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Research article

Functional trait variation predicts distribution of alien plant species across the light gradient in a temperate rainforest

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ABSTRACT

Several interspecific studies have related functional traits to alien plant invasiveness. Few studies have explicitly addressed how intraspecific variation in functional traits influences alien plant distribution across environments. In an old-growth temperate rainforest, we evaluated alien plant distribution across the light gradient, its relationship with native plant diversity and abundance, and variation in functional traits related to light capture that could explain the ecological breadth of alien plant species across the light gradient. In addition, we estimated possible ecological and phylogenetic constraints to intraspecific variation in these functional traits. In sixty 8-m² plots we recorded light availability together with richness and abundance of alien and native plant species. We measured in 14 alien plant species three functional traits (specific leaf area, chlorophyll content and root/shoot ratio) and calculated their coefficient of variation. We estimated ecological constraints by measuring correlations among traits that could limit functional responses to light. We assessed phylogenetic constraints by calculating the phylogenetic signal of those functional traits. Richness and abundance of alien plant species were positively associated with light availability, while abundance was negatively related to native plant species abundance. Dominance of alien species increased with light availability, but some of them were dominant even in the shade. Phenotypic variation of functional traits was positively associated with ecological breadth and dominance of alien plant species. We found little evidence of ecological or phylogenetic constraints on functional trait variation. Light availability and functional trait variation correlated with the distribution and dominance of alien plants in this temperate rainforest. Alien plant species showed considerable phenotypic variation in low light, which may facilitate colonization of the forest understory. This process would not be hindered by ecological or phylogenetic constraints. Intraspecific variation in functional traits can render insightful information on current and future alien plant distribution across environmental gradients.

1. Introduction

Invasion ecology aims to understand the success of alien species beyond their natural range. In absence of propagule dispersal limitation (Simberloff, 2009), factors that determine the establishment of alien species in new habitats are related to either: (1) invasiveness of alien species, the features that promote their ability to be invasive, or (2) invasibility of local communities, the characteristics that make them vulnerable to invasion (Richardson and Pyšek, 2006). To better understand the invasion process, these two issues should be considered together.

Ecological breadth, the extent of an environmental gradient that a given species occupies, is a good predictor of species distribution (Futuyma and Moreno, 1988). Alien species with broad ecological breadth (generalists) are expected to be more successful than specialist

species (Vázquez, 2005; Richards et al., 2006). Plant species with large ecological breadth across a light gradient show ample variation in their functional traits related to light capture (Walters and Field, 1987; Sultan et al., 1998; Saldaña et al., 2005; Gianoli et al., 2012), which may facilitate the colonization of different light environments (Violle et al., 2012). Expected functional responses to light availability in order to optimize or maintain a positive carbon balance include changes in leaf area and thickness (specific leaf area, SLA), chlorophyll content, and root:shoot ratio of biomass allocation (Salgado-Luarte and Gianoli, 2011). Many functional traits have been related to invasiveness in alien plant species after analyses conducted at the interspecific level (e.g., Baruch and Goldstein, 1999; Grotkopp and Rejmánek, 2007; Van Kleunen et al., 2010). Fewer studies have explicitly addressed how intraspecific variation in functional traits influences alien plant species distribution across environments (e.g., Sexton et al., 2002; Godoy et al.,

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2011; Sultan and Matesanz, 2015) despite the fact that it is at the local scale where evolution of environmental tolerance takes place (see Gianoli and Saldaña, 2013).

Biotic and abiotic factors often determine the susceptibility to plant invasion of a community (Lonsdale, 1999; Stotz et al., 2017). High resource availability or resource fluctuation may enhance survival of alien propagules, and thus invaded ecosystems are typically open and disturbed habitats (Davis et al., 2000; Theoharides and Dukes, 2007; Escobedo et al., 2017). Relatively few plant invasion studies have been carried out in less disturbed ecosystems such as mature forests, where pioneer-like invasive plants have been traditionally considered to be excluded from the dark understory (Martin et al., 2009). Regarding biotic factors, high community diversity may confer resistance to invasions (Lodge, 1993; Levine and D'Antonio, 1999). This has been explained in terms of reduced niche availability for invaders in species-rich communities, but the relationship between native species diversity and invasibility is variable and depends on the spatial scale of the analysis (Shea and Chesson, 2002). The abundance of native species in the community may also be relevant for invasibility; dominance of one or a few species may prevent invasions through the sequestration of limiting resources or physical exclusion (Robinson et al., 1995).

In the old-growth temperate evergreen rainforest of southern Chile, light availability determines the distribution of plant species (Lusk et al., 2006; Gianoli et al., 2010; Saldaña et al., 2014). In this temperate rainforest a field study addressed the mechanisms of invasion of the alien perennial *Prunella vulgaris* into the mature forest, showing that the invasion success was explained by phenotypic plasticity and adaptation to local light conditions (Godoy et al., 2011). This mature forest – located within a protected area – is not “immune” to plant invasions (see Martin et al., 2009); in fact, nearly 60 alien plant species have been reported in gaps, roads, trails and the forest understory (Muñoz-Schick, 1980; Mardones et al., 2012). Roads and trails are the most important pathway for introduction of propagules in protected areas, as they facilitate propagule dispersion and modify microclimatic conditions (Parendes and Jones, 2000; Pauchard and Alaback, 2004). Moreover, roads and trails may act as reservoirs of propagules from which alien plant species can establish into the forest understory (Gilbert and Lechowicz, 2005; Godoy et al., 2011).

We conducted a field study across a light gradient in this temperate rainforest, evaluating whether the distribution and abundance of alien plant species is influenced by light availability and native plant diversity. We also evaluated whether the ecological breadth of alien plant species is related to their variation in functional traits (SLA, chlorophyll, and root:shoot biomass ratio) across the light gradient, thus exploring explanatory mechanisms of alien plant invasiveness at the intraspecific level. Furthermore, in view of the trait-mediated successful adaptation to light environments in the alien plant *P. vulgaris* described above (Godoy et al., 2011), we explored possible ecological and phylogenetic constraints to adaptive variation in these functional traits in the alien species. Ecological constraints were estimated by measuring correlations among traits (Etterson and Shaw, 2001; Gianoli and Palacio-López, 2009). Specifically, we tested for associations that could constrain expected functional responses to light availability (Salgado-Luarte and Gianoli, 2011): negative correlations between traits that should increase with low light (SLA and chlorophyll content) and positive correlations between any of these traits and the trait that should decrease with low light (root:shoot). Phylogenetic constraints were assessed by calculating the phylogenetic signal of those traits (Blomberg et al., 2003; Ackerly, 2009), with significant and high phylogenetic signals indicating that trait variation is to some extent constrained by the evolutionary history and features of the species lineage. We hypothesized that i) species richness and abundance of alien plant species would increase with light availability and would decrease with native plant species richness and abundance, and ii) the ecological breadth and dominance of alien plant species in the light gradient would reflect the extent of their functional trait variation.

2. Materials and methods

2.1. Study site

The study was carried out in Anticura, Puyehue National Park, Southern Chile (40°39'S, 72°11'W; 350–400 m). The climate is maritime temperate, with average annual precipitation of 2800 mm and temperature of 9.8 °C (Dorsch, 2003). Soils are well drained, acidic, derived from volcanic ash, and with low availability of nutrients due to low mineralization and high immobilization rates (Lusk et al., 2003; Saldaña and Lusk, 2003). Mature forests are dominated by broadleaf, evergreen species (Lusk et al., 2006; Gianoli et al., 2010). Plant distribution is mainly determined by light availability, but herbivore pressure may also play a role (Lusk, 2002; Salgado-Luarte and Gianoli, 2010, 2012). Regarding alien plant species, Mardones et al. (2012) recorded 57 species for the entire Puyehue National Park, including those originally reported by Muñoz-Schick (1980), and 38 species for the Anticura area. Alien plants are mainly associated with forest gaps and trails (Muñoz-Schick, 1980; Godoy et al., 2011; Mardones et al., 2012).

2.2. Sampling

We sampled 60 plots (4 × 2 m) randomly located across different light environments, from open sites to deep understory, near trails, roads and prairies; plots lay within an area of nearly 200 ha. Plots were at least 15 m apart. We quantified light availability in the middle of each plot using hemispherical photographs as described in Gianoli et al. (2010). The photographs were taken 0.5 m above the ground using a horizontally-levelled digital camera (Nikon Coolpix E4500) with a fish-eye lens with 180° field of view (Nikon FC-8). All photographs were taken under homogeneous sky conditions (cloudy). Using HemiView 2.1 (Delta-T Devices, Cambridge, U.K.), we measured the global site factor, GSF, the fraction of total radiation (diffuse + direct) expected to reach the spot where the photograph was taken. This calculation takes into account the sun trajectory in the sky, based on geographic location of the site and the time of the year. GSF values range from 0 to 1, representing no sunlight and full sunlight, respectively. As propagule pressure can decrease with distance to roads (Pauchard and Alaback, 2004), we measured the minimum distance (m) from a plot to the nearest potential propagule source (main road, trails, prairies, and anthropogenic areas).

In each plot we estimated species richness and abundance (% cover) of alien and native plant species from the herbaceous and shrub layers. Functional traits related to light capture and use were measured in 14 alien plant species from a total of 23 alien plants found (species list in Supplementary data Table S1). These 14 species were chosen due to their contrasting ecological breadth (see below), and together accounted for 89% of total abundance of alien plant species in the study site. For each selected species, we measured specific leaf area (SLA), chlorophyll content (Chl) and root/shoot biomass ratio (R/S). For each species and trait 15 individuals were measured in 5 representative plots of the light conditions used by the species, including the extremes of their distribution across the light gradient. Chl was measured using a hand-held chlorophyll meter (CCM 200, Opti-Sciences, Inc., Tyngsboro, Massachusetts, USA), with three measurements in a single leaf per individual. For SLA (cm² g⁻¹) two leaves per individual were scanned and analysed using ImageJ software (<https://imagej.nih.gov/ij/>) to obtain leaf area, dried at 70 °C for 72 h, and weighed to get dry mass using an analytical balance. For both SLA and Chl we averaged the measurements made in each individual to obtain a single replicate. For R/S, whole plants (15 individuals per species) were collected, dried at 70 °C for 72 h, and weighed to get dry mass of roots and shoots. To collect whole plants we carefully dug soil blocks (20–30 cm sides, 30 cm deep) using hand shovels, with the focus plant in the centre (immediately adjacent plants were not sampled); to facilitate separation of

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