PLANT ANIMAL INTERACTION

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Rodent seed predation promotes differential recruitment among bird-dispersed trees in temperate secondary forests

Abstract We investigated the role of seed predation by rodents in the recruitment of the fleshy-fruited trees *Taxus baccata*, *Ilex aquifolium* and *Crataegus monogyna* in temperate secondary forests in NW Spain. We measured the densities of dispersed seeds, early emerged seedlings, established recruits and adults, at four sites over a period of 2 years. Seed predation among species was compared by seed removal experiments and analysis of rodent larder-hoards. The three species differed markedly in local regeneration patterns. The rank order in the seed rain following decreasing seed density was *Ilex*, *Taxus* and *Crataegus*. However, *Crataegus* established 3.3 times more seedlings than *Taxus*. For all species, there was a positive linear relationship between the density of emerged seedlings and seed density, suggesting that recruitment was seed- rather than microsite-limited. A consistent pattern of seed selection among species was exerted by rodents, which preferred *Taxus* and, secondarily, *Ilex* seeds to *Crataegus* seeds. Predation ranking was the inverse of that of seed protection against predators, measured as the mass of woody coat per mass unit of the edible fraction. Recruitment potential, evaluated as the ratio of seedlings to seeds, was negatively related to seed predation, with the rank order *Crataegus* > *Ilex* > *Taxus*. The selective early recruitment limitation exerted by predation may have a demographic effect in the long term, as judged by the positive relationship between early seedling emergence and the density of established recruits. By modulating the pre-emptive competition for seed safe sites, rodents may preclude the progressive exclusion of species that produce low numbers of seeds (i.e. *Crataegus*) by those dominant in seed number (i.e. *Ilex*, *Taxus*), or at least foster the evenness for site occupation among seedlings of different species.

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Introduction

Post-dispersal seed predation is a major cause of reproductive losses in many plants, with the magnitude of predation usually differing among co-occurring species (Janzen 1971; Crawley 1992; Hulme 1998). This differential predator attack is sometimes related to extrinsic-to-seed, environmental factors, e.g. the taxonomic identity of the predator or the structure of the habitat where a seed is dispersed (Myster and Pickett 1993; Manson and Stiles 1998; Hulme 1997; Rey et al. 2002). More frequently, specific variation in the seed predation rate depends on plant intrinsic factors, such as dispersal phenology (Whelan et al. 1991; Myster and Pickett 1993), seed density (Greenwood 1985; Hulme 1994; but see Hulme and Hunt 1999) and, more importantly, seed traits, among others size (Hulme 1994; Reader 1997; Blate et al. 1998; Moles et al. 2003), nutritional content (Kerley and Erasmus 1991; Kollmann et al. 1998), chemical defence (Blate et al. 1998; Kollmann et al. 1998) and mechanical defence characteristics such as coat thickness (Hulme 1997; Blate et al. 1998; Rey et al. 2002; Moles et al. 2003). When heritable, these traits may be modulated both within and among species by evolutionary selective pressures exerted by predators (Blate et al. 1998; Grubb et al. 1998; Moles et al. 2003).

Post-dispersal seed predation is supposed to play a pivotal role in plant population dynamics, when seed losses lead to significant reductions in the number of established recruits (e.g. Crawley and Long 1995; Hulme 1996a; Maron and Simms 1997). This only happens

when plant recruitment depends more on the absolute number of seeds reaching the available safe sites (seed limitation) than on the number of safe sites (microsite limitation, Andersen 1989; Crawley 1992; Hulme 1998; Turnbull et al. 2000). When this demographic effect is exerted on different species, it drives relative abundance patterns within local communities (e.g. Reader 1993; Hofmann et al. 1995; Edwards and Crawley 1999; Clarke and Kerrigan 2002). Thus, by modulating the recruitment potential of co-occurring species, seed predation may have an ultimate effect on coexistence and local diversity of plant species (Hulme 1996b, 1998; Wright 2002). These differential demographic effects have been demonstrated in annual-dominated arid communities (Brown and Heske 1990) as well as in mesic grasslands (Hofmann et al. 1995; Edwards and Crawley 1999; Howe and Brown 1999), where seed predators favour the regeneration of small-seeded species by selectively killing large-seeded species, which are also often superior competitors relative to small-seeded species. In addition, predators may reduce the encounter among potential competitor plants by determining what seed species, among several dispersed to the same safe site, actually occupies the site (Hulme 1996b, 1998; Wright 2002). Such modulation of pre-emptive competition among co-dispersed seeds has the power to enhance species coexistence even with low availability of safe sites for establishment (Hulme 1996b, 1998; Edwards and Crawley 1999).

Despite the aforementioned findings, the role of post-dispersal seed predation as a major mechanism controlling for specific recruitment differences among woody plants remains controversial. In fact, many woody species show traits, such as vegetative reproduction, that make their population dynamics seldom responsive to seed predation, and even when their regeneration mainly depends on seeds, they may buffer predation by masting (Crawley 1992; Crawley and Long 1995; but see De Steven 1991a, b; Clarke and Kerrigan 2002). The fleshy-fruited, vertebrate-dispersed species that dominate European temperate secondary forests offer an excellent study system for analysing the comparative recruitment effects of post-dispersal predation on woody communities, given plant life-history traits as well as the strong seed attack caused by a small, rodent-dominated predatory guild (e.g. Hulme 1996a; Kollmann et al. 1998; Hulme and Borelli 1999). Furthermore, the spatial patterns of dispersed seeds of these species frequently overlap and the resulting multi-specific seed rain is the raw material for pre-emptive competition among co-occurring seeds (Schupp et al. 2002).

In this study, we assessed whether seed predation by rodents drives the recruitment differences among fleshy-fruited trees in temperate secondary forests in NW Spain. Once proven that tree regeneration is mainly determined by seed availability, we searched for negative covariation between seed predation and recruitment potential across the regional landscape. The specific aims of the study were: (1) to measure the regeneration ability of different tree species in terms of availability of dispersed seeds and abundance of established seedlings; (2) to determine the extent of seed- compared with microsite-limitation in these species, in order to evaluate their susceptibility to seed predation in demographical terms; (3) to compare seed predation attack among species differing in seed characteristics related to mechanical defence; (4) to evaluate the differences in recruitment potential as a function of selective seed predation.

Materials and methods

Study sites and species

This study was carried out during 2001–2003, in secondary-growth forests in the Cantabrian mountain range (Asturias, NW Spain). The forests are mainly composed of fleshy-fruited, bird-dispersed trees (holly *Ilex aquifolium*, hawthorn *Crataegus monogyna*, yew *Taxus baccata*, rowans *Sorbus* sp.) together with hazel *Corylus avellana*. They occur as isolated stands in a pasture matrix or as fringe patches between pasture and mature deciduous forests (beech *Fagus sylvatica*). Sampling was carried out at four different sites, named Aramo, Peña Mayor, Sueve and Teixeu, located on northern-oriented slopes in mid-altitude areas (680–1,400 m a.s.l.) at distances of 5–50 km from each other; see García and Obeso (2003) for a comprehensive description of localities. Sites were chosen to provide a good representation of well-preserved secondary forests containing all the aforementioned species on a regional extent.

Plant species

This study focused on three species: *Taxus baccata* L. (Taxaceae, hereafter referred to as *Taxus*), *Ilex aquifolium* L. (Aquifoliaceae, hereafter *Ilex*) and *Crataegus monogyna* L. (Rosaceae, hereafter *Crataegus*). The choice of species was based on the following criteria:

1. They are the most abundant small trees present, accounting for 44–73% of woody canopy cover in all study sites.
2. They are dispersed by a shared guild of avian frugivores (almost exclusively thrushes *Turdus viscivorus*, *T. iliacus*, *T. philomelos* and *T. merula*) whose foraging activity and post-foraging movements frequently determine a multi-specific seed rain (Obeso and Fernández-Calvo 2002; Martínez 2004).
3. Their seeds strongly differ in the degree of mechanical defence against post-dispersal predators. All three species have a hard lignified coat (testa in *Taxus*, pyrene in *Ilex* and endocarp in *Crataegus*) surrounding the embryo-plus-endosperm fraction (EEF, see Kollmann et al. 1998). We considered the ratio between dry mass of seed coat and EEF as an estimate of the relative protection against post-dispersal

seed predators (Moles et al. 2003). That is, for similar sizes, seeds with a proportionally thicker coat (higher Coat:EEF value) would be better defended, and would be less profitable for predators (in terms of higher seed husking cost, Hulme 1993) than those with an EEF surrounded by a thinner coat. These species show a sharp gradient in the Coat:EEF ratio as follows: *Crataegus > Ilex > Taxus* (see seed characteristics in Table 1). Conversely, they do not represent strong gradients of seed mass, EEF nutrient content or EEF toxicity (compared with the findings of other studies involving fleshy-fruited woody plants, e.g. Kollmann et al. 1998; Rey et al. 2002).

Sampling stations design

At each site, we established 50 permanent sampling stations, isolated from one another by at least 5 m, equally distributed and randomly positioned in five microhabitats that are likely to represent most of the natural variation in seed rain of the studied species: under female yew, under male yew, under female holly, under hawthorn and open interspace among tree canopies. These microhabitats accounted for 68–84% of the total cover in study sites (García and Obeso 2003; García et al. 2005).

Demographic variables of tree species

Seed availability in seed rain

We established one permanent 50×50 cm^2 quadrat per station in which we collected all fallen fruits and bird-dispersed seeds in successive fortnightly surveys during the dispersal season (September to January) in 2001–2002 and 2002–2003. Fruits were opened in the laboratory and all seeds were counted to calculate the density of seeds per sampling station (units = cumulative number of seeds m^{-2}). Despite the sampling being carried out in autumn, a season of low rodent predation activity (see also Hansson 1985; Kollmann et al. 1998 for other temperate areas), this method may underestimate

actual seed rain, due to undetected seed removal from sampled surfaces by predators or abiotic factors. To avoid removal-related bias we also counted the seeds showing signs of predation (open husks, teeth marks) as a part of the dispersed seed pool (see also Alcántara et al. 2000a; García and Obeso 2003; for similar procedures). In addition, to validate the use of sampling quadrats for evaluating seed rain density we set up two seed traps per sampling station in Peña Mayor, during 2001–2002. The traps consisted of $50 \times 25 \times 5$ cm^3 plastic trays covered with a 1.3-cm diameter mesh, and were nailed to the ground adjacent to the seed quadrats. Their contents were collected at the same time as quadrat surveys. Seed densities were similar in traps and quadrats, for *Taxus* and *Crataegus* (Wilcoxon paired test: $Z \leq 1.30$, $P > 0.18$, $n = 50$; for both species). However, seed density for *Ilex* was on average 14% less in quadrats than in traps (Wilcoxon paired test: $Z = 4.51$, $P < 0.001$, $n = 50$), making the estimate for this species conservative. Given the negligible or low loss of seeds from quadrats by predators and the ability of quadrat sampling to cover for the small-scale variability in seed dispersal (García et al. 2005), we considered that this method provided a reliable estimate of seed rain density for comparative purposes.

Seed viability

The species under study may produce variable proportions of sterile, empty seeds, which are equally dispersed by frugivores. We thus estimated the proportion of viable seeds for the 2001 and 2002 seed crops of each species, by dissecting the seeds of 20–30 fruits collected from each of 10–15 plants in the middle of their respective ripening seasons. Viable, sound seeds had endosperm completely filling the seed coat (see also Kollmann et al. 1998). Values for each species, site and year were obtained from averaging among trees.

Seedling recruitment

We established a 50×50 cm^2 quadrat contiguous to the seed rain quadrat at each station where we surveyed seedling emergence. Quadrats were revisited fortnightly

Table 1 Seed characteristics of the species under study (EEF: embryo-plus-endosperm fraction)

	Taxus baccata	*Ilex aquifolium*	*Crataegus monogyna*
Seed dry mass (mg)	66.3 ± 4.8 (111)	28.2 ± 0.2 (2248)	87.1 ± 4.0 (41)
EEF dry mass (mg)	24.6 ± 0.4 (108)	8.4 ± 0.2 (764)	13.2 ± 0.5 (41)
Coat dry mass (mg)	41.7 ± 4.9 (108)	23.5 ± 0.2 (1461)	73.8 ± 3.6 (41)
Coat:EEF	1.69	2.79	5.59
Coat thickness (mm)	0.57 ± 0.07 (10)	0.61 ± 0.10 (10)	1.57 ± 0.30 (10)
Nitrogen in EEF (%)	2.87 ± 0.08 (28)	4.05 ± 0.31 (40)	8.23 ± 0.22 (41)
Toxins	Taxin and cyanogenic glycosides (coat)	Not detected	Not detected

Dry mass was obtained after 48 h in 70°C. The Coat:EEF ratio is considered to be an estimate of seed protection against predation. Coat thickness was measured at the thickest part of the largest seed transverse section. Nitrogen content (percentage of mass) was obtained using a standard automated CNH procedure (PE 2400 Series II, CNHS/O). Information on seed toxicity was taken from Barnea et al. (1993). Means are given $\pm$ 1SE. The number of seeds used for each measurement is shown in parentheses

between May and September of 2002 and 2003 and the presence of emerged seedlings of all three species was recorded (distinguished on the basis of the presence of cotyledons and stem colour, see Peterken and Lloyd 1967; Thomas and Polwart 2003). Each seedling was individually distinguished by positioning it within the quadrat with x, y coordinates (two-dimensional accuracy ≤ 1 cm), and was mapped on a drawing template to discern among seedlings emerging simultaneously from the same point (sharing the same x, y coordinates). The fate (survival) of each marked seedling was followed in successive surveys. We estimated the density of first-year seedlings as the cumulative number of emerged seedlings per square metre at the end of the season, for each station and year. In 2003, we also recorded the presence and survival of 2 year and >2 year (to ≤ 10 cm tall) seedlings, distinguishing age by size, number of leaves and stem colour. Adult densities were estimated in September 2001, by counting the number of trees of each species in ten to fifteen 20×20 m^2 plots randomly distributed through the study sites (García and Obeso 2003; García et al. 2005).

Recruitment limitation and recruitment potential

The importance of seed limitation compared with microsite limitation on seedling recruitment was evaluated separately for each species by analysing the spatial covariation among the densities of dispersed seeds and early emerged seedlings, using the sampling stations as replicates and the average between years for each station. We assumed that a significant positive relationship among seed density and first-year seedling density would imply that seed limitation is stronger than microsite limitation (an increase in seed input would lead to enhanced seedling establishment, Andersen 1989; Eriksson and Ehrlén 1992; De Steven and Wright 2002; Müller-Landau et al. 2002). Absence of a positive relationship would suggest that establishment limitation is more important than seed limitation in determining the levels of seedling recruitment (at least in the absence of compensation by density-dependent losses, Andersen 1989; De Steven and Wright 2002).

For each species and site, we evaluated recruitment potential (RP) as the ratio of first-year emerged seedlings to viable dispersed seeds (i.e., RP = first-year seedling density/(seed density in fallen fruits + seed density in bird-generated seed rain) $\times$ seed viability). Recruitment potential was calculated from the average values among sampling stations per microhabitat, with seed viability being considered to be similar among microhabitats within sites. This spatial scale of analysis allowed us to avoid possible mismatches caused by some sampling stations containing seedlings but not receiving seeds. On the other hand, in order to compensate for any possible bias due to the effects of delayed germination when assigning specific seedling cohorts to specific seed rains, we used the average values for 2001–2002 for seed rain and 2002–2003 for

emerged seedlings (see Clark et al. 1998; De Steven and Wright 2002; for similar procedures). The study species have short-lived (1–3 years) seed banks (Kollmann 2000; Thomas and Polwart 2003; Arrieta and Suárez 2004), and thus, we considered the proportion of emerged seedlings corresponding to the seed rain from earlier years to be low. Fruit crops and seed rain prior to the sampling years were similar in magnitude for all species, the overestimation of recruitment potential due to lower seed rain being highly unlikely.

Seed predation estimates

Post-dispersal removal experiments

Seed predation was studied by recording removal of seeds of the three species offered simultaneously to predators in the field. We placed eight seed depots composed of plastic mesh (1.5-mm pore) triangles (6-cm side), in each sampling station, by nailing them to the ground at a distance of 50 cm from each other. One seed of each of the three target species was glued to a different vertex of the triangle, using a low odour, rainproof thermoplastic glue (see Herrera et al. 1994; Alcántara et al. 2000b; for similar methods). The triangles were arranged in two parallel lines passing through the seed rain quadrat, to ensure a uniform, low density of natural seeds around the seed depots. Depots were monitored after 2 and 4 weeks, and removed after the second monitoring. Seeds were glued firmly to the plastic triangles to prevent removal by wind and rain. We did not record trampling or the digging-up of triangles by animals during experiments. Thus, we considered that a seed had been consumed by a rodent if: (1) it was missing from the plastic mesh; or (2) it was still on the mesh but was gnawed and empty. We considered that seed attack was almost exclusively attributable to forest rodents (woodmouse *Apodemus sylvaticus*, yellow-necked mouse *A. flavicollis* and bank vole *Clethrionomys glareolus*) for the following reasons: (1) we frequently identified rodent predation (by gnaw marks on the seed coat) and visits by rodents to the triangles (by the presence of faeces); (2) consumption of seeds by birds on the ground is highly infrequent in these sites (after bird censuses and field observations we have only recorded occasional predation on *Taxus* by bullfinches (*Phyrrula phyrrula*), which eat seeds before complete aril maturation, and by marsh tits (*Parus palustris*) and nuthatches (*Sitta europaea*), which eat seeds directly from trees) and we did not find sign of either predation nor faeces attributable to granivorous birds; (3) seed removal by ants was precluded by the small size and scarcity of granivorous ants present in the area in that season (see also Hulme 1997; Rey et al. 2002). Removal experiments were performed at all sites between late January and early March in 2002 and 2003, i.e. after the end of seed dispersal.

Seeds in rodent trash heaps

Additional information on seed predation was obtained by the study of seed remains of rodent trash heaps made at the entrance of their burrows, usually at the bottom of old trees (Obeso 1998). In late March 2002, we collected the seeds in 25 heaps in Peña Mayor and 10 hoards in Sueve, discarding old seeds from previous crops (easily distinguishable by external colour and texture). In the laboratory, we recorded the number of seeds of each species under study, distinguishing between eaten (gnawed) and intact seeds. We corrected the number of eaten seeds taking into account that rodents sometimes produce two seed fragments after opening a single seed. Intact seeds were dissected to check for soundness. Trash heap observations also corroborated that seed removal from the experiment was equivalent to predation and not to secondary dispersal, since no significant seedling establishment was observed around the heaps (larder hoards are deep in the burrow, from which successful establishment of seedlings is also unlikely, see also Alcántara et al. 2000b).

Statistical analysis

Differences among species in seed rain, seed viability, first-year seedling density and adult tree density were analysed by using generalized linear models (GLM, Crawley 1993) incorporating normal, Poisson or binomial error distributions when necessary. We evaluated seed limitation by means of the relationship among seed and seedling densities, and after accounting for the potential effects of both the locality and the microhabitat on the variance of both densities. For this, we performed GLMs for each species considering the effects of locality, microhabitat and their interaction on the density of dispersed seeds and the density of emerged seedlings as dependent variables. The error terms of these variables were considered to follow Poisson distributions. The residuals derived from these models were then used to check the covariation among seed density and seedling density, by regression analyses. The *P*-values for these regression tests were calculated by using the degrees of freedom for the error term of previous GLM fitting locality, microhabitat, and their interaction, to prevent spurious significance derived from the use of residuals. We excluded those stations with zero seed density because where there are no seeds there can be no subsequent seedlings, regardless of establishment conditions (Müller-Landau et al. 2002).

Seed predation rate (proportion of seed removal) obtained in experiments was considered to have a binomial error distribution and was compared among species, localities and years. Seed preference by rodents was also analysed by comparing the proportion of seeds of each species in the seed rain with those found in rodent trash heaps using one-tailed χ^2 -tests, and assuming a positive preference for those species showing a signif-

icantly higher occurrence in heaps than in seed rain. The proportion of attacked seeds in rodent heaps was compared among species and localities, considering individual heaps as replicates.

The relationship between seed predation magnitude and recruitment potential was evaluated by plotting the average values of experimental seed predation for each species and locality against the corresponding values of recruitment potential. The regression between the residuals of both variables, after GLM considering species and locality as main factors, enabled us to evaluate possible effects of seed predation on recruitment potential independently of species and site effects. Recruitment potential was considered to have a normal error distribution after transformation by using the formula $p' = 1/2 \ [\arcsin\sqrt{(X/n+1)} + \arcsin\sqrt{(X+1/n+1)}]$ (Zar 1996). For these models, we also calculated *P*-values by using the degrees of freedom for the error term of previous GLMs in which species, locality, and their interaction were fitted (df = 48). Given that average values per species and site did not provide enough replicates for the analysis, we considered the values for each microhabitat within site as replicates (averaging among stations within microhabitat to give five values per species and site). A similar procedure was used to evaluate the relationship among the density of first-year seedlings and the density of > 1 year recruited seedlings after removing the effects of species and site. Means are shown along with one standard error throughout text and tables.

Results

Seed rain, seed viability and seedling establishment

The three study species differed in their relative contribution to the overall seed rain ($F_{2,597} = 67.6$, $P < 0.0001$, Table 2). In most sites and years, *Ilex* showed the most dense seed rain (314.2 ± 25.6 seeds m^{-2}), with a high proportion of bird-dispersed seeds. *Taxus* showed intermediate values of seed density (136.2 ± 13.2 seeds m^{-2}) whereas *Crataegus* showed the lowest values of seed density and low proportions of seeds dispersed by birds (55.4 ± 6.9 seeds m^{-2}, Table 2). Seed viability also varied among species ($F_{2,290} = 163.2$, $P < 0.0001$, Table 2), because *Ilex* fruits always contained a variable proportion of empty pyrenes. Differences in seed viability were insufficient to offset initial differences in seed density. Species also differed significantly in the density of emerged first-year seedlings ($F_{2,597} = 72.9$, $P < 0.0001$, Table 2), but with a pattern that differed from that of seed rain. Although *Ilex* seedlings were dominant, the density of *Crataegus* seedlings was, on average, 3.3 times higher than the density of *Taxus* seedlings. The density of adult trees differed significantly among species ($F_{2,147} = 49.9$, $P < 0.0001$, Table 2), since *Ilex* trees were much more abundant than the remaining species in all sites. *Crataegus* and *Taxus* adult densities

Table 2 Values (mean ± SE) of the density of seed rain, distinguishing seeds from fruits fallen to the ground and seeds dispersed by birds ($n = 50$ sampling quadrats per site), the proportion of viable (sound) seeds per tree ($n = 10$–15 trees per site; 20–30 fruits per tree) and the density of first-year emerged seedlings ($n = 50$ sampling quadrats per site), for different tree species, localities and years (period from September to August through consecutive years). The local number (mean ± SE) of adult trees per ha, estimated in 2001, is also shown

	Aramo		Peña mayor		Sueve		Teixeu	
	2001–2002	2002–2003	2001–2002	2002–2003	2001–2002	2002–2003	2001–2002	2002–2003
Taxus baccata								
Seeds in fruits m^{-2}	0.3 ± 0.3	12.8 ± 8.7	2.2 ± 0.8	4.8 ± 5.3	5.3 ± 1.8	8.9 ± 2.5	5.0 ± 2.9	4.6 ± 3.1
Dispersed seeds m^{-2}	120.1 ± 36.1	114.3 ± 31.6	46.8 ± 10.9	70.5 ± 16.0	245.3 ± 49.2	263.7 ± 56.5	78.2 ± 17.8	104.8 ± 29.6
Seed viability	0.99 ± 0.01	0.98 ± 0.01	0.98 ± 0.09	0.99 ± 0.01	0.99 ± 0.01	0.99 ± 0.00	0.99 ± 0.01	0.99 ± 0.00
First-year seedlings m^{-2}	0.6 ± 0.2	0.2 ± 0.1	1.1 ± 0.4	0.6 ± 0.2	4.2 ± 0.9	1.4 ± 0.4	0.9 ± 0.3	0.2 ± 0.1
Trees ha^{-1}	33.3 ± 9.9		35.0 ± 7.2		67.5 ± 17.9		40.0 ± 10.0	
Ilex aquifolium								
Seeds in fruits m^{-2}	13.0 ± 5.9	155.4 ± 57.9	44.2 ± 10.3	133.7 ± 28.3	32.8 ± 11.7	26.6 ± 11.3	33.4 ± 12.2	71.4 ± 24.1
Dispersed seeds m^{-2}	130.8 ± 27.3	410.0 ± 103.1	222.8 ± 41.9	283.9 ± 76.4	216.9 ± 29.4	115.4 ± 24.8	253.9 ± 62.6	372.2 ± 95.7
Seed viability	0.55 ± 0.04	0.69 ± 0.05	0.78 ± 0.02	0.85 ± 0.03	0.80 ± 0.03	0.71 ± 0.06	0.75 ± 0.06	0.81 ± 0.03
First-year seedlings m^{-2}	12.1 ± 2.7	4.2 ± 1.3	20.8 ± 3.9	8.6 ± 1.8	4.1 ± 1.2	2.7 ± 0.6	10.2 ± 2.3	7.3 ± 1.8
Trees ha^{-1}	280.0 ± 94.8		301.7 ± 49.8		247.5 ± 40.6		125.0 ± 22.9	
Crataegus monogyna								
Seeds in fruits m^{-2}	51.2 ± 19.5	78.5 ± 36.8	25.9 ± 5.9	23.2 ± 5.5	12.6 ± 3.9	6.4 ± 2.9	24.7 ± 6.7	13.4 ± 5.6
Dispersed seeds m^{-2}	31.1 ± 6.8	20.1 ± 6.9	35.7 ± 5.7	29.8 ± 5.4	26.1 ± 3.9	15.8 ± 2.9	36.2 ± 8.2	14.2 ± 3.9
Seed viability	0.81 ± 0.06	0.96 ± 0.03	0.95 ± 0.02	0.99 ± 0.01	0.83 ± 0.06	0.99 ± 0.01	0.87 ± 0.05	0.92 ± 0.03
First-year seedlings m^{-2}	0.7 ± 0.4	2.9 ± 0.9	5.4 ± 1.1	10.1 ± 2.2	0.2 ± 0.1	1.9 ± 0.9	3.3 ± 0.8	5.4 ± 1.4
Trees ha^{-1}	18.3 ± 5.7		96.7 ± 13.8		70.0 ± 11.7		62.5 ± 19.5	

were similar in all sites except Peña Mayor, where hawthorn was more abundant than yew ($P < 0.05$ after post-hoc test; Table 2).

Spatial covariation among seed and seedling densities

The locality and the microhabitat, as well as their interaction, had significant effects on the variation of the density of dispersed seeds and the density of emerged first-year seedlings, for all species (GLM: all main effects and interactions were significant at $P < 0.05$ for both dependent variables). For all tree species, the distribution of residuals of the density of emerged first-year seedlings was positive and significantly related to that of the density of dispersed seeds, after removing the variance accounted for by locality and microhabitat effects (*Taxus*, $F_{1,155} = 4.3$, $P = 0.04$, $b = 0.02 \pm 0.01$; *Ilex*, $F_{1,169} = 68.9$, $P < 0.0001$, $b = 0.09 \pm 0.01$; *Crataegus*, $F_{1,149} = 16.1$, $P < 0.001$, $b = 0.09 \pm 0.02$; Fig. 1).

Seed predation

The three plant species showed marked differences in the percentage of seeds removed from experimental depots, ranging from the lowest values of *Crataegus* seeds (ca. 19% on average) to the strongest attack in *Taxus* seeds (ca. 70%), with *Ilex* seeds showing intermediate values (ca. 56%, Fig. 2). The generalized linear model showed significant differences among species, localities and, marginally, between years, in seed predation rates (Table 3). This model explained 36.6% of the variance in seed predation rate, from which 27.7% corresponded

to the species factor (Table 3). Significant interactions between factors indicated that differences among years and localities in predation rate were species-dependent, since the differences and the rank among species were consistent among sites and years (Fig. 2).

The relative occurrence of the different species in rodent heaps differed significantly from that in the seed rain (Peña Mayor: $\chi^2 = 217.5$, $P < 0.001$, df = 2, 10,320 and 3,808 number of seeds in heaps and in seed rain, respectively; Sueve: $\chi^2 = 459.3$, $P < 0.001$, df = 2, 1,350 and 6,103 number of seeds in heaps and in seed rain, respectively). *Taxus* seeds were significantly more frequent in rodent heaps than in seed rain, in both sites (Peña Mayor: 22.6% in heaps compared with 15.4% in seed rain, partial $\chi^2 = 93.8$, $P < 0.001$, df = 1; Sueve: 79.6% in heaps compared with 50.2% in seed rain, partial $\chi^2 = 414.4$, $P < 0.001$, df = 1). Conversely, the frequency of *Crataegus* seeds was significantly lower in heaps than in seed rain (Peña Mayor: 5.4% in heaps compared with 11.7% in seed rain, partial $\chi^2 = 153.8$, $P < 0.001$, df = 1; Sueve: 0.15% in heaps compared with 5.3% in seed rain, partial $\chi^2 = 115.8$, $P < 0.001$, df = 1). The percentage of seeds in heaps showing signs of predation also differed among species (*Taxus*: 98.1 ± 0.8, *Ilex*: 87.2 ± 2.0, *Crataegus*: 81.6 ± 4.7, $F_{2,91} = 16.2$, $P < 0.0001$) and sites ($F_{1,91} = 5.4$, $P = 0.002$; interaction species × locality $P > 0.05$).

Seed predation and recruitment potential

Recruitment potential, estimated as the ratio of first-year seedlings to viable dispersed seeds for each species and site, was low in *Taxus*, intermediate in *Ilex* and high
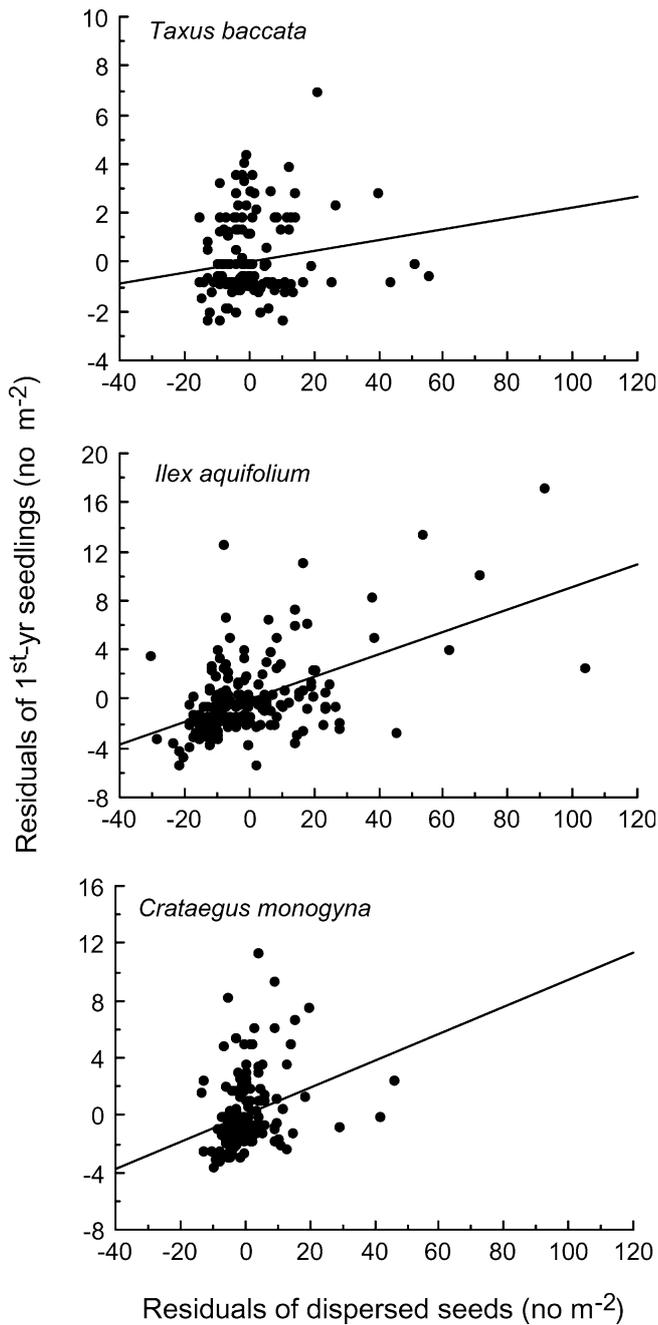
Fig. 1 Relationship between the residuals of the density of dispersed seeds and the residuals of the density of emerged first-year seedlings (after respective GLMs considering the effects of the locality and the microhabitat and their interaction), for different tree species. The regression lines between the variables are also shown (*T. baccata*: $F_{1,155}$ = 4.3, P = 0.04; *I. aquifolium*: $F_{1,169}$ = 68.9, $P<0.0001$; *C. monogyna*: $F_{1,149}$ = 16.1, $P<0.001$). Each point represents the average among years 2001–2002 and 2002–2003 for each sampling station (only stations with seed density higher than zero were included)

in *Crataegus*, and this pattern was consistent among localities (Fig. 3). The residuals of recruitment potential and seed predation were obtained after GLM calculations that removed the effects of species and locality (both main effects and interaction were significant at
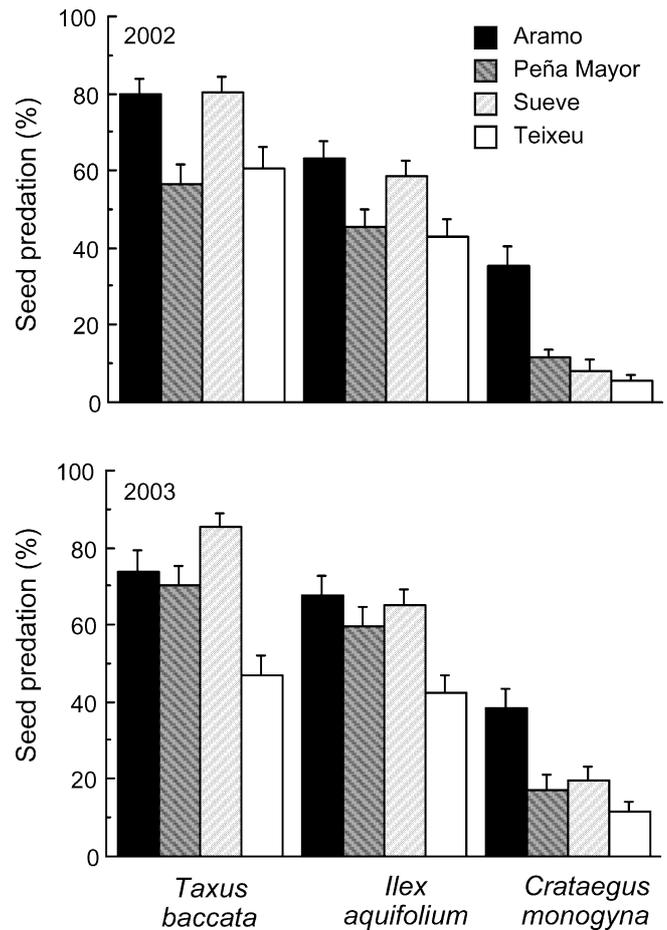
Fig. 2 Mean (+SE) values of the seed predation rate (percentage of removal) in seed removal experiments, for different tree species, localities and years

Table 3 Generalized linear model examining the significance of tree species, locality, year, and the interactions among main factors on the seed predation rate in the seed removal experiment. The model was obtained considering the response variable to have a binomial error

Source	df	Deviance	F	P
Species (S)	2	139.10	254.82	< 0.0001
Locality (L)	3	23.65	28.88	< 0.0001
Year (Y)	1	1.01	3.70	0.055
S × L	6	14.19	8.67	< 0.0001
S × Y	2	1.93	3.54	0.029
L × Y	3	2.15	2.63	0.049
S × L × Y	6	1.94	1.18	0.313
Error	1169	319.07		

$P<0.05$, for both dependent variables). The relationship between these distributions of residuals was negative and significant (Fig. 4a; $F_{1,48}$ = 24.2, $P<0.001$, R^2 = 0.29).

The density of established recruits (> 1-year seedlings surviving at the end of the summer) for each species and locality was positively related to the density of emerged first-year seedlings (Fig. 4b). This positive relationship
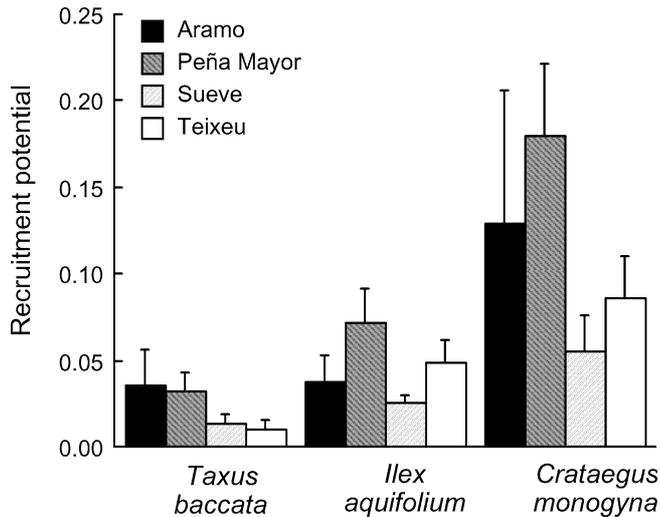
Fig. 3 Mean (+SE) values of the recruitment potential (estimated as the ratio 1st-yr seedling to viable dispersed seed) for different tree species and localities. Each *bar* represents the average for the two study years

was significant and independent of the differences among localities and species on the density of established recruits, as judged by the regression between the residuals of both variables after removing the effects of species and locality ($F_{1,48} = 85.1$, $P < 0.001$, $R^2 = 0.60$). The slope of this regression line was significantly different from $\beta = 1$ ($b = 0.49 \pm 0.05$, $t = 4.9$, $P < 0.001$, $df = 58$).

Discussion

Regeneration ability and seed limitation of temperate fleshy-fruited trees

The regeneration values (seed rain, seed viability, seedling density) estimated for these fleshy-fruited trees in Cantabrian forests were similar to those corresponding to other temperate localities (e.g. Kollmann 1995; Kollmann and Pirl 1995; Obeso and Fernández-Calvo 2002). However, we found marked differences among species in regeneration characteristics. Dispersal efficiency by birds, measured as the quantity of seeds in fallen fruits relative to avian dispersed seeds, was higher in *Taxus* than in *Ilex* and *Crataegus*. These differences are probably related to a proportionally higher consumption of yew arils by frugivores (*Turdus* sp.), due to their higher caloric and lower saponin contents (Snow and Snow 1988; Barnea et al. 1993), and to a higher rate of handling errors when foraging in *Ilex* and *Crataegus* (Sallabanks 1992; Obeso 1998). Species also differed in the proportion of empty seeds (see also Kollmann et al. 1998). Nevertheless, differences in dispersal efficiency by frugivores and in seed viability were not large enough to compensate for seed production differences and thus, *Ilex* and *Taxus* dominated the seed rain, whereas *Crataegus* was the rarest species. Moreover, this species
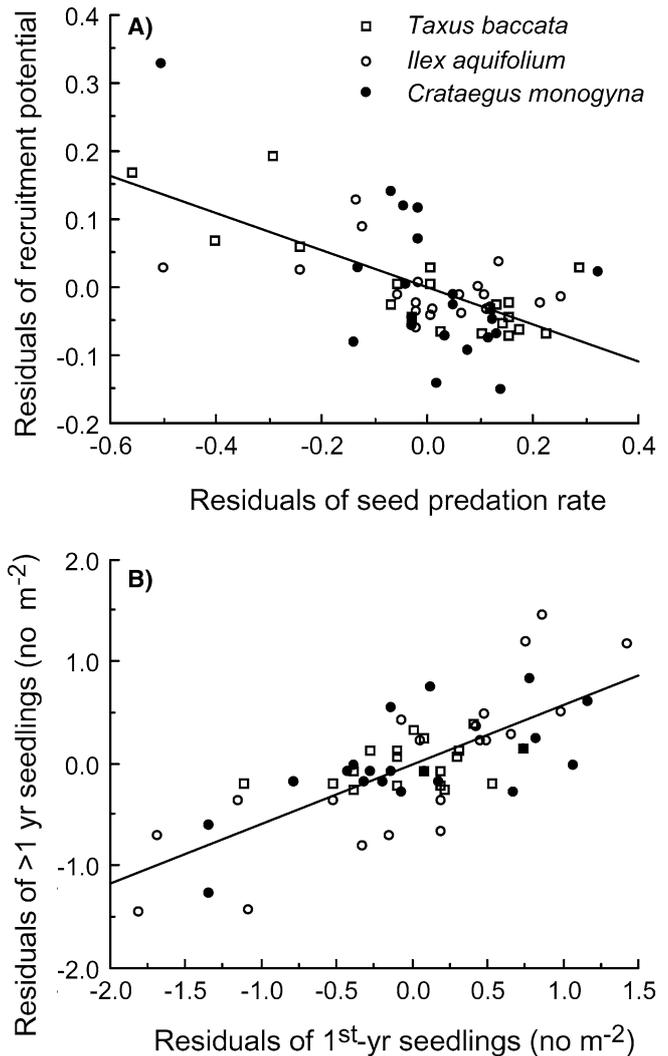
Fig. 4 Relationship between **a** the residuals of the seed predation rate and the recruitment potential, and **b** the residuals of the density of emerged first-year seedlings and the density of > 1-year seedlings surviving at the end of the summer, after GLMs considering, for each variable, the effects of the species, the locality and their interaction. Each point represents the average among sampling stations within microhabitat and the 2 study years. Species are indicated by *different symbols*. The regression lines between the variables are also shown (**a**: $F_{1,48} = 24.2$, $P < 0.001$; **b**: $F_{1,48} = 85.1$, $P < 0.001$)

ranking for seed abundance did not persist for the abundance of emerged seedlings, since many more *Crataegus* than *Taxus* seedlings became established. Since the abundance of established juveniles was directly proportional to the density of emerged seedlings, the differences in early seedling abundance appeared to persist as differences in capability of long-term recruitment, and may have favoured the observed differences in adult density, since *Crataegus* was as abundant as (or even more so than) *Taxus*.

Our results strongly suggest that, at least for the seed density ranking found here, the recruitment of all three studied species was mostly determined by seed limitation, because the density of emerged seedlings related

linear and positively to seed density. If recruitment was mainly limited by the number of suitable microsites, establishment would be unaffected by any increment in the number of seeds, at least above the threshold number of seeds determined by the actual number of microsites (Andersen 1989; Eriksson and Ehrlén 1992). This pattern mostly deals with microsite limitation occurring before and during seedling emergence, by processes such as fungal attack on seeds, germination inhibition by abiotic factors or early death during radicle and epicotyl expansion (Eriksson and Ehrlén 1992). Nevertheless, the low incidence of microsite limitation can probably be extrapolated to the first years of plants' lives, because, as noted above, the abundance of established recruits was correlated with the density of emerged seedlings. The present results are therefore consistent with the generalized, but probably underestimated, seed limitation suggested for temperate forests (Turnbull et al. 2000; and references therein). More importantly, this generalized seed limitation makes possible the demographic effect of any plant–animal interaction, including seed predation, involving a numerical change in the number of seeds arriving to safe sites.

Selective seed predation by rodents

Removal experiments and analysis of seeds in rodent trash heaps provided evidence that rodents selected among tree species, establishing the following ranking of attack of seeds: *Taxus* > *Ilex* > *Crataegus*. This ranking was consistent both in space (different localities within the region) and in time (successive years), as suggested for similar systems in central Europe and Great Britain (Kollmann et al. 1998; Hulme and Borelli 1999). Other comparisons among fleshy-fruited plants in the Mediterranean area have shown high seed predation rates for *Taxus* and low predation rates for *Crataegus* (Hulme 1997; Rey et al. 2002).

The variation in the magnitude of predation among species may be related to extrinsic factors, as occurs when different species are dispersed to habitats or microhabitats that differ in abundance of—or use by—-rodent predators (Manson and Stiles 1998). The pattern presented here hardly fits this case, given the strong spatial consistency in seed selection, which also occurred at the microhabitat level (data not shown). On the other hand, it cannot be attributed to seed segregation among different types of predators (e.g. Hulme 1997; Rey et al. 2002) because rodents were apparently the only seed predators in the study sites. Thus, selective predation seems to be almost entirely caused by differences in intrinsic, seed-related factors. In this sense, a pro-apostatic frequency-dependent selection, in which the rarest species prevails (Greenwood 1985), could account for the low occurrence and attack of *Crataegus* seeds on rodent heaps. However, *Taxus* was less frequent than *Ilex* in the seed rain, and did not achieve enhanced survival. In addition, seed depots contained all species at the same density and showed the same selection pattern, suggesting little pro-apostatic selection (see also Hulme and Hunt 1999).

In contrast to similar systems involving wider among-species comparisons (Kollmann et al. 1998; Rey et al. 2002) our results failed to suggest any effect of seed toxicity or nutritional content on selection among species. In fact, the chemical defence of *Taxus* seeds is probably ineffective for rodents, which easily discard the toxic coat to obtain the undefended EEF (see also Hulme 1997). Additionally, *Crataegus* was the least consumed even having the highest nitrogen content. Alternatively, our data strongly support an effective role of mechanical defence traits, since the seed predation ranking is the inverse of the gradient of seed protection established by Coat:EEF ratio (Table 1; see also Hulme 1997; Kollmann et al. 1998; Rey et al. 2002, for relating *Crataegus* escape in relation to coat thickness). Species with a higher proportion of woody coat in relation to the edible mass would gain enhanced survival through increased husking cost, which also involved differences in handling time among seed species (I. Martinez, unpublished data; see also Hulme 1993). As this relationship among mechanical defence characteristics and differential predation escape prevailed over space and time, there is a potential for seed predation to be a selective pressure modulating the evolutionary trends of seed traits among these co-occurring fleshy-fruited species (Blate et al. 1998; Grubb et al. 1998).

Differential demographic effects of seed predation

This study shows a negative covariation between seed predation and recruitment potential for fleshy-fruited trees. *Crataegus* escaped predatory rodents and showed an enhanced recruitment potential, establishing more seedlings even when producing and dispersing fewer seeds than *Taxus*, the species preferred by seed predators. Although based on observational data, this relationship suggests that seed predators exerted some control on the relative abundance of recruits of different tree species at the local scale. We think it unlikely that the among-species differences in recruitment potential could be accounted for by other post-dispersal factors, leading to spurious relationships with seed predation. In fact, as judged by field germination trials, seed losses other than predation are similar among species (D. García et al., unpublished data). On the other hand, the between-species differences in seed abundance after predation, suggested by our results, are probably unaffected in the long term by differential seed bank dynamics, due to the short-lived character of these species (Kollmann 2000; Thomas and Polwart 2003; Arrieta and Suárez 2004). Moreover, the potential demographic effect by seed predators is probably fostered by other life-history traits of the study species since their population dynamics mostly depend on sexual reproduction (although *Ilex* may show vegetative regeneration;

Peterken and Lloyd 1967; Kollmann 1995; Obeso and Fernández-Calvo 2002), and they show relatively low supra-annual variability in seed production and are probably unable to saturate rodents in large-crop events (Herrera et al. 1998).

The rodent-mediated limitations on seedling recruitment proposed here may be affected by potential compensatory effects from other post-dispersal factors or positive density-dependent seedling mortality (Crawley 1992; Edwards and Crawley 1999; De Steven and Wright 2002). In fact, our results suggested positive density-dependence for all three study species, as shown by the slopes significantly lower than 1 in the regression lines among seed density and seedling density (Fig. 1, $\beta = 1$ indicates the same percent recruitment at all seed densities; Harms et al. 2000; De Steven and Wright 2002). Similarly, some density-dependent mortality of seedlings may be interpreted from the relationship among early-emerged seedlings and established recruits (Fig. 4; see also Obeso and Fernández-Calvo 2002). In any case, these density-dependent effects appear to be insufficient to lead to independence between seed input and seedling emergence, as well as between seedling emergence and long-term recruitment.

Differential recruitment limitation imposed by seed predation may also be considered among the processes driving the coexistence of these fleshy-fruited trees. We therefore propose that rodents exert a primary effect by modulating the pre-emptive competition for available safe sites and precluding the progressive exclusion of species with low seed production by species dominant in propagule number, or at least by fostering the evenness within the seedling community for the occupation of safe sites (see also Hubbell et al. 1999; Wright 2002). This was favoured by the fact that all seed species frequently co-occurred at the same dispersal microsites (>60% of sampling stations received seeds from the three species; Martínez 2004), probably because of the similar post-foraging movement patterns of shared dispersers (Martínez 2004). On the other hand, seed predators may also affect plant coexistence by eliminating dominant species and thus liberating resources for poor competitors (Brown and Heske 1990; Hulme 1996a; Wright 2002). This may also be the case for Cantabrian secondary forests, where *Crataegus* may be competitively excluded in the long-term, due to its poor performance under the deep shade imposed by the dense perennial canopies of *Ilex* or *Taxus* (Grubb et al. 1996; Kollmann and Reiner 1996). Conversely, holly and yew are shade tolerant species, the seedlings of which are able to establish and grow under dense canopy (Peterken and Lloyd 1967; García and Obeso 2003; Thomas and Polwart 2003).

Conclusion

The results of the present study suggest a potential role for post-dispersal seed predation in the processes that shape the composition of temperate secondary forests in NW Spain. By decreasing differences among tree species in the input of propagules, seed predation may modify the outcome of competition for safe site occupation and resource use, ultimately facilitating plant coexistence (Hurtt and Pacala 1995). This differential recruitment effect would depend on the generalized seed-limitation of involved species, as well as on the consistent selective attack by the rodent-dominated predatory guild. In contrast to the results of previous studies, in which the role of predators was found to be driven by seed size (e.g. Brown and Heske 1990; De Steven 1991a; Hoffmann et al. 1995; Edwards and Crawley 1999), we propose that mechanical defence characteristics underpin the differences among species in recruitment. If these seed traits also involve differences in fitness among individuals within species, then seed predators would exert a multi-specific, demographic effect and also evolutionary pressure. Clearly, the consideration of post-dispersal seed predation as a major demographic and evolutionary force may be decisive in understanding both the structure and functioning of temperate woody plant communities.

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