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# Quantifying drylands' drought resistance and recovery: The importance of drought intensity, dominant life history and grazing regime

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Abbreviations: (A)NPP – (Aboveground) net primary production, MAP – Mean annual precipitation

## Abstract

Projected global change will increase the level of land-use and environmental stressors such as drought and grazing, particularly in drylands. Still, combined effects of drought and grazing on plant production are poorly understood, thus hampering adequate projections and development of mitigation strategies. We used a large, cross-continental database consisting of 174 long-term datasets from >30 dryland regions to quantify ecosystem responses to drought and grazing with the ultimate goal to increase functional understanding in these responses. Two key aspects of ecosystem stability, resistance to and recovery after a drought, were evaluated based on standardized and normalized aboveground net primary production (ANPP) data. Drought intensity was quantified using the standardized precipitation index. We tested effects of drought intensity, grazing regime (grazed, ungrazed), biome (grassland, shrubland, savanna) or dominant life history (annual, perennial) of the herbaceous layer to assess the relative importance of these factors for ecosystem stability, and to identify predictable relationships between drought intensity and ecosystem resistance and recovery. We found that both components of ecosystem stability were better explained by dominant herbaceous life history than by biome. Increasing drought intensity (quasi-) linearly reduced ecosystem resistance. Even though annual and perennial systems showed the same response rate to increasing drought intensity, they differed in their general magnitude of resistance, with annual systems being ca. 27% less resistant. In contrast, systems with an herbaceous layer dominated by annuals had substantially higher post-drought recovery, particularly when grazed. Combined effects of drought and grazing were not merely additive but modulated by dominant life history of the herbaceous layer. To the best of our knowledge, our study established the first predictive, cross-continental model between drought intensity and drought-related relative losses in ANPP, and suggests that systems with an

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herbaceous layer dominated by annuals are more prone to ecosystem degradation under future global change regimes.

## Introduction

In today's ecological research, discerning the mechanisms behind, and the quantification of ecosystem responses to global environmental change is a central theme (Reed *et al.*, 2012).

Nevertheless, although 41% of Earth's terrestrial landmass is covered by drylands (MEA, 2005), our understanding of how the structure and functioning of these ecosystems will respond to changing climate and land-use is still surprisingly poor (Maestre *et al.*, 2012, Reynolds *et al.*, 2007).

Drylands, comprising arid, semi-arid and dry subhumid ecosystems, are characterized by water-deficiency during prolonged periods throughout the year (Asner & Heidebrecht, 2005). In these ecosystems, plant growth is mainly limited by low and variable precipitation (Ruppert *et al.*, 2012, Zhao & Running, 2010), which constrains human activities mainly to livestock production. Thus, livelihood security in drylands relies heavily on the provision of ecosystems services from vegetation (Martin *et al.*, in print). These are often estimated by aboveground net primary production (ANPP), a core ecological currency and one of the best documented quantitative estimates for forage provision (Scurlock *et al.*, 2002).

Projected climate change for dryland environments predict most of these regions to face even increased variability in precipitation as well as increased frequency of extreme events, such as floods or drought (IPCC, 2013). Simultaneously, large dryland areas are facing significant population growth (MEA, 2005), leading to increased demand for ecosystem services from vegetation, which itself might negatively feedback on vegetation state, available standing plant biomass as well as production, i.e. degradation (Reynolds *et al.*, 2007).

Although there is ample evidence that terrestrial ecosystems can vary dramatically in their responses to drought (Cherwin & Knapp, 2012, Knapp *et al.*, 2008, Tielbörger *et al.*, 2014) and grazing (Díaz *et al.*, 2007), their combined effects on ecosystems' structure and functioning are

still poorly understood. In particular, very few studies have considered both effects simultaneously (Koerner & Collins, 2014, Zwicke *et al.*, 2013). Furthermore, conceptual and simulation models predict that synergistic interactions between drought and grazing may accelerate the above mentioned degradation processes (Lohmann *et al.*, 2012) and reduce drylands' ability to buffer climatic variability (Martin *et al.*, 2014).

In this context, an ecosystems' ability to retain a healthy and productive state – irrespective of changes in climate or land-use – is of major interest for all agents engaged in the assessment and mitigation of global change (land owners, decision makers, and scientists). This ability is usually called ecosystem stability (Donohue *et al.*, 2013, Pimm, 1984).

Various approaches exist to define and estimate ecosystem stability (Donohue *et al.*, 2013) and its constituents. In this study we focus on two aspects of stability: resistance, that is a system's ability to withstand disturbance (Pimm, 1984), and recovery, that is a system's potential to (or rate of) return to a previous state after a disturbance.

For mesic grasslands, results from experimental studies (Koerner & Collins, 2014, Vogel *et al.*, 2012, Zwicke *et al.*, 2013) suggest that effects of combined drought and management disturbances on recovery and resistance act non-additive. Drought intensity and duration play a crucial role here (Zwicke *et al.*, 2013). Underlying response mechanisms seem to be closely related to functional diversity (Craine *et al.*, 2013, Vogel *et al.*, 2012) and to species' life history and resource allocation (MacGillivray *et al.*, 1995).

Apart from mesic grasslands, our understanding of ecosystems' response to joint effects of drought and grazing is still very restricted. Those limited results we have for drylands suggest that combined effects of drought and grazing disturbances on ecosystem performance are complex, and (as for mesic grasslands) not merely additive (Carlyle *et al.*, 2014). Furthermore, they generally support the crucial role of plant diversity and plant life history (Bai *et al.*, 2004,

Frank & McNaughton, 1991, Miede *et al.*, 2010). However, findings in drylands were mostly obtained for single sites or even individual plants, and we do not know if they also hold for higher levels of aggregation. More importantly, due to vastly varying methodology and spatiotemporal constraints, past findings lack the potential to be easily upscaled and/or to be quantitatively compared across ecosystems or biomes (Reyer *et al.*, 2012).

Generally, there are two options to tackle these problems. The first being '*coordinated distributed experiments*' (CDE; Fraser *et al.*, 2013). CDE initiatives define standardized protocols and common metrics, thus making results from all collaborators highly comparable. However, while considerable efforts are made in setting up drought-related CDEs (e.g. [www.drought-net.org](http://www.drought-net.org), M. Smith pers. comm.) and to combine them with grazing manipulations, it will take some 5-10 years to obtain first reliable results – especially for highly variable dryland ecosystems. The alternative to CDEs are data-fusion or meta-analytical studies, which process and analyze available data.

Here we follow the latter approach and quantify how drought and grazing affect ecosystem stability (resistance and recovery) across dryland sites and biomes, while also utilizing fundamental ideas of CDEs. To accomplish this, we did not merely compile results qualitatively as done in many meta-analyses (Hillebrand & Cardinale, 2010), but established common metrics for quantifying ecosystem responses to drought and grazing.

Our approach is innovative in several aspects. First, we compiled a global dataset on long-term ANPP monitoring studies from drylands to harness the potential of these scattered datasets.

Long-term datasets were selected as they offer the highest probability to observe relatively rare climatic conditions (e.g. extreme to exceptional drought events). Second, we used an ecologically sound definition of drought and its intensity across all relevant climates. Third, to assess drought response, we selected two key aspects of ecosystem stability and operationalized them with

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respect to drought and vegetation metrics: ecosystem resistance (*in-drought* vs. *normal* ANPP) and recovery (*pre-* vs. *post-drought* ANPP). Finally, and to address recent concerns that stability components may not be independent (Donohue *et al.*, 2013), we analyzed these two stability components separately and evaluated potential correlations among them.

With this approach, we aimed to advance the understanding of dryland ecosystem responses to drought and grazing above the level of anecdotal field studies by synthesizing and standardizing available data. Particularly, we addressed the following questions:

- (1) What are the response patterns of drylands' resistance and recovery to drought intensity, grazing regime and vegetation characteristics (biome, dominant life history)?
- (2) What is the relative importance of these factors for ecosystem resistance and recovery?
- (3) Are effects of drought and grazing disturbance additive or interactive?
- (4) Can we identify predictable relationships between the severity of drought events and ecosystem stability? Are there dependencies between the two stability components?
- (5) What are implications for dryland ecosystems in the light of climate change?

## Materials and methods

### Database

The large spatial extent and the high demand for livelihood security in drylands have led to numerous studies addressing effects of various abiotic and biotic drivers on primary production. Taking advantage of this large body of literature and data, we assembled a global database of long-term studies (>5 years consecutive observations), comprising more than 320 datasets derived from about 50 dryland regions and study sites and totaling over 4400 years of observations. At study sites where more than one dataset was available, data were averaged if sites were in close proximity (<5 km), but only if they did not differ in habitat (as defined by soil and topography) or treatment (e.g. varying grazing intensities). Methods of data acquisition are described in Ruppert *et al.* (2012; Supporting Information 1).

For this study, we restricted our selection to near-natural and semi-natural vegetation, and excluded sown, fertilized, and (intentionally or unintentionally) burned sites or observation years. The latter steps were necessary, as fire affects herbaceous vegetation in specific ways (Snyman, 2006, Zimmermann *et al.*, 2010), potentially confounding effects of drought and grazing. In sum, 174 long-term datasets were included that derived from 34 dryland regions (Figure 1). The final dataset contained >3100 observation years, representing all major dryland biomes, i.e. savannas (n = 81 datasets), shrublands (n = 22), and grasslands (n= 71; see Ruppert *et al.*, 2012 for the definitions of biomes). Mean dataset length was 17.9 years, and mean annual precipitation (MAP) ranged from 183 to 838 mm a<sup>-1</sup> across sites (see Supporting Information 1).

To assess relationships between ecosystem properties, drought intensity, and ecosystem stability, we assembled data on (i) ANPP, (ii) precipitation of the hydrological year, (iii) dominant life history of the herbaceous layer (annual or perennial), and (iv) grazing regime (ungrazed or



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grazed). Dominance of herbaceous life histories was determined upon species' contribution to total biomass (>50%); where this information was unavailable, their contribution to vegetation cover was used as proxy. Sites where grazing was only deferred for certain periods of a year were considered as 'grazed'. Consequently, 'ungrazed' refers to prolonged grazing exclusions.

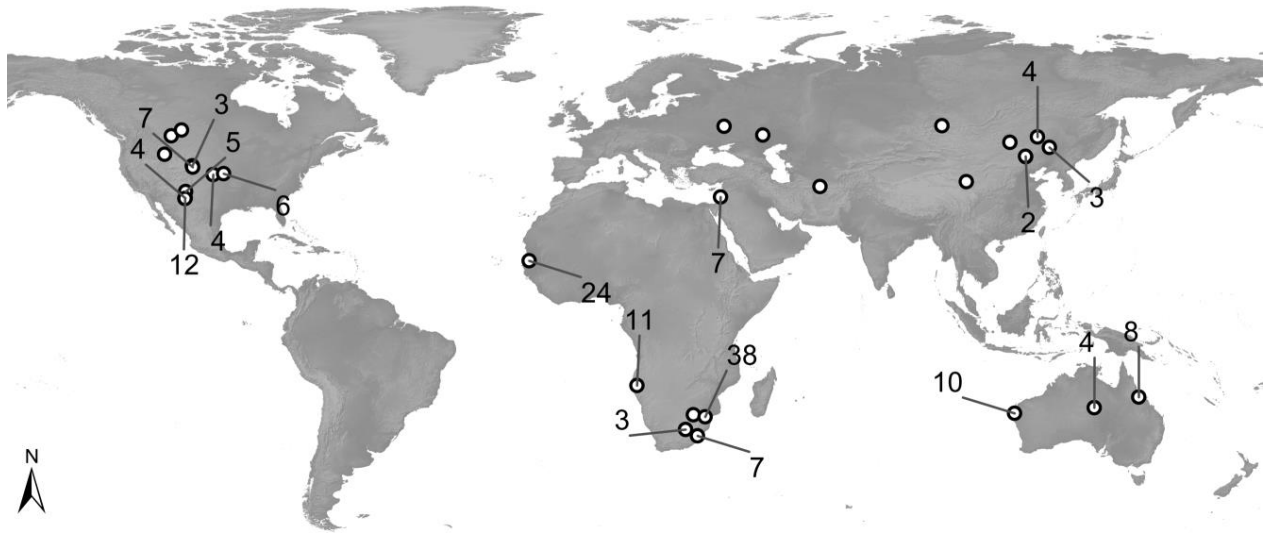


Figure 1: Distribution of the dryland sites used in the study. In total, 174 datasets derived from 35 regions were available for this study. Points indicate locations, numbers refer to datasets at a certain locations if >1.

### Data standardization procedures

*Primary production.* We standardized ANPP as 'peak standing crop'. If ANPP data were not available in this form, we recalculated ANPP either from original biomass data or via conversion rates (Ruppert & Linstädter, 2014; see also Supporting Information 1). For the savanna biome, all datasets only provided data on the grass layer. Thus total ANPP for this biome is underestimated by ca. 30% (Le Houérou, 1989). For grasslands and shrublands, total biomass is included in ANPP estimates.

*Drought intensity.* To compare drought responses across dryland sites, we quantified drought intensity via the standardized precipitation index (SPI; McKee *et al.*, 1993), a well-supported precipitation index in ecology (Vicente-Serrano *et al.*, 2012). We calculated SPI values based on

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annual precipitation sums representing sites' hydrological year. SPI values were assigned to drought intensity classes ('SPI classes') according to the classification of the US National Drought Mitigation Center (<http://droughtmonitor.unl.edu/>), adding the class of 'normal precipitation' (SPI class 0, with SPI values  $\leq 0.5$ ). Further details on the SPI are given in Supporting Information 1.

*Resistance and recovery.* To quantitatively compare ecosystem stability across sites and with respect to drought intensity, a main challenge was to operationalize the generic definitions of resistance and recovery (see Supporting Information 1). For recovery, we adopted definitions from field and experimental studies (in these often interchangeably called 'resilience'; Bai *et al.*, 2004, Tilman & Downing, 1994, Vogel *et al.*, 2012), and defined it as the quotient between pre- and post-drought ANPP for a given site and drought event, expressed as percentage. Values above 100% represent increases in post-drought years as compared to pre-drought; values below 100% represent decreases. To avoid potentially confounding effects of variable pre- and post-drought conditions, we only selected drought events where pre- and post-drought years received normal (= average) precipitation (SPI class 0, see above).

Resistance definitions from the same sources were not suitable for a quantitative comparison, as they usually related in-drought to pre-drought ANPP, irrespective of the precipitation in pre-drought years. We thus defined resistance as the percentage deviation in ANPP of a certain year from a site's 'normal' (benchmark) ANPP, which is the mean ANPP in the second year of two consecutive years receiving 'normal' precipitation (SPI class 0). This standardization was chosen to avoid potentially confounding effects of previous year's rainfall on ANPP (Ruppert *et al.*, 2012, Sala *et al.*, 2012, Wiegand *et al.*, 2004). Negative percentages for resistance represent reductions in ANPP; positive values represent increases. More extreme values represent relatively low or high resistance, respectively.

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For resistance, 167 datasets allowed the estimation of a benchmark ANPP; their ~2000 observation years included 775 drought events. In the case of recovery, the strict criteria for the selection of triplets or even quadruplets (for two-year droughts) reduced usable data to 118 drought events (24 two-year, and 94 single-year droughts).

### Data analysis

To quantify drylands' drought resistance and recovery, we established a series of mixed-effect models. For the response variable 'resistance' we established full-factorial models using the fixed-effect terms 'drought intensity' (SPI class -1 to -5; Table 1), 'grazing regime' (grazed, ungrazed), and 'biome' (grassland, shrubland, savanna) or 'dominant life history' of the herbaceous layer (annual, perennial) to account for potential differences in resistance across grazing regimes and vegetation types, as well as all combinations. Note that 'biome' and 'dominant life history' could not be assessed simultaneously as they were collinear. Instead two contrasting models were established, differing in the inclusion of either of these terms. Furthermore, 'study site' was included as random (intercept) term to account for potential site-specific differences and to counter potential bias towards studies that provided more than one dataset.

Table 1: Classification scheme of drought intensity used in this study, adapted from the classification used by the National Drought Mitigation Center of the USA (<http://droughtmonitor.unl.edu>). In our study, SPI (Standardized Precipitation Index) of hydrological years was calculated to estimate annual drought intensity of all observation years.

SPI class	Description	Impacts on rangeland production	SPI range
0	Normal	-	$+0.5 \leq \text{SPI} \leq -0.5$
-1	Abnormally Dry	Slowing growth of vegetation	$-0.5 < \text{SPI} > -0.8$
-2	Moderate Drought	Some damage to vegetation	$-0.8 \leq \text{SPI} > -1.3$
-3	Severe Drought	Production losses likely	$-1.3 \leq \text{SPI} > -1.6$
-4	Extreme Drought	Major production losses	$-1.6 \leq \text{SPI} > -2.0$
-5	Exceptional Drought	Exceptional and widespread production losses	$-2.0 \leq \text{SPI}$

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For recovery, we tested the same fixed and random terms except 'drought intensity', as this would have reduced the case numbers in some subgroups to  $n < 5$  (see Supporting Information 4). Instead, recovery values were lumped across observations for real drought conditions (SPI class  $\leq -2$ ). We initially established two competing full-factorial models for the response in each stability component, with either 'biome' or 'dominant life history' included. Subsequently, models were subject to a (log-)likelihood-based model selection procedure (Zuur, 2009), eliminating insignificant effect or interaction-terms.

To quantify the relative importance and explanatory power of the fixed predictors 'biome' and 'dominant life history' for resistance and recovery, respectively, the final models were evaluated based on their respective explained variance ( $R^2$ ) and AIC/BIC values (critical values:  $\Delta R^2 > 5\%$ ;  $\Delta AIC > 2$ ;  $\Delta BIC > 2$ ). Following the principle of parsimony (Crawley, 2002), we selected the most parsimonious model as final model for each stability component and used it for further analyses (see Supporting Information 3). The final models were analyzed using ANOVAs (type III) and multiple comparisons of means (with custom contrasts to omit confounding comparisons).

We also performed an ANCOVA to test for linear responses of resistance to SPI (not SPI class). The fixed effect model tested the response of 'resistance' to the continuous predictor 'SPI' across 'dominant life histories' (annual, perennial) for moderate to exceptional drought conditions (SPI  $\leq -0.8$ ). Finally, we calculated correlations between resistance and recovery to evaluate potential trade-offs between these two stability components (Donohue *et al.*, 2013).

Data exploration was performed visually as proposed by Zuur *et al.* (2010). Where necessary, adequate variance structure was incorporated in the models to avoid homoscedasticity and to satisfy regression and ANOVA assumptions. For goodness of fit metrics ( $R^2$ ), we used the method described in Nakagawa & Schielzeth (2013) and extended in Johnson (2014). It

distinguishes between *marginal* and *conditional*  $R^2$ , with the first being the proportion of explained variance by fixed effects, and the second the proportion explained by fixed plus random effects. Hence, *marginal*  $R^2$  is identical to (*multiple*)  $R^2$  in standard fixed-effect models. All statistical analyses were performed in R 3.0.3 (R Core Team, 2014). Mixed-effect modelling was performed using the *nlme*-package 3.1-113 (Pinheiro *et al.*, 2013).  $R^2$  metrics were calculated using the R-implementation from Lefcheck (2014).

## Results

### Importance of biome and life history for drought effects on ecosystem stability

For both resistance and recovery, the life history model outperformed the biome model with respect to  $R^2$ -metrics and AIC/BIC. For resistance, the life history model explained more variance (*conditional*  $R^2_{\text{life history}}$  57.8% vs. *conditional*  $R^2_{\text{biome}}$  51.9%) and had lower AIC ( $\Delta\text{AIC}_{\text{life history}}$  0 vs.  $\Delta\text{AIC}_{\text{biome}}$  26) and BIC ( $\Delta\text{BIC}_{\text{life history}}$  0 vs.  $\Delta\text{BIC}_{\text{biome}}$  62). For recovery, the life history model explained considerably more variance in the data (*marginal*  $R^2_{\text{life history}}$  51.7% vs. *marginal*  $R^2_{\text{biome}}$  18.1%) and was also selected by AIC ( $\Delta\text{AIC}_{\text{life history}}$  0 vs.  $\Delta\text{AIC}_{\text{biome}}$  66) and BIC ( $\Delta\text{BIC}_{\text{life history}}$  0 vs.  $\Delta\text{BIC}_{\text{biome}}$  72). Note that *marginal*  $R^2$  is given for the recovery models, as in both models (biome vs. dominant life history) the random effect ('study site') was removed during model selection (see below).

### Resistance Patterns

We found that resistance was strongly dependent on drought intensity (SPI class), dominant life history, and grazing (Table 2a). These three factors – together with interactions of life history with drought and grazing – explained 57.8% of variance in the data. Increasing drought intensity itself had a strong negative influence on resistance, irrespective of the dominant life history of the herbaceous layer (Figure 2). The only significant difference in ecosystem response was observed under abnormally dry conditions (SPI class -1; see Supporting Information 2). Here annual-dominated systems were more resistant than perennial-dominated systems; they even displayed an increased ANPP (+28%) compared to years with normal rainfall. However, this finding was contrasted by the visual impression that, under more intense drought conditions (SPI class  $\leq -2$ ), annual systems had a consistently lower resistance than perennial systems (Figure 2). We thus

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Table 2: ANOVA (type III) results on ecosystem (a) resistance and (b) recovery in drylands. (a) Results on the mixed-effect model testing the response in resistance to drought intensity (SPI class), dominant life history (annual, perennial), grazing regime (ungrazed, grazed) and significant interactions between those. Study site was incorporated as random-effect to allow for differences across studies and counter potential bias towards larger studies (>1 dataset). (b) Results on the fixed-effect model testing the response of average recovery in real drought years (SPI class  $\leq -2$ ) to dominant life history, grazing regime and significant interactions between those. *Marginal* and *conditional*  $R^2$  represent proportion of explained variance by fixed effects alone and fixed plus random effects, respectively. Results of posthocs for interactions are given in Supporting Information 2 and are presented as letter codes and asterisks in Figures 2 to 4.

(a)	Type III mixed effects		
	Df	F value	P value
<b>Response variable: Resistance</b>			
(Intercept)	1	25.5036	<0.001 ***
Drought intensity	4	64.6586	<0.001 ***
Dominant life history	1	23.3887	<0.001 ***
Grazing regime	1	0.4843	0.487
Drought intensity x Dominant life history	4	23.4568	<0.001 ***
Dominant life history x Grazing regime	1	7.3338	0.007 **
(Denominator Df)	713		
Random effect: ~1 Study site group			
<i>Marginal</i> $R^2$	40.5%		
<i>Conditional</i> $R^2$	57.8%		
(b)	Type III fixed effects		
	Df	F value	P value
<b>Response variable: Recovery</b>			
(Intercept)	1	51.7008	<0.001 ***
Dominant life history	1	3.0335	0.084
Grazing regime	1	15.0764	<0.001 ***
Dominant life history x Grazing regime	1	14.5215	<0.001 ***
(Denominator Df)	114		
<i>Marginal</i> $R^2$	51.7%		

Table 3: ANCOVA (type III) testing differences in response of resistance to SPI (for real drought conditions, SPI  $\leq -0.8$ ) across dominant life histories. ANCOVA found differing intercepts (dominant life history,  $p=0.003$ ), but no differences in slopes (SPI x dominant life history,  $p=0.421$ ). Below ANCOVA results, the derived regression estimates are given (Figure 5).

Response variable: Resistance	Type III fixed effects			
	Df	F value	P value	
(Intercept)	1	14.0639	<0.001 ***	
SPI	1	5.4572	0.020 *	
Dominant life history	1	8.9022	0.003 **	
SPI x Dominant life history	1	0.6482	0.421	
(Denominator Df)	499			
Regression model	Estimate	Std. Err.	t value	P value
(Intercept)	-33.75	6.31	-5.3467	<0.001 ***
SPI	15.92	2.85	5.5872	<0.001 ***
Dominant life history (Perennial)	26.93	3.52	7.6417	<0.001 ***

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decided to test with ANCOVA whether ecosystems dominated by annuals or perennials differed in their linear response to drought intensity (see below). With respect to grazing effects, we found that ungrazed perennial systems showed a slightly higher resistance (-19%) than those being grazed (-27%; Figure 3b). Hence, perennial systems' overall drought resistance (lumped across all drought intensity classes) dropped only by ~8% with grazing.

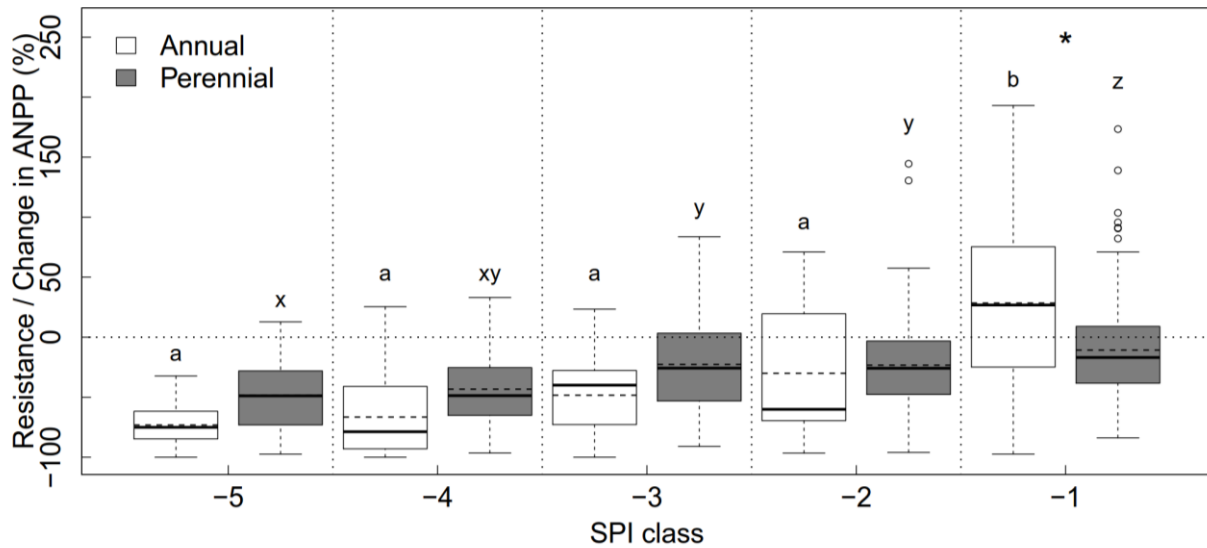


Figure 2: Interacting effects of drought intensity (SPI class) and dominant life history (annual, perennial) on ecosystem resistance to drought. Dashed lines in boxplots represent mean values, and solid lines represent medians. Asterisks indicate significant differences between dominant life forms in the respective SPI class (at  $p < 0.05$ ), letter-codes give significant differences ( $p < 0.05$ ) across SPI classes for annual and perennial systems, respectively.

ANCOVA results (Table 3) showed that resistance was significantly influenced by SPI ( $p = 0.020$ ) and dominant life history ( $p = 0.003$ ), the interaction being not significant ( $p = 0.421$ ).

Hence, annual and perennial systems had a similar response rate to increasing drought intensity (slope of regressions), but perennial systems had a 26.9% ( $\pm 3.5\%$ ) higher resistance under moderate or stronger drought conditions ( $SPI \leq -0.8$ ) than annual systems, shown by significant differences in intercepts (Table 3 and Figure 5).



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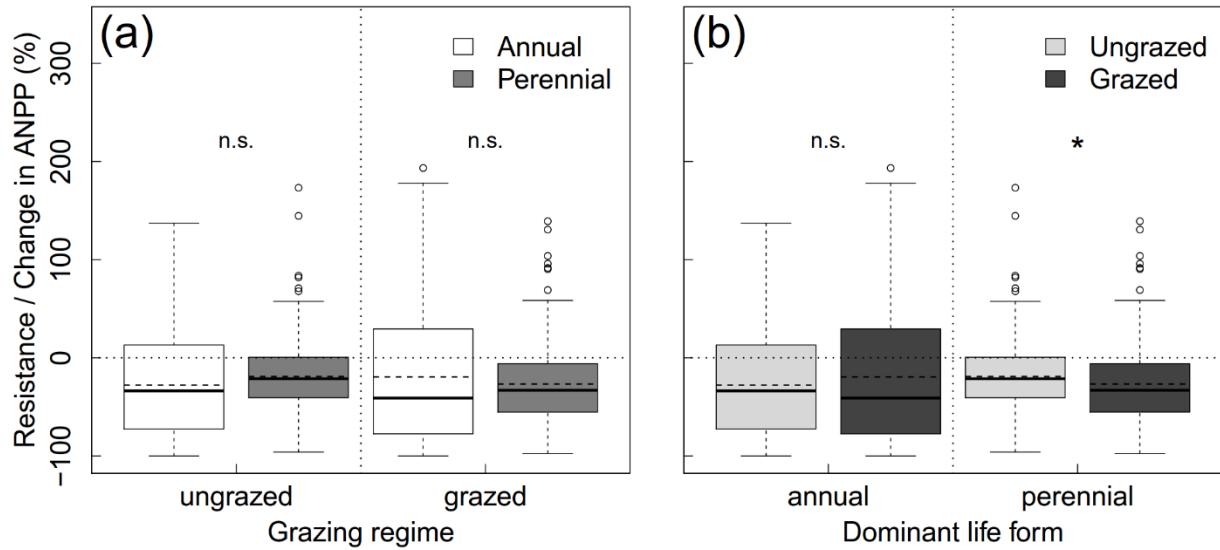


Figure 3: Interactive effect of dominant life history (annual, perennial) and grazing regime (ungrazed, grazed) on ecosystem resistance to drought. Dashed lines in boxplots represent mean values, and solid lines represent medians. Asterisks indicate significant differences within a panel (at  $p < 0.05$ ).

### Recovery Patterns

Unlike for resistance, the random-effect term ('study site') was not included in the final model for recovery, and the model collapsed to a fixed-effect model. ANOVA results showed that drought recovery was significantly influenced by grazing regime and its interaction with dominant life history (Table 2b). In total, the model explained 51.7% of variance in ecosystem recovery from drought. Annual and perennial systems only differed in their drought response when being grazed (Figure 4a and Supporting Information 2). Under grazed conditions, annual systems could even benefit from a drought event, with post-drought ANPP being 189% of pre-drought ANPP. In contrast, grazed perennial systems only displayed a partial recovery (81% of pre-drought ANPP; Figure 4a). These differences diminished under ungrazed conditions.

Recovery of annual systems also differed significantly across grazing regimes (189% when grazed vs. 117% when ungrazed; Figure 4b). Even though, the paucity of observations forbade a systematic assessment of the influence of drought intensity on ecosystem recovery, preliminary

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results show that recovery hardly varied across drought intensities, particularly in perennial systems (Figure S4-2).

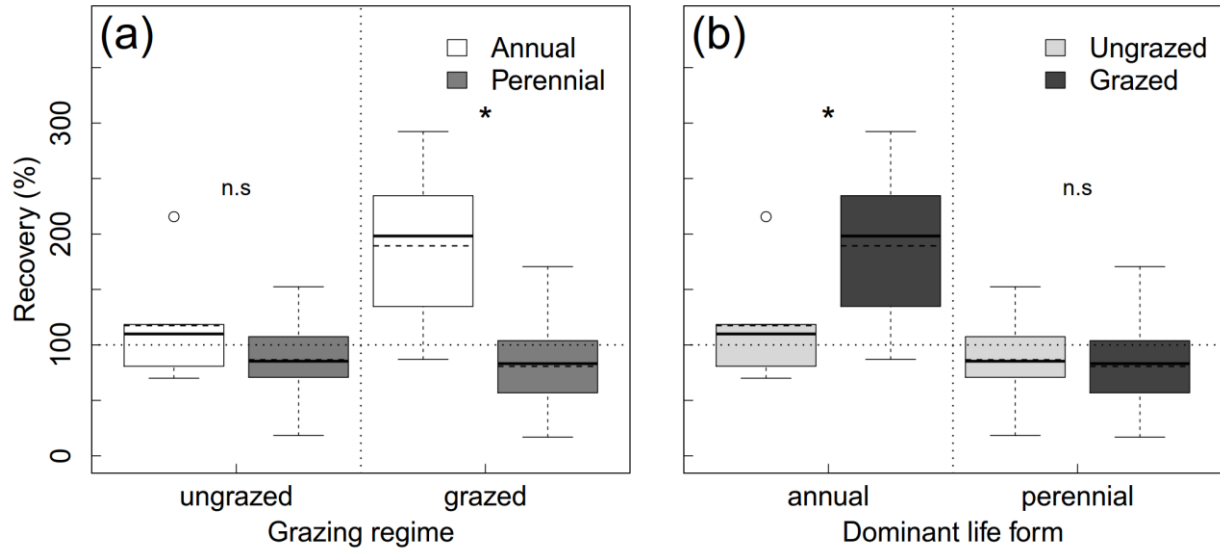


Figure 4: Interactive effect of dominant life history (annual, perennial) and grazing regime (ungrazed, grazed) on ecosystem recovery from drought. Dashed lines in boxplots represent mean values, and solid lines represent medians. Asterisks indicate significant differences within a panel (at  $p < 0.001$ ).

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### Resistance and recovery are not generally related

ANCOVA results on the dependence between resistance and recovery showed that the relationship between these two stability parameters differs across dominant life histories (see Supporting Information 4). Annual systems showed a negative correlation between recovery and resistance ( $Resistance = -2.79 \times Recovery$ ;  $marginal R^2 = 92\%$ ), while no significant correlation was observed for perennial systems ( $Resistance = -82.5$ ; see Supporting Information 4).

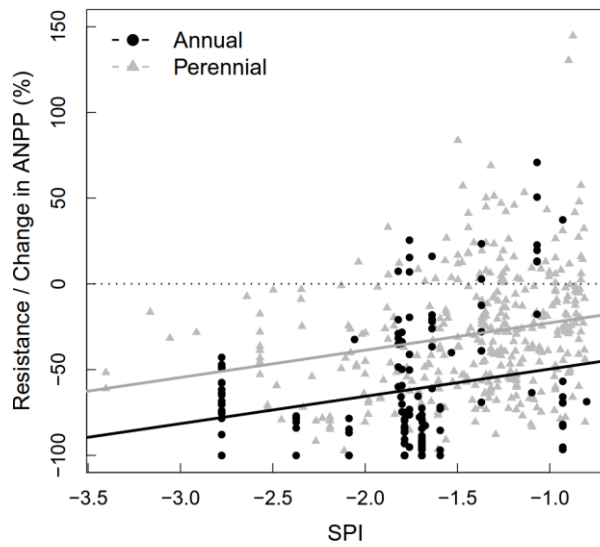


Figure 5: Linear response of resistance to SPI (for real drought conditions,  $SPI \leq -0.8$ ) across dominant life histories. Response rate (slope of regression) to SPI does not differ for either dominant life history, but annuals have lower resistance (difference in intercept). Annuals:  $Resistance = SPI \times 15.92 - 33.75$ . Perennials:  $Resistance = SPI \times 15.92 - 6.82$ .

## Discussion

Under increasing importance of global change effects, dryland ecosystems are projected to experience more frequent drought as well as increased intensities of drought and land-use. In this study, we analyzed dryland ecosystems' stability to these stressors, estimated as resistance during and recovery after a drought, respectively. With this approach, we aimed to advance the functional and quantitative understanding of dryland ecosystem responses to drought and grazing above the level of single field studies. In parts, our results confirmed assumptions from theoretical and site-based studies, but additionally yielded reliable projections for responses of dryland primary production under future drought regimes. Furthermore, our innovative data-integration approach can serve as blueprint for other – not only drought or dryland related – studies.

Relative importance of vegetation characteristics, drought intensity and grazing for resistance and recovery

*Vegetation characteristics.* We found that dominant life history was a considerably better predictor for ecosystem resistance and recovery than biome. Given that plants' life histories are functionally related to principal strategies of resource acquisition and conservation (Grime, 2001), it is of little surprise that life history was important for ecosystem stability in face of drought (MacGillivray *et al.*, 1995). In contrast, the biome classification as used here is relatively coarse and mainly based on structural vegetation properties such as the presence of a tree layer (cf. Olson *et al.*, 2001). Thus, the functional coupling to ecosystem processes is likely to be less immediate. Dominant life history also modulated ecosystems' responses to combined effects of

drought intensity and grazing. Hence, differences between annual and perennial systems can only be discussed together with these interacting predictors.

*Drought intensity.* Generally, drought intensity was a strong, (quasi-) linear predictor for ecosystem resistance. This applied across dominant life histories and irrespective whether drought intensity was assessed as a categorical (SPI class; Figure 2) or continuous predictor (SPI; Figure 5). However, resistance of annual systems was consistently lower under moderate or stronger drought conditions ( $\text{SPI} \leq 0.8$ ).

This can be explained by the principal strategies of perennial and annual plants to cope with high intra-seasonal variability in rainfall, which represent the two 'extreme strategies' in drylands (Stafford Smith & McAllister, 2008). Most importantly, perennials have a higher ability to buffer intra-seasonal variability (Linstädter *et al.*, 2013): Their larger root system allows for early and quick emergence after rainfall events and for persistence between rainfall gaps (Snyman, 2005, Zimmermann *et al.*, 2008). In contrast, annual plants are more prone to intra-seasonal dry spells, especially after the first rainfalls when they have just germinated or as germination might fail altogether (Hamilton *et al.*, 1999). Also during later phenological stages, dry spells lead to reduced productivity (Shao *et al.*, 2008) as annuals invest comparatively less into conservation of acquired resources (Moreno García *et al.*, 2014). Compared to annual-dominated systems, the perennial life-history strategy thus ensures a less severe reduction of in-drought ANPP, leading to a consistently higher resistance across drought intensities (SPI class  $\leq -2$ ).

This trend has an important exception. In abnormally dry years (SPI class -1), slight aridity had beneficial effects on annuals systems' ANPP, leading to positive resistance values (Figure 2).

Such a 'boost' in herbaceous production in years with slightly below-average rainfall has been observed frequently in arid savannas with an annual-dominated herbaceous layer (Le Houérou, 1989, Penning de Vries & Djitéye, 1982). The phenomenon is attributed to a high proportion of

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highly specialized small annual species (e.g. genus *Zornia*). These reach optimum production already under conditions of slightly below-average rainfall, but are outcompeted by other species in years with better rainfall. As a major proportion of data in the respective SPI class originated from such savannas (e.g. Miede *et al.*, 2010, Schulte, 2001), the 'boost' phenomenon might explain the observed positive resistance. If data from these sites were excluded (data not shown) or if resistance was analyzed across biomes (Supporting Information 3), the 'boost' diminished or was restricted to the savanna biome, respectively.

Due to limited data, effects of drought intensity on recovery could not be assessed systematically. Preliminary results for perennial systems suggest that recovery remains constant with increasing drought intensity (Supporting Information 4). Hence, the ability of perennial vegetation to recover from a short-term drought appears to be unaffected by drought intensity, at least under the specific conditions considered in our study (with a drought event framed by two years with average rainfall). Our preliminary results could be attributed to observations that moderate and even severe droughts may drastically reduce ANPP of perennial-dominated dryland ecosystems, but do not substantially affect belowground production (Koerner & Collins, 2014, Shinoda *et al.*, 2010). Perennating buds and the large and deep root system of perennial plants thus provides not only the basis for buffering intra-seasonal variation of rainfall, but also for recovery after a drought (Shinoda *et al.*, 2010, Snyman, 2005).

*Grazing regime:* Grazing regime was less important for ecosystem stability than the other predictors retained in final models. For both stability components, the effect of grazing regime was intermingled with differences between dominant life histories (Figure 3 and 4).

Concerning the relative importance of predictors, we can thus conclude that ANPP-based resistance is mainly driven by drought intensity. Annual and perennial systems have a similar response rate to increasing drought intensity, but differ in their general magnitude of response

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(Figure 5). Grazing regime is of minor importance, and alters resistance only in perennial systems. Similarly, ecosystem recovery is closely connected to the principal dichotomy between annual and perennial plant strategies in drylands (Stafford Smith & McAllister, 2008), representing strategies of fast resource acquisition and effective resource conservation, respectively (Reich, 2014). Here, grazing regime alters recovery only in annual systems. Our findings are supported by empirical studies from drylands (Fuhlendorf *et al.*, 2001, O'Connor, 1995) which assume a hierarchical nature of factors affecting ecosystem processes and place grazing secondary to drought (but see Koerner & Collins, 2014).

Are combined effects of drought and grazing disturbance additive or interactive?

As found before, there is no simple answer to this question (Vogel *et al.*, 2012, Zwicke *et al.*, 2013). For resistance, our results implied additive or synergistic effects. In the case of recovery, restricted data availability forbade a systematic assessment. However, we saw that effects of grazing on drought recovery and overall drought resistance was not uniform: Grazing modulated response patterns of drought resistance and recovery across dominant life histories in specific ways (Figure 3 and 4). Thus, combined effects of grazing and drought seem to be not (only) additive, but (also) interactively related to the dominant life history of the herbaceous layer. This observation is supported by the convergence model of aridity and grazing (Coughenour, 1985, Quiroga *et al.*, 2010), which assumes that aridity and grazing act as convergent selective forces upon plants. Because dominant species and functional groups may have a unimodal response along a gradient of combined forces of aridity and grazing (Linstädter *et al.*, 2014), effects of grazing on drought resistance could either be positive (Koerner & Collins, 2014), suggesting antagonistic interactions, or negative (as found in our study for perennial systems), suggesting synergistic interactions or additive effects. The convergence model implies that positive effects

are more likely to occur in less arid environments, where grazing has shifted vegetation composition towards a dominance of species which are (also) better adapted to drought (Coughenour, 1985).

A similar but inverse pattern was found for recovery. Under grazed conditions (Figure 4), annual systems showed roughly twice the rate of recovery as compared to perennial systems (Figure 4a). However, under ungrazed conditions, this large difference diminished, and life histories did not differ anymore (Figure 4a). Taking into account that life histories coexist at nearly all sites, this effect can be explained by basic assumptions of the plant economics spectrum (Reich, 2014; condensed from CSR-model, Grime, 2001). Under conditions of grazing following a drought, perennials' fitness and competitive strength may be decreased, and annuals may gain dominance (Sander *et al.*, 1998). If these systems fall ungrazed, perennials may reduce the gap in recovery by gradually outcompeting annual plants. On the community level, this may significantly reduce overall ANPP. Hence, as for resistance, our results imply complex additive effects between drought and grazing on ecosystem recovery, which are modulated by life histories.

Are there predictable relationships between the severity of drought events and ecosystem stability?

*Resistance.* Based on data from ~500 drought events, we found a linear relationship between drought intensity and ecosystem resistance, valid across biomes and gradients of climatic aridity (Table 3, Figure 5). To the best of our knowledge, this regression represents the first cross-continental model of dryland resistance derived from field data. We validated model performance by comparing predicted against observed resistance values from two case studies performed at Cedar Creek (USA; Tilman & Downing, 1994) and at the Inner Mongolia Grassland Ecosystem Research Station (IMGERS, China; Bai *et al.*, 2004). To enable meaningful comparison, we only



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selected data representing near-natural vegetation and obtained original precipitation data for the respective sites (for details please refer to Supporting Information 5). For both studies, model predictions showed striking agreement with published results. For Cedar Creek and IMGERS predicted resistance only deviated 1% ( $-29\%_{\text{obs}}$  vs.  $-30\%_{\text{pred}}$ ) or 3% ( $-25\%_{\text{obs}}$  vs.  $-28\%_{\text{pred}}$ ) from observed resistance, respectively. Hence, our cross-continental model performs well in predicting drought resistance, at least in perennial grassland for which published validation data were available.

*Recovery.* For this stability component, we could only assess predictions based on class means from the ANOVA model (Figure 4) and hence projections as well as validation procedure are vague. Mean recovery at IMGERS and Cedar Creek were reported with 121% and 112%, respectively. Although these values are higher than our estimate for ungrazed perennial sites (87%), they fall within the variability of the respective class (Figure 4). The differences in observed vs. predicted recovery are likely to reflect differences in the calculation of recovery: We only assessed drought events where pre- and post-drought years received normal precipitation, the mentioned studies did not correct for potential confounding effects of variable pre- and post-drought precipitation (Ruppert *et al.*, 2012, Wiegand *et al.*, 2004).

*Predicting resistance for a centennial drought.* Given the high accordance between predicted and observed resistance, we took another step and predict resistance during a centennial drought. This is particularly interesting as a 'centennial' drought of today might become a 'quarter-centennial' or even 'decadal' drought in future (Dai *et al.*, 2004, Meehl & Tebaldi, 2004). For resistance, we can benefit from our SPI-based approach, as each SPI value corresponds to a cumulative probability. A SPI of ca. -2.4 corresponds to the cumulative probability of 1% and thus to a centennial drought. At SPI -2.4, our model predicts that in-drought ANPP of perennial systems would suffer a reduction of ca. -45% compared to normal ANPP. For annual systems ANPP

would even be reduced to -72%. It is evident that these differences have important implications for future ecosystem responses under elevated levels of climate change (see below).

### Implications for dryland ecosystems and degradation in the light of climate change

Even though drylands are remarkably adapted to low and erratic water-availability (Davidowitz, 2002), elevated rainfall variability induced by climate change is predicted to detrimentally impact ecosystem response and functioning (MEA, 2005). Here we focused on potential impacts of drought and grazing on ecosystem stability, as these factors are likely to increase in intensity and frequency in the mid- to long-term and have been reported to considerably impact various ecosystem processes and properties (Hsu & Adler, 2014, Koerner & Collins, 2014) and even might trigger degradation (Miehe *et al.*, 2010, Schlesinger *et al.*, 1990).

One major result of this study is that responses in ecosystem stability vary with herbaceous plants' strategies of resource acquisition and allocation. Although not unexpected, this finding has seldom emerged in such clarity. Here, these contrasting strategies are represented through the principal dichotomy between annual and perennial herbaceous plants, which is characteristic for drylands (Stafford Smith & McAllister, 2008). Perennial plants were particularly capable of buffering detrimental effects on ANPP during a drought (high resistance), but failed to fully recover to their pre-drought performance after a drought (low recovery). For annual plants, the opposite applied. These contrasting pathways in achieving stability involve a trade-off between strategies (Miller & Chesson, 2009). However, a reciprocal correlation between resistance and recovery could only be observed for annual systems (Supporting Information 4). Although this suggests differences of response diversity in the respective systems, a profound discussion would be out of focus here. The interested reader may refer to Miller & Chesson (2009; cf. 'storage effect').

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Recalling the marked differences in resistance projections of annual versus perennial systems during centennial droughts, we may postulate that annual systems are more prone to elevated frequencies and intensities of drought. Given the relatively higher losses in ANPP for annual systems, more frequent occurrences of extreme and exceptional droughts in the future will lead to massive declines in annual systems' ANPP accompanied by lowered seed production (Golodets *et al.*, in print, Russi *et al.*, 1992). This might push annual systems towards gradual seed bank depletion and ultimately lead to a partial or complete breakdown of herbaceous plant communities, particularly when (over-) grazed (Kinloch & Friedel, 2005, Miede *et al.*, 2010). Currently high post-drought recovery of annual systems counters these processes. However, under climate regimes with more frequent and potentially longer droughts, the recovery strategy of annual plants might not be sufficient to counter their poor in-drought resistance, and systems might desertify (Kinloch & Friedel, 2005, Miede *et al.*, 2010, Schlesinger *et al.*, 1990). Due to additive effects of drought and grazing, more frequent and severe drought events could trigger degradation of perennial- to annual-dominated systems. Such drought-induced shifts have frequently been observed in dryland vegetation subject to a high grazing pressure (Sander *et al.*, 1998, Vetter, 2009). Altered rainfall regimes in drylands may thus not only be detrimental to ecosystem performance via the direct mechanisms of drought-induced losses of ANPP within and after a drought, but also accelerate degradation and desertification, further reducing ecosystem stability and performance (Lohmann *et al.*, 2012, Miede *et al.*, 2010, Schlesinger *et al.*, 1990). This is particularly problematic as most drylands are primarily used as rangelands for livestock production, and local livelihoods are tightly coupled to revenues from primary production (Martin *et al.*, 2014). Hence, higher inter-seasonal variability induced by climate change will considerably threaten local livelihoods, particularly under further increasing population sizes (MEA, 2005, UN, 2008) and decreasing herd mobility (Martin *et al.*, 2014). Hence, from a

rangeland management perspective, it is utmost important to retain perennial grasses in the system in order to maintain a stable and productive vegetation state in the thread of global change (Lohmann *et al.*, 2012).

### Strengths and weaknesses of our data-fusion approach

Our data-fusion approach was well-suited and effective in quantifying the relative importance of drought intensity, grazing regime and ecosystem characteristics in explaining variation in drylands' stability to drought. However, it also had limitations with respect to variable selection. The focus on ANPP was partially motivated by data availability, and obviously imposes restrictions upon interpretability. Most importantly, we could not complement ANPP dynamics with changes in species composition or diversity, which have shown to be functionally connected to ecosystem stability (Bai *et al.*, 2004, Tilman & Downing, 1994, Vogel *et al.*, 2012).

Also selection of explanatory variables was partly restricted by data availability. Despite having >4400 observation years at hand, data was still insufficient to analyze potentially interfering factors, such as the role of drought intensity for ecosystem recovery (Hoover *et al.*, 2014) , or the legacy effect of precipitation which may modulate drought responses (Sala *et al.*, 2012). For a detailed discussion on our methodological approach, please refer to Supporting Information 1.

Our methodological toolbox – a combination of a large global database, normalization of ANPP and precipitation data, and selection of two key estimates for ecosystem stability – enabled us to assess timely questions on global change-related ecosystem functioning in drylands, which thus far could only be answered on a theoretical or anecdotal basis. In future, this approach will ideally be combined with experimental and modeling studies to overcome caveats of the respective individual methodologies (Reyer *et al.*, 2012).

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