

MECHANISMS AND CONSEQUENCES OF FACILITATION IN PLANT COMMUNITIES

Does the stress-gradient hypothesis hold water? Disentangling spatial and temporal variation in plant effects on soil moisture in dryland systems

Bradley J. Butterfield^{*1}, John B. Bradford^{1,2}, Cristina Armas³, Ivan Prieto⁴
and Francisco I. Pugnaire³

¹Merriam-Powell Center for Environmental Research and Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona, USA; ²U.S. Geological Survey, Southwest Biological Science Center, Flagstaff, Arizona, USA; ³Estación Experimental de Zonas Áridas, Consejo Superior de Investigaciones Científicas, Almería, Spain; and ⁴Centro de Edafología y Biología del Seguro (CEBAS-CSIC), Campus Universitario de Espinardo, PO Box 164, 30100 Murcia, Spain

Summary

1. The nature of the relationship between water limitation and facilitation has been one of the most contentious debates surrounding the stress-gradient hypothesis (SGH), which states that plant-plant interactions shift from competition to facilitation with increasing environmental stress.

2. We take a closer look at the potential role of soil moisture in mediating plant-plant interaction outcomes by assessing effects of climate and soil texture on plant modulation of soil moisture.

3. Using an empirically-parameterized soil moisture model, we simulated soil moisture dynamics beneath shrubs and in un-vegetated coarse and fine soils for 1000 sites in the Western United States with < 700 mm mean annual precipitation. This threshold reflects the transition from dryland (< 600 mm precipitation) to mesic ecosystems.

4. Positive effects of shrubs on shallow soil moisture (i.e. the difference between shrub and interspace soil moisture) decreased along the aridity gradient when long-term average conditions were considered, contrary to expectations based on the SGH. Negative effects of shrubs on deeper soil moisture also increased with aridity.

5. However, when extreme years were considered, positive effects of shrub on soil moisture were greatest at intermediate points along the spatial aridity gradient, consistent with a hump-backed model of plant-plant interactions.

6. When viewed through time within a site, shrub effects on shallow soil moisture were positively related to precipitation, with more complex relationships exhibited in deeper soils

7. Taken together, the results of this simulation study suggest that plant effects on soil moisture are predictable based on relatively general relationships between precipitation inputs and differential evaporation and transpiration rates between plant and interspace microsites that are largely driven by temperature. In particular, this study highlights the importance of differentiating between temporal and spatial variation in weather and climate, respectively, in determining plant effects on available soil moisture. Rather than focusing on the somewhat coarse-scale predictions of the SGH, it may be more beneficial to explicitly incorporate plant effects on soil moisture into predictive models of plant-plant interaction outcomes in drylands.

Key-words: arid, competition, drought, evapotranspiration, facilitation, hydraulic lift, precipitation pulse, shade

*Correspondence author. E-mail: Bradley.Butterfield@nau.edu

Introduction

In their now seminal paper, Bertness & Callaway (1994) proposed an increase in the frequency and importance of facilitation with increasing environmental severity, which became known as the stress gradient hypothesis (SGH). Many examples of facilitation, including some of the earliest (Turner *et al.* 1966; Yeaton 1978), come from dryland ecosystems, thereby anecdotally supporting the prediction of the SGH that facilitation should be important in water-limited relative to mesic ecosystems (Flores & Jurado 2003). Yet *within* dryland ecosystems [those experiencing <600 mm of rain in an average year (Noy-Meir 1973; Sala *et al.* 1988)], the relationship between plant-plant interactions and water deficit is less clear. Meta-analyses have found support for (Lortie & Callaway 2006; Dohn *et al.* 2013; He, Bertness & Altieri 2013) and against (Maestre, Valladares & Reynolds 2005; Soliveres & Maestre 2014; Soliveres *et al.* 2014) the SGH, which have led to recent refinements and alternative models for plant-plant interactions along aridity gradients (Maestre *et al.* 2009; McCluney *et al.* 2012). Contradictory conclusions may stem from variation in functional and life history strategies, resource vs. non-resource stress factors, and a focus on only a small portion of the community (Michalet 2007; Butterfield 2009; He, Bertness & Altieri 2013; Michalet *et al.* 2014). Nevertheless, some field studies in drylands support the SGH (e.g., Pugnaire & Luque 2001; Holzapfel *et al.* 2006; Armas, Rodríguez-Echeverría & Pugnaire 2011; Dohn *et al.* 2013; Ziffer-Berger *et al.* 2014; Pugnaire *et al.* 2015), while others do not (Tielborger & Kadmon 2000; Maestre & Cortina 2004; Butterfield *et al.* 2010). Recent meta-analyses at the individual plant (Soliveres *et al.* 2014) and community levels (Soliveres & Maestre 2014) demonstrate that facilitation is on the whole weakly negative correlated with aridity (a measure of water deficit) across a number of studies, contrary to the SGH, but the variability in this relationship among those studies was incredibly high.

As the primary limiting resource, water plays a central role in mediating plant-plant interactions in drylands, and it stands to reason that interactions mediated by water should play an important role in determining support for or against the SGH. Plants in drylands can also increase soil nutrient content and organic matter compared to interspaces (Pugnaire, Haase & Puigdefabregas 1996; Armas, Pugnaire & Sala 2008), reduce incident radiation and ameliorate microclimatic conditions through shading (Callaway 2007; Holmgren *et al.* 2012), all of which can directly or indirectly ameliorate soil moisture conditions under plants compared to interspaces. These mechanisms are not mutually exclusive, but act simultaneously to determine the outcome of plant-plant interactions (see review in Callaway 2007). Nevertheless, an assessment from first principles of plant effects on soil moisture would help to identify whether plant modulation of soil water along aridity gradients, and by extension effects on the growth, survival and population dynamics of neighboring plants, are

alone likely to provide support for the SGH. Plants can have positive effects on available surface soil moisture by reducing evaporation through shading (Domingo *et al.* 2011), enhancing moisture retention through increased litter or soil organic matter (Pugnaire, Armas & Valladares 2004), and increasing shallow soil moisture via hydraulic redistribution from deeper soil layers (Prieto *et al.* 2011). Plants can also reduce soil moisture via canopy interception (Dunkerley 2000) and of course through uptake by roots (Armas & Pugnaire 2009). Understanding how the combined effects of these mechanisms are expected to influence soil moisture availability along aridity gradients could help direct the study of plant-plant interactions in drylands in new and productive ways.

Plant effects on soil moisture are dependent in large part on the interactions between precipitation inputs, evaporative demand and soil texture. Precipitation can be highly temporally variable within and among years in many dryland ecosystems (Noy-Meir 1973). Variability in precipitation event size and frequency across time and space may play a pivotal role in determining plant effects on available soil moisture, particularly in the extremely wet or dry years that typically drive regeneration and mortality in dryland ecosystems (Holmgren *et al.* 2006). Soil texture can further modulate precipitation inputs and evapotranspiration. In dryland systems, above-ground net primary productivity (ANPP) is expected to be greater on coarse textured (with low-water holding capacity) than on fine-textured soils (with high water-holding capacity), and increasingly so with increasing aridity (Noy-Meir 1973; Sala *et al.* 1988). The rationale behind this expectation is that coarse dryland soils have a high infiltration potential relative to finer-textured soils; this increases percolation to deeper soil layers that may reduce soil evaporation, thereby increasing water availability for vegetation (i.e., sustaining higher ANPP) in coarser soils, but presumably deeper into the soil. Much of the variation in soil texture can in turn be attributed to parent material and landscape position (McAuliffe 1994; Michalet *et al.* 2002). Thus, the effects of plants on available soil moisture and the outcome of plant-plant interactions can be expected to change based on temporal and spatial variation in precipitation, as well as soil texture and depth.

A number of studies have presented conceptual models of plant effects on soil moisture as a function of aridity (Holmgren, Scheffer & Huston 1997; Butterfield 2009; Holmgren & Scheffer 2010), but none have applied process-based soil moisture models to the question of how plants influence water availability, and hence their potential effects on neighbours via facilitation or competition. The complex interactions between exogenous and endogenous factors outlined above indicate that such a modelling exercise could be highly beneficial. Here, we present simulations using an empirically-parameterized soil moisture model to predict variation in plant effects on available soil moisture relative to bare interspaces along an aridity gradient. Specifically, we use 40 years of real weather conditions (daily precipitation and temperature) from a

randomly-selected set of points across drylands of the Western United States to assess both spatial and temporal variation in simulated plant effects on soil moisture. We arrayed these sites along a spatial gradient of aridity based on long-term average precipitation and temperature data. We asked three specific questions: (i) What are the long-term average effects of plants on soil moisture along a spatial gradient of aridity?; (ii) In the most mesic and arid years within a site, what are the effects of plants on soil moisture, and do these effects in extreme weather years exhibit a different relationship along the aridity gradient than do average effects; and (iii) What is the temporal relationship between aridity and plant effects on soil moisture within a site, and does it differ from the relationship across sites in space? We then discuss the answers to these questions in the context of the SGH.

Materials and methods

MODEL DESCRIPTION

We utilized SOILWAT, a multiple soil layer, process-based, simulation model of daily ecosystem water balance (Parton 1978; Bradford & Lauenroth 2006; Lauenroth & Bradford 2006; Bradford, Schlaepfer & Lauenroth 2014a). SOILWAT has been applied and validated in grasslands (Parton 1978; Lauenroth *et al.* 1994), shrublands (Schlaepfer, Lauenroth & Bradford 2012; Bradford *et al.* 2014b) and low-elevation forests (Bradford, Schlaepfer & Lauenroth 2014a). Inputs to SOILWAT include weather, vegetation structure and soil properties. In order to simplify the model assessment, vegetation structure and soil texture were constrained to two states each (see below), whereas real weather data were used in order to assess potential effects of spatiotemporal variation in climate on plant modulation of soil moisture. We randomly selected 1000 points within the Western United States that receive on average <700 mm of annual precipitation (Fig. 1). We set our precipitation threshold at 700 mm in order to ensure that any patterns at and above the typical upper precipitation limit for drylands (600 mm) were observable. Weather inputs to SOILWAT include mean daily temperature and precipitation, mean monthly relative humidity, wind speed, cloud cover and latitude. We extracted temperature and precipitation data for each site for 1970–2010 from 1/8 degree-resolution interpolated data (Maurer *et al.* 2002), and the first year of the simulation period was discarded as a burn-in period to exclude effects of initial conditions. We obtained estimates of relative humidity, wind speed and cloud cover from the 'Climate Maps of the United States' (<http://cdo.ncdc.noaa.gov/cgi-bin/climaps/climaps.pl>).

For the purposes of this study, we applied identical vegetation (no vegetation or plant canopy) and soil property (coarse, intermediate and fine) treatments to each site. The no vegetation (hereafter 'interspace') treatment consisted of bare soil, while the plant canopy treatment consisted of a shrub and associated litter. SOILWAT estimates interception by vegetation and litter, evaporation of intercepted water, snow melt and loss (sublimation and wind redistribution), infiltration into the soil profile, percolation and hydraulic redistribution for each soil layer, bare soil evaporation, transpiration from each soil layer and deep drainage (Lauenroth & Bradford 2006; Schlaepfer, Lauenroth & Bradford 2012). For details of the specific plant characteristics applied here, see Bradford, Schlaepfer & Lauenroth 2014a). We simulated water balance for all sites under three different soil texture conditions: sandy loam (75% sand particles by weight, 15% silt, 10% clay), silt loam (15% sand, 75% silt, 10% clay) and clay loam (33% sand, 37%

silt, 30% clay.) These textures were consistent throughout the soil profile, and are henceforth referred to as sand, silt and clay. We simulated nine soil layers (bottom depths of 5, 10, 20, 30, 40, 60, 80, 100 and 150 cm). Grass, rather than shrub, and a shrub/grass mix as predicted from climate (Bradford, Schlaepfer & Lauenroth 2014a) were analysed in addition to the shrub treatment, but the results were qualitatively similar along aridity gradients, so only the results for simulations with shrubs are presented below. Only results for the coarse and fine soil treatments, hereafter referred to as 'sand' and 'clay', respectively, are reported for brevity, as the intermediate soils produced intermediate simulation results.

MODEL ANALYSIS

We aggregated the SOILWAT output in several ways within each site in order to facilitate interpretation. First, we aggregated results into three soil layers (average of 0–10 cm, 10–30 cm and 30–150 cm) that in general represent distinct rooting zones in drylands. The shallowest depth is likely to have the strongest effect on seed germination and seedling survival, and is most strongly influenced by evaporation and canopy interception. The intermediate depth represents the highest concentration of roots in arid to semi-arid ecosystems (Schenk & Jackson 2002), and is likely to have the strongest soil moisture effects on the establishment and mature phases. The deepest soils may be most relevant to species with a strong tap root and/or greater overall size or longevity (Schenk & Jackson 2002). Second, soil water potential was classified into wet (>-1.5 MPa: a commonly-applied threshold of wilting point; Brady & Weil 1999) and dry (<-3.9 MPa: the soil pressure potential below which 50% cavitation is observed in a common north American dryland shrub; Kolb & Sperry 1999) days for simplicity. These thresholds are more-or-less relevant to growth and mortality, respectively. Alternative thresholds of -3 and -3.5 MPa resulted in patterns that were intermediate and sequential between -1.5 and -3.9 (Fig. S1, Supporting information), indicating that the latter represent physiologically relevant thresholds that fall along a predictable continuum of soil moisture dynamics. Because few days >-1.5 MPa were generated for fine-textured surface soils, >-3 MPa was used as the threshold for wet days in that specific treatment. The latter likely reflects conditions that are above wilting point for many dryland plants (-1.5 MPa is a very conservative estimate of wilting point for dryland species), and should therefore be a useful indicator of wet days in the dryer (relative to sand) clay soils of dryland systems. Third, the difference in number of wet or dry days between shrub and interspace soils (effects of shrubs or shrub effects, henceforth) was used as the response variable in further analyses. Finally, all of the above calculations were conducted separately for each season (Winter, January–March; Spring, April–June; Summer, July–September; Autumn, October–December). Patterns for spring and autumn were qualitatively similar to those for summer (Fig. S2), and effects of shrubs during the winter were minimal, so only simulations for summer are discussed further.

In order to relate our results to the SGH, we analysed the effects of shrubs (the difference in number of wet or dry days between shrub and interspace soils) on the number of wet and dry days as a function of aridity (i.e. the stress gradient) across sites. Specifically, we used the 40 year average climatic water deficit (D) for each site, calculated as potential minus actual evapotranspiration (PET–AET; Stephenson 1998). PET is driven primarily by temperature and AET by precipitation, thus D is a proximate estimate of long-term water stress. Shrub effects on the number of wet and dry days were then analysed in three ways. First, we calculated the 40 year average simulated effects of shrubs at each site and compared them to the long-term D, allowing us to assess average shrub effects as a function of site aridity. Second, we calculated the simulated effects of shrubs during just the wettest and driest years in each site over the 40 years of variation in weather,

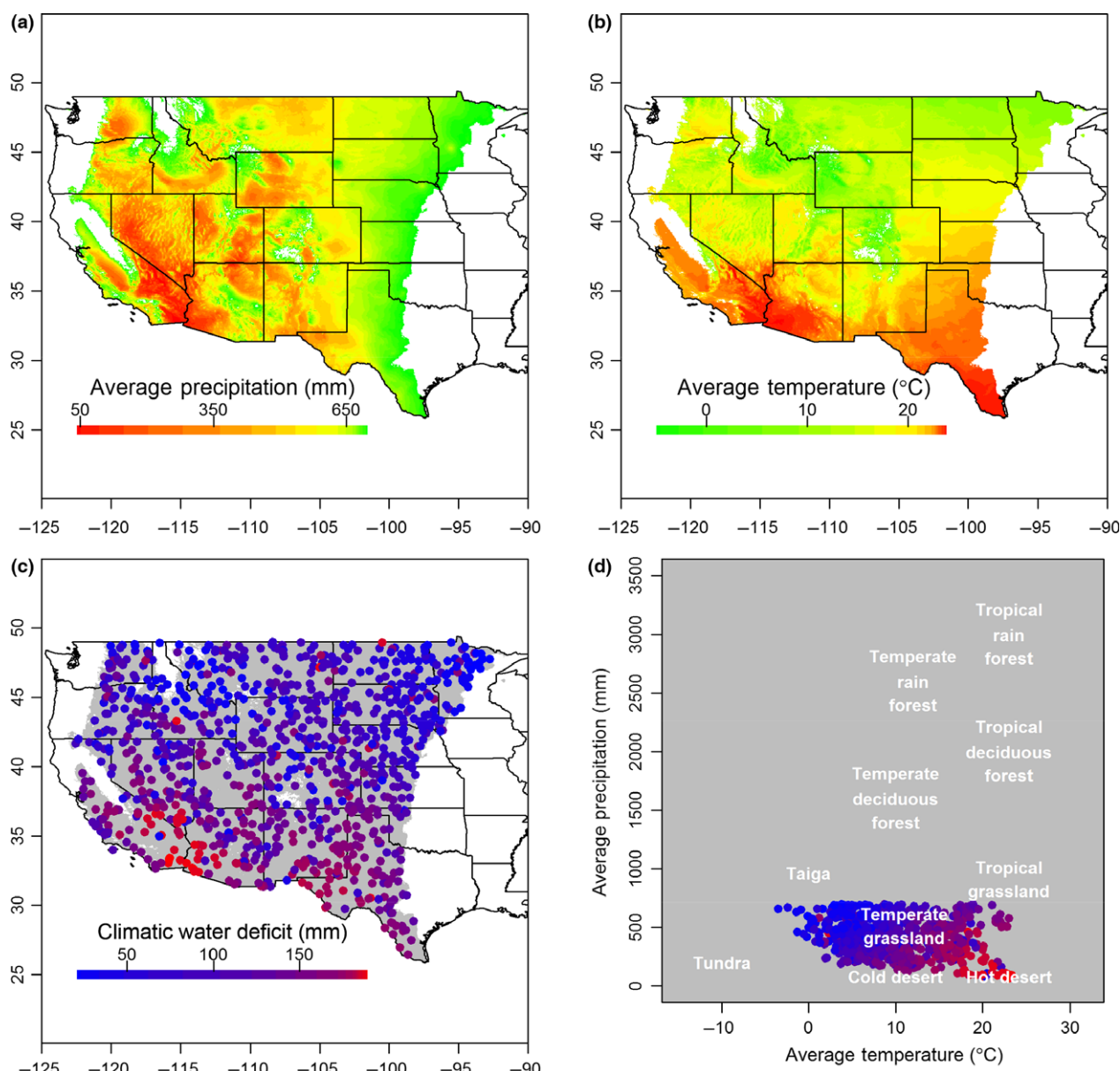


Fig. 1. Distribution of mean annual precipitation (a), mean average temperature (b), climatic water deficit (potential minus actual evapotranspiration) (c), and study sites (by latitude and longitude decimal degrees) with respect to coarse biome categories (d; after Ricklefs 2008). Maps are masked to <700 mm mean annual precipitation.

which can provide insights into the potential role of extreme events in modulating shrub effects on the population dynamics of beneficiary species, both in terms of regeneration and mortality. Third, we estimated the correlation (r) between precipitation and simulated shrub effects across years within each site, then assessed how these temporal relationships within sites varied across the gradient of long-term D in order to compare temporal vs. spatial responses to water availability.

Results

LONG-TERM AVERAGE EFFECTS OF PLANTS ON SOIL MOISTURE ACROSS A SPATIAL ARIDITY GRADIENT

Simulated long-term average effects of shrubs on soil moisture varied with depth and soil texture (Fig. 2). In

both sand and clay surface soils (0–10 cm), shrubs had positive effects on water availability (i.e. more wet days and fewer dry days) at the mesic end of the aridity gradient, shifting toward approximately neutral effects toward the xeric end of the gradient. This decline was more rapid in sand than clay soils. In intermediate and deeper layers, shrubs had nearly universal negative effects on soil moisture. With the exception of deep sand soils (which are relatively wet), shrubs decreased the number of dry days (i.e. drier beneath shrubs than in the open) with increasing aridity. Shrubs had increasingly negative effects on number of wet days with increasing aridity in sand soils, but the opposite pattern in clay soils.

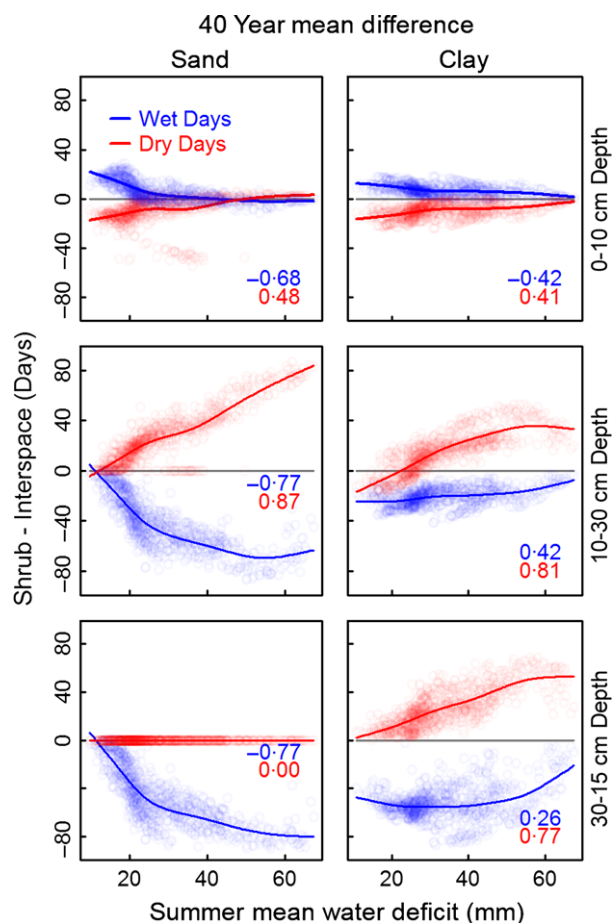


Fig. 2. Effects of shrubs on the 40 year mean number of wet ($\psi_{\text{soil}} > -1.5 \text{ MPa}$ in general; but note $\psi_{\text{soil}} > -3.0 \text{ MPa}$ for 0–10 cm clay soils only) and dry ($< -3.9 \text{ MPa}$) days during the summer as a function of mean summer climatic water deficit (PET-AET), and varying with soil depth and texture. Aridity increases from left to right. Positive values of wet day difference (i.e. more wet days under shrubs than interspaces) indicates a positive effect of shrubs on soil moisture relative to interspaces (bare ground), and negative values of dry day difference (i.e. less dry days under shrubs than interspaces) indicate an ameliorative effect of shrubs on drought. Points indicate values for each of the 999 simulated sites, and lines are smooth-spline regressions. Correlation coefficients are reported for both wet (blue) and dry (red) days.

EFFECTS OF PLANTS ON SOIL MOISTURE IN EXTREME YEARS ACROSS A SPATIAL ARIDITY GRADIENT

In shallow sand soils, shrubs had increasingly positive effects on the number of wet days (i.e. more days where soil moisture was higher beneath shrubs) in wet years with increasing aridity, peaking at moderately high aridity, and shifting toward negative effects in the most xeric sites (Fig. 3). Shrub effects in extreme years were strongly positively related to long-term temperature across sites, contrary to the trend for long-term average effects of shrubs to increase primarily with long-term precipitation across sites (Table 1). The former reflects the strong difference in PET between shrub and interspace microsites in hot environments *during particularly wet years*, such that large

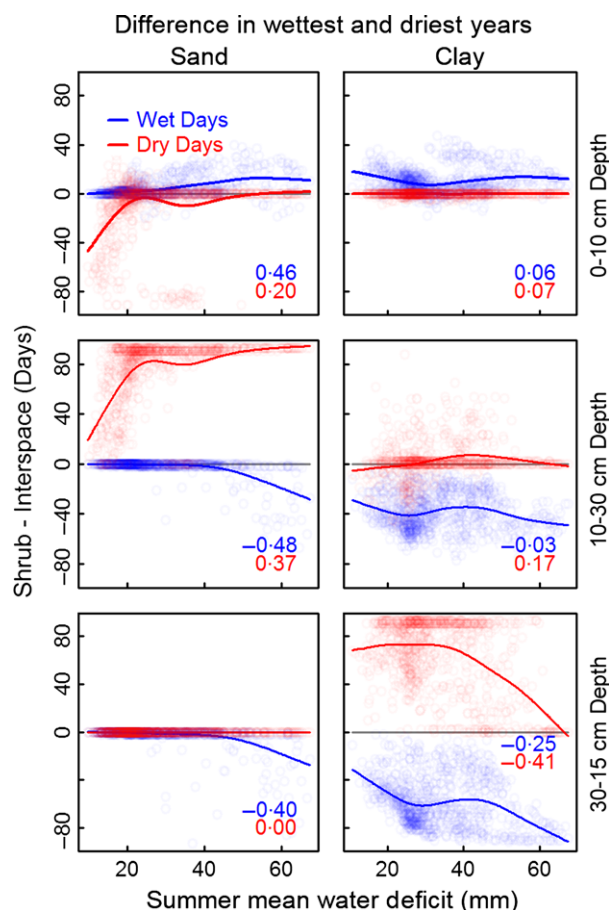


Fig. 3. Effects of shrubs on number of wet days in the wettest year, and number of dry days in the driest year within a site over 40 years. Shrub effects are plotted as a function of long-term mean summer climatic water deficit (PET-AET; i.e. same axis as in Fig. 2), and varying with soil depth and texture. Rest of the legend as in Fig. 2.

precipitation pulses are retained beneath shrubs but evaporate rapidly in interspaces. In contrast to changes between long-term mean and extreme effects on wet days, shrub effects on the number of dry days in dry years were similar to the long-term mean effects, though with a more pronounced negative effect at the mesic end of the gradient (Fig. 3).

In shallow clay soils, shrubs had generally stronger positive effects on number of wet days in wet years than the long-term average effects across most sites, and declined at the xeric end of the gradient, much like the long-term average effects did. The effect of shrubs on number of dry days in dry years was generally neutral, due to both shrub and interspace soils being dry for the entirety of the season in the driest years. In general, shallow clay soils exhibited weaker differences between long-term average and extreme effects of shrubs than did shallow sand soils.

In intermediate and deep soils, shrub effects in extreme years were highly dependent upon texture (Fig. 3). In deeper sand soils, the increase in positive effects of shrubs on dry days found for long-term average conditions became

Table 1. Correlations (Pearson r) between precipitation or temperature (P , T) and the effect of shrubs (i.e., difference between shrub and interspace) on the number of wet or dry days. Correlations are presented for both long-term mean effects of shrubs (Mean) and effects of shrubs in extreme wet and dry years (Extr). Shrubs had no effects on number of dry days in deep sand soils

Depth	Shrub effect	Sand				Clay			
		P		T		P		T	
		Mean	Extr	Mean	Extr	Mean	Extr	Mean	Extr
1–10 cm	Wet days	0.70	–0.07	–0.32	0.61	0.74	0.25	0.06	0.36
	Dry days	–0.51	–0.35	–0.03	0.01	–0.77	–0.28	–0.09	–0.17
10–30 cm	Wet days	0.60	0.30	–0.61	–0.35	–0.74	–0.36	–0.10	–0.35
	Dry days	–0.75	–0.57	0.56	0.11	–0.62	–0.23	0.67	0.13
30–150 cm	Wet days	0.64	0.29	–0.55	–0.25	–0.58	–0.08	–0.19	–0.40
	Dry days	–	–	–	–	–0.76	0.39	0.49	–0.18

more pronounced in dry years, resulting in very strong positive effects on number of dry days in all but the most mesic sites. Shrubs only had moderate negative effects on the number of wet days in wet years at the xeric end of the gradient. Taken together, these patterns indicate that dry years were very dry beneath shrubs vs. interspaces at greater depths, and wet years were relatively similar between shrubs and interspaces, except in the most arid sites. In deeper clay soils, the relationships between shrub effects and aridity in extreme years were the opposite of those for long-term effects in nearly all cases. Negative effects of shrubs on number of wet days became stronger with increasing aridity, and positive effects on number of dry days in dry years became weaker with increasing aridity (in deep, but not intermediate soils). Relationships between long-term climate and shrub effects were generally weaker in extreme years than under average conditions (Fig. 3), and shrub effects on deeper soil moisture (>10 cm) tended to become decoupled from long-term climate in extreme years, which is reflected in the weaker relationships between long-term climate variables and shrub effects in extreme years compared to long-term average conditions (Table 1).

TEMPORAL VARIATION IN PLANT EFFECTS ON SOIL MOISTURE

Within a site through time, the effects of shrubs on water availability were highly dependent upon weather (i.e. between-year variation in precipitation, temperature and water deficit), though the nature of these relationships varied substantially with depth and in some cases texture (Fig. 4). In shallow soil layers, shrub effects on number of wet days were generally positively correlated with precipitation and negatively correlated with climatic water deficit, with temperature having a more moderate negative effect. These relationships were more pronounced in clay than in sand soils. Relationships between shrub effects and weather were weaker at intermediate soil depths, with the notable exception of consistently negative effects of temporal variation in precipitation on the effect of shrubs on

number of dry days. At greater depths, shrub effects on number of wet days exhibited contrasting relationships with precipitation in sand (positive) and clay (negative) soils. Interestingly, shrub effects on wet and dry days exhibited similar responses to variation in weather in deep clay soils.

Temporal variation in precipitation played the most consistent role in driving temporal variation in shrub effects on soil moisture (Fig. 4). When the temporal correlations between shrub effects and precipitation are considered along our gradient of long-term climatic water deficit, we see very strong effects of both soil texture and depth (Fig. 5). In shallow soils, shrub effects on wet days were positively correlated with precipitation, and effects on dry days negatively correlated with precipitation, in all but the most mesic sites. Shallow clay soils exhibited the opposite pattern, with effects on wet and dry days being positively and negative correlated, respectively, with precipitation in all but the most xeric sites. Temporal relationships between shrub effects and precipitation were weakly dependent upon the position of a site along the long-term aridity gradient, exhibiting a negative relationship for number of wet days and a u-shaped relationship for dry days at intermediate depths in sand soils, and positive and negative relationships for wet and dry days, respectively, in deeper clay soils.

Discussion

The original proposition of Bertness & Callaway (1994) regarding the balance of plant-plant interactions was cast in the context of very broad contrasts between productive and unproductive ecosystems. Instead, much of the current debate over the balance between competition and facilitation within dryland systems revolves around variation in interaction outcomes among unproductive ecosystems. Recent models (Butterfield 2009; Maestre *et al.* 2009; Holmgren & Scheffer 2010), meta-analyses (Soliveres & Maestre 2014; Soliveres *et al.* 2014) and the results of the present study suggest that we might do better to shift our focus from the SGH to more precise hypotheses when

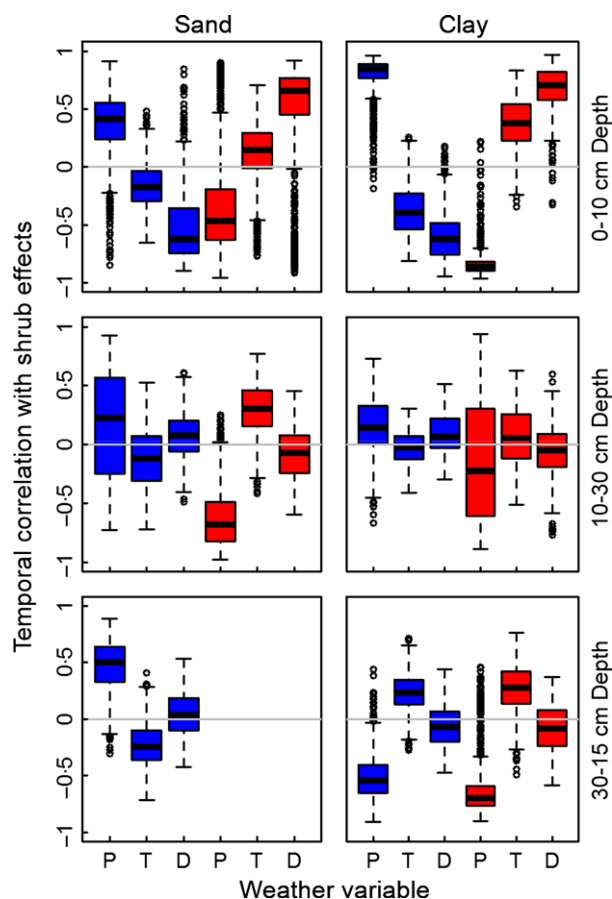


Fig. 4. Distribution of correlations (Pearson r) between temporal variation in weather (precipitation – P ; temperature – T ; and climatic water deficit; D) and shrub effects on number of wet (blue) and dry (red) days (i.e. difference between number of wet or dry days between shrub and interspace, see legend for Fig. 2) over 40 years within each site. Shrubs had no effects on number of dry days in deep sand soils.

discussing variation in plant-plant interaction outcomes along stress gradients within already low productivity, dryland ecosystems. The results of our simulation model suggest that plant-plant interactions mediated primarily by soil moisture are unlikely to result in support for the SGH based on long-term average effects of plants, likely to produce highly variable support for or against the SGH across short gradients or different soil types, and may consistently support a hump-shaped model if extreme years are taken into account (see below). Our results also suggest a critical need for explicitly integrating spatial and temporal variation in plant effects on soil moisture and subsequent consequences for the performance of neighbours if we are to develop better predictive models of plant-plant interactions in drylands.

The simulated long-term average effects of plants are consistent with the idea that decreasing precipitation inputs result in weakening positive effects of plants on shallow soil moisture. Evaporative demand in interspaces is much higher than beneath canopies, even at the relatively mesic end of the dryland continuum. Thus, shallow

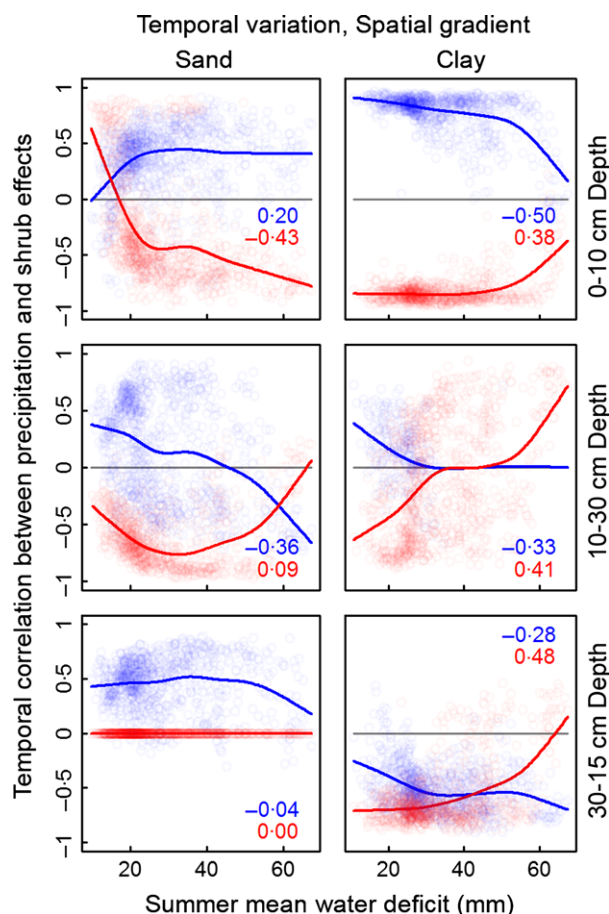


Fig. 5. Temporal correlation over 40 years between summer precipitation and shrub effects on number of wet and dry days, plotted along a spatial gradient of aridity averaged across those 40 years. The horizontal axis is the same as in Figs 2 and 3, but the vertical axis represents temporal relationships between precipitation and shrub effects within a site. Rest of the legend as in Fig. 2.

soil moisture is relatively similar in interspaces in both mesic and xeric sites, whereas the decline in shallow soil moisture from mesic to xeric sites beneath plants is much steeper (Butterfield 2009). The simulated long-term average effects on shallow soil moisture are consistent with a recent meta-analysis of the relationship between aridity and interaction outcomes at the community level (Soliveres & Maestre 2014). In addition to finding a weak negative effect of aridity on facilitation, Soliveres and Maestre demonstrated that studies finding support for the SGH were typically along shorter gradients than those that rejected the SGH, and argued that this could be due to differences between intraspecific responses on short gradients vs. the effects of species turnover across broader gradients. Our results suggest an additional possibility: a great deal of variability in simulated plant effects on available soil moisture was not explained by aridity, thus selection of sites along a short gradient could produce positive, negative or neutral effects of plants on soil moisture as a function of aridity. This variability in plant effects is likely due

to substantial variation in the frequency, timing and size of precipitation pulses among sites that may nonetheless have similar long-term patterns of aridity.

The variable and stochastic nature of weather patterns in dryland systems generated substantial differences between simulated plant effects in extreme vs. average years. Extreme conditions had the general effect of shifting the pattern of plant effects along the gradient, with positive effects of plants in wet years occurring further toward the xeric end of the aridity gradient, and negative effects in dry years extending further toward the mesic end. These extreme years and associated plant effects on soil moisture have the potential to most strongly influence population and community structure. Facilitation has the greatest potential to influence community composition at the regeneration phase, and if seedling establishment is primarily driven by shallow soil moisture in wet years, facilitative effects may in fact peak at moderate to high levels of aridity in fine and coarse soils, respectively, though still declining in the most extremely xeric environments (Fig. 3). Conversely, the greatest potential effects of competition on community composition is through mortality of more mature individuals rather than seedlings, and during extremely dry years plants have increasingly negative effects on water availability in more mesic environments (Fig. 3). Differences in the climatic drivers of plant effects between average and extreme years also indicate an equalizing effect of extreme years on differences in plant effects across sites, as long-term precipitation and temperature generally became weaker predictors of plant effects in extreme relative to average years (Table 1). Considering these patterns together, extreme years could shape community composition by decoupling competitive and facilitative effects on community composition, resulting in greater dominance of competition in driving mortality in less arid environments and greater effects of facilitation on regeneration in more arid environments. Thus, if extreme years are the primary determinants of population and community structure, and plant effects on soil moisture during those years strongly influence regeneration and competition, the hump-shaped model of a shift from competition to facilitation to neutral interactions with increasing aridity may be supported (Michalet *et al.* 2006).

Contrasting temporal and spatial variation in plant effects on soil moisture may help to resolve some contradictory patterns among empirical studies. In shallow soils, where positive effects of plants on soil moisture are observed, precipitation is almost always positively correlated with simulated positive effects of plants on soil moisture (Figs 4 and 5), which would not be expected to provide support for the SGH. This further reinforces the importance of differences in evaporation rates between canopy and interspace microsites in determining the retention of precipitation pulses. Wet years are almost universally wetter beneath shrubs than in interspaces (Fig. 3). This corresponds with the findings of two studies of arid plant communities that found a positive temporal correla-

tion between precipitation and facilitation (Tielborger & Kadmon 2000; Butterfield *et al.* 2010). However, this contrasts with another very large study of plant-plant interactions in afforestation of semi-arid Mediterranean woodlands (Gómez-Aparicio *et al.* 2004), where facilitative effects were greater in two dry, hot years than in one wet, cool year, though they did find that shrubs had the strongest positive effects on soil moisture in the wet year, in agreement with our model. The contradictory patterns between plant effects on soil moisture and the responses of neighbours in the latter study points to direct effects of irradiance on plant performance (Holmgren *et al.* 2012 and citations therein), as the dryer years were much hotter than the wetter one. Thus, while temperature may indirectly influence plant-plant interactions via differential evaporation rates between canopy and interspace microsites, negative covariation between precipitation and temperature across years may result in countervailing direct and indirect effects of temperature in different years.

Many of the patterns found in this study were contingent upon soil type, which adds another layer of complexity to predicting the role of soil moisture in mediating plant-plant interactions in drylands. In general, a shift from coarse to fine soils had the effect of increasing aridity and vice versa (data not shown), and subsequent shifts in the importance of competition and facilitation in influencing soil moisture. In general, plants had stronger effects on water availability in coarse soils, whereas physical processes were more important in fine soils. In coarse soils, plants had increasingly negative effects on deep soil moisture with increasing aridity due to increasingly efficient uptake of declining precipitation inputs, whereas plant effects on number of wet days became weaker with increasing aridity in clay soils. This switch with texture is consistent with an overwhelming effect of physical processes on water availability in fine soils in very arid sites and provides an interesting twist to the hypothesis of Goldberg & Novoplansky (1997) that resource availability should become supply-driven, rather than demand-driven, in particularly arid ecosystems. Our results support this hypothesis for deeper fine soils, but not for deeper coarse soils.

Conclusions

It has been difficult to come to general conclusions about the role of aridity in determining plant-plant interaction outcomes through comparisons of empirical studies with disparate methods, systems, taxa and experimental designs (Lortie & Callaway 2006; Maestre *et al.* 2009). Given that our simulation results do not consistently predict spatial trends in plant-plant interactions in a number of empirical studies, other factors beyond water must play a role in mediating plant-plant interactions in drylands (Callaway 2007; Butterfield & Briggs 2011; Butterfield & Callaway 2013). However, our results also provide baseline expectations for the role of soil moisture in mediating plant-plant interaction outcomes, such that when studies disagree with

these predictions (e.g. Gómez-Aparicio *et al.* 2004), other mechanisms can become the focus. Understanding the scenarios under which specific mechanisms determine interaction outcomes, and those in which they do not, is a critical step toward developing better predictive models of plant-plant interactions and consequences for the distribution of biodiversity.

Acknowledgments

C.A. was supported by a Ramón y Cajal contract from the Spanish Ministerio de Economía y Competitividad (RYC-2012-12277). IP was supported by a 'Juan de la Cierva' research contract (FPDI-2013-16221). F.I.P. was supported by MICINN (grant CGL2014-59010-R). JBB was supported by the USGS Ecosystems Mission area. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Data accessibility

This manuscript does not use data.

References

- Armas, C. & Pugnaire, F.I. (2009) Ontogenetic shifts in interactions of two dominant shrub species in a semi-arid coastal sand dune system. *Journal of Vegetation Science*, **20**, 535–546.
- Armas, C., Pugnaire, F.I. & Sala, O.E. (2008) Patch structure dynamics and mechanisms of cyclical succession in a Patagonian steppe (Argentina). *Journal of Arid Environments*, **72**, 1552–1561.
- Armas, C., Rodríguez-Echeverría, S. & Pugnaire, F.I. (2011) A field test of the stress-gradient hypothesis along an aridity gradient. *Journal of Vegetation Science*, **22**, 818–827.
- Bertness, M.D. & Callaway, R. (1994) Positive interactions in communities. *Trends in Ecology & Evolution*, **9**, 191–193.
- Bradford, J.B. & Lauenroth, W.K. (2006) Controls over invasion of *Bromus tectorum*: the importance of climate, soil, disturbance and seed availability. *Journal of Vegetation Science*, **17**, 693–704.
- Bradford, J., Schlaepfer, D. & Lauenroth, W. (2014a) Ecohydrology of adjacent sagebrush and lodgepole pine ecosystems: the consequences of climate change and disturbance. *Ecosystems*, **17**, 590–605.
- Bradford, J.B., Schlaepfer, D.R., Lauenroth, W.K. & Burke, I.C. (2014b) Shifts in plant functional types have time-dependent and regionally variable impacts on dryland ecosystem water balance. *Journal of Ecology*, **102**, 1408–1418.
- Brady, N.C. & Weil, R.R. (1999) *The Nature and Property of Soils*. Prentice-Hall, Inc., Upper Saddle River, New Jersey, USA.
- Butterfield, B.J. (2009) Effects of facilitation on community stability and dynamics: synthesis and future directions. *Journal of Ecology*, **97**, 1192–1201.
- Butterfield, B.J. & Briggs, J.M. (2011) Regeneration niche differentiates functional strategies of desert woody plant species. *Oecologia*, **91**, 1132–1139.
- Butterfield, B.J. & Callaway, R.M. (2013) A functional comparative approach to facilitation and its context dependence. *Functional Ecology*, **27**, 907–917.
- Butterfield, B.J., Betancourt, J.L., Turner, R.M. & Briggs, J.M. (2010) Facilitation drives 65 years of vegetation change in the Sonoran Desert. *Ecology*, **91**, 1132–1139.
- Callaway, R.M. (2007) *Positive Interactions and Interdependence in Plant Communities*. Springer, Dordrecht, The Netherlands.
- Dohn, J., Dembélé, F., Karembé, M., Moustakas, A., Amévor, K.A. & Hanan, N.P. (2013) Tree effects on grass growth in savannas: competition, facilitation and the stress-gradient hypothesis. *Journal of Ecology*, **101**, 202–209.
- Domingo, F., Serrano-Ortiz, P., Were, A., Villagarcía, L., García, M., Ramírez, D.A. *et al.* (2011) Carbon and water exchange studies in semiarid ecosystems in SE Spain. *Journal of Arid Environments*, **75**, 1271–1281.
- Dunkerley, D. (2000) Measuring interception loss and canopy storage in dryland vegetation: a brief review and evaluation of available research strategies. *Hydrological Processes*, **14**, 669–678.
- Flores, J. & Jurado, E. (2003) Are nurse-protégé interactions more common among plants from arid environments? *Journal of Vegetation Science*, **14**, 911–916.
- Goldberg, D. & Novoplansky, A. (1997) On the relative importance of competition in unproductive environments. *Journal of Ecology*, **85**, 409–418.
- Gómez-Aparicio, L., Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J. & Baraza, E. (2004) Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. *Ecological Applications*, **14**, 1128–1138.
- He, Q., Bertness, M.D. & Altieri, A.H. (2013) Global shifts towards positive species interactions with increasing environmental stress. *Ecology Letters*, **16**, 695–706.
- Holmgren, M. & Scheffer, M. (2010) Strong facilitation in mild environments: the stress gradient hypothesis revisited. *Journal of Ecology*, **98**, 1269–1275.
- Holmgren, M., Scheffer, M. & Huston, M.A. (1997) The interplay of facilitation and competition in plant communities. *Ecology*, **78**, 1966–1975.
- Holmgren, M., Stapp, P., Dickman, C.R., Gracia, C., Grahams, S., Gutierrez, J.R. *et al.* (2006) Extreme climatic events shape arid and semiarid ecosystems. *Frontiers in Ecology and the Environment*, **4**, 87–95.
- Holmgren, M., Gómez-Aparicio, L., Quero, J.L. & Valladares, F. (2012) Non-linear effects of drought under shade: reconciling physiological and ecological models in plant communities. *Oecologia*, **169**, 293–305.
- Holzapfel, C., Tielbörger, K., Parag, H.A., Kigel, J. & Sternberg, M. (2006) Annual plant-shrub interactions along an aridity gradient. *Basic and Applied Ecology*, **7**, 268–279.
- Kolb, K.J. & Sperry, J.S. (1999) Differences in drought adaptation between subspecies of sagebrush (*Artemisia tridentata*). *Ecology*, **80**, 2373–2384.
- Lauenroth, W.K. & Bradford, J.B. (2006) Ecohydrology and the partitioning AET between transpiration and evaporation in a semiarid steppe. *Ecosystems*, **9**, 756–767.
- Lauenroth, W.K. & Bradford, J.B. (2012) Ecohydrology of dry regions of the United States: water balance consequences of small precipitation events. *Ecohydrology*, **5**, 46–53.
- Lauenroth, W.K., Sala, O.E., Coffin, D.B. & Kirchner, T.B. (1994) The importance of soil water in the recruitment of *Bouteloua gracilis* in the shortgrass steppe. *Ecological Applications*, **4**, 741–749.
- Lortie, C.J. & Callaway, R.M. (2006) Re-analysis of meta-analysis: support for the stress-gradient hypothesis. *Journal of Ecology*, **94**, 7–16.
- Maestre, F.T. & Cortina, J. (2004) Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. *Proceedings of the Royal Society of London B: Biological Sciences*, **271**, S331–S333.
- Maestre, F.T., Valladares, F. & Reynolds, J.F. (2005) Is the change of plant-plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. *Journal of Ecology*, **95**, 748–757.
- Maestre, F.T., Callaway, R.M., Valladares, F. & Lortie, C.J. (2009) Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology*, **97**, 199–205.
- Maurer, E.P., Wood, A.W., Adam, J.C., Lettenmaier, D.P. & Nijssen, B. (2002) A long-term hydrologically based dataset of land surface fluxes and states for the conterminous United States. *Journal of Climate*, **15**, 3237–3251.
- McAuliffe, J.R. (1994) Landscape evolution, soil formation, and ecological patterns and processes in Sonoran Desert bajadas. *Ecological Monographs*, **64**, 112–148.
- McCluney, K.E., Belnap, J., Gonzalez, A.L., Holland, J.N., Kotler, F.T., Maestre, S.D. *et al.* (2012) Shifting species interactions in terrestrial dryland ecosystems under altered water availability and climate change. *Biological Reviews*, **87**, 563–582.
- Michalet, R. (2007) Highlighting the multiple drivers of changes in interactions along stress gradients. *New Phytologist*, **173**, 3–6.
- Michalet, R., Gandoy, C., Joud, D., Pages, J.P. & Choler, P. (2002) Plant community composition and biomass on calcareous and siliceous substrates in the northern French Alps: comparative effects of soil chemistry and water status. *Arctic, Antarctic, and Alpine Research*, **34**, 102–113.
- Michalet, R., Brooker, R.W., Cavieres, L.A., Kikvidze, Z., Lortie, C.J., Pugnaire, F.I. *et al.* (2006) Do species interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters*, **9**, 767–773.
- Michalet, R., Le Bagousse-Pinguet, Y., Maalouf, J.-P. & Lortie, C.J. (2014) The two alternatives to the Stress-Gradient-Hypothesis at the edge of

- life: the collapse of facilitation and the switch from facilitation to competition. *Journal of Vegetation Science*, **25**, 609–613.
- Noy-Meir, I. (1973) Desert ecosystems. I. Environment and producers. *Annual Review of Ecology & Systematics*, **4**, 25–52.
- Parton, W.J. (1978) Abiotic section of ELM. *Grassland Simulation Model* (ed. G.S. Innis), pp. 31–53. Springer-Verlag Inc., New York, NY, USA.
- Prieto, I., Padilla, F.M., Armas, C. & Pugnaire, F.I. (2011) The role of hydraulic lift on seedling establishment under a nurse plant species in a semi-arid environment. *Perspectives in Plant Ecology, Evolution and Systematics*, **13**, 181–187.
- Pugnaire, F.I., Haase, P. & Puigdefabregas, J. (1996) Facilitation between higher plant species in a semiarid environment. *Ecology*, **77**, 1420–1426.
- Pugnaire, F.I., Armas, C. & Valladares, F. (2004) Soil as a mediator in plant-plant interactions in a semi-arid community. *Journal of Vegetation Science*, **15**, 85–92.
- Pugnaire, F.I. & Luque, M.T. (2001) Change in plant interactions along a gradient of environmental stress. *Oikos*, **93**, 42–49.
- Pugnaire, F.I., Zhang, L., Li, R. & Luo, T. (2015) No evidence of facilitation collapse in the Tibetan Plateau. *Journal of Vegetation Science*, **26**, 233–242.
- Ricklefs, R.E. (2008) *The Economy of Nature*. W.H. Freeman and Company, New York, NY, USA.
- Sala, O.E., Parton, W.J., Joyce, L.A. & Lauenroth, W.K. (1988) Primary production of the central grassland region of the United States. *Ecology*, **69**, 40–45.
- Schenk, H.J. & Jackson, R.B. (2002) The global biogeography of roots. *Ecological Monographs*, **72**, 311–328.
- Schlaepfer, D.R., Lauenroth, W.K. & Bradford, J.B. (2012) Ecohydrological niche of sagebrush ecosystems. *Ecohydrology*, **5**, 453–466.
- Soliveres, S. & Maestre, F.T. (2014) Plant-plant interactions, environmental gradients and plant diversity: A global synthesis of community-level studies. *Perspectives in Plant Ecology, Evolution and Systematics*, **16**, 154–163.
- Soliveres, S., Maestre, F.T., Bowker, M.A., Torices, R., Quero, J.L., García-Gómez, M. *et al.* (2014) Functional traits determine plant co-occurrence more than environment or evolutionary relatedness in global drylands. *Perspectives in Plant Ecology, Evolution and Systematics*, **16**, 164–173.
- Stephenson, N. (1998) Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. *Journal of Biogeography*, **25**, 855–870.
- Tielborger, K. & Kadmon, R. (2000) Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology*, **81**, 1544–1553.
- Turner, R.M., Alcorn, S.M., Olin, G. & Booth, J.A. (1966) Influence of shade, soil and water on saguaro seedling establishment. *Botanical Gazette*, **127**, 95–102.
- Yeaton, R.I. (1978) A cyclical relationship between *Larrea tridentate* and *Opuntia leptocaulis* in the northern Chihuahuan Desert. *Journal of Ecology*, **66**, 651–656.
- Ziffer-Berger, J., Weisberg, P.J., Cablk, M.E. & Osem, Y. (2014) Spatial patterns provide support for the stress-gradient hypothesis over a range-wide aridity gradient. *Journal of Arid Environments*, **102**, 27–33.

Received 6 May 2015; accepted 7 October 2015

Handling Editor: Richard Michalet

Supporting Information

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

Figure S1. Simulated 40 year average and maximum plant effects on summer soil moisture (difference between shrub and interspace) as a function of 40-year mean summer climatic water deficit at intermediate soil water content thresholds (wet days >-3.0 MPa, dry days <-3.5 MPa) relative to those presented in the body of the manuscript (wet days >-1.5 MPa, dry days <-3.9 MPa).

Figure S2. Simulated 40 year average and maximum plant effects of shrubs (difference between shrub and interspace) on spring (top) and autumn (bottom) soil moisture as a function of 40-year mean spring and autumn climatic water deficit, respectively.