

Understanding neighborhood effects to increase restoration success of woody plant communities

INÉS IBÁÑEZ ^{1,3} AND ALEJANDRO RODRÍGUEZ ²

¹*School for Environment and Sustainability, University of Michigan, Ann Arbor, Michigan 48109 USA*

²*Department of Conservation Biology, Estación Biológica de Doñana – CSIC, Sevilla, Spain*

Citation: Ibáñez, I., and A. Rodríguez. 2020. Understanding neighborhood effects to increase restoration success of woody plant communities. *Ecological Applications* 30(5):e02098. 10.1002/eap.2098

Abstract. Revegetation is the most common procedure in the restoration of disturbed areas; this practice usually aims at reconstructing plant communities that can last without further management. A low-cost strategy to assist these efforts is the application of ecological knowledge in the design of the restoration. Promoting ecological processes that enhance the functioning of the restored community could result in higher restoration success. Among these processes, plant–plant interactions, e.g., facilitation and competition, can play an important role, both facilitating and impeding the development of a self-sustaining plant community. Although these processes have been well-studied in nature, we rarely have sufficient knowledge about the whole plant community. To develop that knowledge, we leverage on a restoration experiment that took place after a mine toxic spill, where ~15,000 woody plants from 13 species were planted and geolocated. Species were planted in three mixtures mimicking natural communities found along soil moisture gradients (xerophyte, intermediate, and hydrophyte). Plantings also varied in density. Approximately 2,600 plants were monitored for damage status, survival, and growth, for 4 yr. We analyzed growth performance of six targeted species as a function of their damage status, planted mixture, and density. Growth was also assessed on the basis of neighboring plants, accounting for the species identity and distance to the focal plant. Results show that survival among planted species was relatively high and was mostly unaffected by mixture or density of the plantings. Only very damaged plants in one species experienced a decrease in survival with increasing density. Neighborhood effects on growth show positive, neutral, and negative interactions among the tested species; these also varied depending on the type of growth performance considered (height, crown area, diameter). The species-specific results ranged from positive to negative, varying between pair of species and growth performance metric. Results gathered from our neighborhood analyses on plant growth provide valuable information for the design of planting schemes that could enhance the performance of the target species. The methods developed can be applied to other systems and species. Given the potential impacts that facilitation and competition may have during revegetation, these interactions could be considered in restoration operations.

Key words: *Crataegus monogyna*; Guadamar toxic spill; *Myrtus communis*; *Olea europaea*; *Phillyrea angustifolia*; *Pistacia lentiscus*; *reclamation*; *Spain*; *Tamarix africana*.

INTRODUCTION

Restoration efforts of degraded land are being undertaken all over the world. Although these usually involve a considerable amount of resources, success is not always granted. Furthermore, most restoration projects either entirely fail or underperform while the underlying causes remain poorly identified (Zedler and Callaway 1999, Suding 2011). Restoration ecology, i.e., the study of the relationships among organisms and their environment in a restoration context (Palmer et al. 2016), aims at applying well known ecological theory and principles

to restoration practices. In restoration, the rationale is that we can accelerate and aid recovery by promoting processes that will lead to the desired outcome. Even where human-caused perturbations are very different from the natural disturbances that may have shaped ecosystems, ecological damage is more readily reversed if restoration can capitalize on natural processes (e.g., Bradshaw 1997, Prach and Pyšek 2001).

Most restoration practices aim at rebuilding degraded ecosystem through revegetation (Greibsson 2011), and multi-species planting is a common practice to speed up ecosystem recovery (Funk et al. 2008). Ecological processes that could be targeted in restoration are the mechanisms by which co-occurring plants interact with each other. Plant–plant interactions, mainly competition and facilitation, play a dominant role in community

Manuscript received 29 March 2019; revised 2 December 2019; accepted 6 January 2020. Corresponding Editor: Emil Cienciala.

³ E-mail: iibanez@umich.edu

assembly (Callaway and Walker 1997). Plant–plant interactions can facilitate (e.g., nurse plants, mycorrhizal networks) or constrain (e.g., competitors, allelopathic species) the establishment and performance of plants (Brooker and Callaghan 1998, Armas and Pugnaire 2005, Maestre et al. 2009). Thus, understanding and quantifying these effects could provide critical information aimed at increasing restoration success. For example, by choosing combinations of species that minimize competition for limiting resources, or plant species that facilitate establishment or performance of other plants, restoration efforts could be improved.

In the context of restoration, facilitation among plant species is widespread in plant communities (Padilla and Pugnaire 2006, Callaway 2007, Brooker et al. 2008). Positive interactions are particularly common among woody species in water-limited ecosystems (Gómez-Aparicio 2009), this is likely due to release from water stress (Gómez-Aparicio 2009). With shading, facilitating plants can ameliorate water scarcity by reducing evapotranspiration in other plants (e.g., Gómez-Aparicio et al. 2004, Holmgren et al. 2012, Caldeira et al. 2014). Plants with deep roots can provide water to the superficial layers of the soil via hydraulic lift (e.g., Dawson 1993, Caldwell et al. 1998, Prieto et al. 2011), benefiting establishing seedlings and plants with shallower root systems. In addition, as different species may exploit different water resources within the soil layers, mixtures of species may also lead to water stress release through root niche partitioning or diversity of hydraulic traits (Pretzsch et al. 2012, Anderegg et al. 2018). In a restoration context, soils and hydrology have often been altered, deeply affecting water holding capacity in the soil (Suding et al. 2016), and strongly influencing the establishment and persistence of the restored vegetation. Thus, facilitative effects may be particularly relevant in this context.

Still, even if facilitation dominates plant–plant interactions under stressful conditions, competition for limiting resources will also contribute to the net effect of the interaction. Under the usually harsh conditions taking place during revegetation (e.g., no shading, bare and degraded soils), nutrients and water are common limiting resources for plant establishment and persistence (Pywell et al. 2002, Suding et al. 2016). In addition, unvegetated sites experience harsher environments for plant growth, being exposed to more extreme conditions, e.g., higher temperatures and wind exposure, which increase the risk of desiccation (Questad et al. 2014), and make competition for water even more relevant. Furthermore, as plants grow and require more resources, communities may experience a shift from neutral dynamics or net facilitation to having competition dominating plant–plant interactions (Miriti 2006). Therefore, in restoration, competition with other plants can constrain the establishment and performance of the target individuals, leading to failure or underperformance of the restoration (Yang et al. 2014, Suding et al. 2016).

Given the potential impacts that facilitation and competition mechanisms may have during revegetation, understanding these processes, and their spatial extent, could provide critical information in the design of the restoration in question. To that extent, neighborhood analyses that identify and quantify interaction between co-occurring plants have been developed for natural communities (e.g., Uriarte et al. 2004, Canham and Uriarte 2006, Ibáñez et al. 2015). These techniques have been used to understand spatial patterns of plant recruitment and growth performance as a function of distance, identity, and/or size of neighboring plants. As such, this same approach could also be applied in the design of restoration activities. Thus, understanding how different neighborhood designs, i.e., plant species composition and spatial arrangement, may affect the outcome of the restoration could be particularly relevant in the success of these projects.

In Mediterranean regions, like the one in our study site, reforestation efforts have focused on using facilitative effects of already established native shrubs on transplanted trees (Cortina et al. 2004, Greipsson 2011). However, in the context of restoration, where all woody vegetation is being established simultaneously, it is not clear what kind of interaction, facilitation, or competition, prevails. We leverage the use of neighborhood analyses in the context of a large-scale restoration project to assess the impact of the neighboring community on plant performance. In particular, we assessed the magnitude, and spatial scales, of positive and negative interactions between neighboring plants. We analyzed woody plant survival and growth data from a restoration effort that took place in southwestern Europe (Fig. 1a,b). For each target species, we addressed the following questions: (1) How does neighborhood density affect survival of these restored species? (2) What are the neighboring species that exert a positive or negative influence on their growth performance? And (3) what are the spatial extent of those effects? Answering these questions allowed us to provide a specific list of positive and negative plant interactions affecting these planted species, information that can now be directly used in the design of future restoration projects at no, or low, additional cost.

METHODS

In April 1998, a toxic spill to the Guadiamar River (southwest Spain; 37°23'46" N, 6°13'46" W; Fig. 1a) took place after the collapse of a dyke in a pyrite mine tailings pond. About six million cubic meters of acidic water and sludge rich in heavy metals breached the dam and flooded more than 4,000 ha of the alluvial plain along 40 km downstream (Grimalt et al. 1999; Fig. 1b). The heavy equipment used first to remove sludge and then to apply alkaline and organic amendments also uprooted existing vegetation (mostly tree crops) and removed topsoil (or thicker soil layers in some areas; OTRG 1998). Buried sludge remains created soil spots

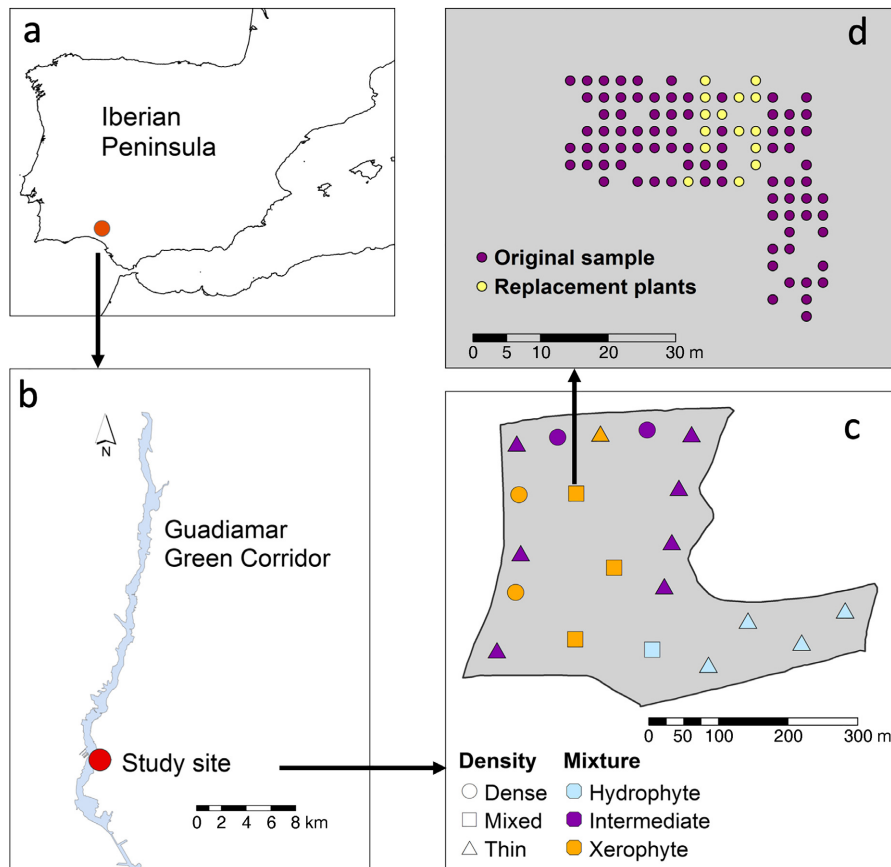


FIG. 1. (a) Location of the Guadiamar River in southwest Spain. (b) Location of the experimental plantation within the restored area (shaded) in the lower Guadiamar River. (c) Distribution of parcels planted with three mixtures of six woody species with variable dependence on soil moisture. Plantations were classified as dense (individuals spaced 1 m), thin (2–2.5 m), or mixed, where the parcel core was densely planted (1.5 m) and density decreased at the parcel periphery (2.5 m). (d) Sample of neighboring plants that were monitored for survival and growth. Some individuals dying during the observations were replaced with other shrubs or trees in order to get a sample size of about 100 plants per parcel and year.

with high trace-element concentration (Cabrera et al. 2008). In 1999, native shrubs and trees began to be planted. On the basis of soil properties, altitude, and distance to the river banks, 14 different plantation models varying in species composition were used (Moreira and Arenas 2003). By 2005, plantation performance exhibited large spatial variability and further efforts were applied to zones where restoration proved unsuccessful, sometimes adopting new plantation models.

Planting effort

In early 2006, approximately 15,500 individuals, distributed in 20 parcels over a 14-ha area (Fig. 1b,c), were planted. At planting, all individuals were 1 yr old except for *Fraxinus angustifolia* and *Quercus* spp. seedlings that were 2 yr old. Three types of plant mixtures were planted, species for each mixture were selected to represent a gradient of plant adaptations to different levels of soil moisture (xerophytes, hydrophytes, and intermediate; Table 1; Fig. 1c). Each mixture included two tree

and four shrub species. Plant density was also manipulated with dense parcels, where individuals were spaced 1 m; thin parcels, where separation doubled to 2.0–2.5 m; and mixed parcels, where parcels featured a dense core (1.5 m) and a thin periphery (2.5 m). Site size and the distribution of soil conditions precluded a balanced factorial design density \times mixture (Fig. 1c).

Herbs and the aerial structures of woody plants surviving from earlier revegetation were removed by dis-harrowing. The site was then planted between January and February 2006. Each planted individual was geolocated within the parcel. In fall 2006, each planted individual surviving the first summer was geolocated. We randomly selected a point in each parcel \times density combination and marked a set of about 100 contiguous individuals around this point. For the next 3 yr, each fall, we monitored survival and growth of marked individuals. When available, dead plants were replaced with nearby individuals in order to keep sample size close to 100 plants per parcel (Fig. 1d). Initial identification and geolocation also included plants naturally growing in the

TABLE 1. Plant species planted at each mixture type and other species found in the parcels, or nearby, assigned to each of the mixtures.

Mixture	Species planted	Other species found in the parcels
Xerophyte	<i>Arbutus unedo</i> (tree), <i>Crataegus monogyna</i> (shrub), <i>Phillyrea angustifolia</i> (shrub), <i>Pistacia lentiscus</i> (shrub), <i>Quercus coccifera</i> (shrub), <i>Quercus ilex</i> (tree)	<i>Celtis australis</i> , <i>Ceratonia siliqua</i> , <i>Fraxinus angustifolia</i> , <i>Myrtus communis</i> , <i>Olea europaea</i> , <i>Prunus</i> spp., <i>Rosa</i> spp., <i>Tamarix africana</i>
Intermediate	<i>Crataegus monogyna</i> (shrub), <i>Olea europaea</i> (tree), <i>Phillyrea angustifolia</i> (shrub), <i>Pistacia lentiscus</i> (shrub), <i>Populus alba</i> (tree), <i>Retama sphaerocarpa</i> (shrub)	<i>Celtis australis</i> , <i>Fraxinus angustifolia</i> , <i>Rosa</i> spp.
Hydrophyte	<i>Fraxinus angustifolia</i> (tree), <i>Myrtus communis</i> (shrub), <i>Nerium oleander</i> (shrub), <i>Salix atrocinerea</i> (shrub), <i>Salix alba</i> (tree), <i>Tamarix africana</i> (shrub)	<i>Crataegus monogyna</i> , <i>Olea europaea</i> , <i>Populus</i> spp., <i>Prunus</i> spp., <i>Retama sphaerocarpa</i> , <i>Rosa</i> spp., <i>Rubus ulmifolius</i>

parcels (114 individuals; resprouts from former vegetation) and other plantings (3,881 individuals).

Data collection

In November of 2006, 10 months after planting, all individuals were checked for survival, damage status, and size. Surviving plants were classified according to their damage status as vigorous (V), low vigor (low V; growth was judged to be abnormally low regarding the average height, volume, branch density, and stem diameter for the species in the parcel), damaged (D; there were signs of at least one of these features: defoliated secondary stems, most leaves showed abnormal color, shape, or size, major branches were torn apart or eaten, the main stem presented severe tissue harm), and high damage (high D; similar signs as D, but affecting at least one-half of the aerial structures, evergreen species were leafless or the main stem was cut below the first bifurcation). After that date, only a targeted number of plants (2,675) were monitored for survival and growth in 2007, 2008, and 2009. Plant size was assessed by measuring height, crown area (estimated from the plant's largest crown diameter and its perpendicular diameter), and diameter at the base in 2007, 2008, and 2009. Growth was estimated as the difference in size between two consecutive years. Negative growth values, mainly due to herbivory or mechanical damage during field operations, were not included in the analyses. To factor out the effect of plant size on growth and to better compare among the different growth measurements, height, crown, and diameter, we used relative growth rates (RGR: $\ln[\text{size}_t / \text{size}_{t-1}]$) in the analyses.

Survival analysis

We had 4 yr of survival data to estimate annual survival probabilities at three period intervals, 2006(fall)–2007, 2007–2008, and 2008–2009. For each species, we estimated survival as a function of mixture (if they were planted in more than one mixture), density of planting, status of the plant the previous year ($t - 1$), and parcel random effects (PRE_{surv}). Survival data ($S = 1$ alive,

$S = 0$ dead) for plant i in time interval t were analyzed as

$$\begin{aligned} \text{likelihood: } S_{i,t} &\sim \text{Bernoulli}(p_{i,t}) \\ \text{process model: } \logit(p_{i,t}) &= \alpha_{\text{mixture}(i), \text{density}(i)} \\ &+ \beta_{\text{status}(i), t-1} + \text{PRE}_{\text{surv}}(\text{parcel}(i)). \end{aligned}$$

We then used the results of this analysis, i.e., parameter means, variances, and covariances, to predict survival (S^{pred}) for the plants still alive in fall 2006 but that were not monitored in subsequent years. We used these predicted survival values in our growth analysis (see details in *Growth analysis*). Naturally occurring seedlings were considered to be alive the whole time period.

Growth analysis

We analyzed relative growth rates (RGR) for the two periods of time for which growth data were available: 2007–2008 and 2008–2009. We analyzed growth data for height, basal diameter, and crown area from targeted plants as a function of mixture, plant status the previous year, neighborhood effects (NE), and parcel random effects (PRE_{grow}). For plant i in year t

$$\begin{aligned} \text{likelihood: } \text{RGR}_{i,t} &\sim \text{Normal}(G_{i,t}, \sigma^2) \text{ (limited to be positive)} \\ \text{process model: } G_{i,t} &= \mu_{\text{mixture}(i)} + \omega_{\text{status}(i), t-1} \\ &+ \text{NE}_{i,t} + \text{PRE}_{\text{grow}}(\text{parcel}(i)). \end{aligned}$$

Neighborhood effects were estimated following Uriarte et al. (2004), where the overall neighborhood effect is the sum of each neighbor's effect. Each neighbor's effect is a function of the neighbor's species identity (parameter λ) and of the distance to the target plant (effects dissipate with distance following a power function; parameter γ). We used a radius of 5 m to define each plant's neighborhood. Using the geolocation data, we identified all the neighbors surrounding a particular plant and the distance between them. We did not include size of the neighbor (which is commonly done; Gómez-Aparicio et al. 2008a) because we did not have size data for unmarked plants; also since all plants were of the

same age, size variability within each species is likely to have been low. To account for plant mortality over time, each neighbor's effect was multiplied by its survival status (S^{obs} observed, for plants monitored each year, or estimated S^{pred} , for those that were not). For target plant i at time t , the overall neighborhood effect was calculated as the sum of all the individual effects from each neighbor j , as

$$NE_{i,t} = \sum_{j=1}^{\text{No. neighbors}_i} \lambda_{\text{species}(j)} \text{distance}_{ij}^{-\gamma_{\text{species}(i)}} S_{j,t}^*$$

Each growth data set, height, crown area, and diameter, was analyzed independently. To better visualize the effects of neighbors on plant growth, we then analyzed neighborhood effects (NE) estimated for each individual as a function of the number of neighbors

$$\begin{aligned} \text{likelihood: } NE_{i,t} &\sim \text{Normal}(NEM_{i,t}, \sigma_{NE}^2) \\ \text{process model: } NEM_{i,t} &= \delta * \text{No. neighbors}_{i,t}. \end{aligned}$$

To better quantify the variability associated with the growth data, fixed effects parameters were estimated for each individual plant (μ_i, ω_i), these individual-level parameters were then estimated from treatment-level hyperparameters ($\mu_{\text{mixture}}, \omega_{\text{status}}$). We estimated parameter values following a Bayesian approach where all parameters were estimated from non-informative distributions; $\alpha_{\text{mixture}}, \text{density}, \beta_{\text{status}}, \omega_{\text{status}}, \lambda_{\text{speciesNeighbor}}, \delta \sim \text{Normal}(0, 1, 000)$, $\mu_{\text{mixture}} \sim \text{LogNormal}(1, 100)$, $\gamma_{\text{speciesNeighbor}} \sim \text{Uniform}(0, 1)$, $1/\sigma^2 \sim \text{Gamma}(0.001, 0.001)$, $\text{PRE}_{\text{SURV}_{\text{parcel}}} \sim \text{Normal}(0, \sigma_{\text{SURV}}^2)$, $\text{PRE}_{\text{GROW}_{\text{parcel}}} \sim \text{Normal}(0, \sigma_{\text{GROW}}^2)$, and $\sigma_{\text{SURV}}^2, \sigma_{\text{GROW}}^2, \sigma_{NE}^2 \sim \text{Uniform}(0, 100)$. Each target species was analyzed independently. Analyses were run in JAGS 3.4 (Plummer 2003) using the rjags package (Plummer et al. 2018) in R (R Development Core Team 2013). Three chains were run until convergence of the parameters, ~100,000 iterations, and run again for another 50,000 to estimate posterior parameter means, variances, and covariances, after thinning every 100th iteration (see DataS1: *Analysis Code*).

RESULTS

Of the ~15,500 individuals planted in the restoration, 10,546 survived the first 10 months. From the 2,676 individuals targeted for long-term monitoring in 2006, 2,429 were alive in 2007, 2,192 in 2008, and 1,994 in 2009. Growth analyses were only performed for species with enough observations, which resulted in six target species: *Crataegus monogyna*, *Myrtus communis*, *Olea europaea*, *Phillyrea angustifolia*, *Pistacia lentiscus*, and *Tamarix africana*. That amounted to 1,645 individuals for which we had data for two growth periods. We used 2,809 estimates of height growth, 2,779 of crown area growth, and 2,609 of basal diameter growth. Species-level breakdown

counts for survival and growth data are included Appendix S1: Table S1, S2.

Survival analysis

In general, survival rates after the initial planting period were high across all the species analyzed (Fig. 2 for target species; for all species see Appendix S2: Table S1). Plants classified under the status categories vigorous, low vigor, and damaged had similarly high survival, but this significantly decreased for the high damage category (Fig. 2). Density of planting did not affect survival in most species (*C. monogyna*, *M. communis*, and *P. angustifolia*), but it had a negative effect for plants in the very damage status for *P. lentiscus*, and a positive effect in *O. europaea* and *T. africana* (Fig. 2).

Growth analysis

Measured values for growth rates varied widely among species. For plants in the vigorous category, average height growth (cm/yr, mean \pm SD) ranged from 57.6 ± 36.0 for *T. africana* to 9.3 ± 6.5 for *M. communis*, with 30.8 ± 20.3 for *C. monogyna*, 17.1 ± 11.5 for *O. europaea*, 18.0 ± 15.6 for *P. angustifolia*, and 24.6 ± 17.5 for *P. lentiscus*. Growth in crown area (m²/yr, mean \pm SD) varied from 1.7 ± 2.9 for *T. africana* to 0.10 ± 0.10 for *P. angustifolia*, with 0.12 ± 0.12 for *C. monogyna*, 0.29 ± 0.28 for *M. communis*, 0.34 ± 0.26 for *O. europaea*, and 0.42 ± 0.78 for *P. lentiscus*. Growth in basal diameter (mm/yr, mean \pm SD) ranged from 13.0 ± 9.1 for *T. africana* to 2.6 ± 0.86 for *C. monogyna*, with 11.2 ± 7.4 for *M. communis*, 6.2 ± 5.7 for *O. europaea*, 2.8 ± 2.9 for *P. angustifolia*, and 6.7 ± 7.1 for *P. lentiscus*.

Analysis of relative growth rate data (RGR) shows an overall fit (i.e., predicted vs. observed R^2 across all species) of 0.93 for height, 0.31 for crown area, and 0.69 for stem basal diameter. In the growth analyses of the target species, height and crown RGR increased with plant's damage status for *C. monogyna*, *P. angustifolia*, *P. lentiscus*, and *T. africana*, and showed no trend with status in *M. communis* and *O. europaea* (Fig. 3). Basal diameter growth also increased with damage status for *C. monogyna* and *P. angustifolia* (Fig. 3). For the three species planted in two mixtures, *C. monogyna*, *P. angustifolia*, and *P. lentiscus*, growth was similar between mixtures (Fig. 3). See Appendix S2: Table S2 for growth analyses parameter values.

The number of neighbors included in the analyses was 2–101 for *C. monogyna*, 2–33 for *M. communis*, 2–99 for *O. europaea*, 6–115 *P. angustifolia*, 2–114 for *P. lentiscus*, and 2–32 for *T. africana*. The neighborhood analyses illustrate how the six target species were affected by their neighbors in many different ways (Table 2); although only a few interactions were statistically significant (i.e., 95% CI around parameter λ did not intercept with zero; see Appendix S2: Table S3 for parameter

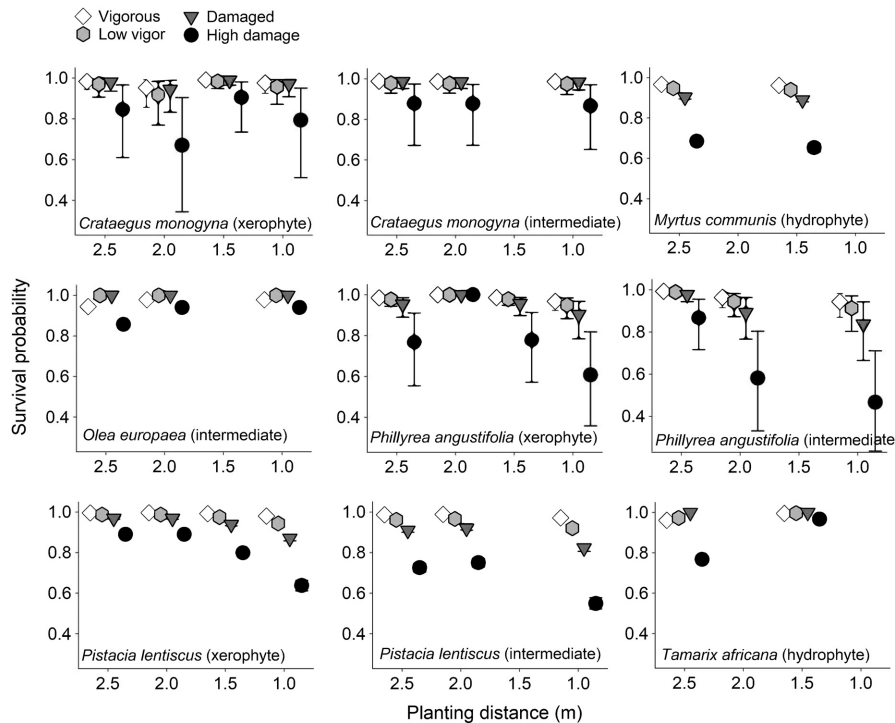


FIG. 2. Predicted survival of the target species by mixture, density of plantings and status. Values are mean and 95% PI (Predicted Interval). Intervals that do not overlap (95% PI) are considered to be significantly different from each other.

values). Only one species, *M. communis*, showed several strong positive interactions, and a negative one, affecting growth. None of the species of neighbors had an overall negative or positive effect on the target species' growth trends (Table 2). The extent of the spatial effects (parameter γ) was very similar in magnitude and variability among the target species (mean \pm SD $\sim 0.93 \pm 0.12$; see Appendix S2: Table S4). Analyses of the neighborhood effects as a function of the number of neighbors reflect the variability of results found among the parameters (Table 2), showing increasing, decreasing, and neutral effects on height, crown and basal diameter growth, as the number of neighbors accumulated (Fig. 4).

DISCUSSION

Plant–plant interactions play an important role in determining the assemblage of plant communities, and this could likely be the case in restoration projects where degraded areas are revegetated. Facilitative interactions could be critical under the suboptimal conditions frequently associated with restoration settings (Gómez-Aparicio et al. 2004, Padilla and Pugnaire 2006). Still, competition for limiting resources may also affect success under the harsh conditions plants often encounter in restored areas. Despite its relevance, a major challenge for designing restoration schemes that promote facilitative interactions, while lessening competition, is the uncertainty in the nature of these plant–plant

interactions (Vallejo et al. 2012). In this study, we leverage on a large-scale restoration experiment, where both plantings and naturally growing vegetation were geolocated, to assess the impact of plant–plant interactions on plant performance. Results from the analyses show that after the initial transplant, survival among planted species was relatively high and was mostly unaffected by density of the plantings. Only for one species very damaged plants experienced a decrease in survival with increased density. Nevertheless, growth increased with damage category among several species, indicating a high recovery potential among surviving plantings. Growth was also impacted by the neighboring plants. Neighborhood effects, i.e., number of neighbors, their species identity, and distance to the plant, were quite idiosyncratic. Outcomes from the analyses show positive, neutral and negative interactions among the tested species, and these varied depending on the type of growth performance considered. The species-specific results gathered from our neighborhood analyses on plant growth provided valuable information for the design of planting schemes that could enhance the performance of the target species.

The restoration project we assessed took place in southwestern Europe, an area within the Mediterranean biome. The region is characterized by mild and wet winters and hot and dry summers; droughts are frequent and can last from weeks to months, making water a key limiting resource in plant establishment (Gómez-

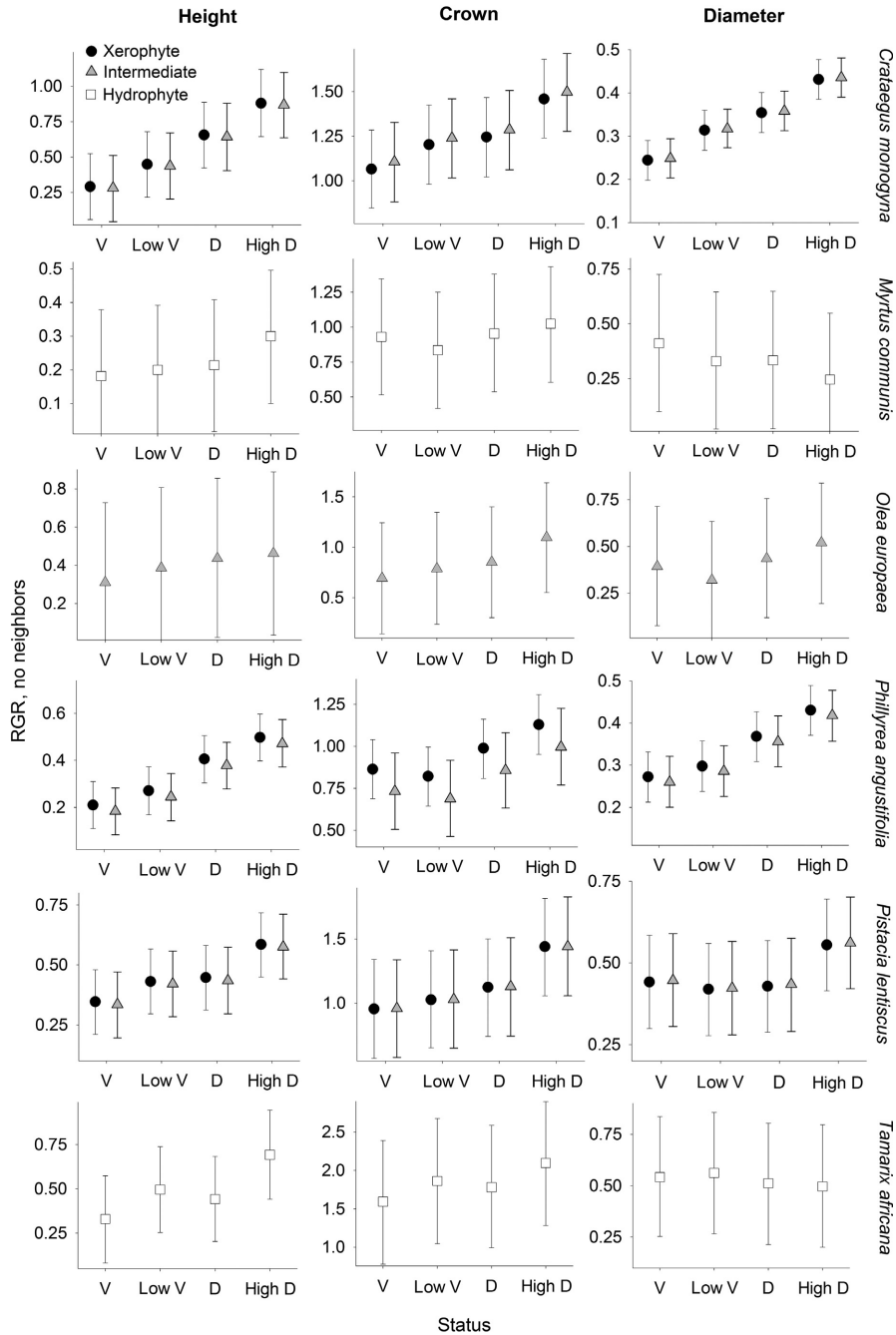


Fig. 3. Predicted relative growth rates, height, crown, and diameter, for each to the target species according to status and mixture planted. Values are mean and 95% PI. Intervals that do not overlap (95% PI) are considered to be statistically different from each other. Status: V, vigorous; low V, low vigor; D, damaged; high D, high damage.

Aparicio et al. 2008b, Caldeira et al. 2014). In restoration, irrigation is rarely an option, thus, careful selection of species is critical to ensure the success of the project. For highly damaged reclamation sites, like our study site, artificial selection of native species is an optimal strategy (Vallejo et al. 2012). Species in this restoration were chosen based on the natural vegetation of the area and on the specific biophysical characteristics of the site. The

three mixtures of species planted represent the gradient of plant adaptations to water availability characteristic of this region, and reflect natural communities common to the area.

Our survival results indicate that the species selected were adequate for this landscape and that the planting of young individuals worked well under those conditions (Fig. 2). After initial transplant shock, survival of these

TABLE 2. Neighbor effects on growth (parameter λ : height/crown/diameter) for the six target species.

Neighbor species	Target species					
	<i>Crataegus monogyna</i>	<i>Myrtus communis</i>	<i>Olea europaea</i>	<i>Phillyrea angustifolia</i>	<i>Pistacia lentiscus</i>	<i>Tamarix africana</i>
<i>Arbutus unedo</i>	+/-†/+	NA	NA	/-/	+/-/-	NA
<i>Crataegus monogyna</i>	/-/+	-/-+	-/++	+/++	+/++	NA
<i>Fraxinus angustifolia</i>	+/+†/+	-/-+	+/-+	/-/	/-/	+†/+/-
<i>Myrtus communis</i>	-/++	+†/++	NA	/-+	/-+	/-/
<i>Nerium oleander</i>	NA	-/++	NA	NA	NA	+†/++
<i>Olea europaea</i>	+/-/-	NA	-/-	+/-/-	+/-/-	NA
<i>Phillyrea angustifolia</i>	/-+	/-/	-/-	+/-/-	/-/	NA
<i>Pistacia lentiscus</i>	+/+/-	+†/-+	+/++	+/++	-/-	NA
<i>Quercus coccifera</i>	/-+	NA	NA	-/+/-	-†/-/-	NA
<i>Quercus ilex</i>	+/+/-	NA	NA	-/++	+/+†/+†	NA
<i>Retama sphaerocarpa</i>	/-/	NA	/-/	/-/-	/-/	NA
<i>Tamarix africana</i>	NA	/-/	NA	NA	/-/-	/-+
<i>Salix</i> spp.	NA	-/-+	NA	NA	NA	+/-/-
<i>Populus alba</i>	+/-/-	NA	+/++	+/-+	+/+†/+	NA
<i>Rosa</i> spp.	+/++	+/++	NA	/-+	-/++	-†/-/-
<i>Quercus</i> spp.	+/++	NA	NA	/-+	+/-+	NA
Other	/-/-†	/-/-	+/-+	-/-+†	+/-+	-/-+

Notes: Plus symbols indicate positive interactions, while minus symbols represent negative interactions. We only report parameter values for those interactions that had at least 10 individuals of the target species being affected by the neighbor species. NA, not applicable (fewer than 10 interactions).

† Statistically significant parameters (95% CI does not intercept zero; for actual parameter values see Appendix S2).

woody species was high and, for most species, density of plantings did not affect survival of healthy plants (Fig. 2). In settings of low resource availability, e.g., water, low plant density could be essential since plants would have to explore the soil beyond their canopy areas (Galatowitsch 2012, Trautz et al. 2017). Our plants were 4 yr old the last time we monitored them, 3 yr after planting may not have been enough time for their root systems to start competing for limiting soil resources (Schwinning and Weiner 1998). Similarly, any canopy interference may not have been sufficient to limit light availability to the point that could have affected survival (Reisman-Bernan 2007; see discussion on growth analyses). Nevertheless, longer time monitoring of these plantings is likely to show stronger competitive interactions in the denser parcels as plants grow (Miriti 2006).

Not only were these individuals unaffected by planting density, neither was the plants' capacity to recover from damage, e.g., herbivory or mechanical damage, jeopardized in any of the planting schemes. Well established individuals seemed to have had the resources to compensate, to a certain extent, for tissue losses (Rosenthal and Kotanen 1994, Hawkes and Sullivan 2001). Growth compensation for leaf and stem removal has been reported in shrubs of the Mediterranean basin (Riba 1998, Focardi and Tinelli 2005, Michielsen et al. 2017). Our analyses revealed that three of the target species responded to damage by increasing their growth rates, while the other three maintained the same growth across all damage categories (Fig. 3), corroborating the choice of species was optimal for this site.

We also explored the characteristics of the neighborhood surrounding each target plant, i.e., species identity and distance to target plant, which could have strong impacts on its establishment and growth performance (McCarthy-Neumann and Ibáñez 2012, Ibáñez et al. 2015, Uriarte et al. 2018). Competition for resources, exposure to soil pathogens, and facilitation effects are the most common mechanisms by which adjacent plants impact each other (Richard et al. 2009, Prieto et al. 2011, Urli et al. 2016). In a restoration setting, the neighborhood, i.e., species selection and design of the plantings, can be easily manipulated and aimed at promoting beneficial interactions while avoiding or minimizing negative effects. In our restoration project, the neighborhood impacted growth of the target species with both positive and negative effects depending on the species involved, the number of neighbors and the growth performance metrics (Table 2; Fig. 4).

In water-limited ecosystems, temperature amelioration and water supply via hydraulic lift are considered common mechanisms of plant-plant facilitation (Gómez-Aparicio 2009, Prieto et al. 2011). In our case, where all individuals were planted at once, root niche partitioning for water resources may also be a relevant mechanism behind the positive interactions we found (Table 2). For example, overall, *C. monogyna* and *P. lentiscus* had positive effects on all target species except their conspecifics, supporting root niche partitioning. Heterospecific neighbors could be using different soil space for water and nutrient resources, while conspecific neighbors would be in direct competition with the target plant (Pretzsch et al. 2012).

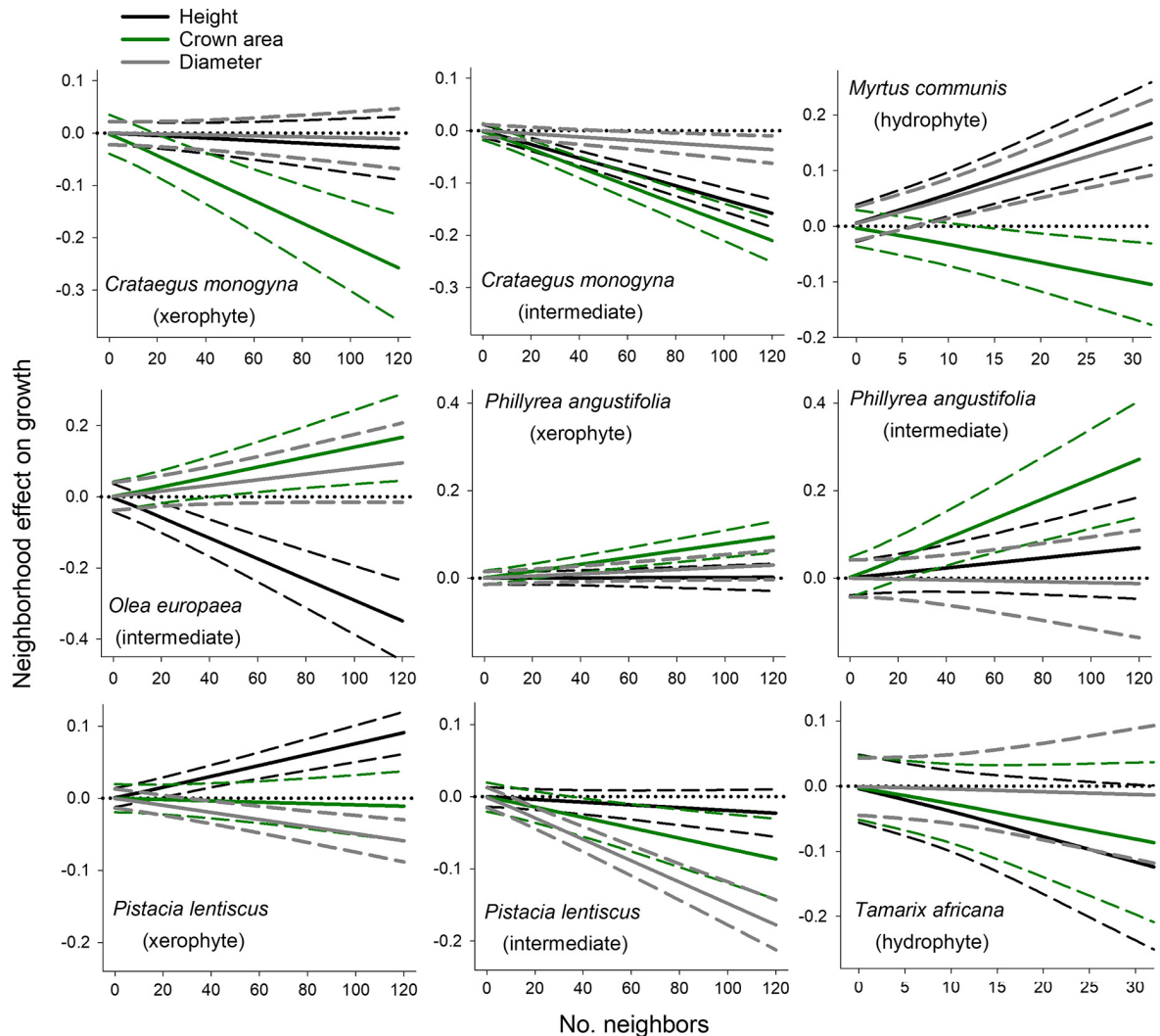


FIG. 4. Predicted neighborhood effects as a function of number of neighbors on height, crown, and diameter growth. Solid lines are means, dashed and dotted lines show 95% PI (Predicted Interval). Intervals (95% PI) including zero indicate a not statistically significant effect of neighbors. Values above zero represent positive effects and values below the zero line indicate negative effects.

How neighborhood effects affected growth of the target species shed some light on the competitive ability of these species in these particular mixtures. For example, *C. monogyna* and *P. lentiscus* seem to be more competitive in the xerophyte mixture than in the intermediate mixture, while *P. angustifolia* showed the opposite pattern (Fig. 4). For the species that were only planted in one mixture, we can also assess their differential growth performance. *Myrtus communis* responded to increasing number of neighbors by allocating resources to stem growth, i.e., height and basal diameter, over crown area; while *O. europaea* prioritized crown and stem diameter growth over height; and *T. africana* showed an overall negative effect on growth with increasing neighborhood density (Fig. 4). Our particular experimental set up precludes us from identifying the actual mechanisms behind those results. Still, the analyses unveil relationships

valuable for directly informing the design of more optimal planting mixtures (Table 2).

Given the increasing need for restoration operations (Hobbs 2012) and the large expense associated with these projects (Kimball et al. 2015), ensuring the success of a restoration should be a priority objective in the field of restoration ecology. Ecological restoration uses ecological theory at low, or no, additional cost to enhance biological and physical processes that optimize the outcome of the restoration (Tongway and Ludwig 2012). Therefore, identifying and quantifying the ecological mechanisms that could contribute to the success of the restoration is essential for the advancement of this discipline. Co-occurring facilitative and competitive mechanisms are rarely accounted for in restoration projects, but could be critical in determining the outcome of the project. Facilitative plants may aid the establishment

and performance of others, especially under stressful conditions. Concomitantly, when resources are limiting, plant competition may determine the performance, and ultimately survival, of other planted shrubs and trees. Therefore, by maximizing facilitation and minimizing constrains, these mechanisms can guide the design of restoration efforts to ensure their success. Our findings assessing plant–plant interactions in the context of a restoration provide concrete information on the nature and strength of the mechanisms affecting the performance of the target species at least in alluvial plains of the Mediterranean Basin (Table 2). They also provide the foundation for incorporating neighborhood interactions into the design of restoration projects. Through the design and active management involved in restoration efforts, we can use our knowledge on how the ecological system works to improve the outcome of these projects.

ACKNOWLEDGMENTS

We thank T. Marañón and J. Fernández-Haeger for discussing the composition of plant mixtures and F. Carrascal for supervising the plantation. We are indebted to J. Quetglas who, aided by other field technicians, thoroughly kept sampled plants identifiable over the years and measured them, and to S. Arenas and J. Monje who helped to ensure the accuracy of plant geolocation. We also thank the Plant Ecology Discussion Group at the University of Michigan for thoughtful comments on the manuscript. This research was funded by the Spanish National Research Agency (AEI; CGL2016-75205-R) and the Andalusian Department of Innovation, Science and Enterprise (P06-RNM-01903), and co-funded by the European Regional Development Fund (FEDER).

LITERATURE CITED

- Anderegg, W. R. L., et al. 2018. Hydraulic diversity of forests regulates ecosystem resilience during drought. *Nature* 561:538–541.
- Armas, C., and F. I. Pugnaire. 2005. Plant interactions govern population dynamics in a semi-arid plant community. *Journal of Ecology* 93:978–989.
- Bradshaw, A. 1997. Restoration of mined lands—using natural processes. *Ecological Engineering* 8:255–269.
- Brooker, R. W., and T. V. Callaghan. 1998. The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. *Oikos* 81:196–207.
- Brooker, R. W., et al. 2008. Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology* 96:18–34.
- Cabrera, F., J. Ariza, P. Madejón, E. Madejón, and J. M. Muriillo. 2008. Mercury and other trace elements in soils affected by the mine tailing spill in Aznalcóllar (SW Spain). *Science of the Total Environment* 390:311–322.
- Caldeira, M. C., I. Ibáñez, C. Nogueira, M. N. Bugalho, X. Lecomte, A. Moreira, and J. S. Pereira. 2014. Direct and indirect effects of tree canopy facilitation in the recruitment of Mediterranean oaks. *Journal of Applied Ecology* 51:349–353.
- Caldwell, M. M., T. E. Dawson, and J. H. Richards. 1998. Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia* 113:151–161.
- Callaway, R. M. 2007. Positive interactions and interdependence in plant communities. Springer, Dordrecht, The Netherlands.
- Callaway, R. M., and L. R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78:1958–1965.
- Canham, C. D., and M. Uriarte. 2006. Analysis of neighborhood dynamics of forest ecosystems using likelihood methods and modeling. *Ecological Applications* 16:62–73.
- Cortina, J., J. Bellot, A. Vilagrosa, R. Caturla, F. Maestre, E. Rubio, J. Martínez, and A. Bonet. 2004. Restauración en semiárido. Pages 345–406 *in* V. Vallejo, and J. Alloza editors. *Avances en el estudio de la gestión del monte mediterráneo*. Fundación CEAM, Valencia, Spain.
- Dawson, T. E. 1993. Hydraulic lift and water use by plants: implications for water balance, performance and plant–plant interactions. *Oecologia* 95:565–574.
- Focardi, S., and A. Tinelli. 2005. Herbivory in a Mediterranean forest: browsing impact and plant compensation. *Acta Oecologica* 28:239–247.
- Funk, J. L., E. E. Cleland, K. N. Suding, and E. S. Zavaleta. 2008. Restoration through reassembly: plant traits and invasion resistance. *Trends in Ecology & Evolution* 23:695–703.
- Galatowitsch, S. M. 2012. *Ecological restoration*. Sinauer Associates Inc., Sunderland, Massachusetts, USA.
- Gómez-Aparicio, L. 2009. The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. *Journal of Ecology* 97:1202–1214.
- Gómez-Aparicio, L., R. Zamora, J. M. Gómez, J. A. Hódar, J. Castro, and E. Baraza. 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. *Ecological Applications* 14:1128–1138.
- Gómez-Aparicio, L., C. D. Canham, and P. H. Martin. 2008a. Neighbourhood models of the effects of the invasive *Acer platanoides* on tree seedling dynamics: linking impacts on communities and ecosystems. *Journal of Ecology* 96:78–90.
- Gomez-Aparicio, L., I. M. Pérez-Ramos, I. Mendoza, Matías, J. I. Quero, J. Castro, R. Zamora, and T. Marañón. 2008b. Oak seedling survival and growth along resource gradients in Mediterranean forests: implications for regeneration in current and future environmental scenarios. *Oikos* 117:1683–1699.
- Greipsson, S. 2011. *Restoration ecology*. Jones & Barlett Learning, Sudbury, Massachusetts, USA.
- Grimalt, J. O., M. Ferrer, and E. Macpherson. 1999. The mine tailing accident in Aznalcóllar. *Science of the Total Environment* 242:3–11.
- Hawkes, C. V., and J. J. Sullivan. 2001. The impact of herbivory on plants in different resource conditions: A meta-analysis. *Ecology* 82:2045–2058.
- Hobbs, R. J. 2012. Restoration in a changing climate. Pages 23–29 *in* J. van Andel, and A. J. Aronson, editors. *Restoration ecology*. Wiley-Blackwell, Oxford, UK.
- Holmgren, M., L. Gómez-Aparicio, J. L. Quero, and F. Valladares. 2012. Non-linear effects of drought under shade: reconciling physiological and ecological models in plant communities. *Oecologia* 169:293–305.
- Ibáñez, B., L. Gómez-Aparicio, P. Stoll, J. M. Ávila, I. M. Pérez-Ramos, and T. Marañón. 2015. A neighborhood analysis of the consequences of *Quercus suber* decline for regeneration dynamics in mediterranean forests. *PLoS ONE* 10:e0117827.
- Kimball, S., M. Lulow, Q. Sorenson, K. Balazs, Y.-C. Fang, S. J. Davis, M. O’Connell, and T. E. Huxman. 2015. Cost-effective ecological restoration. *Restoration Ecology* 23:800–810.
- Maestre, F. T., R. M. Callaway, F. Valladares, and C. J. Lortie. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology* 97:199–205.
- McCarthy-Neumann, S., and I. Ibáñez. 2012. Tree range expansion may be enhanced by escape from negative plant–soil feedbacks. *Ecology* 93:2637–2649.

- Michielsen, M., L. Szemák, A. Fenesi, I. Nijs, and E. Ruprecht. 2017. Resprouting of woody species encroaching temperate European grasslands after cutting and burning. *Applied Vegetation Science* 20:388–396.
- Miriti, M. N. 2006. Ontogenetic shift from facilitation to competition in a desert shrub. *Journal of Ecology* 94:973–979.
- Moreira, J. M., and J. M. Arenas. 2003. La información ambiental de la cuenca del río Guadimar. Consejería de Medio Ambiente y Ordenación del Territorio, Junta de Andalucía, Sevilla, Spain.
- OTRG. 1998. Propuesta de actuaciones para la recuperación del Guadimar. Oficina Técnica para la Recuperación del Guadimar, Consejería de Medio Ambiente, Junta de Andalucía, Sevilla, Spain.
- Padilla, F. M., and F. I. Pugnaire. 2006. The role of nurse plants in the restoration of degraded environments. *Frontiers in Ecology and the Environment* 4:196–202.
- M. A. Palmer, J. B. Zedler, and D. A. Falk, editors. 2016. Foundations of restoration ecology. Island Press, Washington, D.C., USA.
- Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. Proceedings of the 3rd International Workshop on Distributed Statistical Computing, March 20–22 Vienna, Austria.
- Plummer, M., A. Stukalov, and M. Denwood. 2018. Package ‘rjags’. Bayesian graphical models using MCMC. R package version 408. <https://CRAN.R-project.org/package=rjags>
- Prach, K., and P. Pyšek. 2001. Using spontaneous succession for restoration of human-disturbed habitats: experience from Central Europe. *Ecological Engineering* 17:55–62.
- Pretzsch, H., G. Schütze, and E. Uhl. 2012. Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by inter-specific facilitation. *Plant Biology* 15:483–495.
- Prieto, I., F. M. Padilla, C. Armas, and F. I. Pugnaire. 2011. The role of hydraulic lift on seedling establishment under a nurse plant species in a semi-arid environment. *Perspectives in Plant Ecology, Evolution and Systematics* 13:181–187.
- Pywell, R. F., J. M. Bullock, A. Hopkins, K. J. Walker, T. H. Sparks, M. J. W. Burke, and S. Peel. 2002. Restoration of species-rich grassland on arable land: assessing the limiting processes using a multi-site experiment. *Journal of Applied Ecology* 39:294–309.
- Questad, E. J., et al. 2014. Mapping habitat suitability for at-risk plant species and its implications for restoration and reintroduction. *Ecological Applications* 24:385–395.
- R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org
- Reisman-Berman, O.. 2007. Age-related change in canopy traits shifts conspecific facilitation to interference in a semi-arid shrubland. *Ecography* 30:459–470.
- Riba, M. 1998. Effects of intensity and frequency of crown damage on resprouting of *Erica arborea* L. (Ericaceae). *Acta Oecologica* 19:9–16.
- Richard, F., M.-A. Selosse, and M. Gardes. 2009. Facilitated establishment of *Quercus ilex* in shrub-dominated communities within a Mediterranean ecosystem: do mycorrhizal partners matter? *FEMS Microbiology Ecology* 68:14–24.
- Rosenthal, J. P., and P. M. Kotanen. 1994. Terrestrial plant tolerance to herbivory. *Trends in Ecology & Evolution* 9:145–148.
- Schwinning, S., and J. Weiner. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia* 113:447–455.
- Suding, K. N. 2011. Toward an era of restoration in ecology: Successes, failures, and opportunities ahead. *Annual Review of Ecology, Evolution, and Systematics* 42:465–487.
- Suding, K., E. Spotswood, D. Chapple, E. Beller, and K. Gross. 2016. Ecological dynamics and ecological restoration. Pages 27–56 in M. A. Palmer, J. B. Zedler, and D. A. Falk editors. Foundations of restoration ecology. Island Press, Washington, D.C., USA.
- Tongway, D. J., and J. A. Ludwig. 2012. Planning and implementing successful landscape-scale restoration. Pages 30–42 in J. van Andel, and J. Aronson editors. Restoration ecology: the new frontier. Blackwell Publishing, Oxford, U.K.
- Trautz, A. C., T. H. Illangasekare, and I. Rodriguez-Iturbe. 2017. Role of co-occurring competition and facilitation in plant spacing hydrodynamics in water-limited environments. Proceedings of the National Academy of Sciences USA 114:9379–9384.
- Uriarte, M., R. Condit, C. D. Canham, and S. P. Hubbell. 2004. A spatially explicit model of sapling growth in a tropical forest: does the identity of neighbours matter? *Journal of Ecology* 92:348–360.
- Uriarte, M., R. Muscarella, and J. K. Zimmerman. 2018. Environmental heterogeneity and biotic interactions mediate climate impacts on tropical forest regeneration. *Global Change Biology* 24:e692–e704.
- Urli, M., C. D. Brown, R. Narváez Perez, P.-L. Chagnon, and M. Vellend. 2016. Increased seedling establishment via enemy-release at the upper elevational range limit of sugar maple. *Ecology* 97:33058–3069.
- Vallejo, V. R., E. B. Allen, J. Aronson, J. G. Pausas, J. Cortina, and J. R. Gutiérrez. 2012. Restoration of Mediterranean-type woodlands and shrublands. Pages 130–144 in J. van Andel, and J. Aronson editors. Restoration ecology: the new frontier. Blackwell Publishing, Oxford, U.K.
- Yang, L., W. Wei, L. Chen, W. Chen, and J. Wang. 2014. Response of temporal variation of soil moisture to vegetation restoration in semi-arid Loess Plateau, China. *Catena* 115:123–133.
- Zedler, J. B., and J. C. Callaway. 1999. Tracking wetland restoration: Do mitigation sites follow desired trajectories? *Restoration Ecology* 7:69–73.

SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2098/full>

DATA AVAILABILITY

Data are available from DIGITAL.CSIC: <http://dx.doi.org/10.20350/digitalCSIC/10537>.