Comment on “Plant Species Richness and Ecosystem Multifunctionality in Global Drylands”

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Maestre et al. (Reports, 13 January 2012, p. 214) reported a general, but weak, positive relationship between plant diversity and ecosystem multifunctionality in global drylands. We show that the strength of this relationship changes consistently along multiple environmental gradients, becoming strongly positive in stressed habitats. This suggests that biodiversity loss may have especially strong consequences in harsh environments.

In light of global change and its consequences for plant and animal communities, explaining and quantifying the link between biodiversity and ecosystem multifunctionality (B-EMf) has become a priority for ecologists and stakeholders alike (1). Maestre et al. (2) measured 14 ecosystem properties related to the storage and flux of nutrients [carbon (C), nitrogen (N), and phosphorus (P)] in 224 vegetation plots distributed across all major dryland ecosystems. From these, the authors derived an index of ecosystem multifunctionality (M) that was significantly positively related to the richness of perennial vascular plants. Although weak (regression model \( R^2 = 0.03 \)), this pattern persisted even after having accounted for the confounding effects of environmental covariates influencing M. Because of the global scale of the study, the focus on multiple ecosystem processes (1, 3) and the vulnerability of drylands to climate change, this study represents an important contribution to its field. However, we reveal that the association between biodiversity and ecosystem multifunctionality in drylands is more complex than initially thought and highlight how this relationship changes consistently and predictably along different environmental gradients, becoming progressively stronger and more positive as environmental stress increases.

The role of abiotic stress in shaping plant interactions has been extensively studied in ecology and is conceptualized in the stress-gradient hypothesis (SGH), which predicts competition (i.e., negative interactions) to dominate under favorable environments, whereas facilitative processes (i.e., positive interactions) increase as conditions become harsher (4). These same ecological processes (competition and facilitation) help explain how biodiversity may enhance (or impede) ecosystem functioning (5), suggesting that the strength of the B-EMf relationship should vary along environmental gradients in response to changes in the net effect of species interactions (6). Therefore, the most basic expectation is that B-EMf patterns shift from weak or even negative where conditions are favorable and competition is prominent, to strong and positive under harsher environments (6, 7). Maestre et al. (2) focus on drylands, which encompass arid, semi-arid and dry-subhumid ecosystems and exhibit a considerable range of environmental conditions (e.g., mean annual precipitation: 66 to 1219 mm/year; elevation: 69 to 4668 m; soil sand content: 5 to 98%; mean annual temperature: −2 to 28°C). In light of this, we reanalyzed the data presented in the study to determine how accounting for differences in environmental stress would influence the effect of species richness on ecosystem multifunctionality.

We identified environmental stress gradients [as defined in (4)] from data available in Maestre et al. (2) and other data sources. Measures of terrain slope and soil sand content were obtained from the original study, while FetchClimate (http://fetchclimate.cloudapp.net) was used to extract environmental variables related to stress (8). We removed strongly correlated predictors and used principal components analysis (PCA) ordination to obtain a measure of water availability (8). Following Maestre et al.’s (2) method, \( Z \) scores were then computed for the selected environmental stress variables (water availability, sand content, terrain slope, temperature range, frost days, and wind speed), and for each plot a stress index (\( S \)) was calculated by averaging the \( Z \) score of all predictors. Based on this, we divided the data into three equal-number S classes (low, intermediate, and high, specifically low (A), intermediate (B), and high (C) stress. Red and green lines represent the fitted OLS and SAR models, respectively. The shaded region in red corresponds to the 95% confidence intervals of the OLS regression. Linear regression equations (±SE for parameter estimates) are reported for OLS (red) and SAR (green) models. Regression results were (A) OLS, \( R^2 = 0.046, P = 0.065; \) SAR, \( P = 0.113; \) (B) OLS, \( R^2 = 0.083, P = 0.012; \) SAR, \( P < 0.001; \) (C) OLS, \( R^2 = 0.224, P < 0.001; SAR, P < 0.001.

Fig. 1. Scatter plots of ecosystem multifunctionality (M) as a function of species richness (square-root transformed for comparability with (2)) along an increasing environmental stress gradient (from left to right): low (A), intermediate (B), and high (C) stress. Red and green lines represent the fitted OLS and SAR models, respectively. The shaded region in red corresponds to the 95% confidence intervals of the OLS regression. Linear regression equations (±SE for parameter estimates) are reported for OLS (red) and SAR (green) models. Regression results were (A) OLS, \( R^2 = 0.046, P = 0.065; \) SAR, \( P = 0.113; \) (B) OLS, \( R^2 = 0.083, P = 0.012; \) SAR, \( P < 0.001; \) (C) OLS, \( R^2 = 0.224, P < 0.001; SAR, P < 0.001.

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with 74 to 75 plots each) and repeated the authors’ regression analysis [ordinary least-squares (OLS) and simultaneous autoregression (SAR)] for the three groups separately (9). In this way, we were able to test how both the strength (explained variance, $R^2$) and slope (slope parameter, $\beta$) of the B-EMf relationship changes across multiple environmental stress gradients.

We found that B-EMf patterns differed considerably among S classes, and did so in accordance with the predictions of the SGH (Fig. 1). The B-EMf relationship shifted from slightly negative in the low S plots ($R^2 = 0.046; \beta = -0.138$) to increasingly positive in the intermediate ($R^2 = 0.083; \beta = 0.168$) and high ($R^2 = 0.224; \beta = 0.247$) S class, respectively. To highlight the consistency of this result, we also considered each environmental stress variable used to calculate S individually and sorted the data according to their values. We then repeated the regression analysis separately for each of these environmental gradients, highlighting very similar B-EMf patterns across all of them. This common trend can be clearly seen when $R^2$ and $\beta$ estimates of the separate models are compared among stress classes, with $R^2$ becoming increasingly strong and $\beta$ shifting from negative to positive as stress increases (Fig. 2).

Along with focusing on B-EMf, the authors also investigated the effects of species richness on ecosystem functions related to C, N, and P individually. In repeating their analysis while accounting for environmental stress, we found the same pattern of increasing importance described for B-EMf in all three nutrient pools. While unsurprising for C and N (both of which covary strongly with M; $r > 0.93$), this is important to note for P (which is less correlated with M; $r < 0.55$). Although P availability was little affected by species richness in the authors’ initial analysis, a strongly significant relationship emerged once stress had been accounted for.

Collectively, our analyses revealed that the general positive B-EMf relationship in global drylands reported by Maestre et al. (2) masks strong and contrasting underlying patterns. By accounting for the effect of environmental stress on ecological interactions, we considerably improved model predictions and identified a consistent trend of shifting B-EMf patterns in relation to environmental stress. In conjunction with the original study, our results provide a strong basis for research aiming to disentangle large-scale B-EMf patterns in plant communities and highlight the value of considering both general relationships and their underlying variability. A better understanding of how biodiversity interacts to promote ecosystem functioning is crucial if areas of conservation priority are to be identified and attempts to mitigate the effects of global change are made. Our findings indicate that the effect of biodiversity loss on ecosystem multifunctionality might be particularly severe in harsh environments.

References and Notes

8. For each study plot, FetchClimate was used to extract the following environmental variables: near-surface air temperature, precipitation rate, soil moisture, near-surface air humidity, diurnal temperature range, near-surface wind speed, percent of maximum possible sunshine, and frost day frequency. Pearson product-moment correlation coefficients ($r$) were then used to identify strongly correlated variables ($r \geq 0.55$ to 0.89). Based on this, air temperature was excluded from further analysis, while component 1 of a PCA among soil moisture ($r = 0.91$), precipitation rate ($r = 0.87$), sunshine fraction ($r = -0.85$), and air humidity ($r = 0.68$) was included as measure of water availability. Therefore, the selected predictors were terrain slope and soil sand content [available in (2)], water availability, temperature range, frost days, and wind speed ($r < 0.55$).
9. We tested the sensitivity of our results to the criteria adopted for subdividing the data by repeating the analyses with different numbers of subsets (2, 3, 5, and 7 stress classes). In all cases, B-EMf patterns along environmental gradients were highly comparable.

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