. On this way, invader species may be benefited by the novel interactive range, with deep implications for the behavior of the introduced plants and the synergy with the new habitat. For example, recent studies revealed that the notion of closed-canopy forests resistance to invasion based on the common low shade tolerance of alien plants may be inaccurate (Martin et al. 2009; Essl et al. 2011; Godoy et al. 2011; Essl et al. 2012). Therefore, resistance to invasion in intact systems might fall primarily to the competition strength of native species (e.g. Martin and Marks 2006; Martin et al. 2009) which suggests that plant as well as recipient community traits are important to assess invasive threat (Martin and Marks 2006).

Southern subtropical Atlantic forests show a well documented historic of land cover changes throughout the 20th century due to human occupation, which lead to intense habitat lost and fragmentation. At the landscape level, forest remnants are often distributed in patches surrounded by crop production or urban matrix, with larger forest patches located at inaccessible high declivous sites (Decian et al. 2011). These negative trends are expect to reduce biodiversity and may lead to an opportunity to colonization by alien plants. In this study, we aimed to assess the establishment capability and invasiveness of the alien *Hovenia dulcis* in a landscape with intense habitat fragmentation in southern Brazil. Our assessment focused on the features of the landscape matrix, forest remnants distance and connectivity related to surround land use and to community structure. Features of community structure were associated to canopy openness on adult occurrence and sapling regeneration. To achieve these goals, we postulate the following questions: is *H. dulcis* clustered on spatially adjacent forest fragments? Does open canopy environments facilitate *H. dulcis* invasion? Do landscape metrics of connectivity and permeability interact in any extension to invasion of forest fragments? We hypothesize that *H. dulcis* will be clustered on spatially close fragments due to limitations of propagule source. With this prediction, saplings would be found near adult trees. Furthermore, we expect higher canopy openness should facilitate the invasion due to higher resource availability and lower competition with native species. Moreover, small, irregularly shaped fragments surrounded by an agricultural matrix should be more susceptible to *H. dulcis* colonization.

Methods

Species description

The Oriental Raisin Tree, *H. dulcis* (Rhamnaceae) is classified as extremely invasive on moist forest ecosystems (Zenni and Ziller 2011) including subtropical Atlantic forests from southern Brazil where it was initially planted in small agricultural settlements. Adult trees reach 10–15 m height and 20–40 cm mean trunk diameter at breast height (DBH) being capable to reach as high as 25 m and 50 cm DBH (Lorenzi et al. 2003). It has a cylindrical, straight trunk, with a shaft reaching up to 8 m height, branching at the top into a broad, globe shaped crown. It has been classified as rustic, fast growing species and even though exotic, its usage for recovering of disturbed areas and landscaping is being encouraged (Carvalho 1994).

It has intense leaf fall from April to August (Carvalho 1994) and hermaphrodite flowers starting blooming, in Brazil, from August to February (Lorenzi et al. 2003), which produces large quantities of small, palatable pseudo-fruits containing two-four seeds each, from March to October (Carvalho 1994). These fruits are highly sought by birds and small mammals (Hirsch 2011).

Study site

The study was conducted in Alto Uruguai region, Southern Brazil, in a drainage basin with 2121 ha at the coordinates 27°39'38.3"–27°42'48.6"S and 52°14'15.7"–52°17'48.6"W (Fig. 1). The region has humid subtropical climate–Cfa, according to the Köppen classification system. However, local climate analysis suggest a transition between humid

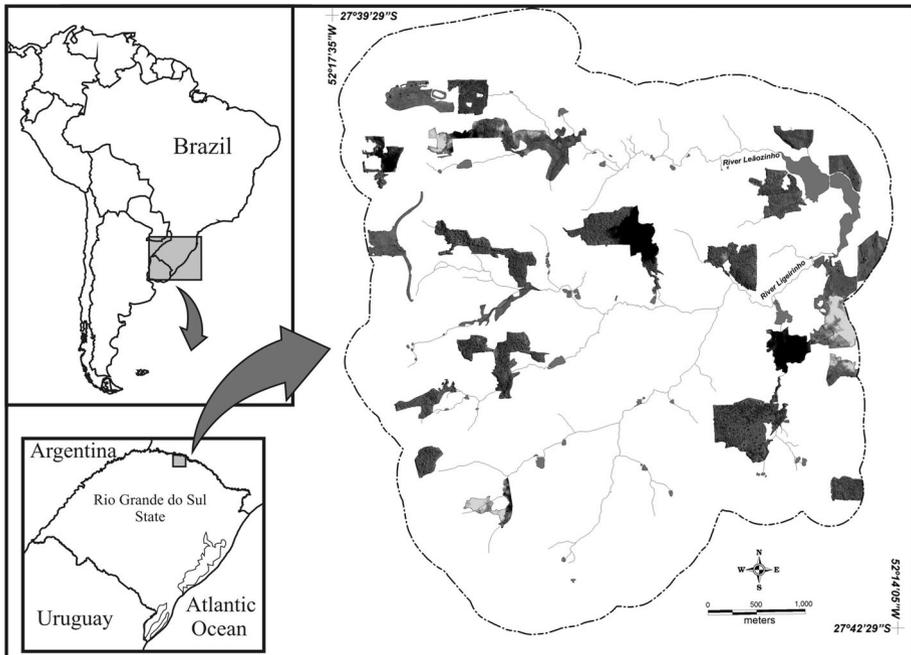


Fig. 1 Landscape including Atlantic forest remnants where *Hovenia dulcis* occurrence and abundance was surveyed. Northern Rio Grande do Sul state, southern Brazil. *Gray-scale* indicates direct satellite imagery, including initial, middle and late successional forest remnants (late successional stages toward more *shadowed areas*) and water surface (*linear gray patches*)

subtropical climate and maritime temperate climate, with mean annual temperature of 17.6 °C and mean annual precipitation of 1912.3 mm (Bernardi and Budke 2010).

The study area spreads in the Atlantic Forest vegetation domain (Oliveira-Filho et al. 2013) and contains species from Atlantic evergreen seasonal *Araucaria* forests to Atlantic semideciduous seasonal forests (Budke et al. 2010). Natural vegetation in the area has been reduced to island-like forest fragments of varying sizes and shapes surrounded mainly by agricultural matrix (Decian et al. 2011).

Map preparation and patch selection

We prepared the land use chart of the study area with a *Quick Bird* satellite image with spatial resolution of 0.6 m dated from February 2010 using the IDRISI *Andes* software to identify each different land use in the landscape. Some of these areas were randomly chosen to be verified in the field for accuracy. We found 567 unconnected forest fragments in the landscape that, after mapped, were classified into initial, middle or late successional stages. Such classes merged from distinct features of color intensity, roughness and canopy properties assessed by IDRISI *Andes* and orbital images (Decian et al. 2011). We then selected the largest ten fragments in each successional stage for population sampling, which totaled 30 replicates.

Landscape variables

Geographic distance (kilometers) among remnants were calculated by using the coordinates of the central point of each fragment, allowing to achieve vectors that contained the distances of each pair of points.

We obtained remnant size (RSi) by measuring their areas with the previous land use chart with the *area calculator tool* in Fragstats 3.3 (McGarigal and Marks 1995). Remnant shape (RSh) was calculated using a circularity index, which compares the current shape of each forest fragment in relation to a circle using an area-perimeter ratio whose values range from zero (most irregular, with thin sections) to one (perfectly circular). We classified the land use surrounding each fragment as the most abundant kind of use in the area immediately adjoined to the remnant. Land uses included urbanized, agricultural cover, forest native remnants or tree plantations (Decian et al. 2011) (see Table 2).

Environmental and population variables

We plotted 20 randomly rectangular plots (15×1.5 m) within each fragment and once we found an adult of *H. dulcis* (fruiting tree) in these plots, we set a circular plot (3 m radius) centered in the adult tree. In these plots, both rectangular and circular, we measured total height and DBH of all *H. dulcis* individuals and grouped them as adult (presence of fruiting traces) or non-adults (regenerative juveniles and/or saplings). In each plot we collected canopy coverage (CC) values (as a proxy of light availability) using a convex densitometer (Brown et al. 2000) in which values range from 0 (completely open areas) to 1 (fully closed canopy). Light availability in each fragment was then averaged from all readings taken in the respective plots.

Data analysis

We used Mantel tests to assess whether occurrence and abundance of *H. dulcis* were related to geographic distance among remnants and thus, spatially autocorrelated. For these tests we used three distinct Euclidean distance matrices. One contained the geographic distance among fragments, the second one contained *H. dulcis* presence–absence (occurrence) and the third one contained the abundance of *H. dulcis* in each fragment.

We applied generalized linear models (GLM) to verify the relative importance of the landscape variables (adjoined land use, fragment size and shape) and environmental variables (plant successional stage and CC, plus occurrence of adults of *H. dulcis*—OAt in the tests with abundance data) for occurrence and abundance of *H. dulcis*. Models to test for the effects of the explanatory variables on occurrence used binomial family distribution and models to test the effects of the explanatory variables on abundance used Poisson family distributions (Bolker et al. 2009). We removed all fragments with no individuals of *H. dulcis* from the abundance model and transformed abundance values to natural logarithms to compensate higher abundance fluctuations. We used saturated models at first, including all variables which were then simplified by removing non significant variables, considering a 5 % significance threshold, until the best model was obtained (lowest AICc value). We carried out all the analyses in R version 3.0.2 (R Development Core Team 2013).

Results

Population, landscape and environmental features

We found 2551 *H. dulcis* individuals within approximately 50 % (14 out of 30) forest fragments (see Table 2). If we consider only those fragments where we found *H. dulcis*, the mean number of individuals per fragment was approximately 182 ± 365 individuals. Of those, 21 were adults and 2530 were non-adults (juvenile trees and/or saplings). The land use adjoined to the fragments was mainly agricultural (83 %). Overall, fragments varied from thin linear sections to almost circular shapes with index values ranging from 0.06 to 0.75 (mean = 0.29 ± 0.18) and had a variation of size that ranged from 0.1 to 31.3 ha^{-1} (mean = 8.3 ± 6.9) (Table 2). Inside the fragments, CC varied from open to highly covered areas with the means for CC index values ranging from 0.07 to 0.93 (mean = 0.65 ± 0.24) (Table 2).

Spatial relationships

The geographic distance among remnants ranged from 0.1 e 11 km (mean = 2.8 km). We found that both occurrence and abundance of *H. dulcis* were not dependent of the presence of individuals on nearby fragments (*Mantel test* $r = 0.09$, $p = 0.05$; $r = 0.05$, $p = 0.27$ for *H. dulcis* occurrence and abundance respectively).

Environmental and biotic filtering

The best model for *H. dulcis* occurrence was explained by CC and RSh (Table 1). In this case, CC has a significative effect on *H. dulcis* occurrence ($z = 2.12$, $p = 0.03$) and RSh

Table 1 Deviance analyses of the generalized linear models (GLMs) to evaluate the effects of occurrence of adult trees (OAt), canopy coverage (CC), remnant shape (RSh) and remnant size (RSi) (simplified models) on the occurrence and abundance of *H. dulcis*

Occurrence model	Variables	z value	Pr ($> z $)	AICc	Abundance model	Variables	z value	Pr ($> z $)	AICc
Initial	CC	2.27	0.02	34.45	Initial	OAt	3.32	<0.01	55.70
	RSh	-1.93	0.05			CC	1.16	0.24	
	RSi	-0.86	0.38			RSh	-0.11	0.90	
One step	CC	2.12	0.03	32.69	One step	RSi	1.38	0.16	53.72
	RSh	1.45	0.14			OAt	3.56	<0.01	
Interaction added	CC:RSh	-1.71	0.08	32.69		CC	1.17	0.24	
Two steps	CC	2.23	0.02	33.31	Two steps	Rsi	1.37	0.16	53.72
	RSh	-1.8	0.07			OAt	3.42	<0.01	
Three steps	CC	3.42	2.26	35.15	Three steps	Rsi	1.78	0.07	53.06
						OAt	3.26	<0.01	

Occurrence model used binomial family distribution and abundance model used Poisson distribution family

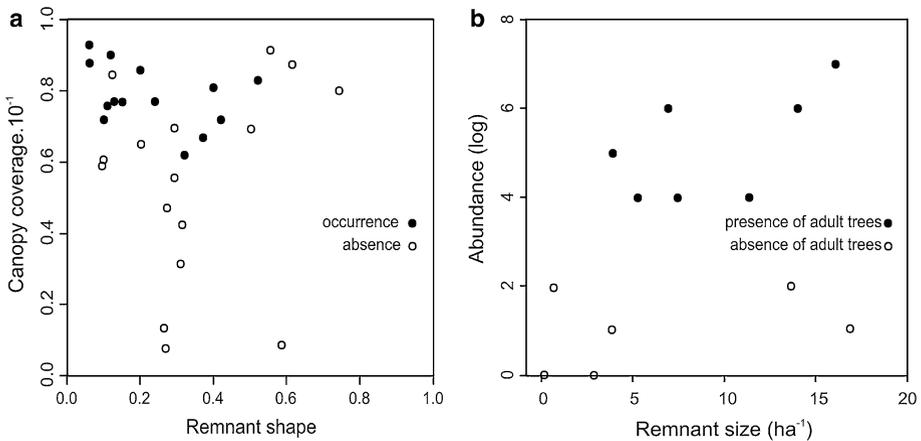


Fig. 2 Relationships between remnant shape and canopy coverage on the occurrence of *Hovenia dulcis* (a); relationships between presence and absence of adult *H. dulcis* trees and remnant size on the overall abundance of *Hovenia dulcis* (b) in forest remnants from a subtropical Atlantic forest landscape

had a marginal effect on *H. dulcis* occurrence ($z = 1.45$, $p = 0.14$) (Table 1). On the other hand, when added an interactive variable combining both CC and RSh, it provided a marginal effect on *H. dulcis* occurrence. The species only occurred in fragments with at least 62 % of CC and showing lower RSh (Fig. 2). To abundance, the best model included the occurrence of adult *H. dulcis* trees (OAt) in the fragment, which has a significant effect on *H. dulcis* abundance ($z = 3.42$, $p < 0.01$) (Fig. 2). The final model also included RSi, which did not have a direct significant effect on *H. dulcis* abundance ($z = 1.78$, $p = 0.07$) but whose removal resulted in a poorer model overall (three steps, Table 1).

Discussion

Considering fragment size, sampled area inside each fragment and lack of evident propagule sources along the study area, the mean number of individuals of *H. dulcis* found at each fragment is remarkable, specially the abundance of juvenile and saplings, which accounted for more than 99 % of total sampled plants. The invasion rate in the area is interesting as well, with occurrence of at least one young individual on 50 % of sampled remnants. As we argued, these results are indicators of the invasion capability of *H. dulcis* at landscape scale and potentially on other fragmented habitats within the same climatic and edaphic conditions.

According to the dispersal limitation (spatial pattern of seed rain, see Terborgh et al. 2011) we expect at landscape level that *H. dulcis* should occur more frequently on fragments spatially closer to ones where adult, fruiting individuals occurred and to less extent on more distant ones. Instead, the lack of any spatial autocorrelation for both abundance and occurrence of *H. dulcis* indicates that the species arrival on fragments may not depend on spatial proximity to potential seed sources. The effect of seed dispersal capability is known to have important influence on spatial patterns of species on multiple scales (Réjou-Méchain et al. 2011). The possible effect of a propagule source outside the sampled area but close to fragments that could have biased these results is rejected in this study because

only one fragment was located near built areas with constant human activities, which were not considered a propagule source.

Most of invasive species are initially introduced by humans (Davis 2005; Richardson and Pyšek 2008). Thus, anthropogenic land uses such as agriculture are commonly associated with propagule sources mainly by cultivation of alien species (Pauchard and Alaback 2004; Essl et al. 2012). However, even though the majority of land use around in the area was agricultural we only observed one site with fewer than 10 individuals clearly planted. On this way, strong influence of direct human introduction was discarded. Also, the land use near remnants had the lowest importance in our models and seems not to be an important factor to explain *H. dulcis* abundance on these forest remnants. Inside the fragments, only a few proportion had recent disturbance and not sufficient to replace the native forest. We can assume then, *H. dulcis* is entering in natural assemblages and potentially competing for resources with native tree species.

Light availability has been pointed out to promote increased growth and abundance of *H. dulcis* (Selle et al. 2010) and is a general indicator of disturbance related to invasions. Open areas could facilitate the arrival of seeds (Pauchard and Alaback 2004) and their establishment for light-demanding plants (Davis et al. 2000). The edge of forest fragments can also contribute to higher exposures to diffuse sunlight (Laurance et al. 2011) mainly on smaller fragments, where edge effect is proportionally higher (Metzger 2000). As we found no relation between *H. dulcis* occurrence and fragment size, we excluded the role of diffuse sunlight as a compensatory for lack of direct incidence. However, as our results suggest *H. dulcis* occurrence on forest fragments is affected significantly by CC not only being completely absent in open areas but also being increasingly common in more shadowed ones, contrary to all expectations, which demonstrate the plasticity of this species on the invasion process.

By studying relationships of community structure and functional groups in contrasting areas with and without *H. dulcis*, Dechoum et al. (2014) observed that the invasion occurred in all early, middle and late successional stages with increased abundance toward semi-open vegetation plots. The authors observed no changes in species richness, functional and taxonomic diversity and the invasiveness of *H. dulcis*. Moreover, they suggested colonization by invasive species was associated to forest openness. Notwithstanding, these plants occurred in all three successional stages, which indicated regeneration may occur independently from successional patches (Dechoum et al. 2014).

The independence of light availability as well as the resistance of old-growth forests to invasion are being discussed and there is evidence that biological invasions is ongoing on these systems and such evidence is not normally noticed because invasion dynamics may need more time to become apparent (Martin and Marks 2006; Martin et al. 2009; Essl et al. 2011; 2012). In our case, the independence of light availability occurred only for *H. dulcis* occurrence. However, the occurrence rate in the study area was close to 50 % of the fragments. Furthermore, the vast majority of the individuals were very young or even just saplings that probably did not grow up to reproductive age yet and as such, the real increment in population size may be small over the reproductive cycles. Thus, we have a situation where the invasion may be undergoing a time lag with small but steady increases in population size.

In fragmented habitats, fragment size should ultimately affect local ecological processes, owing mostly to edge effect (Fischer and Lindenmayer 2007), quite evident on smaller fragments where edge effect is proportionally larger (Metzger 2000). In our study, although fragment size played a minor role, the majority of occurrences were linked to

lower fragment shapes index values (linear-like remnants) that, ultimately, may promote higher edge effects (Kupfer et al. 2006).

By destabilizing forest fragments, edge effects should make them even more susceptible to biological invasions (Laurance and Bierregaard 1997). The colonization of shaded old-growth areas by alien species are not novel in biological invasion studies. By studying the invasive palm *Archontophoenix cunninghamiana* H. Wendl. & Drude, Dislich et al. (2002) did not find associations between human disturbance and the occurrence of the invasive one. Furthermore, they found a positive effect of shading on species occurrence. Agreeing with such results, our findings evidenced that human activity and habitat disturbance are not necessarily related to invasion facilitation, demonstrating thus the competitive potential *H. dulcis* and their capability to invade even natural, undisturbed environments.

As generally documented (Richardson et al. 2000), we observed a small number of adult trees and even smaller number of reproductively ones in contrast to a remarkably high number of saplings and juveniles. As expected, when we assessed the effects of different variables on *H. dulcis* abundance, we found a significant effect of the presence of an adult, fruiting individual for higher abundances, even in large remnants. This was expected as a fruiting adult would be a direct seed source and many of these seeds fall and germinate under the source tree (Decker et al. 2012). However, fragment size had a minor, even though not statistically significant effect on the abundance as well, although, combined with fragment shape, it reflected predominantly on the species occurrence. We argue that fragment size might be important for the successful establishment and growth of *H. dulcis* and thus, have an indirect effect on abundance. This situation is interesting as it goes against the most accepted notion that smaller fragments would facilitate invasion (With 2002).

In conclusion, the consequences of severe fragmentation are widely known as drivers of external pressure on forest remnants, which can advance from edge effects to extinction cascades and ultimately environmental collapse. We proposed that, although these effects are important and understanding their consequences is vital for conservation issues, even areas that are not under such intense stress might be susceptible to environmental threats, such as biological invasions. The occurrence and abundance of the invasive *H. dulcis* at the landscape level are not spatially autocorrelated. At patch level, the species occurrence is related to CC and fragment shape and, once occurring, overall abundance directly reflected the presence of *H. dulcis* adults, which regularly provide seeds to further colonizing new sites of the subtropical Atlantic forests.

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Appendix

See appendix Table 2.

Table 2 Independent and dependent variables measured in subtropical Atlantic forests remnants of southern Brazil

Remnant	Occurrence	Abundance	FSS	CC	RSh	RSi	SLu
1	0	0	Initial	0.07	0.27	1.61	Native
2	0	0	Initial	0.08	0.60	2.23	Agricultural
3	0	0	Initial	0.13	0.27	15.47	Native
4	0	0	Initial	0.32	0.31	2.96	Forestry
5	0	0	Initial	0.42	0.31	1.99	Forestry
6	0	0	Middle	0.46	0.27	8.12	Agricultural
7	0	0	Initial	0.56	0.29	11.74	Native
8	0	0	Initial	0.59	0.09	2.39	Agricultural
9	0	0	Late	0.60	0.10	31.35	Agricultural
10	1	1	Initial	0.62	0.32	0.10	Agricultural
11	0	0	Middle	0.65	0.20	12.96	Forestry
12	1	1	Middle	0.67	0.37	2.90	Forestry
13	0	0	Middle	0.69	0.50	3.96	Native
14	0	0	Initial	0.70	0.29	6.49	Urban
15	1	82	Late	0.72	0.10	5.27	Agricultural
16	1	482	Late	0.72	0.42	6.94	Agricultural
17	1	9	Middle	0.76	0.11	13.68	Agricultural
18	1	332	Late	0.77	0.15	14.05	Agricultural
19	1	3	Middle	0.77	0.13	3.76	Agricultural
20	1	41	Late	0.77	0.24	11.39	Agricultural
21	0	0	Late	0.80	0.75	5.58	Native
22	1	1346	Late	0.81	0.40	16.09	Agricultural
23	0	0	Late	0.85	0.12	8.82	Agricultural
24	1	76	Middle	0.86	0.53	7.48	Agricultural
25	1	11	Middle	0.86	0.20	0.58	Native
26	0	0	Late	0.88	0.61	13.30	Agricultural
27	1	2	Late	0.88	0.06	16.87	Agricultural
28	1	141	Late	0.90	0.12	3.92	Agricultural
29	0	0	Late	0.91	0.56	1.77	Native
30	1	3	Late	0.93	0.06	16.87	Agricultural

Dependent variables included occurrence (presence–absence) and abundance of *Hovenia dulcis*

Independent (explanatory variables) included *FSS* forest successional stage, *CC* canopy coverage (0–1); *RSh* remnant shape (0–1); *RSi* Remnant Size (ha^{-1}) and *SLu* surround land use

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