Are rodents a source of biotic resistance to tree invasion in Pampean grasslands? Tree seed consumption under different conditions

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Abstract   Biotic resistance has been invoked as a major barrier to woody species invasion, although the role of resident generalist consumers and their interaction with seed availability in a local community has received little attention. We assessed tree seed consumption by rodents under two different scenarios: (i) We documented in field spatio-temporal patterns of seed predation by native rodents on two exotic tree species, *Gleditsia triacanthos* or 'honey locust' and *Robinia pseudoacacia* or 'white locust' (family Leguminosae), in five grassland habitats of the Inland Pampa, Argentina. (ii) We conducted laboratory feeding trials to evaluate tree seed consumption in the presence (cafeteria-style feeding trials) and in the absence (non-choice feeding trials) of alternative food supplies. Seed predation was generally higher for *Robinia* than for *Gleditsia* seeds, both in field and laboratory conditions. For both tree species, seed predation varied between habitats and seasons and was higher in the native tussock grassland than in the remaining studied communities, whereas the crop field showed the lowest levels of consumption along with the absence of captured rodents. Seed consumption of *Gleditsia* and *Robinia* among the four grassland communities (which did not differ in rodent abundance) was negatively associated with the availability of alternative food. Laboratory feeding trials showed a higher consumption of *Gleditsia* seeds in the non-choice than in the cafeteria-style feeding trials, while the consumption of *Robinia* seeds did not differ in the absence or presence of alternative seeds. These patterns indicate that the contribution of resident granivores to invasion resistance might depend on colonizer species identity, recipient community type and season of the year. We suggest that rodent preferences for different invader seeds will interact with the availability of alternative food in the local habitat in influencing the amount of predator-mediated biotic resistance to invasion.

Key words: biotic resistance, food availability, grasslands, invasion, rodent, seed consumption.

INTRODUCTION

Along with environmental conditions, biotic interactions determine the performance of species in a community (Jaksic & Marone 2007). For plant communities, competition and both pre- and post-dispersal seed predation are known to influence species composition and relative abundances (Nuñez *et al.* 2008). Post-dispersal seed predation causes considerable seed losses in a wide variety of plants, being a key factor affecting the recruitment and spatial distribution of many species (Edwards & Crawley 1999). For example, granivores can destroy over 95% of seeds produced by preferred species in shrub steppe environments, eucalyptus and temperate deciduous forests (Hulme 1994a,b; Anderson & MacMahon 2001). In

the case of grasslands, it is known that granivory interacts with competitive interactions among plant species, reducing or increasing the effects of dominance (Howe & Brown 2000; Murillo *et al.* 2007).

Resource harvest is highly context-dependent across a range of spatial scales (Ostoja *et al.* 2012) that include plant communities, patches and seed selection within patches. At each scale, foraging decisions are made in light of a range of habitat characteristics, including quality and quantity of food, direct and indirect predation risk, and potential rate of harvest (Ostoja *et al.* 2012). Density-dependent foraging is predicted by optimal foraging theory (Charnov 1976) and has been well demonstrated for granivorous rodents in North American deserts (Ostoja *et al.* 2013), but many authors have shown that consumption of seeds does not depend only on their abundance, quality and preference by the predator, but also on the neighbourhood characteristics. Mixed seeds

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neighbourhoods have been shown to result in associational effects among co-occurring resources that are mediated by generalist consumers (Ostoja *et al.* 2013). In seed neighbourhoods with a mixture of species, some species may confer associational resistance (Ostoja *et al.* 2013), also referred to as apparent mutualism (Holt 1977), when an increase in seeds of one species leads to an increase in the abundance of the second because of a decrease in the intensity of predation (Holt & Kotler 1987; Abrams & Matsuda 1996). Alternatively, being in a mixed seeds neighbourhood might increase the susceptibility of a seed species to predation. This is known as associational susceptibility or short-term apparent competition (Holt & Kotler 1987; Ostoja *et al.* 2013). Optimal foraging can produce short-term apparent competition if a predator behaves opportunistically at both patch and seed selection scales (Veech 2001). On the other hand, the presence of a highly preferred seed type at high density leads to a functional, aggregative or numerical response in the populations of seed predators, which may spend more time searching for food or may be aggregated in sites where the preferred species is present, and so increasing the consumption of alternative prey species (Holt & Kotler 1987).

In the case of species introduced in a new region, the lack of specialist enemies may cause a decrease in the intensity of attacks that may result in favourable conditions for the introduced species with respect to resident species. However, exotic species must cope with the biotic resistance of competitors and generalist enemies in the recipient community (Mitchell *et al.* 2006). In some cases, generalist enemies can exert a great impact in the invader species via seed predation (Brown & Heske 1990; Nuñez *et al.* 2008; Pearson *et al.* 2011, 2014) or herbivory (Vilà & D'Antonio 1998), while in other cases their effect is not significant (Willson & Whelan 1990; Cappuccino & Carpenter 2005; Pearson *et al.* 2011). In addition to the direct effects of predators on exotic species, differential consumption may alter the competitive relations with resident species (Murillo *et al.* 2007). In some cases, greater consumption of resident species promotes the establishment of exotics (Ostfeld *et al.* 1997), whereas in contrast if exotic species are more consumed predation is part of the biotic resistance of the resident community (Nuñez *et al.* 2008), as is the case for many invasive species in different systems (Simberloff 2009).

Rodents represent the main post-dispersal seed predators in many plant communities (Edwards & Crawley 1999; Howe & Brown 2000; Manson *et al.* 2001). However, environments that differ in vegetation structure frequently show different patterns of seed consumption that are probably related to differences in rodent abundance and availability of alternative foods (Brown 1988; Manson *et al.* 2001; Caccia *et al.* 2006; Murillo *et al.* 2007; Busch *et al.* 2012). In the presence

of seeds of different species, rodents may consume them according to innate traits like size, nutritional quality, or morphological and chemical defences (Brown & Heske 1990; Moles *et al.* 2003; Xiao *et al.* 2006), but also depending on the neighbourhood (Ostoja *et al.* 2013).

Around the world, grassland ecosystems are intensively altered by alien plant invasions and human activities, such as agriculture and livestock husbandry (Gibson 2009). Particularly, woody species invasions exert a negative effect in grassland conservation and in the services that these habitats provide (Jackson *et al.* 2002). To what extent granivory by rodents may act as an agent of biotic resistance in these systems depends on the abundance and characteristics of the alternative food, the vegetation structure, rodent abundance, and food requirements (Manson *et al.* 2001; Busch *et al.* 2012). In consequence, the role of rodents in the community biotic resistance to tree invasion in grasslands may vary across different recipient communities and seasons of the year and may depend on their food preferences.

One of the most aggressive invaders in the Pampas grasslands of east-central Argentina is the honey locust (*Gleditsia triacanthos*, family Leguminosae, subfamily Caesalpinioideae), which is present along roadsides, within crop fields forming woodlots and along riparian habitats (Ghersa & León 1999). However, previous studies showed that different plant communities vary in their susceptibility to woody invasion; native tussock grasslands appear to be more resistant to tree invasion than old-field communities dominated by exotic forbs and grasses (Chaneton *et al.* 2004; Mazía *et al.* 2010; Busch *et al.* 2012). In native tussock Pampas grasslands, seed predation by rodents has been found to reduce herbaceous plant invasion (Murillo *et al.* 2007) and seems to affect the emergence of *G. triacanthos* in simulated armadillo diggings (Mazía *et al.* 2010). Also, Mazía *et al.* (2013) found that seed consumption by rodents acted as a first filter to *G. triacanthos* establishment in old-field grasslands dominated by exotic forbs and grasses. These previous studies led us to conduct a more extensive comparison of the effect of rodents on tree seeds in different plant communities with different histories and intensity of agrarian labours. Different plant communities or even similar communities with different disturbance histories likely vary in seed availability, cover and predation risk, resulting in different foraging patterns (Ostoja *et al.* 2012), and may influence the effect of rodents on exotic seed species.

The main goal of this paper was to assess tree seed consumption by rodents under different scenarios. First, we compared different plant communities (field conditions) that represent the most important land uses in Pampean Region (see below), and differ in structure, floristic composition, land use history, susceptibility to invasion, and presumably in the supply of alternative food for resident granivores. Second, we

conducted feeding trials under controlled conditions to evaluate seed consumption in the presence and absence of alternative food supplies. In all cases, woody seeds belonged to two exotic trees, honey locust and white locust (*Robinia pseudoacacia*, family Leguminosae, subfamily Papilionoideae), which represent common woody invaders in the Pampean Region (Ghersa & León 1999).

METHODS

Study site and studied species

The study was conducted at Estancia San Claudio, a farm owned by the University of Buenos Aires in Carlos Casares county (35°53′ S, 61°12′ W), Inland Pampa, Buenos Aires Province, Argentina. The climate is subhumid with mean temperatures 23.4°C in January and 8.2°C in July (data obtained from a meteorological station located 6 km from the study area). Mean annual precipitation was about 1090 mm (standard deviation = 216 mm, 1976–2009). During the study period, climatological conditions were within the average values recorded for the period 1976–2009. The region was originally occupied by mesic perennial grasslands with the absence of native trees (Cabrera 1976). The Inland Pampa has been extensively transformed to row-crop agriculture and livestock grazing. Native grassland communities are presently confined to small relict fragments and narrow corridors (Ghersa & León 1999), being often dominated by tall-tussock grasses (Mazía *et al.* 2010), and many spontaneous herbaceous communities, with both native and exotic species, are confined to semi-natural remnants, abandoned fields, roadsides, railway embankments and pastures. In addition, exotic trees were extensively planted along roadsides and fields, recreation areas, and around farmhouses (Ghersa & León 1999). Old-field grassland communities are developed in abandoned agricultural areas, and after several years of succession become typically dominated by exotic forage grasses (Tognetti *et al.* 2010).

Gleditsia triacanthos and *R. pseudoacacia* are two invasive woody species that have colonized grasslands, abandoned fields, woodlots and riparian corridors in the study area (Facelli & León 1986; Ghersa & León 1999). *Gleditsia triacanthos* is a deciduous dicot species native to eastern USA that was introduced in the region in the mid-1800s as an ornamental and shade plant and was also used for hedges (Chaneton *et al.* 2004). Adult individuals of *G. triacanthos* can reach up to 20 m in height and form dense woodlots of more than 1600 trees per hectare, which greatly reduce herbaceous productivity and prevent the passage of livestock. Seeds are readily dispersed by cattle (Marco & Páez 2000) and native mammals, such as armadillos and foxes. The life history traits of this species, such as high seed production, high germinability, rapid growth and a short juvenile phase, indicate high invasive potential (Marco & Páez 2000; Mazía *et al.* 2010), and hence it is considered the most aggressive invasive woody species in mesic Pampas (Ghersa *et al.* 2002) and a worldwide invasive species (Global Compendium of Weeds: http://www.hear.org/gcw/index.html).

Robinia pseudoacacia is also a deciduous dicot species native to temperate areas of North America and is well adapted to extreme environmental conditions, such as drought, air pollution and high light intensities . Adult individuals can reach up to 25 m in height and form dense woodlots, which reduce herbaceous productivity and prevent the passage of livestock. In the study area, *R. pseudoacacia* is found invading pastures, abandoned fields, woodlots and riparian corridors, but is less frequent than *G. triacanthos*. For both woody species, bud break starts in early spring (September) while ripe fruits fall during autumn (May).

Study sites

The five communities studied were separated approximately by 2–7 km (Fig. 1) and corresponded to the following:
a. A native tussock-grass community located within a 500 m long by 60 m wide corridor extending for 10 km parallel to an abandoned railway line. It is dominated by *Paspalum quadrifarium*, a native tall C$_4$ perennial
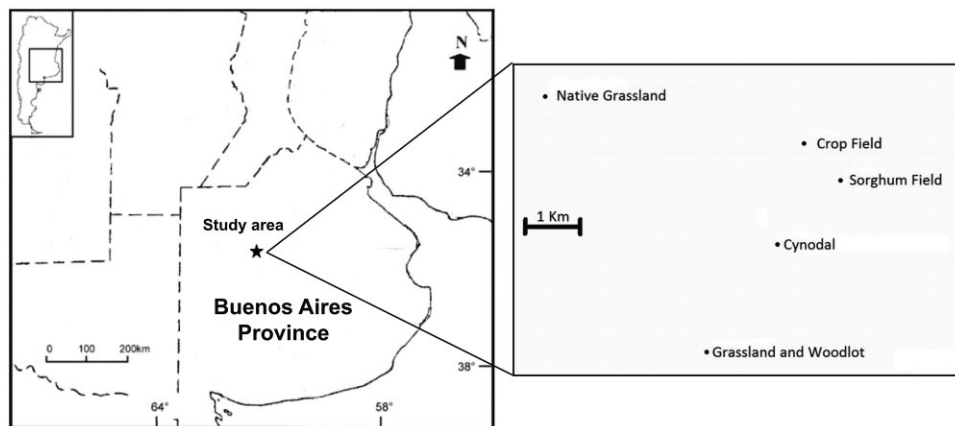

Fig. 1. Map of the study area and the location of the studied communities in Carlos Casares county (35°53′ S, 61°12′ W), Inland Pampa, Buenos Aires Province, Argentina.

bunchgrass, which accounts for 90% of the total standing biomass. Hereafter, we will refer to this community as 'native grassland'.

b. A 32-year-old successional field located in a 4-ha enclosure on a formerly grazed pasture. It comprises a mixture of exotic grasses such as *Lolium multiflorum*, *Bromus catharticus*, *Festuca arundinacea*, *Dactylis glomerata* and *Sorghum halepense*, and tall weeds as *Conium maculatum*, *Carduus acanthoides* and *Cirsium vulgare* (Machera 2006). There is also a patch of about 0.5 ha corresponding to a *G. triacanthos* woodlot. Hereafter, we will refer to this community as 'grassland and woodlot'.

c. A 20-year-old successional field located in a 2-ha enclosure on a formerly grazed pasture dominated by perennial exotic grasses, mainly *Cynodon dactylon*, *S. halepense* and *F. arundinacea* (Tognetti *et al.* 2010). Hereafter, we will refer to this community as 'cynodal'.

d. A 10-year-old successional field in a 1-ha enclosure on a formerly grazed pasture dominated by perennial exotic grasses, mainly *S. halepense*, and tall weeds as *C. maculatum*, *C. acanthoides* and *C. vulgare*. Hereafter, we will refer to this community as 'sorghum field'.

e. An agricultural field that showed typical agrarian labours, such as sowing and harvesting of crops, principally corn, soybeans and wheat. During the study (2010–2011), crop rotation included wheat (winter–spring) and soybean (summer–autumn). Hereafter, we will refer to this community as 'crop field'.

The four grassland communities studied (a–d) showed high (90–95%) plant cover at ground level throughout the year, providing potential shelter and food resources for rodent populations; while the crop field showed strong variations in plant cover (0–100%) according to the phenology of crops. Spatial heterogeneity in plant cover and food availability for rodents was mainly accounted for at the community scale because the communities considered were internally homogeneous with respect to plant composition.

Potential seed predators in the area are birds, ants and small mammals (body mass <45 g). The native sigmodontine rodents, *Akodon azarae*, *Calomys musculinus*, *Calomys laucha*, *Oligoryzomys flavescens* and the Pampa cavy *Cavia aperea* are commonly present in the area (Busch *et al.* 2012). All rodent species, except the Pampa cavy which is considered strictly herbivorous, are omnivorous consumers feeding on invertebrates, green parts of plants, and seeds of grasses and forbs (i.e. *S. halepense* and *C. acanthoides*, Bilenca *et al.* 1992; Ellis *et al.* 1998). Rodent population densities vary temporally in relation to seasonal changes in temperature and precipitation, which affect food availability and energy requirements (Busch & Kravetz 1992).

Data collection

The study was conducted during 2010–2011 at different phases of the rodent population cycle: non-breeding season with moderate abundance (winter, July 2010), breeding season with minimum abundance (spring, October 2010), breeding season with low abundance (summer, February 2011) and non-breeding season with maximum abundance (autumn, April 2011). These phases were established according to previous data (Busch & Kravetz 1992).

In field conditions, seed loss caused by rodents was estimated through the supply of seeds in artificial foraging stations (Busch *et al.* 2012). Seed removal trials were conducted simultaneously at all sites in each season of the year (winter: between July 21 and 31 in 2010; spring: between October 7 and 17 in 2010; summer: between February 1 and 11 in 2011; and autumn: between April 20 and 30 in 2011). At each site, three transects with 10 foraging stations were placed, except in the grassland and woodlot where three transects with nine stations each were located because of the dimensions of the plot. In the latter site, foraging stations were equally distributed between the grassland and the woodlot. Foraging stations were spaced at 10m intervals, and in each of them two containers (feeders) separated by 1 m were placed. Within each site, transects were separated by at least 70 m. Seeds in foraging stations were offered in plastic-lidded containers (500 cm³) which had a circular hole of 2 cm in diameter to allow rodent access (Orrock & Damschen 2005). These containers protected the seeds from the effect of rain and wind, reducing the chances of seed loss or mortality independent of predation. The edges of the openings were covered with adhesive tape to prevent the entry of ants and other insects that could remove seeds, as well as to detect rodent or bird consumption by the recovery of hairs or feathers attached to the tape. At each foraging station, 10 seeds of *G. triacanthos* in one of the containers and 10 seeds of *R. pseudoacacia* in the other were offered, mixed with an artificial substrate constituted by small pieces of rubber (diameter 0.5 cm, thickness 0.01 cm). This substrate was added in order to mimic natural conditions in which rodents must look for seeds that are mixed with plant material and soil (Busch *et al.* 2012).

The total number of foraging stations from which information was obtained varied because of the eventual loss of containers. At the beginning of the study, foraging stations were checked for three consecutive days and no evidence of consumption was found, so exposure time was extended to 10 days. Seed removal was estimated as the difference between the initial and final number of seeds recovered after the exposure period.

Natural seed availability

Seed availability in the seed bank was estimated from the number and species identity of seedlings emerged from soil samples (Ter Heerdt *et al.* 1996). During February 2010, 15 soil samples were randomly collected at each community at distances from foraging stations that are daily covered by the rodent species that are present in the area (between 1 and 20 m, Cittadino *et al.* 1998) in order to allow the comparison between seed consumption and availability. Soil samples covered an area of 7.7 cm² and were extended up to 5 cm in depth. Plant composition did not show great spatial variation within each community and so we considered that these samples were representative of overall seed bank availability. Samples from each community were pooled and placed in an appropriate medium for germination. After 3 months, plants were harvested and then seedlings were counted and identified. This method may have underestimated seed availability because seeds of some species have innate dormancy and may have failed to germinate, while on the other hand

availability may have been overestimated if we counted seeds buried in shallow soil that were not available for rodents. However, these limitations would have affected the estimation of seed availability in a similar way in all communities, and in consequence they might not affect the comparison among communities.

Rodent abundance at each community

In order to assess the composition and abundance of rodent communities in the different communities studied, three lines of 15 Sherman live traps separated by 10 m were set between June 19 and 22 (2011), during a season of high to moderate rodent abundances (autumn–winter). A trapping period of three nights is considered adequate to estimate rodent abundances (Aplin *et al.* 2003). All communities were simultaneously sampled. No rain occurred during this period and the moon was in the full phase. However, abundant cloudiness was registered throughout the sampling period, counteracting the negative effect of moonlight on rodent activity (Longland 1994; Mattos & Orrock 2010). Based on previous studies, differences in abundance among sites were assumed to be consistent throughout the year (Busch *et al.* 2012).

The distance between lines was at least 20 m, depending on the dimension of the habitat. Traps were baited with a mixture of rolled oats, bovine fat and peanut butter, and were checked every morning for three consecutive days. Animals captured were identified to species and were given an individual mark before being released at the site of capture. A rodent density index (RDI) was estimated for each community as the proportion of trap-nights with capture (without considering recaptures within a trapping session): RDI = (number of individuals captured/number of traps × number of nights).

Feeding trials

Rodents captured at the study area were placed in plastic cages of 60 cm (length) × 30 cm (height) × 25 cm (width) with a hermetic cap, perforated with 8–10 holes (1 cm diameter) in order to allow air exchange between the interior of the cage and the external environment. Cotton was added as nesting material inside a cardboard tube attached with glue to the centre of the floor of the experimental cage. The cages were kept outdoors during the experiment, in an environment similar to the sites where rodents were captured. At least 10 h before the start of the experiment, individuals were placed in the experimental cages with water ad libitum (located at the centre of the cage) but without food administration. During the experiment, rodents remained inside the experimental cages from 19:00 of the day of capture to 7:00 of the following day, approximately. This time interval was selected because of the nocturnal habits of rodents.

Seed consumption of woody and herbaceous species that are usually present in the study area was assessed. Seed mass varied over three orders of magnitude from 1 to 200 mg: *Paspalum quadrifarium* (0.73 ± 0.29 mg),

L. multiflorum (2.46 ± 0.47 mg), *S. halepense* (6.88 ± 1.46 mg), *B. catharticus* (13.11 ± 0.80 mg), *R. pseudoacacia* (18.97 ± 4.90 mg) and *G. triacanthos* (171.54 ± 36.42 mg).

In the cafeteria-style feeding trials, the total mass of seeds of each species offered varied between 200 and 300 mg, while the number depended on its mass. The mass of the different species offered was established to force individuals to consume seeds of more than one species. Thus, it could be determined if woody seeds were consumed as a last resort when no other food was available. At the beginning and at the end of the experiment, seeds were weighed and counted using a magnifying glass (Leica, 5×). Seeds of both woody species and grasses were simultaneously offered to each rodent ($n = 21$). Herbaceous and woody species were offered separated in plastic circular containers (feeders) of 3 cm in diameter and 1.4 cm high, which were attached to the walls of the cage by a plastic wire protector in order to facilitate the handling of the feeders by the experimenter at the time of placement and removal of the remaining food at the beginning and at the end of the experiment. The feeders were distributed equidistantly along the walls of the experimental cage. For each rodent, the locations of feeders with seeds of different plant species were selected at random. Before the beginning of the experiment, we waited until the rodent was in the centre of the experimental cage inside the cardboard tube provided as a refuge (neutral start).

In the non-choice feeding trials, 20 seeds of *R. pseudoacacia* were offered to each individual of a first group of rodents ($n = 11$) and 10 seeds of *G. triacanthos* were offered to a second group ($n = 13$). Seeds were offered in feeders randomly distributed within the experimental box.

Data analysis

Tree seeds consumption in field conditions

Seed consumption was estimated by two different variables: seed encounter, as the proportion of the containers with consumption, and seed removal rate, as the mean number of seeds consumed from containers where consumption was detected (Hulme 1994a). Both response variables were modelled assuming binomial error distributions, using analysis of deviance and logit link functions in generalized linear mixed models (GLMM). The effect of species identity (fixed factor, two levels), the studied communities (five levels) and seasons (repeated measures, four levels) on both seed encounter and seed removal rate were assessed using the R statistical package (version 2.15.2; R Development Core Team 2013) and lme4 package (Bates *et al.* 2013). Transects were considered as a random factor nested in each community. Fisher Least Significant Difference comparisons ($\alpha = 0.05$) were conducted when significant differences were found.

A GLMM using stats package (glm library, R Development Core Team 2013) was performed to compare the rodent density indexes (RDI) per transect between the communities where rodents were captured. Since rodent capture was considered to be not limited by the number of traps placed in each community (135), the model assumed Poisson error distributions of the response variable (proportion of traps with capture from a fix number of traps) with overdispersion (quasi-Poisson).

Table 1.   Results of the generalized linear mixed model that assessed the effect of species identity, the community (between factor) and season (repeated measure) on the encounter and removal of *Robinia pseudoacacia* and *Gleditsia triacanthos* seeds in the Inland Pampa, Argentina

	d.f.	Seed encounter		Seed removal	
		χ^2	P	χ^2	P
Species	1	28.48	<0.0001	330.83	<0.0001
Community	4	35.66	<0.0001	7.04	0.1336
Season	3	135.93	<0.0001	242.93	<0.0001
Species × community	4	1.73	0.7847	36.85	<0.0001
Species × season	3	13.13	0.0044	124.93	<0.0001
Community × season	12	156.46	<0.0001	350.41	<0.0001
Species × community × season	12	5.94	0.9189	41.09	<0.0001

Transects were considered as a nested factor in each community.

In order to evaluate the association between food availability and woody seed consumption in the different studied communities, Pearson parametric correlations (Zar 1996) were carried out between food availability and the mean number of seeds removed in all containers. The variable food availability was Ln-transformed to obtain a linear relationship of both variables. The normality and homoscedasticity assumptions were tested using the Shapiro–Wilk W-test and the Levene's test for homogeneity of variances, respectively.

Feeding trials

In non-choice feeding trials, the number of individuals that consumed at least one seed of *G. triacanthos* or *R. pseudoacacia* was compared by a non-parametric Mann–Whitney 'U' test for independent samples (Zar 1996).

A GLMM using stats package was performed to compare the proportion of seeds of each woody species consumed and the proportion of consumption of *G. triacanthos* or *R. pseudoacacia* in the absence (non-choice feeding trials) and in the presence of alternative food (cafeteria-style feeding trials). The models assumed binomial error distributions of the response variables.

In the cafeteria-style feeding trials, differences in the proportions of individuals that consumed at least one seed of each species were evaluated using a classic Cochran non-parametric test for dependent samples (Siegel & Castellan 1988). Then, multiple contrasts for the Cochran test were performed among different plant species (Marasculo & McSweeney 1967).

To compare the proportion of seeds consumed per individual rodent among plant species, a GLMM (lme4 package, Bates *et al.* 2013) was carried out. The model assumed binomial error distributions of the response variable. When significant differences were found, Fisher Least Significant Difference comparisons ($\alpha = 0.05$) were conducted. For all analyses a *P*-value <0.05 was considered statistically significant.

RESULTS

Seed removal

Seed encounter by rodents was 42.6% (in 498 out of 1169 containers at least one seed was removed) and

seed consumption was detected in 49.5% of the containers that contained *R. pseudoacacia* seeds ($n = 584$) and in 35.8% of those containing *G. triacanthos* seeds ($n = 585$). Rodent consumption was confirmed by the presence of remains of seed coats, faeces and hairs. Particularly, rodent faeces and hairs were detected in 86% of the containers where seeds were consumed.

Seed encounter depended on both the interaction between species identity and season and on plant community and season (species × season and community × season, Table 1, Figs. 2, 3). Seed encounter was generally higher for *R. pseudoacacia* in comparison with *G. triacanthos*, and for both woody species the highest number of containers with consumption was detected in autumn. Seed encounter of *R. pseudoacacia* was constant in the remaining seasons, while there were seasonal variations in *G. triacanthos* consumption (Fig. 2).

Seed encounter of both woody species was higher in the native grassland (0.61 ± 0.031) than in the other communities, and it was maximum in autumn and winter, and minimum in spring and summer ($P < 0.05$, Fig. 3). On the other hand, the crop field showed the lowest mean proportion of containers with consumption (0.14 ± 0.022), with higher values in spring in comparison to winter, summer and autumn ($P < 0.05$, Fig. 3). The sorghum field, cynodal and grassland and woodlot communities registered similar and intermediate average values of seed encounter (0.5 ± 0.032, 0.47 ± 0.032 and 0.41 ± 0.34, respectively). The sorghum community showed the highest value of seed encounter in autumn, whereas it was higher in summer than in winter and spring. Seed encounter in the cynodal community also differed among seasons. It was maximum in autumn and minimum in spring. The grassland and woodlot community showed higher seed encounter in autumn than in winter, spring and summer (Fig. 3).

The mean number of seeds removed per container depended on the interaction among species identity, plant community and season (species × community × season, Table 1). In winter, seed removal of both
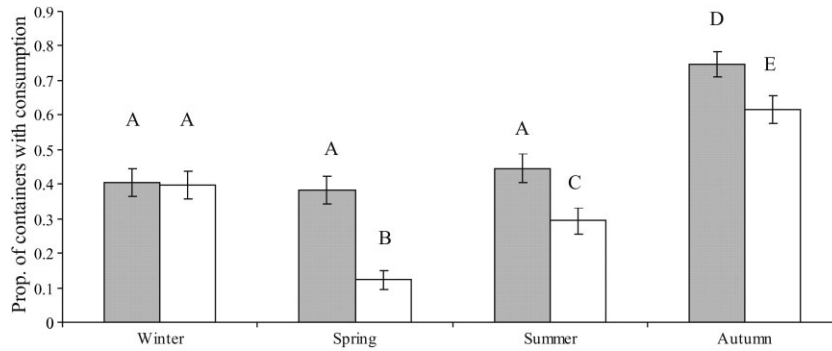
Fig. 2. Mean proportion of containers with consumption (±standard error) for *Robinia pseudoacacia* and *Gleditsia triacanthos* according to seasons in the Inland Pampa, Argentina. Means with the same letters indicate the absence of statistically significant differences (*P* > 0.05, Fisher Least Significant Difference comparisons). (■) Robinia, (□) Gleditsia.
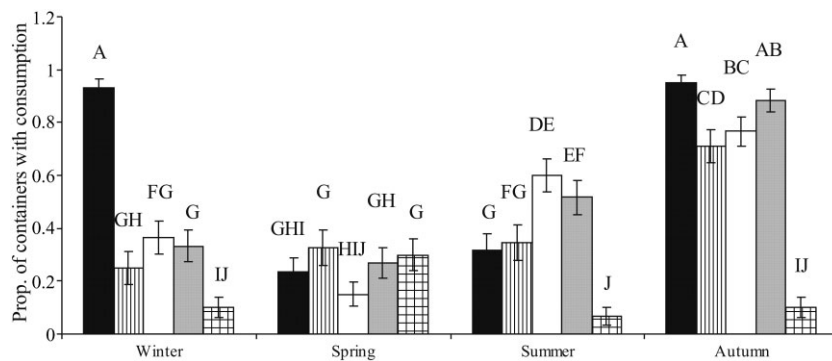

Fig. 3. Mean proportion of containers with consumption of woody seeds (±standard error) according to the season in five communities in the Inland Pampa, Argentina. Data from woody species (*Robinia pseudoacacia* and *Gleditsia triacanthos*) were pooled since the species × communities × seasons and species × communities interactions were not statistically significant. Means that shared at least one letter did not differ significantly (*P* > 0.05, Fisher Least Significant Difference comparisons). (■) NG, (▥) G and W, (□) Cyn, (▨) SF, (▦) CF.

R. pseudoacacia and *G. triacanthos* was higher in the native grassland than in the other communities (*P* < 0.05, Fig. 4a). In spring, removal of *R. pseudoacacia* seeds was higher in the grassland and woodlot than in the remaining communities, while removal of *G. triacanthos* seeds was higher in the grassland and woodlot, sorghum and crop field communities than in the native grassland and cynodal communities (*P* < 0.05, Fig. 4b). In summer, seeds of *R. pseudoacacia* were removed more intensively in the crop field, grassland and woodlot, cynodal, and sorghum field than in the native grassland community (*P* < 0.05, Fig. 4c). In the case of *G. triacanthos*, seed removal was higher in the crop field, cynodal and sorghum field than in the grassland and woodlot and native grassland communities (*P* < 0.05, Fig. 4c). Finally, removal of *R. pseudoacacia* seeds in autumn was higher in the native grassland than in the remaining communities, while seeds of *G. triacanthos* were less removed in the grassland and woodlot community in comparison with the remaining studied communities (*P* < 0.05, Fig. 4d).

Rodent abundance

A total of 114 rodents were captured with a trapping effort of 675 trap-nights. The rodent density index (RDI) was 0 in the crop field and ranged between 0.19 and 0.24 in the remaining communities ($\chi^2_{3;0.95} = 0.55$, $P = 0.91$). Although no rodent was captured at the crop field, it was considered that they were present at low density because there was consumption of seeds (Fig. 2). *Akodon azarae* was the most abundant rodent species in all the communities (Fig. 5), accounting for the 100% of individual captures in the native grassland, the cynodal, and the grassland and woodlot (26, 33 and 26 individuals, respectively), while in the sorghum field it represented 93% (*n* = 29). At this site, the remaining 7% of the captures corresponded to *C. musculinus*.

Alternative food availability in the field

The number of plant species that germinated from soil samples ranged from 6 in the crop field to 14 in the
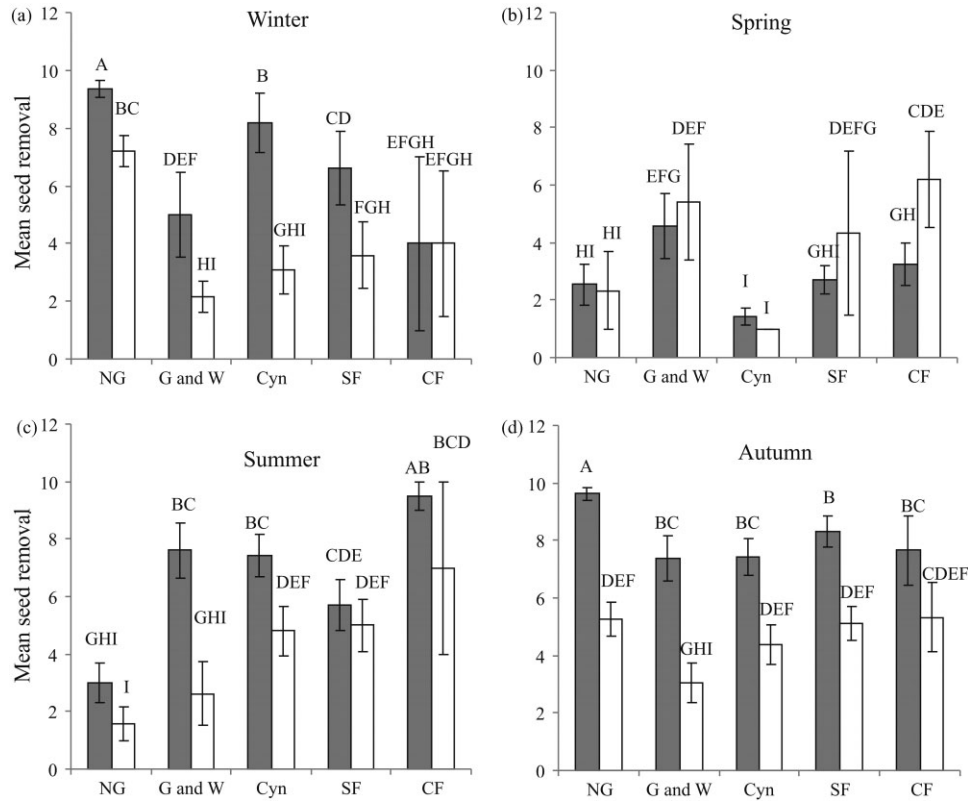
Fig. 4. Mean number of seeds removed from containers where consumption was detected (±standard error) for *Robinia pseudoacacia* and *Gleditsia triacanthos* according to the five studied communities throughout the seasons of the year (a, b, c, d) in the Inland Pampa, Argentina. (C, crop field; Cyn, cynodal; G and W, grassland and woodlot; NG, native grassland; SF, sorghum field). Means that shared at least one letter did not differ significantly (*P* > 0.05, Fisher Least Significant Difference comparisons). (■) Robinia, (□) Gleditsia.
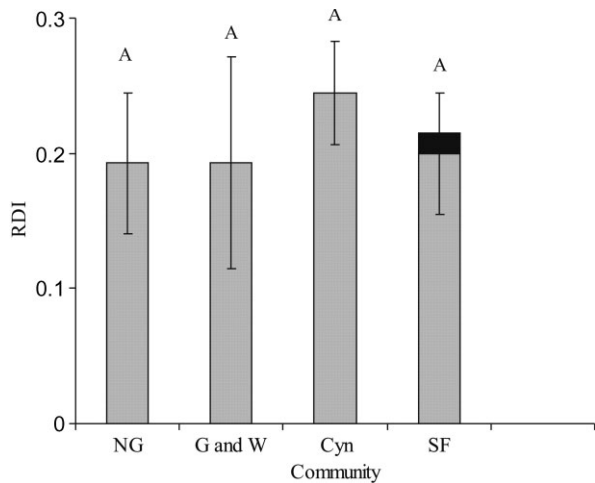

Fig. 5. Rodent density indexes (RDI) (mean ± standard error) in the studied communities during the period of intermediate to high abundance (autumn–winter) in the Inland Pampa, Argentina. (Cyn, cynodal; G and W, grassland and woodlot; NG, native grassland; SF, sorghum Field). Means that shared at least one letter did not differ significantly. (■) *Calomys musculinus*, (□) *Akodon azarae*.

Table 2. Total seedling abundance and number of species emerged from 75 soil samples belonging to the five studied communities in the Inland Pampa, Argentina

Community	Number of emerged seedlings	Number of species
Crop field	12 (0)	6
Sorghum field	65 (42 *Sorghum*)	7
Cynodal	66 (27 *Lolium*, 1 *Bromus*)	7
Grassland and woodlot	169 (16 *Bromus*)	8
Native grassland	25 (11 *Lolium*, 2 *Paspalum*)	14

Between brackets is detailed the number of emerged seedlings corresponding to one of the same species used in the feeding trials.

native grassland (Table 2). Seedling abundance was higher in the grassland and woodlot community than in the crop field and native grassland communities, while the remaining two sites showed almost similar and intermediate abundances (Table 2). Seedlings of woody species were not found in the seed germination trials; however, the species that germinated were a

good reflection of the onsite vegetation (almost 75% of the standing species in each site were found in the seed germination trials).

The crop field showed the lowest levels of consumption (taking in account both seed encounter and the mean number of seeds removed in containers with consumption) of both woody seeds, along with the absence of captured rodents. The variation in the consumption of woody seeds among the other plant communities, which did not significantly differ in rodent abundance, was negatively associated with the increase in availability of alternative food ($r_{pearson} = -0.98$, $P = 0.0237$, d.f. = 2 and $r_{pearson} = -0.96$, $P = 0.0415$, d.f. = 2 for *G. triacanthos* and *R. pseudoacacia*; respectively).

Feeding trials

When seeds of *R. pseudoacacia* and *G. triacanthos* were offered in non-choice feeding trials ($n = 24$), the proportion of rodents that consumed at least one seed was 0.6 (seven individuals) for the first and 0.38 (five individuals) for the latter, but these proportions were not significantly different ($Z = 1.2$, $P = 0.23$, $n = 11$ and $n = 13$, respectively). In turn, the proportion of seeds consumed per individual rodent was also higher for *R. pseudoacacia* than for *G. triacanthos*, and the difference was statistically significant ($\chi^2_{1;0.95} = 27.58$, $P < 0.0001$).

In the cafeteria-style feeding trials ($n = 21$), the proportion of *A. azarae* individuals that consumed at least one seed differed significantly among species ($Q = 67.8$; d.f. = 5; $P < 0.0000$). Seeds of *G. triacanthos* were consumed less in comparison with seeds of grasses and *R. pseudoacacia* ($P < 0.05$; Fig. 6). The proportion of seeds consumed per individual rodent sh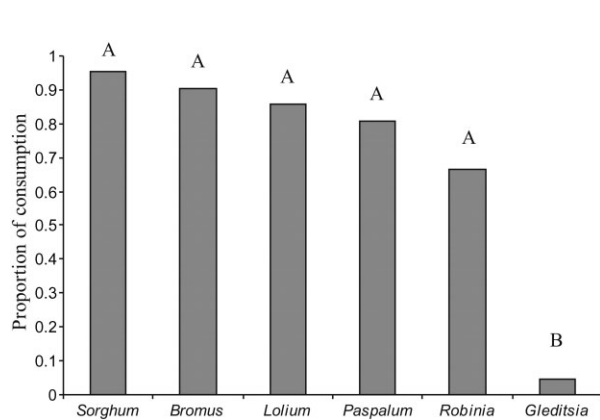owed significant differences among plant species ($\chi^2_{4;0.95} = 1015.52$, $P < 0.0001$). Seeds of *G. triacanthos* and *R. pseudoacacia* were consumed in a lower proportion than those of herbaceous species, but seeds of *R. pseudoacacia* were more consumed than those of *G. triacanthos* ($P < 0.05$, Fig. 7).

There was a higher consumption of *G. triacanthos* seeds in the non-choice than in the cafeteria-style feeding trials ($\chi^2_{1;0.95} = 15.09$, $P < 0.0001$), while the consumption of *R. pseudoacacia* seeds did not differ significantly in the absence or presence of alternative seeds ($\chi^2_{1;0.95} = 2.9$, $P = 0.09$).

DISCUSSION

Our results suggest that, although the intensity of seed consumption varied between communities, seasons and tree species, rodents would be part of the biotic resistance of the resident community to tree invasion since they consumed seeds of both woody species, especially in autumn and winter when there is the major seed rain of *R. pseudoacacia* and *G. triacanthos* (Mazía *et al.* 2013).

Overall consumption (taking into account both seed encounter and the number of seeds removed in containers with consumption) of the seeds of the woody species was higher in the native grassland than all the other studied communities, while the crop field showed both the lowest levels of consumption and abundance of rodents. In this latter habitat, we did not capture any rodents, but they were probably present in low abundance because we registered signs, such as faeces and hairs, in feeders. In consequence, rodent abundance contributed to the differences in seed predation between communities, and as well may explain seasonal variations because seed predation was higher in periods
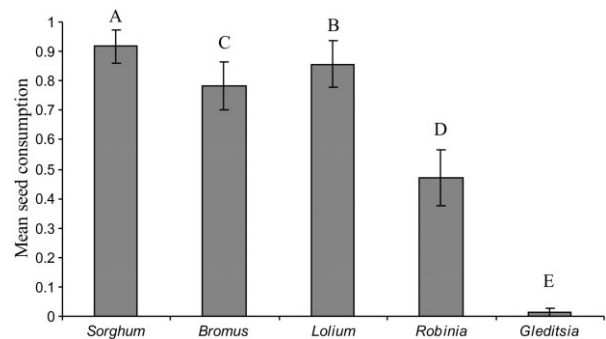

Fig. 6. Proportion of *Akodon azarae* individuals that consumed at least one seed for each of the species included in the cafeteria test. Similar letters indicate the absence of statistically significant differences ($P > 0.05$, Fisher Least Significant Difference comparisons).

Fig. 7. Mean proportion of consumed seeds (±standard error) for *Sorghum halepense*, *Bromus catharticus*, *Lolium multiflorum*, *Robinia pseudoacacia* and *Gleditsia triacanthos* in 21 feeding trials conducted. The small size of *P. quadrifarium* seeds did not allow counting them, and therefore this species was not included in the analysis. Similar letters indicate the absence of statistically significant differences ($P > 0.05$, Fisher Least Significant Difference comparisons).

of high abundance of rodents (autumn–winter). A previous study conducted in the native grassland and in the grassland and woodlot communities found that while the total amount of seeds consumed differed among seasons, consumption per individual rodent was similar, suggesting that differences were related to abundance (Busch *et al.* 2012). However, seasons may not only differ in rodent abundance but also in food requirements and resource availability; therefore, this evidence must be taken with caution.

Differences in consumption among non-cultivated grassland habitats, which showed similar rodent abundance, would support the hypothesis that seed consumption by rodents is context-dependent (Ostoja *et al.* 2012) because consumption of woody species seeds differed among communities according to the availability of alternative food. This effect was also confirmed by the laboratory trials, especially for *G. triacanthos*, which was more consumed in the absence of alternative food than when it was offered with seeds of herbaceous species and *R. pseudoacacia* seeds. Communities with high plant productivity may be more prone to woody plants invasion (because alternative food decreases the intensity of predation on these species) than habitats of low productivity, provided that rodent abundance is not positively correlated to plant productivity. This is verified in our system, since the native grassland, mainly dominated by *P. quadrifarium*, is less productive than the other grassland communities studied (Machera 2006), but rodent abundance was similar. Rodent species of the area are omnivorous, and consumed, in addition to seeds and green parts of plants, insects and other invertebrates; in consequence, their abundance is determined by a variety of alternative foods items (in addition to non-biotic factors). Their effect on seeds must be higher in seasons when insects are rare, such as autumn and winter, as was observed in this study. Food of non-vegetal origin may contribute to maintain higher rodent densities throughout the year than would be expected if the rodents were strictly granivorous or herbivorous. Moreover, cultivated fields, where rodents are less abundant, may be more susceptible to woody invasion if they were abandoned without crops, especially if they are near to woodlots of exotic species or if they are grazed, since livestock are effective seed dispersers that partially digest the seminal cover, thus favouring its subsequent germination (Blair 1990).

The higher consumption of *R. pseudoacacia* seeds with respect to *G. triacanthos* in both field and laboratory trials is probably related to differences in seed sizes, since small-sized rodents present in the study area consume small-sized herbaceous seeds (Bilenca *et al.* 1992; Ellis *et al.* 1998; Murillo *et al.* 2007). A similar result was obtained when comparing the consumption of small-sized seeds of *Prosopis caldenia* with large-sized seeds of *G. triacanthos* (Busch *et al.* 2012). Studies conducted in other grasslands suggest that size may be more determinant than 'novelty' (i.e. lack of consumption of novel items) because small seeds of herbaceous exotic species, such as *Phalaris aquatica* and *C. acanthoides*, were more consumed than seeds of the native *P. quadrifarium* (Murillo *et al.* 2007). On the other hand, the low ranking of *G. triacanthos* seeds in predator preferences agrees with the proposal of Garcia *et al.* (2007), which states that the predation preference ranking is the inverse of that of seed protection against predators because of their hard coat that brings protection against predators. In addition, *G. triacanthos* seeds have a poor nutritional value, with a high proportion of indigestible compounds (Manzi *et al.* 1979).

The higher consumption of *R. pseudoacacia* seeds in comparison with *G. triacanthos* is consistent with the different expansion patterns locally observed for these woody species. *Gleditsia triacanthos* is widely spread forming dense woodlots, while *R. pseudoacacia* is more restricted in distribution and density. *Gleditsia triacanthos* seeds have traits, such as large size and a hard coat, that allow escape from small-sized predators, although its seeds may still be intensively attacked by insects of the bruchiid family (Gold & Hanover 1993). Moreover, its seeds may remain viable in the soil seed bank for long periods and emerge when conditions become favourable (Blair 1990).

Competitive relationships between resident vegetation and invasive woody plants species, such as inhibition of germination by microhabitat conditions and competitive exclusion of seedlings by established vegetation, and the occurrence of disturbances are known to limit tree recruitment (Mazía *et al.* 2001, 2010). However, our results showed that these barriers could be altered in some communities by the seed predator's food preferences. Predator's preference for resident vegetation rather than *G. triacanthos* and *R. pseudoacacia* may increase the propagule pressure of these species and may counteract the negative impacts exerted by the established vegetation. Although woody species were not offered mixed with resident species, taking into account both the negative relation between woody seed consumption and alternative seed availability at the community scale and the preferences of rodents for herbaceous resident seeds with respect to woody species observed in feeding trials, it may be suggested that the resident plant community would exert an apparent mutualism (Holt 1977) or associational resistance (Ostoja *et al.* 2013) on invader seeds via seed predator's food preferences, especially in autumn and winter when woody seed consumption is more intensive. In consequence, in some habitats, these tree species would experience a lower intensity of seed predation, which in turn would increase both the number of propagules available for germination and the chances of population expansion. Our data are consistent with previous studies in different habitats

that also have found that seed predation by rodents on herbaceous and tree species could be an important factor of biological resistance (Ostfeld *et al.* 1997; MacDougall & Wilson 2007), and that its relevance depends on habitats, season of the year and plant species (Murillo *et al.* 2007; Nuñez *et al.* 2008; Pearson *et al.* 2011; Busch *et al.* 2012).

An important limitation of our study was the narrow temporal scale of our observations and the lack of replicates at the community scale. Therefore, caution must be used when making wider generalizations based on the results of this study, and further work is needed. For example, the indirect positive interactions between resident and exotic plant species must be confirmed with new experiments especially designed to test these interactions, particularly offering woody species seeds mixed with resident seeds. On the other hand, larger scale (both in time and space) experiments with rodent removal may clarify if predation influences plant invasion comparing with areas without removal.

In summary, we conclude that rodents consumed seeds of both woody species, that their effect is greater on *R. pseudoacacia*, whereas *G. triacanthos* may probably escape from their control. Habitats with more alternative food of vegetal origin are more prone to be invaded by these woody species than habitats with fewer alternative foods, suggesting that rodent consumption is context-dependent. Thus, the outcome of competitive relationships between resident vegetation and invasive woody plants species (Mazía *et al.* 2001) would be reversed when they interact via a seed predator that prefers to consume resident vegetation.

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