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Post-fire restoration of Mediterranean forests: Testing assembly rules mediated by facilitation

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Abstract

In view of the importance of facilitative interactions between plants, nurse-based planting has been proposed as a restoration technique for Mediterranean vegetation. However, facilitation efficiency is known to depend on the environmental context and the particular pair of interacting species. Understanding these context- and pair-specific dependences is fundamental to understanding Mediterranean vegetation dynamics and to improving the use of nurse-based plantation for restoration. We assessed the effectiveness of nurse-based plantation and the significance for post-fire restoration of some assembly rules mediated by facilitation. In two nearby areas of different burning ages, we compared seedling establishment of 13 tall shrubs and trees planted in open ground and under nurses. Nurses and planted seedlings were selected from different life-forms. Tests of the assembly rules were provided by the partitioning of the statistical interaction effect between nurse and planted seedling life-forms in a two-factor design. Nurse-based plantation increased seedling survival 2–9 times compared to plantation in open ground, depending on the year. The higher efficiency of nurse-based plantation was consistent for the two burned areas and occurred in many species even in years with contrasting rainfall. We detected pair-specific differences in the efficiency of facilitation. This pair-specificity was partly explained by the dependence between life-forms of nurse and guest species, suggesting the existence of assembly rules. Our results confirm that nurse-based plantation would be an appropriate post-fire restoration technique in Mediterranean mountains under dry-subhumid climate, but suggest that attention to the life-form assemblage rules is needed for an efficient implementation of such technique.

Zusammenfassung

In Hinsicht auf die Bedeutung der fördernden Interaktionen zwischen Pflanzen wurde die Pflanzung unter Ammenpflanzen als Renaturierungstechnik für mediterrane Vegetation vorgeschlagen. Die Förderungseffizienz ist jedoch bekanntlich vom Umweltkontext und besonders von den zwei interagierenden Arten abhängig. Ein Verständnis dieser kontext- und paarspezifischen Abhängigkeiten ist fundamental für das Verständnis der mediterranen Vegetationsdynamik und für die Verbesserung der Renaturierung durch Pflanzung unter Ammenpflanzen. Wir schätzten die Effektivität der Pflanzung unter Ammenpflanzen und die Bedeutung für die Wiederherstellung nach Bränden für verschiedene regelmäßige Zusammensetzungen ein, die durch Förderung beeinflusst sind.

Wir verglichen in zwei benachbarten Gebieten mit unterschiedlichen Brandzeitpunkten die Etablierung der Keimlinge von 13 großen Sträuchern und Bäumen, die auf offenen Boden oder unter Ammenpflanzen gepflanzt wurden. Die Ammenpflanzen und die gepflanzten Keimlinge wurden aus verschiedenen Lebensformen ausgewählt.

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Die Tests zum Vergleich der Zusammensetzungsregeln wurden erstellt, indem die statistischen Interaktionseffekte zwischen den Lebensformen der Ammenpflanze und des gepflanzten Keimlings in einem zweifaktoriellen Ansatz aufgeteilt wurden. Die Pflanzung unter Ammenpflanzen erhöhte die Überlebensrate des Keimlings in Abhängigkeit vom Jahr um das 2 bis 9fache im Vergleich zu einer Pflanzung auf offenem Boden. Die höhere Effizienz der Pflanzung unter Ammenpflanzen ergab sich durchgehend in den beiden Brandgebieten und fand bei vielen Arten sogar in Jahren mit gegensätzlichen Niederschlägen statt. Wir entdeckten paarspezifische Unterschiede in der Effizienz der Förderung. Diese Paarspezifität wurde zum Teil durch die Abhängigkeit zwischen den Lebensformen der Ammenpflanze und der Gastart erklärt und lässt vermuten, dass gewisse Zusammensetzungsregeln existieren. Unsere Ergebnisse bestätigen, das die Pflanzung unter Ammenpflanzen nach Brandereignissen eine geeignete Wiederherstellungstechnik in mediterranen Bergen mit trocken-semihumiden Klimaten ist, lassen aber auch vermuten, dass Aufmerksamkeit in Hinsicht auf die Zusammensetzungsregeln in Bezug auf die Lebensformen notwendig ist, damit diese Technik effizient eingesetzt werden kann.

Keywords: Forest restoration; Nurse effects; Nurse plants; Mediterranean fires; Plant–plant interactions; Post-fire regeneration; Succession

Introduction

Wildfires are today a major public concern as every year large areas of forest and scrublands are destroyed by wildfires in California, South Western Australia, Southern Europe, South Africa and Chile. While large efforts are devoted to extinction and prevention of wildfires, ecological restoration of affected areas is seldom undertaken. Since Mediterranean vegetation is known to be resilient to natural fire regimes, it is commonly expected that spontaneous regeneration would make post-fire intervention unnecessary (Keeley & Fotheringham 2001). Such expectation might be correct when it is natural vegetation which burns under a natural fire regime. However, vegetation and fire regimes have been severely altered over the last centuries in most Mediterranean regions, reducing the resilience of plant communities to fire (Díaz-Delgado, Lloret, Pons, & Terradas 2002) and making post-fire restoration an important consideration.

Restoring natural plant communities implies not only to successfully establish a diversity of plant species, but also to favour the recovery of community dynamics. Facilitative interactions (when a plant, the guest hereafter, benefits from growing in the microenvironment provided by another plant, the nurse hereafter) play a key role in the early regeneration stages of many woody species (Callaway, Walker, & Abrams 1997), and its importance has been repeatedly shown in Mediterranean species (García, Zamora, Hódar, Gómez, & Castro 2000; Rey & Alcántara 2000; Gómez-Aparicio et al. 2004; Rey et al. 2004). Based on such evidence, recent studies have proposed the use of shrubs as nurse plants for seedlings of Mediterranean woody species in restoration projects (Castro, Zamora, Hódar, & Gómez 2002; Gómez-Aparicio et al. 2004; Padilla & Pugnaire 2006; Rey, Siles, & Alcántara 2009).

The occurrence of facilitation is dependent on the particular pair of species involved, and on the environmental context (Callaway et al. 1997; Kitzberger, Steinaker, & Veblen 2000; Tielbörger & Kadmon 2000). Specifically, within the Mediterranean region, several studies have shown large differences in the facilitative effect exerted by different nurse species (Gómez-Aparicio et al. 2004). For example, pioneer *Cistus* shrubs (rockroses) show a consistent inhibitory effect on seedlings of tall shrubs and tree species (Robles, Bonin, & Garzino 1999). On the other hand, theoretical models predict that the importance of facilitation relative to competition varies across gradients of biotic and abiotic stress (Bertness & Callaway 1994), increasing as abiotic stress increases (Maestre, Bautista, & Cortina 2003). However, recent findings have generated some controversy on this idea (Kitzberger et al. 2000; Tielbörger & Kadmon 2000; Maestre & Cortina 2004). Maestre and coworkers (Maestre & Cortina 2004; Maestre, Valladares, & Reynolds 2005) have shown that under extreme Mediterranean aridity facilitation may be less frequent than assumed, and that a shift from facilitation to competition is possible. Similarly, when ungulate pressure increases, the protective effect of nurses against browsing may decrease (Smit, Vandenberghe, Ouden, & Müller-Schärer 2007). Thus, the balance between facilitation and competition will depend on the particular environmental conditions (Pugnaire & Luque 2001; Brooker et al. 2008; Veblen 2008). In consequence, before implementing nurse-based plantation for restoration it is necessary to test its effectiveness under different environmental circumstances (Valladares & Gianoli 2007).

This context and pair-specific dependence of facilitation may have important effects on the structure and dynamics of Mediterranean plant communities. For example, pair-specificity of facilitation might be related to the existence of assembly rules (Temperton, Hobbs, Nuttle, & Halle 2004) by which different species, life-forms and/or functional groups of nurse and guest species enter the community successively, according to their degree of dependence on facilitation by previously established plants. This process has been suggested to occur in Mediterranean woody plant communities of southern Spain (Gómez-Aparicio et al. 2004; Castro, Zamora, & Hodar 2006). Therefore, establishment of different combinations of pioneer species (or life-forms) after a disturbance would result in the establishment of different combinations of late successional tree species. Beyond its clear relevance to understand Mediterranean plant community dynamics, investigation of possible facilitation-mediated assembly rules has important implications for projects aimed at restoring the dynamics of disturbed vegetation and to improve the effectiveness of nurse-based restoration practices.

The present study is aimed to experimentally assess the effectiveness of nurse-based plantation in Mediterranean mountains and the significance for post-fire restoration of some assembly rules mediated by facilitation. In order to capture the variability in the nurse facilitative effects, we conducted experiments for 3 years and in two nearby areas which burned 5 and 20 years ago. Planted seedlings and nurse species representing different life-forms (see Appendix A for details) were used to test for the existence of life-form assembly rules. Specifically we address the following questions: (1) How widespread is facilitation by nurse plants in burned areas? (2) Does the efficiency of facilitation depend on the nurse–guest species combination, on the regeneration stage of the vegetation, or on the climatic conditions in the year of planting? (3) Can the different effectiveness of nurse–guest life-form combinations be interpreted in terms of assembly rules driving the successional pathway of the vegetation? From our results we derive suggestions for the most appropriate sequences of nurse–guest life-form combinations for restoration.

Materials and methods

Study area

The present study was conducted in two burned sites (Torre del Vinagre, burnt in 1986 and Puerto de las Palomas, burnt in 2001) in the Natural Park of Sierra de Cazorla, Segura y Las Villas (Jaen province, southeast Spain). The sites are ca. 7.5 km apart, they have the same geological substratum (calcareous limestone) and are exposed to the same climatic conditions. Mean annual rainfall in the closest weather stations ranges between 770.7 and 1155.6 mm (largely concentrated in autumn and spring), with average annual temperatures of 14.2–11.6 °C. The plantations took place in years 2004, 2005 and 2006, with varying annual rainfalls (own data registered with 12 pluviometers placed in the burned areas). Year 2004 suffered a very severe drought (annual rainfall averaged across the 12 pluviometers was 292.9 mm), whereas 2006 was a typical year (1000.5 mm) and 2005 a year below the typical rainfall (672.2 mm).

The potential native vegetation is a mixed forest of *Pinus nigra*, *Quercus ilex* and *Q. faginea* (Valle 2003). Before fire, both sites were covered by pine afforestation stands (*Pinus pinaster*, *P. halepensis*, and *P. nigra*) with poor undergrowth of native shrubs. Because of the different burning ages, the study sites differ in vegetation cover and height of the naturally regenerated vegetation. Nonetheless, the post-fire vegetation in both sites is mainly pioneer shrub, mixed with some resprouting of tall shrubs and tree species and some surviving isolated trees.

Experimental design

We compared the growth and survival of planted seedlings under the canopy of nurse species and in open ground. We planted 1- or 2-year-old seedlings in October and November each year, and determined establishment success in autumn next year. The holes (depth: 30–40 cm; diameter: 12 cm) for planting were drilled with a manual iron drill. For nurse-based plantings, the hole was drilled just below, or adjacent to (less than 10 cm apart), the canopy of nurses, always in north orientation to increase shading effect. Drilling holes minimizes disturbances to nurse and the soil structure (see Gómez-Aparicio et al. 2004, for a similar approach). Planting in open ground was done in the vicinity of shrubs used as nurses but always at least 1–2 m out of the canopy of any spontaneously established woody species. Since we were interested in testing the effectiveness of different combinations of nurse–guest life-forms we used a wide variety of nurse species classified as: leguminous small shrubs (hereafter LG-SS), non-leguminous small shrubs (NLG-SS), rockroses (small shrubs in the family Cistaceae; CIST), spiny tall shrubs (SP-TS), non-spiny tall shrubs (NSP-TS), and trees (TREE). Similarly, a wide variety of guest species were planted. These species were classified on the basis of life-forms as: tall shrubs (spiny and non-spiny, TS), deciduous trees (D) and evergreen trees (E). The species used, the type of life-form assigned to each species and the mean size of nurses and planted seedlings at the time of planting are shown in Appendix A. The plants used as nurses were regenerating spontaneously in the study site. They were randomly selected with no restriction other than avoiding specimens of too small size.

In 2004 and 2006 plantations were done in both study sites (four plots within Puerto de las Palomas and two plots within Torre del Vinagre), whereas in 2005 plantations were conducted only in four plots at Puerto de las Palomas. Since intense browsing was observed in the study sites (43% of the seedlings planted in the open in 2004 were browsed), a further treatment was established at Puerto de Las Palomas in 2006: seedlings were planted in open ground but protected against browsing with tree shelters (60 cm tall, 15 cm diameter and 2.5 cm × 1.5 cm pore, Redplanton®). We assumed that tree shelters did not change the abiotic conditions. Hence, this treatment allowed us to separate the facilitative effect of protection against browsing from the effect of more favourable abiotic conditions.

We used between 20 and 30 replicates for each nurse–guest species combination each year. In total, we planted 1670 seedlings in 2004 (1325 under nurses and 345 in open ground), 1044 in 2005 (804 under nurses and 240 in open ground) and 2021 in 2006 (1325 under nurses, 346 in open ground, and 350 in open ground with tree shelter). The species used in each year are shown in Appendix A.

Data analysis

Seedling survival 1 year after each plantation was analyzed using generalized linear mixed models with binomial error (procedure GLIMMIX in SAS, SAS Institute Inc. 2003). Guest species, plantation treatment (under nurse vs. open ground), and their interaction were considered fixed effects. In 2004 and 2006, a site effect was included to control for possible differences between sites (for example, differences related to burning age, like shrub cover and height or litter accumulation). Site and its interaction with treatment were considered random effects. When interaction terms were statistically significant, we used slice tests (with option SLICEDIFF of LSMEANS statement; SAS Institute Inc. 2003) to check for differences between levels of one factor within each level of the other factor of the interaction.

The effect of the protection with tree shelter was tested in a separate GLM analysis including the effects of plantation treatment (under nurse plants, open ground, open ground with tree shelters), planted species, and their interactions (all considered fixed effects).

To assess the variation in facilitation efficiency of nurse life-forms (nurse-LFs, hereafter) to different life-forms of guest species (guest-LFs, hereafter), we conducted an additional analysis with nurse-LF, guest-LF, and their interaction as fixed effects (only plantations in 2004 and 2006 were considered). We also calculated the facilitation efficiency of the nurses as the difference in mean seedling survival under the canopy of the nurse and in open microsites. We subsequently relativized this absolute difference to the sum of both terms (i.e., we used the relative interaction index, RII, of Armas, Ordiales, & Pugnaire 2004). The important effect in this analysis is the interaction between nurse-LF and guest-LF, which explores if the facilitation efficiency of different guest-LFs depends on the nurse-LF (i.e., whether there are any assembly rules in facilitation).

Results

Seedling establishment in nurse-based and open ground plantation

The nurse effect enhanced survival between 2 and 9 times, depending on the year. The estimated overall survival probability of guests under nurse plants was 0.09 ± 0.07, 0.80 ± 0.11 and 0.68 ± 0.10 (mean ± standard error) for 2004, 2005 and 2006, respectively, while the values in open ground were 0.01 ± 0.01, 0.28 ± 0.15 and 0.29 ± 0.10, respectively.

The effect of treatment on seedling survival depended on the planted species, both in 2005 and 2006 (Table 1). Seedling mortality was very high during 2004. Though the overall survival probability in this year was 9 times higher under nurses than in open ground (Fig. 1), there was no significant nurse effect. In years with intermediate or typical rainfall levels (2005 and 2006) the magnitude and significance of the positive effect of nurses differed between planted species, but the positive direction of the effect was general (Fig. 1): all planted species, except *Prunus mahaleb* (in 2005) and *Q. ilex* (in 2006), had higher survival under nurses.

We did not detect any significant differences on seedling establishment between sites in 2004 and 2006. Further, the effect of planting treatment did not vary between sites in any year (PT × S in Table 1).

Table 1. Analysis of the experiments of plantation under nurses versus open ground carried out in 2004, 2005, and 2006. Data are test statistics obtained from generalized linear mixed models testing, each year, the effects of site (S), plantation treatment (PT: under nurse vs. open ground), planted species (Sp) and the interactions PT × S and Sp × PT, on seedling survival 1 year after planting. Significance of effects is indicated as: (*) marginally significant effect ($p < 0.1$); *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$. "nt", not tested due to small sample size. "na", not available, because samples were taken in only one of the study sites in 2005. Plot effect (not shown) was included in the analyses as a random factor but did never show any significant value.

Effects	Statistic	2004	2005	2006
Site (S)	Z	0.57	na	0.00
Planted species (Sp)	F	5.59***	6.55***	4.97***
Plantation treatment (PT)	F	8.76	9.12*	5.84
PT × S	Z	0.37	na	0.92
PT × Sp	F	nt	13.4***	2.71**

Microclimate amelioration and browsing as nurse effects

Differences in seedling establishment in 2006 remained significant after adding the treatment of plantation in open ground with shelter ($F_{2,\,1963} = 85.9$, $p < 0.001$). There was significantly higher success in nurse-based plantation compared to open ground or open ground with shelter (Fig. 2). Survival was significantly higher in open ground with than without tree shelter.

There was a significant interaction between planted species and treatment ($F_{24,\,1963} = 5.8$, $p = 0.008$). Overall, species tended to show the general pattern with the highest mean survival under nurse, and higher survival in open ground with shelter than in open ground without shelter (data not shown). Exceptions were *Q. ilex*, *P. nigra*, *F. excelsior* and *P. terebinthus*, where shelter did not improve seedling survival.

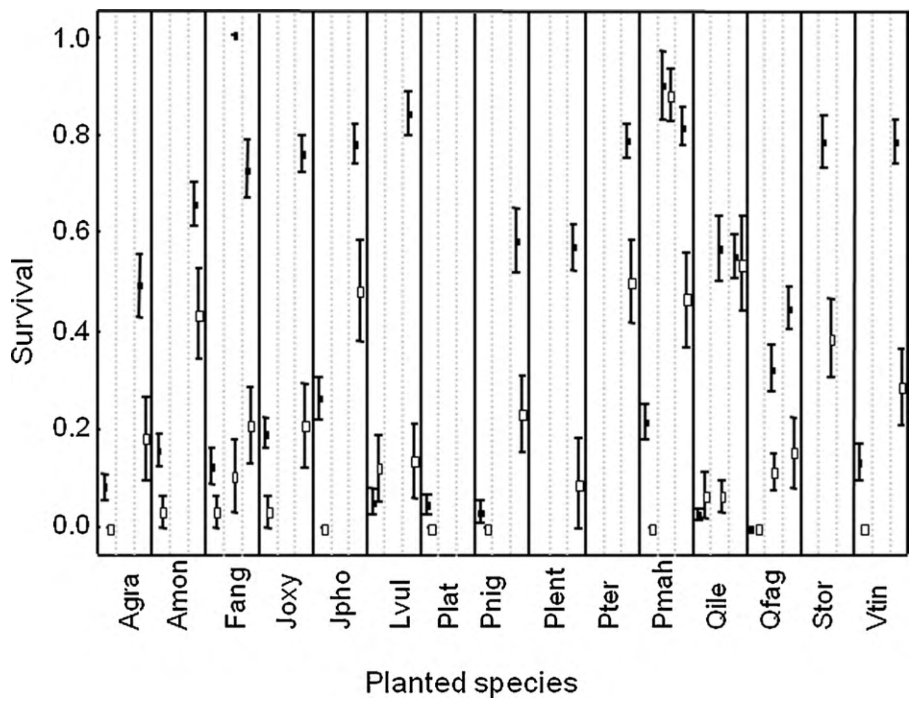

Fig. 1. Observed survival probabilities (±SE) for each planted (guest) species in every year of plantation. The values of different years (2004, 2005 and 2006) are represented in that order, separated by broken lines. For each species and year, survival in open ground is indicated with open symbol and survival under nurses is indicated with filled symbol. Species names are indicated as follows: *Acer granatensis* (Agra), *A. monspessulanum* (Amon), *Fraxinus angustifolia* (Fang), *Juniperus oxycedrus* (Joxy), *J. phoenicea* (Jpho), *Ligustrum vulgare* (Lvul), *Phillyrea latifolia* (Plat), *Pinus nigra* (Pnig), *Pistacia lentiscus* (Plen), *P. terebinthus* (Pter), *Prunus mahaleb* (Pmah), *Quercus ilex* (Qile), *Q. faginea* (Qfag), *Sorbus torminalis* (Stor) and *Viburnum tinus* (Vtin).

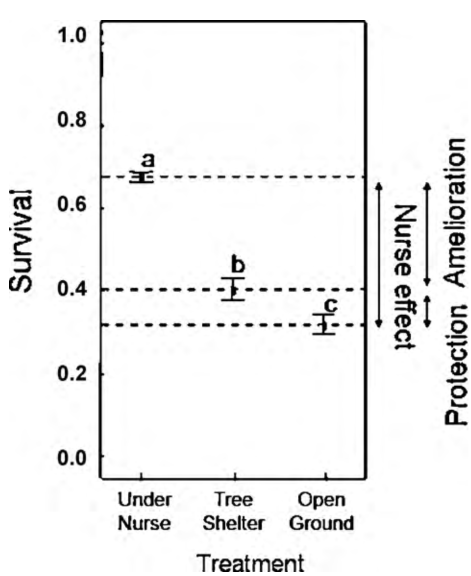

Fig. 2. Observed survival probability (±SE) for three plantation treatments at Puerto de las Palomas in 2006: plantation under nurse plants, plantation in open ground with tree shelters, and plantation in open ground without tree shelters. Total nurse effect and its partition into amelioration and protection effects are indicated on the left *y*-axis. Significant differences between treatments after post hoc tests are indicated by different letters.

Test of assembly rules

Our results showed interdependence between nurse and facilitated life-forms, and this interdependence occurred under very different rainfall regimes. The effect on seedling survival probability of the nurse-LF significantly differed between guest-LFs (Table 2) in both years. In 2004, seedling survival probability of deciduous trees and tall shrubs differed between nurse-LFs but the survival probability for seedlings of evergreen trees was independent of the nurse-LF (Table 2, slice test for the guest-LF factor). In 2006, the effect of nurse-LF on seedling survival probability remained significant for all guest-LFs. On the other hand, in 2004 differences in survival probability among guest-LFs appeared only under non-spiny tall shrub nurses (Table 2, slice test for the nurse-LF). In 2006, each nurse group showed a different effect on seedling survival probability for different life-forms of planted seedlings ($p < 0.05$ in all cases, see Table 2). There was no significant variation among guest life-forms in seedling survival probability in open microsites in any study year.

In absolute terms, facilitation efficiency was clearly higher during the humid 2006-year than during the dry 2004-year (Fig. 1) but it depended on the nurse and guest life-form combination. However, this inter-annual trend changed when we considered RII (Table 3) with facilitation efficiency higher

Table 2. Analyses of nurse and guest life-form (LF) interaction effects on the survival probability of planted seedlings. The slices of the interaction, exploring for each level of a factor the variation among the levels of the other factor (see section "Materials and methods"), are also shown. Nurse life-forms are leguminous small shrubs (LG-SS), non-leguminous small shrubs (NLG-SS), spiny tall shrub (SP-TS) and non-spiny tall shrubs (NSP-TS). Guest life-forms are tall shrubs (TS), deciduous trees (D) and evergreen trees (E) (see Appendix A for details). Open microsites were also considered as a level of the nurse life-form factor to subsequently obtain the facilitation efficiency of the nurse as the difference in mean seedling survival under the canopy of nurses and in open microsites.

Effects	2004 plantation			2006 plantation		
	nDF	dDF	F	nDF	dDF	F
Guest-LF* Nurse-LF	14	1655	4.27***	14	1639	13.25***
Slices of the interaction						
By guest-LF (variation in efficiency of different nurse-LFs to each guest-LF)						
Tall shrubs	4	1655	4.06**	4	1639	24.93***
Evergreen trees	4	1655	0.36	4	1639	2.71*
Deciduos trees	4	1655	6.91***	4	1639	12.53***
By nurse-LF (variation in establishment of different guest-LFs under each nurse-LF)						
Open	2	1655	0.48	2	1639	0.6
LG-SS	2	1655	2.27	2	1639	5.51**
NLG-SS	2	1655	2.07	2	1639	5.08**
SP-TS	2	1655	1.78	2	1639	3.33*
NSP-TS	2	1655	5.45*	2	1639	10.88***

Significance of effects is indicated as: *$p<0.05$, **$p<0.01$, ***$p<0.001$.

in the dry year. Survival of tall shrub seedlings was favoured under the canopy of other shrubs both in the humid and the dry year, particularly under leguminous small shrubs and non-spiny tall shrubs. There was no facilitative effect of shrubs on evergreens in the dry year. During the humid year, there were significant facilitative effects, with small shrubs (both leguminous and non-leguminous) favouring seedling survival of evergreen trees, while the effect of tall shrubs (both for spiny and non-spiny ones) was neutral. Finally, deciduous tree seedling survival was strongly favoured by all types of shrubs both in dry and humid years (Table 3).

Discussion

Plantation under nurse plants was more effective than plantation in open ground and this was spatially consistent. In spite of this generality, there was some variation in the magnitude of the facilitative effects. Such magnitude depended on the ecological context, with inter-annual climatic variation (especially rainfall) and the specificity in the combination of nurse–guest life-forms influencing the variability in the nurse effect.

Table 3. Effect size (RII ± 95% C.I.) of the facilitation efficiency of nurses. Species were classified according to life-form groups. Acronyms for nurse life-forms as in Table 2. Non-significant effects of the nurse facilitation efficiency are indicated in italics. Significant differences between nurse life-forms in their facilitation efficiency for a same guest life-form are indicated with a different letter. Tests of significance for the facilitation efficiency were obtained from differences of absolute means rather than RII (see section "Materials and methods").

Guest life-forms	Nurse life-forms			
	LG-SS	NLG-SS	SP-TS	NSP-TS
2004 (very dry year: 292.86 l/m^2)				
Tall shrub	0.72 ± 0.02a	0.58 ± 0.03b	0.56 ± 0.07ab	0.71 ± 0.02a
Evergreen tree	*0.33 ± 0.13*	*0.00 ± 0.11*	*−1 ± 0.13*	*−0.33 ± 0.14*
Deciduous tree	0.76 ± 0.03b	0.77 ± 0.02b	0.91 ± 0.01a	0.69 ± 0.03b
2006 (normal wet year: 1000.5 l/m^2)				
Tall shrub	0.44 ± 0.01a	0.38 ± 0.01bc	0.29 ± 0.03c	0.41 ± 0.01ab
Evergreen tree	0.22 ± 0.04ab	0.26 ± 0.02c	*0.15 ± 0.04*a	*0.09 ± 0.03*bc
Deciduous tree	0.39 ± 0.01ab	0.31 ± 0.01a	0.45 ± 0.01ab	0.32 ± 0.01b

Nurse facilitative effect during post-fire regeneration

The positive effect of nurse plants on seedling establishment has been widely shown in the Mediterranean Basin (Maestre, Cortina, Bautista, & Bellot 2003; Rey et al. 2004, among others). Similarly, a facilitative effect has been shown in arid environments in other regions in the world (Kitzberger et al. 2000; Tielbörger & Kadmon 2000). This effect is frequently associated with the reduction of water and irradiance stresses through shading in summer or with changes in soil properties, soil retention, and nutrient enrichment (Castro et al. 2002; Gómez-Aparicio, Gómez, Zamora, & Boettinger 2005). As mortality in our study area largely occurred during summer drought we assume that mortality was mainly due to water stress or photoinhibition, and that the facilitative effects of nurses during post-fire regeneration acted mainly through stress mitigation. Another facilitative effect mediated by nurses is protection against ungulate browsing. This effect seems to increase in areas with high herbivory pressure and when the nurse shrub is thorny (Callaway, Kikodze, & Kikvidze 2000; García & Obeso 2003) or has low palatability (Baraza, Zamora, & Hodar 2006). We investigated the possible role of facilitation by protection against herbivore browsing through the use of tree shelters. Our results confirm that protection against browsing is operating as another facilitative effect of nurses in post-fire regeneration, since seedlings protected in open ground increased their survivorship, although not all species benefited of such protection. This facilitative effect happens because our burned area suffers the combined browsing of domestic sheep and wild ungulate populations, mainly red deer (*Cervus elaphus*), fallow deer (*Dama dama*), and wild boars (*Sus scrofa*). Nevertheless, because the probability of survival was still lower for seedlings with tree shelters than for seedlings under nurse shrubs, it seems that the facilitative effect of nurses in post-fire regeneration is mediated both by protection and microhabitat amelioration, with a major effect of the latter (Fig. 2; see also Gómez-Aparicio, Zamora, Castro, & Hodar 2008).

The facilitative effect of nurses was consistent between areas differing in burning age (with different vegetation cover and height or litter accumulation). Experimental trials using shrubs as nurses for seedling plantation in burned areas of other Mediterranean mountains of southern Spain found an overall facilitative effect of the established shrubs, which was consistent across an altitudinal range of 465–2000 m (Gómez-Aparicio et al. 2004). Thus, it seems that nurse facilitative effects are widespread in burned areas under dry to subhumid Mediterranean mountain conditions.

In contrast to this spatial homogeneity of the nurse effect, our results show that the facilitative effect varied between years depending on the guest species. We found significant nurse effects for some guest species in years with rainfall below typical values (2005) or in years with typical rainfall (2006), while in years with extreme drought we could not detect any significant nurse effect on any species. Other studies have shown that a shift from facilitation to competition is frequent under high abiotic stress (Maestre & Cortina 2004; Maestre et al. 2005), when the levels of the most limiting resource are so low that the benefits provided by the nurse cannot outweigh the negative effect its own resource uptake has on the guest. The variation we found in facilitative effects between years with different rainfall seems also consistent with the existence of a humped-back facilitative response proposed in relation to gradients of water stress (Kitzberger et al. 2000; Tielbörger & Kadmon 2000; Maestre & Cortina 2004).

In any case, not all the species were similarly affected by nurses in years of high water stress. In our study the interaction with nurses of seedlings of *Q. ilex* and *Ligustrum vulgare* seemed sensitive to high water stress, and in years of severe drought the interaction with the nurse turned from facilitative to neutral. Other authors have shown that seedling establishment of *Q. ilex* is facilitated by shrubs mainly under dry-subhumid climate (Vilagrosa et al. 1997). The humped-back response has also been proposed regarding ungulate browsing pressure (Smit et al. 2007). Our data do not fit such a response since the year of higher ungulate browsing (incidence of ungulate browsing in open ground was 56.9% of seedlings in 2006 compared to 43.0% in 2004; data registered during surveys of survival) was also the year of the highest facilitation efficiency of nurses.

Assembly rules

To explore the existence of assembly rules we grouped the species into life-forms and estimated each year the relative magnitude of facilitative effect (RII index) of each nurse-LF on each guest-LF. Comparisons of the magnitude of RII between years with different overall mortality may be misleading, so we will avoid such comparisons.

Different nurse-LFs provided different facilitation service to different guest-LFs. Similar results were shown by Gómez-Aparicio et al. (2004) under Mediterranean mountain environment. During an extremely dry year, evergreen trees did not benefit from the facilitative effects of any nurse-LF, and there were even negative effects. Tall shrubs and deciduous trees were facilitated in both typical and dry years suggesting a consistent advantage of nurse-based planting for these groups. Deciduous trees were always best assisted by spiny tall shrubs, which may be related to a double facilitation service provided by these nurses, in terms both of microhabitat amelioration and mechanical protection against ungulates (Brooker, Scott, Palmer, & Swaine 2006; Smit et al. 2007). Since deciduous leaves are usually more palatable than evergreen leaves (Baraza et al. 2006), the benefit of protection against browsing by well-defended nurses would be particularly manifest for deciduous species.

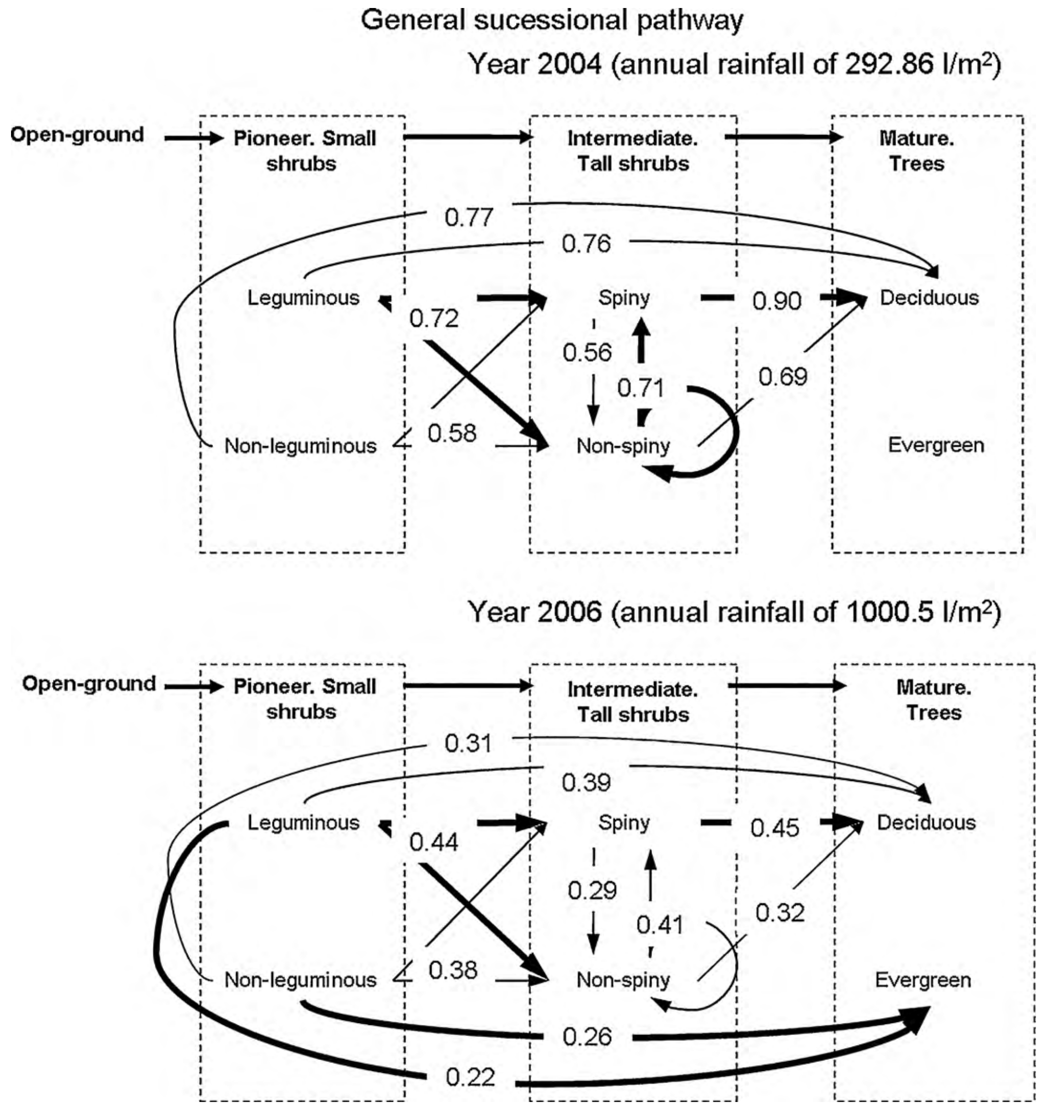

Fig. 3. Graphic representation of the life-form assembly rules and associated successional pathways. The arrows (starting at a nurse-LF and pointing to a guest-LF) indicate facilitation-mediated assembly rules defined as the facilitation efficiency of a nurse-LF on the seedling survival of a guest-LF. Facilitation efficiency was measured as a significant relativized difference between mean survival under the nurse and in open microhabitats (RII, see section "Materials and methods"). The numbers attached to arrows are the respective effect sizes. Best facilitation efficiencies for each guest-LF are highlighted with wider arrows to remark major successional pathways. The theoretical successional sequence is provided in bold type on the top of the panel for each year. Note that each year it is possible to complete a sequential pathway from small shrubs to tall shrubs to deciduous trees, though this possibility does not exist for evergreen trees any year. Evergreen tree establishment may proceed still by facilitation during favourable years, though not sequentially but skipping the intermediate stage of tall shrubs.

Recently, it has been suggested that nurse-based restoration techniques have the advantage of recreating the natural succession of Mediterranean and other ecosystems, minimizing the impact that other practices have on the community (Gómez-Aparicio et al. 2004; Castro et al. 2006; Siles, Rey, Alcántara, & Ramírez 2008; Gómez-Aparicio 2009). It is therefore of interest to place the results of our study in a successional sequence context. The finding of a significant interaction between nurse-LFs and guest-LFs in the survival of planted seedlings and, in particular, the partitioning of such interaction effects (slices test, Tables 2 and 3) is relevant to identify assembly rules and their resulting successional pathways. From a conceptual standpoint, the comparisons reflected in Table 3 can be merged in a successional graph under the assumption that tree species (mature forest phase) will follow tall shrubs (intermediate successional phase) and these will follow pioneer shrubs (see Gómez-Aparicio 2009, for a similar logic). To a large extent, our data support a sequential change of vegetation during post-fire succession which can be mimicked through planting tall shrubs beneath pioneer shrubs, and deciduous trees under tall shrubs (see details in Fig. 3). Establishment of evergreen tree does not follow, however, a sequential facilitative pathway, since they are not facilitated by tall shrubs, which may even inhibit them in dry years (see discussion above). During favourable years, their establishment may proceed still by facilitation, though not sequentially but skipping the intermediate stage of tall shrubs. Some other jumps of this sequence are also possible, but their effectiveness depends on annual rainfall and they are less effective than the sequential pathway.

Management implications

Our results clearly support the use of nurse-based plantation as post-fire restoration technique under dry to subhumid Mediterranean environment. Compared to traditional reforestation, it provides benefits for seedling establishment in terms of microclimate amelioration and protection against ungulate browsing. Beyond the general benefit of the use of nurse plants, our results indicate that attention to life-form assembly rules is needed for an efficient implementation of such a technique (see Temperton et al. 2004). Knowledge of such assembly rules may help increase the success of vegetation restoration projects both by improving the establishment probability of target species and by restoring the successional sequences typical of Mediterranean vegetation dynamics.

After a forest fire it is common to find patches in very different recovery status (see Siles et al. 2008), which is a consequence of the spatial heterogeneity in pre-fire vegetation and the intensity of fire. In this situation a multi-phase reforestation strategy, aimed to attain in each patch the next stage in the succession, would be appropriate (see also Gómez-Aparicio et al. 2004). This multi-phase restoration program would have the additional advantage of maintaining spatially heterogeneous vegetation stands.

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Appendix A. Supplementary data

The online version of this article contains additional supplementary data. Please visit doi:10.1016/j.baae.2010.05.004.

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