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

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ABSTRACT

Biological invasions are a major driver of biodiversity loss on islands. After disturbances, invasive plant species can establish affecting forest regeneration microsites. On Robinson Crusoe Island (33°S, Juan Fernández Archipelago, Chile) small-scale treefall canopy gap microsites are most frequently used by "endemic montane forest" species for regeneration. Regeneration can be hampered when invasive species establish and alter gap conditions. We evaluated the role of small-scale disturbances on regeneration and identified tree regeneration microsites in gaps, gap borders, and closed forest. We collected information on the effects caused by invasive species by sampling 30 gaps with a range of invasive species cover, including gaps where invasive species were removed. We analyzed the impact of native ferns and invasive species, regeneration substrates and light availability on native tree species regeneration and juvenile tree performance traits. Our aim was to analyze small-scale disturbances and identify threshold values for the variables related with tree regeneration presence–absence, density and performance, particularly considering invasive species competition. We used classification and regression trees to identify variables and their threshold values influencing native tree species regeneration. Gap borders and small gaps (<200 m^2) were preferred microsites for regeneration. Native tree species seemed able to compete as long as invasive species cover did not exceed 10%. Fern cover >10% facilitated tree regeneration and performance. Competition from invasive species for space, water and nutrients was likely more important than for light. Restoration should attempt to recreate intermediate disturbance conditions considering the threshold values identified. Thresholds for variables important for restoration processes can help in the control of invasive species.

1. Introduction

Forest composition, structure and function are dependent on the response of tree regeneration to site conditions, disturbances and management practices (Gray et al., 2005). Forest tree species require certain environmental and micro-habitat conditions thereby making forest regeneration a complex and multidimensional process (Smith et al., 1997). Forest ecosystems are affected differently by natural disturbances which influence the spatial, temporal and heterogeneous nature of forest patches (Pickett and White, 1985). In turn, the availability of different resources result in diverse plant regeneration niches (Grubb, 1977). Treefall gaps caused by the fall of one or more trees creating an opening in the forest canopy are the dominant small-scale disturbance in many forest ecosystems worldwide and are known to be important for the self-replacement of temperate and tropical forests (Yamamoto, 2000; Schliemann and Bockheim, 2011; Promis et al., 2010; Durán-Rangel et al., 2013).

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

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

We studied the role of small-scale disturbances and the impact of invasive species on the natural regeneration of endemic tree species on Robinson Crusoe Island (RCI, Juan Fernández Archipelago, Chile 33°37'S, 78°50'W). This island has an extremely high density of endemic vascular species (1.9 endemic species/km^2; Bernardello et al., 2006) and a large number of naturalized exotic plant species (292 exotic vs. 149 native; Danton and Perrier, 2006). It is therefore a good location to study the interactions between native and exotic plants. There are 927 ha of shrublands with invasive species compared to 1014.8 ha of native forest (32.9% and 36% of the total vegetation cover respectively; Smith-Ramirez et al., 2013). *Rubus ulmifolius* (Rosaceae) and *Aristotelia chilensis* (Eleocarpaceae) are aggressive invaders and threaten the montane forest ecosystem (Greimler, Lopez et al., 2002). Annually both species produce a large number of fleshy fruits (containing small seeds <6 mm diameter; Hoffmann, 1992) that are disseminated by native birds, gravity and wind (Smith-Ramirez et al., 2013). These species can also spread asexually and establish more quickly than native tree species in forest gaps (Vargas et al., 2013). The remaining intact montane forest is comprised only of endemic tree species (Danton, 2006) that provide habitat for two threatened endemic land-bird species and more than 40 endangered endemic vascular plant species (Vargas et al., 2011). Without effective invasive species control it has been predicted that half of what remains of the RCI montane forest may become dominated by invasive species by 2080 (Dirnböck et al., 2003). On the other hand it has been shown that the recovery of native species is possible after invasive plants are removed (Vargas et al., 2013). Previous studies in the RCI forest have pointed out the negative effects of invasive plant species on biodiversity and how exotic plant invasions are influenced by: gap size, slope, litter depth and distance to propagule source (Vargas et al., 2013; Arellano, 2011). However, despite the growing understanding of the relationship between invasive and native plants, no study has yet identified neither the thresholds beyond which native plant recovery is compromised or the specific regeneration requirements of endemic forest species. Identifying the threshold values of the variables related with the presence of a species of interest is an approach widely applied in studies that serve to provide information for biodiversity conservation and management activities (Müller and Bütler, 2010; Hothorn and Müller, 2010).

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

2. Materials and methods

2.1. Study area

Field work was carried out in Plazoleta del Yunque, RCI, Juan Fernández Archipelago National Park, an approximately 100 ha area of montane forest between 250 and 550 m.a.s.l (Greimler, Stuessy et al., 2002). The climate is warm temperate with a mean annual temperature of 15.3 °C and an annual precipitation of 1150 mm (Cuevas and Figueroa, 2007). The soils developed from colluvial sediments and ash (Castro et al., 1995). The RCI endemic montane forest tree density ranges between 900 and 1330 trees per ha (>5 cm diameter at 1.3 m, dbh). The dominant tree species is *Myrceugenia fernandeziana* (76% of the individuals per ha), 14–18 m high (Vargas et al., 2010). *Fagara mayu* (9%) is common in the canopy and forms an emergent layer (>22 m), while *Drimys conferifolia* (6.4%) and the invasive tree species *A. chilensis* (6.2%) can be found in the intermediate layer (8–12 m) (Cuevas and Vargas, 2006). *Rhaphithamnus venustus* (1.2%), *Bohemeria excelsa* (1.3%) and *Coprosma pyrifolia* (<1%) are infrequent components of the intermediate and dominant layers. When the forest canopy is broken by gaps, species richness, the proportion of invasive species and the regeneration density of native tree species change (Vargas and Reif, 2009; Arellano, 2011). Gaps were defined as a break of at least 20 m^2 in the forest canopy extending down through all canopy levels to at least two meters above ground (Brokaw, 1982). For our study we used the expanded gap areas (i.e., canopy gap plus the adjacent area extending to the bases of the surrounding border trees >12 m high; Runkle, 1982). About one quarter of the forest canopy in the study area is affected by gaps that range in size between 46 and 777 m^2, and are created mainly by senescent trees falling (Arellano, 2011; Vargas et al., 2013). These gaps are created at a yearly rate of ca 2% of the forest surface (Smith-Ramirez et al., 2013). *A. chilensis* and/or *R. ulmifolius* (i.e.,invasive species) occur in most gaps in the study area (about 85% of 37 gaps sampled by Arellano (2011)). Half of 46 gaps sampled in a previous study were dominated by invasive species (>30% *A. chilensis* and *R. ulmifolius* cover) whereas one third were dominated by native species (<5% invasive species cover; Vargas and Reif, 2009). Since 2004 the invasive species have been removed from some gaps to improve the nesting habitat of the critically endangered hummingbird (*Sephanoides fernandensis*, Hagen et al., 2005). These gaps provided us with an opportunity to study another category of gaps, "treated" with which to compare regeneration microsites under relatively similar conditions. Accordingly, gaps were categorized as: "natural", withno or low (<5%) cover of exotic invasive species (N = 10), "invaded gaps" with a significant cover of *A. chilensis* and *R. ulmifolius* (>30%, N = 9), and "treated gaps", where the invasive exotic plant species were removed (N = 11) by cut-stump control of *A. chilensis* and *R. ulmifolius* by application of Garlon 4® 5% mixture (Tryclopir; Hagen et al., 2005). Invasive species had been removed from the treated gaps for at least one year and at most six years before data collection.

2.2. Sampling design

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