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Large-scale impacts of multiple co-occurring invaders on monkey puzzle forest regeneration, native seed predators and their ecological interactions

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ABSTRACT

Most ecosystems of the world are being increasingly invaded by a variety of alien species. However, little is known about the combined ecological impacts of multiple co-occurring invaders. We assessed the impact of a community of exotic mammals (five domestic and four wild) on forests of monkey puzzle (*Araucaria araucana*), a globally endangered tree restricted to ca 400 km^2 on the slopes of the Andes in Chile and Argentina. Seeds of monkey puzzles provide food during winter to a small community of native mice and Austral parakeets (*Enicognathus ferrugineus*). We recorded the number of uneaten seeds and the number of young seedlings at the end of winter under 516 female monkey puzzle trees located across the species' distribution, and identified the signals of native and exotic species that visited the under-canopy of each tree. Moreover, we studied the diet and foraging behavior of Austral parakeets to explore the potential indirect effects of exotic mammals through the disruption of a key ecosystem service (seed dispersal) supposedly provided by parakeets. All but one tree were visited by at least one seed predator species. Austral parakeets and mice predated seeds from 85% and at least 45% of the trees, respectively, and both the number of remaining seeds and seedlings were significantly larger when only parakeets or mice predated seeds than when exotic mammals also visited the trees. At least 90% of trees were visited by one or more exotic species, and the number of seeds and seedlings dropped drastically when at least two and four exotic species visited the tree, respectively. Austral parakeets mostly foraged on monkey puzzle trees during the winter period and dispersed their seeds in most feeding instances once seeds fell to the ground. The proliferation of exotic mammals may reduce the populations of native seed-predators in the long-term as well as the regeneration of monkey puzzle forests, directly through a reduction of seed availability and seedling survival, and indirectly through the disruption of dispersal processes. Our results show how strategies based on protecting areas may assure the survival of individuals of this long-lived (up to 1300 yr) tree species. However, forest regeneration and the community of native seed-predators and related ecological processes further depend on the proper management of exotic mammal invasions.

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1. Introduction

Biological invasions are one of the major drivers of global change, yet there is considerable uncertainty about the type and intensity of their impacts on native species and their environments. Understanding the magnitude and scope of their impacts is crucial to design and prioritize management actions (Simberloff et al., 2013). Important progress regarding the empirical quantification of impacts has been made in recent decades. This has allowed the development of scoring systems for assessing or predicting the impacts caused by a variety of taxa, ranging from plants to arthropods and vertebrates (e.g., Kumschick et al., 2015). Most empirical studies and meta-analyses focus on the measurement of impacts caused by single alien species on a given environment, despite the fact that most ecosystems of the world are progressively or even simultaneously invaded by a variety of alien species. Co-occurring invaders may not only affect the invasiveness of each of the newly or yet-to-be introduced species, through facilitative or competitive interactions (Glen and Dickman, 2005), but also their net impact on the ecosystem.

Little attention has been paid to the study of combined impacts caused by co-occurring invaders. In a recent literature review, Kuebbing et al. (2013) showed that while over two thirds of important conservation habitats are multiply invaded, less than one-third of studies considered the impacts of co-occurring plant invaders and only 6% of studies focused on invasive plant interactions. Interactions (neutral, facilitative, competitive) between invaders and their additive or non-additive effects may greatly determine their invasiveness and whole impact (Kuebbing et al., 2013). The combined ecological impact of multiple invaders may result from the sum of their independent effects (additive), or be greater than (synergistic) or less than (antagonistic) the sum of their independent effects (Jackson, 2015). Jackson (2015) recently compiled the relatively few studies on co-occurring animal invaders, showing that they generally have neutral or negative impacts on one another and that their combined adverse impacts on native species are often less than predicted by an additive response and were rarely synergistic. Results, however, varied among phyla and environments, and studies were biased towards arthropods and terrestrial ecosystems of the USA (Jackson, 2015). Moreover, studies considering multiple species' impacts have dealt with pairs of co-occurring invaders (e.g., Nyström et al., 2001; Johnson et al., 2009), lacking assessments of the impact of whole invasive communities. Therefore, much more research is needed on the combined impacts of multiple invaders, both for a better understanding of biological invasions and for prioritization of which invasive species – or group of species – to manage (Kuebbing et al., 2013; Jackson, 2015).

Here, we assess the combined and multi-faceted impacts of several exotic mammals in a relatively simple ecosystem, the forest dominated by monkey puzzle trees (*Araucaria araucana*). The monkey puzzle tree is a globally endangered species whose small distribution range (392 km^2) is mostly restricted to the slopes of the Andes in Chile and Argentina (Premoli et al., 2013). The main threats to the species include deforestation, through logging for plantation of exotic tree species and anthropogenic fires, causing a 40% reduction and fragmentation of the monkey puzzle tree range. Moreover, a lack of regeneration due to seed harvesting by animals may also be a key factor and requires urgent evaluation (Premoli et al., 2013). This masting tree produces a large (3.5 g), highly nutritive seed (Sanguinetti and Kitzberger, 2008) that has been traditionally consumed by indigenous Mapuche people (Aagesen, 1998; Herrmann, 2006) and a small community of native seed predators. Among them, the Austral parakeet (*Enicognathus ferrugineus*) is the main pre-dispersal predator, removing matured seeds directly from female cones over several months (Shepherd et al., 2008). Once seeds fall to the ground (post-dispersal period) in autumn, which usually takes place between March and June, they are available over the winter and until the following spring (December) to a few native mice species (greater long-clawed mouse *Chelemys macronyx*, long haired mouse *Abrotrix longipilis*, long-tailed mouse *Oligoryzomis longicaudatus*, and arboreal mouse *Irenomys tarsalis*; Shepherd and Ditgen, 2005). Austral parakeets prey on between 0.6% and 21% of available pre-dispersed seeds in mast and intermast years, respectively (Shepherd et al., 2008). The mice assemblage can prey on between 30% and 70% of the post-dispersed seeds (Sanguinetti and Kitzberger, 2010). Nonetheless, these seed-predator species may also contribute to forest regeneration through seed dispersal (Veblen, 1982; Finckh and Paulsch, 1995; Shepherd and Ditgen, 2005). However, seed predation may have increased to the point of compromising forest regeneration after the introduction in the last century of several exotic mammals for productive (livestock) and hunting purposes, including some game species that became invaders such as wild boar (*Sus scrofa*), European hare (*Lepus europaeus*), European rabbit (*Oryctolagus cuniculus*), and red deer (*Cervus elaphus*) (Novillo and Ojeda, 2008; Speziale et al., 2012). In fact, negative effects on forest regeneration have already been shown independently for free-ranging cattle (Zamorano-Elgueta et al., 2012; Donoso et al., 2014) and wild boars (Sanguinetti and Kitzberger, 2010) in local monkey puzzle stands. A dietary study showed that wild boar feces contained more than 90% of monkey puzzle seeds in autumn (Izquierdo et al., 2001). Given their potential impacts (Vázquez, 2002), our goal was to assess the combined effects of native species and nine exotic (five domestic and four wild) mammals on overwinter seed and seedling availability at a large spatial scale (i.e., most of the tree species distribution). Moreover, we studied the diet and foraging behavior of Austral parakeets for exploring the potential indirect effects of exotic mammals through the disruption of a key ecosystem service (seed dispersal) provided by parakeets.

2. Methods

2.1. Study area and species

The monkey puzzle (family Araucariaceae) is mostly distributed from 600 to 1800 m.a.s.l. throughout the Andean ranges of Chile and Argentina (northwestern Patagonian region, Fig. 1). They form pure stands, mixed forests with *Nothofagus*