

# Stabilizing effects of biodiversity on grassland productivity under climate anomalies depend on the communities' resource use strategy

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## Abstract

The effects of climate changes on the stability of plant communities is a major concern, especially for the maintenance of ecosystem processes and services. Biodiversity may buffer communities from the effects of these disturbances, providing resistance and resilience. Here we assess the interplay between biodiversity facets on resistance and resilience of biomass productivity under anomalous dry and wet conditions in subtropical grasslands. Overall, high levels of taxonomic and functional biodiversity components, coupled to the community type derived from functional traits, positively affected the resistance under anomalous dry and wet conditions, whereas resilience was positively affected in the recovery from wet periods. We conclude that increased diversity of the plant communities can ensure ecosystem stability throughout the climatic anomalies, but this is contingent on the biodiversity component evaluated, the direction and intensity of the climatic anomaly, and the functional structure of the communities.

## Introduction

In the face of climate change, biodiversity may be an important driver of ecosystem stability (Eisenhauer *et al.* 2016; Craven *et al.* 2018; Pillar *et al.* 2018), i.e., the resistance of a given ecosystem function to change and its resilience to recover from disturbances or climate extremes (Tilman & Downing 1994; Isbell *et al.* 2015). Some studies have shown that plant biodiversity can provide resistance of primary productivity to climate extremes, but this relationship depends on the direction and intensity of the event (Isbell *et al.* 2015; Fischer *et al.* 2016; García-Palacios *et al.* 2018; Mackie *et al.* 2019; Biggs *et al.* 2020; Valencia *et al.* 2020). The biotic mechanisms driving ecosystem stability under such anomalies have been mainly addressed through experimental studies based on the manipulation of species composition (Fischer *et al.* 2016; Craven *et al.* 2018; Mackie *et al.* 2019; Biggs *et al.* 2020). Often the available evidence emerges from communities that were artificially assembled from scratch, which also entangles the effects of the disturbance involved in the manipulation (but see Jochum *et al.* 2020). Despite the importance of those findings, experimental studies may not fully translate the natural community assembly effects on the ecosystem stability under climatic anomalies.

With the predicted changes in temperature and precipitation, extreme climatic events are about to become more common (IPCC 2021). In fact, we are already experiencing it. Specifically for southeastern South America, an increase in frequency and intensity of droughts and rainfall events has been predicted (Hoover

*et al.* 2014; Souza & Manzi 2014; Gao *et al.* 2019; NOAA 2020; IPCC 2021). Climate controls vegetation phenology, while the amount and distribution of annual precipitation strongly influences the annual net primary productivity of grasslands (Sala *et al.* 1988; Pardo & Lauenroth 1995; Gordo & Sanz 2010). If water availability is constrained, there is an increasing influence of limited evapotranspiration for grassland biomass production (Vicente-Serrano *et al.* 2010). Thus, as an increase in extreme climatic events would interfere with the seasonal patterns of rainfall distribution (IPCC 2021), it is expected that this will also affect the primary productivity of plant communities. However, plant biodiversity may buffer ecosystems from the effects of these anomalies, providing resistance and resilience (Biggs *et al.* 2020).

According to the insurance hypothesis (Yachi & Loreau 1999), biodiversity should provide stability due to the functional redundancy of different species in nature. Functional redundancy in a community can be operationally defined as the difference between taxonomic and functional diversity based on traits driving ecosystem functions (Pillar *et al.* 2013), i.e., the portion of species taxonomic diversity in a community that plays similar ecosystem functions. Increased functional redundancy for a given ecosystem function implies that the community contains species that can replace each other in case of species losses due to their different environmental sensitivity (Walker *et al.* 1999; Oliver *et al.* 2015). High taxonomic diversity may also imply increased functional diversity in terms of responses to drivers such as extreme climate events, i.e., increased response diversity *sensu* Elmqvist *et al.* (2003) defined by response traits *sensu* Lavorel & Garnier (2002). In other words, on the one hand, ecosystem stability relies on the degree of functional equivalence regarding effect traits (Lavorel & Garnier 2002) of the resident species in the community (Elmqvist *et al.* 2003; Violle *et al.* 2007; Fischer *et al.* 2016). On the other hand, plant functional diversity loss in terms of response traits can be associated with a decrease in ecosystem functioning stability and hence, environmental changes that potentially affect biodiversity may induce long-term changes (Hautier *et al.* 2015).

Closely related to the insurance hypothesis, increased species diversity may induce the “portfolio effect” (Doak *et al.* 1998; Tilman *et al.* 1998). Beyond the simple idea of a statistical averaging of individual species contribution to biomass production, together, these two hypotheses predict a stabilizing effect of species diversity on ecosystem properties through species asynchrony. This mechanism ensures, via species richness and its different environmental responses, that the more species, the greater the probability of asynchronous species responses to environmental fluctuations, thus leading to an increased stability (Yachi & Loreau 1999; Loreau 2010).

Plant traits directly related to environmental conditions (Bruehlheide *et al.* 2018; Testolin *et al.* 2021) reflect a resource acquisition and conservation trade-off known as the “leaf economics spectrum” (Wright *et al.* 2004; Díaz *et al.* 2016; Garnier *et al.* 2016). The conservative side of this spectrum typically comprises species that are able to store resources and use water more efficiently. So, conservative species would withstand anomalous events, providing resistance. In the acquisitive side, species use the resources to grow faster. Therefore, they would offer less resistance during anomalous events. A similar spectrum has been observed at the community level (Bruehlheide *et al.* 2018). It is an open question, however, if communities that differ in terms of resource-use strategy would also differ regarding their stability under extreme climatic conditions. It is plausible to believe that they will. For example, under increased water availability, communities characterized by acquisitive species would benefit from resource-inputs ensuring biomass production and providing resistance. Or they could be more productive than in normal periods, leading to low resistance (Wright *et al.* 2015; Fischer *et al.* 2016). In contrast, communities defined by conservative species could maintain productivity under decreased water availability (García-Palacios *et al.* 2018)

In this study, we address the question whether plant communities with higher diversity provide increased ecosystem stability under climatic anomalies, and if the effects of biodiversity differ regarding the dominant resource-use strategy of the communities. We evaluate the effects of species richness and diversity, functional diversity and functional redundancy on the stability (i.e. resistance and resilience) of biomass production at the ecosystem level. From a taxonomic perspective, (i) we hypothesize that induced by compensatory dynamics, species richness (i.e. number of species) will present a positive effect on resilience, induced by a “portfolio effect” (Doak *et al.* 1998; Tilman *et al.* 1998; Valencia *et al.* 2020), (ii) while species diversity

will have a positive effect on resistance, corroborating the insurance hypothesis (Yachi & Loreau 1999; Loreau 2010). From a functional perspective, (iii) using traits that are relevant for biomass production, we hypothesize that functional redundancy (FR) will guarantee biomass production, with a positive effect on stability (resistance and/or resilience), whereas (iv) increased functional diversity in terms of response diversity (hereafter functional response diversity - FRD) will have a positive effect on stability (resistance and/or resilience).

Overall, high levels of species richness, species diversity, functional redundancy, and functional response diversity were positively related to the resistance of biomass productivity in dry and wet events, whereas resilience of biomass productivity to drought was positively related mostly to species richness.

## Material and methods

### *Study area and biodiversity data*

Our study sites were located in the Campos Sulinos region, southern Brazil. The Campos Sulinos encompasses the northern portion of Río de la Plata grasslands (Soriano *et al.* 1991; Andrade *et al.* 2018), along with grassland enclaves inside the southern tip of the Atlantic Forest (Andrade *et al.* 2016). The climate in the region is humid subtropical with no pronounced dry season, ranging from hot summers (Cfa type) in lowlands to temperate summers (Cfb type) in higher altitudes, according to Köppen’s classification (Alvares *et al.* 2013).

Plant species were surveyed during the growing season, which comprises spring and summer, between 2014 and 2016 (see Menezes *et al.* 2022 for more details). The communities were sampled in 108 250-m long, contour transects nested in twelve 5 x 5 km grids (Figure 1). Each transect was subsampled by 10 quadrats of 1 m<sup>2</sup>, which were pooled for our analyses, thus forming a 250-m long unit we called a “plot” for the sake of simplicity. We characterized the functional community structure of the plots using leaf traits known by their representation of ecological trade-offs involved in biomass production (Lundgren *et al.* 2014; Engel 2017; Bruelheide *et al.* 2018; Testolin *et al.* 2021), thus they were considered effect traits *sensu* Lavorel & Garnier (2002). These traits were leaf area (LA – mm<sup>2</sup>), specific leaf area (SLA – mm<sup>2</sup>.mg<sup>-1</sup>), leaf dry matter content (LDMC – g.g<sup>-1</sup>), leaf nitrogen (leaf N – mg.g<sup>-1</sup>) and photosynthetic pathway (categorical, C<sub>3</sub> or C<sub>4</sub>) which were collected from plant species sampled in situ or obtained from the TRY database (Kattge *et al.* 2011) and TRY gap-filled (Schrodte *et al.* 2015). Missing trait values were imputed (Penone *et al.* 2014) using the *missForest* function of the package *missForest* (Stekhoven & Bühlmann 2012). For all plots, with these traits we calculated single trait community-weighted means (CWM), Gini-Simpson index of species diversity (for simplicity, hereafter “species diversity”) and functional redundancy (FR; difference between Gini-Simpson index of species diversity and Rao entropy) (de Bello *et al.* 2007). Life form, considered as a response trait (Pillar & Orlóci 1993), obtained from Ferreira *et al.* (2020) or collected from virtual herbaria (BFG 2022), was used to calculate Rao’s quadratic entropy (Rao 1982), which was taken as functional response diversity. We computed CWM using the function *functcomp* of package FD (Laliberté *et al.* 2014), and species diversity, Rao entropy and functional redundancy using the function *rao.diversity* from package SYNCSA (Debastiani & Pillar 2012).

### *Functional groups of communities*

We calculated fuzzy-weighted species composition to reflect the functional relatedness among communities (Pillar *et al.* 2009; Duarte *et al.* 2016), using the *matrix.x* function of package SYNCSA (Debastiani & Pillar 2012). For that we considered only the effect traits, thus, not including the life forms. Next, based on Euclidean distances between plots, we submitted the fuzzy-weighted species composition to cluster analysis using Ward’s method. For the derived classifications up to five functional groups of plots, we tested group partition sharpness by using the bootstrap resampling procedure (Pillar 1999). Further, for a synthetic view of the functional patterns across communities we submitted the fuzzy-weighted community composition matrix to covariance-based Principal Components Analysis (PCA) and tested the significance of the ordination axes (Pillar 1999). For these analyses we used the functions *Cluster* and *Ordination* in MULTIV software (available at <http://ecoqua.ecologia.ufrgs.br>).

### Characterizing anomalous climatic events (SPEI base)

To identify climatic anomalies, we chose the standardized precipitation-evapotranspiration index (SPEI, Vicente-Serrano *et al.* 2010). We compiled it for local monthly values at time scales ranging from 1 to 48 months and at the spatial resolution  $5^\circ \times 5^\circ$ . This means that, for a given month, it represents the cumulative water balance over the previous  $n$  months. Here, we used  $n = 3$  months (SPEI-03), which presented the highest correlation with NDVI data. Based on the index values, we identified for each plot, from year 2000 to 2018, dry and wet events outside the normal range ( $-0.68 < \text{SPEI} < 0.68$ ), as well as their intensity: extreme ( $\text{SPEI} > |1.27|$ ) or moderate ( $|0.68| < \text{SPEI} < |1.27|$ ) (Vicente-Serrano *et al.* 2010).

### Biomass productivity data – NDVI

The Normalized Difference Vegetation Index – NDVI is a spectral indicator widely used to quantify photosynthetic activity, which is a proxy for biomass production, an indicator of ecosystem functioning (Pettorelli *et al.* 2005; De Keersmaecker *et al.* 2017). Here, we employed NDVI data at the 250 m resolution for the period of 2000 to 2018, with 23 acquisitions per year for each one of the 108 plots. The original data were obtained from the MODIS product MOD13Q (Didan 2015), available through the Google Earth Engine (Google Earth Engine Team 2015). NDVI values were subjected to a smoothing process (Savitzky & Golay 1964) using the function *savgol* of *pracma* package (Borchers 2021).

### Ecosystem level temporal stability

Temporal stability is a measure of the productivity change (increase or decrease) during a climatic anomaly. We calculated resistance [Eq 1] and resilience [Eq 2] following Isbell *et al.* (2015), for each plot at each anomalous climatic event. We log-transformed the values to smooth outliers with no clear ecological meaning, which also avoided the denominator in the equations approaching zero.

The first step was to use normal SPEI events to calculate the average productivity of each plot for each month in the time series (2000 to 2018). This average for normal periods was adopted as the productivity baseline,  $Y_n$ .

Resistance describes the change of NDVI related to its baseline:

$$\Omega = \log \left( \frac{Y_n}{|Y_e - Y_n|} \right) \text{ [Eq 1]}$$

Resilience describes the return ratio to baseline value:

$$= \log \left( \frac{Y_e - Y_n}{Y_{e+1} - Y_{n+1}} \right) \text{ [Eq 2]}$$

In these equations,  $Y_e$  e  $Y_{e+1}$  are, respectively, the ecosystem productivity during a climatic anomaly, and after a climatic anomaly. We calculated resilience only when an anomalous event with productivity  $Y_e$  at a given month was followed by at least two normal months. Note that the identified anomalous events may not be synchronous across plots at the regional scale, but they were synchronous at the spatial resolution of our  $5 \times 5$  km grids.

### Data analysis

We applied separate linear mixed-effects models to each group of communities defined by their functional similarities and for each type of climatic event (moderate and extreme dry and wet events). Resilience and resistance were treated as response variables and were modeled as a function of a single fixed effect of biodiversity descriptors (taxonomic richness or diversity, functional redundancy or functional response diversity), and the season of the climatic event as a random effect (summer, spring, autumn, winter). The fixed effects were standardized to allow comparison of the effects among biodiversity descriptors. We used the packages *lme4* (Bates *et al.* 2015), *lmerTest* (Kuznetsova *et al.* 2017) and *MuMIn* (Bartoń 2020) to run all models.

For data treatment and manipulation, we used tidyverse package (Wickham *et al.* 2019). The figures were created using ggplot2, from tidyverse package. All data treatment and analyses were performed in R (R Core Team 2019).

## Results

### *Distribution of extreme climatic events*

Across the 18 years we identified a total of 2,724 monthly SPEI-03 values, which were classified as normal periods or anomalous climatic events. Outside normal periods, 36% were wet events, among which 20% were extreme and 16% were moderate wet events. The dry events represented 24%, among which 11% were extreme and 13% were moderate dry events (Figure S1).

### *Taxonomic and functional characteristics of communities*

Based on the fuzzy-weighted species composition, the grassland communities were classified into five groups, which form a functional gradient from groups G1 to G5 (Figure 2). At one end group G1 comprises communities with high LDMC, LA and predominantly C<sub>4</sub> species, whereas at the other end group G5 represents communities with high SLA, leaf N and predominantly C<sub>3</sub>. Most of the variation across communities is related to the leaf economic spectrum, represented in the PCA ordination. The first principal component explained 94.97% (P-value < 0.0001) of the variation and was positively correlated to SLA, leaf N and predominance of C<sub>3</sub> species in the communities, and negatively correlated to LDMC and LA. The second principal component explained only 2.91% (P-value = 0.001) and was positively correlated with high SLA, and leaf N, while negatively correlated with LDMC, LA and C<sub>3</sub> species.

The correlations between biodiversity descriptors varied across community functional groups (Figure 3). The correlations between species richness with species diversity, and between species diversity with FR were positive for all community groups. For G1 and G5 communities, all relationships were positive, however, they were stronger for G1. For G2 communities, the correlations between species richness were negative with both FR and functional response diversity. Moreover, species diversity and functional response diversity were also negatively correlated. Regarding G3 and G4 communities, the correlations between functional response diversity were negative for both, species diversity and FR.

In general, anomalous climatic events triggered more positive than negative effects of biodiversity on both communities' resistance and resilience, and their estimated effects varied across community groups and climatic events (Figures 4, 5, S2, and Tables S1 and S2).

### *Biodiversity effects on resistance*

We found analogous taxonomic components effects on communities' resistance. Such as a gradient in the effects of species richness and species diversity on the resistance of the communities under all anomalous events, ranging from strong and positive in group G1 to weaker and negative in group G5 (Figure 4a-b). Species diversity (Gini-Simpson) effects on resistance were positive in G2 and G3 communities under both extreme dry and wet events, while in G4 and G5, its effects were negative under both moderate and extreme wet events (Figure 4b).

Regarding the functional components of biodiversity, we also found similar effects on communities' resistance. For instance, both functional redundancy and functional response diversity effects on the resistance of G1 communities were strong and positive under all anomalous events, whereas variable and weaker in the other community groups (Figure 4c-d). In addition, functional redundancy effects were positive in G3 and G5 under extreme dry anomalous events, while under extreme wet they were positive in communities G2 and negative in G4 (Figure 4c). The effect of functional response diversity was negative for G2, G3 and G4 communities under extreme dry anomalous events (Figure 4d), yet under moderate dry events, it was positive in G3 and G5 (Figure 4d).

### *Biodiversity effects on resilience*

We found predominant, yet scarce positive effects of all biodiversity predictors on the resilience of communities recovering mainly from wet events (Figure 5a-d), whereas the negative effects, mostly in communities recovering from dry anomalous events (Figure 5a-d).

## Discussion

Despite the productivity of the native grassland communities tended to be lower than the baseline during dry events and higher than the baseline during wet events (Figures S3-5), our results showed that the effects of biodiversity on both resistance and resilience depend on the community functional structure, on the biodiversity component evaluated and the direction and intensity of anomalous climatic events.

Although the effects of biodiversity on the ecosystem resistance were mostly positive, they were closely related to the community type defined in terms of functional traits, irrespective of the direction or intensity of climatic events. To examine this pattern, we grouped the studied grassland communities by their functional relatedness (Figure 2) based on traits that are relevant for biomass production and water and nutrient balance (Lundgren *et al.* 2014; Engel 2017; Bruelheide *et al.* 2018; Testolin *et al.* 2021). Hence, along the first axis (Axis I; Figure 2), positive scores can be interpreted as communities dominated by acquisitive species (high SLA, Leaf N, C3), and therefore, it is expected that they would be predominantly drought sensitive (Griffin-Nolan *et al.* 2018). Along the same first axis, communities with negative scores indicate dominance by conservative species (high LDMC) and thus, predominantly drought resistant (Shi *et al.* 2016; García-Palacios *et al.* 2018). Our results showed that the effects of biodiversity on resistance were predominantly positive and stronger in resource-conservative communities, while they were predominantly negative and weaker in resource-acquisitive communities (Table S1). Considering biodiversity effects on the ecosystem resilience, they were more pronounced for resource-acquisitive communities and mainly positive under wet events (Table S2).

From a taxonomic perspective, species richness and species diversity were negatively correlated with species dominance in all groups. Species richness affects resistance, as we predicted and has already been shown by others (Hautier *et al.* 2015; Isbell *et al.* 2015). However, regardless of the direction or intensity of the climatic events, species richness increased ecosystem resistance in resource-conservative communities', while it decreased resistance in resource-acquisitive communities. Considering resource-acquisitive communities under wet events, species richness negative effects on resistance may indicate an increased biomass production given water/resource inputs (Fischer *et al.* 2016) (Figures 4, S2 and S4). Interestingly, positive effects of species richness on resilience were only observed in communities recovering from wet events, while the effects on the recovery from dry events were negative. According to the portfolio effect (Doak *et al.* 1998; Tilman *et al.* 1998), ecosystem stability may be ensured by maintaining high levels of species richness, but our results show that this may be consistently observed only in resource-conservative communities.

Species diversity also increased the resistance of grassland communities. However, its effect was evidenced under extreme dry and extreme wet climatic events, increasing the ecosystem resistance of resource-conservative communities, thus partially supporting our hypothesis. For resource-acquisitive communities under moderate and extreme wet events, an increased species diversity had a negative effect on resistance and a positive effect on resilience. Therefore, given resource-acquisitive communities facing wet events, species diversity may induce a compensatory stabilizing mechanism of biomass production (Lehman & Tilman 2000; Grman *et al.* 2010; Mackie *et al.* 2019).

From the functional perspective, we observed a consonant result between species diversity and functional redundancy effects on ecosystems' resistance, as we predicted, according to the insurance hypothesis (Yachi & Loreau 1999). Their high positive correlation values indicate that the functional redundancy found in the communities is promoted by species diversity more than by the number of species per se. Functional redundancy had a strong positive effect on the resistance of the most resource-conservative communities facing extreme dry and wet events. In turn, ecosystems' resilience of resource-acquisitive communities was increased by functional redundancy while recovering from moderate dry and extreme wet events.

The effect of functional response diversity on resistance was dependent on the community functional struc-

ture, as it was mainly observed in resource-conservative communities and was independent from the anomalous climatic events. However, given the resource-conservative communities, we observed contrasting effects. While in communities where species richness and functional response diversity were positively related, in general functional response diversity had a positive effect on ecosystem resistance, and in communities where the relationship was negative, its effect was negative. Thus, we may conclude that a positive relationship between species richness and traits reflecting functional response diversity (Lavorel & Garnier 2002; Elmqvist *et al.* 2003) plays an important role on the resistance, according to the insurance hypothesis (Yachi & Loreau 1999).

As already highlighted (Isbell *et al.* 2015; Wright *et al.* 2015), when analyzing empirical data, it may be difficult to completely decouple resistance and resilience, especially when disturbances are recurrent. This implies a challenge to distinguish resistance and resilience over a temporal time series once both may be skewing each other. However, it should be further explored in future studies, for example, by looking for periods when productivity no longer depends on the previous anomalous event. Additionally, this is an important issue considering the already known dangerous effects of climate change on ecosystem stability (Hautier *et al.* 2015; Craven *et al.* 2018; García-Palacios *et al.* 2018; IPCC 2021).

Here we have shown that the ecosystem stability measured as resistance and resilience of native grasslands depend on the biodiversity metric evaluated in the communities and the direction and intensity of the climatic anomaly. In addition, more than a single taxonomic or functional component, communities' functional structure plays an important role in driving the effects of biodiversity on ecosystem resistance and resilience under different anomalous climatic events. This emphasizes the importance to consider different components of biodiversity when investigating ecosystem services under climate change. There is no unified measure able to synthesize all the possible answers of the ecosystems under climate change. Moreover, our results stressed the importance of biodiversity to guarantee grassland biomass productivity under disturbance events generated by climate change. As climate change models indicate that the intensity and frequency of wet events are likely to increase in the Campos Sulinos region (IPCC 2021), there is a pressing need for further studies to help understand ecosystem-level response to such disturbances.

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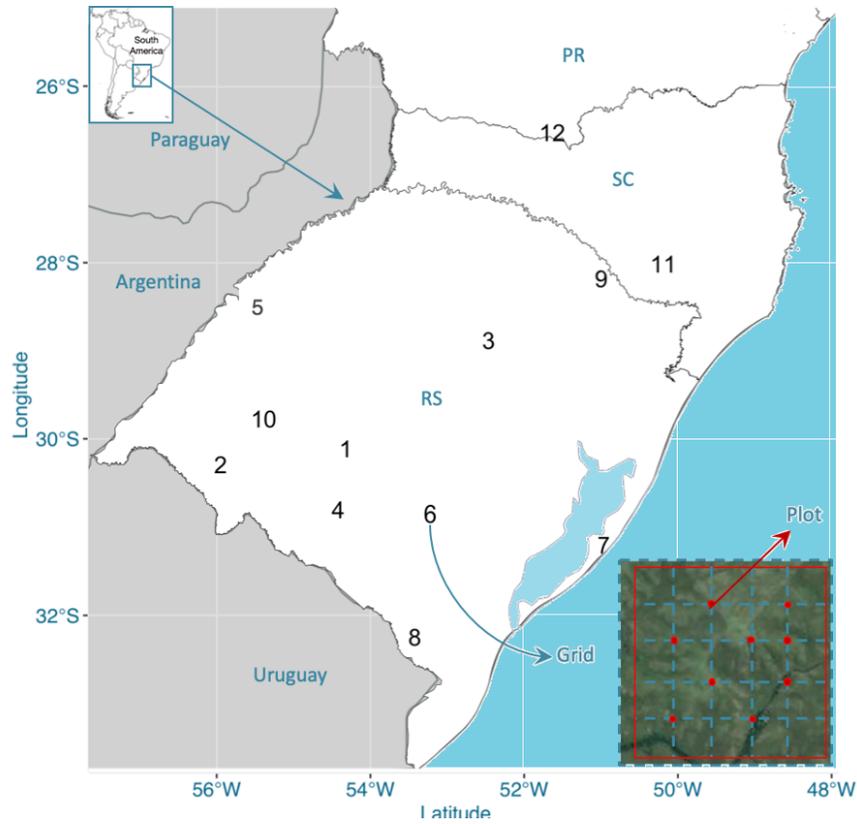
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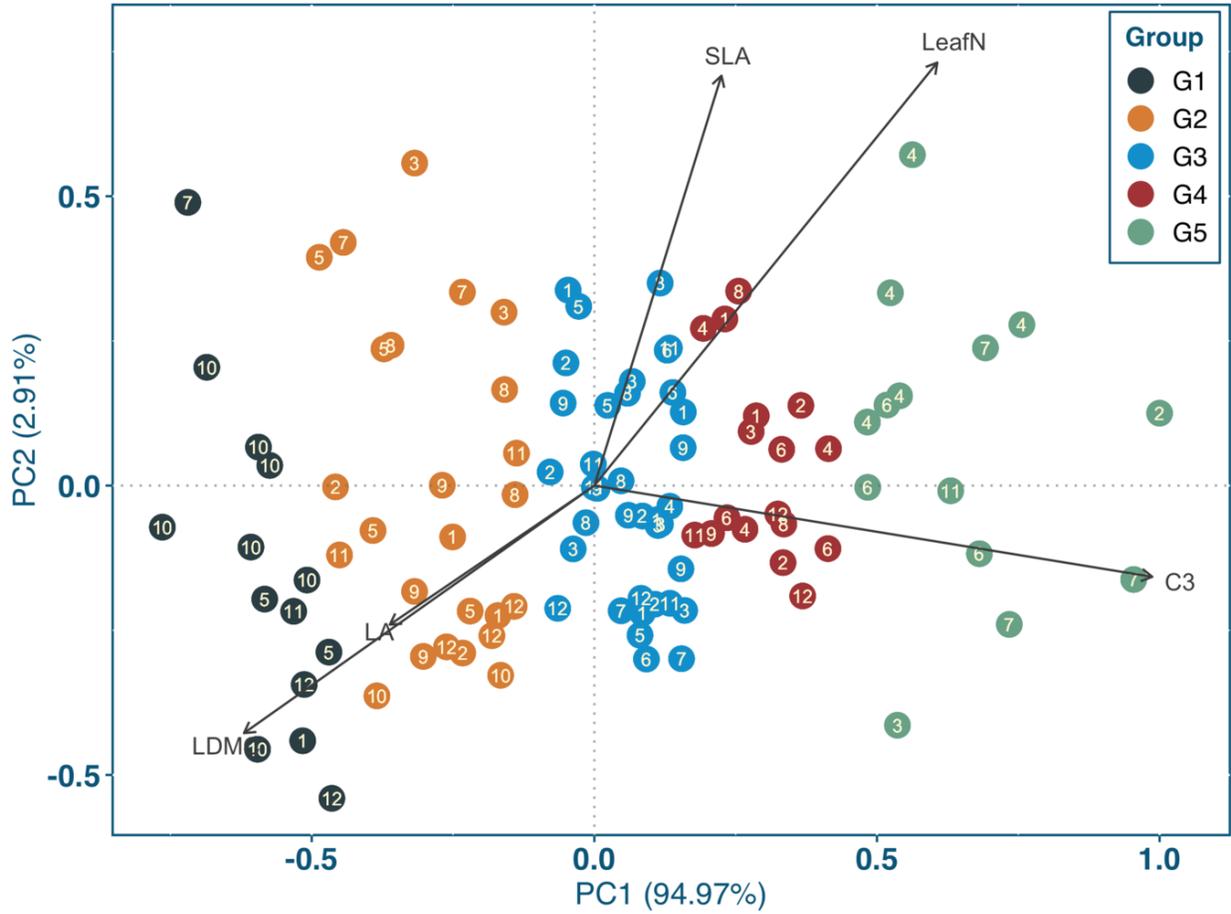
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## Figures



**Figure 1:** Distribution of the twelve grids (represented by numbers: 1 – São Gabriel, 2 – Quaraí, 3 – Soledade, 4 – Lavras do Sul, 5 – Santo Antônio das Missões, 6 – Santana da Boa Vista, 7 – Tavares, 8 – Jaguarão, 9 – Vacaria, 10 – Alegrete, 11 – Paineira, 12 – Palmas) in the Campos Sulinos grasslands in south Brazil. In the representation of one 25 km<sup>2</sup> grid, the red dots point to nine 250-m long contour transects. Each transect (taken as a plot) was subsampled systematically by ten quadrats of 1 m<sup>2</sup>.

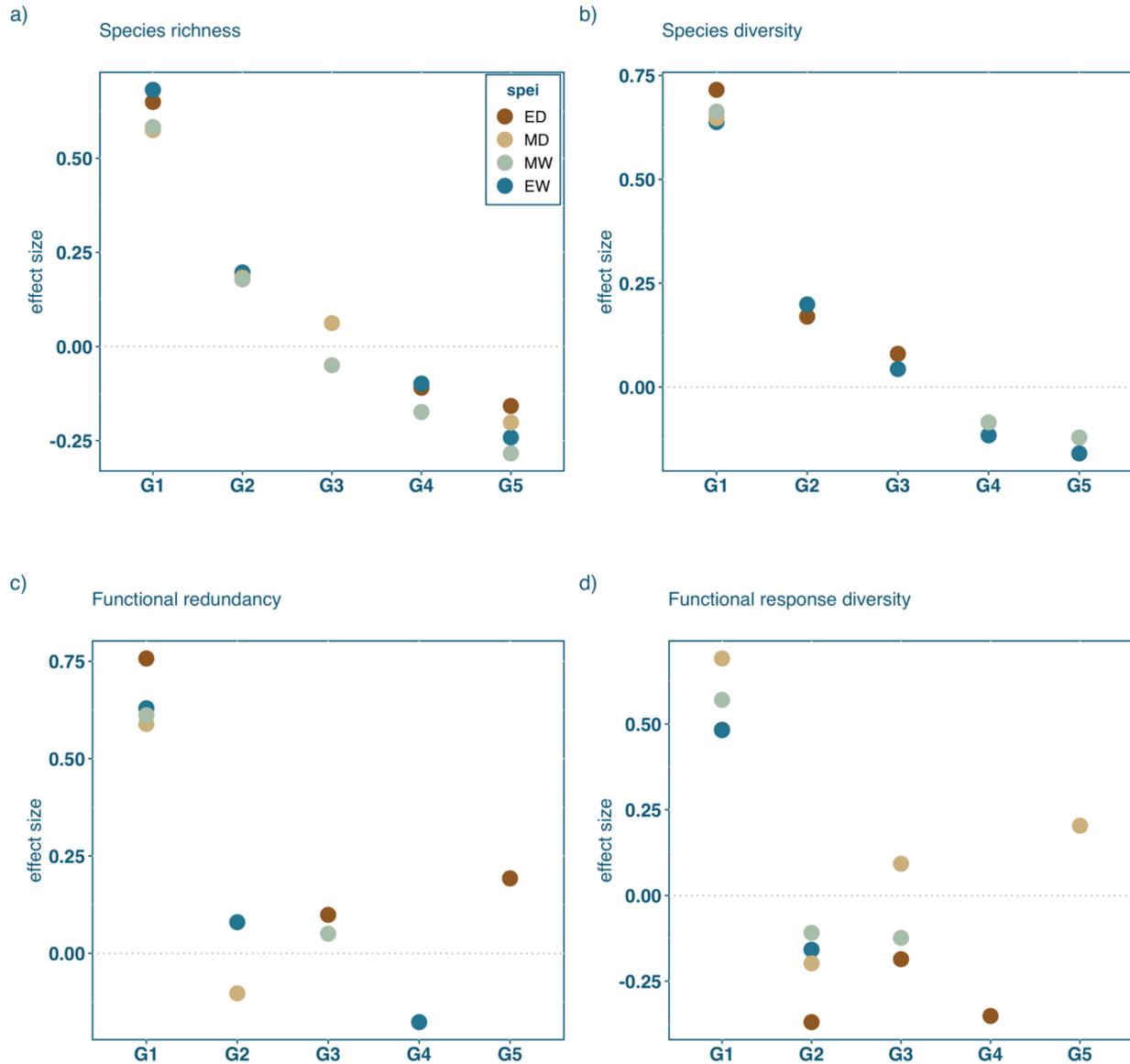


**Figure 2:** Principal Components Analysis ordination of the studied grassland vegetation communities gathered in groups (indicated in the panel) described by fuzzy-weighted species composition based on functional relatedness among species. Post hoc correlations of PCA axes with traits are shown in gray. Arrows indicate community-weighted means for the traits based on their correlations with the ordination axes. The numbers refer to the sites (1 – São Gabriel, 2 – Quaraí, 3 – Soledade, 4 – Lavras do Sul, 5 – Santo Antônio das Missões, 6 – Santana da Boa Vista, 7 – Tavares, 8 – Jaguarão, 9 – Vacaria, 10 – Alegrete, 11 – Paineis, 12 – Palmas, see Fig. 1 for site location) and are repeated nine times each, indicating plots belonging to the same grid. Colors represent groups of functional relatedness, as indicated by the key on the top right.

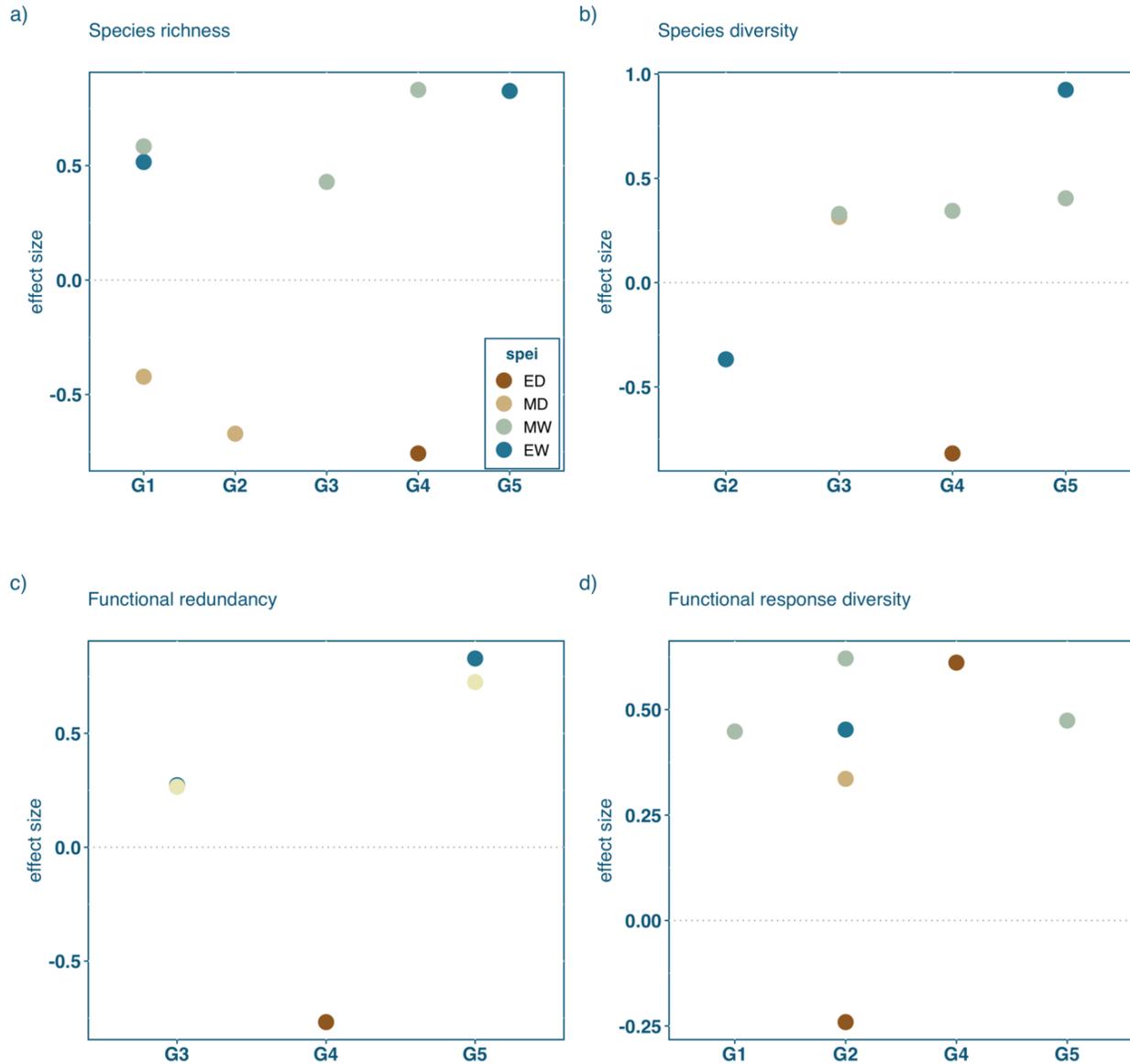
SR	0.589	0.442	0.288	All
SD		0.923	0.541	
FR			0.527	
SR	0.811	0.767	0.589	G1
SD		0.979	0.803	
FR			0.725	
SR	0.282	-0.05	-0.16	G2
SD		0.806	-0.224	
FR			0.003	
SR	0.633	0.304	0.157	G3
SD		0.857	-0.161	
FR			-0.219	
SR	0.575	0.362	0.053	G4
SD		0.75	-0.041	
FR			-0.327	
SR	0.661	0.228	0.32	G5
SD		0.756	0.594	
FR			0.221	
	SD	FR	FRD	

Figure 1:

**Figure 3:** Correlation between biodiversity predictors (SR – species richness, SD – species diversity, FR – functional redundancy, FRD - functional response diversity) considering all plots and separated by groups of functional relatedness (G1-G5).



**Figure 4:** Relative effects (standardized slopes of linear mixed effects) of taxonomic predictors species richness (a), Gini-Simpson index of species diversity (b), functional redundancy (c) and functional response diversity (d) on the resistance of grassland vegetation communities for the distinct community functional groups, representing the resource-use strategy. The parameter estimates (standardized regression coefficients) represent only coefficients that differ from zero. Colors and symbols represent dry: extreme – ED and moderate – MD; and wet: extreme – EW and moderate – MW anomalous climatic events classified according to SPEI-03, as indicated by the key on the top left panel (a).



**Figure 5:** Relative effects (standardized slopes of linear mixed effects) of taxonomic predictors species richness (a), Gini-Simpson index of species diversity (b), functional redundancy (c) and functional response diversity (d) on the resilience of grassland vegetation communities for the distinct community functional groups, representing the resource-use strategy. The parameter estimates (standardized regression coefficients) represent coefficients that differ from zero. Colors and symbols represent dry: extreme – ED and moderate – MD; and wet: extreme – EW and moderate – MW anomalous climatic events classified according to SPEI-03, as indicated by the key on the top left panel (a).