Effects of *Quercus suber* decline on woody plant regeneration: potential implications for successional dynamics in Mediterranean forests

Shortened Title: Successional dynamics in declining forests

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Abstract

In the last decades widespread tree decline and mortality has been documented in forests worldwide. These mortality events usually show certain level of host-specificity, translating into rapid changes in the relative abundance of the adult community. Despite these short-term changes, it is poorly understood whether the decline and mortality of certain tree species are likely to result in long-term vegetation shifts. Trajectories of forest recovery and the probability of occurrence of permanent vegetation shifts are to a large extent determined by post-mortality regeneration dynamics. Using a spatially-explicit neighborhood approach we evaluated the spatial patterns of natural regeneration of the woody plant community in mixed Mediterranean forests affected by the decline of their dominant tree species, *Quercus suber*. We predicted the abundance, survival and richness of the seedling and sapling bank as a function of the distribution and health status of the tree and shrub community. Results indicated that *Q. suber* decline had detectable effects on seedlings and saplings of coexistent woody species from very different functional groups (trees, shrubs and lianas). The sign and magnitude of these effects varied substantially among coexistent species, which could imply shifts in the species ranking of seedling and sapling abundance, affecting successional trajectories and potentially leading to vegetation shifts. Because most of these changes pointed towards a loss of dominance of *Q. suber*, management strategies are urgently needed in order to attenuate adult mortality or promote its regeneration, counteracting the negative effects of global change drivers (exotic pathogens, climate change) on these valuable forests.

Key words: disturbance, global change, Mediterranean forests, neighborhood models, seedling and sapling bank, succession, tree dieback.

Introduction

Over the last two decades widespread tree decline and mortality has been documented in forests of almost every bioregion of the world (Allen et al., 2010, 2015; Breshears et al., 2009; Van Mantgem et al., 2009). Several global change drivers have been identified as potential causes, such as increasing drought frequency and severity, recurrent pest outbreaks or the spread of exotic pathogens (e.g. Axelson et al., 2009; Carnicer et al., 2011; Loo, 2009). A common feature to these mortality processes is that they usually show certain level of host-specificity, some tree species being much more vulnerable to abiotic and biotic sources of stress than others. As a result, they have a large potential to induce selective species removals and changes in community composition (Allen and Breshears, 1998; Collins et al., 2011). For example, in semi-arid *Pinus edulis*-*Juniperus monosperma* woodlands of southwestern USA, recent severe droughts have induced a shift towards *Juniperus* dominated communities due to the higher drought tolerance of this species (Koepke et al., 2010; Mueller et al., 2005). In coastal California forests, the emerging pathogen *Phytophthora ramorum* has caused a rapid decline of *Notholithocarpus densiflorus* and an increase in the relative dominance of coexisting *Umbellularia californica* or *Sequoia sempervirens* (Brown and Allen-Diaz, 2009; Ramage et al., 2012). In Australian forests, the largest susceptibility to both drought and pathogens of the *Eucalyptus* genus compared to the co-dominant *Corymbia* genus has lead to severe alterations in the relative dominance of coexisting tree species (Fensham and Holman, 1999, Cahill et al., 2003). However, despite this evidence for rapid changes in the relative abundance of the adult community, we still have limited information on trajectories of forest recovery after tree decline and mortality and whether they are likely to result in long-term vegetation shifts.

The probability of occurrence of permanent vegetation shifts is to a large extent determined by regeneration dynamics after tree dieback (Galiano et al., 2013; Kayes and

Tinker, 2012; Redmond and Barger, 2013; Suarez and Kitzberger, 2008). Tree defoliation and mortality can induce a series of changes in local environmental conditions that alters the probability of establishment of new tree seedlings, inducing shifts of species abundance rankings in the seedling bank. For example, an increase in radiation levels and drought stress in the gaps opened after tree death could preclude the establishment of late-successional shade-tolerant species, indirectly favoring pioneer drought-tolerant species (Amoroso et al., 2012; Diskin et al., 2011, Ibáñez et al., 2015). It has also been shown that trajectories of recovery after drought- or insect-driven tree mortality might depend not only on new seedling establishment, but also even more strongly on advance regeneration established prior to the disturbance (Collins et al., 2011; Kayes and Tinker, 2012; Redmond and Barger, 2013). For example, tree dieback in mature forests could release suppressed saplings of shade-tolerant species, allowing late-successional species to keep dominating the stands and indirectly limiting the establishment of light-demanding pioneer species otherwise typical of disturbed sites (DeRose and Long, 2010; Veblen et al., 1991). These examples illustrate the complexities inherent to post-mortality regeneration dynamics, with seedlings and saplings of different ages likely responding in different ways (e.g. Galiano et al., 2013), and show the need for further research that helps to elucidate long-term changes in stand composition of disturbed forests.

In this study we analyzed the spatial patterns of natural regeneration of the woody plant community in mixed oak forests of southwestern Spain affected by the decline of its dominant tree species, *Quercus suber*. Our main objective was to elucidate whether the abundance and performance of seedlings and saplings of coexistent shrub and tree species varied depending on the composition and health status of neighboring trees, and whether differential responses among species in the regeneration bank could eventually lead to changes in species dominance at the canopy level. The decline of *Q. suber* has been reported throughout the Mediterranean Basin since the early 1990s (Brasier, 1992; Brasier, 1996), where tree death has occurred progressively along time forming stands of dead trees. Several abiotic (e.g. extreme droughts) and biotic (e.g. insects and pathogens) factors are potentially involved in this decline (Tuset and Sánchez, 2004). However, in the study area, oomycete soil-borne pathogens (*Phytophthora cinnamomi* and *Pythium spiculum*) have been isolated from symptomatic *Q. suber* trees and are suggested to be the main drivers of the species decline (Brasier, 1996; Romero et al., 2007; Sánchez et al., 2006; Sánchez et al., 2002). For the analysis of natural regeneration patterns, we used a spatially-explicit neighborhood approach (Canham and Uriarte, 2006; Gómez-Aparicio et al., 2008a; Gómez-Aparicio et al., 2008b) where the abundance, survival and richness of the seedling and sapling bank was predicted as a function of the distribution and health status of the canopy tree and shrub community. Previous studies in the same study area have shown *Q. suber* to suffer from stronger recruitment limitation than coexistent trees or arborescent shrubs (Pérez-Ramos and Marañón, 2012), mainly due to heavy post-dispersal seed predation and high seedling mortality due to summer drought (Gómez-Aparicio et al., 2008b; Pérez-Ramos and Marañón, 2008). Moreover, in a parallel experimental study, where seeds of *Q. suber* and *Q. canariensis* were sown and the recruits were monitored for 3 years, we found that defoliated and dead *Q. suber* trees generated unsuitable microsites for survival of conspecific seedlings likely due to drought stress and/or high pathogen abundance (Ibáñez et al., 2015). Following this, we hypothesized that the process of *Q. suber* decline might cause the seedling/sapling bank to become even less *Q. suber* dominated, hampering the potential for self-replacement and favoring successional trajectories towards forests dominated by other co-existing woody species.

Material and Methods

STUDY SITES AND SPECIES

The study was conducted in Los Alcornocales Natural Park, a 170 000 ha protected area in Southwestern Spain. The climate is Mediterranean type, with cold and humid winters and warm and dry summers. Mean annual temperature varies from 14.6 to 18.4 °C, with a mean monthly maximum of 36°C (July) and a mean monthly minimum of 2.8°C (January). Mean annual precipitation is 975 mm (mean 1951–1999). The bedrock is dominated by Oligo-Miocene sandstone and originates acidic, nutrient-poor, sandy soils, frequently interspersed with clayish soils derived from layers of marl sediments. Our study was carried out during three consecutive years (2010, 2011 and 2012) which exhibited contrasted climatological conditions. The year 2010 was extremely wet in terms of precipitation (1346 mm annual rainfall, 40 mm summer rainfall), 2011 had an average precipitation (1037 mm annual rainfall, 16 mm summer rainfall) and 2012 was particularly dry (474 mm annual rainfall, 0 mm summer rainfall).

The flora in the Alcornocales Natural Park is dominated by mixed sclerophyll forests of *Q. suber*, located mainly on non-carbonated soils, at altitudes between 100-700 m a.s.l.. Within the park the structure of the forests and its diversity vary depending on orography and soil type. In low altitude sites with clayish soils, *Q. suber* forms mixed open woodlands with the evergreen drought-tolerant *Olea europaea* var. *sylvestris*. The shrub layer in these woodlands is usually dense and largely dominated by the evergreen *Pistacia lentiscus* L. and the deciduous *Crataegus monogyna* Jacq. In sandier, moister and colder sites *Q. suber* coexists with the deciduous, shade-tolerant *Quercus canariensis* forming closed forests. The shrubby understory is diverse and dominated by arborescent shrubs (*Arbutus unedo* L., *Phillyrea latifolia* L.) and heath species (*Erica arborea* L.,*Erica scoparia* L.) (Ojeda et al., 1996). These forests are relatively well conserved since 1989 (declared as Natural Park), and the main management activities are the extraction of cork, game hunting and recreation (Anonymous, 2005).

FIELD SAMPLING

The field work was conducted in six study sites within the Natural Park. Three of the sites were located in open woodlands of *Q. suber* and *O. europaea* var. *sylvestris* (hereafter woodland sites) and three in closed forests of *Q. suber* and *Q. canariensis* (hereafter closed forest sites). The six sites covered a gradient of climate and soil conditions (see Table A in Supplementary Material). During winter 2009, we established a 70 x 70 m plot at each of the six study sites. Each plot was subdivided in 49 10 x 10 m subplots. Within each of the 49 subplots, a smaller 1 x 1 m quadrat was permanently set up for monitoring of natural regeneration (n = 147 sampling quadrats per forest type, 294 quadrats in total).

During early June in 2010, 2011 and 2012 we counted and marked all the seedlings (i.e. individuals emerged that spring) and saplings (i.e. > 1 year-old individuals smaller than 50 cm height) of woody species in each of the 1 m^2 sampling quadrats. We chose this sampling date to ensure that most seedlings had emerged (Pérez-Ramos and Marañón, 2012). Additionally, seedlings and saplings of tree species were revisited in early October 2010 and October 2011 to record survival after the summer, the main mortality period in Mediterranean systems (Gómez-Aparicio 2008; Pérez-Ramos et al. 2012). We also calculated species richness for each quadrat as the number of different woody plant species censured at seedling or sapling stage. Due to the low growth rates of oak species in Mediterranean systems and their resprouting ability, saplings smaller than 50 cm height can be as old as 30 years (Galiano et al., 2013). Therefore, the sapling bank could represent the regeneration accumulated during the last decades and even before the first report of *Q. suber* decline in the area (Brasier, 1992; Brasier, 1996).

To characterize the local neighborhood of each plot, we identified and mapped all live and standing dead trees with a diameter at breast height (dbh) > 2 cm and all shrubs in the 70 x 70 m permanent plots, as well as in a buffer zone 15-m (for trees) or 5-m (for shrubs) wide around each plot. Tree neighborhoods of similar size have been shown to capture the most important aspects of neighborhood interactions in temperate forests (Coates et al., 2009; Gómez-Aparicio et al., 2008a). Although we did not have any reference to choose the maximum shrub neighborhood, we considered a radius of 5 m to be big enough based on the small size of most shrubs in these forests (height usually < 3 m) (Gómez-Aparicio et al., 2012). We measured the dbh of each of the trees mapped (n = 1341 trees). Due to its multi-stem growth form, shrub size was characterized measuring the two diameters of the elliptical projection of its crown (n = 3005 shrubs). In addition, we visually evaluated the crown health status of *Quercus suber*, with a standardized semi-quantitative scale used routinely for monitoring purposes of oak decline (García et al., 2011): (1) healthy reference trees; (2) defoliated trees; and (3) dead trees. No other tree or shrub species in the study area showed symptoms of decline.

DATA ANALYSIS

Neighborhood models of seedling and sapling performance and richness

We used likelihood methods and model selection for the analysis of our data (Canham and Uriarte, 2006; Johnson and Omland, 2004). Following the principles of likelihood estimation, we estimated model parameters that maximized the likelihood of observing the data measured in the field. We fit separate models for each combination of dependent variables (abundance, survival, and richness), life-stage (seedling and sapling), forest type (woodland and closed forest), and woody species/functional group. The dominant tree species were analyzed separately (*Q. suber*, *O. europaea* and *Q. canariensis*), whereas the remaining woody species were divided in three groups according to their life-form and dispersal syndrome: fleshy-fruited shrubs (with endozoochorous dispersal), dry-fruited shrubs (with dispersal syndromes other than endozoochory, mainly abiotic dispersal) and lianas (Table B in Supplementary Material).

Our full regeneration model predicted mean seedling/sapling performance in each quadrat as a function of three components: 1) the potential seedling/sapling performance at each of the three study sites for each forest type in the absence of specific effects of neighboring trees (i.e. site effects); 2) the identity, size, health status and spatial distribution of the trees in the neighborhood (i.e. tree neighborhood effects); and 3) the size and spatial distribution of shrubs in the neighborhood (i.e. shrub neighborhood effects). We tested and compared two different model frameworks (additive vs. multiplicative) to describe neighbor effects (e.g. Baribault and Kobe, 2011):

Additive model $$Y = a_{Site} + b_{Year}*NI_{Tree} + c_{Year}*NI_{Shrub} + \varepsilon \quad (1)$$

Multiplicative model $$Y = a_{Site} *\exp(b_{Year}*NI_{Tree})*\exp(c_{Year}*NI_{Shrub}) + \varepsilon \quad (2)$$

The first term in the models, a_{Site}, represents the site effects. The second term accounts for the tree neighborhood effects, which are assumed to vary as a function of a *neighborhood index* (NI_{Tree}). The parameter *b* defines the steepness of the variation in performance due to an increment in NI_{Tree} and was allowed to vary between years to account for inter-annual differences in tree effects. The tree neighborhood index quantifies the net effect of $j=1,...,n$ neighboring trees of $i=1,...,s$ species on seedling/sapling abundance, survival or richness, and was assumed to vary as a direct function of the size (dbh) and as an inverse function of the distance to neighbors:

$$NI_{Tree_{ij}} = \sum_{i=1}^{s} \sum_{j=1}^{n} \lambda_i \frac{dbh_{ij}^{\alpha}}{dist_{ij}^{\beta}} \qquad (3)$$

where dbh_{ij} is diameter at breast height, $dist_{ij}$ is the distance to the sampling quadrat of the *j*th neighboring tree of the *i*th species, and α and β are estimated parameters that determine the shape of the effect of the dbh (*α*) and the distance to neighbors (*β*) on the target variable. We used NI standardized ($0<NI_i/NI_{max}<1$) to facilitate comparisons across different seedling/sapling species. Because we were particularly interested in exploring whether tree effects varied between individuals of different species or health status, we grouped tree neighbors in four categories: healthy *Q. suber* trees, defoliated *Q. suber* trees, dead *Q. suber* trees, and the coexisting tree species at each site (*O. europaea* or *Q. canariensis*). We initially considered two categories of defoliated trees (<50% and > 50% defoliation, see Gómez-Aparicio et al., 2012 for a similar approach), but since they had similar effects on regeneration we decided to merge them in just one category for simplicity. We then multiplied the net effect of an individual tree by a *per-capita* coefficient (*λ*), one for each category (estimating therefore four different λ values), that ranged from -1 to 1 and allowed for differences between neighbors in their effects (negative or positive) on the target variable.

The third term in equations 1 and 2 accounts for shrub neighborhood effects, and were calculated as a function of a shrub neighborhood index (NI_{Shrub}). The parameter *c* defines the steepness of the variation in performance due to an increment in NI_{Shrub}, and was allowed to vary between years to account for inter-annual differences in shrub effects. This index is a simplified version of the tree neighborhood index, and quantifies the net effect of *j=1,…,n* neighboring shrubs on seedling/sapling abundance, survival or richness following the form:

$$NI_{Shrub_j} = \sum_{j=1}^{n} area_j \qquad (4)$$

The NI_{Shrub} was assumed to vary just as a direct function of the size (crown area) of neighbor shrubs in a 5-m radius neighborhood. We decided not to include distance in the calculation of the index given the already restricted area over which shrubs were mapped and to keep the number of parameters in the models manageable.

Parameter estimation and model selection

Because our main interest was to compare the effect of trees of different species and health status on regeneration, we first fit a simple model where only Tree neighborhood effects were considered ("Only tree" model). We then compared this simple model with more complicated models that included Site, Year or Shrub effects, finally selecting the simplest model that was not a significantly worse fit than any more complicated model. Additive and multiplicative models with the same number of parameters were also compared among them. We used the Akaike Information Criterion corrected for small sample sizes (AIC_c) to select the best model, with lower AIC_c values indicating stronger empirical support for a model (Burnham and Anderson, 2002). We solved for the maximum likelihood parameter values with simulated annealing (Goffe et al., 1994), a global optimization procedure. The likelihood functions used in our models varied according to the data. We used a negative binomial function to model the abundance data (counts) accounting for over-dispersion. We also tested the use of a zero-inflated Poisson distribution, but found the negative binomial to be more appropriate to the error distribution of our data. The survival data were binomial in nature, so a binomial distribution was used for the likelihood function of the corresponding models. Finally, the species richness data (counts) were adequately modeled using a Poisson likelihood function. We used asymptotic 2-unit support intervals (as an approximation to the 95% confidence interval) to assess the strength of evidence for individual maximum likelihood parameter estimates (Edwards, 1992). Coefficients whose 2-unit support intervals did not include zero were considered statistically significant. The slope of the regression (with a zero intercept) of observed versus predicted was used to measure bias (with an unbiased model having a slope of 1). We explored model residuals (i.e. lack of patterns when represented against predicted values and independent variables, and lack of spatial autocorrelation [Mantel test, Legendre & Fortin 1989]) to finally validate the model. All analyses were performed using R (R Development Core Team, 2009) and the “likelihood” package (Murphy, 2012).

Results

Seedling and sapling abundance

A total of 4514 seedlings and 1865 saplings of 21 woody species were counted during the three sampling years at the six study sites (Table B in Supplementary Material). Due to the scarcity of seedlings and saplings of dry-fruited shrubs, this group was only included in the analysis of seedling abundance in woodland sites. All models produced unbiased estimates of seedling and sapling abundance (slope ~1, Table 1), and did not show spatial autocorrelation in their residuals with two exceptions (liana seedlings in woodlands and *Q. suber* saplings in closed forests, Table C in Supplementary Material). It is important to highlight that likelihood-based inference is very robust even in cases of lack of independence, with deviations from independence mostly resulting in underestimates of variance terms but not in biased parameters values. Both the additive and multiplicative approaches were used in best models of seedling abundance, whereas most of the best models of sapling abundance involved a multiplicative approach (Table 1). Most of the best models of seedling (7/9) and sapling (7/8) abundance showed differences among the three sites in regeneration abundance. All models detected tree neighborhood effects on seedling and sapling abundance, as indicated by significant λ values for one or more neighbor categories (Tables D and E in Supplementary Material). These effects did not vary among years (Table 1). Our models did not detect any effect of shrubs on seedling abundance, and only in one species (*Olea europaea*) for sapling abundance (Table 1).

In general, seedling abundance was higher in healthy tree communities (as indicated by positive *λ* values) than in neighborhoods dominated by defoliated or dead trees (as indicated by neutral or negative *λ* values) (Table D in Supplementary Material, Fig. 1a,c,e,g, Fig. 2,a,c,e,g). However, the magnitude of the neighborhood effect varied among species/functional groups, causing shifts in rankings of species abundance among neighborhood types. In woodlands, *Olea* was the dominant seedling species in healthy tree neighborhoods (both conspecific and heterospecific), whereas *Q. suber* dominated the seedling bank in defoliated neighborhoods, and fleshy-fruited shrubs in dead neighborhoods (Fig. 1). In closed forests, lianas and (to a lesser extent) fleshy-fruited shrubs were the dominant groups in all type of neighborhoods (Fig. 2). Among tree species, *Q. suber* and *Q. canariensis* dominated their respective conspecific healthy neighborhoods, whereas the abundance of both species was virtually null in defoliated and dead *Q. suber* neighborhoods (Fig. 2e,g). In most neighborhood models of seedling abundance (7/9), the exponent α of the Neighborhood Index (which controls how neighbor effects scale with tree size, Eq. 3) took high values (> 2), indicating that the effect of neighboring trees scaled roughly with biomass (Table D in Supplementary Material). Low values of the β parameter (which controls the effect of distance to neighbors, Eq. 3) in most models indicated that neighbor effects on seedling abundance slightly decreased with distance (Table D in Supplementary Material).

Sapling abundance of tree species was also generally lower in defoliated and dead neighborhoods than in healthy ones (Table E in Supplementary Material, Fig. 1b,d,f,h, Fig. 2b,d,f,h). However, abundance of fleshy-fruited shrub and liana saplings was not negative affected by tree decline in most situations (as indicated by neutral or positive *λ* values; Table E in Supplementary Material). Shifts in rankings of species abundance among neighborhood types were also found in the sapling community. In woodland sites, whereas healthy neighborhoods of both *Q. suber* and *O. europaea* were dominated by conspecific saplings, the strong negative effects of defoliated and dead trees on *Q. suber* saplings (stronger than on any other species) caused these neighborhoods to be dominated by heterospecific *O. europaea* saplings (Fig. 1f,h). In closed forests, the sapling bank kept being dominated by lianas and fleshy-fruited shrubs in all type of neighborhoods (with the exception of fleshy-fruited shrubs in *Q. canariensis* neighborhoods). Among tree species, *Q. canariensis* dominated the sapling bank in conspecific neighborhoods and was also slightly more abundant than *Q. suber* in healthy *Q. suber* neighborhoods. However, *Q. suber* dominated the sapling bank in defoliated and dead neighborhoods likely as a result of stronger negative effects of decline (more negative λ values) on *Q. canariensis* than on *Q. suber* sapling abundance (Table E in Supplementary Material). In models of sapling abundance, the value of the α parameter was highly variable among species (Table E in Supplementary Material), whereas the β parameter was generally close to 0 indicating that abundance was mostly proportional to neighbor density.

Seedling and sapling survival

All models produced unbiased estimates of tree seedling and sapling survival (slope ~1), except for *O. europaea* and *Q. suber* seedlings in woodlands and closed forests (respectively) where best models tended to overpredict (slope > 1, Table 1). Model residuals did not show spatial autocorrelation, except for *Q. canariensis* saplings (Table C in Supplementary Material). In all cases additive models were a better fit to the data than multiplicative models. Only 25% (2/8) of the best survival models found differences among sites in seedling and sapling survival (Table 1). All models detected tree neighborhood effects on seedling and sapling survival, as indicated by significant λ values of one or more neighbor categories

(Table F, Figures H and I in Supplementary Material). These tree effects remained mostly constant among years, with three exceptions (*Q. suber* seedlings and *O. europaea* saplings in woodlands, *Q. suber* saplings in closed forests; Table 1). Our models did not detect any effect of shrubs on seedling survival (Table 1).

In woodlands, neighbor effects on survival were of generally weak magnitude, as indicated by the low value of most significant λ (Table F in Supplementary Material). Moreover, the sign of the effects on *Q. suber* seedlings and *Olea* saplings varied among years (see sign of parameter *b* in Table F in Supplementary Material), with survival being higher in healthy than defoliated neighborhoods in 2010 (a very wet year) but lower in 2011 (a normal year in terms of rainfall). In closed forests, *Q. canariensis* neighborhoods had the most negative effect (lowest *λ* value, Table F in Supplementary Material) on seedling survival of the two oak species, followed by healthy *Q. suber* neighborhoods. Although seedling survival was lower in healthy than in declining *Q. suber* neighborhoods, sapling survival was higher (more positive *λ* values) in healthy neighborhoods. This was particularly true for *Q. canariensis* saplings, which suffered from strong negative effects of defoliated and dead neighbors (Table F in Supplementary Material). Values of parameters α and β in the Neighborhood Index (Eq. 3) showed a very high variability among best models of seedling and sapling survival (Table F in Supplementary Material).

Seedling and sapling richness

The two richness models produced unbiased estimates of species richness (slope ~1), but showed some spatial autocorrelation in their residuals (Table C in Supplementary Material). In both cases, an additive approach offered a better fit to the data than a multiplicative approach (Table 1). In woodlands, the best model detected an effect of the tree community on richness values, but did not find any site, year or shrub effects (Table 1). In this forest type, species richness was higher in healthy tree communities of *Quercus* and *Olea* (large positive λ values) than in neighborhoods dominated by defoliated and dead *Q. suber* trees (Table G, Figure J in Supplementary Material). In closed forests, the best model was the full model that considered the effect of all the factors tested. Thus, in this forest type richness varied among sites, was lower in *Q. canariensis* neighborhoods than in any *Q. suber* neighborhood (in all years but the dry 2012), and were positively affected by shrubs in the three study years (Table G, Figure J in Supplementary Material). Values of the α and β parameters in the Neighborhood Index of the two best richness models were roughly around 1, indicating that neighbor effects scaled with tree size (α) and declined as a simple inverse function of distance (β) (Table G in Supplementary Material).

Discussion

Our results indicated that the decline of *Q. suber* in Mediterranean forests had detectable effects on both new seedlings and older saplings of coexistent woody species belonging to very different functional groups (trees, shrubs and lianas). Thus, we found total and relative regeneration abundance (both within and among functional groups) to vary depending on the health status of the canopy cover. Our neighborhood approach provided a useful framework that integrates the myriad ways that canopy and seedling species interact under natural conditions helping in this way to improve our understanding of the consequences of tree decline and mortality for regeneration dynamics.

Patterns of natural regeneration in healthy tree neighborhoods

Healthy neighborhoods of the three dominant tree species in the study forests (*Q. suber*, *O. europaea*, and *Q. canariensis*) showed a tree seedling and sapling bank composed largely by conspecifics. It is interesting to note that the positive relationship found between abundance of conspecifics in the canopy and the seedling/sapling bank was stronger for new seedlings than for saplings (Fig. 1a,b for *O. europaea*, Fig. 2a,b for *Q. canariensis*, Fig. 2c,d for *Q. suber*). Stronger positive conspecific effects for seedlings than for saplings could indicate the existence of negative density-dependent processes from conspecifics acting at the seedling stage due to host-specialized antagonists (e.g. Janzen-Connell effects; Connell, 1971; Janzen, 1970), intense competition for resources, or to the generation of unfavorable abiotic conditions (e.g. Bonanomi et al., 2008). Accordingly, we found negative effects of conspecific neighborhoods on seedling survival of the three tree species (negative λ values), in agreement with previous studies (Pérez-Ramos and Marañón, 2012, Ibáñez et al., 2015). Our results however suggest that the magnitude of these negative density-dependent processes on survival were not strong enough to counteract the high number of seedlings emerged in conspecific neighborhoods (Fig. 1a,b,c,d, Fig. 2a,b,c,d). High emergence values under conspecific trees are likely the result of dispersal patterns, with most seeds not being biotically dispersed and arriving under mother trees in both *Olea* (Rey and Alcántara, 2000) and *Quercus* species (Pulido and Díaz, 2005). For tree species in mixed forests, the existence of a conspecific sapling bank under adult canopies might be considered as a guarantee of self-replacement that could favor species coexistence (Catovsky and Bazzaz, 2002; Frelich and Reich, 1995; van Breemen and Finzi, 1998; Wilson and Agnew, 1992). Our results therefore suggest that, in the absence of disturbances, positive canopy-sapling feedbacks could lead to a rather stable stand structure. The process of *Q. suber* decline could however act as a destabilizing force of this structure through its impacts on the regeneration bank.

Effects of Quercus suber *decline on natural regeneration*

A clear consequence of *Q. suber* decline was a reduction in the absolute abundance of regeneration (both seedlings and saplings) in all tree species. The negative impact of *Q. suber* decline on tree species regeneration might explain the lower species richness found in declining neighborhoods at some sites (e.g. in woodlands). However, the magnitude of this effect varied substantially among co-dominant tree species. In woodland sites, the decline of *Q. suber* had a stronger negative effect on conspecific regeneration than on *O. europaea* regeneration, causing a shift in sapling relative abundance towards the dominance of *O. europaea*. Such among-species difference in the magnitude of the negative effects of decline could be due to the high abundance of *Phythopthora cinnamomi* (a soil-borne pathogen with high preference for *Q. suber*) under declining trees in woodlands (Gómez-Aparicio et al., 2012), or to the better capacity of drought-tolerant *O. europaea* seedlings to tolerate stressful abiotic conditions in gaps opened after tree death (e.g. high light levels and evaporation demand, Fetcher et al., 1985; Royer et al., 2011). Abiotic conditions in gaps might be considered to be particularly stressful in woodlands compared to closed forests, since their open structure and smaller tree size determined the formation of larger gaps after the death of individual trees. In closed forests, on the contrary, the somewhat weaker negative effect that *Q. suber* decline had on conspecific regeneration compared to *Q. canariensis* regeneration caused a shift in sapling relative abundance towards a slight advantage in dominance for *Q. suber*. This result was quite unexpected since, in a parallel experimental study where seeds of *Q. suber* and *Q. canariensis* were sown and the recruits monitored, we did not detect clear differences in the response of new seedlings and young saplings (2-3 years old) of the two oak species to neighborhoods of contrasting health (Ibáñez et al., 2015). Because the sapling bank in this study potentially included saplings much older than three years, it is possible that this result reflect the development of among-species differences with ontogeny, with older saplings of the shade-tolerant *Q. canariensis* being more impaired than those of *Q. suber* by the high light levels of the gaps open after tree death.

Whereas the decline of *Q. suber* had important negative effects on abundance and performance of tree seedlings and saplings, other functional groups such as fleshy-fruited shrubs and lianas were more independent of the decline process and even benefited from it in some situations. These findings could be related to the fact that seedling survival of both lianas and fleshy-fruited shrubs has been shown to benefit from high-light microsites in the forest understory (Pérez-Ramos and Marañón, 2012), they are not reported to be affected by *P. cinnamomi*, and they are the dominant woody species recruiting in degraded forests (e.g. post-fire shrublands and reforested stands, Mendoza et al., 2009). Our results therefore suggest that the process of *Q. suber* decline could induce an increase in the relative abundance of functional forms other than trees in the woody community. This finding is in agreement with previous studies that have proposed a potential development of Mediterranean forests towards more open systems with lower tree cover and higher shrub dominance due to global environmental change (Acácio et al., 2007; Matías et al., 2012; Pérez-Ramos and Marañón, 2012).

Implications for successional dynamics in declining forests

The effects of tree dieback on regeneration dynamics is probably one of the less studied aspects of forest die-off, particularly when compared with the abundance of studies exploring the physiological mechanisms underlying tree dieback or its impacts on ecosystem processes (McDowell et al., 2013). Among the scarce regeneration studies available, a large majority has focused on regeneration patterns after insect-decline mortality in mountain forests (Battles and Fahey, 2000; Collins et al., 2011; DeRose and Long, 2010; Kayes and Tinker, 2012; Nigh et al., 2008; Veblen et al., 1991; Vyse et al., 2009), and to a lesser extent after temperature- or drought-driven mortality in water-limited systems (Galiano et al., 2013; Redmond and Barger, 2013; Van Mantgem and Stephenson, 2007). Here we show, for a complex system involving water-limited forests affected by aggressive exotic pathogens, that the decline of the dominant species (*Q. suber*) implies shifts in the ranking of seedling and sapling abundance among tree species, which could affect successional trajectories potentially leading to vegetation shifts (Kayes and Tinker, 2012; but see Redmond and Barger, 2013; Suarez and Kitzberger, 2008).

Yet, predicting trajectories of forest recovery after tree dieback is not an easy task. For tree dieback to induce compositional shifts, it is necessary that the die-off species has a disadvantage in terms of propagule input or that the new conditions created are relatively more favorable for regeneration of coexisting species (Suarez and Kitzberger, 2008). Here we found that in some forest types, like open woodlands, the die-off species *Q. suber* met both requisites, showing much lower seedling and sapling abundance than the co-dominant *O. europaea* in all sites (Table B in Supplementary Material) and a stronger negative response to declining neighborhoods (Fig. 1f,h). Everything being equal, we could therefore expect these oak woodlands to change towards *O. europaea*- dominated systems, in agreement with our initial hypothesis of study. In closed forests, on the contrary, we found *Q. suber* to have much lower regeneration abundance than the co-dominant *Q. canariensis* at the site-level (Table B in Supplementary Material), but to be somewhat less negative affected by the process of adult decline. Therefore, the future dominance patterns in this forest type will likely depend on the extent to which the relative advantage of *Q. suber* over *Q. canariensis* saplings under defoliated and dead trees can compensate for the intrinsic lower regeneration capacity of the species and its increasing seed-limitation as the process of adult decline advances.

Understanding recruitment dynamics in *Q. suber* forests is of major ecological and social importance given the prominent role that this tree species plays in the configuration of the landscape and the economy of the Mediterranean basin, and the problems of regeneration and decline that *Q. suber* suffers throughout its distribution area (Aronson et al., 2009;

Urbieta et al., 2008). Here we have shown that, based on current patterns of woody plant regeneration in declining mixed *Q. suber* forests, we could expect these systems to suffer from important changes in relative abundance among tree species as well as among functional groups (trees, shrubs, lianas) in the near future. Because most of these changes point towards a loss of cover and dominance of *Q. suber*, management strategies are urgently needed in order to either attenuate adult mortality (e.g. adequate phytosanitary measures) or promote its regeneration (e.g. enrichment plantings). Only by looking for stabilizing mechanisms that improve the balance between mortality and recruitment (Lloret et al., 2012) we will be able to counteract the negative effects of global change drivers (exotic pathogens, climate change) on *Q. suber*, and preserve the many ecosystem services provided by these valuable forests.

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Table 1. Comparison of the alternate models for the analysis of seedling and sapling abundance, survival and richness. AIC$_c$ values for trivariate and full models are only given when several bivariate models were a better fit than the "Only Tree" model. The best model is shown in bold. Model type (additive vs. multiplicative), number of parameters (NP) and slope (SL) are also given.

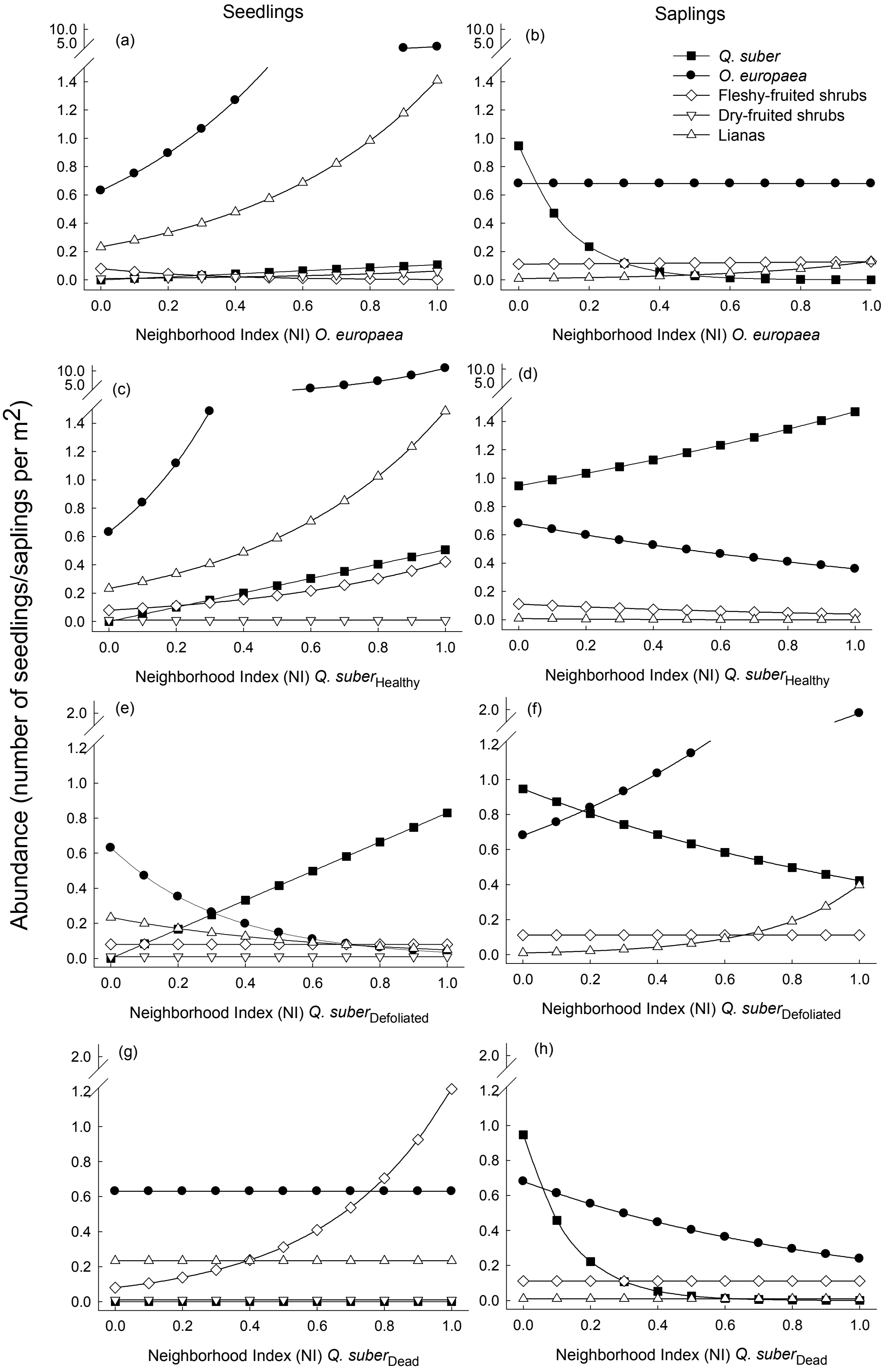
Variable	Life stage	Forest type	Species	AIC$_c$							Model type	NP	SL
				Only Tree	Tree + Site	Tree + Year	Tree + Shrub	Tree + Site + Year	Tree + Site + Shrub	Full			
Abundance	Seedling	Woodland	*Q. suber*	**448.4**	448.8	448.8	450.0				AD	9	1.05
			O. europaea	1001.5	**927.5**	1000.4	1000.1				AD	11	0.91
			Fleshy-fruited shrubs	249.8	**245.0**	249.0	253.7				MT	11	1.02
			Dry-fruited shrubs	137.3	**116.3**	142.1	141.1				MT	11	0.93
			Lianas	480.3	**411.7**	481.1	483.2				MT	11	0.97
		Closed forest	*Q. suber*	342.6	**317.1**	341.0	345.9				AD	11	1.05
			Q. canariensis	**905.5**	904.8	906.6	907.3				AD	9	1.06
			Fleshy-fruited shrubs	809.1	**795.6**	808.7	807.6				AD	11	0.92
			Lianas	1712.3	**1450.3**	1710.9	1716.9				MT	11	0.96
	Sapling	Woodland	*Q. suber*	630.9	**625.7**	633.1	631.6				MT	11	0.98
			O. europaea	994.7	977.8	993.3	988.1		**971.2**		MT	12	1.00
			Fleshy-fruited shrubs	217.4	**203.0**	218.7	219.0				MT	11	1.09
			Lianas	109.4	**95.6**	108.3	115.2				MT	11	1.00
		Closed forest	*Q. suber*	655.1	**590.2**	666.0	658.5				MT	11	1.07
			Q. canariensis	973.2	**968.9**	975.7	973.2				MT	11	1.02
			Fleshy-fruited shrubs	**893.4**	892.3	895.7	894.0				MT	9	1.07
			Lianas	1155.1	**1125.7**	1156.3	1153.4				AD	11	1.08
Survival	Seedling	Woodland	*Q. suber*	98.8	100.8	**91.0**	102.1				AD	9	0.90
			O. europaea	**226.6**	230.8	228.7	228.3				AD	8	2.07
		Closed forest	*Q. suber*	**69.7**	74.4	71.98	73.8				AD	8	1.48
			Q. canariensis	**177.9**	182.1	178.0	180.7				AD	8	1.02
	Sapling	Woodland	*Q. suber*	**151.4**	153.0	153.3	155.4				AD	8	0.96
			O. europaea	221.3	213.0	210.6	227.9	**206.8**			AD	11	0.99
		Closed forest	*Q. suber*	91.9	92.2	**89.6**	91.2				AD	9	0.97
			Q. canariensis	287.2	**237.0**	283.4	290.0				AD	10	0.98
Richness	Seedling + sapling	Woodland	All woody species	**898.8**	903.2	903.3	901.5				AD	8	0.97
		Closed forest	All woody species	1301.1	1163.9	1278.6	1287.1			**1122.4**	AD	15	0.97

Figure legends

Figure 1 Predicted variation in the abundance of seedlings and saplings of different woody species (*Quercus suber*, *Olea europaea*, fleshly-fruited shrubs, dry-fruited shrubs, and lianas) as a function of the neighborhood index (NI) calculated for four different tree neighbor types (*O. europaea* [a,b], healthy *Q. suber* [c, d], defoliated *Q. suber* [e, f] and dead *Q. suber* [g,h]) in woodland sites. NI values of 0 represent neighborhoods without trees, whereas NI values of 1 represent, for each neighbor category, the neighborhoods with the highest observed value of NI (i.e. the highest influence of that neighbor type). Predicted abundance of seedlings and saplings was calculated using the values of the parameters a, b and λ in Eq. 1 or 2, given in Supporting Information (Tables D and E in Supplementary Material).

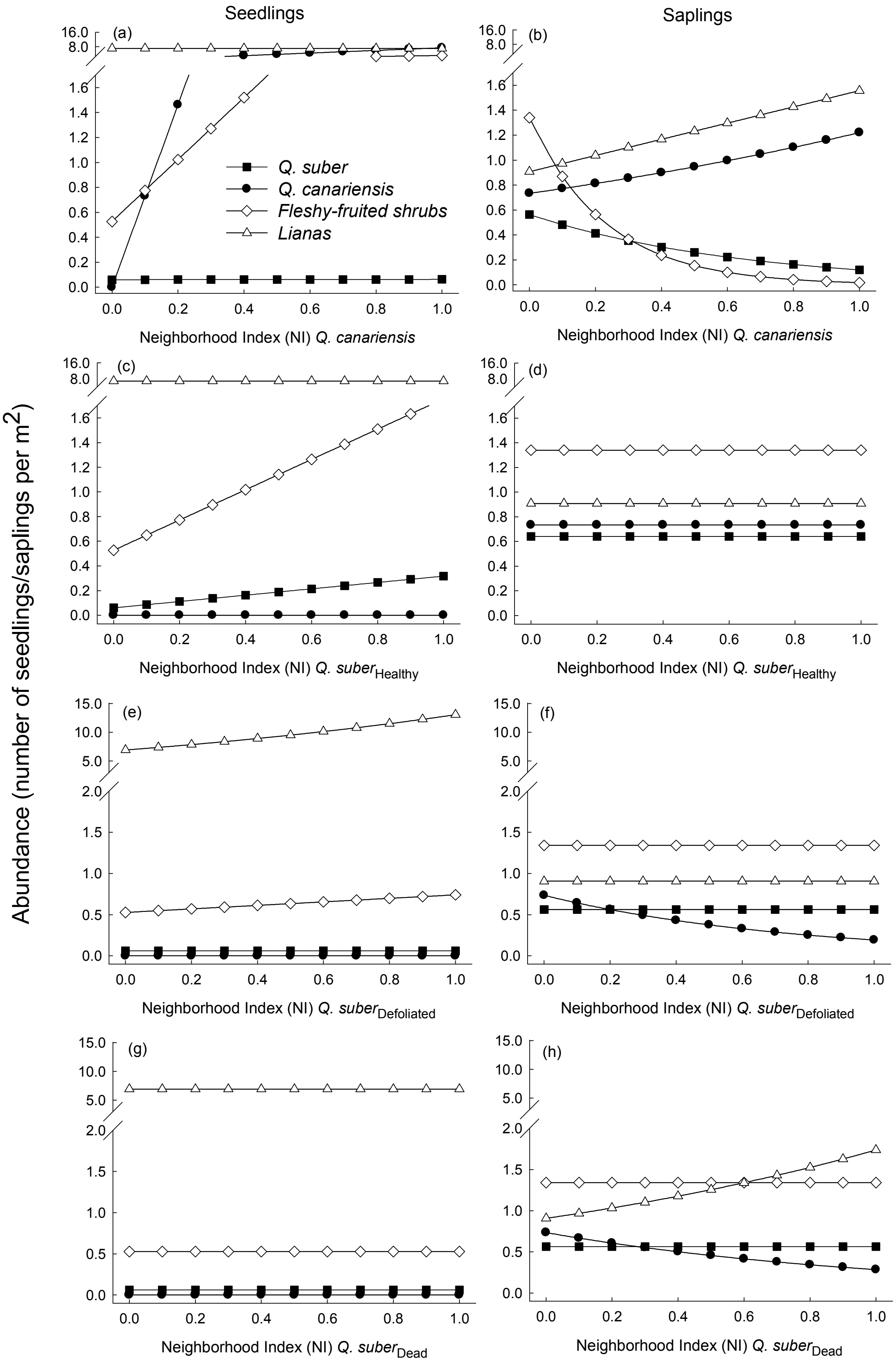
Figure 2 Predicted variation in the abundance of seedlings and saplings of different woody species (*Quercus suber*, *Quercus canariensis*, fleshly-fruited shrubs, and lianas) as a function of the neighborhood index (NI) calculated for four different neighbor types (*Q. canariensis* [a, b], healthy *Q. suber* [c,d], defoliated *Q. suber* [e, f] and dead *Q. suber* [g,h]) in closed forest sites. NI values of 0 represent neighborhoods without trees, whereas NI values of 1 represent, for each neighbor category, the neighborhoods with the highest observed value of NI (i.e. the highest influence of that neighbor type). Predicted abundance of seedlings and saplings was calculated using the values of the parameters a, b and λ in Eq. 1 or 2, given in Supporting Information (Tables D and E in Supplementary Material).

726 Figure 1



727

Figure 2


Seedlings
Saplings
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
Q. suber
Q. canariensis
Fleshy-fruited shrubs
Lianas
Abundance (number of seedlings/saplings per m2)
Neighborhood Index (NI) Q. canariensis
Neighborhood Index (NI) Q. suberHealthy
Neighborhood Index (NI) Q. suberDefoliated
Neighborhood Index (NI) Q. suberDead
16.0
8.0
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
15.0
10.0
5.0
2.0
1.5
1.0
0.5
0.0
0.2
0.4
0.6
0.8
1.0