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# Yew (*Taxus baccata* L.) regeneration is facilitated by fleshy-fruited shrubs in Mediterranean environments

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**Abstract**

Yew *Taxus baccata* is catalogued as a species endangered and prone to extinction in the Mediterranean mountains of southern Spain, due to the small size and senescent status of most populations. In this paper, we study the effects of herbivory and the protective role of woody shrubs in the regeneration ability of the yew in the Sierra Nevada. The estimated density of the yew in the study plot was 287.9 individuals/ha, more than 90% being juveniles (seedlings and saplings), which were mostly located under fleshy-fruited shrubs. Saplings suffered serious herbivore damage when unprotected by shrubs. Thus, fleshy-fruited shrubs proved to be the best habitat for seedling establishment and sapling survival and growth. The abundance of fleshy-fruited shrubs in our study site provides a yew population characterized by an active regeneration under natural conditions. We suggest that the maintenance of healthy populations of yew in Mediterranean mountains is strongly dependent on the conservation of well-developed fleshy-fruit understories and their community of avian dispersers. © 2000 Elsevier Science Ltd. All rights reserved.

*Keywords:* Herbivory on seedlings and saplings; Mediterranean environments; Plant–plant facilitation; Population regeneration; Yew *Taxus baccata*

## 1. Introduction

Yew (*Taxus baccata* L., Taxaceae) is a long-lived native tree species widely distributed throughout Europe but declining sharply over most of its range (Tittensor, 1980; Hulme, 1996, and references therein). In the Mediterranean Basin, as happens with other plant species of boreo-alpine origin (Bennett et al., 1991; Cox and Moore, 1993; García et al., 1999), this species is restricted to the mountain areas, following the climatic regression after the last Ice Age. As a result of climate change and human disturbance over centuries, yew distribution in the Mediterranean Basin is formed by a reduced number of small isolated patches, populations being located mainly in shady ravines on northern montane slopes (Franco, 1986). In Andalusia (southern Spain), yew populations are small, most with less than 10–20 individuals, and dominated by senescent individuals, with a very low proportion of saplings and seedlings. These data imply an apparent regeneration failure of most populations and, consequently, yew has been catalogued as endangered and prone to extinction in these areas (Hernández and Clemente, 1994).

Natural regeneration of the yew in temperate latitudes appears limited by both seed-predator pressure and the scarcity of microsites for recruitment (Hulme, 1996, 1997; Wilson et al., 1996). Moreover, yews are frequently damaged by vertebrate herbivores despite the foliage being strongly poisonous (Tittensor, 1980; Allison, 1990a, b; Font Quer, 1995). Under herbivore pressure, juvenile yews benefit from the protective role of nurse plants which mechanically defend yews from browsers. This idea has been supported by the relationship between the development of prickly shrublands as a seral stage prior to the establishment of well-developed yew populations in Great Britain (Watt, 1926; Tittensor, 1980; Hulme, 1996).

The possible dependence of yews on facilitative nurse shrubs to regenerate might be even more evident in Mediterranean environments, characterised by high ungulate pressure and strong summer drought, both being factors which limit natural regeneration of many boreal-origin woody species [drought for *Abies pinsapo* (Arista,

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1994) and *Juniperus communis* (García et al., 1999); ungulate herbivory for *Pinus sylvestris* var. *nevadensis* (Hódar et al., 1998)]. In this paper, we analyse the effects of herbivores and the potential protective role of woody shrubs in the regeneration ability of the yew in Mediterranean environments. Studying the regenerative traits of the yew in the Sierra Nevada (SE Spain), we seek to determine:

1. The regeneration ability of this population by its age structure.
2. The distribution of juvenile yews by microhabitats and the role of nurse woody shrubs in relation to herbivore damage.

## 2. Material and methods

### 2.1. Natural history and study site

Yew is a slow-growing evergreen tree, its longevity reaching up to 1000 years. Although in central Europe and the British Isles this species can form dense stands or woodlets, in southern Europe it grows in small stands (Tittensor, 1980; Kelly, 1981; Hernández and Clemente, 1994; Hulme, 1996, 1997). Yew is dioecious and wind-pollinated. Every year, female individuals bear axillary cones which in autumn develop fleshy red arils containing a single seed. In the Mediterranean mountain areas, seeds are dispersed mainly by frugivorous birds (*Turdus merula*, *T. torquatus* and *T. viscivorus*; authors' personal observation). Dispersed seeds are strongly dormant but do not form a persistent seed bank (Melzack and Watts, 1982; Zhiri et al., 1994; Hulme, 1996). During this post-dispersal stage, seeds can be predated by rodents [mainly the woodmouse *Apodemus sylvaticus*; see Hulme (1996, 1997)]. Seedlings start to emerge in the second spring after seedfall (Melzack and Watts, 1982). Yews can suffer herbivory by insects and, especially severe, by browsing ungulates which damage leaves, shoots and bark (Tittensor, 1980; Kelly, 1981; Allison, 1990a,b).

This study was conducted in 1998–1999 in an autochthonous montane pine stand located near Trevenque peak (1700 to 1950 m a.s.l.; 37°06′N, 3°21′W; Sierra Nevada, Granada, SE Spain), composed of native *Pinus sylvestris* var. *nevadensis*, with a dense shrub understory. The climate is of Mediterranean mountain type, with rainfall (825 mm year$^{-1}$, average 1990–1998) heaviest in autumn and spring, hot dry summers and cold snowy winters. The area supports natural populations of *Capra pyrenaica* year round and extensive livestock during the summer [domestic goats and sheep; Hódar et al., (1998)]. Furthermore, the forest is visited during autumn and winter by thrushes which actively feed on yew fruits [authors' personal observation; see also Jordano (1993)].

### 2.2. Habitat structure

Habitat structure and vegetation coverage were sampled in the study area by means of 10 linear 50-m transects (Bullock, 1996), randomly located to cover a representative area of the stand (ca. 4 ha). At each meter of the tape the presence/absence and the identity of vegetation covering ground were recorded at two points, 1 m each perpendicular to the transect ($n=100$ sampling points per transect, 1000 points total).

### 2.3. Seedling sampling

Seedling (individuals below 5 years old) abundance and spatial distribution was sampled noting age and herbivore damage for each individual. Seedling counts were made in 30 quadrats of 4 m$^2$ in the following different habitats in the study area: yew, areas under the canopy of adult yews; pine, areas under the canopy of adult Scots pines; open, areas bare of woody shrubs; NFFS, areas below non-fleshy-fruited shrubs; and FFS, areas below fleshy-fruited shrubs. For the microhabitats under shrubs, and due to the difficulty of finding homogeneous surfaces of 4 m$^2$, we used sampling areas of variable surface areas (corresponding to the basal area of the shrub), covering a minimum of 30 sample units and 100 m$^2$ (NFFS: $n=83$ sample units, 123 m$^2$; FFS: $n=35$, 201 m$^2$). Additionally, we considered as a microhabitat the area surrounding a mountain spring ($n=22$ quadrats) located in the study site, in order to control for the possible effects of higher water availability in yew recruitment, as shown for other woody species in Mediterranean montane areas [see García et al. (1999) for *J. communis*].

### 2.4. Spatial distribution of saplings

Saplings (non-reproductive individuals $\geqslant 5$ years old) spatial distribution and habitat was studied using two variables: (1) Angle of contact (°), angle of direct contact between the yew and the surrounding shrubs; and (2) Shrub cover, percentage of soil surface covered by woody vegetation in four 1-m transects in the cardinal axis centered on the sapling and with sampling points at 0.25, 0.5, 0.75 and 1 m from the yew. Depending on the level of association with shrubs described by these variables, the habitat for each sapling was assigned to one of three main categories: (a) open, when the yew grew in a open site or was surrounded by $<180°$ of woody shrubs directly in contact with it; (b) NFFS, when the yew was surrounded by $\geqslant 180°$ of non-fleshy-fruited woody shrubs; and (c) FFS, when the yew was surrounded by $\geqslant 180°$ of fleshy-fruited woody shrubs. We did not consider the habitats pine and yew in the case of saplings because very few saplings were found growing under these tree species, and all of them were simultaneously growing under fleshy-fruited shrubs (and, thus, were classified under this category). In addition, we estimated the age of the saplings as the number of whorls of the main shoot [for this procedure with other conifers, see Edenius et al. (1995); Hódar et al. (1998)].

### *2.5. Herbivore damage on juvenile yews in relation to protection by shrubs*

The intensity of herbivory was quantified for all juvenile yews (seedlings and saplings) by means of three parameters: (1) risk of herbivory, percentage of browsed plants; (2) damage intensity, proportion of shoots damaged by ungulates, quantified by counting the number of total shoots as well as the number of shoots browsed by ungulates; and (3) magnitude of repeated herbivory (% losses). We considered the proportion of losses of apical dominance (that is, the number of apical dominance losses divided by the age of the yew) as an estimate of the herbivory pressure undergone by each juvenile since establishment [see Hódar et al. (1998), for a similar procedure]. The association between the juvenile yews and the surrounding vegetation, in relation to herbivory, was assessed by two complementary indexes: (1) shrub height (cm), maximum height of the shrub making direct contact with the yew; and (2) overgrowth (cm), difference between the height of the yew and the maximum height of the shrub in direct contact with the yew. A negative value of this variable indicates that the shrub overgrows the yew. In addition, the rate of height growth of each tree was estimated by dividing its height by its age [see Danell et al. (1991) for a similar procedure].

### *2.6. Yew population structure*

The following parameters were used to characterize population structure: (1) population density (no. of individuals $ha^{-1}$). This density is expressed using as raw data the total number of adults and saplings in a plot of 1.9 ha located in the centre of the study area. The density of seedlings was calculated by extrapolating to the entire plot, according to the coverage of the different habitats, the data collected in the sampling quadrats (see Section 2.3); (2) age structure, expressed by the percentages of adults, saplings and seedlings in the population; (3) sex ratio; and (4) ratio of seedling to adult density [see also Hulme (1996)]. Adult age was estimated from trunk basal diameter assuming a mean annual growth rate of 1 mm $year^{-1}$ [see Hulme (1996) for a comprehensive description of this assumption]. Sex was determined by the presence of male or female cones.

### *2.7. Statistical analysis*

Most of the statistical analyses were performed using non-parametric statistics. To test whether the growth rate differed between damaged and undamaged saplings, we used an ANCOVA, introducing damage as independent variable, height as covariate and the rate of height growth as a dependent variable (Dowdy and Wearden, 1991). Significance of the statistical analyses was fixed to the standard level, $P<0.05$ (Zar, 1996). However, to avoid type-I error when statistically analysing more than one related variable, we chose the sequential Bonferroni test for fitting the significance level (see Rice, 1989).

## 3. Results

### *3.1. Habitat structure and spatial distribution of juvenile yews*

The study plot was covered mainly by fleshy-fruited shrubs, the dominant species being *Juniperus communis*, *J. sabina*, *Berberis hispanica* and *Rosa* spp. (Table 1).

The density of seedlings varied significantly between habitats, with the areas under fleshy-fruited shrubs showing the highest density values (Fig. 1; $H=22.15$, $P=0.0005$, df $=5$, Kruskall–Wallis test). The areas

Table 1
Habitat structure (percentages of cover of different plant species) in the study plot[a]

| | % cover |
|---|---|
| *Pinus sylvestris* | 21.3 |
| *Taxus baccata* | 3.0 |
| *Acer granatense* | 1.7 |
| *Lonicera arborea* | 2.0 |
| Σ Trees | 28.0 |
| *Amelanchier ovalis* | 0.4 |
| *Berberis hispanica* | 11.6 |
| *Cotoneaster granatensis* | 0.3 |
| *Crataegus granatensis* | 0.4 |
| *Juniperus communis* | 16.9 |
| *Juniperus sabina* | 11.8 |
| *Prunus ramburii* | 3.5 |
| *Rosa* spp. | 4.6 |
| Other fleshy-fruited shrubs | 1.0 |
| Σ Fleshy-fruited shrubs | 50.5 |
| *Astragalus granatensis* | 0.1 |
| *Erinacea anthyllis* | 3.9 |
| *Genista versicolor* | 6.4 |
| *Ononis aragonensis* | 10.5 |
| *Salvia oxyodon* | 0.2 |
| Other non-fleshy-fruited shrubs | 2.2 |
| Σ Non-fleshy-fruited shrubs | 23.3 |
| Grasses | 11.7 |
| Bare ground | 11.6 |
| Rock | 2.7 |

[a] $n=100$ sampling points per transect, 1000 points as a whole.

under yew canopy, as well as those close to the mountain spring showed intermediate densities of seedlings, whereas under pine and non-fleshy-fruited shrubs registered low densities. No seedling was found in the open microhabitat (Fig. 1).

Saplings were associated with fleshy-fruited shrubs more than expected according to shrub cover (see Table 1) in the study plot ($\chi^2 = 18.81$, $P < 0.0001$, df = 2; Fig. 2). Most juveniles (saplings + seedlings) were thickly surrounded by woody shrubs, showing high values in the angle of contact and in the shrub cover in the surrounding patch (Fig. 3). Very few yews overgrew the nurse shrubs, most of these being 50 cm below the upper border of the shrub (Fig. 3).

### 3.2. Herbivore damage in relation to shrub protection

Ungulate herbivores attacked 31.1% of the 103 labelled juvenile yews. Damaged plants lost an average of 23.0 ± 3.6% ($n = 31$) of their shoots to ungulates, damage reaching 67.7% in some individuals. The magnitude of repeated herbivory positively and significantly correlated with damage intensity ($\rho = 0.737$, $P < 0.05$ after Bonferroni adjustment, $n = 101$). In addition, the percentage of losses of apical dominance was significantly higher in damaged plants than in undamaged ones (19.1 ± 2.3% vs. 3.4 ± 1.5%, $U = 171.50$, $Z = -7.35$, $P < 0.0001$, Mann–Whitney test).

Undamaged seedlings and saplings were younger than damaged ones (Table 2). In addition, damage intensity was positively and significantly correlated with height and age ($\rho > 0.260$, $P < 0.05$ after Bonferroni adjustment, $n = 86$, for both Spearman rank correlations).

The risk of being browsed significantly declined with increased the angle of contact, the shrub cover and the height of the nurse shrub above the yew (Table 2). Furthermore, damage intensity decreased significantly with a greater angle of contact, the shrub cover and the height of the nurse shrub ($\rho < -0.260$, $P < 0.05$ after Bonferroni adjustment, $n = 86$). There was a positive

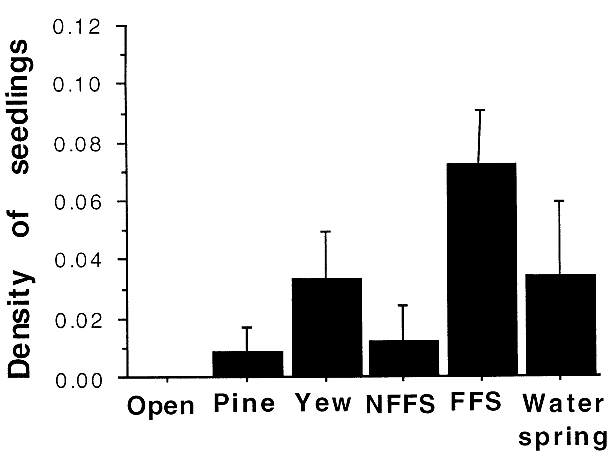


Fig. 1. Mean value (+1 S.E.) of the density of seedlings (no. of seedlings $m^{-2}$) found in different microhabitats in the study site (see Methods for microhabitat description).

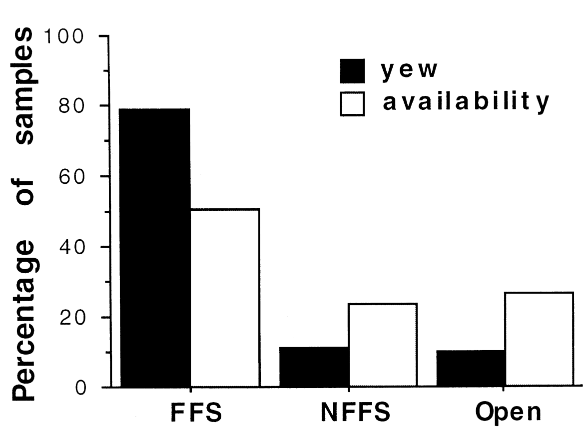


Fig. 2. Comparison between the different habitats occupied by sapling yews in the study plot and the availability of these habitats in the area, estimated as the cover according to Table 1.

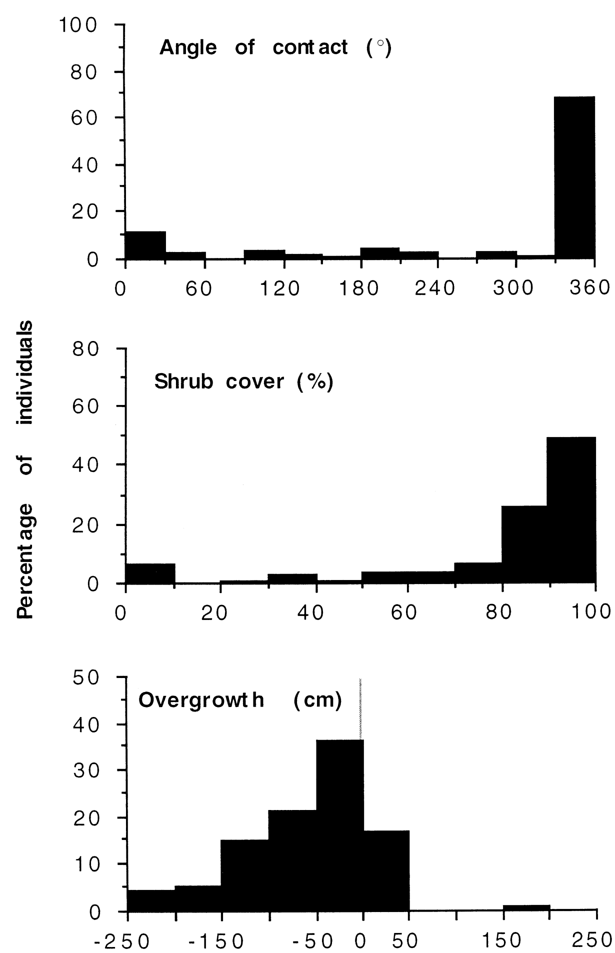


Fig. 3. Distribution of values of the angle of contact with nurse shrubs, the percentage of contacts with woody shrub in the surrounding path and the overgrowth distance with the shrub measured in the juvenile yews. Positive overgrowth values indicate that yew overgrows the shrub and negative values that the shrub overgrows the yew.

Table 2
Mean values (± 1 S.E.) of the individual traits (Height and Age) as well as the characteristics related with the presence of surrounding nurse shrubs (Angle of contact, Shrub cover, Shrub height, Overgrowth) measured on juvenile yews, depending on ungulate herbivory (damaged vs undamaged)[a]

| | Damaged | Undamaged | $\chi^2$ | P |
|---|---|---|---|---|
| Height (cm) | 53.47 ± 5.91 (32) | 38.91 ± 5.96 (69) | 2.16 | 0.141 |
| Age (years) | 15.97 ± 1.85 (32) | 9.27 ± 1.19 (71) | 8.49 | 0.0036 |
| Angle of contact (°) | 226.41 ± 27.42 (32) | 301.97 ± 13.57 (71) | 6.91 | 0.0086 |
| Shrub cover | 69.76 ± 5.69 (31) | 85.87 ± 2.95 (69) | 6.79 | 0.0091 |
| Shrub height (cm) | 81.54 ± 10.94 (26) | 113.76 ± 7.61 (64) | 5.92 | 0.0153 |
| Overgrowth (cm) | −23.58 ± 10.29 (26) | −72.59 ± 8.37 (63) | 11.88 | 0.0006 |

[a] The sample size for each group is shown in parentheses. The results of the logistic regression relating these variables with the probability of being damaged are also shown.

relationship between overgrowth and damage intensity ($\rho = 0.423$, $P < 0.05$ after Bonferroni adjustment, $n = 86$). The more the juveniles were hidden beneath shrubs, the lower was the intensity of damage (Table 2).

Herbivory was associated with a significant growth-rate depression in juvenile yews (Table 3), with damaged plants showing a lower rate of height growth (3.63 ± 0.30 cm/year) than undamaged ones (4.09 ± 0.20 cm/year).

Table 3
Summary of the ANCOVA analysis to compare the rate of height growth values (Height/Age) between damaged and undamaged yew juveniles

| | df | SS | F | P |
|---|---|---|---|---|
| Model | 2 | 3.17 | 10.04 | < 0.0001 |
| Herbivory | 1 | 1.12 | 7.11 | 0.0008 |
| Height | 1 | 2.47 | 15.69 | < 0.0001 |
| Error | 98 | 15.46 | | |

### 3.3. Population structure

The estimated density of yews in the study plot was 287.9 individuals $ha^{-1}$, most individuals being seedlings, and adults and saplings showing similar frequency of appearance (less than 10%; Table 4). The sex ratio was strongly female biased, with 2.3 females per male ($P = 0.003$, binomial test). Adult age ranged from 60 to 1050 years (Fig. 4), with males tending to be younger than females (Fig. 4), although there was no between-sex difference in age ($Z = -0.916$, $P = 0.359$, median test). Most of saplings ranged between 10 and 30 years and seedlings distributed around 3 years (Fig. 4).

Table 4
Density (no. of individuals $ha^{-1}$) and percentage of yews belonging to different stage-classes in the study plot

| | Density | % |
|---|---|---|
| Adults | 22.63 | 7.86 |
| Saplings | 27.89 | 9.69 |
| Seedlings | 237.37 | 82.45 |

## 4. Discussion

Our yew population was characterized by an active regeneration under natural conditions. Considering the density and proportion of seedlings and saplings as an indicator of recruitment, our results are similar to or even more favourable than those from other European populations, outside the Mediterranean climate, where conservation status is favourable (see data from Hulme, 1996). The conservation value of this population is reinforced when considering the current status of this species in southern Spain, where all the reported populations are composed of a few senescent adults and where regeneration appears to have collapsed, presenting a high risk of extinction (Hernández and Clemente, 1994; Junta de Andalucía, 1998). The contrasting picture offered by our population may be due to the high value of fleshy-fruited plant cover [ > 50% in our study site, higher than in other similar mountain localities in SE Spain; García (1998)], the habitat where most of seedlings and saplings appeared. Additionally, the reported differences between our data and those of previous surveys may be related to the specific methodology and the habitat considerations we used to sample seedlings, which are difficult to detect in extensive surveys due to their small size and hidden location under shrubs.

### 4.1. Seedling and sapling association to fleshy-fruited shrubs

Most yew seedlings were under fleshy-fruited shrubs, but also under adults and close to the mountain spring (Fig. 1). The association between fleshy-fruited plants and yew seedlings also applied to saplings which, however, were absent from areas under adults and, especially,

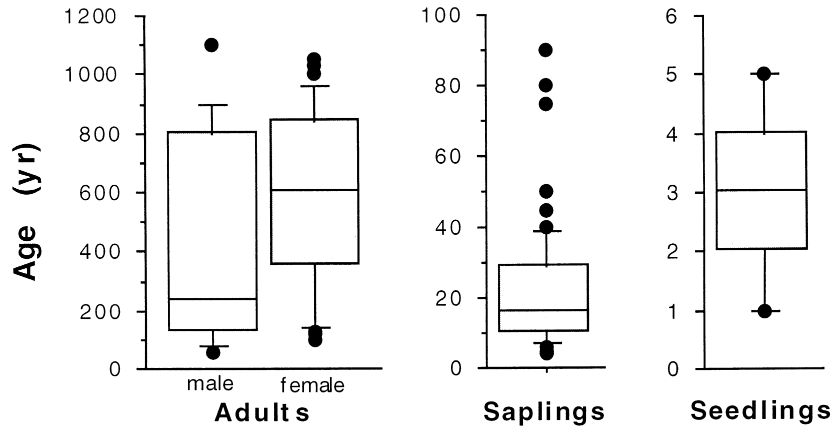


Fig. 4. Box plots representing the age (in years) of adult (males and females), sapling and seedling yews in the population studied.

from the water spring. This situation contrasts with those found for other similar boreal-origin woody species in Mediterranean mountains, where wet meadows close to springs are the habitats most favourable for the recruitment both of seedlings and of saplings [García et al. (1999) for *J. communis*]. Although our study does not discriminate between seed input and seedling establishment, considering that fleshy-fruited shrubs are the best habitats for seedling and sapling establishment, our results suggest a clear spatial concordance throughout different phases of yew recruitment (see also Jordano and Herrera, 1995; Schupp and Fuentes, 1995).

The origin of the association between yew and fleshy-fruited shrubs can be explained by two non-exclusive factors. Firstly, Mediterranean fleshy-fruited plants attract high numbers of avian frugivores during fall and winter, acting as sinks where the seeds of many species, the yew among them, accumulate disproportionately (Izhaki et al., 1991; Debussche and Isenmann, 1994; Herrera et al., 1994; García, 1998). This idea is reinforced by the lack of establishment under non fleshy-fruited shrubs, places where the seed rain by avian frugivores rarely occurs. Secondly, the role of fleshy-fruited shrubs as nurse plants is, primarly, related to the favourable microenvironmental conditions for germination and first-year seedling survival found under shrubs, compared to the situation in open areas. These conditions are related mainly to soil moisture and the consequent protective role against summer drought, soil texture and nutrient availability (Joffre and Rambal, 1993; Callaway, 1995; Verdú and García-Fayos, 1996; Godínez-Alvarez and Valiente-Banuet, 1998). Once established, seedling-to-sapling transition can be favoured under shrubs, due to the characteristic shade tolerance of the juvenile yews for growth (Tittensor, 1980; Hulme, 1996). Thus, the overall outcome of shrub–yew interaction appears to be facilitation in favour of, rather than competition against, the yew.

Our results indicate that the protection of the yew by fleshy-fruited shrubs against herbivores is an additional factor determining the associative pattern between juvenile yews and shrubs. Shrubs provide shelter against ungulates both for their relative unpalatability and imbricate branching structure (in the case of shrubs such as *J. communis* and *J. sabina*, accounting for 29% of total coverage) or to dense spinescence (in the case of *B. hispanica*, *Rosa* spp. and *Prunus ramburii*, accounting for 20% of total coverage). As a result, ungulates attacked almost exclusively plants unprotected by shrubs, juvenile yews suffering serious damage, the main consequence of which is aggravated growth delay in a slow-growing species [Callaway (1995); Zamora et al. (1999); see also Hódar et al. (1998) for a similar effect on *P. sylvestris* in Mediterranean mountains]. Thus, spiny and unpalatable shrubs serve the purpose of fences that are often used to exclude plants from herbivores in conservation programmes. Finally, the mechanism of yew regeneration by shrub facilitation found in this study can be extrapolated to other populations with effective regeneration, even beyond the Mediterranean environment, corroborating the fact that yew populations can establish after the development of shrublands in central Europe (Watt, 1926; Tittensor, 1980; Hulme, 1996).

### 4.2. Ecological consequences for conservation and restoration

The presence of yew in Andalusia is restricted mainly to shady, foggy ravines in northward-facing montane areas (Franco, 1986). However, the senescent status of reported populations (Hernández and Clemente, 1994; Junta de Andalucía, 1998) suggests that these environmental microclimatic conditions are necessary but not sufficient to ensure active regeneration of yew populations. This study suggests that patterns of yew regeneration are strongly dependent on the presence of fleshy-fruited shrublands. Considering a fine spatial scale, fleshy-fruited plants act as establishment microhabitats for yew seedlings and saplings. From a macrohabitat scale, the presence of a well-developed community of fleshy-fruited shrubs determines a site-dependent regeneration in yew populations (see also Crawley and Long, 1995; Hulme, 1996).

This study exemplifies the presence of a complex facilitative system, composed of yews, fleshy-fruited nurse plants and avian dispersers. Yews benefit from fleshy-fruited shrubs that can facilitate yew seed rain (indirect effect, mediated by avian dispersers) but also protect against summer drought during the seedling stage, and against ungulate herbivores during sapling-stage (direct effects). In view of these benefits, two main management guidelines can be suggested: (1) the maintenance of healthy yew populations in Mediterranean mountains is strongly dependent on the conservation of well-developed fleshy-fruited shrublands and their community of avian dispersers; and (2) any restoration planning for the yew in Mediterranean mountains should consider fleshy-fruited shrubs as the optimal sites for man-made planting of seedlings and saplings.

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