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Establishment of invasive plant species in canopy gaps on Robinson Crusoe Island

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Abstract To design preventive and management measures it is crucial to identify the mechanisms that facilitate an invasion process. We evaluated how microsites affect establishment success of the alien small tree *Aristotelia chilensis*, the alien climber *Rubus ulmifolius,* and endemic tree species on Robinson Crusoe Island forest. Seedling and sapling densities were estimated in 65 canopy gaps in two forest stands (PEY and Villagra) along a canopy forest-gap gradient, and in three microsites (mound, pit, and trunk) of canopy gap-maker trees. Two statistical models were applied to evaluate the effects of the position in the gap (center, edge, and close forest) and substrate microsites in relation to topographic and structural variables on invasive and endemic species establishment. The density of invasive species was higher in the center of canopy gaps and forest edges than under forest canopy. Invasive plants were present in 86.5 % ($n = 32$ gaps in PEY) and 89.8 % ($n = 25$ forest gaps) in Villagra. A higher seedling and sapling density of endemic rather than invasive species was found in canopy-gap center and gap edges. However, trunks, mounds, and pits were dominated by invasive species. We found different responses in seedlings, saplings, and juvenile stages in relation to the explanatory variables studied and between the two stands. The decomposition state of gap-maker trees, which was used as a proxy of gap age, was the only variable that showed the same tendency in the two forest stands and for both invasive and endemic seedlings. In this case, we found that the densities of invasive and endemic seedlings were lower in older gaps, but sapling densities were higher in older gaps. Based on the results we cannot conclude a general pattern of seedling, sapling, and juvenile establishment in forest gaps for either invasive species, but in some gaps the invasion seems to start in trunks, mounds, and pits. We recommend focusing invasive species control on mounds and pits in some forest stands; and in general, we recommend controlling invasive saplings, more than seedlings or juveniles.

Keywords *Aristotelia chilensis* · Canopy gaps · Microsites · Natural disturbances · Plant invasions · *Rubus ulmifolius*

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Introduction

Biological invasions are defined as a phenomena in which species expand their distributional range,

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occupying regions in which they have not been found previously (Kolar and Lodge 2001). The invasion process is regulated by the biological features of the invasive species and the environmental conditions of the receptor ecosystem (Hobbs and Humphries 1995; King and Grace 2000) or changes in the disturbance regime (Moles et al. 2012). Among the environmental characteristics, disturbances are considered one of the main factors affecting ecosystem invasibility (Hobbs and Huenneke 1992; Davis et al. 2005; Baret et al. 2008). Natural disturbances are a fundamental feature of all forests (Hubbell and Foster 1986; Kellner et al. 2009) and play a crucial role in community composition and structure (White 1979). At a local scale, the most common disturbance occurring within a forest is canopy-gap creation (Yamamoto 2000). The falling of trees is the main cause of canopy openings in temperate and tropical forests (Hubbell and Foster 1986).

Canopy-gap formation generates considerable changes in the distribution and availability of environmental resources (Pickett and White 1985). These changes allow for the recruitment, establishment, development, and renewal of the forests through natural regeneration dynamics (Brokaw and Busing 2000; Dalling and Hubbell 2002; Numata et al. 2006). Several biotic and abiotic variables are associated with the establishment of plant species in canopy gaps. Among them, sunlight quantity, positively correlated with gap size, has been found to be one of the most important variables in determining seedling density in forest gaps (Canham et al. 1990; McCarthy 2001; Dalling and Hubbell 2002; Montgomery and Chazdon 2002; Beckage et al. 2005, among others). Other variables commonly associated with invasion success are related to forest renewal through gap dynamics, such as elevation, slope, age of the gap, and the distance from a propagule source (Yamamoto 2000; Lockwood et al. 2005; Holle and Simberloff 2005). Also, soil variables such as litter depth, humidity, and nutrients have been found to have a high impact on seed germination and seedling recruitment in forest canopy gaps (Molofsky and Augspurger 1992; Dalling and Hubbell 2002, Christie and Armesto 2003), and could be related to the invasion process in forests.

It is possible to define different microsites for seedling establishment in forest canopy gaps, depending on the type and quantity of resources available in them. Types of microsites are mainly determined by the quantity of light received and by soil changes. Soil changes occur in the uprooted tree sites, where mound, pit, and trunk microsites are found, hereafter referred to as substrate microsites (Beatty 1984; Bazzaz 1991; Chesson and Warner 1981; Clebsch and Busing 1989). In canopy gaps, the light incidence presents a gradient with more light availability in the gap center and less light from the edge towards the interior forests (Vargas et al. 2013). These light gradients directly influence the species composition that will renew the forest (Busing and White 1997). At the same time however, the environmental heterogeneity produced within the canopy gaps provides the conditions needed for some invasive species to establish successfully (Beckage and Clark 2003). Disturbances that remove dominant vegetation encourage quick colonization by light-dependent species (Bazzaz 1979; Poulson and Platt 1989), and frequently facilitate the invasion process (Asner et al. 2008; Pauchard et al. 2008). Even in small disturbances, a forest alien species can invade (Tilman 1994; Suding and Goldberg 2001; Davis 2003; Burnham and Lee 2010), and after a number of years, in some cases dominate and alter the wild ecosystems irreparably (Baret et al. 2008).

Robinson Crusoe, part of Juan Fernandez Archipelago, is located in the South Pacific Ocean 674 km off continental Chile (33°37′ S, 78°51′ W). The island has an area of 4.794 ha, 96 % of which is under the protection category of National Park and World Biosphere Reserve, and is also considered a biodiversity conservation hotspot (Myers et al. 2000). In spite of these titles, the endemic forest is rapidly disappearing due to the advancement of woody invasive plant species (Cuevas and Leersum 2001; Greimler et al. 2002; Dirnböck et al. 2003; Smith-Ramírez et al. 2013). The serious problem of plant invasion on Robinson Crusoe Island (RCI) forests, is produced mainly by two woody species, *Aristotelia chilensis* (Elaeocarpaceae) and *Rubus ulmifolius* (Rosaceae), both of which are light dependent. Where these adult species grow, thick and impenetrable layers are produced, making germination and establishment of native (and, also invasive) species impossible (Greimler et al. 2002). The presence of these invader plants negatively affects the natural forest regeneration dynamics of RCI, producing forest regression and fragmentation (Smith-Ramírez et al. 2013).

The main objective of this study was to evaluate the influence of canopy-gap characteristics and components on the invasion success of two exotic woody species in relation to endemic species. In spite of the favorable seedling establishment conditions produced throughout canopy gaps, we propose that the density of the invasive light-dependent species will be higher in soil microsites produced by uprooted trees (mound, pit, and sometime trunks). The hypotheses of this study are: (1) The regeneration (seedlings, saplings, and juveniles) of invasive species is distributed in a light gradient, with less density in forests and more density in canopy gaps; (2) There is a positive relationship between gap size and regeneration density of invasive but not endemic species; (3) There is more regeneration density of invasive species near to the propagule source; (4) There is a relationship, positive or negative depending on the species, between the age of the gaps and the regeneration density, since it has been found that edaphic effects of blowdown in mound, pit, and trunk needed several years to develop; (5) There is a negative relationship between litter depth and regeneration density, as has been proposed by some authors for species of the same genus as those in this study.

Methods

Study area and invasion problem

This study was conducted on RCI in two forest stands: Plazoleta El Yunque (PEY), a remnant of 30 ha at an elevation range of 253–500 m.a.s.l; and Villagra, a remnant of 40 ha at similar elevation, but steeper. The forest stands contain two woody invader species, *A. chilensis* and *R. ulmifolius* (from here on referred to as *A. chilensis–R. ulmifolius* association). Canopy gaps are part of the forest́s natural physiognomy. It is estimated that approximately 25 % of the forest canopy is affected by canopy gaps in PEY and around 10 % in Villagra (Vargas et al. 2010). The main canopy tree species in RCI is the endemic and monotypic genus *Nothomyrcia fernandeziana,* which is commonly accompanied by *Fagara mayu* and *Drimys confertifolia*, and less frequently by *Boehmeria excelsa* and *Rhaphithamnus venustus* (Vargas et al. 2013).

Field measurements of canopy gaps

Measurement of topographic and structural variables

Field data were recorded in January and February 2010 and 2011. We studied all gaps found in PEY ($n = 37$) and Villagra forest stand ($n = 28$) that were accessible. The geographical position and topographic variables (elevation and slope) were recorded at the gap's center. Also, qualitative measurements of the gap's origins were taken. We classified the gaps into two categories: gaps produced by landslides and gaps produced by windstorm or tree decay (Yamamoto 1992). Structural variables to describe canopy gaps were gap size, mean litter depth and the closest linear distance from an invasive propagule source. Gap size was calculated with the ellipse formula, using the longest and shortest diameters measured from the canopy-gap border trees (Runkle 1982). It is well known that the size of canopy gaps is positively related to light levels (Carlton and Bazzaz 1998), therefore canopy-gap size was used as a surrogate measure of light availability (Canham et al. 1990; Gálhidy et al. 2006).

Mean litter depth was recorded within the canopy-gap area in five plots of 1 m^2. Each gap was divided into five equal parts, and a plot was placed in the center of each subdivision. The species dbh and decomposition state of the canopy gap-maker tree were recorded in endogenous canopy gaps, which had been created by the uprooting and falling of trees. If the canopy gap had been formed by the falling of multiple trees, the tree with the highest dbh was considered to be the gap maker (Veblen 1985). Decomposition state of canopy gap-maker trees, used as a proxy of the gap age, were estimated qualitatively (adapted from Carmona et al. 2002) based on three possible states, (1) no apparent decomposition, (2) medium state decomposition, and (3) advanced state of decomposition.

Linear distance to closest invasive propagule source was estimated using a high-resolution satellite image from 2010 (WorldView-2) and spatial computer algorithm. The continuum *A. chilensis–R. ulmifolius* association, with a minimum coverage of 10 m^2 was considered an invasive source. The medium canopy area of an adult *A. chilensis* tree where *Rubu*s usually climbs, is 10 m^2, approximately. The distance rank was established considering the main dispersal vector of invasive species, the bird *Turdus falcklandii*

(Smith-Ramírez et al. 2013).This distance was estimated only at PEY stand where the border of the invasive scrubland was abrupt, but in Villagra stand this border was not clear. In this case we did not use this variable.

Biological records in transects in different position of the gaps and quadrants in microsites

Records in different position of the gap We recorded the establishment of endemic and invasive species following a gradient from the center of the canopy gaps through their edges, up to five meters under forest canopy (Pauchard et al. 2008). In each gap, transects (with 2 m of width) were systematically performed every three meters. The number of transects depended on canopy-gap size. In gaps less than 50 m² one transect was made and in bigger gaps up to 11 transects were made. The canopy-gap edge was defined in relation to the limit by the vertical projection two meters above the ground of the first canopy tree with a diameter at breast height (dbh) >10 cm. We measured both edges that crossed one transect in a gap. The center gap area was the area crossed by a transect between both edges of the gap. The center gap area is bigger than edge gap area and interior forest area. The direction of each transect that crossed the canopy gap was decided in relation to the falling direction of the canopy gap-maker tree. The number of seedlings (individuals <50 cm), saplings (51 cm < individuals <200 cm), and juveniles (individuals between 2 and 3 m) of all trees and climber species was recorded in the gradient light transects. Juveniles of almost all species produce fruit when they are around three or more meter tall, although it is possible to find *Rubus* individuals smaller than 3 m with fruit in the gaps. Frequently, *R. ulmifolius* found in forests and forest gaps produces fruit when it receives enough light, which occurs when it climbs 2.5–3 m in tall endemic trees and over *A. chilensis*.

Microsite records We defined the microsites in each endogenous canopy gap: stem, mound, and pits of the gap-maker tree. All microsites were located at the border of the gaps since this was the gap-maker trees' location. In microsites per gap, we made 1 plot of 1 m² and recorded seedlings, saplings, and juveniles. We, also recorded the diameter at breast height (dbh) of all gap-maker trees.

Statistical data analysis

The normality test of *Shapiro–Wilk* was applied in a preliminary evaluation of density data and explanatory variables. Since the data did not follow a normal distribution, we proceeded to work with non-parametric statistics. We analyzed only the species that showed the highest density (*A. chilensis, R ulmifolius, N. fernandeziana*, and *F. mayu*). To evaluate the existence of significant differences ($p < 0.05$) in the regeneration density of endemic and invasive species in the forest-gap gradient in the microsites, a multiple comparison test of Kruskal–Wallis and the multiple comparison pairwise test of Dunn (Dunn 1964) were applied.

Linear models (glm) with a Poisson distribution and logarithmic link function were applied to avoid an overestimation of significance levels that might be caused by over dispersion of data (Martin et al. 2005; Hoef and Boveng 2007; Richards 2008; Zuur et al. 2009). Two models were developed, one for microsite data, which was defined mainly by light gradient (center gap, gap edge, and interior forest) and the second by substrate microsite data. These models were applied to seedlings, saplings, or juveniles of each species and species group (invasive and endemic). It was not possible to use the same model for all data sets because in many microsites there was no regeneration (zero data) and the variables to evaluate were different. In Model 1 the dbh data of the canopy gap-maker tree was excluded, because it was collinear to the gap size. The mean litter depth variable was used only for seedlings, not for saplings or juveniles. Distance to source of invasive species was not used for endemic species density. In Model 2 the mean litter depth was excluded because it was measured at the gap floor, but not in microsites.

Similar models were applied to evaluate the existence of collinearity among the predictors. However, due to the high number of combinations among the variables assessed and associated resulting models, these will not be shown. To find the best fitting model for each response variable, the *p-values* from the *z*-statistics were obtained. Iterative processes were made in which every term that was not significant at the 5 % level was dropped, refitting the models until all terms were significant. A stepwise backward selection to choose the best model was developed (Zuur et al. 2009). All the statistical analyses were performed

using R software (R CORE 2015). The main packages used were mvsf, PMCMR, and glm2.

Results

The structure of the gaps in both studied forests was different, especially due to the absence of landslide canopy gaps in Villagra (Table 1). In Villagra stand the main canopy-gap opening mechanism was broken stems (39.2 %), in PEY it was fallen trees (90.9 %). In stand PEY 16.2 % of the gaps were created by the uprooting of multiple trees, with a maximum of five fallen trees inside a single canopy gap (Table 1). Gap sizes greater than 100 m^2 were infrequent in PEY (9.9 %), but not in Villagra (35.6 %). One of the main differences was the composition of the soil cover, dominated almost completely by the fern *Arthropteris altescandens* in Villagra.

In both stands, the most frequent canopy gap-maker tree was *N. fernandeziana* (stand 1: 63 %; $n = 29$; stand 2: 50.4 % $n = 21$). The other endemic species, *F. mayu, D. confertifolia*, and *B. excelsa* were uncommon generators, while *R. venustus* was not involved in canopy-gap creation. The mean canopy-gap size was 88.7 m^2 for PEY and 76.5 m^2 for Villagra, with a total range between 3.5 and 368 m^2 (Table 1).

Of the 65 studied canopy gaps, 86.5 % ($n = 32$ PEY) and 89.8 % ($n = 25$ Villagra) contained seedlings, saplings, or juveniles of the invasive species *A. chilensis* and *R. ulmifolius*. In PEY, mean density of invasive species seedlings was significantly higher in the canopy-gap forest (both center and edges) in relation to the forest (Table 2), especially in the case of *A. chilensis*. This same tendency was found in Villagra, but it was not significant (Table 2). On average, PEY tended to have more density of invasive seedling species in gaps than endemics, where their establishment exceeded almost twice, but these differences were not significant (Table 2). In Villagra this same tendency, the presence of more endemic than invasive seedling species, was significant for seedlings in gap edges. Only *F. mayu* seedling density in PEY showed significant differences in canopy gaps compared to canopy-gap edges and forest (Table 2). This tree species had more regeneration in gap edges in PEY, but no regeneration in the gaps of Villagra. The other endemic species, *D. confertifolia, R. venustus,* and *B. excelsa,* showed in a total less than 8 % of total regeneration recorded in the light gradient (Table 2). We recorded regeneration of juvenile invasive and endemic species in PEY. In Villagra we found a significantly higher regeneration of endemic species than of invasive ones (Table 2).

Of the 33 canopy gaps created by fallen trees on PEY, species establishment on stem, mound, and pit microsites was recorded in 23 of them (69.7 %). Of these, 14 (60.9 % of $n = 23$) had endemic and invasive species individuals, whereas nine showed

Table 1 Canopy-gap characteristics and predictor variables recorded to describe the studied forest gaps of Plazoleta El Yunque (PEY) and Villagra on Robinson Crusoe Island. Regeneration include seedlings, saplings and juveniles of all invasive and endemic species

Gap characteristics	% (N) PEY	% (N) Villagra
Endogenous gaps	89.0 (33)	100 (28)
Exogenous gaps	11.0 (4)	0
Canopy gaps with microsites	81.0 (30)	70.0 (25)
Canopy gaps with regeneration in the microsites	76.7 (23)	22.4 (8)
Formation by single tree uprooting	64.9 (24)	25.2 (9)
Formation by multiple tree uprooting	16.2 (6)	2.8 (1)
Formation by broken stem	8.1 (3)	39.2 (9)
Formation by slope collapse	10.8 (4)	0

| Predictor variables of the gaps	Mean ± SE	Range	Mean ± SE	Range
Elevation (m. a. s. l.)	346.1 ± 8.3	270–490	321 ± 7.8	270–437
Slope (grades)	29.4 ± 1.3	12–46	69.0 ± 2.5	58.7–105
Canopy-gap size (m^2)	88.7 ± 13.8	13–368.1	76.5 ± 7.7	3.5–211.5
Mean litter depth (cm)	2.0 ± 0.2	0.4–4.0	2.4 ± 0.6	1.5–3.5
Closest linear distance from an invader source (m)	38.0 ± 4.2	7.2–99.1	–	–

Table 2 Mean densities (in 100 m^2 ± SE) of seedlings and saplings of endemic and native species in the canopy-gap forest gradient and microsites of Plazoleta El Yunque (PEY) and Villagra

Species	Seedlings			Saplings		
	Canopy gap	Gap edge	Forest	Canopy gap	Gap edge	Forest
Plazoleta el yunque						
Invaders	**288.7 ± 77.2a**	296.6 ± 107.7a	**94.1 ± 44.8A**	**53.6 ± 16.9A**	**43.2 ± 27.3a**	**2.4 ± 1.7A**
Endemics	172.2 ± 28a	191.6 ± 49.8a	155.5 ± 26.7a	88.5 ± 15.1a	119.6 ± 42.5a	155.3 ± 22.3a
Ach	**145 ± 42.7**	**129.9 ± 46.9**	**35.9 ± 20.5**	**15.8 ± 6.5**	18.9 ± 12.2	**0.0**
Rul	**143.7 ± 34.5**	166.8 ± 60.8	**58.2 ± 24.3**	**37.9 ± 10.4**	24.3 ± 15.1	**2.4 ± 1.7**
Mfe	126.6 ± 14.5	135.4 ± 23.5	125.2 ± 11.6	**82.4 ± 11.5**	114.9 ± 38.3	**148.3 ± 17.8**
Fma	**43.6 ± 12.0**	**56.2 ± 26.3**	**28.8 ± 14.1**	2.3 ± 1.1	2.0 ± 1.5	5.6 ± 3.3
Dco	1.4 ± 1.0	0.0	1.3 ± 0.9	3.3 ± 2.1	2.7 ± 2.7	1.1 ± 0.8
Bex	0.1 ± 0.1	0.0	0.0	0.4 ± 0.4	0.0	0.0
Rve	0.4 ± 0.4	0.0	0.1 ± 0.1	0.0	0.0	0.4 ± 0.4

Species	Seedlings			Saplings			Juveniles		
	Canopy gap	Gap edge	Forest	Canopy gap	Gap edge	Forest	Canopy gap	Gap edge	Forest
Villagra									
Invaders	30.8 ± 0.2a	**59.7 ± 0.21A**	29.3 ± 0.14a	**22.3 ± 0.1a**	38.5 ± 0.1a	0A	1.6 ± 0.1A	0.8 ± 0.0A	0A
Endemics	**27.4 ± 0.1a**	**0a**	30.8 ± 0.01a	25.1 ± 0.1a	34.6 ± 0.2a	41.0 ± 0.2a	3.0 ± 0.1a	3.0 ± 0.1a	0.6 ± 0.1a
Ach	11.9 ± 0.1	**30.8 ± 0.2**	13.9 ± 0.1	18.5 ± 0.1	28.9 ± 0.1	0	1.2 ± 0.0	0.8 ± 0.0	0
Rul	18.9 ± 0.1	**28.9 ± 0.1**	15.4 ± 0.1	3.9 ± 0.1	9.6 ± 0.1	0	0.4 ± 0.0	0	0
Nfe	**24.0 ± 0.1**	**0**	26.2 ± 0.1	23.6 ± 0.1	26.9 ± 0.2	33.08 ± 0.1	2.6 ± 0.1	2.6 ± 0.0	0.6 ± 0.1
Fma	0	0	0.8 ± 0.1	0	0	0	0	0	0
Dco	2.4 ± 0.0	0	3.1 ± 0	1.5 ± 0.1	7.7 ± 0.1	7.69 ± 0.1	0.4 ± 0.0	0.4 ± 0.0	0
Rve	0.4 ± 0.0	0	0.8 ± 0.1	0	0	0	0	0	0

Significant differences among the gradient studied for the same species group are in bold

Significant differences between invaders and endemics in the same gradient or microsites are in letters *aa* non-significant, *Aa* = significant (*Kruskal–Wallis* and *Dunn*; $p < 0.05$), *Ach* = *A. chilensis* (invader); *Rul* = *R. ulmifolius* (invader); *Nfe* = *N. fernandeziana*, *Fma* = *F. mayu*, *Dco* = *D. confertifolia*, *Bex* = *B. excelsa*

Fig. 1 Mean densities (in $1 \text{ m}^2 \pm \text{SE}$) of seedlings and saplings of invasive and endemic species (*Aristotelia chilensis* and *Rubus ulmifolius*) in stump, mound, and pit of gap-maker trees of Plazoleta El Yunque and Villagra forest stands on Robinson Crusoe Island
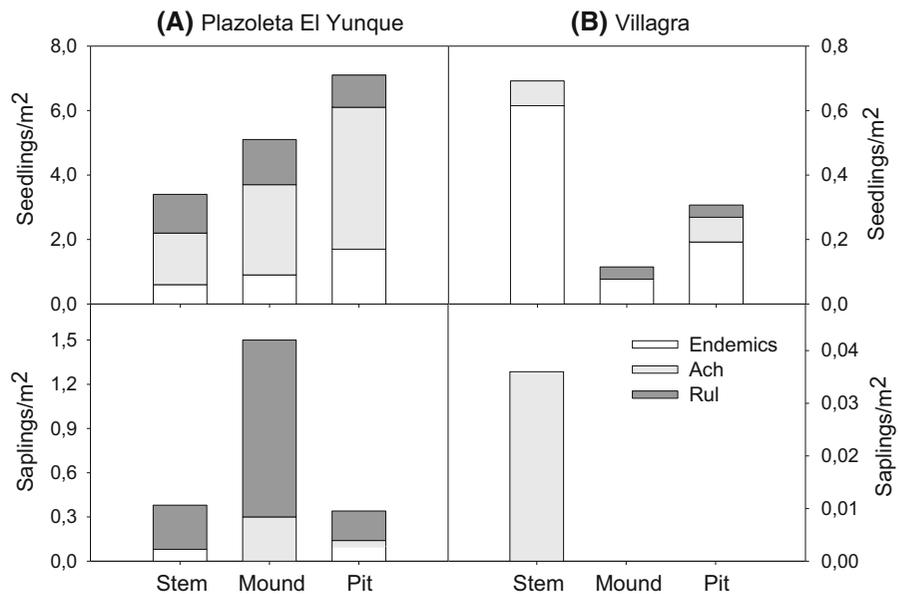
only endemic species. In total, 415 individuals were recorded in the three microsites of the canopy gap-maker tree, 80.7 % of which were *A. chilensis* and *R. ulmifolius*. Endemic species recorded were *N. fernandeziana, F. mayu*, and *D. confertifolia*, the last species having very low densities. *R. venustus* and *B. excelsa* did not regenerate in the studied microsites. In Villagra, 22 (78.6 %) canopy gaps recorded had mound and pit in the canopy gaps. Of these, in nine gaps there were regeneration in mounds and/or pits. 48 seedlings or saplings were recorded in the three microsites. Only in four of these cases (18.2 %) did invasive species account for regeneration. In all these cases the density of regeneration of seedlings and saplings of both invasive and endemics species was low (Fig. 1).

In PEY, seedling and sapling density of invasive species in microsites was higher than endemic species (seedlings: $h = 5.42$, $p = 0.09$; saplings; $h = 6.38$, $p = 0.012$). Here, the microsite that concentrated the highest amount of endemic and invasive species was the pit, while the least preferred by both types of species was the stem (Fig. 1). Approximately two-thirds of the invasive *A. chilensis* and *R. ulmifolius* seedlings were found in mound and pit. The seedling density of *A. chilensis* was higher than *R. ulmifolius* within all microsites (Fig. 1). The only species that showed significant differences in seedling mean density among the three microsites was *N.*

fernandeziana, with the highest values in pits ($h = 10.47$, $p = 0.005$). In Villagra, seedling density of endemics in microsites was a little higher than that of invasives, but these differences were not significant (seedlings: $h = 0.51$, $p = 0.17$; in Villagra only invasive saplings were present, see Fig. 1).

Effects of explanatory variables on species density, canopy gaps, and canopy gap-maker tree microsites

No collinearity among explanatory variables was detected, except dhb of gap-maker tree and gap size. For model 1, invasive (*A. chilensis, R. ulmifolius*) and endemic species (*N. fernandeziana, F. mayu*) differed in their responses to topographic and structural attributes, and sometimes between forest stands (Tables 3, 4). In PEY seedling density of *R. ulmifolius* and *A. chilensis* showed a significant preference for big-sized canopy gaps ($z = 20.03$, $z = 15.41$, respectively). This tendency was negative in Villagra ($z = -11.38$, $z = -6.36$). The same trend was found regarding the influence of mean litter depth on seedling density of *A. chilensis*, which was positive in PEY, but negative in Villagra (PEY: $Z = 25.17$; Villagra: $z = -19.17$). Slope almost always had a positive relationship with seedling density (PEY: Z *R. ulmifolius* = 11.00, Z *A. chilen*sis = 17.00; Villagra:

Table 3 Setting value of linear models (glm) with a Poisson distribution and logarithmic link function for Plazoleta El Yunque (PEY) stand

Species	Significant terms [Pr(>|z|)]	AIC	D^2
Model 1: Within canopy gaps			
Seedlings			
Ach	(−) ELV (<0.001) (+) SLO (<0.001) (+) GSZ (<0.001) (+) LTD (0.006) (−) DECS (<0.001)	6314.2	30.9
Rul	(−) ELV (<0.001) (+) SLO (<0.001) (+) GSZ (<0.001) (+) DPS (<0.001) (−) DECS (<0.001)	5088.3	36.8
Nfe	(+) ELV (<0.001) (+) SLO (<0.001) (+) GSZ (<0.001) (−) LTD (<0.001)	2076.0	6.2
Fma	(−) ELV (<0.001) (+) GSZ (<0.001) (+) LTD (<0.001)	1731.2	43.5
Saplings			
Ach	(−) ELV (<0.001) (+) SLO (<0.001) (+) DECS (<0.001) (−) DPS (<0.001)	600.2	50.4
Rul	(−) ELV (<0.001) (+) SLO (<0.001) (+) GSZ (<0.001) (+) DECS (<0.001) (+) DISTPS (<0.001)	2052.5	13.1
Nfe	(+) ELV (<0.001) (+) SLO (<0.001) (−) GSZ (<0.001) (−) DECS (<0.001)	1593.7	27.5
Fma	(+) ELV (<0.001) (−) GSZ (<0.001) (−) DECS (0.027)	285.3	20.2
Model 2: Within canopy gap-maker tree microsites			
Seedlings			
Invader spp	(+) DBH (<0.001) (−) DECS (<0.001)	153.5	87.0
Endemic spp	(+) DBH (0.002)	110.1	34.0

1 Species relative densities within canopy gaps

2 Substrate microsites: trunk, mound, and pit

The significant terms for predictive variables are shown with the *z*-statistic of goodness of fit, the Akaike Information Criteria (AIC) scores, and the deviance of the optimal model selected

Ach = *A. chilensis* (invader); *Rul* = *R. ulmifolius* (invader); *Nfe* = *N. fernandeziana*; *Fma* = *F. mayu*; *Dco* = *D. confertifolia*; *Bex* = *B. excelsa*; *ELV* = elevation; *SLO* = Slope; *GSZ* = gap size; *DISTPS* = distance propagule source; *DECS* = decomposition state; *LTD* = litter depth; *DBH* = diameter at breast height

Z *R. ulmifolius* = 3.49, Z *A. chilensis* = −12.57). Contrary to what was expected, in PEY a positive relationship between propagule source distance and *R. ulmifolius* seedling density ($z = 19.02$) was found, but no relationship was found for *A. chilensis*. Elevation had a negative relationship with seedling density in both forest stands (PEY: Z *R. ulmifolius* = −33.10, Z *A. chilensis* = −37.13; Villagra Z *R ulmifolius* = −6.23, Z *A chilensis* = −12.37). The decomposition state of gap makers in both stands and models also produced a negative relationship, thus, old gaps had lower densities of invasive species (PEY: Z *R. ulmifolius* = −22.65, Z *A. chilensis* = −13.97; Villagra: Z *R ulmifolius* = −10.91, Z *A chilensis* = −6.48; Tables 3, 4).

Sapling density in PEY and Villagra was not related to gap size, but in Villagra juvenile density of *A. chilensis* was related positively with this variable ($z = 10.56$; Tables 3, 4). As occurred with seedlings,

elevation had a negative influence on saplings in PEY (z *R. ulmifolius* = 10.76, z *A. chilensis* = 14.75), but not in Villagra. Slope and decomposition state had a positive relationship with sapling density in PEY (z *R. ulmifolius* = 12.39 and 4.44, respectively; z *A. chilensis* = 6.29 and 5.95, respectively), but not in Villagra (z *A. chilensis* = −12.88; z = −7.71, respectively, Tables 3, 4).

The seedling density of the native species N. *fernandeziana*, showed a positive relation with gap size in PEY ($z = 24.23$) but not in Villagra, and a positive relation with slope in both forest stands (PEY: $z = 6.86$, Villagra $z = 3.81$; Table 3, 4). In both forest stands, the decomposition state of gap makers had a negative relationship with sapling density (PEY: $z = -2.21$, Villagra: $z = -10.52$; Tables 3, 4).

For Model 2, it was only possible to analyze PEY data, and only by grouping invasive and endemics species separately. As expected, a lower seedling

Table 4 Setting value of linear models (glm) with a Poisson distribution and logarithmic link function for Villagra stand

Species	Significant terms [Pr(>|z|)]	AIC	D^2
Model 1: Within canopy gaps			
Seedlings			
Ach	(−) ELV (<0.001) (+) SLO (<0.001) (−) GSZ (0.002) (−) LTD (<0.001) (−) DECS (<0.001)	444.2	62.1
Rul	(−) ELV (<0.001) (−) SLO (<0.001) (−) GSZ (<0.001) (−) LTD (<0.001) (−) DECS (<0.001)	134.4	95.4
Nfe	(−) ELV (<0.001) (+) SLO (<0.001) (+) LTD (<0.001)	529.9	30.2
Saplings			
Ach	(+) ELV (<0.001) (−) SLO (<0.001) (−) DSZ (<0.001)	375.0	56.9
Nfe	(−) SLO (<0.001) (−) GSZ (<0.001) (−) DSZ (<0.001)	875.8	18.0
Juveniles			
Ach	(+) ELV (<0.001) (+) SLO (<0.001) (+) GSZ (<0.001) (+) DECS (<0.001)	611.5	54.4
Nfe	(+) ELV (<0.001) (+) DECS (<0.001)	329.7	22.2
Model 2: Within canopy gap-maker tree microsites			
Seedlings			
Endemic spp	–	30.2	45.5

1 Species relative densities within canopy gaps

2 Substrate microsites: trunk, mound, and pit

The significant terms for predictive variables are shown with the z-statistic of goodness of fit, the Akaike Information Criteria (AIC) scores and the deviance of the optimal model selected

Ach = A. chilensis (invader); Rul = R. ulmifolius (invader); Nfe = N. fernandeziana; Fma = F. mayu; Dco = D. confertifolia; Bex = B. excelsa; ELT = elevation; SLO = slope; GSZ = gap size; DECS = decomposition state; LTD = litter depth

density of invasive species was found in younger gaps ($z = -4.27$). Endemic species did not show a relationship to the decomposition state of gap-maker trees. For both invasive and endemic species, more seedling density was found in gaps with bigger fallen trees (Table 3). No relationship was found for seedling density in relation to elevation, slope, gap size, and distance to propagule source.

Discussion

The results of this research allow us to partially accept the main hypothesis, which states that microsites generated by the canopy-gap maker trees have a strong influence on the establishment of invasive species on Robinson Crusoe forests, given that this phenomenon occurred in the PEY stand, but not in Villagra. The only place where invasive seedling species exceeded the native ones was in trunk, mound, and pit. The establishment preferences of invasive species in PEY microsites might relate to disrupted soil conditions produced by tree uprooting, along with higher light

incidence in soil patches, which are nutrient enriched due to the gap-maker decomposition roots, and drier than the adjacent undisturbed soil below forest, as has been proposed in other stands by Beatty (1984), Hubbell and Foster (1986) and Peterson et al. (1990), among others. However, we do not know why this same response did not occur in Villagra forest. Villagra is shadier than PEY, it is located in southern exposed slopes, and presents a lower proportion of canopy gaps (Vargas et al. 2010). These environmental conditions could exert some influence on the lower regeneration density found in the substrate microsites. In fact, in some mounds and pits in the Villagra site, ferns were found, but no woody regeneration. We could not find any other studies about the influence of mound, pit, and trunk that compare more than one stand. All the studies we know of have been done in one forest stand, with usually around 20–30 fallen trees. Sometimes the authors do not mention how many mounds and pits were studied (Beatty 1984; McAlister et al. 2000; Mollaei et al. 2014). In those studies, the conclusions obtained in apparently one forest stand have been applied to all forests or tree

species studied. In this case, it was found that in two forest stands 2.5 lineal kilometers apart and at the same elevation but with a different exposure (PEY = NW, Villagra = SW), the regeneration response in substrate microsites was completely different.

As expected, the density of seedlings, saplings, and juveniles of both invasive species was higher in canopy gaps than in forests, which lead us to accept hypothesis 1, that the regeneration of invasive species are distributed in a light gradient, with less density in forests and more density in canopy gaps. However, we found *R. ulmifolius* and some *A. chilensis* seedlings under forest, in spite of the fact they are shade-intolerant species. They were unable to develop as adult individuals, however, which was in accordance with Baret et al. (2008) who found the same behavior for *Rubus alceifolius* in Reunion Island.

Rubus genus is known as one of the largest global invaders, due to its very fast spread and growth rates (Greimler et al. 2002; Baret et al. 2003). *R. ulmifolius* shows higher tolerance in shaded conditions than *A. chilensis,* suggesting that its invasive potential is stronger. However, *A. chilensis* has the advantage of having arrived on RCI around 30 years prior to *R. ulmifolius* (Dirnböck et al. 2003). Greimler et al. (2002) and Dirnböck et al. (2003) stated that *R. ulmifolius* on RCI would be a less invasive species than *A. chilensis*; its growth area would be limited to only RCI town surroundings. Today, nevertheless, a few years after this study, it is possible to find *R. ulmifolius* invading all woodland areas of RCI (Díaz 2012). The success of *Rubus* genus on RCI is also found on other islands and mainlands, like Hawaii (Smith 1985), the Galapagos (Lawesson 1990; Gordillo 1990), Mauritius, Reunion islands (Cronk and Fuller 2001), the Pacific Coast of the USA (Soll 1994), Buenos Aires, Argentina (Mazzolari et al. 2011), South Africa (Richardson and Wilgen 2004), Australia, and others. *A. chilensis,* an endemic species of Chile and Argentina (Muñoz and González 2006), has not been found to invade other islands or continental areas, but has been found as an exotic species in the Pacific Coast of the USA and western Australia (GBIF 2014).

One of the most remarkable results of this analysis is that, in general, in both forest stands the density of saplings and juveniles of endemic species significantly exceeded the density of invasive species, except in the microsites in PEY. In light of these results it is hard to explain how invasive species can be invasive, especially in Villagra. In an attempt to explain this, three years after this study we resampled 14 gaps of the Villagra stand (unpublished data). It was found that three gaps with gap makers in an advanced decomposition state were completely covered by invasive species with no regeneration of any endemic species. Nine out of 11 gaps were still dominated by endemic regeneration. According to the observation of park rangers of RCI, the exclusion of endemic by invasive species happen four to six years after the canopy gap is formed. The PEY gaps could not be resampled, since environmental organizations removed the exotic species in the canopy gaps studied. We believe that this study was made in the early stages of invasion, when the invasive species were not yet dominant. The high dominance of endemic species could be related to the high propagule density (that was not measured by us) or to resistance to invasion (Levine et al. 2004). One way to resist invasion on RCI is the low germination capability in the field of *Rubus* and *A. chilensis*, which occurs in 5 % or less of the seeds sown (Smith-Ramírez et al. 2013). We do not know the germination capability of endemic species.

Regarding hypothesis 2, that there is a positive relationship between gap size and regeneration density of invasive but not endemic species, we found some relationships for which this holds true. However, this pattern was not the same in both forest stands, or for the different development ages studied, so we only partially accept this hypothesis. We believe that only a small quantity of light is required for invasive species to develop, in which case gap size would not be a critical variable related to the abundance of invasive species. In fact, seedlings of invasive species sprout even under canopy. On the other hand, in the canopy gaps, the development of native ferns and herbs, independent of size, can prevent the germination and future development of invasive and endemic species. This has been found or proposed in other studies for shade-intolerant species that are dependent on canopy gaps to persist (Beatty 1984; Carlton and Bazzaz 1998; Bastias 2014).

Regarding hypothesis 3, that there is more regeneration density of invasive species near to the propagule source, we found this to be true for *A. chilensis*, but not for *R. ulmifolius*. We conclude that this hypothesis is species dependent. These results may also be due to multiple factors involved in the

invasion process. The seed dispersal of fleshy fruits of *A. chilensis* and *R. ulmifolius* occurs mainly by two vectors: the austral thrush (*Turdus falcklandii*) and secondarily by wind (Smith-Ramírez et al. 2013). In PEY, the wind comes from northeast and the main invasive sources are in the same direction. After the wind enters the bay, it hits the slopes of El Yunque hill (located south of PEY forest) and generates a strong vortex effect (up to 70 km/hr in summer). The hypothesis that a relationship exists between a spatial dispersion of invasive species and the distance to propagule source as described by Lockwood et al. (2005), Holle and Simberloff (2005), Colautti et al. (2006), and Milton et al. (2007) is likely to take place in scenarios where dispersing agents show linear movements that are constant during the entire fruiting season, which did not occur in the studied case. The fruiting peak of invasive species has a difference of two months, January for *A. chilensis*, and March for *R. ulmifolius*. During these months, the reproductive behavior of *Turdus* changes (Hahn et al. 2009) and the wind speed decreases from January to March (www. meteochile.cl).

Regarding hypothesis 4, which posits a relationship (positive or negative based on the species), between the age of the gaps and the regeneration density, we found a negative relationship between invasive seedling and sapling density (but not juveniles) in edges, canopy gaps, and gap-maker tree microsites in relation to gap age (using decomposition state of the gap-maker trunk). That is, older gaps had less seedling individuals than recent ones. This may be due to several possible factors: changes in the edaphic characteristics of the microsites could act at germination level, seedling mortality caused by competition or because the quantity of uncovered soil necessary for the seed to germinate decreases with the age of the gap. Finally, in relation to the last hypothesis, no general pattern in the relationship between litter depth and the density of seedlings and saplings of invasive and endemic species was found. One of the most important variables that we now think can affect the establishment of species is the amount of germination microsites. Unfortunately, this is a variable that we failed to measure. Much of the soil in the forest is covered by ferns, especially *Arthropteris,* which can prevent any seed germination in a similar way that has been described for litter (Christie and Armesto 2003). However, in this study the seedling density was either

negative or positive or did not have any relation with litter depth, depending on the study site and species, therefore we partially accept hypothesis 5, that there is a negative relationship between litter depth and regeneration density.

Although several studies on gap dynamics in natural forests have been conducted, applications of gap dynamics to forestry practice in relation to invasive species are limited (Gorchov et al. 2011). In this case, based on the results we can recommend mechanically controlling invasive species, especially during sapling stage, due to the natural high mortality in less developed stages. Mechanical control of seedlings is possible but is much work and is tedious. Control during juvenile stage can leave roots in the soil, which can resprout. If the invasive species appear in higher density and cover mound and pit, where the invasion process in some RCI forest gaps may begin, then it is recommended to control these microsites. It is important for managers to consider that invasion dynamics may differ, even in near forest stands of the island, in which case adaptive management strategies must be applied and continuous monitoring must be done. After control, restoration measures could be taken, but this is part of another study.

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