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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 km² 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 km²) 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 mast 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 *Oligoryzomys 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*

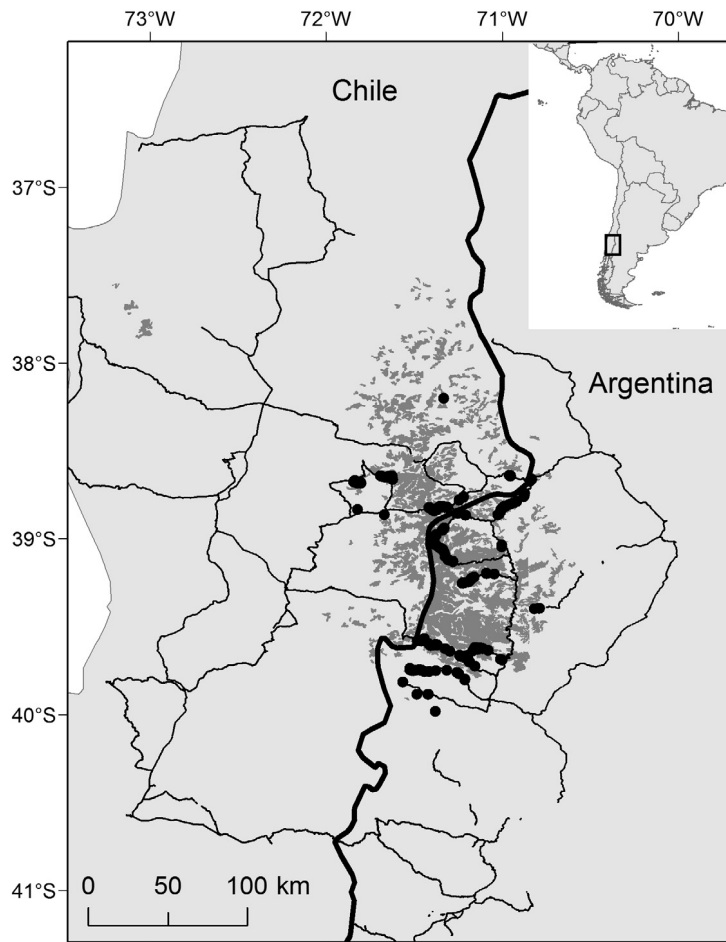


Fig. 1. Study area showing the world distribution of monkey puzzle trees (dark gray patches) at both sides of the border (wider black line) between Chile and Argentina, the 516 sampled trees (black spots, note many of them overlap), and the roads surveyed to look for foraging Austral parakeets (black lines).

pumilio (from 1200 m.a.s.l. to tree line) or *N. antarctica* (lower, drier areas and valley bottoms) and more open areas with shrublands or grasslands as understory. This tree is a long-lived conifer (over 1200 years) that reaches sexual maturity when it has a trunk greater than 20 cm d.b.h. and is more than 30 years old (Muñoz, 1984; Premoli et al., 2013). It is a dioecious species with females producing large cones (15–20 cm in diameter), which are pollinated by wind during the summer. Each cone may produce 100–200 large seeds (3.5 g), which take 16–18 months to mature. Seed production increases with age (Muñoz, 1984). Dispersal through barochory over short distances takes place between March and June (exceptionally September; Muñoz, 1984; Sanguinetti, 2008), but seed dispersal by mice and Austral parakeets may also play a role (Veblen, 1982; Finckh and Paulsch, 1995; Shepherd and Ditgen, 2005). Seed establishment is low but success increases when growing beyond the parent canopy (Finckh and Paulsch, 1995). The monkey puzzle shows masting cycles, with intermittent, moderately fluctuating and highly regionally synchronous reproduction, which improves the species' breeding performance (Sanguinetti and Kitzberger, 2008).

2.2. Seed predation and number of seedlings

Female monkey puzzles were selected throughout the study area to assess the effects of seed predators on the number of unpredated seeds and the number of seedlings at the end of the winter period. This work was conducted between 28 November and 14 December 2013, covering a large part of the world distribution of the species (Fig. 1). Two of the areas surveyed differed from the rest in the way they are subject to seasonal transhumance by ranchers. These high-altitude areas are almost free of goats and sheep in the winter, but large herds of thousands of goats mixed with some sheep are moved into these areas every year from lowlands just after winter. These two areas were visited again on 24–31 January 2014 to assess the effect of the seasonally massive occupation by herds on seed surplus and number of seedlings.

The final number of surveyed trees ($n = 516$) was constrained by the short period of time we defined to avoid confounding time effects on our estimates. Female trees were selected in an attempt to cover variability in tree size, altitude,



Fig. 2. Predated seeds and seedlings of monkey puzzle trees. Seeds eaten by (A) Austral parakeets and (B) native mice, young seedling (C), and overgrazed forest with no regeneration (D).

and land uses through the distribution of the species. Information from local people was obtained to avoid sampling sites where monkey puzzle seeds were collected for human consumption, since the inclusion in our study of human-harvested trees could mask the effects of native and exotic vertebrates on overwinter seed and seedling survival. Selected trees were spaced sufficiently (>40 m) from other unselected female trees to avoid miss-assignment of seeds and seedlings to individual trees, which are usually found within 15 m of the mother tree (Donoso et al., 2014). Each selected tree was georeferenced with a Garmin 62S GPS, recording altitude above sea level and tree height with the help of a laser rangefinder (Leica Geovid 10 \times 42). After selection, the whole seed rain area of each tree (within a radius of 5–20 m around the base of the tree, depending on its height, canopy area, and ground slope) was carefully inspected by two persons (FH plus another researcher) to estimate the number of uneaten seeds and count the number of yearling seedlings (young unramified plants usually <20 cm height, Fig. 2(D); Grosfeld et al., 1999) for 10–15 min. The number of uneaten seeds present under the tree was estimated in two ways. First, we obtained the proportion of eaten and uneaten seeds from the first 30 seeds found under the seed rain area of the tree. Second, we visually estimated the total number of uneaten seeds through a seed index, scoring them in 10 categories (0: 0 seeds, 1: 1–10 seeds, 2: 11–19 seeds, ... 10: 91–100 seeds) after several trials independently made by each researcher for standardization. The number of uneaten seeds obtained from the sample of 30 seeds correlated well with this seed index (Spearman correlation, $r = 0.75$, $n = 516$, $p < 0.001$). However, we ultimately used the seed index for statistical analyses since the proportion of uneaten seeds could be biased through predation by large mammals that can consume in situ the whole seeds or through seed removal by rodents (thus inflating the proportion of uneaten seeds in some cases). Finally, we visually estimated the percentage of soil covered by the under-canopy vegetation (small bushes, grasses and bamboo), since it could affect both seed removal by predators and seed germination.

The identity of seed predator species visiting each tree was obtained in several ways. The numerous observations of Austral parakeets feeding on monkey puzzle seeds (see below) allowed us to clearly identify the seeds eaten by this species through its characteristic method of opening the seed coat to gain access to the seed and its endosperm (Fig. 2(A), see also Shepherd et al., 2008). Rodents, however, nibble the seed coat leaving it with a characteristic shape and tooth marks (Fig. 2(B)). Seeds predated by native rodents were often found in the entrance of small burrows among the roots of the tree or stones, so we actively looked for burrows to confirm seed predation by them. Since we could not identify the rodent species, seeds eaten by rodents were pooled together as eaten by mice. The identity of exotic mammal species visiting the trees was obtained through the easily identifiable feces, dung (see Zamorano-Elgueta et al., 2012 for cattle dung), and footprints of all species, together with characteristic diggings made by European rabbits, pigs and wild boars, and direct observation of the species below the selected trees in some instances. We were able to observe cows, horses, goats, sheep,

Table 1

Diet of Austral parakeets in their late-winter and pre-breeding periods, indicating the number of foraging observations (N obs.) and their proportions (% obs.), the items of the species consumed, the total number of foraging observations and individuals observed, and the number of road-side kilometers surveyed.

	Early—middle October			Late November—early December		
	N obs.	% obs.	Items	N obs.	% obs.	Items
Trees						
<i>Araucaria araucana</i>	960	77.73	Seeds, rubber	429	61.99	Seeds, male cones
<i>Embotrium coccineum</i>				12	1.73	Nectar
<i>Lomatia hirsuta</i>				10	1.45	Flowers
<i>Nothofagus antarctica</i>	2	0.16	Buds	40	5.78	Galls
<i>Nothofagus dombeyi</i>	31	2.51	Buds, galls	56	8.09	Galls
<i>Nothofagus oblicua</i>	87	7.04	Buds			
<i>Nothofagus pumilio</i>	40	3.24	Buds			
<i>Populus sp.</i>	48	3.89	Buds			
<i>Prunus cerasus</i>				1	0.14	Fruits
Herbs						
<i>Acaena splendens</i>				41	5.92	Seeds
<i>Taraxacum officinale</i>				42	6.07	Flowers
Hemiparasite plants						
<i>Misodendrum angulatum</i>				60	8.67	Flowers
Fungus						
<i>Cyttaria harioti</i>	37	3.00	Fungus			
<i>Cyttaria sp.</i>				1	0.14	Fungus
Invertebrates						
Insects	30	2.96				
Total observations	1235			692		
Total individuals	1108			540		
Km surveyed	1011.9			1051.9		

pigs, rabbits and hares consuming monkey puzzle seeds. Moreover, when finding signals of wild boards and red deer we also found rests of seeds eaten by these species under the tree. Nonetheless, our survey relies on signs of presence and thus we cannot assure that exotic mammals consumed seeds in all instances they visited the selected female trees, although it seems highly probable. We should note two authors (FH and JLT) were well familiarized with the four introduced European wild mammal species. However, we could not separate diggings made by wild boars from those made by the related free-ranging pigs (see also Shepherd and Ditgen, 2005), and thus we assigned cases of diggings found close to inhabited houses to pigs, where in some cases we directly observed them. It is worth noting that, while the determination of parakeets preying on seeds was reasonably accurate, the presence of exotic mammals at a number of trees may have been underestimated if they did not leave feces or other signs of presence, or if they visited the tree long-time ago and their signals of presence were lost at the time of our survey. Moreover, some mice could remove seeds without leaving predated seeds under the tree and some mice burrows could had been overlooked. The imperfect detection of these species makes however our results conservative regarding the removal of seeds by seed predators and their impacts on forest regeneration (see also Discussion).

2.3. Diet and foraging behavior of Austral parakeets

Austral parakeets were recorded using road-side transects to investigate their winter diet and foraging behavior. Transects were carried out by two observers driving a car at low speed (ca. 30 km/h) on unpaved roads and in some instances on secondary paved roads with low car transit. This method has been successfully used for other parrot species (Grilli et al., 2012; Tella et al., 2013; Blanco et al., 2015), given their conspicuousness, which is reinforced by their frequent and deep vocalizations that can be heard at large distances. Austral parakeets were visually or aurally detected even at 500 m from the car. The survey covered > 1000 km of roads throughout the distribution of the monkey puzzle, but also throughout the distribution of Austral parakeets from sea level to 1800 m a.s.l. (Fig. 1) to avoid foraging biases towards monkey puzzle seeds. The survey was first conducted between 16 and 26 October 2013, when parakeets were grouped in wintering flocks, and repeated between 28 November and 14 December 2013, when some parakeets were departing flocks and observed in pairs looking for nest sites in tree cavities. Changes in the accessibility of some roads caused small differences in the number of km surveyed in each period (Table 1).

Each time parakeets were detected, we stopped the car to record the number of individuals and their behavior. When foraging, we observed the flock at a distance for ca. 15 min (or until the birds left the foraging site) with binoculars and a telescope, to identify the food plants and the parts of the plant consumed. When needed, we later approached the plant to obtain additional information (traits of the items consumed, identity of the plant species, etc.). In some instances, foraging groups or single individuals switched food plant species within the observation bouts and thus the number of foraging

observations is slightly higher than the number of individuals observed (see Table 1). Flock size (median = 12 individuals, quartiles = 2–40) and distance of detection (median = 70 m, quartiles = 45–110) did not differ between observations of parakeets feeding on monkey puzzles and other food resources ($Z = -1.30$, $p = 0.19$ and $Z = -0.93$, $p = 0.35$ respectively), suggesting that the larger use of monkey puzzle (see Results) did not result from detection biases.

Once the contribution of monkey puzzles to the winter diet of Austral parakeets was determined, we conducted additional surveys (82 field-work days) covering both the pre-dispersal (April–May 2014) and post-dispersal periods of the tree (July–August 2014) to focus just on their handling techniques for consuming monkey puzzle seeds. Particularly, we tried to determine whether Austral parakeets disperse mature seeds from the mother tree as was speculated (Veblen, 1982; Finckh and Paulsch, 1995; Premoli et al., 2013) and, ultimately, to measure dispersal rates and dispersal distances.

2.4. Statistical analyses

Proportions were compared using Yates' Chi-square tests. The number of uneaten seeds (seed index) and number of seedlings followed a Poisson-like distribution. We therefore used Generalized Linear Models (GLM) with Poisson distribution and the log link function to assess the effects of the presence of native and exotic species (explanatory variables) on the availability of uneaten seeds per tree (response variable). In the case of number of seedlings, however, conditional variances were much larger than conditional means thus causing data overdispersion and inflation of parameter estimates in Poisson GLMs. Data overdispersion was avoided using the negative binomial distribution (a particular case of the Poisson distribution), fitting again the presence of native and exotic species as explanatory variables to assess variability on the number of seedlings per female tree (as response variable).

We assessed the effects of potential confounding variables through GLMs. The production of seeds could increase with the age of trees (Muñoz, 1984) and differ among sites due to particular soil conditions, altitude, vegetation, local rain, and other unmeasured variables. The 516 trees surveyed were spatially grouped in 18 areas or sites. The number of uneaten seeds per tree increased with tree size (considered as a proxy of tree age) (Wald $\chi^2 = 31.20$, $df = 1$, $p < 0.001$, estimate = 0.030 ± 0.005) and varied among sites (Wald $\chi^2 = 502.89$, $df = 16$, $p < 0.001$). Number of seedlings also increased with tree size (Wald $\chi^2 = 9.15$, $df = 1$, $p = 0.002$, estimate = 0.098 ± 0.032) and varied among sites (Wald $\chi^2 = 97.84$, $df = 16$, $p < 0.001$). Under-canopy vegetation cover did not influence the number of uneaten seeds (Wald $\chi^2 = 0.13$, $df = 1$, $p = 0.72$) neither the number of seedlings found (Wald $\chi^2 = 1.57$, $df = 1$, $p = 0.21$). Altitude positively influenced both the number of uneaten seeds (Wald $\chi^2 = 18.42$, $df = 1$, $p < 0.001$, estimate = $0.003 + 0.0007$) and the number of seedlings (Wald $\chi^2 = 19.49$, $df = 1$, $p < 0.001$, estimate = $0.002 + 0.0005$). However, both effects turned non-significant when fitted together with tree size and site, suggesting that these variables are absorbing the variability associated with altitude. Sampled trees were located in protected ($n = 226$) and unprotected areas ($n = 290$); however, there were no differences in the number of uneaten seeds (Wald $\chi^2 = 1.04$, $df = 1$, $p = 0.31$) and seedlings (Wald $\chi^2 = 1.41$, $df = 1$, $p = 0.23$) when controlling for the significant effects of site and tree size. Therefore, we only controlled for tree size and site by fitting these variables in all GLMs built for assessing the effects of the presence of predator species on the number of seeds and seedlings. For the comparison of trees in transhumant areas before and after sheep herds arrived, we only controlled for site since the trees surveyed ($n = 70$) were the same in the two time instances. As a proxy of the variance explained, we calculated the percentage of deviance explained by each GLM. All analyses were performed using SPSS v. 15.0.

3. Results

3.1. Effects of native and exotic species on seed surplus

The number of uneaten seeds found under individual female trees ($n = 516$) at the end of winter varied between 0 and ca. 100, although in most cases (65%) was lower than 10. All but one of the 516 trees surveyed was visited by at least one seed predator species. The number of trees visited varied among species (Fig. 3). Austral parakeets predated seeds on ca. 85% of the trees, while seeds predated by native mice (and perhaps introduced rats, see Discussion) were only found in 45% of trees. The proportion of trees visited by each exotic mammal species was lower, ranging from 5% to 35%. Taken together, however, almost 90% of trees were visited by one or more exotic species.

The number of uneaten seeds found under individual female trees at the end of winter was lower in trees visited exclusively by exotic mammals ($n = 29$) than in those visited exclusively by native parakeets ($n = 21$) or native mice ($n = 32$) (Fig. 4(A), Wald $\chi^2 = 16.26$, $df = 2$, $p < 0.001$), while controlling for tree size (Wald $\chi^2 = 11.11$, $df = 1$, $p = 0.001$) and site (Wald $\chi^2 = 52.57$, $df = 13$, $p < 0.001$). This model explained 65.79% of the deviance. Considering the combined effect of all seed predators on the 516 trees surveyed (Fig. 5(A)), the number of uneaten seeds decreased with the number of exotic mammal species visiting them (Wald $\chi^2 = 90.70$, $df = 5$, $p < 0.001$), being higher in trees visited by native parakeets (Wald $\chi^2 = 7.02$, $df = 1$, $p = 0.008$) but not clearly affected by mice (Wald $\chi^2 = 2.88$, $df = 1$, $p = 0.09$), while controlling for tree size (Wald $\chi^2 = 28.69$, $df = 1$, $p < 0.001$) and site (Wald $\chi^2 = 329.26$, $df = 16$, $p < 0.001$). This model explained 48.63% of the deviance.

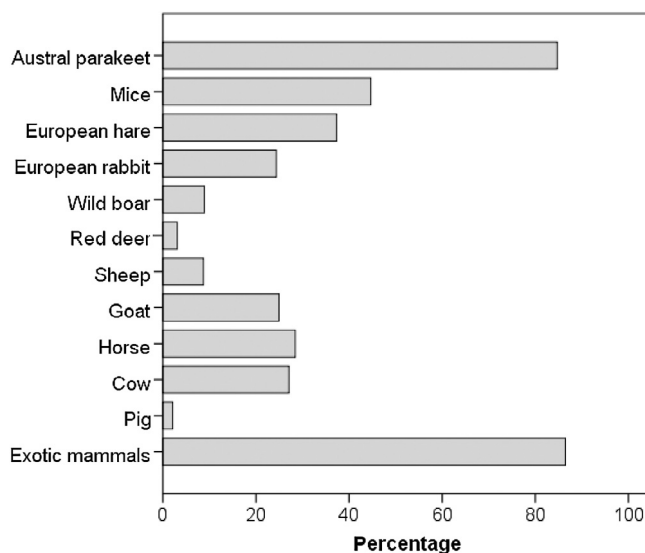


Fig. 3. Percentage of female monkey puzzle trees ($n = 516$) with signals of the presence of different native (parakeets and mice) and exotic (mammals) seed predator species under their canopy. Last bar shows the percentage of trees which were visited by at least one exotic species.

3.2. Effects of native and exotic species on number of seedlings

Although the number of yearling seedlings found under individual female trees ($n = 516$) at the end of winter varied between 0 and ca. 200, in 50% of the cases there were no seedlings. The number of seedlings was lower in trees visited exclusively by exotic mammals ($n = 29$) than in those visited exclusively by native mice ($n = 32$) and native parakeets ($n = 21$) (Wald $\chi^2 = 8.71$, $df = 2$, $p = 0.013$), while controlling for tree size (Wald $\chi^2 = 0.01$, $df = 1$, $p = 0.909$) and site (Wald $\chi^2 = 37.60$, $df = 11$, $p < 0.001$) (Fig. 4(B)). This model explained 55.50% of the deviance. Considering the combined effect of all seed predators on the 516 trees surveyed (Fig. 5(B)), the number of seedlings decreased with the number of exotic mammal species visiting them (Wald $\chi^2 = 999.48$, $df = 4$, $p < 0.001$), being higher in trees visited by native parakeets (Wald $\chi^2 = 6.71$, $df = 1$, $p = 0.010$) and unaffected by mice (Wald $\chi^2 = 0.10$, $df = 1$, $p = 0.74$), while controlling for tree size (Wald $\chi^2 = 50.47$, $df = 1$, $p < 0.001$) and site (Wald $\chi^2 = 380.25$, $df = 15$, $p < 0.001$). This model explained 23% of the deviance.

3.3. Effects of transhumance on seed surplus and seedling production

Before transhumance took place, trees in transhumant sites ($n = 70$ trees) had larger numbers of uneaten seeds (Wald $\chi^2 = 144.97$, $df = 1$, $p < 0.001$, Fig. 6(A)) and seedlings (Wald $\chi^2 = 50.47$, $df = 1$, $p < 0.001$, Fig. 6(B)) than in non-transhumant sites ($n = 446$ trees), taking into account variability among sites (seeds: Wald $\chi^2 = 283.65$, $df = 16$, $p < 0.001$; seedlings: Wald $\chi^2 = 428.14$, $df = 16$, $p < 0.001$) (deviance explained, seeds = 50.42%, seedlings = 33.56%). After transhumance took place, trees in transhumant sites ($n = 70$) had lower numbers of uneaten seeds (Wald $\chi^2 = 198.35$, $df = 1$, $p < 0.001$) than before, taking into account variability among sites (Wald $\chi^2 = 10.84$, $df = 1$, $p = 0.01$) (Fig. 6(C), deviance explained = 52.58%). However, the number of seedlings did not change after transhumance took place (Wald $\chi^2 = 0.036$, $df = 1$, $p = 0.85$; site effect: Wald $\chi^2 = 50.79$, $df = 1$, $p < 0.001$; deviance explained = 26%; Fig. 6(D)).

3.4. Diet of Austral parakeets

A total of 2091 Austral parakeets were recorded during surveys conducted in late winter (October–December), of which 1648 individuals were observed during foraging activities. Although foraging individuals were observed at altitudes ranging from 18 to 1760 m a.s.l., most of them (93.8%) foraged within the altitudinal distribution of the monkey puzzle (600–1800 m a.s.l.). In early October, most foraging observations were obtained from monkey puzzle trees (ca. 78%), with individuals eating mature seeds and in some instances, the rubber obtained after pulling the leaves off the trees. Buds of four tree species (ca. 17% of observations), fungus (3%), galls (0.11%), and insects (3%) complemented the diet of parakeets during this period (Table 1). Foraging on monkey puzzles significantly dropped (Yates $\chi^2 = 63.18$, $df = 1$, $p < 0.001$) to ca. 62% in late November–early December, when parakeets ate both maturing seeds and the new male cones of the trees.

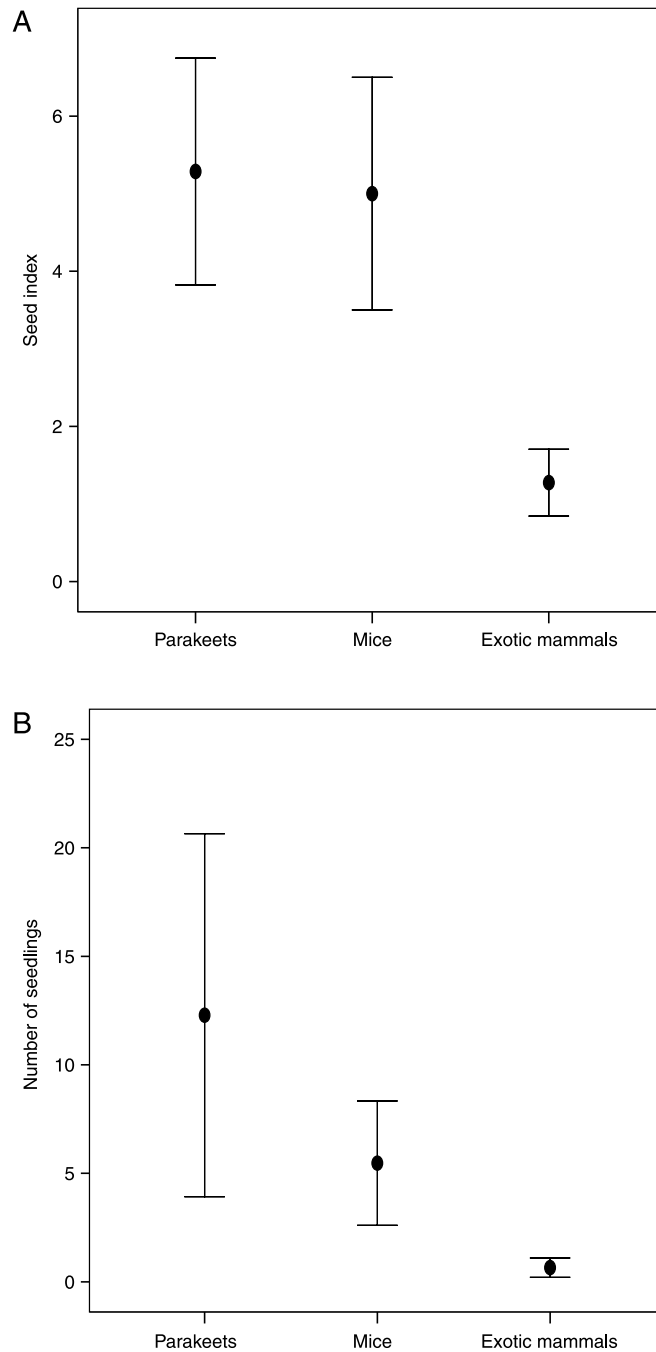


Fig. 4. Uneaten seeds (A) and number of young seedlings (B) found under female monkey puzzle trees in late winter exclusively visited by parakeets, mice or exotic mammals. Bars show 95% CI.

Flowers, galls, seeds and fungus of a larger number of species constituted the rest of the diet of parakeets during this period (Table 1).

3.5. Seed dispersal by Austral parakeets

During the pre-dispersal period of monkey puzzle seeds, we observed 840 Austral parakeets consuming seeds. Parakeets removed mature seeds from female cones and handled them in the same tree, often dropping seeds to the ground. Only one parakeet flew carrying a seed in its beak to handle it in a distant tree. During the post-dispersal period, however, all the observed parakeets ($n = 770$) picked up the seeds from the ground and flew to the same or different trees to handle

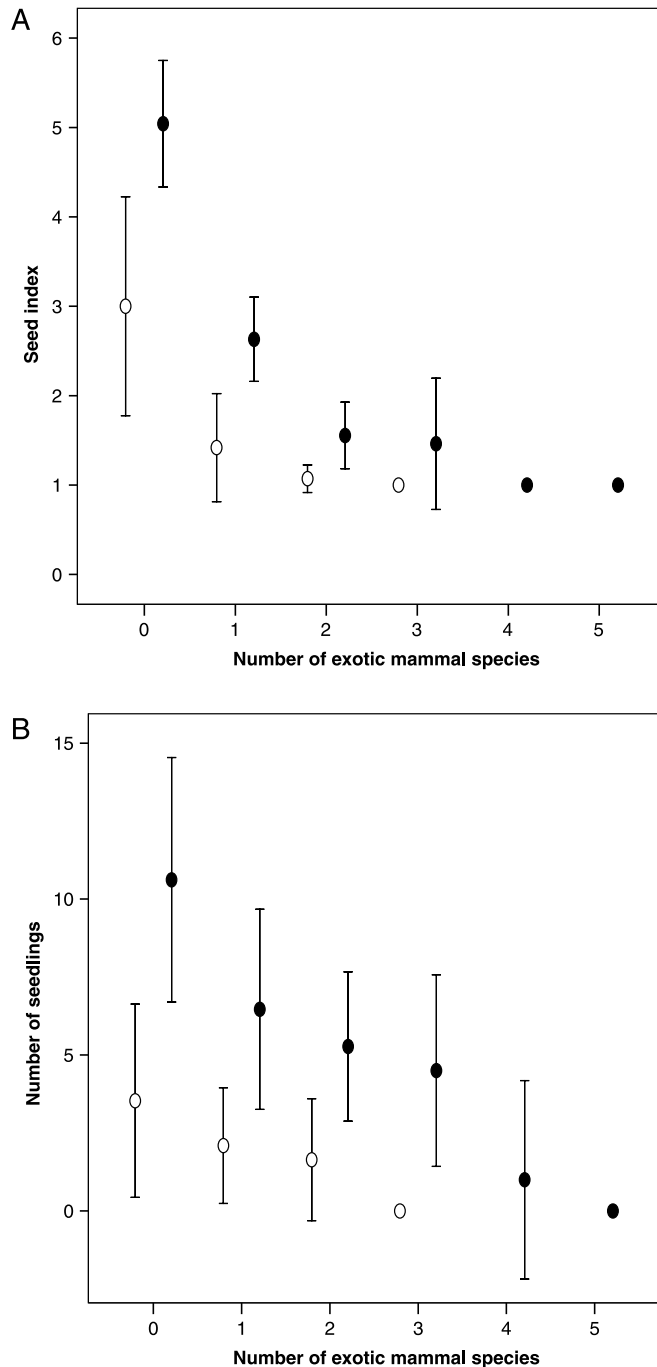


Fig. 5. Uneaten seeds (A) and number of young seedlings (B) found under female monkey puzzle trees in late winter related to the number of exotic mammal species visiting them. Filled circles: trees visited by parakeets, open circles: trees not visited by parakeets. Bars show 95% CI.

them in tree perches. The constant flights of parakeets landing to pick up seeds and further carrying them in their beaks made it difficult to follow all their movements, but at least 57% of them moved the seeds to distant trees. This conservative proportion is significantly higher (Yates $\chi^2 = 63.18$, $df = 1$, $p < 0.001$) than the proportion of parakeets moving seeds during the pre-dispersal period (0.12%). We were able to estimate the distances seeds were moved from the seed rain area of the female tree in 59 instances, distances ranging from 5 to 50 m (mean = 15 m, Fig. 7). Longer distances could be easily overlooked due to the low visibility around the observed female trees. We often saw that undamaged seeds were dropped while parakeets handled them in tree perches, but the constant movements of birds and low visibility when they perched within the tree foliage impeded us from obtaining a rate of seed dropping.

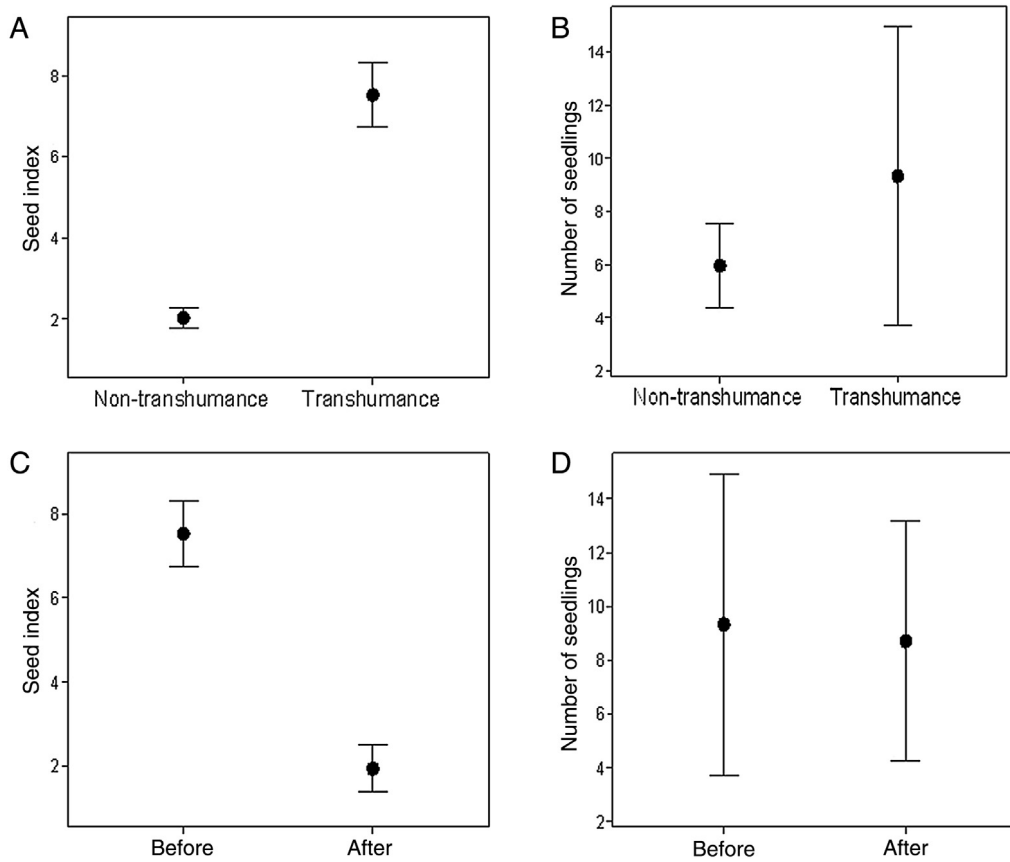


Fig. 6. Number of seeds (A) and seedlings (B) in transhumant and non-transhumant sites before transhumance took place. Number of seeds (C) and seedlings (D) in transhumant sites before and after transhumance took place. Bars show 95% CI.

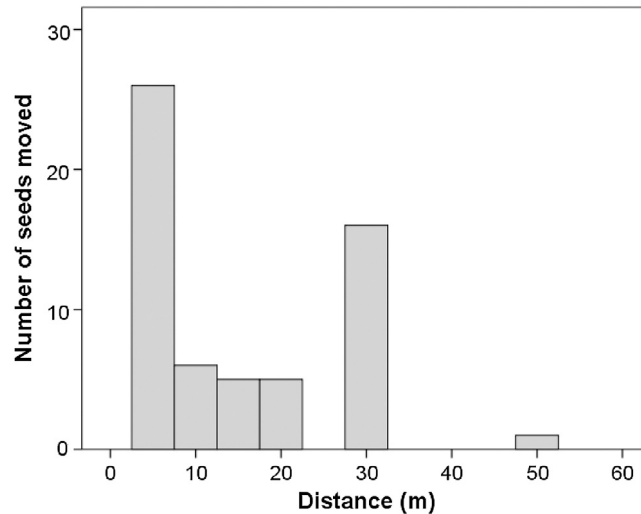


Fig. 7. Distances seeds were moved by Austral parakeets from the seed rain area of female trees.

4. Discussion

4.1. Monkey puzzle and native seed predators

Previous local assessments of seed predation and diets of predators showed that monkey puzzle trees provide a key pre- and post-dispersal resource for native seed eaters (Shepherd and Ditgen, 2005; Díaz, 2012; Díaz et al., 2012; Shepherd et al.,

2008). Our different, large scale approach assessing the overwinter use of seeds by these predators allows generalizing previous results: ca. 45% and 85% of female trees distributed through most of the species range had evidence of seed predation by mice and Austral parakeets, respectively (Fig. 3). The proportion for mice could be even higher if they removed seeds without leaving signs of seed predation under some trees. Regarding the impact of native seed predators on seed survival, our results are unique showing that a number of seeds survive overwinter predation and are sufficient to produce a relatively high number of young seedlings when trees are exclusively visited by mice and parakeets (i.e., not by exotic mammals). Nonetheless, the number of seedlings (but not of seeds) was lower in trees visited by mice than in those visited by parakeets (Fig. 4), suggesting mice could also be predating on germinating seeds. Interestingly, both the number of surviving seeds and seedlings was greater in trees visited by parakeets, independent of predation pressure exerted by other species (Fig. 5). This suggests that winter flocks of Austral parakeets, as in other parrot species (F. Hiraldo obs. pers.), look for the most productive individual trees for foraging and leave the tree before satiating (with additional seeds still available) when the rate between food intake and time to find it decreases, supporting the optimal foraging theory (Pyke, 1984). In this way, parakeet predation seems to affect the most productive trees without over-harvesting, and has less impact on low-producing trees.

It is worth noting that our study was conducted in a mast year (Sanguinetti, 2014; Authors pers. obs.). Seed production in mast years can reach 1000–1500 kg ha⁻¹ (Sanguinetti, 2014), being up to 60-fold the crop of some inter-mast years (Shepherd et al., 2008). Consequently, pre-dispersal seed predation rates by Austral parakeets may increase from 0.6% when seed production is the highest to 20.6% when seed production is the lowest (Shepherd et al., 2008), and post-dispersal predation by mice may reach 70% when seed production is low (Shepherd and Ditgen, 2005). Our results support the predator satiation hypothesis (Shepherd et al., 2008), so that the combined pre- and post-dispersal predation by mice and parakeets still leaves the survival of enough seeds to allow plant recruitment mainly in mast years but also, though in lower numbers, during inter-mast years (Shepherd and Ditgen, 2005; Shepherd et al., 2008).

4.2. Combined impact of multiple invaders on native trees

The introduction of both free-ranging domestic and wild exotic mammals has been recognized as a major problem for the regeneration of monkey puzzle forests. The relative abundance of free-ranging cattle was negatively related to seed availability and the recruitment of monkey puzzle trees in Chile (Zamorano-Elgueta et al., 2012; Donoso et al., 2014). In Argentina, a small-scale study (11 monkey puzzle trees) conducted during four years showed that wild boars consumed between 10% and 30% of seeds disposed artificially within periods of 13 days (Sanguinetti and Kitzberger, 2010). Moreover, there was great concern of the potential, unmeasured effects of other introduced mammals such as red deer, European rabbits, European hares and feral pigs (Shepherd and Ditgen, 2005). Our results show that exotic mammals visited ca. 90% of the monkey puzzle trees surveyed across the species' range, and that the combination of nine exotic species drastically reduced the abundance of overwinter surviving seeds and of young seedlings, when taking trees exclusively visited by mice and parakeets as "controls". Models explained a remarkable amount of variance in both seed availability (65.8%) and the number of seedlings (55.5%), despite many potential factors that could mask the impact of invaders on seed availability such as macro- and microhabitat traits (Shepherd and Ditgen, 2005; Sanguinetti and Kitzberger, 2010) and human seed collection (Aagesen, 1998; Herrmann, 2006). Although we avoided sites affected by human seed harvesting and controlled for significant confounding effects such as tree size and site, any uncontrolled effect could just cause lowering the actual effects of exotic mammals. On the other hand, the detection rates of exotic mammals were surely underestimated since in some instances they could visit a tree and consume seeds without leaving signals of their presence, or had visited the tree long-time ago (see Methods). Moreover, we could not differentiate seed predation by native mice from that of the Norway rat (*Rattus norvegicus*), an invasive species that has already been recorded preying on monkey puzzle seeds (Shepherd and Ditgen, 2012). In any case, the imperfect detection of species made our results conservative regarding the potential effects of exotic species on overwinter seed survival and number of seedlings per tree.

Little is still known on the ways multiple invaders may simultaneously impact native biota and ecosystems (Kuebbing et al., 2013; Jackson, 2015). In contrast with experiments conducted on pairs of co-occurring invaders (e.g., Nyström et al., 2001; Johnson et al., 2009), the large community of exotic mammals makes it difficult to quantitatively evaluate their independent impact on monkey puzzle trees. Exclusion experiments (Sanguinetti and Kitzberger, 2010) only might separate the effects of large (i.e., livestock, wild boar, red deer) and small invasive mammals (European rabbit and hare), and cannot assess the combined effects of native mice and parakeets. Our qualitative approach adds insight to the combined effects of native and exotic species by recording which species visited each individual tree. Exotic species seemed to reduce overwinter seed survival, since the number of seeds dropped drastically to a seed index close to 1 (i.e., less than 10 surviving seeds) when two or more exotic species visited the tree (Fig. 5(A)). Although some species are still patchily distributed across the monkey puzzle range (see below), the large community of exotic species allowed multiple combinations of exotic species at the individual tree level. Unfortunately, the complexity of the data structure did not allow for testing the effects of each combination of species.

A smoother pattern was found for the number of young seedlings related to the number of exotic species visiting the trees, only dropping to an average of 0 seedlings when five or more exotic species visited them (Fig. 5(B)). In this case, species functionally differ in their effects: while some may reduce tree recruitment by overharvesting seed crops, others can also directly predate or destroy young seedlings through trampling. In this sense, our resampling of trees in transhumant

areas showed that the number of seeds but not of seedlings decreased after large herds arrived (Fig. 7), indicating that they may reduce tree recruitment mostly through seed consumption. Other exotic species, such as red deer (Veblen et al., 1989), are known to also browse the vegetation, and rooting wild boars and feral pigs may destroy young seedlings (Shepherd and Ditgen, 2005; Sanguinetti and Kitzberger, 2010). Therefore, the relative specific impact of invaders may be affected by both the local abundance and functional effects of each species, making it difficult to obtain more accurate evaluations. Additionally, these impacts may change with time and future species' distribution scenarios.

There are two ways the individual and combined impacts of invaders may change with time. First, our study was conducted in the highest productive mast year of those recorded in the last 15 years (Sanguinetti, 2014). Sanguinetti and Kitzberger (2010) found that the exclusion of wild boars significantly increased the amount of surviving seeds and the establishment rate of seedlings in intermediate production years, but not in a mast year. Therefore, it is expected that the combined effects of up to nine exotic species could completely deplete seed availability in inter-mast years. With this in mind, we conducted a simpler survey of a subsample of 348 monkey puzzle trees just for recording the availability of fallen seeds in early August 2014, a year with low seed production (Sanguinetti, 2014). No seeds were available under 75% of the trees, and the average seed index was 0.65 (i.e., less than 10 seeds per tree). Since seed availability was so low, it is probable that not a single seed survived the whole winter in this inter-mast year. Second, the monkey puzzle forest is immersed in a contemporary invasion process, and thus the distribution and spatial overlap of exotic mammals will surely increase with time. The wild boar invaded the monkey puzzle forests during the 1970s (Jaksic et al., 2002), with an estimated expansion rate of 3500 ha/yr, and its expansion is expected to continue during the next 50–60 years (Pescador et al., 2009). The expansion of the red deer, European rabbit and hare is also expected, given their invasive behavior in surrounding habitats (Veblen et al., 1989; Vázquez, 2002; Novillo and Ojeda, 2008). Therefore, the high richness of exotic mammals now consuming seeds at the tree population level may translate to the tree individual level in the near future. How the abundance and community composition of invaders will change is however not easy to predict. Nonetheless, our results suggest that the numerical increase and range expansion of just a few exotic species could be sufficient to fully deplete seed availability even in mast years. This reasonable possibility calls for the long-term monitoring of the invader community and its effects on monkey puzzle seed availability and forest regeneration.

4.3. Impact of multiple invaders on native seed eaters

Previous studies on the Austral parakeet, restricted to two forest patches, highlighted the importance of monkey puzzle trees in the diet and population dynamics of the species (Díaz, 2012; Díaz et al., 2012). Our results reinforce and generalize this role; after looking for parakeets throughout its distribution range (Fig. 1), we found most individuals concentrated within the monkey puzzle range, for feeding on its seeds during the wintering and pre-breeding periods. The predominant role of these seeds is even higher in terms of biomass (i.e., 3.5 g per seed) compared to seeds of other species (i.e., 0.1 g, Díaz et al., 2012). Although densities of Austral parakeets were low compared to other parrot species (e.g., Blanco et al., 2015), their movements for tracking seed crops (Shepherd and Ditgen, 2005; Díaz, 2012; Authors unpublished data) meant that ca. 85% of our widely spaced sampled trees were visited by parakeets for winter consumption of fallen seeds. Since breeding success – and probably overwinter survival – of Austral parakeets is related to inter-year variations in monkey puzzle seed crops (Díaz et al., 2012), a continued seed depletion caused by multiple invaders, especially in inter-mast years, could compromise the long-term persistence of the species. Similarly, monkey puzzle seeds constitute a key, highly nutritious resource for winter survival of mice species endemic to Andean forests (Shepherd and Ditgen, 2005). In the case of mice, multiple invaders impact native species not only through food depletion but also by reducing their refuges (forest understory) through overgrazing: mice abundance was found to be 52 times higher where grazing was absent (Shepherd and Ditgen, 2005).

4.4. Disruption of reciprocal feedbacks and mutualistic interactions

Apart from the evident direct impacts of multiple invaders, our work suggests that they may also be disrupting reciprocal feedbacks between native species and their food plants causing multiple indirect, interacting impacts. Three feedbacks were identified. First, we saw in Austral parakeets the typical behavior of parrots dropping a high amount of seeds (Symes and Perrin, 2003; Villaseñor-Sánchez et al., 2010; Blanco et al., 2015) while feeding on female cones. At least a third of partially consumed seeds dropped by Austral parakeets are damaged by less than 50%, thus providing food for the mice community when otherwise seeds would not be available for them (Shepherd and Ditgen, 2005; Shepherd et al., 2008). Therefore, parakeets compete for seeds with mice during the post-dispersal seed period, but provide them seeds during the pre-dispersal period. Second, the removal of mature seeds from the cone often causes many others to fall to the ground and this way 15–29% of fallen seeds are whole or scarcely damaged (Shepherd et al., 2008), thus facilitating secondary dispersal by mice (Shepherd and Ditgen, 2005). Therefore, mice impact seed survival but also provide a mutualistic service to the plant mediated by parakeet foraging behavior. Third, it was suggested that Austral parakeets also act as seed dispersers (Veblen, 1982; Finckh and Paulsch, 1995), but seed-carrying was never observed (Shepherd et al., 2008). This is not surprising given that seed dispersal has been largely overlooked despite it being a widespread behavior in parrots (Blanco et al., 2015; Tella et al., 2015; Blanco et al., in press). We found that, while Austral parakeets do not carry out seeds while feeding on female

cones, it is the rule when seeds fall and are only available on the ground. Parakeets are then forced to pick up the seeds from the ground and carry them for handling in high perches (probably to reduce predation risk) out of the parent tree in at least 57% of the cases, moving seeds 5 to at least 50 m farther from the seed rain. Although further research is needed to determine the rates at which entire seeds are dropped and germinate successfully, even a small rate of effective dispersal should contribute to forest regeneration for this tree species where seedling establishment increases beyond the parent tree (Willson and Whelan, 1990; Finckh and Paulsch, 1995; Iob and Vieira, 2008).

Given all the above evidence, and supporting findings at local scales (Díaz et al., 2012), the reduced food availability at a large scale caused by multiple invaders may reduce the parakeet population, thus also negatively impacting food availability for mice populations (by reducing pre-dispersal seed dropping by parakeets) and forest regeneration by reducing secondary seed dispersal by both mice and parakeets. This may be an example of indirect human effects (through the introduction of exotic animals) disrupting reciprocal feedbacks (Bertness et al., 2015) and causing the disassembly of a mutualistic interaction web, as was shown for the effects of introduced red deer in another Andean forest type (Rodríguez-Cabal et al., 2013).

4.5. Potential cascading effects

Although not examined in our study, cascading effects derived from the introduction of multiple exotic mammals are expected in monkey puzzle forests. For example, Evans et al. (2015) recently demonstrated the effects of cattle overgrazing across trophic levels, including plant and arthropod biomass, small mammals, insectivorous birds, and carnivores. Similarly, the loss of monkey puzzle regeneration and forest understory due to overgrazing (Fig. 2(D)) is probably depleting the diversity and biomass of arthropods and consumers, as well as the diversity of interactions between coexisting species (Vázquez and Simberloff, 2003). On the other hand, some of the introduced exotic mammals may be key prey for predators and trigger hyperpredation processes. As a classic example, the introduction of European rabbits in Australia enhanced negative impacts on native species by supporting larger populations of predators (Glen and Dickman, 2005). It has been shown that, in habitats surrounding the monkey puzzle forests, predators such as foxes and diurnal and nocturnal raptors switched to preying on European rabbits and hares (Hiraldo et al., 1995; Donazar et al., 1997; Palomares and Delibes, 1997; Novaro et al., 2000; Monserrat et al., 2005), which could boost predator populations and further impact native mice. Hyperpredation could also affect larger native species; the puma (*Puma concolor*) is preying on wild boars, rabbits and hares in the monkey puzzle forest (Pescador et al., 2009), and an increase in puma populations could for instance impact the endemic southern pudu (*Pudu pudu*), a globally vulnerable deer species of which we did not find signs of its presence during our surveys.

4.6. Conservation perspectives

Here we show a large-scale impact (Mack et al., 2007) of multiple invaders on the global distribution of a threatened tree species. Conservation implications transcend the conservation of the monkey puzzle tree (Premoli et al., 2013) to affect a whole ecosystem, their ecological interactions and reciprocal feedbacks. The species is listed as Endangered on the IUCN Red List and in Appendix I of the Convention on International Trade in Endangered Species of Wild Flora and Fauna (Premoli et al., 2013), but these categorizations are not sufficient and an ecosystem—rather than a species-oriented conservation approach is needed (Lindenmayer et al., 2007; Zamorano-Elgueta et al., 2012). The extremely long lifespan of monkey puzzles (over 1300 yr, Premoli et al., 2013) might allow the persistence and further recovery of the species after decades without forest regeneration. This is not however the case for the short-lived, r-strategist species such as mice and parakeets, as well as for their key interaction with the tree, if the impact of multiple invaders persists or even increases.

Zamorano-Elgueta et al. (2012) recently highlighted the challenges in managing the negative effects of free-ranging livestock on monkey puzzle forest regeneration, given that cattle often support the economy of local human populations. This conservation scenario is further complicated after showing the combined impact of several introduced wild game species. Part of the monkey puzzle distribution is protected by National Parks and reserves (Premoli et al., 2013), where livestock could be excluded but not the invasion of wild exotic mammals (Sanguinetti and Kitzberger, 2010). In fact, we found that the number of uneaten seeds and seedlings did not differ between protected and unprotected areas. Therefore, conservation actions such as livestock management, anthropogenic fire reduction, and protection of monkey puzzle stands and reforestation (Zamorano-Elgueta et al., 2012; Premoli et al., 2013) must be necessarily combined with the management of invasive wild species. Despite the fact that the control and eradication of these species may not be very successful given their large geographic expansion (Vázquez, 2002; Jaksic et al., 2002; Novillo and Ojeda, 2008), wildlife managers are expected to prioritize their management given their proven ecological impacts (Kuebbing and Simberloff, 2015). Unfortunately, this is not the case for Latin American countries such as Chile and Argentina, where invasive species like the red deer are incorporated in the local culture and highly valued as their own fauna (Speziale et al., 2012), and even protected because of the income they produce (Lambertucci and Speziale, 2011). A great trans-boundary effort is thus needed to inform and convince all stakeholders, from wildlife authorities to local people for whom the monkey puzzle forests also provide resources (Aagesen, 1998), on the impacts of both domestic and exotic mammals for conserving this singular ecosystem.

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