

1 Running title: Mutual benefits along plants life-span

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3 Benefits for nurse and facilitated plants emerge when interactions are considered  
4 along the entire life-span

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23

24 ABSTRACT

25 The structure of plant communities is often influenced by facilitative interactions  
26 where ‘facilitated’ plants gain a benefit from growing associated with ‘nurse’ plants.  
27 Facilitation has been mostly studied from the facilitated plant’s perspective, and  
28 bidirectional effects between nurse and facilitated plants have received less attention.  
29 We hypothesized that reciprocal benefits in plant-plant interactions may emerge when  
30 interactions are considered along the life-span of the plants involved. Over one spring,  
31 we selected five species with similar life-form and growth strategy, and using a full  
32 factorial design, we compared different fitness components along the plants’ life-span  
33 (seedling establishment, juvenile growth and reproductive investment in adult plants).  
34 We compared: a) plants growing in solitary stands and associated with other plants in  
35 vegetation patches; and b) plants that originally functioned as nurse plant (the largest  
36 plant of the vegetation patch) and as facilitated (not the largest plant of the vegetation  
37 patch). Plants growing in vegetation patches displayed higher seedling establishment  
38 and juvenile growth compared to solitary conspecific plants. At a later developmental  
39 stage, nurse plants in vegetation patches experienced higher reproductive investment  
40 (measured as flower production relative to plant size) compared to solitary plants. In  
41 contrast, the originally facilitated plants showed similar reproductive investment  
42 compared to their solitary pair of similar size. Facilitation might be a complex  
43 interaction in which reciprocal benefits for both facilitated and nurse plants can be  
44 detected when interactions are considered along the plants’ life-span. Our results  
45 suggest that mutual benefits in plant-plant interactions could be important to sustain  
46 diversity in plant communities, but they appeared overlooked and deserve further  
47 attention.

48 Keywords: Facilitative interactions, gypsum, long-term interactions, nurse plants'  
49 benefits, plant community, priority effects

50

51

## 52 INTRODUCTION

53 Community assembly processes strongly influence the relative abundance of species  
54 in communities and the spatial distribution of biodiversity (HilleRisLambers et al.  
55 2012, Mittelbach and Schemske 2015). Plant facilitative interactions occur if at least  
56 one of the interacting species gains some benefit (facilitated) from growing in  
57 association with other (nurse) species, and no harm is caused to either (Callaway  
58 2007). During the period of establishment, plants commonly benefit by growing  
59 associated with a nurse plant, but this positive interaction can shift to competitive  
60 once the facilitated plant reaches maturity (Miriti 2006, Schiffers and Tielbörger  
61 2006, Armas and Pugnaire 2009). A less explored component of facilitation is  
62 whether changes in the shared environment caused by adult facilitated plants benefit  
63 the original nurse plant (i.e. the plant that arrived first to the shared environment). In  
64 stressful environments with limited resources, this could result in positive feedbacks  
65 between plants, although these might be detectable at different developmental or  
66 demographic stages for the nurse and the facilitated plants. Unfortunately, the  
67 dynamics of positive feedbacks along the entire life-span and different demographic  
68 stages of plants remains largely unexplored.

69

70 Plant-plant facilitative interactions are commonly assessed from the perspective of  
71 benefits gained by the facilitated species (Callaway 2007). The analysis of costs and  
72 benefits for both facilitated and nurse plants allowed identification of shifts from

73 facilitation to competition associated with plant growth (Valiente-Banuet et al. 1991,  
74 Armas and Pugnaire 2009). However, recent studies demonstrated that the benefits of  
75 plant-plant interactions can be mutual (Sortibrán et al. 2014, Tirado et al. 2015),  
76 which could be explained if the interacting plants shift their role, e.g. if the  
77 beneficiary species becomes benefactor as it grows and becomes an adult plant. For  
78 example, during an early life stage, seedling establishment and growth of juvenile  
79 plants increases if plants grow under the stress-ameliorated micro-environment  
80 provided by the nurse plant (Pugnaire et al. 1996, Gómez-Aparicio et al. 2004,  
81 Callaway 2007, Castillo et al. 2010); as plants become adults, they modify the micro-  
82 environment (Navarro-Cano et al. 2015), which in turns benefits those plants that  
83 share it. Adult plants can provide fungal mutualisms, increase nutrient turn over by  
84 altering soil microbiota, and accumulate nutrients, all of which benefit other plants  
85 (Montesinos-Navarro et al. 2012, 2016, Rodríguez-Echeverría et al. 2013, Lozano et  
86 al. 2014, Navarro-Cano et al. 2014, Sortibrán et al. 2014), including the original nurse  
87 plant. Therefore, as adult plant, the originally facilitated plant can enrich the micro-  
88 environment shared with the nurse plant. The nurse plant might overall gain larger net  
89 benefits compared to the adult facilitated plant, since larger plants are more efficient  
90 at capturing resources (Goldberg and Landa 1991, Keddy et al. 2002, Vogt et al.  
91 2009). Nurse and adult facilitated plants might compete for resources during specific  
92 periods, but in the long term, the association between plants is likely to remain if the  
93 net effects are positive for both nurse and facilitated plant, and overcome the potential  
94 costs (Valiente-Banuet and Verdú 2007). Shifting roles from beneficiary to benefactor  
95 and vice versa might strengthen species coexistence, ultimately increasing  
96 biodiversity at the level of local communities.

97

98 In this study, we focus on a Mediterranean plant community growing on  
99 resource-poor gypsum soils to investigate whether mutual benefits for the nurse  
100 and the facilitated plants may emerge throughout the lifespan of plants. We  
101 compare the performance measures between isolated and aggregated plant  
102 species at different developmental stages (i.e., juveniles and adult plants) and  
103 expect that both the facilitated and the original nurse plant species can benefit  
104 from the interaction, the former at an early developmental stage and the later as  
105 an adult (Fig. 1). Overall, our approach contributes to a better understanding of  
106 the temporal dynamics of plant facilitative interactions, and provides insights  
107 into mutual benefits between nurse and facilitated plants, otherwise overlooked  
108 in the plant-plant facilitation literature.

109

## 110 MATERIALS AND METHODS

111

### 112 Study site

113 The study was conducted in spring-summer 2016 in a semi-arid plant community in  
114 the SE of Spain, 2.21 km NE of Petrer in the province of Alicante (38°29'52.36"N,  
115 0°44'37.62"W), in an area of 4708 m<sup>2</sup> with a 30% of vegetation cover (Delalandre and  
116 Montesinos-Navarro 2018). The average annual temperature and precipitation of the  
117 region is 22.5°C and 381 ml respectively (Cueva 1994). The study site is an outcrop  
118 of gypsum soil surrounded by clay and loam. Gypsum soils are physically unstable  
119 due to lack of plasticity, cohesion, and aggregation (Romão and Escudero 2005),  
120 properties that prevent root penetration of the surface crust after seed germination and  
121 limit establishment of plant juveniles (Meyer 1986). Gypsum soils generally lack  
122 important plant nutrients such as phosphorus, nitrate and potassium (Meyer 1986).

123 Altogether these physical and chemical properties make gypsum soils stressful  
124 environments for plants.

125 The most common plant species in the study site were chamaephytes, including  
126 *Teucrium libanitis* Schreber, *Thymus vulgaris*, *Th. moroderi*, *Fumana ericoides*,  
127 *Helianthemum squamatum* (Jacq.) Dum. Cours., *H. syriacum* L., *Helichrysum*  
128 *stoechas*, *Herniaria fruticosa*, and *Sedum sediforme*. Shrubs such as *Cistus clusii*,  
129 *Ononis tridentata* and *Rosmarinus officinalis* were scattered and uncommon. We  
130 focused the study on the most abundant species, namely *T. libanitis*, *Th. moroderi*, *H.*  
131 *squamatum*, *H. syriacum* and *He. Stoechas*, because they are all dwarf shrubs with  
132 similar size and similar traits related to growth strategies (trait values compiled from  
133 BROT data base, presented in Table 1; Paula et al. 2009, Tavcsanoughlu and Pausas  
134 2018). Therefore, differences among these species are likely to emerge in relation to  
135 temporal differences in plant establishment, especially in gypsum soils, where  
136 secondary growth shows large inter-site and small interspecific differences (Olano et  
137 al. 2011).

138

### 139 Sampling design

140 Over one spring, we studied five species with similar life-form so that their size could  
141 be used as proxy of the sequence order of plant establishment in vegetation patches.

142 We compared performance traits relevant to different life stages between plants that  
143 appeared growing in association with other species (i.e. in vegetation patches where  
144 canopies overlapped) and solitary, in order to estimate the net benefits (or costs) of  
145 growing in vegetation patches. For seedlings and juvenile plants, we quantified the  
146 frequency of establishment and growth of juveniles respectively. In adult plants, we  
147 determined whether net flower production (relative to plant height) varied with the

148 role that the species played in the interaction (nurse or facilitated) (Fig. 1). Therefore,  
149 we quantified the net benefit in pairs of species where the associated individual was  
150 the largest in the vegetation patch (assumed to be the original nurse plant), and in  
151 pairs where it was not the largest (although frequency of establishment and juvenile  
152 growth might have been facilitated by the nurse plant at an earlier life stage). We  
153 focused on key demographic parameters that influence population dynamics, namely  
154 survival, growth and reproduction (Caswell 2001), and selected plant performance  
155 components that inform about these parameters. We used plant height as proxy of  
156 either growth and/or survival, and flower production as a proxy of reproduction.  
157 Then, we followed a widely used approach to quantify the intensity of plant-plant  
158 interactions, which consists of comparing plant performance between treatments  
159 differing in the presence (e.g. associated) or absence (e.g. solitary) of neighbors  
160 (Goldberg et al. 1999, Holzapfel and Mahall 1999, Pugnaire and Luque 2001,  
161 Cavieres et al. 2008, Sch**□**b et al. 2014b, García-Cervigón et al. 2016, Pueyo et al.  
162 2016, Llambí et al. 2017). We applied this general approach for the following fitness  
163 components along the plants' life-span.

164

#### 165 Frequency of juvenile recruitment

166 Recruitment and spatial distribution of juvenile plants (e.g. early life development  
167 stage) was studied by sampling 111 plots of 1.5 m  $\times$  1.5 m randomly distributed across  
168 the study site. We quantified the number of juvenile plants growing in vegetation  
169 patches with other plants, and growing solitarily. We considered juvenile plants those  
170 with soft stems and without signs of stem lignification, and vegetation patches as  
171 groups of plants with overlapping canopies. We calculated the percentage of the total  
172 area covered by plants by measuring the maximum and minimum diameter of the

173 patch per plot, and approximated the patch area to an ellipse. We used binomial tests  
174 to compare the observed number of juveniles in the two conditions (i.e. growing in  
175 association with other plants in patches and solitarily), with those expected based on  
176 the proportion of area covered by plants, using the “binom.test” function implemented  
177 in R version 3.2.3 (R Core Team 2015). The p-values were corrected for multiple  
178 testing through the false discovery rate (FDR) method, using the “p.adjust” function.

179

#### 180 Juvenile growth

181 In an area of 30 m<sup>2</sup>, we compared height of juvenile plants growing in patches and  
182 isolated to test if performance increased in vegetation patches. Plant height was used  
183 as proxy of performance, driven either by an increase in growth rates and/or improved  
184 survival. We used a general linear mixed model and included height as dependent  
185 variable, growing condition (e.g. in association with other plants and in solitary  
186 stands) as fixed effect, and species identity as random effect. The analysis was  
187 conducted using the “lme4” package (Bates et al. 2015), the significance of the fixed  
188 effect was assessed using “lmerTest” package (Kuznetsova et al. 2017), and the mean  
189 estimate of the levels was retrieved using “effects” package (Fox and others 2003), all  
190 implemented in R version 3.2.1 (R Core Team 2015).

191

#### 192 Flower production of adult plants

193 We measured plant height and flower production in 200 adult individuals. We  
194 selected plants distributed in a paired design (hereafter set) so that two plants of the  
195 same species appeared growing in each condition, i.e. in vegetation patches and in  
196 solitary stands within 1 m distance from each other. In half of the sets, the plant  
197 growing in association was the largest of the vegetation patch (assumed to be



198 originally the nurse plant), whereas in the other half the adult plant was not the largest  
199 (assumed to be the originally facilitated plant as seedling) (Fig. 1). For *T. libanitis* and  
200 *Th. moroderi* we counted the number of inflorescence rather than number of flowers  
201 because flowers of these species are too small to obtain accurate counts in the field.  
202 We targeted five species and selected 20 sets per species (40 plants per species),  
203 accumulating a total of 100 sets (sets included paired-individuals, one from the  
204 vegetation patch and one from solitary stands, of a similar size; 200 plants in total). In  
205 some cases, sets of different species shared the same vegetation patch, and this was  
206 incorporated in the analyses (see below).

207 Because plant size and/or age (both likely correlated with height) affects flower  
208 production, we conducted a linear regression for each species to predict flower  
209 production based on plant height. We extracted the residuals and used them as  
210 measure of corrected flower production to remove plant size effects on the response  
211 variable. Within each set, we estimated the difference between the corrected flower  
212 production of plants growing in association and its solitary paired-plant. We used this  
213 measure as proxy of benefits gained (if positive) and costs (if negative) of growing  
214 associated with other plants in a vegetation patch. Two conspecific plants within each  
215 set could slightly differ in height, but using the residuals of flower production  
216 regressed against plant height ensured that detectable differences between plants in  
217 association and its solitary paired-plant were independent of height. We used a  
218 general linear mixed model to test if differences in corrected flower production could  
219 be explained by the fixed factor “role”. “Role” indicated whether the associated plant  
220 was assigned as originally nurse or facilitated plant (largest and not the largest plant  
221 of the patch respectively). In the analysis, plant species and vegetation patch were  
222 included as random factors. All statistical analyses were performed using the package

223 “lme4” (Bates et al. 2015), the significance of the fixed effects was assessed using  
224 “lmerTest” package (Kuznetsova et al. 2017), and the mean estimates and standard  
225 error of the two levels of the fixed factor (largest and non-largest plant) were obtained  
226 using “effects” package (Fox and others 2003), both implemented in R version 3.3.1  
227 (R Core Team 2015).

228

## 229 RESULTS

230

### 231 Juvenile recruitment

232 In the 250 m<sup>2</sup> area sampled, plants covered only 15% of the area surveyed, but the  
233 estimated probability of finding juveniles in vegetation patches was threefold of  
234 solitary juveniles for all plant species (0.52-0.59, Table 2). The binomial test showed  
235 that the proportion of juveniles growing associated with vegetation patches was  
236 significantly larger than expected by chance (Table 2).

237

### 238 Juvenile growth

239 Height was recorded in 314 juvenile plants in 30 m<sup>2</sup> (154 of *H. syriacum*, 82 of *H.*  
240 *squamatum*, 28 of *Th. moroderi*, 21 of *T. libanitis* and 19 of *He. stoechas*). The height  
241 of juvenile plants was significantly explained by growing condition, whether the  
242 plants appeared growing associated vs. in solitary stands (F-value = 6.07<sub>1, 309</sub>, p-value  
243 = 0.01), with an average height (mean ± SE) of 2.88 ± 0.42 cm in vegetation patches  
244 and 2.23 ± 0.40 in solitary stands (Fig. 2). These differences represent an increase of  
245 29% in height for juvenile plants in vegetation patches.

246

### 247 Flower production

248 We detected differences in corrected flower production in relation to the role assigned  
249 to plants. Nurse plants (i.e. the largest individuals in vegetation patches) showed  
250 significantly higher benefits than facilitated conspecifics (not the largest) (N=100, p-  
251 value= 0.003; Fig. 3). Specifically, differences in corrected flower production  
252 between the largest plant in the patch and its paired-solitary conspecific was positive  
253 and statistically significant ( $72.38 \pm 25.22$ ; p-value = 0.02). In contrast, when the  
254 associated plant was not the largest of the patch, flower production was similar  
255 between the plant in the vegetation patch and the paired-solitary conspecific ( $-11.02 \pm$   
256  $25.22$ ; p-value = 0.67).

257

## 258 DISCUSSION

259 From its foundation, coexistence theory emphasized competitive interactions to  
260 predict species composition in communities (Chesson 2000). More recently,  
261 facilitation has been incorporated to this framework (Bulleri et al. 2016) under the  
262 view of being an unidirectional process with benefits for only one plant involved in  
263 the association (Callaway 2007). The integration of a bidirectional and temporal  
264 perspective to plant-plant interactions has provided evidence of shifts from facilitation  
265 to competition, as facilitated plants became adults (Armas and Pugnaire 2009).  
266 However, it remains untested whether adult facilitated plants could change their role  
267 and become benefactors, providing benefits to other plants, including the original  
268 nurse plant. Our study suggests that facilitation is maybe a complex process  
269 maintained throughout the life cycle of the plants involved in the interaction. Here we  
270 propose that as facilitated plants grow and become adults, both plants involved in the  
271 interaction could benefit from being associated with each other. It is therefore  
272 important to investigate the potential benefits gained at different developmental stages

273 by identifying meaningful performance measures relevant to those life stages (e.g.  
274 survival and growth in juvenile vs. flower production as proxy of reproductive  
275 investment in adults). Previous research on plant-plant facilitation quantified changes  
276 in the magnitude and sign of interactions along the ontogeny of facilitated plant  
277 (Armas and Pugnaire 2005) and the effect of neighbours on its population dynamics  
278 (Miriti et al. 2001, Butterfield et al. 2010). However, to our knowledge, the proposed  
279 conceptual frame of mutual benefits for facilitated and nurse species along their life  
280 span has not been integrated in previous studies, and therefore the potential (delayed)  
281 benefits for nurse plants may have been overseen.

282 We investigated plant-plant interactions by testing whether plants growing in  
283 vegetation patches gained benefits compared to those growing in solitary stands. Our  
284 analysis revealed that more juveniles recruited associated to other plants in vegetation  
285 patches compared to solitary, while at a later developmental stage, the original nurse  
286 plant showed an increased flower production compared to solitary conspecifics of  
287 similar size. In similar systems, vegetation patches provide a microenvironment richer  
288 in nutrients and with greater diversity of microbiota compared to bare ground  
289 (Navarro-Cano et al. 2014). Further research is required to assess whether an  
290 improvement of soil properties (e.g. moisture, fertility, enriched microbiota, among  
291 others) could be the underlying mechanism of facilitation.

292 From a theoretical perspective, while experimental manipulations (i.e. plant removal,  
293 addition of nutrients) seem appropriate to evaluate mechanisms for plant facilitation,  
294 it might not be feasible to conduct them in unique edaphic islands with endemic plant  
295 species (Escudero et al. 2015). In addition, manipulations do not necessarily  
296 guarantee the removal of all the effects induced by the association. Hence, non-  
297 experimental approaches like ours might be appropriate to study plant-plant

298 interactions. Nevertheless, in non-experimental approaches other biotic or abiotic  
299 factors could have influenced the performance measurements. Micro-environmental  
300 features of the landscape might affect soil nutrient content or water availability,  
301 conditioning the growth and reproduction of plants establishing in different microsites  
302 (Lundhold 2009, Stover and Henry 2018). The relatively small area (0.5 Ha) and low  
303 slope of the study site selected should have minimized this potential micro-  
304 environmental variation. In addition, the paired experimental design to compare  
305 flower production between associated and solitary plants, where each pair is no more  
306 than one meter apart, should also account for potential micro-environmental variation  
307 present within our study site. In the case of early-stages performance measurements  
308 other factors such as a seed-trap effect might have influenced recruitment of juveniles  
309 in vegetation patches. However, it is unlikely that juvenile growth in vegetation  
310 patches could be attributed to seed-trap effects. Hence, other benefits, such as higher  
311 moisture or nutrient availability influenced by the presence of other plants, might be  
312 present in these environments. We identified some large individuals growing solitary,  
313 maybe reflecting a limited seed dispersal and colonization of all suitable micro-  
314 environments, as well as variability in the plant-plant interactions outcomes as a  
315 balance between competition and facilitation.

316

317 Facilitative priority effects occur when the establishment of a species modifies the  
318 biotic or abiotic environment in ways that favour the establishment of subsequently  
319 arriving species (Fukami et al. 2005). The time of arrival of different species can in  
320 turn affect performance of later arriving species, which is often reflected in the  
321 community structure (von Gillhausen et al. 2014). Although the stage-dependent  
322 responses to plant-plant interactions studied are not equivalent to documenting

323 temporal dynamics, our results describe a pattern that might support the presence of  
324 different effects of facilitative interactions based on the arrival time of the species  
325 involved. In our study, this is supported by the fact that the same species showed  
326 different responses to growing associated vs. solitary, depending on whether they  
327 were the largest plant in the vegetation patch. Although larger size relative to other  
328 plant species in the vegetation patch may not necessarily imply an earlier arrival time,  
329 this might be likely considering that the plant species selected share similar traits  
330 related to growth strategies.

331 Plants that establish first can influence recruitment, growth or reproductive success of  
332 subsequently arriving species (Fukami 2015), and the mechanisms commonly  
333 invoked include niche pre-emption (e.g. a reduction of available niche for plants with  
334 similar requirements), or niche modification (i.e. soil legacies) (Weiner 1990, Grman  
335 and Suding 2010, Cuddington 2011, van der Putten et al. 2013, Helsen et al. 2016).  
336 Different mechanisms of soil modification can give rise to beneficial effects, for  
337 example, by increasing nutrient availability or soil mutualisms (Burkle and Belote  
338 2015), but this modification might depend on the size of the established plants. Our  
339 study suggests that adult plants, particularly when they are the largest of the  
340 vegetation patch, could benefit from the association with other plants. We measured  
341 this by comparing flower production between vegetation patches and solitary  
342 condition. Flower production and associated reproductive traits are often sensitive to  
343 nutrient availability particularly in stressful environments (Muñoz et al. 2005, Burkle  
344 and Irwin 2009). It is possible that plants established in a vegetation patch modify soil  
345 properties improving the microenvironment and resource availability of the patch  
346 (Navarro-Cano et al. 2014). While this can benefit all plants in the patch, the original  
347 nurse plant (i.e. the largest in the patch), which probably presents a more developed

348 root system than other adult plants, may be more efficient at acquiring resources, and  
349 thus more likely to gain greater benefits than relatively smaller plants (Violle et al.  
350 2009, Wang et al. 2010). Nevertheless, further research will help improving a  
351 mechanistic understanding of these interesting patterns.

352

353 Reciprocal benefits in plant facilitative interactions have received little attention, but  
354 the interest is increasingly growing (Pugnaire et al. 1996, Holzappel and Mahall 1999,  
355 Sortibrán et al. 2014, Tirado et al. 2015). Plants interact on a multidimensional scale,  
356 exerting positive and negative effects on their partners depending on the fitness  
357 component considered (i.e. germination, seed production, flower density, fruit set)  
358 (Maestre et al. 2003, Sch**□**b et al. 2014a). However, plant traits vary across the life-  
359 span, implying that the benefits of harbouring complementary suites of traits might  
360 only be detectable when facilitative interactions are considered along the entire life-  
361 span of plants (Montesinos-Navarro et al. 2019). At earlier developmental stages,  
362 seedlings or juvenile plants might be unable to substantially modify the soil  
363 conditions in which they grow (Sortibrán et al. 2014), but their capacity increases  
364 along the ontogeny of the plant (Navarro-Cano et al. 2015). In contrast, adult plants  
365 can reduce insolation, enhance nutrient cycling through litter leaching, alter microbial  
366 communities, and enhance the performance and reproductive success of neighbour  
367 plants (Vetaas 1992, Pugnaire et al. 1996, Montesinos-Navarro et al. 2012, Navarro-  
368 Cano et al. 2014, Rodríguez-Echeverría et al. 2016). Future research should  
369 incorporate a wider and functional perspective of other reproductive estimates, such  
370 as fruit and seed production and quality, or probability of pollen delivery and arrival,  
371 all of which positively correlate with larger floral displays (Karron and Mitchell  
372 2011). Measuring performance at different life stages allows identifying benefits that

373 might be delayed and emerge only when plant-plant interactions are considered along  
374 the life-span of the species involved.

375

376 In conclusion, this study provides a novel view of the stage-dependent benefits that  
377 both nurse and facilitated plants can gain from facilitative interactions. Mutual  
378 benefits in facilitative interactions might promote long-term co-existence in plant  
379 communities, particularly in stressful environments, and create positive feedbacks in  
380 plant-plant interactions. Nevertheless, more research is required to provide a  
381 functional perspective and discover the underlying mechanisms that create positive  
382 feedbacks between plants, and how these structure plant diversity at the community  
383 level.

384

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395

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651

653 Table 1. Trait values related to plant growth for the five focal species of our study  
654 compiled from BROT data base (Paula et al. 2009, Tavcsanouglu and Pausas 2018):  
655 *Helianthemum squamatum* (*H. squamatum*), *Helianthemum syriacum* (*H. syriacum*),  
656 *Helichrysum stoechas* (*He. stoechas*), *Teucrium libanitis* (*T. libanitis*), *Thymus*  
657 *moroderi* (*Th. moroderi*). The similarity in trait values (number of individuals (N),  
658 mean and standard deviation (sd)) across the plant species selected in the study,  
659 supports that they have similar growth strategies. All data comes from specimens  
660 collected in Eastern Spain.  
661

Species traits	N	mean	sd
<b>Height (m)</b>			
<i>H. squamatum</i>	2	0.26	0.20
<i>H. syriacum</i>	5	0.46	0.24
<i>He. stoechas</i>	4	0.48	0.14
<i>T. libanitis</i>	1	0.12	-
<i>Th. moroderi</i>	1	0.10	-
<b>Leaf area (mm<sup>2</sup>)</b>			
<i>H. squamatum</i>	1	69.54	-
<i>H. syriacum</i>	2	44.80	14.42
<i>He. stoechas</i>	3	39.66	32.73
<i>T. libanitis</i>	1	23.44	-
<i>Th. moroderi</i>	1	4.50	-
<b>Leaf Nitrogen content (mg/g)</b>			
<i>H. squamatum</i>	1	13.39	-
<i>H. syriacum</i>	1	12.74	-
<i>He. stoechas</i>	3	12.82	0.79
<b>Root depth (m)</b>			
<i>H. squamatum</i>	2	0.44	0.30
<i>H. syriacum</i>	2	0.39	0.39
<i>He. stoechas</i>	2	0.33	0.27
<i>T. libanitis</i>	1	0.17	-
<i>Th. moroderi</i>	1	0.13	-
<b>Specific leaf area (mm<sup>2</sup>/mg)</b>			
<i>H. squamatum</i>	1	4.56	-
<i>H. syriacum</i>	3	4.84	1.47
<i>He. stoechas</i>	3	10.15	2.04
<i>T. libanitis</i>	1	3.41	-
<i>Th. moroderi</i>	1	6.30	-

663 Table 2. Binomial tests assessing differences in the establishment of juveniles in  
664 vegetation patches and bare ground for the five focal species. The expected proportion  
665 of juveniles growing associated with other plants was 0.15, based on the percentage of  
666 cover of plants in the 30m<sup>2</sup> plot area sampled. For each species, the total number of  
667 juveniles observed (Total N. juveniles), the number of juveniles growing associated  
668 with other plants (N. juv. associated), the estimated probability of growing associated  
669 based on the binomial test (Estim. prob.), and the adjusted p-value corrected for  
670 multiple testing using the false discovery rate method (Adj. p-value) is included. For  
671 all species, the proportion of juveniles growing associated with other plants is  
672 significantly greater than expected by chance.  
673

Species	Total N. juveniles	N. juv. associated	Estim. Prob.	Adj. p-value
<i>T. libanitis</i>	203	120	0.591	<0.001
<i>H. squamatum</i>	539	321	0.596	<0.001
<i>H. syriacim</i>	201	106	0.527	<0.001
<i>T. moroderi</i>	22	13	0.591	<0.001
<i>H. stoechas</i>	23	12	0.522	<0.001

674  
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676



677 FIGURE LEGENDS

678

679 Figure 1. Experimental design. Fitness components for seedling/juveniles and adults  
680 were compared between conspecific plants growing associated with other plants and  
681 solitary (in brackets). In the field, two different situations were selected, vegetation  
682 patches where the focal species was the largest in the patch (i.e. originally acted as the  
683 nurse) and where it was an adult but not the largest of the patch (i.e. originally  
684 facilitated as a seedling). In the case of seedlings fitness components, the seedling  
685 cannot be the largest plant in the patch, and thus this situation is biologically  
686 unavailable. We expect that both the originally facilitated and nurse species will  
687 benefit (blue) from growing associated compared to solitary, the former at an early  
688 developmental stage, increasing its frequency of establishment and growth of  
689 juveniles, and the later at a later developmental stage, increasing flower production.

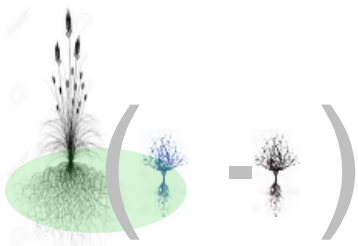
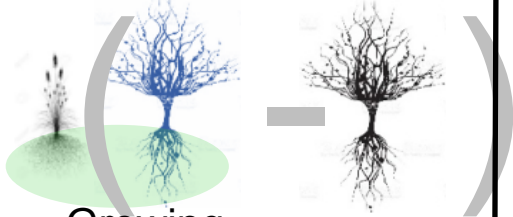
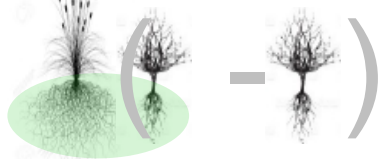
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691 Figure 2. Juveniles size when growing in association with other plants or isolated.  
692 Estimated means and standard errors of the height of juveniles (in cm) for plants  
693 growing in vegetation patches and solitary.

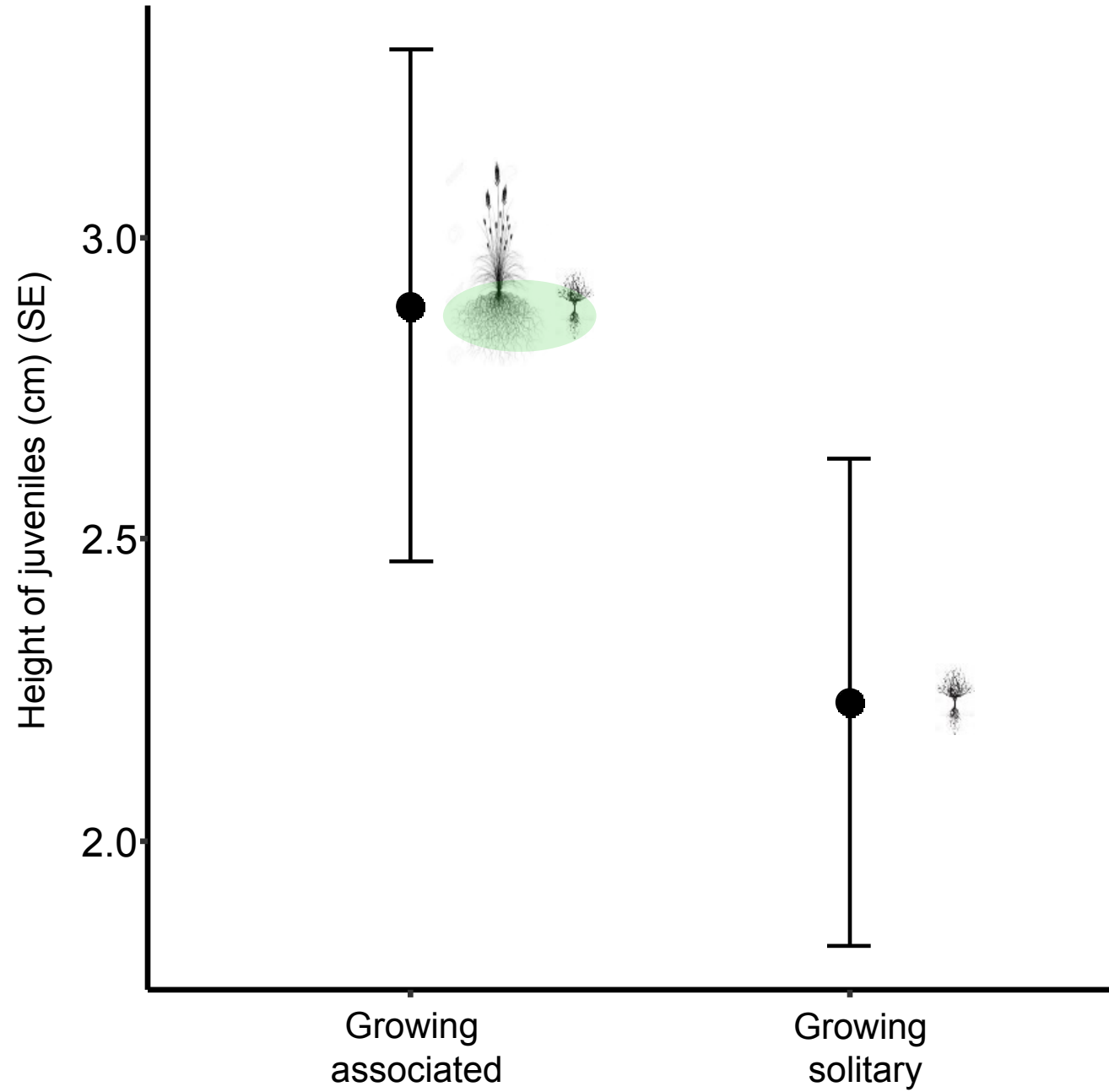
694

695 Figure 3. Benefits of growing in association with other plants in vegetation patches  
696 based on the role of the plant (largest plant of the patch assumed to function originally  
697 as nurse, and not the largest plant assumed to be originally facilitated as a seedling,  
698 see Methods). Estimated means and standard errors of flower production are  
699 presented, based on the residuals of the relationship between flower production and  
700 height. Benefits were calculated as the difference in flower production between paired  
701 individuals growing associated with vegetation patches and solitary.



	Originally nurse	Originally facilitated
Juveniles: seedling establishment and growth of juveniles	Biologically not possible	
Adults: Reproductive investment	 <p>Solitary</p> <p>Growing associated</p>	 <p>Solitary</p> <p>Growing associated</p>

# Juveniles growth



# Benefit of growing associated

