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Comparing seed removal of 16 pine species differing in invasiveness

**M. A. Carrillo-Gavilán · H. Lalagüe ·
M. Vilà**

Abstract Small seed mass is regarded as a robust trait related to invasion success, especially in pines. However, few studies have explored whether invasiveness related to small seed mass is also associated to low levels of seed predation in the recipient community. We conducted field cafeteria seed removal experiments comparing 16 *Pinus* species that differ in seed mass to test if seed removal might impose biotic resistance to *Pinus* spp. and if there are differences between species related to seed mass. Seeds were removed rapidly and in high proportion. In the Mediterranean shrublands, where the experiments were conducted, rodents and ants were the main seed removers. Mean seed survival time was significantly different between species. However, smaller seeds were not the most predated. Our study suggests that, in pine species with high invasiveness, the potential higher seed removal of small seeds can be counterbalanced by larger seed crops.

M. A. Carrillo-Gavilán · M. Vilà (✉)
Estación Biológica de Doñana (EBD-CSIC), Avda.
Américo Vespucio s/n Isla de la Cartuja, 41092 Sevilla,
Spain
e-mail: montse.vila@ebd.csic.es

M. A. Carrillo-Gavilán
e-mail: amparocg@ebd.csic.es

H. Lalagüe
Ecology of Mediterranean Forests Unit, INRA, Domaine
Saint Paul, Site Agroparc, 84914 Avignon, France
e-mail: hadrienlalague@yahoo.fr

Introduction

Invasion success depends mainly on invasiveness (i.e. the intrinsic potential of an alien species to invade), invasibility (i.e. the susceptibility of the recipient community to be invaded) (Lonsdale 1999), and propagule pressure (i.e. the number of individuals introduced and the number of introduction attempts) (Williamson 1996; Lockwood et al. 2005; Colautti et al. 2006), aspects that have tended to be studied in isolation.

Many studies have tried to find life-history traits that determine a high invasive potential (reviewed in Pyšek and Richardson 2007). The most cited studies on the plant traits that determine invasiveness likely correspond to those comparing invasive and non-invasive conifer species particularly pines (Richardson and Rejmánek 2004; Rejmánek and Richardson 1996; Grotkopp et al. 2002). The genus *Pinus* contains approximately 111 species (Price et al. 1998) and 18% are reported to be invasive in at least one country (Richardson and Rejmánek 2004). Three traits characterise pine invader species (Rejmánek and Richardson 1996): a short juvenile period, a short interval between large seed crops and a small seed mass that is correlated with a fast relative growth rate (RGR) (Grotkopp et al. 2002). Small seed mass

seems to be a robust trait related to invasion success at several spatial scales (Hamilton et al. 2005). It may play a significant role in facilitating species arrival to a new range since small seed mass increases successful dispersal, prolongs persistence in the soil (Thompson et al. 1993) and potentially escape from seed removers (Richardson et al. 2000).

Even for native species, however, there is no consensus as to whether small-seeded species escape more often from seed removal than those with large seeds, with the former consequently having a higher establishment success. This depends on a life-history trade-off between seed mass and seed production, viz. small seeds are produced in greater quantities than large seeds (Jakobsson and Eirksson 2000; Henery and Westoby 2001; Moles and Westoby 2004). Moreover, there is a preference for seed size according to predator type (Ordóñez and Retana 2004). For instance, in herbaceous areas in the UK, there is higher predation by rodents on larger (seed size > 1 mg) than on smaller seeds (Hulme 1998) while ants were the main predators on very small seeds (Andersen 1987; Nepstad et al. 1991). In degraded ecosystems, the absence of large mammals can lead to higher predation on smaller than on larger-seeded species (Hang-Hau 1997; Dirzo and Mendoza 2007).

Native seed predators act as barriers to invasion by decreasing the number of seeds available for establishment in the new range (Vilà and Gimeno 2003). Nevertheless, few studies have investigated the link between seed size and post-dispersal seed predation in invasive species. In Argentina, Nuñez et al. (2008) have found that seeds of invasive conifers, two of them pine species, are more consumed than native tree species probably because seeds are larger and more attractive to native rodent and bird seed predators. Large seed predation thus determined lower exotic seedling emergence.

We investigated the likely invasion success of 16 *Pinus* species differing in seed size in disturbed Mediterranean shrublands by conducting field cafeteria seed removal experiments to answer the following questions: (1) Is seed removal imposing a putative biotic resistance to *Pinus* spp. establishment? (2) Are there differences in seed removal between species? (3) Are differences in seed removal explained by seed size? and finally (4) Who are the main seed removers? Our hypothesis is that *Pinus* spp. shows significant differences in seed removal in relation with seed size. We expected small-seeded species to show lower seed removal and to have larger seed-survival times than large-seeded species. Given that many exotic pine species have been experimentally planted in disturbed Mediterranean areas, this study is also an attempt to improve invasion risk analysis for introduced conifer species.

Methods

Study area

The study area was located in disturbed sclerophylous shrublands in Madroñalejo-Aznalcóllar hills (Spain) (37°34′N and 6°20′W) at an average altitude of 292 m a.s.l. The climate is Mediterranean with warm, dry summers and cool, wet winters. According to the nearest meteorological station in El Campillo (Huelva), the mean annual temperature is 18°C. The mean minimum and maximum temperatures are reached in January (5.4°C) and in July (34.8°C), respectively. The mean annual precipitation is 679 mm. Geomorphologically, the area is dominated by ardoise schists rich in iron oxides (Lamy JB, personal communication) and quartzite outcropping at the soil surface. Soils are red, with sandy-loam texture, very poor in organic matter and a very acidic pH (Navarro Cerrillo et al. 1998).

This area has been highly disturbed by forestry management (e.g. clearing, afforestation) and by consecutive fires. The last wildfire was in summer 2004. Prior to the fire, the vegetation was composed of scattered holm oaks (*Quercus ilex* sub. *ballota*), cork oak (*Q. suber*) and reforested *Pinus pinea* with a shrubland understorey (Navarro Cerrillo et al. 1998). Two years after the wildfire the area was mainly reforested by *Q. suber* and *Olea europaea sylvestris*. Currently, the vegetation is dominated by *Cistus salvifolius* (15.4% plant cover) and *C. ladanifer* (13%) followed by *Genista tridendata* (8%), *Ulex eirocladus* (4.25%) *and G. triacanthos* (4%).

Study species

Sixteen *Pinus* species, which are broadly commercialized and planted worldwide, were used for analysis (Table 1). Of these, nine species have been planted in Spain (Montero et al. 2005) but only two

Table 1 Mean (±SE) characteristics of the *Pinus* species assayed

Abbreviation	*Pinus* spp.	Seed traits				Native distribution
		Weight (g)	Strength (Newton)	Length (cm)	Width (cm)	
B[b]	*P. banksiana*	0.004 ± 0.0001	4.2 ± 0.32	0.37 ± 0.005	0.20 ± 0.003	Northern USA and Canada
CT[b]	*P. contorta*	0.004 ± 0.0002	13.5 ± 0.96	0.43 ± 0.012	0.23 ± 0.01	Western North-America
RE[b]	*P. resinosa*	0.009 ± 0.0003	13.3 ± 0.41	0.43 ± 0.006	0.25 ± 0.004	USA and Canada
S[a]	*P. sylvestris*	0.009 ± 0.0004	9.5 ± 0.7	0.47 ± 0.009	0.26 ± 0.004	Europe and Asia
PA[b]	*P. patula*	0.009 ± 0.001	11.9 ± 1.38	0.52 ± 0.121	0.26 ± 0.075	Central America
M[b]	*P. muricata*	0.012 ± 0.0005	11.4 ± 1.06	0.54 ± 0.009	0.30 ± 0.007	Western USA and Northern Mexico
H[a]	*P. halepensis*	0.017 ± 0.0009	13.5 ± 0.63	0.59 ± 0.013	0.34 ± 0.072	Mediterranean Basin
R[b]	*P. radiata*	0.03 ± 0.001	19.2 ± 1.20	0.69 ± 0.015	0.40 ± 0.008	Californian Coast
PO[b]	*P. ponderosa*	0.049 ± 0.002	62.1 ± 3.22	0.71 ± 0.015	0.47 ± 0.007	From Southern Canada until Mexico
P[a]	*P. pinaster*	0.053 ± 0.002	60.5 ± 2.16	0.74 ± 0.022	0.48 ± 0.02	Western Mediterranean and Atlantic area of France and Portugal
PT	*P. palustris*	0.077 ± 0.003	27.6 ± 1.36	0.98 ± 0.037	0.57 ± 0.014	North America
RO[b]	*P. roxburghii*	0.087 ± 0.004	40.8 ± 2.06	1.09 ± 0.028	0.57 ± 0.014	Afganistan, Butan, India, Nepal and Pakistan
C[a]	*P. canariensis*	0.112 ± 0.052	69.4 ± 3.61	1.25 ± 0.032	0.62 ± 0.013	Canary Islands
CO	*P. coulteri*	0.347 ± 0.155	161.2 ± 7.45	1.45 ± 0.021	0.82 ± 0.027	California, Mexico
PI[a]	*P. pinea*	0.62 ± 0.030	509 ± 22.64	1.61 ± 0.026	0.86 ± 0.022	Mediterranean Basin
SA[b]	*P. sabiniana*	0.829 ± 0.021	489.8 ± 26.36	2.09 ± 0.02	0.96 ± 0.014	California

Native species distribution based on Montero et al. (2005) and http://www.arbolesornamentales.com

[a] Native species in Spain; only *P. pinea* occurs in the study area

[b] Exotic species planted in Spain

(*P. radiata* and *P. ponderosa*) have escaped from cultivation but are not considered naturalized in Spain (Sanz-Elorza et al. 2004). Only *P. pinea* is native in the study area.

Seed mass of these species differ in two orders of magnitude ranging from 4 mg (*P. contorta)* to 829 mg (*P. sabiniana*). To guarantee a high seed quality, seeds were purchased in the following nurseries: Intersemillas (Spain), Sheffield's Seed Co. (EE.UU) and Les Semences Du Puy (France) (http://www.intersemillas.es, http://www.sheffields.com/ and http://www.semencesdupuy.com/, respectively).

For each species, 20 seeds were randomly chosen to measure fresh seed mass, length and width. Coat strength was also estimated following Rodgerson's (1998) protocol with a Chatillon Universal Force Tester (Amtek/Chatillon, Largo, FL, USA).

Given that seed mass is strongly positively correlated with strength ($r^2 = 0.95$; $P < 0.001$), seed length ($r^2 = 0.84$; $P < 0.001$) and seed width ($r^2 = 0.77$; $P < 0.001$), seed mass was used as the seed size parameter for our analysis.

Seed removal experiment

In 2007, we placed four 100 × 100 m plots, 0.2–3 km apart. In each plot, we placed ten to fourteen 50 m long transects. In each transect, we randomly placed seeds on the ground surface keeping a distance of approximately 3 m between each other. Each seed was glued to a piece of nylon fishing line that was tied to a wire stake (Schupp 1988). Glue was odourless and tasteless.

In order to consider time variation in seed removal, we repeated the experiment twice during the seasons when pine seed dispersal might occur (Lanner 1998; Tapias et al. 2004). In Summer, we used 14 species ($n = 80 \times 14 = 1,120$ seeds). In Autumn, we used 16 species ($n = 80 \times 16 = 1,280$ seeds). For commercial reasons, we could not use the same number of species in both seasons.

In Summer 2007, seeds were checked for removal after 1, 3, 7, 10, 16, 24, 31, 38, 52 and 59 days. In Autumn 2007, we introduced two more species: *P. pinea* and *P. contorta* and seeds were checked after 1, 2, 3, 7, 13, 21, 34 and 41 days. We considered either missing seeds or the presence of seed coat remnants as evidence of seed removal. We finished the experiment when, after two consecutive visits, the seed removal curves did not vary. After that day, all seeds were removed from the field.

We conducted two analyses. First, differences in seed removal (i.e. percentage of predated seeds at the end of the experiment) between species for each season were analyzed using SAS macro GLIMMIX (Littell et al. 1996) with binomial error and a *logit* link function. Species ($n = 14$ in Summer and $n = 16$ in Autumn) was considered as a fixed factor and plot ($n = 4$) as a random factor. The interaction between species and plot was considered as a random effect. Second, Kaplan–Meier estimations of the mean survival time of seeds were calculated. Differences of mean survival time among species for each season were compared with the Gehan–Wilcoxon test (Pyke and Thompson 1986). Seasonal comparisons were not conducted because the time duration of experiments was different. The software SPSS 14.0 was used for survival analysis (SPSS Inc., Chicago, IL, USA). Additionally, simple regression analysis between seed mass and seed removal and mean survival time were conducted for each season.

Seed removal trials with seed remover exclusion

To ascertain whether species differences in seed removal could be related to seed mass and to discriminate between seed remover guilds, three species with the lowest seed mass, *P. halepensis*, *P. patula* and *P. contorta,* and three with the highest seed mass, *P. sabiniana*, *P. pinea* and *P. coulteri* (Table 1), were chosen in March 2008 to compare the effectiveness of seed removal by birds, ants and rodents.

The device allowing seed access only for birds (i.e. preventing ants and rodents) was composed of a plastic curved tray suspended at a height of 15–20 cm above the ground on a wood stick. This system has been successfully tested with small birds by placing the device at 30 cm height (Castro et al.
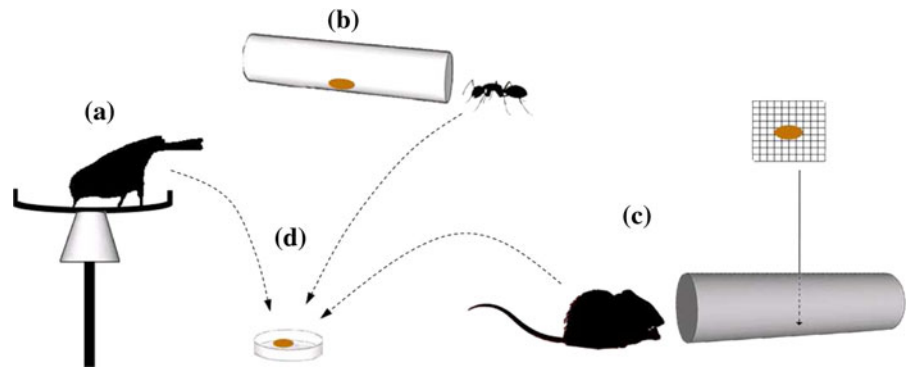
1999). In the study area, however, there are a large number of red-legged partridge (*Alectoris rufa*) that are good walkers but fly with moderation. Therefore, we reduced the height to improve the potential access for seed consumption after testing it in wildfowl hatchery. A plastic cup (9 cm high and 6.5 cm diameter) was positioned against the bottom of the tray in order to prevent rodent access. The bottom of the tray was painted with a Teflon® emulsion (i.e. polytetrafluorethylene) to make the surface of the tray sticky for climbing ants (Hulme 1997; Fedriani et al. 2004). The tray was filled with soil and the seed was placed in the centre of the tray (Fig. 1a).

The device for ants consisted of a transparent plastic tube 8 cm in length and 1.2 cm diameter in which the seed was placed inside. The tube was fixed to the soil with U-shaped wire (Castro et al. 1999; Deveny and Fox 2006; Jacob et al. 2006; Fig. 1b). The diameter was the minimal size that could be used to allow the removal of *P. sabiniana* (Table 1). The treatment revealing rodent activity was made with an opaque plastic tube 20 cm in length and 3.5 cm diameter. The tube was also fixed to the soil with U-shaped wire. To prevent seed displacement by ants, the seeds were glued to 3×3 cm pieces of fine plastic mesh and placed inside the tube (Ordóñez and Retana 2004; Fig. 1c). Finally, the last treatment consisted of small Petri dishes 4.5 cm in diameter and 0.5 cm high fixed to the soil with a wire. This system allows all animals to remove seeds (Fig. 1d, open treatment hereafter).

The four exclusion treatments were randomly placed along 40 parallel transects 70 m long, at approximately 1.5 m intervals. Each transect was approximately 2 m away from the next. There were 80 replicates for each treatment and species. Thus, there were a total of 1,920 seeds displayed in the field (6 species × 4 treatments × 80 replicates = 1,920 seeds). Seed removal was monitored at 2, 6 and 13 days after seed placement.

For this experiment, we also conducted two analyses. Firstly, seed removal at the end of the experiment was compared between exclusion treatments, between species and for larger versus smaller seeded species using SAS PROC GENMOD's with binomial distribution and a *logit* link function (v9.1, SAS Institute Inc.) with species, treatment and seed mass class

Fig. 1 The four excluding experimental devices used to estimate seed removal by each remover taxon. **a** bird access, **b** ant access, **c** rodent access, **d** open access to all

(smaller versus larger seeded species) as fixed factors. Secondly, a survival analysis was also computed following the same procedure as in the previous seed-removal experiments. Mean survival time was compared among treatments, among species within each treatment and between seed mass class.

Identity of seed removers

Rodent trapping was conducted in all four plots at the end of each experiment (Summer, Autumn and Spring). Fifteen Sherman traps (H. B. Sherman Traps, Inc., Tallahassee, FL) were distributed in each experimental plot at dawn keeping a minimum distance of 6 m between them. Traps were surveyed at sunset the next day. Inside each trap, we placed a piece of bread with chocolate spreading. The protocol was repeated during three consecutive days (Fedriani 2005). Simple indexes of relative abundance of rodents were calculated for each plot and season as: the number of captured individuals/trapping effort (number traps x trapped nights). Differences in the relative abundance of rodents between seasons were analysed by using SAS macro GLIMMIX (Littell et al. 1996) with binomial error and a *logit* link function. Season was considered as the fixed factor and plot as a random factor.

Pitfall traps were used to identify ant species foraging on the ground only in spring 2008. Pitfall traps were 6.5 cm-diameter, 9 cm-deep plastic cup partially filled with water, ethanol and soap (Romero and Jaffe 1989). Fifteen traps were in place for 48 h in parallel with the rodent trapping. Ants were then sorted in the laboratory to the species level. Finally, common birds of the study area that might remove

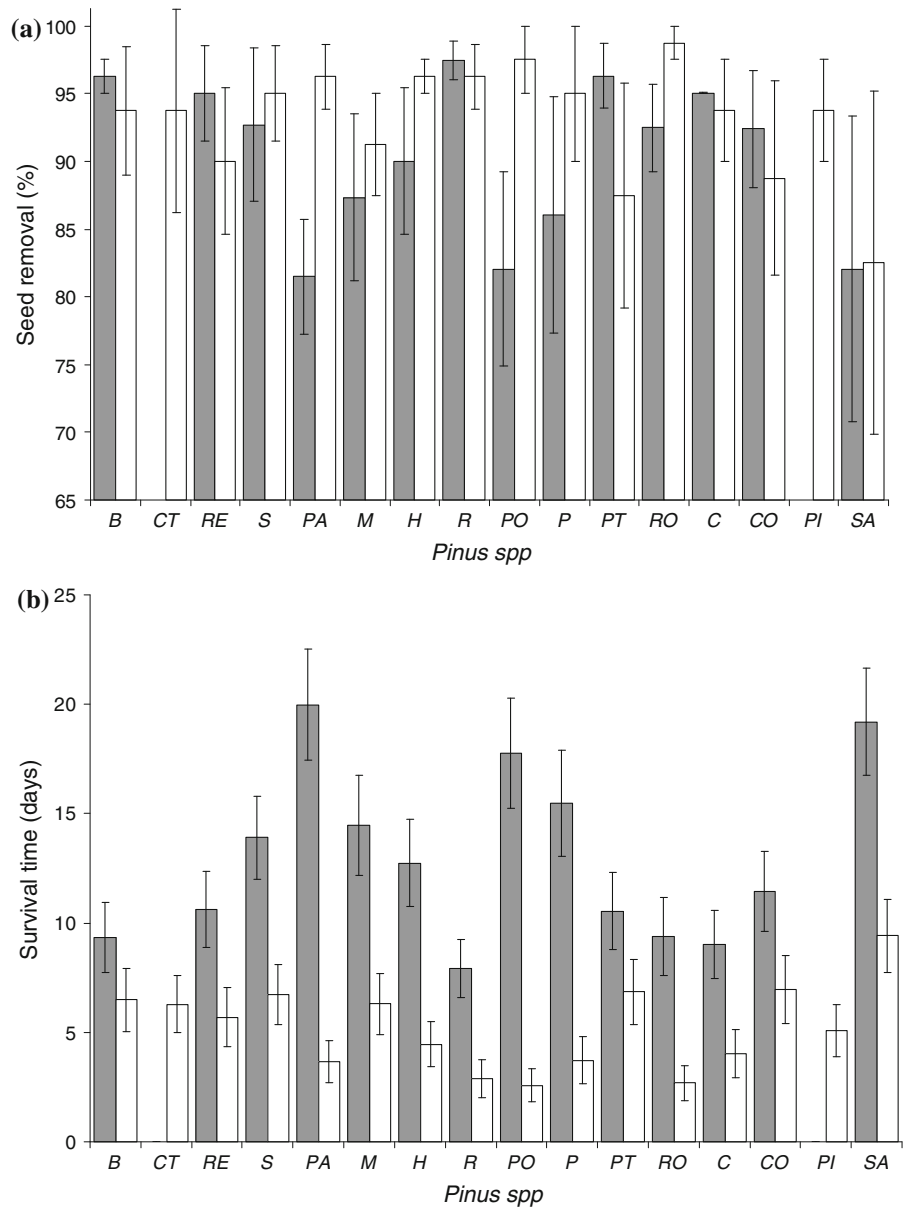seeds were identified in spring 2008 according to visual identification and song.

Results

Seed removal experiment

In both seasons, mean seed removal was very intense for all species at 90.53% in Summer and 93.03% in Autumn (Fig. 2a). There were no significant differences in seed removal between species in any season ($F_{13, 39} = 1.60$; $P = 0.13$ in Summer and $F_{15, 45} = 0.66$; $P = 0.81$ in Autumn).

There was a small significant negative relationship between seed removal and seed mass in Autumn ($r^2 = 0.37$; $P = 0.013$) but not in Summer ($r^2 = 0.107$; $P = 0.254$). However, this correlation was mostly driven by *P. sabiniana,* the species with the largest seeds. The relationship disappeared when this species was removed from the analysis ($r^2 = 0.017$; $P = 0.662$ in Summer and $r^2 = 0.042$; $P = 0.462$ in Autumn).

Mean survival time was shorter in Autumn (5.24 days $\pm$ 0.31) than in Summer (13.11 $\pm$ 0.55). There were significant differences in mean survival time between species for both seasons (Gehan–Wilcoxon test; $\chi^2_{13} = 48.36$, $P < 0.001$ in Summer and Gehan–Wilcoxon test; $\chi^2_{15} = 83.88$, $P < 0.001$ in Autumn) (Fig. 2b). The shortest and longest mean survival times were for *P. radiata* (8 $\pm$ 1.3) and *P. patula* (19.9 $\pm$ 2.5) in Summer and for *P. ponderosa* (2.5 $\pm$ 0.76) and *P. sabiniana* (9.41 $\pm$ 1.67) in Autumn, respectively. Mean survival time, however, was not related to seed mass in any season ($r^2 = 0.001$;

Fig. 2 Mean (±SE) seed removal (**a**) and mean (±SE) survival time (**b**) of pine species in Summer (*grey bars*) and in Autumn (*white bars*). Species are ordered from small to large seed mass. See Table 1 for species identification

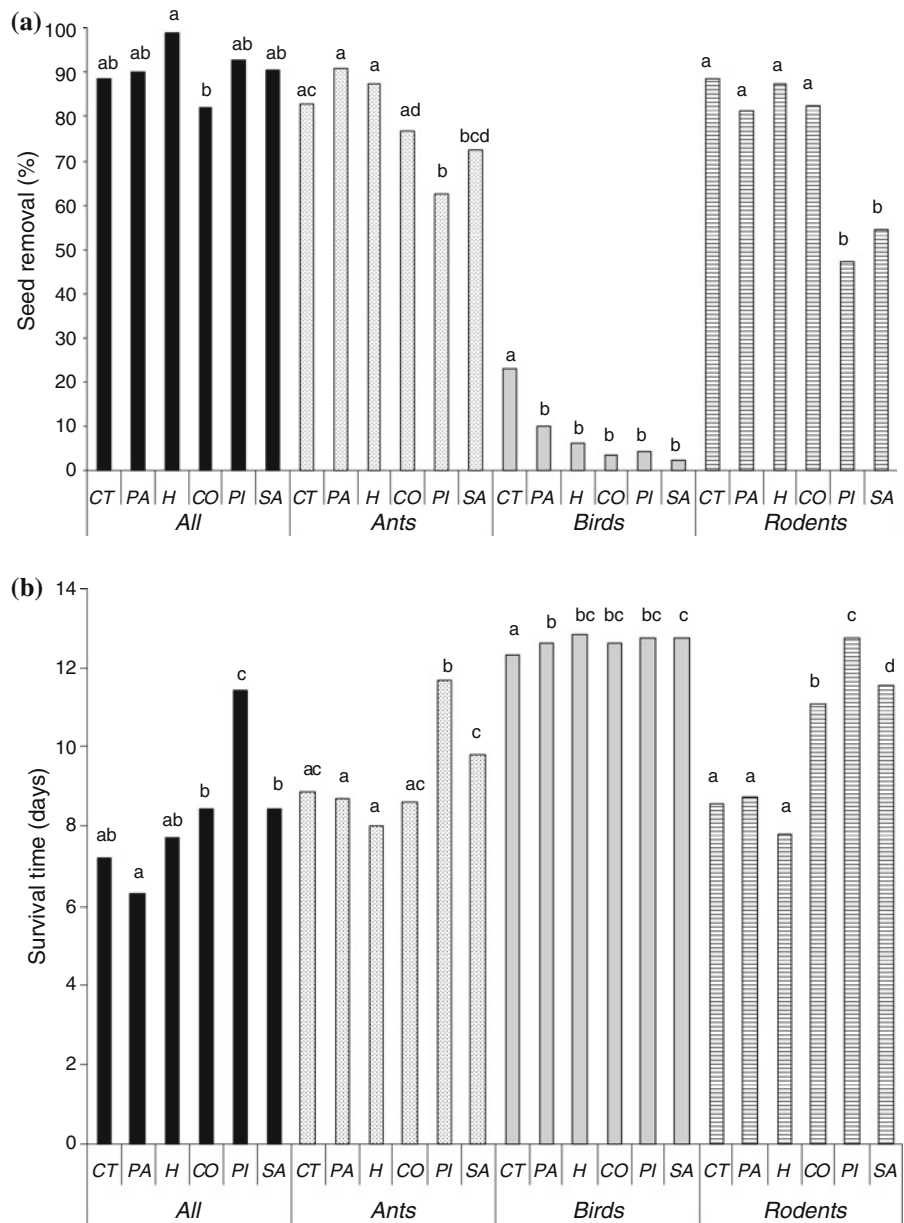P = 0.924 in Summer and $r^2 = 0.201$; $P = 0.082$ in Autumn).

Seed removal trials with seed remover exclusion

Overall, 63.73% of seeds were removed after 13 days. There were significant differences in seed removal between exclusion treatments ($\chi_3^2 = 928.7, P < 0.005$). The highest quantity of seeds removed (94.10%) occurred in the open treatment (Fig. 3a) followed by

ants (79.87%) and rodents (72.03%). The bird treatment had the lowest seed removal (8.94%).

On average, there were significant differences in seed removal between species ($\chi_5^2 = 56.11, P < 0.005$). The most predated species were *P. contorta*, *P. halepensis* and *P. patula* (72.26, 70.86, and 70%, respectively). *P. coulteri* and *P. sabiniana* had an intermediate seed removal percentage (63.30 and 55.22%, respectively), and the least removed was *P. pinea* (50.69%). However, the treatment by species

Fig. 3 Percentage of seed removal (**a**) and mean survival time (**b**) of pine species in different exclusion treatments. *Lower-case* letters represent statistically significant differences ($P \leq 0.05$) between species within treatments. Species are ordered from small to large seed mass. See Table 1 for species identification

interaction was significant ($\chi^2_{23} = 1075.29$, $P < 0.05$) indicating that these differences between species were not consistent across all exclusion treatments. In general, there were also significant differences between seed mass classes ($\chi^2_1 = 46.40$, $P < 0.005$): species with smaller seeds being more predated than larger seeded-species (69.60 and 55.88%, respectively) and this trend was observed for all treatments (open: $\chi^2_1 = 5.03$, $P < 0.05$; ants: $\chi^2_1 = 18.84$, $P < 0.0001$; birds: $\chi^2_1 = 12.93$, $P < 0.005$; rodents: $\chi^2_1 = 40.84$, $P < 0.0001$).

Mean survival time was significantly different between exclusion treatments (Gehan–Wilcoxon test; $\chi^2_3 = 649.6$, $P < 0.0001$) and between species (Gehan–Wilcoxon test; $\chi^2_5 = 186.76$, $P < 0.0001$). Seeds in the open treatment showed the shortest survival time (8.46 ± 0.21) followed by the seeds removed by ants (9.28 ± 0.2), rodents (10.14 days ± 0.19) and, finally birds (12.67 ± 0.08) (Fig. 3b).

Within each treatment, there were significant differences in mean survival time between species (open: $\chi^2_5 = 49.53$, $P < 0.0001$; ants: $\chi^2_5 = 37.19$,

$P < 0.0001$; birds: $\chi^2_5 = 32.4$, $P < 0.0001$; rodents: $\chi^2_5 = 114.12$, $P < 0.0001$ (Fig. 3b). On average, mean survival time for smaller seeded-species (9.14 days $\pm$ 0.15) was significantly shorter than for larger seeded-species (11.03 days $\pm$ 0.12) (Breslow test: $\chi^2 = 88.87$, $P < 0.0001$).

Identity of seed removers

The rodents captured in the area were *Mus spretus* and *Apodemus sylvaticus* (Muridae). In Summer and in Autumn, *M. spretus* was captured in a higher proportion than *A. sylvaticus*. There were significant differences in the relative abundance of rodents between seasons ($F_{2, 6} = 6.62$; $P = 0.03$) being lowest in Spring (Table 2).

We captured nine different ant species of which *Tetramorium impurum*, *Pheidole pallidula* and *T. caespitum* are granivorous. The granivorous birds were predominantly: the red-legged partridge (*Alectoris rufa*, Phasianidae); *Carduelis carduelis*, *C. cannabina*, *Fringilla coelebs*, *Miliaria calandra* and *Serinus serinus* (Fringillidae); *Parus major* (Paridae); and *Galerida cristata* (Alaudidae).

Discussion

Native fauna was very efficient in removing *Pinus* spp. seeds (>90%), exhibiting similar values to other post-dispersal seed removal experiments for pine species (Vander Wall 1992; Castro et al. 1999; Borchert et al. 2003). Although our study should be considered a field cafeteria experiment, it showed evidence that the native fauna can be an important component of biotic resistance to pine establishment

Table 2 Relative abundance index (number of individuals) of rodents in the study area

	Summer 2007	Autumn 2007	Spring 2008
Mus spretus	14.4 (26)	15.5 (28)	1.1 (2)
Apodemus sylvaticus	8.3 (15)	3.8 (7)	1.1 (2)
Total	22.7 (41)	19.4 (35)	2.2 (4)

The relative abundance was calculated as the number of captured individuals/trapping effort, where trapping effort is the number traps × trapped nights

(Elton 1958; Maron and Vilà 2001, Vilà and Gimeno 2003, Nuñez et al. 2008). In our study area, the main seed removers were ants and rodents, which, together with birds, are also considered the main post-dispersal seed removers of the Mediterranean native plant species (Herrera 1984; Hulme and Hunt 1999; Alcántara et al. 2000; Andrieu and Debussche 2007).

There were significant differences in seed survival between pine species. Contrary to expectation, however, the trend was not towards lower seed removal of small-seeded species. Instead, species with smaller seeds tended to be faster removed. Small-seeded species produce seeds in larger quantities than larger-seeded species (Jakobsson and Eirksson 2000; Henery and Westoby 2001) and this can counterbalance the effects of seed loss (Moles et al. 2003; Moles and Westoby 2004). Our finding suggests that, even if pine invasiveness is associated with small seed mass, their seed crop is what might determine invasion success. This is in accordance with the importance that propagule pressure has on invasion success (Lockwood et al. 2005; Colautti et al. 2006). Many pine species that escape from plantations and become invasive are often those that have been cultivated the most widely and for the longest time (Křivánek et al. 2006).

Our negative relationship between seed removal and seed mass increases the percentage of publications where smaller seeded species were removed more than larger ones (e.g. Moles et al. 2003; Myster 2003; Dirzo and Mendoza 2007). There might be several non-exclusive reasons for our results. Firstly, the optimal foraging theory (Krebs 1978) explains that large seeds are consumed more because of their greater energy content and they provide a higher energy intake per travel unit by seed consumers. Moreover, large seeded species have usually adapted to seed removal by seed caching animals (Vander Wall et al. 2006). Nevertheless, smaller seeds are eaten by a larger guild of predators, and, moreover, the absence of large mammals in disturbed ecosystems can lead to higher removal of smaller rather than larger-seeded species (Hang-Hau 1997; Dirzo and Mendoza 2007). The negative relationship between seed removal and seed mass seems to be related to rodent abundance (Ordóñez and Retana 2004; Fedriani 2005) since rodent abundance was significantly lower in Spring than in Summer and Autumn. Secondly, an animal does not remove a seed only

using the mass criterion. All physical (Rodgerson 1998) and chemical traits come into play (Janzen 1969). However, this is beyond the scope of this work. Thirdly, seed removal is only a step towards seedling establishment. Seedlings from larger seeds have higher probability of survival from seedling emergence to adulthood (Moles and Westoby 2006) and perform better during early development than smaller seeds (Moles and Westoby 2004). These explanations highlight the need to incorporate the elements of species invasiveness with those of habitat susceptibility to invasion (Richardson 2006) to reduce the idiosyncrasies found in the importance of species traits for invasion (Kolar and Lodge 2002; Muth and Pigliucci 2006).

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