



Richness, not evenness, varies across water availability gradients in grassy biomes on five continents

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Abstract

We sought to understand the role that water availability (expressed as an aridity index) plays in determining regional and global patterns of richness and evenness, and in turn how these water availability–diversity relationships may result in different richness–evenness relationships at regional and global scales. We examined relationships between water availability, richness and evenness for eight grassy biomes spanning broad water availability gradients on five continents. Our study found that relationships between richness and water availability switched from positive for drier (South Africa, Tibet and USA) vs. negative for wetter (India) biomes, though were not significant for the remaining biomes. In contrast, only the India biome showed a significant relationship between water availability and evenness, which was negative. Globally, the richness–water availability relationship was hump-shaped, however, not significant for evenness. At the regional scale, a positive richness–evenness relationship was found for grassy biomes in India and Inner Mongolia, China. In contrast, this relationship was weakly concave-up globally. These results suggest that different, independent factors are determining patterns of species richness and evenness in grassy biomes, resulting in differing richness–evenness relationships at regional and global scales. As a consequence, richness and evenness may respond very differently across spatial gradients to anthropogenic changes, such as climate change.

Keywords Climate · Diversity · Grasslands · Plant species richness · Precipitation

Introduction

There are two fundamental ways to measure diversity: (1) the number of species in a given area, *richness*, and (2) the equitability of abundances among species, *evenness* (Magurran 2003). Richness is by far the oldest, most frequently used, and least confusing of the two measures (Peet 1974). Thus, it is not surprising that ecology has its early roots in the documentation of patterns of richness at local, regional and global scales, and that countless studies have aimed to understand the mechanisms that generate richness patterns at these different scales (e.g., Gaston 2000; Willis

and Whittaker 2002; Scheiner and Willig 2005; Whittaker et al. 2005). In contrast, far less attention has been devoted to understanding patterns of evenness at the same scales, and when compared to richness (e.g., Palmer 1994), there is a dearth of hypotheses explaining the causes and consequences of evenness patterns (Hillebrand et al. 2008). Yet, evenness is arguably as (or even more) important of a measure of diversity as richness (Hillebrand et al. 2008). Evenness encompasses the variation in traits within a community, which can affect species interactions and coexistence. Furthermore, evenness, or lack thereof (i.e., dominance), directly affects ecosystem functioning (Wilsey and Potvin 2000, Smith and Knapp et al. 2003). Evenness also influences compositional stability (i.e., loss and gain of species). For example, low evenness (high dominance) indicates that a number of small populations occur within a community, and small populations are more vulnerable to extinction under global change (Suding et al. 2005). Thus, understanding

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causes and consequences of evenness are needed to predict how communities may change in the future.

Despite growing recognition of its importance, the lack of focus on evenness may be, in part, due to the ambiguity surrounding how evenness is quantified, given there are numerous ways to calculate this measure of community structure (Peet 1974; Magurran 2003), ranging from simple metrics (e.g., Berger-Parker dominance, Berger and Parker 1970) to more complex measures (See Smith and Wilson 1996 for a review). Nevertheless, because evenness describes a component of diversity—variance in abundances of species—that differs from richness (Gosselin 2006; Wilsey et al. 2005), alternate, independent drivers could be determining richness and evenness and the relationship between these two measures (Ma 2005). Differences in drivers of these two components of diversity could, in turn, have important implications for our ability to predict spatial variation in evenness vs. richness, and their consequences for ecosystem functioning across broad environmental gradients. Moreover, if anthropogenic global changes differentially influence evenness vs. richness, as has been documented in a growing number of studies (e.g., Chapin et al. 2000; Hillebrand et al. 2008; Avolio et al. 2014; Magurran 2016; Jones et al. 2017; Blowes et al. 2019), this could have unknown or difficult to predict consequences for ecosystem functioning compared to if species richness is considered alone.

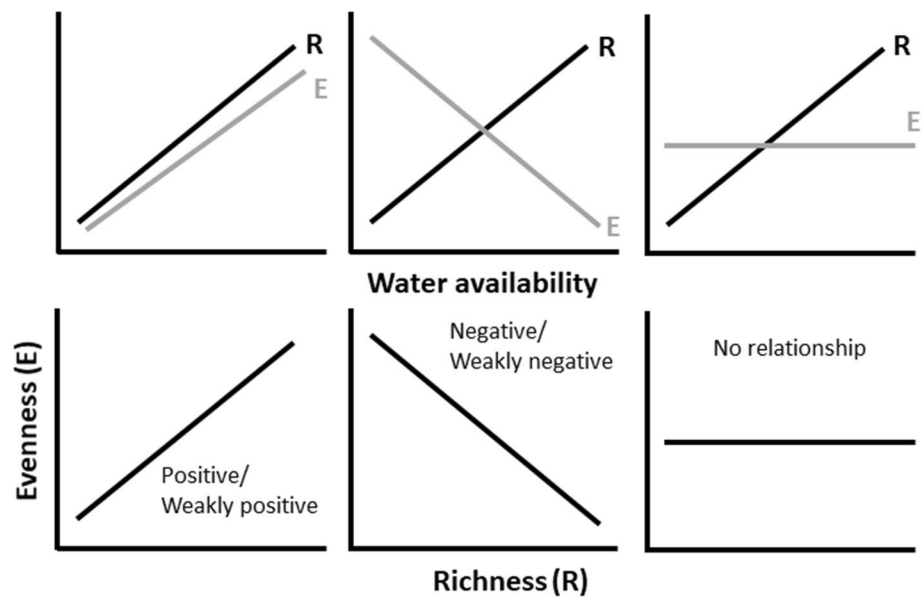
It is often assumed that abiotic factors tend to predict species richness patterns at regional and global scales (e.g., Currie 1991; Rosenzweig 1995). Indeed, it has long been recognized that richness is greater in regions that are warm and wet vs. those that are cold or arid (e.g., A. von Humboldt in 1807, Wulf 2015), and such relationships are borne out not only globally but also within biomes (Currie 1991; Currie et al. 2004). For example, positive relationships between richness and precipitation (as a proxy for resource–water availability) are common across spatial gradients in herbaceous systems (Adler and Levine 2007, Cleland et al. 2013, Wu et al. 2014, Zhang et al. 2014, LaPierre et al. 2016, Lyseng et al. 2018, Harrison et al. 2020). The positive relationship between richness and precipitation is thought to occur because of increasing resource/energy availability and number of individuals allowing more species to co-exist (Currie et al. 2004). Yet, while the spatial relationship between richness and precipitation is well documented, much less is known about the spatial relationship between evenness and precipitation. However, if the same logic were applied as for species richness, the expectation would be for evenness to increase with increasing resource availability (or dominance to decrease with increasing resource availability). The rationale behind this is that abundances would be more equally distributed among a greater number of species in the community and variance in abundances should

decrease as resources become less limiting (e.g., tropical forests, Hubbell 2001). A negative relationship between evenness and precipitation may also be expected. Increasing resources/energy and number of individuals (Currie et al. 2004) can lead to increased competition resulting in skewed dominance–diversity relationship, with a few very abundant species and many rare species, a pattern that is frequently observed in plant communities (e.g., Whittaker 1965; Grime 1998; Smith and Knapp 2003).

Depending on how richness and evenness respond to resource availability at regional or global scales, the expectation is that different richness–evenness relationships could emerge. If we assume a positive relationship between richness and resource availability at regional scales, then a positive richness–evenness relationship would result if evenness shows a similar response as richness (Fig. 1, left panel). Conversely, a negative richness–evenness relationship would result if evenness decreases with increasing resource availability (Fig. 1, middle panel). A lack of relationship would arise if evenness is not related to resource availability (Fig. 1, right panel), but rather other factors determine its variance across spatial scales, such as availability of other resources (nitrogen) or top-down forces (fire, grazing). The array of possible theoretical relationships and the contrasting patterns that have been observed suggest that much is still to be learned about what determines richness–evenness relationships. Recent calls have been made to understand how these two fundamental measures of diversity vary across gradients and in different geographic regions (Soininen et al. 2012; Zhang et al. 2012), particularly given how little we know about variation in evenness when compared to richness.

In this study, we examined relationships between water availability, as measured by an aridity index (and precipitation), and species richness and evenness, and the resulting richness–evenness relationships, in grassy biome plant communities across the globe. Grassy biomes cover more than 40% of the Earth's land surface and encompass relatively broad environmental gradients (Lehmann et al. 2019). As such, they are well suited for testing relationships between resource availability, species richness and evenness, because these measures of diversity vary spatially and with respect to climate. We used water availability as a measure of resource availability, as water availability (precipitation) is a strong determinant of productivity (Knapp and Smith 2001; Huxman et al. 2004; Sala et al. 2012; Forrester et al. 2017) and species richness (Adler and Levine 2007; Cleland et al. 2013; La Pierre et al. 2016; Harrison et al. 2020) in grassy biomes (excluding flooded grasslands). Water availability is determined by precipitation and temperature, and aridity indices integrate these variables to provide a comparable measure across broad geographic extents (Le Houerou 1996).

Fig. 1 Conceptual figure hypothesizing possible relationships between water availability (aridity or precipitation) and richness (R) and evenness (E). It is expected that if richness is primarily abiotically constrained at broad spatial scales, then it should be positively related to water availability. Much less is known about the spatial relationship between water availability and evenness, and a positive, negative, or no relationship are possible. As a consequence, when considering the relationship between richness and evenness, a negative, positive, or no relationship may be expected to result



To examine whether water availability affects richness and evenness differentially to influence richness–evenness relationships within and among grassy biomes, we compiled datasets from eight grassy biomes on five continents that each used consistent methodology to measure plant species richness and abundances and that spanned broad precipitation/aridity gradients. Our focus on water availability as a key abiotic factor affecting richness and evenness does not address other regional factors, such as biogeography, also known to influence patterns of components of diversity at regional or global scales (e.g., Latham and Ricklefs 1993; Kreft and Jetz 2007). Therefore, to account for variation related to regional effects (e.g., biogeography, historical effects), we adjusted richness and evenness values using a z score standardization, which allowed us scale richness and evenness values similarly across the eight biomes. Using these standardized richness and evenness values, we first examined separate relationships between water availability (Aridity Index, mean annual precipitation), richness and evenness both within and among the eight water availability gradients. In line with previous studies, we expected to find a positive relationship between increasing water availability (i.e., decreasing aridity) and plant species richness. For evenness patterns, we hypothesized that there would be either no relationship, indicating other factors (such as biotic interactions, Therriault and Kolasa 1999) were determining spatial patterns of evenness, or either a negative or positive relationship, suggestive of abiotic factors determining both richness and evenness patterns at regional and global scales. We then examined richness–evenness relationships within and among the grassy biome regions to test our conceptual framework (Fig. 1) and determine whether there is global consistency in the relationship across an essential resource

gradient. Given the hypotheses above, we expected that the relationship between richness and evenness at regional and global scales would be either negative or positive, as a result of opposing relationships between richness vs. evenness across the aridity gradients, or that there would be no relationship between the two measures of diversity.

Methods

Global datasets

We compiled a dataset consisting of previously published and unpublished data on plant community composition that spanned eight precipitation/aridity gradients in grassy biome regions on all continents, excluding Europe and Antarctica (Fig. 2, Table 1, Appendix S1). These data were selected because (1) they encompassed relatively broad gradients of precipitation and temperature, and (2) plant composition was sampled using consistent methodology across all sites within each regional biome. We were able to find eight datasets (referred to here as “biome”) that met these criteria; however, it was difficult to control for fire and grazing history (Appendix S1). That said, even though fire and grazing are important factors affecting richness and evenness in grasslands (e.g., Kirkman et al. 2014; Koerner et al. 2018), we believe that at the scales of our analysis (regional, global) that precipitation is likely an overriding factor influencing water availability–diversity patterns. Each dataset consisted of six or more sites located along a precipitation gradient (Table 1). For each biome, plant species composition was determined using the same sampling effort per site (Table 1), using either percent cover or Braun-Blanquet or decimal

Fig. 2 **a** Location of the eight water availability gradients in grassy biomes on five continents. **b** Mean annual precipitation (MAP) and temperature (MAT) parameter space encompassed by the study sites

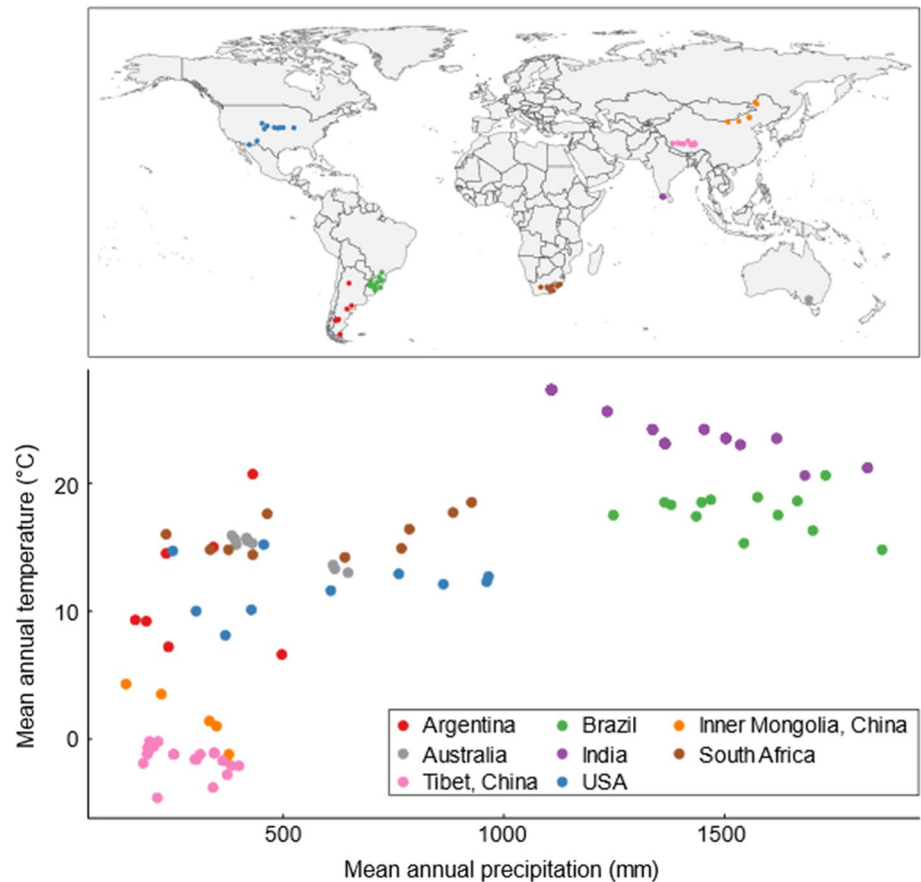


Table 1 Summary of grassy biome gradients by country location, number of sites within a gradient, number of plots per site, plot size, mean annual precipitation (MAP) range, mean annual temperature (MAT) range and aridity index (AI) range

Country/region	Number of sites	Number of plots per site	Plot size (m ²)	MAP range (mm)	MAT range (°C)	AI range	Source
Argentina	7	100	2.25	165–497	6.6–20.7	0.18–0.65	Velasco Ayuso et al. (2020)
Australia	9	5	20	384–687	13.0–15.9	0.28–0.57	
Brazil	13	10	1.0	1248–1857	14.8–20.6	0.96–1.40	Menezes, LS, unpubl. ms
Inner Mongolia, China	6	6	4.0	144–377	– 1.7 to 4.3	0.16–0.51	
India	40	9	1.0	1108–1824	20.6–27.3	0.78–1.61	
South Africa	10	20	1.0	235–927	14.2–18.5	0.15–0.73	Forrestel et al. (2017)
Tibet, China	20	5	0.25	183–400	– 4.6 to – 0.2	0.26–0.58	Wu et al. (2012)
USA	10	20	1.0	250–965	8.1–15.2	0.17–0.86	Forrestel et al. (2017)

If data were previously published, the relevant publication is provided

cover classes (Appendix S1). We obtained datasets directly from investigators rather than from published papers, allowing us to conduct a meta-level analysis (sensu Vetter et al. 2013).

Calculating richness and evenness

For each biome, we calculated the average relative cover or abundance value of each species across all samples (e.g.,

plots or transects) at each site to create a single representation of the community at a site. We then calculated richness (the number of species at a site) and evenness for each site. We chose E_{var} as our evenness metric because it provides an intuitive measure of evenness by calculating the variance of species abundances and converting this variance measure to a bounded 0–1 scale, in which 0 is an uneven community and 1 is a perfectly even community. Unlike Simpson's evenness, if a community only has a single species, no evenness

measure is provided, as opposed to a value of 1 for the Simpson’s evenness metric. E_{var} was calculated as $E_{var} = 1 - \frac{2}{\pi} \text{atan}\left(\frac{s-1}{x} \text{var}(\ln x)\right)$, where s is the number of species in a sample, x is the species abundances in a sample, and var is returned by most statistical software (Avolio et al. 2019). We used `community_structure()` function in the `codyn` R package to calculate richness and evenness (Hallett et al. 2016). We dropped sites with four or fewer species (3 sites out of 115), because evenness metrics are unreliable at low species richness (Magurran 2003).

Because each biome dataset used different sampling methods, we standardized richness and evenness within each gradient using $x_{\text{std}} = \frac{x - x_{\mu}}{x_{\text{sd}}}$, where x represents evenness or richness of a site, and x_{μ} and x_{sd} represent the average and standard deviation, respectively, of evenness or richness across sites within a biome. This standardization also allowed us to account for differences in sampling methodology among biomes and to account for biogeographic variation that occurred within and across biomes. For the standardization, we used the `scale()` function in base R.

Climate data

Mean annual precipitation over a 50-year time period (1950–2000) was obtained from WorldClim 2.0 (Fick and Hijmans 2017) using GPS coordinates from each site. Similarly, mean annual potential evapotranspiration was obtained from CGIAR-CSI Geoportal. Together these climate data were used to calculate the Aridity Index (AI) for each site: $\text{AI} = \text{mean annual precipitation} / \text{mean annual potential evapotranspiration}$. With this AI metric, higher values correspond to more humid conditions (higher water availability), and conversely, lower values correspond to more arid conditions (lower water availability).

Statistical analyses

We examined three relationships, (1) richness versus AI or precipitation, (2) evenness versus AI or precipitation, and (3) richness versus evenness. For the three relationships, we first analyzed them for each biome separately using linear regression models. This regional analysis allowed us to

assess how within each biome richness and evenness were related to measures of water availability, and in turn how these separate relationships then result in the relationship between richness and evenness. We then analyzed each of the three relationships across all biomes. This allowed us to assess global-scale relationships between richness, evenness and water availability. For this global analysis, we employed a mixed effects model with biome as a random factor using the `lmer()` function in the `lme4` package. We compared mixed models that did and did not include a quadratic term and compared the AIC of both models to determine which was a better fit. We determined the model R^2 using the `r.squaredGLMM()` function of the `MuMIn` package (Barton 2019). Lastly, to further explore whether the relationship between richness and evenness is modified by water availability, we used a linear regression model to compare the slopes of the individual linear models of richness versus evenness for each biome to AI. We conducted the same analyses using mean annual precipitation instead of AI as the measure of resource availability to determine if the relationships were appreciably different. All statistical analyses were performed in R (R Development Core Team 2019) and significance was set at $\alpha = 0.05$ for all analyses. To correct for multiple hypothesis testing, we Bonferroni corrected our p values: $p \leq 0.01$ for gradient-level vs. $p \leq 0.016$ for the global analyses.

Results

Richness and evenness patterns across water availability gradients

We found significant linear relationships between water availability and scaled plant species richness for 4 of 8 biomes (Appendix S2, S3). These within-region relationships were positive for drier grassy biomes in South Africa, Tibet and USA and negative for the mesic India biome (Table 2). For relationships between evenness versus AI, only the grassy biome in India was significant (Appendix S2, S4); mirroring richness, the relationship was negative (Table 2).

Table 2 Summary of relationships between water availability (Aridity Index, AI) and richness and evenness for each grassland gradient and across all the gradients (Overall)

	Argentina	Australia	Brazil	Inner Mon-golia, China	India	South Africa	Tibet, China	USA	Overall
Richness vs. AI	–	–	–	–	Neg	Pos	Pos	Pos	Concave down
Evenness vs. AI	–	–	–	–	Neg	–	–	–	–
Richness vs. evenness	–	–	–	Pos	Pos	–	–	–	Concave up

Across all of the biomes, we found a significant quadratic relationship between species richness and AI, with richness increasing with increasing water availability in drier biomes and decreasing with increasing water availability in wetter biomes (Fig. 3a; Quadratic Model: AIC = 291.45; quadratic term = -5.22 , $t_{1,114} = -6.21$, $P < 0.001$; linear term = 0.243 , $t_{1,114} = 0.29$, $P = 0.77$; intercept = $1.35 \cdot 10^{-19}$, $t_{1,114} = 0.0$, $P = 1.0$; Linear Model: AIC = 327.45). In contrast, there was not a significant linear or quadratic relationship between species evenness and AI at the global scale (across biomes; Fig. 3b; Quadratic Model: AIC = 319.10; quadratic term = -1.41 , $t_{1,114} = -1.48$, $P = 0.14$; linear term = -1.77 , $t_{1,114} = -1.87$, $P = 0.06$; intercept = $-9.055 \cdot 10^{-17}$, $t_{1,114} = 0.0$, $P = 1.0$; Linear Model: AIC = 323.96). For both richness and evenness, similar patterns were observed when MAP was substituted for AI in the models (Appendices S5–S8).

Relationships between richness and evenness

Of the eight grassy biomes, scaled evenness and richness were significantly related for 2 of 8 biomes (Appendix S9,

S10). Both were positive relationships, one at the drier end of the water availability gradient (Inner Mongolia, China) and the other at the wetter end (India; Table 2). Overall, we found a weakly concave up relationship between scaled evenness and scaled species richness across all biomes (Fig. 4a; Quadratic Model: AIC = 313.73, quadratic term = 0.609 , $t_{1,114} = 0.655$, $P = 0.51$; linear term = 3.09 , $t_{1,114} = 3.32$, $P = 0.00$; intercept = $-6.23 \cdot 10^{-17}$, $t_{1,114} = 0.0$, $P = 1.0$; Linear Model: AIC = 318.52), and the relationship between the biome-level slopes of scaled evenness and richness and site aridity was not significant (Fig. 4b).

Discussion

Relationships between water availability and richness

In this study, we found a combination of positive, negative and no relationships between water availability (both AI and MAP) and species richness at regional scales; grassy

Fig. 3 Relationship between plant species **a** richness, **b** evenness and water availability (Aridity Index) among grassy biome sites globally. Quadratic models were fitted to the data and R^2 values are reported, with the regression line only shown for significant models. Grey shading indicates the 95% confidence interval. There were 115 datapoints in this analysis

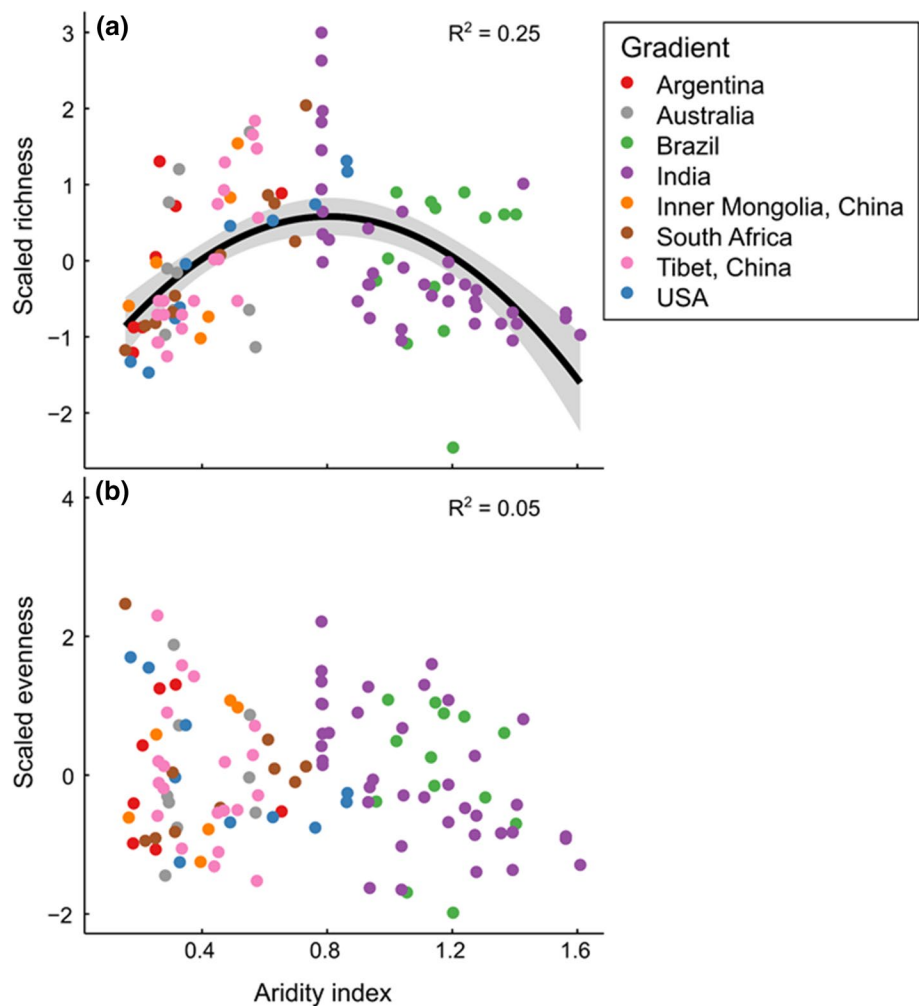
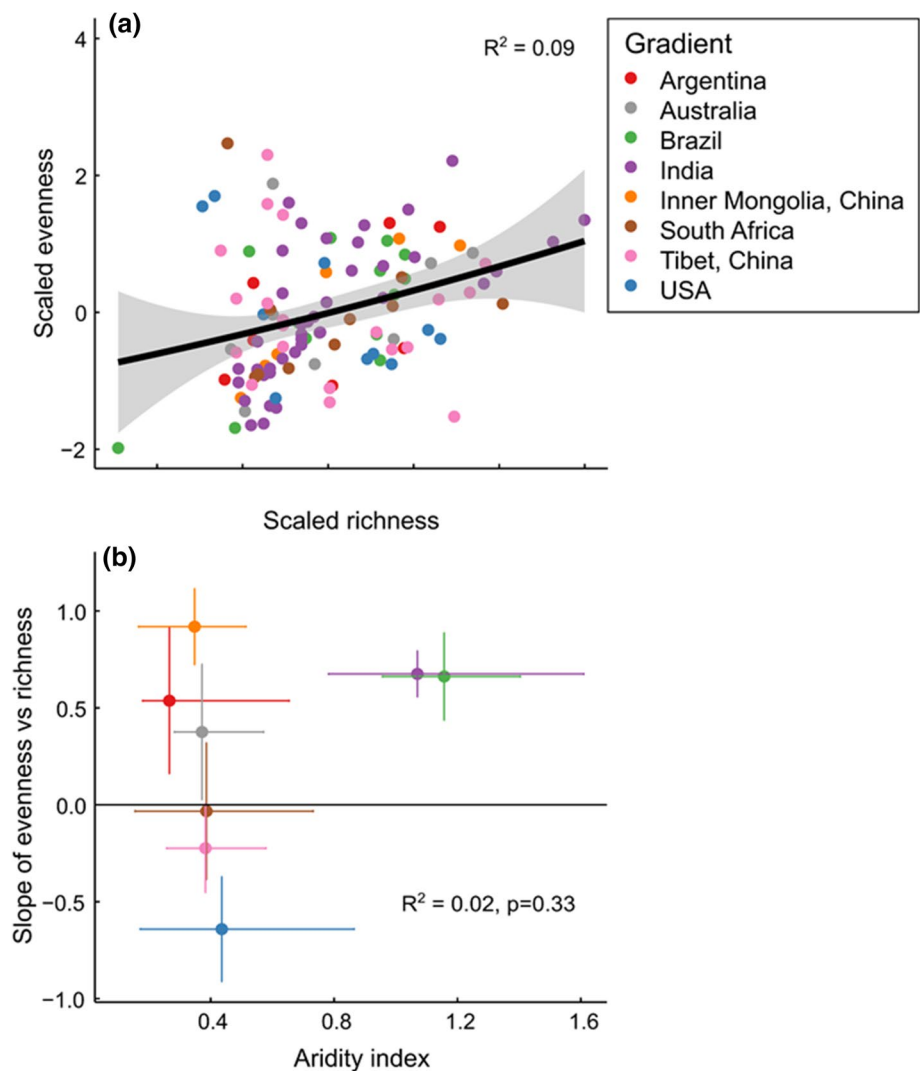


Fig. 4 **a** Relationship between plant species richness and evenness among grassy biome sites globally. Grey shading indicates the 95% confidence interval. **b** Relationship between the slope of the relationship between species richness and evenness and water availability (Aridity Index). There were 115 datapoints in this analysis. The *x*-axis is the geometric mean of the aridity gradient for each biome and the *x*-error bars are the minimum and maximum aridity values for each biome. The *y*-error bars are the error in the slope estimates from the linear regression models



biomes in South Africa, Tibet and USA were positive, whereas only the grassy biome in India was negative. Positive or hump-shaped relationships between resource availability (precipitation or productivity) and richness have been found at regional (among communities) scales in grasslands (Pausas and Austin 2001, Adler and Levine 2007, Cleland et al. 2013, LaPierre et al. 2016). The grassy biomes in South Africa, Tibet and the USA encompass the drier end of the overall water availability gradient captured with our analyses. In contrast, the India biome encompasses the wetter end of the water availability gradient. As has been previously hypothesized (Currie et al. 2004), the increase in water availability at the drier end of the overall water availability gradient likely promotes species coexistence by providing more niche opportunities for species. Thus, abiotic factors are presumed to be the most important factor determining species richness in drier ecosystems (Cleland et al. 2013). In contrast, at the wetter end of the water availability gradient, competition

and light limitation is likely to become more important. Consequently, richness should decline with increasing water availability due to increased importance of biotic factors such as increased competitive effects, rather than water availability per se. Collectively, the grassy biomes included in our study appear to encompass the switch from primarily abiotic factors determining richness to biotic factors limiting membership of species in the community. As a result, when the grassy biomes were combined into a single analysis, we found a humped-shaped relationship between richness and water availability (expressed as AI or MAP), similar to other studies spanning broad resource availability gradients (e.g., Adler et al. 2011). It is important to note that a significant relationship between water availability and species richness was not found for four of the eight grassy biomes. However, the trend was for a positive relationship for drier grassy biomes in Argentina and Inner Mongolia, China.

Relationships between water availability and evenness

In contrast to the role of resource availability in determining species richness, much less is known about how evenness should vary with water availability or other resource gradients. This, in part, may result from the presumption that abundances of species are determined primarily by biotic factors (Therriault and Kolasa 1999) and a greater emphasis in the literature on the effects of evenness rather than its determinants (Hillebrand et al. 2008). We found for all but one grassy biome (India) that evenness was not significantly related to water availability. For the India biome, evenness and water availability were negatively correlated, as was found for species richness. Similar mechanisms may be operating across the water availability gradient as proposed for richness, with competitive interactions becoming more important in determining abundances of species with increasing (high levels) water availability. Indeed, when the relationship between dominance (Berger-Parker index, Berger and Parker 1970) and aridity was examined, dominance increased with increasing aridity for the India biome (data not shown), supporting the idea that competitive interactions may be a factor determining the negative relationship between water availability and evenness. We did not find a relationship between evenness and water availability for the Tibet grassy biome, even though a previous study found a hump-shaped relationship between evenness and soil moisture (Dorji et al. 2014). However, Dorji and colleagues (2014) used a different measure of evenness (Alatolo 1981) than the present study. This raises an important issue for comparing findings of determinants of evenness or relationships between richness and evenness: richness is measured in one way (counts the number of individual species in a sampling unit) though often at different scales, while evenness can be quantified in multiple ways, with different strengths or limitations depending on the metric in question (Smith and Wilson 1996; Gosselin 2006; Tuomisto 2012; Avolio et al. 2019). We chose to use the Evar evenness metric because at higher levels of richness, as represented in all of the datasets included in our analysis (note we dropped sites from the analysis with low species richness following Magurran 2003), species richness and evenness can be viewed as being mathematically decoupled unlike with the Shannon's or Pielou's J metrics (Smith and Wilson 1996). Moreover, Evar provides a good distribution of evenness values and does not allow for an evenness value if the community is only comprised of a single species (unlike Simpson's evenness, Avolio et al. 2019). Overall, with Evar, only one site showed a relationship between evenness and water availability, and there was no relationship across the gradients between evenness and water availability. These findings provide support for biotic factors (grazing), or other physical

factors (disturbance, fire) not captured in our analysis, being more important than water availability for determining species abundances in grassy biomes at regional scales.

Relationships between species richness and evenness

Although significant relationships between richness and evenness have been found for grasslands (e.g., Wilsey et al. 2005; Zhang et al. 2012), only two of the eight grassy biomes in our study showed significant relationships between richness and evenness. For the USA and Tibet biomes, we found no relationship between richness and evenness contrary to previous findings (Wilsey et al. 2005; Zhang et al. 2012). This may be because both studies used a measure of evenness (Simpson's evenness, Pielou's J, respectively) that is considered mathematically non-independent of richness (Smith and Wilson 1996; Jost 2010). A positive relationship between richness and evenness was found for both India and Inner Mongolia, China. For India, relationships between water availability and richness/evenness were positive, and in line with our conceptual framework (Fig. 1), the resulting richness and evenness relationship was positive. However, for the Inner Mongolian biome in China, neither richness nor evenness was significantly related to water availability, though the trend for both was positive. Thus, although there was not clear evidence for increasing water availability promoting both richness and evenness, the positive richness–evenness relationship suggests other factors may be similarly affecting the two measures of diversity in these grasslands. Overall, these results suggest richness and evenness among the grassy biomes we assessed may be responding for the most part independently to either abiotic (e.g., availability of other resources, fire disturbance) or biotic (e.g., degree of dominance, grazing) factors. That is, factors that affect the number of species in a community are often independent of factors that affect the distribution of individuals (relative abundances) among species. These results also suggest there are limitations to our conceptual framework (Fig. 1) for predicting the directionality or significance of relationships between richness and evenness based on separate relationships between water availability and these two measures of diversity.

Despite the variable gradient-level relationships, the relationship between richness and evenness was weakly concave-up across all of the grassy biomes. While such a relationship was not predicted in our framework, this in line with the idea that a relationship between water availability and richness, but no relationship for evenness, can result in no overall relationship between richness or evenness, or one that is (weakly) concave-up (not shown in Fig. 1, but an expectation from the combined relationships

of a hump-shaped water availability–richness relationship, and no relationship between water availability and evenness).

Conclusions

The results from our analysis of variation in richness and evenness with water availability in grassy biomes suggest that different, independent factors are likely determining patterns of species richness and evenness in grassy biomes globally, as well as regionally in some cases. The lack of evidence for significant richness–evenness relationships at regional and global scales has important implications. First, it appears that regardless of the level of species richness, either high or low, the degree of community evenness can be quite similar. Moreover, for any level of richness there can be a broad range of evenness values, and vice versa. This emphasizes the need to improve basic understanding of the processes that promote evenness in communities across spatial gradients. There are numerous hypotheses to explain patterns of richness across broad spatial gradients, but far fewer examples for explaining variation in species abundances or patterns of evenness (or dominance; Hillebrand et al. 2008). Second, our results suggest that richness and evenness may respond very differently across spatial gradients to anthropogenic changes. If this is the case, then it may be difficult to predict the real-world consequences of diversity change, given that richness and evenness likely have different drivers of change, and importantly, that there is strong evidence for more rapid changes in evenness (when compared to richness) to be the norm with anthropogenic change (Chapin et al. 2000; Avolio et al. 2021). Thus, we suggest that future research should focus on a holistic understanding of the determinants of diversity—both richness and evenness—across spatial scales and scenarios of change in the future.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00442-022-05208-6>.

Author contribution statement MDS conceptualized the questions and wrote the manuscript. SEK, MLA, SLC, SE, EJJ, KJK, and KRW contributed to conceptualizing the questions, collecting and analyzing the data, developing the figures and writing the manuscript. MDS, SEK, MLA, SLC, SE, EJJ, KJK, and KRW attended working groups to complete this manuscript, while all other co-authors contributed data to the synthesis; all authors edited the manuscript.

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Data availability The datasets and metadata used in the current study are available in EDI at the following <https://doi.org/10.6073/pasta/5a470cf13ba5576e9be366cf0f7fa6be>.

Declarations

Conflict of interest The authors declare no conflict of interest.


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