



Seed predation and dispersal in relict Scots pine forests in southern Spain

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Abstract

For two years, the seed rain and magnitude of seed losses due to predation were evaluated in Scots pine forests in southern Spain. The Crossbill was the most important pre-dispersal predator, consuming more than 80% of ripening seeds. In addition, other birds, mainly Tits and Siskin, also consumed seeds just before seed dispersal, reaching values of 16 and 51% losses in 1996 and 1997, respectively. Seed rain was monitored in different microhabitats (under pine canopies, under shrubs and in open areas), and was most intense under the canopy of mother plants both years. Post-dispersal seed predators (rodents and birds) consumed up to 96% of seeds reaching the ground. Both pre- and post-dispersal seed predators preferentially harvested filled seeds. Post-dispersal predation was similarly intense in all microhabitats, so predators did not change the spatial distribution of the seed rain. These high predation rates were constant between years, localities and habitats (woodland and treeline). We hypothesize that this high rate of seed predation is a major factor limiting the regeneration of these relict populations of Scots pine in its southernmost limit.

Introduction

Population viability of plants at the ecological limit of their distribution is controlled primarily by abiotic factors (Silvertown & Lovett-Doust 1993). In the Northern Hemisphere, temperature controls the northernmost boundary of plant species distributions (Pigott 1992; Woodward 1990; Bennett 1997), while summer drought controls the southernmost boundary (Pigott & Pigott 1993; Fisher & Gardner 1995; García et al. 1999). In response to changes in these climatic factors, plant populations have continually migrated during glacial-interglacial cycles, moving in a latitudinal and/or altitudinal gradient (Cox & Moore 1993; Bennett et al. 1991; Bennet 1997). As a result, some boreo-alpine tree species have found refuge in the Mediterranean high mountains since the last Ice Age (Bennett et al. 1991), forming relict populations isolated from the current more northerly main distribution.

At the distribution limit, where the viability of plant populations is severely constrained by current

climatic conditions, the additional effect of biotic factors may severely limit chances for regeneration (Miller & Cummins 1982; Zackrisson et al. 1995). Further, these negative effects may dramatically increase where the species is restricted to a cluster of isolated populations instead of a continuous homogeneous population. For instance, seed predation may be higher in small, isolated stands compared to larger stands (Nilsson & Wästljung 1987; Wästljung 1989; Santos & Tellería 1994, 1997), and thus may decrease seedling recruitment (e.g., Santos & Tellería 1994, 1997; Jules 1998).

Seed predation can limit population recruitment not only by a quantitative effect of reducing seed availability (Janzen 1971; Louda 1989; Crawley 1992), but also by a qualitative effect of changing the spatial distribution of seeds in the initial seed rain (Schupp 1995; Schupp & Fuentes 1995). This alters the proportion of seeds available in different microhabitats, and implies that the availability of safe sites for seeds depends on the interaction between seed-rain distribution, habitat

structure, and foraging preferences of post-dispersal seed predators.

Scots pine, *Pinus sylvestris* L. (Pinaceae), is a clear example of a plant species that is presently abundant in boreal and northern areas but isolated in Mediterranean high mountains. This species reaches its southernmost distribution area in Andalusia, southern Spain (Boratynski 1991), forming relicts, isolated populations that are further fragmented into smaller stands due to historical causes or high local environmental heterogeneity. In this work, we investigate the effects of seed predation on regeneration of these isolated stands of Scots pine. Taking into account the qualitative and quantitative consequences of seed predation, the specific objectives of the study were to determine: (1) the degree to which pre- and post-dispersal seed predators decrease seed number, (2) the spatio-temporal variation in seed predation, and (3) the consequences of seed predation for population recruitment.

Materials and methods

Study sites and natural history of Andalusian Scots pine

Study areas were located in two mountain ranges in SE Spain separated by about 80 km, Sierra Nevada and Sierra de Baza. In these areas, the Scots pine, which is considered the variety *nevadensis* Christ of the species, forms relict forests between 1600 and 2100 m asl and forms the treeline. In each area, we selected a study site: Trevenque in Sierra Nevada (37°10'30" N, 3°27'10" W) and Boleta in Sierra de Baza (37°23'01" N, 2°51'45" W). In each site, we studied two habitats: interior of the forest (woodland) and the treeline. Scots pine was the most abundant tree in all sites (Table 1). Woody shrubs taller than 50 cm also represent a high proportion of cover (Table 1), outnumbering *Juniperus communis*, *J. sabina*, *Berberis hispanica* and *Prunus ramburii*.

In our study areas, Scots pine pollination occurs in late May. Seeds mature at 22 months, and dispersal starts in early February, lasting around 3 months. Scots pines produce filled seeds as well as unfilled seeds, generally of similar size but easily identifiable (hereafter referred to as aborted). Filled seeds have a high germination rate (96% in both growth chamber and field experiments) and are not dormant.

All aspects of the study were conducted at the locality of Trevenque in 1996 and 1997, while only the

post-dispersal seed predation experiment in the second year was conducted at Boleta.

Initial seed production

Proportion of filled and aborted seeds per cone was sampled at Trevenque. Healthy cones collected in January from 11 randomly chosen trees per year were individually stored in the laboratory at room temperature until cone opening (15 cones per tree in 1996, totalling 4231 seeds; 10 cones per tree in 1997, totalling 1533 seeds), and then were shaken vigorously until all seeds were released. We then noted the number of filled and aborted seeds.

Pre-dispersal seed predation

Birds were the main pre-dispersal seed predators. The Crossbill (*Loxia curvirostris* L.), feeds on ripening cones from July to December, and all attacked cones fall under the canopy of pines. Crossbill pre-dispersal seed predation was monitored at Trevenque by locating three permanent plots of 1 m² under the canopy of 12 randomly chosen trees in the woodland and 12 at the treeline. Plots were checked every 15 days during 1995 (maturation period of seeds dispersed in 1996) and 1996 (maturation period of seeds dispersed in 1997), noting and collecting the number and types (intact or depredated) of cones found. To evaluate whether the fallen cones contained viable seeds, we allowed the collected cones to open in the laboratory (grouped by plot and sample), and counted the number of filled seeds per cone. We used only cones collected during November and December, since cones collected before November contained unripe seeds.

Paridae (mainly Coal tit, *Parus ater* L., and Crested tit, *P. cristatus* L.) and the Siskin (*Carduelis spinus* L.) were also observed consuming seeds just before dispersal, by feeding on recently opened cones. These birds extract the seeds from the cones and detach the seed wing, which falls to the soil (see Lescourret & Genard 1986, for a similar observation). Pre-dispersal seed predation caused by these birds was registered by counting the number of wings without seeds in relation to the total number of seeds with wings appearing in trays used to collect the seed rain (see below). We used this method because from 5784 seeds counted from shaken cones (see *Initial seed production*, above), only 8 wings lacked seeds. Thus, considering that seeds normally fall with the wing attached, we regarded wings without seeds to be depredated seeds.

Table 1. Habitat structure in study areas (1000 points sampled per habitat and area). Numbers are percentage of cover. # *Acer granatensis*, *Taxus baccata* and *Pinus nigra* (this latter only in Boleta). *Mainly *Prunus ramburii*, *Berberis hispanica*, *Juniperus communis*, *J. sabina* and *Genista versicolor*. ** Mainly *Salvia oxyodon*, *Vella spinosa*, *Ononis aragonensis*, *Erinacea anthyllis* and *Astragalus granatense*.

	Trevenque		Boleta	
	Wood	Treeline	Wood	Treeline
<i>Pinus sylvestris</i>	21.3	2.5	16.0	4.0
Other trees#	4.7		4.9	0.4
Shrubs (>50 cm heigh)*	56.2	27.1	43.1	42.3
Scrubs (<50 cm heigh)**	16.0	38.2	9.6	8.0
Open areas	26.1	34.4	46.9	46.3
Others	1.7	0.3	0.4	0.4

Seed rain

Seed rain was monitored at Trevenque in 1996 and 1997 by placing four aluminium trays (each 425 cm²) covered with 1.3-cm diameter mesh as a sampling unit at each of 24 stations, each centered around an adult pine (12 in treeline and 12 in woodland). At each station, we considered the following microhabitats: (1) *pine*, under the canopy of Scots pine, (2) *open*, in the open interspaces between woody vegetation and (3) *shrubs*, under the canopy of woody shrubs. Both shrub and open microhabitat sampling units were 5–10 m from the dripline of the focal pine. Trap contents were sampled every 15 days during the dispersal period, and the numbers of filled, aborted, and depredated seeds were noted.

Post-dispersal seed predation

During 1996, we performed an experiment at Trevenque to determine the magnitude of post-dispersal seed predation, its spatial distribution between habitats and microhabitats, and the ability of predators to select filled seeds. We selected 10 sampling stations in each habitat. At each station, we placed two groups of 5 seeds open to all predators, and one group which excluded vertebrate predators by a wire cage of 1.3 cm mesh (control treatment) in each of the microhabitats considered for seed-rain sampling. In each station, microhabitats were 10 to 15 m apart and seed supply points were separated by at least 1 m. The seeds were placed in Petri dishes (9 cm in diameter) fixed to the soil and camouflaged with soil. The seeds used, from a pool collected before dispersal, contained a natural proportion of filled (63%) and

aborted (37%) seeds, and were previously dewinged to prevent losses due to abiotic factors (mainly wind and rain). Sampling stations were checked at 7 and 20 days from the beginning of the experiment, recording losses and the type of seeds that remained after losses (filled or aborted). As a means of minimizing potential abiotic losses, data reported for the analyses of the 1996 experiment are those registered at 7 days (from 5 to 12 April), since cumulative seed losses at this period represented 80.7% of those registered after 20 days, and patterns of seed losses were similar at 7 and 20 days.

Following the same procedure, in 1997 we studied again the magnitude of post-dispersal seed predation and its spatial distribution between habitats and microhabitats. Furthermore, this experiment was also designed to assess two additional aspects of post-dispersal seed predation, (1) the type of predators, and (2) the large-scale spatial variation of predation, by simultaneously performing the experiment in both Trevenque and Boleta. To study the type of predators, the following treatments were established: (1) *Predator exclusion* (control); seeds were excluded from predator activity by a wire cage and the addition of a granular insecticide. (2) *Insects*; seeds were protected by a wire cage without insecticide, allowing access only to insects. (3) *Birds*; seeds were placed in Petri dishes (9 cm in diameter) that were fixed to the top of a stick 30 cm high. Petri dishes were filled with soil, leaving a depression in the middle. Only birds had access to this treatment. (4) *Rodents*: seeds were covered by a wire cage of 20 × 8 cm and 3 cm height opened on the sides, permitting the access to rodents but not birds. Granular insecticide was placed

around the dishes to exclude insects. (5) *All predators*; as in 1996, with no exclusion treatment. Within rodents, the Woodmouse (*Apodemus sylvaticus* L.) is the most common species in the study area, as revealed by field observation and trapping. Common birds of the study areas that depredate pine seeds after dispersal are *Fringilla coelebs* L., *F. montefringilla* L., *Carduelis spinus* L., *C. chloris* L., *Emberiza* spp. and *Alectoris rufa* L.

The insecticide used was chlorpyrifos 5% w/w (CHAS® 5G, Agrodan), used at maximum dosage recommended in agriculture, and wire used in exclusions was 1.3 cm mesh. The effectiveness of exclusions was later assessed during data sampling as revealed by types of remains left by different predators (excrement and seed fragments). We placed 5 filled seeds per replicate, and there was a replicate of each experimental treatment per sample station ($n = 10$). The experiments lasted 7 days, since most seeds are removed within this time span, according to the 1996 experiment (see above). Two trials were conducted at each locality, one month apart (3 to 10 April and 9 to 16 May). However, the first trial of Boleta was seriously damaged by an intense storm, and was therefore excluded from the analyses.

Proportion of seed types on the forest floor

During the two study years in Trevenque, we sampled the number of filled, aborted, and depredated seeds found on the forest floor in late winter after the peak of seed rain by establishing plots (from 2 to 5 m² in surface) in the two habitats. In neither year did it snow or rain during the 8 days prior to sampling, and therefore we considered the sampling period adequate to represent the activity of the different predators. In 1996, snow covered the major part of the surface during the sampling period, and plots (24 plots in the woodland and 24 at the treeline, totalling 628 seeds) were established exclusively over snow cover, a substrate where seeds are readily apparent. In 1997, however, snow cover was lower, and sampling was done either over snow (17 plots in the woodland and 13 at the treeline, totalling 2589 seeds) or in snow-free plots, which were located exclusively under the canopy of pines (20 plots and 1794 seeds counted, without distinction between habitats). The accumulation period of seeds on bare-ground areas was longer than those with snow. However, as seed deposition and predation are likely to happen continuously, we concluded that this difference of time accumulation would not affect

final proportion of seed types. Predation registered in these samples correspond both to certain pre-dispersal predators (Tits and Siskins feeding at the time of cone opening) and to post-dispersal predators.

Data analysis

All observational data were analysed with non-parametric statistics (Zar 1996). For the Crossbill predation analysis, we pooled the contents of the 3 plots placed under each tree, and the analysis was performed on a cone m⁻² basis. Similarly, for seed-rain analysis we pooled the contents of 4 traps placed in each microhabitat for every sample station, and performed the analyses only for filled seeds, again on a seeds m⁻² basis. Post-dispersal seed predation was analysed by a multivariate contingency test, examining the effect of habitat, microhabitat and type of predator on seed losses (considered nominal variable with six levels, from 0 to 5 seeds lost). This technique enables the simultaneous consideration of three factors and first-order interactions. When interactions proved non-significant, they were pooled with the error df to improve the model (Zar 1996). When a factor with more than 2 levels proved significant after the contingency analysis, the differences between levels were established by a non-parametric multiple comparison for balanced (Nemenyi test) or unbalanced (Dunn test) data, prior to applying the Kruskal-Wallis test (Zar 1996).

Results

The initial proportion of filled seeds in healthy cones was $67.2 \pm 1.3\%$ in 1996 and $59.8 \pm 2.5\%$ in 1997, the rest being aborted seeds. The number of filled seeds per healthy cone was 17.2 ± 0.8 in 1996 and 8.1 ± 0.6 in 1997.

Predispersal seed predation

We found 10.9 ± 2.2 attacked cones m⁻² by the Crossbill during 1995, and 1.7 ± 0.9 cones m⁻² in 1996, with no differences between habitats (ns, Mann-Whitney test). Crossbill destroyed almost all cones they attacked, since only 6.2% of attacked cones fell intact to the soil in 1995 and no cones were found intact in 1996. Furthermore, cones collected in sample plots during November and December contained only 0.30 ± 0.15 filled seeds per cone in 1995, and no filled seeds in 1996. Therefore, we estimated seed

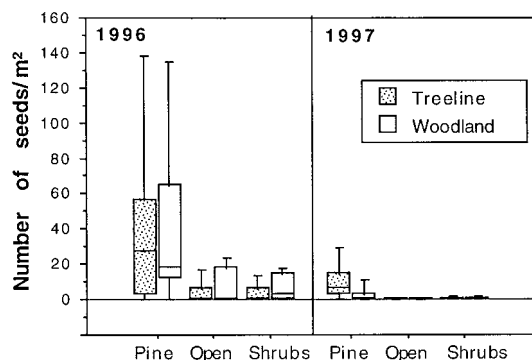


Figure 1. Density of seed rain in different microhabitats, considering only filled seeds. For each habitat (treeline or woodland), there were between-microhabitats differences in both years. All comparisons were performed with Kruskal–Wallis test, $H = 10.22$ to 29.62 , $df = 2$, p -values from 0.006 to <0.0001 .

predation by each year by multiplying the number of cones collected in 1 m^2 times the average number of filled seeds borne by cones, giving 188.2 ± 37.8 filled seeds m^{-2} that were consumed by crossbills in 1995 and 13.8 ± 7.7 in 1996.

Of those seeds that escaped Crossbill predation, 16.2% in 1996 and 51.2% in 1997 were depredated by Tits and Siskins before dispersal. In both years, the proportion of filled vs aborted seeds collected in seed traps changed with respect to that found in cones (1996: 62.7% filled and 37.2% aborted seeds in seed traps, 67.2 and 32.8 in cones; 1997: 27.4 filled and 72.6 aborted in seed traps, 59.8 and 40.2 in cones) although differences were significant only in 1997 (1996: $\chi^2 = 2.96$, $df = 1$, $p < 0.1$; 1997: $\chi^2 = 43.07$, $df = 1$, $p < 0.0001$).

Seed rain

Most filled seeds were dispersed directly beneath the canopy of mother plants in both years and both habitats (Figure 1), whereas a low and similar number of seeds arrived in open and shrub microhabitats. On the other hand, seed rain was, overall, significantly higher in 1996 than 1997 (18.9 ± 4.9 seeds m^{-2} vs 2.3 ± 0.7 seeds m^{-2} , respectively, Mann–Whitney U-test, $Z = 4.88$, $n = 140$, $p < 0.0001$).

Post-dispersal seed predation

In the 1996 experiment, the percentage of seeds removed in the all-predator treatment was much higher (61.2%, habitats and microhabitats pooled) than in the predator-exclusion treatment (12.2%), and this

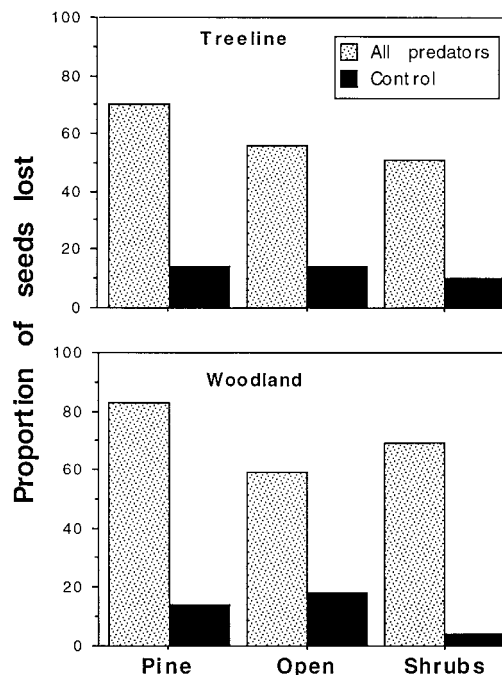


Figure 2. Seed losses in 1996 at Trevenque in the experiment of post-dispersal seed predation. Microhabitats are Pine, Open and Shrub.

Table 2. Effect of different factors on seed losses at Trevenque in the 1996 experiment of post-dispersal seed predation. Treatment refers to the type of predator.

Source	df	Wald χ^2	p
Habitat	5	4.39	0.4950
Microhabitat	10	12.70	0.2407
Treatment	5	11.78	0.0379
Model	20	108.12	<0.0001

between-treatment difference was significant (Table 2, Figure 2). However, neither the habitat nor the microhabitat effects were significant (Table 2). On the other hand, predators actively selected filled seeds and rejected aborted ones, as the proportion of filled vs aborted seeds after predation (44.8 and 55.2%, respectively) differed significantly from the initial proportion (63 and 37%, respectively; $\chi^2 = 21.10$, $df = 1$, $p < 0.001$).

In 1997, values of seed removal for the all-predator treatment ranged from 80% (trial 1 of Trevenque, values of habitat and microhabitat pooled) to 96% (Boleta). Overall, there were no significant between-trials

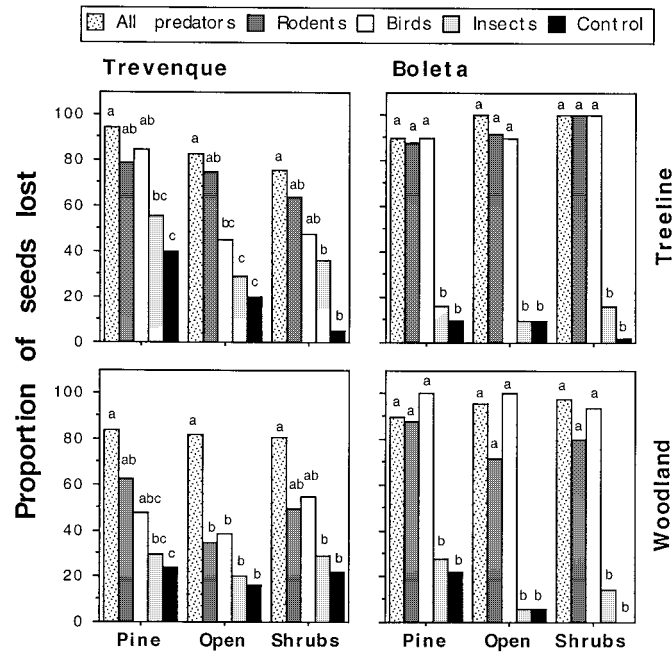


Figure 3. Seed losses registered in 1997 in experiments of post-dispersal seed predation. In Trevenque, we have pooled data from trial 1 and 2 for simplicity (sample size from 16 to 20). In Boleta we used only data from trial 2 ($n = 10$). Posteriori comparisons within sources of removal have been performed for each microhabitat with either Nemenyi (for balanced data) or Dunn (for unbalanced data) test. Different letters indicate differences at p -level of 0.05. Microhabitats are Pine, Open and Shrub.

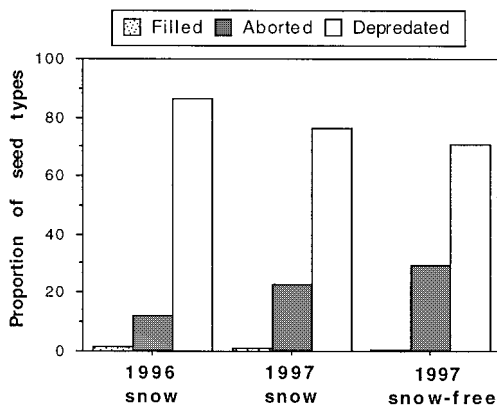


Figure 4. Proportion of seed types found on the forest floor considering snow-covered areas (both years) and snow-free areas located under the canopy of pines (1997 only).

differences in seed predation at Trevenque (Mann–Whitney U-test, $Z = 0.36$, $n = 584$, $p > 0.05$). In the two localities, the only factor accounting for differences was the type of predator; neither habitat nor microhabitat had a significant effect (Table 3). Rodents and birds were the main seed predators, especially in Boleta, whereas the insect seed predation was negligible (Figure 3).

Proportion of seed types on the forest floor

Most seeds found in samples over snow or in snow-free plots had been depredated (Figure 4), whereas a small proportion (from 0.2 to 0.6%) were filled. On the other hand, the percentage of filled, aborted or depredated seeds found in 1997 in snow-free plots did not differ from that found in plots with snow (Mann–Whitney U-test, $U_{20,30} = 335.50$, 339.00 and 357.50 , respectively; $p > 0.05$ in all cases), indicating that predators found filled seeds irrespective of the substratum. In addition, there were no within-year differences in the percentage of filled seeds found in the two habitats (woodland vs treeline, Mann–Whitney U-test, $U_{24,24} = 289.0$ for 1996; $U_{17,13} = 117.5$ for 1997; $p > 0.05$ in both cases).

Discussion

Seed rain

The values for seed rain calculated in this study are considerably lower than those found in large homogeneous stands in the main distribution area of the species ($10 \text{ seeds m}^{-2} \text{ year}$ vs 100 seeds reported in

Table 3. Effects of different factors on seed losses at Trevenque and Boleta in the 1997 experiment of post-dispersal seed predation. Treatment refers to the type of predator.

Source	df	Trevenque				Boleta	
		Trial 1		Trial 2		Wald χ^2	<i>p</i>
		Wald χ^2	<i>p</i>	Wald χ^2	<i>p</i>		
Habitat	5	9.20	0.1014	8.50	0.1307	5.35	0.3746
Microhabitat	10	14.50	0.1516	16.23	0.0933	9.36	0.4985
Treatment	20	74.78	<0.0001	80.15	<0.0001	82.36	<0.0001
Model	35	142.31	<0.0001	154.40	<0.0001	345.84	<0.0001

Koski 1991), perhaps due in part to low tree density (Table 1). In addition, most seeds fell directly under the canopy of the focal pine, whereas only a very small proportion reached other microhabitats (Figure 1). Thus, the distribution of seeds appears to be more affected by distance from a seed source than by the physical structure of the microhabitat (e.g., Russell & Schupp 1998), implying that the availability of seeds to colonize new areas is limited by both the low production and the dispersion pattern.

Effects of seed predators on seed number

Scots pine lost seeds to several types of predators during pre-dispersal as well as post-dispersal periods. Firstly, cones were consumed during the maturation period by the Crossbill, which is an important pre-dispersal mortality factor of many other species of conifers (e.g., Benkman 1993). Considering both the number of seeds ingested by the Crossbill and the values for seed rain in our study years, we estimated that the Crossbill depredated more than 80% of filled seeds each year during seed ripening (seeds consumed / [seeds consumed + seed rain]). In addition, some species of Tits and Siskins depredated up to 51% of the seeds in newly-opened cones surviving the Crossbill attack. This implies that predispersal seed loss is dramatic, greatly decreasing the number of seeds available for dispersal.

After dispersal, Scots pine still lost, in our study sites, a large number of seeds due to predators (Figures 2 and 3). This post-dispersal seed predation ranged from 61% in 1996 (when we used a mixture of filled and aborted seeds similar to the natural proportion) to 96% in 1997 (the year in which we used only filled seeds), values that are equivalent to or higher than those reported previously for vertebrate predation in other coniferous species (Gashwiler 1967, 1970;

Radvanyi 1970; Acherar et al. 1984; Johnson & Fryer 1996). Furthermore, both pre- and post-dispersal seed predators actively selected filled seeds (see VanderWall & Balda 1977; Senar 1981; Jordano 1990; for similar results), increasing the deleterious effect of predators on Scots pine reproduction. As a result, 60 to 67% of filled seeds in cones was reduced to only 0.2 to 0.6% of filled seeds on the ground after the different predation events (Figure 4).

Spatio-temporal constancy in seed predation

The proportion of seeds lost to each post-dispersal seed predator was similar in the different microhabitats (Tables 2 and 3), and rodents and birds appeared to be the main seed predators (Figure 3). Other authors have reported that small rodents and granivorous birds tend to concentrate their activity under or near shrubs, where they find protection from predators (Lima 1985; Simonetti 1989; Hulme 1993) thereby augmenting seed predation in those microhabitats (e.g., Bartholomew 1970; Herrera 1984; Hulme 1997; Manson & Stiles 1998). However, in our study areas, shrub cover was high in all cases (>50%, see Table 1) and is homogeneously mixed with the remaining microhabitats, creating a matrix where seed predators could easily find shelter. This between-microhabitat similarity in high seed-predation intensity has two main consequences. Firstly, the microhabitat pattern of seeds from the seed rain translates to the next regeneration stage, and therefore most of the surviving seeds continue to be found under the focal pine. Secondly, there are no safe microhabitats for seeds because they have the same probability of being consumed by predators, irrespective of the spatial location.

At the larger spatial scales of habitat (treeline vs woodland) and locality (Trevenque vs Boleta), seed predation pressure was also quite constant. The main

consequence of this lack of differences is that both forest regeneration within the stand, as well as the possibility of colonization of the zones above the tree-line, are severely limited, and this applies to both pine populations considered. In addition, seed-predation pressure showed similar levels of intensity in different years irrespective of the magnitude of the seed crop. This spatio-temporal constancy in seed predation could result because the pressures of post-dispersal seed predators were very strong, and either rodents or birds proved capable of depredating most of the Scots pine seeds (Figure 3). Consequently, the probability of seeds eventually escaping predation in years of high seed production or of low population levels of some species of predators appear to be very low. Therefore, these two forests of Andalusian Scots pine are highly affected by seed predation.

Consequences of seed predation for Scots pine forest regeneration

Some features of this species reinforce the impact of seed predators on its population regeneration in Mediterranean environments, which are characterized by summer drought, high herbivory pressure, and fire: (1) Scots pine is not able to reproduce vegetatively, being totally dependent on sexual regeneration (Zasada et al. 1992); (2) Seed production in those relict, scattered forests is low, which may make it difficult to satiate predators, increasing the negative effect of predators (Nilsson & Wästljung 1987; Kelly 1994); (3) Since most filled seeds fall directly beneath the canopy of the mother plant, the possibility of escaping in space is strongly limited, and the probability of recolonizing new potentially suitable areas is very low; (4) Seed predation was similarly intense irrespective of the temporal and spatial scale considered, implying that the few seeds dispersed far away probably do not find safe sites either; (5) Scots pine seeds are not dormant and therefore there is no permanent seed bank to buffer the high seed predation; and (6) seedling survival of Scots pine in Mediterranean environments is severely reduced by the dry season (Hódar et al. 1998, see also Arista 1994, García et al. 1999, for other coniferous species in Mediterranean mountains), implying that Scots pine forest regeneration relies heavily on a high number of seeds available to germinate.

All these points suggest that predation of Scots pine seeds must be considered a main demographic bottle-neck severely reducing the recruitment proba-

bility. This seed predation, together with other factors, causes the expansion of these small isolated fragments of forest, as well as the natural regeneration within the stands, to be severely constrained in Mediterranean environments.

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