Assessing the long-term contribution of nurse plants to restoration of Mediterranean forests through Markovian models

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Summary

1. Based on short-term experimental data, facilitative interactions between woody plants (nurse-recruit interactions) have been described as essential for the restoration of Mediterranean forests. However, the long-term effects of nurse plants on vegetation dynamics are unknown. This study aims to project post-fire vegetation dynamics from easily retrieved data, and to asses the long-term contribution of nurse plants to forest restoration.

2. In an area burned 20 years ago, we compared post-fire dynamics in three states of regeneration: pioneer scrubland; spontaneous pine regeneration stands; and late successional scrubland. For each regeneration state, we obtained an interaction matrix with the frequency of recruitment of a given species under the canopy of every other species in the community. These matrices provided the raw data to develop Markov chain models of community dynamics. We used sensitivity analyses to explore how small shifts in replacement probabilities between species (or between functional groups) may affect the similarity of the projected community to an undisturbed reference community.

3. Plots in the pioneer state had the lowest frequency of facilitative interactions. Matrix projection showed that, under the current frequency of facilitation, these pioneer scrublands would remain so in the long term. By contrast, the building state had the highest frequency of facilitation, and its projection suggested that it should reach a steady state very similar to the reference community. These results confirm that nurse facilitative effects are fundamental for a secondary successional trajectory of the post-fire dynamics.

4. Sensitivities showed that secondary succession may be launched in the pioneer state by increasing the frequency of seedlings of tall shrubs, evergreen and deciduous trees under small shrubs.

5. *Synthesis and applications*. Our Markov chain successional model is an analytical tool which can be applied rapidly and easily to determine successional trajectories for forest restoration. It allows: (i) evaluation of post-fire dynamics and identification of areas in need of intensive intervention (i.e. where secondary succession remains arrested leading to stasis in the pioneer state); (ii) assessment of the role of long-term facilitative nurse effects on restoration; and (iii) identification of species-pair combinations and functional nurse groups of value for further planting efforts.

Key-words: forest dynamics, facilitation, Markov chains, post-fire restoration, secondary succession, sensitivity, plant–plant interactions

Introduction

Mediterranean ecosystems worldwide are suffering from an increase in the number and extent of forest fires over the past decades (Pausas & Vallejo 1999). More than ever, the development and implementation of ecological restoration practices specifically tailored for Mediterranean ecosystems must become the focus of active research. The ample available knowledge of Mediterranean post-fire regeneration dynamics and plant strategies in response to fire and other perturbations is especially useful for this purpose. For example, species have been characterized by their post-fire regeneration ability (Pausas 1999; Pausas *et al.* 2004) by resprouting of surviving organs (resprouter species) vs. increased seed germination

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after fire (seeder species). Similarly, the long-term changes in vegetation cover, structure and composition, which define different successional pathways (Franquesa 1989; Moreno & Oechel 1994; Bonet & Pausas 2005), are also well known. Autosuccession has been claimed to be the most frequent post-fire successional pathway under Mediterranean climate (Hanes 1971; Trabaud 1987; Moreno & Oechel 1994). However, recent modelling argues that secondary succession should be a frequent alternative pathway under favourable climatic conditions in the Mediterranean region (Zavala 2000, 2003). The eventual pathway is thought to be determined by aridity and by disturbance regimes. In arid and semi-arid conditions and under high frequency of disturbance, the vegetation dynamics are characterized by autosuccession. By contrast, under a mesic Mediterranean climate and low recurrence of disturbance, secondary succession is more likely.

The study of plant–plant interactions is increasingly an issue in applied forest ecology. Much of the research on this subject comes from the Mediterranean (Maestre *et al.* 2001; Castro *et al.* 2004; Gómez-Aparicio *et al.* 2004; Padilla & Pugnaire 2006). It has been proposed that planting under the canopy of nurse species should accelerate secondary succession of Mediterranean vegetation (Gómez-Aparicio *et al.* 2004), and would thus reduce considerably the high rates of early sapling mortality of traditional afforestation practices. Compared to open areas, the canopy of nurse species can favour seedling performance by reducing radiation, temperature and grazing, and by increasing soil humidity (Rey-Benayas 1998; Maestre 2002; Rey-Benayas *et al.* 2002; Rey *et al.* 2004; Gómez-Aparicio *et al.* 2005). Therefore, as in other stressful environments (Bertness & Callaway 1994; Callaway, Walker & Abrams 1997), the spatial proximity among plants in Mediterranean ecosystems is believed to have positive rather than negative effects on seedling and sapling performance. A number of studies claim that this positive effect will increase under increased abiotic stress (Pugnaire & Luque 2001; Callaway *et al.* 2002; but see Maestre, Valladares & Reynolds 2005). However, practical reasons preclude the direct study of how short-term nurse facilitative effect may affect the long-term community dynamics. The most viable approach for such a long-term exploration is through modelling.

Markov chains have been used to model succession in a variety of different disturbance scenarios. Several authors have modelled succession through a transition matrix composed of replacement probabilities calculated on a community- to-community, species-to-species, or individual-to-individual basis (e.g. Horn 1975; Hill, Witman & Caswell 2004). In most cases, this modelling assumed discrete and homogeneous time intervals, invariant environmental conditions, and probabilities of replacement based on the ontogeny of the tree species best representing each plant community (Logofet & Lesnaya 2000; Korotkov, Logofet & Loreau 2001; Benabdellah *et al.* 2003). Nonetheless, to our knowledge, no study has modelled post-fire succession incorporating sequential facilitative effects as a major inter-action in community dynamics. This study shows how Markov chain models can be developed to accommodate

species-by-species probabilities of replacement and nurse effects, and to separate objectively autosuccession-driven and secondary succession-driven areas. This should prove useful in diagnosis of community dynamics prior to restoration.

This study is intended to project post-fire vegetation dynamics in the Mediterranean, and to analyse the long-term contribution to such dynamics of facilitation through nurse effects. We develop Markov chain models of community dynamics based on observed interactions between established and recruiting plants. Using these models, we aim: (i) to assess the role of facilitation on the rate at which a community approaches a steady state of mature vegetation by comparing models of vegetation dynamics in three states of recovery after fire in the same burned area; (ii) to assess the role of various functional nurse groups and/or particular vegetation components on the projected vegetation dynamics by sensitivity analyses of matrix models.

Materials and methods

STUDY AREA

The study site is located in Torre del Vinagre, Natural Park of 'Sierras de Cazorla, Segura y Las Villas' (37°00′00″ N, 3°54′00″ W, Jaén province, SE Spain), and covers 1000 ha affected by wildfire in 1986. The soil type (calcareous limestone), aspect and precipitation are fairly homogeneous throughout. Environmental heterogeneity in the study area arises from variation in altitude (ranging from 900 to 1300 m above sea level), slope and soil depth (with zones of rocky outcrops at higher altitudes and deeper soils in middle and basal zones). Apparently, the environmental heterogeneity is not enough to determine substantial differences in potential native vegetation, which is a mixed forest of *Pinus nigra*, *Quercus ilex* and *Q. faginea* (Valle 2003; plant nomenclature through the text follows Castroviejo & col (eds) (1986–2007). However, as a result of traditional management for forestry and cattle (Nieto 2005), the vegetation is dominated by old afforested stands of *Pinus pinaster*, *P. nigra* and *P. halepensis*, with a sparse understorey of native shrub and tree species, and small patches of open native scrubland (Luque 1995). The area underwent largely unsuccessful pine reforestation (1988–1989; *Pinus pinaster* and *P. halepensis*) after fire. Currently, the vegetation can be classified into three types of regeneration states: (i) native late successional scrubland established in basal zones with deep soils (hereafter, building state or BUI); (ii) spontaneous regeneration pine stands in rocky soil at medium to high elevation (hereafter, pine regeneration state or PIN); and (iii) early successional pioneer shrub-dominated community in non-rocky substrates and relatively deep soils at medium and high elevations (hereafter, pioneer state or PIO). Mean annual temperatures and rainfall in the two weather stations closest to the study area are 770·7 and 1155·6 mm (concentrated in autumn and spring) and 11·6 and 14·2 °C, respectively.

DATA COLLECTION

Survey of natural vegetation

We randomly delimited 100-m linear transects in areas of each regeneration state, and sampled ten 25 m² plots evenly distributed along each transect. Overall, we sampled 44 plots in BUI, 35 in PIN, and 30 in PIO. Monitoring focused only on interactions between
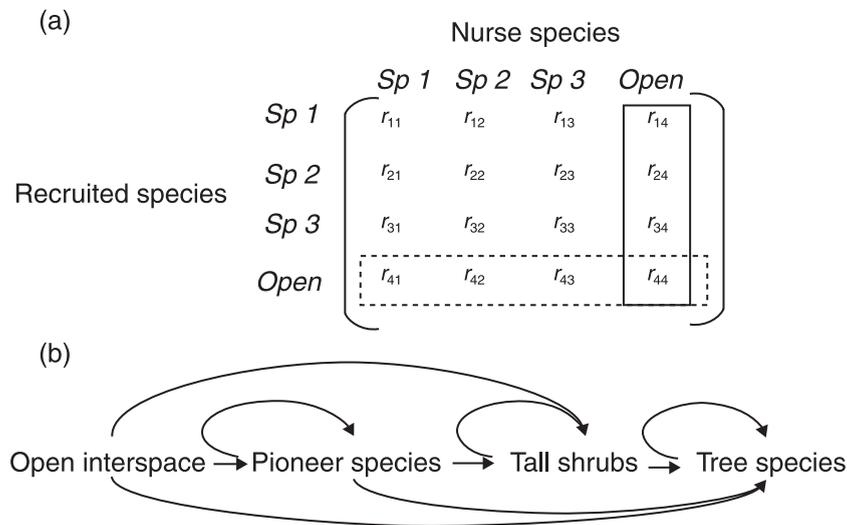
(a)

Nurse species

(b)

Fig. 1. (a) Species replacement matrix **R**. Four types of elements can be found in the matrix: elements indicating the frequency of substitution of a given species by another (r_{ij} *where* $i \neq j$); elements indicating the frequency of auto-replacement (r_{ij} *where* $i = j$); elements indicating substitution of open ground by a given species (framed in a rectangle with unbroken line); and elements indicating the substitution of a given species by open ground (framed in a rectangle with broken line; these are structural zeros in our modelling). (b) Diagram describing the assumed successional dynamics in our modelling. Only r_{ij} elements meeting the assumptions in the diagram are allowed to differ from zero. Note that pioneer species (heliophilous small shrubs) do not replace later successional species (tall shrubs and trees), because they will be outgrown by the latter. Coexistence of tall shrubs and trees is allowed (see Supporting Information Appendix S1 for the mechanistic basis of these assumptions). Thus, the model of succession proposed follows the facilitation model of Connell and Slatyer (1977), as suggested by Gómez-Aparicio *et al.* (2004).

woody plants. In each plot, we recorded the identity of species recruiting under the canopy of every woody species present in the plot (nurse species in the broad sense). This sampling allowed building, for each regeneration state, a matrix whose entries are the observed absolute frequencies of interactions between pairs of species (hereafter, interaction matrix; see Supporting Information Appendix S1).

Identification of facilitative interactions

From the interaction matrix of each regeneration state, we calculated the proportion of observed pairwise interactions (occurrence of recruits of a species under the canopy of the same or other species) relative to the total possible. We tested the difference in this proportion between pairs of regeneration states using Two Proportions Comparison Tests in Statistica (Statsoft Inc 1998). Additionally, we elaborated for the whole burned area a presence/absence matrix of interactions between nurse and recruited target species (i.e. tall shrubs and tree species commonly subject to restoration plans). We analysed this matrix with binomial probability tests in order to identify: (i) nurse species hosting a number of target species higher or lower than expected at random, and (ii) target species recruiting under more or fewer nurse species than expected at random.

Community dynamics modelling and analysis

Following Horn (1975), we modelled the successional dynamics as a Markov chain model under the assumption of invariant environmental conditions (time-homogeneous deterministic model; Binkley 1980; Usher 1981; Hill *et al.* 2004). Modelling was implemented in MATLAB (The Mathworks Inc. 2005). Details of the construction of the matrix models are given in the Supporting Information Appendix S1.

For each regeneration state, we built a replacement matrix, **R**, containing all the pairwise interactions of the woody species in the

study sites (Fig. 1). The r_{ij} elements of this matrix are estimates of the probability that species *i* will replace species *j* during a projection interval of 2 years (the shortest generation time among the species in the matrix). Our estimates of r_{ij} elements also account for the different generation times between each pair of interacting species. Some elements of the matrix were assumed to be zero based on the known successional status of the nurse and recruited species (see specifications for calculation and assumptions of **R** elements in the Supporting Information Appendix S1; see also Fig. 1). An initial state vector, **x**(0), was defined for each regeneration state by the current relative abundance of each species. The community state vector, **x**(*t*), defines the relative abundance of species in the modelled community at the projection interval *t*, scaled so that their elements add up to 1. The multiplication of **R** by the state vector generates the state vector in the next projection interval (**x**(*t* + 1) = **R x**(*t*)). Iterations of this multiplication enable projection of the vegetation dynamics. For each regeneration state, we determined the steady state community vector (**w**) as the relative frequency of species obtained after projecting the successional dynamics over 10^4 projection intervals. To calculate the time needed to reach **w**, we computed the distance between $\mathbf{x_t}$ and **w** at each projection interval using Keyfitz's Δ (Caswell 2001). The maximum distance value for Δ(**x**,**w**) is 1, and it takes the value of 0 when vectors are identical. We considered that stabilization was reached when Δ(**x**,**w**) < 0·01.

Of particular interest to our applied approach is to determine: (i) whether the steady states projected by our models resemble a mature forest community, and (ii) the rate at which communities starting from different regeneration states reach their maximum similarity to the mature communities identified in our study area. To this end, we established a reference vector, **z**, by sampling species composition in well-preserved natural vegetation stands near the study site (G. Siles *et al.* unpublished data). For each regeneration state, we compared **z** against **w** using the proportional similarity index, PS, which takes values between 0% and 100% (Hovirtz & Schemske 1995); see

Supporting Information Appendix S1. Hereafter, we refer to PS(**w**,**z**) as the 'reference similarity'. To estimate the time needed to reach the final similarity, we measured the similarity between **x**$_t$ and **z** after each projection interval. We considered that the final similarity was reached when PS(**w**,**z**) – PS(**x**(t),**z**) < 1.

Sensitivity of reference similarity to replacement probabilities

To explore which pairwise interactions could be manipulated (e.g. by planting juveniles of target species i under the canopy of an established nurse of species j) to improve the regeneration of the communities, we analysed in each regeneration state the sensitivity of PS(**w**,**z**) to small changes in r_{ij} (i.e. how small changes in each r_{ij} would move **w** closer or further from **z**; see Supporting Information Appendix S1 for details). The effect of perturbations on multiple matrix elements can be calculated in terms of sums of sensitivities (Caswell 2001). As examples of the usefulness of this approach, we explored the effect that different nurse functional types (same functional types described in Gómez-Aparicio *et al.* 2004) have on community dynamics through their interaction with plants of different life habits. Specifically, the nurse groups defined were: rockroses (Cistaceae), leguminous small shrubs (LSS), non-leguminous small shrubs (NLSS), spiny-tall shrubs (STS) and non-spiny tall shrubs (NSTS). In order to know whether the nurse species actually form groups that function similarly with respect to facilitation, we calculated the similarity (Sorensen's qualitative index) between pairs of nurses in the list of species hosted. After such calculations, we averaged pairwise similarities within each group and compared these mean similarities across groups (no statistical comparison was possible, because pairwise similarities from a matrix are not truly independent).

Results

TYPES OF REGENERATION STATES

Building state

The community was formed by 32 species (see Supporting Information Table S1). Tall shrubs and tree species accounted for 62·5% of the community, while pioneer species formed the remaining 37·5%. *Quercus ilex* and *Pinus halepensis* were the most frequent species in this state: they amount to 13% and 4% of plant cover, respectively, and occur in over 80% of samples.

Pine regeneration

The community was formed by 23 species (see Supporting Information Table S1). Tall shrubs and tree species accounted for 47·8% of the community, while the remaining 52·2% was formed by pioneer species. *Pinus halepensis*, *Quercus ilex* and *Rosmarinus officinalis* occurred in over 80% of samples, with a mean cover of 12%, 10% and 15%, respectively.

Pioneer state

The community was formed by 29 species (see Supporting Information Table S1). Only 27·6% of the community is formed by tall shrubs and trees, while the remaining 72·4% is formed by pioneer species. Dominant species here were *Rosmarinus officinalis* and *Halimium atripicipholium*, which occurred in over 80% of samples, with a mean cover of 32 and 6%, respectively. *Quercus ilex* appeared in 50% of samples, but its mean cover was only 6%.

FREQUENCY OF FACILITATIVE INTERACTIONS

The proportion of observed to all possible interactions was lower in PIO (88 observed out of 289 possible; proportion: 0·30) than in PIN state (137 out of 361; proportion: 0·38; two proportions comparison test: *P* < 0·05) or in BUI state (163 out of 400; proportion: 0·41; two proportions comparison test: *P* < 0·01). No significant differences were found in the frequency of interactions observed in PIN and BUI states (two proportions comparison test: *P* > 0·05).

Considering species occurring in at least five plots, the resulting interaction matrix was composed of 12 target species and 28 nurse species (Table 1). According to binomial probability tests, individuals of *Quercus ilex*, *Rosmarinus officinalis*, *Pinus halepensis*, *Pistacia terebinthus* and *Juniperus oxycedrus* housed under their canopies a higher number of species than expected to occur at random, while *Echinospartum boissieri*, *Thymus zygis*, *Berberis hispanica*, *Helianthemun croceum*, *Lavandula latifolia*, *Thymus mastichina*, *Acer monspessulanum*, *Cistus albidus* and *Thymus orospedanus* housed under their canopies fewer species than expected at random. On the other hand, recruits of *Quercus ilex* and *Pinus* sp. occurred under a higher number of nurse species than expected at random, while *Acer monspessulanum*, *Berberis hispanica*, *Phillyrea latifolia* and *Rosa* sp. recruited under a number of nurse species were lower than expected at random.

Mean pairwise similarities in the target species hosted were always higher within each nurse group than between groups (rockroses: 0·58 vs. 0·46; LSS: 0·83 vs. 0·56; NLSS: 0·50 vs. 0·45; STS: 0·49 vs. 0·39; and NSTS: 0·69 vs. 0·52, within and between group similarities, respectively). These results confirm our definition of groups to be functional in terms of facilitation of seedlings of target species.

MODELLING COMMUNITY DYNAMICS

The reference community is dominated by tall shrubs and tree species (see Supporting Information Table S2). It suggests a mature community dominated by *Quercus ilex*, *Quercus faginea*, *Pistacia lentiscus* and *Crataegus monogyna*. The projection of vegetation dynamics from the three regeneration states is shown in the Supporting Information Appendix S1).

Building state

The time required to reach the steady state is 58 years (Fig. 2). The steady state is composed of 15 species, all of tall shrubs or trees. The stable community is formed mainly by *Quercus ilex* (relative abundance = 0·27), *Juniperus oxycedrus* (0·17), *Pistacia lentiscus* (0·14) and *Phillyrea latifolia* (0·11). Other well-represented species are *Ulmus minor*, *Sorbus torminalis*

Table 1. Presence/absence interaction matrix between nurse and target species (tall shrubs and trees). N_1 is the number of species recruiting under the canopy of each nurse species. N_2 is the number of interactions with different nurse species for each recruited species. Xs show a target species detected as recruit under a given nurse species

Target species	Acer monspessulanum	Berberis hispanica	Cistus albidus	Cistus clusii	Cistus monspeliensis	Cistus salvifolius	Daphne gnidium	Dorycnium pentaphyllum	Echinospartum boissieri	Halimium atripicifolium	Helianthemum croceum	Juniperus oxycedrus	Lavandula latifolia	Phillyrea angustifolia	Phillyrea latifolia	Pinus halepensis	Pistacia lentiscus	Pistacia terebinthus	Quercus coccifera	Quercus faginea	Quercus ilex	Rosa sp.	Rosmarinus officinalis	Rubus ulmifolius	Thymus mastichina	Thymus orospedanus	Thymus zygis	Ulex parviflorus	N_2
Acer monspessulanum																		x			x								2
Berberis hispanica																		x						x					2
Juniperus oxycedrus			x		x	x	x			x		x		x	x	x	x	x	x	x	x		x						15
Phillyrea angustifolia			x							x					x	x		x			x		x						7
Phillyrea latifolia			x							x		x				x	x	x	x		x								8
Pinus sp.			x	x	x	x	x	x		x		x	x	x	x	x	x	x	x	x	x		x	x		x		x	21
Pistacia lentiscus				x	x	x	x	x		x		x		x	x	x		x	x	x	x		x	x				x	17
Pistacia terebinthus	x	x				x				x		x		x	x			x		x	x		x					x	12
Quercus coccifera				x	x	x	x	x		x		x		x	x	x	x				x		x	x					14
Quercus faginea							x					x		x	x	x	x		x		x		x	x				x	11
Quercus ilex	x			x	x	x	x	x		x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x		x	23
Rosa sp.							x											x	x		x		x	x					6
N_1	2	1	2	4	7	5	7	5	0	7	1	9	1	5	7	9	8	9	7	5	11	2	10	7	1	2	0	7	

Fig. 2. Long-term projection of the similarity to the reference community and to the steady state corresponding to each regeneration state. The vertical line indicates the time needed by the projected community to become stable. Note that the pattern is very similar for building or pine regeneration states, but stabilization is faster in the building state. Note also that despite the most rapid stabilization of the pioneer state, the projected community decreases in similarity to the reference community over time.

and *Acer monspessulanum* (see Supporting Information Table S2). The proportional similarity of the steady state to the reference community is 62%.

Pine regeneration

The time required to reach a steady state is 70 years. At the projected steady state, the community has nine species, all tall shrubs or trees. The stable community is formed mainly by *Quercus ilex* (0·23), *Pistacia lentiscus* (0·18), *Quercus coccifera* (0·14), *Juniperus oxycedrus* (0·11) and *Phillyrea latifolia* (0·11). The proportional similarity to the reference vector at the projected steady state is 61%.

Pioneer state

The time required to reach a steady state is 18 years. The stable state has a species richness of 28, with seven tall shrubs
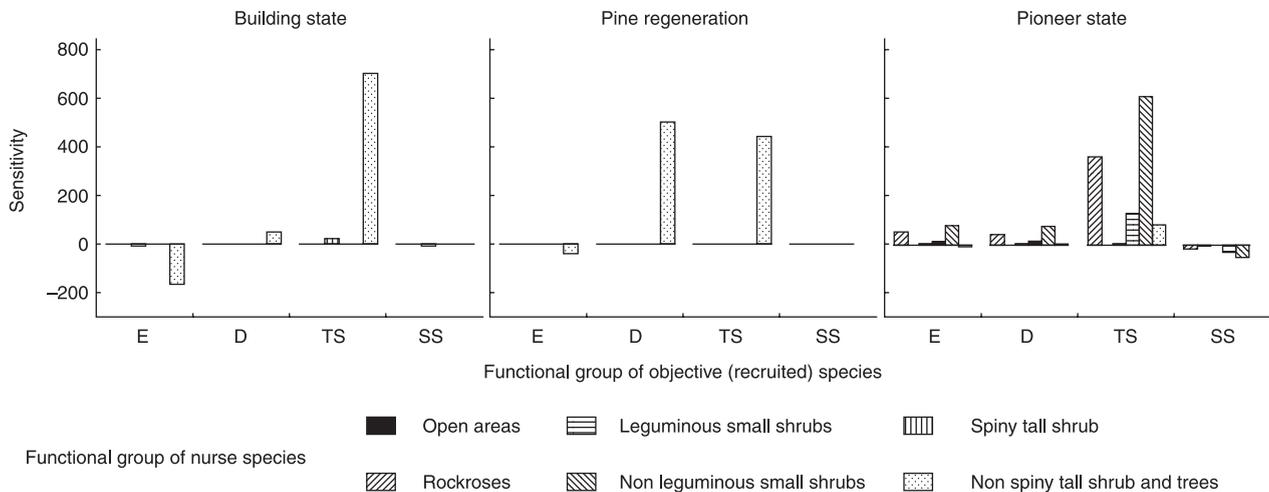
Fig. 3. Sensitivity after changes in the probability of substitution between species. The bars show the change (positive or negative) in the similarity between the projected steady state community vector and the vector indicating the species composition of the reference mature forest community caused by small changes in the probability of replacement between functional nurse groups. Acronyms for functional groups of objective species are: deciduous tree (D), evergreen tree (E), tall shrub (TS) and small shrub (SS).

or trees. The stable community is formed mainly by *Rosmarinus officinalis* (0·27) and *Halimium atripicifolium* (0·12).

The proportional similarity to the reference vector at the steady state is 9% (Fig. 2). Thus, although stabilization is reached quickly, the stable community has little similarity to the reference natural community.

Sensitivity analysis. Exploring the contribution to community dynamics of different functional nurse groups

The sensitivity matrices for the building, pine regeneration and pioneer states are square matrices of 32, 23 and 29 species, respectively.

Building state

The cumulative sensitivity for this state was 606·0, that is to say, the overall effect of small shifts in the probability of replacement between species is to increase the similarity of the projected steady state to the reference vector. Sensitivity ranges between −25·2 and 118·6 for individual r_{ij} elements. The most negative effects (decreases in similarity to the reference vector) would come from an increase in the probability for *Prunus spinosa*, *Sorbus torminalis*, *Juniperus phoenicea*, *Ulmus minor* or *Phillyrea angustifolia* to replace *Quercus ilex* (sensitivity = −25·1, −25·0, −25·0, −24·2 and −24·2 respectively). The most positive effects (increases in similarity) would be reached by increasing the probability of *Quercus ilex* replacement by *Crataegus monogyna* (118·6), *Quercus coccifera* (104·3) or *Quercus faginea* (103·1). By functional groups (Fig. 3), the highest similarity to the reference vector arises when tall shrubs or deciduous trees replace non-spiny tall shrubs and trees (704·4 and 48·9, respectively). Nevertheless, the increase in the probability of replacement of spiny-shrubs

by tall shrubs or deciduous trees also causes positive changes in the similarity to the reference vector (20·6 and 1·0, respectively). A decrease in similarity to the reference vector would appear after an increase in the probability of non-spiny tall shrubs and trees replacement by evergreen trees.

Pine regeneration

Sensitivity in this state shows a cumulative value of 906·7. Sensitivity ranged between −12·4 and 112·7 across matrix elements. The most negative effects would come from an increase in the probabilities of replacement of *Pistacia terebinthus* by *Juniperus oxycedrus* or *Phillyrea angustifolia* (−12·4 and −12·2, respectively). The maximum similarity with the reference vector comes with the increased probability of replacement of *Quercus ilex* or *Pistacia lentiscus* by *Quercus faginea* (112·7 and 95·7, respectively). In the analysis by functional groups (Fig. 3), we found that the replacement of non-spiny tall shrubs and trees by other tall shrubs or deciduous trees would yield the highest similarities to the reference vector (447·0 and 501·4, respectively). This similarity would decrease most with the replacement of non- spiny-tall shrubs and trees by evergreen trees.

Pioneer state

Sensitivity showed a cumulative value of 1356·5. Sensitivity ranges between −14·7 and 95·3 across elements. The most negative effects would come from an increase in the probability of replacement of *Rosmarinus officinalis* by *Lavandula latifolia* or *Echinospartum boissieri* (−14·7 and −12·3, respectively), while the most positive ones would come from an increase in the probability of replacement of *Rosmarinus officinalis* by *Pistacia terebinthus*, *Phillyrea latifolia* or *Juniperus oxycedrus*

(95·29, 93·47 and 79·07, respectively). By functional nurse groups (Fig. 3), we found negative effects on the similarity to the reference vector with: (i) an increased probability of recruitment of small shrubs under rockroses (−17·4), leguminous shrubs (−31·5) or non-leguminous small shrubs (−53·9); (ii) an increased probability of replacement of non-spiny tall shrubs and trees by evergreen trees (−7·3). The most positive effects were obtained by increasing the probabilities of replacement of rockroses and non-leguminous small shrubs by tall shrubs (sensitivity = 349·3 and 611·3, respectively). Increased replacement probability of small shrubs by trees (deciduous or evergreen) always increases the reference similarity, especially when replacing non-leguminous small shrubs (72·2 and 78·8, respectively).

Discussion

This study was intended to project post-fire vegetation dynamics and to analyse the long-term contribution of facilitation through nurse effects to vegetation dynamics. Our Markov chain models suggest that sequential positive (facilitative) interactions between plants may drive post-fire vegetation dynamics in the Mediterranean towards mature vegetation. Our models were parameterized with data on recruits found under established woody plants. The sampling protocols to obtain such data are simple, and consequently, information can be attained quickly. This study also shows that such information and modelling can serve as a diagnostic tool to determine whether the successional pathway of the existing vegetation is leading it towards a desired reference community or is constraining it to develop to some other state. For example, our model allowed us to identify objectively, undesirable autosuccessional dynamics in our study area. Thus, we have shown that zones in pioneer state may remain so for a long time. This implies a collapse (in terms of human-generation time-scale) of the vegetation dynamics towards a mature stand. Therefore, a diagnosis allowing identification of areas in such a state should be a desirable tool for restoration and land management practices. In contrast, by projecting successional community dynamics from the other two regeneration states (building and pine regeneration zones), we envisage a progressive displacement of pioneer species by shrub and tree species, whose relative abundance increases steadily through succession. Similar patterns were found by Benabdellah *et al.* (2003) in forest successions in the Erzgebirge, Germany, using time-homogeneous Markov chain models.

Facilitation of seedling establishment by nurse plants is commonly held to be a fundamental process to population and community dynamics in the Mediterranean. Based on observed short-term positive nurse effects on establishment, research has recently suggested the use of nurse plants in forest restoration (Castro *et al.* 2002; Castro *et al.* 2004; Gómez-Aparicio *et al.* 2004). However, for practical reasons, nurse facilitative effects have been measured only in the short term, and their long-term effects on the natural regeneration of populations and communities are poorly known. Our approach partly fills this gap and allows projection of future dynamics

by assuming facilitation as a major determinant in Mediterranean community dynamics. Thus, it may serve to test if the use of nurse plants for restoration will successfully project the vegetation towards the intended target community. We confirmed that the building state involved the highest frequency of facilitative interactions and required the shortest time to reach a more diverse (in terms of tall shrubs and trees species) steady state community. In contrast, areas in the pioneer state involved the lowest frequency of facilitation, and while they quickly reached a steady state, this was markedly dissimilar to the reference natural community (in fact, it remained as a pioneer community). This suggests that the higher the proportion of facilitative interactions, the more diverse is the steady state obtained and the shorter the time needed to reach a mature vegetation steady state. In the absence of long-term data on facilitative effects, models are a good complementary approach to critically assess the adequacy of restoration practices based on the use of nurse plants.

The low occurrence of recruits under established plants in the pioneer state may be due to a number of non-mutually exclusive reasons. A major reason would be that, in this state, inhibition, not facilitation, determines plant establishment. This would be genuine autosuccession, mediated by mutual inhibition between species. Autosuccession probably occurs in our study area, because many rockroses and other heliophilous vegetation, which are major components of the community in this state, are known to inhibit establishment of late successional plants (Gómez-Aparicio *et al.* 2004; Pulido & Díaz 2005; Acacio *et al.* 2007). A second reason may be the occurrence of stochastic repeated perturbations. It is well-known that fires at short intervals and recurrent grazing (both by domestic and wild ungulates) affect vegetation dynamics and composition (Lloret, Pausas & Vilà 2003) and arrest secondary succession in the Mediterranean (e.g. Franquesa 1989; Zavala 2003). In fact, recurrent grazing is widespread in the study area and is a major problem for post-fire natural regeneration (both by resprouting and seedling establishment) of forest plants (Siles 2008; P.J. Rey *et al.* unpublished data). A third reason is a scarce pre-fire presence of resprouting species. In the pioneer state, 46% of the present species were resprouters compared to 59% and 68% in pine regeneration and building state. The percentage of late successional resprouter species in the pioneer state was 25%, while in pine regeneration and building state, the percentages were 41% and 53%, respectively. The last reason is dispersal limitation due to low rate of seed arrival of shrubs and tree species; this is a widespread barrier to secondary succession (Pickett, Cadenaso & Bartha 2001; Acacio *et al.* 2007). Most Mediterranean late successional species are dispersed by birds and mammals which may not find appropriate habitats in pioneer vegetation. Under these limitations, the list of 'potentially non-effective nurse species' could be overestimated, because the low diversity of recruited species beneath them might be due to the low probability of seed arrival rather than to a lack of facilitation.

In forest restoration it is helpful to know the level of intervention needed throughout a landscape. Sensitivity analyses of the dynamics of different regeneration states allow

identification of areas which should be more intensively managed in reforestation practices. The cumulative sensitivity of our species replacement matrices reached positive values in all the regeneration states. This means that an increase in the probability of species replacement enhanced in all cases the similarity between the projected and the reference community. Minor cumulative sensitivities appeared in the building state, while the pioneer state had the highest ones. This indicates that the increase of species replacement in pioneer zones would greatly increase the development of the existing community to the reference natural community. Human intervention favouring such species replacement is both possible and necessary in pioneer zones in order to avoid autosuccession of heliophilous vegetation, to assist secondary succession and accelerate recovery of mature woodlands. Intervention in pine afforestation and building zones seems not to be so necessary.

Development of forest restoration practices using nurse plants will require identification of what specific pairs of nurse and recruited species disproportionately increase the probability of reaching a reference mature community. We have shown that we can identify them from sensitivity analysis. For example, in the pioneer state, the reference similarity shows maximum sensitivity to the replacement of *Rosmarinus officinalis* by *Pistacia terebinthus*. This means that mature vegetation recovery in future restoration works would benefit from planting seedlings of *Pistacia terebinthus* under the canopy of *Rosmarinus officinalis* to favour its replacement. Although the determination of such species pairs illustrates the possibilities of this kind of analysis, reforestation practice would normally require broader functional categorization of nurse groups. In their experimental work on seedling establishment success using nurse shrubs, Gómez-Aparicio *et al.* (2004) distinguished several functional nurse groups. We have confirmed here that these pre-defined groups are functionally meaningful in terms of the list of species hosted. They showed that (i) leguminous and deciduous spiny shrubs are adequate nurses, but rockroses are not; and (i) late-successional shrubs under early successional shrubs was the most effective way of accelerating succession in degraded sites. We have obtained similar results by experimental planting in our study site (G. Siles *et al.* unpublished data). By pooling species according to functional groups in our matrix models, we evaluated the role of different functional groups in the forest dynamics. Our models suggest that restoration in pioneer zones can be accelerated by increasing the frequency of seedlings of target species (evergreen and deciduous trees, and tall shrubs) under rockroses and small shrubs (sensitivity values for these functional groups were positive). Since rockroses seem to hinder the establishment of late successional species, the probability of replacements for rockroses may not be improved by planting, while other replacements succeed by planting (Gómez-Aparicio *et al.* 2004). It has been mentioned that regeneration dynamics in building and pine regeneration zones may not be substantially improved. However, intervention in these zones should focus on increasing the occurrence of recruits of tall shrubs (e.g. *Pistacia terebinthus*) and deciduous trees (e.g. *Quercus faginea*) under non-spiny tall shrubs, as

indicated by the disproportionately high sensitivity values for these combinations of recruit and nurse functional groups. Taking into consideration both our long term replacement models and the results of short-term experimental planting under different nurse functional groups (Gómez-Aparicio *et al.* 2004; G. Siles *et al.* unpublished data), it can be concluded that restoration of degraded zones can be accelerated by planting seedlings of late successional species under early successional small shrubs.

All in all, matrix substitution models proved to be a rapid and useful analytical tool for forest management and restoration projects, because they allow: (i) evaluation of possible post-fire dynamics, identifying areas in the landscape in need of intervention (i.e. where the secondary succession is arrested in favour of autosuccession of pioneer vegetation); (ii) assessment of the role of long-term facilitative nurse effects on secondary succession; and (iii) identification of species pair combinations and functional nurse groups in need of special effort in restoration practices with nurse plants. Future modelling work should test to what extent specific replacement probabilities could be enhanced by planting under various yearly weather conditions.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Community dynamics modelling

Table S1. Relative frequency of occurrence (f) and mean cover (Cov) for species appearing in three regeneration states (BUI, building state; PIN, pine afforestation; and PIO, pioneer state) of the study area. Each species is classified according to nurse functional group (NFG) and recruited functional group (RFG). NFGs are: leguminous small shrub (LEG), non-leguminous small shrub (NLSS), rockroses (small shrubs in the family *Cistaceae*; CIST), spiny tall shrub (SPIN) and non-spiny tall shrubs and trees (STRE). RFG groups are: deciduous tree (D), evergreen tree (E), tall shrub (TS) and small shrub (SS)

Table S2. Relative abundance of each species in the mature forest reference community (z), in the observed state (x_o) and the projected steady state (w_0) of the community for zones in each regeneration state of the study area (BUI: building state; PIN: pine afforestation; and PIO: pioneer state)

Fig. S1. Projection of vegetation dynamics in three post-fire regeneration states: building, pine regeneration and pioneer states.

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