

LETTER

Enhanced interannual precipitation variability increases plant functional diversity that in turn ameliorates negative impact on productivity

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Abstract

Although precipitation interannual variability is projected to increase due to climate change, effects of changes in precipitation variance have received considerably less attention than effects of changes in the mean state of climate. Interannual precipitation variability effects on functional diversity and its consequences for ecosystem functioning are assessed here using a 6-year rainfall manipulation experiment. Five precipitation treatments were switched annually resulting in increased levels of precipitation variability while maintaining average precipitation constant. Functional diversity showed a positive response to increased variability due to increased evenness. Dominant grasses decreased and rare plant functional types increased in abundance because grasses showed a hump-shaped response to precipitation with a maximum around modal precipitation, whereas rare species peaked at high precipitation values. Increased functional diversity ameliorated negative effects of precipitation variability on primary production. Rare species buffered the effect of precipitation variability on the variability in total productivity because their variance decreases with increasing precipitation variance.

Keywords

Arid zones, climate change, ecosystem functioning, functional diversity, grassland, interannual, precipitation variability, productivity, stability.

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INTRODUCTION

Climate change will result in increased precipitation variability due to higher water-holding capacity of a warmer atmosphere and changes in atmospheric circulation modes (Räisänen 2002; Fischer *et al.* 2013; IPCC 2013). Increase in precipitation variance will occur at intra-annual, interannual and decadal scales. Although the importance of extreme events is part of the public narrative and resulted in a special assessment from the Intergovernmental Panel on Climate Change on extreme events (IPCC 2012), impacts of climate variability in ecosystem structure and functioning have received much less attention than effects of changes in the mean state of climate. Most studies have focused on global warming, atmospheric CO₂ concentration and drought effects overlooking precipitation variability *per se* as a driver of community and ecosystem change. Scarce but interesting work demonstrates that precipitation variation plays an important role in community dynamics across grasslands (Hallett *et al.* 2013). Here, we aim at studying the effect of interannual precipitation coefficient of variation on plant functional diversity and its consequences for the functioning of a grassland ecosystem.

The role of precipitation variability in affecting biodiversity in water-limited ecosystems is particularly relevant to the predictions of global change models (Loik *et al.* 2004). Enhanced precipitation variability may impact species diversity and coexistence because of differential nonlinear response of plant species to precipitation (Chesson *et al.* 2004). In order for several plant species to co-exist in an environment where resource availability changes through time, different plant species must

exhibit a competitive advantage at different points in time (Tilman & Pacala 1993). Interannual precipitation variability determines the temporal heterogeneity of soil-water availability through sequences of wet and dry years. The temporal variance of a limiting resource such as soil water is likely to affect plant diversity (D'Odorico *et al.* 2008) that, in turn, impacts ecosystem processes (Loreau *et al.* 2001).

Plant functional types are groups of species that share morphological and physiological characteristics that result in similar responses to environmental conditions (Sala *et al.* 1997). The number of plant functional types represented in an ecosystem is a better predictor of the rate of ecosystem processes than the number of species (Tilman *et al.* 1997). Consequently, some studies have focused specifically on functional diversity as determinant of ecosystem productivity and stability (Díaz & Cabido 2001; Cadotte *et al.* 2011). Here, we investigate the effect of precipitation interannual coefficient of variation on functional diversity and its consequences for ecosystem functioning.

Mechanisms explaining the relationship between diversity and ecosystem functioning include deterministic processes, such as complementarity effect, and stochastic processes such as sampling effect (Loreau & Hector 2001). The complementarity effect is based on the idea that different plant species or functional types utilise resources differently so higher diversity leads to a more thorough exploitation of resources and higher productivity. The sampling effect states that higher diversity results in increased probability of including a species or functional type with the highest performance and therefore results in higher productivity (Sala 2001).

Plant diversity also affects ecosystem temporal stability (Tilman *et al.* 2006), which is calculated as the coefficient of variation of plant species abundance through time (Tilman 1996). Diverse ecosystems may exhibit high stability because they include species that resist disturbance and species that take advantage of favourable conditions. This is known as the 'portfolio effect' (Tilman 1996) stating that diversity buffers the effect of the resource availability variance through time. The stability of dominant plant functional types has been proposed as an alternative mechanism explaining ecosystem stability in communities where the contribution to ecosystem productivity is not evenly distributed among plant types (Hillebrand *et al.* 2008). The stability of the dominant plant functional type may largely determine overall ecosystem stability because it contributes the largest proportion of the biomass. Therefore, diversity changes due to increased inter-annual precipitation variance may impact ecosystem stability in different directions. If the portfolio effect is the dominant mechanism, increased diversity would result in relatively high stability in response to sequences of dry and wet years. If ecosystem stability is tightly associated with the stability of the dominant plant functional type, functional diversity would have no effect and ecosystem stability would follow the stability of the dominant plant type.

Three hypotheses guided our work:

(1) **Increased interannual precipitation variability increases functional diversity as a result of nonlinear responses of plant functional types to annual precipitation.** If this hypothesis holds true, some plant functional types outperform others at different points in time when their optimal environmental conditions prevail. Increased precipitation coefficient of variation implies a decrease in the frequency of modal precipitation

conditions and an increase in the frequency of extremely wet and dry years. Therefore, increased variability may benefit plant types that do best under both, rare wet or dry years, increasing their relative abundance and functional diversity.

(2) **Enhanced functional diversity resulting from high precipitation variability increases ecosystem productivity despite direct effects of precipitation.** Although precipitation variance may *per se* impact productivity, high functional diversity increases the probability of occurrence of species complementarity (Loreau & Hector 2001). Complementary use of resources leads to high resource-use efficiency and increased productivity.

(3) **Increased functional diversity due to high precipitation variability enhances ecosystem stability.** Increased diversity results in higher abundance of plant types capable of exploiting extreme years compensating negative responses of plant types best adapted to modal conditions.

In order to test these hypotheses, we experimentally manipulated interannual precipitation coefficient of variation applying sequences of wet and dry years for 6 years. Precipitation manipulations consisted of five levels of precipitation: -80% , -50% , ambient, $+50\%$ and $+80\%$ relative to ambient precipitation. We switched these treatments every year resulting in five levels of interannual precipitation coefficient of variation during a 6-year period while keeping mean precipitation virtually constant (Fig. 1). On 50 plots, we estimated plant cover, functional diversity and aboveground net primary production. Our experimental design aimed at exploring the sensitivity of plant functional diversity and ecosystem functioning to changes in precipitation variation instead of exploring specific climate-change scenarios (Sala *et al.* 2015). This approach will contribute to the understanding of responses to many projected changes in precipitation variability.

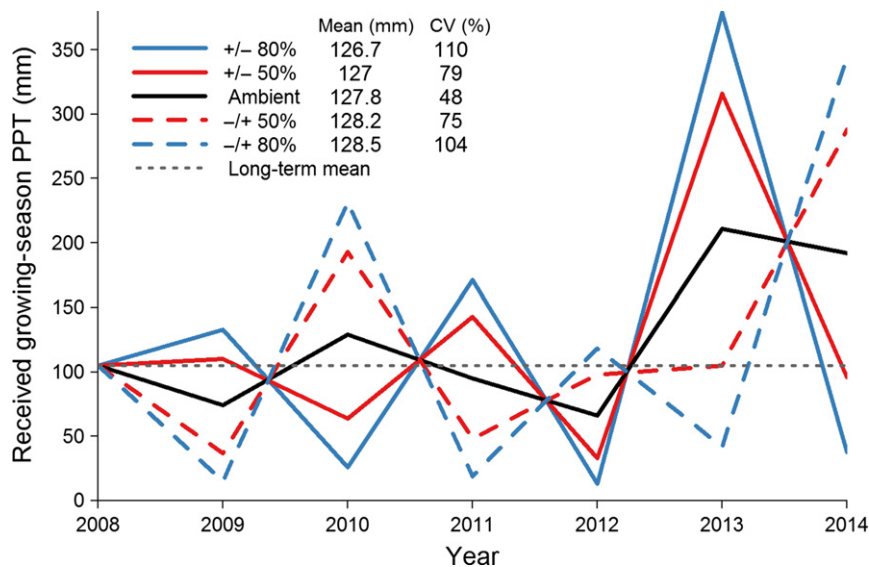


Figure 1 Growing-season precipitation per treatment, including five different levels of precipitation manipulation $+80\%$, $+50\%$, ambient, -50% and -80% all relative to ambient precipitation resulting in five levels of interannual precipitation coefficient of variation. Treatments were switched every year from wet to dry and dry to wet. Different colours indicate different treatments and solid lines indicate ambient growing-season precipitation and treatments starting from irrigation, and dashed lines indicate treatments starting from drought. The grey dashed line indicates the long-term mean growing-season precipitation for reference. Inset legend indicates mean and coefficient of variation for growing-season precipitation for each treatment received during the 6 years of the experiment.

METHODS

Site description

The experiment was carried out in New Mexico, USA, at the Jornada Basin Long Term Ecological Research site (32.5° N, 106.8° W, 1188 m.a.s.l.). A 100-year long climate record indicates a long-term mean growing-season precipitation of 105 mm with an average interannual coefficient of variation for a 6-year time window of 38% ranging from 18 to 67%. Specifically, our experimental site is located on desert grassland dominated by *Bouteloua eriopoda* (Torr.) with presence of *Prosopis glandulosa* Torr. Soils are coarse textured with a petrocalcic horizon varying in depth from 64 to 76 cm (Havstad & Schlesinger 2006).

Experimental design

In order to increase interannual precipitation variance without altering the average precipitation, we alternated annual rainfall interception and irrigation treatments for 6 years. In the first year, the experiment started with five levels of rainfall manipulations (ambient, +80%, +50%, -50% and -80% of ambient precipitation, Fig. 1). During the second year, plots that received water addition in the first year, received drought treatment of the same proportion, and plots that received drought during the first year, received water addition treatment of the same proportion during the second year (-50% plots were inverted to +50%, +50% to -50%, -80% to +80%, and +80% plots to -80%). Subsequent years received alternations of first and second year manipulations resulting in five different levels of interannual precipitation coefficient of variation and virtually constant mean precipitation across treatments (Fig. 1 inset table). These manipulations successfully modified soil-water content in the top 30 cm of the soil profile (Appendix 1, Fig. S1). We kept the number and timing of rainfall pulses similar to natural conditions and constant across treatments. The reasoning behind our design was isolating the effect of year-to-year precipitation variance from the effects of pulse number and timing studied elsewhere. With this design, we also kept constant among plots all other climatic factors. We used an automated rainfall manipulation system (ARMS) (Gherardi & Sala 2013) that consisted of rainout shelters (Yahdjian & Sala 2002) that collected either 50 or 80% of the incoming rainfall from exclusion plots and diverted it by means of a solar-powered pump to irrigation plots, control plots received ambient precipitation. We used 10 replicates totalling 50 plots of 2.5 × 2.5 m that were trenched down to 60 cm or to petrocalcic layer and lined with six mil PVC film to prevent lateral movement of water and roots in or out of the plots.

Response variables

Aboveground net primary production (ANPP)

We measured herbaceous species plant cover to 1 cm precision on three 2.5 m permanent cover lines per plot and two perpendicular diameters and height of shrubs every year at peak biomass. In order to avoid clipping effects in our multi-year experiment, we estimated ANPP utilising a non-destructive method that uses plant species cover and

shrub volume as proxies for ANPP (Flombaum & Sala 2007). We derived ANPP allometric equations for each plant functional type on site (Perennial Grass_{ANPP} = -13 + 506 × Cover, Annual Grass_{ANPP} = 0 + 138 × Cover, Forb_{ANPP} = -5 + 160 × Cover, Sub-Shrub_{ANPP} = 0 + 260 × Cover and Shrub_{ANPP} = 2 + 4e^{-0.5} × Volume; Appendix 1, Fig S2). We are confident of our ANPP estimation method because it matches long-term measurements done with a different method. For example, in 2009 the mean ANPP for our control plots was 104.8 g m⁻² year⁻¹ and ANPP for the IBP site (similar vegetation structure to our site) was 103.2 g m⁻² year⁻¹.

Plant functional diversity

We calculated diversity using species ANPP aggregated by plant functional type and analysed results using both Shannon's and Simpson's indices. We also estimated correspondent evenness for each index and plant functional type richness. We estimated the diversity indices using Hill numbers (Hill 1973):

$${}^qD = 1 / \sqrt[q-1]{\sum_{n=1}^S (p_i p_i^{q-1})}$$

where p_i is the proportion of each plant functional type ANPP, S represents the number of types and q is an index that gives more or less weight to rare and dominant species (Tuomisto 2010). We calculated diversity using $q = 1$ that after taking log (1D) equals Shannon's index (H'), and $q = 2$ that can be transformed into the Simpson's index ($1/{}^2D$) (Tuomisto 2012). Our ANPP estimation method is linearly related to cover (Fig. S2) allowing for direct comparisons with most published work that use cover data.

Ecosystem stability

We estimated stability as the temporal coefficient of variation of ANPP for each plot along the duration of the experiment. Although higher values mean less stability, this index is straightforward and has been traditionally used as a proxy of ecosystem stability (Tilman 1996).

Soil moisture

We measured soil moisture in the top 30 cm of the soil profile every 30 min in four replicates of each treatment using Campbell Scientific CS625 probes. Data were logged onto Campbell Scientific CR200× data loggers (Campbell Scientific, Logan, UT, USA) during 3 years of the experiment showing the success of our manipulations (Fig. S1).

Data use and statistical analyses

We tested 6-year interannual precipitation coefficient of variation effects on mean 6-year responses for total and plant functional type ANPP. Relative abundance changes were addressed on endpoint measurements. Annual ANPP results were used to test mechanisms related to nonlinear responses to growing-season precipitation. Six-year mean responses were used again to test indirect effects through structural equation modelling.

We used a combination of analyses ranging from simple linear regression (Appendix 1), to linear and nonlinear model selection through AIC criterion (Appendix 4), to structural equation models (Appendix 5). We performed all analyses and created all figures using R version 3.0.2 (R Core Team 2013). We ran packages: MASS (Venables & Ripley 2002), car (Fox *et al.* 2011), psych (Revelle 2013) and doBy (Højsgaard *et al.* 2011). For the structural equation modelling, we used the lavaan package (Yves 2012) and made structural equation model plots using semPlot package (Epskamp 2013).

We fit a structural equation model (Grace 2006) to specifically test for indirect effects of precipitation variance on ecosystem productivity. The model included 6-year precipitation coefficient of variation indirect effects on 6-year mean ecosystem productivity through 6-year mean functional diversity and dominant plant functional type productivity.

RESULTS

Six-year mean functional diversity increased as a function of the 6-year interannual precipitation coefficient of variation ($F_{1,48} = 9.35$, $P = 0.003$, Fig. 2a). This diversity pattern was driven by changes in 6-year mean functional evenness that also showed a positive response to precipitation coefficient of variation ($F_{1,48} = 12.65$, $P < 0.001$; Fig. 2b). On the other hand, plant functional type richness did not respond to precipitation coefficient of variation ($F_{1,48} = 2.861e^{-05}$, $P = 0.99$; Fig. 2c).

The increase in evenness resulted from decreased relative abundance of perennial grasses, the dominant plant functional type, and increased cover of all other plant functional types (Fig. 3). After 6 years, increased precipitation variance treatments showed a decrease in perennial grass abundance and an increase in the abundance of all other plant functional types (Fig. 3).

Annual ANPP of dominant and rare plant functional types showed contrasting nonlinear responses to growing-season precipitation (Fig. 4). Dominant species showed a significant hump-shape response with a peak around modal precipitation ($t_{47} = -19.43$, $P < 0.001$), while rare species showed an exponentially increasing response to precipitation ($t_{47} = 15.65$, $P < 0.001$). Both fits were tested against linear models through AIC criterion (Appendix 4). These contrasting responses evidenced a trade-off with rare species doing better under extremely wet conditions and dominant species doing better under modal site conditions.

Six-year interannual precipitation coefficient of variation had a negative effect on 6-year mean productivity of the dominant functional group, perennial grasses (Fig. 5; standardised coefficient = -0.64 , $Z_{\text{value}} = -5.94$, $P < 0.001$), that resulted in a negative effect on 6-year mean total ANPP (standardised coefficient = -0.67 , $Z_{\text{value}} = -5.39$, $P < 0.001$). On the other hand, precipitation variance had a positive effect on functional diversity (standardised coefficient = 0.45 , $Z_{\text{value}} = 3.61$, $P < 0.001$) that in turn enhanced ecosystem productivity as a result of a positive significant biodiversity effect that ameliorates the negative impact of precipitation variance on ANPP (standardised coefficient = 0.07 , $Z_{\text{value}} = 1.64$, $P < 0.1$). It is remarkable that the positive effect of precipitation variance

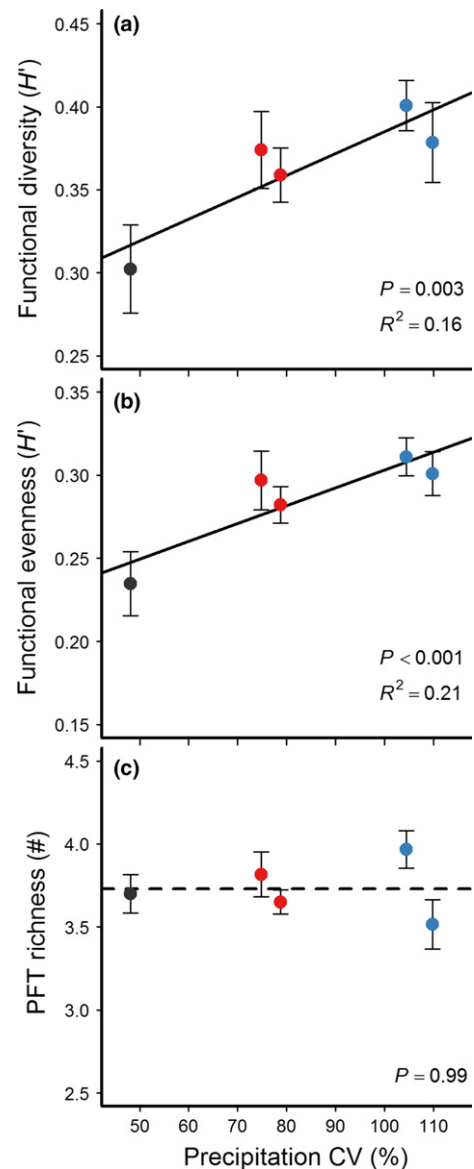


Figure 2 Effect of interannual precipitation coefficient of variation on functional diversity. Six-year mean response for: (a) functional diversity Shannon's index (H'), (b) functional evenness and (c) plant functional type richness to 6-year precipitation coefficient of variation. Points indicate mean values (\pm SE) for each treatment ($n = 10$). Black for ambient precipitation, red for 50% and blue for 80% precipitation manipulations.

through functional diversity ameliorated the negative impact of precipitation variance on productivity. However, the total net effect of precipitation variance on ANPP was negative (standardised coefficient = -0.6 , $Z_{\text{value}} = -5.75$, $P < 0.001$, Appendix 5).

Temporal coefficient of variation of total ANPP increased with 6-year precipitation coefficient of variation (Slope = 0.30 , $F_{1,48} = 10.79$, $P = 0.004$, $R^2 = 0.15$). Dominant and rare plant functional types responded in different directions to increased precipitation variance (Fig. 6). The dominant plant functional type, perennial grasses, showed a positive response (slope = 1.13 , $F_{1,48} = 31.58$, $P < 0.001$, $R^2 = 0.30$), increasing

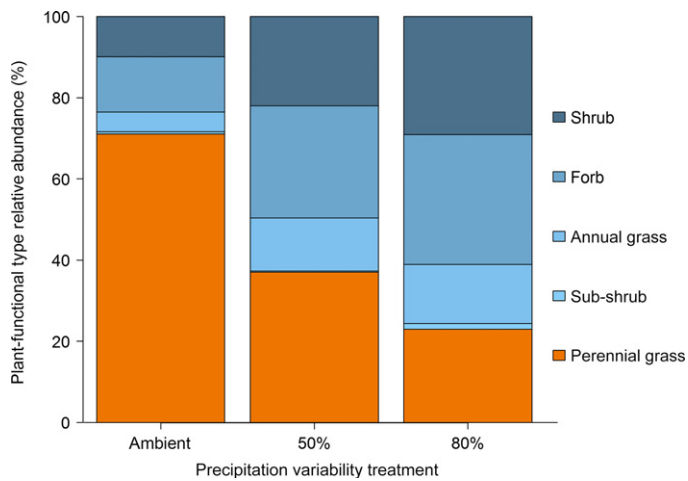


Figure 3 Plant functional type relative abundance. Mean functional-type relative abundance for the two last years of the experiment across precipitation variability treatments. Orange colour indicates dominant plant functional type (perennial grass) and blue colours indicate rare functional types (shrub, sub-shrub, annual grass and forb).

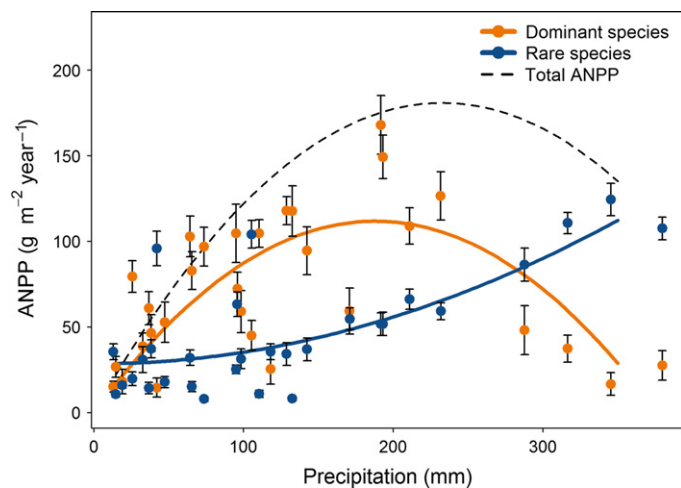


Figure 4 Productivity response to growing-season precipitation amount. Aboveground net primary production (ANPP) as a function of growing-season precipitation. Blue dots represent mean (\pm SE) and blue line best fit for rare species, and orange dots represent mean (\pm SE) and orange lines best fit for dominant species ($n = 10$). Dashed line corresponds to total ANPP for reference. Model fits selected through AIC criterion; see Appendix 4 for complete output.

ANPP variance with interannual precipitation variance. On the contrary, rare plant functional types showed either non-significant responses or surprisingly negative responses either maintaining their ANPP coefficient of variation or reducing it as precipitation variance increased. Shrub, sub-shrub and annual grass species showed slopes that were not significantly different from zero ($F_{1,48} = 1.5$, $P = 0.22$; $F_{1,48} = 0.39$, $P = 0.53$ and $F_{1,48} = 0.32$, $P = 0.57$ respectively); and forb species showed negative response (slope = -0.41 , $F_{1,48} = 4.25$, $P = 0.04$, $R^2 = 0.08$), where forb ANPP variability decreased as precipitation coefficient of variation increased.

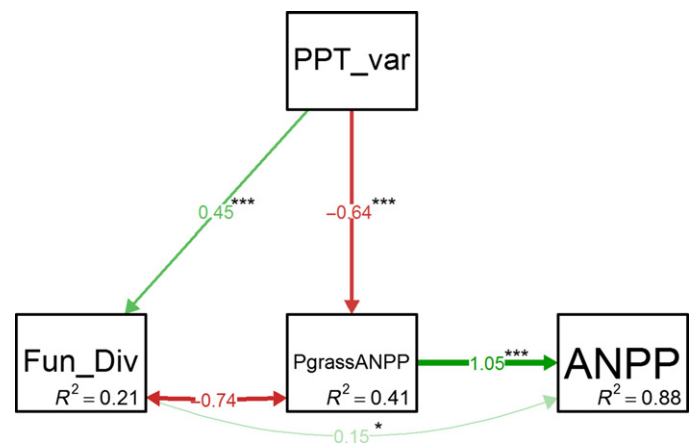


Figure 5 Structural equation model of precipitation variance effect on ANPP through functional diversity. The model includes the direct effect of 6-year interannual precipitation coefficient of variation on 6-year mean ecosystem productivity. Indirect effects of precipitation variation occur through 6-year mean functional diversity and perennial grass ANPP. Coefficients are standardised by the mean so they are comparable to each other. Green single-headed arrows mean positive effect and red single-headed arrows mean negative effects. Double headed arrows mean non-causal correlation. Indirect effects result from the multiplication of two consecutive direct effects. For detailed description of analysis and output see Appendix 5. Significance codes mean: * $P < 0.10$, ** $P < 0.05$ and *** $P < 0.001$. The model fit our data ($\chi^2 = 0.085$, d.f. = 1, $P = 0.77$), other goodness of fit measures also support this model (RMSE < 0.001 , $P = 0.78$; SRMR = 0.003, CFI = 1.000, TLI = 1.031).

DISCUSSION

Our long-term manipulative experiment provides substantial evidence to support our first hypothesis that increased precipitation variability increases diversity. As found by a previous study where within-season soil-moisture variance increased plant diversity (Knapp *et al.* 2002), increased interannual precipitation coefficient of variation had a positive effect on plant diversity (Fig. 2a). Changes in functional diversity resulted from changes in functional evenness that were in turn explained by the increase in the relative abundance of rare plant functional types in high precipitation variance treatments (Fig. 3). Evenness changes are usually the first step in anthropogenic transformation of grasslands and occur through changes in relative abundance. In a second stage, transformations occur through changes in species composition as a result of local extinctions followed by invasions (Reynolds *et al.* 2004).

Theoretical and empirical work support the idea that species coexistence requires important ecological differences among plant types that often involve tradeoffs (Chesson 2000) that result from nonlinear responses to a limiting resource (Hsu *et al.* 2012). In order to increase diversity, such tradeoffs must allow different plant functional types to be dominant at different points in time (Tilman & Pacala 1993). Increased interannual precipitation variance results from a decrease in the frequency of modal precipitation years and an increase in the frequency of extreme precipitation years. The hump-shape relationship between perennial grass ANPP and growing-sea-

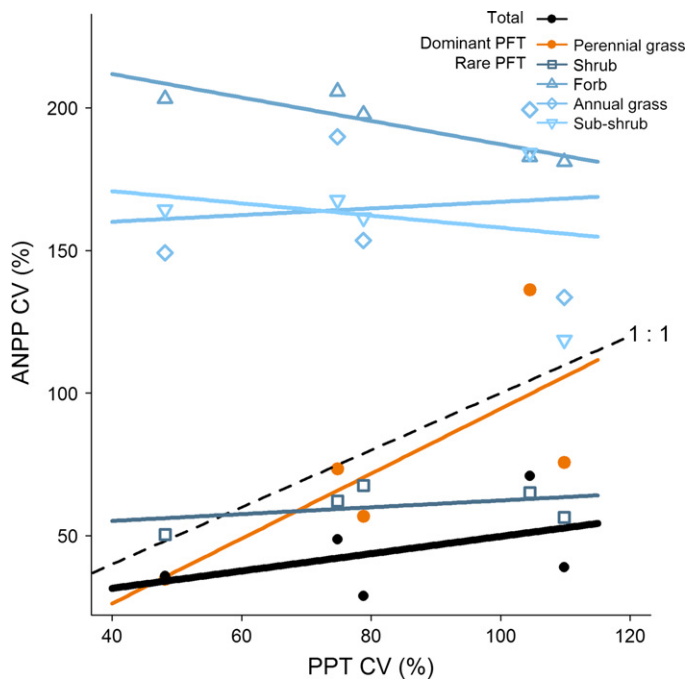


Figure 6 Productivity variation versus precipitation variation. ANPP coefficient of variation as a function of interannual precipitation coefficient of variation. Black solid line and black filled circles correspond to total ANPP (slope = 0.30, $F_{1,48} = 8.81$, $P = 0.004$, $R^2 = 0.15$). Orange-coloured filled circles and line correspond to the dominant plant type, perennial grasses (slope = 1.13, $F_{1,48} = 20.8$, $P < 0.001$, $R^2 = 0.3$). Blue gradient-coloured empty symbols and lines correspond to rare plant types: squares for shrub species ($F_{1,48} = 1.5$, $P = 0.22$), upward triangles for forb species (Slope = -0.41 , $F_{1,48} = 4.25$, $P = 0.04$, $R^2 = 0.08$), diamonds for annual grass species ($F_{1,48} = 0.33$, $P = 0.57$) and downward triangles for sub-shrub species ($F_{1,48} = 0.39$, $P = 0.54$). The black dashed line indicates the one to one ratio for reference.

son precipitation explains the negative response of this dominant plant type to increased precipitation variance (Fig. 4). This unimodal relationship is modulated by biophysical interactions (Munson *et al.* 2015) and can be explained by the interaction between the water distribution in the soil in dry vs. wet years and the shallow root distribution of grass roots. In arid ecosystems, wet years are caused by a small number of very large precipitation events that penetrate deep into the soil profile (Sala *et al.* 1992; Knapp *et al.* 2015). Therefore, most of the water resulting from this rare large events is not accessible by the relatively shallow root system of grasses that are still water limited during interpulse periods (Sala *et al.* 2015). Under increased interannual precipitation variability, wet years follow dry years that diminish grass abundance and decrease their capacity to respond to large rain pulses accentuating this phenomenon. On the other hand, rare plant functional types are exploiters of extreme years by growing rapidly under favourable conditions and resisting dry years (Fig. 4). We suggest that the decline in grass production in wet years results from the competitive effect of rare plant functional types that outperform grasses under these conditions. Rare plant functional types include four plant types that encompass a relatively large set of functional traits (Adler *et al.* 2014) ranging from deep-rooted shrubs that tolerate drought to fast

growing annual grasses and forbs that take advantage of wet years. Therefore, tradeoffs in responses to water availability seem to be the mechanism behind the functional diversity response to increased interannual precipitation variability.

Our results supported our second hypothesis showing that increased interannual precipitation variability resulted in increased diversity, which in turn ameliorated the negative impact of enhanced precipitation coefficient of variation on ecosystem ANPP (Fig. 5). This positive biodiversity effect on ecosystem functioning may be explained through species complementarity (Huston *et al.* 2000; Loreau & Hector 2001). Our data show temporal complementarity among plant functional types with rare plant types taking advantage of extreme years and dominant species outperforming other plant types during years with modal conditions. Other forms of complementarity may co-occur as different plant types may utilise water from different soil layers (Sala *et al.* 1989) or uptake different nitrogen species (Gherardi *et al.* 2013). As previously hypothesised by theoretical developments (Tilman & Pacala 1993; Chesson 2000) and supported by scarce empirical evidence (Knapp *et al.* 2002), we argue that temporal variability in resource availability is important in determining plant diversity and ecosystem functioning.

Our results did support our third hypothesis showing that increased functional diversity enhances ecosystem stability (Tilman *et al.* 2006). Although ecosystem ANPP coefficient of variation showed a trend in the same direction as that of dominant species, the coefficient of variation of total ANPP increased at one-half the rate of perennial grass coefficient of variation as precipitation variance increased (Fig. 6). Therefore, the response of the dominant plant functional type was not fully driving ecosystem stability. On the other hand, the ANPP coefficient of variation in one rare plant functional type decreased and the other three rare plant types did not change with increasing precipitation coefficient of variation up to values that doubled the historical mean. The diverse plant community of this grassland site led to a portfolio effect determining the coefficient of variation of total ANPP to be much lower than expected based on the dominant functional-type response.

The magnitude of the applied experimental treatments matches treatments of model simulations (Sala *et al.* 2015) that resulted in reduction of extreme precipitation return periods ranging from within to slightly above those projected by the IPCC special report on extreme events for the next century (IPCC 2012). Our objective was not to simulate a specific scenario at one point in time but to assess diversity and productivity sensitivity to enhanced climate variability. Our improved understanding of sensitivity can be coupled with predictions of future precipitation variability to assess the impact of this understudied dimension of climate change.

Although 6 years is a relatively long duration for a manipulative experiment, it does not reflect the effect of directional climate change at the centennial scale. Continued exposure to elevated precipitation variability conditions may cause the ecosystem to transition into a novel state dominated by what were originally rare plant types. This novel ecosystem may result in increased erosion (Schlesinger *et al.* 1990) and decrease productivity affecting the ecosystem services provided

to society (Anadón *et al.* 2014). Alternatively, the ecosystem may reach a plateau at current community composition without major changes in physiognomy. Our results, based on this 6-year experiment and current theory do not allow us to predict the effect of enhanced precipitation at the scale of decades to centuries.

Increased precipitation coefficient of variation resulted in increased diversity that ameliorated the impact of expected precipitation change on ecosystem functioning. If climate change in the American Southwest brings both drought and increased precipitation variability (Seager *et al.* 2007), then one effect of climate change partially offsets the other. However, the variability effect is constrained by the biodiversity pool that may be affected by other global change drivers. In general land-use change affects biodiversity (Newbold *et al.* 2015); and in grasslands specifically, overgrazing reduces biodiversity (Milchunas *et al.* 1988). This reduction of biodiversity may constrain the positive effect of precipitation variability and enhance the negative impact of climate change. Our results represent a concrete example of the recent proposal that avoiding ecosystem degradation may buffer the impact of climate change (Scheffer *et al.* 2015).

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AUTHOR CONTRIBUTIONS

L.A.G. and O.E.S. conceived and designed the experiment, L.A.G. carried out the experiment, L.A.G. and O.E.S. analysed the data and wrote the paper.

REFERENCES

- Adler, P.B., Salguero-Gómez, R., Compagnoni, A., Hsu, J.S., Ray-Mukherjee, J., Mbeau-Ache, C. *et al.* (2014). Functional traits explain variation in plant life history strategies. *Proc. Natl Acad. Sci.*, 111, 740–745.
- Anadón, J.D., Sala, O.E., Turner, B.L. & Bennett, E.M. (2014). Effect of woody-plant encroachment on livestock production in North and South America. *Proc. Natl Acad. Sci.*, 111, 12948–12953.
- Cadotte, M.W., Carscadden, K. & Mirotnick, N. (2011). Beyond species: functional diversity and the maintenance of ecological processes and services. *J. Appl. Ecol.*, 48, 1079–1087.
- Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.*, 31, 343–366.
- Chesson, P., Gebauer, R.L.E., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.S.K. *et al.* (2004). Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia*, 141, 236–253.
- R Core Team (2013). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing Vienna, Austria.
- Díaz, S. & Cabido, M. (2001). Vive la difference: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.*, 16, 646–655.
- D'Odorico, P., Laio, F., Ridolfi, L. & Lerdau, M.T. (2008). Biodiversity enhancement induced by environmental noise. *J. Theor. Biol.*, 255, 332–337.
- Epskamp, S. (2013). semPlot: path diagrams and visual analysis of various SEM packages' output. *R package*.
- Fischer, E.M., Beyerle, U. & Knutti, R. (2013). Robust spatially aggregated projections of climate extremes. *Nature Clim. Change*, 3, 1033–1038.
- Flombaum, P. & Sala, O.E. (2007). A non-destructive and rapid method to estimate biomass and aboveground net primary production in arid environments. *J. Arid Environ.*, 69, 352–358.
- Fox, J., Bates, D., Firth, D., Friendly, M., Gorjanc, G., Graves, S. *et al.* (2009). CAR: Companion to applied regression, R Package version 1.2-16. Online at <http://cran.r-project.org/web/packages/car/index.html> (accessed on August 2012).
- Gherardi, L.A. & Sala, O.E. (2013). Automated rainfall manipulation system: a reliable and inexpensive tool for ecologists. *Ecosphere*, 4, art18.
- Gherardi, L., Sala, O. & Yahdjian, L. (2013). Preference for different inorganic nitrogen forms among plant functional types and species of the Patagonian steppe. *Oecologia*, 173, 1075–1081.
- Grace, J. (2006). *Structural Equation Modeling and Natural Systems*. Cambridge University Press, New York, p. 378.
- Hallett, L.M., Hsu, J.S., Cleland, E.E., Collins, S.L., Dickson, T.L., Farrer, E.C. *et al.* (2013). Biotic mechanisms of community stability shift along a precipitation gradient. *Ecology*, 95, 1693–1700.
- Havstad, K.M. & Schlesinger, W.H. (2006). Introduction. In: *Structure and Function of a Chihuahuan Desert Ecosystem* (eds Havstad, K.M., Schlesinger, W.H., Huenneke, L.F.). Oxford University Press, Oxford, UK, pp. 3–15.
- Hill, M.O. (1973). Diversity and evenness: a unifying notation and its consequences. *Ecology*, 54, 427–432.
- Hillebrand, H., Bennett, D.M. & Cadotte, M.W. (2008). Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology*, 89, 1510–1520.
- Højsgaard, S., Halekoh, U., Robison-Cox, J., Wright, K. & Leidi, A. (2011). doBy: groupwise summary statistics, general linear contrasts, LSMEANS (least-squares-means), and other utilities. *R package version*, 4.
- Hsu, J.S., Powell, J. & Adler, P.B. (2012). Sensitivity of mean annual primary production to precipitation. *Global Change Biol.*, 18, 2246–2255.
- Huston, M.A., Aarssen, L.W., Austin, M.P., Cade, B.S., Fridley, J.D., Garnier, E. *et al.* (2000). No consistent effect of plant diversity on productivity. *Science*, 289, 1255.
- IPCC (2012). *Managing the Risks of Extreme Events Disasters to Advance Climate Change Adaptation*. A Special Report of working groups I and II of the Intergovernmental Panel on Climate Change (eds Field, C.B., Barros, V., Stocker, T.F., Qin, D., Dokken, D. & Ebi, K.L. *et al.*). Cambridge University Press, Cambridge, UK and New York, NY, p. 582.
- IPCC (2013). *Climate Change 2013: The Physical Science Basis*. Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change (eds Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K. & Boschung, J. *et al.*) Cambridge University Press, Cambridge, UK and New York, NY, p. 1535.
- Knapp, A.K., Fay, P.A., Blair, J.M., Collins, S.L., Smith, M.D., Carlisle, J.D. *et al.* (2002). Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science*, 298, 2202–2205.
- Knapp, A.K., Hoover, D.L., Wilcox, K.R., Avolio, M.L., Koerner, S.E., La Pierre, K.J. *et al.* (2015). Characterizing differences in precipitation regimes of extreme wet and dry years: implications for climate change experiments. *Global Change Biol.*, 21, 2624–2633.
- Loik, M., Breshears, D., Lauenroth, W. & Belnap, J. (2004). A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. *Oecologia*, 141, 269–281.

- Loreau, M. & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412, 72–76.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A. *et al.* (2001). Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, 294, 804–808.
- Milchunas, D.G., Sala, O.E. & Lauenroth, W.K. (1988). A generalized model of the effects of grazing by large herbivores on grassland community structure. *Am. Nat.*, 132, 87–106.
- Munson, S.M., Webb, R.H., Housman, D.C., Veblen, K.E., Nussner, K.E., Beever, E.A. *et al.* (2015). Long-term plant responses to climate are moderated by biophysical attributes in a North American desert. *J. Ecol.*, 103, 657–668.
- Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A. *et al.* (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, 520, 45–50.
- Räsänen, J. (2002). CO₂-Induced changes in interannual temperature and precipitation variability in 19 CMIP2 experiments. *J. Clim.*, 15, 2395–2411.
- Revelle, W. (2013). *psych: Procedures for Personality and Psychological Research*. Northwestern University, Evanston. *R package version*, 1.
- Reynolds, J.F., Kemp, P.R., Ogle, K. & Fernández, R.J. (2004). Modifying the ‘pulse–reserve’ paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia*, 141, 194–210.
- Sala, O.E. (2001). Price put on biodiversity. *Nature*, 412, 34–36.
- Sala, O., Golluscio, R., Lauenroth, W. & Soriano, A. (1989). Resource partitioning between shrubs and grasses in the Patagonian steppe. *Oecologia*, 81, 501–505.
- Sala, O.E., Lauenroth, W.K. & Parton, W.J. (1992). Long term soil water dynamics in the shortgrass steppe. *Ecology*, 73, 1175–1181.
- Sala, O.E., Lauenroth, W.K. & Golluscio, R.A. (1997). Plant functional types in temperate semi-arid regions. In: *Plant functional types. Their relevance to ecosystem properties and global change* (eds Smith, TM, Shugart, HH & Woodward, FI). Cambridge University Press, pp. 217–233.
- Sala, O., Gherardi, L. & Peters, D.C. (2015). Enhanced precipitation variability effects on water losses and ecosystem functioning: differential response of arid and mesic regions. *Clim. Change.*, 131, 213–227.
- Scheffer, M., Barrett, S., Carpenter, S.R., Folke, C., Green, A.J., Holmgren, M. *et al.* (2015). Creating a safe operating space for iconic ecosystems. *Science*, 347, 1317–1319.
- Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A. *et al.* (1990). Biological feedbacks in global desertification. *Science*, 247, 1043–1048.
- Seager, R., Ting, M.F., Held, I., Kushnir, Y., Lu, J., Vecchi, G. *et al.* (2007). Model projections of an imminent transition to a more arid climate in southwestern North America. *Science*, 316, 1181–1184.
- Tilman, D. (1996). Biodiversity: population versus ecosystem stability. *Ecology*, 77, 350–363.
- Tilman, D. & Pacala, S. (1993). The maintenance of species richness in plant communities. In: *Species Diversity in Ecological Communities* (eds Ricklefs, R.E. & Schluter, D.). University of Chicago Press, Chicago, pp. 13–25.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997). The influence of functional diversity and composition on ecosystem processes. *Science*, 277, 1300–1302.
- Tilman, D., Reich, P.B. & Knops, J.M.H. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, 441, 629–632.
- Tuomisto, H. (2010). A consistent terminology for quantifying species diversity? Yes, it does exist. *Oecologia*, 164, 853–860.
- Tuomisto, H. (2012). An updated consumer’s guide to evenness and related indices. *Oikos*, 121, 1203–1218.
- Venables, W.N. & Ripley, B.D. (2002). *Modern Applied Statistics with S*, 4th edn. Springer, New York, NY, pp. 1–501.
- Yahdjian, L. & Sala, O.E. (2002). A rainout shelter design for intercepting different amounts of rainfall. *Oecologia*, 133, 95–101.
- Yves, R. (2012). lavaan: an R package for structural equation modeling. *J. Stat. Softw.*, 48, 1–36.

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