

1 Running Head: Pioneer shrubs facilitate forest restoration

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

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Abstract

1
2 After a millenarian history of over-exploitation, most forests in the Mediterranean
3 Basin have disappeared, leaving many degraded landscapes that have been recolonized
4 by early-successional shrub-dominated communities. Common reforestation techniques
5 treat these shrubs as competitors against newly planted tree seedlings, thus shrubs are
6 cleared before tree plantation. However, empirical studies and theory governing plant-
7 plant interactions suggest that, in stress-prone Mediterranean environments, shrubs can
8 have a net positive effect on recruitment of other species. Between 1997 and 2001, we
9 carried out experimental reforestations in the Sierra Nevada Protected Area (SE Spain)
10 with the aim of comparing the survival and growth of seedlings planted in open areas
11 (the current reforestation technique) with seedlings planted under the canopy of pre-
12 existing shrub species. Over 18,000 seedlings of 11 woody species were planted under
13 16 different nurse shrubs throughout a broad geographical area. We sought to explore
14 variations in the sign and magnitude of interactions along spatial gradients defined by
15 altitude and aspect. In the present work, we report the results of a meta-analysis
16 conducted with seedling survival and growth data the first summer following planting,
17 the most critical period for reforestation success in Mediterranean areas. The facilitative
18 effect was consistent in all environmental situations explored (grand mean effect size
19 $d_{++}=0.89$ for survival and 0.27 for growth). However, there were differences in the
20 magnitude of the interaction depending on the seedling species planted as well as the
21 nurse shrub species involved. Additionally, nurse shrubs had a stronger facilitative
22 effect on seedling survival and growth at low altitudes and sunny, drier slopes than at
23 high altitudes or shady, wetter slopes. Facilitation in the dry years proved higher than in
24 the wet one. Our results show that pioneer shrubs facilitate the establishment of woody,

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

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

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Introduction

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

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

20 Environmental conditions in Mediterranean mountains are particularly variable
21 in both time and space (Blondel and Aronson 1999). Their complex orography and high
22 altitudes, together with an unpredictable climate, foster the coexistence of many
23 contrasting ecological scenarios at local scales. Differences in environmental conditions
24 appearing at a scale of meters may cause intense shifts in the net outcome of plant
25 interactions. Facilitation often increases with intensified stress, as has been reported in

1 south-facing *versus* west-facing slopes in rocky plant communities (Callaway et al.
2 1996), in dry *versus* mesic adjacent sites in the Chilean matorral (Holmgren et al. 2000),
3 in higher *versus* lower depths in coastal ecosystems (Bertness et al. 1999), or in high
4 *versus* low altitudes in alpine and semiarid environments (Pugnaire and Luque 2001,
5 Callaway et al. 2002). Interspecific interactions can also vary at the same site between
6 years depending on climatic conditions, although the relationship between climatic
7 variability and the net result of the interaction is still unclear. Some studies report
8 stronger facilitation in dry and hot years compared to relatively benign years (Greenlee
9 and Callaway 1996, and Ibañez and Schupp 2001) whereas other studies reached the
10 opposite conclusion (Casper 1996, and Tielbörger and Kadmon 2000). Therefore, an
11 understanding of how the interaction between shrubs and tree seedlings vary spatio-
12 temporally is crucial to assess the generality of the utility of shrubs as nurse plants for
13 forest regeneration and restoration.

14 According to the above theoretical and empirical framework, we hypothesise
15 that an alternative reforestation technique using shrubs as planting microsites in
16 Mediterranean areas would give better results (in terms of seedling survival and growth)
17 than would standard techniques using open spaces without vegetation, especially in hot
18 and dry sites and years. To test this hypothesis, between 1997 and 2001, we carried out
19 experimental reforestations in the Sierra Nevada mountains in SE Spain, encompassing
20 the broad range of abiotic as well as biotic conditions provided by this Mediterranean
21 high-mountain. We considered both variability in space as well as in time, a
22 fundamental but barely explored combination of factors, in order to understand the
23 nature and strength of plant-plant interactions related to woody plant establishment.
24 Specifically, we addressed the following questions: 1) How does the use of shrubs as
25 microsites for planting improve tree seedling survival and growth? 2) How does the

1 effect of shrubs on seedling survival and growth vary depending on the shrub and tree
2 species? 3) How do the sign and magnitude of the interaction between shrubs and
3 woody seedlings depend on spatial characteristics of the study site, such as altitude and
4 aspect? and 4) How do the sign and magnitude of the interaction between shrubs and
5 woody seedlings depend on climatic conditions in the year of planting?

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Methods

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Study area and species

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

21 The experiments were conducted in seven sites of the Sierra Nevada mountains
22 (Table 1), for a total of 36-ha plots (see Appendix 1). The bedrock was siliceous in 2
23 study zones and calcareous in 5, and in all cases the predominant soils were regosols
24 and cambisols (Delgado et al. 1989). All study areas were burned within the last 20
25 years. Consequently, current vegetation is pioneer shrubs (>60% of cover in all cases)

1 mixed with annual and perennial grasses and herbs, together with some surviving
2 isolated trees. The most abundant shrub species in every study site are shown in Table
3 1.

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

11

12 *Experimental design*

13 Seedlings one- or two-year-old were planted in spring (March-April) between 1997 and
14 2001 at each study site using two reforestation techniques: (i) a traditional technique of
15 planting target seedlings in open interspaces without vegetation (Open microsite), and
16 (ii) an alternative technique of planting seedlings under the canopy of shrubs (Shrub
17 microsite) intermingled with the open microsites. Seedlings, provided by the Junta de
18 Andalucía (Consejería de Medio Ambiente), were grown in nurseries under similar
19 conditions. In the case of *Acer opalus* subsp. *granatense* and *Pinus sylvestris* var.
20 *nevadensis*, rarely available in nurseries, seedlings came from seeds collected from
21 adults near the planting sites and seeded in a nursery located at La Cortijuela Botanical
22 Garden (Sierra Nevada National Park). The most abundant shrub species at each site
23 were chosen as nurse plants. In total, we used 16 nurse plant species and 11 target
24 species, for a total of 146 different plot-nurse shrub-target species combinations
25 (experimental cases, hereafter; see Appendix 1). Between 50-60 individually-tagged

1 seedlings were planted per plot-nurse shrub-target species combination. In both Shrub
2 and Open microsites, an automatic auger 12 cm in diameter was used to dig the planting
3 holes 40 cm deep, in an attempt to minimize disturbance to nurse and soil structure.

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

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

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

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

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

1 Intensity (RCI) because RCI has no minimum value, and therefore gives extreme
2 negative values when plant performance is greater in the presence than in the absence of
3 neighbours. For seedling survival, RNE was calculated as the difference in survival with
4 and without nurse shrubs relative to the case with the greatest survival in the pair. For
5 growth, RNE was calculated using means of seedling growth in each plot. Because
6 survival and growth can be influenced by the initial seedling height, we checked the
7 correlation between them, which proved non-significant. Thus, we deleted initial
8 seedling height data throughout all the study. All indices, as well as subsequent
9 statistical analyses, were performed using one-year survival and growth data in order to
10 standardize time scales between experiments. Our previous experience shows that, in
11 Mediterranean environments, the first summer after planting is the main mortality factor
12 for seedling survival (with mortalities of even 90% of the individuals planted), and so
13 the success of a reforestation can be properly evaluated on the basis of first-summer
14 results (Vilagrosa et al. 1997, Rey-Benayas 1998, Maestre et al. 2001, Castro et al.
15 2002).

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

1 mortality was summer drought, whereas the remaining 2% was attributable to herbivore
2 damage (trampling, uprooting, browsing).

3 The effect of shrubs significantly differed between target species ($Q_B = 49.55$, df
4 $= 3$, $P < 0.0001$). Whereas the effect was significantly different from zero for
5 Mediterranean evergreen, deciduous and shrubs, it was not significant for mountain
6 pines (Figure 2a). The magnitude of the effect varied from low for mountain pines,
7 through large for deciduous, to very large for Mediterranean evergreen and shrubs.
8 Between nurses, the effect varied from significantly large and positive for legumes and
9 small shrubs (facilitation), through non-significantly medium and positive for deciduous
10 spiny, to significantly large and negative for rockrose (antagonism; Figure 2b).

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

19 Comparisons between years revealed a significant effect of shrubs on seedling
20 survival in 2000 and 2001 (“dry years”), but not in 1997 (“wet year”) ($Q_B = 48.51$, $df =$
21 2 , $P < 0.0001$; Figure 2e).

22

23

Growth

24 The RNE for growth could be calculated only in 68% experimental cases, where more
25 than one seedling survived. Of these cases, 76% showed higher growth in Shrubs

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

17

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

19 We found relevant differences between target species in their response to the presence
20 of nurse shrubs. Among trees, *Quercus* spp. and *Acer opalus* subsp. *granatense* showed
21 the greatest response both for survival and growth, possibly as a consequence of being
22 late-successional, shade-tolerant species (Zavala et al. 2000, Gómez et al. 2001b).
23 Montane pines had the lowest response in accordance with their shade-intolerant nature
24 (Ceballos and Ruíz de la Torre 1971, Nikolov and Helmisaari 1992), although
25 association with shrubs was still beneficial, given the harsh conditions of Mediterranean

1 summer (Gómez et al. 2001a, Castro et al. 2002). However, shrub seedlings responded
2 more than any tree species to the presence of nurse shrubs, with *Rhamnus alaternus* and
3 *Crataegus monogyna* showing the greatest and *Retama sphaerocarpa* the lowest
4 increase in survival and growth (see Appendix 1). This result, together with the higher
5 values of survival in comparison to any other target species, makes the planting of late-
6 successional shrubs under primary-successional shrubs the most effective way of
7 accelerating succession in degraded sites where the direct recovery of the tree cover can
8 be very difficult, if not impossible.

9 Our work also demonstrates differences between shrubs in their facilitative
10 effect. The magnitude and sign of the nurse effect on seedling survival varied from large
11 and positive for legumes and small shrubs, through medium and positive for deciduous
12 spiny shrubs, to large and negative for rockroses. The differential effect of nurse shrubs
13 may be related to characteristics of the functional groups. Legumes may increase
14 survival and growth by improving soil-nutrients composition due to nitrogen fixation, a
15 scarce nutrient in Mediterranean soils (Callaway 1995, Alpert and Mooney 1996,
16 Franco-Pizaña et al. 1996). On the other hand, radiation during summer in
17 Mediterranean environments is usually excessive, causing photoinhibition of
18 photosynthesis in many plant species (Valladares 2003). In this context, shrub canopy
19 shade can favour seedling performance by reducing radiation in comparison to open
20 areas. In fact, additional experiments conducted in two of the study zones included in
21 the meta-analysis (Gómez et al. 2001b) show that the modification of the microclimate
22 under the canopy of the nurses (e.g. lower radiation and temperature and higher
23 atmosphere and soil humidity) is a main facilitative mechanism of woody seedling
24 establishment (see also Rey-Benayas 1998, Rey-Benayas et al. 2002, Maestre 2002).
25 Finally, in the case of rockroses, the negative effect on the survival of target species is

1 presumably due to allelopathic leachates characteristic of this family (Robles et al.
2 1999), particularly for *Cistus albidus*. Although the grouping of experimental cases that
3 involved the use of meta-analytical techniques prevented the analysis of differences at
4 the species level, these results show that the identity of the nurses matters. This should
5 be taken into account when designing reforestation programmes, in order to choose the
6 nurse shrub species that maximize survival probabilities.

7

8 *The importance of environmental variability in plant-plant interactions*

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

19 With respect to the spatial gradient, the strength of the positive interaction was
20 significantly higher at low altitudes and sunny slopes than at high altitudes or shady
21 slopes. These results indicated a shift in the balance of competitive *versus* facilitative
22 intensity on stress gradients (Bertness and Callaway 1994, Bruno et al. 2003). At low
23 elevation and sunny slopes, low precipitation and high temperatures result in an intense
24 summer drought, limiting seedling survival and growth more than does resource
25 acquisition. Alleviation of such severe stress by nurse shrubs may benefit seedlings,

1 outweighing any effects of their competition for resources (Callaway and Walker 1997).
2 On the contrary, at high elevations and shady slopes, with lower summer temperatures
3 and higher precipitation (and thus less intense summer drought), the abiotic
4 environment barely limits the uptake of resources for plants, and consequently the
5 positive effects of shrubs is less notable (Callaway and Walker 1997).

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

21

22 *Management implications*

23 Our experimental results have clearly shown that the use of nurse shrubs facilitates
24 seedling establishment in many different ecological settings in Mediterranean
25 mountains (altitude, exposure, successional phase of the pre-existing vegetation, level

1 of local environmental stress). Although we monitored one-year survival, the benefit of
2 planting seedlings under shrubs could be translated beyond this stage to sapling or
3 reproductive stages, since natural regeneration in Mediterranean ecosystems is mainly
4 limited at the seedling stage (Herrera et al. 1994, Rey and Alcantara 2000, Gómez
5 2003), and experimental reforestations reveal the bottleneck of first-summer mortality
6 (Maestre et al. 2001, Castro et al. 2002, Castro et al. *in press*).

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

18 Our study implies that the removal of shrubs is not appropriate for reforestation
19 in Mediterranean mountains. This traditional procedure is rooted in techniques
20 developed in Central and Northern Europe (Groome 1989, Bauer 1991), where summer
21 mesic climatic conditions and dense plant cover often result in competition for light and
22 nutrients. This ecological context strongly differs from Mediterranean environments,
23 where stressful conditions, primarily summer drought, severely limit the uptake of
24 resources by the plant, allowing habitat amelioration provided by pioneer shrubs to
25 become the major determinant of spatial distribution of woody seedlings. Therefore, a

1 new paradigm for the science of restoration of Mediterranean forests, based on the
2 natural spatial patterns of regeneration of woody vegetation (with shrubs as microsites
3 for recruitment), emerges from the results of the present work as well as other previous
4 studies (Castro et al. 2002, Maestre et al. 2001, 2002). Furthermore, given that the
5 facilitative effect increases with abiotic stress, this technique might be more relevant
6 under the predicted rise in temperatures, dryness and rainfall variability (with more
7 episodes of drought) for the Mediterranean region under global warming (IPCC 2001).
8 Thus, benefits of this technique will be greater in coming years under a scenario of
9 climatic change.

10

11

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1 **Appendix 1.** Summary of the 146 experimental cases (=plot-nurse shrub- target species
 2 combination) integrating the meta-analysis. N_c and N_e refer to the number of seedlings
 3 planted in control (Open) and experimental (Shrubs) microsites. RNE values show the
 4 sign and magnitude of the interaction between shrubs and woody seedlings, both for
 5 survival and growth. This index ranges from -1 to 1, with negative values indicating
 6 facilitation and positive values competition. Spiny = *Crataegus monogyna*, *Berberis*
 7 *hispanica* and *Prunus ramburii*. EC = experimental case.
 8

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

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

40	1997	10	Spiny	<i>P. sylvestris</i>	96	50	- 0.10	- 0.13
41	1997	10	Spiny	<i>P. nigra</i>	95	60	0.13	- 0.21
42	1997	11	<i>S. lavandulifolia</i>	<i>P. sylvestris</i>	43	50	- 0.48	0.31
43	1997	11	<i>S. lavandulifolia</i>	<i>P. nigra</i>	46	55	- 0.31	0.24
44	1997	11	Spiny	<i>P. sylvestris</i>	102	50	- 0.13	0.14
45	1997	11	Spiny	<i>P. nigra</i>	99	55	0.42	0.59
46	1997	12	<i>S. lavandulifolia</i>	<i>P. sylvestris</i>	44	49	- 0.65	0.12
47	1997	12	<i>S. lavandulifolia</i>	<i>P. nigra</i>	45	47	- 0.19	0.02
48	1997	12	Spiny	<i>P. sylvestris</i>	87	49	- 0.54	- 0.02
49	1997	12	Spiny	<i>P. nigra</i>	94	47	- 0.06	- 0.12
50	1998	13	<i>S. lavandulifolia</i>	<i>Q. pyrenaica</i>	48	48	- 0.36	----
51	1998	14	<i>S. lavandulifolia</i>	<i>Q. pyrenaica</i>	51	47	- 0.05	----
52	1998	15	<i>S. lavandulifolia</i>	<i>Q. pyrenaica</i>	45	45	- 0.38	----
53	1997	16	Spiny	<i>A. opalus granatense</i>	15	15	- 0.13	- 0.39
54	1997	16	Spiny	<i>P. sylvestris</i>	13	15	- 0.04	0.18
55	1997	16	Spiny	<i>P. nigra</i>	16	15	- 0.27	- 0.11
56	1997	16	Spiny	<i>Q. ilex</i>	15	14	0.07	- 0.16
57	1997	17	Spiny	<i>A. opalus granatense</i>	12	12	- 0.40	- 0.34
58	1997	17	Spiny	<i>P. sylvestris</i>	11	12	- 0.08	0.43
59	1997	17	Spiny	<i>P. nigra</i>	13	12	0.34	0.05
60	1997	17	Spiny	<i>Q. ilex</i>	10	11	- 0.39	0.38
61	1997	18	Spiny	<i>A. opalus granatense</i>	12	11	- 0.08	- 0.32
62	1997	18	Spiny	<i>P. sylvestris</i>	10	11	0.45	- 0.85
63	1997	18	Spiny	<i>P. nigra</i>	10	12	0.34	0.09
64	1997	18	Spiny	<i>Q. ilex</i>	10	10	0.3	- 0.15

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65	2001	19	<i>S. lavandulifolia</i>	<i>A. opalus granatense</i>	7	16	0.24	1
66	2001	19	<i>S. lavandulifolia</i>	<i>Q. ilex</i>	19	20	0.73	----
67	2001	19	<i>P. ramburii</i>	<i>A. opalus granatense</i>	14	16	0.52	0.18
68	2001	19	<i>P. ramburii</i>	<i>Q. ilex</i>	21	20	- 0.16	- 1
69	2001	19	<i>C. monogyna</i>	<i>A. opalus granatense</i>	10	16	0.47	- 0.67
70	2001	19	<i>C. monogyna</i>	<i>Q. ilex</i>	19	20	- 0.53	- 1
71	2001	20	<i>S. lavandulifolia</i>	<i>A. opalus granatense</i>	8	17	- 0.06	- 1
72	2001	20	<i>S. lavandulifolia</i>	<i>Q. ilex</i>	20	21	- 0.04	----
73	2001	20	<i>P. ramburii</i>	<i>A. opalus granatense</i>	13	17	- 0.43	- 1
74	2001	20	<i>P. ramburii</i>	<i>Q. ilex</i>	14	21	- 0.89	- 1
75	2001	20	<i>C. monogyna</i>	<i>A. opalus granatense</i>	17	17	- 0.50	- 1
76	2001	20	<i>C. monogyna</i>	<i>Q. ilex</i>	19	21	- 0.93	-----
77	2001	21	<i>S. lavandulifolia</i>	<i>A. opalus granatense</i>	22	13	- 1	- 1
78	2001	21	<i>S. lavandulifolia</i>	<i>Q. ilex</i>	30	47	- 1	-----
79	2001	21	<i>B. hispanica</i>	<i>A. opalus granatense</i>	32	13	- 1	- 1
80	2001	22	<i>C. monogyna</i>	<i>A. opalus granatense</i>	29	24	- 0.81	- 0.87
81	2001	22	<i>C. monogyna</i>	<i>Q. ilex</i>	46	37	- 1	-----
82	2001	22	<i>T. mastichina</i>	<i>A. opalus granatense</i>	39	24	- 0.85	- 0.64
83	2001	22	<i>T. mastichina</i>	<i>Q. ilex</i>	31	37	- 1	-----

ROSALES

84	2000	23	<i>S. lavandulifolia</i>	<i>P. nigra</i>	45	65	0.04	- 0.07
85	2000	23	<i>S. lavandulifolia</i>	<i>Q. ilex</i>	42	61	- 0.42	- 0.41
86	2000	23	<i>C. albidus</i>	<i>P. nigra</i>	42	65	1	-----
87	2000	23	<i>C. albidus</i>	<i>Q. ilex</i>	40	61	0.29	- 0.23

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

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

134	2001	35	<i>U. parviflorus</i>	<i>Q. faginea</i>	20	18	- 1	-----
135	2001	35	<i>U. parviflorus</i>	<i>Q. ilex</i>	21	22	- 0.52	- 0.51
136	2001	35	<i>U. parviflorus</i>	<i>P. nigra</i>	14	10	- 1	-----
137	2001	35	<i>U. parviflorus</i>	<i>J. oxycedrus</i>	13	13	- 0.71	0.17
138	2001	35	<i>U. parviflorus</i>	<i>R. alaternus</i>	24	25	- 0.36	- 0.92
139	2001	35	<i>U. parviflorus</i>	<i>C. monogyna</i>	20	23	- 0.51	- 0.72
140	2001	35	<i>U. parviflorus</i>	<i>R. sphaerocarpa</i>	24	19	- 0.16	-----
141	2001	36	<i>U. parviflorus</i>	<i>Q. ilex</i>	47	45	- 0.04	- 0.47
142	2001	36	<i>U. parviflorus</i>	<i>P. nigra</i>	22	10	1	-----
143	2001	36	<i>U. parviflorus</i>	<i>J. oxycedrus</i>	38	22	- 0.26	0.73
144	2001	36	<i>U. parviflorus</i>	<i>R. alaternus</i>	52	32	- 0.46	0.65
145	2001	36	<i>U. parviflorus</i>	<i>C. monogyna</i>	51	35	0.10	0.93
146	2001	36	<i>U. parviflorus</i>	<i>R. sphaerocarpa</i>	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	37°05'N 3°28'W	1850	N-NE	Calcareous	<i>Salvia lavandulifolia</i> , <i>Ononis aragonensis</i> , <i>Genista scorpius</i>
Panaderos					<i>Crataegus monogyna</i> , <i>Berberis hispanica</i> , <i>Prunus ramburii</i>
Cortijuela	37°05'N 3°28'W	1650	N-NE	Calcareous	<i>S. lavandulifolia</i> , <i>C. monogyna</i> , <i>B. hispanica</i> , <i>P. ramburii</i> , <i>Thymus mastichina</i> , <i>Echinopartium bosissiere</i> , <i>Genista cinerea</i>
Rosales	37°04'N 3°30'W	1800	S	Calcareous	<i>Cistus albidus</i> , <i>S. lavandulifolia</i>
Lanjarón	36°56'N 3°29'W	1230 - 1900	S	Siliceous	<i>Genista umbellata</i> , <i>Cistus monspeliensis</i> , <i>Ulex parviflorus</i> , <i>Santolina canescens</i> , <i>Artemisia campestris</i> , <i>Thymus vulgaris</i>
Lújar	36°52'N 3°23'W	465	N-NE	Calcareous	<i>Rosmarinus officinalis</i> , <i>C. monspeliensis</i> , <i>U. parviflorus</i>
Válor	37°02'N 3°06'W	1820 - 2000	S	Siliceous	<i>S. canescens</i> , <i>Festuca</i> sp., <i>Adenocarpus decorticans</i> , <i>A. campestris</i>
Huétor	37°15'N 3°27'W	1400	N-NE	Calcareous	<i>U. parviflorus</i> , <i>C. monogyna</i>

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.

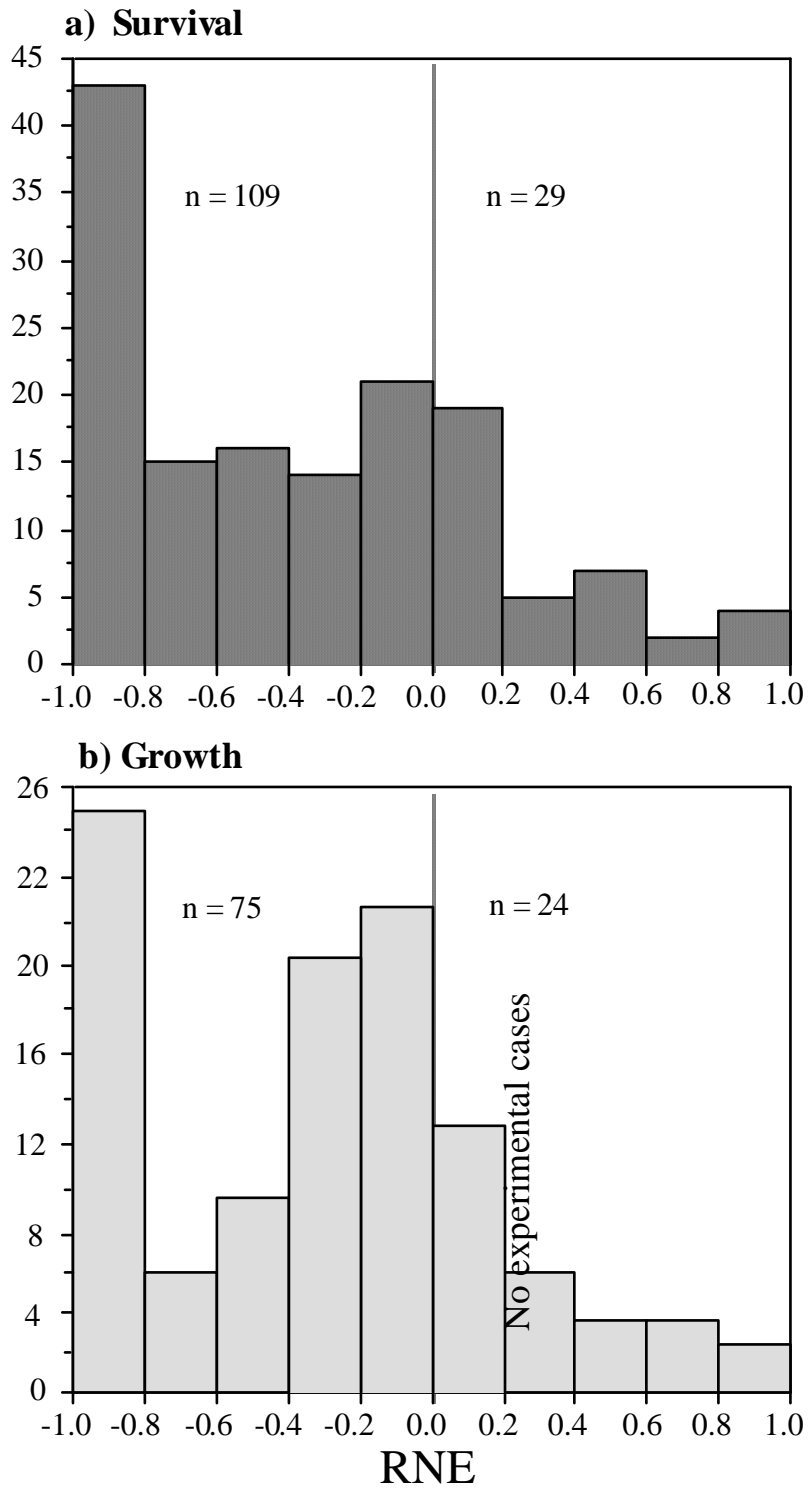


Figure 2.

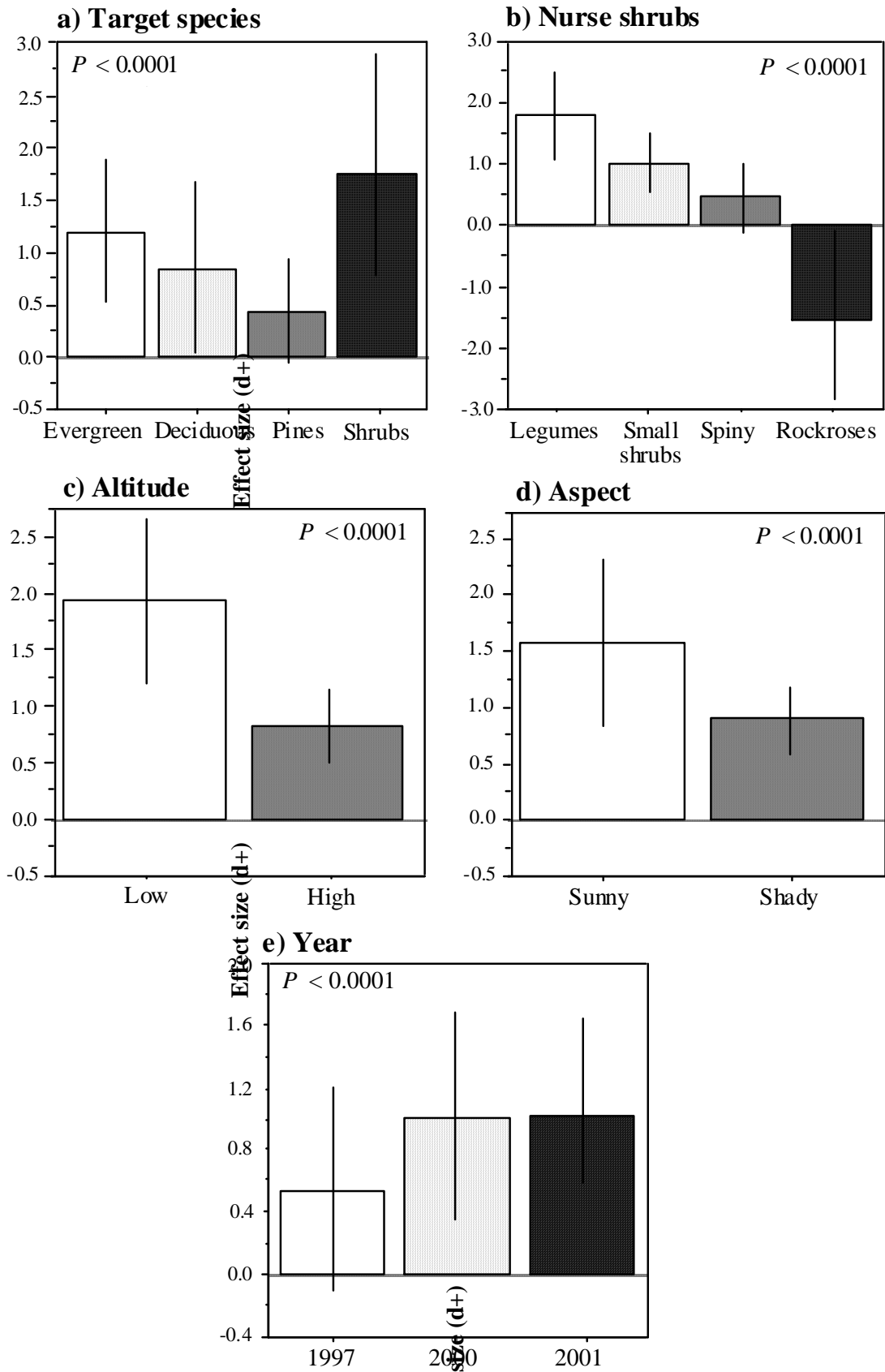


Figure 3.

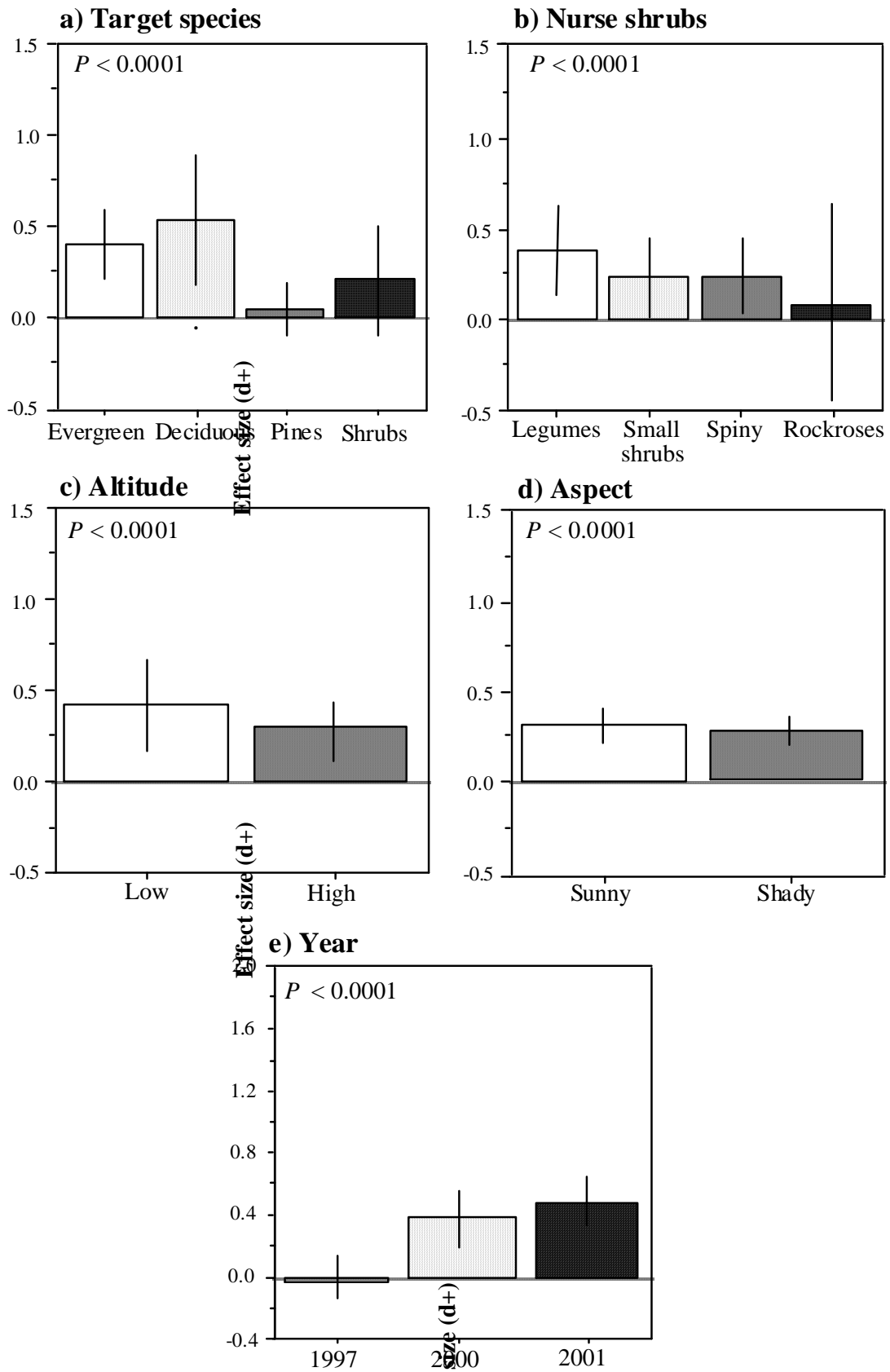


Figure 4.

