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Response to Comment on "Plant Species Richness and Ecosystem Multifunctionality in Global Drylands"

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Jucker and Coomes claim that the relationship between plant species richness (biodiversity) and ecosystem multifunctionality (B-EMf) reported in our study changes along environmental gradients. We point out flaws in their analytical approach and then reanalyze our data to further demonstrate that the B-EMf relationship does not substantially change along environmental gradients.

We reported the existence of a positive and significant relationship between plant species richness (biodiversity) and ecosystem multifunctionality (B-EMf) in global drylands (*1*). Jucker and Coomes (*2*) extended our analyses to explore the effects of "environmental stress" on the B-EMf relationship. They constructed a stress index (S) based on abiotic variables and showed that the slope and R^2 of the B-EMf relationship varies with stress. We first discuss the lack of suitability of their analytical approach and conceptual framework and then reanalyze our data in light of the interesting question raised by these authors.

There are technical flaws that invalidate the analyses made by Jucker and Coomes. First, they incorrectly calculated Z scores for water stress. We found a perfect negative correlation between their Z score for water availability and their untransformed variable (Fig. 1A). As a consequence, their measure of stress (S index) is positively correlated with average water availability (Fig. 1B), a correlation that makes no ecological sense in drylands (*3*). Second, their S index is based on averages of the Z scores of negatively correlated environmental variables (sand content and slope, Spearman's $\rho = -0.464$, $n = 224$, $P < 0.001$). Different, but inversely correlated, stress factors can cancel one another out when calculating S and may suggest a relatively low stress level when it is actually high. This problem has been previously discussed in the context of multifunctionality indices (*4*), as we stated in our manuscript [page 7 of the supporting online material (SOM) in (*1*)]. These analytical flaws led Jucker and Coomes to misclassify our sites into inappropriate stress categories. For example, some sites in Chile (numbers 52 to 54 in our database) with annual rainfall well below 100 mm and a high sand content (~80%), but low slopes and no important frost or wind damage, were classified as "low stress" by Jucker and Coomes. In fact, these sites are extremely arid and are classified as highly stressed, following international and well-established classification schemes for drylands (*5*).

Apart from the analytical problems, Jucker and Coomes invoked the stress-gradient hypothesis (SGH) (*6*) to explain the stronger B-EMf relationship under harsher conditions. Claims made by these authors, such as "We found that B-EMf patterns differed considerably among S classes, and did so in accordance with the predictions of the SGH," are incorrect because the predictions of the SGH have nothing to do with B-EMf relationships, but rather with the relationship between plant-plant interactions and stress. Although these interactions can help to explain the relationship between species richness and ecosystem functioning (*7*), they are not the only, nor even the most important, mechanism invoked to explain the B-EMf relationship. The sampling effect, the insurance hypothesis, and the resource complementarity hypothesis [reviewed in (*8*)] are other plausible explanations, which cannot be evaluated properly with the data gathered in our study.

Despite the analytical errors found in Jucker and Coomes´ contribution, they raise an interesting question (does the B-EMf relationship change along environmental gradients), which clearly deserves exploration. We therefore repeated our model selection analysis (*9*), introducing interaction terms (species richness by abiotic variables) as potential predictors. Each interaction term was calculated as the product of the centered variables (plant species richness

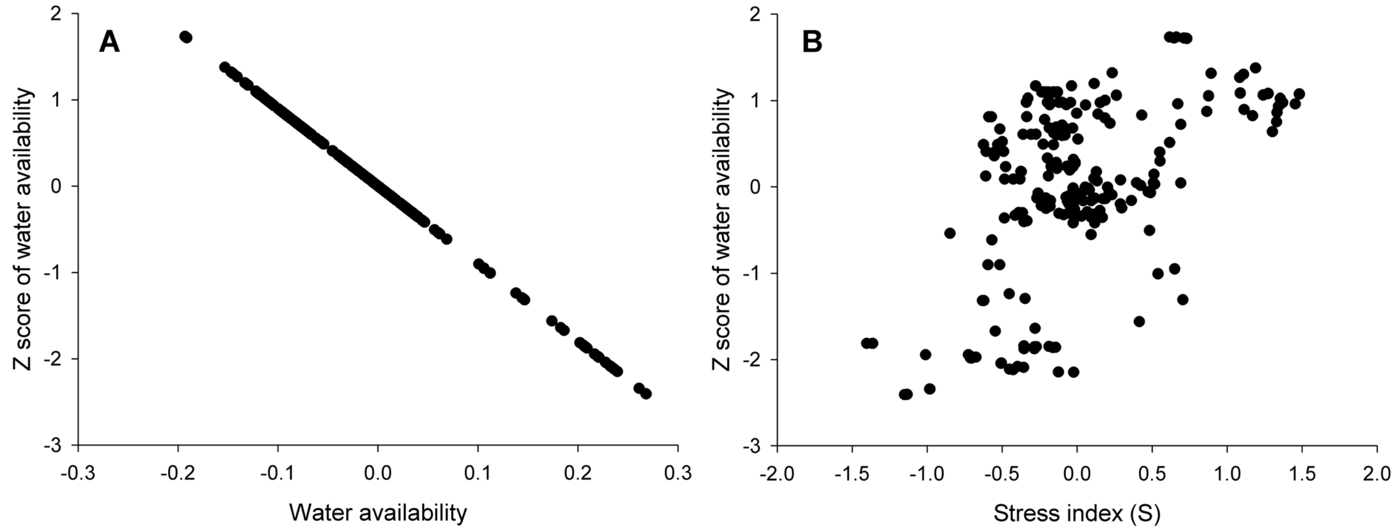

Fig. 1. Relationships between the Z score of water availability and the untransformed values of this variable (**A**), and between the Z score of water availability and the S index used by Jucker and Coomes (**B**). Results of nonparametric correlations in (B) are as follows: Spearman's $\rho = 0.420$, $n = 224$, $P < 0.001$.

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and the corresponding abiotic measure) (*10*). If the inclusion of these interaction terms modifies the regression coefficients of other predictors, or substantially increases the variance explained by the model, it would imply that the B-EMf relationship changes along environmental gradients. We ran two new sets of models with our multifunctionality index as the dependent variable and compared them with our original set of models (Fig. 2A). Model set A included the original variables, plus four interaction terms between plant species richness and the four principal components analysis (PCA) components describing major climatic features of our study sites (*1*) (Fig. 2B). Model set B included the original variables plus four interaction terms between plant species richness and abiotic variables related to the degree of environmental stress (average rainfall, average annual temperature, annual temperature range, and sand content) (Fig. 2C). We quantified the relative importance of the different predictors as described in our original manuscript [page 9 of the SOM in (*1*)].

Regardless of the combination of variables chosen, our results were robust and virtually identical to those presented in our original analyses (Fig. 2). The inclusion of the new interaction terms did not modify the regression coefficients of other predictors. Annual mean temperature and sand content were the two most important predictors of multifunctionality, followed by plant species richness, slope, and elevation. The interaction terms were always weaker than the original variables, and they collectively increased the variance explained by less than 0.5%. In both model sets, one of the richness by abiotic interaction terms were chosen in the best model. However, the addition of these interactions terms did not improve our original model. [Difference in Akaike information criterion (AIC) between the best model and our original model was below 2 in both cases (Table 1).] We also repeated the analyses using other interactions, and their outcome was the same (*11*). Overall, these results suggest that the significant relationship between plant species richness and ecosystem multifunctionality that we originally described does not substantially change along environmental gradients. We never claimed that the relationship between species richness and multifunctionality was universal, or even that it was constant, and acknowledged in our paper that other abiotic and biotic factors that are known to affect ecosystem functioning can be responsible for the

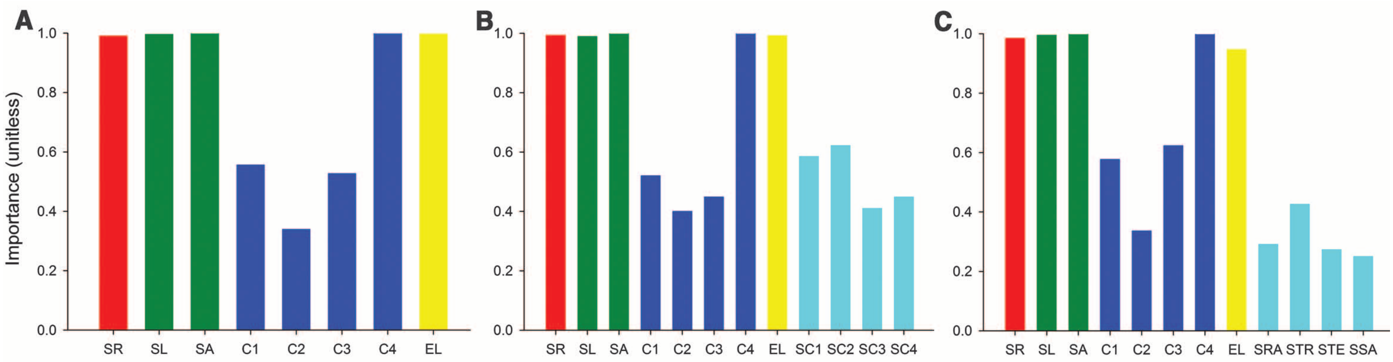

Fig. 2. Relative importance of perennial plant species richness (red column, SR) and other predictor variables in models of ecosystem multifunctionality. The height of each bar is the sum of the Akaike weights of all models that included the predictor of interest, taking into account the number of models in which each predictor appears. Interaction terms between plant species richness and abiotic variables are shown in light blue. (**A**) Original model analysis from Maestre *et al*. (*1*). (**B**) Original variables plus interaction terms with climate PCA variables. (**C**) Original variables plus interactions with aridity-related variables. C1, C2, C3, and C4, first, second, third, and fourth components of a PCA conducted with climatic variables; SA, sand content; SL, slope angle (square root–transformed); EL, elevation (square root–transformed); SRA, STR, STE, and SSA, interaction terms between plant species richness and average annual rainfall, temperature range, and annual temperature and sand content, respectively; SC1, SC2, SC3, and SC4, interaction terms between plant species richness and C1, C2, C3, and C4, respectively.

Table 1. Best-fitting regression models of ecosystem multifunctionality of the new sets of models analyzed (A and B). Each column represents a different predictor variable (red, perennial plant species richness; green, abiotic variables; blue, climatic variables; gold, geographic variables; light blue, richness by abiotic variables interaction terms). The three best models within each set are presented, ranked according to their second-order AIC (AIC_c) value. In set A, we also include the model originally presented in Maestre *et al*. (*1*) to allow comparison of the amount of variance explained and the differences in AIC_c. This model is the second-best model in set B. AIC_c measures the relative goodness of fit of a given model; the lower its value, the more likely it is that this model is correct. Unshaded cells indicate variables that were not included in a particular model. w_i, Akaike weights; ΔAIC_c, difference between the AIC_c of each model and that of the best model (ΔAIC_c values below 2 indicate that the models being compared are approximately equivalent in explanatory power). Other abbreviations as in Fig. 2.

Model	Abiotic			Climatic				Geographic			Interaction terms				R^2	AIC_c	ΔAIC_c	w_i
set	SR	SL	SA	C1	C2	C3	C4	LA	LO	EL								
											SC1	SC2	SC3	SC4				
A	🟥	🟩	🟩		🟦		🟦	🟨	🟨	🟨		🟦			0.567	281.35	–	0.024
	🟥	🟩	🟩	🟦			🟦	🟨	🟨	🟨	🟦	🟦			0.571	281.36	0.014	0.023
	🟥	🟩	🟩		🟦			🟨	🟨	🟨		🟦		🟦	0.571	281.63	0.285	0.020
	🟥	🟩	🟩	🟦		🟦	🟦	🟨	🟨	🟨					0.564	282.75	1.405	0.012
											SRA	STR	STE	SSA				
B	🟥	🟩	🟩	🟦		🟦	🟦	🟨	🟨	🟨		🟦			0.569	282.72	–	0.047
	🟥	🟩	🟩	🟦		🟦	🟦	🟨	🟨	🟨					0.564	282.75	0.033	0.046
	🟥	🟩	🟩	🟦			🟦	🟨	🟨	🟨					0.559	283.23	0.509	0.036

scatter found in our results (*1*). We also believe that the amount of variance in the B-EMf relationship not explained by the variables we measured clearly deserves further attention (*12*). However, the main take-home message of both our original manuscript and this response is that, despite the multiple sources of variation, there is a significant positive B-EMf relationship in global drylands and that species richness is an important positive predictor of ecosystem multifunctionality. The latter result was consistent after accounting for other major environmental factors and their interactions with plant species richness.

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11. Apart from the models described in the text, two additional sets of models were evaluated. One of them included the original variables plus four interaction terms between plant species richness and the climatic variables most correlated with the four PCA components (average rainfall, mean temperature and rainfall during the driest quarter, and mean temperature during the wettest quarter) [page 6 of the SOM in (*1*)]. The other set of models included the original variables plus the interaction between species richness and a widely used aridity index (precipitation/potential evapotranspiration) (*5*). The analyses of these sets of models produced virtually identical results to those presented in the text; the best models for each of the two model sets described here did not include any of the richness by abiotic variables interaction terms. Collinearity among independent variables in all the new sets of models conducted was negligible.
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