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Coping with changing plant–plant interactions in restoration ecology: Effect of species, site, and individual variation

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Abstract

Question: Nurse–beneficiary plant interactions are often used to restore degraded habitats. However, whether and how shifts in plant–plant interactions along the facilitation–competition continuum alter revegetation success has been seldom considered. To test whether and how shifts in plant–plant interactions (due to woody species identity, study site, early life stage, and individual nurse) might alter plant recruitment and thus the success of revegetation projects, we chose a system comprising the Mediterranean dwarf palm (*Chamaerops humilis*) and seven common woody plant species.

Location: Two human-degraded sites within Doñana National Park (southwestern Spain).

Methods: We carried out several well-replicated field experiments to compare plant performance (seed survival, seedling emergence, seedling survival, seedling recruitment) in the presence and absence of *Chamaerops humilis*.

Results: *Chamaerops humilis* had marked effects on the performance of woody species that, however, changed among life stages. Depending on woody species identity, seed survival was up to 193 times greater in adjacent open spaces than beneath *Chamaerops humilis*. Conversely, seedling survival and recruitment were up to 19 times greater beneath *Chamaerops humilis* than in open spaces. Importantly, none of the studied woody species showed greater accumulated recruitment in open spaces than beneath *Chamaerops humilis*. Interestingly, we found strong inter-individual palm variation in the sign and strength of their effect on woody plant performance.

Conclusions: We found strong seed–seedling conflicts the strength of which was species-specific. The strong inter-individual palm variation depicts a facilitation–competition continuum with important implications for restoration. We propose several management recommendations across different hierarchical levels (i.e., from individuals to communities) that may increase plant recruitment and therefore the success of revegetation projects. Our results are particularly relevant for restoring arid, semi-arid and alpine landscapes worldwide where the nurse–beneficiary plant interactions are critical to ameliorating stressful conditions.

KEYWORDS
facilitation–competition continuum, human-degraded sites, nurse–beneficiary interactions, relative interaction index, revegetation, seed survival, seedling facilitation, seed–seedling conflicts

1 | INTRODUCTION

Rather than being fixed, most ecological interactions can vary in sign and strength depending on the balance between benefits and costs for the involved partners (Bronstein, 2001; Fedriani & Delibes, 2011; Michalet et al., 2011; Schöb et al., 2014). Identifying these trades-offs between benefits and costs is essential to comprehensively understand changing interactions along the mutualism–antagonism continuum and their potential ecological, evolutionary, and applied implications (Bronstein, 2015; Perea et al., 2013; Gómez et al., 2019). Plant–plant interactions (Brooker et al., 2008; Callaway, 2007; Pugnaire, 2010) are crucial to increasing the revegetation success of restoration programs (Gómez-Aparicio et al., 2004; Rey-Benayas et al., 2008; Costa et al., 2017; Jankju, 2013; Torroba-Balmori et al., 2015; Fedriani et al., 2019; Ibáñez & Rodríguez, 2020; Castro et al., 2021; Díaz-Hernández et al., 2021; but see Noumi et al., 2015). These interactions are known to change from facilitation to competition (and vice versa) depending on the ecological context (Brooker et al., 2008; Chaieb et al., 2021; Michalet et al., 2014). Therefore, detecting whether and how the outcome of presumed nurse–beneficiary plant interactions shifts along a facilitation–competition continuum may be crucial for successful ecological restoration.

Extreme droughts and high temperatures are strong environmental filters for plant species in arid and semi-arid landscapes (Pugnaire & Valladares, 2007). Early plant life transitions such as seed survival, seedling emergence, and seedling survival are usually the most critical stages for microhabitat-dependent recruitment (Pérez-Ramos et al., 2012; Schupp, 2007). Improved microhabitat suitability (e.g., microclimatic conditions) beneath shrubs with respect to their adjacent open spaces may be favorable for seedling survival and recruitment in arid and semi-arid landscapes such as those occurring in the Mediterranean Basin. By contrast, shrubs may be also unfavorable microsites for early plant life stages such as seed survival due to seed predation, yielding seed–seedling conflicts (*sensu* Schupp, 1995; Drezner, 2015). Further, plant–plant interactions may differ in sign and strength depending on the interacting species, the biotic and abiotic conditions in which such interactions occur, and even the characteristics of nurse individuals (Violle et al., 2012; Costa et al., 2017; Miranda-Jácome & Flores, 2018; Díaz-Hernández et al., 2021; but see Holland & Molina-Freaner, 2013). For instance, Schöb et al. (2013) found that compact and large individuals of a nurse cushion species in the Sierra Nevada Mountains (southeastern Spain) showed stronger facilitative effects, in terms of beneficiary species richness, compared with loose and small individuals (see also Alday et al., 2014). Accounting for context-dependency and potential seed–seedling conflicts in plant–plant interactions could be critical for guiding restoration actions (Jones et al., 2019; Larkin et al., 2019).

Many Mediterranean nurse plants are small-sized, compact, and/or thorny shrubs that provide shade, ameliorating the prevailing severe climatic conditions, among other positive effects (Filazzola & Lortie, 2014). These shrubs usually represent favorable microhabitats for seedling emergence, survival, and recruitment of many woody plant species, although they may be also preferred sites for multiple seed predators such as granivore rodents (Rey & Alcántara, 2000; Alday et al., 2014; but see Ziffer-Berger et al., 2017). In this sense, previous studies have found conflicts or shifts from facilitation to inhibition of sequential life stages in single nurse–beneficiary species pairs (Castanho et al., 2015; Fujita & Yamashina, 2018; Loayza et al., 2017). However, rigorous evaluations of such conflicts throughout several early life stages at the plant-community level are scarce (Bruno et al., 2017; Paterno et al., 2016; Schiffers & Tielbörger, 2006). Even less common are studies that investigate how the nature of these plant–plant interactions changes among interacting individuals (but see Anthelme et al., 2017).

The Mediterranean dwarf palm (*Chamaerops humilis*) plays a key role in the recolonization of human-driven degraded areas by facilitating the establishment of diverse woody plant species (Garrote et al., 2021). Specifically, we recently found strong positive spatial associations with adult plants of several recolonizing woody species (Garrote et al., 2019a). Such spatial associations possibly relate to the shading micro-environment and numerous needle-sharp thorns on this palm, which facilitate plant recruitment (Saiz & Alados, 2012) through strong alleviation of abiotic stress compared with adjacent open spaces, and protect against vertebrate herbivores (e.g., ungulates and rabbits) by acting as a mechanical barrier. However, this shrubby palm could also represent a selected microhabitat for granivore rodents, potentially limiting local woody recruitment (Brown & Kotler, 2004). Here, we chose a system comprising *Chamaerops humilis* and seven common woody species to test how shifts in plant–plant interactions (due to species identity, study site, early life stage, and individual nurse) may alter plant recruitment and thus the success of revegetation projects. To this end, we conducted seed survival and sowing field experiments using seven woody species in the presence and absence of *Chamaerops humilis* in two degraded sites in southwestern Spain. Specifically, we seek to answer three questions: (a) does the effect of *Chamaerops humilis* on woody species performance vary throughout the early life stages (i.e., from seed survival to seedling recruitment); (b) does the cumulative probability of establishment (i.e., the accumulated effect after all life stages) of woody species vary with the presence of *Chamaerops humilis* and, if so, is such variation consistent across woody species identity, study sites, and/or individual nurse; and finally, (c) to what extent does potential inter-individual variation in the interaction between *Chamaerops humilis* and woody plants depict a facilitation–competition continuum?

2 | METHODS

2.1 | Study area

The study was conducted at Doñana National Park (37°9′N, 6°26′W) in southwestern Spain between October 2018 and December 2019. The climate is Mediterranean sub-humid (537.7 ± 30.7 mm; mean ± 1 *SE*), with dry (8.4 ± 1.4 mm) and hot summers (38.5 ± 0.3°C and 10.7 ± 0.2°C; maximum and minimum, respectively). The remaining seasons are cooler and wetter than summer. The mean maximum and minimum temperatures were 20.5 ± 0.2°C and 29.2 ± 0.4°C (spring) and 0.1 ± 0.3°C and 4.8 ± 0.3°C (winter). Most rain falls during winter (74.0 ± 7.3 mm) and autumn (87.6 ± 7.6 mm). The accumulated precipitation during our study period (i.e., October 2018 to December 2019) was 420.9 mm. Therefore, we consider this period relatively dry in terms of historical averages (percentile 24; $N = 40$; 1979–2019, data from Natural Processes Monitoring Group, Doñana Biological Station).

The Doñana area is an anthropogenic and fragmented landscape, where habitat patches of Mediterranean scrubland, oak and pine forests are isolated by cropland, towns, marshes, or dunes. To evaluate possible between-site variation, we set up field experiments at two degraded sites (Matasgordas and Reserva) located 10 km apart that have similar climatic conditions owing to their proximity. Both sites have been intensively exploited for livestock ranching and cultivation that have degraded their original state for decades, although there were some differences in human management between sites (Garrote et al., 2019a). Specifically, in Matasgordas, all shrubs and most trees were mechanically removed in 1970 to create an open area of pastureland with scattered cork oak trees and sparse patches of scrubland. The area was used for intensive cattle grazing until 1996, when the land was expropriated, the cows removed and, afterward, the area protected by the Spanish National Park Service. Historically, in Reserva, the human management of vegetation has been more prolonged, intensive and harsher. Most cork oak and wild olive trees were cut down and controlled rotation was applied every 25–30 years. In 1964, the area was declared a biological reserve, and cultivation and livestock ranching ended. Cattle still graze in this area, although the grazing is not as intensive as it was few decades ago. Both sites differ in terms of the nutrient content of the topsoil, with organic matter, phosphorus and nitrogen in Reserva double that in Matasgordas (Appendix S1, Table S1), and in the availability of groundwater, which is more superficial in Reserva (2.39 m) than in Matasgordas (4.56 m) (CHG, 2019).

Many animal-dispersed native plants such as *Chamaerops humilis*, *Asparagus* spp., *Pyrus bourgaeana*, *Rubus ulmifolius* and *Phillyrea angustifolia* among others are currently recolonizing these human-degraded areas since their protection within National Park boundaries. Fruits of these fleshy fruited species include drupes (*Daphne gnidium*, *Phillyrea angustifolia* and *Pistacia lentiscus*), berries (*Asparagus aphyllus*) or pomes (*Pyrus bourgaeana*). These fruits ripen from August to December and contain seeds that vary in mass by several orders of magnitude (Table 1). These plant species are bird-dispersed except *Pyrus bourgaeana*, which in Doñana is mainly dispersed by mammals (Table 1). Seed dispersal of these woody plants into human-perturbed habitats is increased by the 'perching effect' (*sensu* Debussche et al., 1982) exerted by *Chamaerops humilis* (González et al., unpublished). Dispersed seeds in Doñana are often consumed by rodent species such as *Apodemus sylvaticus*, *Mus spretus*, and *Rattus* spp. (Fedriani et al., 2020; Suárez-Esteban et al., 2018). Seedlings usually emerge during the late winter and spring, and most die during summer owing to extreme drought and severe temperatures.

2.2 | Seed survival experiment

To assess the effect of *Chamaerops humilis* (compared with adjacent open spaces) on seed survival in our target woody plant species (Table 1), we offered seeds beneath *Chamaerops humilis* and in adjacent open spaces at both study sites in October 2018 and 2019. To capture spatial variation in abiotic conditions, we delimited 15 blocks (adjacent blocks were ~20 m apart) in each study site. Each block included one *Chamaerops humilis* individual and one adjacent open space (~5 m apart). We selected these microhabitats because together they include 63.1% ($N = 2426$) of seedlings, saplings, and adults of all the woody species in the study sites (Garrote et al., 2019a). For each block, we placed six Petri dishes (one per studied woody species) with 10 fresh seeds (i.e., collected that year) per dish

TABLE 1 Woody plant species used during field experiments

Woody plant species	Family	Fruit	Seed dry mass (g)	Seed disperser	Positive spatial association with *Chamaerops humilis*[d]
Asparagus aphyllus	Asparagaceae	Black berry	0.019[a]	Birds	Yes (Matasgordas) / Yes (Reserva)
Daphne gnidium	Thymelaeaceae	Orange drupe	0.008[a]	Birds	Yes/No
Olea europaea var. *sylvestris*	Oleaceae	Black drupe	0.221[b]	Birds	Yes/No
Phillyrea angustifolia	Oleaceae	Blue drupe	0.029[a]	Birds	No/No
Pistacia lentiscus	Anacardiaceae	Black drupe	0.025[a]	Birds	Yes/No
Pyrus bourgaeana	Rosaceae	Green pome	0.087[c]	Mammals	Yes/No
Rubus ulmifolius	Rosaceae	Black polydrupe	0.002[a]	Birds	No/No

[a] Data from Jordano (1995).

[b] Data from Perea et al. (2013).

[c] Data from Garrote et al. (2019b).

[d] Data from Garrote et al. (2019a). These spatial associations were detected using Spatial Point Pattern Analysis techniques.

in each microhabitat (i.e., beneath *Chamaerops humilis* and in open space; Appendix S1, Figure S1). Because of the limited abundance of *Phillyrea angustifolia* at Matasgordas and *Pistacia lentiscus* at Reserva, we offered seeds from *Phillyrea angustifolia* and *Pistacia lentiscus* only at Reserva and Matasgordas, respectively. In total, we offered 7,200 seeds (Appendix S1). Each year, we recorded the number of remaining seeds early in the morning during four consecutive (non-rainy) days (see Appendix S1 for additional details). Based on observations of hulls from predated seeds, rodent droppings, and the absence of elaiosomes in the offered seeds, we assumed that seed removal was equivalent to seed predation (Suárez-Esteban et al., 2018; but see Vander Wall et al., 2005).

2.3 | Seedling emergence and survival experiment

To assess the effect of *Chamaerops humilis* (compared with adjacent open spaces) on seedling emergence and survival of our target woody species, we conducted a sowing experiment using the same 15 experimental blocks. In November 2018, seeds were shallowly (~5 mm depth) covered using in situ sandy substrate. Before the start of the experiment, we carefully checked the sand substrate on a flat surface and removed by hand any non-experimental seeds (or fruits) present in the sowing locations. It was not necessary to sieve the sand substrate because seeds from our target woody species were visually detectable given their size (from *Rubus ulmifolius* with ~4–5 mm to *Olea europaea* var. *sylvestris* with ~1 cm). To prevent predation by vertebrates, we covered all sowing locations (beneath *Chamaerops humilis* and in open spaces) with a 1-cm wire mesh cage (28 cm × 18 cm × 13 cm). We monitored the emergence and survival of seedlings in both microhabitats once a month from November 2018 to December 2019. In total, we sowed 3,600 seeds (Appendix S1). We also recorded maximum and minimum daily temperatures from January to December 2019 by setting (~1 cm depth) four Hobo Pendant UA-002-08 data loggers (two beneath *Chamaerops humilis* and two in adjacent open spaces) to verify a milder microenvironment beneath dwarf palms (Figure 1). Further, we measured the temperature beneath every *Chamaerops humilis* individual (n = 30) and in the adjacent open spaces (n = 30) with a 62459 LACOR thermometer during the monthly checks from April to October 2019 (Appendix S1, Figure S2). We recorded the temperature of the upper sandy substrate (2–3 cm depth) for both microhabitats (Appendix S1, Figure S3).

2.4 | Transition probabilities and relative interaction index

We calculated four transition probabilities (TPs) and the cumulative probability of establishment (CPE) for the woody species in both microhabitats and in the two study sites. TPs were calculated as the proportion of individuals completing a life stage with respect to the number of individuals entering that same stage (Fedriani et al., 2012). Specifically, we calculated the following TPs from a dispersed seed: (a) seed survival (surviving seeds/offered seeds), (b) seedling emergence (emerged seedlings/sown seeds), (c) early seedling survival (surviving seedlings before the summer/emerged seedlings), and (d) late seedling survival (surviving seedlings by the end of the study/surviving seedlings before the summer). We then calculated CPE as the product of all stage-specific TPs. We also calculated accumulated seedling recruitment after 1 year as surviving seedlings by the end of the study relative to seeds sown.

To evaluate the consistency of the *Chamaerops humilis* effect among woody plant species identity, study sites, life stages, and blocks (i.e., dwarf palm–open space pairing), we estimated the effect on such species using adjacent open spaces as ‘controls’ and calculating the relative interaction index (RII) for each palm–woody plant pair (Armas et al., 2004):

$$\mathrm{RII} = \frac{B_w - B_0}{B_w + B_0}$$

where B_w and B_0 denote the number of individuals (seeds or seedlings) for each woody species beneath *Chamaerops humilis* and in adjacent open spaces (i.e., ‘controls’), respectively (Paterno et al., 2016). RII ranges between −1 (maximum competition) and 1 (maximum facilitation).

2.5 | Statistical analyses

We evaluated the effect of *Chamaerops humilis* (regarding adjacent open spaces) on seed survival and seedling performance (i.e., emergence, early and late survival, and recruitment). We modeled the following response variables: seed survival (surviving seeds by the end of the field experiment/offered seeds), seedling emergence (emerged seedlings/sown seeds), early seedling survival (surviving seedlings before the summer/emerged seedlings), late seedling survival (surviving seedlings by the end of the study/surviving seedlings before the summer), and accumulated seedling recruitment (surviving seedlings at the end of the study/sown seeds). We fitted Generalized Linear Mixed models (GLMM; Zuur et al., 2009) using the R *lme4* package (version 1.1-7; R Core Team, R Foundation for Statistical Computing, Vienna, AT) with a binomial error distribution and logit link function. We included woody species identity, microhabitat, study site, and their second- and third-order interactions as fixed factors for all models. Year, and block nested within study site were included as random factors. We tested whether the variables were significant based on the likelihood ratio test with χ^2 distribution. The number of surviving seedlings was zero for some species; in these cases, we examined differences in seedling performance between microhabitats using chi-squared tests. Finally, we calculated estimated marginal means and standard errors. To compare different levels of any significant factor, we calculated Tukey's-adjusted *p*-values for all pairwise comparisons with the R *emmeans* package (Lenth & Lenth; version 1.7.2; R Core Team, R Foundation for

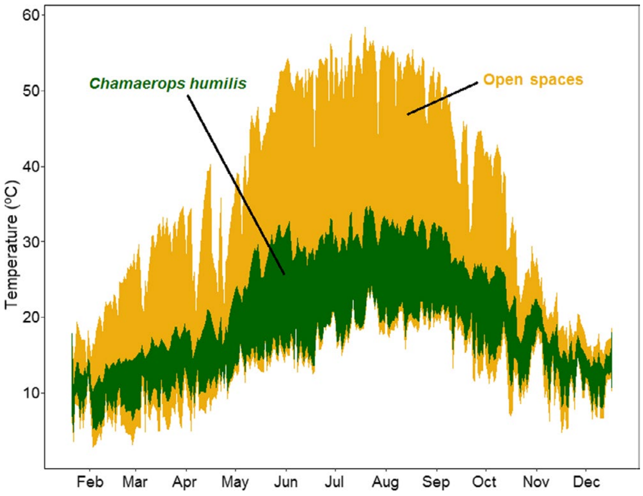

FIGURE 1 Daily range in temperatures of topsoil in Doñana National Park from February to December 2019 beneath *Chamaerops humilis* (green) and in adjacent open spaces (yellow) recorded with four Hobo Pendant UA-002-08 data loggers

Statistical Computing, Vienna, AT). In addition, to estimate the relative importance of woody species identity, microhabitat, study site, and experimental blocks on seed and seedling performance, we estimated the variance partitioning among woody species, among microhabitats, among study sites, and among blocks using the standard analyses of variance components described by Quinn and Keough (2002). To do this, and by contrast with GLMM analyses, we considered all these variables to be random effects, as required for variance partitioning. Finally, to assess whether the potential variation among blocks in seed and seedling performance was mostly related to the variation among *Chamaerops humilis* individuals or to the variation among adjacent open spaces, we calculated the variance for each life stage (i.e., seed survival, seedling emergence, early and late seedling survival, and accumulated seedling recruitment) in both microhabitats. All statistical analyses were conducted using R version 4.0.5. (R Core Team, R Foundation for Statistical Computing, Vienna, AT).

3 | RESULTS

3.1 | Transition probabilities and cumulative probability of establishment

Seed and seedling survival were the stages most critical for the CPE for all woody species, at least by the end of the first year of seedling life. On the one hand, TP to seed survival in open spaces was up to 10.2 times (*Phillyrea angustifolia* in Reserva) greater than beneath *Chamaerops humilis* (Figure 2). On the other hand, early seedling survival beneath *Chamaerops humilis* showed TPs up to 6.1-fold (*Asparagus aphyllus* in Matasgordas) greater than that found in open spaces. This trend was true for all woody species except *Pyrus bourgaeana*, which showed slightly greater probability of seedling survival in open spaces from Reserva (Figure 2). Finally, CPE by the end of the experiment was, on average, 2.5-fold greater beneath *Chamaerops humilis* than in open spaces (Figure 2). For instance, the CPE of *Asparagus aphyllus* in Matasgordas was 5.9 times greater beneath *Chamaerops humilis*. There was also non-negligible inter-block variation; for instance, some *Chamaerops humilis* individuals did not recruit any *Asparagus aphyllus* seedlings, whereas others recruited up to 10 seedlings (100% of sown seeds).

3.2 | Seed survival

Some 4,125 of the 7,200 offered seeds (57.2%) survived to the end of the field experiment. Proportion of seed survival strongly varied among microhabitat ($p < 0.001$), woody species identity ($p < 0.001$), and study site ($p < 0.05$; Table 2). Interestingly, second- and third-order interactions had strong significant effects on seed survival (Table 2). Specifically, microhabitat interacted with woody species identity ($p < 0.001$), the proportion of surviving seeds being between 2.1 (*Daphne gnidium*) and 5.63 times (*Asparagus aphyllus*) greater in open spaces than beneath *Chamaerops humilis* (Appendix S2, Figure S1a). We also found significant differences in seed survival between study sites depending on woody species identity ($p < 0.001$), with *Asparagus aphyllus* and *Pyrus bourgaeana* showing the greatest differences (Appendix S2, Figure S1b). Differences in seed survival between both microhabitats varied strongly between study sites ($p < 0.001$), the proportion of surviving seeds in open spaces for *Chamaerops humilis* being almost five times greater in Reserva than in Matasgordas (Appendix S2, Figure S1c). Taken together, among-block and among-microhabitat variance explained most of the total variance in seed survival (35.1% and 36.3%, respectively; Figure 3). The strong variation in seed survival among blocks was due to variance among both open spaces ($\sigma = 14.9$) and dwarf palms ($\sigma = 12.7$).

3.3 | Seedling emergence

We counted 1,031 emerged seedlings from the 3,600 sown seeds (28.6%). Woody species had a strong significant effect on seedling emergence ($p < 0.0001$; Table 2). Microhabitat as a main factor did not have any effect on seedling emergence ($p = 0.23$), but significantly interacted with woody species identity ($p < 0.001$; Table 2). This interaction indicates that although for most species there were no differences in emergence between microhabitats, emergence of *Olea europaea* var. *sylvestris* was 3.7 times greater beneath *Chamaerops humilis* than in open spaces, and emergence of *Daphne gnidium* was 1.2 times greater in open spaces than beneath *Chamaerops humilis* (Appendix S2, Figure S2a). Microhabitat also interacted with study site ($p < 0.05$), seedling emergence in Matasgordas being 1.2-fold greater beneath *Chamaerops humilis* than in open spaces, whereas in Reserva there were no differences between microhabitats (Appendix S2, Figure S2b). Woody species identity ($p < 0.001$) and study site ($p < 0.05$) had significant effects on seedling emergence, both separately and when interacting ($p < 0.001$; Table 2). For example,

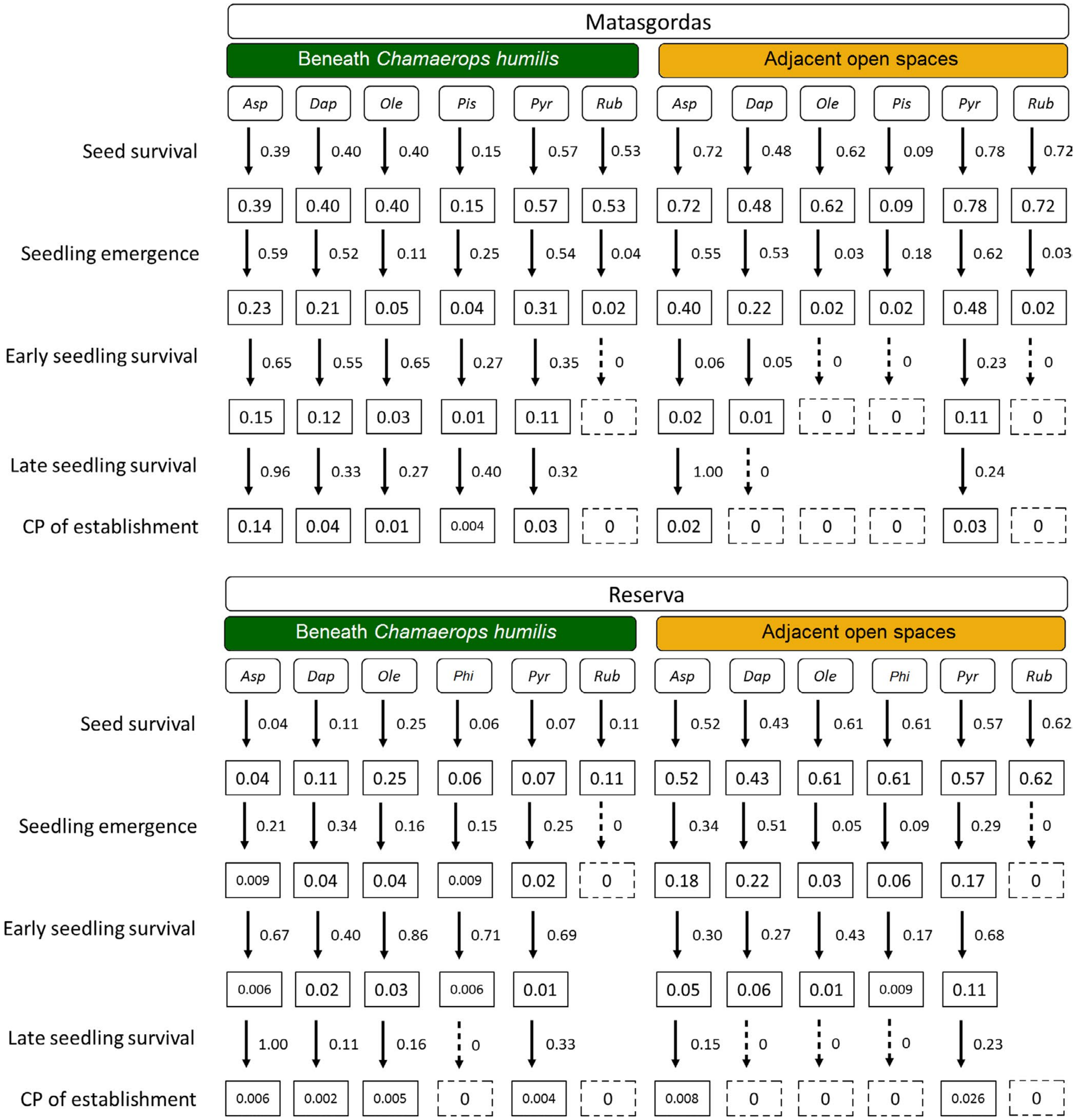

FIGURE 2 Diagram of the propagule fate of woody species showing the proportion of seeds and seedlings moving from one life stage to the next (i.e., transition probabilities; values next to the arrows) and the proportion of the initial propagules still alive at each life stage (values inside the boxes). Overall cumulative probability (CP) of establishment for each treatment combination (i.e., study site and microhabitat) is also shown. Dashed arrows and boxes indicate zero propagules

seedling emergence of *Asparagus aphyllus* and *Pyrus bourgaeana* in Matasgordas was double that found in Reserva (Appendix S2, Figure S2c). Although 70% of the total variance was explained by variations among woody species, 17.6% and 12.15% was due to among-study site and among-block variation, respectively (Figure 3). Variance in seedling emergence among *Chamaerops humilis* individuals ($\sigma = 7.7$) was similar to that among adjacent open spaces ($\sigma = 6.8$).

3.4 | Early seedling survival

Only 413 of 1,031 emerged seedlings (40.1%) survived before the summer (until May 2019). The proportion of surviving seedlings before the summer varied significantly among microhabitats ($p < 0.001$), woody species identity ($p < 0.001$), and study sites ($p < 0.001$; Table 2). Second-order interactions between these factors had strong

TABLE 2 Likelihood ratio tests for Generalized Linear Mixed Models testing the effects of microhabitat, woody species and study sites, and their second- and third-order interactions on seed survival, seedling emergence and survival, as well as on overall seedling recruitment after 1 year of monitoring

	Seed survival			Seedling emergence			Early seedling survival			Late seedling survival			Seedling recruitment		
	df	χ^2	*p*-value	*df*	χ^2	*p*-value	*df*	χ^2	*p*-value	*df*	χ^2	*p*-value	*df*	χ^2	*p*-value
Microhabitat (MH)	1	772.3	**<0.001**	1	1.5	0.23	1	158.9	**<0.001**	1	9.5	**<0.01**	1	81.5	**<0.001**
Woody species (WS)	4	117.9	**<0.001**	3	305.5	**<0.001**	3	74.4	**<0.001**	2	55.5	**<0.001**	2	53.2	**<0.001**
Study site (SS)	1	4.9	**<0.05**	1	6.3	**<0.05**	1	46.9	**<0.001**	–	–	–[a]	–	–	–[a]
MH × WS	4	66.7	**<0.001**	3	25.3	**<0.001**	3	39.3	**<0.001**	1	8.9	**<0.01**	1	13.9	**<0.001**
SS × WS	4	101.2	**<0.001**	3	42.4	**<0.001**	3	11.8	**<0.01**	–	–	–[a]	–	–	–[a]
MH × SS	1	131.0	**<0.001**	1	4.6	**<0.05**	1	19.2	**<0.001**	–	–	–[a]	–	–	–[a]
MH × WS × SS	4	16.4	**<0.01**	–	–	–[a]	–	–	–[a]	–	–	–[a]	–	–	–[a]

Significant results ($p < 0.05$) are shown in bold.

[a] Models with these variables did not converge.

significant effects on seedling survival (Table 2). The interaction between microhabitat and woody species identity influenced seedling survival in different ways ($p < 0.001$). For instance, for *Olea europaea* var. *sylvestris* the proportion of surviving seedlings was 9.6-fold greater beneath *Chamaerops humilis* than in open spaces, whereas for *Pyrus bourgaeana* there were no differences between microhabitats (Appendix S2, Figure S3a). Similarly, seedling survival of our target woody species significantly varied between study sites ($p < 0.001$), and was always greater in Reserva (between 2.3 and 3.9 times) than in Matasgordas (Appendix S2, Figure S3b). The significant interaction between study site and microhabitat ($p < 0.001$; Table 2) indicated that in Matasgordas the proportion of surviving seedlings beneath *Chamaerops humilis* was 10 times greater than in open spaces, whereas in Reserva this difference was only 1.8 times greater (Appendix S2, Figure S3c). Among-microhabitat variation accounted for 56.5% of the total variance in early seedling survival; the remaining 43.5% was explained in similar proportions by the variation among blocks, study sites, and woody species (Figure 3). The variance in seedling recruitment before the summer was 2.3 times greater among *Chamaerops humilis* individuals ($\sigma = 4.5$) than among adjacent open spaces ($\sigma = 1.9$).

3.5 | Late seedling survival

Only 164 of the 413 seedlings surviving before the summer (40.0%) survived to the end of the experiment. Microhabitat significantly affected late seedling survival ($p < 0.01$; Table 2), the overall proportion of surviving seedlings being 799.4 times greater beneath *Chamaerops humilis* than in open spaces. Woody species identity also had a significant effect on late seedling survival ($p < 0.001$). The interaction between microhabitats and woody species identity was significant ($p < 0.01$), indicating that for some species (*Asparagus aphyllus*, *Daphne gnidium* and *Pistacia lentiscus*) late survival was up to 3.8 times greater beneath *Chamaerops humilis*, whereas for others (*Olea europaea* var. *sylvestris* and *Pyrus bourgaeana*) there were no differences between microhabitats (Appendix S2, Figure S4a). Among-woody species and among-block variation accounts for up to 48.1% and 37.0% of the total variance, respectively (Figure 3). We found that variance in seedling survival by the end of the experiment was 6.6 times greater among *Chamaerops humilis* individuals ($\sigma = 2.6$) than among adjacent open spaces ($\sigma = 0.4$).

3.6 | Accumulated seedling recruitment

Finally, of the 4,200 sown seeds, we counted 164 surviving seedlings (3.9%) by the end of the experiment (i.e., recruits after 1 year). Microhabitat ($p < 0.001$), woody species identity ($p < 0.001$), and their second-order interaction ($p < 0.001$) had significant effects on the proportion of recruited seedlings (Table 2). No species recruited more individuals in open spaces than beneath *Chamaerops humilis*, at least by the end of the first year of seedling life. *Asparagus aphyllus*, *Daphne gnidium*, and *Pistacia lentiscus* showed seedling recruitment

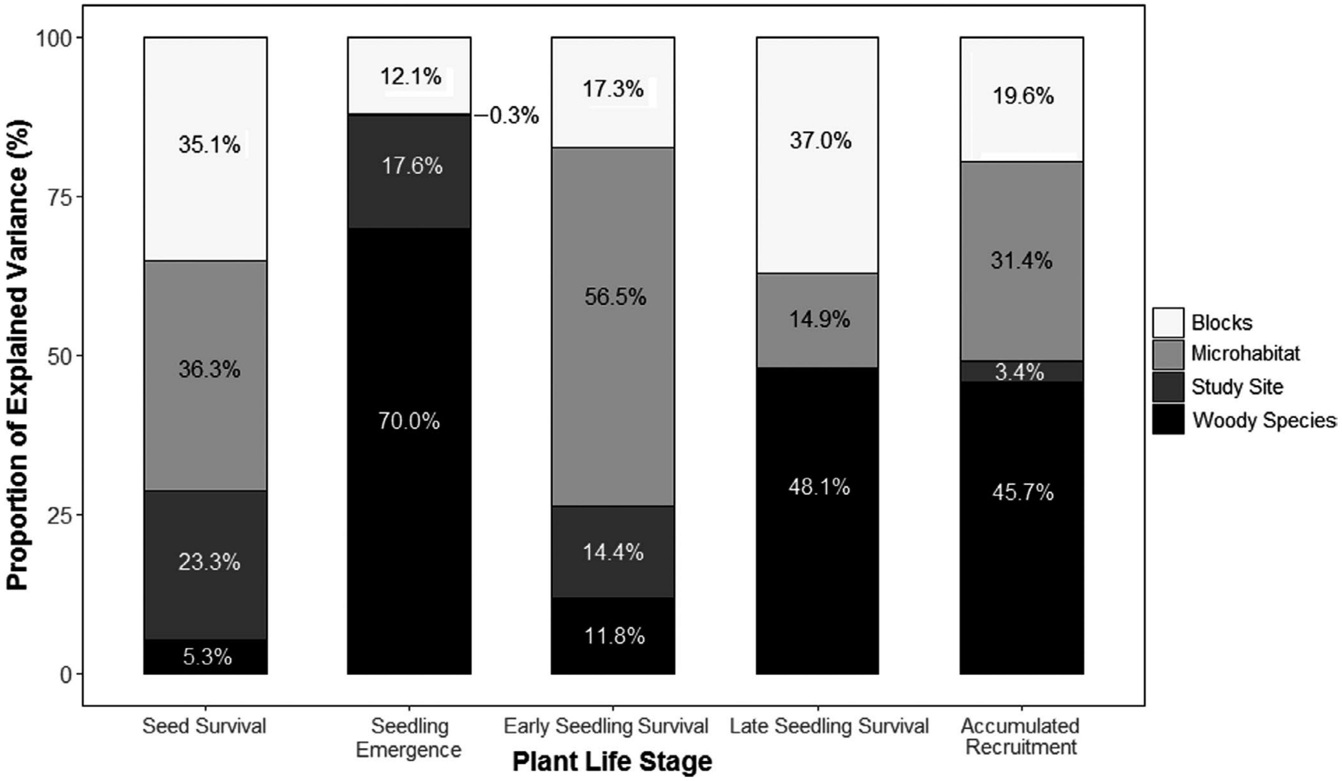

FIGURE 3 Proportion of variance in seed survival, seedling emergence, (early and late) seedling survival as well as accumulated recruitment explained by variation among experimental blocks (i.e., *Chamaerops humilis*–open space pairings), microhabitats, study sites and woody species identity

up to 10.6 times greater beneath *Chamaerops humilis* than in open spaces (Appendix S2, Figure S4b). Other species such as *Olea europaea* var. *sylvestris* and *Pyrus bourgaeana* showed no recruitment differences between the two microhabitats (Appendix S2, Figure S4b). Some 77.1% of the total variance in accumulated seedling recruitment was explained by among-woody species (45.7%) and among-microhabitat (31.4%) variation (Figure 3); 19.6% of the total variance was explained by variation among blocks (Figure 3). Interestingly, variance in accumulated seedling recruitment was 6.7 times greater among *Chamaerops humilis* individuals ($\sigma = 2.9$) than among adjacent open spaces ($\sigma = 0.4$).

3.7 | Relative interaction index

RII varied by life stage and woody species identity, ranging from strongly negative (seed survival) to strongly positive (late seedling survival) (Figure 4). Overall, the accumulated RII was generally neutral to positive after one monitoring year in both sites (Figure 4). Some exceptions with negative accumulated RII were *Asparagus aphyllus* in Reserva and *Pyrus bourgaeana* in both sites. Interestingly, we also found wide ranges in RII depicted by inter-block variation across all life stages (Figure 4). For instance, RII varied between −1 and 0.56 for *Daphne gnidium* seed survival and between −1 and 1 for *Pistacia lentiscus* seedling emergence among blocks. Therefore, depending on the *Chamaerops humilis*–open space pairings, interactions with woody plants shifted along the facilitation–competition continuum as life stages progressed. For example, interactions for seed survival tended to be competitive (i.e., RII negative), whereas for seedling emergence and survival, interactions were generally positive (i.e., RII positive) (Figure 4). Finally, we found neutral interactions during the late life stages (late seedling survival and accumulated recruitment), which were probably due to the progressive decrease in the numbers of surviving seedlings.

4 | DISCUSSION

Using field experiments, we showed that the sign and strength of the *Chamaerops humilis* effect on seven woody plants was rather species-specific and varied strongly across woody plant life stages, as well as between study sites. The fact that woody species explained half or more of the variance in seedling emergence, late seedling survival, and accumulated recruitment strongly suggests a unique relationship for each species. Moreover, substantial variation in the sign of the studied plant–plant interactions among *Chamaerops humilis* individuals depicts a shift from competition to facilitation along the continuum as life stages progress (Gómez et al., 2019; Jácome-Flores et al., 2020; Perea et al., 2013). These shifts along the continuum should be accounted for in revegetation projects.

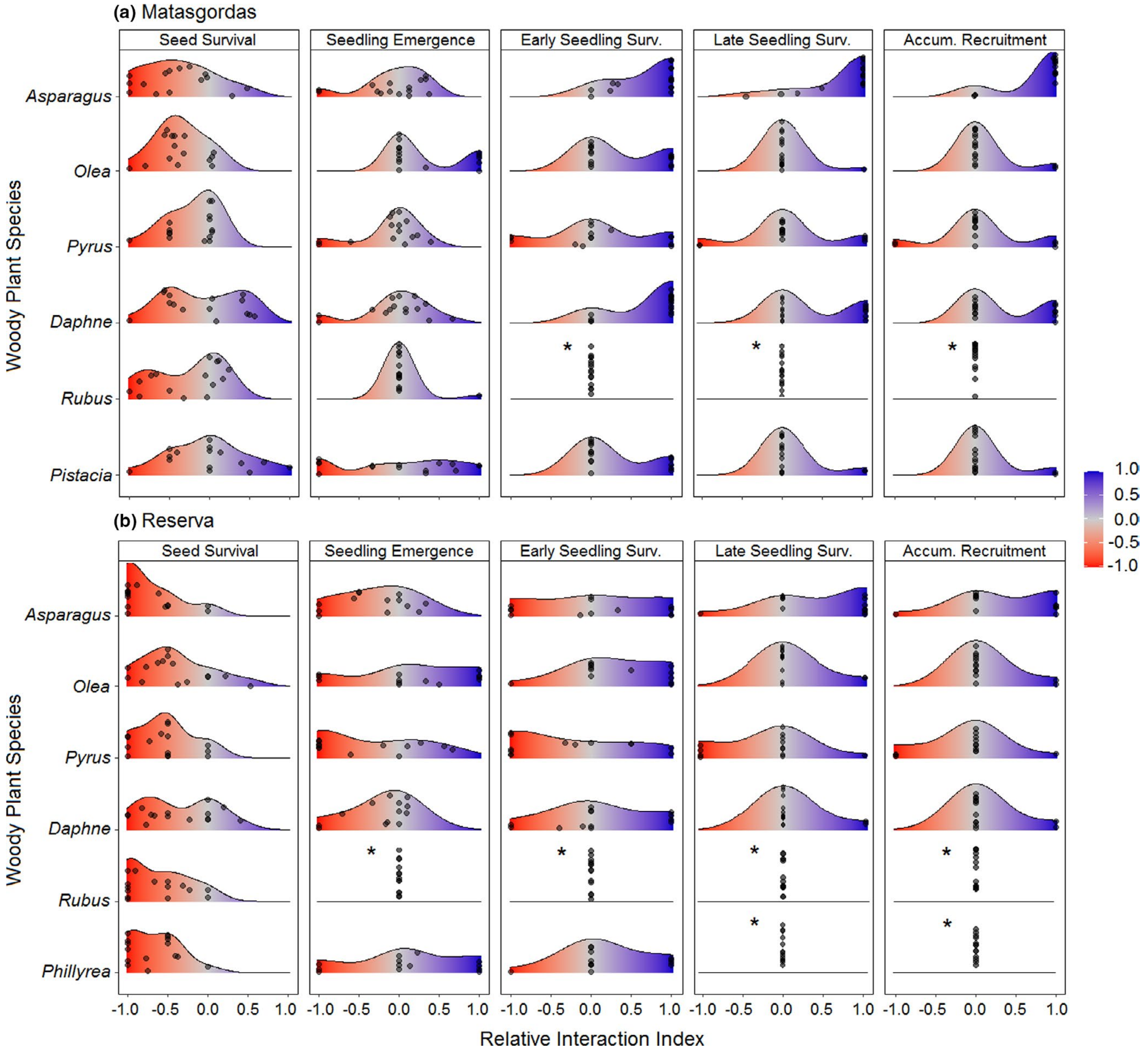

FIGURE 4 Relative interaction index between *Chamaerops humilis* and target woody plant species in Matasgordas (a) and Reserva (b) throughout the studied early life stages. Density function represents the facilitation–competition continuum from −1 (maximum competition in red) to 1 (maximum facilitation in blue). *Chamaerops humilis*–adjacent open spaces pairings (points) interacting with woody species are placed along the continuum depending on the effect sign. Points location yield peaks in the density functions. Asterisks mark life stages with no surviving seedlings and therefore without density functions

4.1 | Seed–seedling conflicts

Microhabitat suitability is crucial for plant recruitment in arid and semi-arid landscapes, but is strongly context-dependent (Pérez-Ramos et al., 2012). We found seed–seedling conflicts (Drezner, 2015; Schupp, 1995) beneath *Chamaerops humilis* for seven Mediterranean woody plant species. The higher seed survival seen in adjacent open spaces compared with beneath *Chamaerops humilis* was primarily due to rodents, which usually predate seeds beneath shrubs (Fedriani et al., 2020; Suárez-Esteban et al., 2018). The thorny and shading microhabitat beneath *Chamaerops humilis* represents a safe site for rodents by sheltering them from predators (Brown & Kotler, 2004; but see Ziffer-Berger et al., 2017).

Conversely, the effect of *Chamaerops humilis* on seedling survival depended on the life stage and identity of the woody species. The strength of the facilitative effect of *Chamaerops humilis* on seedling survival was greater before the summer (until May) than by the end of the experiment (until December). This facilitative effect was probably related to the strong alleviation of thermic stress (Caldeira et al., 2014) and consequently, direct or indirect prevention of increased evaporative demand and reduced soil moisture through higher temperatures. For instance, Rey et al. (2004) found that the major cause of mortality in *Olea europaea* var. *sylvestris* seedlings was water stress. Interestingly, we expect a greater positive effect of *Chamaerops humilis* on seedling survival during the summer because it can strongly alleviate severe temperatures. However, our results suggest that summer remains a significant bottleneck for plant recruitment in Mediterranean areas even after accounting for the facilitative effects of nurse species. In fact, despite the limitations of 1-year studies of plant recruitment, especially in dryland regions, our study period was relatively dry with respect to historical local precipitation. Alternatively, and especially in the Reserva site, the amelioration of environmental conditions by *Chamaerops humilis* might not be enough to satisfy the water requirements of woody seedlings during stressful periods (e.g., two consecutive high summer droughts; Torroba-Balmori et al., 2015). From our findings, we encourage restoration practitioners to conduct sowing field experiments to evaluate whether the outcome of these plant–plant interactions is consistently positive throughout early life stages. Finally, we did not investigate the facilitative role of *Chamaerops humilis* in protecting seedlings from vertebrate herbivores (e.g., ungulates and rabbits). Nonetheless, it is well-known that shrubs act as a mechanical barrier against ungulates, which decreases browsing and rooting damage in seedlings (Alday et al., 2016; Perea & Gil, 2014; Torroba-Balmori et al., 2015).

4.2 | Changing plant–plant interactions

Plant–plant interactions may shift from facilitation to competition (and vice versa) depending on the ecological context (see recent reviews Lortie et al., 2021; Soliveres et al., 2015 and references therein). Here, we found variation in *Chamaerops humilis*–woody species interactions at three levels: plant community, study site, and inter-block. Overall, *Asparagus aphyllus*, *Daphne gnidium* and *Pistacia lentiscus* recruited significantly more seedlings beneath *Chamaerops humilis*, whereas for the remaining species, seedling recruitment after 1 year was low or nonexistent. Nonetheless, we frequently observed juvenile and adult individuals (i.e., different plant cohorts accumulated throughout time) of these three woody species within or spatially associated with *Chamaerops humilis* (Garrote et al., 2019a). Our experimental results demonstrate, for the first time, that such spatial associations are due, at least in part, to *Chamaerops humilis*'s facilitation of such later-successional plant species. In addition, we observed that several frugivorous bird species tend to defecate seeds of these woody species while perching on *Chamaerops humilis* (González et al., unpublished), which may trigger nucleation (Holl et al., 2020; Pausas et al., 2006). To thoroughly assess how plant–plant interactions vary at the plant community level, evaluation of several species (both nurses and beneficiaries) is mandatory (Castro et al., 2004). In this sense, we evaluated the effect of one nurse species (i.e., *Chamaerops humilis*) and additional field experiments using other potential nurse shrub species present in the study areas (e.g., *Halimium halimifolium* and *Stauracanthus genistoides*) will probably confirm the changing nature of these plant–plant interactions.

Accounting for context-dependency among sites of nurse–beneficiary plant interactions is also crucial to guide successful revegetation (Soliveres et al., 2015; Suding et al., 2015). In particular, the nursing effect of *Chamaerops humilis* had a stronger positive impact on seedlings of woody species in Matasgordas than in Reserva, which probably relates to a deficit of two major resources. First, the soil nutrient content (organic matter, phosphorus and nitrogen) for the two microhabitats (open spaces and beneath shrubs) was on average double in Reserva compared with in Matasgordas (Appendix S1). Second, the availability of groundwater was more superficial in Reserva (2.39 m) than in Matasgordas (4.56 m). Thus, although seedlings cannot develop roots to reach these depths in 1 year, seedlings growing in Reserva probably had greater water availability because of greater moisture in the topsoil compared with seedlings growing in Matasgordas. For example, Armolaitis et al. (2013) showed how a relatively higher groundwater level in Scots pine plantations favored most soil moisture conditions. However, accumulated seedling recruitment was unexpectedly greater (especially beneath dwarf palm) in Matasgordas relative to Reserva, which is surprising given the lower nutrient and water availability in the former. Disentangling additional biotic and abiotic factors leading to these among-sites differences requires further experimental studies. In addition, differences in the time since cessation of human activities between the sites (Reserva in 1964 and Matasgordas in 1996) could have led to differences in the current stage of ecological succession. Because human activities in Matasgordas ended more recently, succession is in the initial phases when a nursing effect of pioneer species on woody late-successional plants is more frequent (Callaway, 2007).

Interestingly, we found strong variation in RII among experimental blocks, i.e., among *Chamaerops humilis*–open space pairings (Anthelme et al., 2017; Violle et al., 2012). This noticeable variation seems to be related more to the much higher variance in accumulated seedling recruitment beneath *Chamaerops humilis* compared with adjacent open spaces. *Chamaerops humilis* not only exerts strong temperature amelioration (Figure 1), but also has other important facilitative effects such as protection against vertebrate herbivores (e.g., ungulates, lagomorphs; Alday et al., 2016; Perea & Gil, 2014) and nutrient enrichment (e.g., through leaves, fruits, seeds, and invertebrate decomposition; Rodríguez-Echeverría & Pérez-Fernández, 2003). Although we did not detect any significant relationship between *Chamaerops humilis* size and seedling performance (Garrote et al., unpublished), there was a positive relationship between *Chamaerops humilis* size and its association with the adult plants of several woody species (e.g., *Asparagus aphyllus* or *Olea europaea* var. *sylvestris*; Appendix S2; see also Alday et al., 2014). However, caution is advised, simply because in principle, the greater the *Chamaerops humilis* size, the greater the probability of woody species being present beneath it. Nevertheless, these positive relationships were not linear and showed a size threshold after which the probability of a woody species being present beneath *Chamaerops humilis* does not increase further. Taking into account these findings, the detected strong variation in seedling recruitment among *Chamaerops humilis* individuals supports that *Chamaerops* *humilis*–woody species interactions shift along a facilitation–competition continuum (Bronstein, 2015).

4.3 | Management implications

We highlight the importance for restoration practitioners of considering the possibility that the outcome of plant–plant interactions may shift in sign and strength along a facilitation–competition continuum that is shaped by variation among individual plants. Indeed, our results exemplify a case in which it cannot be assumed that nurse plants always exert positive effects on beneficiary plants. For this reason, in large-scale restoration activities where high investment costs are budgeted, it might be more efficient to carry out small-scale field experiments to identify the species, restoration treatments, and environmental conditions under which facilitative effects among target plants are most likely (Havrilla et al., 2020; Ibáñez & Rodríguez, 2020). Furthermore, identifying which nurse plant phenotypes (e.g., size, shape) provide better results in putative beneficiary species (Violle et al., 2012) might also be an important task in large-scale restoration programs. For instance, in their seminal study, Pugnaire et al. (1996) found that the effects of nurse plant size on multiple variables, such as beneficiary species diversity or soil composition, were always positive (see also Losapio et al., 2018). Thus, adequate selection of plant species phenotype may increase revegetation success.

We also revealed that the effect of *Chamaerops humilis* on the performance of woody species varied along the continuum depending on the plant's life stage. In particular, seed survival and seedling emergence showed the greatest shifts along the continuum due to strong variation among blocks. Therefore, it would be highly recommendable to focus on these life stages during the selection of more positive nurse phenotypes and microhabitats. For instance, when managers use direct seeding beneath nurse plants (Palma & Laurance, 2015), sowings should be protected (e.g., with wire mesh cages) to prevent seed predation by vertebrates (e.g., rodents; Díaz-Hernández et al., 2021; Torroba-Balmori et al., 2015). Also, when the nurse–beneficiary plant association is positive, it may be worthwhile to use seedlings from greenhouses, which may be directly transplanted under nurse plants to avoid the cost of increased seed predation.

Considering the strong variation in seedling establishment observed among target woody species, we suggest careful selection of plant species (both nurse and beneficiary) during the decision-making stage in restoration projects. For example, Navarro-Cano et al. (2019) suggested trait-based species selection because the greater the functional distance between nurse and beneficiaries, the greater the success of seedling establishment (see also Ladouceur et al., 2021; Verdú et al., 2012). Given that facilitative effects can be coupled with disproportionate seed arrival due to activity by frugivorous birds (i.e., perching effect; *sensu* Debussche et al., 1982) around and beneath nurse plants, restoration practitioners should account for the potential generation of nucleation processes (Holl et al., 2020; Pausas et al., 2006), which are key to the restoration of heavily degraded landscapes worldwide. Thus, they could design interconnected local networks of isolated nucleation patches choosing particular nurse–beneficiary species associations depending, for instance, on which frugivorous species are present in the target area.

Finally, we strongly emphasize the importance of accounting for changing interactions between nurse and presumed beneficiary plants in revegetation projects, given that the outcome of such interactions can shift along a facilitation–competition continuum and thus alter restoration success. Our recommendations could be relevant for many other potential nurse plant species present in multiple landscapes such as, for example, *Myrcianthes coquimbensis* in the hyper-arid Atacama Desert of Chile (Loayza et al., 2017), *Larrea tridentata* in the Mojave Desert of California (Mahall et al., 2018) or *Azorella compacta* in the dry, alpine tropics of Bolivia (Anthelme et al., 2017). Indeed, we expect that our results will lead to similar studies involving other plant–plant interactions in degraded habitats worldwide. Thus, these research efforts will allow identification of how these changing interactions might influence the outcome of revegetation projects (Hobbs et al., 2014), especially in the ongoing Decade on Ecosystem Restoration 2021–2030 (Aronson et al., 2020; UN, 2019).

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AUTHOR CONTRIBUTIONS

PJG, ARC and JMF conceived and designed the research and undertook the field work. PJG analyzed the data. PJG and JMF led the writing of the manuscript. All authors contributed critically to the final draft and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are provided in Appendices S3, S4, S5 and S6.

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REFERENCES

Alday, J.G., Santana, V.M., Marrs, R.H. & Martínez-Ruiz, C. (2014) Shrub-induced understory vegetation changes in reclaimed mine sites. *Ecological Engineering*, 73, 691–698.

Alday, J.G., Zaldívar, P., Torroba-Balmori, P., Fernández-Santos, B. & Martínez-Ruiz, C. (2016) Natural forest expansion on reclaimed coal mines in Northern Spain: the role of native shrubs as suitable microsites. *Environmental Science and Pollution Research*, 23, 13606–13616.

Anthelme, F., Meneses, R.I., Valero, N.N.H., Pozo, P. & Dangles, O. (2017) Fine nurse variations explain discrepancies in the stress-interaction relationship in alpine regions. *Oikos*, 126, 1173–1183.

Armas, C., Ordiales, R. & Pugnaire, F.I. (2004) Measuring plant interactions: a new comparative index. *Ecology*, 85, 2682–2686.

Armolaitis, K., Varnagirytė-Kabašinskienė, I., Stupak, I., Kukkola, M., Mikšys, V. & Wójcik, J. (2013) Carbon and nutrients of Scots pine stands on sandy soils in Lithuania in relation to bioenergy sustainability. *Biomass and Bioenergy*, 54, 250–259.

Aronson, J., Goodwin, N., Orlando, L., Eisenberg, C. & Cross, A.T. (2020) A world of possibilities: six restoration strategies to support the United Nation's Decade on Ecosystem Restoration. *Restoration Ecology*, 28, 730–736.

Bronstein, J.L. (2001) The costs of mutualism. *American Zoologist*, 41, 825–839.

Bronstein, J.L. (Ed.) (2015) *Mutualism*. USA: Oxford University Press.

Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G. et al. (2008) Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology*, 96, 18–34.

Brown, J.S. & Kotler, B.P. (2004) Hazardous duty pay and the foraging cost of predation. *Ecology Letters*, 7, 999–1014.

Bruno, J.F., Rand, T.A., Emery, N.C. & Bertness, M.D. (2017) Facilitative and competitive interaction components among New England salt marsh plants. *PeerJ*, 5, e4049.

Caldeira, M.C., Ibáñez, I., Nogueira, C., Bugalho, M.N., Lecomte, X., Moreira, A. et al. (2014) Direct and indirect effects of tree canopy facilitation in the recruitment of Mediterranean oaks. *Journal of Applied Ecology*, 51, 349–358.

Callaway, R.M. (Ed.) (2007) *Positive interactions and interdependence in plant communities*. Dordrecht: Springer Science and Business Media.

Castanho, C.T., Oliveira, A.A. & Prado, P.I. (2015) Does extreme environmental severity promote plant facilitation? An experimental field test in a subtropical coastal dune. *Oecologia*, 178, 855–866.

Castro, J., Morales-Rueda, F., Navarro, F.B., Löf, M., Vacchiano, G. & Alcaraz-Segura, D. (2021) Precision restoration: a necessary approach to foster forest recovery in the 21st century. *Restoration Ecology*, 29(7), e13421.

Castro, J., Zamora, R., Hódar, J.A., Gómez, J.M. & Gómez-Aparicio, L. (2004) Benefits of using shrubs as nurse plants for reforestation in Mediterranean mountains: a 4-year study. *Restoration Ecology*, 12, 352–358.

Chaieb, G., Abdelly, C. & Michalet, R. (2021) A regional assessment of changes in plant-plant interactions along topography gradients in Tunisian Sebkhas. *Ecosystems*, 24, 1024–1037.

CHG (Confederación Hidrográfica del Guadalquivir) (2019) *Informe de estado de los acuíferos del entorno de Doñana*.

Costa, A., Villa, S., Alonso, P., García-Rodríguez, J.A., Martín, F.J., Martínez-Ruiz, C. et al. (2017) Can native shrubs facilitate the early establishment of contrasted co-occurring oaks in Mediterranean grazed areas? *Journal of Vegetation Science*, 28, 1047–1056.

Debussche, M., Escarré, J. & Lepart, J. (1982) Ornitochory and plant succession in Mediterranean orchards. *Vegetatio*, 48, 255–266.

Díaz-Hernández, R., Vicente Villardón, J.L., Martínez-Ruiz, C. & Fernández-Santos, B. (2021) The effects of native shrub, fencing, and acorn size on the emergence of contrasting co-occurring oak in mediterranean grazed areas. *Forests*, 12, 307.

Drezner, T.D. (2015) Regional environmental conditions affect microsite response in a keystone desert species. *Journal of Arid Environments*, 116, 89–95.

Fedriani, J.M., Calvo, G., Delibes, M., Ayllón, D. & Garrote, P.J. (2020) The overlooked benefits of synzoochory: rodents rescue seeds from aborted fruits. *Ecosphere*, 11, e03298.

Fedriani, J.M. & Delibes, M. (2011) Dangerous liaisons disperse the Mediterranean dwarf palm: fleshy-pulp defensive role against seed predators. *Ecology*, 92, 304–315.

Fedriani, J.M., Garrote, P.J., Calvo, G., Delibes, M., Castilla, A.R. & Żywiec, M. (2019) Combined effects of seed provenance, plant facilitation and restoration site on revegetation success. *Journal of Applied Ecology*, 56, 996–1006.

Fedriani, J.M., Żywiec, M. & Delibes, M. (2012) Thieves or mutualists? Pulp feeders enhance endozoochore local recruitment. *Ecology*, 93, 575–587.

Filazzola, A. & Lortie, C.J. (2014) A systematic review and conceptual framework for the mechanistic pathways of nurse plants. *Global Ecology and Biogeography*, 23, 1335–1345.

Fujita, T. & Yamashina, C. (2018) Do consumer-mediated negative effects on plant establishment outweigh the positive effects of a nurse plant? *Ecology and Evolution*, 8, 3702–3710.

Garrote, P.J., Calvo, G., Żywiec, M., Delibes, M., Suárez-Esteban, A., Castilla, A.R. et al. (2019b) Extrinsic factors rather than seed traits mediate strong spatial variation in seed predation. *Perspectives in Plant Ecology, Evolution and Systematics*, 38, 39–47.

Garrote, P.J., Castilla, A.R. & Fedriani, J.M. (2019a) The endemic Mediterranean dwarf palm boosts the recolonization of old-fields: implications for restoration. *Journal of Environmental Management*, 250, 109478.

Garrote, P.J., Castilla, A.R. & Fedriani, J.M. (2021) Assessing the relative importance of nurse species on Mediterranean human-altered areas. *Restoration Ecology*, 29(4), e13402.

Gómez, J.M., Schupp, E.W. & Jordano, P. (2019) Synzoochory: the ecological and evolutionary relevance of a dual interaction. *Biological Reviews*, 94, 874–902.

Gómez-Aparicio, L., Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J. & Baraza, E. (2004) Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. *Ecological Applications*, 14, 1128–1138.

Havrilla, C.A., Munson, S.M., McCormick, M.L., Laushman, K.M., Balazs, K.R. & Butterfield, B.J. (2020) RestoreNet: an emerging restoration network reveals controls on seeding success across dryland ecosystems. *Journal of Applied Ecology*, 57, 2191–2202.

Hobbs, R.J., Higgs, E., Hall, C.M., Bridgewater, P., Chapin, F.S. III, Ellis, E.C. et al.(2014) Managing the whole landscape: historical, hybrid, and novel ecosystems. *Frontiers in Ecology and the Environment*, 12, 557–564.

Holl, K.D., Reid, J.L., Cole, R.J., Oviedo-Brenes, F., Rosales, J.A. & Zahawi, R.A. (2020) Applied nucleation facilitates tropical forest recovery: Lessons learned from a 15-year study. *Journal of Applied Ecology*, 57, 2316–2328.

Holland, J.N. & Molina-Freaner, F. (2013) Hierarchical effects of rainfall, nurse plants, granivory and seed banks on cactus recruitment. *Journal of Vegetation Science*, 24, 1053–1061.

Ibáñez, I. & Rodríguez, A. (2020) Understanding neighborhood effects to increase restoration success of woody plant communities. *Ecological Applications*, 30, e02098.

Jácome-Flores, M.E., Jordano, P., Delibes, M. & Fedriani, J.M. (2020) Interaction motifs variability in a Mediterranean palm under environmental disturbances: the mutualism–antagonism continuum. *Oikos*, 129, 367–379.

Jankju, M. (2013) Role of nurse shrubs in restoration of an arid rangeland: effects of microclimate on grass establishment. *Journal of Arid Environments*, 89, 103–109.

Jones, H.P., Jones, P.C., Barbier, E.B., Blackburn, R.C., Rey-Benayas, J.M., Holl, K.D. (2019). We agree with Larkin et al. 2019: restoration is context specific. *Proceedings of the Royal Society B*, 286, 20191179.

Jordano, P. (1995) Angiosperm fleshy fruits and seed dispersers: a comparative analysis of adaptation and constraints in plant-animal interactions. *The American Naturalist*, 145, 163–191.

Ladouceur, E., McGowan, J., Huber, P., Possingham, H., Scridel, D., van Klink, R. et al. (2021) An objective-based prioritization approach to support trophic complexity through ecological restoration species mixes. *Journal of Applied Ecology*, 59, 394–407.

Larkin, D.J., Buck, R.J., Fieberg, J. & Galatowitsch, S.M. (2019). Revisiting the benefits of active approaches for restoring damaged ecosystems. A Comment on Jones HP et al. 2018 Restoration and repair of Earth's damaged ecosystems. *Proceedings of the Royal Society B*, 286, 20182928.

Loayza, A.P., Herrera-Madariaga, M.A., Carvajal, D.E., García-Guzmán, P. & Squeo, F.A. (2017) Conspecific plants are better 'nurses' than rocks: consistent results revealing intraspecific facilitation as a process that promotes establishment in a hyper-arid environment. *AoB Plants*, 9, plx056.

Lortie, C.J., Zuliani, M., Ghazian, N., Haas, S., Braun, J., Owen, M. et al. (2021) Too much of a good thing: shrub benefactors are less important in higher diversity arid ecosystems. *Journal of Ecology*, 109, 2047–2053.

Losapio, G., Pugnaire, F.I., O'Brien, M.J. & Schöb, C. (2018) Plant life history stage and nurse age change the development of ecological networks in an arid ecosystem. *Oikos*, 127, 1390–1397.

Mahall, B.E., Fonteyn, P.J., Callaway, R.M. & Schlesinger, W.H. (2018) A 37-year experimental study of the effects of structural alterations on a shrub community in the Mojave Desert, California. *Journal of Ecology*, 106, 1057–1072.

Michalet, R., Le Bagousse-Pinguet, Y., Maalouf, J.P. & Lortie, C.J. (2014) Two alternatives to the stress-gradient hypothesis at the edge of life: the collapse of facilitation and the switch from facilitation to competition. *Journal of Vegetation Science*, 25, 609–613.

Michalet, R., Xiao, S., Touzard, B., Smith, D.S., Cavieres, L.A., Callaway, R.M. et al. (2011) Phenotypic variation in nurse traits and community feedbacks define an alpine community. *Ecology Letters*, 14, 433–443.

Miranda-Jácome, A. & Flores, J. (2018) Effects of nurse plants and the granivore guild in the associational susceptibility of seeds from the columnar cactus *Pilosocereus leucocephalus*. *Journal of Arid Environments*, 151, 9–14.

Navarro-Cano, J.A., Goberna, M. & Verdú, M. (2019) Using plant functional distances to select species for restoration of mining sites. *Journal of Applied Ecology*, 56, 2353–2362.

Noumi, Z., Chaieb, M., Michalet, R. & Touzard, B. (2015) Limitations to the use of facilitation as a restoration tool in arid grazed savanna: a case study. *Applied Vegetation Science*, 18, 391–401.

Palma, A.C. & Laurance, S.G. (2015) A review of the use of direct seeding and seedling plantings in restoration: what do we know and where should we go? *Applied Vegetation Science*, 18, 561–568.

Paterno, G.B., Siqueira Filho, J.A. & Ganade, G. (2016) Species-specific facilitation, ontogenetic shifts and consequences for plant community succession. *Journal of Vegetation Science*, 27, 606–615.

Pausas, J.G., Bonet, A., Maestre, F.T. & Climent, A. (2006) The role of the perch effect on the nucleation process in Mediterranean semi-arid oldfields. *Acta Oecologica*, 29, 346–352.

Perea, R., Delibes, M., Polko, M., Suárez-Esteban, A. & Fedriani, J.M. (2013) Context-dependent fruit–frugivore interactions: partner identities and spatio-temporal variations. *Oikos*, 122, 943–951.

Perea, R. & Gil, L. (2014) Tree regeneration under high levels of wild ungulates: the use of chemically vs. physically-defended shrubs. *Forest Ecology and Management*, 312, 47–54.

Pérez-Ramos, I.M., Urbieta, I.R., Zavala, M.A. & Marañón, T. (2012) Ontogenetic conflicts and rank reversals in two Mediterranean oak species: implications for coexistence. *Journal of Ecology*, 100, 467–477.

Pugnaire, F. (Ed.) (2010) *Positive plant interactions and community dynamics*. Boca Raton: CRC Press.

Pugnaire, F.I., Haase, P., Puigdefábregas, J., Cueto, M., Clark, S.C. & Incoll, L.D. (1996) Facilitation and succession under the canopy of a leguminous shrub, *Retama sphaerocarpa*, in a semi-arid environment in south-east Spain. *Oikos*, 76(3), 455–464.

Pugnaire, F.I. & Valladares, F. (Eds) (2007) *Functional plant ecology*. Boca Raton: CRC Press.

Quinn, G. & Keough, M. (2002) *Experimental design and data analysis for biologists*. Cambridge: Cambridge University Press.

Rey, P.J. & Alcántara, J.M. (2000) Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. *Journal of Ecology*, 88, 622–633.

Rey, P.J., Alcántara, J.M., Sánchez-Lafuente, F., Garrido, A.M., Ramírez, J.L. & Manzaneda, A.J. (2004) Seedling establishment in Olea europaea: seed size and microhabitat affect growth and survival. *Ecoscience*, 11, 310–320.

Rey-Benayas, J.M., Bullock, J.M. & Newton, A.C. (2008) Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. *Frontiers in Ecology and the Environment*, 6, 329–336.

Rodríguez-Echeverría, S. & Pérez-Fernández, M.A. (2003) Soil fertility and herb facilitation mediated by *Retama sphaerocarpa*. *Journal of Vegetation Science*, 14, 807–814.

Saiz, H. & Alados, C.L. (2012) Changes in semi-arid plant species associations along a livestock grazing gradient. *PLoS One*, 7, e40551.

Schiffers, K. & Tielbörger, K. (2006) Ontogenetic shifts in interactions among annual plants. *Journal of Ecology*, 94, 336–341.

Schöb, C., Armas, C., Guler, M., Prieto, I. & Pugnaire, F.I. (2013) Variability in functional traits mediates plant interactions along stress gradients. *Journal of Ecology*, 101, 753–762.

Schöb, C., Prieto, I., Armas, C. & Pugnaire, F.I. (2014) Consequences of facilitation: one plant's benefit is another plant's cost. *Functional Ecology*, 28, 500–508.

Schupp, E.W. (1995) Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *American Journal of Botany*, 82, 399–409.

Schupp, E.W. (2007). The suitability of a site for seed dispersal is context-dependent. In: Dennis, A.J., Green, R.J., Schupp, E.W. & Westcott, D.A. (Eds.), *Seed dispersal: theory and its application in a changing world*. Wallingford, UK: CABI. pp. 445–463.

Soliveres, S., Smit, C. & Maestre, F.T. (2015) Moving forward on facilitation research: response to changing environments and effects on the diversity, functioning and evolution of plant communities. *Biological Reviews*, 90, 297–313.

Suárez-Esteban, A., Delibes, M. & Fedriani, J.M. (2018) Dangerous life at the edge: Implications of seed predation for roadside revegetation. *Applied Vegetation Science*, 21, 55–63.

Suding, K., Higgs, E., Palmer, M., Callicott, J.B., Anderson, C.B., Baker, M. et al. (2015) Committing to ecological restoration. *Science*, 348, 638–640.

Torroba-Balmori, P., Zaldívar, P., Alday, J.G., Fernández-Santos, B. & Martínez-Ruiz, C. (2015) Recovering Quercus species on reclaimed coal wastes using native shrubs as restoration nurse plants. *Ecological Engineering*, 77, 146–153.

United Nations (2019) *Resolution 73/284: United Nations Decade on Ecosystem Restoration (2021–2030).*

Vander Wall, S.B., Kuhn, K.M. & Beck, M.J. (2005) Seed removal, seed predation, and secondary dispersal. *Ecology*, 86, 801–806.

Verdú, M., Gómez-Aparicio, L. & Valiente-Banuet, A. (2012) Phylogenetic relatedness as a tool in restoration ecology: a meta-analysis. *Proceedings of the Royal Society B: Biological Sciences*, 279, 1761–1767.

Violle, C., Enquist, B.J., McGill, B.J., Jiang, L.I.N., Albert, C.H., Hulshof, C. et al. (2012) The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution*, 27, 244–252.

Ziffer-Berger, J., Weisberg, P.J., Cablk, M.E., Moshe, Y. & Osem, Y. (2017) Shrubs facilitate pine colonization by controlling seed predation in dry Mediterranean dwarf shrublands. *Journal of Arid Environments*, 147, 34–39.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed effects models and extensions in ecology with R* Vol. 574. New York: Springer.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix S1. Additional details of experimental design.
Appendix S2. Results of generalized linear mixed models.
Appendix S3. Data of seed survival and seedling emergence and survival experiments.
Appendix S4. Data of seed survival and seedling emergence and survival experiments.
Appendix S5. R code for seed survival analysis.
Appendix S6. R code for seedling emergence and survival analyses.

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