

Conditional outcomes in plant–herbivore interactions: neighbours matter

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Spatial distribution of palatable and unpalatable plants can influence the foraging behaviour of herbivores, thereby changing plant–damage probabilities. Moreover, the immediate proximity to certain plants can benefit other plants that grow below them, where toxicity or spines act as a physical barrier or concealment against herbivores. This paper presents the results of a multi-scale experiment performed to test the effect of shrubs as protectors of tree saplings against herbivores and the mechanism involved in Mediterranean ecosystems. We performed a factorial design in two mountain ranges, similar in physiognomy and vegetation, planting saplings of a palatable tree, the maple (*Acer opalus* subsp. *granatense*), and an unpalatable tree, the black pine (*Pinus nigra*), under three different types of shrubs. We considered four experimental microhabitats: highly palatable shrub (*Amelanchier ovalis*), palatable but spiny shrub (*Crataegus monogyna* or *Prunus ramburii*), unpalatable spiny shrub (*Berberis vulgaris* subsp. *australis*) and control (gaps of bare soil without shrubs). Three main factors were found to determine the probability of sapling attack: sapling palatability, experimental microhabitat and plot. Palatable saplings (maples) were browsed much more than unpalatable ones (pines). The degree of protection provided by the shrub proved greater as its palatability decreased with respect to sapling palatability, the unpalatable spiny shrub being the safest microhabitat for palatable saplings and bare soil for unpalatable ones. The differences found in number of attacked saplings between plots may be attributable to differences in herbivore pressure. The community context in which interaction takes place, namely the characteristics of the neighbours and the intensity of herbivore pressure, are determining factors for understanding and predicting the damage undergone by a target plant species. The mechanism that best explains these results is associational avoidance of saplings that grow near to unpalatable shrubs. It is necessary to introduce this neighbour effect in theoretical models and food-web approaches that analyse the plant–herbivore relationships, since it can strongly determine not only the intensity of the interaction, but also the spatial distribution and diversity of the plant community.

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Herbivory has traditionally been viewed as a binary interaction, focusing on a simple pair of interacting elements (one plant vs one herbivore; reviewed by Zamora et al. 1999). Consequently, most of the classical plant–herbivore theories have been founded on the way in which intrinsic plant traits influence herbivore preference, i.e. plant appearance, nutritional quality or

effectiveness and quantity of defences (Rhoades and Cates 1976, Bryant et al. 1983, Coley et al. 1985, Herms and Matson 1992). This species-to-species view of plant–herbivore interactions has been challenged by an increasing body of studies showing that plant–herbivore interactions strongly depend, in a predictable way, by the community context (Grubb 1992, Björkman and

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Hambäck 2003, Strauss and Irwin 2004). In this respect, differences in palatability of coexisting plant species can affect the interaction of a particular herbivore species with a particular plant species (Augner et al. 1991, Baraza et al. 2005). This conditionality should be particularly outstanding when the herbivore has a generalist trophic habit, and the plant community is composed of a diverse array of species differing in chemical and/or physical traits (Provenza et al. 2002).

Large generalist herbivores make foraging choices in a hierarchical fashion: plant communities at the landscape scale, feeding stations at the plant-community, and individual plants or plant parts at the bite scale (Senft et al. 1987). At the plant-community scale, spatial distribution of palatable and unpalatable plants can influence the foraging behaviour of herbivores, changing the plant-damage probability (Edwards et al. 1994, Etzenhouser et al. 1998). The surrounding matrix can be positive (attractive) or negative (repellent) in the herbivore's choice of a particular target plant. For example, palatable plants in a matrix of unpalatable vegetation may remain undetected by the herbivore and thereby escape consumption. This process is called associational resistance, associational defence, associational refuge, or plant-defence guilds (Tahvanainen and Root 1972, Pfister and Hay 1988, Holmes and Jepson-Innes 1989). However, when the herbivore is very selective, the result of the association with unpalatable plants can shift to greater consumption or damage of the edible species, a process called associational susceptibility, associational damage or shared doom (Atsatt and O'Dowd 1976, McNaughton 1978, White and Whitham 2000, Hambäck et al. 2000).

The immediate proximity to certain plants can benefit other plants that grow below them, when toxicity or spines act as physical barrier or concealment against herbivores (Callaway et al. 2000), acting as biotic refuges. We followed Milchunas and Noy-Meir (2002) definitions considering associational avoidance as an external defence mechanism that depends on foraging-behaviour decisions of the herbivore and palatability of a target plant individual relative to surrounding vegetation matrixes. Meanwhile biotic refuges have a structural component that grants direct physical protection to the potential target plant.

A considerable number of studies demonstrate a grazing protection component of woody and perennial plants that harbor other species growing under them (Milchunas and Noy-Meir 2002), enhancing community diversity (Olf et al. 1999, Callaway et al. 2000, Rebollo et al. 2002). Shrubs can protect saplings against herbivores (Callaway 1995, García and Obeso 2003), facilitating the regeneration of palatable tree species that would be untenable without shrub presence (Rousset and Lepart 1999, Meiners and Martinkovic 2002). Most of these studies represent shrubs as biotic refuges providing

physical barriers by means of their spines or toxicity. However, the importance of different protective mechanisms has rarely been evaluated, although the result of the interaction depends not only on the species involved, but also on the mechanisms of the interactions (Hambäck et al. 2003). When the interaction between species of different palatability was evaluated, such mechanisms as associational avoidance or susceptibility could become more important than biotic refuges (Rousset and Lepart 2002).

Mediterranean ecosystems constitute an ideal system to test the effect of neighbour vegetation on plant–ungulate interactions and their consequences for woody-plant diversity. Firstly, the very high diversity and heterogeneity of Mediterranean ecosystems, even at small spatial scales (Blondel and Aronson 1999), result in a great variety of shrub species intermingled with tree species within the same plot, producing a myriad of interacting combinations between sapling and shrub species (Vilá and Lloret 1996, Rousset and Lepart 1999, Gómez et al. 2001). Secondly, studies analysing spatial patterns of woody-plant establishment in Mediterranean ecosystems found that many woody species typically regenerate under pre-established vegetation (Herrera et al. 1994, Rey and Alcántara 2000, Castro et al. 2004, Gómez-Aparicio et al. 2004). Furthermore, high livestock pressure (of both wild and domestic livestock) persisting over thousands of years in Mediterranean habitats (Le Houérou 1981, Papanastasis and Peter 1998) has severely affected the regeneration ability of the most palatable tree species, changing the plant community at different levels (species diversity, spatial structure, ecological succession; Le Houérou 1981).

The present study presents the results of a multi-scale experiment performed to test the existence and mechanism involved sapling protection against herbivores by different kinds of shrubs. We represent the spatial heterogeneity of environmental factors determining herbivory by using a hierarchical model, where the continuous variation of heterogeneity with space is categorized in three nested scales of patchiness: 1) mountain ranges (regional level), 2) plot within mountains (local scale), 3) microhabitats within localities (microsite level). We evaluate the hypothesis that shrubs can protect saplings against herbivory, thereby potentially increasing plant-species diversity, and that this protection varies depending on the relative palatability both of the shrubs and the sapling. Specifically, our aim was to answer the following questions:

- 1) Is there a relationship between the degree of protection and the sapling palatability?
- 2) Is there a relationship between the degree of protection and the shrub palatability?

- 3) Which process best describes the phenomenon: biotic refuges, associational avoidance or associational susceptibility?
- 4) Is the shrub effect on the sapling-damage probability affected by differences in herbivore pressure at different spatial and temporal scales?

Material and methods

We performed the study in two mountain ranges, similar in physiognomy and vegetation, and selected two common forest tree species that represent the two extremes of palatability, according to previous studies in the area (Baraza et al. 2003). We also chose four shrubs species – similar in size and common as well as abundant in the study areas – which represent a gradient of palatability (Baraza 2004).

Study areas

The experiment was conducted in two Mediterranean mountain ranges of SE Spain: the Sierra Nevada National Park and the Sierra de Baza Natural Park. At both localities, the trees grow in open woodlands with a well-developed shrub understory. The tree species are mainly Scots (*Pinus sylvestris*) and black (*P. nigra*) pines, with some scattered individuals of Holm oak (*Quercus ilex*) and maple (*Acer opalus* subsp. *granatense*). Both mountains have a diverse array of intermingled shrubs, creating a fine-grained spatial mosaic of woody vegetation.

Wild ungulates (*Cervus elaphus* and/or *Capra pyrenaica*) are present on both mountains, and during summer, herds of domestic goat (*Capra hircus*) and sheep (*Ovis aries*) notably increase the grazing pressure.

Experimental design

We performed a factorial design to explore the result of the interaction between saplings of a palatable tree, the maple, and an unpalatable tree, the black pine, combined with a highly palatable shrub, (the grape pear *Amelanchier ovalis*), a palatable but spiny shrub, hawthorn

(*Crataegus monogyna*) or sloe (*Prunus ramburii*), and an unpalatable spiny shrub, the Spanish barberry (*Berberis vulgaris* subsp. *australis*) (see Castroviejo et al. 1986 and Muñoz-Garmedia and Navarro 1998 for species nomenclature and description). As a control, we used gaps of bare soil without shrubs (Table 1). Hereafter, the different shrub species and the bare soil are called experimental microhabitats.

Species palatability was determined as a function of their chemical and physical characteristics. Maple was considered more palatable than pines due its higher nitrogen concentration, lower fibre concentration and the lack of terpenes as defences (Baraza et al. 2003, Baraza 2004). With respect to shrub species, grape pear was considered highly palatable because of its chemical characteristics and lack of mechanical defences (Baraza 2004). Hawthorn and sloe were considered to be a single experimental microhabitat because of their similar palatability. Both species have lower nutritive qualities than grape pear (lower nitrogen and higher condensed tannin concentration, Baraza 2004) showing intermediate palatability, and bear caulinar spines as mechanical defence. Spanish barberry was considered unpalatable due to its strong defences, high content of alkaloids (Hartmann 1991) and high density of stipular spines (Illius et al. 2002).

In April 2003, three experimental one-hectare plots were established in each mountain range. Plots were separated by 300–1200 m. Each plot received eight saplings of each species in each experimental microhabitat, for a total of 384 saplings, 192 per species and 48 per experimental microhabitat. The saplings used in this experiment were 3 years old and 30–40 cm in height (large enough to be attractive to ungulates, Baraza 2004), coming from a nursery. Shrubs for planting were chosen with similar branching pattern and size (1–2 m height, 1–3 m wide), within and between plots. Saplings were planted in the inner part of the corresponding shrub, in order to maximize its potential protective role. Planting holes were dug 40 cm deep with a mechanical augur (10 cm in diameter). During the first month of the experiment, saplings were watered several times in order to encourage their survival. However, some of the saplings failed to root and were quickly replaced.

Since plant height can influence the probability of the sapling being eaten (Hartley et al. 1997), saplings were measured at the beginning of the experiment. No

Table 1. Experimental units according to the type of interaction between saplings and shrubs, depending on their palatability and presence of spines.

Sapling	Shrub			
	Highly palatable	Palatable with spines	Unpalatable with spines	Control
Maple (palatable)	maple with grape pear	maple with hawthorn-sloe	maple with barberry	maple in bare soil
Black pine (unpalatable)	black pine with grape pear	black pine with hawthorn-sloe	black pine with barberry	black pine in bare soil

significant differences were found between experimental microhabitats for sapling height (ANOVA, $F_{3,380} = 1.37$; $P = 0.2525$).

Saplings were visited several times during summer, when both survival and herbivore damage were recorded as the percentage of consumed twigs. For statistical analysis, we chose the data from two different time periods: June, corresponding to the beginning of the summer drought, and September, the end of summer drought, when the accumulated herbivory for the entire summer is evident. To estimate of the herbivory pressure in the plots, we registered the percentage of consumed twigs in the experimental shrubs. For each shrub, we counted 100 twigs throughout the shrub crown, noting the percentage of these consumed by ungulates. Furthermore, since herbaceous plants (grass and forbs) may attract ungulate herbivores (Palmer et al. 2003), we also estimated the cover of such plants in the experimental microhabitats, taking as unit a circle of 1 m radius, around the sapling in the microhabitat bare soil and below the canopy of the shrub in the other experimental microhabitats.

Statistical analysis

Herbivory was recorded first as a continuous variable (percentage of browsed twigs); however, the distribution of data was far from normality, since a high proportion of saplings were not attacked (% herbivory = 0) while others were completely consumed (% herbivory = 100). Consequently, to analyse the effect of different factors in the sapling consumption, we constructed a categorical variable with two levels: consumed or intact (Quinn and Keough 2002). This variable was analysed by using log-linear models (Quinn and Keough 2002), taking mountain range, plot nested in mountain range, sapling species, and experimental microhabitat as factors, while the state of the sapling at the beginning and at the end of summer drought were taken as response variables. The non-significant interactions between factors were excluded in order to increase the degrees of freedom of the model (Zar 1996). Furthermore, due to the complexity of the model and the data distribution (some cells always consumed, some cells always intact), interactions

including plot[mountain range] were discarded since they made the model unstable.

The relationship between herbivore damage in saplings, herbaceous cover in each experimental microhabitat, and herbivore pressure in each experimental microhabitat was explored by using Spearman rank correlations, since their distributions were far from normality (Shapiro–Wilk, $P < 0.05$, Zar 1996). Correlations were performed separately for maple and pine, because the quantity and distribution of saplings undergoing herbivory for each species were quite different. In the same way, differences in herbaceous cover between experimental microhabitats and in herbivore damage undergone by shrubs between experimental plots were analysed with the Kruskal–Wallis test (Zar 1996).

Results

At the beginning of the summer drought, the mountain range, sapling species and experimental microhabitat factors significantly affected the sapling probability of been eaten (Table 2, Fig. 1). Differences between species were outstanding, since 45% of the maples, but only one pine, were attacked. Furthermore, the probability of attack significantly differed among experimental microhabitats, decreasing in the order: bare soil, grape pear, hawthorn-sloe and barberry (Fig. 1). The proportion of attacked maples was greater in Sierra de Baza than in Sierra Nevada (Fig. 1).

Differences between sapling species persisted at the end of the summer drought (Table 2) since pines underwent very scant damage, while more than half of the maples had been attacked by herbivores (Fig. 2). The probability of attack also significantly differed depending on the experimental microhabitat (Table 2, Fig. 2). Maple saplings planted in bare soil were the most severely attacked, with 100% of the saplings damaged in some of the plots, but differences with saplings planted under grape pear were scant (Fig. 2). The protective role of hawthorn-sloe differed between plots, with a probability of attack sometimes lower than and sometimes similar to that of saplings planted under grape pear (Fig. 2). Barberry was the safest microhabitat

Table 2. Results of the logistic model: effect of different factors on the probability of the sapling to undergo herbivory at beginning of drought ($R^2 = 0.500$) and at the end of drought ($R^2 = 0.5837$).

	Beginning of drought			End of drought		
	df	χ^2	P	df	χ^2	P
Species	1	32.2165	<0.0001	1	82.4400	<0.0001
Microhabitat	3	36.4742	<0.0001	3	15.4823	0.0014
Mountain range	1	17.8776	<0.0001	1	4.0742	0.0435
Plot[mountain range]	4	5.4737	0.2420	4	50.0331	<0.0001
Species \times microhabitat				3	18.2605	0.0004
Model	9	207.9502	<0.0001	12	299.9196	<0.0001

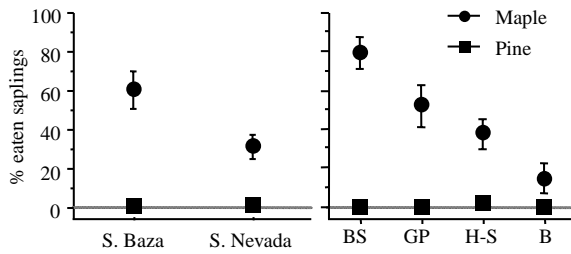


Fig. 1. Percentage of saplings browsed in each mountain range and in each experimental microhabitat (BS = bare soil, G = grape pear, H-S = hawthorn-sloe, and B = barberry) at the beginning of drought. Vertical lines in points represent SE when plots are considered as units.

in most cases (Fig. 2). The species \times microhabitat interaction proved significant (Table 2) since the protective effect of shrubs in relation to maple saplings did not extend to pine saplings.

At the end of summer drought the difference between mountain ranges for the total saplings attacked was smaller than at the beginning, while the difference in the distribution of attacked saplings between plots within each mountain range was significant (Table 2). For instance, in Sierra Nevada, saplings in plot 3 were less damaged than in plot 1 and 2 (Fig. 2).

The herbivore damage undergone by shrubs consistently showed significant differences between plots (grape pear: $H = 37.09$, $P < 0.0001$; hawthorn-sloe: $H = 22.08$, $P = 0.0001$; barberry: $H = 14.11$, $P = 0.0149$; Kruskal–Wallis). Barberry invariably showed the lowest damage intensity, hawthorn-sloe intermediate, and grape pear the highest, with up to 90% of twigs attacked (Fig. 3). Conversely, the herbaceous cover was higher under barberry and hawthorn-sloe (20% of median in

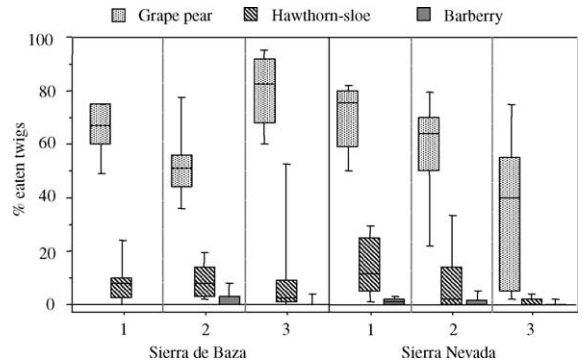


Fig. 3. Box plot for the distribution of damage intensity (percentage of twigs removed by ungulates) undergone by the different shrub species in each plot.

both) than under grape pear or in bare soil (10 % of median in both; $H = 36.90$, $P < 0.0001$, Kruskal–Wallis). These wide variations in damage undergone by the shrubs and in the herbaceous cover were not correlated with the herbivore damage of pine saplings (Table 3), mainly because herbivore damage in pines was very low. In the case of maple saplings, variations in herbivore damage revealed a positive and significant relationship with shrub damage, while the relationship with the herbaceous cover was negative and only marginally significant (Table 3).

Discussion

According to our results, three main factors determine the probability of sapling attack: the sapling species, the experimental microhabitat, and the plot, these

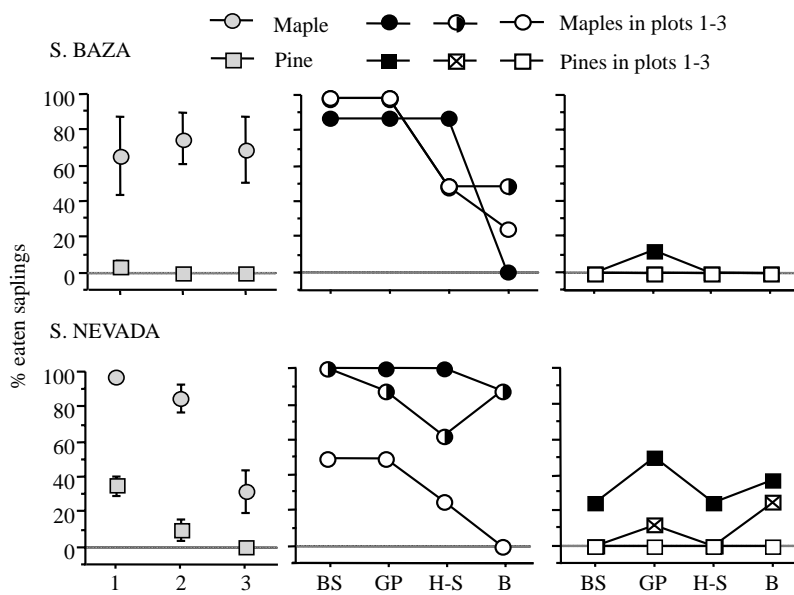


Fig. 2. Percentage of saplings browsed (maples circles and pines square) at the end of drought, in each mountain range (Sierra de Baza, upper, and Sierra Nevada, low), in each plot (different symbols) and in each microhabitat (BS = bare soil, G = grape pear, H-S = hawthorn-sloe, and B = barberry). Vertical lines in points represent SE when plots are considered as units.

Table 3. Spearman-rank correlation between herbivory intensity suffered by saplings and both herbivory intensity suffered by shrubs and herbaceous cover surrounding the sapling.

Sapling	Variable	Variable	ρ	P
Pine	% herbivory	% shrub herbivory	0.1172	0.1633
	% herbivory	% herbaceous cover	0.0005	0.9942
Maple	% herbivory	% shrub herbivory	0.3940	<0.0001
	% herbivory	% herbaceous cover	-0.1428	0.0481

corresponding to three levels of herbivore food selection: the bite, the plant and the feeding area (Danell and Bergström 2002). Thus, palatable species such as maple are usually attacked whereas unpalatable species such as black pine only rarely are. Moreover, sapling damage depends both on sapling and shrub palatability (Callaway 1992, Rousset and Lepart 2002). The degree of protection offered by the shrub is greater as its palatability decreases with respect to sapling palatability. A palatable sapling such as maple showed a positive and significant relationship between herbivory undergone by each shrub species and herbivory on saplings planted below them, suggesting that the probability a sapling being attacked depends on the attractiveness of the shrub. A highly palatable shrub promotes high herbivory in the sapling beneath it; while an unpalatable shrub reduces the probability of attack (Rousset and Lepart 2002). In any case, none of the shrubs used in this experiment, even those heavily armed with spines, provided total protection. In fact, saplings under hawthorn or sloe had a higher probability of being attacked than under barberry, which indicates that spines are not the only factor determining the protective role of the shrub. A different case resulted with the pine saplings. The pines, although without significant differences, tended to be attacked mainly under shrubs, thus corresponding to a case of associational susceptibility (Milchunas and Noy-Meir 2002). Bare soil was advantageous for black pine, since its palatability was lower than most of the shrubs, and therefore it did not attract herbivore attention when growing alone. Similar results were found by Gómez et al. (2001) in a closed area with Scots pine, where saplings growing in open patches far from the shrubs escaped from herbivory more frequently and incurred less damage than did saplings growing close to shrubs.

The herbaceous cover could constitute a secondary attraction to herbivores, as suggested by the negative relationship between the percentage of herbaceous cover and the intensity of herbivory in maple saplings. In most cases, a grazing herbivore attracted to the shrub by the herbaceous cover beneath does not consume the sapling, but during the summer drought, with most of the grasses already dry, the probability of damage to the woody plants increases (Posse et al. 1996, Bartolomé et al. 1998). Thus, plot 1 in Sierra Nevada showed a net increase in herbivore attack for sapling under shrubs

(both maple and pine) from the beginning to the end of drought. Once the herbivore was attracted by the shrub, the probability of attack upon the sapling depended on its palatability, and this progressively increased as other feeding resources (as herbaceous cover) decreased.

With respect to the selection of the feeding area, the differences found in number of attacked saplings between plots in each mountain range may be attributable to a non-uniform distribution of the herbivores in the landscape. In our case, differences in herbivore pressure between plots resulted in different numbers of saplings browsed. In fact, most of the pines attacked were in the plot 1 in Sierra Nevada, which overall showed both the highest proportion of attacked saplings and the highest level of shrub herbivory.

Similarly, the protection against herbivory varied widely among the different shrubs, depending on herbivore pressure. For instance, barberry did not effectively protect maple saplings situated beneath them when the herbivore pressure was high (in plot 1 in Sierra Nevada, more than 75% of maples under barberry were attacked), or when abiotic conditions were extreme, and animals were forced to eat less palatable plants (at the end of drought). Accordingly, spiny but palatable shrubs such as hawthorn and sloe provided protection only when herbivory pressure was low. In this manner, the external defence of a sapling growing below a shrub depended on herbivore plant selection and on the abundance of other feeding resources, and no physical barrier was completely successful. This is more in agreement with a framework of associational avoidance than of biotic refuges (Milchunas and Noy-Meir 2002). Moreover, herbivore pressure acts as one of the most important and potentially variable factors affecting the degree of sapling protection by shrubs. In this context, we propose a conceptual scheme that shows the different result of the interaction between ungulates, shrubs and saplings (Fig. 4). With high herbivore pressure, only unpalatable shrubs can protect palatable saplings, while for unpalatable saplings the probability of attack tends to increase when growing near shrubs. On the contrary, with a low herbivore pressure, shrubs of intermediate palatability may protect palatable saplings from herbivores, while the protective role of unpalatable shrubs increases, and unpalatable saplings are safe in any microhabitat. With intermediate herbivore pressures, palatable saplings decrease their probability of attack by growing under

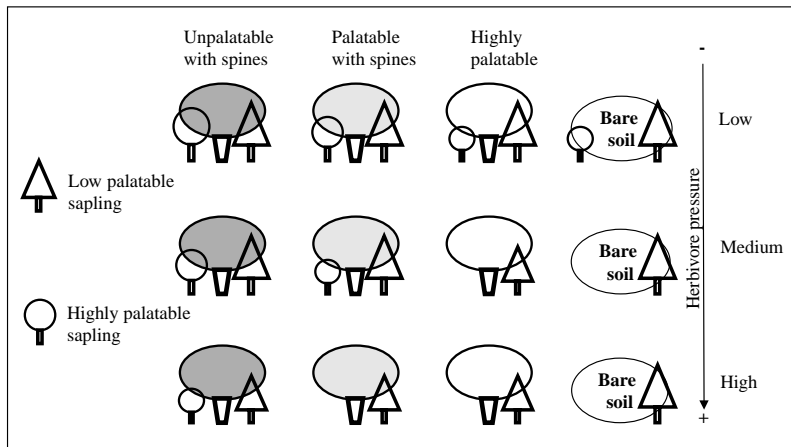


Fig. 4. Sapling damage probability depends on sapling palatability, microhabitat of growth and herbivore pressure. Smaller sapling figures represent more probability of been eating and as a result less probability of establishment. With high herbivore pressure (lower row) palatable saplings escape ungulate damage only when growing under unpalatable shrubs, while for unpalatable saplings the probability of attack increases when growing near shrubs. On the contrary, with a low herbivore pressure (upper row), palatable saplings can occupy all microhabitats, but damage probability is lower under shrubs of intermediate or no palatability, while the damage probability for unpalatable saplings is close to zero

for all microhabitats. With intermediate herbivore pressure (mid row), palatable saplings decrease their probability of attack growing under shrubs of intermediate palatability or no palatable. In this case the proximity of palatable shrubs can increase damage to unpalatable saplings.

shrubs of intermediate or low palatability, whereas unpalatable saplings will start to undergo damage when growing under shrubs (Fig. 4). These findings show that the quality of a microhabitat for recruitment is highly dependent on the degree of herbivore pressure, together with palatability of saplings and shrub. Consequently, the landscape can change from being, at a low herbivory level, a high-quality matrix (both open and shrubs) for sapling recruitment to becoming, at high herbivore levels, a low-quality matrix where only unpalatable shrubs constitute available patches for recruitment.

The high shrub diversity in the Mediterranean ecosystems can promote the appearance of reliable associational avoidance processes for palatable saplings, as happened with maple in this study. This protection of the understory diversity in Mediterranean woodlands can be of special importance, especially when herbivore pressure is moderate or high (Callaway 1995, Rousset and Lepart 1999, Meiners and Martinkovic 2002, García and Obeso 2003), in order to enhance the regeneration of the tree species of the woodlands. Thus, nurse plants can provide protection from browsing, increasing plant-community diversity by harbouring sensitive species (Milchunas and Noy-Meir 2002, Rebollo et al. 2002). From the sapling standpoint, the neighbourhood effect conditions regeneration capacity depending on the vegetation matrix and therefore on its spatial distribution. Open gaps would preferentially allow regeneration of the less palatable tree species, whereas palatable species regenerate only in patches having an abundant cover of less palatable shrubs (Olf et al. 1999, Rousset and Lepart 1999). Thus, high herbivory pressure would favour the coexistence of different tree species in different patches of the same plot (Jeltsch et al. 1996). From the herbivore perspec-

tive, the neighbourhood effect determines the importance that one plant has in its diet in comparison with other species, influencing how the herbivore can filter the plant-species composition (Provenza et al. 2002).

In conclusion, the community context in which interaction takes place, namely the characteristics of the neighbours and the intensity of herbivore pressure, are determining factors for understanding and predicting the damage undergone by a target plant species. There are different examples where the characteristics of the matrix can affect the trophic selection of a mobile generalist consumer looking for a sessile resource: insect and vertebrate herbivores, both in terrestrial and aquatic systems (Atsatt and O'Dowd 1976, Hay 1986, Holmes and Jepson-Innes 1989, Hjältén et al. 1993, Karban 1997, Mulder and Ruess 1998, Hambäck et al. 2000, Gagnon et al. 2003, Palmer et al. 2003, Poore 2004). Thus, it is necessary to quantify this neighbour effect accurately over a broad range of ecological scenarios when analysing plant-herbivore relationships, since these kinds of indirect effects can strongly determine: 1) the likelihood or intensity of paired interactions in plant-animal food webs, 2) the spatial distribution of the vegetation, with the more sensitive species restricted to safe sites whereas the least palatable spread everywhere, and 3) the diversity of woody plant communities, by harbouring sensitive species.

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