



Tree regeneration in the threatened forest of Robinson Crusoe Island, Chile: The role of small-scale disturbances on microsite conditions and invasive species



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ABSTRACT

Biological invasions are a major driver of biodiversity loss on islands. After disturbances, invasive plant species can establish affecting forest regeneration microsites. On Robinson Crusoe Island (33°S, Juan Fernández Archipelago, Chile) small-scale treefall canopy gap microsites are most frequently used by “endemic montane forest” species for regeneration. Regeneration can be hampered when invasive species establish and alter gap conditions. We evaluated the role of small-scale disturbances on regeneration and identified tree regeneration microsites in gaps, gap borders, and closed forest. We collected information on the effects caused by invasive species by sampling 30 gaps with a range of invasive species cover, including gaps where invasive species were removed. We analyzed the impact of native ferns and invasive species, regeneration substrates and light availability on native tree species regeneration and juvenile tree performance traits. Our aim was to analyze small-scale disturbances and identify threshold values for the variables related with tree regeneration presence–absence, density and performance, particularly considering invasive species competition. We used classification and regression trees to identify variables and their threshold values influencing native tree species regeneration. Gap borders and small gaps (<200 m²) were preferred microsites for regeneration. Native tree species seemed able to compete as long as invasive species cover did not exceed 10%. Fern cover >10% facilitated tree regeneration and performance. Competition from invasive species for space, water and nutrients was likely more important than for light. Restoration should attempt to recreate intermediate disturbance conditions considering the threshold values identified. Thresholds for variables important for restoration processes can help in the control of invasive species.

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1. Introduction

Forest composition, structure and function are dependent on the response of tree regeneration to site conditions, disturbances and management practices (Gray et al., 2005). Forest tree species require certain environmental and micro-habitat conditions thereby making forest regeneration a complex and multidimensional process (Smith et al., 1997). Forest ecosystems are affected differently by natural disturbances which influence the spatial, temporal and heterogeneous nature of forest patches (Pickett and White, 1985). In turn, the availability of different resources result in diverse plant regeneration niches (Grubb, 1977). Treefall gaps caused by the fall of one or more trees creating an opening in the forest canopy are the dominant small-scale disturbance in many forest ecosystems worldwide and are known to be important for the

self-replacement of temperate and tropical forests (Yamamoto, 2000; Schliemann and Bockheim, 2011; Promis et al., 2010; Durán-Rangel et al., 2013).

Invasive plant species can affect site conditions particularly after disturbances (Brown et al., 2006). In different forest types they can take advantage of gaps and interfere with native tree regeneration (Burnham and Lee, 2010; Gorchoy et al., 2011; Webster et al., 2006). In island ecosystems invasive plant species are especially competitive mainly due to the high availability of resources and because the native species are usually unable to easily preempt the resources available (Denslow, 2003). Native plant species on islands are often adapted and specialized to local conditions while naturalized exotics are mostly generalist species that can easily displace the noncompetitive native flora (Daehler et al., 2004). To develop and implement restoration measures to manage invasive species, a good understanding of forest species' regeneration requirements is essential (Lamb and Gilmour, 2003). Few studies have analyzed the effect of invasive plants on

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natural regeneration in gaps (Burnham and Lee, 2010; Kueffer et al., 2010; Totland et al., 2005) and the challenges for endangered tree species conservation that result (Baret et al., 2008). Detailed restoration management plans have been developed and carried out but little is known about the effectiveness of removing invasive species from gaps on islands or mainland ecosystems (Loh and Daehler, 2008; Kueffer et al., 2010; Fagan and Peart, 2004).

We studied the role of small-scale disturbances and the impact of invasive species on the natural regeneration of endemic tree species on Robinson Crusoe Island (RCI, Juan Fernández Archipelago, Chile 33°37'S, 78°50'W). This island has an extremely high density of endemic vascular species (1.9 endemic species/km²; Bernardello et al., 2006) and a large number of naturalized exotic plant species (292 exotic vs. 149 native; Danton and Perrier, 2006). It is therefore a good location to study the interactions between native and exotic plants. There are 927 ha of shrublands with invasive species compared to 1014.8 ha of native forest (32.9% and 36% of the total vegetation cover respectively; Smith-Ramirez et al., 2013). *Rubus ulmifolius* (Rosaceae) and *Aristotelia chilensis* (Eleocarpaceae) are aggressive invaders and threaten the montane forest ecosystem (Greimler, Lopez et al., 2002). Annually both species produce a large number of fleshy fruits (containing small seeds <6 mm diameter; Hoffmann, 1992) that are disseminated by native birds, gravity and wind (Smith-Ramirez et al., 2013). These species can also spread asexually and establish more quickly than native tree species in forest gaps (Vargas et al., 2013). The remaining intact montane forest is comprised only of endemic tree species (Danton, 2006) that provide habitat for two threatened endemic land-bird species and more than 40 endangered endemic vascular plant species (Vargas et al., 2011). Without effective invasive species control it has been predicted that half of what remains of the RCI montane forest may become dominated by invasive species by 2080 (Dirnböck et al., 2003). On the other hand it has been shown that the recovery of native species is possible after invasive plants are removed (Vargas et al., 2013). Previous studies in the RCI forest have pointed out the negative effects of invasive plant species on biodiversity and how exotic plant invasions are influenced by: gap size, slope, litter depth and distance to propagule source (Vargas et al., 2013; Arellano, 2011). However, despite the growing understanding of the relationship between invasive and native plants, no study has yet identified neither the thresholds beyond which native plant recovery is compromised or the specific regeneration requirements of endemic forest species. Identifying the threshold values of the variables related with the presence of a species of interest is an approach widely applied in studies that serve to provide information for biodiversity conservation and management activities (Müller and Bütler, 2010; Hothorn and Müller, 2010).

We analyzed the effect of small-scale disturbances and invasive species on forest regeneration by sampling 30 treefall gaps with a range of invasive species cover, including gaps from which invasive species have been removed. Our main objective was to analyze how small-scale disturbances provide a window of opportunity for invasive species to establish, and how this influences native tree species regeneration. Consequently, we also identified the role microsite conditions play in forest regeneration on RCI. We considered floristic components like ferns and invasive species that co-occur with tree regeneration along a disturbance gradient in canopy gaps, gap borders, and closed forest in the montane forest of RCI. We examined regeneration substrates, light conditions and individual tree performances. The results were analyzed to learn where the main endemic tree species establish successfully. We examined regeneration success in terms of (a) presence-absence (b) density, and (c) performance traits (i.e., height/root collar diameter ratio). We identified microsite conditions that were related to the density and performance of endemic tree regeneration to find

thresholds for regeneration success, especially considering invasive species. We identified those variables related with the microsite conditions and their threshold values that influence native forest species regeneration to be used as guidelines for restoration activities. We provide this approach to identify microsite variables and their threshold values influencing native forest species regeneration, to be used by restoration practitioners in endangered ecosystems.

2. Materials and methods

2.1. Study area

Field work was carried out in Plazoleta del Yunque, RCI, Juan Fernández Archipelago National Park, an approximately 100 ha area of montane forest between 250 and 550 m.a.s.l (Greimler, Stuessy et al., 2002). The climate is warm temperate with a mean annual temperature of 15.3 °C and an annual precipitation of 1150 mm (Cuevas and Figueroa, 2007). The soils developed from colluvial sediments and ash (Castro et al., 1995). The RCI endemic montane forest tree density ranges between 900 and 1330 trees per ha (>5 cm diameter at 1.3 m, dbh). The dominant tree species is *Myrceugenia fernandeziana* (76% of the individuals per ha), 14–18 m high (Vargas et al., 2010). *Fagara mayu* (9%) is common in the canopy and forms an emergent layer (>22 m), while *Drimys confertifolia* (6.4%) and the invasive tree species *A. chilensis* (6.2%) can be found in the intermediate layer (8–12 m) (Cuevas and Vargas, 2006). *Rhaphithamnus venustus* (1.2%), *Bohemeria excelsa* (1.3%) and *Coprosma pyrifolia* (<1%) are infrequent components of the intermediate and dominant layers. When the forest canopy is broken by gaps, species richness, the proportion of invasive species and the regeneration density of native tree species change (Vargas and Reif, 2009; Arellano, 2011). Gaps were defined as a break of at least 20 m² in the forest canopy extending down through all canopy levels to at least two meters above ground (Brokaw, 1982). For our study we used the expanded gap areas (i.e., canopy gap plus the adjacent area extending to the bases of the surrounding border trees >12 m high; Runkle, 1982). About one quarter of the forest canopy in the study area is affected by gaps that range in size between 46 and 777 m², and are created mainly by senescent trees falling (Arellano, 2011; Vargas et al., 2013). These gaps are created at a yearly rate of ca 2% of the forest surface (Smith-Ramirez et al., 2013). *A. chilensis* and/or *R. ulmifolius* (i.e., invasive species) occur in most gaps in the study area (about 85% of 37 gaps sampled by Arellano (2011)). Half of 46 gaps sampled in a previous study were dominated by invasive species (>30% *A. chilensis* and *R. ulmifolius* cover) whereas one third were dominated by native species (<5% invasive species cover; Vargas and Reif, 2009). Since 2004 the invasive species have been removed from some gaps to improve the nesting habitat of the critically endangered hummingbird (*Sephanoides fernandensis*, Hagen et al., 2005). These gaps provided us with an opportunity to study another category of gaps, “treated” with which to compare regeneration microsites under relatively similar conditions. Accordingly, gaps were categorized as: “natural”, with no or low (<5%) cover of exotic invasive species ($N = 10$), “invaded gaps” with a significant cover of *A. chilensis* and *R. ulmifolius* (>30%, $N = 9$), and “treated gaps”, where the invasive exotic plant species were removed ($N = 11$) by cut-stump control of *A. chilensis* and *R. ulmifolius* by application of Garlon 4® 5% mixture (Tryclopir; Hagen et al., 2005). Invasive species had been removed from the treated gaps for at least one year and at most six years before data collection.

2.2. Sampling design

Within and around 30 canopy gaps we sampled the natural regeneration and variables describing their microsites. Therefore

we laid out a transect in each gap starting at the base of the northern most (N) border tree (>5 cm dbh >12 m high). We established 2×2 m plots (in the following, fine scale plots) systemically in pairs running through the gap center and gap border into the closed forest (S). Thus, the number of plots per gap was dependent on the gap size. We considered gap borders as transitional areas that began at the base of gap border trees and extended up to 5 m into the closed forest (Dyer et al., 2010). A total of 795 trees were sampled in 634 fine scale plots (Fig. 1).

2.2.1. Assessment of tree regeneration

We recorded the following characteristics of the juvenile trees (<5 cm dbh) found in the fine scale plots: species, forest zone (gap, gap border or forest), root collar diameter (cm, measured at the base approximately 1 cm above ground), and total height (m). We categorized the likelihood of survival for each tree as very probable (no symptoms of damage), probable (<10% leaves with chlorosis/necrosis), or poor (>10% leaves with chlorosis/necrosis) (Kulla et al., 2009). The density of tree regeneration was sampled in four additional larger plots (25 m^2 ; Fig. 1). These larger plots that overlapped the fine scale plots had a variable shape depending on the forest zone they were set: inside expanded gaps, at the gap center (5×5 m) and near the internal gap border (2×12.5 m below border trees facing north); on gap borders (2×12.5 m in the shade below bordering trees facing south), and within closed forest (5×5 m). In these plots the juvenile trees <5 cm dbh were counted by species and size category (small seedlings: ≤ 0.5 m; seedlings >0.5–2 m, and saplings >2 m).

2.2.2. Assessment of microsite conditions and vegetation

In each fine scale plot we measured additional variables describing the microsites for natural regeneration considering (a) the cover estimation of: native ferns, *A. chilensis* and *R. ulmifolius* (using 5% intervals; Mueller-Dombois and Ellenberg, 1974). We sampled the (b) regeneration substrate, as cover by: moss and liverworts, litter, mineral soil, rock and coarse woody debris (>3 cm diameter). To estimate the (c) solar radiation transmittance, hemispherical photos were taken under continuous cloud cover from the center of each fine scale plot at 0.45 and 1.45 m above the

ground (Nikon Coolpix 990 fitted with a Nikon FC-E8 converter[®]). Further explanatory variables (d) were attributed to each fine scale plot including: gap type (natural, invaded, treated) forest zone (gap, gap border, closed forest), gap size (m^2 , calculated with the ellipse formula using NS, EW axes; only for plots within gap and gaps borders), elevation (m.a.s.l.), slope (%), slope contour (straight, convex, concave), time after invasive species treatment (only for treated gaps: long >4 years ago, intermediate >2–4 years ago, recent <2 years ago), and estimated gap age. The estimated gap age was derived from the state of decay of the gapmakers (i.e., canopy tree creating a gap; Lertzman et al., 1996). Gapmakers found were categorized as: little decay: having intact twigs and bark; intermediate decay: absence of twigs, fragmented bark; and mostly decayed: absence of twigs and bark (adapted from Carmona et al., 2002). The presence of a single mostly decayed gapmaker log indicated an “old” gap and in the absence of mostly decayed logs, the next decay category was assigned, either “intermediate” or “newly formed” gap (Lertzman et al., 1996).

2.3. Data analysis

2.3.1. Microsites and tree regeneration

We separately compared the microsites and tree regeneration on the different forest zones (gaps, gap borders and closed forest) and gap types (natural, invaded or treated). Because of the unbalanced design we resampled the fine scale (4 m^2) and regeneration plots (25 m^2) with 1000 bootstrap permutations to stabilize the sampling effort for the mean and standard errors (Canty, 2002). Since most variables were not normally distributed we used the non-parametric Kruskal Wallis test in combination with pairwise Wilcoxon comparisons (Kent, 2012). These and all following statistical analyses were conducted in R (v. 2.15.1; R Development Core Team, 2012).

2.3.2. Estimation of percentage of above canopy light (PACL)

The hemispherical photos were analyzed with HemIMAGE[®] following the protocol of Brunner (2002). This software estimates the solar radiation transmittance as the relationship between the total (i.e., above canopy) and current light (i.e., below canopy) reaching

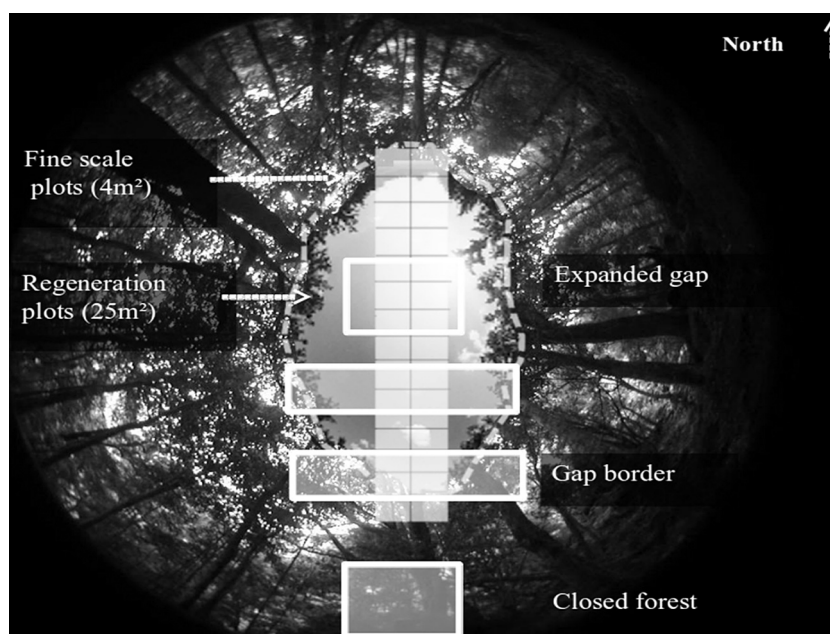


Fig. 1. Horizontal scheme of the field sampling based on a hemispherical photograph. Forest zones are given at right (gap, gap border, forest). The transect established to include: gap, gap borders and closed forest zones is represented considering fine scale (2×2 m) and regeneration plots (5×5 and 2×12.5).

Table 1

Variables describing the microsites for natural regeneration of native tree species in 30 canopy gaps in the montane forest of RCI. (a) Native ferns and invasive species, (b) regeneration substrate, (c) estimated light transmittance, and (d) density of juvenile trees, are compared among natural, invaded and treated areas in a transect gap-forest. Expanded canopy gaps, gap borders (southern border) and closed forest are compared, values in the table are means \pm standard errors. Significant differences are shown with different letters (Wilcoxon test, $P < 0.05$). Sampling effort was stabilized through 1000 random samples based on 634 fine scale plots (4 m², for: a, b, c) and 120 regeneration plots (25 m², for: d).

Forest zones Gap types	Expanded canopy gap (n = 489 fine scale plots/ 60 regeneration plots)			Gap borders (n = 89 fine scale plots/30 regeneration plots)			Closed forest (n = 56 fine scale plots/30 regeneration plots)		
	Natural (n = 160)	Invaded (n = 141)	Treated (n = 188)	Natural (n = 28)	Invaded (n = 29)	Treated(n = 32)	Natural (n = 24)	Invaded (n = 16)	Treated (n = 16)
<i>(a) Native ferns and invasive species (in% cover)</i>									
Ferns (%)	34.3 \pm 0.7 a	8.3 \pm 0.3 b	35.7 \pm 1.0 a	48.8 \pm 0.7 a	19.6 \pm 0.5 b	22.6 \pm 0.6 b	27.4 \pm 0.6 a	25.6 \pm 0.6 a	26.4 \pm 0.3 a
<i>Rubus ulmifolius</i> (%)	0.4 \pm 0.0 a	54.3 \pm 1.0 b	5.3 \pm 0.3 c	0.2 \pm 0.0 a	26.9 \pm 0.8 b	0.8 \pm 0.1 a	0.0 \pm 0.0 a	0.5 \pm 0.1 a	0.5 \pm 0.1 a
<i>Aristolelia chilensis</i> (%)	0.5 \pm 0.1 a	16.8 \pm 0.6 b	5.3 \pm 0.3 c	0.3 \pm 0.0 a	9.8 \pm 0.5 b	2.0 \pm 0.1 ab	0.4 \pm 0.0 a	5.9 \pm 0.3 a	0.0 \pm 0.0 a
Invasives (%)	1.0 \pm 0.1 a	71.2 \pm 1.2 b	10.6 \pm 0.5 c	0.5 \pm 0.0 a	36.8 \pm 0.9 b	2.8 \pm 0.1 a	0.4 \pm 0.0 a	6.4 \pm 0.4 a	0.5 \pm 0.1 a
<i>(b) Regeneration substrate(in% cover)</i>									
Mosses and Liverworts (%)	7.3 \pm 0.2 a	13.4 \pm 0.6 b	14.9 \pm 0.7 b	6.4 \pm 0.1 a	24.5 \pm 1.0 b	6.3 \pm 0.2 a	13.9 \pm 0.7 a	9.6 \pm 0.2 a	7.2 \pm 0.1 a
Coarse woody debris (%)	16.6 \pm 0.5 a	38.1 \pm 0.7 b	20.4 \pm 0.7 a	1.7 \pm 0.1 a	27.1 \pm 0.7 b	15.8 \pm 0.4 b	2.1 \pm 0.1 a	14.3 \pm 0.4 b	3.9 \pm 0.2 a
Litter (%)	75.5 \pm 0.4 a	59.0 \pm 0.6 b	52.5 \pm 0.8 b	81.2 \pm 0.3 a	65.1 \pm 0.7 b	67.4 \pm 0.7 b	80.6 \pm 0.7 a	87.8 \pm 0.2 a	86.3 \pm 0.4 a
Mineral soil (%)	5.1 \pm 0.1 a	5.9 \pm 0.1 b	5.5 \pm 0.1 ab	3.0 \pm 0.1 a	4.7 \pm 0.1ac	6.8 \pm 0.1 c	2.5 \pm 0.1 a	4.2 \pm 0.1 a	1.0 \pm 0.0 a
Rock cover (%)	16.7 \pm 0.3 a	21.7 \pm 0.3 b	15.7 \pm 0.4 a	15.8 \pm 0.3 a	26.5 \pm 0.3 b	12.0 \pm 0.2 a	26.0 \pm 0.3 ac	15.6 \pm 0.2 b	20.0 \pm 0.3 c
<i>(c) Estimated light transmittance (PACL, percentage above canopy light)</i>									
Total PACL 0.45 m (%)	10.0 \pm 0.2 ac	8.7 \pm 0.2 b	10.8 \pm 0.2 c	4.8 \pm 0.1 a	7.0 \pm 0.2 a	6.2 \pm 0.1 a	4.1 \pm 0.1 a	3.5 \pm 0.0 a	3.7 \pm 0.0 a
Total PACL 0.145 m (%)	11.6 \pm 0.2 a	11.2 \pm 0.2 a	13.7 \pm 0.3 a	5.2 \pm 0.1 a	8.7 \pm 0.2 a	6.1 \pm 0.1 a	5.4 \pm 0.1 a	3.9 \pm 0.0 a	3.9 \pm 0.0 a
<i>(d) Density of juvenile tree species (number of individuals < 5 cm dbh/ha)</i>									
	(n = 20)	(n = 18)	(n = 22)	(n = 10)	(n = 9)	(n = 11)	(n = 10)	(n = 9)	(n = 11)
<i>Myrceugenia fernandeziana</i>	5215.6 \pm 93.5 a	1860 \pm 80.6 b	3211.2 \pm 132.8 b	6731.2 \pm 78.4 a	7480.8 \pm 163.8 a	6768.4 \pm 117.4 a	3024.4 \pm 59.6 a	3216.8 \pm 79.6 a	3455.2 \pm 59.5 a
<i>Fagara mayu</i>	650.4 \pm 38.9 a	118 \pm 14.9 a	432.4 \pm 61.6 a	420 \pm 27.6 a	0 \pm 0.0 a	0 \pm 0.0 a	123.2 \pm 13.5 a	0 \pm 0.0 a	0 \pm 0.0 a
<i>Drimys confertifolia</i>	200 \pm 18.4 a	20 \pm 2.8 a	199.2 \pm 18.1 a	0 \pm 0.0 a	0 \pm 0.0 a	239.2 \pm 19.4 a	0 \pm 0.0 a	96 \pm 8.2 a	0 \pm 0.0 a
<i>Rhaphithamnus venustus</i>	40 \pm 3.8 a	0 \pm 0.0 a	65.6 \pm 5.8 a	0 \pm 0.0 a	0 \pm 0.0 a	146 \pm 16.5 a	0 \pm 0.0 a	0 \pm 0.0 a	0 \pm 0.0 a
<i>Bohemeria excelsa</i>	0 \pm 0.0 a	48.8 \pm 6.1 a	131.2 \pm 20.1 a	0 \pm 0.0 a	0 \pm 0.0 a	0 \pm 0.0 a	0 \pm 0.0 a	0 \pm 0.0 a	0 \pm 0.0 a
Standing dead	84 \pm 10.1 a	23.6 \pm 3.0 a	0 \pm 0.0 a	80.8 \pm 7.6 a	0 \pm 0.0 a	68 \pm 7.1 a	206 \pm 6.3 a	48 \pm 4.1 a	453.2 \pm 13.8 a
Regeneration \leq 0.5 m	1019.2 \pm 28.7 a	724 \pm 32.2 a	1061.6 \pm 35.2 a	1462 \pm 34.3 a	1882.8 \pm 45.4 a	1916 \pm 48.7 a	566.8 \pm 25.3 a	914.8 \pm 18.1 a	1128.8 \pm 10.4 a
Regeneration 0.5–2 m	2120.4 \pm 44.5 a	527.2 \pm 31.7 b	1584 \pm 57.5 ab	2747.6 \pm 41.9 a	3248.4 \pm 85.2 a	3006.8 \pm 68.9 a	1306.8 \pm 28.4 a	1170 \pm 38.6 a	1425.6 \pm 32.0 a
Regeneration >2 m	2966.4 \pm 71.0 a	795.6 \pm 37.9 b	1394 \pm 64.0 ab	2941.6 \pm 37.1 a	2349.6 \pm 46.0 a	2230.8 \pm 30.1 a	1274 \pm 22.6 a	1228 \pm 41.8 a	900.8 \pm 29.1 a
Total regeneration	6106 \pm 113.2 a	2046.8 \pm 91.7 b	4039.6 \pm 141.7 ab	7151.2 \pm 81.7 a	7480.8 \pm 163.8 a	7153.6 \pm 132.6 a	3147.6 \pm 59.0 a	3312.8 \pm 76.1 a	3455.2 \pm 59.5

the forest floor for a defined period by calculating the percentage above canopy light (PACL%; Brunner, 2002). The five warmest months on RCI (December 1st–April 30th) were used as the calculation period assuming that 50% of the light was diffuse light due to cloudiness (Hajek and Espinoza, 1987).

2.3.3. Estimating performance of native tree species regeneration

To evaluate tree performance (i.e., vitality), the ratio height–root collar diameter of the individuals (m/cm; furthermore called height–diameter ratio) was selected as an indicator. It combined two morphological traits and provided good differentiation between the performance classes defined based on chlorosis/necrosis (Trubat et al., 2010; Kulla et al., 2009). To test the significance of this performance indicator we did a binary logistic regression. We wanted to detect if an increase in the height–diameter ratio (independent variable) brought about an increase in the individuals categorized as “performing good” (dependant binomial variable; function glm; R Development Core Team, 2012; Dobson, 2001).

2.3.4. Classification and regression trees

We used classification and regression trees to determine how environmental variables influenced native tree species regeneration. This was performed within a conditional inference framework to explain variation in the response variables as a function of the explanatory variables. We used recursive partitioning to derive classification trees for categorical response variables: explaining the regeneration of the native tree species as the presence or absence of juvenile individuals (<5 cm dbh). We considered regen-

eration presence-absence for species all together and separately for the main forest species in gaps and gap borders. We created regression trees for the continuous response variables: density and performance, considering only individuals of the most frequent species (<5 cm dbh, <2 m high), which was *M. fernandeziana*. All other tree species had a low frequency ($n < 50$). Analyses were executed with the non-parametric conditional inferences tree methods implemented in the ‘ctree’ function in the R package ‘party’ (Hothorn et al., 2006). At each step of the analysis one explanatory variable was selected from all available variables based on the best separation of two homogenous groups using a permutation test; this point was determined by a numerical value (threshold) of the explanatory variable (Hothorn et al., 2006). The relationships between the response variable and explanatory variables are presented in a dichotomous tree diagram. The explanatory variables were: (a) cover estimation of: native ferns, *A. chilensis* and *R. ulmifolius*, (b) regeneration substrates, (c) estimated solar radiation transmittance and (d) other explanatory variables such as gap types (natural, invaded, treated), forest zone (gap, gap border, closed forest), gap size, elevation, slope, shape of slope contour, time after invasive species treatment and estimated gap age.

3. Results

3.1. Small-scale disturbances create favorable microsite conditions for the regeneration of tree species

Overall, differences in microsites and densities of juvenile trees were significantly more frequent in gaps and gap borders. Under

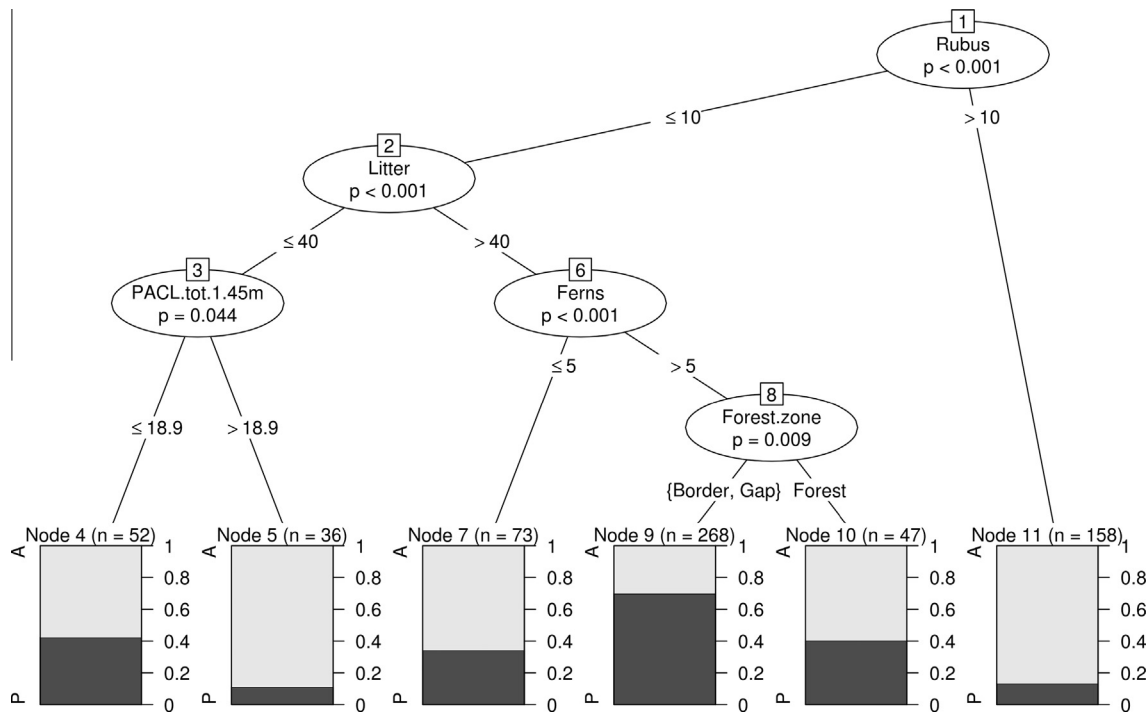


Fig. 2. Classification tree to predict the presence–absence of forest regeneration in the RCI forest (<5 cm dbh, including all species) based on the conditional inference tree model. The circled explanatory variables are those showing the strongest association to the response variable. Values on lines connecting explanatory variables indicate splitting criteria; for example, the first split separated plots with $\leq 10\%$ cover of Rubus (left split) from with $> 10\%$ Rubus (right side of the split). Numbers in boxes above the explanatory variable indicate the node number. P-values at each node represent the test of independence between the listed independent variable and the response variable. “n = ” over terminal nodes indicates the number of plots classified in that node. The predicted presence or absence of regeneration is given by the terminal block representing the probability of regeneration presence (P, dark part of blocks) or absence (A, gray part) based on 634 fine scale plots (4 m²). Explanatory variables included were: estimated cover (%) of: native ferns = Ferns, *Rubus ulmifolius* = Rubus, and *Aristolotelia chilensis*; regeneration substrate (cover of: mosses and liverworts, coarse woody debris, litter = Litter; mineral soil and rocks); estimated total light transmittance (percentage above canopy light = PACL.tot.1.45 m, at 1.45 m above ground, and PACL at 0.45 m); and other explanatory variables (Forest zone: gap, borders, forest; gap size, elevation, slope, shape of the slope contour, time after invasive species treatment, and estimated gap age).

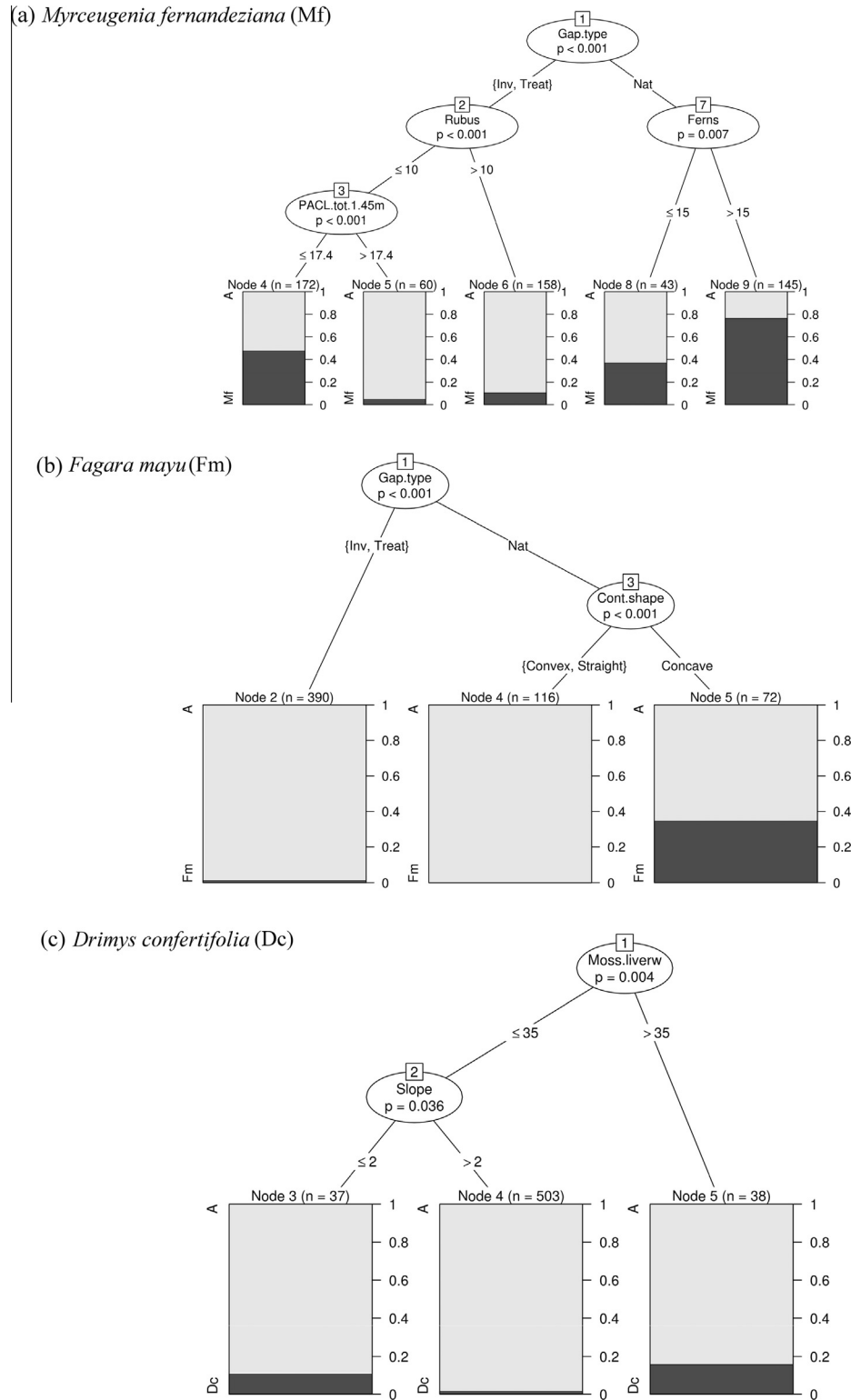


Fig. 3. Classification tree to predict presence–absence of regeneration of the main tree species (<5 cm dbh) based on a conditional inference tree model (Hothorn et al. 2006). Trees were sampled in 578 plots (4 m²) in gaps and gap borders in the RCI forest. The terminal blocks represent the probability of regeneration presence (dark part of blocks) or absence (A, gray part) for (a) Mf = *M. fernandeziana*, (b) Fm = *F. mayu* and (c) Dc = *D. confertifolia*. The encircled explanatory variables show the strongest association to the response variable (regeneration presence or absence). Values on lines connecting explanatory variables indicate splitting criteria. Numbers in boxes above the explanatory variable indicate the hierarchical node number. *P*-values at each node represent the test of the relationship between the listed independent variable and the response variable. The “n =” over terminal nodes indicate the number of plots classified in that node. Explanatory variables included were: estimated cover of: ferns = Ferns, *Rubus ulmifolius* = Rubus, and *Aristotelia chilensis*; regeneration substrate (cover of: mosses and liverworts = Moss.liverw, coarse woody debris, litter, mineral soil and rocks), estimated light transmittance (percentage above canopy light at 0.45 m and at 1.45 m above ground = PACL .tot.1.45 m), and other explanatory variables (gap types = Gap.type; forest zone, gap size, elevation, slope, shape of the slope contour = Cont.shape; time after invasive species treatment, and estimated gap age). See Fig. 1 for further explanation.

closed forest there were almost no differences in microsite or regeneration densities among gap types (Table 1). Among the gap types (natural, invaded, treated) there were significant differences in the cover of native ferns, *A. chilensis* and *R. ulmifolius* (Kruskal Wallis $H = 154, 204, 371$; respectively, $P < 0.001$), in the proportion of regeneration substrates ($H = 175, 64, 175$, for litter, mineral soil and coarse woody debris respectively, $P < 0.001$), light transmittance ($H = 96, 132$ for PACL at 0.45 and 1.45 m high respectively, $P < 0.001$) and total density of tree regeneration ($H = 54, P < 0.01$). Invaded gaps and borders had 25–30% less fern cover than natural areas and about 35–70% more invasive species cover (*A. chilensis* + *R. ulmifolius*). The cover of invasive species in treated areas was found to be intermediate between natural and invaded areas and these treated gaps had almost the same fern cover as natural gaps (Table 1). The cover of mosses, liverworts and coarse woody debris were higher in invaded and treated gaps and gap borders compared to natural areas. Litter covered more ground in natural gaps and borders. Out of the two invasive species, *R. ulmifolius* covered more surface than *A. chilensis*. Solar radiation transmittance was only lower in invaded gaps (compared at the 0.45 m height, $P < 0.01$).

Independent of gap type, the highest density of juvenile trees was found in gap borders. Natural gaps had on average 4000 more juvenile trees/ha than invaded gaps and about 2000 more juvenile trees than treated gaps. Gap types did not vary in the density of standing dead juvenile individuals. We found significant differences in densities between gap types but only for the most frequent tree species *M. fernandeziana*. This species comprised about 85, 90 and 80% of the forest regeneration in natural, invaded and treated gaps respectively. Other tree species established mostly inside gaps. *F. mayu* had the second highest regeneration density (Table 1). Compared with natural areas, *F. mayu* had ca 80% fewer individuals per ha in invaded gaps, and 34% less in treated areas although differences were non-significant. The regeneration of *Drimys confertifolia* was also concentrated in gaps with around the same number of individuals per ha in natural and treated areas (Table 1). Other regenerating tree species like *R. venustus* and *B. excelsa*, were considerably less abundant (<150 individuals/ha).

3.2. Microsite variable thresholds defining the presence of native tree species regeneration

When *R. ulmifolius* cover was >10% of a fine scale plot, the probability of finding regeneration of any native tree species was <15% (Fig. 2). Other significant factors determining regeneration were litter proportion, total light transmittance, fern cover, and forest zone (gap, gap borders, closed forest; Fig. 2).

We examined the likelihood of encountering the three most common species *M. fernandeziana* (Fig. 3a), *F. mayu* (Fig. 3b) and *D. confertifolia* (Fig. 3c) within plots located in gaps or in the gap borders because this was where the highest probability of finding juvenile trees and also where the highest density was found (Table 1, Fig. 2). *M. fernandeziana* and *F. mayu* were both found with a higher probability in natural gaps while it was less likely to find them in invaded or treated gaps (Fig. 3a and b, node 1; Gap type). *M. fernandeziana* (Fig. 3a, node 7) occurred with a higher probability in natural gaps with >15% fern cover. In invaded and treated gaps >10% *R. ulmifolius* cover reduced the probability of finding seedlings of *M. fernandeziana* (Fig. 3a, node 2). But even if the *Rubus* cover was below the threshold, light transmittance >17.4% PACL seemed to hamper the occurrence of *M. fernandeziana*. The probability of finding *F. mayu* and *D. confertifolia* regeneration was very low (Fig. 3b and 2c). Concave slopes in natural gaps provided more favorable regeneration conditions for *F. mayu*. The presence of *D. confertifolia* regeneration seemed to be linked with

a higher proportion of mosses and liverworts, and flat areas (>35%, ≤2% slope; Fig. 3c).

3.3. Density and performance of *M. fernandeziana*

The density (number of individuals/100 m²) of *M. fernandeziana* appeared to be affected by *R. ulmifolius* cover (Fig. 4, node 1). If *R. ulmifolius* cover exceeded 10%, then it was very unlikely to find *M. fernandeziana* regeneration. The highest density was found in areas with ≤10% of *R. ulmifolius* cover and light transmittance ≤9.2% PACL (Fig. 4 node 2). If the aforementioned conditions were met, then natural gaps (Fig. 3, node 4) showed a higher likelihood of finding higher densities of juvenile *M. fernandeziana*. Regeneration density was lowest in invaded and treated areas with light transmittance >13.5% PACL and ≤5% cover of the invasive *A. chilensis*. The cover of *A. chilensis* increased the probability of finding a higher density of *M. fernandeziana* regeneration in invaded and treated gaps with 13.5% PACL (Fig. 4 node 10).

The height-diameter ratio (m/cm) was positively related with the performance categories and significantly ($P < 0.01$) predicted the presence of high performance trees. Based on this result we assumed that the higher the height-diameter ratio value, the higher the performance (Fig. 5). High performing individuals were most likely found in gap borders rather than in the gaps (Fig. 5, node 1). The height-diameter ratio was highest in the borders of gaps with a size range of 161 to 199 m² (Fig. 5 node 2 and 3). In the borders of larger gaps, fern cover >35% was related to an increase in the height-diameter ratio (Fig. 5 node 6). In gap zones the highest height-diameter ratio was likely to be found in invaded or natural gaps (Fig. 5). If gaps were treated, lower percentages of canopy light (<8.3 PACL) seemed to enhance the height-diameter ratio.

4. Discussion

4.1. How do small-scale disturbances impact tree regeneration?

In the montane forest of Plazoleta del Yunque of RCI, treefall canopy gaps affected the regeneration conditions for native tree species significantly by influencing: the cover of ferns and the cover of invasive species, changes in light transmittance, proportions of coarse woody debris, mineral soil exposure, moss and liverworts cover, and amount of litter. These effects are similar to the natural patch dynamics found in many of the world's forests whereby canopy gaps contribute to the maintenance of uneven-aged forest structure, nutrient cycling, preservation of soil and plant species diversity, and changes in micro-topography (Pickett and White, 1985; Schliemann and Bockheim, 2011). Our results confirm that invasive species currently alter the direction of these changes in the montane forests of RCI and in particular by reducing the chances of native tree species regeneration. Fern cover, litter cover and light transmittance were higher in natural gaps while invasive species, coarse woody debris and mosses and liverworts were more dominant in invaded and treated gaps. Among gap types, differences in the proportions of microsites and juvenile tree densities were significant inside canopy gap areas, less pronounced in gap borders and tended to disappear below the closed forest where in all cases, invasive species cover declined. This shows that the higher resource availability in gap and border zones (e.g. increases in light intensity and nutrients due to the decomposition of fallen trees, and less competition for water uptake; Baret et al., 2008; Pickett and White, 1985) provide regeneration opportunities for native as well as for invasive species. Similar findings have been reported on other islands where canopy gaps are shown to be favorable for invasive species that interrupt the forest regeneration cycle by outcompeting native species (Baret et al., 2008; Loh and Daehler, 2008).

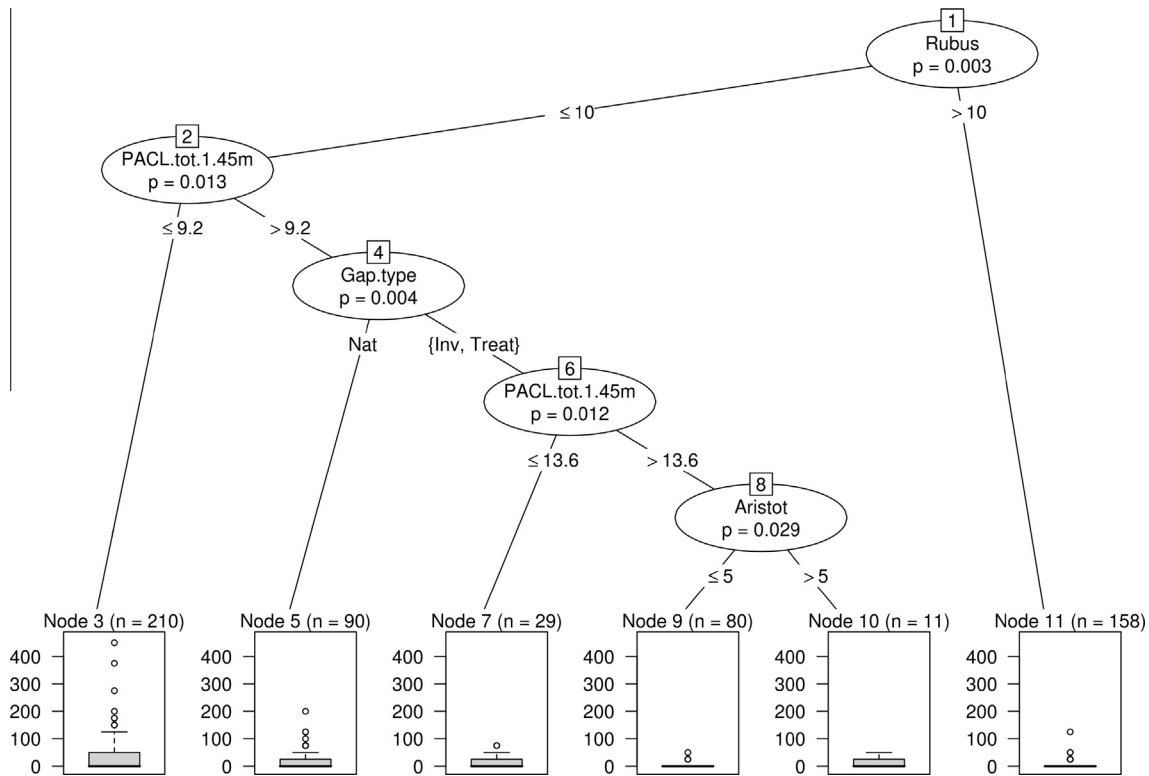


Fig. 4. Regression tree to predict the density of *M. fernandeziana* regeneration (<5 cm DBH <2 m high) located in gap and gap borders in the RCI forest within the conditional inference framework. The encircled explanatory micro-habitat variables, are those showing the strongest association to the response variable (seedlings density/100 m²). *P*-values listed at each node represent the test of independence between the listed independent variable and the response variable. Numbers in boxes above the explanatory variable indicate the node number and values on lines connecting explanatory variables indicate splitting criteria. The “*n* =” above terminal nodes indicate the number of plots classified in that node. The boxplots at the terminal node represent the density of regeneration for all the plots within that branch. Boxes represent the inner-quartile range of the data, dark horizontal lines within the boxes represent the median. Circles above and below the whiskers represent data points outside of this range. Explanatory variables included were estimated cover of: ferns = Ferns, *Rubus ulmifolius* = Rubus, and *Aristotelia chilensis* = Aristot; regeneration substrate (cover of: mosses and liverworts = Moss.liverw, coarse woody debris, mineral soil and rocks); estimated light transmittance (percentage above canopy light at 0.45 m and at 1.45 m above ground = PACL.tot.1.45 m); and other explanatory variables (gap types = Gap.type; forest zone, gap size, elevation, slope, shape of the slope contour, time after invasive species treatment, and estimated gap age). The regeneration substrate: litter, presented the strongest association with the density of *M. fernandeziana* when covered >75% (not shown); we excluded it from the analyzed variables, to enable identifying other independent variables highly related with the response. See Fig. 1 for further explanation.

4.2. What determines the presence of native tree regeneration?

The invasive species *R. ulmifolius* had the greatest negative effect on the occurrence of juvenile native trees on RCI and seemed more aggressive than *A. chilensis*. The reduction in light availability due to invasive species seemed not to affect the establishment of regeneration. In the absence of invasion, open areas showed a lower probability of the occurrence of juvenile trees than did more shaded areas. This suggests that none of the native forest species on RCI are adapted to act as pioneers and able to colonize extremely open conditions. Instead, the native tree species seemed to require semi-shade, or more likely, some protection against environmental stress to establish. Even *F. mayu*, the most shade-intolerant tree species in this forest type, (Vargas et al., 2010) may have dispersal limitations that prevent it from taking advantage of open areas (e.g., gap centers). Competition from invasive species for other resources like water and nutrients may be more influential in limiting forest regeneration than low light availability does. Light, space, water and nutrient deficits and increased root competition are well known consequences of invasive species at the stand level (Gordon, 1998; Vilà et al., 2011). The probability of regeneration establishing was greater in plots with fern cover >5%. In a previous study we found that tall forbs and ferns facilitate the establishment of *M. fernandeziana* and *D. confertifolia* (Vargas et al., 2010). A complementary species may facilitate the establishment of other species by reducing abiotic or biotic environmental

stress (Levine, 1999). Ferns may reduce light availability, but they also may protect the soil from drying out and limit the establishment of invasive species particularly in gaps and gap borders. Fern cover has shown to have a positive impact on tree regeneration in Australian rainforests by protecting it from bird disturbances (Song et al., 2012) and similarly, understory of bamboo in Patagonia was found to facilitate the early survival of seedlings by slowing the rate at which soil dried (Caccia et al., 2009).

The regeneration of the main forest species on RCI was concentrated in expanded gaps and gap borders but the species showed differences in their requirements for establishment and early growth. For *M. fernandeziana* the highest probability of regeneration was found in non-invaded areas with fern cover, which suggest that fern cover facilitates the establishment of *M. fernandeziana*. The plots with the lowest regeneration probability of *M. fernandeziana* were in invaded and treated gaps with open conditions and the result was the same even when the cover of *R. ulmifolius* was low, which suggests that *M. fernandeziana* does not require much light to establish. Similar conclusions have been arrived at based on the spatial distribution pattern of the species (Vargas et al., 2010), and is also in agreement with the findings for the *Myrceugenia* genus in continental Chile where Donoso (2006a,b), stated that this genus has a high degree of shade tolerance. The probability of finding regeneration of *M. fernandeziana* decreased when *R. ulmifolius* cover increased above 10%. The negative impacts that invasive species have on the abundance and diversity of native tree

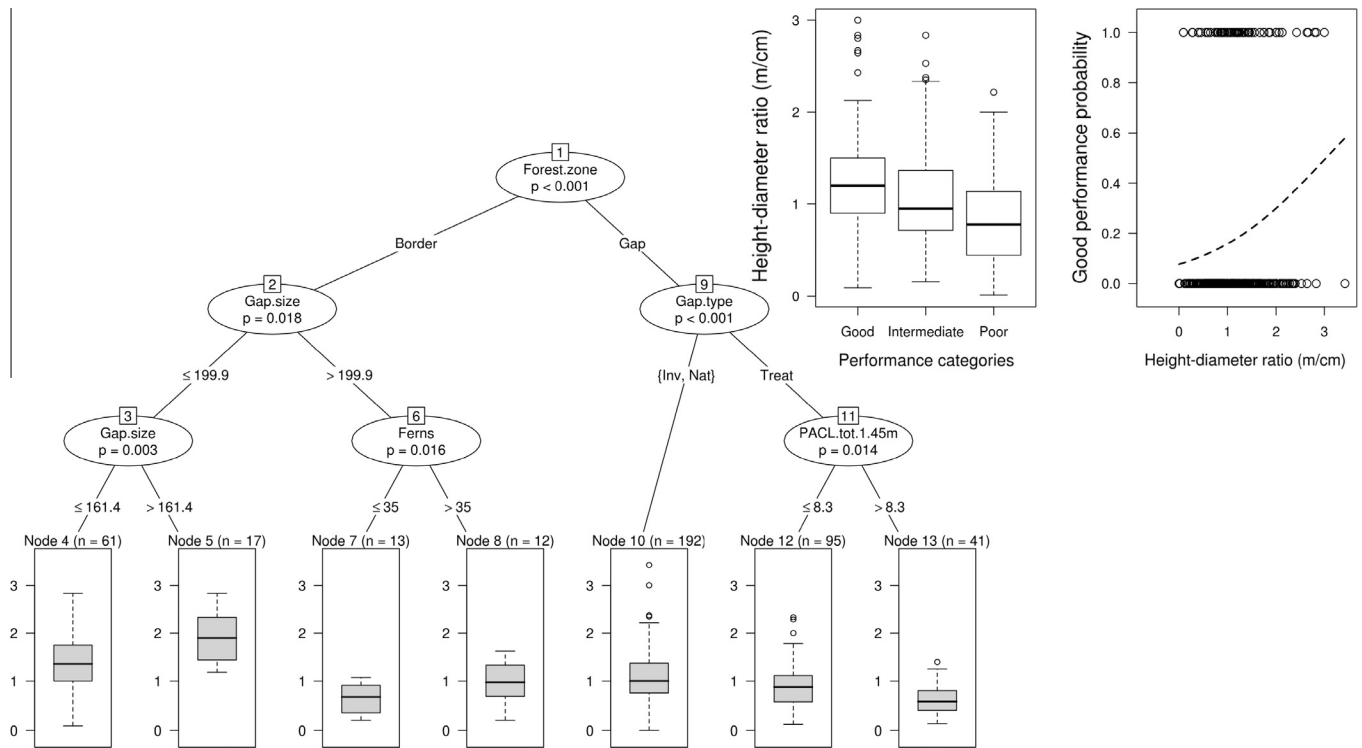


Fig. 5. Regression tree to predict the performance (High-diameter ratio m/cm) of seedlings of *Myrceugenia fernandeziana* based on a conditional inference tree model. Individuals located in gap and border zones in the RCI forest were included (<5 cm DBH, <2 m high, $N = 431$). Micro-habitat explanatory variables encircled, represent the strongest association to the response (height-diameter ratio of seedlings as performance indicator). P -values represent the test of independence between the listed variable and the height-diameter ratio. The boxplots below represent the values of the height-diameter ratio (total height/root collar diameter, m/cm), for the seedlings within each branch in the terminal nodes. Boxes represent the inner-quartile range of the data, dark horizontal lines within the boxes represent the median and circles above and below the whiskers represent data points outside of this range. Explanatory variables included were: estimated cover (%) of: native ferns = Ferns, *Rubus ulmifolius* = Rubus, and *Aristolelia chilensis* = Aristot); regeneration substrate (cover of: mosses and liverworts, and rocks); estimated light transmittances (percentage above canopy light at 1.45 m and at 1.45 m above ground = PACL .tot.1.45 m); and other explanatory variables (gap types = Gap.type; forest zone = Forest.zone; gap size = Gap.size; elevation, slope, shape of the slope contour, time after invasive species treatment, and estimated gap age). In the upper right corner, the boxplots show the values of height-diameter ratio of the juvenile trees classified in performance categories (good, intermediate, poor) and the scatter plot show the logistic regression between high-diameter ratio and the probability of good performance occurrence (P value < 0.01). See Fig. 1 for further explanation.

regeneration have also been reported for other forest ecosystems (Gordon, 1998; Vilà et al., 2011). Invasive species on RCI have faster growth rates than *M. fernandeziana* and are probably more efficient in water and nutrient uptake. Native forest species with water stress symptoms have been observed in invaded shrublands on RCI (Vargas et al., 2011). With increasing drought, competition from *Rubus fruticosus* increased water stress levels for the temperate tree species *Fagus sylvatica* in Europe thereby limiting its growth (Fotelli et al., 2001). Drought stress and mortality in late summer have been observed on the regeneration of *M. fernandeziana* in low montane forests of RCI (Cuevas, 2002). This suggests that competition from *R. ulmifolius* could likely influence water stress on *M. fernandeziana* juvenile trees.

There was a higher probability of finding juvenile *F. mayu* in natural gaps and in gap borders situated in depressions (concave shape). In these natural areas there was negligible competition by invasive species. The higher frequency of *F. mayu* in depressions suggests that it prefers sites where water and nutrients may accumulate. Such accumulation areas, like the bottom of slopes might be key for the establishment of this species. In the temperate forests of Japan, lower slopes provided sites where *Fagara mantchurica* established as pioneer species (Okubo et al., 2005). Juvenile *D. confertifolia* were significantly more likely to be found in flat areas that had a thick carpet of mosses and liverworts. The establishment of *D. confertifolia* seems to be promoted by the removal of invasive species which was done mostly in level areas (Hagen et al., 2005) where the liverwort *Marchantia polymorpha* was also more common, particularly in treated gaps and borders

(Pers. Observation). Facilitation by bryophytes after clear cuts and large natural disturbances has been documented for coastal temperate forests of southern Chile. There the bryophytes enhanced water retention and promoted the establishment of tree species (Díaz and Armesto, 2007).

4.3. What influences the density and performance of *M. fernandeziana*?

Independent of the gap type and the forest zones, *M. fernandeziana* was the dominant regeneration species. The plasticity of *M. fernandeziana* allows it to take advantage of all types of microsites in the RCI forests. This helps explain its structural dominance in all layers of this forest (Vargas et al., 2010). Light availability also seems to be essential for high densities of *M. fernandeziana*. In invaded and treated gaps with low cover of *R. ulmifolius*, the cover of the invasive species *A. chilensis* was associated with the establishment of *M. fernandeziana*. Such facilitation has also been found in Hawaii where invasive species promote the establishment of endemic species in semi-natural forests (Fischer et al., 2009).

The performance of *M. fernandeziana* individuals regenerating in gaps and gap borders was very well indicated by their height-diameter ratio. The best performance shown by juvenile trees was found in gap borders. We found that gap borders represent intermediate areas between disturbed and closed forests. They have semi-shaded conditions, less cover of invasive species, more advanced regeneration, less mineral soil exposure and more litter accumulation than the open and disturbed expanded gap

zone. The enhanced growth of the juvenile trees could be due to the litter accumulation which is associated with higher nutrient availability (Prescott, 2002). Performing particularly well were those individuals located in the border areas of the gaps with a size between 160 and 200 m². Here they seem to have higher establishment and growth rates. Gaps in this size range are commonly found in the forests of RCI where 1–3 gapmakers frequently create openings of less than 500 m² (Arellano, 2011; Vargas et al., 2013). The cover of ferns was positively associated with the performance of *M. fernandeziana* in the borders of gaps larger than 200 m². Thus, fern cover seems not only to facilitate the regeneration of *M. fernandeziana*, but also its performance in areas where large disturbances occur. The performance of *M. fernandeziana* in gaps was found to be the same whether in natural or invaded plots suggesting that invasive species have no direct affect. On the other hand, individuals located in treated gaps, where there was a moderate to high light availability, performed poorly suggesting that *M. fernandeziana* is a plastic shade tolerant species that needs intermediate to low light conditions to perform well.

5. Conclusions and management recommendations

Small-scale disturbances such as falling trees creating canopy gaps changed the microsite conditions and affected tree regeneration in the forests of RCI. Gap border areas provided the best conditions for the regeneration of native tree species. These areas are protected by the adjacent forest and have intermediate light conditions. The native forest species of RCI are able to establish in the presence of *R. ulmifolius* as long as its cover does not exceed 10%. When this threshold is surpassed, the probability of finding tree regeneration is reduced to <20%. *R. ulmifolius* seems to be more aggressive than *A. chilensis*. It currently covers considerably more area in gaps and gap borders and seems to spread more rapidly asexually than *A. chilensis*. Invasive species significantly reduce the light availability in gaps, but this reduction in itself was not found to be problematic because even non-invaded areas that were highly exposed had a lower probability of tree regeneration. The highest densities of juvenile *M. fernandeziana*, the most important tree species on RCI, were found under light conditions similar to that of invaded gaps. Space preemption and competition from invasive species for water and nutrients are likely more important than the reduction in light has on limiting forest regeneration on RCI. Fern cover had a positive effect on the performance of *M. fernandeziana* in the gap borders of large gaps (>200 m²). Therefore, we conclude that fern cover plays an important role in the natural regeneration dynamics on RCI. Although ferns reduce the light availability, they also can compete with invasive species and may prevent soil drying.

Restoration treatments should attempt to recreate intermediate disturbance conditions and focus on gap borders and small gaps (<200 m²) as the best microsites for native tree regeneration on RCI. Promoting fern cover and limiting invasive species and in particular the cover of *R. ulmifolius* to <10% seem to be key factors. Large-scale interventions (>300 m²) are not preferable considering that native tree species do not perform well in exposed areas and that large interventions may also be associated with higher rates of erosion. Future treatments should explore methods that mimic natural microsites required for establishment by native forest tree species, for example treating but not removing mature *A. chilensis*, in combination with treatment of *R. ulmifolius* and promotion of fern cover. The identification of key variable thresholds important for restoration processes can help guide practitioners to manage invasive species and create conditions suitable for successful native species regeneration.

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