

1 **A missing link between facilitation and plant species coexistence: nurses**
2 **benefit generally rare species more than common ones**

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13
14 **Running headline:** Facilitation and coexistence

15 **Summary**

- 16 1. Positive interactions among plants can increase species richness by relaxing
17 environmental filters and providing more heterogeneous environments. However, it is
18 not known if facilitation could affect coexistence through other mechanisms. Most
19 studies on plant coexistence focus on negative frequency-dependent mechanisms
20 (decreasing the abundance of common species); here we test if facilitation can
21 enhance coexistence by giving species an advantage when rare.
- 22 2. To test our hypothesis, we used a global dataset from drylands and alpine
23 environments and measured the intensity of facilitation (based on co-occurrences with
24 nurse plants) for 48 species present in at least 4 different sites and with a range of
25 abundances in the field. We compared these results with the degree of facilitation
26 experienced by species which are globally rare or common (according to the IUCN
27 Red List), and with a larger database including over 1200 co-occurrences of target
28 species with their nurses.
- 29 3. Facilitation was stronger for rare species (i.e., those having lower local abundances or
30 considered endangered by the IUCN) than for common species, and strongly
31 decreased with the abundance of the facilitated species. These results hold after
32 accounting for the distance of each species from its ecological optimum (i.e., the
33 degree of functional stress it experiences).
- 34 4. *Synthesis*: Our results highlight that nurse plants not only increase the number of
35 species able to colonize a given site, but may also promote species coexistence by
36 preventing the local extinction of rare species. Our findings illustrate the role that
37 nurse plants play in conserving endangered species and link the relationship between
38 facilitation and diversity with coexistence theory. As such they provide further
39 mechanistic understanding on how facilitation maintains plant diversity.

40 **Key-words:** biodiversity, coexistence, conservation biology, competition, frequency-
41 dependent mechanisms, plant-plant interactions, stabilizing mechanisms

42 **Introduction**

43 Positive interactions among plants are ubiquitous in nature, being present in biomes ranging
44 from tundra, deserts or alpine environments to rainforests (Brooker *et al.* 2008; Holmgren &
45 Scheffer 2010; McIntire & Fajardo 2013). These interactions are widely acknowledged to
46 increase plant diversity either because nurse plants improve environmental conditions beneath
47 their canopies (Bruno, Stachowicz & Bertness 2003; Brooker *et al.* 2008) or reduce
48 competitive exclusion among their neighbours (Levine 1999; Soliveres *et al.* 2011). Indeed,
49 facilitation helps to preserve evolutionary lineages that are less well adapted to the local
50 environment (Valiente-Banuet *et al.* 2006), and over a quarter of plant species from dryland
51 and alpine environments may depend on facilitative interactions globally (Soliveres &
52 Maestre 2014). However, to effectively maintain diversity, facilitation needs to not only
53 increase the number of species able to colonize a given site, but also to promote stable
54 coexistence between them. The large research effort devoted to understanding the
55 implications of facilitative interactions for the maintenance of diversity has mostly focused on
56 how these interactions reduce environmental constraints, and therefore increase the number of
57 species able to colonize a given site (e.g., Hacker & Gaines 1997; Cavieres & Badano 2009;
58 Soliveres & Maestre 2014). However, the role of these interactions in promoting species
59 coexistence has rarely been addressed, and the few attempts have used theoretical or
60 modelling approaches (Molofsky, Bever & Antonovics 2001; Gross 2008; Greenspoon &
61 M`Gonigle 2013; but see Hart & Marshall 2013; Gross *et al.* 2015).

62 Species coexistence is enhanced by stabilizing mechanisms, which result in negative
63 frequency-dependent population growth rates, or through processes that equalize fitness
64 between species (Chesson 2000). Most studies of coexistence conducted to date have focused

65 on negative interactions such as increased herbivore or pathogen attack on abundant species,
66 or higher competition within than between species. These mechanisms lead to lower
67 population growth rates for abundant species and prevent them from competitively excluding
68 other species (e.g. Levine & HilleRisLambers 2009; Bagchi *et al.* 2014). However, much less
69 attention has been paid to the potential for positive interactions to benefit species when they
70 are rare and to increase their abundance (but see Gross 2008; Hart & Marshall 2013; Gross *et*
71 *al.* 2015).

72 We hypothesize that positive interactions among plants can be an important
73 mechanism enhancing the populations of rare, rather than abundant, plant species, and
74 therefore promoting species coexistence. This notion of facilitation as a coexistence
75 mechanism differs from, and complements, that of microhabitat amelioration (or niche
76 creation), which is often invoked as the main mechanism behind the positive effect of
77 facilitation on diversity (reviewed in Bruno *et al.* 2003; McIntire & Fajardo 2013). Habitat
78 amelioration increases the performance of species less adapted to local environmental
79 conditions regardless of their abundance. Indeed, some manipulative experiments using
80 relatively common species have successfully shown that they are facilitated under
81 environmental conditions to which they are less well adapted (e.g., Tielbörger & Kadmon
82 2000; Callaway *et al.* 2002). Negative frequency-dependent facilitation, instead, might
83 increase the populations of species that are locally rare, regardless of whether they are under
84 optimal ecological conditions or not. Rare species might be rare simply because they are poor
85 competitors or because they show low reproductive performance (see Dawson, Fischer & Van
86 Kleunen 2012 and references therein), and do not need to be suffering more stress than the
87 species that are more common in the same location. Several mechanisms may operate to
88 promote stronger facilitation for locally rare than for common species, although these have
89 been rarely addressed. First, nurses provide heterogeneous habitats that could help rare plants

90 to escape from competition by altering the identity of neighbouring species, and the
91 competitive interactions among them, beneath their canopies (Levine 1999; Soliveres *et al.*
92 2011; McIntire & Fajardo 2013). Second, the beneficial effects of nurse plants on
93 reproduction (e.g, Tielbörger & Kadmon 2000; Callaway *et al.* 2002) may be particularly
94 strong for rarer species because they have lower seed set than common species (e.g., Holmes,
95 James & Hoffmann 2008). Third, nurse plants can reduce the amount of pathogens present in
96 soil (Van der Puten 2009), which would benefit rare species as they are especially sensitive to
97 them (Klironomos 2002).

98 Here, we hypothesize that rare species generally benefit more from facilitation than
99 common species. To test this hypothesis, we used co-occurrence data for 48 species, which
100 varied strongly in local abundance across the different sites in which they occurred. We
101 compare these results with a global database including over 1200 co-occurrences of target
102 species and their potential nurses. Finally, for some species we were also able to acquire data
103 on rarity from the International Union for Conservation of Nature (IUCN) red list and to test
104 whether facilitation was more likely for globally rare than globally common species. A
105 relationship between abundance and facilitation could be due to: i) negative frequency-
106 dependence (i.e., facilitation is more important for rare species), or ii) stronger facilitation for
107 a species when it is at low abundance because it is far from its ecological optimum (Choler,
108 Michalet & Callaway 2001; Greiner La Peyre *et al.* 2001; Liancourt, Callaway & Michalet
109 2005; Valiente-Banuet *et al.* 2006; Gross *et al.* 2010; Soliveres *et al.* 2011). To separate these
110 processes we used both i) the average abundance of each species (a widely accepted measure
111 of rarity; Gaston 1994; Pimm & Jenkins 2010) and ii) the distance of each species to its
112 ecological optimum (i.e., functional stress; Lortie 2010) as predictors of facilitation.

113

114

115 **Materials and Methods**

116 THE DATABASE

117 We used the database presented in Soliveres & Maestre (2014) and extracted the available
118 information on pairwise co-occurrences between the dominant nurse plant species and the rest
119 of the species present in the community. From the 2685 pairwise combinations obtained, we
120 selected those species occurring in at least 4 sites in the database (48 species accounting for
121 320 occurrences in total) for further analyses. These occurrences came from 18 different
122 studies performed along elevational, latitudinal or aridity gradients, and covered sites in 10
123 different countries (see details in Appendix S1; full database in Appendix S2). To
124 complement these results, we also used all the pairwise combinations from Soliveres &
125 Maestre (2014) in which the target species had a minimum of 10 individuals ($N = 1215$), and
126 analyzed whether or not they were facilitated and how this changed with their level of local
127 rarity.

128 We used two different and complementary criteria for the quantification of rarity: i)
129 local abundance (as a continuous variable) and ii) IUCN category (as a categorical variable).
130 First, we measured rarity as the average number of individuals present in areas away from the
131 nurse plants, across all sites in which each species occurred. Together with range size,
132 abundance is widely used as a measure of rarity (e.g., Rabinowitz 1981; Gaston 1994). A low
133 average number of individuals indicates that the species is locally rare (Pimm & Jenkins
134 2010), although the spatial scale at which this abundance is measured is, of course, important
135 (Gaston 1994). We used abundance at the local scale because it is the most relevant spatial
136 scale to quantify the role of facilitation as a coexistence mechanism. In order to coexist
137 species must be able to increase from rare (Chesson 2000; Levine & HilleRisLambers 2009)
138 and therefore for facilitation to promote coexistence it must be stronger for species that are at
139 low abundance within a community than for those which are dominant. We used species'

140 abundances in areas away from nurse plants (i.e., open interspaces) as the measure of rarity
141 because this excludes the effect of plant-plant interactions. Our second criterion (IUCN's
142 category) is probably the most widespread formal use of "rarity" in ecology (Gaston 1994),
143 and directly links our results with biological conservation. It therefore provides a
144 complementary definition of rarity, which is fully independent from our measure of
145 facilitation (see below), adding confidence to our results. In this regard, we were able to
146 classify 32 species from the database according to their extinction risk, using data from the
147 IUCN red list (<http://www.iucnredlist.org/search>; see details below).

148

149 MEASURING FACILITATION

150 We quantified facilitation by comparing the number of individuals of a given species found
151 beneath nurse plants vs. those found in areas away from neighbours (hereafter open
152 interspaces), taking into account the sampling effort spent in each microsite (nurse and open
153 areas). From these co-occurrence data we calculated the Relative Interaction Index (RII
154 hereafter; Armas, Ordiales & Pugnaire 2004), which is a relativized metric of facilitation
155 ranging from -1 (strong competition) to 1 (strong facilitation). $RII = (P_N - P_O) / (P_N + P_O)$, where
156 P_N is the number of individuals beneath the nurse and P_O the number in the open.

157 Observational approaches are insufficient to tease apart whether spatial associations are
158 caused by facilitation or by other mechanisms (e.g. habitat sharing). This is a clear limitation
159 that should be considered when interpreting the results of any observational study. However,
160 although this might affect an overall estimate of facilitation we do not expect it to affect the
161 relationship between facilitation and abundance because it is unlikely that these other
162 processes would lead to rare rather than common species occurring more frequently with
163 nurses.

164

165 The number of individuals of each species in the areas away from the nurse plants was
166 used both as our measure of rarity and to derive the facilitation metrics used, which may
167 cause spurious correlations between our measures of facilitation and local abundance. To
168 avoid these spurious correlations, appropriate randomizations are required to isolate the
169 spurious effects (those when all biological mechanisms are removed) and test the significance
170 and effect size of the relationship between facilitation and abundance, (Brett 2004). Thus, we
171 performed 1000 randomizations of the occurrence of individuals (see Cavieres & Badano
172 2009, Dvorsky *et al.* 2013 for related approaches). We did this for each pairwise interaction
173 by swapping individuals between the two microsites (nurse and open) whilst keeping the total
174 number of individuals observed per target species constant. This ensures that the relative
175 abundance of each species did not vary. From these randomizations we calculated the
176 standardized effect size (SES) of the observed RII as $SES = (M_{obs} - M_{sim}) / SD_{sim}$ (Gotelli
177 2000), where M_{obs} are the RII values obtained from our data, and M_{sim} and SD_{sim} are the
178 average and standard deviations, respectively, of the RII values obtained from the 1000
179 randomizations. Standardized effect sizes are frequently used in other contexts (e.g., analyses
180 of species co-occurrence or phylogenetic dispersion; Gotelli 2000; Kembel *et al.* 2010) to
181 produce a metric corrected for the effect of spurious correlations that allows comparison
182 between communities differing in species richness or species differing in local abundances.
183 Hence, we use the SES of the RII (RII_{ses} , hereafter) for further analyses. Positive values of
184 RII_{ses} are interpreted as more positive associations of the target species with the nurse than
185 expected by chance (i.e. more facilitation than expected by chance), while negative values
186 indicate the opposite. Results comparing the raw data with the randomizations instead of the
187 RII_{ses} were qualitatively the same (Appendix S3; Fig. S3.1) and these are not further
188 discussed.

189

190 STATISTICAL ANALYSES

191 We conducted four analyses to test the relationship between rarity and facilitation:
192 first, we tested whether generally rare species (i.e., those with low abundances in all the sites
193 of our dataset) are more facilitated than generally common ones. To do this, we fitted a linear
194 regression to evaluate the relationship between the mean abundance (individuals in the open)
195 and mean RII_{ses} (across all sites where the species was present) for each of the 48 species
196 present in four or more sites.

197 Second, we used all co-occurrence data from target species with more than 10
198 individuals in total (including those in the open and beneath a given nurse; 1215 pairwise co-
199 occurrences in total). We divided these co-occurrences in 11 abundance classes based upon
200 the number of individuals of the target species in the open (our surrogate of rarity): 0-5 ($N =$
201 299), 6-10 ($N = 245$), 11-15 ($N = 160$), 16-20 ($N = 119$), 21-25 ($N = 97$), 26-30 ($N = 60$), 31-
202 35 ($N = 26$), 36-40 ($N = 35$), 41-45 ($N = 24$), 46-50 ($N = 19$), 51-60 ($N = 23$), 61-70 ($N = 21$),
203 71-100 ($N = 21$), 101-200 ($N = 35$), 201-300 ($N = 9$) and > 300 ($N = 22$) individuals in the
204 open. We then plotted the number of individuals in the open (x-axis) vs. the number of
205 individuals beneath the nurse (y-axis). Values higher than the 1:1 line would indicate
206 facilitation, whereas those below would indicate competition. We compared significant
207 departures from the 1:1 line (individuals in the open = individuals beneath the nurse) by using
208 t-tests including all species within each abundance class.

209 Third, we used a widely accepted global classification of rarity, the IUCN red list,
210 to support results from the first two analyses, and to provide a link between facilitation
211 research and conservation biology. Within the 2685 occurrences in our dataset, 27 species (71
212 occurrences in our data) were considered common (“least concern” according to the UICN
213 classification), and five species (9 occurrences) were considered rare (“endangered” or
214 “threatened” according to the IUCN). When the same species was found in several sites,

215 results were averaged across all sites to obtain a single measure for each one of the 32 species.
216 We compared the RII_{ses} between these two groups (rare and common). For each group
217 separately we also tested whether the RII was significantly different to 0 by using t-tests.

218 Fourth, it may be argued that our target species have low average abundances
219 because they are far from their environmental optimum rather than because they are generally
220 rare. We therefore tested whether or not target species that were far from their environmental
221 optimum experienced greater facilitation. In each site ($N = 320$) we calculated the abundance
222 of each of the 48 species (from analysis one) relative to its maximum abundance across any
223 site in our database (hereafter relative abundance). A lower relative abundance in areas away
224 from neighbours indicates that a given species is at a greater distance from its optimum in a
225 given site, and thus that the species is experiencing greater stress in that location (Lortie
226 2010). We then analysed the effect of relative abundance and the average frequency of a
227 given species (our measure of overall rarity; log-transformed to obtain a linear relationship)
228 on facilitation. Both variables were only weakly correlated ($\rho = -0.21$); thus, they could both
229 be included as predictors in the same model. The fourth analysis, therefore, was a linear
230 mixed model with average frequency and relative abundance as fixed effects and with study
231 site and species as random effects. If average frequency remains a significant predictor in this
232 model, after accounting for changes in the abundance relative to the maximum (i.e. distance to
233 the ecological optimum), then functional stress could not entirely account for negative
234 frequency-dependence in facilitative interactions. We assessed the significance of fixed
235 effects using Likelihood ratio tests. We did not measure functional stress as the decline in
236 abundance across environmental gradients because i) some sites were not sampled across such
237 gradients, and this would reduce our sample size, and ii) some species were sampled across
238 more than one environmental gradient, which could confound our results.

239 Simulations were performed using MATLAB version 7.0 (The MathWorks Inc.,
240 Natick, Massachusetts). The rest of analyses were performed using the lme4 version 1.0-5
241 (Bates, Maechler & Bolker 2011) package for R version 3.0.2 (R Development Core Team
242 2013).

243

244 **Results**

245 Rare species were more strongly facilitated than common species (Figs. 1 and 2). Facilitation
246 decreased with the average number of individuals of each target species in open areas, our
247 surrogate of rarity (Fig. 1). Comparison between these results and the null envelope formed by
248 the 1000 random simulations (shown as grey boxes in Fig. 1) indicated that this relationship
249 was much weaker when analyzing randomized data, and therefore the relationship between
250 rarity and facilitation was ecologically significant and not only a spurious correlation (Fig. 1).
251 The weaker relationship in the simulated data is shown by a shallower slope, and lower
252 intercept and R^2 than in the observed data (see box-plots in Fig. 1). The analysis of the larger
253 database gave the same result and also showed that target species were generally more
254 facilitated when they were at low local abundance in the open (Fig. 2). Facilitative
255 interactions, instead, shifted to neutral or negative (i.e. competition) when the target species
256 became locally abundant.

257 We also found evidence of higher facilitation for endangered than common species
258 according to the IUCN classification. Rare ("endangered" or "threatened") species ($RII_{ses} =$
259 0.85 ± 0.44 , mean \pm SE, $N = 5$) experienced more facilitation than common ones ($RII_{ses} =$
260 0.06 ± 0.19 , $N = 27$), although this difference was not significant, probably because of the
261 small number of rare species in our sample (Fig. 3). For both rare and common species, RII_{ses}
262 was not significantly different from zero ($t < 2$; $P > 0.10$ in both cases). However, 80% of the
263 RII_{ses} for rare species were positive, and removing an outlier resulted in a significantly

264 positive RII_{ses} for rare species ($t = 3.8$; $df = 3$; $P < 0.05$; $t = 3.9$; $df = 7$; $P < 0.01$ if using all
265 data available instead of the averages by species). Conversely, ~56% of the RII_{ses} for common
266 species were negative. This indicates that a large majority of the interactions involving rare
267 species were facilitative, whereas for common species competition was as common as
268 facilitation.

269 The stronger facilitation for rare than for common species remained even after
270 accounting for functional stress, suggesting that this result was not only driven by the distance
271 of each target species to its optimum (linear mixed model [effect of rarity on facilitation]: $\chi^2 =$
272 20.8 ; $P < 0.0001$; $\beta = -1.009 \pm 0.201$; $t = -5.01$). The relative abundance of the species (our
273 measure of functional stress), which varied between 0 and 100% within our dataset, was also
274 an important predictor of facilitation. RII_{ses} linearly decreased with reduced functional stress
275 (increased relative abundance; Fig. 4). This indicates that species growing in conditions
276 further from their ecological optimum, and therefore experiencing greater stress, did benefit
277 more from facilitation. These results are also very unlikely to be driven by spurious
278 correlations as our response variable (percentage decline in abundance regarding the
279 maximum observed) is not directly a function of the predictor (facilitation metric calculated
280 with local abundances; see Fig. S3.2 in Appendix S3). These results indicate that facilitation
281 is stronger for both rarer species and those suffering more stress.

282

283 **Discussion**

284 The role that positive interactions among plants play in the maintenance of biodiversity has
285 received considerable attention (e.g., Hacker & Gaines 1997; Brooker *et al.* 2008; Cavieres &
286 Badano 2009; McIntire & Fajardo 2013; Soliveres & Maestre 2014). However, previous
287 research efforts have focused on how facilitation increases the number of species that can
288 colonize a given site, but have rarely evaluated how facilitation can enhance coexistence by

289 benefiting the rare species within a community more than the common ones (see also Gross
290 2008; Hart & Marshall 2013; Gross *et al.* 2015). Our results, although observational, suggest
291 that facilitation is stronger for rare species, meaning that this mechanism could help maintain
292 diversity and stabilize coexistence. The empirical evidence from multiple species and sites
293 provided here builds upon previous modelling (Gross 2008), two-species (Hart & Marshall
294 2013) and regional (Gross *et al.* 2015) studies, and suggests a link between facilitation and
295 plant coexistence. To fully test for density dependence in facilitation further studies should
296 manipulate species abundances and measure facilitation, however our results provide
297 evidence that a key condition for facilitation to promote coexistence is met in natural
298 communities.

299 Most facilitation research to date has focused on the increase in facilitation intensity
300 with functional stress or across environmental gradients (Choler *et al.* 2001; Greiner la Peyre
301 *et al.* 2001; Liancourt *et al.* 2005; Gross *et al.* 2010; Fig. 4). Our results indicate that, in
302 addition to these effects frequency-dependent processes could be major drivers of facilitation.
303 This pattern proved to be general across a database of 18 different studies covering a wide
304 range of environmental conditions and community types (Figs. 1 and 2). This result is of
305 particular importance, as it places changes in the strength of pairwise interactions across
306 multiple species within the context of population dynamics, a fundamental first step to link
307 facilitation with species coexistence (Hart & Marshall 2013). Additionally, our findings help
308 to link the spatial storage effect (Sears & Chesson 2007) and facilitation. The operation of the
309 spatial storage effect relies on the correlation between response to environment (E) and
310 competition (C) for the dominant species. In short, this means that dominant species occupy
311 the most productive patches but it comes at a cost of a much higher intra-specific competition
312 that controls their population growth rates. However, the spatial storage effect also assumes
313 the lack of E-C correlations for the rare species (Sears & Chesson 2007). In this regard, our

314 results and previous literature suggests that nurse plants may provide environmentally
315 favorable sites for the rare species that are free from strong competition by the dominant ones
316 (see also Soliveres *et al.* 2011; McIntire & Fajardo 2014). To further support these results and
317 to fully test the conditions necessary for the operation of the spatial storage effect,
318 competition-removal experiments performed beneath and outside the nurse (such as in Cuesta
319 *et al.* 2010) combined with a manipulation of target species abundance would be needed.
320 Such experiments could fully test the idea that nurses increase coexistence by providing
321 competition free sites for species as they become rarer.

322 Our observational study does not allow us to test the potential mechanisms behind the
323 positive effect of nurses on rare species; however, these may include the provision of safe
324 sites from competition (discussed above), the beneficial effects of neighbours on reproductive
325 performance, or a reduction in pathogen damage for rare species. Interestingly, these factors
326 have been shown separately to be important drivers of rarity within communities (Klironomos
327 *et al.* 2002, Holmes *et al.* 2008, Dawson *et al.* 2012) and have also been identified as
328 mechanisms of facilitation (Tielbörger & Kadmon 2000, Van der Puten 2009, McIntire &
329 Fajardo 2013). However, to the best of our knowledge, no study to date has assessed the role
330 of these factors as mechanisms driving negative frequency-dependence in facilitation,
331 something that certainly deserves further attention. Experiments addressing the effect of
332 control vs. sterilized soil from beneath the nurse (e.g., Rodríguez-Echevarría *et al.* 2013) on
333 species differing in local rarity, or quantifying the abundance of pathogens (e.g., Gómez-
334 Aparicio *et al.* 2012), can help to disentangle the role of pathogens in the frequency-
335 dependent component of facilitation. Lastly, we also see great potential for experiments
336 calculating population growth rates in response to neighbours (number of seeds or new
337 seedlings per capita; e.g., Hart & Marshall 2013) of species differing in local abundance (see

338 also Choler *et al.* 2001) and quantifying niche and fitness differences (e.g., Godoy, Kraft &
339 Levine 2014) for species in the presence and absence of nurses.

340 Interestingly, our results reconcile the highly unstable dynamics and species
341 extinctions predicted by mathematical models for systems governed by facilitative
342 interactions (“evolutionary suicide”; Gyllenberg & Parvinen 2001; Kéfi *et al.* 2008) with the
343 positive relationships between facilitation and diversity found in many studies (e.g., Cavieres
344 & Badano 2009; Soliveres & Maestre 2014). Evolutionary suicide occurs when facilitated
345 species, which depend on nurses to recruit, grow and competitively exclude their own nurses.
346 This prevents the further recruitment of this species along with other facilitated species, and
347 theoretically leads to species extinctions or to sharp reductions in population size (Gyllenberg
348 & Parvinen 2001). However, our results suggest that facilitation predominantly occurs for the
349 rarer species, which constitute the majority of the species in communities (Odum 1954;
350 Gaston 1994). Thus, the facilitated species are less likely to reach densities high enough to
351 outcompete their nurses, and they may benefit less from facilitation the more common they
352 become, meaning that facilitation will generally increase species richness. This is in line with
353 a recent global study on bidirectional relationships between nurse species and their
354 neighbours, in which the authors found that cover, but not richness, of the facilitated species
355 reduced nurse performance (Schöb *et al.* 2014). Facilitating dominant species (those
356 accounting for a major proportion of plant cover) could drive a nurse to local extinction, as
357 anticipated by mathematical models; however, facilitating rare species (those forming the
358 bulk of species richness) might not reduce nurse performance. Facilitating rare species could
359 even be beneficial. For example, Schöb *et al.* (2014) found that a higher richness amongst the
360 facilitated species increased the reproductive performance of nurses. This example illustrates
361 how the often overlooked frequency-dependent component of facilitative interactions helps to

362 reconcile the contrasting empirical and modelling results regarding the role of facilitation in
363 the maintenance of species diversity.

364

365 CONCLUSION

366 Facilitation (measured as spatial association between species) has an important frequency-
367 dependent component and it is stronger for rare than for common species. This may enhance
368 species coexistence by reducing local extinctions of rare species, and also has important
369 implications for the conservation of globally endangered species. Most studies seeking
370 mechanisms by which rare species can be maintained in communities have focused on the
371 processes reducing the abundance of dominant species, and thus have seldom considered
372 positive interactions that could increase the abundance of rare species. Our findings
373 empirically show negative frequency-dependence in facilitation, a mechanism previously
374 ignored by most theories attempting to explain how facilitation can maintain plant diversity. It
375 also adds to previous attempts to introduce facilitation into mainstream ecological theory by
376 providing a necessary link between the known positive effects of facilitation on diversity and
377 modern coexistence theory.

378

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393

394 **Data Accessibility**

395 The data used in this study are fully accessible as Appendix S2 and in figshare:
396 Soliveres, S. & Maestre, F.T. (2014) Data from "plant–plant interactions, environmental
397 gradients and plant diversity: a global synthesis of community-level studies". *figshare*,
398 <http://dx.doi.org/10.6084/m9.figshare.963585>

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Supporting Information

524 Additional supporting information may be found in the online version of this article:

525 **Appendix S1.** Details of the dataset

526 **Appendix S2.** Main dataset used in this study

527 **Appendix S3.** Sensitivity analyses

528

529 **Figure legends**

530 **Figure 1.** The relationship between facilitation and rarity for those species occurring in, at
531 least, four different sites ($N = 48$ species, 320 occurrences). The relationship between the
532 standardized effect size of our facilitation metric (Relative Interaction Metric; RII_{ses}) and the
533 number of individuals of each target species across all the sites in which it was present is
534 plotted. The regression line (black) and 95% confidence interval (blue) fitted to the data are
535 shown. The regression line (red) and 95% confidence interval (grey) of the 1000 random
536 simulations are also shown for comparison with the observed results. The inset panel shows
537 the comparison between the regression parameters of the observed data (blue dash) and the
538 1000 random simulations (box plots showing the median, 25% and 75% quartiles).

539

540 **Figure 2.** Relationship between the number of individuals found in the open and those found
541 associated to a nurse for 11 different local abundance classes (see *Material & Methods*). For
542 this analyses all species from our database with more than 10 individuals in a given site were
543 selected ($N = 1215$). Significant departures (t-test comparing individuals in the open vs. nurse
544 microsites) from the 1:1 line are shown in green (competition) or red (facilitation).

545

546 **Figure 3.** The degree of facilitation metric for those species from our database considered rare
547 ($N = 5$) or common ($N = 27$) in the IUCN Red List.

548

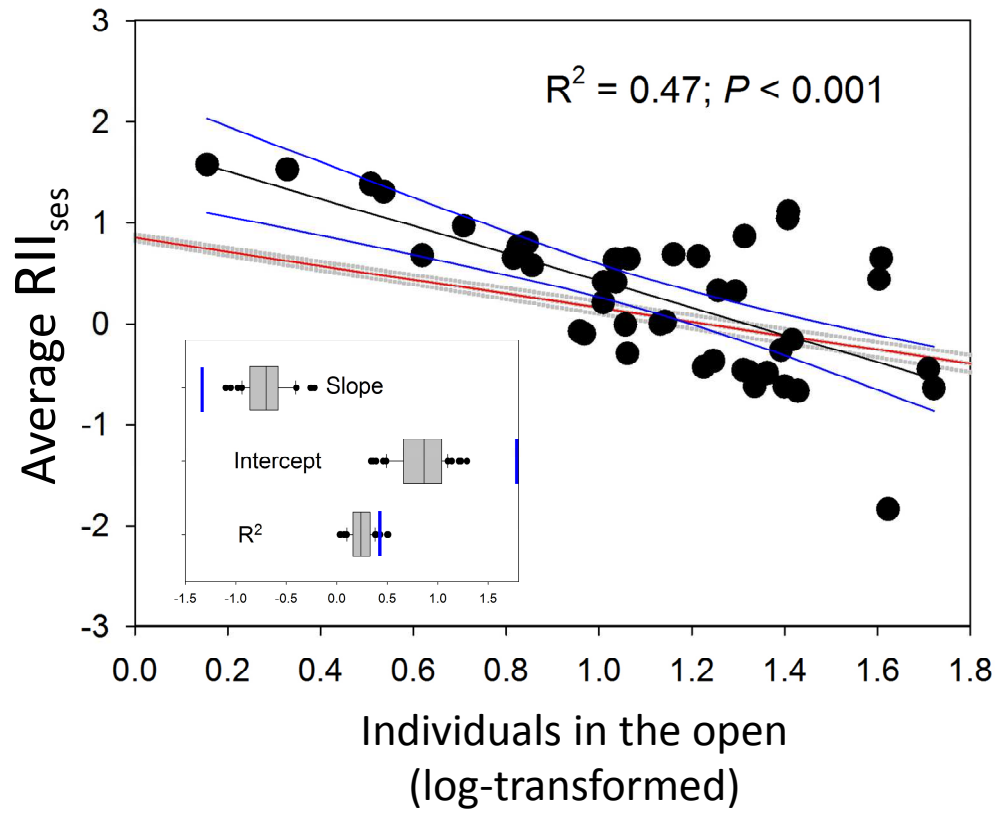
549 **Figure 4.** Relationship between the standardized effect sizes of our facilitation metric
550 (Relative Interaction Metric; RII_{ses}) and functional stress of all species occurring in, at least,
551 four sites ($N = 48$ species, 320 occurrences). Functional stress was calculated based on
552 relative abundance (% of change in local abundance relative to the maximum observed for
553 each species). Slopes, t-values and p-values for the effect of functional stress come from

554 linear mixed models. These parameters were obtained after accounting for study site, species
555 and average frequency (the latter centered to ease interpretation).

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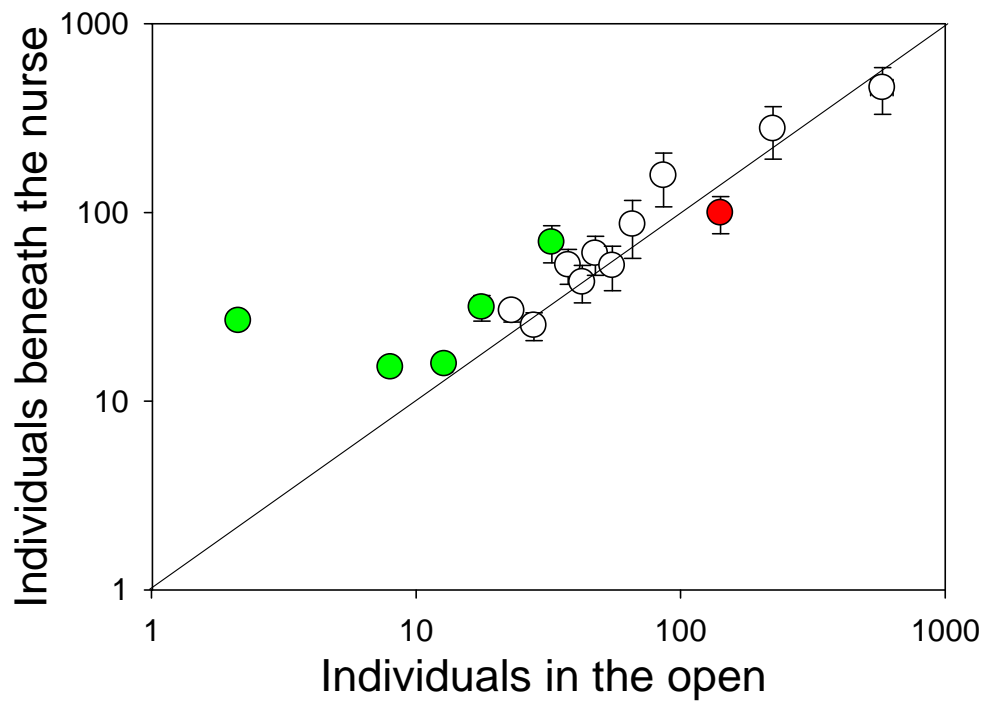
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560 **Figure 1**

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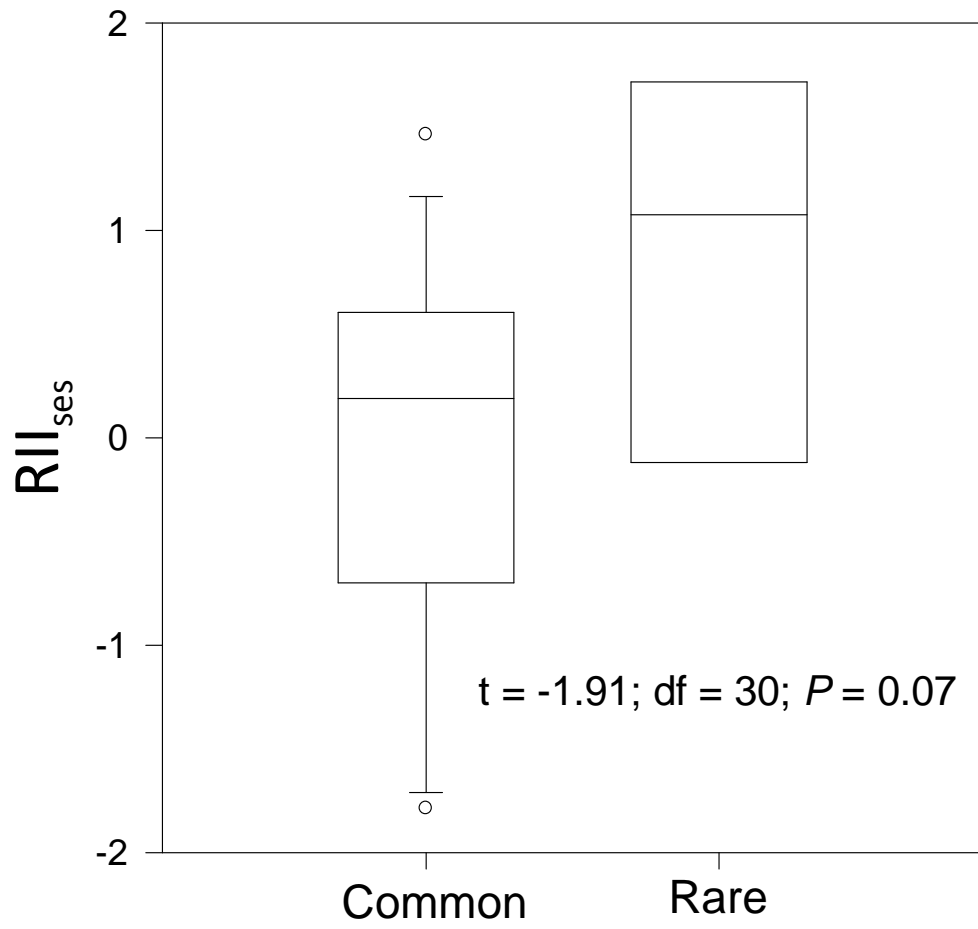


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563 **Figure 2**

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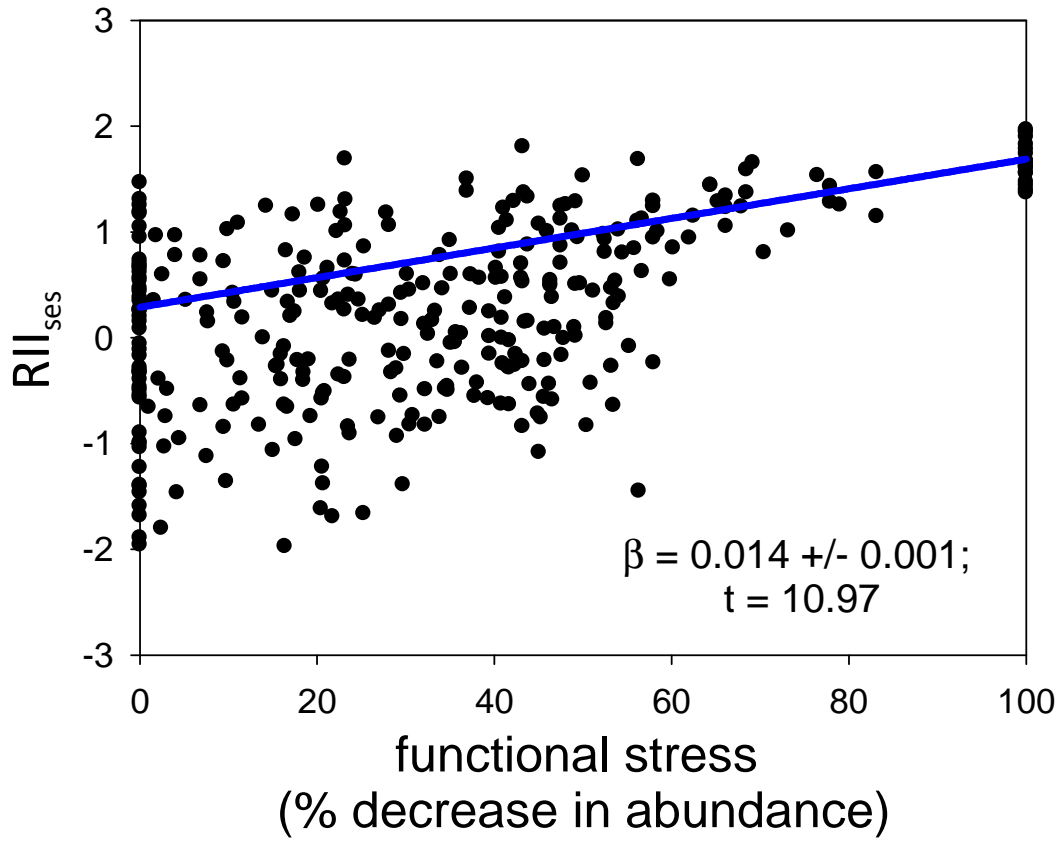
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567 **Figure 3**

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571 **Figure 4**