Ungulate damage on Scots pines in Mediterranean environments: effects of association with shrubs

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Abstract: The spatial structure of plant communities as well as the quality and abundance of neighbours can strongly influence the intensity of herbivory suffered by a plant. In this paper, we study the effect of the association with shrubs on the ungulate herbivory suffered by Scots pine (*Pinus sylvestris* var. *nevadensis* Christ., Pinaceae) saplings in two isolated, fragmented populations in southeastern Spain. For this, we monitored herbivory on saplings with regard to the microhabitat in which they grew. We distinguished pines growing in open interspaces, on the edge of shrubs and within the canopy of shrubs, and also we distinguished four functional types of shrubs: thorny shrubs, nonthorny shrubs, thorny scrubs, and nonthorny scrubs. Our results show that association with shrubs increases the damage inflicted on Scots pine saplings. In fact, saplings growing in the open patches, far from the shrubs, escaped from herbivory more frequently and incurred less damage than did saplings growing close to shrubs. However, herbivory was also reduced when pine saplings were completely surrounded by shrubs, since then they served as a mechanical barrier. The type of neighbouring shrub did not affect the overall damage suffered by pines, despite the fact that the ungulates damaged the nonthorny scrubs more intensely than the other kinds of shrubs. Consequently, saplings have an advantage when growing within the canopy of shrubs; these constitute key microsites for pine recruitment in these Mediterranean forests.

Key words: associational resistance, associational susceptibility, mammalian herbivory, Mediterranean high mountain, neighbouring effects, *Pinus sylvestris* var. *nevadensis*.

Résumé : La structure spatiale des communautés végétales ainsi que la qualité et l'abondance des voisins peuvent fortement influencer l'intensité de l'herbivorie subie par les plantes. Les auteurs ont étudié l'effet de l'association avec des arbustes sur l'herbivorie subie de la part des ongulés par de jeunes plants de pin sylvestre (*Pinus sylvestris* var. *nevadensis* Christ., Pinaceae) dans deux populations isolées et fragmentées du sud-est de l'Espagne. A cette fin, ils ont suivi l'herbivorie chez les jeunes plants en relation avec le microhabitat où ils poussent. Ils ont distingué les pins poussant dans les espaces ouverts, près d'arbustes et sous la canopée des arbustes, et ont également identifié 4 types fonctionnels d'arbustes : arbustes épineux, arbustes non-épineux, rebuts (scrubs) épineux, rebuts non-épineux. On observe que l'association avec les arbustes augmente le dommage subi par les jeunes plants de pin sylvestre. En fait, les jeunes plants poussant dans les espaces ouverts, loin des arbustes, échappent à l'herbivorie plus souvent et subissent moins de dommages que les jeunes plants poussant près des arbustes. Cependant, l'herbivorie est également réduite lorsque les jeunes plants de pin sont complètement entourés d'arbustes, qui servent alors de barrière mécanique. Le type d'arbuste avoisinant n'affecte pas les dommages en général subis par les pins en dépit du fait que les ongulés s'attaquent plus intensément aux rebuts non-épineux qu'aux autres types d'arbuste. Conséquemment, les plantules ont avantage à pousser sous la canopée des arbustes, qui constitue des microsites déterminants pour le recrutement des pins dans ces forêts méditerranéennes.

Mots clés : résistance d'association, susceptibilité d'association, herbivorie des mammifères, hautes montagnes méditerranéennes, effets de voisinage, *Pinus sylvestris* var. *nevadensis*.

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Introduction

The risk of attack by a generalist herbivore depends not only on the plant's traits, such as chemistry, morphology, or phenology, but also on the spatial structure of the plant community and the quality and abundance of the neighbours (Holmes and Jepson-Innes 1989; Wahl and Hay 1995; Zamora et al. 1999). Accordingly, the defensive and nutritional traits of a plant species are not absolute but rather context-dependent properties, relative to the defence and nutritive traits displayed by co-occurring plant species (Huntly 1991; Belovsky and Schmitz 1994; Wahl and Hay 1995).

Interactions among neighbouring individuals are rarely simple, and association with other plant species can have both positive or negative outcomes (Miller 1994; Callaway and Walker 1997; Brooker and Callaghan 1998; Olofsson et al. 1999). Protection by growing close to a neighbour, a phenomenon called "associational plant refuge" or "associational resistance" (Huntly 1991; Hjältén et al. 1993; Wahl

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and Hay 1995; Hjältén and Price 1997), can result from several mechanisms. In some cases, a plant species escapes damage by growing beneath a protective mechanical barrier produced by other species (Jaksic and Fuentes 1980; Herrera 1991; García et al. 2000). In other cases, herbivory can be avoided by associating with unpalatable or less-preferred plants (repellent plant scenario; Atsatt and O'Dowd 1976), since generalist herbivores usually seek the highest quality patches within the habitat (Danell et al. 1991*a*, 1991*b*; Hjältén et al. 1993; Hjältén and Price 1997; WallisDeVries et al. 1999). Nevertheless, plants can also gain protection from being surrounded by more preferred species (attractant or decoy scenario; Hay 1986; Holmes and Jepson-Innes 1989; Danell et al. 1991*a*; Hjältén et al. 1993; Wahl and Hay 1995; Hjältén and Price 1997), because at a within-patch spatial scale, herbivores would again select high-quality plants against low-quality or repellent plants (Hjältén et al. 1993; Hjältén and Price 1997; WallisDeVries et al. 1999).

However, in some cases, instead of associational resistance, less palatable species may encounter accidental herbivory when associating with highly palatable ones, because these high-quality patches attract many herbivores, a phenomenon called "associational susceptibility" (Huntly 1991) or "shared doom" (Hay 1986; Wahl and Hay 1995). This usually occurs when the protection provided by the neighbour is mechanical rather than nutritional, and the protection is not complete (Wahl and Hay 1995). Since palatability of a plant species is not an absolute property but varies with changes in the co-occurring community, associational resistance and shared doom can be two extremes of the same gradient (Brooker and Callaghan 1998), depending on the relative palatability of the neighbours and the way that herbivores are deterred (mechanically or nutritionally).

Mediterranean environments provide many scenarios in which to study neighbouring effects on herbivory. The heterogeneity and diversity in these environments, being very high even at small spatial scales (Blondel and Aronson 1999), increases the probability of a plant being surrounded by other species. In addition, mammalian herbivory is extremely frequent in Mediterranean habitats, most being overgrazed and overbrowsed (Zamora et al. 1996). Finally, the Mediterranean mammalian herbivores are generalists, consuming disparate types of herbs and shrubs (Martínez 1988, 1990, 1995; García-González and Cuartas 1989, 1992*a*, 1992*b*; Fandós 1991; Cuartas and García-González 1992), often resulting in serious damage to Mediterranean woody plants (Cuartas and García-González 1992; Bartolomé et al. 1998).

Scots pine (*Pinus sylvestris* L.) is widely distributed throughout the western Palearctic, although it is relict in many Mediterranean mountains (Boratynski 1991). In Andalusia, southeastern Spain, this pine species (*Pinus sylvestris* var. *nevadensis* Christ.) inhabits only two mountain ranges, the Sierra Nevada and Sierra de Baza, the southernmost populations in the distribution area of this pine species (Boratynski 1991). In these Mediterranean areas, Scots pines are frequently browsed by ungulates: domestic goats (*Capra hircus*) and Spanish ibex (*Capra pyrenaica* Shinz.) in Sierra Nevada and domestic sheep (*Ovis aries*) in Sierra de Baza (Hódar et al. 1996, 1998; Zamora et al. 2001*a*). These generalist herbivores constitute a major factor inhibiting the regeneration of these Scots pine woodlands, since they severely retard the growth rate and first-reproductive age of saplings (Zamora et al. 2001*a*). In this paper, we analyse how ungulate herbivory in Scots pine saplings is affected by association with shrubs. Specifically, we studied the herbivore damage in saplings in relation to (*i*) the associational relationships with neighbouring shrubs, (*ii*) the type of shrubs closely associated with the saplings, and (*iii*) the consequences for forest regeneration.

Study sites and natural history of the system

This study was conducted in the two Scots pine forests remaining in southern Spain. The first is a small isolated forest (approximately 1850 m a.s.l.) located in the Sierra Nevada, near Trevenque peak (37°10′30″N, 3°27′10″W; Trevenque, hereafter), and composed of native Scots pine (*Pinus sylvestris* var. *nevadensis*), maple (*Acer granatense* Boiss.), and yew (*Taxus baccata* L.). The second forest (37°23′01″N, 3°51′45″W; Boleta, hereafter) is located in Sierra de Baza, 80 km north of Trevenque, and is part of an autochthonous forest (1700–2100 m a.s.l.) composed of Scots and black pines (*Pinus nigra* var. *salzmanni* (Donald) Franco) growing intermingled. Both forests have a well-developed understory composed mainly of *Juniperus communis* L., *Juniperus sabina* L., *Berberis hispanica* Boiss. & Reuter, *Prunus ramburii* Boiss., *Astragalus granatensis* Lam., and *Hormathophylla spinosa* (Küpfer) (see Castro et al. 1999 for a further description).

Methods

In 1995, we tagged all pine saplings lower than 2 m (the upper threshold to suffer ungulate damage in apical shoots in the study sites; Zamora et al. 2001*a*) growing within two plots (approximately 2 ha surface area each) per forest, by using aluminum tags to ensure individual monitoring. In total, we studied 466 pines in the two relict forests.

For each tagged pine, we recorded the following.

(1) Age (years) was estimated as the number of whorls (Edenius et al. 1995; Zamora et al. 2001*a*).

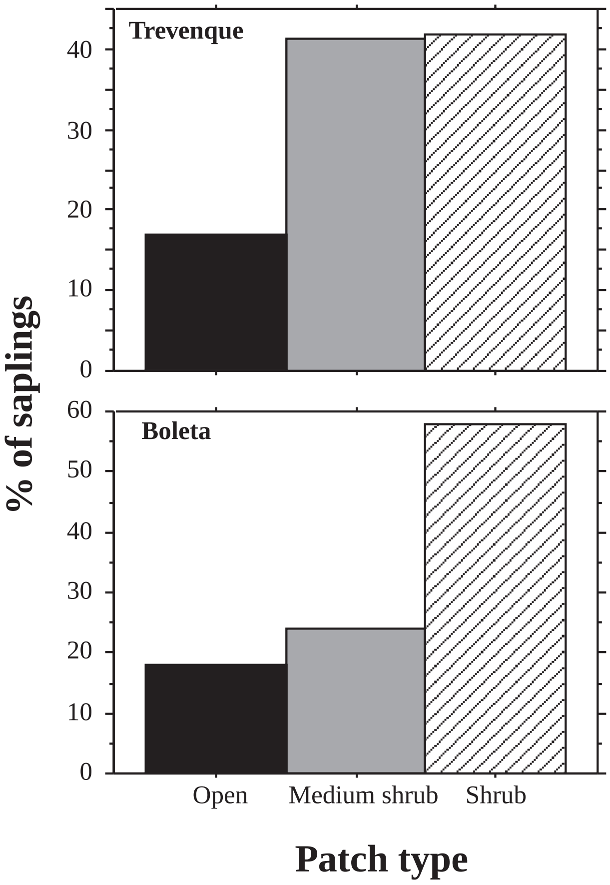
(2) Height was measured in centimetres.

(3) Relative internode growth ($\mathrm{cm \cdot cm^{-1} \cdot year^{-1}}$) was estimated as the net growth of each sapling per year divided by the height of the sapling at the beginning of the study, to control for among-sapling differences in height and growth rate (Zamora et al. 2001*a*). This parameter measures the height change in proportion of overall height. To avoid the effect of herbivory on growth, we quantified this variable only for those saplings unbrowsed during the study period.

(4) The patch type in which the sapling was growing was classified according to the shrub cover. Shrub cover was estimated as the percentage of soil surface covered by woody vegetation in a 1 m radius circular plot centered on the pine sapling (Zamora et al. 2001*a*). Three main types of patches were differentiated according to the shrub cover: (*i*) open, when the shrub cover was less than 25%, with pines growing mostly in bare soil; (*ii*) medium shrub, when the shrub cover was 25–75%, with pines growing at the edge of neighbouring shrubs but remaining physically accessible to ungulates; and (*iii*) shrub, when the shrub cover was higher than 80% (in most cases 100%) with pines completely surrounded and frequently covered by shrubs.

(5) The shrub type surrounding the saplings associated with shrubs (patch types medium shrub and shrub) was determined. Since the diversity of shrubs was very high in all our study sites, we

Fig. 1. Spatial distribution of *Pinus sylvestris* var. *nevadensis* saplings in the two forests studied, expressed as the percentage of saplings growing in each patch type.



classified the neighbouring shrubs into four physiognomic categories: (*i*) thorny shrub, mainly *Prunus ramburii*, *Crataegus granatense* Jacq., *Rosa* spp., and *Berberis hispanica*; (*ii*) nonthorny shrub, mainly *Juniperus communis* and *J. sabina*; (*iii*) nonthorny scrub, mainly *Ononis aragonensis* Asso and *Genista versicolor* Boiss. at the Trevenque site, and *O. aragonensis*, *Satureja alpina*, and *Sideritis* sp. at the Boleta site; and (*iv*) thorny scrub, mainly *Astragalus granatensis*, *Erinacea anthyllis* Link, *Vella spinosa* Boiss., and *Hormathophylla spinosa*. Shrub diversity was so high in the study sites that most pine saplings were surrounded by several types of shrubs. For this reason, to assign the patch to a single category, we used the type of shrub that covered the highest proportion of its surface area.

(6) Overgrowth (cm) was quantified as the difference between the height of the Scots pine sapling and the maximum height of the shrubs in direct contact with it. A negative value of this variable indicates that the shrub overgrows the sapling (see García et al. 2000 for similar procedure). For saplings located in the open patches, the value of the overgrowth corresponds to the total height of the plant.

Quantifying herbivory on pine saplings

We quantified the herbivory intensity affecting each sapling during all the years of the study, using the following three parameters.

(1) Risk of herbivory was interpreted as the probability of a sapling being browsed. For this, at the end of the growing season each year we checked all tagged saplings, scoring them as browsed or unbrowsed. Risk of herbivory was calculated as the percentage of damaged plants.

(2) Damage intensity was quantified as the percentage of apical shoots lost to ungulates during the overall study period. This was quantified by marking the apical shoots of each pine and by counting yearly the proportion of those damaged by ungulates (Zamora et al. 2001*a*).

(3) Chronic herbivory was estimated as the number of losses of leader shoots divided by the pine age. This is an accurate estimate of the herbivory that each sapling has undergone since its establishment, since ungulate herbivory causes more than 98% of the losses of apical dominance in Scots pine in the study areas (Hódar et al. 1996; Zamora et al. 2001*a*). Both risk of herbivory and damage intensity were averaged over all the study years for each pine sapling.

Quantifying herbivory on neighbouring shrubs

We quantified the percentage cover of each shrub type at the study sites by means of linear transects (10 per plot, 50 m each; Bullock 1996; see García et al. 2000 for details), in which we recorded the presence–absence and the identity of the vegetation. To estimate the herbivory intensity in the shrubs, in 1998 we labelled 110 shrubs of each type at each study site (880 shrubs in total), half of them located close to a pine saplings, and the remaining half located far from any pine saplings (at least 1.5 m from a sapling). The palatability of each shrub type was estimated by relating availability and damage by means of W_i (Savage's index of selectivity), and the significance of W_i values was tested with χ^2 (see Manly et al. 1993 for a full description of the procedure). Data from the four plots were pooled for simplicity.

Statistical analysis

All analyses were performed using procedures in the SAS 6.12 statistical package (SAS Institute Inc.1997). To examine the effect of the patch and the type of neighbouring shrub on herbivory, we performed a log–linear model (PROC CATMOD) when the response variable was nominal, as in risk of herbivory, and a general linear model (PROC GLM) when the response variable was continuous, as in damage intensity or chronic herbivory. We also introduced sapling height and shrub overgrowth as independent variables. Nonsignificant interactions among sources of variation were pooled with the error term to improve the test (Zar 1996). Damage intensity on neighbouring shrubs was analysed by a two-way ANOVA (PROC GLM), with type of shrub and distance from focal sapling as fixed factors.

We used type III sum of squares because of the unbalanced data. Although this type of SS does not correct for unbalanced design, it provides the most readily interpretable test of the null hypotheses of no main effect of factors when all treatment combinations are observed but the number of observations varies among cells, and it is preferred over the other types with unbalanced data (Shaw and Mitchell-Olds 1993). To control for the experiment wise type I error produced by multiple comparisons, we adjusted the probabilities of error to $\alpha = 0.05$, by using the sequential Bonferroni technique (Rice 1989). Prior to all these parametric analyses, we arcsine transformed the ratio variables and log transformed the remaining variables when they departed from normality (Zar 1996). Through this paper, means are shown ±1 SE.

Results

Spatial distribution of pine saplings

Most saplings in both Trevenque and Boleta forest were associated with shrubs (Fig. 1). Only 17% of the saplings were growing in the open interspaces despite that this microhabitat covered 30.2% of the Trevenque and 46.6% of the

Table 1. Summaries of the log–linear analysis (χ^2) for the risk of herbivory (yes or no), and the general linear model ANOVA (F) for damage intensity and chronic herbivory testing the effect of patch type (open, medium shrub, shrub) and overgrowth.

	Trevenque				Boleta			
Source of variation	df	χ^2	F	p	df	χ^2	F	p
Risk of herbivory		28.88		<0.0001		20.59		<0.0001
Height	1	2.51		0.11	1	1.52		0.22
Patch type	2	12.60		0.002	2	6.02		0.04
Overgrowth	1	3.87		0.049	1	1.77		0.26
Damage intensity			5.62	<0.0001			3.59	0.0005
Height	1		6.83	0.0001	1		2.18	0.2
Patch type	2		3.96	0.01	2		6.07	0.01
Overgrowth	1		2.22	0.1	1		3.56	0.1
Error	279				152			
Chronic herbivory			9.02	<0.0001			5.28	<0.0005
Height	1		0.31	0.57	1		0.01	0.91
Patch type	2		10.37	0.0001	2		7.10	0.001
Overgrowth	1		4.02	0.046	1		1.54	0.22
Error	268				155			

Note: Nonsignificant interactions were pooled with the error terms to increase dfs.

Boleta plots (see Castro et al. 1999). For this reason, the pine saplings were associated with shrubs more than expected in both forests ($\chi^2 > 5.00$, $p < 0.0001$ for both sites).

Effect of shrub cover on sapling growth

For those saplings unbrowsed by ungulates during the study period, the relative internode growth was significantly higher for those located in the open microhabitat (Trevenque: 0.153 ± 0.036 $\text{cm}\cdot\text{cm}^{-1}\cdot\text{year}^{-1}$, $n = 18$; Boleta: 0.128 ± 0.012, $n = 17$) than for those located in medium shrub (Trevenque: 0.101 ± 0.005, $n = 59$; Boleta: 0.090 ± 0.010, $n = 10$) and in the shrub (Trevenque: 0.107 ± 0.006, $n = 54$; Boleta: 0.105 ± 0.007, $n = 33$), with these figures being significantly different in both forests (Trevenque: $p = 0.017$; Boleta: $p = 0.014$, one-way ANOVA).

Effect of shrub cover on herbivory

The patch type occupied by saplings was a main factor affecting the risk of herbivory in both sites (Table 1), with pines growing in medium shrub having significantly the highest probability of being browsed, followed by shrub and open (Fig. 2). Overgrowth had an effect only in Trevenque, with saplings overgrowing the shrubs being browsed more frequently (69% of pines) than those remaining underneath (37%). The respective difference in Boleta (73 vs. 46%), was not statistically significant (Table 1).

The patch type affected the other two herbivory indicators, damage intensity and chronic herbivory both in Trevenque and Boleta (Table 1). In all cases, pines incurred the most damage when located in medium shrub, whereas those least damaged were located in open patches (Fig. 2). In general, overgrowth did not affect either of these two herbivory indicators (Table 1).

Effect of type of neighbouring shrub

In the saplings growing close to neighbouring shrubs, no herbivory indicator was affected by the type of shrub in either site (Table 2). Sapling height did not influence the herbivory indicator (Table 2), although it differed between types of shrubs ($p = 0.0001$). Thus, saplings located under scrubs were much shorter (nonthorny scrub, 42.98 ± 10.50 cm; thorny scrub, 64.05 ± 9.79 cm) than saplings located under shrubs (nonthorny shrubs, 93.37 ± 6.10 cm; thorny shrubs, 94.48 ± 8.57 cm).

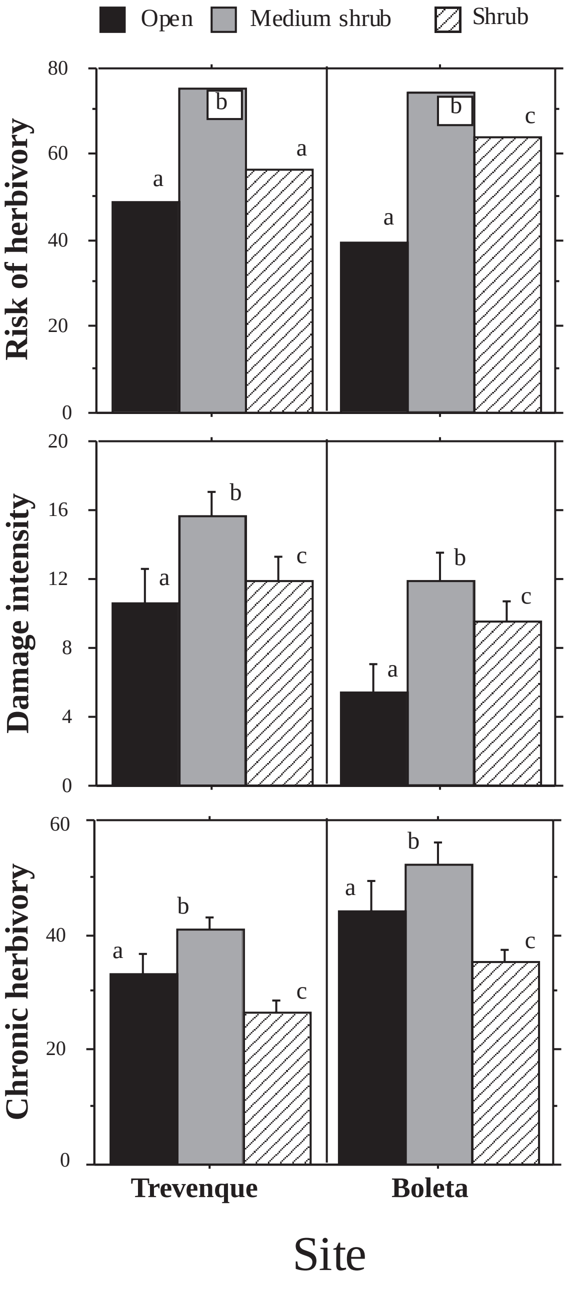
Herbivory on shrubs

The main factor affecting herbivory on neighbouring shrubs was the type of shrubs (Table 3). Nonthorny scrubs were much more damaged than expected (6.85% cover, 72.44 ± 2.89% of shoots removed by ungulates, $W_i = 10.58$, $p < 0.0001$ after Bonferroni correction), while thorny shrubs (13.16% cover, 13.78 ± 1.56% damage) and, above all, thorny scrubs (9.68% cover, 4.12 ± 0.68% damage) and nonthorny shrubs (26.64% cover, 2.77 ± 0.93% damage) were much less damaged and showed neither selection nor rejection (W_i between 0.10 and 1.95, $p > 0.10$ for all). By contrast, the distance from Scots pine saplings did not correlate with the herbivory suffered by shrubs in Trevenque, although it did correlate in Boleta. At this latter site, shrubs far from saplings underwent a herbivory intensity of 23.11 ± 2.41%, whereas among those close to saplings the herbivory intensity was 10.30 ± 2.92% (Table 3, Fig. 3).

Discussion

Our results show that the type of patch occupied by Scots pine saplings is a major factor affecting the damage caused by ungulates. Saplings growing in the open patches, far from the shrubs, escaped from herbivory more frequently and incurred less damage than did saplings growing close to shrubs (Fig. 2). Shrubs in these Mediterranean environments constitute a primary food source for ungulates (Martínez 1988, 1990, 1995, 1997; García-González and Cuartas 1989, 1992*a*, 1992*b*; Fandós 1991; Cuartas and García-González 1992; Valderrábano and Torrano 2000). Indeed, ungulates at our study sites browsed on some types of shrubs more frequently

Fig. 2. Differences in the herbivory suffered by *Pinus sylvestris* var. *nevadensis* saplings depending on the patch types. All herbivory indicators are mean percentages. Error bars are SEs. Bars with different letters are significantly different ($P < 0.05$) according to one-way ANOVAs.



than on pines, since damage intensity to pines averaged less than 11% (see Fig. 2), whereas the percentage of shoots consumed in some kinds of shrubs (e.g., the nonthorny scrubs *Ononis aragonensis*, *Satureja alpina*, or *Sideritis* sp.) approached 75%. In addition, the fact that shrubs were not intensively damaged when growing close to pine saplings (Fig. 3) suggests that ungulates feed on shrubs irrespective of pine presence.

The shrubs are distributed at our study site in discrete patches of a few square metres surrounded by a matrix of open interspaces of similar size composed mainly of bare soil, ephemeral herbs that dry up during the summer, or unpalatable species such as the toxic geophytes *Asphodelus* sp. Therefore, since the only food plants available are woody species, ungulates must move from one shrubby patch to another while foraging, spending little time in the open. In addition, the shrubby patches are usually composed of several shrub species growing closely together. Although mammals attack pines more than some shrubs (e.g., *J. sabina*), some highly palatable shrubs are likely to appear in most shrubby patches. This also explains why, despite the significant difference in damage intensity found between the different types of shrub, shrub type did not affect the herbivory suffered by pine saplings (Table 2). Consequently, when growing at the edge of shrubs, pine saplings are almost always close to the only food plants available and, thus, tend to attract herbivore attention (Holmes and Jepson-Innes 1989; Danell et al. 1991*a*; Hjältén et al. 1993; WallisDeVries et al. 1999), which causes incidental herbivory on this less palatable species.

Growing far from shrubs appears to be advantageous to avoid herbivory because of the low palatability of Scots pine. For example, Rousset and Lepart (1999) suggest that Scots pine, because of its lower palatability, can colonize grasslands more rapidly than *Quercus humilis*, because ungulates avoid pines but heavily damage oaks located in these unprotected habitats. Danell et al. (1991*a*), Heikkilä and Härkönen (1996), and Härkönen et al. (1998) found that young Scots pines growing in monospecific stands are less damaged by moose (*Alces alces*) than those growing in mixed stands containing some other highly palatable tree species, such as aspen (*Populus tremula*), willows (*Salix* spp.), or rowan (*Sorbus aucuparia*). Similarly, we have observed that highly palatable tree species, such as *Quercus pyrenaica* or *Acer granatense*, inhabiting Mediterranean mountains are much more heavily damaged in the open than Scots pine saplings (Hódar et al. 1998).

Our results also show that neighbouring shrubs can deter herbivory on pine when completely surrounding the saplings. Saplings located in patches with 50% of shrub cover were significantly more damaged than were saplings in the middle of patches with 100% shrub cover. Direct and indirect evidence suggest that reduced herbivory was due to merely mechanical effects that interfere with the discovery of, access to, and consumption of tree seedlings and saplings, irrespective of the relative palatability of the saplings and the shrubs (Hay 1986; Callaway 1992). The type of neighbouring shrub did not affect the overall damage suffered by pines, despite that the ungulates more intensely damaged the nonthorny scrubs than the other kind of shrubs. Damage to saplings increased as the pines overgrew the shrubs. The benefit of growing completely protected by shrubs has been shown in the same study area for both other less-palatable tree species, such as *Taxus baccata* (García et al. 2000), as well as for highly palatable species, such as *Acer granatense* (Hódar et al. 1998; Castro 2000). The trophic generalism of the domestic and wild Mediterranean ungulates (e.g., Martínez 1995; García-González and Cuartas 1992*b*; Fandós 1991; Bartolomé et al. 1998) is probably the main factor decreasing the possibility of associational resistance based on nutritional or chemical attributes of neighbouring plants. As a consequence, pine saplings in

Table 2. Summaries of the log–linear analyses (χ^2) for the risk of herbivory (yes or no), and the general linear model ANOVA (*F*) for damage intensity and chronic herbivory testing the effect of shrub type, patch type (only medium shrub and shrub), and overgrowth.

	Trevenque				Boleta			
Source of variation	df	χ^2	*F*	*p*	df	χ^2	*F*	*p*
Risk of herbivory		24.76		0.0001		0.26		0.97
Overgrowth	1	11.26		0.0008	1	0.14		0.93
P	1	0.85		0.65	1	0.04		0.98
S	3	9.61		0.14	2	0.18		0.99
P × S	3	1.01		0.98	2	0.52		0.97
Damage intensity			2.78	<0.0001			0.69	0.55
Overgrowth	1		6.51	0.01	1		0.61	0.44
P	1		0.18	0.67	1		0.01	0.90
S	3		0.87	0.46	2		0.58	0.56
P × S	3		2.86	0.01	2		1.32	0.27
Error	227				122			
Chronic herbivory			3.23	<0.002			0.74	0.53
Overgrowth	1		0.42	0.52	1		0.13	0.72
P	1		4.59	0.03	1		8.82	0.003
S	3		1.70	0.17	2		0.06	0.94
P × S	3		0.99	0.39	2		0.65	0.52
Error	213				123			

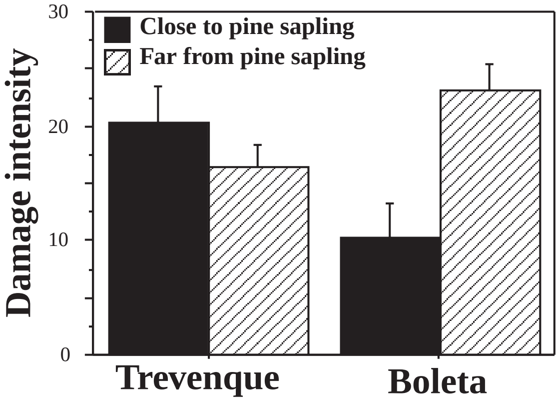
Note: Nonsignificant interactions were pooled with the error terms to increase dfs. Sapling height has been removed from the models, because no effect on herbivory was observed. P, patch type; S, shrub type.

Table 3. Summaries of the two-way ANOVAs analysing herbivory on nurse shrubs.

Source of variation	df	SS	*F*	*p*
Trevenque				
D	1	0.07	0.27	0.601
S	3	115.15	153.54	0.0001
D × S	3	0.12	0.15	0.928
Error	322	80.49		
Boleta				
D	1	1.74	7.23	0.008
S	3	60.83	84.42	0.0001
D × S	3	4.58	6.35	0.0003
Error	299	71.82		

Note: Distance from focal saplings refers to shrubs located close to or far from any pine sapling. Some shrubs have been removed from analyses, because the herbivory intensity could not be accurately determined. D, distance from focal sapling; S, shrub type.

Fig. 3. Damage intensity (percentage of shoots removed by ungulates) suffered by the neighbouring shrubs, close and far from *Pinus sylvestris* var. *nevadensis* saplings. Error bars are SEs.



our study sites seem not to benefit from any deterrent property of neighbouring shrubs other than mechanical barriers against the ungulates.

From our results, we would expect to find most Scots pine saplings growing in open interspaces or in places completely covered by shrubs, since these patches present less threat of damage. This idea is reinforced by the fact that mammalian herbivory has proven deleterious for saplings, severely retarding their growth rate and first-reproductive age (Zamora et al. 2001*a*). However, open interspaces are unsuitable patches for seedling establishment in these Mediterranean environments, because most seedlings die because of summer drought (Castro 2000). Consequently, the density of saplings is much higher in shrubby microhabitats than in open interspaces, the former ones representing the key microsites for pine-forest recruitment. The final spatial structure of Scots pines in the study site depends on the relative effect that each factor (summer drought (Castro et al. 2001) vs. mammalian herbivory) has on the dynamic of pine populations. The importance of shrubs may increase with the degree of drought stress (Bertness and Callaway 1994): more herbivory and more drought increase the importance of shrub cover as nurse plant for pine sapling. These results agree with additional experimental evidence (Castro et al. 2001; Zamora et al. 2001*b*) and allow us to conclude that shrubs play an important role in protecting saplings when their cover is high, by providing an amelioration of the harsh abiotic conditions (i.e., summer drought) and an effective protection against ungulates. In brief, the natural recruitment of pines in Mediterranean environments is favoured by shrubby microhabitats, and consequently, strategies for restoration must use shrub canopy as seeding or planting sites.

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