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

Santiago Soliveres[1*], Fernando T. Maestre[2], Miguel Berdugo[2] and Eric Allan[1]

[1]Institute of Plant Sciences, University of Bern, Altenbergrain 21, 3013 Bern, Switzerland

[2]Área de Biodiversidad y Conservación, Departamento de Biología y Geología, Física y Química Inorgánica, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, Calle Tulipán S/N, 28933 Móstoles, Spain

[*]Correspondence author. E-mail: Santiago.soliveres@ips.unibe.ch.

Running headline: Facilitation and coexistence

Summary

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

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

Introduction

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

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

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

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

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

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

Materials and Methods

THE DATABASE

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

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

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

MEASURING FACILITATION

We quantified facilitation by comparing the number of individuals of a given species found beneath nurse plants vs. those found in areas away from neighbours (hereafter open interspaces), taking into account the sampling effort spent in each microsite (nurse and open areas). From these co-occurrence data we calculated the Relative Interaction Index (RII hereafter; Armas, Ordiales & Pugnaire 2004), which is a relativized metric of facilitation ranging from -1 (strong competition) to 1 (strong facilitation). RII = $(P_N-P_O)/(P_N+P_O)$, where P_N is the number of individuals beneath the nurse and P_O the number in the open. Observational approaches are insufficient to tease apart whether spatial associations are caused by facilitation or by other mechanisms (e.g. habitat sharing). This is a clear limitation that should be considered when interpreting the results of any observational study. However, although this might affect an overall estimate of facilitation we do not expect it to affect the relationship between facilitation and abundance because it is unlikely that these other processes would lead to rare rather than common species occurring more frequently with nurses.

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

STATISTICAL ANALYSES

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

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

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

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

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

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

Results

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

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

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 data available instead of the averages by species). Conversely, ~56% of the RII_{ses} for common species were negative. This indicates that a large majority of the interactions involving rare species were facilitative, whereas for common species competition was as common as facilitation.

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

Discussion

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

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

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

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

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

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

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

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

CONCLUSION

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

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Data Accessibility

The data used in this study are fully accessible as Appendix S2 and in figshare:

Soliveres, S. & Maestre, F.T. (2014) Data from "plant–plant interactions, environmental gradients and plant diversity: a global synthesis of community-level studies".*figshare*, http://dx.doi.org/10.6084/m9.figshare.963585

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Supporting Information

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

Appendix S1. Details of the dataset

Appendix S2. Main dataset used in this study

Appendix S3. Sensitivity analyses

Figure legends

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

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

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

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

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

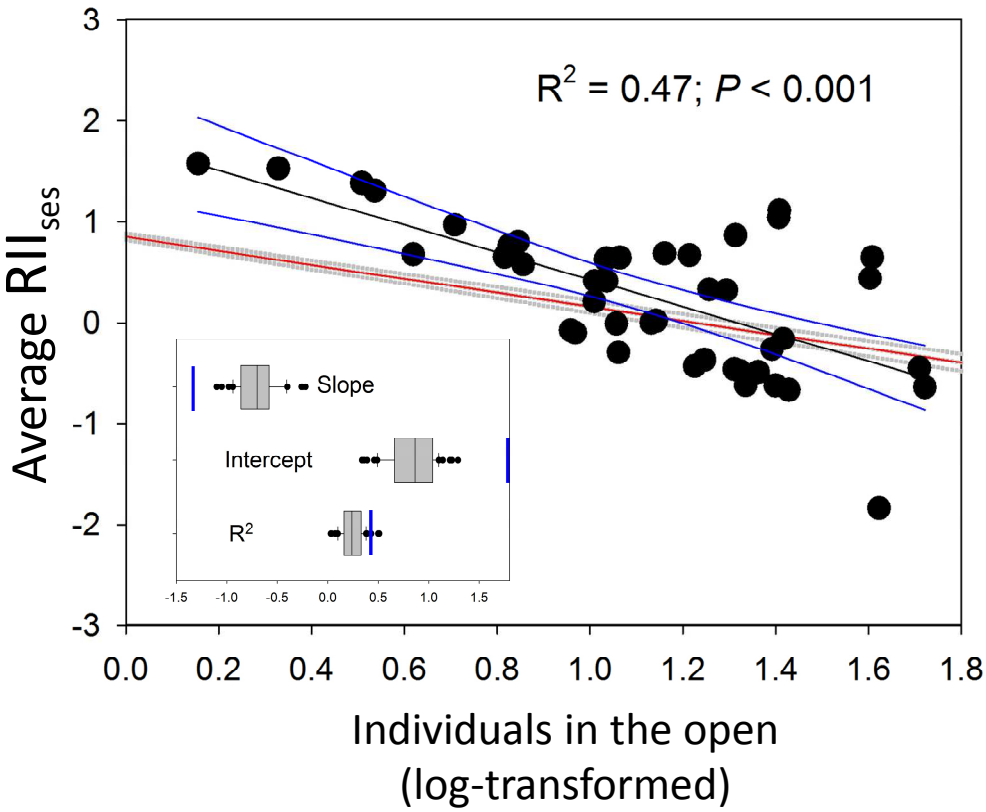
R2 = 0.47; P < 0.001
Average RIIses
Individuals in the open
(log-transformed)
Slope
Intercept
R2
3
2
1
0
-1
-2
-3
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5

Figure 1

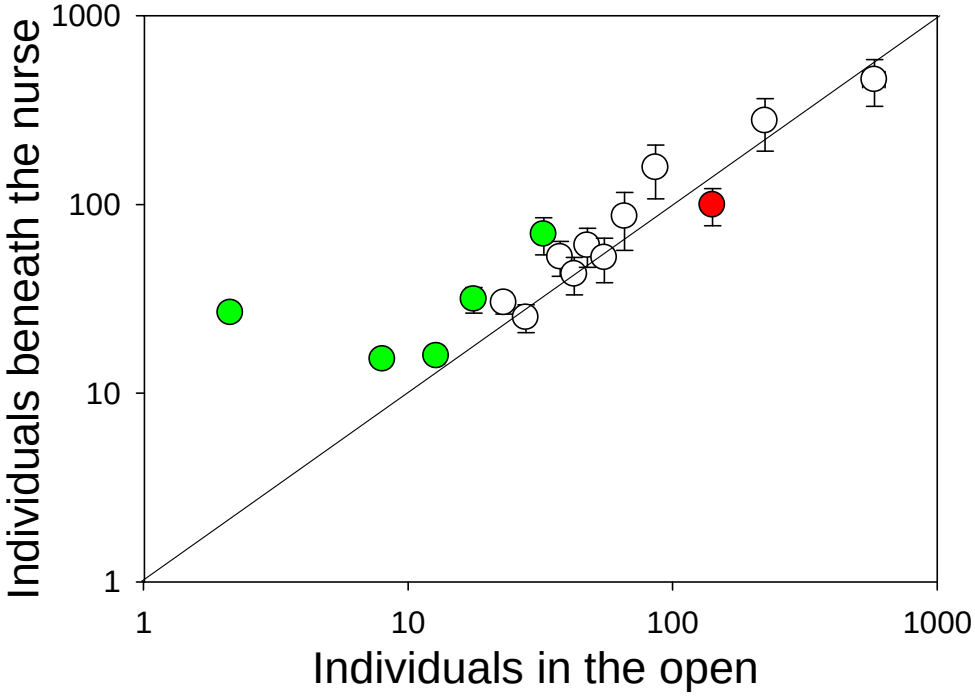
Individuals beneath the nurse
1000
100
10
1
1
10
100
1000
Individuals in the open

Figure 2

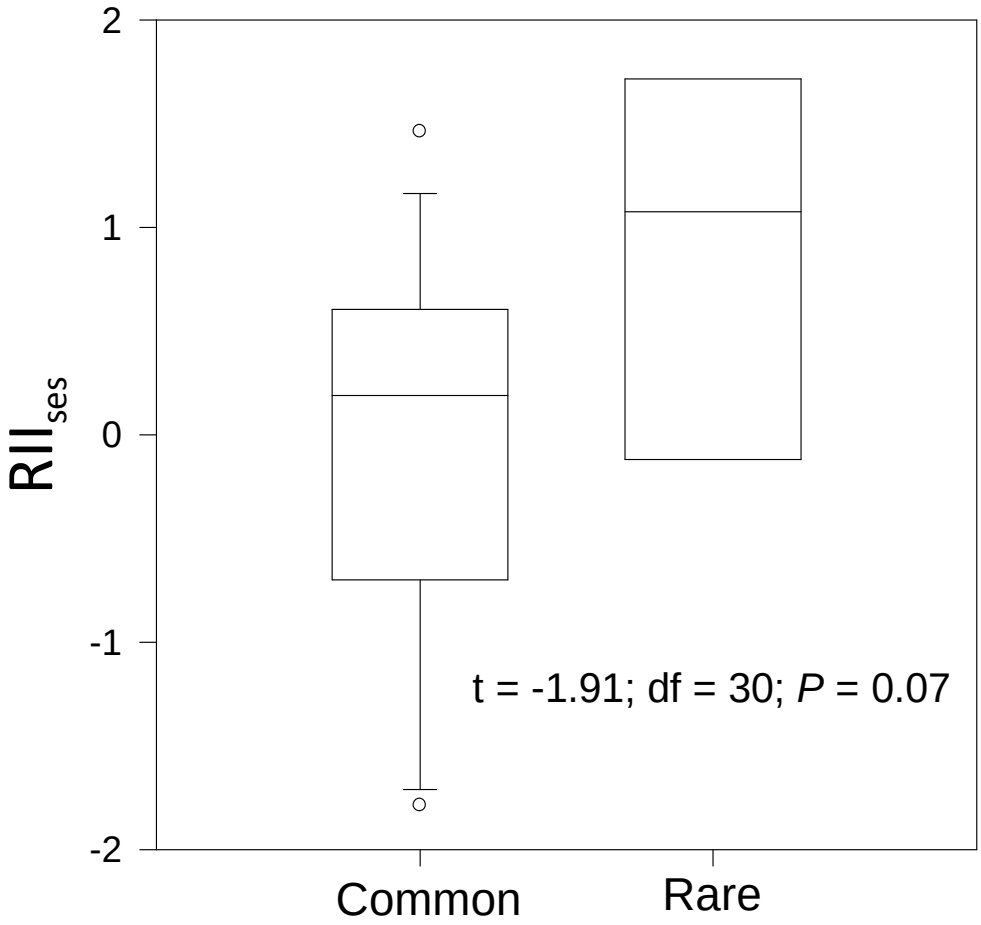

Figure 3

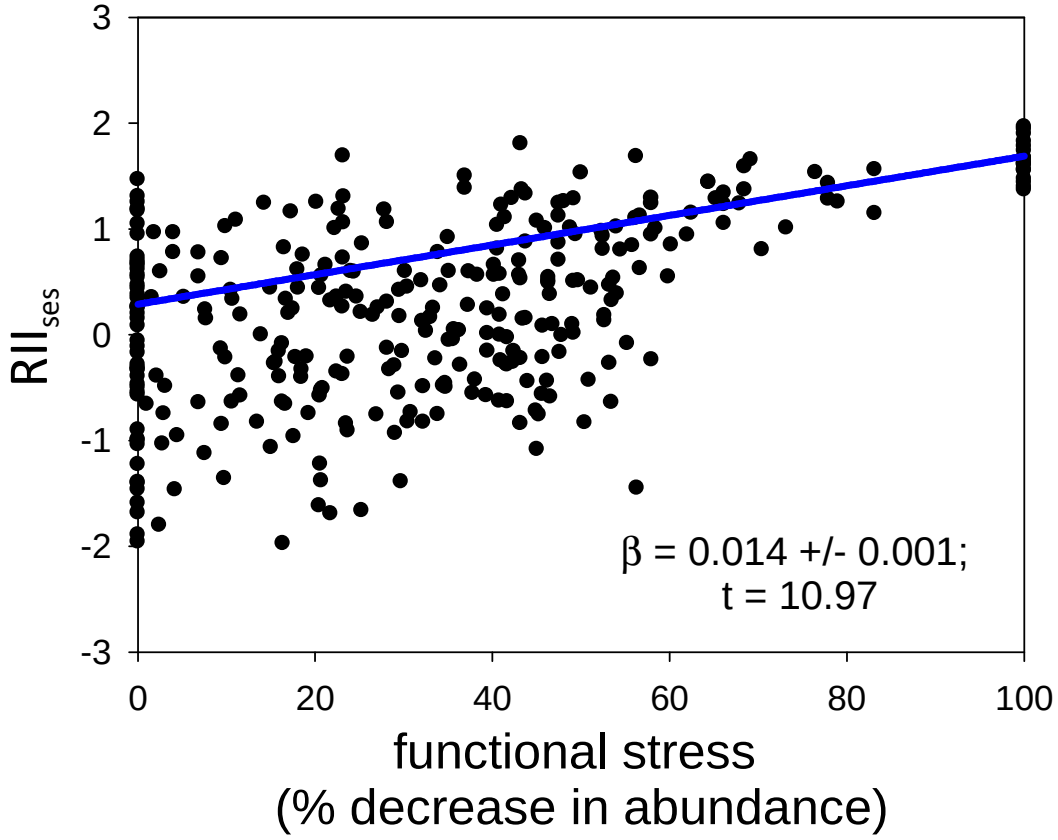
3
2
1
0
-1
-2
-3
RII$_{ses}$
0
20
40
60
80
100
functional stress
(% decrease in abundance)
β = 0.014 +/- 0.001;
t = 10.97

Figure 4