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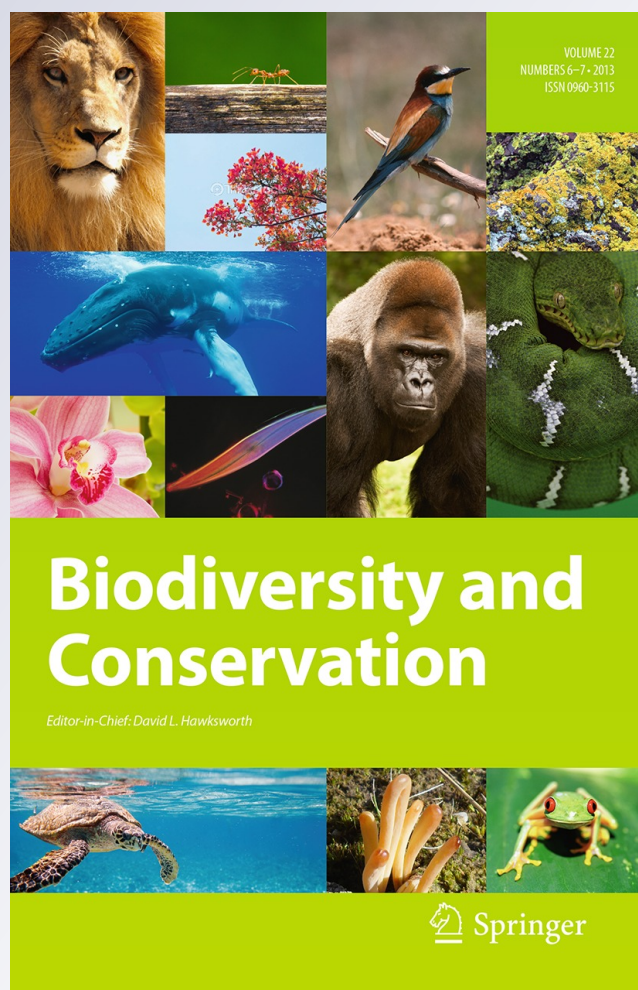
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# Does restoration help the conservation of the threatened forest of Robinson Crusoe Island? The impact of forest gap attributes on endemic plant species richness and exotic invasions

R. Vargas · S. Gärtner · M. Alvarez · E. Hagen · A. Reif

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**Abstract** Invasive plant species are major drivers of biodiversity losses, especially on islands which are prone to invasions and extinctions. In the “endemic montane forest” of Robinson Crusoe Island (Pacific Ocean, Chile) invasive exotic plant species threaten conservation efforts by establishing in gaps and outcompeting native tree species regeneration. We compared gap attributes and ground vegetation cover in three gap types: those dominated by native species (<5 % cover of invasive species), invaded gaps (>30 % cover by invasive species), and treated gaps (invasive species removed). We examined (a) which gap attributes favored native and exotic species, (b) the relationship between gap size and species richness, and (c) species responses to invasion and treatment. Gaps ranged in size from 46 to 777 m<sup>2</sup> caused mainly by uprooted and snapped trees. Multi response permutation procedures showed a different floristic composition between natural, invaded and treated gaps. The presence of *Myrceugenia fernandeziana* (native species) and *Aristotelia chilensis* (invasive species) as gap border trees was positively and negatively correlated with native species richness, respectively. New gaps had more native species than old gaps, and smaller gaps contained relatively more native species than larger ones. An increase in invasive species cover was related to a decline in native species cover and richness. 1–6 years after treatment gaps tended to recover their native floristic composition. Highly effective conservation management programs will concentrate on monitoring gap creation, early control of invasive species, and by treating smaller gaps first.

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R. Vargas · S. Gärtner · A. Reif

Chair of Vegetation Science and Site Classification, Faculty of Environment and Natural Resources,  
Institute of Forest Sciences, Albert-Ludwigs University, Freiburg, Germany

R. Vargas (✉)

Tennenbacherstr. 4, 79106 Freiburg im Brsg., Germany  
e-mail: rodrigo.vargasgaete@gmail.com

M. Alvarez

Institute for Crop Science and Resource Conservation (INRES), University of Bonn, Bonn, Germany

E. Hagen

Island Conservation, Santiago, Chile

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## Introduction

Invasive plant species are important globally as drivers of biodiversity losses (Kueffer et al. 2010). In contrast to mainland ecosystems, islands contain smaller floras characterized by species unable to take advantage of resources that suddenly become available due to disturbances. These plant communities are easily invaded and less resilient (Denslow 2003). Islands make up only 3.6 % of the world's terrestrial surface but account for 26.1 % of the known vascular plant species (Kier et al. 2009). Plant endemism and extinction rates are higher on oceanic islands underscoring their importance for species preservation and suitability for species conservation efforts (Kier et al. 2009).

Robinson Crusoe Island (RCI, Juan Fernández Archipelago; 33°S 78°W, Pacific Ocean, Chile) has more endemic species per unit area than any other island in the world (1.9 species/km<sup>2</sup>, Bernardello et al. 2006). Currently >65 % of all vascular plant species on RCI (292 of 441) are naturalized exotics (Danton and Perrier 2006).

Natural and anthropogenic disturbances, such as gap creation, facilitate the establishment and naturalization of exotic species because in gaps competition from native species and their ability to capitalize on available resources is low (Denslow 2003). In the “endemic montane forests” of RCI (Greimler et al. 2002) the main natural disturbances are tree-fall canopy gaps (Vargas et al. 2010). Similar to other forest ecosystems, gaps on RCI are important for the maintenance of vascular plant species richness (Brokaw and Busing 2000; Schnitzer and Carson 2001). Therefore, understanding gap dynamics is especially relevant for conservation considering that most endangered plant and land bird species, all endemic, occur in the montane forests (Vargas et al. 2011).

Since the discovery of RCI in 1574 native species have been affected by land clearing fires, selective timber harvesting, and introduced animal and plant species that became feral and invasive (Skottsberg 1953). Their impacts contributed to the extinction of at least five endemic plant species during the last century e.g. *Santalum fernandezianum* (Santalaceae) around 1910, and *Robinsonia berteroi* (Asteraceae) in 2004 (Danton and Perrier 2006). Currently 115 of the islands 149 native vascular plant species are classified as vulnerable, endangered or critically endangered (IUCN, Danton and Perrier 2006). Moreover, population declines in the endemic birds, Juan Fernández firecrown (*Sephanoides fernandensis*) and Juan Fernández tit-tyrant (*Anairetes fernandezianus*), have been attributed to habitat loss, predation by introduced mammals, and forest degradation by invasive plant species (Hahn et al. 2011).

The most invasive exotic plant species in the montane forests are *Aristotelia chilensis* (Eleocarpaceae) and *Rubus ulmifolius* (Rosaceae) (Dirnböck et al. 2003). These species produce berries which are dispersed by gravity, wind and the native Austral thrush (*Turdus falcklandii magellanicus*) (Skottsberg 1953; Smith-Ramirez et al. 2013). Once established at lower altitudes (200–250 m.a.s.l) these plant species can spread asexually eventually becoming invasive in open shrublands (Skottsberg 1953), or by colonizing canopy gaps in forests (Vargas et al. 2010; Arellano 2011).

Once established, exotic species can influence species composition, site conditions and disturbance regimes, including canopy gap creation frequency and attributes (Hobbs et al. 2006; Vilà et al. 2011). Greimler et al. (2002) estimated that circa 36 % of the RCI montane forest was affected by invasive species. Once woody invasive species become

established in an area their removal and the restoration and recovery of native vegetation in the area can be technically challenging and costly (Tassin et al. 2006). On RCI since 2004 invasive plants have been removed from forest gaps containing critical nesting habitat for the endangered endemic Juan Fernández firecrown (*S. fernandensis*) (Hagen et al. 2005). After 2–4 years of treatment, these managed gaps have ~60 % of the native tree regeneration per ha observed in non-invaded natural gaps (Vargas and Reif 2009), however the recovery of floristic composition and overall species richness and diversity is unknown.

Gap site characteristics like size and topography have different impacts on species composition (Brokaw and Busing 2000; de Lima and de Moura 2008). The montane forest canopy gaps on RCI have greater tree and vascular plant species richness than does closed forest (Vargas and Reif 2009). But gaps also facilitate the invasion of exotic plant species which hamper the establishment of native species (Arellano 2011). Considering RCI's urgent conservation needs, it is important to understand the mechanisms and roles played by canopy gap attributes and their impacts on native and exotic plant species.

We examined the influence that altitude, slope, gap size and gap border tree attributes have on plant species richness, abundance and ground vegetation composition in RCI forests. To understand the effect of invasive species we sampled gaps with a range of invasive species cover. We categorized the gaps as being: (a) natural gaps with no or low (<5 %) cover of exotic invasive species, (b) invaded gaps with a significant cover of exotic invasive species (>30 %), or (c) treated gaps where the invasive exotic plant species were removed mechanically and chemically as part of a management program. Our research questions were related to the influence that gap attributes have on endemic and exotic species richness: (1) which gap attributes foster native and which foster exotic species richness? (2) What role does gap size play in species richness? And (3) how do native and exotic plant species respond to plant invasion and management? We assessed how invasive plant species currently affect forest gap vegetation diversity to provide immediate management recommendations for the maintenance of native species richness.

## Study area

Robinson Crusoe Island is a part of the Juan Fernández Archipelago National Park, a UNESCO World Biosphere Reserve considered a biodiversity conservation hotspot (Myers et al. 2000). Robinson Crusoe Island (RCI; 4,794 ha) is located in the Pacific Ocean, 667 km from mainland Chile, and is the only permanently inhabited island of the Archipelago (ca. 850 inhabitants). The climate of RCI is warm-temperate and humid, with short dry summers. Mean annual temperature and annual precipitation are 15.3 °C and 1,150 mm respectively (Cuevas and Figueroa 2007). The RCI formed over a volcanic hotspot about 4 million years ago (Stuessy et al. 1984), the soils developed from colluvial sediments and ash (Castro et al. 1995). The topography is rugged with few flat areas, the highest peak El Yunque, reaches 915 m.a.s.l.

The upper and lower endemic montane forest types of RCI (total area 1,014.8 ha, Smith-Ramirez et al. 2013), have been referred to as the upper and lower Myrtisylva due to the dominance of the Myrtaceae tree, *Myrceugenia fernandeziana* (Danton 2006, synonymous with *Nothomyrcia fernandeziana* Murillo-Aldana and Ruiz 2011). These forests are habitat for more than 40 endemic plant species which account for around 70 % of the vascular species endemism and provide more habitat for endangered plant and bird species than does any other vegetation type on RCI (Hahn et al. 2011; Vargas et al. 2011).



The study area was located in a forest classified as part of the endemic upper montane forest communities (250–550 m.a.s.l. Greimler et al. 2002). The forest averages between 900–1,330 trees per hectare (Vargas et al. 2010). The dominant tree layer (12–18 m high) is largely composed of *M. fernandeziana*, with emergent *Fagaya mayu* (>20 m) and less common *Bohemeria excelsa* and *Coprosma pyrifolia*. *Drimys confertifolia* is usually present in the intermediate layer (6–12 m) where it sometimes coexists with the invasive exotic *A. chilensis*, while in the lowest tree layer (< 6 m) *Rhaphithamnus venustus* grows. Frequent in the understory are the ferns *Arthropteris altescandes*, *Megalastrum inaequalifolium* and *Blechnum cordatum*, and the angiosperm species *Dysopsis hirsuta*, *Halorragis masatierrana* and *Erigeron fernandezianum* (Greimler et al. 2002). In forest gaps the endemic species *Gunnera peltata*, *Gunnera bracteata* and *Dicksonia berteriana*, and the invasive species *Rubus ulmifolius* and *A. chilensis* are regularly found (Danton and Perrier 2006).

The Plazoleta del Yunque (ca 100 ha, Fig. 1) was selected as a study site where around one quarter of the forest area is considered to be in a gap phase (>20 m<sup>2</sup>, Vargas et al. 2010). The site includes gaps containing native species and others that have been invaded by exotics providing an opportunity for comparisons under relatively similar site conditions. The forest structure and floristic composition were representative of the forest type at this altitude (Greimler et al. 2002; Vargas et al. 2010), and the abundance of tree regeneration suggests that there has been less browsing by introduced mammalian herbivores than in other parts of the RCI forest (Cuevas 2002).

## Methods

Gaps were defined as an interruption in the forest canopy of at least 20 m<sup>2</sup> extending down through all canopy levels to at least two meters above ground (Brokaw 1982). The gap area was expanded outwards to the bases of the gap border trees that were over 12 m tall and had a diameter >5 cm at 1.3 m (DBH) (Runkle 1981, 1982). In a pre-survey, four 100 m transects were sampled in 2008 and two 240 m transects were added in 2010. Transects were 300 m apart running perpendicular to the slope (forest stand data, see Vargas and Reif 2009; Vargas et al. 2010). All canopy gaps ( $n = 46$ ) crossed by the transects were characterized by their slope position (bottom, middle or upper slope), origin (fallen tree or landslide), size in m<sup>2</sup> (calculated with the ellipse formula using the longest and shortest diameters measured from the canopy gap border tree boles i.e., expanded gap sensu Runkle 1982) and by visually categorizing the degree of invasion as: “invaded” i.e., >10 % cover by exotics inside the expanded gap; or non-invaded with <10 % cover by exotics. In some of the gaps, the invasives: *A. chilensis* and *R. ulmifolius* had been removed using cut-stump treatment with Garlon 4<sup>®</sup> 5 % (Tryclopipir) mixture (Hagen et al. 2005).

Most gaps found along the pre-survey transects were created by tree falls (44 of 46) and were located mid-slope (33 of 46). Therefore, we additionally sampled 48 gaps created by tree falls in mid-slope positions. They were stratified into three categories of invasiveness to contrast extremely invaded gaps with non invaded and treated gaps. Hence we considered “natural gaps” <5 % cover of invasive exotics inside the expanded gap ( $n = 15$ ), “invaded gaps” >30 % cover of invasive exotic species ( $n = 16$ ) and “treated” where invasive exotics were removed ( $n = 17$ ). We aimed to include a broad gap size range (<100 to >400 m<sup>2</sup>) in each category.



**Fig. 1** Location of Juan Fernández Archipelago, Robinson Crusoe Island (RCI) is shown with the main vegetation units. The study site Plazoleta del Yunque is indicated (adapted from Bernardello et al. 2006; Greimler et al. 2002; Díaz 2012)

## Data collection

For each expanded gap ( $N = 48$ ) we recorded: (a) topographical and structural attributes, (b) gap border tree attributes, (c) gapmaker attributes and (d) vegetation cover attributes. Thus we sampled: (a) altitude (m.a.s.l), slope (%), and gap size ( $m^2$ ), including (b) number and species of trees forming the gap border, and the (c) number, length and diameter (average of measurements taken at the butt, middle and top) of the gapmakers, reason for the demise of the gapmaker (uprooted, snapped, standing dead, cut) and (d) the vascular plant species cover. The cover was sampled using a modified Braun-Blanquet scale (Glavac 1996): (1) 0.01 % = 1–2 individuals <1 % cover, (2) 0.5 % = 3–10 individuals <1 % cover, (3) 3 % = 10–50 individuals <1 % cover, (4) 4 % = > 50 individuals <5 % cover, (5) 10 % = 5–15 % cover, (6) 20 % = 15–25 % cover, (7) 37.5 % = 25–50 % cover, (8) 62.5 % = 50–75 % cover, (9) 87.5 % = 75–100 % cover. The decompositional state of the gapmakers was evaluated and recorded 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). Within treated and invaded gaps some trees had been cut. We therefore added the category “cut”, as a gapmaker tree (i.e., cut *A. chilensis*). We assumed that the gapmaker decomposition state was related to gap age and based on this, derived an “estimated age” that we used as an additional structural attribute: “new”, “intermediate” and “old” gaps. The presence of a single mostly decayed gapmaker log indicated the “oldest” gaps and in the absence of mostly decayed logs, the next decay category was assigned the “intermediate” or “newly formed” gap age category (Lertzman et al. 1996). The treated gaps we sampled were removed from invasive species at least 1 year, and at most 6 years before data collection.

## Data analysis

Most variables were not normally distributed therefore we used the non-parametric Kruskal–Wallis test, and post hoc, pairwise Wilcoxon tests to identify statistical differences among natural, invaded and treated gaps (Kent and Coker 1992). We considered: (a) topographical and structural attributes, (b) gap border tree attributes, (c) gapmaker attributes, and (d) vegetation cover attributes. To enable comparisons between the gaps of different sizes, variables were scaled to percentages or averages (per gap or per  $m^2$ ), e.g. number of border trees/ $m^2$  of gap area, number of uprooted trees/total gapmaker logs  $\times 100$ . Plant species evenness for each gap was calculated using the Pielou index, which indicates the similarity of the relative abundance of the species and ranges from 0 (single species dominance) to 1 (equal abundance of all species, maximum diversity) (Stirling and Wilsey 2001). All statistical analyses were performed with R 2.15 (R Development Core Team 2012).

To visualize floristic composition differences among gap types we carried out non-metrical multidimensional scaling ordination (NMDS) using Bray–Curtis distance (function metaMDS Vegan 2.02, R Oksanen et al. 2011). We conducted the analysis for all gap types together (i.e., natural, invaded, treated), and separately for natural and invaded gaps. To identify relationships between gap attributes and floristic composition, we fit gap attributes as explanatory variables onto the species ordination (function envfit; Vegan, Oksanen et al. 2011). Variables included were: gap types (natural, invaded or treated), topographical and structural attributes, bordering tree attributes, and gapmaker attributes.

We considered only attributes significantly correlated with the floristic ordination ( $r^2 > 0.15$ ;  $P < 0.05$ ) and tested significance through 999 permutations using the coefficient of determination ( $r^2$ ) to choose the best fit (McCune et al. 2002). Multi-response



permutation procedures (MRPP) were used to test differences in the floristic composition among gap types using post hoc pairwise comparison (function `mrpp` in `Vegan`, Bray–Curtis distance, 999 permutations, weighted by group size; Oksanen et al. 2011). The MRPP compares floristic dissimilarities within and among groups. Groups are different if the average distance within the group samples (i.e., gap type), is less than the average distance of all possible partitions (permutations) of the whole population (McCune et al. 2002). The agreement statistic “A” describes if the within group homogeneity is higher than randomly expected. When samples are floristically identical within groups, A reaches its maximum ( $A = 1$ ). If within-group heterogeneity equals expectations at random, then  $A = 0$ .  $P$  values express the likelihood of getting a difference among groups, similar or smaller as the observed one within the groups (McCune et al. 2002).

### Species richness and cover

To know if the gap size was influencing species richness we used the SLOSS analysis. This method quantifies whether a single large or several small areas are more suitable to conserve species richness (SLOSS controversy, see: Quinn and Harrison 1988; Oertli et al. 2002). Species-area accumulation curves were displayed for the gaps ordered from small to large, and from large to small. An index was obtained by calculating the ratio of the integrals of the curves displayed (i.e., “SLOSS-index” according to Quinn and Harrison 1988). When large areas support more species than several smaller areas whose combined surface is similar, SLOSS-index values are  $<1$ . Values  $>1$  indicate that smaller gaps support more species per area (Quinn and Harrison 1988). The analyses for native and exotic species were done separately (by a SLOSS function written within R 2.15, available on request). A species coverage accumulation curve was included to analyze the species cumulative coverage within the gap types following the same SLOSS sorting. To compare species accumulation among gap types we used the same number of samples selecting 15 gaps per type by randomly removing one invaded and two treated gaps.

### Analysis of individual species response

We performed an indicator species analysis to identify taxa associated with natural, invaded and treated gaps. This procedure selects species representatives of a group, considering their specificity and fidelity (McCune et al. 2002). The analysis calculates a species indicator value which integrates the frequency and relative abundance to an importance value of the species for a group, using the overall largest value to select the indicator group for each species (Dufrière and Legendre 1997). A random reallocation procedure was used to test the significance of the indicator value for each species considering the probability of obtaining as high an indicator value as observed over 1,000 iterations (Indval, package `labdsv` 1.4.1; Roberts 2012). Only species with an indicator value  $>20\%$  ( $P < 0.05$ ) were considered significant indicator species (Dufrière and Legendre 1997). To evaluate how species reacted to invasion and treatment we subtracted the indicator value of each species on natural gaps (used as reference), from the indicator value obtained on invaded and on treated gaps. Thus a positive (+) or a negative (–) change in importance was obtained for invaded and treated gaps corresponding to an increase or decrease in frequency and abundance compared to the frequency and abundance that each plant species had in natural gaps.

## Results

The studied gaps in the montane forest on RCI were located between 260 and 428 m a.s.l. Invaded canopy gaps were found, in most cases, on steep slopes while the natural and particularly the treated gaps were predominantly on more level sites. Gap sizes ranged from 46 to 777 m<sup>2</sup> and there were no significant differences among gap types (Table 1).

The most frequent canopy tree species bordering the gaps was *M. fernandeziana*, however its occurrence was significantly lower around invaded gaps (Table 1). Most gaps were formed by two gapmakers (range 1–7). In natural gaps the gapmakers were thicker and taller ( $P < 0.05$ ; Table 1).

Compared to natural gaps invaded and treated gaps had 44 and 24 % less native species vegetation cover. There was no significant difference in average species richness (Table 1) but the maximum number of native as well as of exotic species (18 and 8 respectively) were found in natural gaps. Species diversity (evenness) was significantly lower in invaded areas where exotics cover was highest (Table 1).

### Floristic composition within the gaps

The floristic differences among gap types were significant in the MRPP ( $A = 0.19$ ,  $P = 0.001$ ). Natural and invaded gaps showed the greatest floristic differences ( $A = 0.28$ ,  $P = 0.001$ ). This gradient in floristic composition can be recognized along the first NMDS axis (Fig. 2a). Natural and treated gaps were floristically more similar, but still significantly different ( $A = 0.05$ ,  $P = 0.003$ ). Floristic composition differed between invaded and treated gaps as well ( $A = 0.14$ ,  $P = 0.001$ ). While the floristic gradient from natural to treated to invasive gaps correlated with the altitude and slope gradient (NMDS axis 1, Fig. 2a), the floristic differentiation between gap types along the gap size gradient was much smaller (NMDS axis 2, Fig. 2a).

The isolines in the ordination diagram describe native species richness in the floristic space, whereby invaded gaps represent areas with lower richness compared to natural gaps (Fig. 2b). The floristic differentiation between natural and invaded gaps was related to a different canopy composition around the gaps. *Myrceugenia fernandeziana* was more frequent around natural gaps while around invaded gaps the relative frequency of *A. chilensis* was higher (Table 1, univariate tests). Recently created gaps (Age.New) had higher native species richness than older gaps (Age.Interm and Age.Old) that were associated with higher degrees of invasion.

### Species richness and gap-size

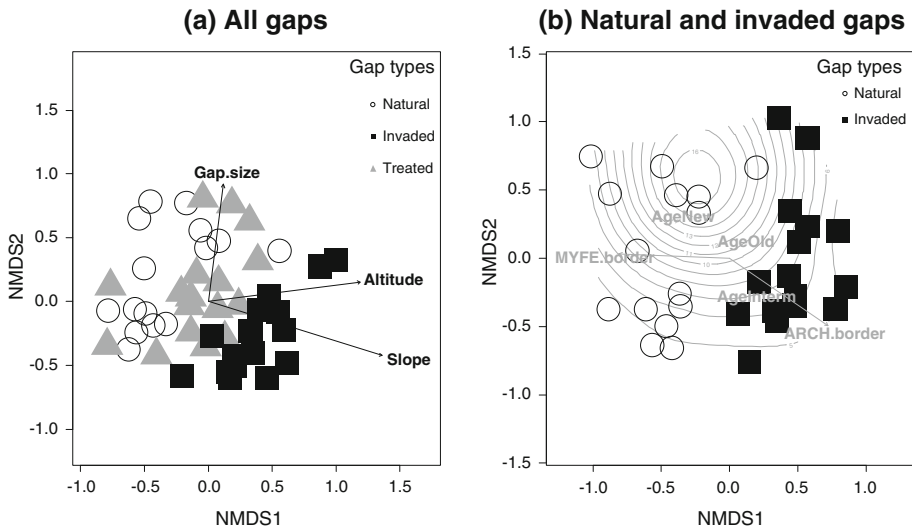
In smaller gaps we found proportionally more native species than in larger gaps (Fig. 3a). This pattern was constant for all gap types and for overall and native species richness (SLOSS index  $> 1$ ). On the other hand, exotic species covered proportionally more area in larger gaps (SLOSS index  $< 1$ , Fig. 3b).

When the cover of several smaller gaps was combined it was consistently higher than the cover in a single large gap of the same area (cumulative species cover, right axis in grey, Fig. 3). Native and exotic species contributed about 50 % of the overall ground vegetation cover found. Exotic species contributed the most cover in invaded gaps (ca. 40 % of the 50 % total exotic plant cover found overall gap types). On the other hand, native species accounted for about 25 % of the 50 % total native species cover in natural gaps, around 15 % cover in invaded gaps, and ca. 8 % in those treated (Fig. 3 right axis).

**Table 1** Attributes of the 48 gaps sampled in the montane forest of RCI (median and range)

	All gaps (n = 48)		Natural (n = 15)	Invaded (n = 16)	Treated (n = 17)
a) Topographical and structural attributes		Kruskal–Wallis P			
Altitude (m.a.s.l)	316 (260–428)	**	320 (260–380) ab	323 (303–428) a	306.5(269–329) b
Slope (%)	37 (2–94)	***	33 (14–85) ab	54 (34–94) a	30 (2–53) b
Area (m <sup>2</sup> )	162.4 (46–777)	n.s	152.7 (82–259) a	198.6 (46–580) a	160.2 (61–777) a
b) Bordering tree species attributes					
Bordering trees (m <sup>2</sup> )	0.06 (0.01–0.19)	n.s	0.05 (0.03–0.1) a	0.07 (0.01–0.2) a	0.08 (0.01–0.17) a
<i>Myrceugenia fernandeziana</i> (% of border trees)	68.5 (15–100)	***	80 (70–90) a	49 (15–100) b	67 (40–100) a
<i>Fagara mayu</i> (%)	11 (0–43)	n.s	6.5 (0–29) a	10.5 (0–43) a	13 (0–27) a
<i>Drimys confertifolia</i> (%)	9.5 (0–33)	*	10 (0–18) a	19 (0–33) b	7.5 (0–20) a
<i>Bohemeria excelsa</i> (%)	0 (0–40)	*	0 (0–10) a	0 (0–31) ab	6 (0–40) b
<i>Raphithamnus venustus</i> (%)	0 (0–60)	n.s	0 (0–60)a	0 (0–38) a	0 (0–37) a
<i>Aristotelia chilensis</i> (%)	0 (0–67)	**	0 (0–5) a	13 (0–67) b	0 (0–23) a
c) Gapmaker attributes					
Number (No./gap)	2 (1–7)	n.s	1 (1–3) a	2 (1–3) a	2 (1–7) a
Diameter (cm)	32 (10–127)	*	39.5 (26–127) a	27.2 (24–40) b	24.8 (10–47) b
Mean total length (m)	8.7 (1.1–23)	***	13.2 (8.6–23) a	7.5 (3–12) b	6.3 (1–12) b
Uprooted (%)	0 (0–100)	n.s	0 (0–100) a	50 (0–100) a	0 (0–100)a
Snapped (%)	0 (0–100)	n.s	33 (0–100)a	0 (0–50) a	0 (0–50) a
Standing dead (%)	0 (0–100)	n.s	0 (0–100)a	0 (0–50) a	0 (0–33) a
Cut (%)	0 (0–100)	***	0 (0–0) a	0 (0–100) a	50 (0–100) b
Undetermined origin (%)	0 (0–100)	*	0 (0–0) a	0 (0–100) b	0 (0–0) a
Gapmaker debris least decay (%)	50 (0–100)	n.s	0 (0–100) a	0 (0–100) a	50 (0–100) a
Gapmaker debris intermediate decay (%)	0 (0–100)	n.s	0 (0–100) a	0 (0–100) a	0 (0–100) a
Gapmakers debris most decay (%)	0 (0–100)	n.s	0 (0–100)a	0 (0–100) a	10 (0–100) a
d) Vegetation cover and richness inside extended gaps					
Native spp. cover (%)	33.8 (1.5–103)	***	58.5 (17–103) a	15 (1.5–48) b	34.5 (4–83)c
Exotic spp. cover (%)	18 (0–150.5)	***	3 (0–10.5) a	86.3 (38–151) b	17.5 (0–91.5) c
Native spp. richness (N° spp.)	6.5 (3–18)	n.s	7 (4–18) a	6 (4–10) a	8 (3–14) a
Exotic spp. richness (N° spp.)	2 (0–8)	n.s	2 (0–8) a	2 (1–5) a	2 (0–6) a
Evenness (Pielou index)	0.36 (0.07–0.66)	***	0.42 (0.2–0.6)a	0.28 (0.07–0.43) b	0.42 (0.16–0.6) a

Natural, invaded and treated gaps are compared; significant differences are shown with different letters; n.s= non significant differences (Kruskal Wallis and post-hoc Wilcoxon test, P < 0.05)

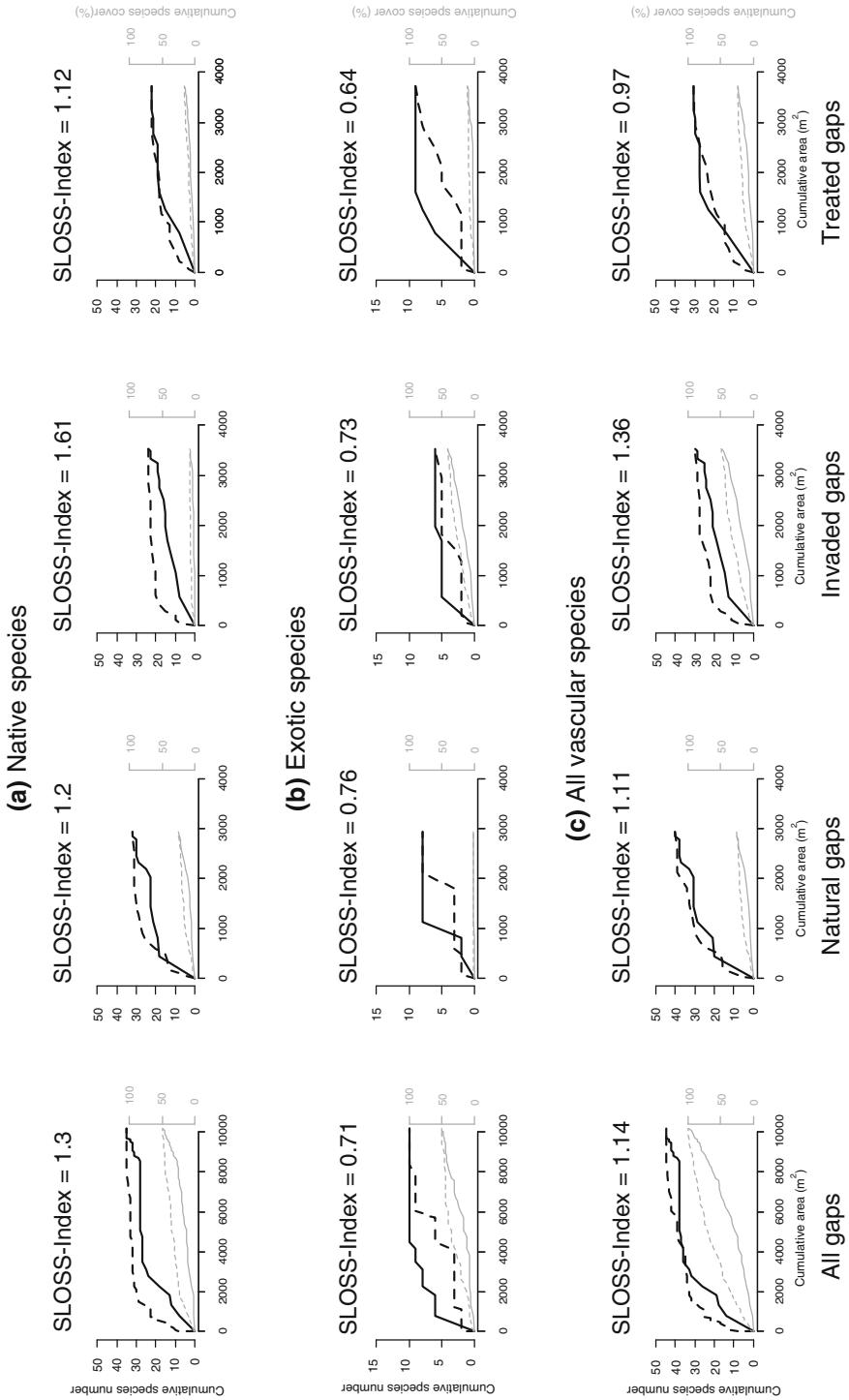


**Fig. 2** NMDS ordination produced with Bray–Curtis distance, based on the composition of vascular flora in 15 natural, 16 invaded and 17 treated gaps in the endemic montane forest of RCI. At left, **a** Ordination of all gaps (stress 23.8) showing significant gap attributes (95 %) including gap type (squared correlation coefficient  $r^2 = 0.35$ ,  $P = 0.001$ ), altitude ( $r^2 = 0.33$ ,  $P = 0.002$ ), slope ( $r^2 = 0.46$ ,  $P = 0.001$ ), gap size ( $r^2 = 0.19$ ,  $P = 0.01$ ). **b** Ordination of natural and invaded gaps (stress 20.8) where isolines represent native species richness in each gap (ordisurf Vegan; Oksanen et al. 2011) showing significant gap attributes correlated with the ordination (95 %); ARCH.border: species *A. chilensis* as border tree ( $r^2 = 0.44$ ,  $P = 0.009$ ), MYFE.border: species *M. fernandeziana* as border tree ( $r^2 = 0.37$ ,  $P = 0.01$ ), Age.New: “newly formed gaps”, Age.Old: “older gaps”; Age.Interm: “intermediate gaps” ( $r^2 = 0.21$ ,  $P = 0.04$ )

### Species associated with natural, invaded and treated gaps

We found a total of 46 vascular plant species growing in 48 sampled gaps. Out of the 46 species 36 were native (27 endemic) and 10 exotic. In natural gaps all of the significant indicator species (7) were either endemic or native (Table 2). The two most invasive exotic species (*A. chilensis*, *R. ulmifolius*) were indicators of invaded gaps whereas in treated gaps the only significant indicator species was the exotic herb *Sonchus oleraceus* (Table 2). The ratio of exotic to native species number increased from 1:21 in natural reference gaps to 2:8 in invaded gaps and to 7:17 in treated gaps.

More than half of all vascular species (mostly native) were either less abundant or frequent in invaded and treated gaps compared to natural gaps (i.e., negative difference with reference areas, Table 2). It was mostly exotics and infrequently found native species that increased their frequency and abundance in treated and invaded gaps (Table 2). Native species that decreased most in frequency and abundance compared to natural gaps were *M. fernandeziana*, *A. altescandens*, *F. mayu*, *R. venustus* and *P. macrocarpa*. Besides *A. chilensis* and *R. ulmifolius* there were no species that increased their importance more than 35 % in either invaded or treated areas (Table 2). In treated gaps *D. confertifolia* increased in abundance and frequency when compared with natural gaps. In treated gaps a reduction in abundance and frequency of targeted exotic species could be confirmed for *A. chilensis* and *R. ulmifolius* (with >50 % reduction in importance).



◀ **Fig. 3** Cumulative species-area curves of Canopy gaps in the endemic montane forest of RCI. **a** Native, **b** exotic, and **c** all vascular species are represented separately for: all gaps, natural gaps, invaded gaps and treated gaps. *Dotted lines* represent gaps ordered by size, from small to large, and *continued lines* represent gaps ordered from large to small. In *grey* (right axis) the cumulative species cover (i.e. cumulative species cover in each gap) is shown. The SLOSS or Saturation index was calculated according to Quinn and Harrison (1988). Where SLOSS-index is  $>1$ , smaller gaps gather more species for the same cumulative area; where SLOSS-index is  $<1$ , larger gaps accommodate more species than smaller ones

## Discussion

What are the main gap characteristics in the endemic montane forest?

The gap sizes that we measured in the RCI forest (mean: 223.2 m<sup>2</sup>, range: 46–777 m<sup>2</sup>) are comparable to average gap sizes in other south Chilean coastal temperate forests (197 m<sup>2</sup>, 28–972 m<sup>2</sup> in Chiloé Island; Armesto and Fuentes 1988). However the gaps we measured on RCI were considerably larger when compared to forest gaps on some other oceanic islands at similar latitudes, for example, in the *Juniperus*–*Laurus* forests on the Azores with (25.1 m<sup>2</sup>, 4–52.6 m<sup>2</sup>; Elias and Dias 2009) or those gaps in the *Laurisilva* forests on the Canary islands (77.6 m<sup>2</sup>, 17–125 m<sup>2</sup>; Arévalo and Fernández-Palacios 1998). Gap sizes smaller than our study gaps have also been reported for natural gaps on RCI (88.7 m<sup>2</sup>, 13–368 m<sup>2</sup>; Arellano 2011). This size difference can be partly explained by our use of the expanded gap area, which results in larger gap sizes compared with the effective canopy opening method (Arellano 2011). We used the expanded gap area because gap influences extend beyond the effective canopy opening (Runkle 1982).

The most common canopy border tree for all gap types was *M. fernandeziana*. This is not surprising since the forest type name *Myrtisilva* comes from this species family (Danton 2006), and because of the dominance of *M. fernandeziana* which represents  $>90\%$  of stocking and  $>65\%$  of basal area (Vargas et al. 2010). But around invaded gaps there were significantly more individuals of *A. chilensis* (invasive exotic species). The success of this invader in gaps can be best explained by its multiple dispersal strategies (mainly endozoochory by thrush, followed by barochory and wind; Smith-Ramirez et al. 2013). Natural gaps presented the highest number of native species (18) and exotic species (14 species, with low cover), which suggests that site factors similar to those that determine natural diversity, may promote exotic species establishment, as has been reported for tropical forests (Denslow 2003).

Which attributes were associated with native and exotic species?

We found a reduction in species evenness in gaps invaded by exotic species due to the dominance of *A. chilensis* and *R. ulmifolius*. However, there were no differences in evenness between natural and treated gaps suggesting that species diversity tends to increase after treatment. The floristic composition in the canopy gaps of the RCI forests was most different between invaded gaps and natural gaps while treated gaps showed an intermediate position in the floristic space. This suggests that when *A. chilensis* and *R. ulmifolius* were removed, the floristic composition tended to revert to a pre-invasion state. However, in our case, this recovery was not complete because natural and treated gaps still had significantly different floristic compositions (1–6 years after treatment).

The ordination revealed a floristic differentiation between the different gap types due to slope, altitude and size. It has to be taken into account that gap treatment (invasive plant



**Table 2** Results of indicator species analysis

No.	Dist.	Species	Indicator value	Difference with reference gaps	Gap type	P-value
1	E	<i>Myrceugenia fernandeziana</i>	0.683	-45%	Nat	<b>0.001</b>
2	E	<i>Arthropteris altescandes</i>	0.596	-35%	Nat	<b>0.001</b>
3	E	<i>Pleopeltis macrocarpa</i>	0.512	-30%	Nat	<b>0.001</b>
4	E	<i>Fagara mayu</i>	0.450	-25%	Nat	<b>0.006</b>
5	E	<i>Raphithamnus venustus</i>	0.281	-15%	Nat	<b>0.009</b>
6	N	<i>Blechnum mochaenum</i>	0.356	-10%	Nat	<b>0.011</b>
7	N	<i>Adiantum chilense</i>	0.200	-5%	Nat	<b>0.028</b>
8	E	<i>Uncinia douglasii</i>	0.133	-2%	Nat	0.095
9	E	<i>Polypodium intermedium</i>	0.133	-2%	Nat	0.110
10	E	<i>Gunnera peltata</i>	0.153	-3%	Nat	0.121
11	E	<i>Halorragis masatierrana</i>	0.193	-4%	Nat	0.238
12	E	<i>Megalastrum inaequalifolium</i>	0.365	-6%	Nat	0.260
13	E	<i>Dysopsis hirsuta</i>	0.199	-5%	Nat	0.260
14	N	<i>Hymenophyllum ferrugineum</i>	0.067	-1%	Nat	0.298
15	E	<i>Gunnera bracteata</i>	0.067	-1%	Nat	0.311
16	Ex	<i>Lardizabala biternata</i>	0.067	-1%	Nat	0.318
17	E	<i>Peperomia berteroaana</i>	0.065	-1%	Nat	0.525
18	E	<i>Thyrsopteris elegans</i>	0.066	-1%	Nat	0.537
19	N	<i>Lophosoria quadripinnata</i>	0.052	-0.5%	Nat	0.539
20	E	<i>Machaerina scirpoidea</i>	0.035	-0.5%	Nat	0.545
21	N	<i>Hymenophyllum sp</i>	0.052	-0.5%	Nat	0.556
22	Ex	<i>Aristolelia chilensis</i>	0.834	+45%	Inv	<b>0.001</b>
23	Ex	<i>Rubus ulmifolius</i>	0.577	+35%	Inv	<b>0.006</b>
24	E	<i>Blechnum schotti</i>	0.234	+10%	Inv	0.085
25	E	<i>Pteris berteroaana</i>	0.164	+5%	Inv	0.738
26	E	<i>Blechnum cycadifolium</i>	0.125	+3%	Inv	0.201
27	N	<i>Hymenophyllum plicatum</i>	0.122	+3%	Inv	0.247
28	E	<i>Trichomanes ingae</i>	0.113	+2%	Inv	0.383
29	E	<i>Dicksonia berteroaana</i>	0.050	+1%	Inv	0.887
30	Ex	<i>Sonchus oleraceus</i>	0.327	+10%	Treat	<b>0.028</b>
31	E	<i>Drimys confertifolia</i>	0.381	+15%	Treat	0.109
32	N	<i>Blechnum hastatum</i>	0.379	+15%	Treat	0.169
33	N	<i>Blechnum cordatum</i>	0.252	+10%	Treat	0.127
34	E	<i>Rumohra berteroaana</i>	0.233	+10%	Treat	0.656
35	E	<i>Polystichum tetragonum</i>	0.161	+5%	Treat	0.972
36	Ex	<i>Myosotis sylvatica</i>	0.146	+5%	Treat	0.270
37	N	<i>Juncus spp</i>	0.118	+4%	Treat	0.335
38	Ex	<i>Poa pratensis</i>	0.113	+4%	Treat	0.596
39	E	<i>Histiopteris incisa</i>	0.098	+3%	Treat	0.422
40	E	<i>Boehmeria excelsa</i>	0.078	+2%	Treat	0.824
41	Ex	<i>Acaena argentea</i>	0.059	+1%	Treat	1.000
42	E	<i>Coprosma pyrifolia</i>	0.059	+1%	Treat	1.000
43	E	<i>Erigeron fernandezianum</i>	0.059	+1%	Treat	1.000
44	Ex	<i>Rumex spp</i>	0.057	+1%	Treat	1.000
45	Ex	<i>Oenothera rosea</i>	0.056	+1%	Treat	1.000
46	Ex	<i>Sonchus asper</i>	0.049	+1%	Treat	1.000

All 46 species found in the studied gaps are listed considering their distribution (Dist: *E* endemic, *N* native, *Ex* exotic). The highest indicator value obtained for each species is given considering the gap type where the species mainly occurred (*Nat* natural, *Inv* invaded, *Treat* treated). The probability value of obtaining as high an indicator value as observed by 1,000 iterations is provided (*P* value); significant values are in bold ( $P < 0.05$ , sensu Dufrière and Legendre 1997). Differences in the importance that species presented compared to reference gaps (i.e., natural) are shown in the graph. Positive (+) or negative (–) change in importance, correspond to an increase or decrease in frequency and abundance compared to natural gaps

control) was done, for the most part, on sites with little or no slope and at lower altitude (<350 m.a.s.l) near to invasive shrubland formations (*Aristotelia–Rubus*) and human modified habitats (Hagen et al. 2005). The ruggedness of the island terrain was found to influence changes in vegetation composition over short distances. Steeper areas had more species common to the transitional and upper montane forests while level areas reflected the flora found in the lower montane forests (Greimler et al. 2002). It is known from coastal forests of Brazil that slope and topography can explain species distribution in canopy gaps, particularly that of advanced regeneration which is influenced by the community surrounding the gap (de Lima and de Moura 2008).

The proximity of *M. fernandeziana* and the exotic *A. chilensis* to gaps seemed to have a significant impact on the floristic composition of natural and invaded gaps. The age of the gaps also influenced floristic composition. Floristically, newly created gaps tended to have higher native species richness, whereas older gaps were associated with invasive species. This seems to confirm that invasive species colonize gaps after a disturbance and go on to change the floristic composition and bring about the reduction of native species richness.

How does gap size influence native species richness and the invasion of exotics?

Gap size can modify site conditions, such as soil temperature, which in turn influences seed germination and long-term changes in the floristic composition of forests (Marthews et al. 2008). However, in the RCI forest, gap size was not linked with an increase in species number. A set of smaller gaps combined had a higher number of native species than single larger gaps of the same area. Smaller gaps also had higher overall species richness and contained a greater proportion of native species (36 out of 46 species) than larger gaps. This might be explained by the fact that many smaller gaps have more combined edge than one large gap with the same area. The more edge the greater is the likelihood that the regeneration of different bordering species will contribute to species diversity (Quinn and Harrison 1988). Smaller areas usually have less cover of the two main invasive exotic species (Arellano 2011) which hamper native species establishment. We found more native species in smaller invaded gaps than in the larger ones indicated by the higher SLOSS-index of invaded gaps. However, the number of exotic species increased when going from large to small gaps (SLOSS Index < 1). This may be because exotic species require more light, space and disturbed soil to establish in the RCI forest. Larger gaps enable more solar radiation to reach the forest floor and border trees in larger gaps may compete less for the available water with plants growing within the gap (Marthews et al. 2008). The most common exotic species, *A. chilensis* and *R. ulmifolius*, benefit from the effects of larger gaps particularly in areas where invaded sites are nearby (Arellano 2011). Similarly, *Rubus alceifolius* preferably invades large sized gaps in the Reunion Island forest (Baret et al. 2008) and the density of the widespread invasive species: *Lantana camara* is positively related to gap size in tropical forests (Totland et al. 2005). Our findings show that not only the main invasive species, but that exotic species in general take advantage of larger gaps on RCI.

Larger gaps were also more prone to reinvasion by exotic species following treatment (Lowest SLOSS index, always <1). After exotic species are removed, resources became available and may be exploited by reinventing ruderal species (Jäger and Kowarik 2010). The larger treated gaps examined in our study provided more space and resources which might explain the increase in exotic species number observed in them (overall species SLOSS-index < 1 on treated gaps).

Species cover was always higher in smaller gaps compared to larger ones (Fig. 3), and there was no difference in response to gap size between native and exotic species cover. Smaller gaps usually had lower levels of disturbance, indicated by a lower number of gapmakers, thereby promoting advanced regeneration that can explain the relatively higher vegetation cover in smaller gaps.

#### How respond species to invasion and treatment?

Invasive species threaten native vascular plant species richness in the RCI forest canopy gaps. Out of 46 native species, 20 occurred with a higher frequency and abundance in natural gaps, while only 7 were found in invaded gaps. The endemic species naturally growing in RCI forest gaps were significantly reduced in frequency and abundance after gap invasion but tended to recover slowly following treatment. *Myrceugenia fernandeziana*, the main RCI forest tree species was reduced by about 60 % in invaded gaps but increased (+20 %) after the gaps were treated. A similar trend was observed in the common creeping climbing fern *A. altescandes*. Yet other species declined after invasion and did not increase after treatment (e.g. *P. macrocarpa*, *A. chilense*), and some significant indicator species were slightly less frequent and abundant in treated gaps than in invaded gaps (e.g. *F. mayu*, *R. venustus*).

As expected the main invasive species (*A. chilensis* and *R. ulmifolius*) were reduced after treatment. Nevertheless, both species were still more frequent and abundant in treated gaps than in natural gaps. *Rubus ulmifolius* seemed to be more frequent than *A. chilensis* (Table 2). Arellano (2011) reported that *A. chilensis* and *R. ulmifolius* prevailed over native forest species inside gap and border areas, but they did not seem to prosper below forest cover in RCI. The persistence of invasive species in gaps could be due to the perseverance of their propagules in gap bordering areas and their ability for seed banking and for vegetative regeneration (Smith-Ramirez et al. 2013). These same strategies help invasive species invade newly created open areas where they out grow and develop more rapidly than native species.

The persistence of invasive species due to seed bank reservoirs and seed rain as well as invasions by new exotic species were common problems experienced after attempts at control were taken on other islands such as Galapagos (Jäger and Kowarik 2010) and Hawaii (Loh and Daehler 2008). Compared to the natural areas the ratio of exotic over native species was considerably higher in treated gaps. This highlights the importance of ongoing monitoring to prevent the spread of new invasive species. Exotic species appeared to take advantage of the space, lack of competition and increased resources available following gap treatment. The control of invasive species often creates different micro habitats and may influence dispersal processes (Jäger and Kowarik 2010). Wind dispersal (e.g. *Sonchus* spp.; *Rumex* spp.) and epizoochory dispersal (e.g., *Acaena*, *Myosotis*) assists those exotic species with mechanical dispersal adaptations. Propagules dispersal by introduced mammals (rodents, rabbits, coati, dogs), and those people doing the treatment work, as well as rangers, scientists and tourists; (epianthropochory sensu Vibrans 1999) could help explain the relatively high number of exotic species in treated areas.

#### Conclusions

Invasive species have significantly altered the abundance and diversity of native flora in forest canopy gaps of RCI. The removal of invasive plant species suggests a trend towards

floristic recovery, but the process is still incomplete after 1–6 years. Although plant species diversity was similar in treated gaps and natural gaps, treated gaps had more exotic species. This situation requires active monitoring and further evaluation of treated areas. Conservation management efforts involving native species should focus treatments on smaller gaps (<150 m<sup>2</sup>) as they have fewer exotic species and were shown to be more important for native species conservation than larger gaps in our study. Controlling invasive species will be most effective if initiated within 2 years of gap formation as the newer gaps had higher native species richness than older gaps. Restoration should be prioritized in these areas before invasive species have a chance to suppress the native vegetation. Sooner or later the tendency is for invasive species to reduce diversity, particularly in the larger gaps surrounded by *A. chilensis* trees. Based on our results, the most effective conservation management plan for the maintenance of endemic forests on RCI involves the regular monitoring of gap formation followed by the control of exotic plant species beginning with the smaller gaps.

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## References

- Arellano G (2011) Evaluación de la dinámica de invasión de *Aristotelia chilensis* (Eleocarpaceae) y *Rubus ulmifolius* (Rosaceae) en claros de dosel en un bosque de la isla Robinson Crusoe, Archipiélago Juan Fernández, Chile. Msc Áreas Silvestres y Conservación, Universidad de Chile, Santiago, Chile
- Arévalo JR, Fernández-Palacios JM (1998) Treefall gap characteristics and regeneration in the laurel forest of Tenerife. *J Veg Sci* 9:297–306
- Armesto J, Fuentes E (1988) Tree species regeneration in a mid-elevation, temperate rain forest in Isla de Chiloé, Chile. *Plant Ecol* 74:151–159
- Baret S, Cournac L, Thébaud C, Edwards P, Strasberg D (2008) Effects of canopy gap size on recruitment and invasion of the non-indigenous *Rubus alceifolius* in lowland tropical rain forest on Réunion. *J Trop Ecol* 24:337–345
- Bernardello G, Anderson G, Stuessy TF, Crawford D (2006) The angiosperm flora of the Archipelago Juan Fernández (Chile): origin and dispersal. *Can J Bot* 84(8):1266–1281
- Brokaw N (1982) The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica* 14:158–160
- Brokaw N, Busing RT (2000) Niche versus chance and tree diversity in forest gaps. *Trends Ecol Evol* 15:183–188
- Carmona MR, Armesto JJ, Aravena JC, Pérez CA (2002) Coarse woody debris biomass in successional and primary temperate forests in Chiloé Island, Chile. *For Ecol Manag* 164:265–275
- Castro C, Brignardello L, Cereceda P (1995) Determinación de áreas con riesgo morfoodinámico en San Juan Bautista, Isla Robinson Crusoe, comuna de Juan Fernández, V Región. *Revista Geográfica de Chile Terra Australis*. *Revista Geográfica de Chile Terra Australis* 40:43–61
- Cuevas JG (2002) Distribución y abundancia de la flora vascular del Archipiélago de Juan Fernández. II Parte y Final
- Cuevas JG, Figueroa JA (2007) Germinación de semillas de especies del Archipiélago de Juan Fernández en condiciones de laboratorio. *Gayana Botánica* 64:60–80

- Danton P (2006) The “myrtisylva” of the Juan Fernández Archipelago (Chili), a threatened forest. *Acta Botanica Gallica* 153(2):179–199
- Danton P, Perrier C (2006) Nouveau catalogue de la flore vasculaire de l’archipel Juan Fernández (Chili). *Acta Botanica Gallica* 153:399–587
- de Lima R, de Moura LC (2008) Gap disturbance regime and composition in the Atlantic Montane rain forest: the influence of topography. *Plant Ecol* 197:239–253
- Denslow JS (2003) Weeds in paradise: thoughts on the invasibility of tropical islands. *Ann Mo Bot Gard* 90:119–127
- Díaz RI (2012) Análisis y modelación de la evolución espacio-temporal de la invasión de *Rubus ulmifolius*, *Aristotelia chilensis* y *Ugni molinae*, en la Isla Robinson Crusoe. Tesis Ingeniería en Recursos Naturales Renovables. Universidad de Chile, Facultad de Ciencias Forestales y de la Conservación de la Naturaleza
- Dirnböck T, Greimler J, López P, Stuessy TF (2003) Predicting future threats to the native vegetation of Robinson Crusoe island, Juan Fernández archipelago, Chile. *Conserv Biol* 17:1650–1659
- Duffrêne M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol Monogr* 67:345–366
- Elias RB, Dias E (2009) Gap dynamics and regeneration strategies in *Juniperus–Laurus* forests of the Azores islands. *Plant Ecol* 200:179–189
- Glavac V (1996) Vegetationsökologie: Grundfragen, Aufgaben. Methoden. Jena, Gustav Fischer
- Greimler J, Lopez PS, Stuessy TF, Dirnböck T (2002) The vegetation of Robinson Crusoe island (Isla Masatierra), Juan Fernández Archipelago, Chile. *Pac Sci* 56:263–284
- Hagen E, Odum P, Johow F, Wainstein M (2005) Conservación del picaflor de Juan Fernández (*Sephanoides fernandensis*), especie endémica en peligro de extinción. Informe Parque Nacional Juan Fernández. 10p
- Hahn I, Vergara PM, Römer U (2011) Habitat selection and population trends in terrestrial bird species of Robinson Crusoe island: habitat generalists versus forest specialists. *Biodivers Conserv* 20:2797–2813
- Hobbs RJ, Arico S, Aronson J, Baron JS, Bridgewater P, Cramer VA, Epstein PR, Ewel JJ, Klink CA, Lugo AE et al (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. *Glob Ecol Biogeogr* 15:1–7
- Jäger H, Kowarik I (2010) Resilience of native plant community following manual control of invasive *Cinchona pubescens* in Galápagos. *Restor Ecol* 18:103–112
- Kent M, Coker P (1992) Vegetation description and analysis: a practical approach. Belhaven, London
- Kier G, Kreft H, Lee TM, Jetz W, Ibisch PL, Nowicki C, Mutke J, Barthlott W (2009) A global assessment of endemism and species richness across island and mainland regions. *Proc Natl Acad Sci* 106:9322–9327
- Kueffer C, Schumacher E, Dietz H, Fleischmann K, Edwards PJ (2010) Managing successional trajectories in alien-dominated, novel ecosystems by facilitating seedling regeneration: a case study. *Biol Conserv* 143:1792–1802
- Lertzman KP, Sutherland GD, Inselberg A, Saunders SC (1996) Canopy gaps and the landscape mosaic in a coastal temperate rain forest. *Ecology* 77:1254–1270
- Loh RK, Daehler CC (2008) Influence of woody invader control methods and seed availability on native and invasive species establishment in a Hawaiian forest. *Biol Invasions* 10:805–819
- Mathews TR, Burslem DFR, Phillips RT, Mullins CE (2008) Modelling direct radiation and Canopy gap regimes in tropical forests. *Biotropica* 40:676–685
- McCune B, Grace JB, Urban DL (2002) Analysis of ecological communities. MjM Software Design Gleneden Beach, Oregon
- Murillo-Aldana J, Ruiz E (2011) Revalidación de *Nothomyrcia* (Myrtaceae), un género endémico del Archipiélago de Juan Fernández. *Gayana. Botánica* 68:129–134
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GA, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858
- Oertli B, Joye DA, Castella E, Juge R, Cambin D, Lachavanne JB (2002) Does size matter? The relationship between pond area and biodiversity. *Biol Conserv* 104:59–70
- Oksanen J, Blanchet GF, Kindt R, Legendre P, O’Hara RB et al (2011) vegan: Community Ecology Package. R package version 117–118. <http://cran.r-project.org/web/packages/vegan>. Accessed 2 March 2012
- Quinn JF, Harrison SP (1988) Effects of habitat fragmentation and isolation on species richness: evidence from biogeographic patterns. *Oecologia* 75:132–140
- R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

- Roberts D (2012) labdsv: Ordination and Multivariate Analysis for Ecology. R package version 15-0. <http://CRAN.R-project.org/package=labdsv>. Accessed 5 June 2012
- Runkle JR (1981) Gap regeneration in some old-growth forests of the eastern United States. *Ecology* 62:1041–1051
- Runkle JR (1982) Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* 63(5):1533–1546
- Schnitzer S, Carson W (2001) Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology* 82(4):913–919
- Skottsberg C (1953) The vegetation of Juan Fernández islands. In: The natural history of Juan Fernández and Easter island, Uppsala, pp 793–960
- Smith-Ramirez C, Arellano, G, Mora, JP, Hagen E, Vargas R, Miranda A (2013) El rol de *Turdus falcklandii* (Ave: Passeriforme) como dispersor de plantas invasoras en el archipiélago de Juan Fernández. *Revista Chilena de Historia Natural* (in press)
- Stirling G, Wilsey B (2001) Empirical relationships between species richness, evenness, and proportional diversity. *Am Nat* 158:286–299
- Stuessy TF, Foland KA, Sutter JF, Sanders RW, Silva M (1984) Botanical and geological significance of potassium–argon dates from the Juan Fernandez islands. *Science* 225:49–51
- Tassin J, Riviere J-N, Cazanove M, Bruzzese E (2006) Ranking of invasive woody plant species for management on Réunion island. *Weed Res* 46:388–403
- Totland Ø, Nyeko P, Bjerknes AL, Hegland SJ, Nielsen A (2005) Does forest gap size affects population size, plant size, reproductive success and pollinator visitation in *Lantana camara*, a tropical invasive shrub? *For Ecol Manag* 215(1–3):9–338
- Vargas R, Reif A (2009) The structure, regeneration and dynamics of the original forest of Robinson Crusoe's island (Juan Fernández Archipelago, Chile): guidelines for its restoration. In: proceedings World Forestry Congress, Buenos Aires, 2009
- Vargas R, Cuevas JG, Le-Quesne C, Reif A, Bannister J (2010) Spatial distribution and regeneration strategies of the main forest species on Robinson Crusoe island. *Revista Chilena de Historia Natural* 83:349–363
- Vargas R, Reif A, Faúndez MJ (2011) The forest of the Robinson Crusoe island, Chile: an endemism hotspot in danger. *Bosque* 32:61–70
- Vibrans H (1999) Epianthropochory in Mexican weed communities. *Am J Bot* 86:476–481
- Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol Lett* 14:702–708