Running Head: Pioneer shrubs facilitate forest restoration

Applying plant facilitation to forest restoration in Mediterranean ecosystems: a meta-analysis of the use of shrubs as nurse plants

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Abstract

After a millenarian history of over-exploitation, most forests in the Mediterranean Basin have disappeared, leaving many degraded landscapes that have been recolonized by early-successional shrub-dominated communities. Common reforestation techniques treat these shrubs as competitors against newly planted tree seedlings, thus shrubs are cleared before tree plantation. However, empirical studies and theory governing plant-plant interactions suggest that, in stress-prone Mediterranean environments, shrubs can have a net positive effect on recruitment of other species. Between 1997 and 2001, we carried out experimental reforestations in the Sierra Nevada Protected Area (SE Spain) with the aim of comparing the survival and growth of seedlings planted in open areas (the current reforestation technique) with seedlings planted under the canopy of pre-existing shrub species. Over 18,000 seedlings of 11 woody species were planted under 16 different nurse shrubs throughout a broad geographical area. We sought to explore variations in the sign and magnitude of interactions along spatial gradients defined by altitude and aspect. In the present work, we report the results of a meta-analysis conducted with seedling survival and growth data the first summer following planting, the most critical period for reforestation success in Mediterranean areas. The facilitative effect was consistent in all environmental situations explored (grand mean effect size d_{++}=0.89 for survival and 0.27 for growth). However, there were differences in the magnitude of the interaction depending on the seedling species planted as well as the nurse shrub species involved. Additionally, nurse shrubs had a stronger facilitative effect on seedling survival and growth at low altitudes and sunny, drier slopes than at high altitudes or shady, wetter slopes. Facilitation in the dry years proved higher than in the wet one. Our results show that pioneer shrubs facilitate the establishment of woody,

late-successional Mediterranean species, and thus can positively affect reforestation success in many different ecological settings

Key words: abiotic stress; ecological succession; Mediterranean mountains; meta-analysis; nurse shrubs; plant-plant interactions; reforestation; spatial and temporal variability; tree and shrub seedlings.

Introduction

A fundamental problem currently facing the Mediterranean basin is the loss of most primeval forests after a millenarian history of over-exploitation (Bauer 1991, Blondel and Aronson 1999). No more than 9-10% of the Mediterranean area is currently forested, and in the Iberian Peninsula only 0.2% can be considered natural or semi-natural forests (Marchand 1990). Simultaneously, the surface area covered by shrublands has increased, representing stages of degradation of mature forests as well as stages of vegetation recovery in abandoned agricultural lands (di Castri 1981, Grove and Rackham 2001). In both cases, local and regional characteristics, such as resource availability or the lack of tree propagules, act as barriers to succession (Pickett 2001), and result in self-perpetuating systems that hardly return to the structure and complexity of the original mature community (Blondel and Aronson 1999). In this situation, human intervention is necessary to assist secondary succession at the shrubland or even grassland stage, and to accelerate recovery of woodlands. Reforestation is a common approach to achieve this aim. However, in Mediterranean areas, reforestation undergoes extremely high rates of early plant mortality (Mesón and Montoya 1993, García-Salmerón 1995), making these efforts unprofitable both in ecological as well as economic terms.

In traditional reforestation techniques used in Mediterranean areas, shrubs growing close to newly planted trees are commonly considered heavy competitors, and consequently, they are removed before planting (Mesón and Montoya 1993, García-Salmerón 1995, Savill et al. 1997). However, evidence is growing that the spatial proximity among plants is beneficial rather than detrimental in environments such as Mediterranean-type ecosystems that are characterized by abiotic stress (Bertness and Callaway 1994, Callaway and Walker 1997, Brooker and Callaghan 1998). Summer drought is a main source of stress in Mediterranean environments, that limits recruitment of both natural and planted seedlings (Herrera et al. 1994, Rey and Alcántara 2000, Castro et al. 2002). Under such conditions, tree seedlings may benefit from the habitat amelioration by shrubs, which buffer against high radiation and temperatures, and can increase soil nutrient and moisture content (Callaway 1995). The survival and performance of plants in Mediterranean-type ecosystems usually improves when associated with neighbours (Pugnaire 1996a, b, Maestre et al. 2001, Callaway et al. 2002), resulting in a positive association of seedlings and saplings of tree species with shrubs (García et al. 2000, Gómez et al. 2001a, 2003). As a consequence, the spatial pattern of the Mediterranean vegetation is commonly aggregated (Callaway and Pugnaire 1999, Maestre 2002). Thus, the removal of pre-established shrubs prior to reforestation would not be an appropriate technique to apply in these ecosystems.

Environmental conditions in Mediterranean mountains are particularly variable in both time and space (Blondel and Aronson 1999). Their complex orography and high altitudes, together with an unpredictable climate, foster the coexistence of many contrasting ecological scenarios at local scales. Differences in environmental conditions appearing at a scale of meters may cause intense shifts in the net outcome of plant interactions. Facilitation often increases with intensified stress, as has been reported in south-facing *versus* west-facing slopes in rocky plant communities (Callaway et al. 1996), in dry *versus* mesic adjacent sites in the Chilean matorral (Holmgren et al. 2000), in higher *versus* lower depths in coastal ecosystems (Bertness et al. 1999), or in high *versus* low altitudes in alpine and semiarid environments (Pugnaire and Luque 2001, Callaway et al. 2002). Interspecific interactions can also vary at the same site between years depending on climatic conditions, although the relationship between climatic variability and the net result of the interaction is still unclear. Some studies report stronger facilitation in dry and hot years compared to relatively benign years (Greenlee and Callaway 1996, and Ibañez and Schupp 2001) whereas other studies reached the opposite conclusion (Casper 1996, and Tielbörger and Kadmon 2000). Therefore, an understanding of how the interaction between shrubs and tree seedlings vary spatio-temporally is crucial to assess the generality of the utility of shrubs as nurse plants for forest regeneration and restoration.

According to the above theoretical and empirical framework, we hypothesise that an alternative reforestation technique using shrubs as planting microsites in Mediterranean areas would give better results (in terms of seedling survival and growth) than would standard techniques using open spaces without vegetation, especially in hot and dry sites and years. To test this hypothesis, between 1997 and 2001, we carried out experimental reforestations in the Sierra Nevada mountains in SE Spain, encompassing the broad range of abiotic as well as biotic conditions provided by this Mediterranean high-mountain. We considered both variability in space as well as in time, a fundamental but barely explored combination of factors, in order to understand the nature and strength of plant-plant interactions related to woody plant establishment. Specifically, we addressed the following questions: 1) How does the use of shrubs as microsites for planting improve tree seedling survival and growth? 2) How does the effect of shrubs on seedling survival and growth vary depending on the shrub and tree species? 3) How do the sign and magnitude of the interaction between shrubs and woody seedlings depend on spatial characteristics of the study site, such as altitude and aspect? and 4) How do the sign and magnitude of the interaction between shrubs and woody seedlings depend on climatic conditions in the year of planting?

Methods

Study area and species

This study was carried out in the Sierra Nevada mountains (SE Spain). The general climate is Mediterranean, characterized by cold winters and hot summers with heavy summer drought (July-August). Rainfall is concentrated mainly in autumn and spring. In these mountains, temperature drops and rainfall increases with altitude, with areas below 1400 m a.s.l. having a dry climate with precipitation of less than 600 mm per year, while areas above this threshold have a subhumid climate with precipitation between 600 and 1000 mm per year (García-Canseco 2001). Additionally, the complex orography of the mountains causes strong climatic contrasts between the sunny and dry south-facing slopes and the shaded and wetter north-facing slopes (Rodríguez-Martínez and Martín-Vivaldi 1996). From a temporal perspective, in southern Spain, annual rainfall fluctuates markedly, making it possible to identify dry and wet years (Rodó and Comín 2001).

The experiments were conducted in seven sites of the Sierra Nevada mountains (Table 1), for a total of 36-ha plots (see Appendix 1). The bedrock was siliceous in 2 study zones and calcareous in 5, and in all cases the predominant soils were regosols and cambisols (Delgado et al. 1989). All study areas were burned within the last 20 years. Consequently, current vegetation is pioneer shrubs (>60% of cover in all cases) mixed with annual and perennial grasses and herbs, together with some surviving isolated trees. The most abundant shrub species in every study site are shown in Table 1.

We planted seedlings of the following target shrub and tree species: *Crataegus monogyna*, *Rhamnus alaternus*, *Retama sphaerocarpa*, *Quercus faginea*, *Q. ilex*, *Q. pyrenaica*, *Pinus halepensis*, *P. nigra*, *P. sylvestris* var. *nevadensis*, and *Acer opalus* subsp. *granatense*. These species are either commonly found in natural forests in Mediterranean mountains (e.g. *C. monogyna*, *R. alaternus*, *P. halepensis*, *P. nigra*, *Q. ilex*, *Q. pyrenaica)* or are endemic species of interest in conservation (*P. sylvestris* var. *nevadensis* and *A. opalus* subsp. *granatense)*.

Experimental design

Seedlings one- or two-year-old were planted in spring (March-April) between 1997 and 2001 at each study site using two reforestation techniques: (i) a traditional technique of planting target seedlings in open interspaces without vegetation (Open microsite), and (ii) an alternative technique of planting seedlings under the canopy of shrubs (Shrub microsite) intermingled with the open microsites. Seedlings, provided by the Junta de Andalucía (Consejería de Medio Ambiente), were grown in nurseries under similar conditions. In the case of *Acer opalus* subsp. *granatense* and *Pinus sylvestris* var. *nevadensis*, rarely available in nurseries, seedlings came from seeds collected from adults near the planting sites and seeded in a nursery located at La Cortijuela Botanical Garden (Sierra Nevada National Park). The most abundant shrub species at each site were chosen as nurse plants. In total, we used 16 nurse plant species and 11 target species, for a total of 146 different plot-nurse shrub-target species combinations (experimental cases, hereafter; see Appendix 1). Between 50-60 individually-tagged seedlings were planted per plot-nurse shrub-target species combination. In both Shrub and Open microsites, an automatic auger 12 cm in diameter was used to dig the planting holes 40 cm deep, in an attempt to minimize disturbance to nurse and soil structure.

Seedlings were examined in June, before the summer drought, and those that died from transplant shock were excluded from the experiment. By September-October, following first autumn rains, we recorded two variables per seedling: 1) survival, and the cause of mortality in case of death; and 2) growth, quantified as the elongation of the apical shoot after the first growing season.

The dataset was sorted according to five grouping variables to respond to the specific questions posed in this study:

1) Target species were classified into four functional groups based on life habits and ecological similarity: shrubs (which included *Juniperus oxycedrus*, *Rhamnus alaternus*, *Crataegus monogyna* and *Retama sphaerocarpa*), deciduous (which included *Acer opalus* subsp. *granatense*, *Quercus pyrenaica* and *Quercus faginea*), Mediterranean lowland evergreen (which included *Quercus ilex* and *Pinus halepensis*) and mountain pines (which included *Pinus nigra* and *Pinus sylvestris* var. *nevadensis*).

2) Nurse shrubs were classified into four functional groups based on architectural and ecological traits: 1) legumes (*Ulex parviflorus*, *Genista versicolor*, *Genista umbellata*, *Ononis aragonensis*, *Adenocarpus decorticans*); 2) small shrubs (*Salvia lavandulifolia*, *Thymus mastichina*, *Thymus vulgaris*, *Rosmarinus officinalis*, *Santolina canescens*, *Artemisia campestris*); 3) deciduous spiny shrubs (*Prunus ramburii*, *Crataegus monogyna*, *Berberis hispanica*); and 4) rockroses (*Cistus albidus*, *Cistus monspeliensis*).

3) Altitude, by classifying experimental cases into both low (below 1400 m a.s.l.) and high altitude sites (above 1400 m a.s.l.).

4) Aspect, by classifying experimental cases into two classes: sunny (south-facing slopes) or shady (north-facing slopes).

5) Year, based on the start of the study (1997, 2000, 2001). Experimental cases conducted in 1998 were not included in this analysis because of their low number (n = 3).

Data analysis

The effect of planting technique (Open *versus* Shrub microsites) in reforestation success was analysed using meta-analysis. We employed this procedure because the heterogeneity in the different experiments performed with respect to several factors, such as initial conditions, timing, and nurse and tree identity, did not fulfil the requirements of ordinary statistic analyses. Nevertheless, meta-analysis is a powerful statistical tool to synthesize results from independent studies beyond their differences, emphasizing patterns that are not obvious looking at single studies (Goldberg et al. 1999). Specifically, when sample sizes are small or the intensity of an effect is low (as it was in some of our studies), meta-analysis controls for Type II statistical error (Arnquist and Wooster1995). This characteristic of meta-analytical techniques has much relevance in the field of applied ecology where management decisions based on erroneous research results can have significant negative repercussions.

Prior to the meta-analysis, we summarized our database by the calculation of the Relative Neighbour Effect index (RNE, *sensu* Markham and Chanway 1996) for each experimental case (either for seedling survival or growth). This index is an estimation of the magnitude and sign of the interspecific interaction, and ranges from –1 to 1, with negative values indicating facilitation between neighbours and positive values indicating competition. We used RNE instead of the common Relative Competitive

Intensity (RCI) because RCI has no minimum value, and therefore gives extreme negative values when plant performance is greater in the presence than in the absence of neighbours. For seedling survival, RNE was calculated as the difference in survival with and without nurse shrubs relative to the case with the greatest survival in the pair. For growth, RNE was calculated using means of seedling growth in each plot. Because survival and growth can be influenced by the initial seedling height, we checked the correlation between them, which proved non-significant. Thus, we deleted initial seedling height data throughout all the study. All indices, as well as subsequent statistical analyses, were performed using one-year survival and growth data in order to standardize time scales between experiments. Our previous experience shows that, in Mediterranean environments, the first summer after planting is the main mortality factor for seedling survival (with mortalities of even 90% of the individuals planted), and so the success of a reforestation can be properly evaluated on the basis of first-summer results (Vilagrosa et al. 1997, Rey-Benayas 1998, Maestre et al. 2001, Castro et al. 2002).

We used the mixed-model procedure which appears to be more accurate than the fixed-model because it assumes random variation between studies within a class instead of the sharing of a single true effect size (Gurevitch and Hedges 2001). We chose the standardized difference between means (*d index*) to estimate the effect of the presence of shrubs on two response variables: seedling survival and seedling growth. To calculate the effect sizes using survival data, we grouped the experimental cases carried out in the same study site and year with the same target and nurse shrub species, and calculated the means of the two groups (experimental and controls) as well as the standard deviations for these means. To calculate the effect sizes using growth data, we used each of the 146 experimental cases independently with the condition that at least two individuals survived in both treatments. The magnitudes of effect sizes were interpreted *sensu* Cohen (1969).

Sensitivity analyses were used to control dependence between data (Gates 2002). We performed an additional analysis restricting the data to one data point for each study site. The effect of shrubs on planted seedlings was first assessed for the entire dataset. Then we evaluated the homogeneity of results among groups of each of the five, grouping variables by using the Q statistic (Hedges and Olkin 1985, Cooper and Hedges 1994). We found a significant covariation between some grouping variables: *P. halepensis* and shrubs were always at low altitudes, whereas deciduous species, *P. nigra* and *P. sylvestris* var. *nevadensis* were always at high altitudes ($\chi^2 = 44.37$, df = 3, $p<0.001$). Therefore, the difference between altitudes in the effect of shrubs may reflect differences between target species. To correct for this, we also examined altitudinal effects for *Q. ilex*, the only species appearing at both altitudes.

Results

Survival

In 109 of the 146 experimental cases (75%), shrubs increased seedling survival (negative RNE values). A neutral interaction (RNE = 0) was found in 8 cases (5%), whereas only in 29 (20%) of the cases there was a negative RNE indicating antagonism (Figure 1a). The result from this “vote-counting” approach was consistent with results from the meta-analysis. Across all studies, shrubs had a large positive significant effect on seedling survival, with a grand mean effect size of $d_{++} = 0.89$ (CI = 0.51 - 1.27). The sensitivity analysis showed a similar general result at the study-site level, but with a substantially higher absolute total effect size ($d_{++} = 1.15$; CI = 0.49 - 1.81). Thus, we can assume that interdependence caused little bias. In 98% of the cases, the cause of mortality was summer drought, whereas the remaining 2% was attributable to herbivore damage (trampling, uprooting, browsing).

The effect of shrubs significantly differed between target species ($Q_B = 49.55$, df $= 3$, $P < 0.0001$). Whereas the effect was significantly different from zero for Mediterranean evergreen, deciduous and shrubs, it was not significant for mountain pines (Figure 2a). The magnitude of the effect varied from low for mountain pines, through large for deciduous, to very large for Mediterranean evergreen and shrubs. Between nurses, the effect varied from significantly large and positive for legumes and small shrubs (facilitation), through non-significantly medium and positive for deciduous spiny, to significantly large and negative for rockrose (antagonism; Figure 2b).

On average, shrubs provided stronger facilitation at the low altitude than at the high altitude ($Q_B = 41.42$, df = 1, $P < 0.0001$; Figure 2c). The same result was found when the relative contribution of altitude to the variation in the shrub effect was analysed for *Q. ilex* alone, with a significantly higher effect size at the low altitude than at the high altitude ($Q_B = 14.92$, df = 1, $P < 0.0001$). Facilitation by shrubs had a significant effect both in the sunny group and in the shady group, the effect size significantly being larger ($Q_B = 43.59$, df = 1, $p<0.0001$) in the sunny slopes than in the shady ones (Figure 2d).

Comparisons between years revealed a significant effect of shrubs on seedling survival in 2000 and 2001 (“dry years”), but not in 1997 (“wet year”) ($Q_B = 48.51$, df = 2, $P < 0.0001$; Figure 2e).

Growth

The RNE for growth could be calculated only in 68% experimental cases, where more than one seedling survived. Of these cases, 76% showed higher growth in Shrubs compared to Open (negative RNE values), and the remaining 24% reported higher growth in Open (positive RNE; Figure 1b). These results also agreed with those from the meta-analysis. On pooling studies, we found a significant, but small mean effect of shrubs on seedling growth on average (d_{++} = 0.27;CI = 0.15 - 0.39). Seedlings planted under shrubs grew more during the first growing season than did seedlings planted in open areas. The sensitivity analysis showed a similar general result at the study-site level (d_{++} = 0.3; CI = 0.05 - 0.55). Thus, interdependence did not bias the results.

There were significant differences between target groups in the effect of shrubs on growth (Q_B = 82.20, 1 df, $P < 0.0001$); statistically significant differences were only found for Mediterranean evergreen and deciduous (Figure 3a). Among nurses, the effect was significant for legumes, stunted and spiny, but not for rockroses; legumes registered the highest values of any group (Figure 3b).

As in survival, the effect was significantly larger at the low than at the high altitude (Q_B = 59.34, 1 df, $P < 0.0001$; Figure 3c). Significant differences were found between aspect categories (Q_B = 84.49, 1 df, $P < 0,0001$), both showing a small effect of shrubs over growth (Figure 3d).

Finally, the effect of shrubs varied from non-significant in the wet year of 1997 to significantly positive in the dry years of 2000 and 2001 (Q_B = 98.03, 2 df, $P < 0.0001$), when seedling planted under shrubs grew more than did seedlings planted in open areas (Figure 3e).

Discussion

Our results demonstrated that pioneer shrubs have a generally positive effect on woody-seedling survival and initial growth in Mediterranean mountains. Seedling survival under shrubs more than doubled in comparison to Open microsites, and even up to four

-fold in some experimental cases (see Appendix 1). Of our 146 experimental cases, less than a 20% showed positive RNE for survival (indicating competitive interactions). In most cases, RNE was lower than 0.2, showing a very weak negative effect. Similarly, in the 76% of the experimental cases seedlings planted under shrubs grew more than did seedlings planted in open areas (giving a negative RNE). Therefore, we found a consistent beneficial effect in both survival and initial growth, in contrast to studies that have reported a negative nurse effect in seedling growth, despite the positive effects at other life cycle stages (Holzapfel and Mahall 1999, Kitzberger et al. 2000). These results agree with the hypothesis that there is little competition between shrubs and tree seedlings in the Mediterranean Basin (Vilá and Sardans 1999). Thus, our experiments show that facilitation between shrubs and tree seedlings in Mediterranean environments is not a local or sporadic phenomenon restricted to a few species assemblages and environmental conditions, but a more widespread phenomenon. From a conceptual standpoint, these results show that pioneer shrubs benefit the establishment of woody, late-successional species (Clements 1916, Addicot 1984), according to the model of succession by facilitation (Connell and Slatyer 1977).

The role of the interacting species in the net effect of shrubs

We found relevant differences between target species in their response to the presence of nurse shrubs. Among trees, *Quercus* spp. and *Acer opalus* subsp. *granatense* showed the greatest response both for survival and growth, possibly as a consequence of being late-successional, shade-tolerant species (Zavala et al. 2000, Gómez et al. 2001b). Montane pines had the lowest response in accordance with their shade-intolerant nature (Ceballos and Ruíz de la Torre 1971, Nikolov and Helmisaari 1992), although association with shrubs was still beneficial, given the harsh conditions of Mediterranean summer (Gómez et al. 2001a, Castro et al. 2002). However, shrub seedlings responded more than any tree species to the presence of nurse shrubs, with *Rhamnus alaternus* and *Crataegus monogyna* showing the greatest and *Retama sphaerocarpa* the lowest increase in survival and growth (see Appendix 1). This result, together with the higher values of survival in comparison to any other target species, makes the planting of late-successional shrubs under primary-successional shrubs the most effective way of accelerating succession in degraded sites where the direct recovery of the tree cover can be very difficult, if not impossible.

Our work also demonstrates differences between shrubs in their facilitative effect. The magnitude and sign of the nurse effect on seedling survival varied from large and positive for legumes and small shrubs, through medium and positive for deciduous spiny shrubs, to large and negative for rockroses. The differential effect of nurse shrubs may be related to characteristics of the functional groups. Legumes may increase survival and growth by improving soil-nutrients composition due to nitrogen fixation, a scarce nutrient in Mediterranean soils (Callaway 1995, Alpert and Mooney 1996, Franco-Pizaña et al. 1996). On the other hand, radiation during summer in Mediterranean environments is usually excessive, causing photoinhibition of photosynthesis in many plant species (Valladares 2003). In this context, shrub canopy shade can favour seedling performance by reducing radiation in comparison to open areas. In fact, additional experiments conducted in two of the study zones included in the meta-analysis (Gómez et al. 2001b) show that the modification of the microclimate under the canopy of the nurses (e.g. lower radiation and temperature and higher atmosphere and soil humidity) is a main facilitative mechanism of woody seedling establishment (see also Rey-Benayas 1998, Rey-Benayas et al. 2002, Maestre 2002). Finally, in the case of rockroses, the negative effect on the survival of target species is presumably due to allelopathic leachates characteristic of this family (Robles et al. 1999), particularly for *Cistus albidus*. Although the grouping of experimental cases that involved the use of meta-analytical techniques prevented the analysis of differences at the species level, these results show that the identity of the nurses matters. This should be taken into account when designing reforestation programmes, in order to choose the nurse shrub species that maximize survival probabilities.

The importance of environmental variability in plant-plant interactions

The facilitative effect was consistent in all the environmental situations explored. However, as predicted by our initial hypothesis, the strength of the interaction was significantly lower (and not statistically significant) in the plantings carried out in the wet year (1997) than in the two dry years (2000, 2001). The summer of 1997 was mild and wet compared to the other summers of the study period, and, in accordance soil-water content in the middle of the summer was significantly greater in 1997 than in the other two years (Figure 4). This water availability in the soil, although limited, may have relieved stressed plants in 1997, helping them to survive until the arrival of autumn rains. Consequently, the benefit of living in the shade of shrubs was less evident in the wetter 1997 than in the drier 2000 and 2001.

With respect to the spatial gradient, the strength of the positive interaction was significantly higher at low altitudes and sunny slopes than at high altitudes or shady slopes. These results indicated a shift in the balance of competitive *versus* facilitative intensity on stress gradients (Bertness and Callaway 1994, Bruno et al. 2003**)**. At low elevation and sunny slopes, low precipitation and high temperatures result in an intense summer drought, limiting seedling survival and growth more than does resource acquisition. Alleviation of such severe stress by nurse shrubs may benefit seedlings, outweighing any effects of their competition for resources (Callaway and Walker 1997). On the contrary, at high elevations and shady slopes, with lower summer temperatures and higher precipitation (and thus less intense summer drought), the abiotic environment barely limits the uptake of resources for plants, and consequently the positive effects of shrubs is less notable (Callaway and Walker 1997).

In conclusion, the higher the temperature and irradiance in open areas, the more important the protection of shrubs can be for a good water and temperature balance of the seedlings, and thus the stronger the facilitative effect on their survival and initial growth. Consequently, sites and years with stressful summer droughts promise the best advantage of nurse plants for the recovery of degraded vegetation (Whisenant 1999, Pickett et al. 2001). In these stressful scenarios, the presence of a habitat-modifying pioneer shrub may enhance species diversity by providing structural refuge to a broad array of woody species (Hacker and Gaines 1997, Stachowicz 2001). Additionally, by their positive effect in a very sensitive life-history stage of woody species (seedling), habitat-modifiers can increase the regional and local distribution of plants, allowing woody species to colonize a broad range of ecological conditions. Given that nurse plants facilitated some woody species more than others**,** pioneer shrubs in Mediterranean ecosystems could be considered *foundation species* (Dayton 1972) or *ecosystem engineers* (Jones et al. 1994) able to influence the species composition, abundance and the spatial structure of the plant community.

Management implications

Our experimental results have clearly shown that the use of nurse shrubs facilitates seedling establishment in many different ecological settings in Mediterranean mountains (altitude, exposure, successional phase of the pre-existing vegetation, level of local environmental stress). Although we monitored one-year survival, the benefit of planting seedlings under shrubs could be translated beyond this stage to sapling or reproductive stages, since natural regeneration in Mediterranean ecosystems in mainly limited at the seedling stage (Herrera et al. 1994, Rey and Alcantara 2000, Gómez 2003), and experimental reforestations reveal the bottleneck of first-summer mortality (Maestre et al. 2001, Castro et al. 2002, Castro et al. *in press*).

Since most shrub species studied acted as nurses, and most planted species were effectively facilitated, this technique could be used to design multi-specific reforestations. To plant many woody species would avoid problems derived from mono-specific plantations such as fire propagation (Moreno 1999) or soil impoverish (Scott et al. 1999), and additionally would increase the diversity and heterogeneity of the recovered woodlands. Moreover, since the response of shrub seedlings to the presence of a nurse plant was larger than the response of tree seedlings, this technique could be used to design a two-phase reforestation strategy, mimicking the natural process. During the first phase, shrubs and sun-tolerant early-successional trees would be planted in association with pioneer shrubs, and in a second phase the shade-tolerant late-successional trees would be introduced under the canopy of the former ones.

Our study implies that the removal of shrubs is not appropriate for reforestation in Mediterranean mountains. This traditional procedure is rooted in techniques developed in Central and Northern Europe (Groome 1989, Bauer 1991), where summer mesic climatic conditions and dense plant cover often result in competition for light and nutrients. This ecological context strongly differs from Mediterranean environments, where stressful conditions, primarily summer drought, severely limit the uptake of resources by the plant, allowing habitat amelioration provided by pioneer shrubs to become the major determinant of spatial distribution of woody seedlings. Therefore, a new paradigm for the science of restoration of Mediterranean forests, based on the natural spatial patterns of regeneration of woody vegetation (with shrubs as microsites for recruitment), emerges from the results of the present work as well as other previous studies (Castro et al. 2002, Maestre et al. 2001, 2002). Furthermore, given that the facilitative effect increases with abiotic stress, this technique might be more relevant under the predicted rise in temperatures, dryness and rainfall variability (with more episodes of drought) for the Mediterranean region under global warming (IPCC 2001). Thus, benefits of this technique will be greater in coming years under a scenario of climatic change.

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Appendix 1. Summary of the 146 experimental cases (=plot-nurse shrub- target species combination) integrating the meta-analysis. N_c and N_e refer to the number of seedlings planted in control (Open) and experimental (Shrubs) microsites. RNE values show the sign and magnitude of the interaction between shrubs and woody seedlings, both for survival and growth. This index ranges from -1 to 1, with negative values indicating facilitation and positive values competition. Spiny = *Crataegus monogyna*, *Berberis hispanica* and *Prunus ramburii.* EC = experimental case.

EC	**Year**	**Plot**	**Nurse shrub**	**Target species**	**N_c**	**N_e**	**RNE survival**	**RNE growth**
LOMA PANADEROS								
1	2001	1	*S. lavandulifolia*	*A. opalus granatense*	23	30	- 0.74	0.72
2	2001	1	*S. lavandulifolia*	*Q. ilex*	53	48	- 0.72	- 0.68
3	2001	2	*S. lavandulifolia*	A. *opalus granatense*	8	19	0	----
4	2001	2	*S. lavandulifolia*	*Q. ilex*	25	23	- 0.64	- 0.85
5	2000	3	*S. lavandulifolia*	*P. sylvestris*	25	29	- 0.88	- 0.11
6	2000	3	*S. lavandulifolia*	*P. nigra*	25	26	- 1	----
7	2000	3	*S. lavandulifolia*	*Q. ilex*	29	30	- 0.34	- 0.30
8	2000	4	*S. lavandulifolia*	*P. sylvestris*	27	29	- 0.92	- 0.88
9	2000	4	*S. lavandulifolia*	*P. nigra*	26	28	- 0.84	- 0.08
10	2000	4	*S. lavandulifolia*	*Q. ilex*	28	28	- 0.28	- 0.4
11	2000	5	*S. lavandulifolia*	*P. sylvestris*	25	29	- 0.63	- 0.37
12	2000	5	*S. lavandulifolia*	*P. nigra*	28	26	- 0.42	- 0.56
13	2000	5	*S. lavandulifolia*	*Q. ilex*	29	30	- 0.35	- 0.09
14	2001	6	*S. lavandulifolia*	*A. opalus granatense*	20	39	- 1	----

15	2001	6	*S. lavandulifolia*	*Q. pyrenaica*	34	45	0	----
16	2001	6	*S. lavandulifolia*	*Q. ilex*	37	41	- 1	----
17	2001	6	*O. aragonensis*	*A. opalus granatense*	44	39	0	----
18	2001	6	*O. aragonensis*	*Q. pyrenaica*	46	45	- 1	----
19	2001	6	*O. aragonensis*	*Q. ilex*	42	41	- 1	----
20	2001	6	*B. hispanica*	*A. opalus granatense*	30	39	0	----
21	2001	6	*B. hispanica*	*Q. pyrenaica*	45	45	0	----
22	2001	6	*B. hispanica*	*Q. ilex*	44	41	- 1	----
23	2001	7	*S. lavandulifolia*	*A. opalus granatense*	29	40	- 1	----
24	2001	7	*S. lavandulifolia*	*Q. pyrenaica*	39	17	- 0.14	- 1
25	2001	7	*S. lavandulifolia*	*Q. ilex*	55	23	- 0.37	- 1
26	2001	7	*P. ramburii*	*A. opalus granatense*	37	40	- 1	----
27	2001	7	*P. ramburii*	*Q. pyrenaica*	55	17	0.59	- 1
28	2001	7	*P. ramburii*	*Q. ilex*	63	23	0.02	- 1
29	2001	7	*G. versicolor*	*A. opalus granatense*	45	40	- 1	----
30	2001	7	*G. versicolor*	*Q. pyrenaica*	57	17	0.40	- 1
31	2001	7	*G. versicolor*	*Q. ilex*	61	23	- 0.20	- 1
32	2001	8	*C. monogyna*	*A. opalus granatense*	20	10	- 1	----
33	2001	8	*C. monogyna*	*Q. ilex*	58	34	- 1	----
34	2001	8	*C. monogyna*	*P. nigra*	40	24	0	----
35	2001	9	*C. monogyna*	*A. opalus granatense*	28	29	- 1	----
36	2001	9	*C. monogyna*	*Q. ilex*	40	42	- 0.52	- 0.30
37	2001	9	*C. monogyna*	*P. nigra*	44	45	- 0.66	- 0.92
38	1997	10	*S. lavandulifolia*	*P. sylvestris*	37	50	0.08	- 0.06
39	1997	10	*S. lavandulifolia*	*P. nigra*	47	60	0.04	- 0.11

40	1997	10	Spiny	*P. sylvestris*	96	50	- 0.10	- 0.13
41	1997	10	Spiny	*P. nigra*	95	60	0.13	- 0.21
42	1997	11	*S. lavandulifolia*	*P. sylvestris*	43	50	- 0.48	0.31
43	1997	11	*S. lavandulifolia*	*P. nigra*	46	55	- 0.31	0.24
44	1997	11	Spiny	*P. sylvestris*	102	50	- 0.13	0.14
45	1997	11	Spiny	*P. nigra*	99	55	0.42	0.59
46	1997	12	*S. lavandulifolia*	*P. sylvestris*	44	49	- 0.65	0.12
47	1997	12	*S. lavandulifolia*	*P. nigra*	45	47	- 0.19	0.02
48	1997	12	Spiny	*P. sylvestris*	87	49	- 0.54	- 0.02
49	1997	12	Spiny	*P. nigra*	94	47	- 0.06	- 0.12
50	1998	13	*S. lavandulifolia*	*Q. pyrenaica*	48	48	- 0.36	----
51	1998	14	*S. lavandulifolia*	*Q. pyrenaica*	51	47	- 0.05	----
52	1998	15	*S. lavandulifolia*	*Q. pyrenaica*	45	45	- 0.38	----
53	1997	16	Spiny	*A. opalus granatense*	15	15	- 0.13	- 0.39
54	1997	16	Spiny	*P. sylvestris*	13	15	-.04	0.18
55	1997	16	Spiny	*P. nigra*	16	15	- 0.27	- 0.11
56	1997	16	Spiny	*Q. ilex*	15	14	0.07	- 0.16
57	1997	17	Spiny	*A. opalus granatense*	12	12	- 0.40	- 0.34
58	1997	17	Spiny	*P. sylvestris*	11	12	- 0.08	0.43
59	1997	17	Spiny	*P. nigra*	13	12	0.34	0.05
60	1997	17	Spiny	*Q. ilex*	10	11	- 0.39	0.38
61	1997	18	Spiny	*A. opalus granatense*	12	11	- 0.08	- 0.32
62	1997	18	Spiny	*P. sylvestris*	10	11	0.45	- 0.85
63	1997	18	Spiny	*P. nigra*	10	12	0.34	0.09
64	1997	18	Spiny	*Q. ilex*	10	10	0.3	- 0.15

CORTIJUELA								
65	2001	19	*S. lavandulifolia*	*A. opalus granatense*	7	16	0.24	1
66	2001	19	*S. lavandulifolia*	*Q. ilex*	19	20	0.73	----
67	2001	19	*P. ramburii*	*A. opalus granatense*	14	16	0.52	0.18
68	2001	19	*P. ramburii*	*Q. ilex*	21	20	- 0.16	- 1
69	2001	19	*C. monogyna*	*A. opalus granatense*	10	16	0.47	- 0.67
70	2001	19	*C. monogyna*	*Q. ilex*	19	20	- 0.53	- 1
71	2001	20	*S. lavandulifolia*	*A. opalus granatense*	8	17	- 0.06	- 1
72	2001	20	*S. lavandulifolia*	*Q. ilex*	20	21	- 0.04	----
73	2001	20	*P. ramburii*	*A. opalus granatense*	13	17	- 0.43	- 1
74	2001	20	*P. ramburii*	*Q. ilex*	14	21	- 0.89	- 1
75	2001	20	*C. monogyna*	*A. opalus granatense*	17	17	- 0.50	- 1
76	2001	20	*C. monogyna*	*Q. ilex*	19	21	- 0.93	--------
77	2001	21	*S. lavandulifolia*	*A. opalus granatense*	22	13	- 1	- 1
78	2001	21	*S. lavandulifolia*	*Q. ilex*	30	47	- 1	--------
79	2001	21	*B. hispanica*	*A. opalus granatense*	32	13	- 1	- 1
80	2001	22	*C. monogyna*	*A. opalus granatense*	29	24	- 0.81	- 0.87
81	2001	22	*C. monogyna*	*Q. ilex*	46	37	- 1	--------
82	2001	22	*T. mastichina*	*A. opalus granatense*	39	24	- 0.85	- 0.64
83	2001	22	*T. mastichina*	*Q. ilex*	31	37	- 1	--------
ROSALES								
84	2000	23	*S. lavandulifolia*	*P. nigra*	45	65	0.04	- 0.07
85	2000	23	*S. lavandulifolia*	*Q. ilex*	42	61	- 0.42	- 0.41
86	2000	23	*C. albidus*	*P. nigra*	42	65	1	--------
87	2000	23	*C. albidus*	*Q. ilex*	40	61	0.29	- 0.23

88	2000	24	*S. lavandulifolia*	*P. nigra*	55	58	- 0.7	- 0.34
89	2000	24	*S. lavandulifolia*	*Q. ilex*	54	50	- 0.45	- 0.01
90	2000	24	*C. albidus*	*P. nigra*	58	58	0.83	- 0.43
91	2000	24	*C. albidus*	*Q. ilex*	55	50	- 0.05	0.56
92	2000	*25*	*S. lavandulifolia*	*P. nigra*	40	49	0.05	0.03
93	2000	*25*	*S. lavandulifolia*	*Q. ilex*	40	50	0.02	- 0.43
94	2000	*25*	*C. albidus*	*P. nigra*	40	49	1	--------
95	2000	*25*	*C. albidus*	*Q. ilex*	40	50	0.62	- 0.53
LÚJAR								
96	2000	26	*R. officinalis*	*P. halepensis*	78	47	- 0.17	- 0.18
97	2000	26	*R. officinalis*	*Q. ilex*	64	25	- 0.49	- 1
98	2000	26	*U. parviflorus*	*P. halepensis*	57	47	- 0.11	- 0.24
99	2000	26	*U. parviflorus*	*Q. ilex*	65	25	- 0.69	- 1
LANJARÓN								
100	2000	27	*U. parviflorus*	*P. halepensis*	19	50	- 1	--------
101	2000	27	*U. parviflorus*	*Q. ilex*	23	49	- 0.51	- 0.05
102	2000	27	*G. umbellata*	*P. halepensis*	21	50	- 1	--------
103	2000	27	*G. umbellata*	*Q. ilex*	23	49	- 0.82	- 0.08
104	2000	28	*U. parviflorus*	*P. halepensis*	26	50	- 1	--------
105	2000	28	*U. parviflorus*	*Q. ilex*	31	50	- 0.90	--------
106	2000	28	*G. umbellata*	*P. halepensis*	28	50	- 1	--------
107	2000	28	*G. umbellata*	*Q. ilex*	29	50	- 0.91	--------
108	2000	28	*C. monspeliensis*	*P. halepensis*	28	50	- 1	--------
109	2000	28	*C. monspeliensis*	*Q. ilex*	30	50	- 0.92	--------
110	2000	29	*U. parviflorus*	*P. halepensis*	57	48	- 0.80	- 0.19

111	2000	29	*U. parviflorus*	*Q. ilex*	48	50	- 0.82	- 0.37
112	2000	29	*S. canescens*	*P. halepensis*	46	48	- 0.95	- 0.17
113	2000	29	*S. canescens*	*Q. ilex*	48	50	- 0.84	- 0.35
114	2000	30	*T. vulgaris*	*Q. pyrenaica*	109	63	- 0.63	- 0.24
115	2000	30	*T. vulgaris*	*Q. ilex*	107	91	- 0.74	- 0.47
116	2000	30	*A. campestris*	*Q. pyrenaica*	104	63	- 0.02	- 0.30
117	2000	30	*A. campestris*	*Q. ilex*	100	91	- 0.53	- 0.03
VÁLOR								
118	2000	31	*Festuca* sp.	*P. nigra*	50	50	- 0.75	- 0.31
119	2000	31	*Festuca* sp.	*Q. ilex*	7	46	- 0.95	- 1
120	2000	32	*Festuca* sp.	*P. nigra*	50	100	0	- 0.21
121	2000	32	*Festuca* sp.	*Q. ilex*	27	70	0.53	- 0.12
122	2000	32	*A. decorticans*	*P. nigra*	50	100	1	--------
123	2000	32	*A. decorticans*	*Q. ilex*	14	70	0.44	0.26
124	2000	33	*S. canescenes*	*Q. ilex*	25	25	0	--------
125	2000	33	*S. canescenes*	*P. nigra*	89	114	- 0.32	0.12
126	2000	33	*S. canescenes*	*Q. pyrenaica*	59	43	- 0.39	- 0.17
HUÉTOR								
127	2001	34	*U. parviflorus*	*Q. faginea*	29	26	- 1	--------
128	2001	34	*U. parviflorus*	*Q. ilex*	30	31	- 0.67	0.39
129	2001	34	*U. parviflorus*	*P. nigra*	27	12	- 1	--------
130	2001	34	*U. parviflorus*	*J. oxycedrus*	30	25	- 0.06	- 0.24
131	2001	34	*U. parviflorus*	*R. alaternus*	26	36	- 0.62	- 0.87
132	2001	34	*U. parviflorus*	*C. monogyna*	30	39	- 0.49	- 0.75
133	2001	34	*U. parviflorus*	*R. sphaerocarpa*	34	32	- 0.11	--------

134	2001	35	*U. parviflorus*	*Q. faginea*	20	18	- 1	--------
135	2001	35	*U. parviflorus*	*Q. ilex*	21	22	- 0.52	- 0.51
136	2001	35	*U. parviflorus*	*P. nigra*	14	10	- 1	--------
137	2001	35	*U. parviflorus*	*J. oxycedrus*	13	13	- 0.71	0.17
138	2001	35	*U. parviflorus*	*R. alaternus*	24	25	- 0.36	- 0.92
139	2001	35	*U. parviflorus*	*C. monogyna*	20	23	- 0.51	- 0.72
140	2001	35	*U. parviflorus*	*R. sphaerocarpa*	24	19	- 0.16	--------
141	2001	36	*U. parviflorus*	*Q. ilex*	47	45	- 0.04	- 0.47
142	2001	36	*U. parviflorus*	*P. nigra*	22	10	1	--------
143	2001	36	*U. parviflorus*	*J. oxycedrus*	38	22	- 0.26	0.73
144	2001	36	*U. parviflorus*	*R. alaternus*	52	32	- 0.46	0.65
145	2001	36	*U. parviflorus*	*C. monogyna*	51	35	0.10	0.93
146	2001	36	*U. parviflorus*	*R. sphaerocarpa*	47	35	- 0.01	--------

Table 1. Main characteristics of the seven study sites. Main shrub species represent species covering > 5% of the study area. a.s.l. = above sea level.

Study site	**Coordinates**	**Altitude (m a.s.l.)**	**Aspect**	**Soil**	**Main shrub species**
Loma Panaderos	37º05'N 3º28'W	1850	N-NE	Calcareous	*Salvia lavandulifolia, Ononis aragonensis, Genista scorpius Crataegus monogyna, Berberis hispanica, Prunus ramburii*
Cortijuela	37º05'N 3º28'W	1650	N-NE	Calcareous	*S. lavandulifolia, C. monogyna, B. hispanica, P. ramburii, Thymus mastichina, Echinospartium bosissiere, Genista cinerea*
Rosales	37º04'N 3º30'W	1800	S	Calcareous	*Cistus albidus, S. lavadulifolia*
Lanjarón	36º56'N 3º29'W	1230 - 1900	S	Siliceous	*Genista umbellata, Cistus monspeliensis, Ulex parviflorus, Santolina canescens, Artemisia campestris, Thymus vulgaris*
Lújar	36º52'N 3º23'W	465	N-NE	Calcareous	*Rosmarinus officinalis, C. monspeliensis, U. parviflorus*
Válor	37º02'N 3º06'W	1820 - 2000	S	Siliceous	*S. canescens, Festuca* sp., *Adenocarpus decorticans, A. campestris*
Huétor	37º15'N 3º27'W	1400	N-NE	Calcareous	*U. parviflorus, C. monogyna*

Figures

FIG. 1. Summary of results from experimental cases. We give Relative Neighbour effect (RNE) as an estimation of the magnitude of the effect of shrubs on seedling survival and growth. This index ranges from -1 to 1, with negative values indicating facilitation and positive values competition. Eight cases were removed from the figure because RNE = 0.

FIG. 2. Results of the mixed-model for survival. Values reported are the mean effect size ($d+$) and the 95% confidence interval. *P* shows the significance of the Q statistic for the difference between groups in the effect of nurse shrubs on survival. See *Methods* for a description of the grouping variables.

FIG. 3. Results of the mixed-model for growth. Values reported are the mean effect size ($d+$) and the 95% confidence interval. *P* shows the significance of the Q statistic for the difference between groups in the effect of nurse shrubs on growth. See *Methods* for a description of the grouping variables.

FIG. 4. Variability in summer abiotic conditions (soil water content, rainfall, and mean maximum temperature) among the three years of study. Climatic data were obtained in a meteorological station located in La Cortijuela Botanical Garden. This meteorological station is situated in the centre of the geographical area including all the study sites, representing the general climatic conditions in Sierra Nevada mountains. Volumetric soil-water content was recorded in an adjacent area at 15 cm depth during the first week of August using ThetaProbe sensors (Delta-T Devices Ltd., Cambridge, UK).

Figure 1.

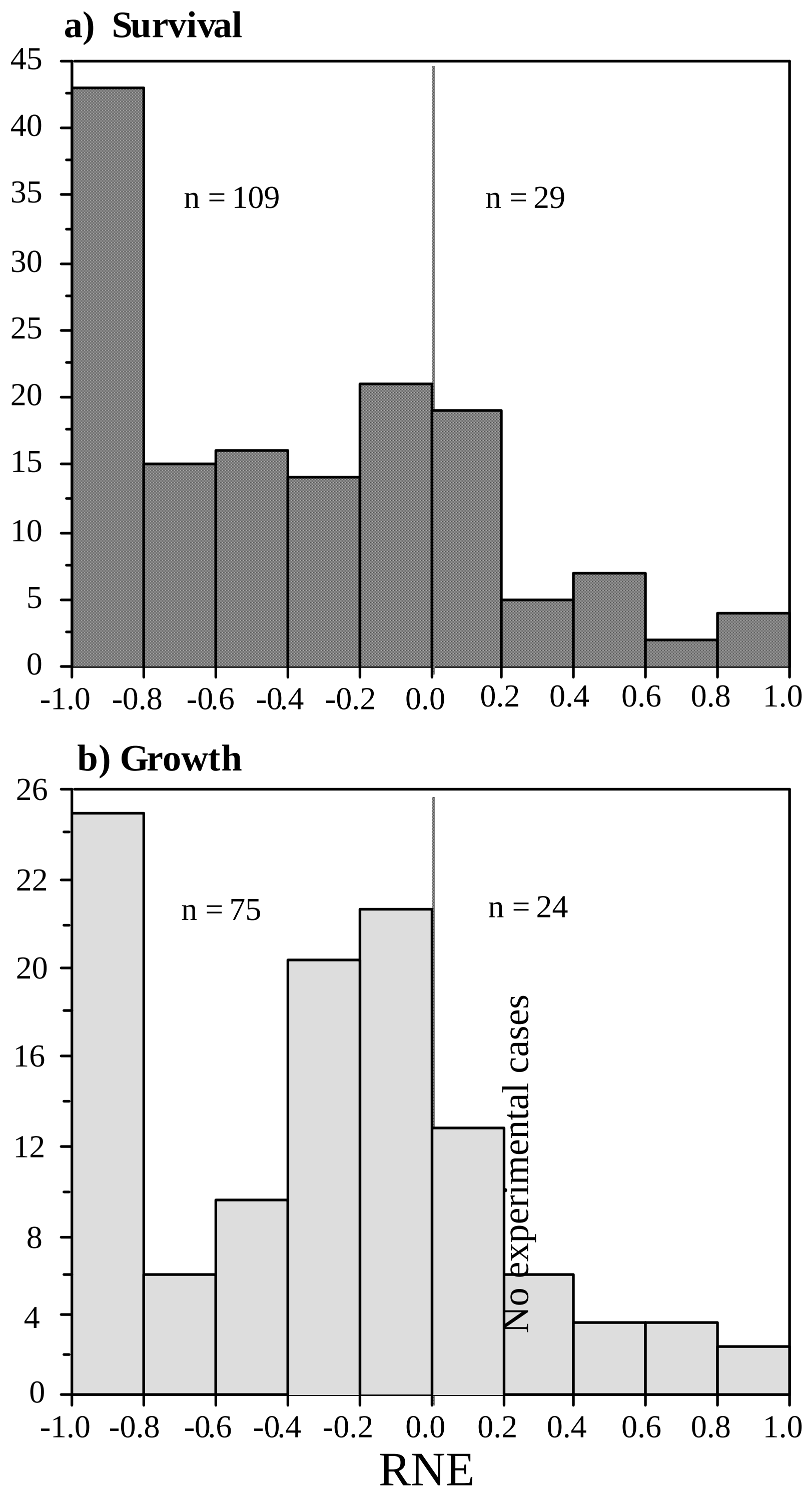
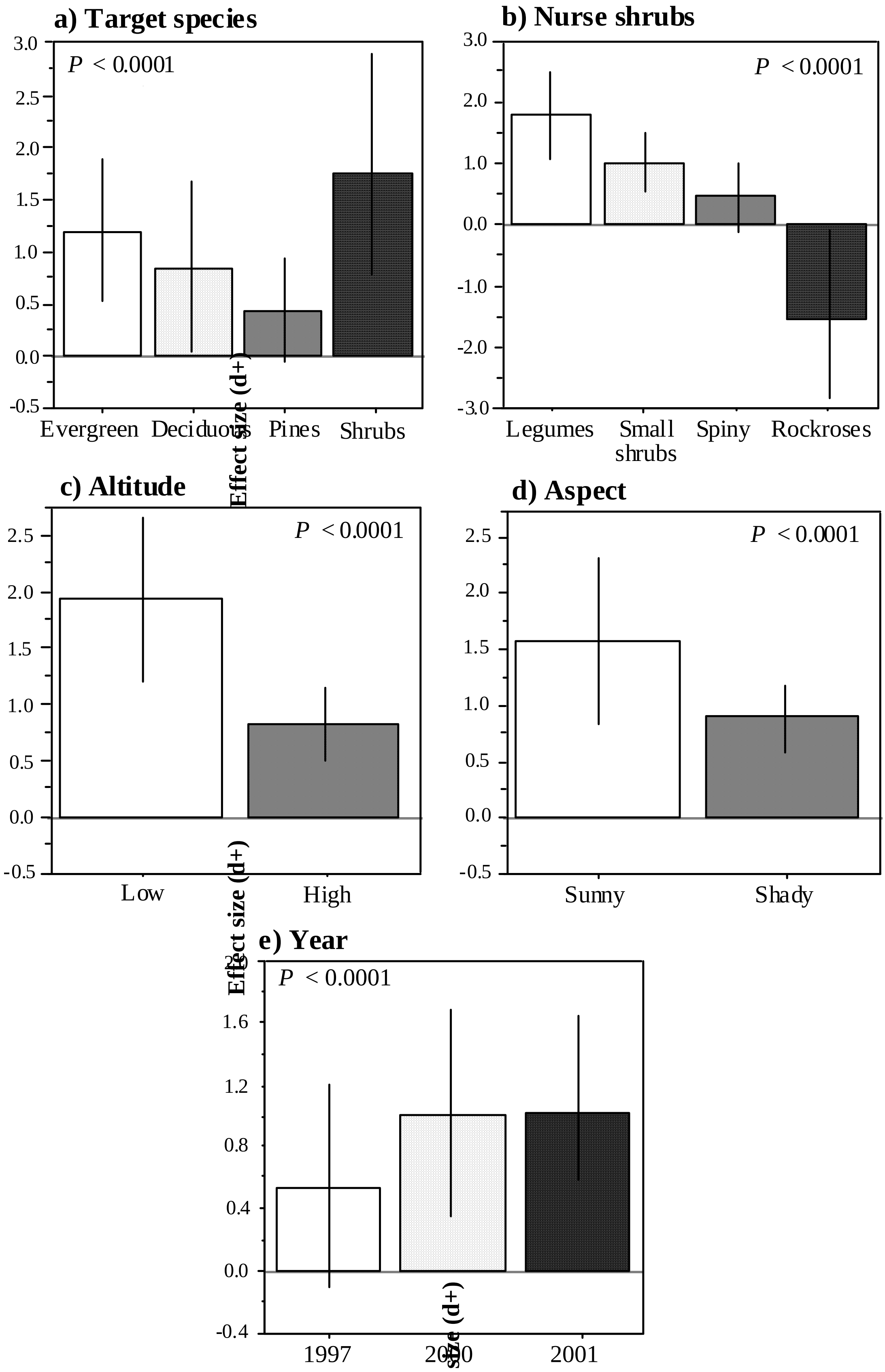

a) Survival
45
40
35
30
25
20
15
10
5
0
n = 109
n = 29
-1.0 -0.8 -0.6 -0.4 -0.2 0.0 0.2 0.4 0.6 0.8 1.0
b) Growth
26
22
20
16
12
8
4
0
n = 75
n = 24
No experimental cases
-1.0 -0.8 -0.6 -0.4 -0.2 0.0 0.2 0.4 0.6 0.8 1.0
RNE

Figure 2.



a) Target species
P < 0.0001
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
Evergreen
Deciduous
Pines
Shrubs
b) Nurse shrubs
P < 0.0001
3.0
2.0
1.0
0.0
-1.0
-2.0
-3.0
Legumes
Small shrubs
Spiny
Rockroses
Effect size (d+)
c) Altitude
P < 0.0001
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
Low
High
d) Aspect
P < 0.0001
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
Sunny
Shady
Effect size (d+)
e) Year
P < 0.0001
1.6
1.2
0.8
0.4
0.0
-0.4
1997
2000
2001

Figure 3.

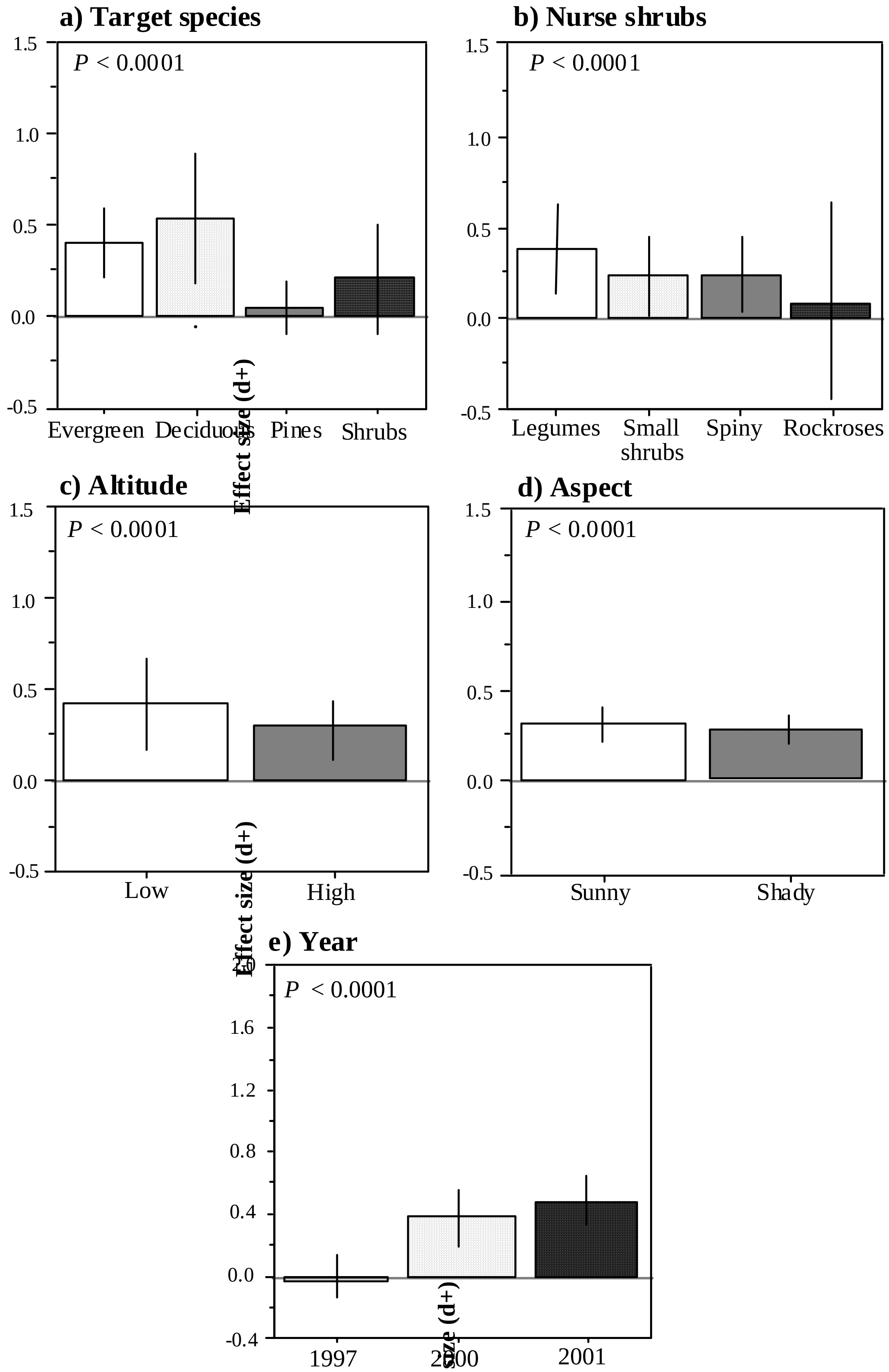
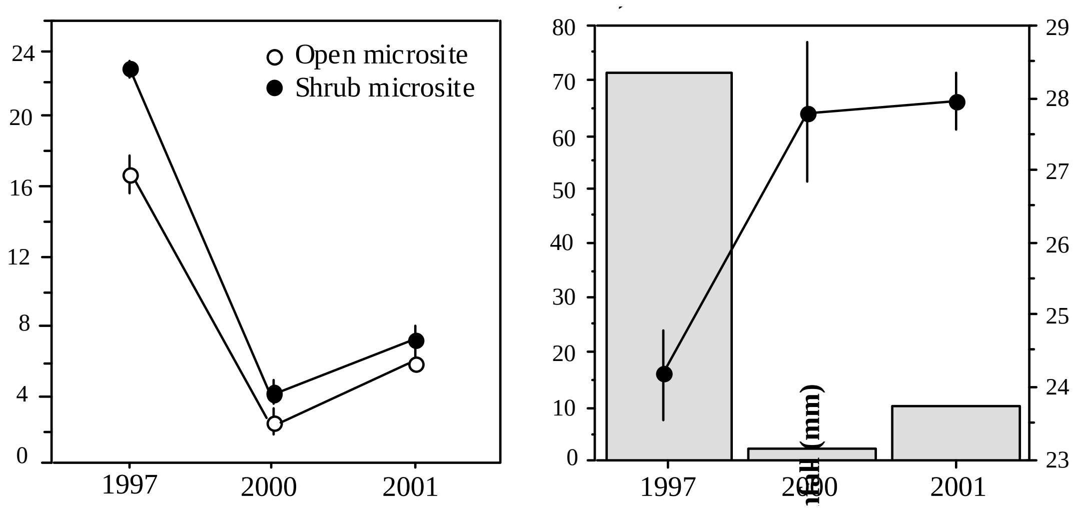

a) Target species
P < 0.0001
1.5
1.0
0.5
0.0
-0.5
Evergreen
Deciduous
Pines
Shrubs
b) Nurse shrubs
P < 0.0001
Legumes
Small shrubs
Spiny
Rockroses
Effect size (d+)
c) Altitude
P < 0.0001
Low
High
d) Aspect
P < 0.0001
Sunny
Shady
e) Year
P < 0.0001
1.6
1.2
0.8
0.4
0.0
-0.4
1997
2000
2001

Figure 4.


Open microsite
Shrub microsite
24
20
16
12
8
4
0
1997
2000
2001
80
70
60
50
40
30
20
10
0
29
28
27
26
25
24
23
1997
2000
2001
(mm)