

Seed predation of non-native species along a precipitation gradient

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Abstract Generalist seed predators are an important factor shaping non-native species invasion. Their effect is highly influenced by abiotic conditions, yet how the importance of this biotic filter changes in a gradient of abiotic conditions is still poorly understood. In this study, we assessed seed predation of non-native conifer species along a precipitation gradient in north-western Argentinean Patagonia. We performed a seed removal experiment over a 15-day period during the fall in sites where annual precipitation ranges from 600 to 1600 mm and vegetation ranges from steppe to forest. We used the three most common forestry species in the study area, including two species known to invade areas adjacent to plantations and one native species. Seed predation was higher in

sites with higher precipitation, but no significant differences in seed predation were found among species. Small mammals were the dominant group preying seeds on this gradient. These findings highlight the importance of abiotic conditions mediating plant-granivore interactions, and the influence that abiotic conditions may have on biotic resistance to invasion.

Keywords Environmental conditions · Non-native · Plant invasion · Plant–granivore interactions

Introduction

Ecologists have long focused on how different biotic interactions influence plants abundance and distribution (Maron et al. 2014). For instance, granivory can affect plant demography and community composition (Brown and Heske 1990; Hulme and Benkman 2002). The removal of kangaroo rats (*Dipodomys* spp.) in a Chihuahuan desert shrub, for example, led to an increase of perennial and annual grasses (Brown and Heske 1990), while the abundance of the non-native species *Tragopogon dubius* was decreased by native generalist rodents in North American grasslands (Pearson et al. 2012). Hence, seed predation is an important biotic filter influencing both native and non-native species' abundance and distribution.

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Seed predation, however, can affect native and non-native species differently (Nuñez et al. 2008; Maron et al. 2012; Connolly et al. 2014). For instance, seed removal was higher for native and naturalized species compared to non-native species in a steppe and adjacent coniferous forest in North America (Connolly et al. 2014) and for native and weak invaders compared to strong invaders in an inter-mountain grassland in Montana (Pearson et al. 2011). In contrast, in a native forest in north-western Patagonia Nuñez et al. (2008) found that seed predators preferred seeds of the non-native *Pinus contorta*, *Pinus ponderosa*, and *Pseudotsuga menziesii* over seeds of the natives *Austrocedrus chilensis* and *Nothofagus dombevi*. Despite apparent contradictions, together previous studies suggest that seed predation may differentially affect native and non-native species.

At the same time, abiotic environmental conditions can shape seed predation patterns by influencing the abundance and activity of animals. For instance, seed predation of *Avena sativa* in North American grasslands was positively related to annual evapotranspiration and precipitation (Orrock et al. 2015). Thermal conditions of the environment can directly influence aboveground activity and foraging decisions of predators (Orrock and Danielson 2009). For example, seed predation of *Peromyscus leucopus* was higher on warm and cloudy nights in a riparian woodland (Orrock and Danielson 2009). Indirectly, conditions that favor plant biomass production may also support higher densities and abundance of granivores and hence result in higher levels of seed consumption (Orrock et al. 2015). Additionally, greater vegetation productivity may increase the availability of sheltered habitats for granivores (Caccia et al. 2006). These alternative mechanisms jointly highlight the context dependency of the strength of plant-granivore interactions.

Given the importance of abiotic conditions on biotic interactions (Rodríguez-Castañeda 2013; Orrock et al. 2015; Pearson et al. 2017), it is plausible that abiotic conditions may also influence biotic resistance to invasion (sensu Elton 1958). In a recent meta-analysis, Stotz et al. (2016) found that native plants' resistance to invasion was greater in warmer and wetter conditions. In marine ecosystems, predation of non-native tunicates was higher in the tropics compared to temperate locations (Freestone et al. 2013). Exploring how biotic resistance changes along environmental gradients may help explain spatial

patterns of invasions in natural settings. Communities may resist invasion by a wide variety of biotic interactions (Levine et al. 2004). Seed predators can provide biotic resistance by inhibiting an invader's establishment or by regulating an invader's populations once established (Levine et al. 2004; Larios et al. 2017). Recruitment of non-native conifer species is regulated by seed predation in north-western Patagonia (Caccia and Ballaré 1998; Nuñez et al. 2008). Other studies have shown negative effects of seed predation on non-native plant abundance in grasslands and forests (Pearson et al. 2012, 2014). However, how the importance of seed predation on non-native species changes in a gradient of abiotic conditions is still poorly understood.

In this study, we evaluated the hypothesis that seed predation increases with precipitation because conditions that favor plants may also support higher densities and abundance of granivores. Additionally, we expected seed predation to affect native and non-native species differently. To test these hypotheses, we evaluated seed predation of native and non-native conifer species at ten sites where annual precipitation ranges from 600 to 1600 mm and vegetation ranges from steppe to forest in north-western Argentinean Patagonia (ca. 40°S). The following questions were addressed: (1) Do abiotic conditions mediate plant-granivore interactions? (2) Does seed predation affect native and non-native species in this gradient differently?. In north-western Argentinean Patagonia, treeless and open woodlands in drier areas are notably more affected by conifer invasions than more humid areas (Simberloff et al. 2002; Sarasola et al. 2006). Exploring our hypothesis may help to explain these invasion patterns. Assessing how plant-granivore interactions change in a gradient of abiotic conditions may improve our understanding of the factors influencing biotic resistance, and more generally, the drivers of community assembly (Larios et al. 2017).

Materials and methods

Study system

We evaluated seed predation at a regional level at ten sites with varying precipitation (Fig. 1, see Online Resource 1). Patagonia is a temperate or cold-temperate region where precipitation increases from

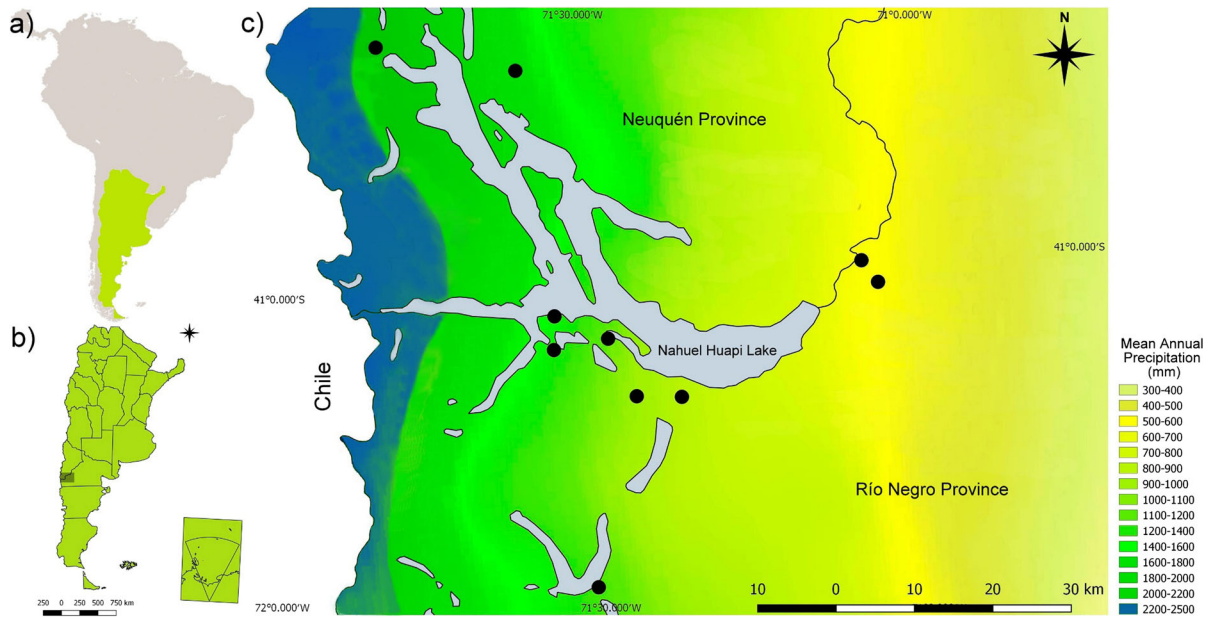


Fig. 1 Distribution of experimental sites in north-west Patagonia, Argentina. South America map with Argentina in green (a), Argentina map with shaded study area (b), and map with ten experimental sites (black dots) and precipitation information in

north-west Patagonia (c). Precipitation information was extracted from Bianchi and Cravero (2010). (Color figure online)

east to west (Paruelo et al. 1998) due to the Andes' rain shadow. This precipitation gradient influences the type of vegetation; in the dry part of the gradient, the dominant vegetation is a grass-shrub steppe community, while in the wet part the characteristic vegetation is a perennial or deciduous forest dominated by species of the genus *Nothofagus* (Cabrera 1994). Consequently, this system provides an ideal opportunity to evaluate the importance of abiotic factors mediating biotic interactions.

In this area of Patagonia, the most planted forestry species are *Pinus ponderosa*, *Pseudotsuga menziesii*, and *Pinus contorta*. *Pinus contorta* is a common invasive species in the steppe ecosystem (Sarasola et al. 2006, Pauchard et al. 2016), while *P. menziesii* is a common invader in native *Nothofagus dombeyi* and *Austrocedrus chilensis* forests (Simberloff et al. 2002; Sarasola et al. 2006; Peña et al. 2007). *Pinus ponderosa* seems not to become invasive in the area (Sarasola et al. 2006).

Seed removal experiment

To evaluate whether seed predation changes along a climatic gradient, we conducted a seed removal

experiment at ten sites with different precipitation levels using seeds from the three non-native species mentioned earlier: *P. contorta*, *P. ponderosa*, and *P. menziesii* and one native species: *Austrocedrus chilensis*. *Austrocedrus chilensis* is an endemic conifer of southern Patagonia that occurs both in forests and steppe (Veblen et al. 1995). The species included in our experiment differ in seed size, a factor known to influence seed predation (Reader 1993; Moles et al. 2003; Nuñez et al. 2008). Seeds of *A. chilensis* are two, three, and 17 times smaller than those of *P. contorta*, *P. menziesii*, and *P. ponderosa*, respectively (see Online Resource 2). At each site, there were four randomized complete blocks separated by 30–40 m. In all cases, the blocks were in open microsites (i.e., no woody understorey plants were present) within closed-canopy forests, except for the two drier treeless sites. In each block, *per* species, we installed four wooden popsicle sticks with three seeds of the same species each in a 1 m × 1 m area within a total block size of 2 m × 2 m block. We fixed sticks to the ground with stakes to prevent their removal by small mammals. Seeds were glued to the sticks with a non-toxic odor-free adhesive (Nuñez et al. 2008). We did not place seeds on the ground as in other studies (see Moles et al.

2003; Orrock et al. 2015) because of strong Patagonian winds. *Chusquea culeou*, a species known to increase seed predation by providing sheltered habitats (Caccia et al. 2006; Kitzberger et al. 2007), was present in the neighborhood of four of our sites but at low density. We visited sites at two, seven, and 15 days after experiment establishment to register seed predation. Since we glued seeds to sticks and seeds were not removed intact (Fig. 2a), we considered seed removal as evidence of seed predation and not secondary seed dispersal (Nuñez et al. 2008). Also, at each site we installed a camera trap (Bushnell Outdoor Product, Overland Park, KS) to document the main groups of granivorous animals preying upon the seeds. We carried out the experiment during fall (May–June) because this is the time of the year when seeds would naturally be available (Moles et al. 2003) and when rodent community abundance tends to peak (Guthmann et al. 1997). Rodents are considered to be the

main group preying seeds in the system (Caccia et al. 2006; Nuñez et al. 2008). The small mammal community varies in abundance and richness in the study area; there are forest species (e.g., *Chelemys macronyx*), steppe species (e.g., *Eligmodontia* spp. and *Ctenomys* spp.), and habitat generalist species that are present in both steppe and forests (e.g., *Abrothrix longipilis* and *Oligoryzomys longicaudatus*; Pearson and Pearson 1982; Pearson 1995; Pardiñas and Teta 2013).

We obtained mean annual precipitation data of each site from the software FetchClimate (Grechka et al. 2016). We used long-term climatic information rather than interannual or seasonal variability because we were interested in exploring whether long-term climate tendencies relate to seed predation (Orrock et al. 2015). Mean annual precipitation for the year the study was conducted (2017) was normal in the area (not within either extreme quartile of its distribution in

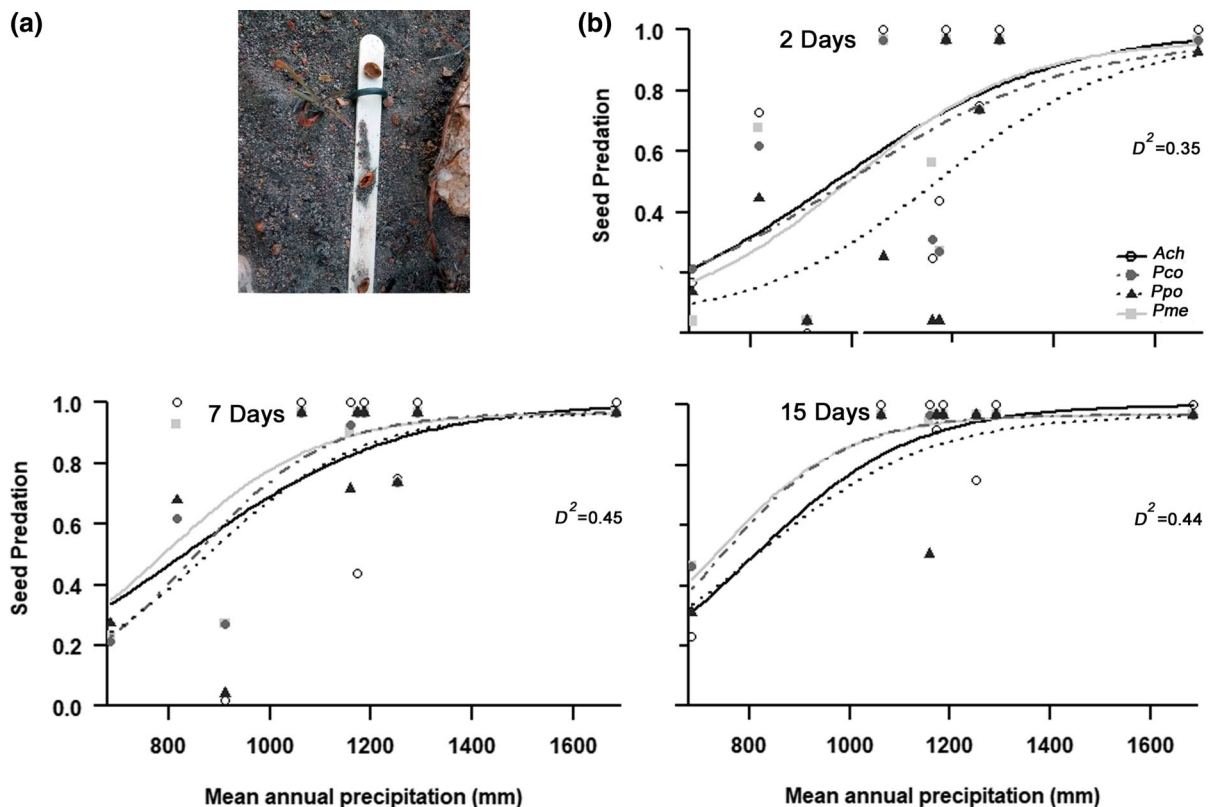


Fig. 2 a Seed consumption of *Pinus ponderosa* in the field. Photo: Jaime Moyano. b Proportion of seed predation along the precipitation gradient at 2, 7, and 15 days after experiment establishment. Symbols represent the mean seed predation for a site, as a proportion. Empty symbols for native species, filled

symbols for non-native species. Not all symbols are visible due to overlap. Ach, *Austrocedrus chilensis*; Pco, *Pinus contorta*, Ppo, *Pinus ponderosa*. Pme, *Pseudotsuga menziesii*. The lines represent the fitted line for quasibinomial models

the 1987–2017 period) (Servicio Meteorológico Nacional, national weather organization, <https://www.smn.gob.ar/>).

Statistical analysis

To determine whether seed predation varies along the precipitation gradient, we used general linear models with quasibinomial error distributions and a logit-link function. We used a quasibinomial distribution because data exhibited overdispersion (residual deviance > residual degrees of freedom). In the models, predictors were mean annual precipitation, species, and their interaction. Seed predation *per* species was calculated as the proportion of seeds eaten *per* block. Because models including blocks as a random effect had convergence problems (several warnings), we used averaged data for each species at a site level instead. We performed analyses separately for 2, 7, and 15 days after experiment establishment. Significance of terms was assessed using *F*-tests from analysis of deviance. We report significance of terms for all quasibinomial models and the D^2 statistic, equivalent to R^2 (Guisan and Zimmermann 2000). All analyses were performed using R 3.5.0 (R Development Core Team 2018).

Results

We found that seed predation increased with precipitation. The proportion of seeds predated for native and non-native conifer species was positively related to precipitation on all observation dates (2 days: $F_{1,38} = 19.2681$, $p < 0.001$; 7 days: $F_{1,38} = 28.6728$, $p < 0.001$; 15 days: $F_{1,38} = 22.4625$, $p < 0.001$). Although the slope of the curves at 7 and 15 days decreases with increasing precipitation suggesting a point of saturation (approximately at 1400 mm) (Fig. 2). Seed predation did not differ among the native and the three non-native conifer species (2 days: $F_{3,35} = 0.762$, $p = 0.523$; 7 days: $F_{3,35} = 0.2141$, $p = 0.885$; 15 days: $F_{3,35} = 0.5549$, $p = 0.648$) (Fig. 2). Precipitation effect did not depend on species identity (mean annual precipitation \times species, 2 days $F_{3,32} = 0.0495$, $p = 0.985$; 7 days $F_{3,32} = 0.2217$, $p = 0.881$; 15 days: $F_{3,32} = 0.1096$, $p = 0.954$). The main group detected by camera traps eating seeds was small mammals; no birds were

detected eating seeds. In our videos, it was possible to identify *Oligoryzomys longicaudatus* both in forests and steppe, and *Eligmodontia morgani* in steppe.

Discussion

In this study, we evaluated seed predation of native and non-native species on a precipitation gradient. As hypothesized, we found that seed predation was higher in sites with more precipitation, but there was no evidence that native and non-native species were predated differentially along the gradient. Small mammals were the dominant seed predators registered. These findings thus highlight the importance of abiotic environmental conditions mediating plant–granivore interactions, and the influence that abiotic conditions may have on biotic resistance to invasion.

Few studies have explored how seed predation changes with climatic conditions, here we found evidence supporting the expectation of seed predation increasing with precipitation. Although many factors could influence this pattern (e.g., lower predation risk in cloudier site, seed quality), our results conform with the idea that the increase in vegetation towards wetter sites may support higher abundances of granivore populations by providing more food and sheltered habitats (Caccia et al. 2006; Orrock et al. 2015), while in drier sites seed availability may be lower and predatory risk higher. Similar to our results, predation of seeds of *Avena sativa* in North American grasslands was positively related to mean annual precipitation (Orrock et al. 2015). Our results add evidence to the idea that general patterns of biotic interactions change with abiotic conditions (Rodríguez-Castañeda 2013; von Euler et al. 2014; Orrock et al. 2015; Pearson et al. 2017; Reynolds et al. 2018).

We found no significant differences in seed predation among tree species. Consuming all types of seeds resources is the optimal strategy when there are many granivores simultaneously predated upon available seeds (Brown and Mitchell 1989). This could explain the lack of selectivity in our study since we performed the experiment during the peak of rodent abundance (Guthmann et al. 1997). Our findings contrast to the many studies showing that seed predation differentially affects native and non-native species to either facilitate (Pearson et al. 2011; Connolly et al. 2014) or inhibit invasion (Nuñez et al. 2008). It has been

suggested that this could be because non-native species may have novel seed defences or lower nutritional value than native species (Pearson et al. 2011; Connolly et al. 2014) in the case of facilitation, or alternatively, because bigger sized non-native seeds would offer a higher energy resource in the case of inhibition (Nuñez et al. 2008). In a previous study with the same species and in the same area, Nuñez et al. (2008) found that seed predation of non-native bigger species was greater than those of native species. Difference in the season in which experiments were performed, winter versus fall, may help to explain the contrasting results between the two studies. Seed availability is low during winter, while fall is the peak of seed release and the peak of abundance of rodent community. Both seed availability and granivore abundance are known to influence seed predation selectivity behavior of foragers (Brown and Mitchell 1989).

In north-western Patagonia, drier areas are more invaded by conifer species than humid areas (Simberloff et al. 2002; Sarasola et al. 2006). Our results support the hypothesis that seed predation could influence this invasion pattern. However, to better understand the extent to which this invasion pattern is explained by seed predation it is necessary to perform additional experimental studies. Specifically, experiments exploring how seed predation affects recruitment and whether the effects of seed loss translate to patterns of invasive species abundances (Pearson et al. 2012; Clair et al. 2016). Previous research in the study area has identified *Chusquea culeou* cover, food availability, vegetation cover, and tree patch composition as factors influencing seed predation (Caccia and Ballaré 1998; Caccia et al. 2006; Kitzberger et al. 2007). Future research should address how these factors interact with abiotic conditions to influence seed predation. Also, even though our experiment duration is longer than other seed removal studies (Morton 1985; Moles et al. 2003; Orrock et al. 2015), longer-term experiments should be performed to evaluate the generality of our findings. It is possible that the effect of precipitation dilutes over time if all seeds are eaten eventually. Although it is also possible that predation in our study was higher than normal because of the way seeds are presented (easily detectable), in which case the effects could be more important over longer times. Additionally, the importance of seed predation versus other biotic and abiotic

factors influencing plants abundance should also be evaluated in environmental gradients.

Overall, our study shows that seed predation of native and non-native species increases with precipitation. In doing so, it provides evidence of the importance abiotic conditions may have in biotic resistance to invasion and it may help to predict responses of plant-granivore interactions to climate change.

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