

1 **Facilitation mediates species presence beyond their environmental optimum**

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9 Abstract: 300 words

10 Main text: 4327 words

11 3 Figures; 63 References

12 **Abstract**

13 Species distributions are driven by abiotic conditions that filter species with specific traits
14 and physiological tolerances and match them with their suitable environment. Plant–plant
15 interactions can constrict (through competition) or loosen (through facilitation) the strength of
16 these environmental filters, which in turn inhibit or enhance establishment and recruitment of
17 plant species at a finer spatial scale. Although competition is often the focus of community
18 assembly processes that further impede the entry of plant species into a site, facilitation is also
19 important for potentially loosening environmental filters (especially climatic filters such as
20 temperature and precipitation), ultimately enhancing species occurrence beyond their
21 physiological optimum. We used multiple data sets from the arid site of Rambla del Saltador
22 Valley to test the hypothesis that facilitation by a nurse-plant promotes the presence of
23 herbaceous, beneficiary species beyond their environmental optimum relative to open sites.
24 Furthermore, we propose that the median elevation and community composition of herbaceous
25 species expands with the age of the nurse-plant, and we tested this hypothesis by examining 105
26 beneficiary species under 50 nurse-plant shrubs varying in age from 6 to 48 years old. We found
27 nurse-plants both facilitate herbaceous species occurrence beyond their median elevation and
28 support more diverse and a distinctly different composition of species in contrast to open sites.
29 Specifically, herbaceous species that originate from a median elevation more than 600 to 700 m
30 above the site only existed beneath nurse-plants, and below this median elevation, half the
31 species only occurred below the nurse-plant. Moreover, the richness and elevation provenance of
32 the herbaceous species increased with increasing nurse-plant age. Our results highlight the
33 importance of facilitation for alleviating physiological strain (in support of the strain hypothesis)

34 and mediating regional species distributions, which has implications for understanding species
35 movements and community assembly at larger-scales under hotter and drier climates.

36 **Keywords**

37 Species distributions, climate change, community assembly, environmental filters, nurse-plants,
38 plant-climate interactions

39 **Introduction**

40 Understanding the processes that underlie patterns of species distribution is a cornerstone
41 of ecology (MacArthur, 1972; Whittaker and Niering, 1975), which is increasingly relevant for
42 predicting community assembly in a changing climate (Alexander et al., 2016, 2015; Soliveres et
43 al., 2015). Species diversity at any location is governed by large-scale biogeographic and
44 evolutionary processes as well as by local biotic and abiotic mechanisms (Brooker et al., 2008;
45 Cavieres et al., 2014; Harrison and Cornell, 2008; Ricklefs, 2008, 2004). Within the suite of
46 plant–plant interactions, competitive exclusion can inhibit species occurrence (Alexander et al.,
47 2015; Chesson, 2000; Hart and Marshall, 2013; Kraft et al., 2015; Schöb et al., 2013) while, in
48 contrast, facilitation can increase the realized niche of plant species at local and regional scales
49 by ameliorating environmental filters — such as climatic conditions across environmental
50 gradients — thereby promoting species presence beyond their environmental optimum (Armas et
51 al., 2011; Gross et al., 2010; Liancourt et al., 2017; Schöb et al., 2014a; Soliveres et al., 2015;
52 Valiente-Banuet et al., 2006; Wisz et al., 2013). Assessing the influence of nurse-plants on
53 regional-scale species distribution can help our understanding of species dynamics and
54 community assembly under a changing environment (Bruno et al., 2003; Cavieres et al., 2016;
55 Liancourt et al., 2017; O’Brien et al., 2017b; Pugnaire et al., 1996; Schöb et al., 2012).

56 Facilitation is a widespread process particularly important for species coexistence in low
57 resource or stressful climatic environments (Callaway, 2007; Filazzola and Lortie, 2014; Fugère
58 et al., 2012; He et al., 2013). In plant communities, facilitation is often, but not solely, shown as
59 the effect of a nurse-plant on beneficiary species whereby the nurse promotes the establishment,
60 growth or reproduction of stress-sensitive species under their canopy (Bertness and Callaway,
61 1994). The relative importance of facilitation for the persistence of a species increases as the

62 environmental conditions at a site diverge from the physiological optimum of the species — i.e.
63 the more strain (termed the strain hypothesis) on a species at a site (Gross et al., 2010; Liancourt
64 et al., 2017). In arid systems, this hypothesis would imply that facilitation is asymmetric with
65 species from higher elevations (cooler and wetter sites) benefitting more from facilitation than
66 species from lower elevations (hotter and drier sites) due to the greater physiological tolerance to
67 arid conditions of lower elevation species and more physiological strain on higher elevation
68 species (Liancourt et al., 2017). In other words, nurse species can expand niche space within sub-
69 optimal environments thereby allowing species to exist in locations beyond their environmental
70 optimum (Wiens, 2011). This process can in turn increase local community diversity and
71 productivity, which mediates geographic distributions at larger scales (Bulleri et al., 2016;
72 Cavieres et al., 2014; Ettinger and HilleRisLambers, 2017; Kraft et al., 2015; Schöb et al., 2012).

73 Common mechanisms underpinning facilitation are amelioration of microclimate
74 conditions and improvement of understory soil properties, and as nurse-plants grow older, the
75 complexity and heterogeneity of soil and climatic conditions will increase (Lozano et al., 2017;
76 Pugnaire et al., 2011, 1996). This correlation between the complexity of the understory niche
77 and nurse-plant age suggests that older nurse-plants will support more beneficiary species by
78 providing niche space to a larger breadth of physiological optimum. Pugnaire et al., (1996) found
79 older and larger nurse-plants host more than twice the number of beneficiary species than
80 younger nurse-plants. This was mainly attributed to the increase of organic matter, N and P
81 availability and water availability with increasing nurse-plant age (Pugnaire et al., 2011, 1996).
82 Although such increases in resource availability with nurse-plant age may enhance competition
83 in the understory, the facilitation effects of the nurse often overshadow negative interactions
84 among beneficiary species (Pugnaire et al., 1996; Schöb et al., 2013).

85 Climatic conditions in many ecosystems are becoming hotter and drier (O'Brien et al.,
86 2017a), and for plant species to avoid extinction (either local, regional or global) under novel
87 climatic regimes, they will need to either change their distributions to track their current climatic
88 conditions or persist under novel climatic conditions in their current distributions (Alexander et
89 al., 2015; Ettinger and HilleRisLambers, 2017). For example, in alpine systems, climate change
90 is increasing temperatures across the elevation gradient, and plant species will need to either
91 move upward in elevation to avoid warming or persist under warmer conditions at their current
92 elevation (Alexander et al., 2015; Valiente-Banuet et al., 2006). In arid systems such as the
93 Mediterranean, temperatures decrease but precipitation increases with increasing elevation
94 (Liancourt et al., 2017; Schöb et al., 2014b), so that hotter, drier conditions are moving up in
95 elevation under climate change (Scherrer and Körner, 2010). Nurse-plants may buffer species
96 from warmer and drier conditions thereby providing refugia from the changing climate (O'Brien
97 et al., 2017b). The presence of beneficiary species at lower and more arid elevations beyond their
98 preferred environment would indicate the buffering ability of nurse-plants in novel climatic
99 conditions, and as nurse-plants age and grow larger, they may be able to buffer a greater quantity
100 and diversity of beneficiary species. Particularly, the more beneficiary species deviate from their
101 physiological optimum the greater the importance of nurse-plants for mediating higher diversity.

102 We propose a concept whereby nurse-plants alleviate environmental conditions (i.e.
103 reduce physiological strain) at an arid site (Fig. 1) that allows species occurrence far from their
104 environmental optimum (i.e. median elevation). Using the model nurse-plant, *Retama*
105 *sphaerocarpa* (*Retama*; Pugnaire et al., 1996), we tested the hypothesis that the diversity and
106 breadth of median elevation of the beneficiary species increases with *Retama* age. We posit that
107 older nurse-plants support species far from their median elevation due to a greater complexity of

108 microsites and accumulation of resources beneath them. We expect that species originating from
109 higher elevations and cooler and wetter climates can occur in lower and more arid elevations due
110 to facilitation, while the relative importance of facilitation will be weaker on species moving
111 from more arid elevations.

112 **Materials and Methods**

113 *Field site and data collection*

114 All species occurrence data were collected from the Rambla del Saltador valley in the
115 Almeria province, Southeast Spain (37°07'43" N, 2°22'13" W; 630 m elevation). The site is arid
116 with a dry season from May to September and a wetter season from December to March
117 (Puigdefábregas et al., 1996). The average rainfall is 256 mm per year with irregular intra- and
118 inter-annual distribution. The valley is alluvial detritus with low water holding capacity, organic
119 matter and nutrient concentrations. It is dominated by randomly and sparsely distributed *Retama*
120 *sphaerocarpa* (*Retama*) individuals from the Fabaceae family, a leafless leguminous shrub with
121 a deep root system which performs hydraulic lift (Prieto et al., 2011). Other vascular plants are
122 concentrated around *Retama* with sparse vegetation between shrubs dominated by drought
123 tolerant plants (Pugnaire et al., 1996), especially in low rainfall years where few plants occur in
124 open sites (O'Brien et al., 2017b). *Retama* shrubs improve their understorey environment by
125 increasing soil water content and soil organic matter and nutrients (Pugnaire et al., 1996). Shrub
126 canopies also buffer solar radiation reaching the soil up to ~40%, leading to a decrease in mean
127 daily temperatures of up to 3°C compared to gaps and 7°C in max temperature (Moro et al.,
128 1997b). Combined, microclimate conditions and litter accumulation under the canopy produce a
129 number of strong gradients –often opposing each other (Moro et al., 1997a), that increase niche
130 availability (Michalet et al., 2015; O'Brien et al., 2017b) and allow for the establishment of a

131 great diversity of plant species. The positive effects of *Retama* on understorey productivity and
132 diversity has been widely shown in previous studies (Michalet et al., 2015; Moro et al., 1997b;
133 O'Brien et al., 2017b; Prieto et al., 2010; Pugnaire et al., 1996; Pugnaire and Luque, 2001),
134 although the facilitative effects of *Retama* decrease with increasing elevation (Pugnaire and
135 Luque, 2001).

136 Two data sets were used for this analysis. The first dataset was from Pugnaire and Lázaro
137 (2000) which includes the herbaceous beneficiary species under 50 *Retama* shrubs that ranged
138 from 6 to 48 years of age (measured from destructive harvests and ring counts) and with crown
139 areas ranging from 0.4 to 44 m² (estimated allometrically from length and width). The second
140 dataset was compiled from a number of experiments that were carried out at the same field site
141 over multiple years (Armas et al., 2011; Hortal et al., 2015; O'Brien et al., 2017b; Schöb et al.,
142 2013). These data were of herbaceous plants collected in open spaces between *Retama* in
143 sampled areas ranging from 0.2 to 11.3 m² (total sample area of 12.6 m²) and provided an open
144 site contrast to the herbaceous community under *Retama*.

145 Elevation ranges of beneficiary species were compiled from Blanca et al., (2009). We
146 used the median elevation of the recorded range of each species (i.e. median point of the lower
147 and upper limits) as the unit to define their optimal elevation. Using median elevation is a robust
148 measure of central tendency of species distribution but limits between-species comparison as it
149 ignores the shape (i.e. assumes normal distribution) and width of the distribution such that two
150 species with a median elevation of 500 m are assumed the same even though one could exist
151 from 400 to 600 m and the other from 200 to 800 m. However, our goal was to assess the level of
152 deviation between our study site elevation and the optimal elevation for each species rather than
153 specifically contrasting the differences among species. For practical reasons, we assumed that

154 the median elevation \pm 200 m from the elevation of the site were native to the site (Scherrer and
155 Körner, 2010). Based on these assumptions, species were assigned to three elevation categories:
156 1) less than 430 masl (low elevation compared to our study site), 2) 430 – 830 masl (home
157 elevation of our study site) and 3) greater than 830 masl (high elevation compared to our study
158 site). We tested the importance of this categorization by altering the cut-off of elevations for
159 these three levels and found that our results were qualitatively robust regardless of the width of
160 the category examined (see Figure S1 and S2 in Appendix).

161 *Statistical analysis*

162 To assess the importance of *Retama* for species richness of plants originating from
163 different median elevations, we calculated the ratio of the number of species present only under
164 *Retama* from a median elevation versus the total number of species from that median elevation
165 present under *Retama* and in open sites. Therefore, if all species from a median elevation were
166 only found under *Retama*, the ratio would be one, and if all species were only found in open
167 sites, the ratio would be zero. We calculated this ratio at 100 m increments from greater than
168 1000 m difference downward (species with a median elevation above 1630 m) to greater than
169 500 m difference upward (species with a median elevation of less than 130 m). We used a simple
170 loess smoother to show the trend across the change in elevation.

171 To test for differences in composition between *Retama* and open site, we calculated the
172 dissimilarities in the herbaceous community compositions using the Jaccard index based on
173 species presence–absence per plot. We performed constrained analysis of proximities on the
174 Jaccard distance matrix to test the effect of the constraining terms site (a fixed factor with 2
175 levels; *Retama* and open) and age (a continuous variable; open were considered zero). We tested
176 the significance of the constraining terms with a permutation test. If the inertia in the permuted

177 models was lower than in the constrained model, then the association was considered statistically
178 significant. These analyses were done with R statistical software (version 3.3.2; [http://r-](http://r-project.org)
179 [project.org](http://r-project.org)). The `vegdist` function in the `vegan` package (Oksanen et al., 2015) was used to
180 calculate Jaccard dissimilarities. The constrained analysis of proximities was performed with the
181 `capscale` function (Legendre and Anderson, 1999), and the permutation test was done with the
182 `anova` function in the `vegan` package.

183 Species richness was analysed as a function of *Retama* age (a continuous variable), origin
184 elevation of the species (a fixed factor with 3 levels; low, home and high elevation) and their
185 interaction using a generalized-linear mixed model with a Poisson distribution and a log link
186 function (see ANOVA Table S1 of Wald statistics in the Appendix). We included a random
187 effect for *Retama* plant (a random term with 50 levels, the number of individual shrubs
188 assessed). We included a covariate for *Retama* canopy area to control for the effects of plant size.

189 To estimate the significance of the observed species richness across the age gradient, we
190 used a null model approach. Random communities were assigned according to a probabilistic
191 null model that builds communities from the community matrix considering the probability of
192 species presence-absence among *Retama* shrubs (Bascompte et al., 2003). In particular, the
193 community matrix ($M = \text{Retama} \times \text{Species}$) indicates the presence or absence of a beneficiary
194 species j beneath a *Retama* i . For each *Retama*–species pair, the probability that a species j
195 occurs beneath a *Retama* i is drawn from a binomial distribution with density

$$196 \quad d = \frac{1}{2} \left(\frac{a_{\text{Species}}}{\text{Retama}} + \frac{a_{\text{Retama}}}{\text{Species}} \right)$$

197 where a_{Species} is the number of *Retama* a beneficiary species j is occurring beneath, a_{Retama} is the
198 number of beneficiary species occurring beneath a *Retama* i , ‘Retama’ is the total number of

199 *Retama* and open plot, ‘Species’ is the total number of beneficiary species. Thus, the occurrence
200 probability of a beneficiary species beneath *Retama* depends on both the distribution of each
201 beneficiary species among *Retama* shrubs and on the capability of each *Retama* of hosting
202 beneficiary species. To test whether the observed species richness was significantly different
203 from the probabilistic null model, we calculated species richness from 1000 probabilistic
204 communities and used linear mixed-effects model of richness as a function of area sampled and
205 age (see ANOVA Table S2 of Wald statistics in Appendix). This analysis was performed
206 separately for the community of beneficiary species from low, home and high elevation. We also
207 assessed the standardized effect size with a z-score, which was calculated as the difference
208 between the observed richness and mean simulated richness under a *Retama* divided by the
209 standard deviation of the simulated richness. We analyzed this as a function of *Retama* age in a
210 linear model separately for the community of beneficiary species from low, home and high
211 elevation (see ANOVA Table S3 of Wald statistics in Appendix). The mixed effects models
212 were performed with the asreml-R package (ASReml 3, VSN International, UK) in the R
213 statistical software (version 3.3.2; <http://r-project.org>).

214 **Results**

215 After examining species distributions based on the most up-to-date taxonomy and
216 floristic data (Blanca et al., 2009), a total of 105 species were identified in our *Retama* dataset
217 (see Table S4 for full species list in Appendix), and one species, *Polycarpon tetraphyllum*, was
218 removed from analysis due to the uncertainty of the subspecies. Of the 104 species analysed, 60
219 species (~58% of the total) had their median elevation within 200 m of the elevation of the site
220 (home origin; Fig. 2a). Of the remaining species, *Retama* provided habitat for 11 species (~11%)
221 with a lower median elevation, and 33 species (32%) species with a higher median elevation

222 (Fig. 2a). In open site data, 61 species were identified (see Table S4 for full species list) with 35
223 species (57%) from the home origin while 9 species (15%) were from a lower elevation and 17
224 species (28%) were from a higher elevation.

225 The range of species found in open plots was much narrower with species originating
226 from 200 – 1200 m in the open versus 200 – 1850 m under *Retama*. Therefore, the range of
227 median elevations of species at the study site was more than 1.5 times larger with facilitation by
228 *Retama* than without. In support of our hypothesis, moving up in elevation was less common —
229 *Silene littorea* was the lowest species found with a distribution between 0 and 400 m — although
230 there is a lower elevation limit of 0 m as species are not moving up from below sea-level.
231 Alternatively, species moved down in elevation as much as 1220 m (e.g. *Alyssum granatense*
232 found at an elevation range of 1600 – 2100 masl), and the community under *Retama* had twice as
233 many species from higher elevations than open sites. Furthermore, 100% of the species
234 originating from a median elevation above 1300 m were only found under *Retama* (Fig. 2b) as
235 no species from the high elevations occurred in open sites. Below this elevation, 50% of the
236 species on average from all other median elevations were found solely under *Retama*. This
237 resulted in *Retama* hosting a distinctly different community than that found in open sites ($P <$
238 0.001), and beneficiary community composition under older *Retama* was significantly different
239 from younger *Retama* communities ($P < 0.001$; Fig 2c). The results in figure two were robust if
240 the largest shrubs ($> 12 \text{ m}^2$) were removed from the analysis to control for differences in
241 sampling area between open and *Retama* plots (Figure S3 in Appendix).

242 Overall species richness increased with increasing *Retama* age regardless of median
243 elevation origin (Fig. 3a). Species richness under the youngest *Retama* shrubs (6 years old) was
244 highest for beneficiary species originating from the home site (12.0 species, 95% CI: 10.1 –

245 14.3), lowest for species from low elevations (2.8 species, 95% CI: 2.1 – 3.6) and intermediate
246 from the high elevations (6.4 species, 95% CI: 5.2 – 7.8). After controlling for *Retama* canopy
247 area, species richness significantly increased with *Retama* age for the home and high elevation
248 groupings but not for the species from the low elevation (Fig. 3b-d). The increase in species
249 richness was greatest for home elevation species (slope of age on log scale = 0.03, 95% CI: 0.01
250 – 0.04) followed by high elevation species (slope of age on log scale = 0.02, 95% CI: 0.0004 –
251 0.03) while the richness of low elevation species was similar across all *Retama* ages (slope of
252 age on log scale = 0.01, 95% CI: -0.01 – 0.03). Therefore, home elevation species richness
253 increased by ~15 species from 6-year-old *Retama* to 27-year-old *Retama* while low elevation
254 species richness increased by ~1 species and high elevation species richness increased by ~3
255 species across the same *Retama* age range. This resulted in a near doubling of species richness
256 between younger and older *Retama*. Our analysis compared to a probabilistic null model
257 confirmed these results as the difference between the observed and null community increased
258 with increasing *Retama* age (see Figure S4 in Appendix). The standardized z-scores also
259 significantly increased with *Retama* age.

260 **Discussion**

261 Our combined analyses of beneficiary species under and outside canopies of nurse-plants
262 shows that nurse-plants support species from a larger median elevation breadth, and the relative
263 importance of facilitation increases as the median elevation of the beneficiary species increases.
264 These results provide direct evidence in support of reduced physiological strain hypothesis
265 (Gross et al., 2010). However, nurse-plants also supported distinctly different species than the
266 open sites even for beneficiary species that originated from a similar median elevation as the site,
267 suggesting facilitation also functions to support species unable to survive in open areas. These

268 processes led to a distinct community composition under *Retama* relative to open sites,
269 confirming that facilitation is an important process affecting community assembly and diversity
270 (Brooker et al., 2008; Tirado and Pugnaire, 2005). Specifically, these results highlight that the
271 importance of facilitation increases with increasing differences between beneficiary-species
272 average habitat and nurse-plant habitat. In addition, our results from multiple analyses indicate
273 that older *Retama* plants support nearly twice as many species and from a larger breadth of
274 median elevation than younger *Retama* plants.

275 Mechanisms of facilitation for reducing physiological strain are due to effects of
276 facilitator shrubs on climatic conditions under their canopy (Pugnaire et al., 1996) with
277 fundamental consequences for relaxing environmental filters associated with elevation gradients
278 in arid ecosystems (Moro et al., 1997b). Therefore, nurse-plants in arid environments provide
279 refugia from high temperatures and low availability of resources, particularly water and nutrients
280 (Pugnaire et al., 2011), which allowed the presence of beneficiary species far from their optimal
281 environmental conditions, especially species from higher elevations (wetter and cooler sites).
282 These results have implications for the distribution of species due to changing climates because it
283 suggests that plant–plant interactions can supersede climatic filters that limit species
284 establishment and survival, and in turn may allow species to either persist in altered climates or
285 more effectively track shifting climatic conditions. Models forecasting the presence of species
286 (i.e. distributions) under climate change should therefore consider the effects of nurse-plant
287 refugia.

288 Our results show that plant–plant interactions at the local-scale influence meso-scale
289 diversity patterns, which directly supports the results of Cavieres et al., (2014) that showed
290 similar processes shape diversity in alpine ecosystems worldwide. Species distributions are often

291 defined by bioclimatic envelopes (Elith and Leathwick, 2009; Sexton et al., 2009), since climate
292 variables are primary determinants of the species richness and composition of vascular plant
293 communities (Marini et al., 2008; Moser et al., 2005). However, the presence of favourable
294 habitats (including microhabitats under facilitator species) may have higher predictive power at
295 smaller spatial resolutions. Indeed, our study indicates not only that the structure of plant
296 communities is driven by local biotic interactions but also that local plant–plant interactions can
297 shape the large-scale distribution of species. These results imply that macroecological patterns
298 may result from microecological processes (Wiszniewski et al., 2013). Even though the data from open
299 locations also supported some species originating from higher and lower elevations, the overall
300 distribution of the median elevation of species was smaller, and no species from above 1300 m
301 were found in open sites. This smaller range was found despite the fact that the open data came
302 from multiple years and also included the 2009 to 2010 year, which had significantly higher than
303 average rainfall (O’Brien et al., 2017b). These multiple years of sampling and high rainfall years
304 likely inflated the species richness found in open sites. Our analysis of species composition
305 further supported the importance of *Retama* presence and age for harbouring unique beneficiary
306 species unable to persist outside the *Retama* canopy. Therefore, facilitation relaxed climatic
307 filters on plant diversity that restricted establishment and recruitment of species from other
308 environments while also supporting species originating locally that are unable to exist outside the
309 nurse-plant canopy (Armas et al., 2011; O’Brien et al., 2017b; Schöb et al., 2013).

310 In support of our prediction, more species from higher elevations than from lower
311 elevations benefitted from facilitation. A primary component of facilitation in these arid sites is
312 reduced temperatures from increased shading and hydraulic lift from deeply rooted nurse-plants
313 (Butterfield et al., 2010; López-Pintor et al., 2006; Moro et al., 1997b), which would create

314 environmental conditions more suitable to plants originating from cooler and wetter sites at
315 higher elevations than from warmer and drier sites at lower elevations. This result supports the
316 strain hypothesis (Gross et al., 2010; Liancourt et al., 2017). The elevation in this arid system is
317 associated with temperature and precipitation patterns that influence plant growth and lead to
318 changes in species composition and physiognomy of plant communities over large
319 environmental gradients (Austin, 1987; Körner, 2007; Pendry and Proctor, 1997; Proctor et al.,
320 1988), but *Retama* sustained species that originated from sites as much as 1200 m above the
321 study site. Therefore, *Retama* substantially relaxed environmental constraints, which may
322 ultimately result in higher species diversity. Dispersal is also a likely secondary component of
323 the greater number of species from high elevation at the site because it is easier to disperse
324 downslope via wind and water than upslope (Thompson and Katul, 2009; Venable et al., 2008).
325 Therefore, introduction rates of species from higher elevations would be greater than that of
326 species from lower elevations. There was a constraint on the median elevation limit of lower
327 elevation species (i.e. species were limited to 630 m below the site due to sea-level), but the
328 results show the proportion of species richness that depended on facilitation was decreasing with
329 decreasing median elevation.

330 Not surprisingly, most species were from the same environmental belt as the field site
331 (Thermomediterranean semiarid; Lázaro et al., 2001). However, the herbaceous communities
332 were comprised of many species found in wetter environments. For example, Armas et al.,
333 (2011) reported 10 species from this site that are distributed across a gradient from 250 to 2000
334 mm of annual rainfall (4-fold change in mean annual precipitation). Therefore, it is important to
335 note that the elevation gradient is an indicator of both a temperature and precipitation gradient,

336 and facilitation at the site is also contributing to the distribution of species across latitudinal and
337 longitudinal precipitation gradients.

338 Temperatures are increasing in many terrestrial systems around the globe, and plants will
339 either need to track the current climate associated with their home elevation range or persist in
340 novel climates (Alexander et al., 2016). In addition to warming, precipitation is also changing
341 worldwide, and many places are already facing reductions in precipitation and more variable
342 rainfall patterns (O'Brien et al., 2017a). Our results suggest that plants are already moving in the
343 attempt to find suitable microhabitats to escape these climatic stresses. Facilitation may support
344 biodiversity by providing refugia for plants to persist under hotter and drier conditions at their
345 native sites (O'Brien et al., 2017b) as well as mediate the movement of species tracking climatic
346 conditions. Recent work from Ettinger and HilleRisLambers (2017) showed that interactions
347 between juvenile and adult trees were facilitative at the upper elevation limits, which improved
348 establishment of juveniles. Therefore, it is important to consider facilitation as a factor
349 promoting community assembly as climate change drives interactions among novel species
350 neighbours (Alexander et al., 2015).

351 Our analysis highlights the importance of facilitation for reducing physiological strain for
352 species outside of their climatic optimum while also maintaining local species sensitive to arid
353 conditions. Both processes promote large-scale species distributions along elevational gradients
354 in arid systems (i.e. gradients of temperature and moisture). These results suggest that the
355 influence of older nurse-plants on micro-environmental conditions is especially important for the
356 presence of species far from their physiological optimum.

357 **Acknowledgements**

358 This work was funded by AEI (çCGL2017-84515-R). MOB was supported by the Swiss
359 National Science Foundation through an Advanced Postdoc Mobility Fellowship
360 (P300PA_167758).

361 **Author contributions**

362 FIP conceived the experiment, provided community data and contributed to data compilation.
363 MOB analyzed the data and wrote the manuscript. LFT compiled the data. KAB contributed to
364 data compiling and provided an initial version of the manuscript. GL performed the null model
365 testing. All authors contributed to revisions.

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565 **Appendix**

566 **Table S1: The ANOVA table for species richness.**

567 **Table S2: The ANOVA table for species richness of the probabilistic null model.**

568 **Table S3: The ANOVA table for z-scores of the probabilistic null model.**

569 **Table S4: List of species.**

570 **Figure S1: Identical analysis of Figure 3 with ± 100 elevation categories.**

571 **Figure S2: Identical analysis of Figure 3 with ± 300 elevation categories.**

572 **Figure S3: Identical analysis of Figure 2 after removing shrubs greater than 12 m².**

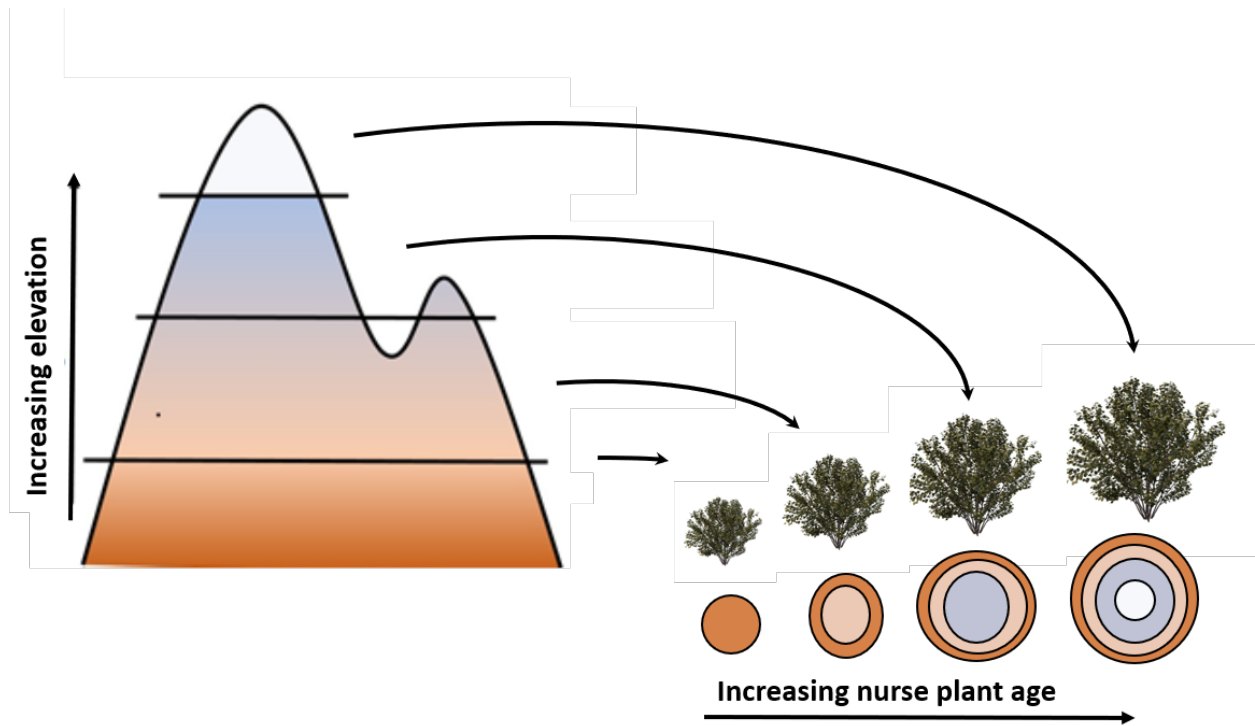
573 **Figure S4: Boxplot of null communities built from the probability model.**

574 **Figure captions**

575 **Fig. 1 Microclimate under nurse-plants increase with age providing establishment for**
576 **species from different elevations.** The distribution of a species is determined by a matching of
577 species characteristics to specific environmental conditions (i.e. environmental filtering). We
578 propose that nurse-plants mediate species from outside their optimal environment and that
579 facilitation is more important the further from that optimal environment a species deviates
580 (greater physiological strain). Here we show an example that species from higher elevations
581 (colours represent increasing elevation and decreasing aridity from brown to white) can persist at
582 lower elevations due to environmental modification by nurse-plants and that older nurse-plants
583 have more microsites beneath them that facilitate a greater range of species (i.e. only local
584 species from the same site under younger *Retama* and a range of high elevation to local species
585 under older *Retama*). Arrows match elevation colours to *Retama* size.

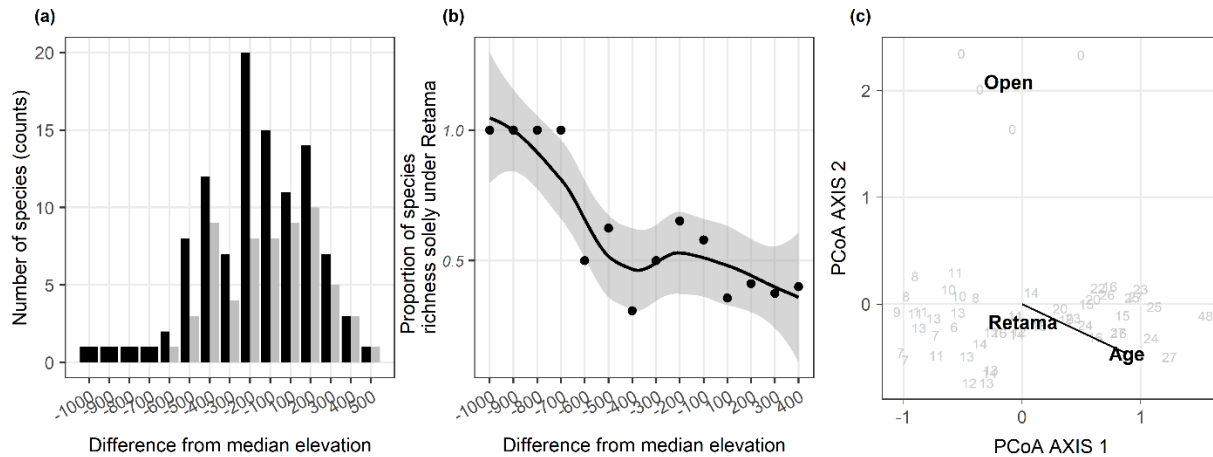
586 **Fig. 2 Elevation range and composition of species under *Retama* and open sites.** The site
587 used in this study is at 630 masl. Expansion of home elevation was calculated as the difference in
588 median home elevation reported for the species and the elevation of the site. (a) The number of
589 species found under all *Retama* (black) and in open areas (grey) that originated from elevations
590 greater than 1000 m above the site (-1000 m difference) to 500 m below the site (500 m
591 difference). There were 104 species in total found under *Retama* shrubs and 61 species in total in
592 open areas. (b) The proportion of the number of species found under *Retama* relative to the total
593 species richness found from that median elevation both under *Retama* and in open sites. The
594 black line represents a loess smoother with 95% CI. (d) The composition was statistically
595 different between open and *Retama* communities as well as from older to younger *Retama*.
596 Numbers represent *Retama* age, and the line represents the directional effect of age.

597 **Fig. 3 Beneficiary species richness as a function of *Retama* age and origin elevation.** Species
598 richness (95% CI) significantly increased with *Retama* age, after controlling for the effects of
599 area, for beneficiary species originating at elevations from and above the site but not from below
600 the site (a). Average species richness was lowest for beneficiary species originating from low
601 elevation (b), highest for beneficiary species from the home elevation (c) and intermediate for
602 beneficiary species from high elevation (d). Therefore, older *Retama* had more species than
603 younger *Retama* and expanded the elevation range of more species than younger *Retama*.



604

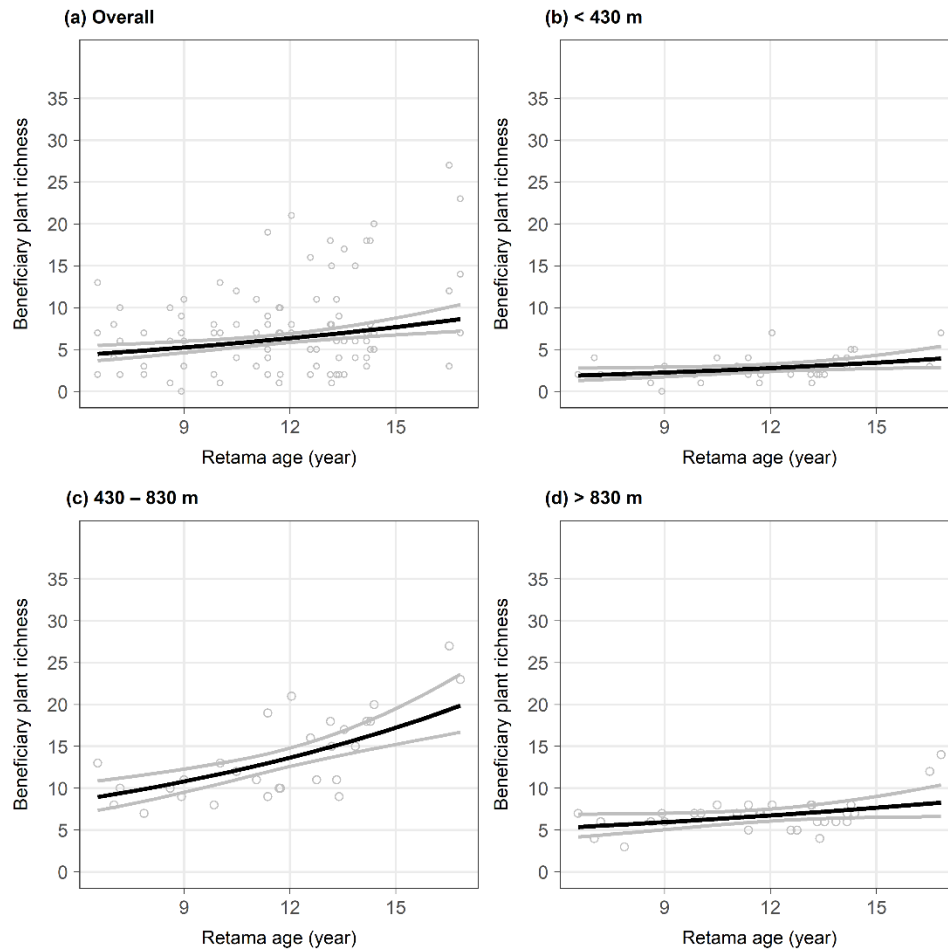
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637

638 **Appendix 1**

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648

649 **Facilitation mediates species presence beyond their environmental optimum**

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658 **Table S1.** The ANOVA tables of Wald statistics from the mixed-effects model of species
 659 richness using a Poisson distribution and log link function with a covariate for canopy area.

Source of variation	d.f.	denominator d.f.	F
<i>Retama</i> area	1	44.2	57.4***
<i>Retama</i> age	1	39.8	14.6***
Elevation	2	74.5	596.4***
Age x elevation	2	62.1	4.5*
Variance components	Var.	SE	
Shrub	0.05	0.01	
Shrub:elevation	0.00	0.01	
Residual	0.44	0.11	

660 d.f., degrees of freedom; denominator d.f., denominator degrees of freedom,
 661 F, conditional F-statistic; Var., variance component estimate and SE, standard errors for random
 662 effects; **P < 0.01, ***P < 0.001
 663

664 **Table S2.** The ANOVA tables of Wald statistics from the mixed-effects model of species
 665 richness compared to a probabilistic null model using a Poisson distribution and log link function
 666 for a) low, b) home and c) high elevation communities.

Source of variation	d.f.	denominator d.f.	F
a			
Sampled area	1	32995	2322***
Age	1	32995	70***
Variance components	Var.	SE	
Simulation	-0.001	0.000	
Residual	0.791	0.006	
b			
Sampled area	1	32998	3395***
Age	1	32998	3101***
Variance components	Var.	SE	
Simulation	0.000	0.000	
Residual	0.877	0.007	
c			
Sampled area	1	32999	327***
Age	1	32999	1538***
Variance components	Var.	SE	
Simulation	0.000	0.000	
Residual	0.818	0.006	

667 d.f., degrees of freedom; denominator d.f., denominator degrees of freedom,
 668 F, conditional F-statistic; Var., variance component estimate and SE, standard errors for random
 669 effects; **P < 0.01, ***P < 0.001

670

671 **Table S3.** The ANOVA tables of linear model of z-scores from a probabilistic null model as a
 672 function of *Retama* age for a) low, b) home and c) high elevation communities.

Source of variation	d.f.	denominator d.f.	F
a			
Age	1	52	8.3**
Variance components	Var.	SE	
Residual	0.30	0.06	
b			
Age	1	52	48.7***
Variance components	Var.	SE	
Residual	0.60	0.12	
c			
Age	1	52	9.4**
Variance components	Var.	SE	
Residual	0.32	0.06	

673 d.f., degrees of freedom; denominator d.f., denominator degrees of freedom,
 674 F, conditional F-statistic; Var., variance component estimate and SE, standard errors for random
 675 effects; **P < 0.01, ***P < 0.001

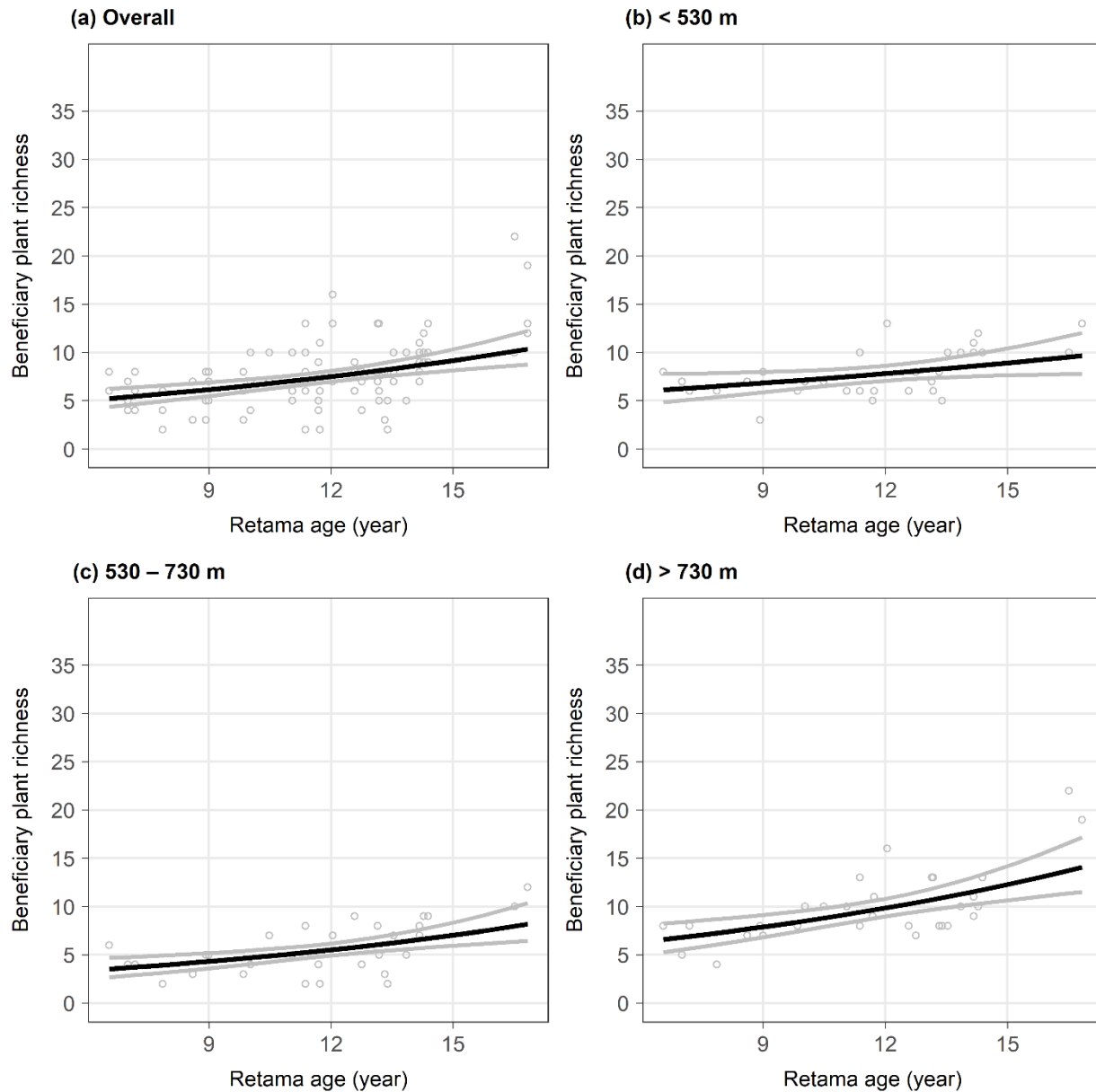
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677 **Table S4. Species list and elevation.** The starred (*) species was removed from analysis due to
 678 uncertainty over the subspecies.

Species	Lower limit	Upper limit	Median	Saltador elevation	Elevation difference	Site
Alyssum_granatense	1600	2100	1850	630	-1220	Retama
Spergularia_rubra	700	2500	1600	630	-970	Retama
Juncus_bufonius	0	3000	1500	630	-870	Retama
Capsella_bursa-pastoris	0	2500	1250	630	-620	Retama
Logfia_minima	300	2100	1200	630	-570	Retama, Open
Galium_spurium	300	2000	1150	630	-520	Retama
Andryala_ragusina	0	2200	1100	630	-470	Retama, Open
Cirsium_arvense	300	1800	1050	630	-420	Retama
Erodium_cicutarium	0	2100	1050	630	-420	Retama, Open
Geranium_molle	0	2100	1050	630	-420	Retama
Paronychia_suffruticosa	100	2000	1050	630	-420	Retama, Open
Senecio_malacitanus	0	2100	1050	630	-420	Retama
Silene_portensis	300	1800	1050	630	-420	Retama
Sonchus_oleraceus	0	2100	1050	630	-420	Retama
Aegilops_truncialis	300	1700	1000	630	-370	Retama
Daucus_durieua	300	1700	1000	630	-370	Retama
Lamarkia_aurea	0	2000	1000	630	-370	Retama, Open
Leontodon_longirostris	0	2000	1000	630	-370	Retama, Open
Papaver_pinnatifidum	0	2000	1000	630	-370	Retama, Open
Paronychia_argentea	0	2000	1000	630	-370	Retama, Open
Rumex_induratus	0	2000	1000	630	-370	Retama
Silene_colorata	300	1700	1000	630	-370	Retama, Open
Clypeola_jonthlaspi	0	1900	950	630	-320	Retama, Open
Eryngium_ilicifolium	0	1900	950	630	-320	Retama
Petrorhagia_prolifera	100	1800	950	630	-320	Open
Sonchus_tenerrimus	0	1900	950	630	-320	Retama, Open
Trigonella_polyceratia	0	1900	950	630	-320	Retama, Open
Trifolium_scabrum	0	1800	900	630	-270	Retama
Thymus_baeticus	0	1750	875	630	-245	Retama
Carlina_corymbosa	100	1600	850	630	-220	Retama
Hypochaeris_glabra	0	1700	850	630	-220	Retama, Open
Medicago_minima	0	1700	850	630	-220	Retama, Open
Rumex_bucephalophorus	0	1700	850	630	-220	Retama, Open
Spergularia_purpurea	100	1600	850	630	-220	Open
Vulpia_hispanica	0	1700	850	630	-220	Retama
Aegilops_ovata	100	1500	800	630	-170	Retama
Anacyclus_clavatus	100	1500	800	630	-170	Retama
Atractylis_cancellata	0	1600	800	630	-170	Retama
Avena_sterilis	0	1600	800	630	-170	Retama
Centaurea_melitensis	0	1600	800	630	-170	Retama

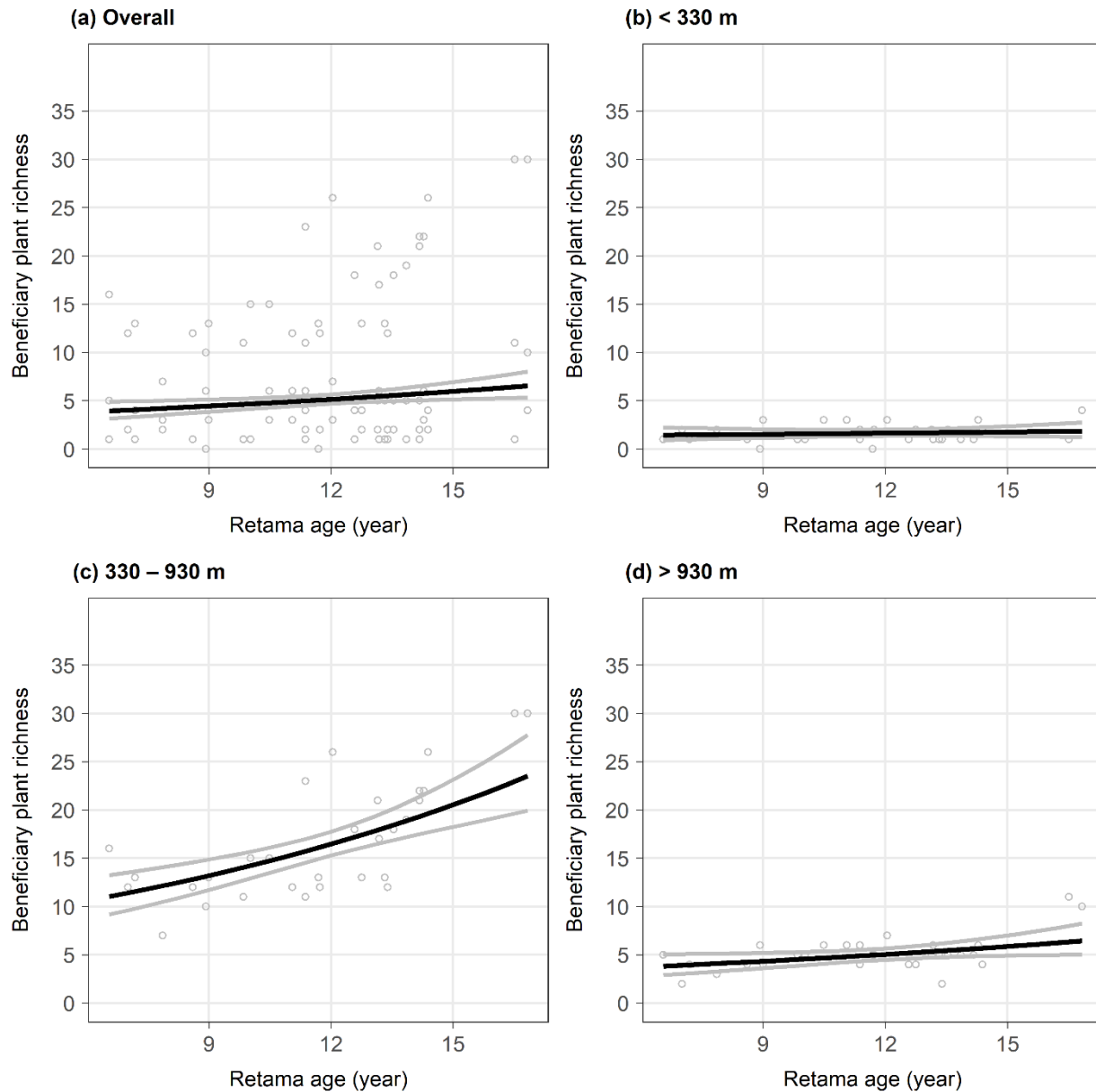
Cynodon_dactylon	0	1600	800	630	-170	Retama
Dactylis_glomerata	0	1600	800	630	-170	Retama
Helianthemum_ledifolium	0	1600	800	630	-170	Retama, Open
Lagurus_ovatus	0	1600	800	630	-170	Retama
Neatostema_apulum	0	1600	800	630	-170	Retama
Scabiosa_monspeliensis	0	1600	800	630	-170	Retama
Silene_tridentata	100	1500	800	630	-170	Retama
Bromus_rubens	0	1500	750	630	-120	Retama, Open
Catapodium_rigidum	0	1500	750	630	-120	Retama
Euphorbia_falcata	0	1500	750	630	-120	Open
Linum_strictum	0	1500	750	630	-120	Retama, Open
Malcolmia_africana	0	1500	750	630	-120	Retama
Marrubium_vulgare	0	1500	750	630	-120	Retama
Medicago_truncatula	0	1500	750	630	-120	Retama, Open
Plantago_afra	0	1500	750	630	-120	Retama
Plantago_albicans	0	1500	750	630	-120	Open
Reseda_undata	0	1500	750	630	-120	Retama, Open
Silene_nocturna	0	1500	750	630	-120	Open
Bromus_diandrus	0	1400	700	630	-70	Retama
Chenopodium_murale	0	1400	700	630	-70	Retama
Euphorbia_helioscopia	0	1400	700	630	-70	Retama, Open
Lathyrus_angulatus	0	1400	700	630	-70	Retama
Ononis_ornithopodioides	0	1400	700	630	-70	Retama
Reichardia_intermedia	0	1400	700	630	-70	Retama
Tolpis_umbellata	0	1400	700	630	-70	Retama
Valantia_muralis	0	1400	700	630	-70	Retama
Artemisia_barrelieri	50	1300	675	630	-45	Retama, Open
Anthyllis_cytisoides	0	1300	650	630	-20	Retama
Convolvulus_althaeoides	0	1300	650	630	-20	Retama
Crassula_tillaea	0	1300	650	630	-20	Open
Erodium_malacoides	0	1300	650	630	-20	Open
Hypecoum_imberbe	200	1500	650	630	-20	Open
Lasiopogon_muscoides	300	1000	650	630	-20	Open
Logfia_clementei	0	1300	650	630	-20	Retama, Open
Lolium_rigidum	200	1100	650	630	-20	Retama
Reichardia_tingitana	0	1300	650	630	-20	Retama, Open
Urospermum_picroides	0	1300	650	630	-20	Retama
Asphodelus_fistulosus	0	1200	600	630	30	Open
Asterolinon_linum-stellatum	0	1200	600	630	30	Retama, Open
Brachypodium_distachyon	0	1200	600	630	30	Retama
Carrichtera_annua	0	1200	600	630	30	Retama, Open
Desmazeria_rigida	0	1200	600	630	30	Open
Foeniculum_vulgare	0	1200	600	630	30	Retama
Hedypnois_cretica	0	1200	600	630	30	Retama

<i>Lycocarpus_fugax</i>	400	800	600	630	30	Retama, Open
<i>Pipthaterum_miliaceum</i>	0	1200	600	630	30	Retama, Open
<i>Plantago_lagopus</i>	0	1200	600	630	30	Retama, Open
<i>Avena_barbata</i>	0	1100	550	630	80	Retama, Open
<i>Gynandriris_sisyrrinchium</i>	0	1100	550	630	80	Open
<i>Lobularia_maritima</i>	0	1100	550	630	80	Retama
<i>Papaver_hybridum</i>	0	1100	550	630	80	Retama
<i>Atractylis_humilis</i>	0	1000	500	630	130	Retama
<i>Echium_creticum</i>	0	1000	500	630	130	Retama, Open
<i>Leysera_leyseroides</i>	0	1000	500	630	130	Retama, Open
<i>Loeflingia_hispanica</i>	0	1000	500	630	130	Retama
<i>Malva_parviflora</i>	0	1000	500	630	130	Retama
<i>Schismus_barbatus</i>	0	1000	500	630	130	Retama
<i>Silene_decipiens</i>	0	1000	500	630	130	Retama, Open
<i>Silene_sclerocarpa</i>	0	1000	500	630	130	Open
<i>Stipa_capensis</i>	0	1000	500	630	130	Retama, Open
<i>Trigonella_foenum-graecum</i>	400	600	500	630	130	Open
<i>Asphodelus_tenuifolius</i>	0	900	450	630	180	Retama, Open
<i>Calendula_tripterocarpa</i>	0	900	450	630	180	Retama, Open
<i>Cistanche_phelypaea</i>	0	900	450	630	180	Retama
<i>Herniaria_fontanesii</i>	0	900	450	630	180	Retama
<i>Hordeum_leporinum</i>	0	900	450	630	180	Retama, Open
<i>Linaria_nigricans</i>	0	900	450	630	180	Open
<i>Matthiola_parviflora</i>	0	900	450	630	180	Retama
<i>Erodium_chium</i>	0	800	400	630	230	Retama, Open
<i>Eryngium_campestre</i>	0	800	400	630	230	Retama, Open
<i>Ifloga_spicata</i>	0	800	400	630	230	Open
<i>Lavandula_multifida</i>	0	800	400	630	230	Retama
<i>Limonium_thouinii</i>	0	800	400	630	230	Retama
<i>Notoceras_bicorne</i>	0	800	400	630	230	Retama
<i>Ononis_viscosa</i>	0	800	400	630	230	Retama, Open
<i>Rostraria_pumila</i>	0	800	400	630	230	Retama, Open
<i>Diploaxis_ilorcitana</i>	0	600	300	630	330	Retama, Open
<i>Leontodon_hispidulus</i>	0	600	300	630	330	Retama
<i>Linaria_oligantha</i>	0	600	300	630	330	Open
<i>Plantago_ovata</i>	0	500	250	630	380	Open
<i>Volutaria_lippii</i>	0	500	250	630	380	Retama
<i>Silene_littorea</i>	0	400	200	630	430	Retama, Open
<i>Polycarpon_tetraphyllum*</i>	0	50	25	630	605	Retama



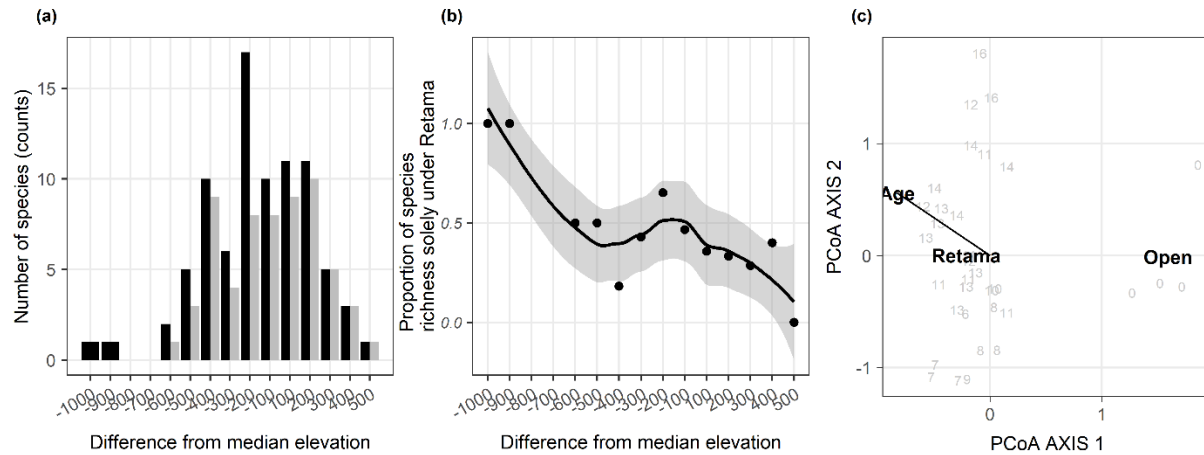
679

680 **Figure S1. Beneficiary species richness as a function of Retama age and origin elevation**
 681 **±100 home elevation.** Species richness (95% CI) significantly increased with Retama age, after
 682 controlling for the effects of area, for beneficiary species originating at elevations from and
 683 above the site but not from below the site (a). Average species richness was lowest for
 684 beneficiary species originating from low elevation (b), highest for beneficiary species from the
 685 home elevation (c) and intermediate for beneficiary species from high elevation (d). Therefore,
 686 older Retama had more species than younger Retama and expanded the elevation range of more
 687 species than younger Retama.



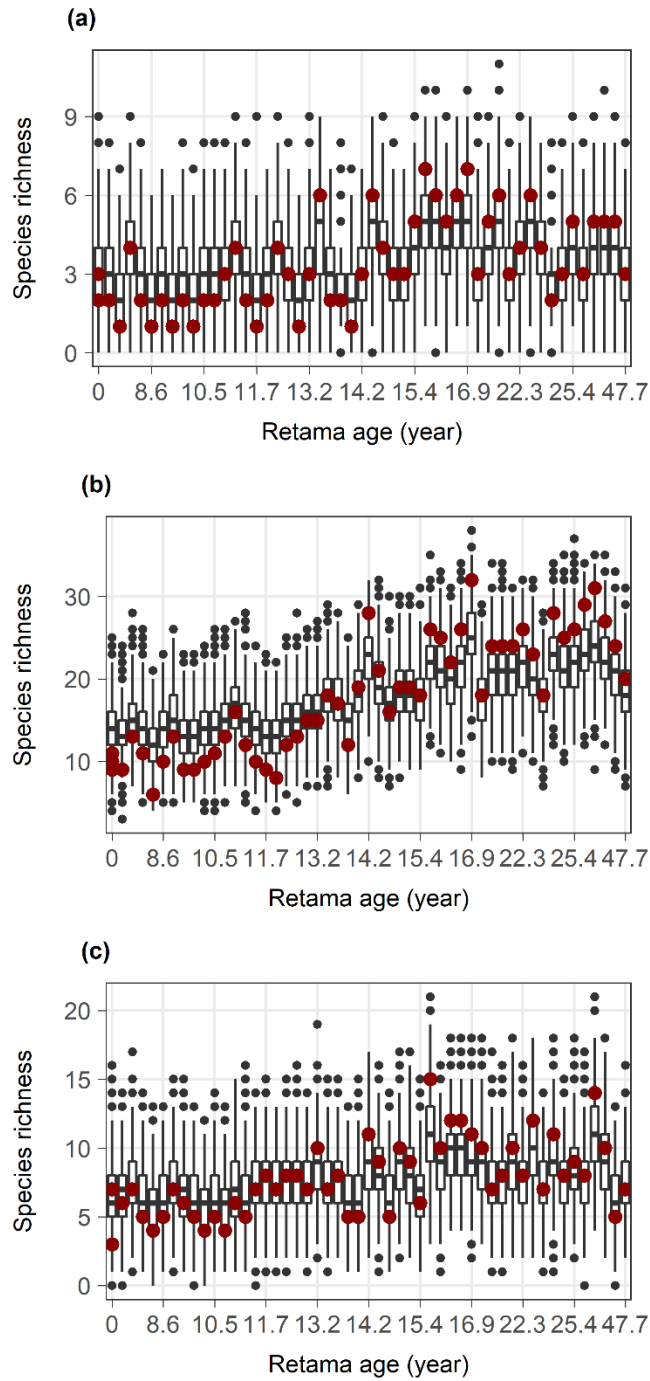
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689 **Figure S2. Beneficiary species richness as a function of Retama age and origin elevation**
 690 **±300 home elevation.** Species richness (95% CI) significantly increased with Retama age, after
 691 controlling for the effects of area, for beneficiary species originating at elevations from and
 692 above the site but not from below the site (a). Average species richness was lowest for
 693 beneficiary species originating from low elevation (b), highest for beneficiary species from the
 694 home elevation (c) and intermediate for beneficiary species from high elevation (d). Therefore,
 695 older Retama had more species than younger Retama and expanded the elevation range of more
 696 species than younger Retama.



697

698 **Figure S3. Elevation range and composition of species under Retama 12 m² or less and**
 699 **open sites.** The site used in this study is at 630 masl. Expansion of home elevation was
 700 calculated as the difference in median home elevation reported for the species and the elevation
 701 of the site. (a) The number of species found under all Retama (black) and in open areas (grey)
 702 that originated from elevations greater than 1000 m above the site (-1000 m difference) to 500 m
 703 below the site (500 m difference). There were 104 species in total found under Retama shrubs
 704 and 61 species in total in open areas. (b) The proportion of the number of species found under
 705 Retama relative to the total species richness found from that median elevation both under Retama
 706 and in open sites. The black line represents a loess smoother with 95% CI. (d) The composition
 707 was statistically different between open and Retama communities as well as from older to
 708 younger Retama. Numbers represent Retama age, and the line represents the directional effect of
 709 age.



710

711 **Figure S4. Boxplot of probability model.** The distribution of random communities (box-
 712 whisker plots with black points) built from the species matrix based on the probability model for
 713 the species originating from below, from and above the site. The red points are the observed
 714 species richness found at open sites (0 year old) and under *Retama*.