




Invasive plant species thresholds in the forests of Robinson Crusoe Island, Chile

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ABSTRACT

Background: Invasion by exotic plants worldwide can lead to the loss of native species, particularly on islands with a high proportion of endemic plants, such as Robinson Crusoe Island (RCI).

Aims: We studied the two most invasive exotic plant species occurring in the forest of RCI: *Aristotelia chilensis* and *Rubus ulmifolius*. We aimed at establishing thresholds for environmental and microsite variables related to invasion.

Methods: Environmental and forest understorey variables, including canopy gaps and invasive species cover were measured in non-invaded and invaded forest sites. We expected more invasion in plots located close to invasive shrublands, and in large gaps with high solar radiation.

Results: We found no relationship between the distance to invasive shrublands and invasion probability. Solar radiation tended to be slightly related with a higher cover of *R. ulmifolius*, the most abundant invasive exotic plant in RCI forests. Overall, the cover of native ferns appeared to inhibit invasion.

Conclusions: The identification of variable thresholds related to invasion can be useful for guiding management decisions. Our results suggest that management should consider monitoring forest canopy gap formation and promote the establishment of ferns to reduce the probability of invasive species establishing.

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Introduction

The ecological impact of invasive plant species on native communities they invade has been well documented, especially on islands (Hejda et al. 2009; Vilà et al. 2011). Invasive plant species are those introduced by humans into a region in which they did not evolve and where they can compete with native species, alter natural habitats and affect nutrient cycling and/or interfere with native food webs, impacting on the natural resources and may affect economic activities (Heleno et al. 2010). Invasive plants may prevent tree seedling recruitment in forest by direct competition for light, water, nutrients and/or space (Burnham and Lee 2010). Furthermore, invasive species may persist for several years in seedbanks or as seedlings (Vilà et al. 2011), and they can promote the expansion of other exotic invasive species (Vargas et al. 2013) leading to changes in forest structure and

the loss of species dependent on natural forest characteristics and composition, such as birds (Minden et al. 2010) and smaller vascular species. These impacts are particularly striking on island ecosystems where invasive plant species can be particularly successful due to the high availability of resources and niches and the fact that native species are usually specialists that are easily displaced by exotics (Daehler et al. 2004).

Most plant invasions occur in forests altered by human disturbances, open canopy and/or canopy gaps (Totland et al. 2005; Baret et al. 2008). Canopy gaps caused by the death and fall of trees or large branches are the dominant small-scale disturbance in temperate forests (Oliver and Larson 1990; Schliemann and Bockheim 2011). Such disturbances increase resource availability, and facilitate the colonisation by species with greater competitive abilities than the natives (Prieur-Richard and Lavorel 2000). Canopy gaps provide safe sites

for tree species to germinate, particularly light-demanding taxa (Yamamoto 2000). Consequently, invasive species may take advantage of these areas with higher radiation to establish (Funk 2013; Driscoll et al. 2016). This process occurs in several island ecosystems worldwide where invasive plants establish in canopy gaps, affecting forest regeneration, leading to fragmentation, loss of forest area and eventually to species extinctions (Baret et al. 2008; Vargas et al. 2013; Denslow 2003). Thus, it is relevant to understand which environmental and microsite variables promote plant invasions on island ecosystems so that their impact on biodiversity could be reduced.

Robinson Crusoe Island (RCI) (33° 38' 29" S 78° 50' 28" W, Juan Fernández Archipelago) has the highest rate of plant endemism in the world (1.9 species km⁻²) Bernadello et al. 2006). Canopy gaps affect, on average, 22 ± 15.8% of the native forests (Smith-Ramírez et al. 2017). The montane forests of RCI (Greimler et al. 2002), referred to as *Myrtisylva* due to the dominance of *Nothomyrcia fernandeziana* of the Myrtaceae (Danton 2006), covers an area of 1,015 ha (Smith-Ramírez et al. 2013). This forest contains around 50 to 60 endemic vascular plant species (ca. 70% endemism) and is the main habitat of critically endangered plant and bird species (Hahn et al. 2011; Vargas et al. 2011). Plant invasion in the forests of RCI mainly involves two exotic plant species: *Aristotelia chilensis* and *Rubus ulmifolius*, that arrived from continental Chile around 1864 and 1927, respectively (Dirnbörk et al. 2003). The fleshy fruits of these invasive plants are principally spread into the forest gaps by gravity, wind and the native austral thrush (*Turdus falcklandii*) (Mora and Smith-Ramírez 2016). Once established, both invasive species spread vegetatively, often by stolons (*R. ulmifolius*), quickly occupying the disturbed area. In canopy gaps, where invasive species dominate, the abundance (−69%) and richness (−28%) of native plants are reduced (Lara et al. 2014) and can even lead to the local extinction of some native species in some instances (Vargas et al. 2013).

Although there is some knowledge about the biotic interactions of invasive species in RCI (Cuevas and Van Leersum 2001; Dirnböck et al. 2003; Arellano-Cataldo and Smith-Ramírez 2016), the mechanisms related to environmental

and biotic factors promoting invasion at the microsite scale, remained unclear. Understanding which environmental and microsite variables are important for invasion success is fundamental for scientific and management/conservation purposes, including forest restoration in the Juan Fernández Archipelago, as well as on other islands with natural forest remnants. We regard microsite as the space where a plant is rooted, above which its foliage develops and expands, i.e., a space of similar environmental conditions such as: vegetation cover, sunlight, temperature, soil and physical characteristics (Whittaker and Levin 1977). Identifying environmental and microsite variables could help to understand the biotic resistance to exotic species invasion within natural communities (Levine et al. 2004). Some variables have been considered important to explain invasion in forest communities worldwide. They include the distance to roads, distance to the nearest large source of propagules of invasive species (Von Holle and Simberloff 2005) and the forest canopy cover, which relates with solar radiation that usually correlates with invasive species presence (Pauchard and Alaback 2004; Reinhart et al. 2006). Similarly, the proportion of forest gaps and the time since gap formation (i.e., gap age) have also been found to be related to invasion, because the probability of invasion tends to increase with time (Burnham and Lee 2010).

Defining thresholds of ecological variables related with the occurrence of a given species can be very useful to guide management activities (Hothorn and Müller 2010). Thresholds go a little further than just identifying a positive or negative relationship of a predictor variable with, for example, the presence of an endangered species (Müller and Butler 2010). They provide a limit to the relationship found, hence an improvement in actions can be used to promote or prevent certain species (e.g., number of standing dead trees snags for birds, microsites for tree regeneration; Müller and Bütler 2010; Vargas et al. 2013). Although there exists a large body of knowledge about environmental and microsite characteristics that invasive species generally prefer (e.g., vacant niches, disturbed and/or recently changed ecosystems; Moles et al. 2008; Martin et al. 2009), direct, applied examples cannot easily be found (Forrest Meekins and McCarthy 2001; Hothorn and Müller 2010). However, such information could be useful in

areas such as RCI, where urgent restoration measures are needed (Smith-Ramírez et al. 2017).

In this work, we focused on the environmental and microsite variables that determine the presence and abundance of two invasive woody shrubby species in the forest ecosystems of RCI. We studied the two most invasive woody species (*A. chilensis* and *R. ulmifolius*) in treefall gaps and in closed forest. We aimed at identifying the variables that facilitated (predicted) the presence and abundance of these invasive species and quantified the relationship. Our principal objective was to assess threshold values of critical environmental and microsite variables that were related to the invasiveness of *A. chilensis* and *R. ulmifolius*. We hypothesised that: (a) the closeness to shrublands containing the invasive species, (b) higher solar radiation and (c) the time since canopy gap formation would positively influence the presence and abundance of the invasive species in forest areas of RCI. Alternatively, larger distances to the shrublands, percent closed canopy cover and recently formed canopy gaps would limit invasion. Establishing these relationships, and particularly the thresholds involved, may help to guide conservation and restoration actions.

Materials and methods

Study area

RCI is part of the Juan Fernández Archipelago National Park, a UNESCO World Biosphere Reserve, considered a biodiversity conservation hotspot (Myers et al. 2000). It is located in the Pacific Ocean, 667 km from mainland Chile. RCI is the only permanently inhabited island of the Archipelago (ca. 850 inhabitants). The climate is warm-temperate and humid, with short and dry summers. Mean annual temperature is 15.3°C, and annual precipitation is 1150 mm (Cuevas and Figueroa 2007). The RCI formed as a result of a volcanic hotspot about 4 million years ago (Stuessy et al. 1984), and the soils developed from colluvial sediments and ash (Castro et al. 1995). The topography is rugged with few flat areas; the highest peak is El Yunque at 915 m a.s.l.

Our study was carried out in the Plazoleta del Yunque forest, an area of native transitional and upper montane forest of around 100 ha (250–550 m a.s.l. Greimler et al. 2002). Tree density >

5 cm diameter at breast height (1.3 m, dbh) varies between 900–1330 trees ha⁻¹ with the dominant tree layer being 12–18 m tall and largely composed of *N. fernandeziana* (Vargas et al. 2010). According to Vargas et al. (2010), emergent individuals of *Fagara mayu* (> 20 m high) represent around 9% of the tree density; *Bohemeria excelsa* (1.3% trees/ha⁻¹) while *Coprosma pyrifolia* (< 1%) are less frequent in the dominant layer. *Drimys confertifolia* (6.4%) is usually present in the intermediate layer (6–12 m high) where it sometimes coexists with the invasive exotic *A. chilensis* (6.2%). About 1.2% of the trees are *Rhaphithamnus venustus* that usually grow in the lowest tree layer (< 6 m). Fern species are frequent in the understory and account for most of the vascular species richness (Greimler et al. 2002). Canopy gaps are created mainly by fallen senescent trees, affecting in average about 0.04 ha year⁻¹ in the study area (Smith-Ramírez et al. 2017). Over 75% of the gaps in the study area have cover of one or both of the two exotic invasive species *A. chilensis* and *R. ulmifolius* (Arellano 2011).

Sampling design and data collection

We established six transects of 100 to 240 m in Plazoleta del Yunque forest, to characterise the forest stand structure. Transects were separated by ca. 300 m. All gaps intersected by transects ($n = 31$) were described by considering their slope position (i.e., upper, mid, and bottom), size, origin, and vegetation cover. We defined gaps as an interruption in the forest canopy of a size larger than 20 m², extending down through all canopy layers to at least 2 m above ground (Brokaw 1982). Most canopy gaps found in the transects were of endogenous origin, created by fallen trees (94%), and located in mid-slope positions (87%). Gaps were dominated by either the main invasive exotics (*A. chilensis* and *R. ulmifolius*) or native plant species, 52% and 48% of them, respectively. We focused on a subset of 19 canopy gaps of similar attributes, created by fallen trees and positioned mid-slope. Gaps were classified according to the degree of invasion by the exotics into invaded (10) and non-invaded (9) gaps. We established 398 squared sampling units (4 m²) inside gaps, at gap borders and closed forest considering among 16–36 sampling units per gap site. Consequently, we considered three levels for the factor forest zone (i.e., gap, border and forest) and

two levels for the factor invasion (invaded, non-invaded). The number of sampling units established depended on the gap size, so, larger gaps presented more sampling units than smaller ones. Gap borders were considered as the transitional areas from gap border trees (> 5 cm dbh; > 12 m height) and extending up to 5 m into the closed forest (Dyer et al. 2010).

Environmental and microsite variables related to invasion were sampled within each 4 m² sampling unit. We considered a manifold of variables aimed at representing the following aspects: (a) abiotic conditions, (b) forest understorey, (c) juvenile trees and (d) invasive species. Abiotic conditions and gap-related variables included: the linear distance to the nearest *A. chilensis*-*R. ulmifolius* shrubland, determined in a GIS, using geographical coordinates taken by GPS at the centre of each gap (Diaz 2012). Solar radiation transmittance was estimated via hemispherical photographs, following the protocol of Brunner (2002). The camera (Nikon Coolpix 990 fitted with a Nikon FC-E8 converter[®]) was set at the centre of each plot at ca. 0.5 and 1.5 m heights to contrast conditions below and above the level of invasive species cover. If present, invasive shrubs were removed so that they would not affect the photograph taken. Furthermore, the time since gap formation (gap age) was estimated from the decay state of the gap makers found (i.e., fallen canopy tree creating a gap; Lertzman et al. 1996). Gap-maker trees were categorised by degree of decay: little, intermediate or high. The presence of a single mostly decayed gap-maker log indicated an 'old' gap and in the absence of mostly decayed logs, the next decay category was assigned, either 'intermediate' or 'newly-formed' (Vargas et al. 2013a, b). Moreover, the distance from each plot to the nearest closed forest area was obtained using a metric tape, and the size of the canopy gaps related to each plot was calculated using the ellipse formula by measuring the largest and shortest gap axes. Each plot was assigned to one of the following categories: forest zone (gap, gap border, closed forest), slope shape (straight, convex, concave), elevation (m a.s.l.) and slope (%). To characterise forest understorey, the cover of native ferns, mosses and liverworts, coarse woody debris (> 3 cm diameter), litter, and the cover of mineral soil and rocks were estimated (using 10% classes; Müller-Dombois and Ellenberg 1974). To characterise

juvenile trees (< 5 cm dbh) at each sampling unit, the density, basal area (using the root collar diameter) was estimated. Moreover, for each sampling unit, we calculated the total crown area (assuming circular crowns), based on the average of two perpendicular diameter estimates. Finally, the percent cover was estimated for *A. chilensis* and/or *R. ulmifolius* in each sampling unit. Hemispherical photographs were analysed with HemIMAGE[®] software to estimate percent above canopy light (PACL %; Brunner 2002) considering the five warmest months on RCI (1 December–30 April; i.e., plant growing season), assuming 50% of diffuse light due to cloudiness (Hajek and Espinoza 1987).

Data analyses

To avoid pseudoreplication, the data collected in each sampling unit was averaged by gap, border and closed forest zones for analysis. From the 19 gaps, two of them presented only one forest zone possible to find in the field, and in two others, only two forest zones were found. The 51 plots were obtained then, as 15 gaps with three forest zones (45 plots), two gaps with one forest zone (2) and two gaps with two forest zones (4). From the 51 plots, 30 were non-invaded and 21 invaded (< 10% or, > 10% cover of *A. chilensis* and/or *R. ulmifolius*, respectively). We considered medians and interquartile ranges (25–75% of the distribution, Kent and Coker 1992) as better statistics for representing the central tendency and variability of the variables than the mean.

We focused the statistical analysis of the response variables: presence/absence of invasive plant species and percent of cover of *A. chilensis* and *R. ulmifolius*. Since we were not focused on hypotheses testing, but on pointing out differences on the variables related with invaded and non-invaded sites, as well as on analysing factors determining invasion, we deliberately avoid reporting *P*-values. Furthermore, we think that in ecological analysis, the *P*-values are generally misleading on focusing just on this number rather than in the potential relationships among variables (White et al. 2014).

We used classification and regression trees (CART) to determine how the presence and abundance of invasive species were related to environmental and microsite variables (Hothorn et al. 2012). To first identify a broad

pattern for the occurrence of invasive species on RCI, classification trees was implemented using the dichotomous response variable option: combined presence or absence of both invasive species. We were able to do this since both invasive species conform a shrubland (Skottsberg 1953; Greimler et al. 2002; Danton and Perrier 2006), they both have edible fruits, similar dispersal agents and germination patterns (Smith-Ramírez et al. 2013; Mora and Smith-Ramírez 2016). Afterwards, analyses were made on the estimated percent cover values (proxy for abundance) individually for the two invasive species (Hothorn and Müller 2010; Hothorn et al. 2012). 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. 2012). The minimum sum of weights considered in the analyses were 10 plots for splitting, and 7 plots for terminal nodes (Hothorn et al. 2012). The explanatory variables included were: (a) abiotic and gap-related variables, (b) forest understorey and (c) characteristics of the juvenile trees. All statistical analyses were conducted in R (v. 3.0.2., R Development Core Team 2013) using the package ‘party’ for CART (Hothorn et al. 2012).

Results

Almost all environmental and microsite variables differed among non-invaded and invaded forest sites (Table 1). Invaded plots were located about 20 m closer to the nearest shrubland containing the invasive species, than non-invaded sites. Estimated light transmittance values differed between invaded and non-invaded sites, and were on average about 1.3% lower at invaded sites, measured either at 0.45 m or at 1.45 m. There were some slight differences among invaded and non-invaded sites: gap size associated with non-invaded sites was larger and sites were located at lower elevations and on flatter slopes than those invaded (Table 1). The cover of ferns and litter was higher in non-invaded sites than in invaded gaps and surrounding forest while the cover of mosses and liverworts, coarse woody debris, mineral soil, and rocks was higher in invaded sites. Non-invaded sites had about 4000 native trees ha⁻¹ (< 5 cm dbh), while in invaded sites the median was about 625 plants ha⁻¹. This resulted in higher basal and crown areas in non-invaded sites. Overall, non-invaded plots ($n = 30$) had negligible cover of invasive species. Invaded plots instead ($n = 21$), presented 0–19% *A. chilensis* cover, whereas 0–51% of *R. ulmifolius* (Table 1).

Table 1. Environment and microsite variables in non-invaded and invaded plots on Robinson Crusoe Island (median and interquartile range).

Variable/forest areas	Non-invaded sites ($n = 30$)	Invaded sites ($n = 21$)
(a) Abiotic and gap-related characteristics		
Distance to invasive shrubland (m)	66.6 (46–129)	48.3 (0–77)
Distance to closed forest (m)	1.0 (0–2.8)	3.0 (1–5)
Light at 0.45 m (Percentage of full light, PACL %)	5.3 (4.1–6.3)	4 (3–9)
Light at 1.45 m (Percentage of full light, PACL %)	6.9 (4.9–8.6)	5.6 (4.4–11.4)
Associated Gap size (m ²)	186 (127–297)	161 (97–272)
Elevation (m.a.s.l)	315 (305–325)	321 (312–330)
Slope (%)	32.7 (21–40)	42 (38–60)
(b) Forest understorey (%)		
Ferns	30.8 (25–45)	12.7 (6.5–25)
Bryophytes	7 (4.7–10)	8.3 (6–15)
Coarse woody debris	2 (0–14)	36.1 (15–43)
Litter	84 (75–88)	75 (58–87.5)
Mineral soil	0.8 (0–2.5)	4.4 (2–12.5)
Rocks	18.5 (14–24)	20.7 (18–27.5)
(c) Characteristics of the juvenile trees (< 5 cm dbh)		
Total basal area (cm ²)	1.8 (1–3.1)	0.08 (0–0.6)
Total crown area (m ²)	0.2 (0.07–0.35)	0.02 (0–0.07)
Native tree regeneration (N)	1.6 (0.7–2.5)	0.25 (0.05–0.67)
(d) Invasive species presence and cover (%)		
Plots with presence of <i>A. chilensis</i> only	0	4
Plots with presence of <i>R. ulmifolius</i> only	0	5
Plots with <i>A. chilensis</i> and <i>R. ulmifolius</i>	0	7
Cover by <i>Aristotelia chilensis</i> (%)	0.0 (0–0)	10 (0–19)
Cover by <i>Rubus ulmifolius</i> (%)	0.0 (0–0)	30.0 (0–51)

Presence and cover of invasive species

There was a negative relationship between the cover of ferns and invasive species. When ferns covered more than 15% of the plots, invasive species were less likely to be found (ca. 30% probability; Figure 1).

R. ulmifolius had higher cover than *A. chilensis*, with an interquartile range of 0–51% cover in invaded plots, while *A. chilensis* cover was between 0 and 19% (Table 1). The cover of *A. chilensis* was higher in sites where native fern species covered less than 7.5% (Figure 2, node 2) than where fern cover was higher. When fern cover was more than this threshold, we found in general less than 5% cover of *A. chilensis* in the plots (Figure 2, node 3)

Ferns were also the most important variable related to the cover of *R. ulmifolius*. The abundance of *R. ulmifolius* was highest (~ 50% cover) when fern species covered less than 12.7% of the plot (Figure 3, node 2). Sites with more than 12.7% fern cover were generally associated with less than 5% cover of *R. ulmifolius* (Figure 3, right side of the split). Sites that surpassed 12.7% cover of ferns were related with some more cover of *R. ulmifolius* only when light transmittance was more than 7.3% (Figure 3, node 5).

Discussion

Variables and thresholds that influence invasive species

In RCI forests, the cover of native ferns seems to contain the invasion of exotic species. Invasion was significantly related with areas that lack substantial fern cover (< 15%). When ferns covered more than 15% of the site area, the amount of invasion reduced dramatically, presenting always less than 30% probability of presence. Our results showed that invasion was not directly influenced by the distance to the shrublands that contained the invasive species (propagule source), or the time since disturbance occurred (canopy gap formation). In general, we did not find a broad trend between invasion and solar radiation received by the forest site. This contrasts with what has been reported in other forests affected by similar exotic species, where radiation was strongly related to invasion in gaps (Baret et al. 2008; Gaudio et al. 2008).

Although invaded plots were located closer to shrublands than non-invaded plots, lower distances seemed not to increase significantly the invasion probability. This contrasted with previous studies that identified a positive relationship between the distance from invasive species shrubland and the density of invasive species in the RCI

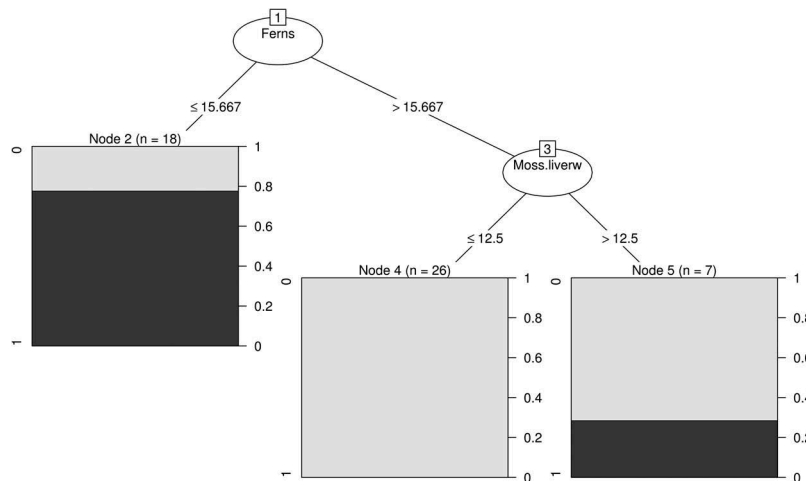


Figure 1. Classification tree to predict presence-absence of invasive species (*A. chilensis* + *R. ulmifolius*) in plots located in the forest of Robinson Crusoe Island (RCI). The circled explanatory variables presented the strongest association with the response (presence or absence of invasive species). Values on lines indicate the splitting criteria. For example, the first split is given by the cover of ferns (% of cover). Number in boxes above the explanatory variables indicate the hierarchical node number. The predicted presence or absence of invasive species is shown in the terminal blocks, representing the probability of invasive species presence (1, dark part of blocks), or absence (0, gray grey part of blocks), based on 51 plots (4 m²). Significant explanatory variable selected by the analysis was the ferns cover (Ferns) and the cover by mosses and liverworts (Moss.liverw). Other abiotic and gap-related variables, attributes of the forest understorey and characteristics of the juvenile that were included on the analyses but resulted non-significant were: distance of the plot to the next invasive shrubland, estimated age of gaps, forest zones where plots were located (Gap, gap border or Forest), distance in meters from the plot to the next closed forest area, estimation of total light transmittances, gap size, total regeneration of tree species in plots, total basal area of trees in plots and total crown area of tree species in plots.

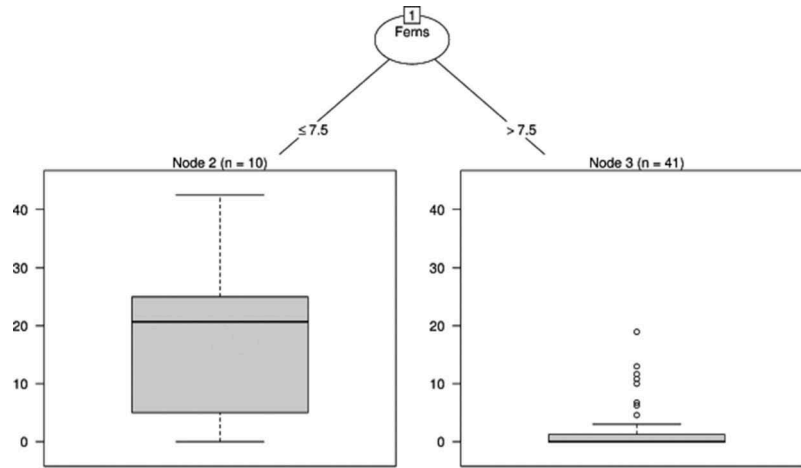


Figure 2. Regression tree to predict the abundance of *A. chilensis*, located in forest sites of RCI within the conditional inference framework. The encircled explanatory variables are those showing the strongest association with the response (cover percentage % of *A. chilensis*, inside 4 m² plots). Values on lines connecting explanatory variables indicate the splitting criteria. The only significant explanatory variable selected by the analysis was the ferns cover (Ferns).

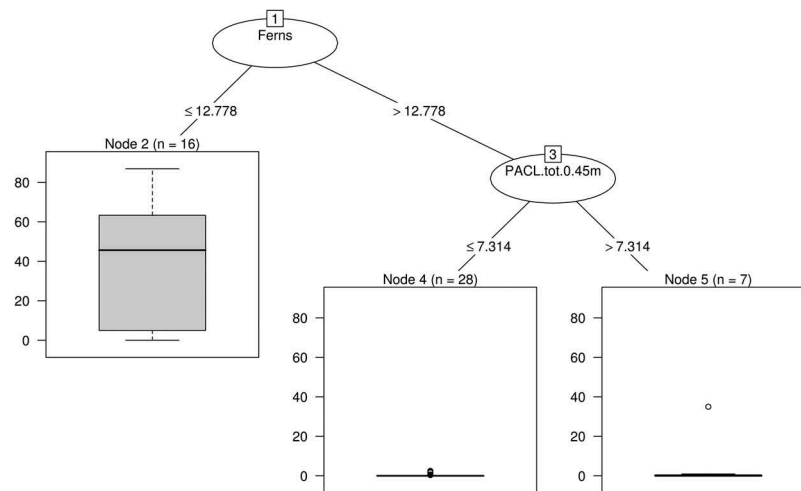


Figure 3. Regression tree to predict the abundance of *R. ulmifolius* located in forest sites of RCI within the conditional inference framework. The encircled explanatory variables are those showing the strongest association with the response (cover percentage % of *R. ulmifolius*, inside the 4 m² plot). Values on lines connecting explanatory variables indicate the splitting criteria. Explanatory variables selected by the analysis were: percent cover by ferns (Ferns); and estimation of total light transmittances (percentage above canopy light; PACL.tot.0.45 m).

forests (Arellano 2011; Arellano-Cataldo and Smith-Ramírez 2016). On average, our invaded plots were located not more than 18 m closer to shrublands, than non-invaded plots. Furthermore, across the study area there are several invaded sites (e.g., canopy gaps, trails) closer to the gaps studied than invasive the shrublands dominated by the invasive species, thus, creating a diffuse propagule pressure, reducing the importance of the distance to the main propagule source. Moreover, both invasive species present several dispersal agents, including endozoochory by the austral thrush, which enables them to be dispersed up to 50–60 m from the propagule source (Mora and Smith-Ramírez 2016).

Similarly, our results did not indicate a direct influence of the time since disturbance (i.e., estimated age of canopy gaps) on invasion probability. Contrary to what we hypothesised, the time since gap formation was not related to a greater invasion probability, or to a higher cover of invasive species. This might be explained by considering that plots were considered ‘invaded’, when invasive species, cover was > 10%. Our sampling units were rather small (4 m²) and invasive species when present, may take advantage of the available site in a short period of time, probably covering more than 0.5–1 m² per year, which corresponded to more than 10% of the analysed plots. Canopy gaps were categorised as

recently created up to two years since formation, which seems to be long enough for ‘invasion’, given the abundant seeds and multiple propagation strategies that the two invasive species have (Mora and Smith-Ramírez 2016). For instance, tree ring studies have documented the fast growth of *A. chilensis* in RCI, in that in 20 years it reaches the size of ca. 140-year-old individuals of *N. fernandeziana*, the main endemic tree species in the forest of RCI (Rojas-Badilla et al. 2017).

Solar radiation was only slightly related to a higher cover of *R. ulmifolius* in the RCI forests. This contrasts with what has been reported in other forests affected by similar exotic species, where radiation was strongly related to invasion presence in gaps (Baret et al. 2008; Gaudio et al. 2008). This difference might have been caused by the fact that our study was not established to contrast shaded with non-shaded areas. The sampling units we used, running from gaps into closed forest, and the radiation measurements (made at a maximum of 1.5 m) resulted in gradual changes of light, not contrasting very exposed areas with covered sites. Higher solar radiation was slightly related with a higher cover of *R. ulmifolius* at sites where fern cover was >12%, suggesting that the relationship: radiation-invasion might be clearer when there is some competition (Rentería et al. 2012; Flory et al. 2009).

In general our results show that invasive plant species do not co-occur with native ferns. When ferns cover more than 15% of the plots, the probability of finding any invasive plant is reduced to less than 30%. Competition from ferns might reduce the chances for invasive species to establish, which appears to inhibit or at least delay invasion. Similarly, higher species richness and cover of native species seem to prevent invasive species in the Galapagos (Rentería et al. 2012).

Microsites and implications for forest restoration

Establishing/maintaining fern cover might be the best preventive measure against invasive species in RCI forests. The likelihood of finding invasive species was considerably reduced in gaps with substantial fern cover. Since 2004, invasive plants have been controlled in forest gaps on RCI to improve the nesting habitat for the endangered endemic Juan Fernández firecrown (*Sephanoides*

fernandensis; Vargas et al. 2014; Smith-Ramírez et al. 2017). The re-invasion by the two plant species along with other opportunistic exotics have made it essential to continuously employ expensive control measures in managed areas (Vargas et al. 2013, 2013b). Due to the lack of knowledge of fern species propagation and cultivation, establishing ferns in RCI is difficult. Planting juvenils of native tree species which have been naturally regenerating in managed areas appears as an option. However, considering our results, fern planting might be effective in controlling invasive species. Ferns cover the ground more rapidly than trees and shade better than young native forest individuals, which have small crowns. Moreover, ferns do not provide easy perching for the austral thrush, so the dispersion of invasive species seeds could be also reduced.

Invasive species management activities should consider monitoring forest gaps for early detection and removal of invasive species to facilitate native species recruitment. This option might be used to prevent invasion on strictly protected sites (Kueffer et al. 2010). A promotion of establishment for ferns before the gaps are invaded (and control measures are instituted), would ensure a reduction in the probability of invasive species from establishing. Unlike in other ecosystems, ferns on RCI do not act as ecological filters for tree seedlings; rather they appear to facilitate the regeneration of endemic tree species (George and Bazzaz 1999; Vargas et al. 2013).

Conclusions

Our assessment of invasive plants in the forest of RCI shows a strong association between invasion and some environmental and microsite variables. Overall, fern cover (>15%) appears to reduce the probability of the presence of the two invasive species in gaps to less than 30%. This study not only improves our current knowledge on the dynamics of two extremely invasive species, but also could provide restoration directions for protecting a highly threatened forest ecosystem. The monitoring of gap creation followed by the prompt control of exotic species to prevent invasion is a management strategy not yet tested in the endangered forest of RCI. Further research is needed to understand fern and tree species recruitment, propagation and establishment to

use ferns as natural agent in preventing colonisation by invasive shrubs.

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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). Santiago (Chile): Universidad de Chile. p. 61.
- Arellano-Cataldo G, Smith-Ramírez C. 2016. Establishment of invasive plant species in canopy gaps on Robinson Crusoe Island. *Plant Ecology*. 217:289–302.
- 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 Reunion. *Journal of Tropical Ecology*. 24:337–345.
- Bernardello G, Anderson GJ, Stuessy TF, Crawford DJ. 2006. The angiosperm flora of the Archipelago Juan Fernández (Chile): origin and dispersal. *Canadian Journal of Botany*. *Journal Canadien De Botanique*. 84:1266–1281.
- Brokaw NV. 1982. The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica*. 1982:158–160.
- Brunner A. 2002. hemIMAGE, a hemispherical image analysis program. Version 15-09-2002. Danish Forest and Landscape Research Institute, Hørsholm, Denmark. p.18.
- Burnham KM, Lee TD. 2010. Canopy gaps facilitate establishment, growth, and reproduction of invasive *Frangula alnus* in a *Tsuga canadensis* dominated forest. *Biological Invasions*. 12:1509–1520.
- Castro C, Brignardello L, Cereceda P. 1995. Determinación de áreas con riesgo morfodinámico en San Juan Bautista, Isla Robinson Crusoe, comuna de Juan Fernández, V Región. *Revista Geográfica De Chile Terra Australis*. 40:43–61.
- Core Team R. 2013. R: A language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. "<http://www.r-project.org/>" "<http://www.R-project.org/>".
- Cuevas JG, Figueroa J. 2007. Seed germination of species of the Juan Fernández archipelago under laboratory conditions. *Gayana Botánica*. 64:60–80.
- Cuevas JG, Van Leersum G. 2001. Proyecto conservación, restauración y desarrollo de las Islas Juan Fernández, Chile. [Project "conservation, restoration, and development of the Juan Fernández islands, Chile"]. *Revista Chilena De Historia Natural*. 74:899–910.
- Daehler CC, Denslow JS, Ansari S, Kuo HC. 2004. A risk-assessment system for screening out invasive pest plants from Hawaii and other Pacific Islands. *Conservation Biology*. 18:360–368.
- Danton P. 2006. The myrtisylva of the Juan Fernández Archipelago (Chile), a threatened forest. *Acta Botanica Gallica*. 153:179–199.
- Danton P, Perrier C. 2006. Nouveau catalogue de la flore vasculaire de l'archipel Juan Fernández (Chile). *Acta Botanica Gallica*. 153:399–587.
- Denslow JS. 2003. Weeds in Paradise: thoughts on the Invasibility of Tropical Islands. *Annals of the Missouri Botanical Garden*. 90:119–127.

- Diaz R **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]. [Santiago (Chile)]: Universidad de Chile, Facultad de Ciencias Forestales y de la Conservación de la Naturaleza. p. 55.
- Dirnböck T, Greimler J, López P, Stuessy TF. **2003**. Predicting future threats to the native vegetation of Robinson Crusoe Island, Juan Fernández archipelago, Chile. *Conservation Biology*. 17:1650–1659.
- Driscoll AG, Angeli NF, Gorchov DL, Jiang Z, Zhang J, Freeman C. **2016**. The effect of treefall gaps on the spatial distribution of three invasive plants in a mature upland forest in Maryland 1, 2. *The Journal of the Torrey Botanical Society*. 143:349–358.
- Dyer JH, Gower ST, Forrester JA, Lorimer CG, Mladenoff DJ, Burton JL. **2010**. Effects of selective tree harvests on aboveground biomass and net primary productivity of a second-growth northern hardwood forest. *Canadian Journal of Forest Research*. 40:2360–2369.
- Flory SL, Clay K. **2009**. Invasive plant removal method determines native plant community responses. *Journal Of Applied Ecology*. 46(2):434–442.
- Forrest Meekins J, McCarthy BC. **2001**. Effect of environmental variation on the invasive success of a nonindigenous forest herb. *Ecological Applications*. 11(5):1336–1348.
- Funk JL. **2013**. The physiology of invasive plants in low-resource environments. *Conservation Physiology*. 1:1–16.
- Gaudio N, Balandier P, Marquier A. **2008**. Light-dependent development of two competitive species (*Rubus idaeus*, *Cytisus scoparius*) colonizing gaps in temperate forest. *Annals of Forest Science*. 65:1–5.
- George LO, Bazzaz FA. **1999**. The fern understory as an ecological filter: growth and survival of canopy-tree seedlings. *Ecology*. 80:846–856.
- Greimler J, Lopez PS, Stuessy TF, Dirnböck T. **2002**. The vegetation of Robinson Crusoe Island (Isla Masatierra), Juan Fernández Archipelago, Chile. *Pacific Science*. 56:263–284.
- Hahn IJ, Vergara PM, Römer U. **2011**. Habitat selection and population trends in terrestrial bird species of Robinson Crusoe Island: habitat generalists versus forest specialists. *Biodiversity and Conservation*. 20(12), p2797.
- Hajek E, Espinoza G. **1987**. Meteorología, climatología y bioclimatología de las Islas Oceánicas Chilenas. En *Islas oceánicas chilenas: conocimiento científico y necesidades de investigaciones*. Castilla JC, Editor. Santiago Chile: Ediciones Universidad Católica de Chile. p. 55–84
- Hejda M, Pyšek P, Jarošík V. **2009**. Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology*. 97:393–403.
- Heleno R, Lacerda I, Ramos JA, Memmott J. **2010**. Evaluation of restoration effectiveness: community response to the removal of alien plants. *Ecological Applications*. 20:1191–1203.
- Holle BV, Simberloff D. **2005**. Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology*. 86:3212–3218.
- Hothorn T, Hornik K, Zeileis A. **2012**. Party: a laboratory for recursive partytioning (version 1.0–2). *Computer software manual*. p 37.
- Hothorn T, Müller J. **2010**. Large-scale reduction of ungulate browsing by managed sport hunting. *Forest Ecology and Management*. 260:1416–1423.
- Kent M, Coker P. **1992**. *Vegetation Description and Analysis: A Practical Approach*. CRC Press, Boca Raton, 363 p.
- 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. *Biological Conservation*. 143:1792–1802.
- Lara A, Amoroso A, Bannister J, Donoso C, Gonzalez M, Vargas R, Smith-Ramirez C, Arellano-Cataldo G, Gutierrez AG. **2014**. Sucesión y dinámica de bosques templados en Chile. In: *Ecología Forestal. Bases Para El Manejo Sustentable y Conservación de Los Bosques Nativos de Chile*. Valdivia (Chile). Donoso C, González M, Lara A, Editores. Universidad Austral de Chile. p. 323–408.
- Lertzman KP, Sutherland GD, Inselberg A, Saunders SC. **1996**. Canopy gaps and the landscape mosaic in a coastal temperate rain forest. *Ecology* 77(4): 1254–1270.
- Levine JM, Adler PB, Yelenik SG. **2004**. A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters*. 7:975–989.
- Martin PH, Canham CD, Marks PL. **2009**. Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. *Frontiers in Ecology and the Environment*. 7:142–149.
- Minden V, Jacobi J, Porembski S, Boehmer H. **2010**. Effects of invasive alien kahili ginger (*Hedychium gardnerianum*) on native plant species regeneration in a Hawaiian rainforest. *Applied Vegetation Science*. 13:5–14.
- Moles AT, Gruber MA, Bonser SP. **2008**. A new framework for predicting invasive plant species. *Journal of Ecology*. 96:13–17.
- Mora JP, Smith-Ramírez C. **2016**. Are birds, wind and gravity legitimate dispersers of fleshy-fruited invasive plants on Robinson Crusoe Island, Chile? *Flora-Morphology, Distribution, Functional Ecology of Plants*. 224:167–171.
- Müller J, Bütler R. **2010**. A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. *European Journal of Forest Research*. 129:981–992.
- Müller-Dombois D, Ellenberg H. **1974**. *Aims and methods of vegetation ecology*. New York (NY): Wiley. p. 45–66.
- Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J. **2000**. Biodiversity hotspots for conservation priorities. *Nature*. 403:853–858.
- Oliver CD, Larson BC. **1990**. *Forest stand dynamics*. New York. McGraw-Hill Pub. Co. p. 467.
- Pauchard A, Alaback PB. **2004**. Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of South-Central Chile. *Conservation Biology*. 18:238–248.

- Prieur-Richard AH, Lavorel S. 2000. Invasions: the perspective of diverse plant communities. *Austral Ecology*. 25:1–7.
- Reinhart KO, Gurnee J, Tirado R, Callaway RM. 2006. Invasion through quantitative effects: intense shade drives native decline and invasive success. *Ecological Applications*. 16:1821–1831.
- Rentería JL, Gardener MR, Panetta FD, Atkinson R, Crawley MJ. 2012. Possible impacts of the invasive plant *Rubus niveus* on the native vegetation of the *Scalesia* forest in the Galapagos Islands. *PLoS ONE* 7(10): e48106.
- Rojas-Badilla M, Le Quesne C, Álvarez C, Velásquez-Álvarez G, Rozas V. 2017. Crecimiento radial de la especie endémica *Nothomyrcia fernandeziana* (Hook. & Arn.) Kausel y la invasora *Aristotelia chilensis* (Molina) Stuntz en la isla Robinson Crusoe, Archipiélago de Juan Fernández, Chile. *Gayana Botanic*. 74:1.
- Schliemann SA, Bockheim JG. 2011. Methods for studying treefall gaps: a review. *Forest Ecology and Management*. 261:1143–1151.
- Skottsberg C. 1953. The vegetation of Juan Fernández Islands. In: *The natural history of Juan Fernández and Easter Island*. Uppsala (Sweden): Almqvist & Wiksells Boktrickeri AB. p. 793–960
- Smith-Ramírez C, Arellano G, Hagen E, Vargas R, Castillo J, Miranda A. 2013. El rol de *Turdus falcklandii* (Aves: Passeriforme) como dispersor de plantas invasoras en el archipiélago de Juan Fernández. *Revista Chilena De Historia Natural*. 86:33–48.
- Smith-Ramírez C, Vargas R, Castillo J, Mora JP, Arellano-Cataldo G. 2017. Woody plant invasions and restoration in forests of island ecosystems: lessons from Robinson Crusoe Island, Chile. *Biodiversity and Conservation*. 26(7): 1507–1524.
- Stuessy T, 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.
- 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? *Forest Ecology and Management*. 215:329–338.
- 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, Gärtner S, Alvarez M, Hagen E, Reif A. 2013. 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. *Biodiversity and Conservation*. 22(6-7): 1283–1300.
- Vargas R, Reif A, Faúndez MJ. 2011. The forest of the Robinson Crusoe Island, Chile: an endemism hotspot in danger. *Bosque*. 32:61–70.
- Vargas R, Smith-Ramírez C, González C, Fernández M. 2014. El Archipiélago Juan Fernández: Endemismo en peligro para conservar. In: *Reservas de Biósfera de Chile: Naturaleza y Ser Humano*. Santiago (Chile): U Católica. p. 126–143
- Vilá 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. *Ecology Letters*. 14:702–708.
- White JW, Rassweiler A, Samhouri JF, Stier AC, White C. 2014. Ecologists should not use statistical significance tests to interpret simulation model results. *Oikos*. 123(4):385–388.
- Whittaker RH, Levin SA. 1977. The role of mosaic phenomena in natural communities. *Theoretical Population Biology*. 12:117–139.
- Yamamoto SI. 2000. Forest gap dynamics and tree regeneration. *Journal of Forest Research*. 5:223–229.