Functional components of biodiversity mediate stability of grasslands under extreme drought

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Abstract

How different biodiversity components underpin ecosystem resistance and recovery and thus stability under extreme climatic events is a timely question in Ecology. To date, most studies have focused on the role of taxonomic diversity, neglecting how community functional composition and diversity beget stability under exceptional climatic conditions. In addition, land use potentially modulates how biodiversity and ecosystem functions respond to extreme climatic conditions. Using an 11-year time-series of plant biomass from 150 permanent grassland plots spanning a gradient of land-use intensity, we examined how different biodiversity components affected resistance and recovery of biomass production under extreme drought. The association between biodiversity, land use, and biomass production varied across years, especially in the driest years. Species rich and functionally diverse communities buffered extreme droughts better, while species poor communities dominated by fast-growing species had higher recovery capabilities after a moderate to extreme drought. Our results show that plant community functional and taxonomic components determine grasslands resistance and recovery under severe drought. In turn, this points to the importance of designing landscapes with both extensively and intensively managed grasslands. Functionally and taxonomically rich communities (favoured under low land-use intensity) would preserve biomass production under extreme droughts, whereas species-poor, fast-growing communities (favoured by high land-use intensity) would restore biomass production after extreme droughts.

Running title: grassland stability under extreme drought

Keywords: resistance, recovery, plant biomass, standardised precipitation-evapotranspiration index, land-use intensity, extreme climatic events.

1. Introduction

A growing effort has been devoted to understanding how ecosystems respond to *extreme climatic events* (hereafter ECE) such as heat waves and/or droughts (De Boeck et al. 2018). The frequency, magnitude, and impact of ECE will increase in the near future (EEA 2017), so determining the capacity of ecosystems to respond to these phenomena is a pressing task (Smith 2011; De Boeck et al. 2018). Extreme climatic events can strongly impact the stability of ecosystem functions or nature contributions to people (Diaz et al. 2018; Xu et al. 2019; Bastos et al. 2020; Xu et al. 2020; Domeisen et al. 2022). Ideally, to withstand ECE, ecosystems should be able to (i) maintain their properties under strong environmental perturbations (i.e., show high resistance), and to (ii) quickly recover their functioning after environmental perturbations (i.e., show high recovery) (Isbell et al. 2015; de la Riva et al. 2017; Neilson et al. 2020). Ecosystems with low resistance and recovery are expected to be more vulnerable to the effect of ECE (Oliver et al. 2015). Which biological features make ecosystems resist to and recover from ECE is, however, still a subject of research (Mahecha et al. 2022).

Under average climate, biodiversity should stabilise ecosystem functions over time, although the paradigm 'biodiversity begets stability' has long been debated (Lepš et al. 1982; McCann 2000; Diaz & Cabido 2001; Tilman et al. 2006; Li et al. 2022). In principle, biodiversity can support stability via several mechanisms related to species richness, abundance, and temporal fluctuation. More diverse communities can be more stable because they can harbour species with different responses to environmental fluctuations, which insures ecosystems against loss of functioning (i.e., 'insurance effect'; Ives et al. 2000; McCann 2000; Diaz & Cabido 2001). However, in line with the 'mass ratio hypothesis' (Grime 1998), species' contribution to stability is proportional to their relative abundance, so that few but abundant species can determine stability (i.e., 'dominant species effect'; Lisner et al. 2022). Apart from community composition, asynchrony of individual species' population sizes can also stabilise ecosystem functions (Allan et al. 2011; Lepš et al. 2019). Empirical and experimental studies found that taxonomic diversity has a positive (Tilman et al. 1994, Isbell et al. 2015), negative (Pfisterer et al. 2002; Fischer et al. 2016), or no effect (Caldeira et al. 2005; Dormann et al. 2017; Kreyling et al. 2017; De Boeck et al. 2018) on resistance, recovery, or both under ECE. Somewhat surprisingly, the role of community functional composition and diversity has been poorly investigated in the context of ECE (De Boeck et al. 2018; Stampfli et al. 2018; but see Gazol et al. 2016; Fischer et al. 2016; de la Riva et al. 2017). Yet, accounting for it may explain how biodiversity begets stability under ECE, as functional traits can reveal a mechanistic link between ecosystem functioning and environmental variability (Diaz & Cabido 2001; Suding et al. 2008; Polley et al. 2013; Cadotte 2017).

Recently, de Bello et al. (2021) reviewed different biodiversity-related mechanisms possibly involved in ecosystem resistance and recovery from ECE, and concluded that they generally operate *via* functional traits (see also Naeem et al. 2012). On one hand, dominant species can exert the largest effect on the resistance and recovery of ecosystem functions through their traits (de Bello et al. 2021). For this reason, the dominant trait composition of plant communities, as measured by community weighted means, has been used to locate communities along leaf-economic continuum ('slow' *vs* 'fast' communities; Craven et al. 2018). This has shown that communities dominated by traits associated with conservative strategies ('slow communities') are better at withstanding perturbations (Lepš et al. 1982; Isbell et al. 2015; de Bello et al. 2021) than fast communities, which, instead, seem to more quickly restore their functioning after perturbations (Ghazoul et al. 2015; Craven et al. 2018; Karlowsky et al. 2018). On the other hand, the 'insurance effect' hypothesis predicts that high diversity of response traits, which relate to plant response to environmental variability (Lavorel & Garnier 2002), promotes stability of ecosystem functioning under strong environmental perturbations (Craven et al. 2018; Griffin-Nolan et al. 2019). Under this scenario, the loss of species lacking the appropriate functional traits to resist a specific environmental perturbation (e.g., drought) should be compensated by less sensitive species. However, the impact of species loss on the stability of ecosystem functioning would only be minimised if extinct and persistent species share the same effect traits, i.e. traits producing an impact on ecosystem processes (Diaz & Cabido 2001; de Bello et al. 2021). Nevertheless, both measures of trait composition and diversity can be important predictors of ecosystem resistance and recovery under ECE (Griffin-Nolan et al. 2019).

Here we analysed how multiple biodiversity components (functional composition, functional diversity and taxonomic diversity) support the resistance and recovery of plant biomass production of managed grasslands undergoing extreme drought. Specifically, by measuring year-to-year changes in plant aboveground biomass, we derived yearly estimates of resistance and recovery, which we related to the yearly values of variables associated with plant community functional and taxonomic characteristics. We tested this in a gradient of land-use intensity representing realistic management conditions of central European grasslands. Our aims were to: (i) assess how functional composition, functional diversity, and taxonomic diversity mediate the fluctuation of plant biomass production along a gradient of land-use intensity; (ii) test whether these relationships change under exceptional climatic conditions (i.e., moderate-to-extreme drought, hereafter also referred to as severe drought); and (iii) investigate whether and how biodiversity-related mechanisms mediated by functional traits, such as dominant species and insurance effects, support ecosystem resistance and recovery during and after severe drought. To this end, we analysed an 11-year grassland time-series of field-collected plant biomass, biodiversity and land-use data from Germany.

2. Materials and methods

2.1. Data from the Biodiversity Exploratories

We gathered data on vegetation characteristics and land-use intensity from the German Biodiversity Exploratories, a long-term project aiming at exploring and monitoring the relationships among land use, biodiversity, and ecosystem functioning (Fischer et al. 2010). The Exploratories consist of a network of permanent plots in three regions, which cover a wide latitudinal extent: Schorfheide-Chorin (hereafter North-East; North-East Germany: 52°470 to 53°130N; 13°230 to 14°090E); Hainich-Dün (hereafter Central; Central Germany: 50°940 to 51°380N; 10°170 to 10°780E); and Schwäbische Alb (hereafter South-West; South-West Germany: 48°340 to 48°530N; 9°180 to 9°600E) (Figure 1; also see Fisher et al. 2010 for a thorough description of the three regions). The BE regions span a wide range of altitude (South-West: 460-860 m; Central: 285-550 m; North: 3-140 m), as well as a considerable range of precipitation (South-West: 700-1000 mm; Middle: 500-800 mm; North-East: 500-600 mm) and temperature (South-West: 6-7 °C; Central: 6.5-8 °C; North-East: 8-8.5 °C). In each region, 50 permanent grassland plots of 50 m x 50 m size were randomly placed within larger management units and have been surveyed yearly since 2008 to measure aboveground plant biomass (from 2009), and collect data on several biotic (e.g., plant composition based on estimated cover), abiotic (e.g., soil humidity) and anthropogenic (e.g., land-use intensity) variables.

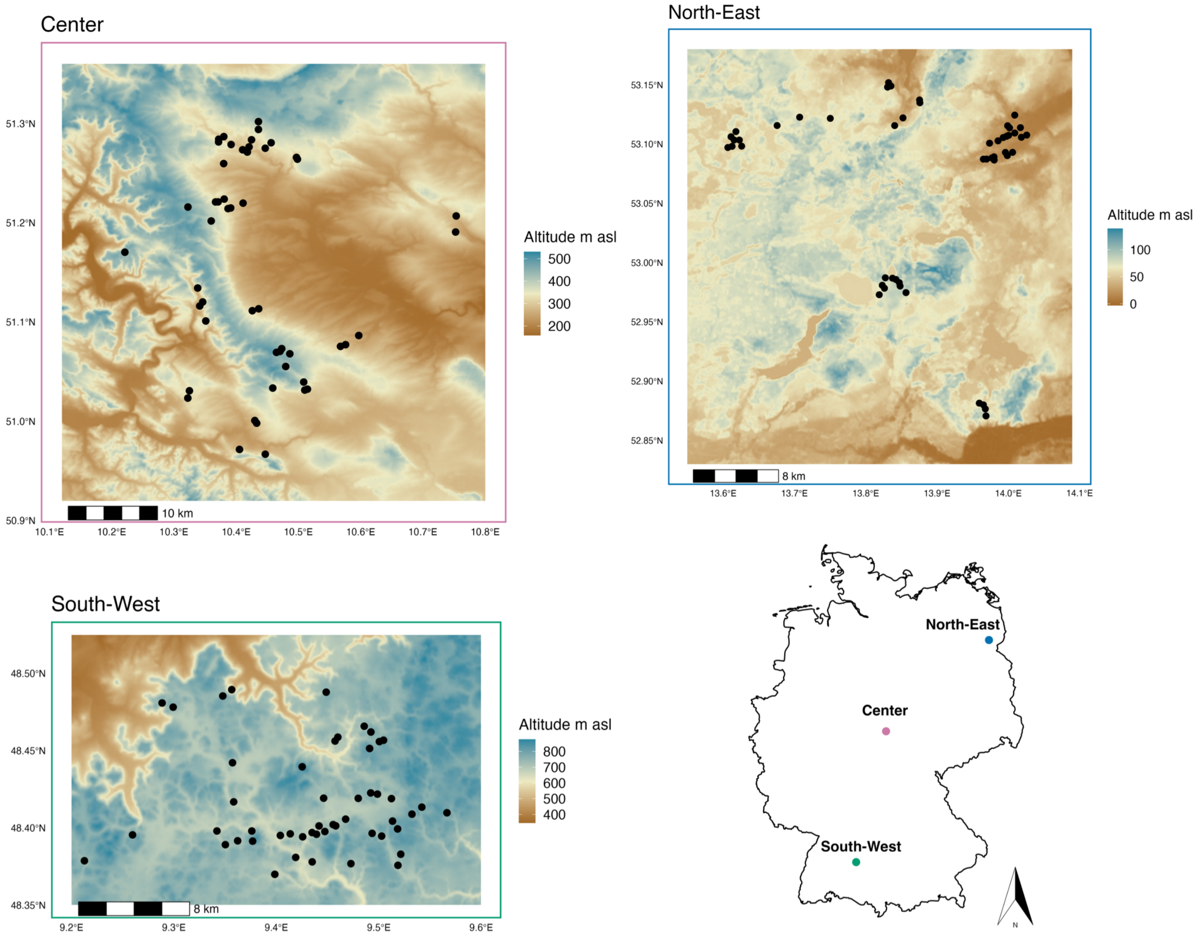

Figure 1 - Study area. Panels show the location of grassland plots in each region of the Biodiversity Exploratories overlaid to an altitude layer (m asl: metres above the sea level).

2.1.1. Measures of biomass fluctuation

Plant aboveground biomass was harvested yearly in-situ during spring over the period 2009-2019 (11 years; Hinderling et al. 2023). The harvest period, as averaged over the time series, ranged from mid-April to early June (average min./max. day of the year: 135th/151st in South-West, 129th/146th in Central, and 132nd/158th in North-East). Biomass was collected in each vegetation plot within 8 sub-quadrats of 0.5 m x 0.5 m from 2009 to 2018 and within 2 sub-quadrats of 1 m x 1 m in 2019. All plants in the sub-quadrats were harvested at 4 cm height, and the resulting organic matter was oven dried until constant weight and weighted. We then computed the average of the biomass measured in the sub-quadrats to obtain a single value for each vegetation plot, namely the average biomass per square metre. The area on which plant biomass was harvested was temporarily fenced in spring to exclude livestock. The date of plant biomass harvesting was also recorded.

We quantified temporal changes in plant biomass using three log response ratios (Lloret et al 2011; Nimmo et al. 2015; Gazol et al. 2016; Stuart-Haëntjens et al. 2018; Mathes et al. 2021).

A first measure was computed as:

$$\mathrm{LogR} = ln\left(\frac{biomass_{plot\ i,\ year\ t}}{biomass_{plot\ i,\ year\ t-1}}\right),$$

where ln is the natural logarithm. The LogR quantified the year-by-year change in plant biomass collected in a plot (Figure 2). In other words, this measure considers as a reference the biomass of the previous year to assess biomass response to environmental fluctuations. When focusing on years immediately after a moderate or extreme drought event, we used the LogR (hereafter also referred to as **annual log ratio**) to quantify grassland recovery (Schäfer et al. 2019).

A second measure of plant biomass change was computed as:

$$\mathrm{LogR}_{\text{ref-plot}} = ln(\frac{biomass_{plot\ i,\ year\ t}}{median\ biomass_{plot\ i}}),$$

where $median\ biomass_{plot\ i}$ is the median value of the biomass collected in $plot_i$ over the time-series. This measure was used to quantify the year specific biomass budget of $plot_i$ with respect to the plot reference value (i.e. $median\ biomass_{plot\ i}$) (Figure 2). When focusing on years featuring severe drought, we used the $\mathrm{LogR}_{\text{ref-plot}}$ (hereafter also referred to as **plot reference log ratio**) to measure grassland resistance.

Finally, we computed a third measure as:

$$\mathrm{LogR}_{\text{ref-reg}} = ln(\frac{biomass_{plot\ i,\ year\ t}}{median\ biomass_{region\ z}}),$$

where $median\ biomass_{region\ z}$ is the median of the year-specific median biomass collected in region z over the time-series. This measure quantified the year specific biomass budget of $plot_i$ with respect to the region specific reference value (i.e. $median\ biomass_{region\ z}$). As such, the $\mathrm{LogR}_{\text{ref-reg}}$ (hereafter also referred to as **regional reference log ratio**) is a measure of plant productivity, scaled to be comparable across regions. We compared the $\mathrm{LogR}_{\text{ref-reg}}$ to the LogR and the $\mathrm{LogR}_{\text{ref-plot}}$ to assess how the influence of several parameters on plant biomass changed under average water availability conditions *vs* extraordinary droughts.

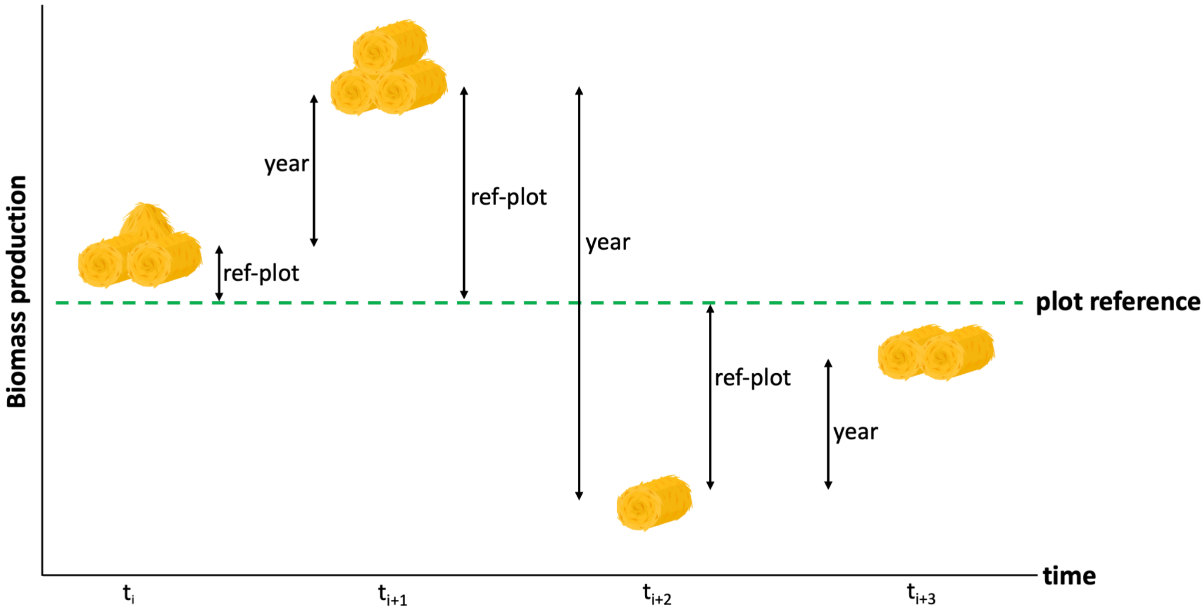

Figure 2 - Rationale behind the computation of the LogR and the $\mathrm{LogR}_{\text{ref-plot}}$, which, in the case of a moderate or extreme drought, we used to quantify grassland recovery and resistance, respectively. The LogR (annual log ratio, year in the figure) measures the drop (or increase) in plant biomass in $plot_i$ from t_{i+1} to t_i. The $\mathrm{LogR}_{\text{ref-plot}}$ (plot reference log ratio, ref-plot in the figure) measures the drop (or increase) in plant biomass in $plot_i$ at t_i with respect to the plot-specific reference, i.e. median value of the biomass collected in $plot_i$ over the time-series. Hay bales represent biomass production.

2.1.2. Plant community characteristics

We calculated several characteristics of grassland communities:

Taxonomic diversity (species richness) is the number of plant species recorded yearly in each vegetation plot within a 4 m x 4 m sub-quadrat (Bolliger et al. 2021).

Functional traits. We used multiple above-ground traits to summarise the functional composition and diversity of grassland communities. These were: plant height (m); leaf dry matter content (mg/g); specific leaf area (m^2/kg); seed mass (mg); leaf nitrogen and phosphorus content (mg/g). Data on specific leaf area (hereafter SLA) and leaf dry matter content (hereafter LDMC) are from both the BE and TRY datasets, while data for all the other traits are from the TRY database (Kattge et al. 2020). We preferred measured values from the BE (available for SLA and LDMC, and for a total of 317 species; Breitschwerdt et al. 2018; Prati et al. 2021) and, when these were not available, we filled the gaps with trait data from TRY, cleaned and aggregated at the species level (Neyret & Manning 2023).

Functional composition. As a measure of functional composition, for each plot, we computed the (year-specific) community weighted mean of each of the above-ground plant traits, and performed a principal component analysis (PCA) on their correlation matrix. We used the first axis of the PCA as a proxy of the leaf-economic spectrum (hereafter *slow-fast continuum*). Positive values of the slow-fast continuum were associated with plant communities dominated by species with acquisitive strategies (fast-growing species), whereas negative values represented plant communities characterised by species with conservative strategies (slow-growing species).

Functional and phylogenetic diversity. For each plot and year separately, and using the above-mentioned traits, we computed a combined measure of functional and phylogenetic diversity following the approach proposed by de Bello et al. (2017). In a nutshell, this approach uses a phylogeny as a proxy to integrate missing information on traits values. Phylogenetic distance between species is added to measured functional trait diversity to account for unmeasured (and conserved) traits. However, the functional and phylogenetic components are added without double-counting the signal they inevitably share. Here, as we were mainly interested in the effect of functional traits, we added the non-overlapping phylogenetic part to the functional dissimilarity. This way, we derived a matrix of combined functional and phylogenetic dissimilarity, on which we computed the plot specific Rao's diversity index (Rao 1982). For simplicity, we refer here to this as functional diversity. For all this, we used Daphne, a dated ultrametric supertree of European plant species (Durka & Michalski 2012).

Mycorrhizae. Finally, using data from TRY (Neyret & Manning 2023), we computed the community weighted mean of the intensity of mycorrhizal colonisation (expressed in %) to account for the interaction between mycorrhizae and vegetation under drought (Fu et al. 2022).

2.1.3. Land-use intensity

Land use intensity. The land-use intensity gradient covered by our study plots affects grassland biomass production (Allan et al. 2015). To account for this, we used the plot-specific, yearly value of a *land-use intensity index* developed by Blüthgen et al. (2012), which combines the individual contributions of grazing, fertilisation and mowing (Lorenzen et al. 2022). We computed the land-use intensity index as the global mean of grassland management for the three BE regions for the years 2009-2019 (see Blüthgen et al. 2012), which allows comparison of land-use intensity across regions. We computed the index using the index calculation tool (Ostrowski et al. 2020) from the Biodiversity Exploratories Information System (http://doi.org/10.17616/R32P9Q).

Soil humidity. Soil characteristics were considered in the selection of sites with different land uses (see Fischer et al. 2010). However, environmental factors may have still partially influenced the relationships between land use and biomass fluctuation. For example, plant communities in wet areas are generally less intensively managed than communities on dry soils. To account for that, when analysing the relationship between land use, biomass fluctuation, and grasslands resistance and recovery, we simultaneously controlled for the plot-specific soil humidity. As an overall measure of soil humidity, we computed the average value of the soil humidity at 10 cm depth (in %) recorded over the time-series by climatic loggers placed within each vegetation plot (Wöllauer et al. 2022). Note that data on soil humidity had to be aggregated over the time-series due to missing values.

2.2. Data on annual drought

To analyse the response of grasslands to different drought severities, we gathered data from the Global SPEI database (SPEIbase, version 2.6; Vicente-Serrano et al. 2010). We downloaded the **Standardised Precipitation-Evapotranspiration Index** (hereafter **SPEI**; data available until 2018), which is a multiscalar, site-specific drought indicator of deviations from average water balance. In contrast to other drought indices (e.g., the Standardised Precipitation Index), the SPEI not only accounts for precipitation, but also incorporates the influence of temperature on drought severity (see Vicente-Serrano et al. 2010). The SPEI has been used in several studies assessing the effect of drought on plant biomass production and stability (Isbell et al. 2015; Ivits et al. 2016; Slette et al. 2019; Matos et al. 2020; Chen et al. 2022). Also, it is expressed in z-scores, which facilitates the classification of drought events of different magnitude (see Isbell et al. 2015). For example, an annual value of SPEI equal to (or lower than) -1.28 indicates that the associated annual drought event (or a more extreme one if lower than -1.28) is likely to occur once every 10 years.

We considered SPEI aggregating data on cumulative water balance over 3, 12 and 24 months (hereafter SPEI-3/-12/-24) before the peak of biomass production (i.e., May). This allowed analysing resistance and recovery from drought measured at multiple time-scales. The SPEI values for all time-scales were obtained for each year of the time-series (see Figure A1, Appendix A1 for SPEI-3/-12/-24 temporal trend). Data on SPEI were gathered as rasters of 0.5 degrees resolution from which we extracted, separately for each region, the index value at the geographical centroid of the ensemble of vegetation plots in a region.

Following Isbell et al. (2015), continuous SPEI-3/-12/-24 were categorised to extreme drought ($SPEI < -1.28$); moderate drought ($-1.28 <= SPEI <= -0.67$); normal water balance ($-0.67 < SPEI < 0.67$); moderate wetness ($0.67 <= SPEI <= 1.28$); extreme wetness ($SPEI > 1.28$). Table A1 (Appendix 1) provides the numbers of dry (or wet) years in each time series and BE region.

2.3. Analysis of grassland resistance and recovery

2.3.1. Year specific analysis of change in plant biomass production

The LogR, $LogR_{ref\text{-}plot}$ and $LogR_{ref\text{-}reg}$ were modelled (using linear regression) separately for each year as a function of land-use intensity, slow-fast continuum, functional diversity, intensity of mycorrhizae colonisation, soil humidity, and plant species richness (Table 1). Also, we included a categorical variable with three levels, each representing one of the three BE regions, to account for mean region-specific differences. We compared model results for the annual and the plot reference log ratios against those for the regional reference log ratio to understand how predictors affected grasslands productivity under extraordinary *vs* average drought conditions, respectively.

To minimise the effect of multicollinearity on the width of regression parameters' confidence intervals, we computed the variance inflation factor (vif) of each predictor, and removed from the models those with vif equal to or greater than 3 (R function *vif*, *car* package; Fox & Weisberg 2019). Plant species richness scored vif values systematically (i.e., across years) greater than 3. Species richness was indeed correlated with the slow-fast continuum (mean Pearson correlation computed over the time-series: -0.43), functional diversity (0.51), and land use intensity (-0.40). Therefore we analysed species richness separately, i.e. repeating analyses including species richness in the models and excluding slow-fast continuum and functional diversity.

Model assumptions (i.e., linearity, heteroscedasticity and normality) were checked using the *performance* R package (Lüdecke et al. 2021).

Table 1 - R formulas of models for the year specific analysis of change in plant biomass production. [a] species richness was analysed in a separate set of models excluding slow-fast continuum and functional diversity (see 2.3.1.).

Response variable	Predictors
LogR	(slow-fast continuum + functional diversity) | [a]species richness + land-use intensity + intensity of mycorrhizae colonisation + soil humidity + region
$\text{LogR}_{\text{ref-plot}}$	
$\text{LogR}_{\text{ref-reg}}$	

2.3.2. Effect of community functional composition and diversity on resistance and recovery

To test for the effect of community functional composition and diversity, and taxonomic diversity on resistance and recovery under drought, we fitted linear mixed effects models including the statistical interaction between the functional and taxonomic components and the categorical SPEI (Table 2). As done in 2.3.1., analyses were carried out separately for functional composition and diversity, and for species richness. Also, separate models were fitted for the different SPEI time-scales, i.e. SPEI-3/-12/-24. Along with the interaction between slow-fast continuum, functional diversity, species richness and the categorical SPEI, we included the following predictors: land-use intensity, intensity of mycorrhizae colonisation, day of biomass harvest (i.e., day of the year) and region (Table 2). By including region as a predictor in the models, we allowed for mean region-specific differences to be accounted for. At the same time, we assumed that the interaction between biodiversity components and drought intensity, as well as the association between recovery, resistance and the other predictors, was the same within each region. This way we focused on the overall trend of the relationship between recovery, resistance, biodiversity and drought. All predictors were centred before fitting the models. The plot unique identifier was included as a random intercept to account for the non-independence of observations collected from the same plot over the time-series. Model diagnostics were used to assess residuals' normality and homoscedasticity. We fitted linear mixed models using the *nlme* R package (Pinheiro et al. 2021).

To analyse recovery (models for the annual log ratio), we used observations from the year immediately after one or more consecutive events of either moderate or extreme drought. This way we assessed whether and how functional composition, and functional and taxonomic diversity of plant communities support recovery of plant biomass production after severe droughts, and we tested this under different conditions of water availability (from normal water budget to extreme wetness). For the resistance analysis (models for the plot reference log ratio), we focused on variables measured in years of moderate or extreme drought, which allowed us to examine the role of functional composition, functional and taxonomic diversity in buffering grasslands under water shortage.

Model for recovery and for the categorical SPEI-24 was fitted using linear regression, as there were no repeated measures associated with the individual plot identifiers. Note that according to the categorical SPEI-24, events of moderate or extreme drought were followed only by years of normal water budget conditions. Therefore, recovery was analysed under a lower number of water availability conditions than for SPEI-3 and -12.

Table 2 - R formulas of models testing the effect of community functional composition and diversity on recovery (LogR) and resistance ($\text{LogR}_{\text{ref-plot}}$). '*' represents the statistical interaction between slow-fast continuum, functional diversity, and SPEI (i.e., SPEI-3/-12/-24). [a] the statistical interaction between species richness and drought intensity was analysed in a separate set of models excluding slow-fast continuum and functional diversity. Note that lower-order interaction terms were also included in the model. We specified the plot identifier (in italics) as a random intercept.

Response variable	Predictors
LogR	(slow-fast continuum + functional diversity)*SPEI | [a]species richness*SPEI + land-use intensity + intensity of mycorrhizae colonisation + day of the year + region + *plot*

$\text{LogR}_{\text{ref-plot}}$	*identifier*

3. Results

The three regions showed similar trends in plant biomass production. Overall, productivity was higher in South-West and North-East than in Central Germany over the time-series (Figure 3a). In Central and North-East Germany plant biomass peaked in 2014, while in the South-West it peaked in 2013. According to all SPEI time-scales, 2013 featured average or above average water budgets in all regions (Figure 3b, Figure A1, Appendix A1). Biomass production was lower than overall productivity in all regions in 2011 and 2017 (Figure 3a), both years which featured severe droughts at different time-scales (Figure 3b, Figure A1, Appendix A1).

3.1. Year-specific association between land use, biodiversity and log response ratios

The influence of the biodiversity components (slow-fast continuum, functional diversity, species richness) and land-use intensity on biomass production ($\text{LogR}_{\text{ref-reg}}$) did not change across time (Figure 3c), indicating that these predictors consistently affected biomass production over the time-series. On the contrary, the sign of the relationships between LogR as well as $\text{LogR}_{\text{ref-plot}}$ and the predictors varied across the years. In particular, in 2010, 2012, 2014, 2016 and 2017 (which either featured or were preceded by moderate-to-extreme drought in at least one of the regions), the two log response ratios exhibited an opposite relationship with the slow-fast continuum, functional diversity and species richness than the relationship consistently observed for the regional reference log ratio over the time-series. This means that the three biodiversity components affected biomass change in these years differently than overall biomass production over the time-series.

The $\text{LogR}_{\text{ref-reg}}$ always showed a positive relationship with the slow-fast continuum and a negative association with functional diversity and species richness (Figure 3c), indicating that functionally and species poor communities dominated by fast-growing species were more productive. Also, land-use intensity consistently and positively affected the $\text{LogR}_{\text{ref-reg}}$ over the time-series in both models including either functional or taxonomic components (Figure 3d), meaning that overall intensively managed plant communities produced more biomass than extensively managed. Results for intensity of mycorrhizae colonisation and soil humidity are presented in Appendix A2.

Results for the annual (LogR) and plot reference log ratio ($\text{LogR}_{\text{ref-plot}}$) indicate that grasslands with different functional composition, functional diversity and species richness responded differently to drought. The relationship between LogR and the slow-fast continuum turned from negative to positive between 2017 and 2018 (Figure 3c). Specifically, in 2017 plant communities dominated by fast-growing species produced less (or lost more) biomass compared to the previous year than communities dominated by slow-growing species. On the contrary, in 2018, which was extremely dry according to the SPEI-3 but normally-to-moderately wet according to SPEI-12 (Figure 3b), plant communities with prevalence of fast-growing species produced more (or lost less) biomass than the previous year than communities dominated by slow-growing species. Both species rich and functionally diverse communities produced more biomass in 2012, which featured (and was preceded by) extremely dry conditions in all three regions according to the SPEI-3, while having an overall normal water budget according to SPEI-12 (Figure 3b). Also, in 2012, extensively managed plant communities produced more biomass than intensively managed (Figure 3d).

The $\text{LogR}_{\text{ref-plot}}$ negatively correlated with slow-fast continuum in 2014 and 2017 (when all regions experienced severe droughts according to SPEI-12), indicating that communities dominated by slow-growing species produced more biomass than fast-growing communities (Figure 3c). Species rich communities produced more biomass than species poor communities in 2012, 2014, 2016 and 2017.

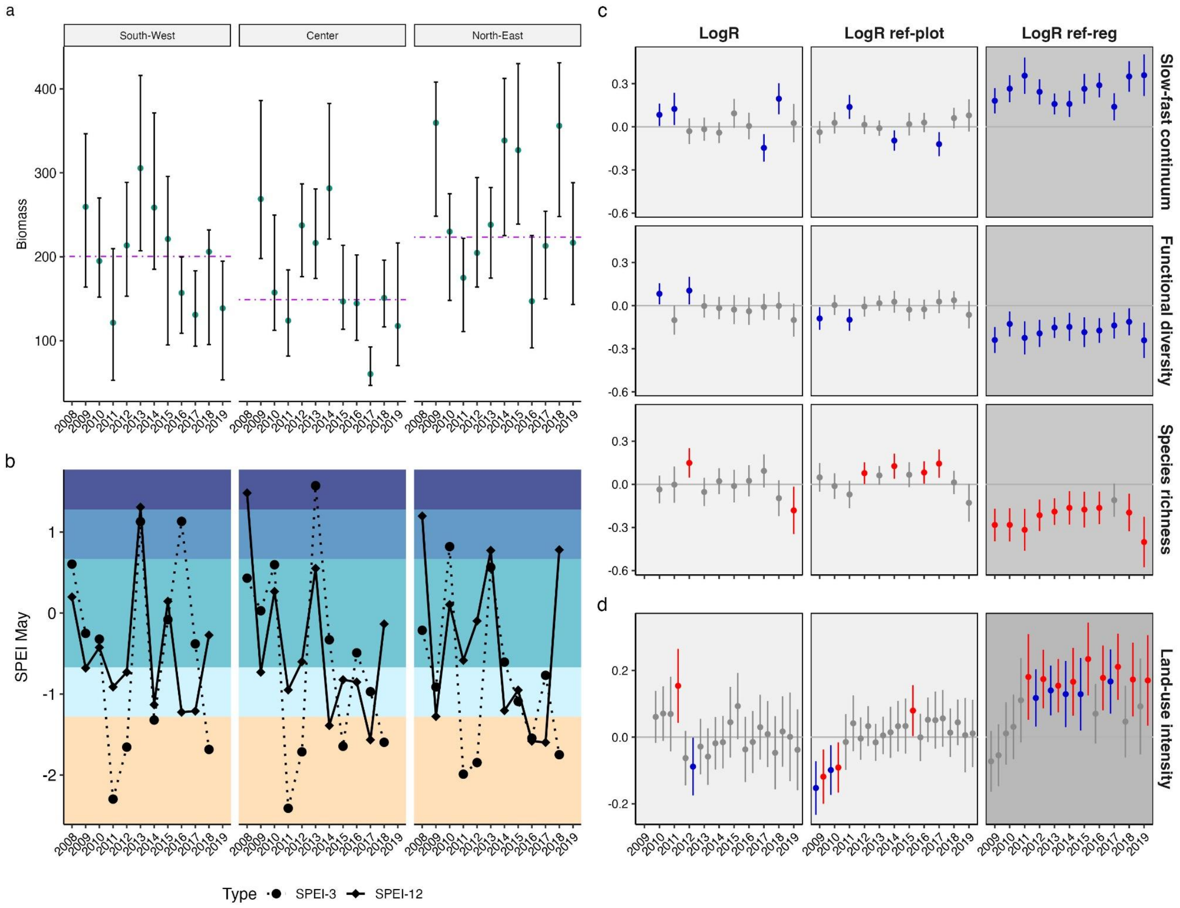

Figure 3 - Panel a) Green points represent median biomass collected in each year in each region (South-West, Central and North-East). Bars delimit the interquartile range of biomass values and the purple dotted lines represent the regional median biomass across the time-series. Panel b) Temporal trend of 3- and 12-months Standardised Precipitation-Evapotranspiration Index (SPEI-3 and -12). Temporal trend for SPEI-24 is reported in Appendix A1 (Figure A1). Colours of horizontal bands are associated with water budget conditions, with light blue and ochre colours representing moderate and extreme drought, respectively. Panel c) Results of the year specific linear regressions. Columns refer to the results for the three log response ratios (i.e., LogR, $\mathrm{LogR}_{\mathrm{ref\text{-}plot}}$ and $\mathrm{LogR}_{\mathrm{ref\text{-}reg}}$), while rows report results for slow-fast continuum, functional diversity, species richness and land-use intensity (results for intensity of mycorrhizae colonisation and soil humidity are reported in Figure A2, Appendix A2). Dots represent regression coefficients derived from models fitted using predictors standardised to have zero mean and unit variance, while error bars are 95% confidence intervals for the parameters. Blue and red dots (and bars) are associated with statistically significant relationships in models including the functional and taxonomic components, respectively.

3.2. Effect of the interaction between functional composition, functional diversity and SPEI on resistance and recovery

At SPEI-3, the effect of slow-fast continuum and functional diversity on plant community recovery depended on water availability after drought (i.e., SPEI categories: normal, moderate and extreme wet) (Wald's F test with Kenward-Roger df; slow-fast continuum: F = 5.41, p-value < 0.05; functional diversity: F = 7.24, p-value < 0.05), while there was no evidence of such an interaction at SPEI-12 (full summary of Type II Analysis of Deviance reported in Table A3.3, Appendix A3). In particular, functionally poor and fast-growing plant communities showed a more pronounced production of plant biomass (i.e., higher recovery) when drought was followed by normal water conditions, whereas more functionally diverse and slow-growing communities seemed favoured when drought was followed by moderate wetness (Figures 4, A3.1, Appendix A3).

Concerning taxonomic diversity, at SPEI-3 species poor communities produced more biomass when drought was followed by normal water budgets, while species rich communities exhibited higher recovery capabilities when drought was followed by moderate wetness (Wald's F test with Kenward-Roger df: F = 23.37, p-value < 0.05) (Figures 4, A3.1, Appendix A3). On the contrary, at SPEI-12 species poor communities produced more biomass when drought was followed by moderate wetness (Wald's F test with Kenward-Roger df: F = 3.60, p-value < 0.05) (full summary of Type II Analysis of Deviance reported in Table A3.4, Appendix A3). We found no evidence of an association between functional composition, functional diversity, species richness and recovery at SPEI-24, according to which severe drought was followed only by normal water budget (Figure 4, Figure A3.1, Tables A3.3, A3.4, Appendix A3).

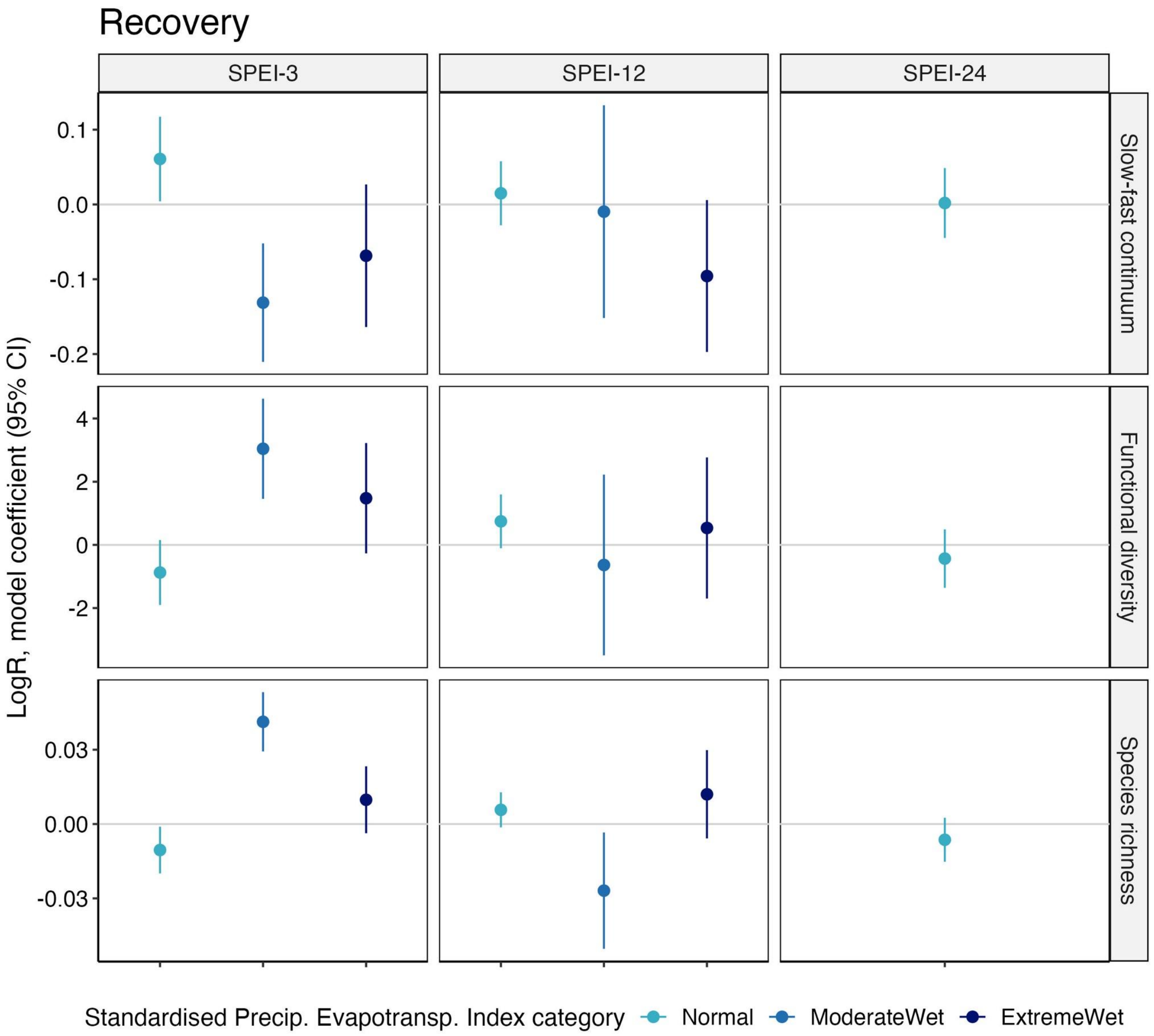

Figure 4 - Regression coefficients (and 95% confidence intervals for parameters) for models testing the effect of the interaction between slow-fast continuum, functional diversity, and species richness (rows) and the categorical Standardised Precipitation Evapotranspiration Index (SPEI-3/-12/-24, columns) on recovery. Normal (normal water budget) is the 'reference level' of the statistical interaction between slow-fast continuum, functional diversity, species richness and SPEI. Interaction terms (i.e., all coefficients except those for Normal) should be compared to the reference level to interpret how functional and taxonomic components supported grasslands recovery under different water availability (regression slopes and model tables are shown in Figure A3.1, Tables A3.1, A3.2, Appendix A3).

At SPEI-3, resistance, as measured by the $\text{LogR}_{\text{ref-plot}}$, appeared to be affected by the interaction between drought intensity and functional diversity (Wald's F test with Kenward-Roger df: F = 11.89, p-value < 0.05), but not by the interaction between drought intensity and slow-fast continuum (Wald's F test with Kenward-Roger df: F = 1.80, p-value > 0.05) (full summary of Type II Analyses of Deviance reported in Table A4.3, Appendix A4). Specifically, functionally diverse communities had greater resistance (i.e., more pronounced biomass production or lower biomass loss) under extreme drought (Figure 5, Figure A4.1, Appendix A4). We found no statistically significant interaction between slow-fast continuum, functional diversity and drought intensity at SPEI-12 and -24 (Table A4.3, Appendix A4).

Species richness interacted with drought intensity in affecting resistance at SPEI-3 and -12 (Table A4.4, Appendix A4). At both time-scales, species rich communities had a more pronounced biomass production (or lower biomass loss) than species poor communities under extreme drought (Figure 5, Figure A4.1, Appendix A4). We found no statistical interaction between species richness and drought intensity at SPEI-24 (Table A4.4, Appendix A4).

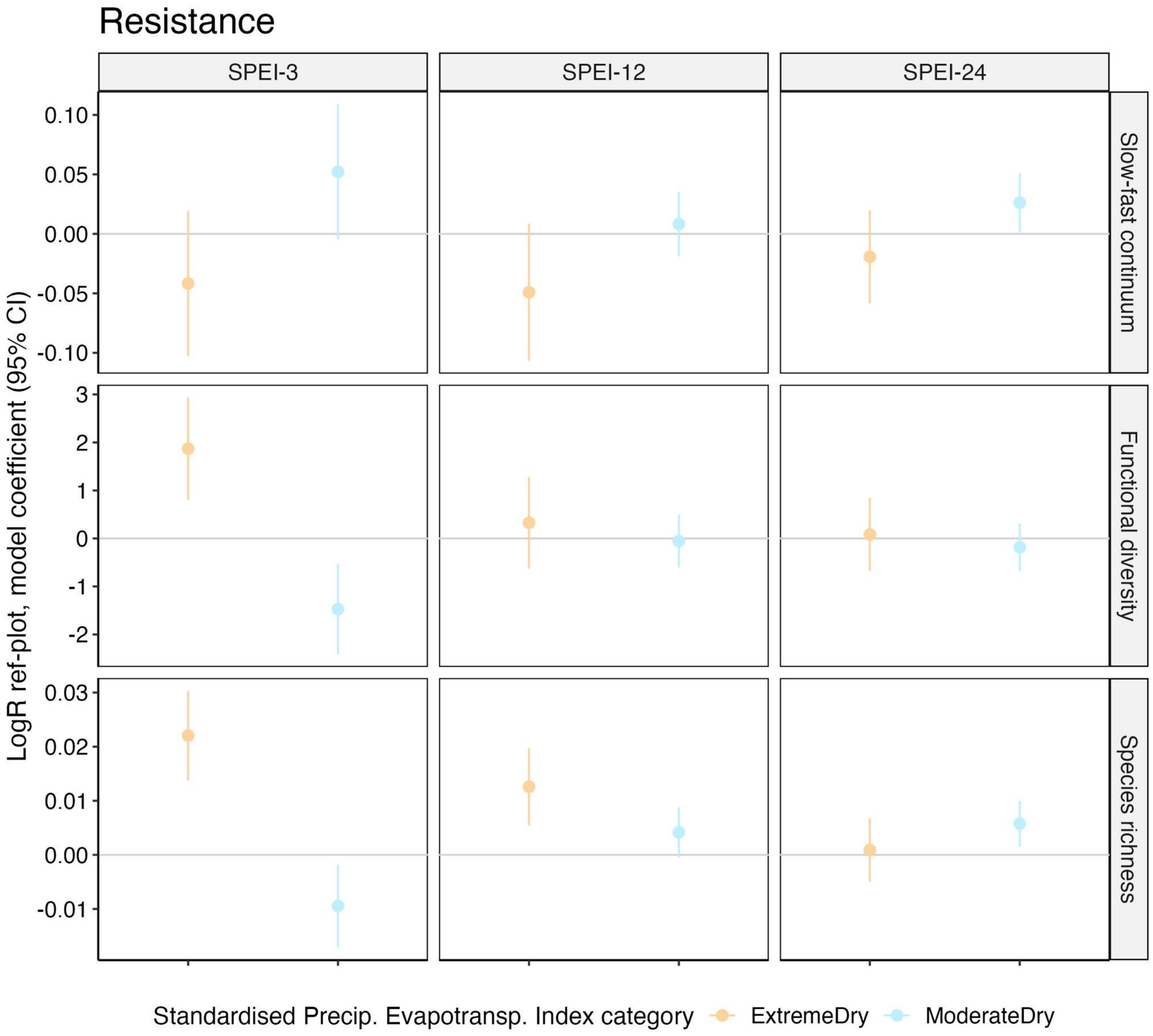

Figure 5 - Regression coefficients (and 95% confidence intervals for parameters) for models testing the effect of the interaction between slow-fast continuum, functional diversity, and species richness (rows) and the categorical Standardised Precipitation Evapotranspiration Index (SPEI-3/-12/-24, columns) on resistance. ModerateDry is the 'reference level' of the statistical interaction between slow-fast continuum, functional diversity, species richness and SPEI. Interaction terms for ExtremeDry should be compared to the reference level to interpret how functional and taxonomic components supported grasslands resistance under different drought intensity (regression slopes and model tables are shown in Figure A4.1, Tables A4.1, A4.2, Appendix A4).

4. Discussion

When focusing on short-term water budgets (i.e., SPEI-3), we found that functionally and taxonomically diverse communities buffered extreme droughts better, whereas species-poor, fast-growing communities had higher recovery capabilities when severe drought was followed by normal water conditions. This shows that mechanisms such as insurance (Diaz & Cabido 2001) and dominant species effect (Lisner et al. 2022) support resistance and recovery of grasslands experiencing unfavourable environmental conditions.

4.1. Community composition and land use *vs* temporal fluctuation of biomass

We observed that the relationship between biodiversity, land use and plant biomass was stationary over time. Our results suggest that land use is the main determinant of grassland productivity, likely through its influence on community functional and taxonomic composition (Socher et al. 2012; Blüthgen et al. 2016). In this regard, we observed that species poor plant communities with fast-growing species, low functional diversity (Figure 3c), and subject to high land-use intensity (Figure 3d), produced more biomass. On the contrary, species rich plant communities with abundant slow-growing species and high functional and taxonomic diversity were less productive (Figure 3c, d). These findings are in line with Allan et al. (2015) and Májeková et al. (2016), who previously described such a relationship in grasslands.

However, we found that the association between biodiversity and plant biomass fluctuation (i.e., LogR and $\mathrm{LogR_{ref\text{-}plot}}$) had opposite signs than those found for the $\mathrm{Log_{ref\text{-}reg}}$ in years with severe drought (2011, 2012, 2014, 2016 and 2017; see Figure 3b). This supports the idea that biodiversity mediates the response of grassland productivity to drought. Under average climatic conditions, land use determines plant community composition, with intense land use shifting vegetation towards fast-growing competitive species, and thus highly productive but functionally poor communities (Laliberté & Tylianakis 2012; Májeková et al. 2016). However, in dry years fast communities produce less (or lose more) biomass than functionally and species rich communities, thus pointing to high biodiversity as a factor promoting long-term stability of ecosystem functions (Isbell et al. 2017; Craven et al. 2018 and references therein).

4.2. Community composition and diversity *vs* resistance and recovery

We observed a positive effect of functional diversity and species richness on the *resistance* of grassland biomass production. In particular, species rich communities with high functional diversity withstood extreme droughts better than species poor communities with low functional diversity. The buffering effect of taxonomic diversity was already observed by Isbell et al. (2015), who found that species richness positively correlated with the resistance of biomass production to both dry and wet extreme events in experimental settings, and our study extends this result to real-world communities. Concerning functional diversity, previous empirical studies found its positive effect on overall ecosystem stability under drought (Polley et al. 2013; Gazol et al. 2016; Hallett et al. 2017; Miller et al. 2019), but only few reported such a positive effect on resistance specifically (Lepš et al. 1982; Symstad & Tilman 2001). Thus, we add evidence that biodiversity-related mechanisms mediated by functional diversity may kick in under extreme drought to maintain grasslands biomass production. Here we see the insurance effect (Diaz & Cabido 2001) as the most likely trait-based mechanism explaining our results: specifically, functionally diverse communities, characterised by species with varying responses to environmental fluctuations, maintain more stable ecosystem properties under environmental perturbations (Ives et al. 2000; Diaz & Cabido 2001, Mariotte et al. 2013; de Bello et al. 2021). In this regard, previous studies evidenced that communities with high evenness of SLA values were the least sensitive to drought (Griffin-Nolan et al. 2019; Miller et al. 2019). Along with root traits, leaf traits are indeed relevant for resistance to drought, as, for example, leaf dimension is related to water consumption efficiency (Griffin-Nolan et al. 2019; Walde et al. 2021). In line with the insurance effect, functionally diverse plant communities, and more specifically those with large variability of leaf traits, may include species that better resist extreme drought (Walde et al. 2021). Also, communities with high functional diversity are usually constituted by stress-tolerant species, which can resist harsh perturbations (Lepš et al. 1982).

Concerning *recovery*, in line with previous studies (Lepš et al. 1982; Stampfli et al. 2018), we observed that species poor communities dominated by fast-growing species recovered better, especially when severe drought was followed by average water availability. We ascribe this to the dominant species effect, whereby few, yet abundant (in terms of biomass) species exert the largest effect on ecosystem functions through their traits (de Bello et al. 2021). In our study, fast-growing communities were dominated by species with resource-acquisitive strategies, which match the typical ecological profile of competitive-ruderals with rapid growth of biomass (Lepš et al. 1982). Moreover, recovery of these species was likely higher under high intensity of land use, corresponding to high content of nitrogen and other nutrients. Indeed, even low inputs of nitrogen foster recovery of biomass production after drought (Mackie et al. 2019). Also, intensively managed grasslands of the Biodiversity Exploratories, and particularly those subject to high fertilisation, have large proportions of grasses (Socher et al. 2013), which outperform other plant types (e.g., forb) in post-drought compensatory growth (Hoover et al. 2014; Stampfli et al. 2018; Wilcox et al. 2020).

In line with Oram et al. (2020), at SPEI-3 we found that species rich, slow-growing communities recovered better than species poor, fast communities when drought was followed by moderate wetness. This can be ascribed to conservative species being usually tolerant to stressful environmental conditions. On the contrary, we found that species poor communities recovered better under moderate wetness at SPEI-12. Such a contrasting association between species richness and recovery under wet conditions measured at different SPEI time-scales was also reported by Isbell et al. (2015). However, our results for recovery under above-average wetness should be interpreted with caution due to the low number of moderate and extreme events at all SPEI time-scales in our time-series (Table A1, Appendix A1).

4.3. Generality over SPEI time-scales

We found that functional components of biodiversity mediated the response of biomass production to drought only at SPEI-3, which in our study quantified water availability right before and at the peak of biomass production. On the contrary, we observed that species richness and resistance were positively associated at all SPEI time-scales (although they negatively correlated under moderate short-term drought). Similarly, species richness affected recovery of biomass production under both short- (SPEI-3) and long-term (SPEI-12) drought. Our results thus suggest that biodiversity mechanisms mediated by functional traits and taxonomic diversity may operate at different temporal scales: functional traits, which are more mechanistically linked to plants ecophysiological response to water shortage (Fatichi et al. 2016), may be better at capturing vegetation response to short-term drought (e.g., right before the peak of biomass production), whereas taxonomic diversity may also catch vegetation response to long-term droughts. We acknowledge that our results do not allow us to conclude that there is an interaction between drought duration (i.e., press *vs* pulse drought) and biodiversity facets, but we believe that it would be worth further investigating this research question in more targeted studies.

Our results show the importance of considering different biodiversity facets (i.e., functional and taxonomic) when analysing the stability of grasslands under extreme climatic events and varying land-use intensity. Also, using multiple measures of biomass change (here, log response ratios), as compared to different reference values, allows (i) predicting temporal changes in plant biomass production, and (ii) understanding how grasslands respond to both average and extraordinary environmental conditions. This will help develop more effective grassland management strategies to address the new challenges posed by increasing extreme drought events. Our results indicate that promoting landscapes with varying land-use intensity can increase the overall stability of grassland biomass production, with slow communities (subject to low land-use intensity) preserving productivity during droughts due to high resistance, and fast communities (subject to high land-use intensity) restoring biomass production after droughts due to high recovery capabilities.

Authors contribution

MB, FdB, MG conceptualised the study. MB analysed the data with MGS. MB wrote the first version of the manuscript, which was commented on, improved and approved by all authors.

Data availability statement

This work is based on data elaborated by several projects of the Biodiversity Exploratories program (DFG Priority Program 1374). The datasets are publicly available in the Biodiversity Exploratories Information System (http://doi.org/10.17616/R32P9Q), (Breitschwerdt et al. 2018; Bolliger et al. 2021; Prati et al. 2021; Lorenzen et al. 2022; Wöllauer et al. 2022;Hinderling et al. 2023; Neyret & Manning 2023).

Code availability statement

Data and R code for reproducing the results presented in this manuscript can be found at: https://github.com/ManueleBazzichetto/ResistRecoverDrought (or at: https://doi.org/10.5281/zenodo.7924836).

Conflict of interest statement

Authors have no conflict of interest to declare.

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Appendix A1 - Temporal trend in the SPEI value

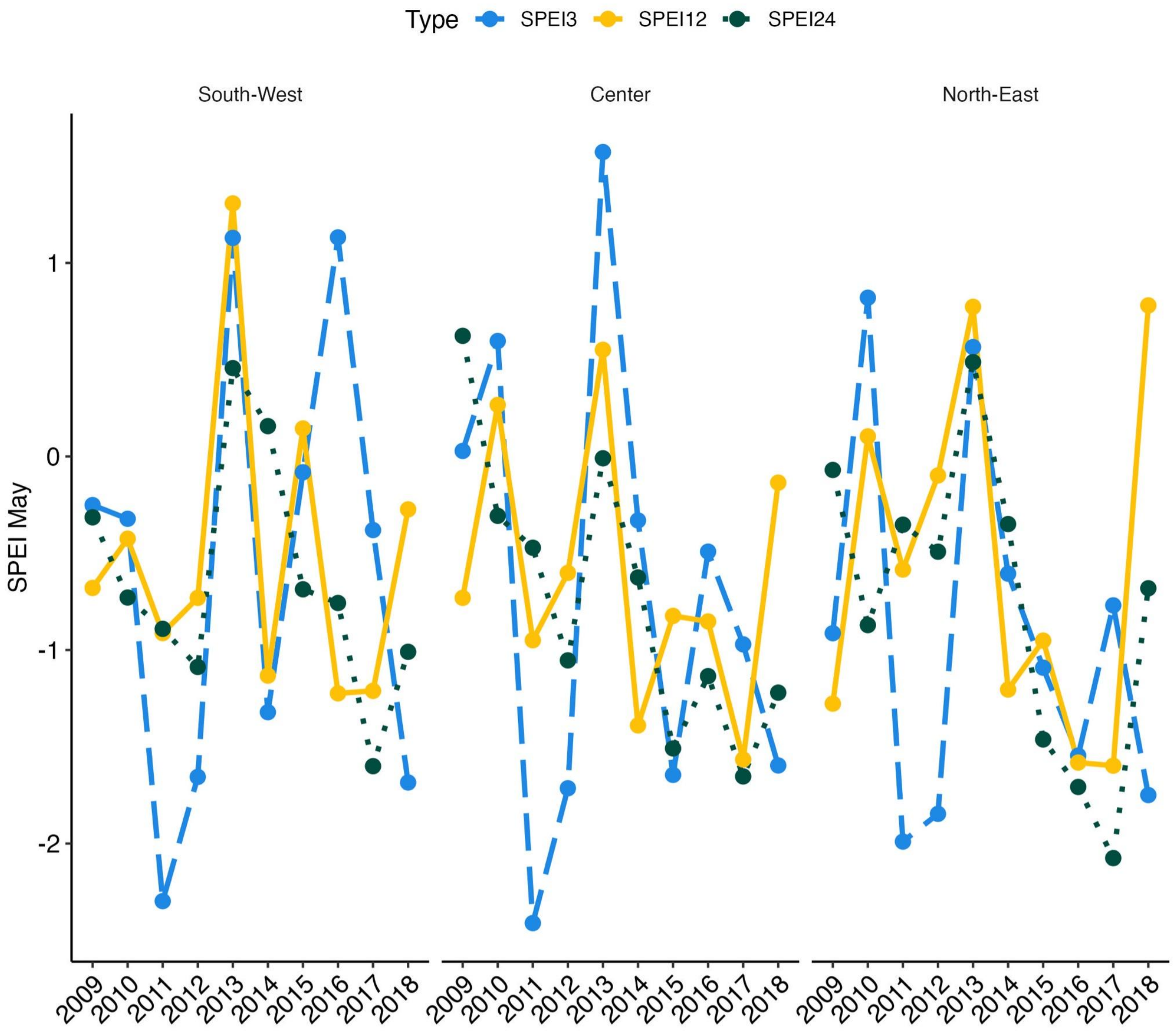

Figure A1 - Trend of the SPEI (of May) value in the three regions of the Biodiversity Exploratories: Schwäbische Alb (South-West); Hainich-Dün (Central); Schorfheide-Chorin (North-East).

Table A1 - Number of dry or wet years included within each class of the categorised SPEI-3/-12/-24. Number of years is given for each region: South-West (Schwäbische Alb); Central (Hainich-Dün) and North-East (Schorfheide-Chorin). Normal stays for normal water balance.

	SPEI-3/-12/-24		
	South-West	Central	North-East
Extreme drought	4, 0, 1	4, 2, 2	4, 2, 3
Moderate drought	0, 6, 6	1, 4, 3	3, 3, 2
Normal	5, 4, 4	5, 4, 6	3, 3, 6
Moderate wetness	2, 0, 0	0, 0, 0	1, 3, 0
Extreme wetness	0, 1, 0	1, 1, 0	0, 0, 0

Appendix A2 - Results of year specific analysis of biomass fluctuation

The intensity of mycorrhizae colonisation was significantly and negatively associated with the three log response ratios in 2019 (except for the LogR in the model including species richness instead of the functional components) (Figure A2). Also, it showed a positive association with the plot reference log ratio in 2009 in both models including slow-fast continuum and functional diversity, and species richness (Figure A2). Soil humidity showed a common trend of association with all log response ratios, indicating that average plot humidity similarly correlated with both biomass production ($\text{LogR}_{\text{ref-reg}}$) and fluctuation (LogR, $\text{LogR}_{\text{ref-plot}}$).

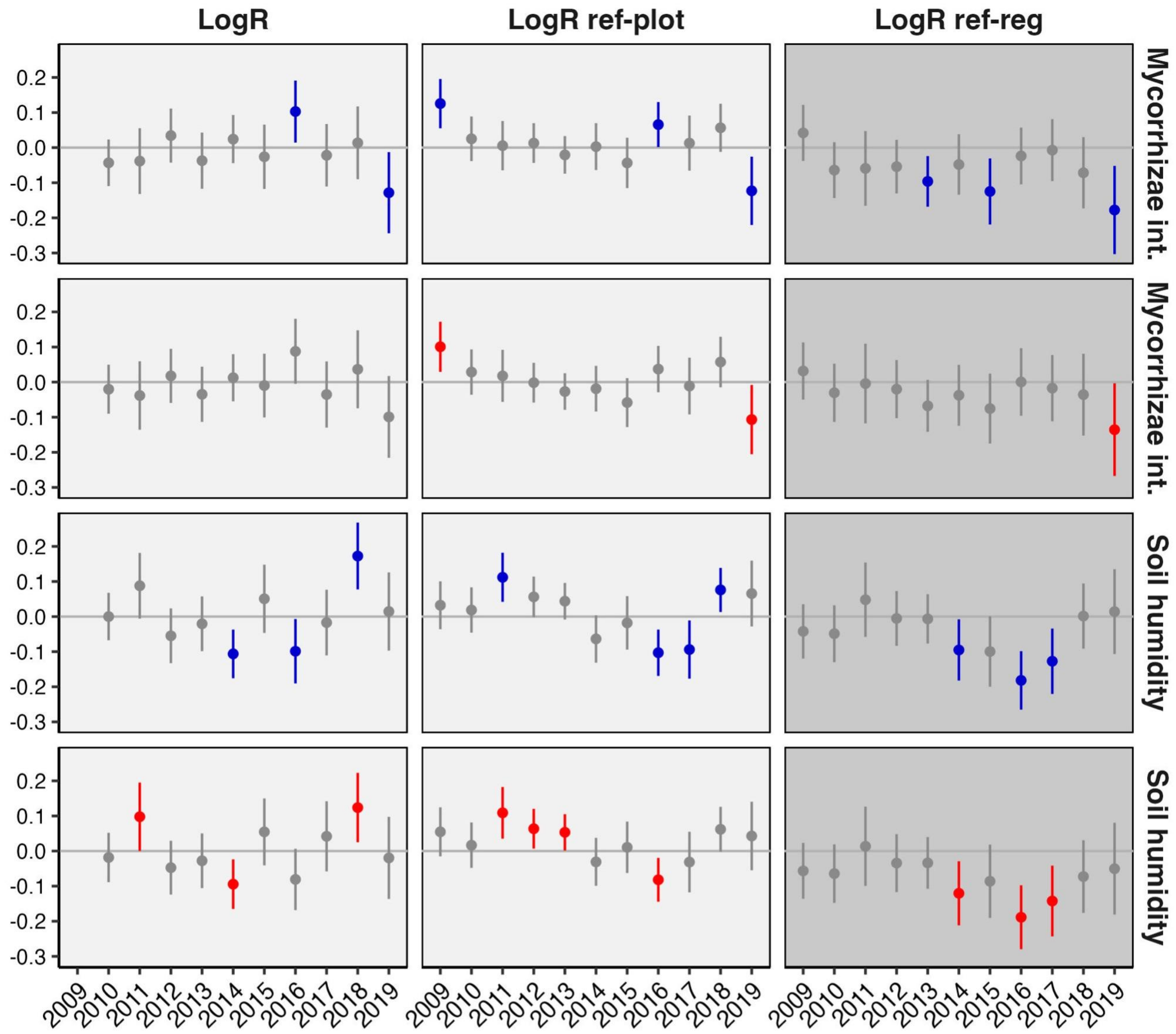

Figure A2 - Results of the year specific linear regressions for intensity of mycorrhizae colonisation and soil humidity. Columns refer to the results for the three log response ratios (i.e. LogR, $\text{LogR}_{\text{ref-plot}}$ and $\text{LogR}_{\text{ref-reg}}$), while rows report results for the two predictors (in blue results of models including slow-fast continuum and functional diversity, in red results of models including species richness). Dots represent the value of the regression coefficients derived from models fitted using predictors standardised to have zero mean and unit variance, while error bars are 95% confidence intervals for the parameters. Blue dots (and bars) are associated with statistically significant relationships.

Appendix A3 - Effect of the interaction between functional composition, functional diversity, species richness and SPEI on recovery

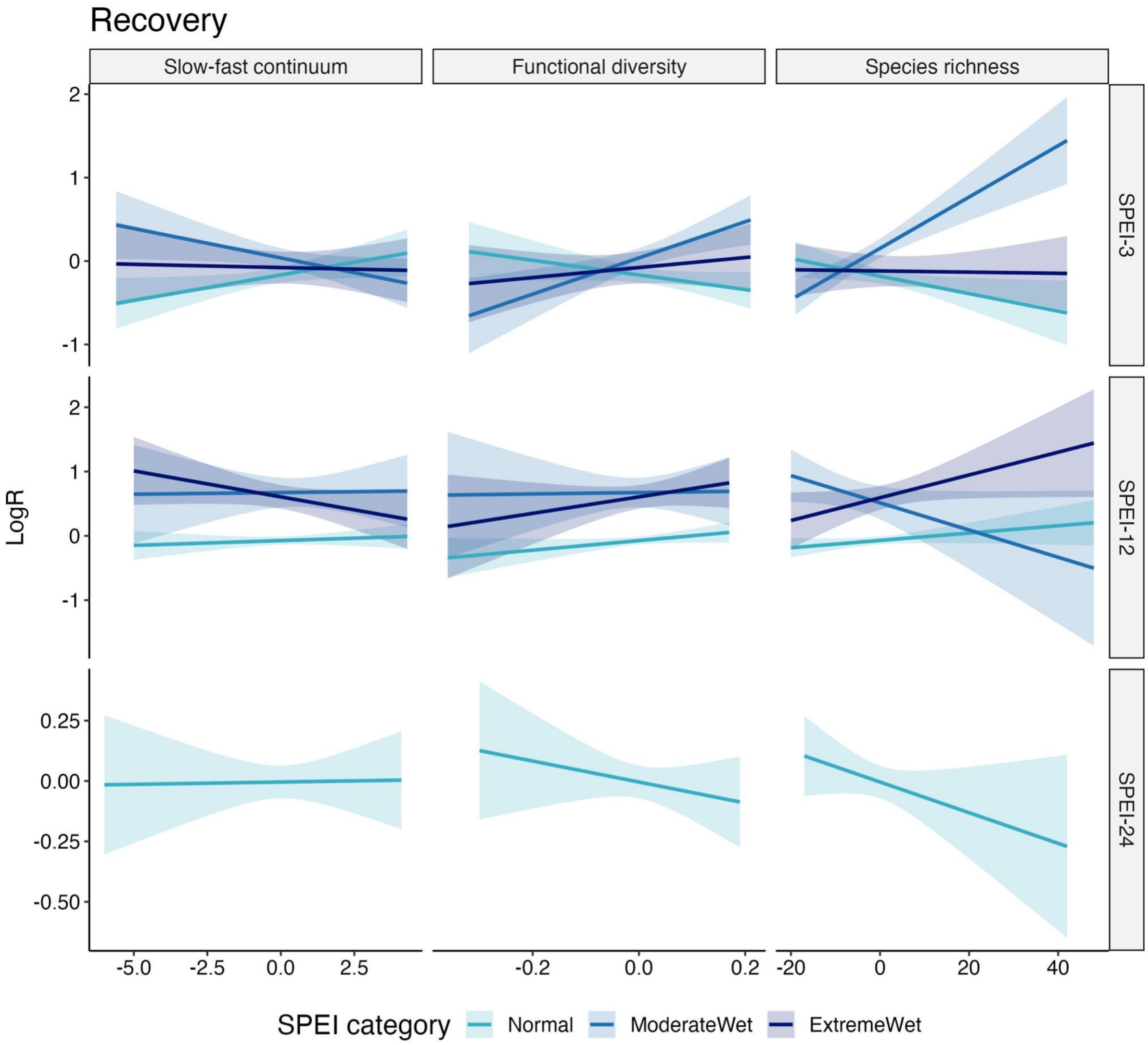

Figure A3.1 - Effect of the statistical interaction between water availability (SPEI categories: normal, moderate and extreme wet) and slow-fast continuum, functional diversity and species richness (columns) on recovery (LogR). Results are reported for the different SPEI time-scales (i.e., -3/-12/-24; see rows) and pertain to models fitted on data from the year immediately after one or more (in a row) events of either moderate or extreme drought. Predictors were centred before fitting the models. Line colours represent different water availability conditions: from normal water budget (light blue) to extreme wet (purple). Bands represent 95% confidence intervals for conditional means.

Table A3.1 - Table of results for models including slow-fast continuum and functional diversity. Estimates of regression parameters are reported along with associated standard error of coefficient estimators (p-value for the test statistic in brackets). Num. Obs.: number of observations. R2 Marg.: marginal R-squared. R2 Cond.: conditional R-squared. The symbol ‘:’ represents the interaction between two terms.

	SPEI-3	**SPEI-12**	**SPEI-24**

	Estimate Std. error (p-value)	Estimate Std. error (p-value)	Estimate Std. error (p-value)
Intercept	-0.133 0.062 (0.033)	-0.215 0.050 (<0.001)	0.380 0.064 (<0.001)
ModerateWet	0.204 0.083 (0.016)	0.747 0.126 (<0.001)	-
ExtremeWet	0.089 0.116 (0.448)	0.680 0.099 (<0.001)	-
Central	0.030 0.111 (0.788)	0.465 0.073 (<0.001)	-0.363 0.106 (<0.001)
North-East	-0.132 0.075 (0.082)	-0.063 0.106 (0.549)	-0.805 0.107 (<0.001)
Slow-fast continuum	0.061 0.029 (0.035)	0.015 0.022 (0.493)	0.002 0.024 (0.935)
Functional diversity	-0.875 0.519 (0.094)	0.745 0.432 (0.086)	-0.434 0.468 (0.356)
Land-use intensity	-0.003 0.054 (0.955)	0.030 0.051 (0.560)	-0.066 0.067 (0.328)
Mycorrhizae intensity	-0.012 0.005 (0.031)	-0.008 0.006 (0.197)	0.002 0.006 (0.792)
Day of harvest	-0.007 0.006 (0.257)	-0.023 0.004 (<0.001)	0.013 0.007 (0.091)
ModerateWet:Slow-fast continuum	-0.131 0.040 (0.001)	-0.010 0.072 (0.894)	-
ExtremeWet:Slow-fast continuum	-0.069 0.048 (0.157)	-0.096 0.052 (0.065)	-
ModerateWet:Funct. diversity	3.043 0.801 (<0.001)	-0.637 1.453 (0.662)	-
ExtremeWet:Funct. diversity	1.476 0.883 (0.097)	0.535 1.135 (0.638)	-
SD PlotID	0.00002	0.00001	-
SD Residual	0.472	0.566	-

Num. Obs.	293	440	148
R2 Marg. (R2 for SPEI-24)	0.126	0.286	0.345
R2 Cond. (Adj-R2 for SPEI-24)	0.126	0.286	0.313

Table A3.2 - Table of results for models including species richness. Estimates of regression parameters are reported along with associated standard error of coefficient estimators (p-value for the test statistic in brackets). Num. Obs.: number of observations. R2 Marg.: marginal R-squared. R2 Cond.: conditional R-squared. The symbol ':' represents the interaction between two terms.

	SPEI-3 Estimate Std. error (p-value)	**SPEI-12** Estimate Std. error (p-value)	**SPEI-24** Estimate Std. error (p-value)
Intercept	-0.211 0.062 (<0.001)	-0.215 0.048 (<0.001)	0.386 0.062 (<0.001)
ModerateWet	0.333 0.080 (<0.001)	0.584 0.139 (<0.001)	-
ExtremeWet	0.062 0.113 (0.584)	0.664 0.099 (<0.001)	-
Central	0.117 0.107 (0.275)	0.428 0.070 (<0.001)	-0.323 0.102 (0.002)
North-East	-0.025 0.085 (0.772)	0.003 0.109 (0.982)	-0.866 0.117 (<0.001)
Species richness	-0.010 0.005 (0.030)	0.006 0.004 (0.113)	-0.006 0.004 (0.160)
Land-use intensity	-0.009 0.051 (0.866)	0.066 0.049 (0.178)	-0.088 0.066 (0.182)
Mycorrhizae intensity	-0.011 0.005 (0.037)	-0.006 0.006 (0.262)	0.003 0.006 (0.610)
Day of harvest	-0.008 0.006 (0.166)	-0.024 0.004 (<0.001)	0.014 0.007 (0.055)
ModerateWet:Species richness	0.041 0.006 (<0.001)	-0.027 0.012 (0.025)	-

ExtremeWet:Species richness	0.010 0.007 (0.154)	0.012 0.009 (0.186)	-
SD PlotID	0.00002	0.00002	-
SD Residual	0.453	0.565	
Num. Obs.	293	440	148
R2 Marg. (R2 for SPEI-24)	0.185	0.287	0.350
R2 Cond. (Adj-R2 for SPEI-24)	0.185	0.287	0.323

Table A3.3 - Models for recovery including slow-fast continuum and functional diversity. Analysis of deviance table (Type II Wald F-tests with Kenward-Roger degrees of freedom) for SPEI-3 and -12. Analysis of variance table (Type II F-test) for SPEI-24. SPEI: categorical predictor representing the different SPEI categories for recovery models (Normal, ModerateWet and ExtremeWet for SPEI-3 and -12). n.s.: not significant (i.e., p-value > 0.05).

	SPEI-3				**SPEI-12**				**SPEI-24**		
	F	Df	Df.res	p-value	F	Df	Df.res	p-value	F	Df	p-value
SPEI	4.5706	2	181.52	*	48.2582	2	311.81	***	-	-	-
Slow-fast continuum	0.0405	1	200.68	n.s.	0.0389	1	219.54	n.s.	0.0066	1	n.s.
Functional diversity	0.5359	1	254.01	n.s.	3.5783	1	353.18	n.s.	0.8590	1	n.s.
Land-use intensity	0.0031	1	211.67	n.s.	0.3366	1	255.22	n.s.	0.9626	1	n.s.
Region	2.0923	2	212.31	n.s.	24.2009	2	269.29	***	30.3001	2	***
Day of harvest	1.2777	1	272.28	n.s.	25.6633	1	422.58	***	2.8965	1	n.s.
Mycorrhizae intensity	4.6909	1	240.28	*	1.6561	1	334.44	n.s.	0.0699	1	n.s.
SPEI:Slow-fast c.	5.4093	2	226.32	**	1.7114	2	407.81	n.s.	-	-	-
SPEI:Fun. div.	7.2379	2	256.11	***	0.2262	2	421.88	n.s.	-	-	-

Table A3.4 - Models for recovery including species richness. Analysis of deviance table (Type II Wald F-tests with Kenward-Roger degrees of freedom) for SPEI-3 and -12. Analysis of variance table (Type II F-test) for SPEI-24. SPEI: categorical predictor representing the different SPEI categories for recovery models (Normal, ModerateWet and ExtremeWet for SPEI-3 and -12). n.s.: not significant (i.e., p-value > 0.05).

	SPEI-3				**SPEI-12**				**SPEI-24**		
	F	Df	Df.res	p-value	F	Df	Df.res	p-value	F	Df	p-value
SPEI	5.4288	2	181.97	**	46.3865	2	320.23	***	-	-	-
Species richness	0.5671	1	197.16	n.s.	1.4900	1	263.69	n.s.	1.9978	1	n.s.
Land-use intensity	0.0283	1	202.08	n.s.	1.8044	1	261.21	n.s.	1.8012	1	n.s.
Region	0.8531	2	228.15	n.s.	19.7339	2	256.19	***	31.7304	2	***
Day of harvest	1.9145	1	277.84	n.s.	28.9862	1	428.06	***	3.7401	1	n.s.
Mycorrhizae intensity	4.4072	1	247.27	*	1.2490	1	360.00	n.s.	0.2615	1	n.s.
SPEI:Sp. richness	23.3725	2	210.29	***	3.5965	2	413.73	*	-	-	-

Appendix A4 - Effect of the interaction between functional composition, functional diversity, species richness and SPEI on resistance

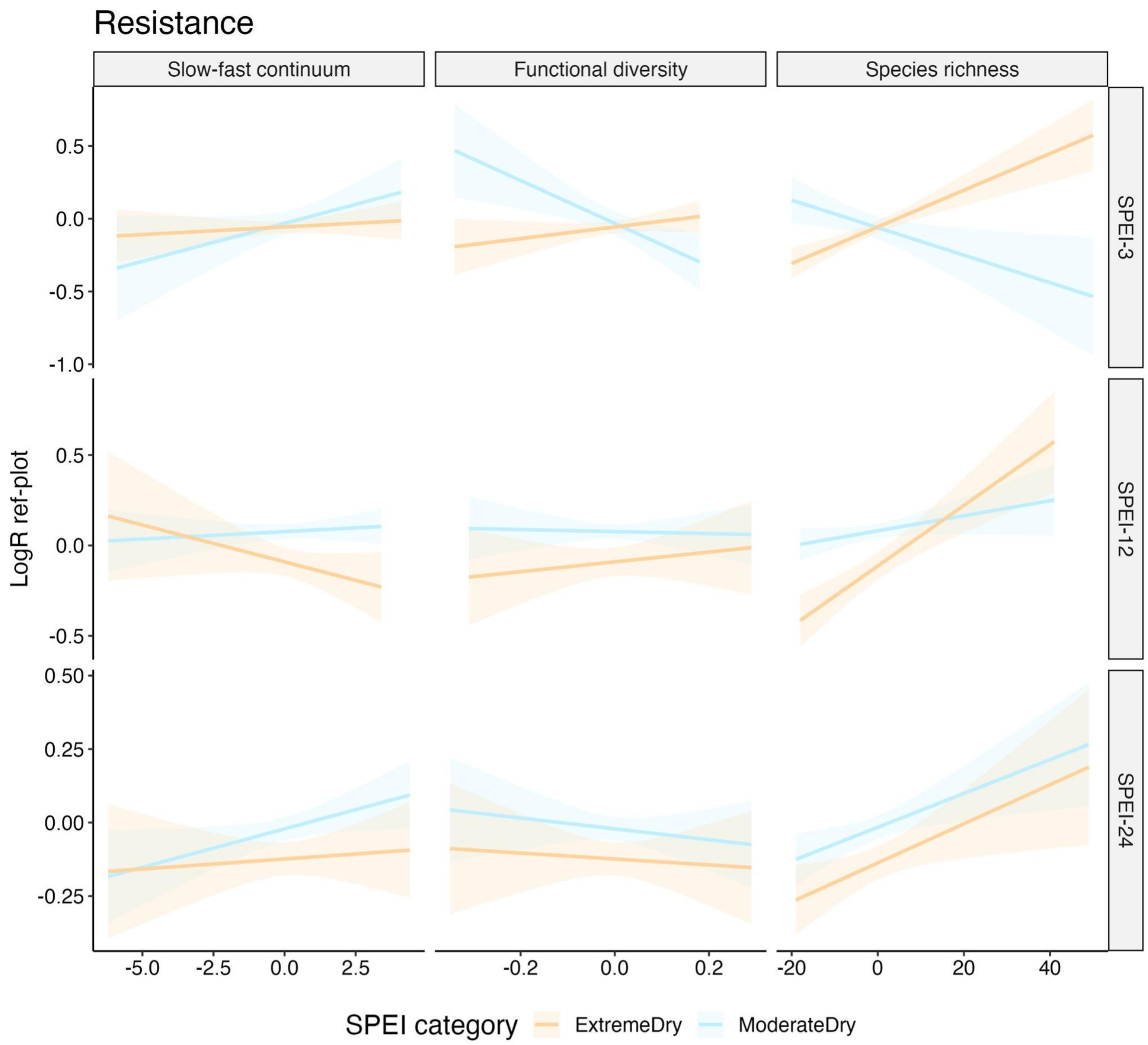

Figure A4.1 - Effect of the statistical interaction between water availability (SPEI categories: moderate and extreme dry) and slow-fast continuum, functional diversity and species richness (columns) on resistance ($LogR_{ref\text{-}plot}$). Results are reported for the different SPEI time-scales (i.e., -3/-12/-24; see rows) and pertain to models fitted on data from the years featuring either moderate or extreme drought. Predictors were centred before fitting the models. Line colours represent different water availability conditions: from extreme (ochre) to moderate drought (light blue). Bands represent 95% confidence intervals for conditional means.

Table A4.1 - Table of results for models including slow-fast continuum and functional diversity. Estimates of regression parameters are reported along with associated standard error of coefficient estimators (p-value for the test statistic in brackets). Num. Obs.: number of observations. R2 Marg.: marginal R-squared. R2 Cond.: conditional R-squared. The symbol ':' represents the interaction between two terms.

	SPEI-3 Estimate	**SPEI-12** Estimate	**SPEI-24** Estimate

	Std. error (p-value)	Std. error (p-value)	Std. error (p-value)
Intercept	-0.032 0.063 (0.608)	-0.035 0.031 (0.255)	-0.145 0.027 (<0.001)
ExtremeDry	-0.025 0.049 (0.615)	-0.168 0.048 (<0.001)	-0.102 0.038 (0.007)
Central	-0.049 0.054 (0.371)	0.096 0.047 (0.042)	0.210 0.043 (<0.001)
North-East	0.034 0.056 (0.541)	0.266 0.051 (<0.001)	0.211 0.043 (<0.001)
Slow-fast continuum	0.052 0.029 (0.072)	0.008 0.014 (0.546)	0.026 0.012 (0.036)
Functional diversity	-1.472 0.477 (0.002)	-0.055 0.279 (0.844)	-0.184 0.252 (0.465)
Land-use intensity	0.067 0.035 (0.060)	0.035 0.032 (0.269)	0.049 0.028 (0.077)
Mycorrhizae intensity	-0.0007 0.004 (0.839)	0.005 0.004 (0.164)	-0.0009 0.003 (0.769)
Day of harvest	0.015 0.002 (<0.001)	0.024 0.002 (<0.001)	0.026 0.002 (<0.001)
ExtremeDry:Slow-fast continuum	-0.042 0.031 (0.179)	-0.049 0.029 (0.095)	-0.019 0.020 (0.331)
ExtremeDry:Funct. diversity	1.872 0.542 (<0.001)	0.326 0.487 (0.503)	0.084 0.387 (0.829)
SD PlotID	0.00002	0.00002	0.00002
SD Residual	0.509	0.491	0.430
Num. Obs.	786	839	836
R2 Marg.	0.130	0.240	0.252
R2 Cond.	0.130	0.240	0.252

Table A4.2 - Table of results for models including species richness. Estimates of regression parameters are reported along with associated standard error of coefficient estimators (p-value for the test statistic in brackets). Num. Obs.: number of observations. R2 Marg.: marginal R-squared. R2 Cond.: conditional R-squared. The symbol ':' represents the interaction between two terms.

	SPEI-3 Estimate Std. error (p-value)	**SPEI-12** Estimate Std. error (p-value)	**SPEI-24** Estimate Std. error (p-value)
Intercept	-0.089 0.060 (0.140)	-0.047 0.029 (0.111)	-0.161 0.026 (<0.001)
ExtremeDry	0.005 0.048 (0.915)	-0.195 0.047 (<0.001)	-0.121 0.038 (0.001)
Central	-0.078 0.051 (0.128)	0.088 0.043 (0.044)	0.201 0.042 (<0.001)
North-East	0.117 0.054 (0.031)	0.329 0.051 (<0.001)	0.291 0.043 (<0.001)
Species richness	-0.009 0.004 (0.016)	0.004 0.002 (0.077)	0.006 0.002 (0.007)
Land-use intensity	0.149 0.033 (<0.001)	0.078 0.030 (0.010)	0.112 0.026 (<0.001)
Mycorrhizae intensity	-0.004 0.004 (0.254)	0.0009 0.004 (0.823)	-0.006 0.003 (0.081)
Day of harvest	0.013 0.002 (<0.001)	0.023 0.002 (<0.001)	0.025 0.002 (<0.001)
ExtremeDry:Species richness	0.022 0.004 (<0.001)	0.013 0.004 (<0.001)	0.0009 0.003 (0.763)
SD PlotID	0.00002	0.00002	0.00002
SD Residual	0.501	0.484	0.428
Num. Obs.	786	839	836
R2 Marg. (R2 for SPEI-24)	0.156	0.260	0.257
R2 Cond. (Adj-R2 for SPEI-24)	0.156	0.260	0.257

Table A4.3 - Models for resistance including slow-fast continuum and functional diversity. Analysis of deviance table (Type II Wald F-tests with Kenward-Roger degrees of freedom). SPEI: categorical predictor representing the different SPEI categories for resistance models (ModerateDry and ExtremeDry). n.s.: not significant (i.e., p-value > 0.05).

	SPEI-3				**SPEI-12**				**SPEI-24**			
	F	Df	Df.res	p-value	F	Df	Df.res	p-value	F	Df	Df.res	p-value
SPEI	1.0674	1	653.85	n.s.	14.4491	1	704.81	***	7.5176	1	718.61	**
Slow-fast continuum	1.6299	1	309.90	n.s.	0.0027	1	262.97	n.s.	3.4341	1	232.63	n.s.
Functional diversity	0.0706	1	514.12	n.s.	0.0246	1	459.63	n.s.	0.5441	1	467.67	n.s.
Land-use intensity	3.5251	1	437.73	n.s.	1.2160	1	352.56	n.s.	3.1115	1	316.26	n.s.
Region	1.3863	2	242.18	n.s.	13.7265	2	201.14	***	17.2422	2	238.47	***
Day of harvest	63.5673	1	756.02	***	168.8402	1	808.98	***	162.0432	1	809.65	***
Mycorrhizae intensity	0.0411	1	416.17	n.s.	1.9297	1	481.32	n.s.	0.0854	1	440.25	n.s.
SPEI:Slow-fast c.	1.7990	1	771.03	n.s.	2.7827	1	820.85	n.s.	0.9418	1	814.33	n.s.
SPEI:Fun. div.	11.8943	1	758.89	***	0.4463	1	827.98	n.s.	0.0465	1	820.88	n.s.

Table A4.4 - Models for resistance including species richness. Analysis of deviance table (Type II Wald F-tests with Kenward-Roger degrees of freedom). SPEI: categorical predictor representing the different SPEI categories for recovery models (ModerateDry and ExtremeDry). n.s.: not significant (i.e., p-value > 0.05).

	SPEI-3				SPEI-12				SPEI-24			
	F	Df	Df.res	p-value	F	Df	Df.res	p-value	F	Df	Df.res	p-value
SPEI	0.9572	1	654.97	n.s.	18.4205	1	713.08	***	10.1539	1	722.68	**
Species richness	10.5737	1	325.57	**	12.8326	1	281.42	***	10.3214	1	329.87	**
Land-use intensity	20.3826	1	381.04	***	6.6814	1	340.96	*	19.2471	1	294.79	***
Region	6.8856	2	237.04	**	21.8697	2	189.18	***	27.1158	2	235.70	***
Day of harvest	48.7655	1	754.36	***	157.7066	1	807.61	***	139.5074	1	812.29	***
Mycorrhizae intensity	1.2881	1	389.75	n.s.	0.0495	1	470.19	n.s.	3.0355	1	473.19	n.s.
SPEI:Sp. richness	27.3594	1	743.16	***	11.8585	1	821.37	***	0.0909	1	801.49	n.s.