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Tese de Doutorado

Stabilizing mechanisms of grassland communities under disturbance

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Dedico esta tese a todos os cientistas que lutam e lutaram as mais diversas

batalhas para estarmos vivos hoje.

Viva a ciência.

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1 Resumo

2   O objetivo geral desta tese foi avaliar os efeitos da biodiversidade nativa

3 campestre sobre a estabilidade ecossistêmica diante de anomalias climáticas de

4 precipitação pluvial. No **primeiro capítulo**, *Grassland stability: the role of biodiversity*

5 *in the face of climate change*, avalio o efeito de distintos componentes da

6 biodiversidade campestre na estabilidade ecossistêmica sob anomalias climáticas

7 de precipitação. Nesse capítulo foram utilizados dados obtidos nos levantamentos

8 florísticos do projeto PPBio para os Campos Sulinos. Os resultados indicam que a

9 estabilidade ecossistêmica dos Campos Sulinos está relacionada positivamente com

10 a biodiversidade, porém isso depende da métrica de diversidade avaliada e da

11 direção e intensidade das anomalias climáticas. No **segundo capítulo**, *A global*

12 *assessment on the effects of plant functional redundancy on grassland ecosystems'*

13 *stability during climatic anomalies*, emprego o arcabouço analítico desenvolvido no

14 capítulo I para avaliar os efeitos da diversidade taxonômica e funcional na resistência

15 e na resiliência de sistemas campestres sob influência de eventos climáticos

16 anômalos em uma escala global. Nesse capítulo, utilizo a base de dados sPlot para

17 obter informações sobre comunidades campestres amostradas ao redor do mundo.

18 Os resultados indicam que a biodiversidade da vegetação é preditiva da resistência

19 e resiliência nos ecossistemas campestres ao redor do mundo, no entanto, a relação

20 entre biodiversidade e estabilidade depende da métrica avaliada, da estrutura

21 funcional da comunidade e da direção e intensidade da anomalia climática.

22 Finalmente, no **terceiro capítulo** *Biodiversity manipulation via removals*, que está

23 estruturado como um reporte metodológico, apresento um arcabouço para

24 experimentos de remoção de BEF, juntamente com um algoritmo que se propõe a

minimizar erros associados à falta de controle de alguns componentes da diversidade que não são alvo do estudo. Aplicamos essa estrutura experimental em um experimento de remoção com comunidades campestres nativas, nas quais manipulei a diversidade para avaliar o efeito da redundância funcional na resistência e na resiliência da produtividade sob condições hídricas extremas.

Abstract

The main objective of this thesis was to evaluate the effects of native grassland biodiversity on ecosystem stability in the face climatic anomalies. In the **first chapter**, *Grassland stability: the role of biodiversity in the face of climate change*, I assessed the effect of different components of grassland biodiversity on ecosystem stability under climatic precipitation anomalies. In this chapter, data obtained from floristic surveys of the PPBio project for Campos Sulinos were used. The results indicate that the Campos Sulinos ecosystem stability is positively related to biodiversity, but this depends on the diversity metric evaluated and the direction and intensity of climatic anomalies. In the **second chapter**, *A global assessment on the effects of plant functional redundancy on grassland ecosystems' stability during climatic anomalies*, I use the analytical framework developed in the first chapter to assess the effects of taxonomic and functional diversity on the resistance and resilience of grassland systems under influence of anomalous climatic events on a global scale. In this chapter, I use the sPlot database to obtain information about grassland communities sampled around the world. The results indicate that vegetation biodiversity is predictive of resistance and resilience in grassland ecosystems around the world, however, the relationship between biodiversity and stability also depends on the

evaluated metric, the functional structure of a community and the direction and intensity of the climatic anomaly. Finally, in the **third chapter** *Biodiversity manipulation via removals*, which is structured as a methodological report, I present a framework for BEF removal experiments, along with an algorithm that proposes to minimize biases associated with the lack of control of some diversity components that do not are the target of the study. We applied this experimental framework to a removal experiment with native grassland communities, in which I manipulated functional redundancy via species richness removal to assess its the effect on resistance and resilience under extreme dry and wet conditions.

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1 Introdução geral

2   Eventos climáticos extremos e o manejo pastoril são distúrbios que podem

3 alterar a biodiversidade, a resistência e a resiliência de comunidades, interferindo

4 assim na manutenção dos serviços ecossistêmicos. A biodiversidade assegura

5 processos ecossistêmicos conferindo estabilidade às comunidades, de forma que

6 quanto mais biodiversidade existe em uma área, maior é a probabilidade de que as

7 funções ecossistêmicas sejam mantidas em caso de distúrbios que levem à perda

8 de espécies (Yachi & Loreau 1999; Pillar et al. 2013; Isbell et al. 2015).

9   Define-se como distúrbio qualquer evento discreto relativo no tempo que

10 interrompe a estrutura do ecossistema, da comunidade ou da população e altera a

11 disponibilidade de recursos (Pickett & White 1986). Por sua vez, a estabilidade pode

12 ser definida para uma determinada função desempenhada pela biodiversidade,

13 como por exemplo, a produção de biomassa (utilizada como sinônimo de

14 produtividade). É possível particionar a estabilidade em dois componentes:

15 resistência e resiliência. Enquanto a primeira métrica indica o quanto a produtividade

16 aumenta ou diminui em função de um distúrbio, a outra serve para avaliar a taxa de

17 retorno a níveis de produtividade anteriores ao distúrbio (Pimm 1984; Tilman &

18 Downing 1994a; Isbell et al. 2015). Comunidades mais diversas em sua composição

19 de espécies podem assegurar a manutenção de funções ecossistêmicas durante

20 distúrbios, devido ao aumento da probabilidade de que nelas existam espécies

21 capazes de responder rapidamente ao distúrbio e desempenhar a função deixada

22 vaga pela espécie excluída (Tilman & Downing 1994b; Elmqvist et al. 2003; Isbell et

23 al. 2011). Assim, a presença de espécies menos resistentes nas comunidades pode

24 ser compensada por outras mais tolerantes ao distúrbio (Yachi & Loreau 1999). O

que determinará a capacidade de a espécie resistir ao distúrbio é o conjunto de seus atributos funcionais. Atributos são as características que mensuramos nas espécies para descrever sua relação com as demais espécies e o meio. Numa perspectiva ecossistêmica, os atributos podem auxiliar no esclarecimento do efeito de um conjunto de espécies em uma determinada propriedade ecossistêmica, como a produtividade, diante de alterações ambientais, como as mudanças climáticas.

Apesar de muitos retrocessos no âmbito ambiental, há um crescente reconhecimento e preocupação em relação às mudanças climáticas. Dentre elas, alterações na intensidade e frequência de anomalias na precipitação pluviométrica (IPCC 2021). Dado que serviços ecossistêmicos são dependentes de determinadas condições climáticas (Sala et al. 1988; Paruelo & Lauenroth 1995; Gordo & Sanz 2010), é fundamental que se avance na compreensão de como anomalias climáticas podem alterar as relações entre a biodiversidade e o funcionamento ecossistêmico, e em consequência, o bem-estar humano

Ao longo desta tese, testo a hipótese geral de que comunidades vegetais campestres mais diversas em sua composição de espécies, bem como em seus atributos funcionais, são mais estáveis frente a distúrbios. E proponho a avaliação dos efeitos da biodiversidade campestre sobre a estabilidade ecossistêmica diante de anomalias climáticas de precipitação pluvial. A tese é composta por três capítulos que integram diferentes abordagens metodológicas em diferentes escalas espaciais. No primeiro capítulo, "Grassland stability: the role of biodiversity in the face of climate change", avalio o efeito da redundância funcional na estabilidade ecossistêmica de comunidades campestres sob anomalias climáticas de precipitação. As análises integram dados obtidos nos levantamentos florísticos de um projeto de pesquisa em

biodiversidade (PPBio), atributos funcionais das espécies campestres e o índice NDVI do satélite MODIS como indicativo do funcionamento ecossistêmico, um proxy da produção mensal de biomassa. No segundo capítulo, "A global assessment on the effects of functional redundancy on grassland ecosystems' stability during climatic anomalies", emprego o arcabouço analítico desenvolvido no primeiro capítulo para avaliar os efeitos da diversidade taxonômica, da estrutura funcional e da redundância funcional na resistência e na resiliência de sistemas campestres sob influência de eventos climáticos extremos, em uma escala global. Nesse capítulo, utilizo a base de dados sPlot para obter informações sobre comunidades campestres amostradas ao redor do mundo, o índice de NDVI como proxy da produtividade e o índice SPEI para classificar eventos climáticos anômalos. No terceiro capítulo, "Biodiversity manipulation via removals", apresento algumas lacunas de conhecimento relacionadas a experimentos de remoção de biodiversidade e proponho como abordar essas questões. Finalmente, apresento um experimento de remoção, desenvolvido com comunidades naturais, onde manipulei a diversidade para avaliar o efeito da redundância funcional na resistência e na resiliência da produtividade sob condições hídricas extremas.

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Capítulo 1

Grassland stability: the role of biodiversity in the face of

climate change

Grassland stability: the role of biodiversity in the face of climate change[1]

Running title: Biodiversity role in the face of climate change

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1   **Abstract**

2   Climate changes are expected to increase frequency and intensity of extreme

3   climatic events. The effects of such disturbances on the stability of plant communities

4   is a major concern, especially for the maintenance of ecosystem processes and

5   services needed to ensure human welfare. Yet, biodiversity may buffer communities

6   from the effects of these anomalies, providing resistance and resilience. Here we

7   assess the relations between biodiversity and the stability of biomass productivity

8   under anomalous climatic events of drought and rainfall on subtropical grasslands in

9   southern Brazil. We used data on plant species composition, functional traits, and

10   ecosystem productivity for 250-m long plots located in twelve 5-km grids. For each

11   plot, we retrieved a monthly based 18-year time series of NDVI, as a proxy for plant

12   productivity, using MODIS data. We defined climatic events using the SPEI-03 index,

13   which quantifies temporal variations in water balance on a 0.5-degree spatial

14   resolution. This allowed us to classify every month for each plot into dry or wet events

15   outside the normal range, as well as their intensity: extreme or moderate. For each

16   plot, using normal SPEI months, we calculated the baseline as the mean monthly

17   NDVI observed. We quantified resistance as the relative change of NDVI from its

18   baseline, and resilience as the rate of return to the baseline. We found that the

19   resistance and the resilience of native grassland communities are related to

20   biodiversity, but it depended on the metric evaluated and the direction and intensity

21   of the climatic anomaly. Overall, high levels of species richness, species diversity,

22   functional diversity, and functional redundancy were positively related to the

23   resistance of biomass productivity in dry and wet events, whereas resilience of

24   biomass productivity to drought was positively related mostly to species richness.

1   We conclude that high diversity of the plant communities can ensure ecosystem

2   stability throughout the climatic anomalies registered so far in the studied grasslands.

3   Further, detecting the effects of biodiversity on the stability depends on the

4   biodiversity dimension and the functional characteristics considered.

5

6

8

9   **Introduction**

10   Understanding the impacts of climate change should include evaluating the

11   effects of biodiversity on the stability of ecosystem functions and processes

12   (Eisenhauer *et al.* 2016; Pillar *et al.* 2018). There is evidence that biodiversity can

13   provide ecosystem stability (Isbell *et al.* 2015). Ecosystem stability can be defined for

14   a given function as the resistance to change and the resilience to recover from

15   disturbance (Tilman & Downing 1994; Isbell *et al.* 2015). According to the insurance

16   hypothesis (Yachi & Loreau 1999), biodiversity provides stability of a given ecosystem

17   function due to the redundancy of species roles in nature; thus, once some species

18   may go extinct due to their response to changes in some drivers, others may stay

19   and maintain the ecosystem functions. Therefore, plant diversity loss is associated

20   with a decrease in stability and hence, environmental changes that potentially affect

21   biodiversity may induce long-term ecosystem changes (Hautier *et al.* 2015).

22   Communities may suffer changes in biomass production due to disturbances

23   caused by extreme climatic events, compromising ecosystem stability. The biomass

24   production (hereafter used as synonym of productivity) during normal climatic periods

1 is the productivity baseline. Under anomalous climatic events, productivity may

2 increase or decrease, and its deviation from the baseline is a measure of resistance.

3 The farther from the baseline, the lower the resistance (Isbell *et al.* 2015). Meanwhile,

4 resilience is the rate of return to the productivity baseline after the disturbance (Isbell

5 et al. 2015). The faster the recovery, the higher the resilience. Both resistance and

6 resilience result from interactions between biodiversity and disturbances. Closely

7 related to the insurance hypothesis, increased species diversity may induce the

8 "portfolio effect" (Doak *et al.* 1998; Tilman *et al.* 1998). Beyond the simple idea of a

9 statistical averaging of individual species contribution to biomass production,

10 together, these hypotheses predict a stabilizing effect of species diversity on

11 ecosystem properties through species asynchrony. This mechanism ensures, via

12 species richness and their different environmental responses, that the more species,

13 the greater the probability of asynchronous species responses to environmental

14 fluctuations, thus leading to an increased stability (Yachi & Loreau 1999; Loreau

15 2010).

16   If we consider the functional component of biodiversity, dominant species that

17 are functionally dissimilar in their responses to environmental drivers but are similar

18 (redundant) in their roles in ecosystem functions, may enable a community to

19 overcome climatic anomalies and keep ecosystem functions, thus being more

20 resistant and/or resilient. Functional redundancy of a community can be defined as

21 the difference between taxonomic and functional diversity regarding their roles in

22 ecosystem functions (Pillar *et al.* 2013), i.e., the portion of species taxonomic diversity

23 in a community that plays similar ecosystem functions. Therefore, it is expected that

24 increased functional redundancy for a given ecosystem function implies that the

community contains several species that can maintain the same function such as biomass production. It is also expected that such high taxonomic diversity may also imply increased functional diversity in terms of responses to drivers such as disturbances, i.e., increased response diversity sensu Elmqvist *et al.* (2003) defined by response traits sensu Lavorel & Garnier (2002). In other words, ecosystem stability relies on the degree of functional equivalence, in terms of effect traits (Lavorel & Garnier 2002) of the resident species in the community and the direction and intensity of the climatic anomaly (Elmqvist *et al.* 2003; Violle *et al.* 2007; Fischer *et al.* 2016).

Plant traits related to environmental conditions (Bruelheide *et al.* 2018; Testolin *et al.* 2021) reflect a resource acquisition and conservation trade-off known as the "leaf economics spectrum" (Díaz *et al.* 2016). The conservative side of this spectrum typically comprises species that are able to allocate resources and use water in a more efficient way. Therefore, conservative species could withstand water restrictions maintaining the biomass production, thus providing resistance. Acquisitive species, use the resources to grow faster. Under increased water inputs these species may ensure biomass production, providing resistance, or even overshoot its normal levels, leading to low resistance. Given that communities can share a great similarity in terms of their organization and function (Elmqvist *et al.* 2003), even if they are not spatially close or sharing species, resistance and resilience should be defined by the functional structure. So, the communities are described not only by their taxonomic or functional characteristics, but by merging the concept of functional redundancy in the context of a given ecosystem function and environmental factors.

Some studies have shown that biodiversity can provide resistance to disturbance, but not resilience, and that this relationship is not only mediated by climate itself, as it also depends on the direction and the intensity of the disturbance (Isbell *et al.* 2015; Fischer *et al.* 2016; García-Palacios *et al.* 2018; Mackie *et al.* 2019). Further, there is increasing knowledge about the importance of species functional diversity and functional redundancy on the stability of ecosystems (Fischer *et al.* 2016; Mackie *et al.* 2019; Biggs *et al.* 2020). Therefore, the use of biodiversity and its functional descriptors should be considered as predictors, instead of response, to understand the impacts of climatic anomalies on ecosystem functioning (Craven *et al.* 2018; Pillar *et al.* 2018). The biotic mechanisms driving ecosystem stability under such anomalies have mainly been addressed through experimental studies, where species manipulation is a common practice (Fischer *et al.* 2016; Craven *et al.* 2018; Mackie *et al.* 2019; Biggs *et al.* 2020). Consequently, the available evidence emerges from artificially assembled communities, and its inherent manipulations. Despite the importance of those findings, experimental studies may not fully translate the natural community assembly effects on stability under climatic anomalies.

With the predicted changes in temperature and precipitation, extreme climatic events are about to become more common. In fact, we are already experiencing it. Specifically in terms of precipitation, 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; Paruelo & 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, we can expect that an increase in extreme climatic events would interfere with the seasonal patterns of rainfall distribution (IPCC 2021), affecting the primary productivity of vegetation communities. However, plant biodiversity may buffer ecosystems from the effects of these anomalies, providing resistance and resilience (Biggs *et al.* 2020).

Our question is whether plant communities with higher diversity provide increased ecosystem stability under climatic anomalies. Here, we propose to evaluate the effects of richness, species 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 species richness will present a positive effect on resilience, induced by a "portfolio effect" (Doak *et al.* 1998; Tilman *et al.* 1998), (ii) while species diversity will have a positive effect on resistance, led by the insurance hypothesis (Yachi & Loreau 1999; Loreau 2010). From a functional perspective, (iii) using traits that are relevant for biomass production, we hypothesize that FR will guarantee biomass production, with a positive effect on stability (resistance and/or resilience). Whereas (iv) increased FD 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 diversity, and functional redundancy 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

1   Our studied sites were located within the Campos Sulinos region, southern

2   Brazil. The Campos Sulinos encompasses the northern portion of Río de la Plata

3   grasslands (Soriano *et al.* 1991; Andrade *et al.* 2018), along with grasslands enclaves

4   from the southern tip of Atlantic Forest – highland grasslands, Andrade *et al.* (2016).

5   The climate in the region is humid subtropical with no pronounced dry season,

6   ranging from hot summers (Cfa type) to temperate summers (Cfb type) in higher

7   altitudes, according to Köppen's classification (Alvares *et al.* 2013).

8   Plant species were surveyed during the growing season between October

9   2014 and March 2015 (see Menezes *et al*. 2020 for more details). The communities

10   were sampled in 108 250-m long transects nested in twelve 5 x 5 km grids (Figure 1).

11   Each 250-m long transect was subsampled by 10 quadrats of 1 m^2, which were

12   pooled for our analyses, thus forming a 250-m long unit we called a "plot" for the

13   sake of simplicity. We characterized the functional community structure of the plots

14   using leaf traits known by their representation of ecological trade-offs involved in

15   biomass production (Lundgren *et al.* 2014; Engel 2017; Bruelheide *et al.* 2018;

16   Testolin *et al.* 2021) The traits leaf area (LA – mm^2), specific leaf area (SLA – m^2.kg^{-1}),

17   leaf dry matter content (LDMC – g.g^{-1}), leaf nitrogen (leaf N – mg.g^{-1}) and

18   photosynthetic pathway (categorical, C$_3$ or C$_4$) were collected from plant species

19   sampled in situ or obtained from the TRY database (Kattge *et al.* 2011) and TRY gap-

20   filled (Schrodt *et al.* 2015). Missing traits were imputed (Penone *et al.* 2014) using

21   *missForest* function of the package missForest (Stekhoven & Bühlmann 2012). Life

22   form, considered as a response trait (Pillar & Orlóci 1993), was obtained from Ferreira

et al. (2020) or collected from virtual herbaria ("Flora do Brasil 2020" 2021) Flora do Brasil 2020 and JBRJ. For all plots, we calculated single trait community-weighted means (CWM) using the function *functcomp* of package FD (Laliberté *et al.* 2014). Gini-Simpson index of species diversity (for simplicity, hereafter "species diversity"), functional diversity as Rao's quadratic entropy (Rao 1982), and functional redundancy (FR; difference between Gini–Simpson index of species diversity and Rao entropy) (de Bello *et al.* 2007) using 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 & Duarte 2010), using fuzzy-weighting defined by the *matrix.x* function of package SYNCSA (Debastiani & Pillar 2012). For this we considered only the effect traits, thus, not including the life forms. Next, based on the fuzzy-weighted species composition we computed Euclidean distances between plots using the multiv package (Debastiani & Pillar 2019), which was then submitted to cluster analysis using Ward's method. For the derived classifications up to five groups, 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 axes using the function *Ordination* of multiv package (Debastiani & Pillar 2019).

1   *Characterizing anomalous climatic events (SPEI base)*

2   To identify climatic anomalies, we chose the standardized precipitation-

3   evapotranspiration index (SPEI). It provides local monthly values at time scales

4   ranging from 1 to 48 months and at a 5 x 5 km spatial resolution. This means that, for

5   a given month, it represents the cumulative water balance over the previous *n*

6   months. Here, we used *n* = 3 months (SPEI-03), due to the high correlation with NDVI

7   data. Based on the index values, we identified for each plot, from year 2000 to 2018,

8   dry and wet events outside the normal range ($-0.68 < SPEI < 0.68$), as well as their

9   intensity: extreme ($SPEI > |1.27|$) or moderate ($|0.68| < SPEI < |1.27|$) (Vicente-Serrano

10   *et al.* 2010).

11

12   *Biomass productivity data – NDVI*

13   The Normalized Difference Vegetation Index – NDVI is a spectral indicator

14   widely used to quantify photosynthetic activity, which is a proxy for biomass

15   production, an indicator of ecosystem functioning (Pettorelli *et al.* 2005; De

16   Keersmaecker *et al.* 2017). Here, we employed NDVI data at the 250 m resolution for

17   the period of 2000 to 2018, with 23 acquisitions per year for each one of the 108

18   plots. The original data were obtained from the MODIS product MOD13Q (Didan

19   2015), available through the Google Earth Engine (Google Earth Engine Team 2015).

20   NDVI values were subjected to a smoothing process (Savitzky & Golay 1964) using

21   the function *savgol* of pracma package (Borchers 2021).

1	*Ecosystem level temporal stability*

2	Temporal stability is a measure of the productivity change (increase or

3	decrease) during a climatic anomaly. We calculated resistance [Eq 1] and resilience

4	[Eq 2] following Isbell et al. (2015), for each plot at each anomalous climatic event.

5	We log transformed the values to smooth outliers with no clear ecological meaning,

6	which also avoided the denominator in the equations approaching zero

7	The first step was to use normal SPEI events to calculate the average

8	productivity of each plot for each month in the time series (2000 to 2018). This

9	average was adopted as the productivity baseline, $\overline{Y_n}$.

10	Resistance describes the change of NDVI related to its baseline:

11	$\Omega = log\left(\frac{\overline{Y_n}}{|Y_e - \overline{Y_n}|}\right)$ [Eq 1]

12	Resilience describes the return ratio to baseline value:

13	$\Delta = log\left(\left|\frac{Y_e - \overline{Y_n}}{Y_{e+1} - \overline{Y_{n+1}}}\right|\right)$ [Eq 2]

14	Where Y_e e Y_{e+1} are, respectively, the ecosystem productivity during a climatic

15	anomaly, and after a climatic anomaly. We calculated resilience only when an

16	anomalous event with productivity Y_e at a given month was followed by at least two

17	normal months. Note that the identified anomalous events may not be synchronous

18	across plots at the regional scale.

19

20	*Data analysis*

21	We applied separate linear mixed-effects models to each group of

22	communities defined by their functional similarities and for each type of climatic event

23	(moderate and extreme dry and wet events). Resilience and resistance were treated

24	as response variables and were modeled as a function of a single fixed effect of

biodiversity descriptors (taxonomic richness and diversity, and functional redundancy and response diversity) and season of the climatic event as a random effect (summer, spring, autumn, winter). The fixed effects were standardized in order 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 or anomalous climatic events. Outside normal climatic 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 (SI – Figure S1).

Taxonomic and functional characteristics of communities

Based on the fuzzy-weighted species composition, the grassland communities were classified into five groups, G1 to G5 (Figure 2 and Supplementary Figure S2). Group G1 comprises communities with high LDMC, LA and predominantly C4 species, whereas group G5 represents communities with high SLA, leaf N and predominantly C3. 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% ($p < 0.0001$) of the variation and was positively correlated to high taxonomic and functional richness and diversity, SLA, leaf N and predominance of C3 species in the communities, and negatively correlated to LDMC and LA. The second principal component explained only 2.91% ($p = 0.001$) and was positively correlated with high functional response diversity (FRD), SLA, and leaf N, while negatively correlated with species richness, species diversity, FR, LDMC, LA and C3 species.

The relationships between biodiversity components varied across community groups (Figure 3). The correlation between species richness with species diversity and species diversity with FR were positive in all community groups. In G1 and G5 communities, all relationships were positive, however, they were stronger in the former group. In G2 communities, the correlations between species richness were negative with both FR and FRD. Moreover, species diversity and FRD were also negatively correlated. Regarding G3 and G4 communities the correlations between FRD 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 (Figure 4, Supplementary tables 1, 2 and 3).

Biodiversity effects on resistance

Under extreme dry events, the effect of species richness (Figure 4a) was positive on the resistance of G1, while it was negative in G4 and G5 communities.

Under moderate dry events, the effect of species richness was positive in G1, G2 and G3, whereas it was negative in G5 communities (Figure 4a). Under wet events, it was positive for G1 and G2, while it was negative for G4 and G5 communities (Figure 4b). In addition, the species richness effect was negative for G3 communities facing moderate wet events.

The effect of species diversity (Gini-Simpson) on resistance was positive under all anomalous events for G1 communities (Figure 4c-d). Furthermore, its effect was positive under extreme events for G2 and G3 communities (Figure 4c-d). Under wet events, it was negative for G4 and G5 communities (Figure 4d).

The effect of functional redundancy on the resistance of G1, G3 and G5 communities was positive under extreme dry climatic events (Figure 4e). Under moderate dry events, it was positive for G1 and negative for G2 (Figure 4f). Under extreme wet events, the effect of FR was positive for G1 and G2, while negative for G4 communities (Figure 4f). Under moderate wet events, it was positive for G1 and G3 communities (Figure 4f).

The effect of functional response diversity (FDR) on the resistance was positive under extreme dry events for G1, meanwhile, it was negative for G2, G3 and G4 (Figure 4g). Under moderate dry events, the effect of FDR was positive for G1, G3 and G5, and negative for G2 communities (Figure 4g). Under wet events (Figure 4h), its effect was positive for G1, while negative for G2 communities. In addition, FDR also had a negative effect for G3 communities under moderate wet events.

1   *Biodiversity effects on resilience*

2   Species richness negatively affected the resilience of G4 communities

3   recovering from extreme dry events, and G1 and G2 from moderate dry events (Figure

4   4a). Its effects, however, were positive of G1 and G5 communities recovering from

5   extreme wet events (Figure 4b). Moreover, after moderate wet events, its effect was

6   positive for G1, G3 and G4 communities (Figure 4b).

7   The effect of species diversity was positive on the resilience of G3

8   communities recovering from moderate dry events (Figure 4c). Moreover, its effect

9   was positive for G5 recovering from extreme wet, and for G3, G4 and G5 communities

10   recovering from moderate wet events (Figure 4d). Species diversity had negative

11   effects for G4 and G2 recovering from extremes dry (Figure 4c) and wet (Figure 4d),

12   respectively.

13   After moderate dry and wet events, the effect of FR was positive on the

14   resilience of G3 and G5 communities (Figure 4e-f). After extreme dry events, the effect

15   of FR was negative for G4 communities (Figure 4e).

16   Considering FRD effect on resilience after extreme dry events, it was positive

17   for G4 and negative for G2 communities (Figure 4g). After moderate dry (Figure 4g)

18   and extreme wet (Figure 4h) its effect was positive for G2 communities. After

19   moderate wet events, the effect of FRD was positive for G1, G2 and G5 communities

20   (Figure 4h).

21

22   **Discussion**

23   Our results showed that the effects of biodiversity on both resistance and

24   resilience of native grassland communities 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. That is, the effects of biodiversity on the resistance were predominantly positive in resource-conservative communities, while they were predominantly negative in resource-acquisitive communities. Considering biodiversity effects on the ecosystem resilience, they were more pronounced for resource-acquisitive communities and mainly related to moderate events.

We grouped the grassland communities evaluated in this study by their functional relatedness (Figure 2) based on traits that are relevant for biomass production and water and nutrient balance. Hence, along the first axis (Axis I; Figure 2), positive scores can be interpreted as communities dominated by acquisitive species (high SLA, Leaf N, C_3), 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).

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 shown by others (Hautier *et al.* 2015; Isbell *et al.* 2015). However, regardless of the direction or intensity of the climatic events, resource-conservative communities' resistance was increased by species richness, while resource-acquisitive communities had their resistance decreased.

1 Considering resource acquisitive communities under wet events, species richness

2 negative effects on resistance may indicate an increased biomass production given

3 water/resource inputs (Fischer et al. 2016). Interestingly, positive effects of species

4 richness on resilience were only observed in communities recovering from wet

5 events, while the effects on the recovery from dry events were negative. Therefore,

6 according to the portfolio effect (Doak *et al.* 1998; Tilman *et al.* 1998) ecosystem

7 stability of resource-conservative communities may be ensured by maintaining high

8 levels of species richness.

9 Species diversity also increased the resistance of grassland communities.

10 However, its effect was predominant under extreme dry and wet climatic events,

11 increasing the ecosystem resistance of resource-conservative communities, thus

12 partially supporting our hypothesis. For resource acquisitive communities under

13 moderate and extreme wet events, an increased species diversity had a negative

14 effect on resistance and a positive effect on resilience. Therefore, given resource

15 acquisitive communities facing wet events, species diversity may induce a

16 compensatory stabilizing mechanism of biomass production (Lehman & Tilman 2000;

17 Grman *et al.* 2010; Mackie *et al.* 2019).

18 From the functional perspective, we observed a consonant result between

19 species diversity and functional redundancy effects on ecosystems' resistance, as

20 we predicted, according to the insurance hypothesis (Yachi & Loreau 1999). Their

21 high positive correlation values indicate that the FR found in the communities is

22 promoted by species diversity more than by the number of species *per se*. Functional

23 redundancy had a predominant positive effect on the resistance of resource-

24 conservative communities facing extreme events. In turn, ecosystems' resilience of

resource acquisitive communities was increased by FR while recovering from moderate dry and extreme wet events.

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

As already highlighted (Isbell 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 (resistance and the resilience) of native grassland depend on the biodiversity metric evaluated in the communities and the direction and intensity of the climatic anomaly. Yet, the effects

were mostly positive, indicating that the high plant biodiversity in Campos Sulinos region (Andrade et al. 2018) has ensured ecosystem stability throughout the climatic anomalies registered so far. The effects of biodiversity on the stability depend on the functional characteristics of the communities, and also, upon which dimension of biodiversity we are taking in count. This emphasizes the importance to consider different components of biodiversity when investigating the relationships between ecosystem services and 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. Also, models of climate change indicate high possibility of increasing intensity and duration of wet events for the Campos Sulinos region, pressing the need for more studies that help understanding ecosystem level response to this kind of disturbance.

Acknowledgements

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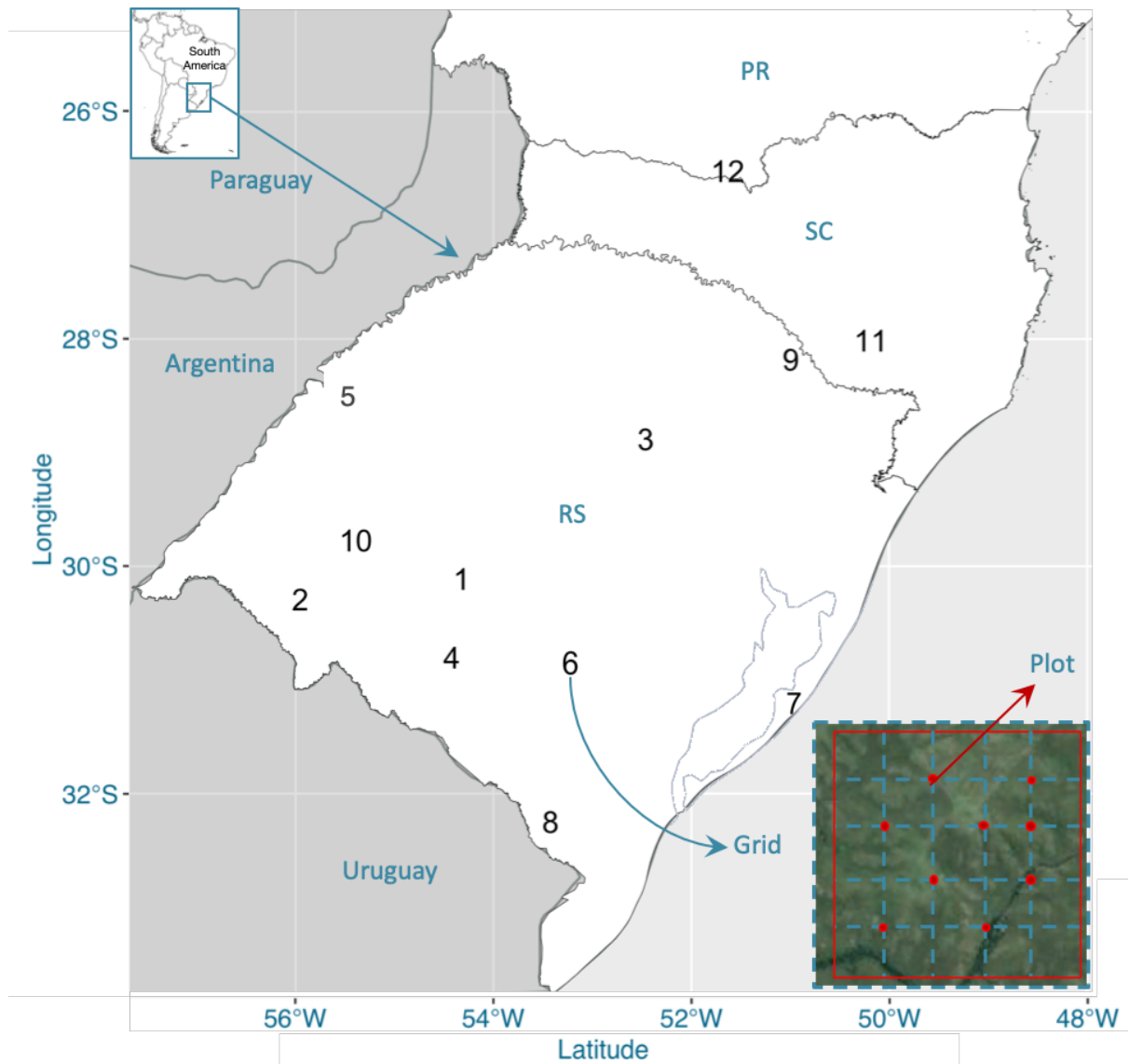
Figure 1: Distribution of the eleven grids (represented by numbers: 1 – São Gabriel, 2 – Quaraí, 3 – Soledade, 4 – Lavras do Sul, 5 – Santo Antônio das Missões, 6 – Santana da Boa Vista, 7 – Tavares, 8 – Jaguarão, 9 – Vacaria, 10 – Alegrete, 11 – Painel, 12 – Palmas) in the Campos Sulinos grasslands and the representation of the 25 km² grid, red dots are the location of the nine plots in this grid. Each plot consisted of ten equidistant subsampling quadrats of 1 m².
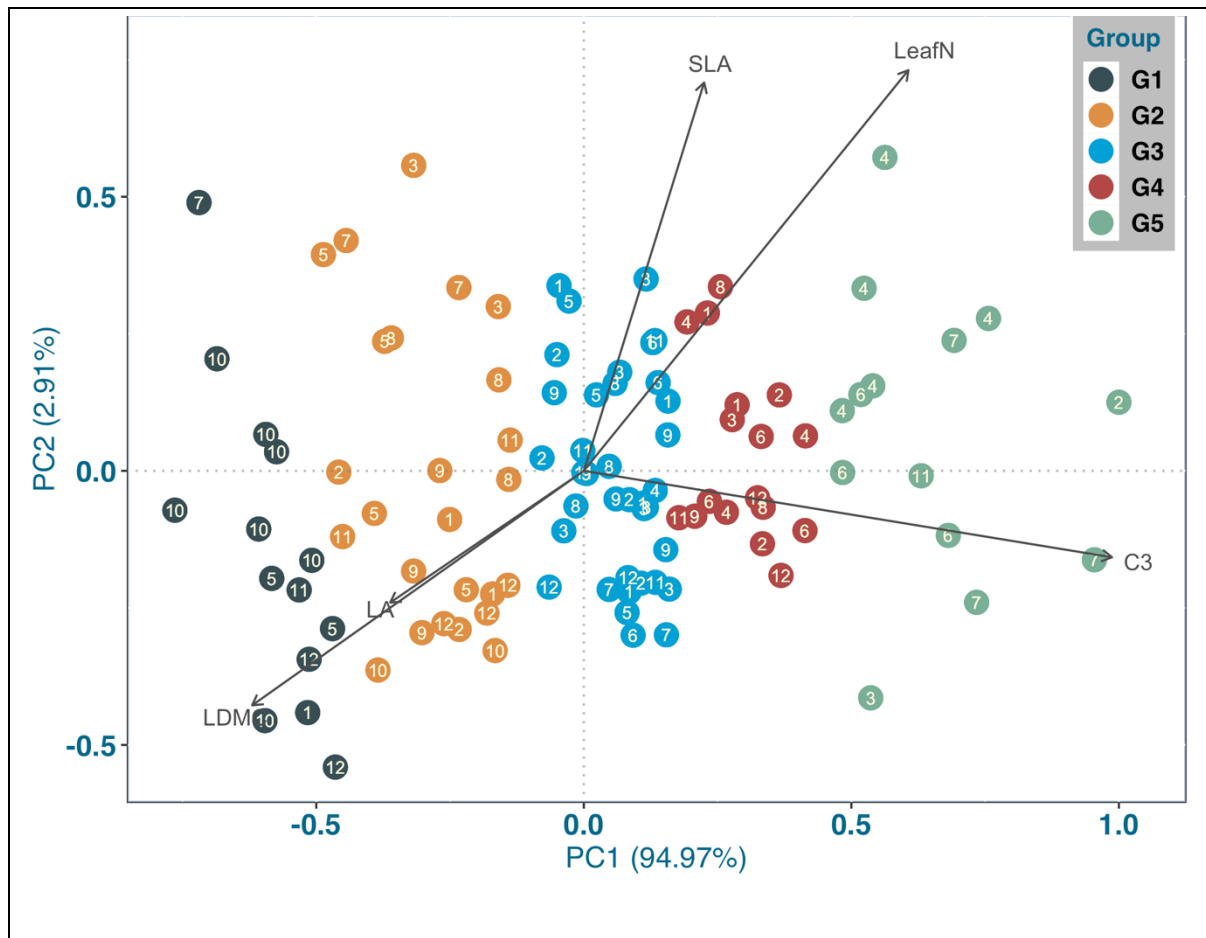
Figure 2: Principal Components Analysis ordination of the studied grassland vegetation communities gathered in groups (indicated in the panel) described by fuzzy-weighted species composition based on functional relatedness among species. Post hoc correlations of PCA axes with traits and taxonomic and functional diversity descriptors are shown in grey and red, respectively. Arrows indicate community-weighted means for the traits based on their correlations with the ordination axes. The 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 – Painel, 12 – Palmas) are repeated nine times each, to indicate plots from same grids. Colors and symbols represent groups of functional relatedness, as indicated by the key on the top right.

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

Figure 3: Correlation between biodiversity predictors (SR – species richness, SD – species diversity, FR – functional redundancy, FRD - functional response diversity)

a) SR - Dry Events
b) SR - Wet Events
c) SD - Dry Events
d) SD - Wet Events
e) FR - Dry Events
f) FR - Wet Events
g) FRD - Dry Events
h) FRD - Wet Events

Direction
▽ extreme
△ moderate

Group
G1
G2
G3
G4
G5

Resilience (Δ)

Resistance (Ω)

45

Figure 4: Relative effects (standardized slopes of linear mixed effects) of predictors taxonomic richness (a), Gini-Simpson index of species diversity (b), functional redundancy (c) and functional response diversity, using response traits (d) on the resistance (Ω, on the abscissa) and resilience (Δ, on the ordinate) of grassland vegetation communities by community functional group and climatic events (dry: extreme – ED, moderate – MD; wet: extreme – EW, moderate – MW). The parameter estimates (standardized regression coefficients) of the model predictors are shown with their associated 95% confidence intervals, calculated a posteriori. Solid lines represent coefficients that differ from zero, dashed lines represent coefficients that did not differ from zero. Colors and symbols, respectively represent climatic events and groups, as indicated by the key on the top left panel (a).
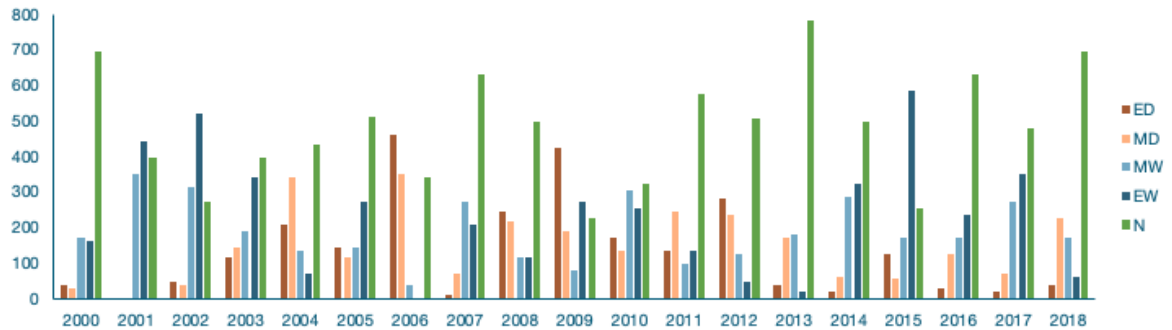
Supplementary figure 1: Occurrence of the climatic events (N – normal, dry: extreme – ED, moderate – MD; wet: extreme – EW, moderate – MW) classified according to SPEI-03 during the period from 2000 to 2018 for the studied area. The frequency of events corresponds to the total number of events in each year and type of event irrespective of the studied grid.
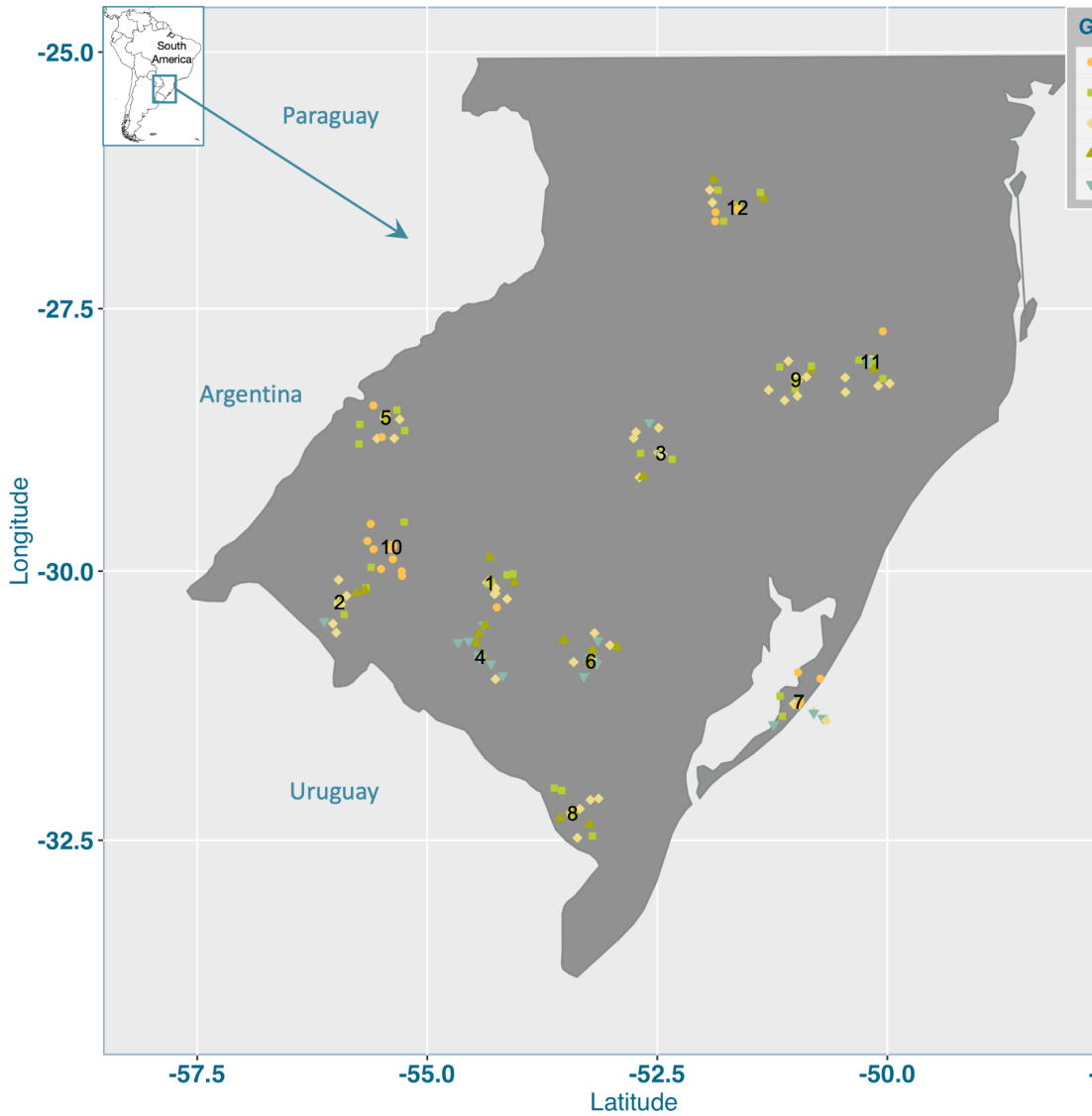
Supplementary figure 2: Geographical distribution of the studied grassland vegetation communities gathered in groups (indicated in the panel) described by fuzzy weighted species composition based on functional relatedness among species. The numbers (1 – São Gabriel, 2 – Quaraí, 3 – Soledade, 4 – Lavras do Sul, 5 – Santo Antônio das Missões, 6 – Santana da Boa Vista, 7 – Tavares, 8 – Jaguarão, 9 – Vacaria, 10 – Alegrete, 11 – Painel, 12 – Palmas) are repeated nine times each, to indicate plots from same grids. Points have been jittered for clarity; therefore, we show the grids' centroid geographic coordinate location. Colors and symbols represent groups of functional relatedness, as indicated by the key on the top right.
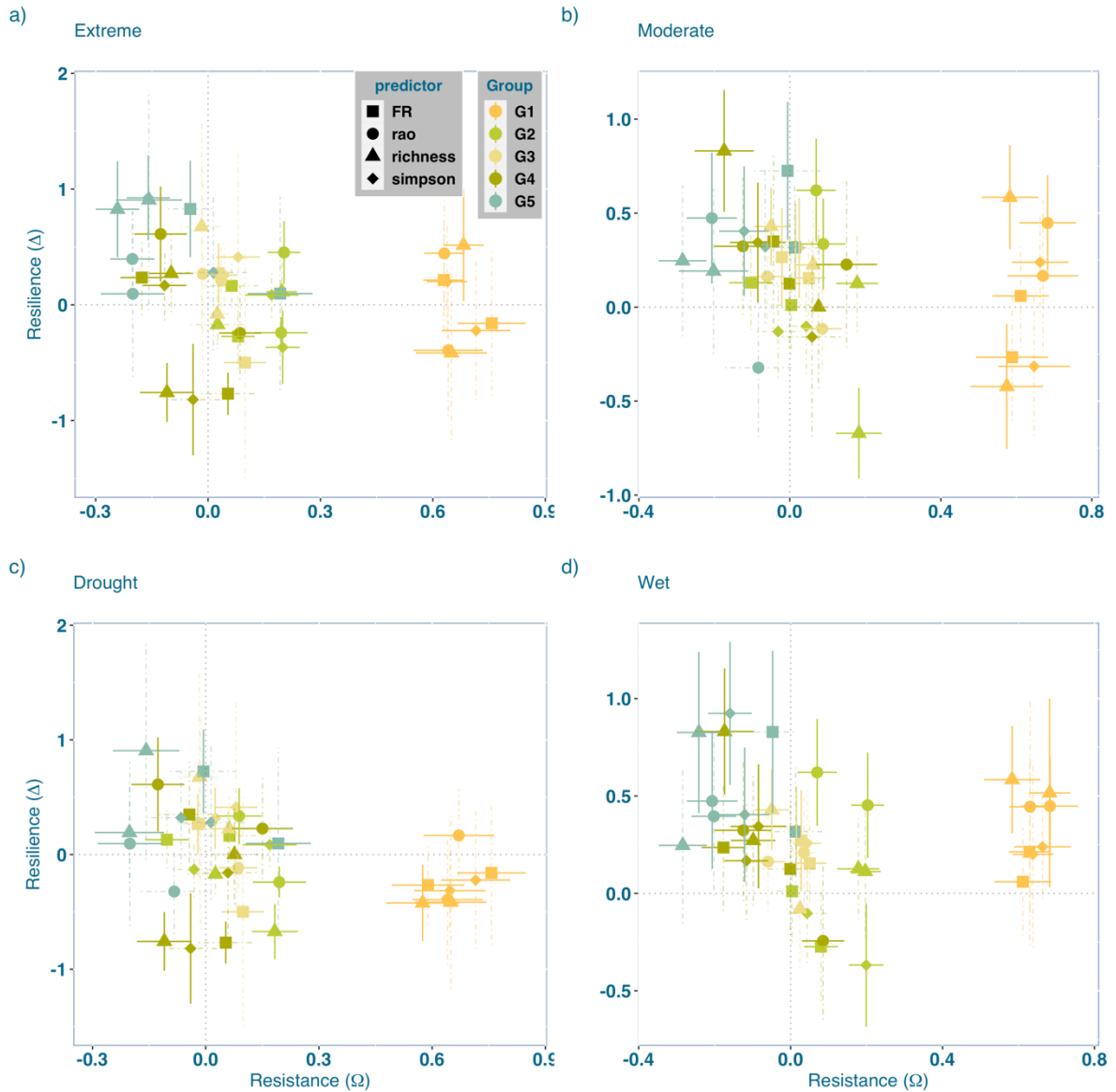
Supplementary figure 3: Relative effects of predictors on the resistance (*Ω*, on the abscissa) and resilience (Δ, on the ordinate) of the studied grassland vegetation communities gathered into groups of functional relatedness under climatic events: extreme (a), moderate (b), dry (c) and wet (d). The parameter estimates (standardized regression coefficients) of the model predictors are shown with their associated 95% confidence intervals. Solid lines represent coefficients that differ from zero. Colors and symbols, respectively represent groups and biodiversity, as indicated by the key on the top left panel (a).

a) Group 1

b) Group 2

c) Group 3

d) Group 4

e) Group 5
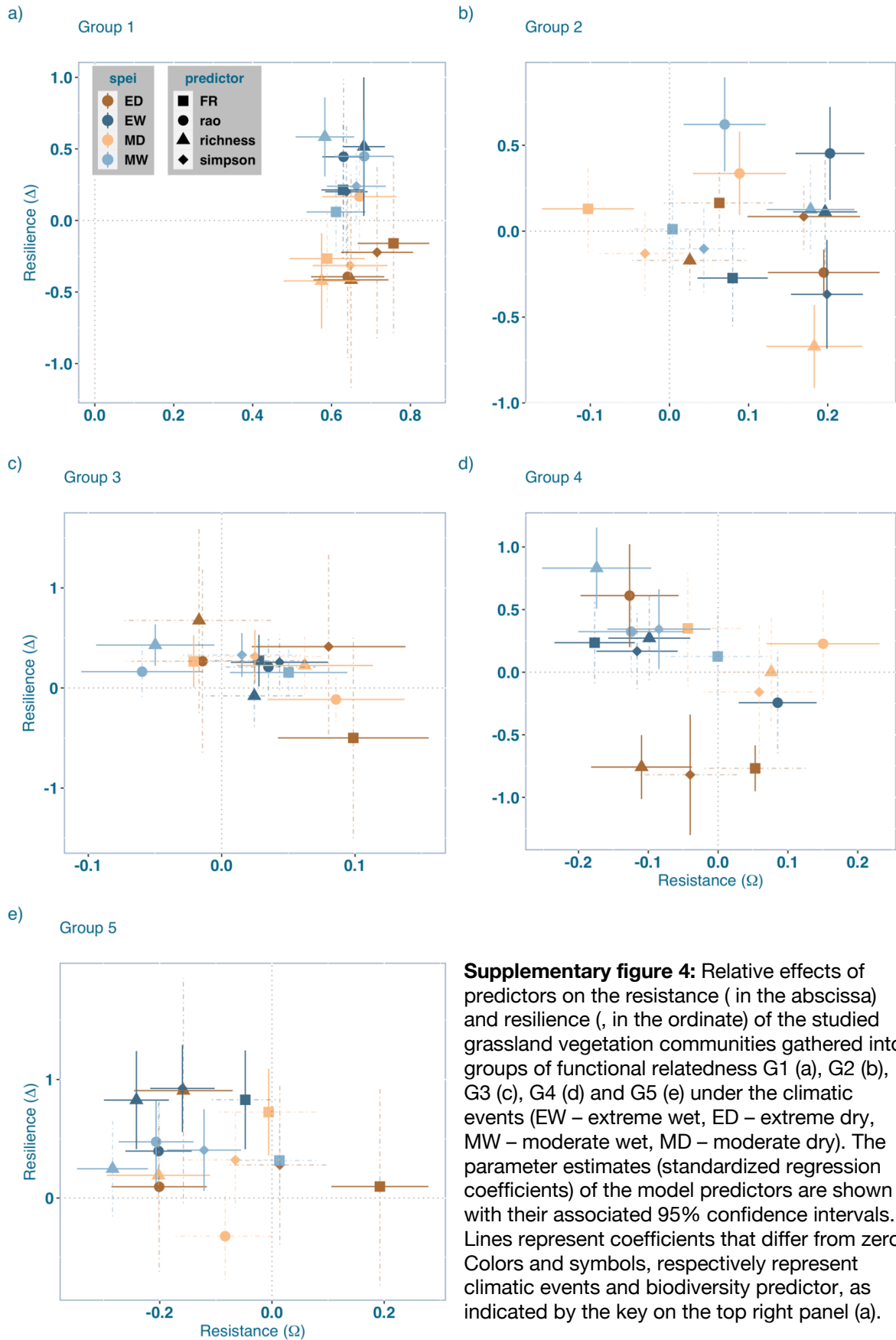
Supplementary figure 4: Relative effects of predictors on the resistance (in the abscissa) and resilience (, in the ordinate) of the studied grassland vegetation communities gathered into groups of functional relatedness G1 (a), G2 (b), G3 (c), G4 (d) and G5 (e) under the climatic events (EW – extreme wet, ED – extreme dry, MW – moderate wet, MD – moderate dry). The parameter estimates (standardized regression coefficients) of the model predictors are shown with their associated 95% confidence intervals. Lines represent coefficients that differ from zero Colors and symbols, respectively represent climatic events and biodiversity predictor, as indicated by the key on the top right panel (a).
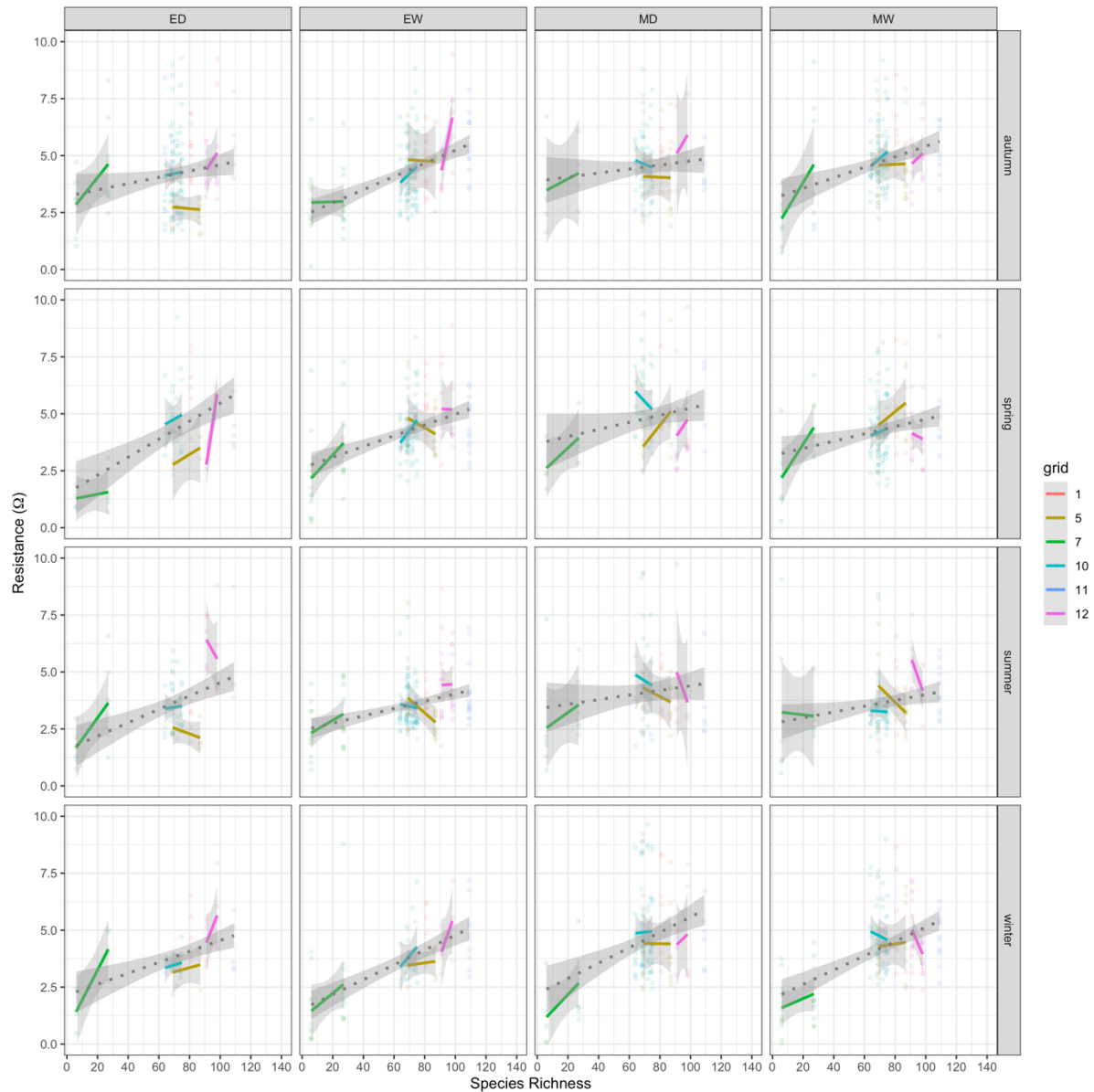
Supplementary figure 5: Relative effects of species richness (solid lines with bands indicating 95% confidence intervals) on the resistance of grassland vegetation communities that functionally comprises group G1 (dotted line represents the average species richness effect on group G1). Each panel combines the effects of species richness per season and climatic events (extreme wet – EW, extreme dry – ED, moderate wet – MW, moderate dry – MD).
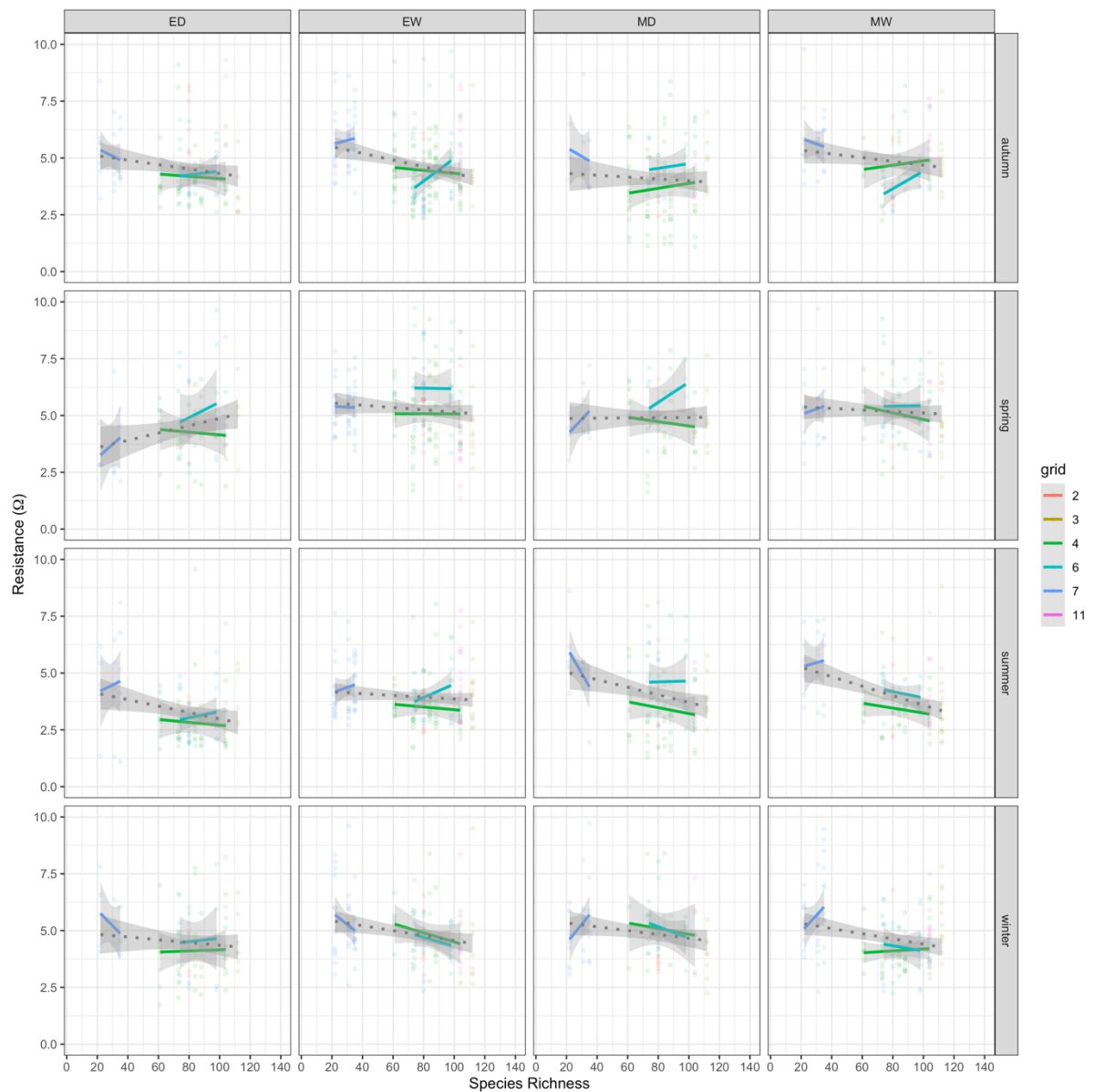
Supplementary figure 6: Relative effects of species richness (solid lines with bands indicating 95% confidence intervals) on the resistance of grassland vegetation communities that functionally comprises group G5 (dotted line represents the average species richness effect on group G5). Each panel combines the effects of species richness per season and climatic events (extreme wet – EW, extreme dry – ED, moderate wet – MW, moderate dry – MD).

Supplementary table 1: Relative effects of the biodiversity predictors (SR – species richness, SD – species diversity, FR – functional redundancy, FD – functional diversity) on the resistance (Ω) of the studied grassland vegetation communities gathered into groups of functional relatedness under the climatic events (EW – extreme wet, ED – extreme dry, MW – moderate wet, MD – moderate dry). The parameter estimates (standardized regression coefficients) of the model predictors are shown with their associated 95% confidence intervals (upper and lower limits).

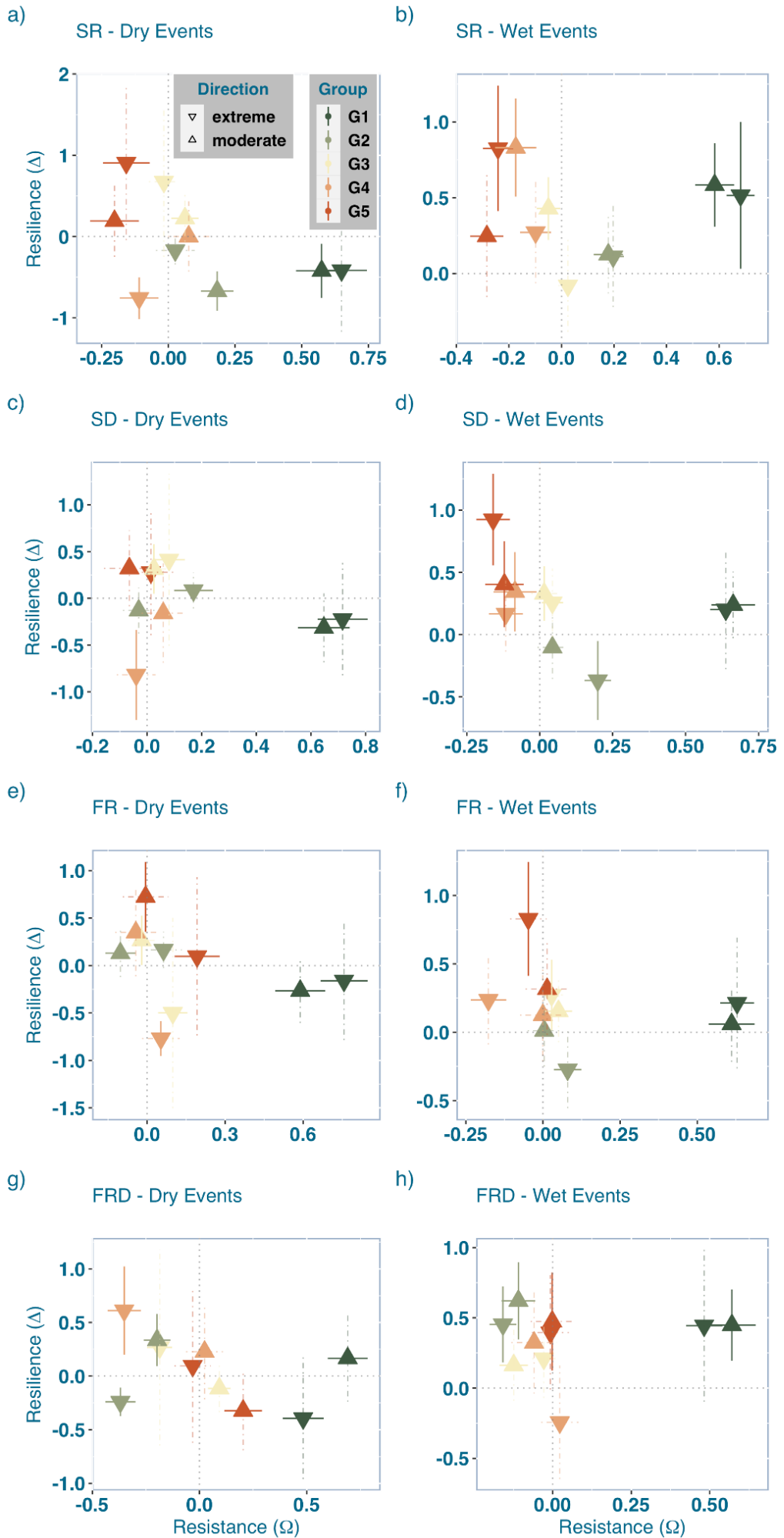| Groups	SPEI-03 class	Predictor	Estimate	Standard Error	Upper Limit	Lower Limit	df	*t*-value	*p*-value	R²
G1	ED	**SR**	**0.650**	0.095	0.744	0.555	341	6.851	3.44E-11	0.142
		SD	**0.715**	0.091	0.807	0.624	340	7.835	6.07E-14	0.173
		FR	**0.757**	0.091	0.848	0.666	340	8.355	1.69E-15	0.192
		FRD	**0.483**	0.096	0.579	0.388	342	5.045	7.39E-07	0.092
	MD	**SR**	**0.575**	0.096	0.671	0.479	418	5.978	4.85E-09	0.090
		SD	**0.647**	0.095	0.742	0.552	418	6.826	3.09E-11	0.111
		FR	**0.589**	0.096	0.684	0.493	418	6.153	1.78E-09	0.094
		FRD	**0.691**	0.093	0.784	0.598	418	7.450	5.38E-13	0.126
	EW	**SR**	**0.682**	0.053	0.735	0.628	603	12.763	3.43E-33	0.265
		SD	**0.638**	0.054	0.692	0.584	603	11.842	3.09E-29	0.241
		FR	**0.629**	0.055	0.684	0.574	603	11.459	1.22E-27	0.234
		FRD	**0.482**	0.058	0.540	0.424	604	8.311	6.28E-16	0.158
	MW	**SR**	**0.583**	0.074	0.657	0.509	566	7.850	2.10E-14	0.169
		SD	**0.663**	0.075	0.738	0.588	566	8.889	8.23E-18	0.189
		FR	**0.611**	0.075	0.686	0.537	566	8.178	1.91E-15	0.174
		FRD	**0.570**	0.075	0.645	0.495	566	7.577	1.45E-13	0.157
G2	ED	SR	0.026	0.072	0.098	-0.047	590	0.354	0.723	0.047
		SD	**0.170**	0.071	0.241	0.099	590	2.388	0.017	0.057
		FR	0.063	0.070	0.133	-0.007	591	0.901	0.368	0.049
		FRD	**-0.369**	0.070	-0.299	-0.440	591	-5.251	2.12E-07	0.084
	MD	**SR**	**0.183**	0.061	0.244	0.122	684	3.017	0.003	0.089
		SD	-0.031	0.057	0.027	-0.088	684	-0.538	0.591	0.075
		FR	**-0.103**	0.058	-0.045	-0.161	684	-1.772	0.077	0.080
		FRD	**-0.198**	0.062	-0.136	-0.260	684	-3.186	0.002	0.086
	EW	**SR**	**0.197**	0.040	0.237	0.156	1087	4.858	1.36E-06	0.111
		SD	**0.199**	0.045	0.244	0.154	1087	4.380	1.30E-05	0.106
		FR	**0.080**	0.044	0.124	0.035	1087	1.795	0.073	0.094
		FRD	**-0.158**	0.043	-0.115	-0.201	1087	-3.694	0.0002	0.105
	MW	**SR**	**0.178**	0.055	0.234	0.123	939	3.217	0.001	0.115
		SD	0.043	0.051	0.095	-0.008	938	0.845	0.398	0.102
		FR	0.004	0.054	0.058	-0.050	938	0.072	0.943	0.101
		FRD	**-0.109**	0.054	-0.055	-0.163	938	-2.033	0.042	0.105

Continues

Groups	SPEI-03 class	Predictor	Estimate	Standard Error	Upper Limit	Lower Limit	df	*t*-value	*p*-value	R²
G3	ED	SR	-0.017	0.056	0.039	-0.073	922	-0.304	0.762	0.068
		SD	**0.080**	0.058	0.138	0.023	922	1.392	0.164	0.069
		FR	**0.099**	0.056	0.155	0.042	922	1.748	0.081	0.071
		FRD	**-0.186**	0.058	-0.128	-0.244	922	-3.195	0.001	0.076
	MD	**SR**	**0.062**	0.051	0.113	0.011	1014	1.217	0.224	0.066
		SD	0.025	0.051	0.076	-0.026	1014	0.492	0.623	0.064
		FR	-0.021	0.051	0.030	-0.072	1015	-0.410	0.682	0.064
		FRD	**0.092**	0.053	0.145	0.040	1014	1.759	0.079	0.068
	EW	SR	0.024	0.036	0.061	-0.012	1709	0.675	0.500	0.092
		SD	**0.043**	0.036	0.080	0.007	1709	1.191	0.234	0.093
		FR	0.028	0.036	0.064	-0.008	1709	0.767	0.443	0.092
		FRD	-0.028	0.037	0.009	-0.065	1709	-0.767	0.443	0.093
	MW	**SR**	**-0.050**	0.044	-0.005	-0.094	1362	-1.121	0.262	0.113
		SD	0.015	0.044	0.059	-0.029	1362	0.344	0.731	0.113
		FR	**0.050**	0.044	0.094	0.006	1362	1.141	0.254	0.114
		FRD	**-0.124**	0.045	-0.079	-0.169	1362	-2.740	0.006	0.117
G4	ED	**SR**	**-0.110**	0.072	-0.037	-0.182	474	-1.518	0.130	0.114
		SD	-0.040	0.071	0.031	-0.111	474	-0.562	0.574	0.112
		FR	0.053	0.072	0.125	-0.019	474	0.735	0.463	0.113
		FRD	**-0.351**	0.078	-0.274	-0.429	474	-4.520	7.83E-06	0.142
	MD	SR	0.076	0.078	0.154	-0.001	484	0.982	0.327	0.024
		SD	0.059	0.079	0.138	-0.021	482	0.741	0.459	0.024
		FR	-0.043	0.080	0.036	-0.123	483	-0.544	0.587	0.024
		FRD	0.024	0.086	0.110	-0.063	485	0.273	0.785	0.024
	EW	**SR**	**-0.099**	0.059	-0.040	-0.157	793	-1.680	0.093	0.096
		SD	**-0.116**	0.058	-0.058	-0.174	793	-1.996	0.046	0.099
		FR	**-0.177**	0.058	-0.119	-0.234	793	-3.075	0.002	0.104
		FRD	0.023	0.059	0.082	-0.037	794	0.382	0.702	0.093
	MW	**SR**	**-0.174**	0.078	-0.096	-0.252	556	-2.225	0.026	0.119
		SD	**-0.085**	0.074	-0.011	-0.159	555	-1.148	0.251	0.113
		FR	-0.001	0.074	0.073	-0.074	556	-0.008	0.994	0.111
		FRD	-0.059	0.072	0.013	-0.131	555	-0.821	0.412	0.113
G5	ED	**SR**	**-0.158**	0.088	-0.070	-0.246	376	-1.797	0.073	0.134
		SD	0.014	0.089	0.103	-0.075	376	0.156	0.876	0.124
		FR	**0.192**	0.087	0.279	0.106	376	2.223	0.027	0.134
		FRD	-0.032	0.085	0.053	-0.117	376	-0.376	0.707	0.125
	MD	**SR**	**-0.202**	0.092	-0.110	-0.294	405	-2.200	0.028	0.061
		SD	-0.065	0.092	0.027	-0.158	403	-0.706	0.481	0.055
		FR	-0.006	0.088	0.082	-0.094	403	-0.067	0.947	0.054
		FRD	**0.203**	0.088	0.291	0.116	403	2.315	0.021	0.068
	EW	**SR**	**-0.242**	0.058	-0.184	-0.300	689	-4.171	3.41E-05	0.138
		SD	**-0.160**	0.057	-0.102	-0.217	689	-2.776	0.006	0.125
		FR	-0.048	0.059	0.012	-0.107	689	-0.801	0.424	0.117
		FRD	-0.007	0.059	0.052	-0.066	689	-0.123	0.902	0.117
	MW	**SR**	**-0.284**	0.063	-0.221	-0.347	451	-4.500	8.66E-06	0.135
		SD	**-0.121**	0.066	-0.055	-0.187	451	-1.837	0.067	0.108
		FR	0.013	0.070	0.083	-0.056	451	0.190	0.849	0.104
		FRD	-0.001	0.069	0.068	-0.071	451	-0.021	0.984	0.103

Supplementary table 2: Relative effects of the biodiversity predictors (SR – species richness, SD – species diversity, FR – functional redundancy, FRD – functional diversity) on the resilience (Δ) of the studied grassland vegetation communities gathered into groups of functional relatedness under the climatic events (EW – extreme wet, ED – extreme dry, MW – moderate wet, MD – moderate dry). The parameter estimates (standardized regression coefficients) of the model predictors are shown with their associated 95% confidence intervals (upper and lower limits).

Groups	SPEI-03 class	Predictor	Estimate	Standard Error	Upper Limit	Lower Limit	df	*t*-value	*p*-value	R^2
G1	ED	SR	-0.415	0.755	0.340	-1.170	5	-0.550	0.608	0.230
		SD	-0.222	0.602	0.379	-0.824	4	-0.370	0.731	0.219
		FR	-0.160	0.626	0.466	-0.786	5	-0.256	0.809	0.206
		FRD	-0.393	0.568	0.174	-0.961	5	-0.693	0.519	0.229
	MD	**SR**	**-0.422**	0.333	-0.089	-0.755	30	-1.267	0.215	0.342
		SD	-0.315	0.369	0.054	-0.684	30	-0.853	0.401	0.273
		FR	-0.266	0.339	0.073	-0.605	29	-0.785	0.439	0.279
		FRD	0.167	0.406	0.573	-0.240	31	0.410	0.685	0.273
	EW	**SR**	**0.516**	0.484	1.000	0.031	23	1.065	0.298	0.398
		SD	0.201	0.478	0.679	-0.277	24	0.420	0.678	0.388
		FR	0.214	0.479	0.692	-0.265	24	0.446	0.659	0.393
		FRD	0.445	0.542	0.987	-0.097	25	0.820	0.420	0.409
	MW	**SR**	**0.584**	0.276	0.860	0.308	52	2.116	0.039	0.316
		SD	0.239	0.267	0.506	-0.028	52	0.895	0.375	0.189
		FR	0.060	0.276	0.335	-0.216	52	0.216	0.830	0.164
		FRD	**0.448**	0.254	0.702	0.194	50	1.767	0.083	0.226
G2	ED	SR	-0.170	0.174	0.004	-0.344	3	-0.979	0.400	0.193
		SD	0.085	0.193	0.278	-0.108	2	0.441	0.701	0.064
		FR	0.164	0.191	0.356	-0.027	3	0.858	0.454	0.155
		FRD	**-0.241**	0.134	-0.107	-0.374	2	-1.804	0.204	0.791
	MD	**SR**	**-0.671**	0.241	-0.430	-0.912	53	-2.783	0.007	0.450
		SD	-0.130	0.246	0.116	-0.376	52	-0.529	0.599	0.385
		FR	0.130	0.253	0.383	-0.123	52	0.514	0.610	0.375
		FRD	**0.336**	0.243	0.579	0.093	53	1.382	0.173	0.413
	EW	SR	0.112	0.334	0.446	-0.222	51	0.336	0.738	0.223
		SD	**-0.368**	0.317	-0.051	-0.685	50	-1.161	0.251	0.228
		FR	-0.273	0.282	0.008	-0.555	50	-0.970	0.337	0.234
		FRD	**0.453**	0.271	0.723	0.182	51	1.673	0.100	0.267
	MW	SR	0.126	0.258	0.384	-0.132	65	0.488	0.627	0.047
		SD	-0.102	0.254	0.152	-0.356	67	-0.403	0.688	0.040
		FR	0.011	0.263	0.274	-0.252	68	0.043	0.966	0.042
		FRD	**0.621**	0.274	0.896	0.347	67	2.265	0.027	0.098

Continues

Groups	SPEI-03 class	Predictor	Estimate	Standard Error	Upper Limit	Lower Limit	df	*t*-value	*p*-value	R²
G3	ED	SR	0.675	0.926	1.601	-0.251	7	0.729	0.490	0.062
		SD	0.413	0.920	1.332	-0.507	7	0.449	0.667	0.025
		FR	-0.499	1.003	0.503	-1.502	7	-0.498	0.634	0.167
		FRD	0.267	0.914	1.181	-0.647	7	0.292	0.779	0.014
	MD	SR	0.225	0.287	0.512	-0.063	79	0.782	0.436	0.245
		SD	**0.315**	0.266	0.581	0.049	78	1.183	0.240	0.248
		FR	**0.265**	0.260	0.526	0.005	78	1.019	0.311	0.249
		FRD	-0.115	0.222	0.107	-0.337	78	-0.519	0.605	0.245
	EW	SR	-0.080	0.304	0.224	-0.383	71	-0.262	0.794	0.208
		SD	0.257	0.274	0.531	-0.017	69	0.937	0.352	0.236
		FR	**0.272**	0.257	0.530	0.015	69	1.058	0.294	0.231
		FRD	0.210	0.281	0.490	-0.071	70	0.747	0.457	0.224
	MW	**SR**	**0.429**	0.207	0.636	0.222	98	2.073	0.041	0.266
		SD	**0.329**	0.219	0.548	0.110	98	1.501	0.137	0.260
		FR	0.155	0.227	0.382	-0.073	97	0.680	0.498	0.254
		FRD	0.163	0.253	0.416	-0.090	98	0.644	0.521	0.249
G4	ED	**SR**	**-0.757**	0.255	-0.502	-1.013	5	-2.965	0.031	0.594
		SD	**-0.819**	0.481	-0.338	-1.300	5	-1.702	0.150	0.326
		FR	**-0.768**	0.183	-0.585	-0.951	5	-4.186	0.009	0.745
		FRD	**0.611**	0.411	1.023	0.200	5	1.487	0.197	0.269
	MD	SR	0.001	0.433	0.433	-0.432	34	0.002	0.998	0.089
		SD	-0.159	0.531	0.373	-0.690	35	-0.299	0.767	0.076
		FR	0.350	0.463	0.813	-0.114	33	0.755	0.456	0.114
		FRD	0.227	0.443	0.670	-0.216	27	0.512	0.613	0.158
	EW	SR	0.272	0.336	0.607	-0.064	29	0.810	0.425	0.419
		SD	0.168	0.304	0.471	-0.136	29	0.552	0.585	0.397
		FR	0.236	0.325	0.560	-0.089	29	0.725	0.474	0.396
		FRD	-0.244	0.404	0.160	-0.648	32	-0.603	0.551	0.388
	MW	**SR**	**0.831**	0.324	1.155	0.507	33	2.567	0.015	0.545
		SD	**0.344**	0.319	0.663	0.026	33	1.080	0.288	0.426
		FR	0.125	0.339	0.465	-0.214	33	0.369	0.714	0.380
		FRD	0.324	0.363	0.687	-0.040	33	0.891	0.380	0.336
G5	ED	SR	0.906	0.950	1.856	-0.044	5	0.954	0.388	0.549
		SD	0.279	0.673	0.953	-0.394	7	0.415	0.691	0.460
		FR	0.097	0.834	0.932	-0.737	6	0.116	0.911	0.465
		FRD	0.095	0.718	0.813	-0.623	6	0.133	0.899	0.451
	MD	SR	0.192	0.441	0.632	-0.249	29	0.436	0.666	0.341
		SD	0.322	0.407	0.728	-0.085	28	0.791	0.436	0.317
		FR	**0.725**	0.366	1.091	0.359	28	1.979	0.058	0.332
		FRD	-0.322	0.371	0.049	-0.693	26	-0.869	0.393	0.381
	EW	**SR**	**0.826**	0.414	1.240	0.412	23	1.997	0.058	0.595
		SD	**0.924**	0.367	1.292	0.557	23	2.516	0.019	0.664
		FR	**0.829**	0.417	1.245	0.412	23	1.988	0.059	0.645
		FRD	0.396	0.407	0.803	-0.011	23	0.973	0.341	0.545
	MW	SR	0.247	0.402	0.648	-0.155	26	0.613	0.545	0.386
		SD	**0.404**	0.345	0.749	0.059	24	1.172	0.253	0.446
		FR	0.317	0.336	0.653	-0.020	24	0.941	0.356	0.470
		FRD	**0.474**	0.349	0.823	0.125	24	1.360	0.187	0.493

Supplementary table 3: Relative effects of the biodiversity predictors (SR – species richness, SD – species diversity, FR – functional redundancy, FRD – functional diversity) on the resistance and resilience of the studied grassland vegetation communities gathered into groups of functional relatedness under the climatic events (dry: extreme – ED, moderate – MD; wet: extreme – EW, moderate – MW).

Stability	Effect	Community group / SPEI	SR ED	SR MD	SR EW	SR MW	SD ED	SD MD	SD EW	SD MW	FR ED	FR MD	FR EW	FR MW	FRD ED	FRD MD	FRD EW	FRD MW
Resistance	+	G1	ED	MD	EW	MW	ED	MD	EW	MW	ED	MD	EW	MW	ED	MD	EW	MW
		G2		MD	EW	MW	ED		EW				EW					
		G3		MD			ED		EW					MW		MD		
		G4																
		G5									ED					MD		
	–	G1																
		G2										MD			ED	MD	EW	MW
		G3				MW									ED			MW
		G4	ED		EW	MW			EW	MW			EW		ED			
		G5	ED	MD	EW	MW			EW	MW								
Resilience	+	G1			EW	MW												MW
		G2														MD	EW	MW
		G3				MW		MD		MW		MD	EW					
		G4				MW				MW					ED			
		G5			EW				EW	MW		MD	EW					MW
	–	G1		MD														
		G2		MD					EW						ED			
		G3																
		G4	ED				ED				ED							
		G5																

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Capítulo 2

A global assessment on the effects of plant functional redundancy on grassland ecosystems' stability during climatic anomalies

A global assessment on the effects of plant functional redundancy on grassland ecosystems' stability during climatic anomalies[2]

Running title: Functional redundancy affects ecosystem stability globally

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1   **Abstract**

2 *Aim*

3 Biodiversity may provide stability on ecosystem functions in the face of climatic

4 anomalies. Biodiversity changes and their effects on ecosystem functioning are

5 mainly studied at fine spatial scales, through experimental approaches, and under a

6 limited set of climatic conditions. A global analysis across continents has not been

7 yet attempted. In this study we evaluate how plant communities' functional

8 redundancy, and its interaction with the functional structure, affects resistance and

9 resilience in grassland ecosystems worldwide.

10 *Location*

11 1212 grassland plots globally

12 *Time period*

13 2000-2018

14 *Major taxa studied*

15 Grassland vegetation

16 *Methods*

17 Plot-based data on functional community structure were obtained from the global

18 vegetation plot database sPlot in combination with the plant trait database TRY.

19 Using 18 ecologically relevant plant traits, we calculated the community weighted

20 means and functional redundancy. For each plot location, we extracted a monthly

21 based 18-year time series of NDVI at a spatial resolution of 250 m using the MODIS

22 product MOD13Q. We identified climatic anomalies using the SPEI-03 index, which

23 quantifies temporal variations in water balance on a 0.5-degree spatial resolution. For

this we classified every month for each plot as normal, dry or wet and also the intensity: extreme or moderate. For each plot, using normal SPEI months, we calculated the baseline as the mean monthly NDVI observed. We quantified resistance as the relative change of NDVI from its baseline, and resilience as the rate of return to the baseline. Linear Mixed models were used to test whether plant communities with higher diversity and redundancy provide increased ecosystem stability under climatic anomalies.

Results

We found that plant biodiversity is predictive of resistance and resilience in grassland ecosystems worldwide, but the direction and strength of the effect depended on the evaluated diversity metric, the community functional structure, and the direction and intensity of the climatic anomaly.

Main conclusions

At the global extent, detecting the effects of biodiversity on the stability depends on the biodiversity dimension, the functional characteristics considered, and the climatic events.

Keywords

plant functional ecology, biodiversity, ecosystem functioning, NDVI, sPlot, global ecology, resilience, resistance.

1   Introduction

2   The year 2021 can be considered as a hallmark regarding the effects of climate

3   change on ecosystem functioning (IPCC 2021). For the first time it was explicitly

4   recognized in a technical document that anthropogenic effects are responsible for a

5   range of climate changes, such as the increase in frequency and intensity of

6   precipitation anomalies. Since basic ecosystem services, e.g, primary productivity,

7   are highly dependent on a range of climatic conditions (Sala et al. 1988; Paruelo &

8   Lauenroth 1995; Gordo & Sanz 2010), understanding how the intensity and direction

9   of climatic anomalies influences biodiversity and its effects on ecosystem stability is

10   of paramount importance in mitigating the consequences of climate change on basic

11   ecosystem functioning and, consequently, human well-being.

12   It is known that biodiversity stabilizes the ecosystem's productivity (Tilman &

13   Downing 1994). This maintenance of normal levels of biomass production may be

14   promoted by plant biodiversity effects, such as increased species richness, functional

15   and phylogenetic diversity (Craven et al. 2018), as suggested by previous studies on

16   the relationships between biodiversity and ecosystem functioning (BEF). However,

17   the effects of these different components of biodiversity can be very contingent

18   depending on the functional composition of communities (García-Palacios et al.

19   2018, Hoss et al. in prep); the type of climatic anomaly (Fischer et al. 2016; Wilcox et

20   al. 2017; García-Palacios et al. 2018; Craven et al. 2018); or even the type of sampling

21   design used to investigate the BEF relationships (Isbell et al. 2015). For example,

22   disturbances such as extreme dry or rainfall events may trigger different effects of

23   biodiversity on two important aspects of stability: resistance and resilience (Isbell et

24   al. 2015). This way, it has been hypothesized that ecosystem stability is ensured by

the redundancy of some species that differ in their response to environmental change (insurance hypothesis, Yachi & Loreau 1999). In other words, some species will be more resistant than others to environmental changes, thus compensating the others that decline, maintaining the function (Yachi & Loreau 1999; Pillar et al. 2013; Mackie et al. 2019).

Another important issue to be considered in the investigation of BEF relationships is the limited framework in which the majority of the studies have been conducted. Ecosystem stability has been assessed mainly at fine spatial scales (e.g., Chalcraft 2013), through experimental approaches (e.g., Isbell et al. 2015), and under a restricted set of climatic conditions (e.g., Fischer et al. 2016, Shi et al. 2016), thus limiting our inferences about processes that may mitigate the effects of climate change on ecosystem functioning. Current knowledge of BEF relationships often supports the insurance hypothesis for grassland ecosystems, demonstrating a positive relationship between biodiversity and ecosystem stability (Isbell et al. 2015, García-Palacios et al. 2018). However, these results may present an incomplete picture of the problem, which may bias the interpretation of biodiversity effects on ecosystem stability. If biodiversity buffers ecosystem functioning from climate changes that impose increased stress on ecosystems and may jeopardize services that ecosystems provide, these findings have a potential to guide decision makers on climate change adaptation actions. In this sense, management actions that guarantee biodiversity levels may increase ecosystems' stability under climate change without compromising the services they provide.

Therefore, if we want to understand the effects of climate change on BEF relationships we must consider all factors above mentioned in an integrated study

that approaches BEF relationships under different climatic anomalies, natural communities and different facets of biological diversity. So, in this study we evaluate how plant communities' diversity, specifically functional redundancy and its interaction with the functional structure, affects resistance and resilience in grassland ecosystems worldwide.

Material and methods

Study area and biodiversity data - sPlot database

We used the sPlot database (Bruelheide et al. 2019) to access grassland vegetation communities distributed throughout the world. For so, the main criteria to filter plots were that (1) the sampling occurred after the year 2000, (2) they consisted of grassland vegetation, (3) with homogeneous landscapes in their surroundings, (4) with precise geographic information, and (5) at with at least 50% of the relative vegetation cover consisting of plant species represented in the TRY database (see below) (see Engel et al *in prep.* for more details on the filtering plot procedure).

To characterize the functional community structure at all selected plots, 18 ecologically relevant plant traits were selected. Among them were traits related to the leaf economics spectrum (e.g., specific leaf area), plant size (e.g., height) and reproduction (e.g., seed mass). Species mean traits were retrieved from TRY (Kattge et al. 2011) and gap-filled using Bayesian Hierarchical Probabilistic Matrix Factorization (Schrodt et al. 2015). The gap-filled trait data were available for 88.7% of all species occurrences in sPlot (Bruelheide et al. 2018). We log-transformed all trait values for downstream analysis.

1   *Functional characteristics at the community level*

2   With the 18 traits community weighted means (CWM) were computed for each

3 plot and analyzed by Principal Components Analysis (Engel et al. *in prep*.). We used

4 the first PCA axis (hereafter acquisitive-conservative axis) of the CWM space that

5 explained 27.42% of the trait variation to characterize the community's functional

6 structure. Most of the variation across communities was related to the resource

7 economics spectrum (Wright et al. 2004; Díaz et al. 2016). For this reason, we used

8 the scores of each community as a metric of functional structure, where plots with

9 negative scores on acquisitive-conservative axis were associated with communities

10 dominated by "acquisitive" species, while positive values on this axis were related to

11 "conservative species". For some analysis, we partitioned the acquisitive-

12 conservative axis into three community groups (G1, G2, and G3, respectively from

13 acquisitive to conservative).

14   In addition, we used only the traits most related to the leaf economics spectrum

15 (traits correlation values higher than 0.5 to the PCA first axis; Engel et al. *in prep*.),

16 that were: Specific Leaf Area, Leaf P concentration, Leaf N concentration, Leaf Area,

17 Leaf N/P ratio, Leaf N per Area, Leaf Dry Matter Content and Stem density, as we

18 were interested on the effect traits (sensu Lavorel & Garnier 2002) for resistance and

19 resilience. With these traits, we computed for each plot the functional redundancy

20 (difference between Gini–Simpson index of species diversity and Rao entropy) (Pillar

21 et al. 2013).

1   *Characterizing anomalous climatic events (SPEI base)*

2   To identify climatic anomalies, we choose the standardized precipitation-

3   evapotranspiration index (SPEI - SPEIbase version 2.6). It provides local monthly

4   values at time scales ranging from 1 to 48 months and at a 0.5° spatial resolution.

5   This means that, for a given month, it represents the cumulative water balance over

6   the previous *n* months. Here, we used *n* = 3 months (SPEI-03). Based on the index

7   values, we identified for each plot, from year 2000 to 2018, dry and wet events outside

8   the normal range (-0.68 < SPEI < 0.68), as well as their intensity: extreme (SPEI >

9 |1.27|) or moderate (|0.68| < SPEI < |1.27|) (Vicente-Serrano et al. 2010).

10

11   *Biomass productivity data – NDVI*

12   The Normalized Difference Vegetation Index – NDVI is a spectral indicator

13   widely used to quantify photosynthetic activity, which is a proxy for biomass

14   production, an indicator of ecosystem functioning (Pettorelli et al. 2005; De

15   Keersmaecker et al. 2017). Here, we employed NDVI data at the 250 m resolution for

16   the period of 2000 to 2018, with 23 acquisitions per year for each one of the 1,212

17   plots (Figure 1). The original data were obtained from the MODIS product MOD13Q

18   (Didan 2015), available through the Google Earth Engine (Google Earth Engine Team

19   2015). NDVI values were subjected to a smoothing process (Savitzky & Golay 1964)

20   using the function *savgol* of pracma package (Borchers 2021).

21

22   *Ecosystem level temporal stability*

23   Temporal stability is a measure of the productivity change (increase or

24   decrease) during a climatic anomaly. We calculated for each plot the resistance [Eq

1   1] and resilience [Eq 2] which describes, respectively, the change of NDVI related to

2   its baseline and the return ratio to baseline (Isbell et al. 2015).

3   The first step to obtain resistance and resilience was to use normal SPEI

4   events to calculate the average productivity of each plot for each month in the time

5   series (2000 to 2018). This average was adopted as the productivity baseline ($\overline{Y_n}$ in

6   Equation 1). In order to guarantee that the vegetation described at the plots was not

7   affected by anomalous climatic events, we selected plots sampled in normal months

8   according to SPEI03. For each plot sampling date surveyed in a normal period we

9   searched for the 11 previous and 11 subsequent months. Within this ten-month

10   temporal window, for a given plot we selected the months that presented NDVI values

11   subjected to an anomalous climatic event (Y_e in Equation 1) to calculate the resistance

12   following Equation 1.

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

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

15   We calculated resilience by first identifying anomalous climatic events (Y_e in

16   Equation 2) that were followed by a sequence of three normal months. For a given

17   plot and anomalous climatic event at month e, the denominator of Eq. 2 was the

18   difference between the NDVI value of the third normal month (Y_{e+1} in Eq 2) and the

19   productivity baseline of that third normal month ($\overline{Y_{n+1}}$ in Eq 2). The closer the NDVI of

20   the third normal month was to the NDVI baseline, the greater the resilience for that

21   plot. It is worth to note that the identified anomalous events were not synchronous

22   across plots at the global scale. Finally, we log transformed the values of resistance

23   and resilience to smooth outliers.

1   *Data analysis*

2   We modelled both resistance and resilience using a linear mixed model for

3   each class of climatic event (moderate and extreme dry and wet events). In this model

4   we used as the fixed term the resistance and resilience modelled as a function of

5   species richness (richness), functional redundancy (FR) and functional structure of

6   each plot (acquisitive-conservative axis), and a random term with an intercept only

7   variation represented by the different biome types (Equations 3 and 4). The fixed

8   effects were standardized in order to allow comparison of the effects among

9   biodiversity descriptors. We used the nlme package (Pinheiro et al. 2021) to run the

10   model.

11

12   $\Omega \sim richness + FR + PCA1 + richness : PCA1 + FR : PCA1 + richness : FR$

13   $\qquad : PCA1,$

14   $random = \sim 1| Biome$ [Eq 3]

15

16   $\Delta \sim richness + FR + PCA1 + richness : PCA1 + FR : PCA1 + richness : FR$

17   $\qquad : PCA1,$

18   $random = \sim 1| Biome$ [Eq 4]

19

20   For data treatment and manipulation, we used tidyverse package (Wickham et

21   al. 2019). The figures were created using ggplot2, from tidyverse package. All data

22   treatment and analyses were performed in R (R Core Team 2019).

23

Results

Biodiversity effects on the resistance of ecosystem productivity were in general significant under extreme and moderate dry and wet events (Table 1, Figures 2 to 5). The effects of functional redundancy on the resistance were positive under extreme dry events (Figure 2a). Communities functional structure had a negative effect on resistance, however, acquisitive communities had higher values of resistance than conservative communities (Figure 2b). During moderate dry events, the effect of FR on resistance depended on communities' functional structure. While the effect of FR on resistance was negative in conservative communities (Figure 3), its effect was positive in communities dominated by acquisitive species (Figure 3). Species richness affected resistance positively during extreme wet events (Figure 4a). In turn, the functional structure of communities showed a negative effect on resistance, i.e., the resistance values of acquisitive communities were higher than those of conservative communities (Figure 4b). When communities faced moderate wet events, the effect of FR on resistance was negative (Figure 5). However, the strength of this effect depended on species richness and the functional community structure, and the negative effect increased from low to high species richness (Figure 5).

Regarding ecosystem resilience, we found significant effects on the recovery from wet events (Figures 6 and 7). The recovery from extreme wet events, on the one hand, was positively affected by species richness mediated by acquisitive communities (Figure 6). On the other hand, the effect of species richness mediated by acquisitive-conservative character of the communities had a negative effect on resilience (Figure 6). After moderate wet events, the effect of species richness on

1   resilience was positive, but mediated by communities' functional structure, with

2   increasing strength from conservative to acquisitive communities (Figure 7a). In

3   contrast, the effect of FR on resilience was negative (Figure 7b).

4

5   **Discussion**

6   Our results support the hypothesis that the effects of biodiversity on

7   ecosystem stability (resistance and resilience) are context dependent on the

8   biodiversity facet and the climatic anomaly considered. As a general pattern,

9   biodiversity effects on resistance during dry events were positive, whereas negative

10   under wet anomalous climatic events. Therefore, no single metric can capture all the

11   effects of climate change on the stability of ecosystem functioning, specifically

12   resistance and resilience.

13   We showed that considering the functional structure is paramount in BEF

14   research since the effects of the different biodiversity facets on ecosystem stability

15   are contingent to it. As far we know, this is the first time in which the functional

16   structure is considered when analyzing BEF effects on stability considering

17   anomalous climatic events in a macroecological scale. Functional diversity was

18   already used to investigate BEF relationships García-Palacios et al. (2018); Craven et

19   al. 2018), however as we show in our study the effect of functional diversity is also

20   dependent on the functional structure of communities, highlighting the need to

21   consider the later when investigating BEF relationships. It is also worth to highlight

22   that different from previous studies (García-Palacios et al. 2018; Craven et al. 2018))

23   we considered the functional structure as an important factor to explain the outcomes

24   of BEF effects on resistance and resilience. Once depending on the dominant

resource use strategies of a community its response to anomalous climatic driving

forces may will differ. In other words, consider the functional structure is not just a

matter of statistical control, but is an important ecological factor to be considered.

Further, our work evaluated the effects of resource use strategies in a

community level, differently from the usual approach of many experimental studies

(but see Craven et al. 2018). Also, the majority of studies investigating BEF effects on

resistance and resilience rely on fine to medium scale experiments or studies that are

focused on a particular Biome or Ecosystem type (e.g. arid ecosystem (García-

Palacios et al. 2018). Our work combines natural communities spread across different

locations globally, comprising one of the few studies to investigate BEF relationships

in a macroecological scale.

In the context of climate change the current evidence shows that biodiversity

buffers the effects of climate change over productivity stability (Isbell et al., 2015),

however our study shows that in face of climatic extreme events there are no single

biodiversity effect in ecosystem stability.

Despite the gaps that our work fills, to elucidate BEF relationship effects on

stability in the context of climate change, some possible drawbacks must be further

addressed. First, the range of ecosystem types evaluated must be enhanced, for

example due to the filtering criteria our sample did not include vegetation plots from

South America, despite the recognized importance and representativeness of

grassland communities present in this continent (Baldi & Paruelo 2008; Staude et al.

2018). Second, regarding the calculation of stability measures, further investigation

should investigate the dependence of frequent or consecutive anomalous climatic

events on the productivity values. Specifically, to date there is no formal evaluation

on how resilience values are affected by the time span between the occurrence of an anomalous climatic event and the next evaluation of productivity in the studied communities. In our analyses we defined Y_{e+1} as the productivity at the third month after the anomalous month for the SPEI, conditional on that no anomalous month occurred in between.

As a take-home message we emphasize that mitigating the effects of climate changes need specific actions depending on the direction and the intensity of the anomalous climatic events, the related biodiversity component and the underpinned ecosystem functions.

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Figures
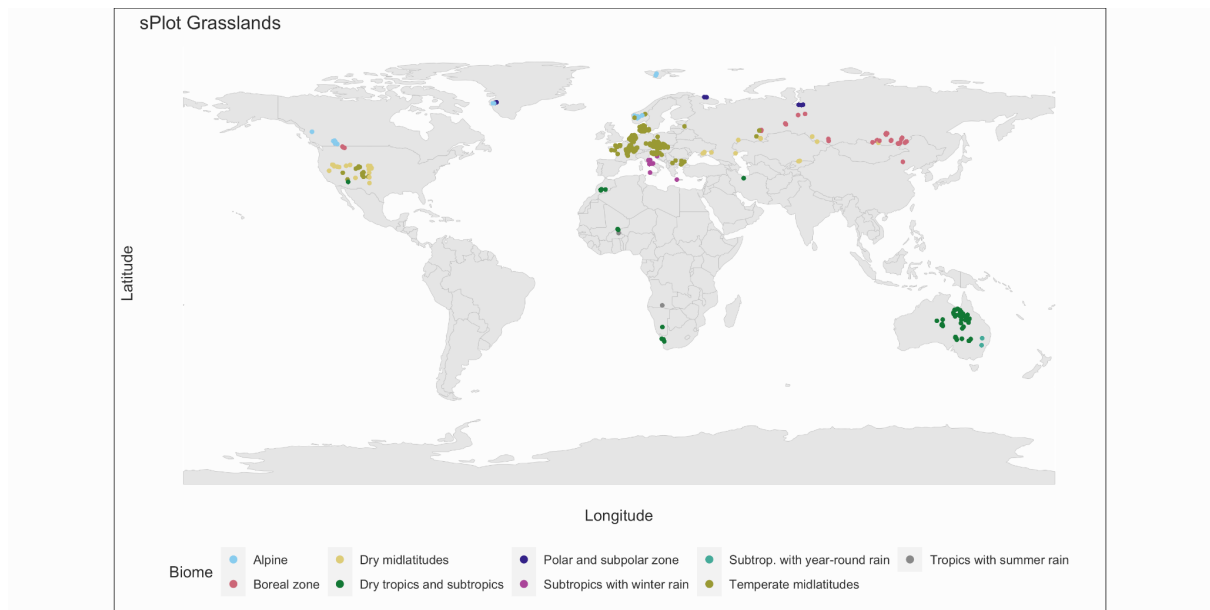
Figure 1: Locations of included vegetation sPlot plots (Bruelheide et al. 2019) colored by biome types (Alpine, Boreal zone, Dry midlatitudes, Dry tropics and subtropics, Polar and subpolar zone, Subtropics with winter rain, Subtropics with year-round rain, Temperate midlatitudes, Tropics with summer rain).

Extreme Dry anomalous climatic events

Figure 2: Predicted values from the linear mixed model effects of functional redundancy (a) and the acquisitive-conservative axis (b) on the resistance (log transformed) of grassland vegetation communities under extreme dry climatic events. The parameter estimates (standardized regression coefficients) of the model predictors are shown with their associated 95% confidence intervals.

Moderate Dry anomalous climatic events

Figure 3: Predicted values from the linear mixed model effects of the interaction between functional redundancy and the acquisitive-conservative axis (PCA1 scores increasing from G3 conservative to G1 acquisitive) on the resistance (log transformed) of grassland vegetation communities under moderate dry climatic events. The parameter estimates (standardized regression coefficients) of the model predictors are shown with their associated 95% confidence intervals.
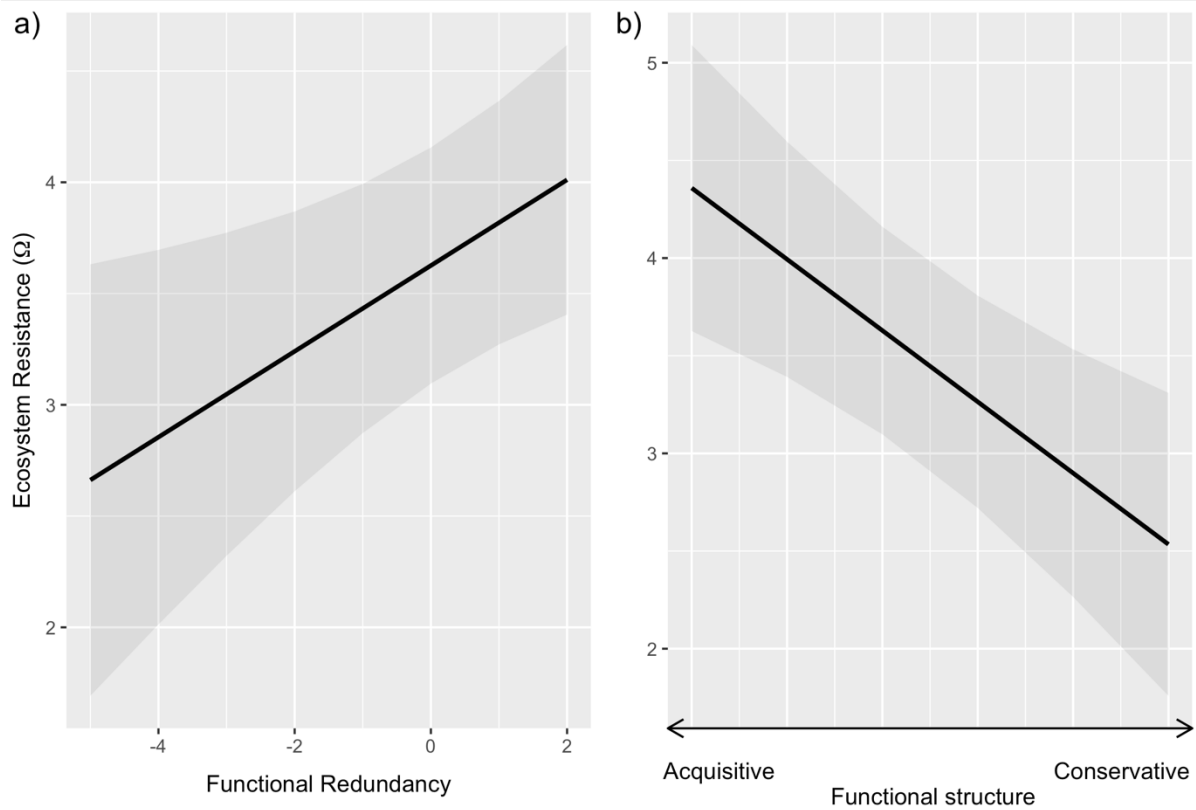
Extreme Wet anomalous climatic events

Figure 4: Predicted values from the linear mixed model effects of species richness (a) and the acquisitive-conservative axis (b) on the resistance (log transformed) of grassland vegetation communities under extreme wet climatic events. The parameter estimates (standardized regression coefficients) of the model predictors are shown with their associated 95% confidence intervals.
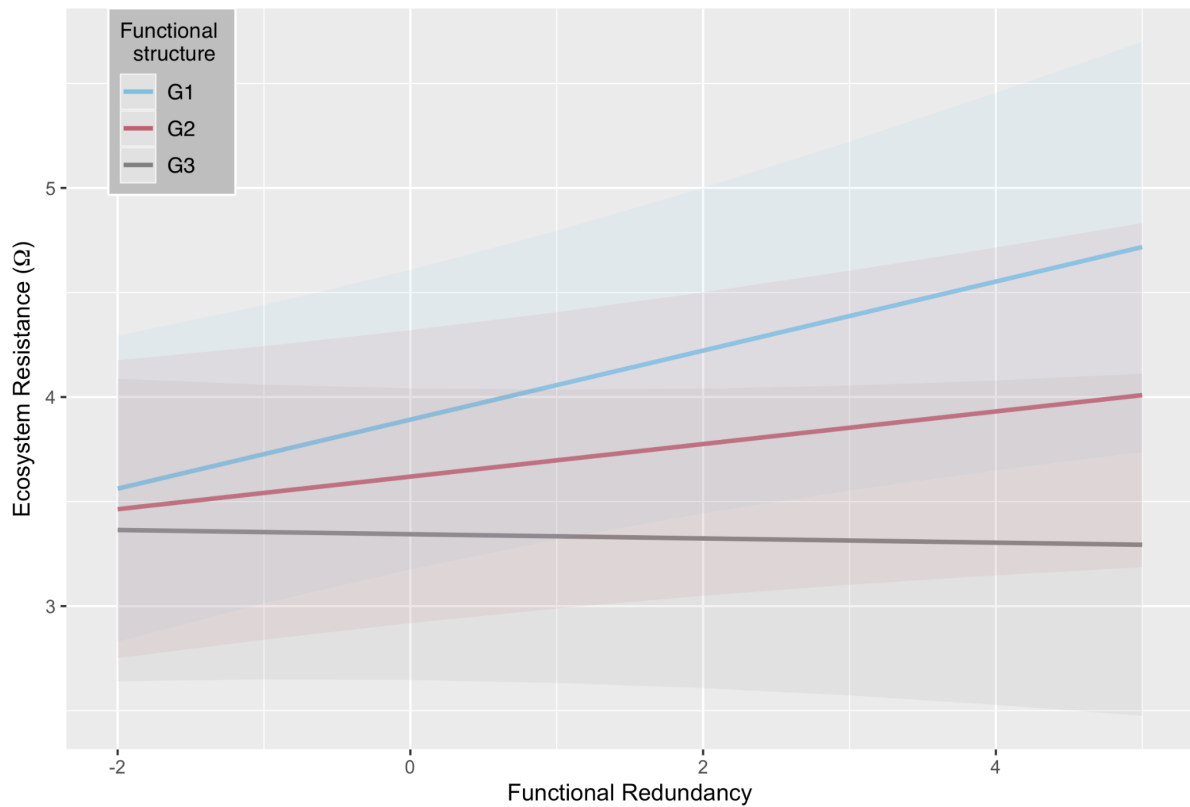
Moderate Wet anomalous climatic events

Figure 5: Predicted values from the linear mixed model effects of the interaction between functional redundancy, the acquisitive-conservative axis (PCA1 scores decreasing from G1 acquisitive to G3 conservative) and species richness on the resistance (log transformed) of grassland vegetation communities under moderate wet climatic events. The parameter estimates (standardized regression coefficients) of the model predictors are shown with their associated 95% confidence intervals.

Extreme Wet anomalous climatic events
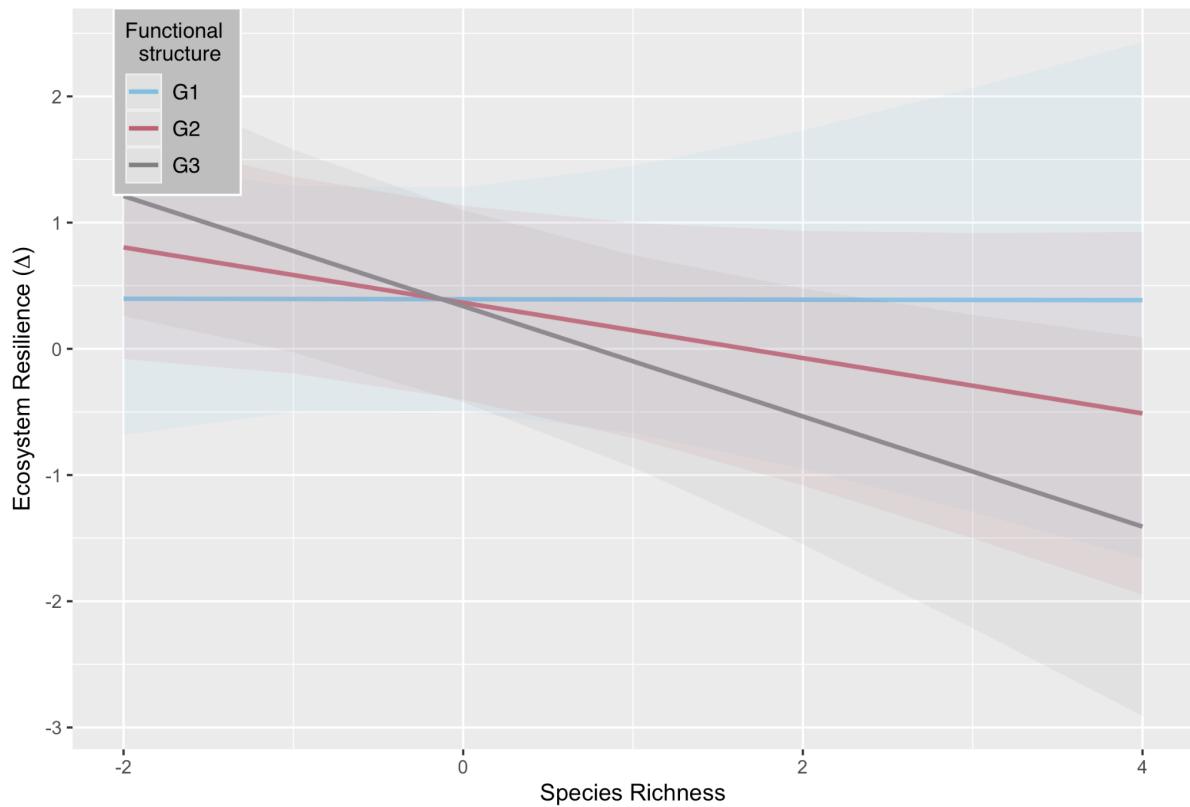
Figure 6: Predicted values from the linear mixed model effects of the interaction between species richness and the acquisitive-conservative axis on the resilience (log-transformed) of grassland vegetation communities under extreme wet climatic events. The parameter estimates (standardized regression coefficients) of the model predictors are shown with their associated 95% confidence intervals.
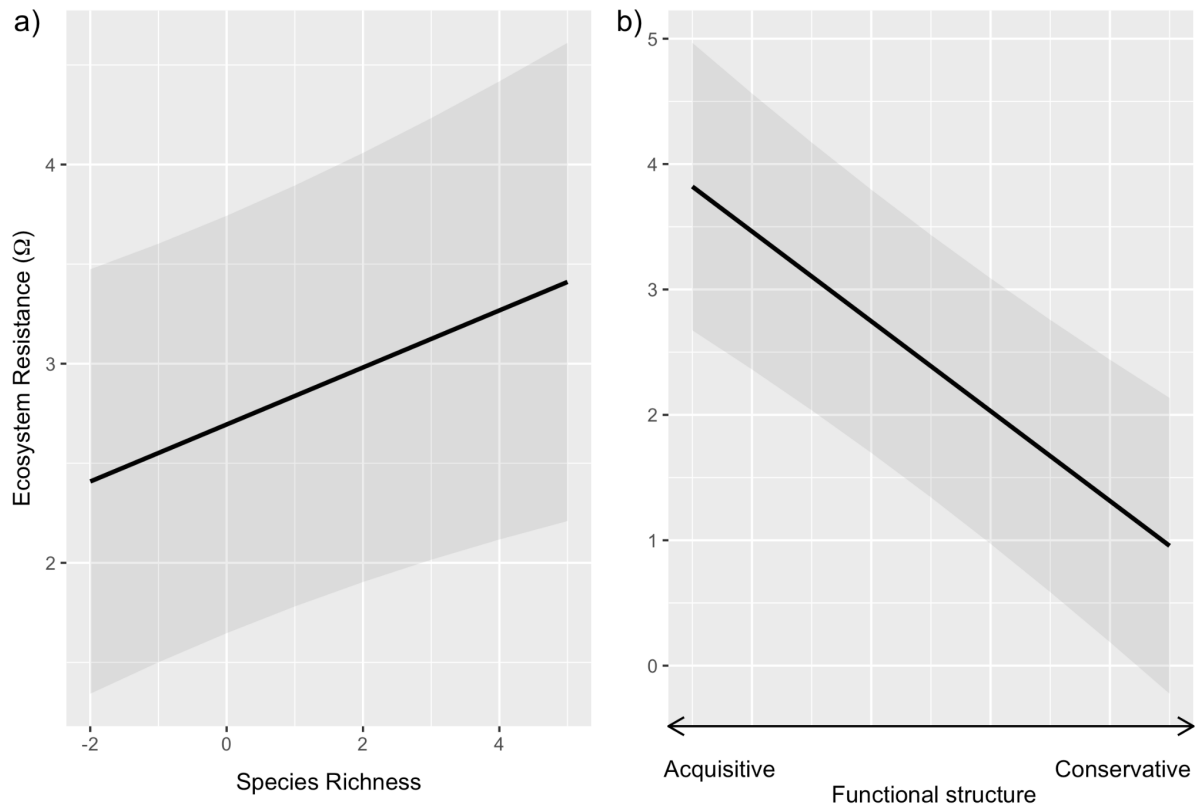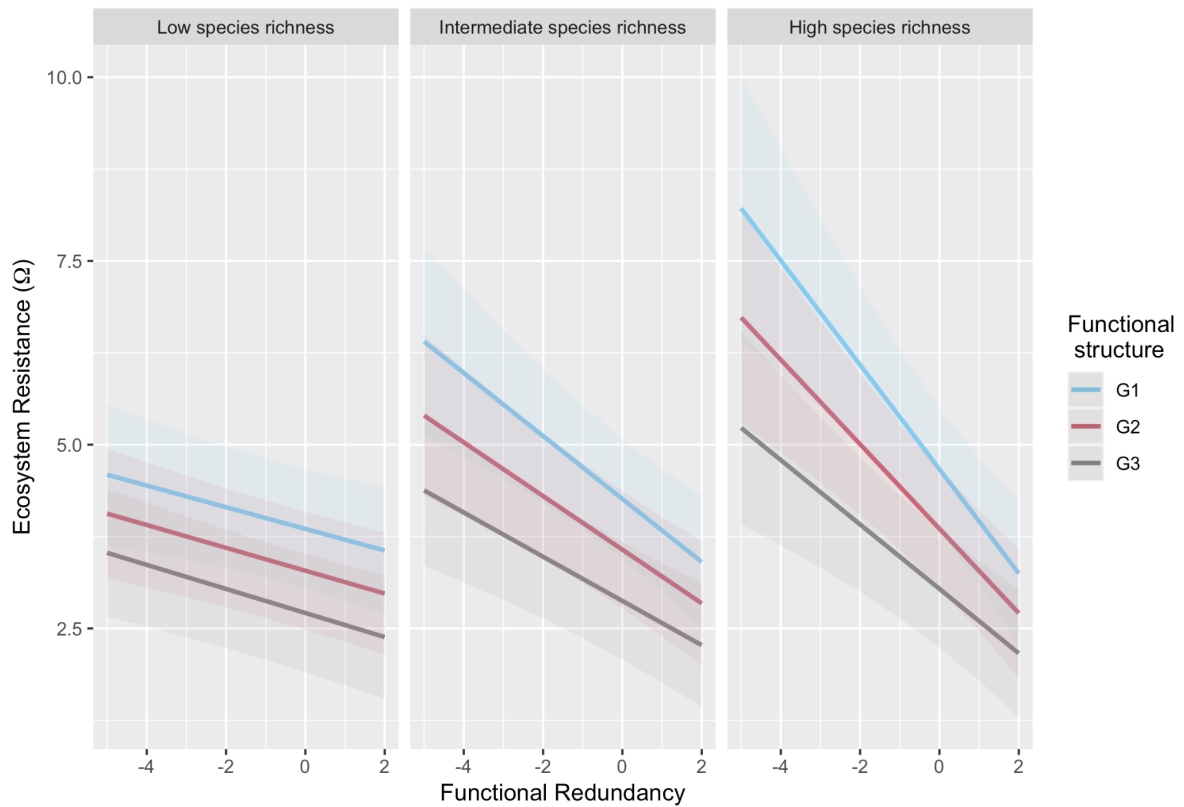
Moderate Wet anomalous climatic events

Figure 7: Predicted values from the linear mixed model effects of the interaction between species richness and the acquisitive-conservative axis (PCA1 scores) (a) and functional redundancy (b) on the resilience (log-transformed) of grassland vegetation communities under moderate wet climatic events. The parameter estimates (standardized regression coefficients) of the model predictors are shown with their associated 95% confidence intervals.
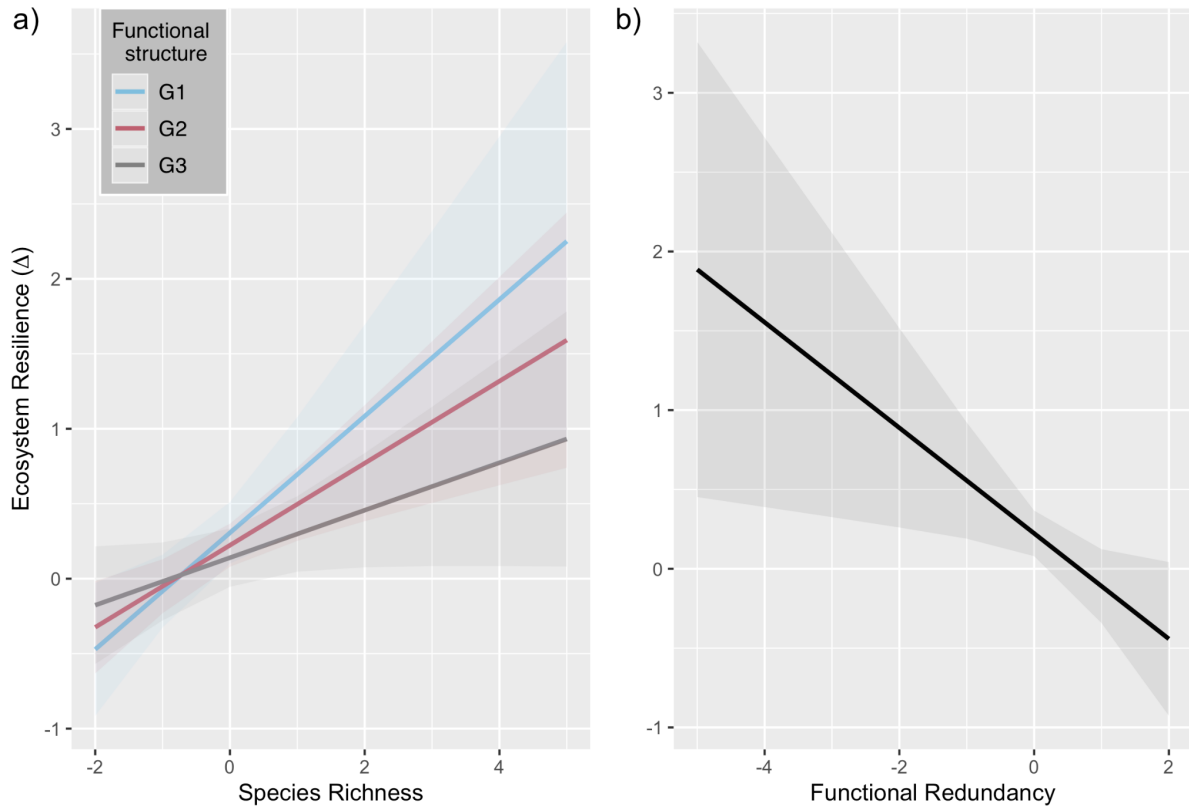
Table 1. Estimated effects of biodiversity descriptors on grassland ecosystems' stability (Resistance and Resilience) during climatic anomalies (ED – Extreme dry, EW – Extreme wet, MD – Moderate dry, MW – Moderate wet). SR – Species richness, Dim1 – Functional structure[1], FR – Functional redundancy, SE – Standard Error, DF – degrees of freedom.

SPEI-03	Fixed Effect	Resistance (Ω)					Resilience (Δ)				
		Estimate	SE	DF	t-value	p-value	Estimate	SE	DF	t-value	p-value
ED	Intercept	3.634	0.27	3272	13.416	**5.40E-40**	0.107	0.29	529	0.366	0.714
	SR	-0.009	0.05	3272	-0.19	0.849	0.013	0.11	529	0.12	0.905
	Dim1	-0.182	0.06	3272	-3.298	**0.001**	0.161	0.13	529	1.209	0.227
	FR	0.193	0.08	3272	2.364	**0.018**	-0.037	0.2	529	-0.19	0.852
	SR:Dim1	0.029	0.04	3272	0.757	0.449	-0.131	0.09	529	-1.5	0.135
	Dim1:FR	0.004	0.04	3272	0.107	0.915	-0.002	0.09	529	-0.02	0.983
	SR:FR	0	0.05	3272	0.004	0.997	-0.082	0.13	529	-0.65	0.518
	SR:Dim1:FR	0.014	0.03	3272	0.414	0.679	-0.032	0.07	529	-0.46	0.648
MD	Intercept	3.619	0.36	5185	10.131	**6.70E-24**	0.038	0.08	1077	0.463	0.643
	SR	0.077	0.04	5185	1.917	**0.055**	-0.091	0.09	1077	-0.98	0.326
	Dim1	-0.286	0.05	5185	-5.824	**6.10E-09**	0.039	0.08	1077	0.515	0.606
	FR	0.081	0.07	5185	1.161	0.246	0.045	0.16	1077	0.278	0.781
	SR:Dim1	-0.091	0.04	5185	-2.493	**0.013**	0.016	0.08	1077	0.209	0.834
	Dim1:FR	0.033	0.04	5185	0.808	0.419	-0.131	0.09	1077	-1.47	0.143
	SR:FR	0.012	0.04	5185	0.275	0.783	0.045	0.1	1077	0.45	0.653
	SR:Dim1:FR	0.023	0.03	5185	0.811	0.417	-0.093	0.06	1077	-1.47	0.141
EW	Intercept	2.744	0.54	2813	5.126	**3.20E-07**	0.365	0.39	559	0.933	0.351
	SR	0.142	0.06	2813	2.395	**0.017**	-0.219	0.14	559	-1.55	0.123
	Dim1	-0.358	0.07	2813	-5.553	**3.10E-08**	-0.027	0.16	559	-0.18	0.860
	FR	-0.05	0.1	2813	-0.516	0.606	-0.038	0.21	559	-0.18	0.858
	SR:Dim1	0.01	0.05	2813	0.217	0.829	-0.217	0.12	559	-1.78	**0.076**
	Dim1:FR	0.048	0.05	2813	0.974	0.33	0.127	0.11	559	1.116	0.265
	SR:FR	-0.062	0.07	2813	-0.968	0.333	-0.018	0.14	559	-0.13	0.899
	SR:Dim1:FR	0.06	0.04	2813	1.591	0.112	0.065	0.09	559	0.712	0.477
MW	Intercept	3.486	0.41	5186	8.553	**1.60E-17**	0.223	0.07	1102	3.051	**0.002**
	SR	0.284	0.04	5186	6.835	**9.10E-12**	0.274	0.08	1102	3.365	**0.001**
	Dim1	-0.736	0.05	5186	-14.35	**8.30E-46**	-0.083	0.07	1102	-1.18	0.24
	FR	-0.35	0.07	5186	-4.945	**7.90E-07**	-0.333	0.14	1102	-2.41	**0.016**
	SR:Dim1	-0.135	0.04	5186	-3.485	**5.00E-04**	-0.115	0.07	1102	-1.65	0.098
	Dim1:FR	0.065	0.04	5186	1.558	0.119	0.02	0.07	1102	0.275	0.783
	SR:FR	-0.21	0.05	5186	-4.71	**2.50E-06**	-0.13	0.09	1102	-1.54	0.125
	SR:Dim1:FR	0.08	0.03	5186	2.661	**0.008**	0.041	0.05	1102	0.79	0.43

Note 1 – The functional structure was accessed by a Principal Coordinates Analysis using the community weighted means for leaf traits.

Supplementary information
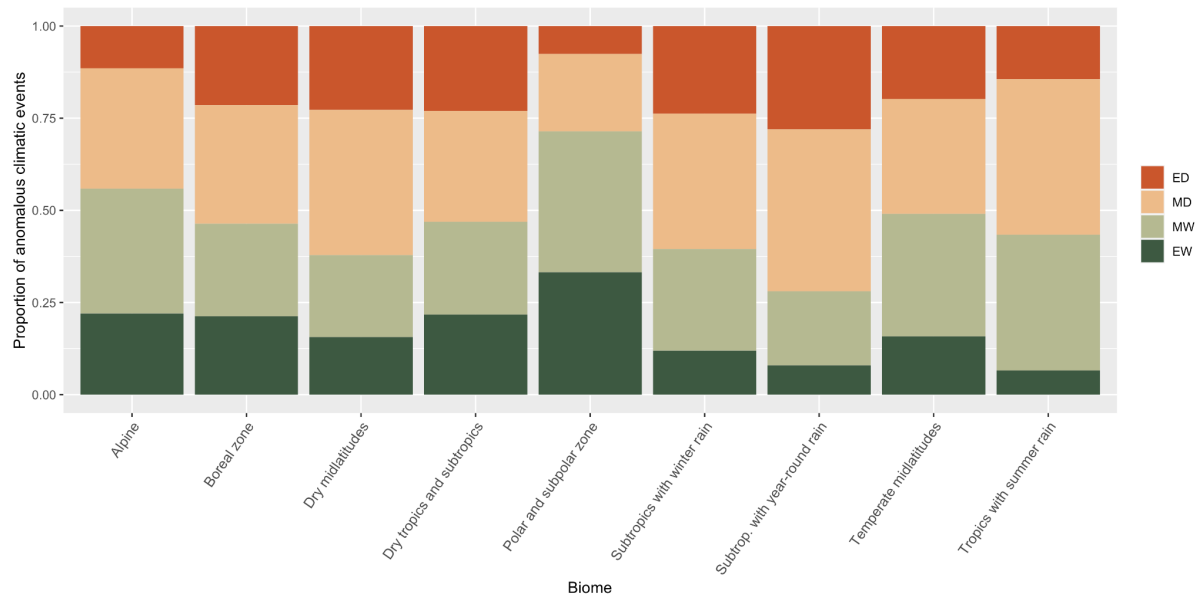
Supplementary figure 1 – Proportion of climatic anomalous climatic events by biome classified using SPEI-03

Capítulo 3

Biodiversity manipulation via removals

Biodiversity manipulation via removals

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1   **Abstract**

2   Biodiversity changes and their effects on ecosystem functioning (BEF) are

3   mainly studied through experimental approaches, either by target species removal

4   (removal experiments) in natural communities, or by synthetic communities created

5   through planting and seeding target species combinations (synthetic experiments).

6   While removal experiments preserve the community assembly process, the synthetic

7   experiments allowed to a great control of confounding effects in BEF studies. Despite

8   the advantages, none of those experiments deal with methodological pitfalls

9   associated with the lack of control in some biodiversity components while

10   manipulating others and the effects of the mechanical removal (experimental

11   manipulation) on the ecosystem function considered. In this report we will present an

12   experimental design for removal BEF experiments, coupled with an R function that

13   accounts to the above-mentioned pitfalls. We applied this experimental framework

14   on a removal experiment with natural grassland communities. The removals were

15   targeted to reduce functional redundancy in order to assess its effect on the

16   resistance and resilience of the ecosystem productivity when simulated extreme

17   climatic events were applied. As far as we know, this is the first experimental attempt

18   to circumvent some confounding factors in BEF experiments. We argue that this type

19   of experiments and methodological procedure should be adopted whenever the aim

20   is to investigate the effects of a biodiversity component in BEF experiments.

21

22   *Keywords*: Biodiversity Ecosystem Function; Removal Experiment; Climate

23   change; Precipitation manipulation; Resistance; Resilience

Introduction

1

2   Natural communities are the result of assembly processes, which are generally

3   non-random. This means that regional and local assembly processes affect local

4   species composition, and this in turn drives ecosystem functioning (Leibold et al.

5   2017). One of the main challenges of community ecology is to unify the existing

6   theories about community assembly, understand whether and how they relate to

7   each other, and how we can use their insights to predict the ecosystem functioning

8   in a changing world (Korell et al. 2020; Thompson et al. 2020). This also applies to

9   the biodiversity and ecosystem functioning (BEF) approach. BEF experiments have

10   been established using a large range of different designs that vary with respect to

11   which degree community assembly processes are allowed and considered. Despite

12   BEF studies provide important evidence on the significance of biodiversity to

13   ecosystem functioning (Eisenhauer et al. 2016; Jochum et al. 2020), some do not

14   consider community assembly (synthetic communities experiments) or, when

15   considered, do not account for the variation in different dimensions of diversity or,

16   even, the effects of the experimental manipulation itself. Therefore, findings of

17   existing approaches have been questioned regarding their applicability to natural

18   communities (e.g., Wardle 2016) and to what extent biodiversity and ecosystem

19   process are related.

20   While natural communities are experimentally manipulated through target

21   species removal (hereafter, removal experiments), synthetic communities are created

22   through planting and seeding target species combinations (hereafter, synthetic

23   experiments). Removal experiments account for community assembly by preserving

24   inherent patterns produced by natural processes and hence, incorporating drivers

underlying community assembly that operate on a regional scale (Díaz et al. 2003; van der Plas 2019). Instead, synthetic experiments use artificially assembled communities from a given species pool, and by controlling for species richness (or functional composition) synthetic experiments impose strong constraints on community assembly. However, both experiments do not usually control for two important confounding factors that can blur the BEF relationships: the effects of the manipulation itself, involved in the maintenance by weeding or removal of non-target species, and the effects the manipulation of a given biodiversity component causes on other components. Therefore, removal experiments can offer better insights on BEF relationship if the above-mentioned confounding factors could be properly addressed.

In this report, we propose a new methodological framework to be adopted in removal experiments that allows to differentiate in BEF experiments the effects of biodiversity manipulation and at the same time preserving other biodiversity characteristics of communities while modifying the target biodiversity component. To achieve this, we propose a modification in the design of current removal experiments and a R function that allows guiding the removal of species during the experiment.

Methods

I – Differentiating the effects of experimental manipulation in BEF experiments through the experimental design

In order to allow a correct interpretation of the results in removal BEF experiments, it is necessary to compare the effect of the removal treatment with the control (Figure 1A). The target removal allows to evaluate the response of the

community in the absence of it. However, to evaluate the true target effect (the effect of target biodiversity component) of the experimental manipulation, it is necessary to control the side-effects of removals, that is, if not controlled, the removal disturbance effect itself may be taken as a biodiversity effect (Figure 1C).

II – Controlling biodiversity effects

The target removal may have other side-effects that need to be controlled. Since biodiversity components may be highly correlated, while we manipulate one component we need to minimize the variation in others, relative to the removal treatment (Figure 1B). Once studying natural communities, with their inherent variation, it can be challenging to find a solution that at the same time maximizes the target biodiversity effect and minimizes the variation on the other biodiversity components of the communities. For example, if we are interested on the effects of functional redundancy on an ecosystem function (Pillar et al. 2013), we need to change by removals the level of redundancy while maintaining the other components of biodiversity closer to the original values in the communities.

Therefore, we developed an algorithm that help us to select a set of combinations of candidate species to be removed. This algorithm simulates all the possible combinations from 1 to *n-1* species to be removed in a given community and computes diversity metrics for the remaining species. With this information we can select the combination which satisfies the pre-defined thresholds. Depending on the original number of species in a community, and on the number of parameters we define, the algorithm may provide more than one solution.
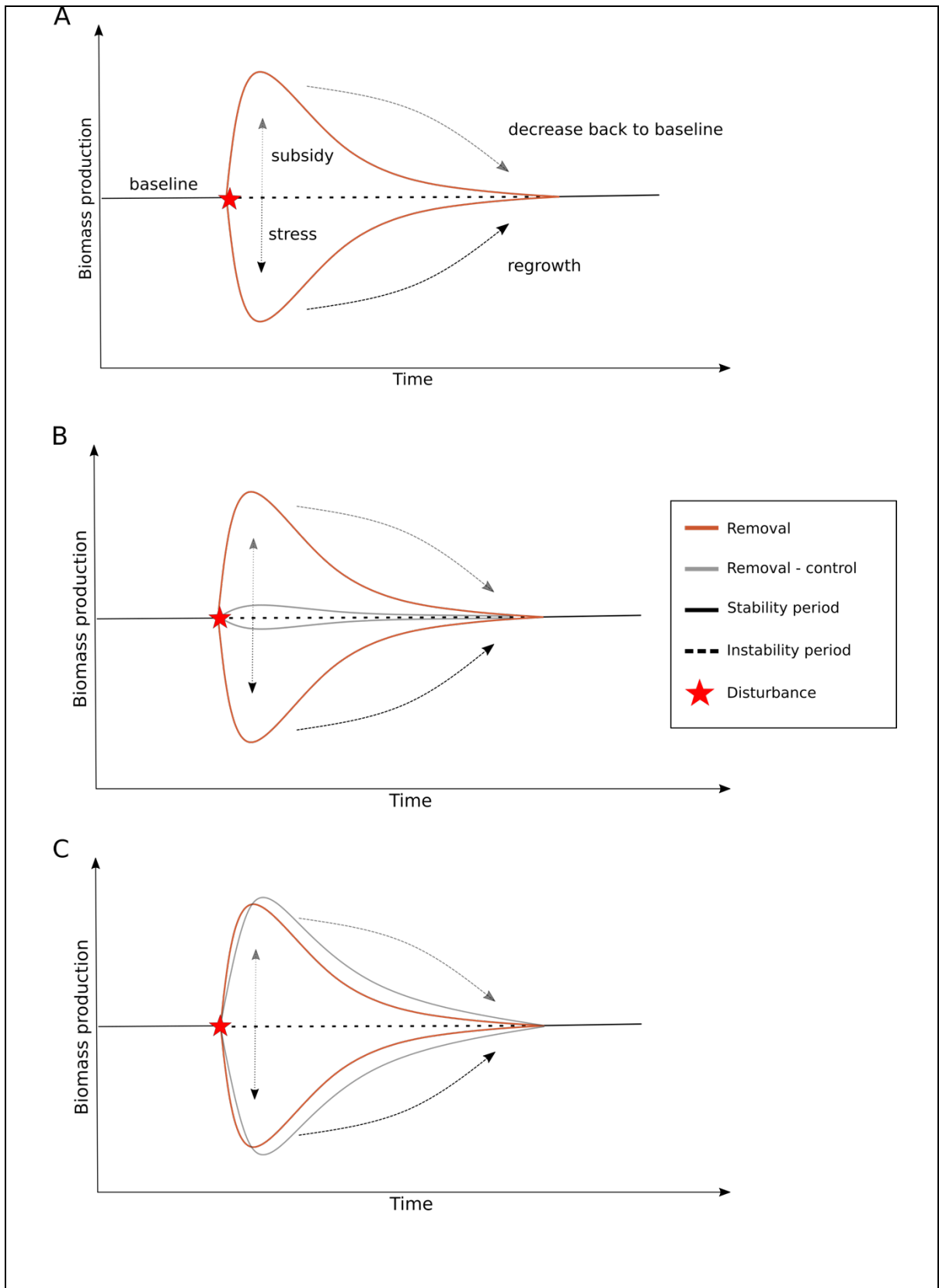
Figure 1: Schematic figure (modified from Fischer et al. 2016). We showed a common outcome of a BEF experiment that analyzed ecosystem stability (A). However, this outcome can be a true result of the effect of a biodiversity facet (B) or just a side effect of experimental manipulation (C).

1   *III – An empirical illustration: removal BEF in face of climate change events*

2   In order to illustrate how our proposed methodological approach can be applied to

3   improve removal experiments, in the next section we show an example of a removal

4   experiment that adopted the above-mentioned experimental design.

5

6   *Study site and abiotic conditions*

7   Intact vegetation-soil monoliths with approximately 20 cm soil depth and 30

8   cm diameter were collected in June 2019 from a native grassland (30°15'45.6"S

9   52°14'00.2"W) in the municipality of Rio Pardo in southern Brazil. The grassland site

10   had been managed under moderate grazing, and we collected the monoliths in well

11   grazed patches (grazing lawns).

12

13   *Experimental setup*

14   We assembled the grassland monoliths in the beginning of July 2019 in 60

15   cylindrical PVC pots of 30 cm in diameter and 30 cm high. Hereafter we refer to each

16   grassland monolith as a community. The pots with the communities were placed in a

17   greenhouse located within the UFRGS Campus do Vale, in Porto Alegre. After a

18   month of acclimatization to the new conditions, we conducted the first vegetation

19   survey to record species identities and visual estimation of percentage cover. We

20   defined the blocks of the experiment based on species composition. For this, we

21   submitted the community composition matrix to cluster analysis using Ward's

22   method based on Euclidean distances between communities using the Multiv

23   package (Debastiani & Pillar 2019). We partitioned the 60 communities into seven

1   groups and tested group partition sharpness by bootstrap resampling procedure

2   (Pillar 1999).

3   Once the best community clusters (blocks) were defined, we randomly

4   allocated each pot in a block to one treatment. The treatments consisted of a

5   combination of three levels of two factors: removal and irrigation water.

6

7   *Definition of removal treatments*

8   To avoid unwanted confounding factors, while manipulating a given

9   biodiversity component to achieve the desired experimental level of functional

10   redundancy, we should also minimize the variation on other components. Therefore,

11   we defined critical thresholds to select the set of target species that should be

12   removed from each community. Thus, for target species removal (Removal

13   treatment), the following criteria evaluated at the community level must be satisfied:

14   i) the difference between the final community evenness relative to its initial value could

15   be no more than 10%; ii) the difference between the functional diversity (Rao) relative

16   to its initial value could be no more than 5%; iii) as for the functional redundancy, the

17   target was to achieve a reduction of at least 40% relative to its initial value; while iv)

18   the species cover in the pot, due to the removals, could not be reduced by more than

19   40% of its initial value.

20   The three levels of this treatment are: i) Control – no manipulation to remove

21   species; ii) Removal treatment (above mentioned); and Removal-control. For the later,

22   we used the same algorithm developed to find the set of species to be removed on

23   the Removal treatment. However, we chose the combination that minimized the

24   variation of biodiversity parameters at the community level, guaranteeing the original

1   richness in each pot, and at the same time reducing an equivalent amount of biomass

2   to its relative pair within the block.

3

4   *Definition of water treatments*

5   To define the water treatments, first we used the function *get_power* from

6   nasapower package (Sparks, 2018) to retrieve daily precipitation (mm) and

7   temperature (°C) values between January 1981 to June 2019, for Rio Pardo, RS.

8   Second, using the SPEI package (Beguería & Vicente-Serrano 2017), we computed

9   monthly potential evapotranspiration (PET) with the *thornthwaite* function. Then we

10   fitted monthly SPEI-03 values by applying the *spei* function to the calculated water

11   balance (difference between precipitation and PET). Third, based on the SPEI-03

12   index values, we identified for every month, from year 1981 to 2019, dry and wet

13   events outside the normal range (-0.68 < SPEI < 0.68), as well as their intensity:

14   extreme (SPEI > |1.27|) or moderate (|0.68| < SPEI < |1.27|) (Vicente-Serrano et al.

15   2010).

16   As our interest was to evaluate the effects of extreme dry and wet climatic

17   events, we excluded moderate values. Using normal SPEI-03 events we defined the

18   water control treatment as the average precipitation baseline for each month (Figure

19   2). Using the average precipitation for extreme dry and extreme wet months, we

20   defined the extreme dry treatment and the extreme wet treatment, respectively.

21   Finally, we adjusted the amount of water each pot would receive according to the

22   water treatment, relative to its volume.

23   We installed a tensiometer in each pot in order to monitor their humidity. For

24   this purpose, a hole was made in the center of each pot using a hollow cylinder of

1   the same diameter as the tensiometer tube. This method allowed the removal of the

2   soil avoiding compaction. The tube of each tensiometer was inserted into the hole to

3   a depth of around 15 cm and then filled with water until the formation of a meniscus.

4   A glycerin-filled manometer was inserted into each tube and the water level was

5   readjusted as necessary to avoid air pockets. The humidity of each pot was

6   monitored from the measurement of the differential pressure read in each

7   tensiometer, where the higher the indicated pressure, the drier the soil in the pot. In

8   addition to the tensiometers, five dataloggers were distributed among the pots for

9   monitoring the local temperature and humidity in each block.

10
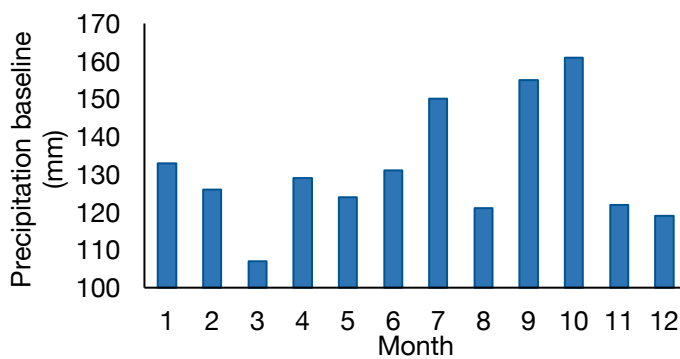
11 **Figure 2**: Monthly baseline precipitation (mm) for Rio Pardo, RS, Brazil.

12

13   *Experiment maintenance*

14   All pots were irrigated with the same amount of water, adjusted to simulate

15   monthly rainfall during normal periods. Biomass was maintained by clipping at time

16   intervals defined by 350°C growing degree days, and species composition surveys

17   were repeated quarterly in each community.

18

19   **Results**

20   A total of 85 species were identified, with *Paspalum notatum*, *Axonopus affinis*,

Desmodium incanum, *Hypoxis decumbens*, *Richardia humistrata*, *Soliva sessilis*, *Dichondra sericea*, and *Elephantopus mollis* as the most abundant species.

Consideration and perspectives

We defined objective criteria for selecting the species to be removed from each experimental community: to reduce functional redundancy by minimizing the variation caused by removal in functional diversity and equitability. This is the first approach, as far as we know, that circumvent confounding factors in BEF experiments. We argue that this type of experiments and methodological procedure should be adopted whenever the aim is to investigate the effects of a biodiversity component in BEF experiments.

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1 Considerações finais

Nesta tese investigamos o papel da biodiversidade vegetal campestre em promover a estabilidade (resistência e resiliência) do funcionamento ecossistêmico diante de alterações anômalas na precipitação pluvial. Integramos diferentes abordagens metodológicas, e utilizamos bases de dados disponíveis, que viabilizaram o teste das hipóteses apresentadas para avaliar a relação entre biodiversidade e estabilidade em três escalas: experimental (capítulo 3), regional (capítulo 1) e mundial (capítulo 2).

A partir dos resultados, demonstramos a importância da biodiversidade para assegurar a produtividade frente aos distúrbios causados pelas mudanças climáticas. Além disso, a estabilidade ecossistêmica em sistemas campestres é dependente de diferentes componentes da biodiversidade e a importância deles varia de acordo com a direção e ou intensidade dos eventos anômalos. Ainda, mostramos que os efeitos dos componentes da biodiversidade são contingentes da estrutura funcional dominante na comunidade da qual fazem parte.

A erosão da biodiversidade vem aumentando a passos largos. Isso pode significar perda permanente de biodiversidade, dadas as dificuldades de restauração. Por fim, enfatizamos que a mitigação dos efeitos das mudanças climáticas em curso depende do tipo de evento anômalo, do componente da biodiversidade e da função que ela assegura. Comunidades vegetais campestres sujeitas a diferentes anomalias climáticas requerem planos de ações específicos, de acordo com os distúrbios preditos para uma dada região.

Finalmente, propomos uma forma objetiva para avaliar experimentalmente a ação combinada entre a perda da biodiversidade e distúrbios hídricos, levando em

1   consideração alguns procedimentos para minimizar erros associados à falta de

2   controle de alguns componentes da diversidade que não são alvo do estudo.