Facilitation contributes to Mediterranean woody plant diversity but does not shape the diversity–productivity relationship along aridity gradients

Pedro J. Rey, Julio M. Alcántara, Antonio J. Manzaneda and Alfonso M. Sánchez-Lafuente

Department of Biología Animal, Biología Vegetal y Ecología, Universidad de Jaén, E-23071 Jaén, Spain

Author for correspondence:
Pedro J. Rey
Tel: +34 953 212145
Email: prey@ujaen.es

Summary

- The diversity–productivity relationship (humped-back model (HBM)) and the stress-gradient (SGH) hypotheses may be connected when productivity is limited primarily by aridity. We analytically connect both hypotheses and assess the contribution of facilitation to woody plant richness along the aridity gradient of the Western Mediterranean floristic region.
- We monitored regeneration niches of woody plants, obtaining rarefied species richness and plant relative interaction indices in 54 forests and scrublands in a 1750-km geographical range across Spain, Morocco and the Canary Islands.
- We verified the monotonic increase in facilitation with aridity postulated by SGH and the humped-shape pattern of species richness expected from HBM, which became manifest after expanding the aridity gradient or crossing vegetation types. Along the gradient, interaction balance turned into facilitation earlier in forest than in scrublands. The effects of aridity and interaction balance on species diversity were additive rather than interdependent.
- Facilitation is an important driver of woody species richness at macroecological scales because it added up to diversity in most sites, with enhanced contribution with increased stress. The HBM was not shaped by species interactions. Results suggest that facilitation may act in Mediterranean vegetation buffering against critical transitions between states allowing woody plant communities to cope with the rise in aridity expected with global warming.

Introduction

Understanding the factors that shape species diversity at local, regional and global scales is a major challenge in ecology (Ricklefs, 2004; Harrison & Cornell, 2008; Allesina & Levine, 2011). Species interactions are considered determinants of community diversity, with competition and predation thought to play leading roles in community organization (e.g. Menge & Sutherland, 1976; Tilman, 1982). Likewise, productivity, which is strongly linked with environmental/climatic factors, likely determines macroecological and regional gradients in species richness (e.g. Grime, 1973; Abrams, 1995). Grime's humped-back model (HBM) of species richness (Grime, 1973) was an important conceptual advance that merged the effects of productivity (or environmental stress) and species interactions (primarily through competition) on species diversity. According to this hypothesis, species richness peaks at intermediate levels along productivity–stress gradients, with competitive species dominating towards the high productivity extreme, stress-tolerant species dominating towards the stressful extreme and both strategies coexisting at intermediate levels. Grime's influential model continues to be evaluated, with persistent debate and refinements based on studies with animal and plant communities (Mittelbach

et al., 2001; Michalet *et al.*, 2006; Adler *et al.*, 2011; Fraser *et al.*, 2015). However, in the last two decades, studies on the influence of plant–plant interactions on community structure, assembly and diversity have moved the focus from competition towards facilitation in stressful environments (Bertness & Callaway, 1994; Bruno *et al.*, 2003; Valiente-Banuet *et al.*, 2006; Verdú *et al.*, 2009). Since Bertness & Callaway (1994) formulated the stress gradient hypothesis (SGH), information on the importance of facilitative interactions for plant performance in stressful environments, such as alpine, arid or salt marsh ecosystems, has accumulated rapidly (Brooker *et al.*, 2008; Soliveres *et al.*, 2015); however, consensus is far from being reached on the generality and the exact form (whether a monotonic increase or unimodal) of the relationship between the frequency (and intensity) of positive interactions and the level of the environmental stress (Maestre *et al.*, 2005; Lortie & Callaway, 2006; He *et al.*, 2013; Michalet *et al.*, 2014; Soliveres & Maestre, 2014).

Water availability is one of the most general limiting resources for plant productivity worldwide, and aridity is among the most important stresses influencing plant community diversity and productivity and ecosystem functioning (Maestre *et al.*, 2012). In particular, aridity is a widespread stress in the Mediterranean region and the one influencing species interaction and plant

community composition and structure throughout the region most obviously (Armas *et al.*, 2011; Pugnaire *et al.*, 2011; Gross *et al.*, 2013). In this study, we examine how the balance between facilitation and competition contributes to the species diversity of woody plant communities over most of the productivity–aridity gradient of the Western Mediterranean floristic region (a plant biodiversity hotspot; Médail & Quézel, 1997). We do this by assessing both the HBM and the SGH, two influential hypotheses that more commonly have been examined independently in previous studies.

Studies connecting the HBM and the SGH have been largely theoretical (Hacker & Gaines, 1997; Michalet *et al.*, 2006). Moreover, there have been few attempts to evaluate empirically how the competition–facilitation balance affects species diversity at the community level across stress gradients (Soliveres *et al.*, 2011, 2012), with even fewer studies at macroecological scales (Cavieres *et al.*, 2014). One clear connection between HBM and SGH emerges when productivity is limited primarily by aridity, a condition typical in Mediterranean ecosystems. In this case, both the balance between competition and facilitation and species richness theoretically will covary with aridity. Therefore, unlike recent studies that examined the contribution of facilitation to the macroecological patterns of species diversity (e.g. Cavieres *et al.*, 2014) but did not explicitly address such hypotheses, we tested both hypotheses and examined whether the stress gradient and the plant–plant interaction balance have synergistic (i.e. interactive) or independent (i.e. additive) effects on species diversity. Merging both hypotheses answers the recent calls for efforts to understand the multivariate drivers of species richness (Adler *et al.*, 2011; Fraser *et al.*, 2015). It is notable that the HBM and further modifications of this model to incorporate facilitation (e.g. Michalet *et al.*, 2006) mechanistically postulate that the influence of species interactions on community species richness across productivity–stress gradients acquires different weights depending on the position on the gradient. Thus, we should expect synergistic effects of the balance of interactions and productivity/aridity on species richness. By contrast, the independent effects of both drivers would imply that the competition–facilitation balance affects species richness over the entire gradient in a relatively comparable manner and that the humped-back distribution, when it occurs, is not shaped by species interactions but rather by some alternative mechanism (see later).

Crossing over boundaries of vegetation types is important to detect macroecological hump-shaped patterns of species richness across productivity–stress gradients for vascular plants (Mittelbach *et al.*, 2001) and to envisage the mechanisms involved in such patterns; however, few studies have been conducted at a sufficient scale to be conclusive (Fraser *et al.*, 2015). Moreover, most insights in this direction have come from meta-analyses rather than from studies conducted simultaneously at many sites and at different scales using homogenous sampling protocols (but see Adler *et al.*, 2011; Fraser *et al.*, 2015). Across the productivity–aridity gradient of the Mediterranean region, a transitional shift from forest to scrub communities typically occurs, and the different dominant lifeforms and physiognomies of these communities may affect both the balance of the interaction between plant

species and species richness. Furthermore, the western range of the floristic Mediterranean region extends to Mediterranean Europe, northwestern Africa, and the Canary Islands (Quézel, 1985; Médail & Quézel, 1997), and the contemporary floras of these three areas differ in regional species pools, biogeographical origins and turnovers of species (Médail & Quézel, 1999; Lavergne *et al.*, 2013). Modelling species richness in the overall context of the region may confound some of these issues that influence diversity. Therefore, as another goal of this study, we explored whether the HBM and the SGH are maintained independently of geographic scale, vegetation type (forest vs scrublands) and/or biogeographical region. To summarize, the wide productivity–aridity gradient of the Mediterranean region and its complex biogeographic history make it an ideal subject to assess the occurrence of diversity–productivity relationships and examine the mechanisms, in addition to species interactions, that may be involved in such a pattern.

Linking the HBM and SGH at macroecological scales can provide new insights with which to understand gradients of species diversity; however, the studies conducted to date have lacked a clear macroecological context. By our empirical combination of both hypotheses, we also provide novel insights enhancing understanding of the consequences of global warming on the maintenance of plant communities and species diversity (Soliveres *et al.*, 2015), a concern particularly relevant in the Mediterranean Basin.

Materials and Methods

Study sites and vegetation types

We sampled 54 study zones belonging to 16 woody plant communities (one to five zones per community, most commonly four), from mesic forests to arid scrublands in Spain (25 zones), Morocco (21) and the Canary islands (8), spanning a geographical range of *c*. 1750 km. The study zones were occupied by mature communities typical of the environmental conditions of the study area, and, when possible, the study sites were within protected and/or low-impact areas to minimize anthropogenic effects on recruitment. Largely disturbed sites were excluded because land-use history and management change the form of the regional- and global-scale relationships of species richness and productivity (Adler *et al.*, 2011), inflating the chance of a humped-back relationship. We studied a representative sample of the forest and scrubland types of the study region. Data and locations of the study zones and communities surveyed in this work are provided in Supporting Information Table S1 and Fig. 1. Based on the dominant life-forms, 32 of these zones were considered forests and 22 scrublands (Fig. 1; Table S1).

Sampling design

The surveys were conducted in five 65×50 m plots in each study zone, with the plots separated by > 100 m and arranged in parallel lines, topography permitting. Plots were planned to cross relatively heterogeneous canopy coverage to allow for the open
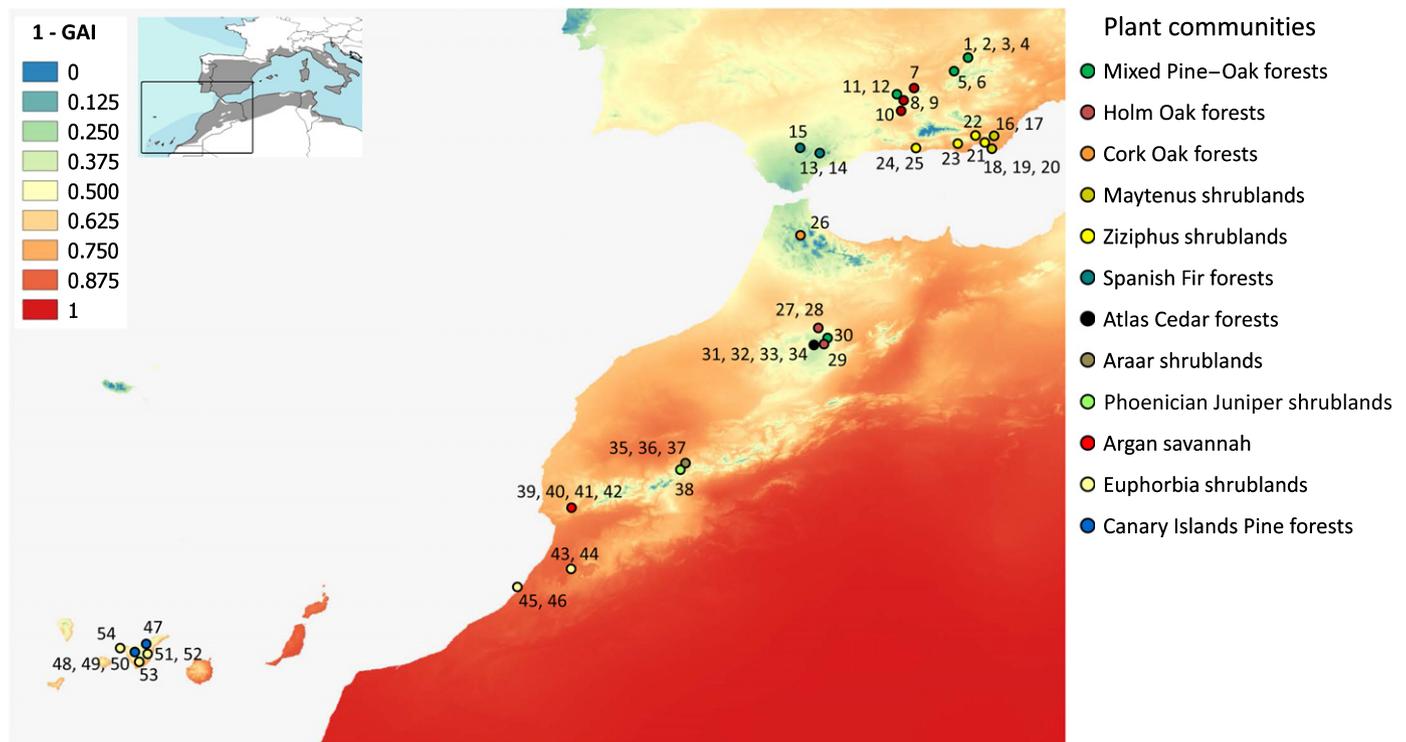
Fig. 1 Study site locations and major plant communities considered in this study. Plant communities considered forests were *Pinus canariensis* forests, *Cedrus atlatica* forests, *Argania spinosa* forests, several types of mixed Pine–oak forests (*Pinus halepensis*–*Q. faginea*; *P. nigra*–*Q. pyrenaica*, *P. pinaster*–*Q. faginea*, *P. halepensis*–*Q. ilex*), *Abies pinsapo* forests, *Quercus ilex* and *Quercus suber* oak forests. Plants communities considered scrublands were: Morocco and Canary Islands *Euphorbia* scrublands, *Juniperus phoenicea* scrublands, *Tetraclinis articulata* scrublands, *Maytenus senegalensis* scrublands and *Ziziphus lotus* scrublands. Numbering of study site localities follow that given in Supporting Information Table S1, where further details of each locality is provided. The inset represents the Mediterranean floristic ecoregion (ecoregion of Mediterranean forest, woodlands and scrublands. Global terrestrial Ecoregions, WWF). GAI, global aridity index.

interspaces and small gaps that are generated by natural disturbances (e.g. tree falls and wild ungulates) or patches of shallow soil. Within each of these plots, surveys of juveniles were conducted using paired samples, with each pair composed of the ground under the canopy of an adult of the most common plant species in the community (here considered the nurses) and an adjacent open of similar area outside the cover of that adult. The cover of the adult of each pair was assessed with the measurement of two perpendicular diameters of the canopy. Paired sampling of established juveniles has been used in previous studies to assess variation in the intensity of facilitative interactions in relation to climatic variation and/or or stress gradients (e.g. Soliveres *et al.*, 2011; Cavieres *et al.*, 2014). Moreover, the use of standing regeneration niches is common in studies that evaluate facilitation, test the stress-gradient hypothesis (SGH) and/or explore the contribution of facilitation to species richness at the community level (Valiente-Banuet *et al.*, 2006; Soliveres *et al.*, 2011, 2012; Cavieres *et al.*, 2014). The cover of each plant species was estimated in the 65 × 50 m plots along a 65 × 5 m transect centred in the plot.

Species interaction balance estimation

Advocates of the SGH have noted several uncertainties that potentially alter its verification, such as misdefined or incomplete stress gradients, confounding effects of multiple stresses,

incomplete or disparate datasets for meta-analytical tests and use of barely stress-sensitive life stages (He *et al.*, 2013; He & Bertness, 2014). We attempted to control some of these uncertainties: our study encompassed nearly the entire productivity–aridity gradient in the Mediterranean region from a value of 0.1 in *Abies pinsapo* forests to semidesertic areas with aridity up to 0.9; we avoided alpine scrublands with freezing temperatures to prevent a confounding stress; we defined clearly that the scale of examination of the SGH was at the community level of response rather than at a species-pairwise level (Soliveres *et al.*, 2015); we focused on pre-reproductive life-stages, which are preferred to adults for tests of the SGH; and our data were all obtained with the identical sampling protocol.

The estimate of the interaction balance was based on the comparison of established juveniles (i.e. saplings, not seedlings) beneath adult plants vs open. To estimate the result of the interaction between species, we used the relative interaction index, RII (Armas *et al.*, 2004), which is frequently used to characterize variation in facilitation across stress gradients (Armas *et al.*, 2011; Soliveres *et al.*, 2011; Cavieres *et al.*, 2014). The index has values between −1 (competition) and +1 (facilitation) and is based on the performance of a species when growing alone or when interacting with other species. Here, RII was calculated for each recruiting species using the following equation: RII = (juveniles beneath nurses − juveniles in open)/(juveniles beneath nurses + juveniles in open). Once the RII for each species in a

community was obtained, values were averaged across species to obtain a community-level RII, which was used in the analyses. The RII was calculated only for those species with at least five juveniles in the samples of the juvenile bank.

Species richness estimation

Congruent with the estimation of the interaction balance, species richness here referred only to juveniles (not seedlings) of woody species (trees and scrubs) from each study zone. Caution was used in determining juveniles of resprouting species, and some species with clonal and rhizomatous growth (e.g. *Rubus*, *Smilax*, *Jasminum*, *Osyris*, *Clematis*, *Rubia*) were not included in the analyses. Restricting the monitoring of species richness to woody species was relevant because, first, it focused on relatively similar growth forms and therefore richness estimates were directly comparable and, second, the counts were, to some extent, independent of yearly variation in production. Despite the similar sampling effort within each zone, the number of juveniles detected varied greatly among communities and zones. Thus, we used rarefaction to estimate juvenile species richness, and adopted the projections of species richness from rarefaction curves using ESTIMATES v.9.0 (Colwell, 2013; see Fig. S1 for some examples on estimated rarefaction curves). For each zone, species richness from rarefaction curves was standardized to 200 individuals (S200). We complemented this estimation with a species richness estimator that accounted for rarity (Chao1). Both estimates were strongly correlated across zones ($r = 0.87$) and with the total number of species detected as juveniles ($r = 0.90$ for S200; $r = 0.94$ for Chao1). The estimates of S200 and Chao1 were based on the number of juveniles detected rather than on the number of samples (or area sampled) because each sample of surveyed juveniles was from a very different area and depended on the cover area of the adult specimen and the species lifeform. The use of individual-based rarefaction curves to estimate species richness is common in ecology (Gotelli & Colwell, 2001; Gotelli & Chao, 2013) and is particularly convenient to control for sampling efforts when very different total numbers of individuals are sampled in each community.

Contribution of facilitation to species richness

Following Cavieres *et al.* (2014), we evaluated the magnitude of the contribution of facilitation to species richness by estimating the increase in species richness index (ISR), which measures the proportion of the species in the community that do not recruit in the open (i.e. obligate facilitated). This index was calculated by obtaining total juvenile species richness and juvenile species richness in open by rarefaction. ISR = $(S_{TOTAL} - S_{OPEN})/S_{TOTAL}$, where S is the species richness.

Aridity

We used the global aridity index (GAI) of CGIAR-CSI (http://www.cgiar-csi.org; Zomer *et al.*, 2007, 2008) to the resolution of 30 arc s (*c.* 1 km at the equator). This index combines mean annual precipitation and potential evapotranspiration. With an increase in this index, an increase in humidity in the environment is indicated; therefore, our analyses and graphs were based in 1-GAI for a straightforward interpretation. Climatic indices calculated both on an annual and a seasonal basis are relevant for vegetation and, in particular, for estimating climatic stress and the influence on the balance of interactions (Soliveres & Maestre, 2014). We used annual climatic data rather than seasonal data because annual-based climatic indices are commonly used in studies on facilitative interactions that consider rainfall, temperature or aridity as the primary stressors (e.g. Soliveres *et al.*, 2012) and, more commonly, are better descriptors of the relationships between facilitative interactions and climatic stress than seasonal variables (see recent review of Soliveres & Maestre, 2014).

Because the humped-back model (HBM) is formulated as a species diversity–productivity relationship, we also used indirect estimates of productivity to demonstrate that the aridity gradient was inversely related to productivity. We estimated productivity (net primary production, NPP) in each plot using remote sensing images from MODIS (Running *et al.*, 2015) at a resolution of 200M × 200M pixels (see Gaitán *et al.*, 2014 for a similar approach). Furthermore, we used the sum of the woody plant cover of the different vegetation layers as a surrogate for productivity.

Statistical analyses

General linear models (GLMs) were used to analyse the variation among regions and between vegetation types (both treated as fixed effects) for species richness, RII and ISR.

Because of the nonlinear relationships proposed by the HBM and the SGH, these hypotheses were first assessed independently for the overall dataset using nonlinear quadratic regressions (e.g. Mittelbach *et al.*, 2001; Maestre & Cortina, 2004). The response variables in these regressions were species richness and RII for the HBM and SGH, respectively, whereas the predictors were simple and quadratic terms of 1-GA (aridity) in the tests of both models. Quadratic regressions were conducted using GLM models in STATISTICA v.8 (StatSoft Inc., 2007). Because the estimators of species richness (S200 and Chao1) are typically continuous rather than counts, and the RII is typically normally distributed (Armas *et al.*, 2004), we adopted normal error and identity link functions in our tests of the HBM and SGH. The HBM and SGH were subsequently assessed within each region and for each vegetation type independently.

The possibility of synergistic effects of aridity and interaction balance on species richness was tested using surface regression. Surface regression is a type of GLM that includes linear, quadratic and interaction terms between two continuous predictors (*X* and *Y*) on a single response variable (*Z*):

$$Z = a + b_1X + b_2Y + b_3X^2 + b_4Y^2 + b_5XY$$

Thus, it permits the modelling of the independent effects of each predictor (whether linear or quadratic) on the response variable and also the possibility of interdependence (i.e. that the

effects of both predictors covary or depend on one another; the XY term in the equation earlier). It is particularly useful when the combination of continuous variables is likely to affect a response variable in complex ways, for example, nonlinearly, that is, giving rise to a surface that depicts the combination of values of the predictors that renders maximum and minimum in the response variable. Interpretation of the effects of the surface regression is similar to that for other factorial GLMs (e.g. ANOVA, ANCOVA). When no significant interaction of the predictors occurs (i.e. the XY term is not significant), the effects are additive (when both predictors have significant effects, linear or quadratic, on the response variable). By contrast, when the interaction of the predictors is significant, the effects of the predictors are interpreted as synergistic (i.e. dependent on one another). Surface regression is an appropriate statistical technique to merge the SGH and HBM analytically because productivity–aridity is the common axis (predictor) of the relationships depicted by these hypotheses. Moreover, both productivity–aridity and facilitation influence species diversity, but their link to explain species richness is unresolved. Therefore, with surface regression, we tested for linear and quadratic relationships of species richness to productivity–stress (as is typically conducted in HBM tests), linear or quadratic relationships of species richness to the relative interaction index (i.e. the contribution of facilitation–competition balance to species richness), and whether the effects of productivity–aridity and facilitation–competition on species richness covaried (as implicit in the mechanistic basis formulated by Grime for the HBM and further modifications; Michalet *et al.*, 2006).

Because species richness and/or RII could vary among regions and types of vegetation (forests and scrublands), we additionally tested the HBM, SGH and the surface regression by incorporating region and vegetation type separately as blocking effects in the overall models. Moreover, aridity also influences other variables that can affect productivity and the outcome of plant–plant interactions (e.g. soil nutrients and effects of human activities such as grazing; e.g. Ulrich *et al.*, 2014). Spatial covariation of aridity and these environmental variables along a geographical gradient may result in confounding effects. To avoid this

possibility, we repeated all analyses of the SGH, the HBM and the surface regression with and without geographic coordinates (longitude and latitude) as covariables. Incorporation of spatial coordinates did not change the statistical significance of any linear or quadratic coefficient. Therefore, in favor of simplicity, we opted to maintain the analyses, tables, figures and results without the geographic coordinates. Tests with geographic coordinates are provided in Table S2.

The assumptions of the statistical tests used were met without transformation of the original variables.

Results

In total, we recorded 26 844 juveniles of woody plants (mean across zones = 497.1; median = 278.5) belonging to 206 species, 102 genera and 42 families (Table S3). The mean observed juvenile species richness per zone was 13.9 (range 5–28; median = 13). Some species in the community were not observed as juveniles. Thus, the average total richness per zone was 17.2 (range 6–48; median = 15), with the average juvenile species richness representing 80.8% of the total. The total species richness and juvenile species richness were strongly correlated ($r = 0.90$; $P << 0.001$; $n = 54$ sites) and, therefore, juvenile species richness was an adequate representation of the total species richness of the community.

Species richness varied regionally (Table 1), with higher values in southern Spain than in Morocco and the Canary Islands, but not between forests and scrublands. Similarly, RII varied regionally from mean negative values in the Canary Islands to positive values in southern Spain and in Morocco, particularly (Table 1); however, RII did not vary between vegetation types.

Aridity varied among the study zones and ranged from 0.11 to 0.87, which covered most of the aridity gradient of the Mediterranean region. Across sites, the variation in productivity, estimated by both the sum of different layers of woody cover and from remote sensing images using MODIS, was inversely correlated with aridity ($r = -0.65$; $P < 0.0001$, for correlation with cover; $r = -0.73$; $P < 0.0001$, for NPP). Vegetation types differed in aridity ($F_{1,52} = 58.37$; $P < 0.0001$), with the aridity of

Table 1 Regional and between vegetation type variation in species richness (S200 and Chao1 richness estimators), balance of the interactions (relative interaction index, RII), and contribution of facilitation to (indigenous) species richness (ISR)

	Region (LS means ± 1 SE)					Vegetation type (LS means ± 1 SE)			
	Southern Spain	Morocco	Canary Islands	$F_{2,51}$	P	Forests	Scrublands	$F_{1,52}$	P
Species richness									
S200	**14.80 ± 0.79**	**11.41 ± 0.87**	**9.20 ± 1.41**	**7.67**	**0.0012**	12.79 ± 0.79	12.44 ± 0.96	0.08	0.78
Chao1	**20.13 ± 1.22**	**12.90 ± 1.33**	**10.96 ± 2.15**	**11.25**	**0.00009**	16.36 ± 1.27	15.38 ± 1.54	0.24	0.63
Balance of interactions									
RII	**0.14 ± 0.05**	**0.32 ± 0.05**	**−0.12 ± 0.09**	**9.44**	**0.0003**	0.180 ± 0.05	0.152 ± 0.06	0.12	0.73
Contribution of facilitation to species richness									
ISR estimated from S200	**0.114 ± 0.037**	**0.264 ± 0.040**	**0.128 ± 0.065**	**4.07**	**0.02**	0.153 ± 0.034	0.204 ± 0.041	0.89	0.35
ISR estimated from Chao1	**0.182 ± 0.041**	**0.325 ± 0.044**	**0.215 ± 0.072**	**2.90**	**0.06***	0.242 ± 0.038	0.243 ± 0.055	0.00	0.99

Separate general linear model tests were conducted for each dependent variable. Significant differences at $P < 0.05$ are shown in bold type and marked with an asterisk if $P < 0.1$.

scrublands higher than the aridity of forests (LS-mean = 0.75 ± 0.03 vs 0.48 ± 0.02, respectively); however, the mean aridity did not vary among regions ($F_{2,52} = 0.26$; $P = 0.77$).

Contribution of facilitation to species richness

Based on the estimates with S200 and Chao1, nurse species contributed to species richness (positive ISR) in 83.3% and 77.8% of the study sites, respectively. The ISR values varied considerably, ranging between 0 and 0.79 (as estimated from S200) and between 0 and 0.80 (from Chao1), and this variation was influenced by region, with higher ISR in Morocco than in the Canary Islands or southern Spain (Table 1). Although the ISR did not vary by vegetation type, it increased linearly with aridity, based on estimates of both S200 (b = 0.40 ± 0.13; $t = 3.16$; $P = 0.003$) and Chao1 (b = 0.29 ± 0.15; $t = 2.01$; $P = 0.050$).

Tests of HBM and SGH for Mediterranean woody communities

The HBM was strongly supported when all study zones were considered together, as indicated by the highly significant negative quadratic coefficient for aridity in polynomial regressions (Table 2; Fig. 2a,b). The humped-back curve remained significant even after controlling for regional variation and vegetation type (Table 2). The HBM was further corroborated in each biogeographic region (Fig. 3; Table 3). According to the negative quadratic trends shown in Table 3 and Fig. 3, the maximum in species richness was attained at increasingly higher aridity values from southern Spain to Morocco and to the Canary Islands. By contrast, when considering forests and scrublands separately, the negative quadratic term was significant only for scrublands with S200 (Table 3). Nevertheless, the slopes of the linear relationships between species richness and aridity varied from positive in forests to negative in scrublands, based on an ANCOVA that compared slopes between both vegetation types (illustration and test in Fig. 3).

Regarding the SGH, when all study zones were considered, we did not find a general quadratic relationship (Table 2) but a linear increase of RII with aridity (b = 0.52 ± 0.19; $t = 2.70$; $P = 0.0099$; $R^2 = 0.123$; Fig. 2c). When the SGH was tested separately for each region, significant quadratic terms were never detected (Table 3), although the linear increase in facilitation with aridity was verified in Morocco (b = 0.67 ± 0.25; $t = 2.62$; $P = 0.0168$; $R^2 = 0.265$) but not in southern Spain or the Canary Islands (Fig. 3). However, after controlling for vegetation type, we detected a positive quadratic term that increased the R^2 of the model to 41% and reinforced the occurrence of a monotonic, nonlinear increase of facilitative interactions throughout the aridity gradient. In Fig. 3, largely parallel monotonic trends of increasing RII with aridity in both vegetation types are indicated, with facilitation appearing earlier in forests than in scrublands along the stress gradient. Whereas the nonlinear increase of RII with aridity was significant for forests, the positive quadratic term was not significant for scrublands (Table 3; Fig. 3), although there RII increased linearly with aridity (b = 2.42 ± 0.81; $t = 2.99$; $P = 0.007$; $R^2 = 0.308$).

Merging HBM and SGH to model species richness

The surface regression conducted without data blocking showed no significant effect of aridity or RII for both Chao1 and S200 (Table 4). However, incorporating region as blocking effect revealed a humped-back relationship of species richness to aridity (significant negative quadratic term) and a nonlinear effect of RII (positive quadratic term of RII), although the interaction term between RII and aridity was not significant. This result indicates that the effects of aridity and interaction balance on species richness were largely additive (i.e. independent). Notably, these

Table 2 Tests of the humped-back model (HBM) and the stress gradient hypothesis (SGH)

	Humped-back model of species richness								Stress gradient			
	Estimate	SE	t	P	Estimate	SE	t	P	Estimate	SE	t	P
General pattern	Chao1 ($R^2 = 0.154$)				S200 ($R^2 = 0.166$)				RII ($R^2 = 0.132$)			
1-global aridity	**80.79**	**26.53**	**3.05**	**0.0037**	**50.13**	**16.36**	**3.06**	**0.0035**	−0.24	1.07	−0.23	0.8204
(1-global aridity)^2	**−71.31**	**23.87**	**−2.99**	**0.0043**	**−41.99**	**14.72**	**−2.85**	**0.0062**	0.70	0.97	0.73	0.4711
Intercept	−4.29	6.90	−0.62	0.5367	−0.79	4.25	−0.19	0.8532	0.04	0.28	0.15	0.8790
Blocking by region model	Chao1 ($R^2 = 0.479$)				S200 ($R^2 = 0.434$)				RII ($R^2 = 0.374$)			
1-global aridity	**86.88**	**21.69**	**4.00**	**0.0002**	**55.84**	**14.08**	**3.97**	**0.0002**	0.59	0.95	0.63	0.5348
(1-global aridity)^2	**−75.46**	**19.57**	**−3.86**	**0.0003**	**−46.55**	**12.67**	**−3.67**	**0.0006**	−0.10	0.86	−0.12	0.9045
Intercept	−7.86	5.69	−1.38	0.1734	−3.42	3.68	−0.93	0.3573	−0.20	0.25	−0.81	0.4220
Blocking by vegetation type model	Chao1 ($R^2 = 0.155$)				S200 ($R^2 = 0.180$)				RII ($R^2 = 0.408$)			
1-global aridity	**79.41**	**27.36**	**2.90**	**0.0055**	**46.94**	**16.74**	**2.80**	**0.0072**	−1.15	0.92	−1.26	0.2133
(1-global aridity)^2	**−68.80**	**26.20**	**−2.63**	**0.0114**	**−36.13**	**16.03**	**−2.25**	**0.0286**	**2.37**	**0.88**	**2.70**	**0.0094**
Intercept	−4.52	7.03	−0.64	0.5231	−1.32	4.30	−0.31	0.7596	−0.11	0.24	−0.46	0.6468

Tests were conducted independently for a general pattern and using region and vegetation types as blocks. Estimate, SE, t-test and P-level of significance are provided for each coefficient in the model. Significant coefficients at $P < 0.05$ are in bold type. Two estimates of species richness (S200 and Chao1) are used in tests of the HBM. The block effect was statistically significant in the *blocking by region model* ($F_{2,49} = 15.29$, $P < 0.0001$, for Chao1; $F_{2,49} = 11.60$, $P < 0.0001$, for S200) but not in the *blocking by vegetation type model* ($F_{1,50} = 0.06$, $P = 0.81$, for Chao1; $F_{1,50} = 0.86$, $P = 0.36$, for S200). Here we show only the coefficients and statistical significance of the effects of interest.
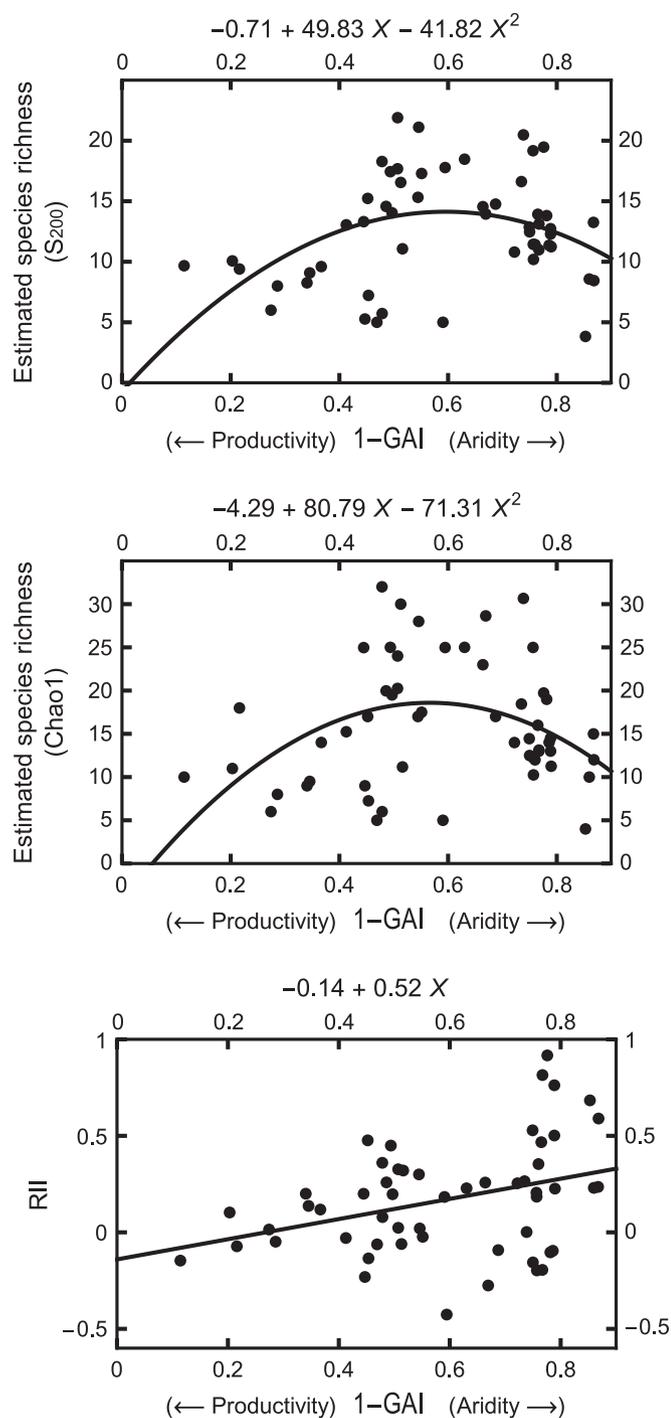
$-0.71 + 49.83\,X - 41.82\,X^2$

$-4.29 + 80.79\,X - 71.31\,X^2$

$-0.14 + 0.52\,X$

Fig. 2 Overall patterns of the humped-back model (HBM) and the stress gradient hypothesis (SGH) across the study region. The humped-shape relationship of species richness to aridity was corroborated (upper and middle panels), whereas balance of interaction (RII) showed a significant linear monotonic increase of facilitation with aridity (lower panel). S(200), species richness standardized to 200 juveniles from rarefaction curves; Chao1, nonparametric species richness estimator accounting for rarity; RII, relative interaction index; GAI, global aridity index.

surface regressions, which control for regional variation in mean species richness with the blocking effect, increased the variance explained by the polynomial regressions (compare the R^2 values

in Tables 2, 4) and probe the contribution of plant interaction balance to the variation in species richness.

Discussion

The stress gradient hypothesis

Considerable debate has occurred in the last decade on the shape of the relationship between variation in positive species interactions and environmental stress. It has been argued that the monotonic shift from competition to facilitation along stress gradients postulated by the stress-gradient hypothesis (SGH; Bertness & Callaway, 1994) should be moved towards a unimodal relationship (Maestre & Cortina, 2004; Holmgren & Scheffer, 2010). Thus, at a certain high level of stress, facilitation collapses and may turn into competition under extreme stress (Michalet *et al.*, 2014). However, based on our results, a monotonic increase in facilitation at the community level occurred along the entire aridity gradient of the Mediterranean region (confirming SGH) and facilitation did not collapse under extreme stress. This pattern continued to be reinforced after controlling for differences in relative interaction index (RII) induced by the type of vegetation.

Although support for the SGH along aridity gradients in the Mediterranean is controversial, some supporting evidence is found when expanding the study area to include the distribution range of primary nurse species or stretching the gradient to include most of the productivity–aridity values found regionally (Holzapfel *et al.*, 2006; Armas *et al.*, 2011). For example, the nurse effect at the community level of *Retama sphaerocarpa* increases monotonically throughout its aridity range (Armas *et al.*, 2011; but see Michalet *et al.*, 2015). By contrast, lack of support for a monotonic increase of positive interactions along the gradient or evidence of a unimodal relationship was found in studies conducted along short stress gradients and/or in species-pairwise comparisons rather than at the community level (e.g. Maestre & Cortina, 2004). Our results are also consistent with the conceptual model of Soliveres *et al.* (2011), in which the relationship between environmental gradients and the frequency of facilitative interactions can be predicted at the community level when the gradient is driven by a single primary stressor (here, aridity).

The investigation of the SGH at the regional scale and within types of vegetation provided new insights. We did not detect any relationship between RII and aridity in southern Spain and the Canary Islands, but there was a monotonic increase in Morocco, where the gradient expands into greater severity. This illustrates that the portions of the gradients not sampled may account for the lack of detection of the SGH (Lortie & Callaway, 2006; He & Bertness, 2014). The SGH was corroborated within forests and within scrublands (either through a linear or nonlinear monotonic increase in RII). Notably, facilitation appeared earlier along the stress gradient in forests than in scrublands (Fig. 3); therefore, at the same level of aridity, forest species are more reliant on facilitation for recruitment than shrub species (Gómez-Aparicio *et al.*, 2004; Siles *et al.*, 2010). This observation is consistent with the well-known pattern of increasing aridity imposing increasing inhibition of the establishment of typical
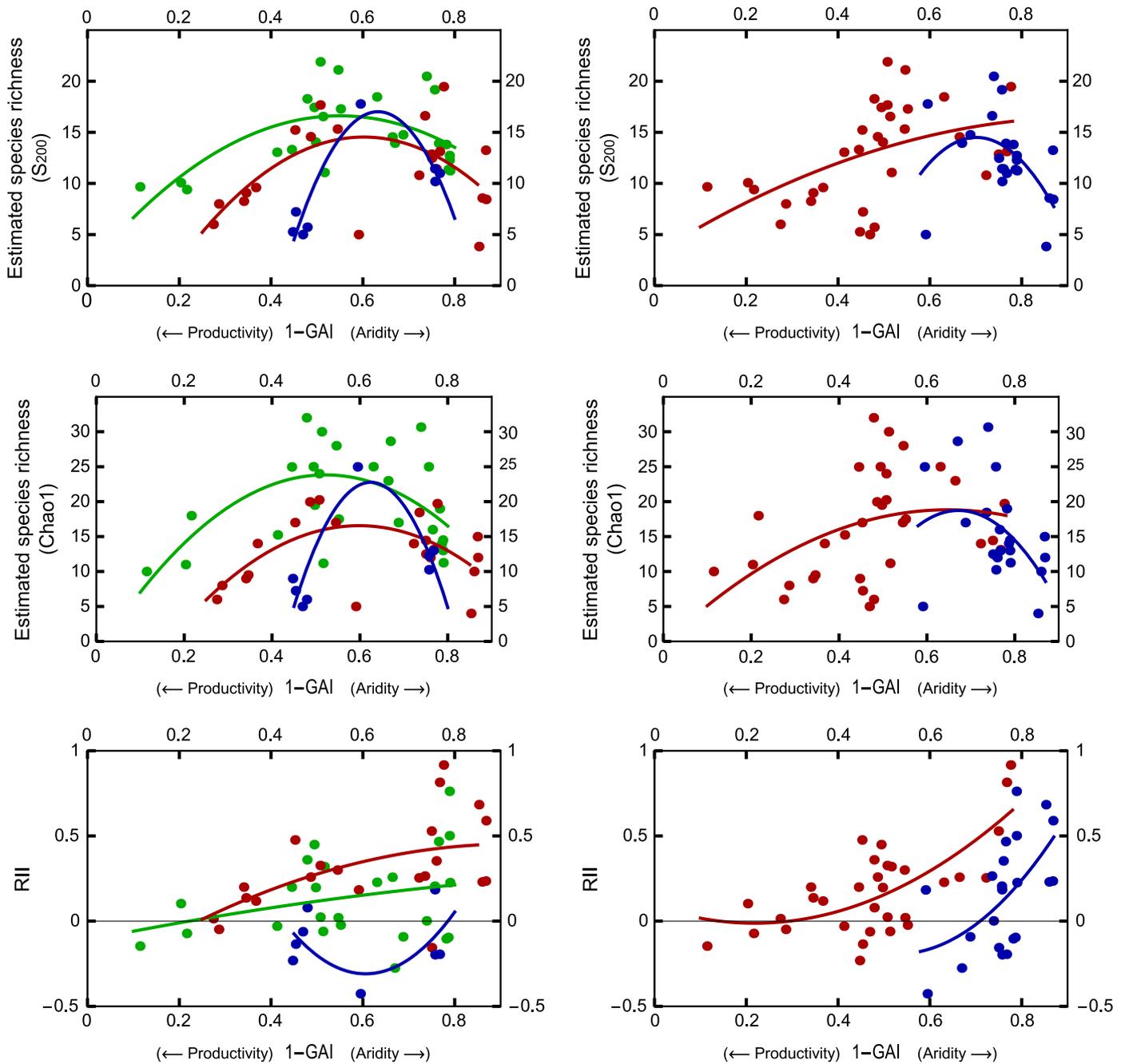
Fig. 3 Test of the humped-back model (HBM) and the stress gradient hypothesis (SGH) at each biogeographical region (left panels: green, South Spain; red, Morocco; blue, Canary islands) and vegetation type (right panels: red, forest; blue, scrublands). The humped-shape curve was corroborated at each region with both richness estimators (see also Table 2) but not in each type of vegetation with the slopes differing significantly from positive in forest to negative in scrublands (ANCOVA, interaction vegetation type × 1-GA, $F_{1,50} = 5.18$, $= 0.027$ with S200; $F_{1,50} = 4.96$, $P = 0.03$ with Chao1). The balance of interaction (RII) did not show any significant nonlinear trends in any region; it shows a significant monotonic increase (but linear) only in Morocco, and depicted parallel monotonic increase in both types of vegetation (ANCOVA: $F_{1,50}$, 3.04, $P = 0.09$). S(200), species richness standardized to 200 juveniles from rarefaction curves; Chao1, nonparametric species richness estimator accounting for rarity; RII, relative interaction index; GAI, global aridity index.

temperate forest species and that, at a certain level of stress, trees require facilitation by shrubs to persist in the local flora. Indeed, taxa present in the region before the onset of the Mediterranean climate (typically trees) are facilitated by taxa that evolved after the onset of this climate (typically small shrubs) (Valiente-Banuet *et al.*, 2006; Verdú *et al.*, 2009).

Test of the humped-back diversity–stress relationship

The spatial and geographic scales, productivity range and the type of community to which the humped-back model (HBM) applies also have been debated (Mittelbach *et al.*, 2001; Whittaker & Heegaard, 2003; Adler *et al.*, 2011; Fraser *et al.*, 2015), in

Table 3 Tests of the humped-back model (HBM) and stress-gradient hypothesis (SGH) at each biogeographical pattern and vegetation type level considered in the study

	Humped-back model of species richness								Stress gradient			
	Estimate	SE	t	P	Estimate	SE	t	P	Estimate	SE	t	P
Biogeographical pattern												
South Spain	Chao1 ($R^2 = 0.345$)				S200 ($R^2 = 0.388$)				RII ($R^2 = 0.087$)			
1-global aridity	**98.54**	**28.94**	**3.41**	**0.0025**	**54.14**	**14.86**	**3.64**	**0.0014**	0.55	1.23	0.45	0.6606
(1-global aridity)²	−**94.44**	**28.26**	−**3.34**	**0.0030**	−**49.24**	**14.51**	−**3.39**	**0.0026**	−0.17	1.20	−0.15	0.8857
Intercept	−1.88	6.95	−0.27	0.7899	1.73	3.57	0.49	0.6323	−0.11	0.29	−0.38	0.7067
Morocco	Chao1 ($R^2 = 0.317$)				S200 ($R^2 = 0.319$)				RII ($R^2 = 0.277$)			
1-global aridity	**104.78**	**36.46**	**2.87**	**0.0101**	**90.47**	**31.55**	**2.87**	**0.0102**	1.78	2.08	0.85	0.4050
(1-global aridity)²	**87.59**	**31.14**	−**2.81**	**0.0115**	−**75.15**	**26.94**	−**2.79**	**0.0121**	−0.95	1.78	−0.53	0.5983
Intercept	−14.78	9.64	−1.53	0.1427	−12.70	8.34	−1.52	0.1455	−0.37	0.55	−0.68	0.5063
Canary islands	Chao1 ($R^2 = 0.740$)				S200 ($R^2 = 0.853$)				RII ($R^2 = 0.181$)			
1-global aridity	**725.84**	**211.66**	**3.43**	**0.0187**	**472.18**	**109.18**	**4.32**	**0.0075**	−11.63	11.29	−1.03	0.3498
(1-global aridity)²	−**581.04**	**173.27**	−**3.35**	**0.0203**	−**372.93**	**89.38**	−**4.17**	**0.0087**	9.60	9.24	1.04	0.3463
Intercept	−**203.91**	**61.40**	−**3.32**	**0.0210**	−**132.44**	**31.67**	−**4.18**	**0.0086**	3.22	3.27	0.98	0.3709
Vegetation type pattern												
Forest	Chao1 ($R^2 = 0.167$)				S200 ($R^2 = 0.2406$)				RII ($R^2 = 0.499$)			
1-global aridity	59.33	35.03	1.69	0.1010	28.16	21.44	1.31	0.1993	−0.92	0.96	−0.96	0.3451
(1-global aridity)²	−45.84	36.26	−1.26	0.2162	−14.75	22.19	−0.66	0.5116	**2.10**	**0.99**	**2.13**	**0.0422**
Intercept	−0.37	8.16	−0.04	0.9644	3.09	4.99	0.62	0.5409	0.09	0.22	0.39	0.6958
Scrubland	Chao1 ($R^2 = 0.201$)				S200 ($R^2 = 0.277$)				RII ($R^2 = 0.327$)			
1-global aridity	347.20	275.04	1.26	0.2221	**333.69**	**154.00**	**2.17**	**0.0431**	−6.22	11.96	−0.52	0.6087
(1-global aridity)²	−258.37	186.97	−1.38	0.1830	−**237.81**	**104.68**	−**2.27**	**0.0349**	5.89	0.13	0.72	0.4776
Intercept	−97.91	100.60	−0.87	0.3427	−102.56	56.32	−1.82	0.0844	1.45	4.37	0.33	0.7436

Estimate, SE, t-test and P-level of significance are provided for each coefficient in the model. Significant coefficients at $P < 0.05$ are in bold type. Two estimates of species richness (S200 and Chao1) are used in tests of the HBM.

Table 4 Surface regression controlling for interdependence of the effects of the interaction balance (RII) and aridity (1-GA) on species richness

	Estimate	SE	t	P	Estimate	SE	t	P
Simple surface regression	Chao1 ($R^2 = 0.182$)				S200 ($R^2 = 0.208$)			
RII	21.46	19.49	1.10	0.2765	17.85	11.98	1.49	0.1428
RII²	8.54	10.48	0.82	0.4189	7.09	6.44	1.10	0.2760
1-global aridity	56.57	32.02	1.86	0.0690	34.61	19.66	1.76	0.0849
(1-global aridity)²	−49.83	30.41	−1.61	0.1148	−26.68	18.68	−1,43	0.1598
RII×(1-global aridity)	−38.48	31.02	−1.24	0.2209	−28.83	19.06	−1.51	0.1370
Intercept	−0.40	7.68	−0.05	0.9583	2.08	−4.72	0.44	0.6615
Blocking by region model	Chao 1 ($R^2 = 0.535$)				S200 ($R^2 = 0.4911$)			
RII	10.36	15.82	0.65	0.5160	10.49	10.29	1.02	0.3135
RII²	**17.43**	**8.29**	**2.10**	**0.0410**	**11.87**	**5.39**	**2.20**	**0.0327**
1-global aridity	**75.48**	**25.79**	**2.93**	**0.0053**	**45.51**	**16.77**	**2.71**	**0.0093**
(1-global aridity)²	−**62.51**	**24.39**	−**2.56**	**0.0137**	−**36.05**	**15.86**	−**2.27**	**0.0277**
RII×(1-global aridity)	−31.81	24.18	−1.32	0.1949	−23.80	15.72	−1.51	0.1369
Intercept	−6.34	6.26	−1.01	0.3166	−1.72	4.07	−0.42	0.6743

The region blocking effect was statistically significant in this model ($F_{2,46} = 17.46$, $P < 0.0001$, for Chao1, $F_{2,46} = 12.68$, $P < 0.0001$, for S200). Here we only show the coefficients and statistical significance of the effects of interest. Significant coefficients at $P < 0.05$ are in bold type.

addition to the mechanisms shaping the relationship between species richness and productivity–stress (Michalet *et al.*, 2006; Michalet & Touzard, 2010).

The meta-analytical review of Mittelbach *et al.* (2001) showed that for vascular plants the humped-back relationship is found more frequently in studies conducted at scales < 4000 km. Independent of the geographic scale, this type of relationship is also more frequent in studies that crossed community types (i.e. shifts in vegetation types from predominant tree lifeforms to shrubs or herbs) than in studies conducted within a single type of community. Our results are consistent with the findings of Mittelbach *et al.* (2001). We corroborated the HBM at the scale of both the entire study area (2000 km) and within each biogeographical region, independent of an impoverishment of the flora from southern Spain to Morocco and the Canary Islands, but not within each vegetation type. As shown in Fig. 3, the overall humped-back pattern is shaped after merging the trends of increasing diversity with increasing aridity in forests and decreasing

diversity with increasing stress in scrublands. Notably, the humped-shape relationship also was found after controlling for variation in mean species richness among regions, which, to some extent, is equivalent to controlling for historical and biogeographical differences across the region (Molina-Vanegas *et al.*, 2013) in the species pool.

The most recent debate on diversity–productivity relationships emerged from studies on grassland communities conducted at a global scale (Adler *et al.*, 2011; Fraser *et al.*, 2015) that gathered their own data with homogeneous field protocols but rendered very contrasting results. From these studies, it is evident that detection of the humped-back relationship may depend on the sampling effort and the width of the productivity range. There are few tests of the HBM across productivity–aridity gradients in the Mediterranean region, and these tests examined productivity–aridity gradients that were considerably narrower than the gradient of this study. Soliveres *et al.* (2011) found a humped-shape relationship between perennial plant richness and drought and radiation in the semiarid range of central and southeastern Spain. However, Armas *et al.* (2011) did not find support for a humped-shape relationship in communities that grow along the range of *R. sphaerocarpa*. We believe that the failure to cross communities (Mittelbach *et al.*, 2001) or expand the productivity–aridity range (Fraser *et al.*, 2015) may account for such discrepancies and that both are required to properly assess the HBM and its underlying mechanisms.

Merging SGH and HBM

With the merger of these two influential hypotheses, we can try to answer two major questions in plant ecology.

Does facilitation contribute to species diversity along the aridity gradient? The occurrence of positive interactions within plant communities implies that when one species occurs in a locality the chances for other species to co-occur increases; thus, positive interactions can contribute to species diversity (Cavieres & Badano, 2010). Studies comparing species richness beneath and outside nurses in arid environments have produced contrasting results (reviewed in Cavieres & Badano, 2010), which reflects the idiosyncratic nature of species richness at the patch scale (Michalet, 2006; Soliveres *et al.*, 2012). We found positive ISR values for most study sites, which indicated that some species were most likely occurring there as obligate beneficiaries of positive plant–plant interactions and that, in most communities, the diversity was increased by facilitation. Cavieres *et al.* (2014) found a similar result for alpine cushion communities that experience freezing temperatures and strong winds. We also found a significant positive linear relationship of indigenous species richness (ISR) with aridity, which indicated a higher contribution of facilitation to species diversity at the harsh extremes of the stress gradient (Holzapfel *et al.*, 2006); all five localities with ISR values over 0.5 had aridity > 0.75 (Table S1). Consistent with this idea the ISR was lower in the Canary Islands and southern Spain than in Morocco, where the aridity expands to the most severe values. Likewise, Cavieres *et al.* (2014) found that the increase in species

richness by facilitation declines with productivity in alpine communities at a global scale. Assuming a unimodal relationship between frequency (or intensity) of positive interactions and stress, with a collapse of facilitation at the extremes of the gradient, Michalet *et al.* (2006) hypothesized that facilitation would contribute to species richness with maximum scores at intermediate levels of stress. Our results did not confirm this hypothesis. We found increasing ISR with aridity which, indeed, could be expected from the incorporation into the species diversity curve of the monotonic increase in facilitation postulated by the SGH.

The relevance of facilitation for species richness was also manifested after controlling for the interdependence of species richness with the productivity–aridity gradient. According to our surface regression models, RII might positively affect species diversity independent of the level of aridity, which means that benefits other than an amelioration of aridity stress are also achieved for the recruits that grow under adults in the local communities studied. These benefits include protection against herbivory, provision of soil nutrients and reduced interspecific belowground competition for shared mycorrhizal networks (Moora & Zobel, 2010; Pugnaire *et al.*, 2011; Soliveres *et al.*, 2012). Notably, our models also suggest increased richness at highly negative RII values (Fig. S2), which might reflect the occurrence of species strictly recruiting in the open (nurse avoiders) and also account for some additional richness through niche differentiation mediated by functional trait divergence (Gross *et al.*, 2013). This situation could occur with the shade-intolerant species in Mediterranean forests that require recurrent disturbance to persist (Alcántara *et al.*, 2015).

In short, facilitation was an important driver of woody species richness at a macroecological scale because it added up to diversity in most sites and the contribution to diversity increased with aridity.

Does the balance of interactions shape the humped-back diversity–aridity relationship? As stated in the introduction, if the species interaction balance shaped the relationship between species richness and productivity–aridity, we would expect interdependent effects of aridity and RII on species richness. However, we found that the humped-back relationship between species richness and aridity was maintained in Mediterranean woody plant communities at a continental scale and did not depend on how the interaction balance varied across the aridity gradient. Thus, other drivers are responsible for the humped-back relationship. In a recent review, Michalet & Touzard (2010) proposed that the relative importance of the primary ecological filters of plant diversity depends on the geographic scale. They suggested that at regional (< 1000 km) and continental (> 1000 km) scales the patterns of community richness are driven primarily by stress and chance biogeographical events (Huston, 1999; Lortie *et al.*, 2004). Our continental humped-back pattern might be consistent with this proposal. On the one hand, the complex biogeographical history of the Mediterranean region has repeatedly melded species pools (*sensu* Cornell & Harrison, 2014) and lineages of different biogeographical origins (i.e. Eurosiberian, Mediterranean, Irano-Turanian and Saharo-

Arabian; Thompson, 2005), that would be particularly pronounced at intermediate positions of the gradient. On the other hand, parallel to and to a large extent shaped by the aridity gradient of the Mediterranean region, there is a transition from typical temperate forest to savanna-like woodlands and finally to arid scrublands. We propose that the turnover of these vegetation formations inherently shapes the unimodal relationship of species richness with aridity. Supporting this proposal, our analysis of the HBM by vegetation type showed that the overall humped-back relationship was depicted as a trend of species richness to increase with aridity in forests and decrease in scrublands, which is linked with the replacement of lifeforms (trees to scrubs) along the aridity gradient (Fig. 3). We hypothesize that vegetation type turnover involves a concomitant transition of predominant plant functional traits and of the level in which functional traits are filtered by environment (Gross *et al.*, 2013). With these two nonexclusive explanations, we would expect that the patterns of functional, biogeographical or phylogenetic diversity would reflect the species diversity pattern across the aridity gradient; the evaluation of these possibilities is currently under investigation.

Concluding remarks: implications for climate change concerns

Our study is based on spatial correlations and therefore some caution is needed to interpret our results. Although HBM can be strongly supported with spatial patterns, further experimental evidence is needed in case of SGH tests. Keeping this in mind, our results provide insights to improve our understanding of the consequences of global warming for woody plant communities and the maintenance of species diversity in the Western Mediterranean floristic region. Drylands are ecosystems prone to critical transitions from vegetated to nonvegetated stable states under global change drivers such as climate change and intensified land use (Kéfi *et al.*, 2007a; Verwijmeren *et al.*, 2013). In fact, the humped-back pattern of diversity–aridity relationship, that was detected at a continental scale and shaped across community boundaries, suggests that the Western Mediterranean floristic region may undergo critical transitions from forest to scrubland and from scrubland to nonvegetated states with an increase in aridity. Recent connections between critical transition theory and facilitation have led to the proposal that declines in facilitation with stress would increase the chances of critical transitions from vegetated to nonvegetated stable states in arid ecosystems (Verwijmeren *et al.*, 2013; and references therein). We propose that when the relationship of facilitation and aridity is unimodal then increased drought in the region resulting from climate change would cause a decline in the frequency and intensity of facilitative interactions in communities located at present on the high aridity side of the gradient, which could potentially trigger the critical transition to nonvegetated states. By contrast, our finding of a monotonic increase of facilitation intensity with aridity would suggest that the Mediterranean woody vegetation is, to some extent, resistant to critical transitions from forest to scrubland and to desert, because facilitation would act as a buffering mechanism against such transitions. Additionally, with a monotonic increase, the persistence of species would increase and, consequently, maintain the ecosystem multifunctionality of drylands through species diversity (Maestre *et al.*, 2012). It has been suggested that the intensity of facilitation may determine the position of a critical transition threshold (Kéfi *et al.*, 2007b) and serve as a warning signal in the forecasting of transition. Our study illustrates that a relatively rapid and repeatable protocol of juvenile monitoring produces indices of facilitation intensity and species richness that are useful to such ends.

Author contributions

P.J.R. developed the conceptual framework of this study; P.J.R., J.M.A. and A.J.M. designed the sampling protocols; P.J.R. and J.M.A. analysed the data; P.J.R., J.M.A., A.J.M. and A.M.S-L. participated in data collection, processing and interpretation; and P.J.R., J.M.A. and A.J.M. wrote the paper.

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Supporting Information

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

Fig. S1 Estimated rarefaction curves for a sample of 12 study localities.

Fig. S2 Contour plots of species richness in surface response regression models.

Table S1 Compiled data in each study site

Table S2 Complete set of tests of the humped-back model, the stress gradient hypothesis, and their combined analysis, incorporating latitude and longitude of the study sites as covariates

Table S3 Complete list of plant species and families found as juveniles in this study

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