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Plant diversity and ecosystem multifunctionality peak at intermediate levels of woody cover in global drylands

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ABSTRACT

Aim The global spread of woody plants into grasslands is predicted to increase over the coming century. While there is general agreement regarding the anthropogenic causes of this phenomenon, its ecological consequences are less certain. We analysed how woody vegetation of differing cover affects plant diversity (richness and evenness) and the surrogates of multiple ecosystem processes (multifunctionality) in global drylands, and how these change with aridity.

Location Two hundred and twenty-four dryland sites from all continents except Antarctica, widely differing in their environmental conditions (from arid to dry-subhumid sites) and relative woody cover (from 0 to 100%).

Methods Using a standardized field survey, we measured the cover, richness and evenness of perennial vegetation. At each site, we measured 14 soil variables related to fertility and the build-up of nutrient pools. These variables are critical for maintaining ecosystem functioning in drylands.

Results Species richness and ecosystem multifunctionality were strongly related to woody vegetation, with both variables peaking at a relative woody cover (RWC) of 41–60%. This relationship shifted with aridity. We observed linear positive effects of RWC in dry-subhumid sites. These positive trends shifted to hump-shaped RWC–diversity and multifunctionality relationships under semi-arid environments. Finally, hump-shaped (richness, evenness) or linear negative (multifunctionality) effects of RWC were found under the most arid conditions.

Main conclusions Plant diversity and multifunctionality peaked at intermediate levels of woody cover, although this relationship became increasingly positive in wetter environments. This comprehensive study accounts for multiple ecosystem attributes across a range of levels of woody cover and environmental conditions. Our results help us to reconcile contrasting views of woody encroachment found in the current literature and can be used to improve predictions of the likely effects of encroachment on biodiversity and ecosystem services.

Keywords

Aridity, semi-arid, shrub encroachment, soil, species evenness, species richness, thickening.

INTRODUCTION

Overgrazing or alterations in rainfall patterns and atmospheric CO₂ concentrations due to human activity are among the

major causes of widespread increases in the cover and abundance of woody vegetation into former grasslands world-wide (Schlesinger *et al.*, 1990; Van Auken, 2000; Sankaran *et al.*, 2008). This phenomenon, hereafter referred to as woody

encroachment, is likely to increase in intensity and extent under predicted future environmental scenarios (Kulmatinski & Beard, 2013; Blois *et al.*, 2013). Woody encroachment is known to affect the structural and functional attributes of ecosystems, including plant spatial patterns (Schlesinger *et al.*, 1990), composition and diversity (Ratajczak *et al.*, 2012; Quero *et al.*, 2013; Soliveres & Eldridge, 2013) and nutrient cycling (Throop & Archer, 2007; Knapp *et al.*, 2008; Eldridge *et al.*, 2013). Alteration to nutrient cycles results in substantial changes in the provision of key ecosystem services such as forage production (Riginos *et al.*, 2009), carbon storage (Jackson *et al.*, 2002; Knapp *et al.*, 2008;) and the regulation of climate (Blois *et al.*, 2013). Woody encroachment is particularly prominent across arid, semi-arid and dry-subhumid ecosystems (drylands; Van Auken, 2000; Sankaran *et al.*, 2008; Maestre *et al.*, 2009), where it has been traditionally linked to land degradation and desertification (Schlesinger *et al.*, 1990; Millennium Ecosystem Assessment, 2005). In these areas, many billions of dollars have been spent world-wide in reducing the cover of woody plants to enhance the pastoral value for livestock using a range of chemical and mechanical techniques (e.g. Teague, 1997; Daryanto & Eldridge, 2010).

While the links between woody encroachment and desertification have dominated scientific and management efforts for years, there are multiple lines of evidence for positive or neutral effects of encroachment on ecosystem structure and functioning (Maestre *et al.*, 2009; Barger *et al.*, 2011; Quero *et al.*, 2013). Indeed, a recent review found little evidence to support the contention that woody encroachment has an overall negative impact on dryland ecosystems (Eldridge *et al.*, 2011). Current research suggests that the magnitude, and particularly the sign, of the effects of woody encroachment on ecosystems is highly variable, and may depend on both environmental factors and the degree of shrub dominance (Breshears, 2006; Soliveres & Eldridge, 2013). Environmental conditions are particularly important for an understanding of the impacts of woody encroachment. For example, aridity alters the effects of encroachment on carbon sequestration or herbaceous productivity (Jackson *et al.*, 2002; Knapp *et al.*, 2008; Blaser *et al.*, 2013) and the increase in grazing pressure influences the effects of encroachment on plant diversity and several ecosystem processes (Eldridge *et al.*, 2013). Additionally, despite a lack of strong empirical support, it has been suggested that the effects of woody encroachment vary with the degree of encroachment (i.e. the density or cover of woody species; Breshears, 2006). Positive effects are expected under intermediate levels of encroachment for attributes such as diversity (Blaum *et al.*, 2007; Sirami *et al.*, 2009), while the capture of resources, such as carbon or water, may increase linearly towards higher woody densities (Breshears, 2006; Riginos *et al.*, 2009; Eldridge *et al.*, 2013). These major drivers of the effect of woody encroachment (the degree of encroachment and environmental conditions) are likely to simultaneously and interactively influence the structure and functioning of natural ecosystems. However, they are generally considered in isolation. Most studies on encroachment have tended to focus on either a single site or similar environ-

mental conditions (reviewed in Archer *et al.*, 2001; House *et al.*, 2003; Breshears, 2006), or consider paired plots (encroached versus unencroached) without accounting for true gradients in woody encroachment. This narrow focus hinders our capacity to develop general models of the effects of woody plants on dryland ecosystems across a broad range of environments. Furthermore, most previous research on the ecological effects of woody encroachment has evaluated a limited set of ecosystem attributes at any one time (see Eldridge *et al.*, 2011, for a review), despite the facts that ecosystems are valued primarily for the multiple processes and services they provide and woody encroachment can affect multiple structural and functional variables simultaneously (Millennium Ecosystem Assessment, 2005; Eldridge *et al.*, 2011; Quero *et al.*, 2013).

Using a space-for-time substitution, we address the role of different degrees of woody abundance (which might help to explain the ecological consequences of woody encroachment; Breshears, 2006) on multiple structural and functional variables of ecosystems across a wide variety of communities and environmental conditions. We used data from 224 dryland sites from all continents except Antarctica to analyse the effect of differing degrees of woody dominance on ecosystem structure and multiple ecosystem processes, and to explore how environmental conditions alter such effects. We measured the relative cover of woody species together with plant diversity (species richness and evenness) and 14 soil variables related to fertility and the build-up of nutrient pools, which were analysed both separately and simultaneously by using an index of ecosystem multifunctionality (Maestre *et al.*, 2012). Our results show how both aridity and woody dominance interact to affect plant diversity and ecosystem multifunctionality in global drylands. As drylands are particularly sensitive to climate change and woody encroachment (Van Auken, 2000; Kulmatinski & Beard, 2013), our results provide new insights into the potential consequences for dryland biodiversity and ecosystem functioning of a widespread increase in woody plants.

MATERIALS AND METHODS

Study sites and environmental data

We sampled 224 dryland sites located in 16 countries from all continents except Antarctica (Argentina, Australia, Brazil, Chile, China, Ecuador, Iran, Israel, Kenya, Mexico, Morocco, Peru, Spain, Tunisia, the USA and Venezuela). These sites covered a wide range of woody cover (0–100% relative woody cover, RWC), environmental conditions (average annual rainfall 66–1219 mm, average annual temperature -1.8°C to 27.8°C), elevations (69–4668 m a.s.l.), total plant cover (3–83%), more than 25 different soil types according to the FAO (UN Food and Agricultural Organization) classification, and various vegetation (grasslands, shrublands and savannas) and land management (from protected areas to rangelands) types (see Maestre *et al.*, 2012, for more details).

In all of these sites, we established four 30-m long transects in which the total plant and woody coverage were measured using

a line-intercept method. From these data, we calculated the RWC as the percentage of the total plant cover that was occupied by woody species (i.e. woody cover \times 100/total plant cover). We used RWC instead of woody cover per se to account for the marked differences in total cover among the sampled sites, which could potentially influence any conclusions about the effects of total plant cover on ecosystem functioning in drylands (Greene *et al.*, 1994; Maestre & Escudero, 2009). Within each site, we also registered the total number of perennial plant species (woody and non-woody) and their cover within 80 1.5 m \times 1.5 m sampling quadrats (see Maestre *et al.*, 2012). These data were used to calculate species richness (total number of plant species found within each site) and species evenness [Hurlbert's PIE (probability of inter-specific encounter); Hurlbert, 1971].

We acknowledge that woody encroachment is pre-eminently a temporally dynamic process, and that repeated measurements through time or historical records would be necessary to properly assess it. However, space-for-time substitutions have proven useful in assessing temporal dynamics (reviewed in Hammond & Kolasa, 2014), and are particularly suitable when such continuous measurements are simply not possible due to the scale and extent of a study such as ours. Moreover, studying ecosystems across a whole shrubland–grassland continuum (i.e. differing in RWC), such as that used here, can provide important insights into the ecological implications of woody encroachment (Breshears, 2006).

For every site, we obtained climatic variables derived from digital models using the WorldClim database (<http://www.worldclim.org>; Hijmans *et al.*, 2005), from which an aridity index (mean annual precipitation/potential evapotranspiration) was derived. To facilitate the interpretation of our results, we used 1 – aridity index in our analyses (higher values of aridity mean lower water availability; see Delgado-Baquerizo *et al.*, 2013).

Measuring ecosystem multifunctionality

Dryland ecosystems are naturally heterogeneous (e.g. Schlesinger *et al.*, 1990). Therefore, an appropriate way of analysing soil properties is by using a stratified sampling design in which the heterogeneity of soil properties is taken into account. Thus, we used a stratified sampling design taking into account the dominant microsites within each site. We sampled the top 7.5 cm of the soil from up to three different microsites per site; these microsites always included a location from areas of bare soil devoid of vascular plants as well as microsites dominated by perennial vegetation (e.g. under trees, shrubs or tussock grasses, depending on the dominant growth forms within each site). Five samples were collected for each microsite, yielding between 10 and 15 samples per site, which were sieved (< 2 mm fraction) and air-dried at room temperature before physicochemical analyses. In each soil sample, we measured (in the same laboratory to avoid experimental noise) 14 variables: nitrate (NO₃⁻) and ammonium (NH₄⁺) availability, organic carbon (C), total nitrogen (N), available inorganic phosphorus (P), amino acids,

proteins, pentoses, hexoses, aromatic compounds, phenols, potential N transformation rate and the activity of two extracellular enzymes (β -glucosidase and phosphatase). These variables, which were evaluated as detailed in Maestre *et al.* (2012), provide a good proxy of key ecosystem processes linked to soil fertility, the ability of soils to capture and retain water, nutrient cycling, biological productivity and build-up of nutrient pools (see Maestre *et al.*, 2012, and Delgado-Baquerizo *et al.*, 2013, for a full rationale). Most of these variables are also considered to be supporting ecosystem services, as other types of ecosystem services depend on them (Millennium Ecosystem Assessment, 2005; Balvanera *et al.*, 2006; Isbell *et al.*, 2009). Data from individual replicates were averaged to obtain site-level estimates by using the mean values observed in bare ground and vegetated areas, weighted by their respective cover at each site. With these site-level estimates, we obtained a multifunctionality index (*M*) representing the ability of each site to maintain high levels of multiple ecosystem processes simultaneously (Zavaleta *et al.*, 2010). This index was calculated as the average of the Z-scores of each of the 14 variables measured (Maestre *et al.*, 2012). The *M*-index is statistically robust (Maestre *et al.*, 2012), is being increasingly used (e.g. Pendleton *et al.*, 2014; Wagg *et al.*, 2014) and is related to other widely used multifunctionality metrics (Byrnes *et al.*, 2014).

Multifunctionality measurements may obscure specific responses for the different soil variables measured. Thus, we analysed the effect of both aridity and woody cover on them separately. The variables evaluated were either positively correlated or uncorrelated. The only exception was the relationship between organic C and available P, which was slightly negative ($r = -0.15$, $P < 0.05$, $n = 224$). The relationships of aridity and woody cover, and their interaction, with these variables were also relatively consistent (see Results). Overall, this suggests that there were no trade-offs among the different variables measured; therefore we will not discuss them separately here (detailed results for each variable are presented in Appendix S1 in Supporting Information).

Statistical analyses

The statistical analyses included two sequential steps. First, we assessed the relationship among the several geographical, environmental, plant and soil variables evaluated using structural equation modelling (SEM; Grace, 2006) with the whole dataset. This modelling approach is a synthesis of path analysis, factor analysis and maximum likelihood techniques that has been widely used as a tool for causal inference and for partitioning causal influences among multiple variables. The first step in SEM is to establish an a priori causal model establishing the expected relationships among the variables introduced based on previous knowledge. In our case, we established an a priori model assuming that both geographical variables (latitude and longitude; to account for the spatial structure in our data) and aridity affect to some degree the rest of the variables introduced in the model (plant species richness, plant species evenness, total plant cover, relative woody cover and ecosystem

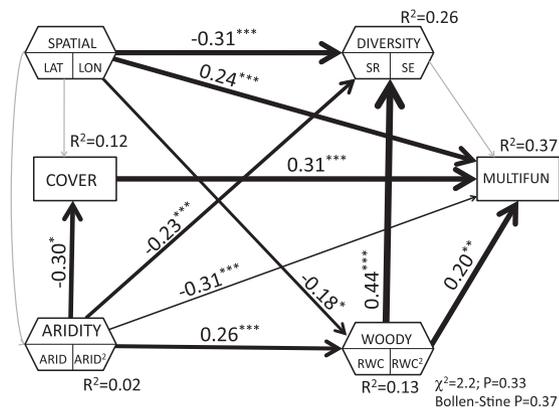


Figure 1 Structural equation modelling depicting the effects of aridity, geographical variables and plant variables upon ecosystem multifunctionality. Composite variables are shown with hexagons. The width of the arrows is proportional to the path coefficient, with continuous (positive), dashed (negative) and grey (non-significant) lines indicating the sign of the relationships. The overall goodness-of-fit test and the R^2 for each variable introduced are included. P -values of path coefficients are as follows: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$. Key: ARID, aridity level; RWC, relative woody cover; LAT, latitude; LON, longitude; WOODY, woody dominance, represented by relative woody cover (RWC); COVER, total plant cover; SR, species richness; SE, species evenness; MULTIFUN, multifunctionality.

multifunctionality; e.g. Lomolino *et al.*, 2006; Sankaran *et al.*, 2008). Total plant cover was expected to affect ecosystem multifunctionality (Maestre & Escudero, 2009) and to correlate with both species richness and evenness due to shared causal influences external to the model. RWC, in turn, was expected to affect plant richness and evenness, together with ecosystem multifunctionality (Eldridge *et al.*, 2013). There is ample evidence that both species richness and evenness affect ecosystem multifunctionality (e.g. Isbell *et al.*, 2009; Maestre *et al.*, 2012, and references therein); thus, we also considered this relationship in our a priori model.

The second step in SEM is to estimate path coefficients and their associated P -values from the field data. We estimated coefficients with bootstrapping because some of our data were positively kurtotic or non-normal, and this technique is preferred to maximum likelihood estimation in these cases. The path coefficient is analogous to a partial correlation coefficient, and describes the strength and sign of the relationships among the introduced variables (Grace, 2006). Apart from estimating single path coefficients, SEM tests the overall goodness of fit of the model against the dataset. To do this, we used the traditional χ^2 test, the root mean square error of approximation (RMSEA) index and the Bollen–Stine bootstrap test. All of these indices (Fig. 1) show that our model fits the data, and that our proposed model structure is a plausible network of causal relationships among our variables. We acknowledge that other a priori model structures would be possible, and that inferring causality from observational studies is always a challenge. However, the goodness-of-fit metrics of our model (Fig. 1), and the ample

evidence demonstrating causality in the effect of both diversity (richness and evenness) and woody cover on multiple ecosystem processes such as those measured here (e.g. Isbell *et al.*, 2009; Eldridge *et al.*, 2011), clearly support the direction of the paths chosen.

Nevertheless, we also considered an alternative a priori model structure including the effects of multifunctionality on species richness, evenness, total plant cover and RWC. Although less likely, according to current literature, this a priori model structure was also a plausible causal scenario ($\chi^2 = 0.54$, d.f. = 1, $P = 0.46$; Fig. S1). However, the path from multifunctionality to RWC was not significant [standardized path coefficient (SPC) = 0.11, $P = 0.12$], and neither were those paths linking multifunctionality with richness (SPC = 0.12, $P = 0.09$) or evenness (SPC = 0.12, $P = 0.10$). While the causal links from diversity and woody cover to multifunctionality have previously been widely demonstrated, the sign of the effect of woody encroachment on both diversity and multifunctionality – and its interaction with the environment – are poorly understood. We believe that the structure of our proposed model can provide important insights into this topic and do not consider the alternative model structure further.

Inspection of our data indicated that both aridity and RWC had a hump-shaped relationship with ecosystem multifunctionality, which could be well modelled with a second-order polynomial regression. To model these nonlinear relationships, we included a *composite* variable in our model including both x and x^2 , x being the raw predictor (aridity or RWC). Composite variables were also used to model the cumulative effects of multiple geographical predictors (latitude and longitude) and the cumulative effect of the two elements of plant diversity measured (richness and evenness). The use of these composite variables does not alter the underlying model, but collapses the effects of the variables included (two in our case) into a single path coefficient, aiding interpretation of model results (Grace, 2006).

We also explored the interactions between aridity and woody dominance as drivers of diversity and multifunctionality, as they are very likely to interact (Jackson *et al.*, 2002; Knapp *et al.*, 2008). To do this we first tested the interaction between RWC and aridity with generalized linear models (GLMs), one for each response variable (richness, evenness and multifunctionality). In these GLMs, we introduced latitude and longitude, to control for the spatial structure in our data, total plant cover, aridity (as a three-categorical factor, to ease interpretation), RWC (as a polynomial term to model nonlinear relationships) and the interaction between aridity and RWC. To illustrate the significant RWC \times aridity interactions that were found for most variables (see Results), we divided our study sites into dry-subhumid (aridity level = 0.55–0.2, $n = 27$), semi-arid (aridity level = 0.54–0.79, $n = 151$) and arid (aridity level = 0.80–1.00, $n = 46$) environments. We fit separate regressions (linear or quadratic, depending on the shape of the relationship) for each variable and aridity level to assess for the effect of RWC on species richness, evenness and ecosystem multifunctionality. Species richness and evenness were square root- and arcsine-

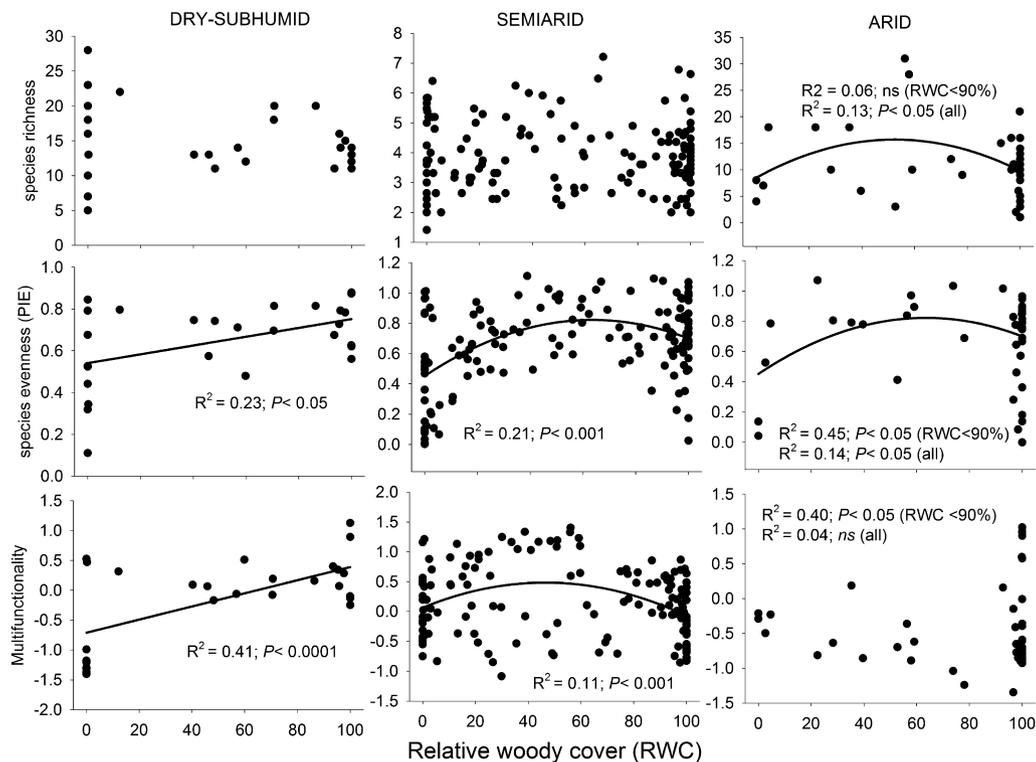


Figure 2 Relationships between relative woody cover (RWC) and species richness, evenness or ecosystem multifunctionality across differing aridity levels. Significant relationships and their statistics are shown within each panel. For arid environments, regression results with (all) and without (RWC < 90%) the sites with RWC > 90% are shown. $n = 27$, 151 and 46 for dry-subhumid, semi-arid and arid environments, respectively. Statistical results for the aridity \times RWC interaction are shown for each variable in the left panel.

transformed, respectively, before statistical analyses to normalize them. SEM analyses were performed using AMOS for Windows (SPSS Inc., Chicago, IL, USA), the rest of the analyses were conducted with SPSS 13.0 for Windows (SPSS Inc.).

RESULTS

Our SEM explained 37% of the variance in multifunctionality (Fig. 1); its relationships with both aridity (based on FAO's aridity level) and RWC (proportion of total plant cover occupied by woody species) were positively hump-shaped, with multifunctionality peaking under semi-arid conditions and with RWC values between 41 and 60%. The effects of both RWC and aridity were relatively homogeneous when considering the 14 measured soil variables separately, with most peaking at values of 50–60% RWC and an aridity level of 0.5–0.6 (Appendix S1). Our structural model also showed that plant diversity (richness and evenness) decreased with aridity or latitude (Fig. 1). However, RWC was its strongest predictor, and the relationships between species richness or evenness and RWC were similarly hump-shaped, with both variables peaking at RWC values of 61–80% (Fig. 2).

Woody encroachment is the increase in woody abundance in former grasslands. An alternative way of assessing the role of woody encroachment, therefore, would be to test how absolute woody cover (irrespective of total plant cover within each site) affected diversity and multifunctionality considering only those

sites in our database located in grasslands, excluding shrublands and other vegetation types (Fig. S3). Using absolute woody cover instead of RWC yielded similar results, with substantial positive effects of woody cover on multifunctionality and species evenness up to values of 40%, the maximum value recorded in grasslands within our global survey. Species richness, in turn, peaked at woody cover levels of *c.* 25%.

Aridity altered the effect of RWC on species evenness and multifunctionality (as well as for 10 out of 14 functional variables separately; Table S1), but not richness (Fig. 2). The positive linear trend in evenness and multifunctionality with increasing RWC found in dry-subhumid sites changed to a unimodal relationship under semi-arid conditions. Under the most arid conditions, the unimodal relationships were retained for evenness and richness, but shifted to a linear negative relationship for multifunctionality. The negative relationship between RWC and multifunctionality or species evenness in arid environments was obscured by the high variability found at sites with very high RWC (> 90%). When these high-cover sites were excluded, trends were more clearly defined for evenness ($R^2 = 0.45$, $P < 0.05$) and multifunctionality ($R^2 = 0.40$, $P < 0.05$), but not for species richness (Fig. 2).

DISCUSSION

Examining trends in ecosystem structure and functioning across gradients of varying woody dominance helps us to understand

the ecological consequences of woody encroachment, and guides management and policy for key environmental areas such as desertification, deforestation, grazing, fire management and climate change (Breshears, 2006, and references therein). Despite the considerable interest in woody encroachment from land managers, scientists and government agencies, very few studies have attempted to assess how both aridity and woody encroachment simultaneously affect plant diversity and ecosystem functioning at the global scale (Jackson *et al.*, 2002) and none has considered how the degree of woody dominance influence such effects in global drylands.

Hump-shaped RWC–diversity and RWC–multifunctionality relationships

The results of our global study are remarkably consistent with the few existing regional studies that indicate hump-shaped responses of diversity across gradients of woody cover (Blaum *et al.*, 2007; but see Báez & Collins, 2008; Sirami *et al.*, 2009). They provide clear evidence that these hump-shaped relationships are also applicable at the global scale, and extend these relationships to include critical variables related to soil fertility, productivity and the ability of ecosystems to capture and retain resources.

The ecological mechanisms behind the hump-shaped responses of diversity across gradients of woody cover have been discussed previously, and relate mainly to heterogeneity in environmental conditions and resources between canopy and intercanopy microsites, and to connectivity among vegetated patches (Huxman *et al.*, 2005; Breshears, 2006; Riginos *et al.*, 2009). Woody canopies reduce incident radiation and typically increase water infiltration and soil fertility compared with intercanopy microsites (Breshears, 2006; Throop & Archer, 2007; Maestre *et al.*, 2009). These markedly different environmental conditions increase the amount of available niche space (e.g. Moro *et al.*, 1997; Dean *et al.*, 1999), and may increase overall species richness at the site level (Maestre *et al.*, 2009; Soliveres *et al.*, 2012). However, once a given threshold in woody density or cover is reached, higher woody densities create a more homogeneous environment, with shading extending to the open interspaces (Martens *et al.*, 2000) and similar water availabilities in woody and open microsites due to the overlap of the roots of woody plants (Breshears, 2006). Once a threshold in woody dominance has been reached, shade-intolerant species or those that cannot compete with woody plants for soil moisture disappear. Put simply, our results indicate that, at low woody plant densities, increases in woody cover and density increase habitat heterogeneity and therefore niche space, leading to greater diversity of both plants and animals and increased heterogeneity of resources. At higher woody plant densities, however, increasing densities have a homogenizing influence. Our study is unique in that the comprehensive global database used provides strong evidence that this cover threshold lies between a RWC of 41 and 60% (Fig. 2), or close to 25% absolute woody cover (Fig. S3).

Interestingly, the hump-shaped relationship found between plant richness and woody cover has also been observed in bird

(Sirami *et al.*, 2009) and mammal (Blaum *et al.*, 2007) assemblages. Like plants, animals can also benefit from the increase in heterogeneity, and therefore niche space, within the landscape at average levels of woody encroachment (e.g. more insect species to feed from, increase in fleshy fruited plants or more available nesting spaces; e.g. Dean *et al.*, 1999). However, at higher woody densities those species requiring open areas for habitat will disappear, promoting the same hump-shaped response as observed for plants. Interestingly, observations of woody thresholds based on empirical data for bird (c. 40%; Sirami *et al.*, 2009) and mammal (c. 20%; Blaum *et al.*, 2007) richness are similar to our values for plants (Figs 2 & S3).

Our results for ecosystem multifunctionality track those found with plant diversity, but are likely to be driven by different mechanisms. Although soil C is hypothesized to increase linearly with increasing woody cover (Reich *et al.*, 2001; Breshears, 2006), we failed to detect such a pattern when evaluating ecosystem multifunctionality at the high end of our RWC gradient (see also top panels in Fig. S2a). Two potential mechanisms might explain this observation: (1) consistent with the Jornada desertification model (Schlesinger *et al.*, 1990), dominance of woody plants over herbaceous plants at high levels of RWC might be expected to enhance wind erosion and removal of topsoil (Huxman *et al.*, 2005), compromising the ability of the soil to sequester resources; and (2) the higher water demands of woody dominated areas (RWC > 80%) create intense plant–plant competition for moisture, compromising their ability to capture and recycle nutrients (Breshears, 2006; Knapp *et al.*, 2008). These mechanisms might explain why some studies show increases in soil fertility with increasing woody cover (Maestre *et al.*, 2009; Barger *et al.*, 2011; Eldridge *et al.*, 2011) while others demonstrate decreases (Schlesinger *et al.*, 1990; Archer *et al.*, 2001). These contrasting results might be explained, at least in part, by the different woody densities in which each study was performed – for example a woody cover of 26% in Maestre *et al.* (2009), which showed a positive effect of shrubs, versus 60% in Archer *et al.* (2001), which showed a negative effect of shrubs – and hence highlight the need to consider differing levels of woody dominance to properly assess the role of woody encroachment in global nutrient cycles.

Interactions between woody dominance and aridity

Surprisingly few studies have addressed how the availability of water influences the effects of woody plants on ecosystem structure and functioning. These studies stem from very divergent degrees of woody encroachment and show contradictory results (Jackson *et al.*, 2002; Knapp *et al.*, 2008). Our global survey showed that, within drylands, an increasing dominance of woody plants increases plant diversity and ecosystem multifunctionality under the wettest situations, and linearly decreases multifunctionality under the driest situations (although the trend under the driest conditions was much less consistent; see below and Appendix S1). Intermediate semi-arid situations, however, exhibited a hump-shaped relationship between woody dominance and plant diversity and ecosystem

multifunctionality, and this hump-shaped relationship was also found for diversity in the most arid environments. Our results contrast with those previously found under a similar range of rainfall conditions (Jackson *et al.*, 2002), which might be explained by (1) differing degrees of woody cover between their database and ours (discussed extensively above) or (2) the influence of soil depth sampled (Jackson *et al.*, 2002; Dean *et al.*, 2012). These authors took samples at deeper soil depths than we did and soil nutrients are more widely distributed across the soil profile, and therefore might be showing lower values at the surface when woody plants become more dominant (Jackson *et al.*, 2000). Thus, the negative effect of RWC that we found under arid conditions could be derived from the lower amounts of C in shallow soils in situations where woody plants are more dominant. An alternative explanation is the extreme intersite variability in the RWC–ecosystem functioning relationships found in arid areas (see Fig. S2a,b). For example, both positive and neutral responses of soil C across gradients of woody encroachment have been previously found in sites within the same area under arid conditions (Eldridge *et al.*, 2013), and both strongly positive (Wheeler *et al.*, 2007) and negative (Schlesinger *et al.*, 1990; Archer *et al.*, 2001) responses of soil C to woody encroachment have been reported in arid areas of the south-western USA. Indeed, the high variability in our own results resulted in non-significant trends in many soil variables (Figs 2 & S2a,b). The high variability among arid sites might be due to differences in management across study sites (i.e. grazing pressure). For example, overgrazing might lead to a loss of plant diversity at a time that prevents herbaceous cover from growing sufficiently to reduce the risk of erosion (Schlesinger *et al.*, 1990; Greene *et al.*, 1994). Grazing effects, which are particularly relevant in the most arid sites (Illius & O'Connor, 1999), can dampen the positive effects of woody encroachment on both diversity and multifunctionality under arid conditions (Eldridge *et al.*, 2013; Soliveres & Eldridge, 2013). High intersite variability might also result from the fact that arid environments frequently experience extreme climatic events, to which woody-dominated systems show more variable responses than grasslands (Breshears, 2006; Knapp *et al.*, 2008). The variable response of woody plants to such extreme climatic events may explain the overall dampening (if we exclude those sites with RWC < 90%) of the positive effect of woody plants on ecosystem functioning in arid areas.

The more positive effect of woody cover on ecosystem multifunctionality that we found in wetter environments is consistent with findings from North American grasslands where the positive effect of woody encroachment on aboveground net primary production increases with increasing precipitation (Knapp *et al.*, 2008). Because more water is stored within deeper soil layers in more mesic environments (Scholes & Archer, 1997; Kulmatinski & Beard, 2013) the higher water demand of woody plants does not stifle nutrient capture and storage (Knapp *et al.*, 2008), and may increase productivity at the site level when woody plants are more abundant (Hughes *et al.*, 2006). Overall, our results show that the increase in aridity predicted under future climatic scenarios may compromise the generally positive

role of woody dominance in dryland structure and functioning (Eldridge *et al.*, 2011). This reduction in the positive effects of woody dominance on ecosystem structure and functioning seems to be particularly relevant in those areas shifting from semi-arid to arid climates, which are already more sensitive to increasing aridity due to important changes in nutrient stoichiometry (Delgado-Baquerizo *et al.*, 2013).

In summary, our study provides clear evidence that increasing dominance of woody plants has a positive influence on plant diversity and ecosystem multifunctionality in drylands, with both diversity and multifunctionality peaking at 41–60% of RWC. The interactions found between aridity and RWC suggest that the increase in aridity predicted for drylands with climate change (Feng & Fu, 2013) will tend to counteract the positive effect of woody encroachment, particularly in those areas shifting from semi-arid to arid climates. By investigating the inter-relationships among climate and woody dominance using a global survey, our results not only provide a major advance for forecasting the ecological consequences of woody encroachment, but can also help to refine management and policy actions in drylands world-wide.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1 Results of structural equation modelling according to an alternative a priori model structure.

Figure S2 (a) Relationships between relative woody cover and soil variables related to nutrient pools across differing aridity levels. (b) Relationships between relative woody cover and soil variables related to nutrient fluxes across differing aridity levels.

Figure S3 Analysis only with grasslands.

Table S1 GLM results for each of the response variables and predictor introduced in the model.

Appendix S1 Analyses and results with each functional variable separately.

BIOSKETCH

Santiago Soliveres has a range of interests in dryland community ecology ranging from plant–plant interactions, diversity–ecosystem functioning relationships, restoration of roadsides and mine sites, the effect of grazing or climate on plant diversity and the ecology of biological soil crusts. However, his latter research has mainly focused on woody encroachment, its ecological consequences and how the widely extended woody encroachment phenomenon interacts with differing environmental conditions to simultaneously drive the diversity and functioning of drylands.

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