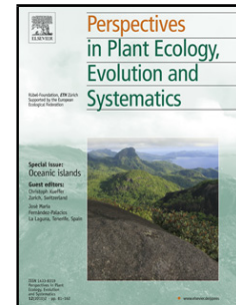


Accepted Manuscript

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PII: S1433-8319(14)00045-6
DOI: <http://dx.doi.org/doi:10.1016/j.ppees.2014.05.001>
Reference: PPEES 25229

To appear in:

Received date: 26-1-2014
Revised date: 2-5-2014
Accepted date: 3-5-2014

Please cite this article as: Soliveres, S., Maestre, F.T., Bowker, M.A., Torices, R., Quero, J.L., García-Gómez, M., Cabrera, O., Cea, A., Coaguila, D., Eldridge, D.J., Espinosa, C.I., Hemmings, F., Monerri, J.J., Tighe, M., Delgado-Baquerizo, M., Escolar, C., García-Palacios, P., Gozalo, B., Ochoa, V., Blones, J., Derak, M., Ghiloufi, W., Gutiérrez, J.R., Hernández, R.M., Noumi, Z., Functional traits determine plant co-occurrence more than environment or evolutionary relatedness in global drylands, *Perspectives in Plant Ecology, Evolution and Systematics* (2014), <http://dx.doi.org/10.1016/j.ppees.2014.05.001>

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1 **Functional traits determine plant co-occurrence more than environment or**
2 **evolutionary relatedness in global drylands**

3

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21 **Key Words:** aridity; biotic interactions; competition; facilitation; phylogenetic distance;
22 plant functional traits; semi-arid; soil fertility

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24

1 **Abstract**

2 Plant-plant interactions are driven by environmental conditions, evolutionary
3 relationships (ER) and the functional traits of the plants involved. However, studies
4 addressing the relative importance of these drivers are rare, but crucial to improve our
5 predictions of the effects of plant-plant interactions on plant communities and of how
6 they respond to differing environmental conditions. To analyze the relative importance
7 of –and interrelationships among– these factors as drivers of plant-plant interactions, we
8 analyzed perennial plant co-occurrence at 106 dryland plant communities established
9 across rainfall gradients in nine countries. We used structural equation modeling to
10 disentangle the relationships between environmental conditions (aridity and soil
11 fertility), functional traits extracted from the literature, and ER, and to assess their
12 relative importance as drivers of the 929 pairwise plant-plant co-occurrence levels
13 measured. Functional traits, specifically facilitated plants' height and nurse growth
14 form, were of primary importance, and modulated the effect of the environment and ER
15 on plant-plant interactions. Environmental conditions and ER were important mainly for
16 those interactions involving woody and graminoid nurses, respectively. The relative
17 importance of different plant-plant interaction drivers (ER, functional traits, and the
18 environment) varied depending on the region considered, illustrating the difficulty of
19 predicting the outcome of plant-plant interactions at broader spatial scales. In our
20 global-scale study on drylands, plant-plant interactions were more strongly related to
21 functional traits of the species involved than to the environmental variables considered.
22 Thus, moving to a trait-based facilitation/competition approach help to predict that: 1)
23 positive plant-plant interactions are more likely to occur for taller facilitated species in
24 drylands, and 2) plant-plant interactions within woody-dominated ecosystems might be
25 more sensitive to changing environmental conditions than those within grasslands. By

- 1 providing insights on which species are likely to better perform beneath a given
- 2 neighbour, our results will also help to succeed in restoration practices involving the use
- 3 of nurse plants.

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1 **Introduction**

2 Plant-plant interactions influence the structure and composition of ecological
3 communities, and therefore may play important roles in determining the distribution of
4 species, secondary succession, ecosystem productivity and stability (reviewed in
5 Brooker et al., 2008; Soliveres and Maestre, *in press*). Plants compete for resources, but
6 also may improve the microclimate of their neighbours via shading, run-off capture or
7 grazing protection (Callaway, 2007). Thus, both negative (competition) and positive
8 (facilitation) effects of plants on their neighbours often co-occur in nature, with the net
9 outcome of their interaction depending on species-specific and environmental factors
10 (Maestre et al., 2009a; Soliveres et al., 2012a; He et al., 2013).

11 Although most research has focused on the behaviour of plant-plant interactions
12 across environmental gradients, there is a lack of agreement on how such plant-plant
13 interactions respond to environmental gradients (see He et al., 2013; Soliveres and
14 Maestre, *in press* for last reviews in the topic). The most influential theory in this regard
15 (the Stress Gradient Hypothesis; Bertness and Callaway, 1994) predicts a monotonic
16 increase of the frequency of positive plant-plant interactions with environmental stress.
17 However, unimodal relationships with a collapse of facilitative interactions under
18 extreme stressful conditions have been also empirically observed and theoretically
19 predicted (Hacker and Gaines, 1997; Tielbörger and Kadmon, 2000; Maestre and
20 Cortina, 2004). A third scenario, moreover, has been recently suggested in which the
21 relationship between plant-plant interactions and environmental conditions can be nil
22 when variability in species' responses to the environment within the community is high
23 (e.g., Soliveres et al., 2011).

24 Part of the controversy regarding the relationship between plant-plant interactions
25 and environmental conditions may be solved when considering the specific features of

1 the interacting species and their relationship with the prevailing environmental
2 conditions (Maestre et al., 2009a). Whether environmental conditions are more or less
3 important than species-specific (functional traits or evolutionary relatedness of the
4 interacting species) attributes, or how do these different drivers relate to each other, is
5 poorly known (but see Schöb et al., 2012; Soliveres et al., 2012b; Butterfield and
6 Callaway, 2013). Additionally, the different drivers of plant-plant interactions do not act
7 in isolation, and thus they need to be studied together. Environmental conditions,
8 functional traits and evolutionary relatedness among interacting species are strongly
9 related to each other (Webb et al., 2002). For example, the prevailing environment
10 determines to a certain degree the trait values or the evolutionary lineages present
11 within a community (Weiher and Keddy, 2001; Cornwell and Ackerly, 2009) and thus
12 those that are able to interact with each other (but see Schöb et al., 2012). Evolutionary
13 information, conversely, is often regarded as an indirect measure of important
14 functional traits that could be either unknown to be important or unmeasured under the
15 assumption of evolutionary conservatism of important functional traits (Webb et al.,
16 2002; but see Mayfield and Levine, 2010). Indeed, although current literature suggests
17 that environmental conditions are the main driver of plant-plant interactions (e.g., He et
18 al., 2013), the combination of environmental measurements with phylogenetic
19 information (Soliveres et al., 2012b; Verdú et al., 2012) or functional traits (Liancourt et
20 al., 2005, Schöb et al., 2012; Gross et al., 2013) has proven more useful to better predict
21 the outcomes of pairwise plant-plant interactions. Thus, simultaneously studying the
22 importance of environmental conditions, phylogeny and functional traits as drivers of
23 plant-plant interactions will clarify how such interactions influence species distribution
24 under changing environmental conditions. Furthermore, such a comprehensive approach
25 would shed light on how plant-plant interactions affect the functional and phylogenetic

1 diversity of plant communities. However, such a holistic framework has been rarely
2 applied when studying the outcome of the variety of pairwise interactions existing
3 within local communities, which range from strongly negative to strongly positive.

4 Here, we use a field study conducted in 106 drylands worldwide involving 929
5 pairwise plant-plant interactions (measured as their level of co-occurrence) to test the
6 relative importance of species-specific features vs prevailing environmental conditions
7 as drivers of plant-plant interactions. Specifically, we aimed to answer the following
8 questions: i) what is the relative importance of environment, evolutionary relatedness
9 and functional traits as drivers of plant-plant interactions?, ii) how do these drivers
10 relate to, and co-determine the effects of, each other?, and iii) does the relative
11 importance of them vary with the geographical region studied? Apart from being one of
12 the biomes in which facilitative interactions among plants have been more extensively
13 studied (Callaway, 2007; Brooker et al., 2008), drylands occupy a large proportion of
14 the terrestrial surface, and provide ecosystem services that are essential for the
15 maintenance of life on Earth (Reynolds et al., 2007). The use of facilitative interactions
16 among plants has been invoked to restore dryland diversity in degraded environments
17 (Cortina et al., 2011), which can help to mitigate negative impacts of climate change
18 and desertification in these areas (Maestre et al., 2012). Therefore, solving the above-
19 stated questions will further refine our predictions regarding how these interactions will
20 respond to a changing environment, and will enhance the success of restoration
21 practices involving the use of nurse plants.

22

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1 **Materials and methods**

2 **Study sites and sampling protocol**

3 Field data for this study were obtained from 106 sites established across rainfall
4 gradients within nine countries (Australia, Chile, Ecuador, Morocco, Peru, Spain,
5 Tunisia, USA and Venezuela; see Table 1). The sites surveyed encompass the major
6 vegetation types found in drylands: grasslands (Peru, Morocco, Spain, Tunisia and
7 Venezuela), shrublands (Chile, Ecuador, Spain, USA) and open woodlands (Australia).
8 Water availability is widely accepted as the main abiotic stressor in drylands and
9 therefore was the predominant factor considered in the environmental gradients studied
10 within each country. The different regional rainfall gradients established covered
11 differences in annual rainfall ranging from 50 to 341 mm among sites within each
12 region, from 4 to 30 points sampled along the different gradients, and from regions
13 supporting grassland communities dominated by a single species to species-rich
14 shrublands with different potential nurse species (Table 1). The fact that the plant-plant
15 interactions studied vary widely across the different environments considered (from
16 very positive to very negative pairwise co-occurrences [Appendix A] and from 0 to
17 100% facilitated species within the community [Soliveres and Maestre, under review])
18 clearly show that the range of environmental conditions sampled suffices to test plant-
19 plant interactions-environment relationships.

20 For every site, we obtained climatic variables derived from digital models using
21 the Worldclim database (<http://www.worldclim.org>; Hijmans et al., 2005), from which
22 an aridity index (precipitation/potential evapotranspiration) was derived (data from
23 Maestre et al., 2012). To give a more readily interpretable result, we calculated Aridity
24 as 1- aridity index, which is directly related to drought stress (higher values mean higher
25 drought stress).

1 All the sites studied were sampled following the same protocol. At each site, we
2 surveyed 30 0.5 m × 0.5 m quadrats under the canopy of the dominant plant species,
3 which were treated as potential nurses, and the same number of quadrats in open areas
4 far from such potential nurses (hereafter Nurse and Open microsites). These potential
5 nurses were mainly trees or shrubs in open woodlands or shrublands, and large tussocks
6 in grasslands (Table 1). The sampling quadrats were distributed beneath at least three (if
7 the potential nurse was a tree), five (for shrubs) or ten (if the potential nurse was a
8 grass) individuals at each site. Open microsites were those located > 2 m away from any
9 adult individuals of the selected nurses, except for trees in which case open microsite
10 were located at a distance equal to the canopy width. Composition or dominant species
11 within these open microsites varied widely due to the range of vegetation and soil types,
12 plant composition and productivity included in the 106 study sites. Average cover (%)
13 and density of individuals per quadrat in the open ranged from 1.1% and 0.3 to 7.3%
14 and 3.4, respectively. At each quadrat, we measured the number of individuals of every
15 perennial plant species to quantify the degree of co-occurrence between each one of
16 them and the potential nurse species. Annual plant composition substantially changes
17 through the year, and among different years, in drylands worldwide (Whitford, 2002).
18 Thus, we did not include annual species in our observational design to avoid
19 confounding effects in our results or in the differences among study sites derived from
20 sampling 'incomplete' communities depending on the time of the year that each site was
21 sampled.

22 Co-occurrence between the potential nurse species and the rest of species forming
23 the community is a widely used metric to assess plant-plant interactions (e.g., Badano
24 and Cavieres, 2006; Schöb et al., 2013). Obviously, observational approaches such as
25 that used here have some limitations, as they cannot differentiate between the outcome

1 of plant-plant interactions *per se* and other drivers of plant co-occurrence such as
2 dispersal or habitat sharing. However, co-occurrence is often assumed to be a good
3 indicator of – and has proven to be tightly associated to- positive interactions among
4 plants in drylands such as those studied here (Tirado and Pugnaire, 2005; Pueyo et al.,
5 2008). Moreover, we also controlled to a certain degree for those functional traits that
6 may drive co-occurrence among plants due to dispersal (see below), which is other main
7 driver of co-occurrence among plants.

8 From the co-occurrence data, we assessed interactions at the pairwise level by
9 performing χ^2 tests using the observed number of individuals of a given species within
10 each site beneath the potential nurse and in the open inter-spaces as the response
11 variable. Hereafter, we refer to these χ^2 tests as the plant-plant interaction metric. The
12 metric is based on comparing the occurrence of the individuals of a given target species
13 in the open vs. beneath the nurse in comparison with a random expectation according to
14 the sampling effort invested for each microsite. Thus, the “expected values” were
15 calculated as the total number of individuals of each target species observed by the
16 relative number of quadrats within each microsite. If, say, 100 quadrats would be
17 sampled in a given site: 50 in the open, 30 in nurse species A and 20 in nurse species B,
18 the relative sampling effort would be 0.5, 0.3 and 0.2 for open, nurse A and nurse B
19 microsites, respectively. Imagine a total of 100 individuals of a given target species
20 observed in this site. Then, the expected values for this target species would be $100 \times$
21 0.5 for open, 100×0.3 for nurse A and 100×0.2 for nurse B. That is, assuming that the
22 individuals are randomly distributed regardless of the microsite and their number only
23 depends on the number of quadrats sampled. This random expectation (the expected
24 values) would be compared against the observed individuals within each microsite by
25 using the χ^2 test. To aid in the interpretation of this metric, it was multiplied by -1 or 1

1 in non-facilitated or facilitated species (those with less or more individuals under a
2 given nurse than in open areas) respectively. The size and the sign of our plant-plant
3 interaction metric were mostly independent of sample size (*i.e.*, the number of
4 individuals recorded for each species only explained 0.8% of the variance in our plant-
5 plant interaction metric; see Appendix A). However, to avoid confounding the effect of
6 plant-plant interactions on either the total number of individuals or on how these
7 individuals were distributed, we included both the number of individuals and the plant-
8 plant interaction metric as response variables in our models (see below).

9

10 **Assessment of plant functional traits, evolutionary relatedness, and the** 11 **environmental gradient**

12 We compiled from the literature available data on functional traits known to affect the
13 co-occurrence, establishment, competitive ability and drought tolerance of plants. These
14 were: height, growth form (grass, forb, woody), photosynthetic pathway (C3, C4/CAM)
15 and dispersal mode (dispersed by wind, vertebrates, or other vectors). Plant height is
16 strongly related to the ability of plants to compete for light, plant performance
17 characteristics like growth rate, and demographic features such as longevity, time to
18 reproduction or seed mass (Cornelissen et al., 2003; Moles et al., 2009). Growth form
19 plays an important role in defining the outcome of interactions between individuals and
20 their neighbors (Gómez-Aparicio, 2009; Verdú et al., 2012), and is associated with how
21 they use the available resources, climatic factors and land use (Cornelissen et al., 2003).

22 In our case, we sorted our plant species into three growth forms: grass, woody and
23 forbs. Despite its simplicity, this classification follows the basic functional grouping
24 used in current plant-plant interactions literature (e.g. Cahill et al., 2008; Gómez-
25 Aparicio, 2009; Verdú et al., 2012). The photosynthetic pathway is a key functional

1 attribute of any plant species, with C4 and CAM species associated with higher water-
2 use efficiencies but lower shade tolerances (Ehrlinger et al., 1991). Finally, dispersal
3 mode influences the degree of co-occurrence among plants, with vertebrate-dispersed
4 species more likely to co-occur with other plant species (particularly shrubs or trees)
5 through nucleation processes (Pueyo et al., 2008; Soliveres et al., 2012b).

6 In the case of the nurse species, we added to the traits described above the ability
7 to fix nitrogen (N) and the shape of the canopy (in contact with the soil surface or not).
8 Although important for all the species, these additional traits are crucial to define the
9 degree of microclimatic amelioration provided by the potential nurse and to know the
10 mechanisms through which it ameliorates environmental conditions for other species to
11 successfully establish underneath. Plants able to fix N are more likely to improve soil
12 fertility, and therefore to facilitate growth and survival of other species, especially in
13 nutrient-poor soils (see Callaway, 2007 for a complete review). Canopy shape, on the
14 other hand, was roughly divided in pyramidal canopy or canopy in full contact with the
15 soil surface (unattached and attached to the soil, respectively). These two different
16 canopy classes differ in their ability to capture water and nutrients coming from run-off
17 (those in full contact with the soil capture more; Maestre et al., 2009b), to reduce
18 incident radiation (e.g., Jankju, 2013) or to protect neighbors from grazing (e.g.,
19 Rebollo et al., 2002). Furthermore, differing nurse shapes are also known to influence
20 seed movement and, therefore, co-occurrence among plant species (e.g., Caballero et al.,
21 2008; Giladi et al., 2013). These features are very likely to affect how a given nurse
22 interacts with its neighbors. Major sources of functional traits data were the BROT
23 (Paula et al., 2009) and LEDA (Kleyer et al., 2008) databases, flora descriptions and
24 databases available on internet (e.g. <http://data.kew.org/sid/> for seeds;
25 <http://www.floravascular.com/> for Spain; <http://plantnet.rbgsyd.nsw.gov.au/> for

1 Australia; <http://plants.usda.gov/java/> for USA; all accessed between January and July
2 of 2012); and Wright et al., (2004).

3 Those species for which we could not acquire data on all of these traits were
4 removed from the database. We retained 929 pairwise interactions (45.5% of the 2,040
5 pairwise interactions sampled), which contained information of all the traits, for further
6 analyses. We acknowledge that other qualitative and quantitative traits, such as the
7 specific leaf area or seed mass for beneficiaries and the leaf area index, the presence of
8 spines or allelopathy for nurses are important drivers of plant-plant interactions (e.g.,
9 Callaway, 2007; Schöb et al., 2012, Soliveres et al., 2012a; Butterfield and Callaway,
10 2013; see Adler et al., 2013 and references therein for more examples where these traits
11 are drivers of species interactions). We could gather information on the specific leaf
12 area or seed mass for a relatively important fraction of our species, and they were
13 included in our analyses whenever possible (“models of maximum R^2 ” in Table 2;
14 Appendix B). The categorical functional traits (all traits excepting plant height) were
15 organized into a set of binomial variables, and summarized by using a non-metric
16 multidimensional scaling ordination (NMDS, Anderson et al., 2008). This ordination
17 technique is well suited to handle non-normal and non-continuous data (McCune and
18 Grace, 2002) and allowed us to reduce our matrix of categorical plant trait data prior to
19 modeling. This accomplishes the synthesis of a smaller number of vectors that correlate
20 with sets of traits that are most informative, and summarize the separation in the trait
21 space of the species considered. We considered the alternative of introducing multiple
22 binomial or multi-level categorical variables to be more difficult to model and unlikely
23 to perform any better. The NMDS ordinations were performed separately for nurse and
24 facilitated species, and for the three different sets of analyses considered in this study
25 (global, regional and growth form, see below). These ordinations can have solutions

1 with either two (2D) or three (3D) dimensions or axes (McCune and Grace, 2002;
2 Anderson et al., 2008). The 2D solution of all the ordinations conducted here showed
3 stress values between 0.05 and 0.1. Stress values below 0.2 provide a good
4 representation of the distance among samples (McCune and Grace, 2002; Anderson et
5 al., 2008), and therefore we selected the 2D solution. We conducted NMDS ordinations
6 with the PRIMER v6 statistical package for Windows (PRIMER-E Ltd., Plymouth
7 Marine Laboratory, UK), using the Euclidean distance for the resemblance matrix and
8 25 re-starts to calculate stress values.

9 We assembled a phylogenetic tree for these species using the Phylocom 4.1
10 software (Webb et al. 2008), standard phylogenetic protocols and published phylogenies
11 (see details in Appendix C). After assembling the phylogenetic tree, we calculated the
12 phylogenetic distance between each species pair by using the 'cophenetic' command of
13 the R statistical software (R Foundation for Statistical Computing, Vienna, AT).

14 As a surrogate for the environmental conditions, we used the aridity level
15 described above, with higher values of this index indicating more arid conditions. We
16 also included soil variables widely accepted as indicators of soil fertility: organic C (%),
17 available P ($\text{mg P} \cdot \text{g}^{-1}$ of soil) and N (the sum of ammonium, nitrate and dissolved
18 organic N, in $\text{mg N} \cdot \text{Kg}^{-1}$ of soil; Appendix B, data extracted from Maestre et al., 2012).
19 To reduce the amount of variables introduced in our models, soil variables (standardized
20 by their maximum) were summarized by conducting a principal components analysis
21 (PCA), which first axis explained 44.5% of the variance in the three variables globally
22 (loadings for C, N and P were -0.67, -0.74 and -0.08, respectively). The second axis of
23 this PCA ordination, more related to P, was not used since it did not increase the
24 amount of variability explained in the model and further complicated it. In some of the
25 regional models, and in the grass as nurse model, the addition of the first axis of this

1 PCA (hereafter fertility) introduced multicollinearity with aridity, and therefore it was
2 not included in the analyses of these data.

3

4 **Data organization and statistical analyses**

5 We used structural equation modeling (SEM) to evaluate the relationships between the
6 environment (aridity and soil fertility), the traits and phylogenetic distance of the
7 interacting species and the plant-plant interaction metric. We used SEM because it can
8 partition causal influences among multiple variables, allowing the separation of direct
9 and indirect effects of the different predictors (Grace, 2006). These unique properties of
10 SEM make this technique particularly suitable to answer the questions posed in this
11 study. In particular, we evaluated: i) the relative importance of the different predictors
12 (plant traits, phylogenetic distance and environmental conditions), ii) the
13 interrelationships among such predictors, and iii) the amount of the variance in the
14 outcome of plant-plant interactions (the χ^2 metric) that is directly or indirectly
15 (mediated by a third variable) explained by each predictor. We used three separate sets
16 of SEMs to analyze our data: a global analysis (including data from all the sites),
17 regional analyses (using environmental gradients located in different regions of the
18 world), and growth form analyses (using grass vs. woody species as nurses).

19 The first step in SEM is to establish an *a priori* causal model based on previous
20 knowledge. In our case, this model included: i) a direct effect of plant traits,
21 phylogenetic distance and environmental conditions on our proxy of plant-plant
22 interactions, ii) a direct effect of the environment on plant functional traits and
23 phylogenetic relationships between the interacting species caused by environmental
24 filtering (Webb et al., 2002, Schöb et al., 2012), and iii) the influence of phylogeny on

1 plant functional traits by evolutionary conservatism in the selected traits (Prinzing et al.
2 2001; see full description in Appendix C).

3 We applied this basic model to the different SEM analyses described in detail
4 below. The second step in SEM is to estimate path coefficients, with their associated P -
5 values, from the field data. We did this estimation with bootstrapping because our data
6 were positively kurtotic, and this technique is preferred to maximum likelihood
7 estimation in these cases. The path coefficient is analogous to a partial correlation
8 coefficient, and describes the strength and sign of the relationships among the
9 introduced variables (Grace, 2006). It must be noted that SEM assumes linearity in the
10 relationships between each introduced variable and all the relationships presented here
11 fulfill this assumption. Apart from estimating single path coefficients, SEMs test the
12 overall goodness-of-fit of the model against the dataset; for doing this we used the
13 traditional χ^2 test, the RMSEA index and the Bollen-Stine bootstrap test. It must be
14 noted that in these indices high P -values indicate that the proposed model is a plausible
15 causal scenario. Since all the indices rendered very similar results, we only show the χ^2
16 tests here. Another important output of SEM analyses is the standardized total effects,
17 which account for all the (direct and indirect) paths from a given explanatory variable to
18 the response variable. The details of the SEMs conducted are given below. Our models
19 also make use of composite variables (Grace and Bollen, 2008). Composites allow the
20 effects of multiple conceptually related, but not necessarily statistically correlated,
21 variables to be pooled into a single path to more closely match broader theoretical
22 concepts. Error terms are fixed to zero during the construction of the composite
23 variables, so they include all the variance of the response variable explained by the
24 predictors introduced into a single comprehensive variable (the composite).

25

1 -Global scale analysis

2 At this scale, we used all of our pairwise interactions ($N = 929$), introducing
3 latitude and longitude of each site to account for the spatial autocorrelation present in
4 our data (gradients were nested within spatial clusters of sites; see Maestre et al. 2012
5 for a related approach). At the global scale, we had a large number of categorical plant
6 traits which would have required a complex model to include, likely with minimal
7 information gains. The traits used in our model at the global scale were plant height
8 (log-transformed to improve linearity in the relationships), and the first or second axis
9 of the non-metric multidimensional scaling ordination (NMDS) conducted with our
10 categorical functional traits for facilitated or nurse species, respectively. The remaining
11 two NMDS axes (axis 2 for beneficiaries and axis 1 for nurses) were not considered as
12 they were highly correlated with height, which was already introduced in the model.
13 The first NMDS axis of the ordination conducted with the facilitated species was
14 negatively correlated with grass growth form (Spearman's $\rho = -0.67$), wind-dispersion
15 ($\rho = -0.70$) and C4 photosynthetic pathway ($\rho = -0.61$; $P < 0.001$ in all cases, $N = 167$).
16 The second NMDS axis of the ordination for the nurse species was positively related to
17 dispersal by vertebrates ($\rho = 0.70$) and to the canopy shape attached to the soil ($\rho =$
18 0.40 ; $P < 0.005$ in all cases, $N = 53$). The remaining binomial traits were not well
19 correlated with the selected NMDS axis, but were significantly correlated with nurse
20 plant height (woody growth form $\rho = 0.55$; C3 photosynthetic pathway $\rho = 0.35$; $P <$
21 0.05 in both cases), thus their inclusion would have added little new information. We
22 did not include the additional NMDS axes of both ordinations because they were
23 correlated with plant height, did not improve the amount of variance explained, and
24 further complicated the model and its interpretation. The same reason prevented us from

1 introducing the environment \times traits and environment \times phylogenetic distance
2 interactions terms in our models.

3 After fitting the model, we built four composite variables (Grace, 2006), each of
4 which combine the effects of two conceptually related variables: “Spatial” (latitude +
5 longitude), “Stress” (aridity + fertility), “Nurse” (Nurse height + NMDS axis), and
6 “Benefit” (Facilitated height + NMDS axis)” (shown as hexagons in Fig. 1; see
7 Appendix S3 for details). The use of these composite variables does not alter the
8 underlying model, but collapses the effects of the variables included into a single path
9 coefficient that aids with the interpretation of results. The latent variable, another type
10 of synthetic variable often used to model broader theoretical constructs in SEM, was not
11 used because latent variables seek to develop a linear vector from multiple highly
12 correlated indicators. The ecologically meaningful concepts addressed in our models
13 generally were not represented by highly correlated indicators (e.g., environmental
14 conditions [climate and soils]), and thus composite variables were a better option to
15 include these concepts in our models.

16

17 *-Regional analyses*

18 In a second step, we reorganized our data into ten different “regional groups”
19 (Table 1; see Appendix C for details). As spatial autocorrelation was no longer a
20 problem in the within-region level, we did not include geographical predictors (latitude
21 and longitude) in this model. To facilitate comparisons among different regions, we
22 fitted a general and simple model structure to all of them (“common structure” in Table
23 2). In these models, we used aridity as our environmental measurement, phylogenetic
24 distance between the interacting species and the height of facilitated as the only measure
25 of plant traits. Fertility was not included in order to keep models’ structure simple and

1 because in several regions it was highly related with aridity, which might induce
2 multicollinearity problems. We only considered height because the NMDS ordination
3 axis did not significantly increase the amount of variance explained nor improved the
4 model fit in most cases, and data on specific leaf area and seed mass were not available
5 for enough species in half of the regions. To complement these analyses, we fitted each
6 regional model separately by introducing, from the variables available, those that
7 explained most of the variance in our plant-plant interaction metric (“model maximum
8 R^2 ” in Table 2, see full description in Appendix B). Nurse functional trait data were not
9 included into these models for three main reasons: i) nurse plants were so similar within
10 most regions that not enough variability in their functional traits was recovered to add it
11 as a variable in the regional models, and ii) only a simple structure such as that used
12 could be fitted to all regions.

13

14 *-Nurse growth form analyses*

15 The outcome of plant-plant interactions is known to depend on the growth form
16 of the interacting species (Gómez-Aparicio, 2009); thus it is likely that growth form
17 influences the effect of other drivers of plant-plant interactions (e.g., Verdú et al., 2012).
18 While the rest of predictors assessed here are continuous variables (aridity, soil fertility,
19 phylogenetic distance or plant height), plant growth form is not. This may obscure the
20 influence of a widely acknowledge plant-plant interaction driver on the previous SEMs.
21 Therefore, we evaluated changes in the relative importance of the different plant-plant
22 interaction drivers depending on the growth form of the nurse species involved by
23 constructing different SEMs for those pairwise interactions involving woody and grass
24 nurses, respectively. As with the global model, we included latitude to control for
25 spatial autocorrelation in our data (longitude could not be introduced due to

1 multicollinearity problems when both latitude and longitude were included). SEM
2 analyses were performed using AMOS for windows (SPSS Inc., Chicago, IL, USA).

3

4 **Results**

5 **The relative importance of environment, evolutionary relatedness and functional** 6 **traits as drivers of plant-plant interactions**

7 Overall, facilitated plant traits (represented mainly by height) were more influential than
8 environmental conditions or evolutionary relatedness in determining co-occurrence
9 among plants. When the global data were analyzed, the height of the facilitated species
10 (standardized total effect [STE] = 0.11), the longitude (STE = -0.12) of the study sites
11 and soil fertility (STE = -0.10) were the best predictors of co-occurrence among plant
12 plant species, with aridity (STE = -0.06) and the evolutionary relatedness (STE = 0.07)
13 playing secondary roles as their effect on plant-plant interactions, once accounting for
14 the other predictors, were weaker than those of plant height or longitude. In general,
15 positive interactions were prevalent for taller facilitated species, more fertile soil
16 conditions or eastern regions (Fig. 1).

17 Separate analyses for the ten major regions sampled (Table 2), and for the major
18 nurse growth forms (grass vs. woody; Fig. 2), provided additional support for the
19 importance that plant functional traits have as drivers of plant-plant interactions. Even
20 after considering the environmental influence on plant functional traits with the
21 standardized total effects, traits of facilitated species were more important for plant-
22 plant interactions than the environment and the evolutionary relatedness in four of the
23 ten regional models analyzed (Table 2, left side), and in the two models conducted for
24 the dominant growth forms (Fig. 2). When we introduced other important functional

1 traits that could drive species interactions in our models, such as specific leaf area or
2 seed mass, the total amount of variance explained by the regional models increased by
3 an additional 10% on average and plant traits were the most important driver in six of
4 the ten models (see “models maximum R^2 ” in Table 2). In the latter case, plant height
5 was the most important trait (i.e., the biggest path coefficient) acting as driver of plant-
6 plant interactions in three of the five regions analyzed (Australia trees, Spain sprouter
7 shrubs, and Venezuela), but SLA was a better indicator of plant co-occurrence in the
8 remaining regions (Australia shrubs and Spain non-sprouter shrubs; see full details in
9 Appendix B).

10

11 **Relationship among drivers of plant-plant interactions**

12 As expected, all the different drivers of plant-plant interactions interrelated with each
13 other (Figs. 1 and 2). Those paths from aridity to functional traits or phylogenetic
14 distance, from phylogenetic distance to functional traits and from nurse to facilitated
15 functional traits were significant. The stronger drivers of plant functional trait values
16 were the spatial component (STE = -0.70 and -0.33 for nurse and facilitated traits),
17 followed by aridity (STE = -0.29 and -0.25 for nurse and facilitated traits). The latter
18 was the best predictor (i.e., biggest path coefficient) of pairwise phylogenetic distance
19 (STE = 0.22). We found a relatively weak, although significant relationship between
20 phylogenetic distance and both nurse or facilitated traits. This relationship, however,
21 disappeared in the models separated by nurse growth-form. We found a significant
22 relationship between nurse and facilitated traits (0.11; Fig. 1) which was much stronger
23 for woody than for grass nurses (Fig. 2).

24 Conversely, the analyses conducted separately for grass and woody nurses
25 revealed that the growth form of nurses significantly altered the importance of other

1 plant-plant interaction drivers studied (Fig. 2). Aridity was more important in those
2 interactions involving woody than grass nurses (STE = -0.16 vs 0.08), while the
3 evolutionary relatedness was a much stronger driver of the effects of grass -but not
4 woody- nurses on their neighbors (STE = 0.01 for woody nurses vs STE = 0.34 for
5 grass nurses). The functional traits of the interacting species, however, were equally
6 important for the interactions involving both grass and woody nurses (STE = 0.11 and
7 0.12, respectively).

8

9 **Does the relative importance of the drivers of plant-plant interactions vary with**
10 **the geographical region studied?**

11 Even after accounting for the three major drivers of plant-plant interactions as
12 acknowledged in current literature, we found a large effect of the geographical
13 predictors (latitude and longitude) in both the global model and in those divided by
14 nurse growth-form. This suggests a strong idiosyncrasy of the relative strengths of the
15 different drivers of plant-plant interactions, as further demonstrated by the regional
16 models (Table 2). We found a strong variability in the main drivers of plant-plant
17 interactions (as measured by plant co-occurrence) depending on the region. For
18 example, aridity turned out to be the major predictor of plant-plant interactions in three
19 of the studied regions (two when considering more functional traits). Evolutionary
20 relatedness was the most important predictor of plant-plant interactions in Venezuela,
21 Ecuador and Australia (shrubs as nurse), and for those pairwise interactions involving
22 grass nurses (Fig. 2). Lastly, plant height was the most important predictor in four of the
23 studied regions, and this number increase to six when considering other important traits
24 available in the literature (Table 2).

25

1 **Discussion**

2 We quantified the relative importance and interrelationships among environment,
3 functional traits and evolutionary relatedness as drivers of plant-plant interactions in
4 drylands. Our findings illustrate the wide array of mechanisms driving plant-plant
5 interactions, and the complex relationships that exist among their major drivers. Our
6 study also highlights the difficulty of adequately predicting the outcomes of plant-plant
7 interactions using simple models based solely on a subset of these drivers. In spite of
8 this complexity, we showed that readily measurable plant traits, such as plant height or
9 growth form, can be informative predictors of plant co-occurrence in global drylands.
10 Our results suggest that moving forward from an “abiotic/biotic stress point of view”,
11 which has dominated the facilitation literature over the last decades, to a trait-based
12 framework can have far reaching implications in our ability to successfully predict how
13 these interactions, and thus whole plant communities, will respond to environmental
14 factors (see also Butterfield and Callaway, 2013; Gross et al., 2013). The use of a trait-
15 based framework has proven very useful to advance our knowledge in topics such as the
16 biodiversity-function relationship (Polley et al., 2013), the response of plant
17 communities to environmental changes (Frenette-Dussault et al., 2012), and the
18 mechanisms underlying plant coexistence (Adler et al., 2013). Thus, moving towards a
19 trait-based framework when studying plant-plant interactions could also help to better
20 link these often separate, albeit tightly related, research topics (Butterfield and Briggs,
21 2011, Schöb et al., 2012).

22

23 **The importance of plant height**

24 The height of beneficiaries was our most informative predictor of the variance in plant
25 species co-occurrence in drylands. In spite of the obvious limitations of not accounting

23

1 for other important functional traits missing for some of our species, our results
2 demonstrate that target plants tend to benefit more from the presence of a neighbor the
3 taller they are. It must be noticed that the importance of facilitated plants' height (i.e.,
4 the size of this path coefficient) prevailed for some regions even after including other
5 important functional traits such as SLA or seed mass. These findings agree with studies
6 from other desert systems, which identify facilitated plant height as a fundamental trait
7 defining the outcome of plant-plant interactions (Butterfield and Briggs, 2011). The
8 high importance of facilitated plant height as a driver of plant-plant interactions might
9 be related to the fact that taller plants can be in disadvantage in the open (taller plants
10 normally have bigger canopies and higher transpiration rates; Butterfield and Briggs,
11 2011). Thus, species holding these features might benefit from the ameliorated
12 conditions beneath a nurse. In some cases, an alternative explanation to this high
13 importance of facilitated height might be derived from competition by light, which
14 seems more important than previously thought (Forseth et al., 2001; Soliveres et al.,
15 2010). The higher growth rates that characterize taller plants may allow them to overtop
16 their neighbors, and thus avoid the deleterious effects of shading.

17 Previous studies have reported an important influence of nurse height, and its
18 interaction with the environment, as a driver of the effects of woody plants - especially
19 trees- on the biomass of understory species (Callaway et al., 1991; Moustakas et al.,
20 2013). However, we failed to detect such influence, since neither nurse height (Fig. 2)
21 nor its interaction with the environment (data not shown) affected the degree of co-
22 occurrence between plant species. A plausible explanation for these contrasting results
23 is the different performance measures used (number of individuals vs. biomass), which
24 are known to affect the results gathered when studying plant-plant interactions (e.g.,
25 Maestre et al., 2005). A complementary explanation is that plant-plant interactions are

1 highly species-specific, and thus the influence of nurse height might be obscured by the
2 mixing of different woody nurses and a variety of facilitated species in our analyses.

3

4 **Interrelationship among the different drivers of plant-plant interactions**

5 The growth form of the nurse plant strongly influenced the outcome of plant-plant
6 interactions, and modulated the effect of both the environment and the evolutionary
7 relatedness on such outcome. Environmental conditions and evolutionary relatedness
8 were important mainly for interactions involving woody and graminoid nurses,
9 respectively. The graminoid growth form is often associated with poor nurses (Gómez-
10 Aparicio, 2009), but we found that negative interactions involving grass nurses might
11 shift to positive ones for evolutionary distant taxa. Indeed, grass nurses can facilitate the
12 establishment of woody seedlings beneath them, and have been recommended for the
13 restoration of degraded drylands (Maestre et al., 2001). We speculate that the strong
14 effect of the evolutionary relatedness on interactions involving grass, but not woody,
15 nurses (Fig. 2) might be caused by two simple mechanisms: i) grasses are monocots and
16 have relatively poor competitive ability against dicots (Cahill et al., 2008), and ii) the
17 traits included in our analyses could adequately include the niche segregation between
18 woody nurses and their neighbors, but did not adequately account for relevant
19 differences among grass nurses and their neighbors, which were better represented by
20 their evolutionary relatedness.

21 Nurse growth form also interacted with the environment to influence plant-plant
22 interactions. Environmental conditions were more important drivers of interactions
23 involving woody nurses than facilitated plant height or the evolutionary relatedness of
24 the species involved (Fig. 2B). The overwhelming importance of aridity when woody
25 nurses are involved has been illustrated previously, with works showing either an

1 increase in the importance of facilitation in tree (nurse)-grass (facilitated) interactions
2 with rainfall scarcity (Dohn et al., 2013) and shifts towards positive interactions with
3 higher stress when shrubs act as nurses (Gómez-Aparicio et al., 2004; He et al., 2013).
4 The relationship between aridity and the outcome of plant-plant interactions in drylands,
5 however, seems to be obscured when other nurse growth forms are considered in the
6 analyses (Maestre et al., 2005; He et al., 2013; Fig. 1). The latter supports the inter-
7 relationships between nurse growth-form and the environment found in this study.

8

9 **Idiosyncratic changes in the relative importance of plant-plant interaction drivers**

10 The highly idiosyncratic effects of different drivers of plant-plant interactions across
11 different regions (Table 2) or nurse growth forms (Fig. 2) may partly explain the overall
12 low variance covered by our global model (Fig. 1; see also Appendix S1). Our multi-
13 site approach provides us with a potential explanation of these idiosyncratic results. The
14 importance of environmental conditions increased with environmental harshness, while
15 the importance of functional traits was augmented as the number of facilitated species
16 involved increased (Appendix S4). We speculate that, in those environmental gradients
17 where the stress experienced by plants is more multi-dimensional (not driven by a single
18 dominant stress factor but by different uncorrelated ones such as low temperatures,
19 salinity or poor soils), the degree of plant facilitation will be less related to the
20 individual environmental gradient and neither a disadvantage of particular functional
21 trait values nor a clear relationship between the degree of microclimatic amelioration
22 provided by nurses and the environmental gradient will be seen (Soliveres et al., 2011,
23 Soliveres and Maestre, 2014). The relationship between environmental conditions and
24 the outcome of plant-plant interactions is also expected to vanish when the variability
25 across the trait space is higher, and therefore the variability in species-specific responses

1 to the prevailing environment present in the target community is higher; Appendix D;
2 Soliveres et al., 2011).

3 Mechanisms not considered here could also be invoked to explain the results
4 observed in the global model, that is, the relatively low explanation power of our
5 predictors even after accounting for three of the major drivers of plant-plant interactions
6 simultaneously. These include other well-known drivers of plant-plant interactions such
7 as changes in grazing pressure (Smit et al., 2009; Soliveres et al., 2012a), indirect
8 interactions among multiple species clusters (Levine, 1999; Brooker et al., 2008), the
9 different ontogenetic stages of the individuals measured (Miriti, 2006; Soliveres et al.,
10 2010), more complex functional classifications of the interacting plants including other
11 important functional traits not considered here (Callaway, 2007; Appendix B), and the
12 complex interplay between (un)measured functional traits and the multiple possible
13 prevailing stress factors across the study sites (Butterfield and Callaway, 2013).
14 Furthermore, two methodological issues might also account in part for the
15 idiosyncrasies found: i) we only considered perennial plant species; however, annual
16 species are an important fraction of the species in some of the studied regions (e.g.,
17 Chile, Australia or USA) but not in others (e.g., the Mediterranean Basin), which could
18 generate differing results between annual- or perennial dominated communities, and ii)
19 the link between plant co-occurrence (what we measured) and plant-plant interactions
20 may vary with the environmental conditions or habitat-type, which could confound to a
21 certain degree the importance of the different plant-plant interactions drivers studied.
22 All these mechanisms could account up to some degree for the differences in the degree
23 of co-occurrence among plant species and the idiosyncratic results found here.

24

25

1 **Conclusion**

2 The classification of species and communities into the functional trait space has proven
3 to be a useful improvement in our understanding of important ecological questions,
4 including the assemblage of ecological communities and how they scale to the
5 ecosystem level, the response of ecosystems to global change, or the relationship
6 between biodiversity and ecosystem functioning (Frenette-Dussault et al., 2012; Schöb
7 et al., 2012; Gross et al., 2013; Polley et al., 2013). We provide strong empirical support
8 for a plant-plant interaction theory based on functional traits and their relationships with
9 other drivers of such interactions and conclude that functional traits of the interacting
10 plants are more important than –and modulate the effects of– the environment or the
11 evolutionary relatedness in defining pairwise interactions. Two significant testable
12 hypotheses derive from this trait-based theory: i) plant-plant interactions at the
13 community level may behave differently across environmental gradients depending on
14 the nature of the gradient (i.e., the gradient is driven by one or several stress factors),
15 and ii) the relationship between environmental gradients and plant-plant interactions at
16 the community level may wane when a variety of functional groups are present within
17 this community. Although we provide some results supporting these two hypotheses
18 (i.e., Appendix D) future research should further evaluate them. Furthermore, and
19 although we covered an important proportion and variety of dryland ecosystems, future
20 studies focused on other dryland areas poorly studied here and including annual plant
21 communities will undoubtedly improve our knowledge on the generality of the patterns
22 found in our study. In addition, our findings provide insights on which species are likely
23 to benefit from the presence of a given neighbour, which can be used for designing
24 effective restoration strategies based on afforestation using nurse plants, and for

1 devising methods to increase plant species diversity in order to mitigate the negative
2 impacts of climate change and desertification in drylands.

3

4 **Acknowledgements**

5 Christoph Kueffer, Florian Jeltsch and two anonymous reviewers provided numerous
6 comments that improved a previous version of this manuscript. This research was
7 funded by the European Research Council under the European Community's Seventh
8 Framework Programme (FP7/2007-2013)/ERC Grant agreement 242658 (BIOCOM).
9 The Ciencia y Tecnología para el Desarrollo (CYTED) program funded networking
10 activities (EPES, Acción 407AC0323). The authors deeply thank to those people who
11 measured and allowed access to the functional trait data used in this study, especially to
12 the creators and administrators of the LEDA and BROT databases, and to I. Wright, T.
13 Navarro and C. Frenette-Dussault for kindly providing published and unpublished data.
14 C. Smit provided helpful comments on a previous version of the manuscript. JRG
15 thanks ICM PO-5, CONICYT BFP-23, and FONDECYT 1110255 for financial support.

16

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1

2 **Table 1.** Details of the different regional gradients considered.

3

Country	Regional group	Ecosystem type	Range in aridity index	Number of study sites along the gradient	Number of potential nurse species	Dominant nurse type
Australia	AUSsh	Open woodland	0.211-0.312	9	5	Shrub
Australia	AUStr	Open woodland	0.211-0.337	10	3	Tree
Chile	Chile	Shrubland	0.059-0.154	4	4	Shrub
Ecuador	Ecuador	Shrubland	0.431-0.739	16	9	Shrub and Tree
Peru	Peru	Grassland	0.245-0.458	9	4	Grass and Shrub
United States	USA	Shrubland	0.102-0.340	8	10	Shrub
Venezuela	Venezuela	Grassland	0.656-0.702	6	9	Grass
Morocco, Spain, Tunisia	Mediterranean	Grassland	0.125-0.416	30	1	Grass
Spain	SPAspo	Grassland	0.247-0.416	15	5	Shrub
Spain	SPANon	Shrubland	0.241-0.431	22	4	Shrub

4

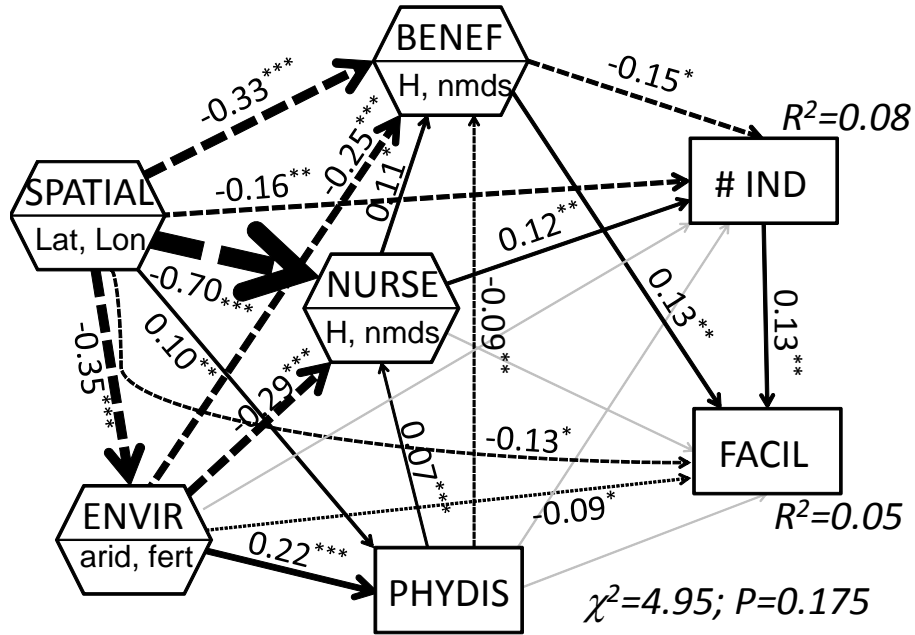
Table 2. Summary of the standardized total effects on plant-plant interactions (sum of direct + indirect effects, standardized from 0-1) for the Structural Equation Models performed for the ten regions surveyed. Two different sets of models were performed: 1) those only including aridity and plant height as indicators of environmental conditions and plant traits, respectively (“common structure”), 2) those models including more environmental variables and traits to maximize the amount of variance explained (“model maximum R²”). PhyDis = evolutionary relatedness between interacting plants; Height = facilitated plant height; R² = amount of variance explained in the number of individuals/plant-plant interaction metric (the latter in bold); Envir = variable(s) indicative of environmental conditions (* = only aridity, † = only fertility, ‡ = aridity + fertility), Traits = facilitated plant height and specific leaf area (height and NMDS axis in the case of Venezuela).

Regional groups	common structure				model maximum R ²			
	Aridity	PhyDis	Height	R ²	Envir	PhyDis	Traits	R ²
Chile	-0.30	0.07	0.11	0.15/ 0.41	-0.30*	0.07	0.11	0.15/ 0.41
Ecuador	-0.03	-0.07	-0.05	0.02/ 0.11	-0.03*	-0.07	-0.05	0.02/ 0.11
Peru	0.29	0.11	0.24	0.05/ 0.38	0.29*	0.11	0.24	0.05/ 0.38
USA	-0.09	0.04	0.33	0.15/ 0.37	-0.09*	0.04	0.33	0.15/ 0.37
Venezuela	0.20	0.21	0.07	0.21/ 0.12	0.20‡	0.22	0.11	0.22/ 0.15
Australia (shrubs as nurses)	0.01	0.21	-0.14	0.07/ 0.08	-0.03*	0.20	0.23	0.16/ 0.18
Australia (trees as nurses)	-0.22	-0.19	0.32	0.00/ 0.21	0.24†	-0.20	0.31	0.06/ 0.25
Mediterranean (Spain, Morocco and Tunisia)	-0.05	-0.19	0.31	0.03/ 0.11	-0.07†	-0.19	0.31	0.02/ 0.20
Spain (sprouting shrubs)	0.04	0.07	0.10	0.02/ 0.12	0.06‡	0.07	0.27	0.01/ 0.19
Spain (non-sprouting shrubs)	-0.10	-0.02	0.04	0.06/ 0.07	-0.11‡	-0.01	0.17	0.08/ 0.08

Figure legends

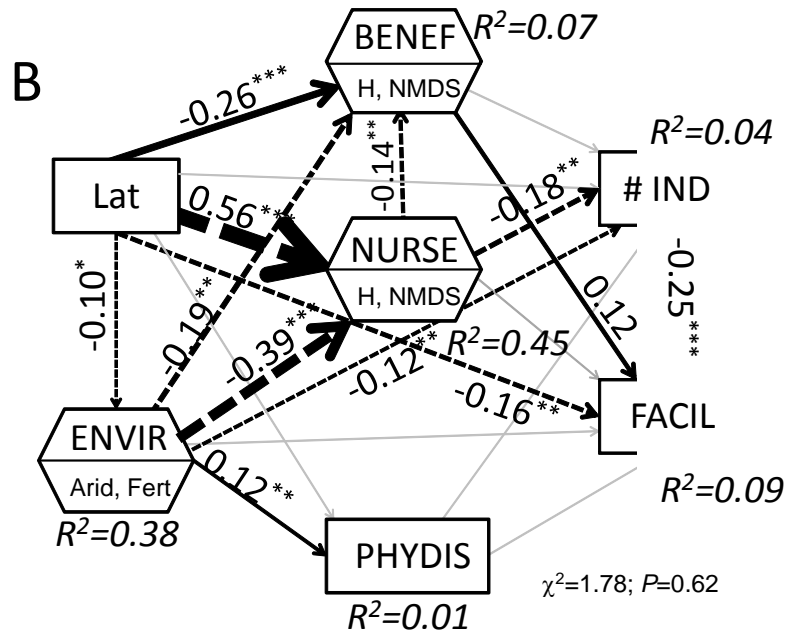
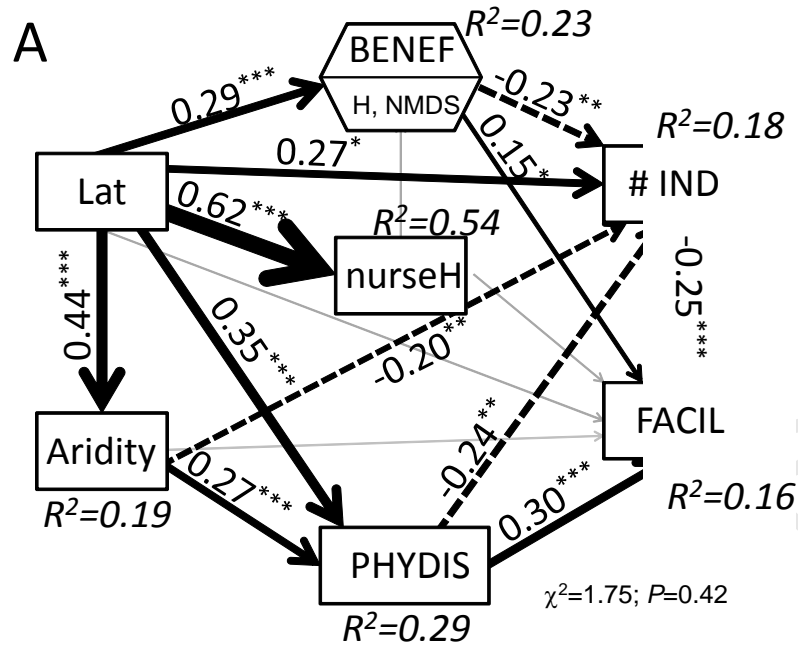
Figure 1. Global structural equation model, depicting effects of environmental conditions (ENVIR; aridity [arid] and fertility [fert]), phylogeny (PHYDIS), and functional traits of the beneficiaries (BENEF) and the nurse (NURSE) species (see main text for details) upon our plant-plant interaction metric (FACIL) and the number of individuals of the facilitated species (# IND). H = plant height; NMDS = NMDS ordination axis performed with qualitative functional traits. Composite variables are shown with hexagons. Standardized path coefficients are shown. The width of arrows is proportional to the path coefficient, with continuous and dashed lines for positive and negative relationships, respectively. The overall goodness-of-fit test and the R^2 for each variable introduced are given. *P*-values are: *** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$. The table shows the standardized total and direct effects on FACIL of the predictors included.

Figure 2. Global structural equation models for grasses (A) and woody (B) plants as nurses, depicting effects of environmental conditions (aridity and fertility), phylogeny and functional traits upon our plant-plant interaction metric (FACIL) and the number of individuals of the facilitated species (# IND). Rest of legend as in Fig. 1.



	SPATIAL		ENVIR		PHYDIS	NURSE		BENEF	
	Lat	Lon	arid	fert		H	nmds	H	nmds
Total effects	-0.01	-0.11	-0.06	-0.10	0.07	-0.01	0.03	0.11	0.03
Direct effects	0.03	-0.12	-0.04	-0.08	0.06	-0.02	0.02	0.12	0.03

Figure 1



1

2 **Figure 2**

3