Biodiversity promotes resistance but dominant species shape recovery of grasslands under extreme drought

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Abstract

1. How biodiversity underpins ecosystem resistance (i.e., ability to withstand environmental perturbations) and recovery (i.e., ability to return to a pre-perturbation state) 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.

2. Using an 11-year time-series of plant biomass from 150 permanent grassland plots spanning a gradient of land-use intensity, we examined how taxonomic and functional components of biodiversity affected resistance and recovery of biomass under extreme drought.

3. The association between biodiversity, land use, and biomass varied across years, especially in the driest years. Species rich or functionally diverse communities (associated with low land-use intensity) buffered extreme droughts better, while species poor communities or those dominated by fast-growing species (associated with high land-use intensity) had higher recovery capabilities after a moderate-to-extreme drought.

Synthesis. Our results show that plant community functional and taxonomic components determine grasslands resistance and recovery under moderate-to-extreme drought. In turn, this points to the importance of designing landscapes with both extensively and intensively managed grasslands. Functionally or taxonomically rich communities (favoured under low land-use intensity) would preserve biomass under extreme droughts, whereas species-poor or fast-growing communities (favoured by high land-use intensity) would restore biomass 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, ecosystem function and services.

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 of population sizes. More diverse communities can be more stable because they can harbour species with different responses to environmental fluctuations, which insures ecosystems against loss of functions (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, asynchronous fluctuations 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, namely any biological feature measurable at the individual level (Violle et al. 2007), 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 species lost during an environmental perturbation and those that persist 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 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 functional and taxonomic characteristics of plant communities. 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 plant biomass fluctuation along a gradient of land-use intensity; (ii) test whether the association between biodiversity, biomass and land use changes under exceptional climatic conditions (i.e., moderate-to-extreme drought, hereafter also collectively 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 Biodiversity Exploratories (hereafter BE) 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 moisture) and anthropogenic (e.g., land-use intensity) variables.

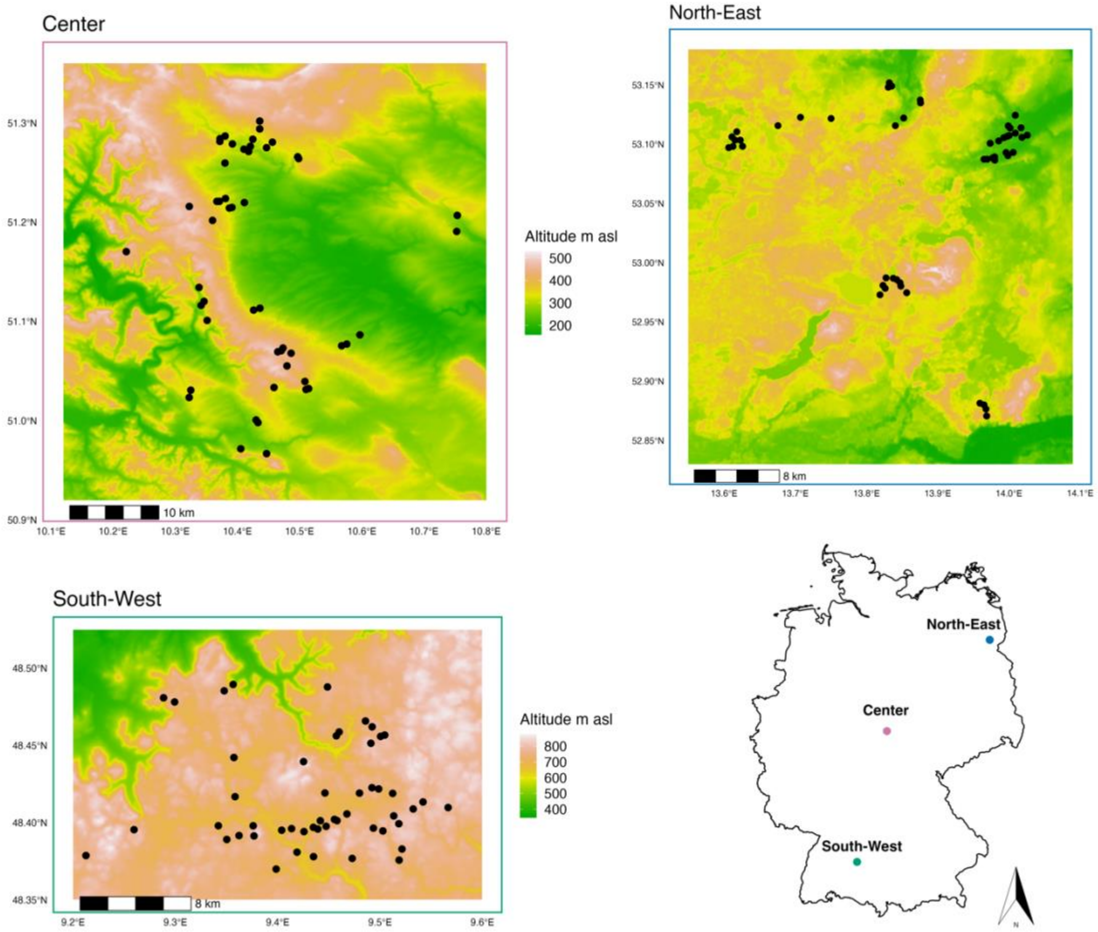

Figure 1 - Study area. Panels show the location of grassland plots in each region of the Biodiversity Exploratories overlaid to an altitude layer (m asl: metres above the sea level).

2.1.1. Measures of biomass fluctuation

Plant aboveground biomass was harvested yearly during spring over the period 2009-2019 (11 years; Hinderling et al. 2023). The harvest period varied across BE regions, but mainly occurred in mid/late May. The median, first and third quartile of the day of harvest, as averaged over the study period, were: 142nd, 138th-147th in South-West; 137th, 134th-141st in Central; 141st, 137th-145th 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 for 48 hours at 80 °C until constant weight and weighed. 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. We recorded the date on which plant biomass was harvested in each vegetation plot (hereafter *day of the year*), and used it in the analyses (as a continuous variable) to account for the effect of the harvesting period when testing the association between biodiversity, resistance and recovery of biomass.

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

The first was:

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

where ln is the natural logarithm. The LogR quantified the year-by-year change in plant biomass collected in a plot. 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:

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

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., $median\ biomass_{plot\ i}$). When focusing on years featuring severe drought, we used the $\text{LogR}_{\text{ref-plot}}$ (hereafter also referred to as **plot reference log ratio**) to measure grassland resistance.

See Figure 2 for the hypothesised association between biomass recovery, resistance, biodiversity and slow- *vs*. fast-growing strategies, and for scenarios of recovery and resistance arising under extreme drought.

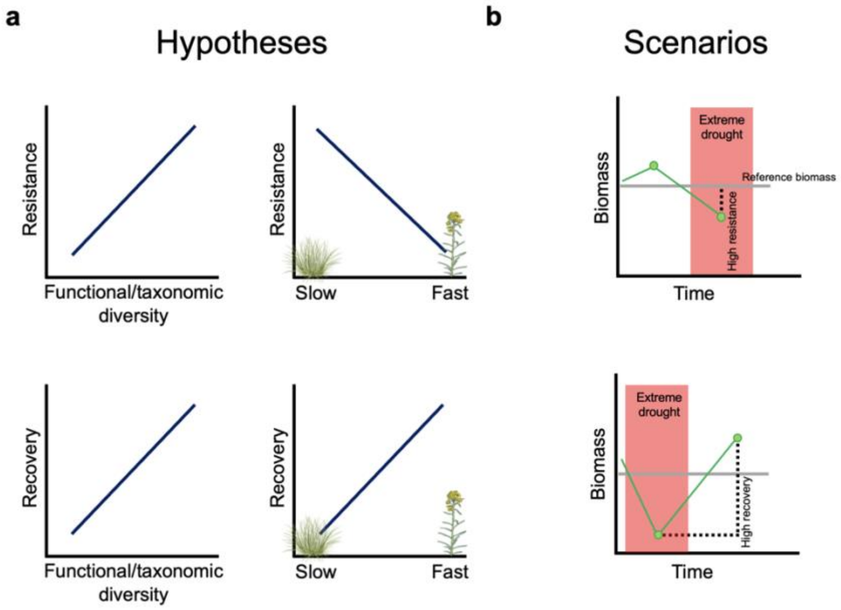

Figure 2 - Hypotheses about the association between biomass recovery, resistance, biodiversity and slow- *vs*. fast-growing strategies (panel a), and scenarios of recovery and resistance under extreme drought (panel b). Plant icons (*Festuca* spp. on the 'slow side' and *Euphorbia esula* on the 'fast' side) by Tracey Saxby (Integration and Application Network, ian.umces.edu/media-library), CC BY-SA 4.0 DEED. No changes were made to the original icons.

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 leaf phosphorus content (mg/g). Plant height is associated with competitiveness for light and the overall plant fecundity; specific leaf area (hereafter SLA), leaf dry matter content (hereafter LDMC), leaf nitrogen and leaf phosphorus content are related to resource acquisition, growth and photosynthetic rate; seed mass is associated with plant persistence and dispersal capacity (Perez-Harguindeguy et al. 2013). Data on SLA and 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, which explained 48% of the variance, as a proxy of the leaf-economic spectrum (hereafter *slow-fast continuum*) (see Figure A1, Appendix A1 for supplementary information on the PCA). 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). Note that, to compute community weighted means, trait values were weighted by species cover, which we measured (on a percentage scale) in the same 4 m x 4 m sub-quadrats where we also recorded species richness.

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 to this as functional diversity, where high values of functional diversity are associated with communities characterised by high dissimilarity in species' plant traits. For all this, we used Daphne, a dated ultrametric supertree of European plant species (Durka & Michalski 2012).

2.1.3. Land-use intensity and soil moisture

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 moisture. 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 relationship 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 moisture. As an overall measure of soil moisture, we computed the average value of the soil moisture at 10 cm depth (in %) recorded over the time-series by climatic loggers placed within each vegetation plot (Wöllauer et al. 2022).

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 and ecosystem 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 growth (i.e., May). This allowed analysing resistance and recovery from drought measured at multiple time-scales, and, in turn, to assess biomass response to short- and long-term drought. The SPEI values for all time-scales were obtained for each year of the time-series (see Figure A2, Appendix A2 for SPEI-3/-12/-24 temporal trend). Data on SPEI were gathered as raster layers 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 A2 (Appendix A2) 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. Time-series analysis of plant biomass change

Using generalised least squares models, we analysed how the LogR and $LogR_{ref-plot}$ related to land-use intensity, slow-fast continuum, functional diversity, day of the year (day of biomass harvest), soil moisture and plant species richness over the time-series. Also, we included a categorical variable with three levels, each representing one of the three BE regions, to account for mean region-specific differences. Species richness was correlated with 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.

We assumed that time affected how the log response ratios related with land-use intensity, slow-fast continuum, functional diversity, day of the year, soil moisture and plant species richness. We therefore included the statistical interactions between the predictors and year, i.e. a categorical variable with each level representing a year of the time-series. To account for the dependence among observations sampled from the same vegetation plots over time, we considered the following temporal autocorrelation models: a first- and a second-order autoregressive process (AR-1, AR-2), and an autoregressive-moving average process (ARMA) with a correlation parameter for the autoregressive model and one for the moving average (see Pinheiro & Bates 2006). Among the different temporal autocorrelation structures, we selected the most parsimonious one (i.e., including the lowest number of parameters), which allowed reducing (normalised) residuals' temporal autocorrelation. We found that ARMA was the most adequate model for the LogR, while an AR-1 best fitted the temporal autocorrelation of the $LogR_{ref-plot}$ model.

Although the 'repeated measures' structure of our dataset would call for the use of a plot-level random effect (in a mixed-effects model design) to further account for the non-independence of observations from the same plots, we did not include it. The reason is that both log response ratios were computed by standardising biomass collected in a plot and year by a plot-specific refence value (see 2.1.1.). This substantially absorbs the 'between plots' variability in the log ratios, making the plot-level random effect ineffective (i.e., explaining zero 'between plots' variance).

We fitted generalised least squares models using the *nlme* R package (Pinheiro et al. 2021). All numeric (non-categorical) predictors were centred before fitting the models. Models' predictions on the association between the log response ratios *vs*. slow-fast continuum, functional diversity, species richness and land-use intensity were compared with the observed relationship between these predictors and biomass. This allowed determining whether the former predictors related differently to overall biomass and biomass change (here measured by the two log response ratios). Models' predictions were computed using the *effects* R package (Fox & Weisberg 2018, 2019).

2.3.2. Effect of functional composition, functional and taxonomic 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 models including the statistical interaction between the functional and taxonomic components and the categorical SPEI. To analyse recovery (models for the annual log ratio, LogR), 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 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, $\text{LogR}_{\text{ref-plot}}$), we focused on observations from 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.

We fitted separate models for the different SPEI time-scales, i.e. SPEI-3/-12/-24. As done in 2.3.1. analyses were carried out separately for functional composition and diversity, and for species richness. Land-use intensity, day of the year, soil moisture and region were included as predictors in the model but were excluded from the interaction with the categorical SPEI. 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. 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. All numeric (non-categorical) predictors were centred before fitting the models. Model assumptions of normality, linearity and homoscedasticity were assessed using the *performance* R package (Lüdecke & Mattan 2021). Models' predictions were computed using the *effects* R package (Fox & Weisberg 2018, 2019).

3. Results

The three regions showed similar temporal trends in plant biomass production, which, overall, 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 production was highest in 2009 and 2014, while in the South-West it was highest in 2013. According to all SPEI time-scales, 2009, 2013 and 2014 either featured or were preceded by average or above average water budgets in all regions (Figure 3b, Figure A2, Appendix A2). Biomass production was lower than the overall trend in all regions in 2011 and 2017 (Figure 3a), both years which featured severe droughts at different time-scales (Figure 3b, Figure A2, Appendix A2).

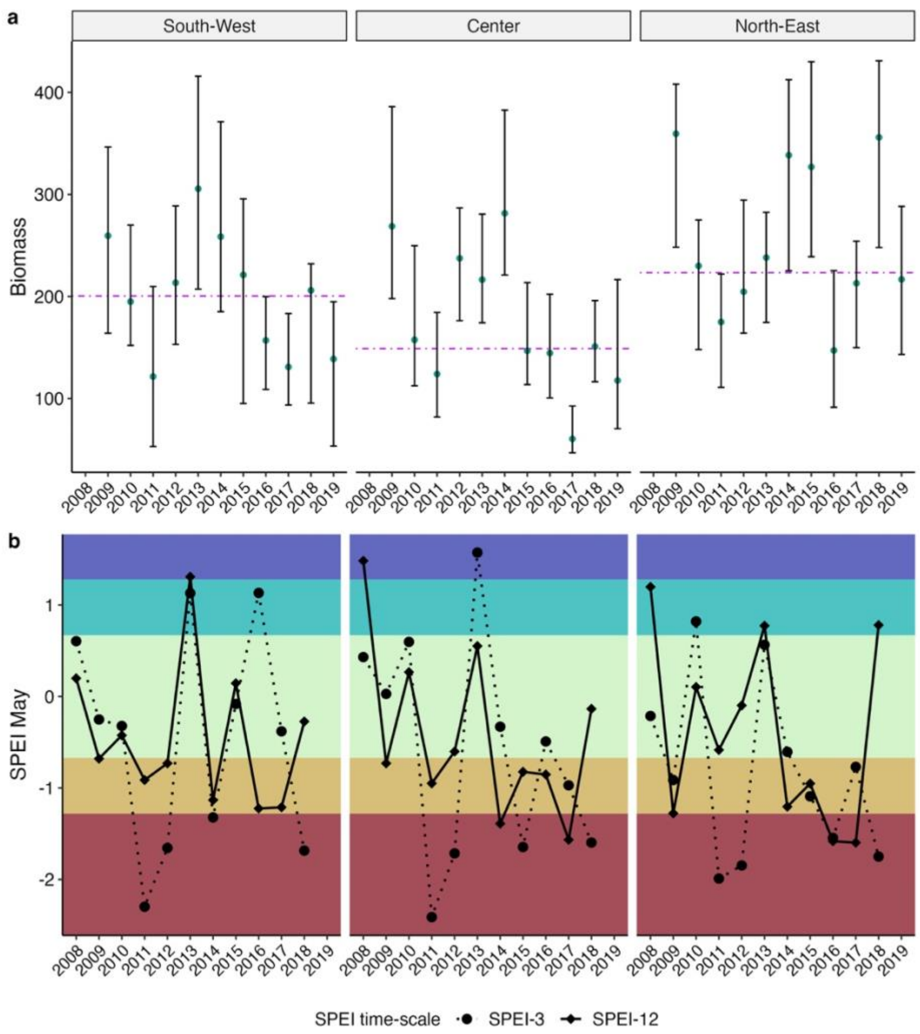

Figure 3 - Temporal trends in biomass (panel a) and Standardised Precipitation-Evapotranspiration Index (panel b) in the three regions of the Biodiversity Exploratories. Panel a) Green points represent median biomass collected in each year in each region (South-West, Center and North-East). Bars delimit 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 SPEI. Temporal trend for SPEI-24 is reported in Appendix A2 (Figure A2). Colours of horizontal bands are associated with water budget conditions, with ochre and reddish colours representing moderate and extreme drought, respectively (following the classification of continuous SPEI values into categories of water availability conditions reported in 2.2.).

3.1. Association between biomass, biomass change, biodiversity and land use over time

Biomass showed an overall positive association with slow-fast continuum and a negative relationship with functional diversity and species richness (Figure A3.1, Appendix A3), indicating that functionally and species poor communities dominated by fast-growing species were more productive. These communities appeared to be associated with high land-use intensity (Figure A3.2, Appendix A3). As a result, biomass was also positively associated with land-use intensity (Figure A3.1, Appendix A3), meaning that intensively managed plant communities produced more biomass than extensively managed.

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 the years 2009, 2010, 2012 and 2016 (Figures A4.1,3, Appendix A4), the two log response ratios exhibited an opposite relationship with the slow-fast continuum, functional diversity and species richness to the overall relationship observed for biomass (Figure A3.1, Appendix A3). This means that the three biodiversity components affected biomass change in these years differently than overall biomass growth.

Results for the annual (LogR) and plot reference log ratio ($\mathrm{LogR}_{\text{ref-plot}}$) suggest that grasslands with different functional composition, functional diversity and species richness responded differently to drought. Concerning the LogR, 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). In 2017, which featured severe droughts in all regions according to all SPEI time-scales, land-use intensity negatively affected the LogR (although significantly only in the model including species richness), indicating that communities subject to low land-use intensity produced more (or lost less) biomass in that year than in the previous year. Overall, vegetation plots harvested later in the sampling season were predicted to have higher LogR values (Figure A4.2, Appendix A4), while soil moisture seemed not to consistently affect the LogR.

In 2009, 2010, 2012 and 2016, the $\mathrm{LogR}_{\text{ref-plot}}$ correlated positively with species richness, indicating that species rich communities produced more (or lost less) biomass (with respect to the plot refence median biomass) than species poor communities (Figure A4.3, Appendix A4). According to SPEI-12, all regions experienced moderate drought in 2009, while they all undergone extreme drought in 2012 (according to SPEI-3) and moderate-to-extreme drought in 2016 (according to SPEI-12) (Figure 3b). Land-use intensity significantly (and positively) affected the $\mathrm{LogR}_{\text{ref-plot}}$ only in 2013, and exclusively in the model including species richness. As observed for the LogR, vegetation plots harvested later in the sampling season were predicted to have higher $\mathrm{LogR}_{\text{ref-plot}}$ values (Figure A4.4, Appendix A4). Finally, soil moisture positively affected the $\mathrm{LogR}_{\text{ref-plot}}$ from 2009 to 2013, meaning that vegetation plots located in wetter areas produced more (or lost less) biomass (with respect to the plot reference median biomass) in these years.

3.2. Effect of the interaction between functional composition, functional and taxonomic 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) (slow-fast continuum: F = 4.89, p-value < 0.05; functional diversity: F = 7.27, p-value < 0.05), while there was no evidence of such an interaction at SPEI-12 (full summary of Type II analysis of variance reported in Table A5.3, Figures A5.1,2, Appendix A5). In particular, functionally poor and fast-growing plant communities showed a more pronounced plant biomass growth (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, A5.2, Appendix A5).

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 (F = 23.05, p-value < 0.05) (Figures 4, A5.2, Appendix A5). On the contrary, at SPEI-12 species poor communities were predicted to produce more biomass when drought was followed by moderate wetness, although the interaction between species richness and water availability after drought was only marginally significant (F = 2.98, p-value = 0.05) (Figures A5.1,2; full summary of Type II analysis of variance reported in Table A5.4, Appendix A5). 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 A5.1,2, Tables A5.3, A5.4, Appendix A5).

At SPEI-3, resistance, as measured by the $\mathrm{LogR}_{\text{ref-plot}}$, appeared to be affected by the interaction between drought intensity and functional diversity (F = 10.86, p-value < 0.05), but not by the interaction between drought intensity and slow-fast continuum (F = 2.21, p-value > 0.05) (full summary of Type II analyses of variance reported in Table A6.3, Appendix A6). Specifically, functionally diverse communities had greater resistance (i.e., more pronounced biomass growth or lower biomass loss) under extreme drought (Figures 4, A6.2, Appendix A6). We found no statistically significant interaction between slow-fast continuum, functional diversity and drought intensity at SPEI-12 and -24 (Table A6.3, Figures A6.1,2, Appendix A6).

Species richness interacted with drought intensity in affecting resistance at SPEI-3 and -12 (Table A6.4, Appendix A6). At both time-scales, species rich communities had a more pronounced biomass growth (or lower biomass loss) than species poor communities under extreme drought (Figures 4, A6.1,2, Appendix A6). We found no statistical interaction between species richness and drought intensity at SPEI-24 (Table A6.4, Appendix A6).

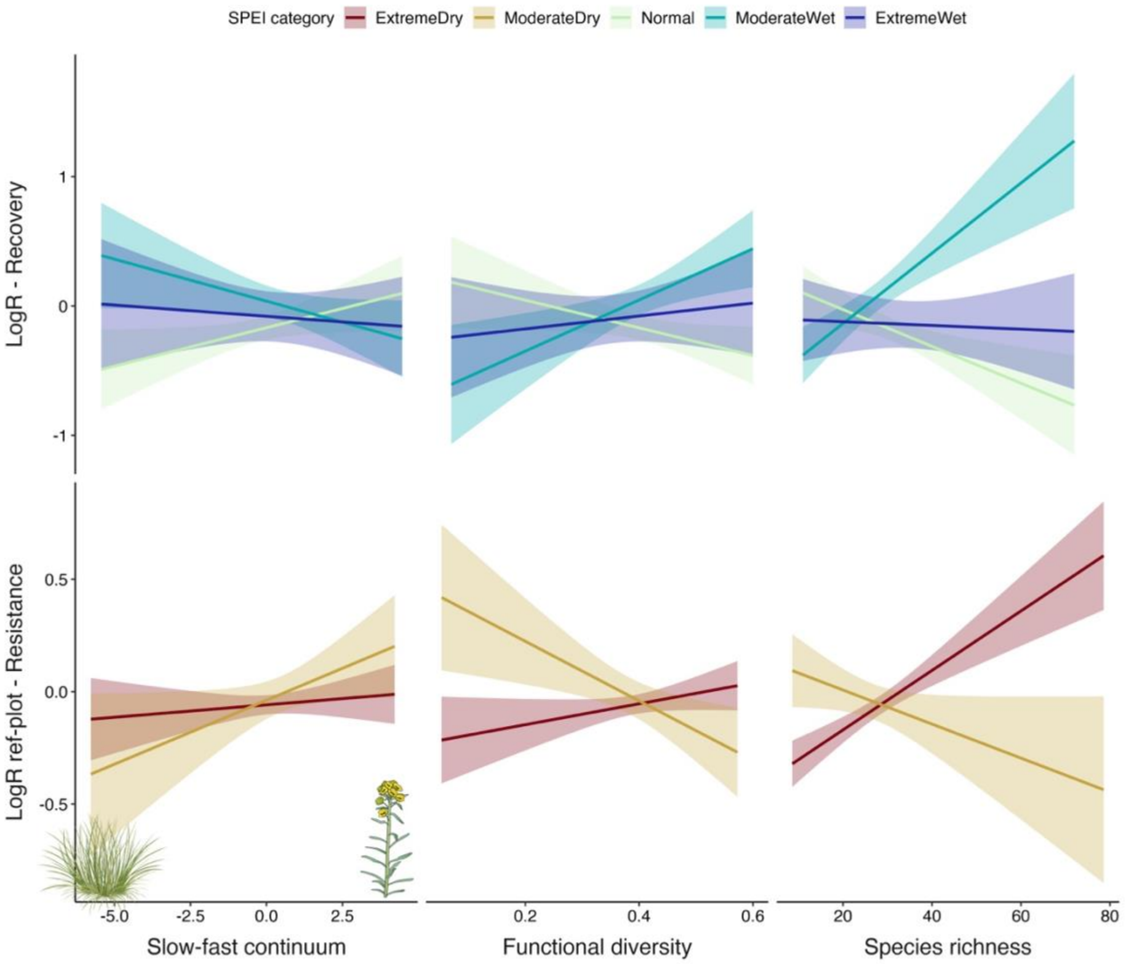

Figure 4 - Effect of the interaction between slow-fast continuum, functional diversity, and species richness (columns) and the categorical 3-months Standardised Precipitation-Evapotranspiration Index (SPEI-3: from extreme drought, in reddish, to extreme wet, in blue) on recovery (upper panel) and resistance (bottom panel). Bands represent 95% confidence intervals for conditional means. An example of a slow-growing species (*Festuca* spp.) is located at the leftmost end of the slow-fast continuum, while an example of a fast-growing species (*Euphorbia esula*) is located at the rightmost end of the spectrum. Plant icons by Tracey Saxby (Integration and Application Network, ian.umces.edu/media-library), CC BY-SA 4.0 DEED. No changes were made to the original icons.

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

Our results suggest that land use is the main determinant of grassland biomass production, likely through direct management (e.g., fertilisation) that influences 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 A3.1, Appendix A3), and subject to high land-use intensity (Figure A3.1,2, Appendix A3), 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 A3.1, Appendix A3). 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 $\text{LogR}_{\text{ref-plot}}$) had opposite signs to those found for biomass in several years with severe drought (2009, 2012 and 2016; see Figure 3b). This supports the idea that biodiversity mediates the response of grassland biomass 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 functionally and species rich communities produce more (or lose less) biomass than functionally and species poor 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. 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 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. 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 such as extreme climatic events (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 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). Thus, the effect of (functional) diversity should be always considered together with the effect of functional composition, particularly the effect of the strategies of dominant species – in our case, represented by the slow-fast continuum.

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 A2, Appendix A2).

4.3. Generality over SPEI time-scales

We found that functional components of biodiversity mediated the response of biomass to drought only at SPEI-3, which in our study quantified water availability right before and at the peak of biomass growth. 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 under both short- (SPEI-3) and long-term (SPEI-12) drought, although the interaction between species richness and SPEI was only marginally significant in the latter case. 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 biomass peak), whereas taxonomic diversity may also catch vegetation response to long-term droughts. We acknowledge that our results do not prove that there is an interaction between drought duration (i.e., press *vs*. pulse drought) and biodiversity facets, and this is worth a more targeted study in the future.

5. Conclusion

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. Using multiple measures of biomass change (here, log response ratios) allows (i) predicting temporal changes in plant biomass, 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, with slow communities (subject to low land-use intensity) preserving biomass during droughts due to high resistance, and fast communities (subject to high land-use intensity) restoring biomass 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.10518333).

Conflict of interest statement

Authors have no conflict of interest to declare.

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Appendix A1 - Computation of the slow-fast continuum variable

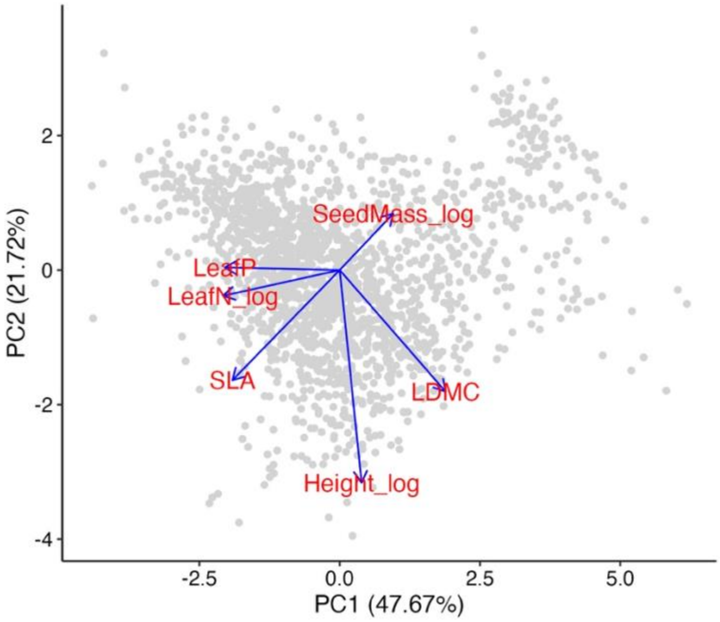

Figure A1 - Biplot showing the correlation between the community weighted means of the functional traits (specific leaf area, SLA; leaf dry matter content, LDMC; leaf nitrogen and phosphorus content, LeafP and LeafN; plant height, Height; seed mass, SeedMass) and the first two axes of the principal component analysis (PCA) that was used to derive the slow-fast continuum variable. The community weighted means of leaf nitrogen content, plant height and seed mass were computed on the log-transformed trait values. The slow-fast continuum was derived as the negative of the first principal component, so that low values of the axis were associated with slow-growing strategies, while large values indicated fast-growing strategies.

Appendix A2 - Temporal trend in the SPEI value

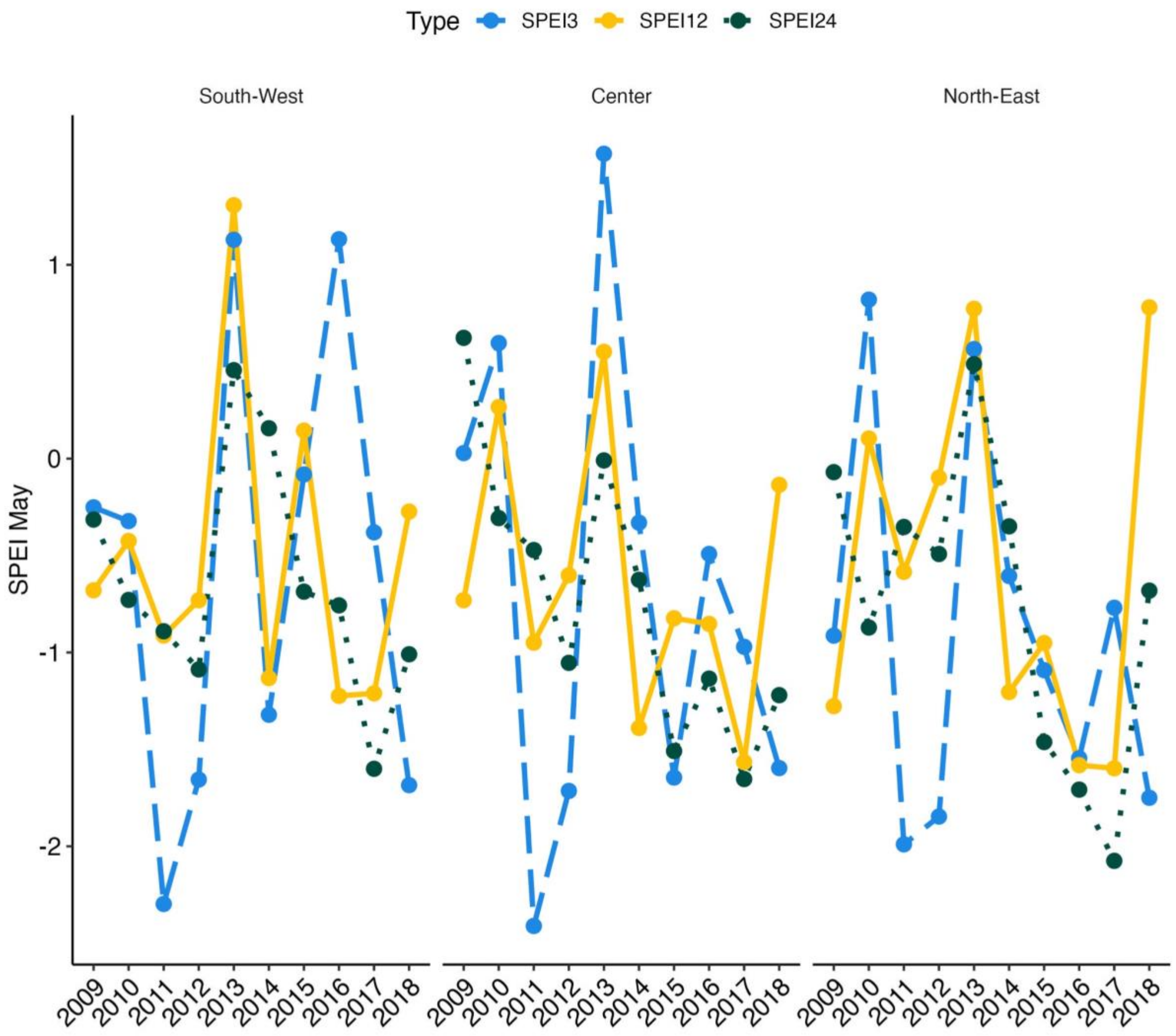

Figure A2 - Trend of the SPEI (of May) value in the three regions of the Biodiversity Exploratories: Schwäbische Alb (South-West); Hainich-Dün (Central); Schorfheide-Chorin (North-East).

Table A2 - 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' indicates 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 A3 - Association between biomass, functional and taxonomic diversity, slow-fast continuum, and land-use intensity

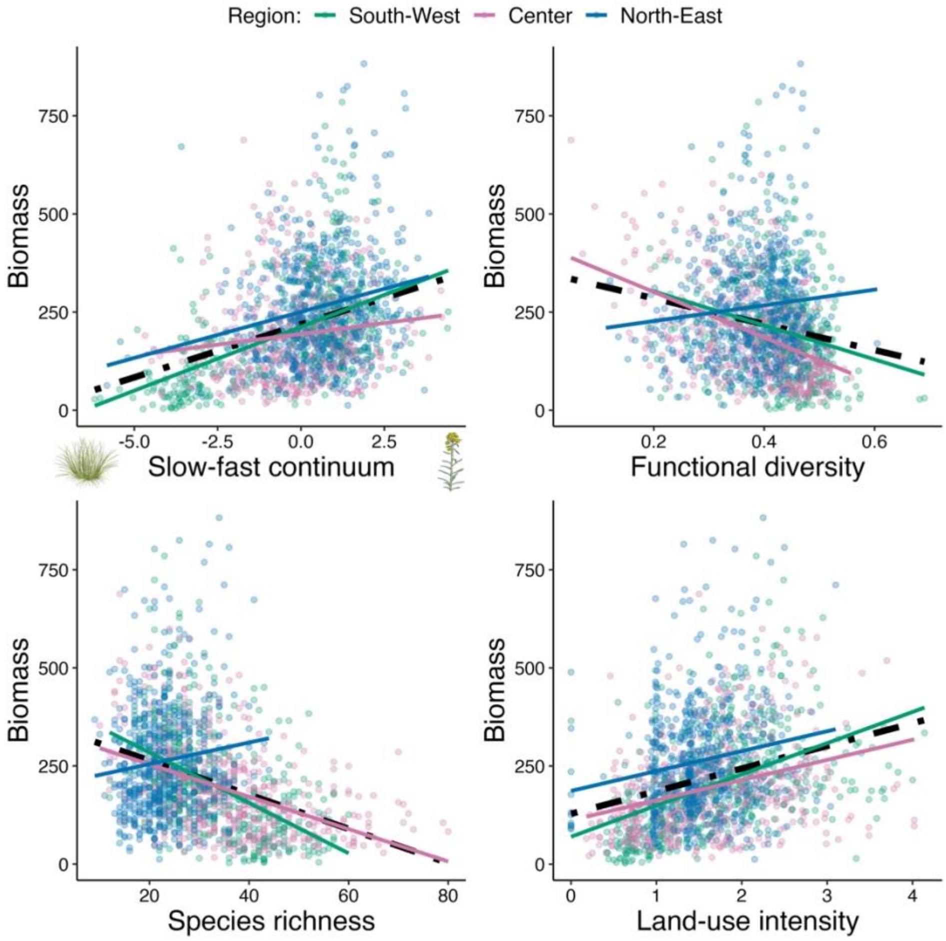

Figure A3.1 - Association between biomass *vs*. slow-fast continuum, functional diversity, species richness and land-use intensity. The black dot-dash line represents the overall association in the Biodiversity Exploratories (i.e., data from the three regions pooled together), whereas the coloured continuous lines represent the association within each region. An example of a slow-growing species (*Festuca* spp.) is located at the leftmost end of the slow-fast continuum, while an example of a fast-growing species (*Euphorbia esula*) is located at the rightmost end of the spectrum. Plant icons by Tracey Saxby (Integration and Application Network, ian.umces.edu/media-library), CC BY-SA 4.0 DEED. No changes were made to the original icons.

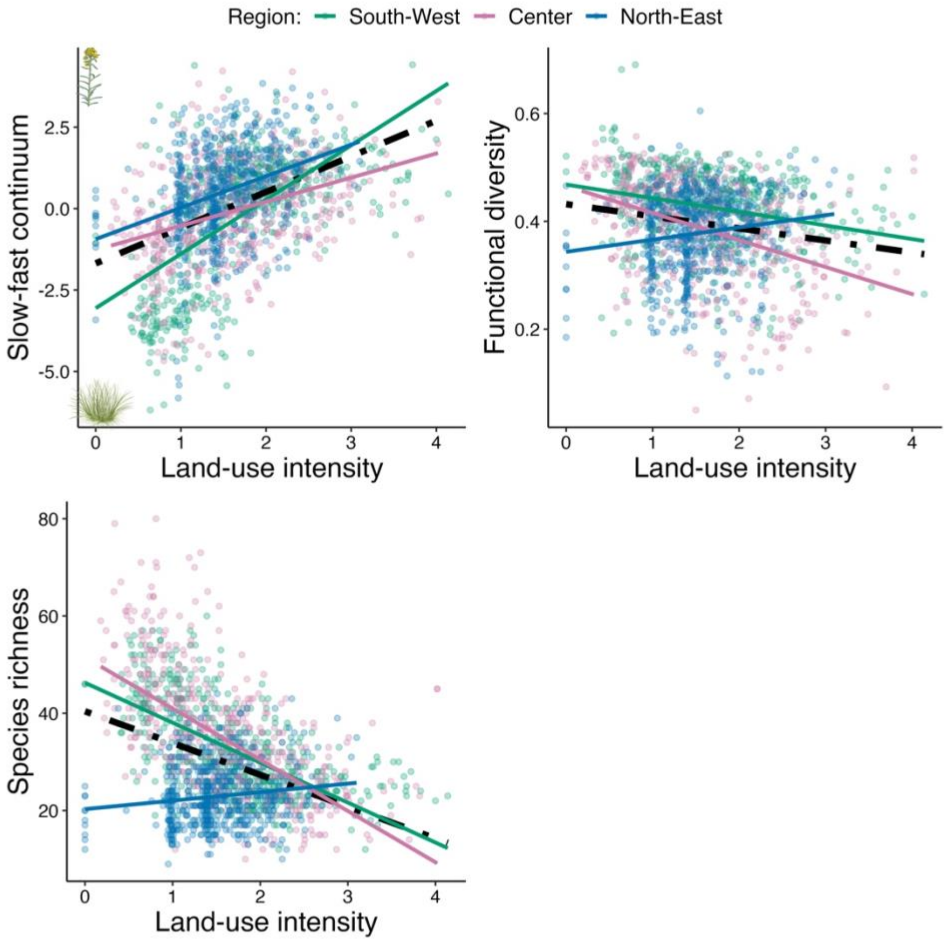

Figure A3.2 - Association between land-use intensity *vs*. slow-fast continuum, functional diversity and species richness. The black dot-dash line represents the overall association in the Biodiversity Exploratories (i.e., data from the three regions pooled together), whereas the coloured continuous lines represent the association within each region. An example of a slow-growing species (*Festuca* spp.) is located at the bottom end of the slow-fast continuum, while an example of a fast-growing species (*Euphorbia esula*) is located at the top end of the spectrum. Plant icons by Tracey Saxby (Integration and Application Network, ian.umces.edu/media-library), CC BY-SA 4.0 DEED. No changes were made to the original icons.

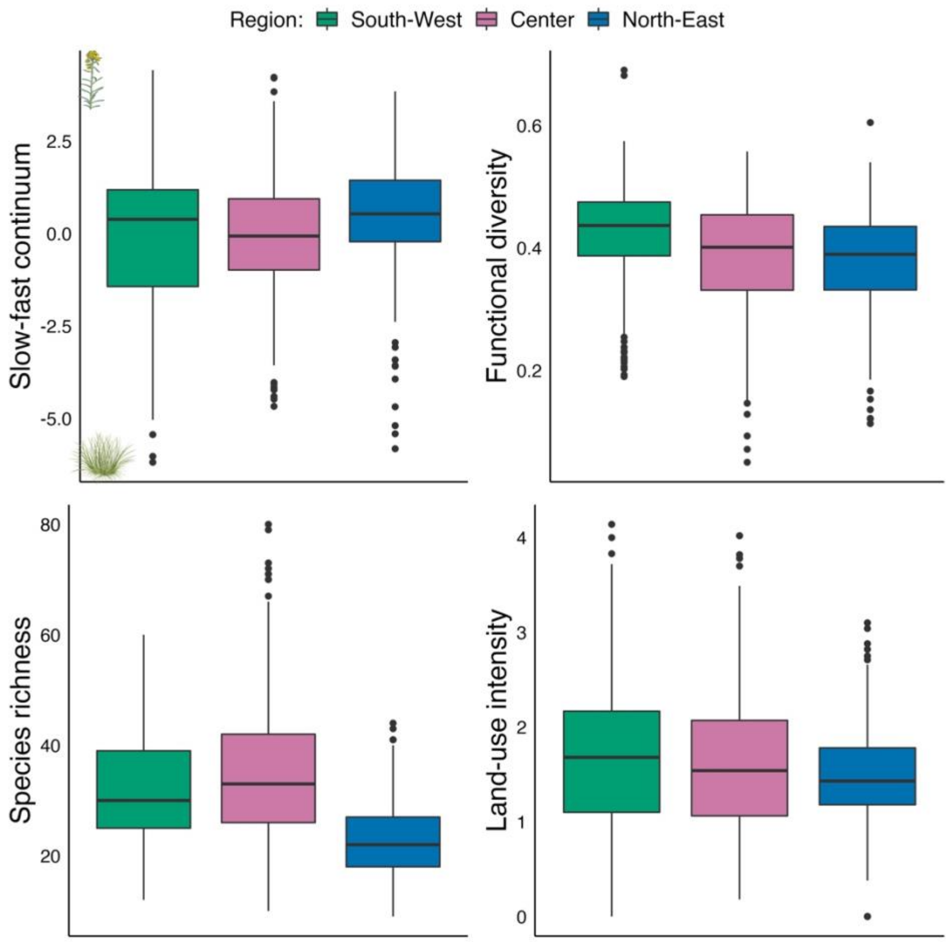

Figure A3.3 - Distribution of slow-fast continuum, functional diversity, species richness and land-use intensity in the three regions of the Biodiversity Exploratories (i.e., South-West, Center and North-East). An example of a slow-growing species (*Festuca* spp.) is located at the bottom end of the slow-fast continuum, while an example of a fast-growing species (*Euphorbia esula*) is located at the top end of the spectrum. Plant icons by Tracey Saxby (Integration and Application Network, ian.umces.edu/media-library), CC BY-SA 4.0 DEED. No changes were made to the original icons.

Appendix A4 - Association between log response ratios, biodiversity and land use over time

Results for LogR (annual log ratio)

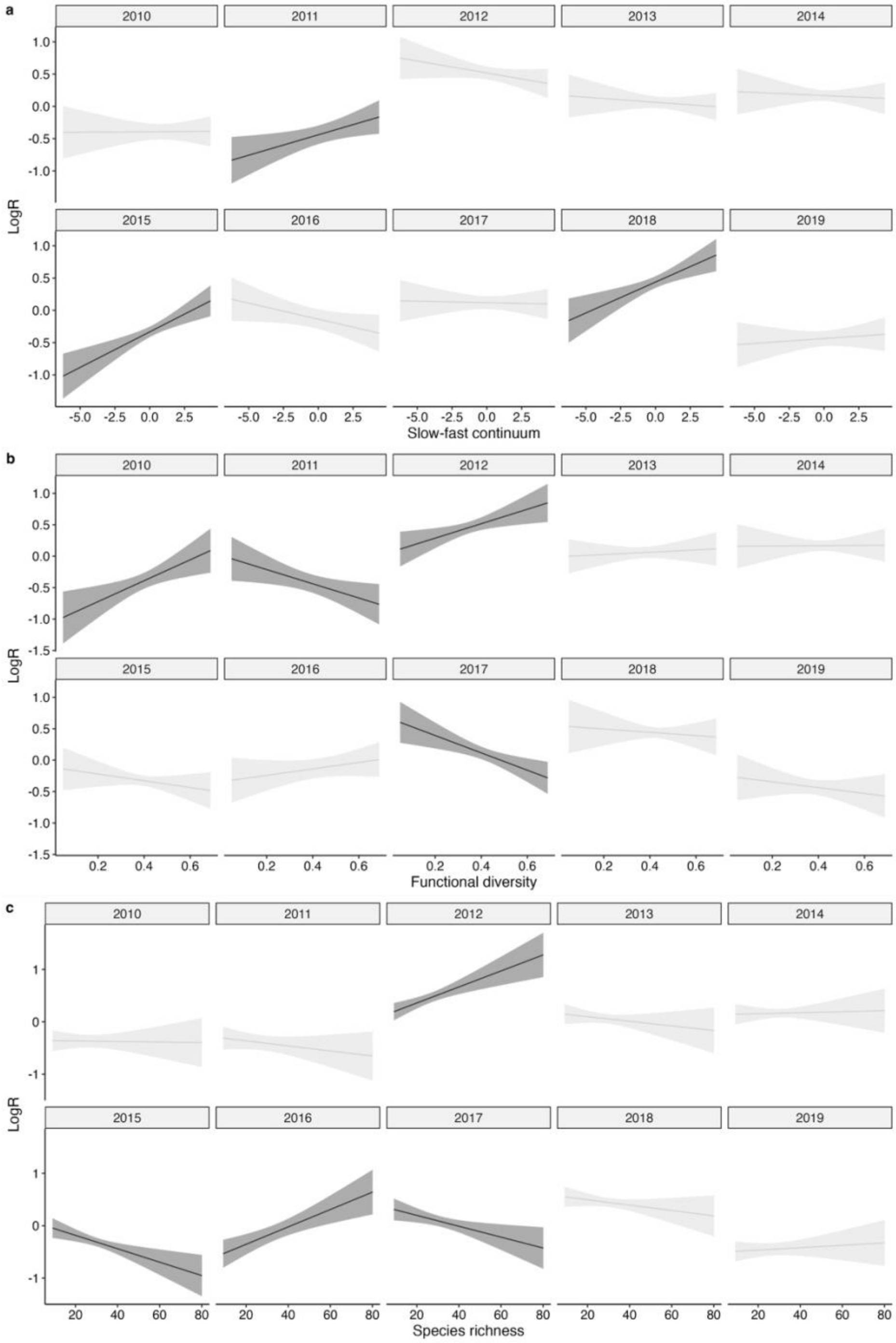

Figure A4.1 - Association between the LogR and slow-fast continuum (panel a), functional diversity (panel b) and species richness (panel c). The relationships between the functional components (slow-fast continuum and functional diversity), species richness and the LogR were analysed in separate models. Dark grey lines and ribbons highlight statistically significant relationships (not statistically significant relationships are reported in light grey).

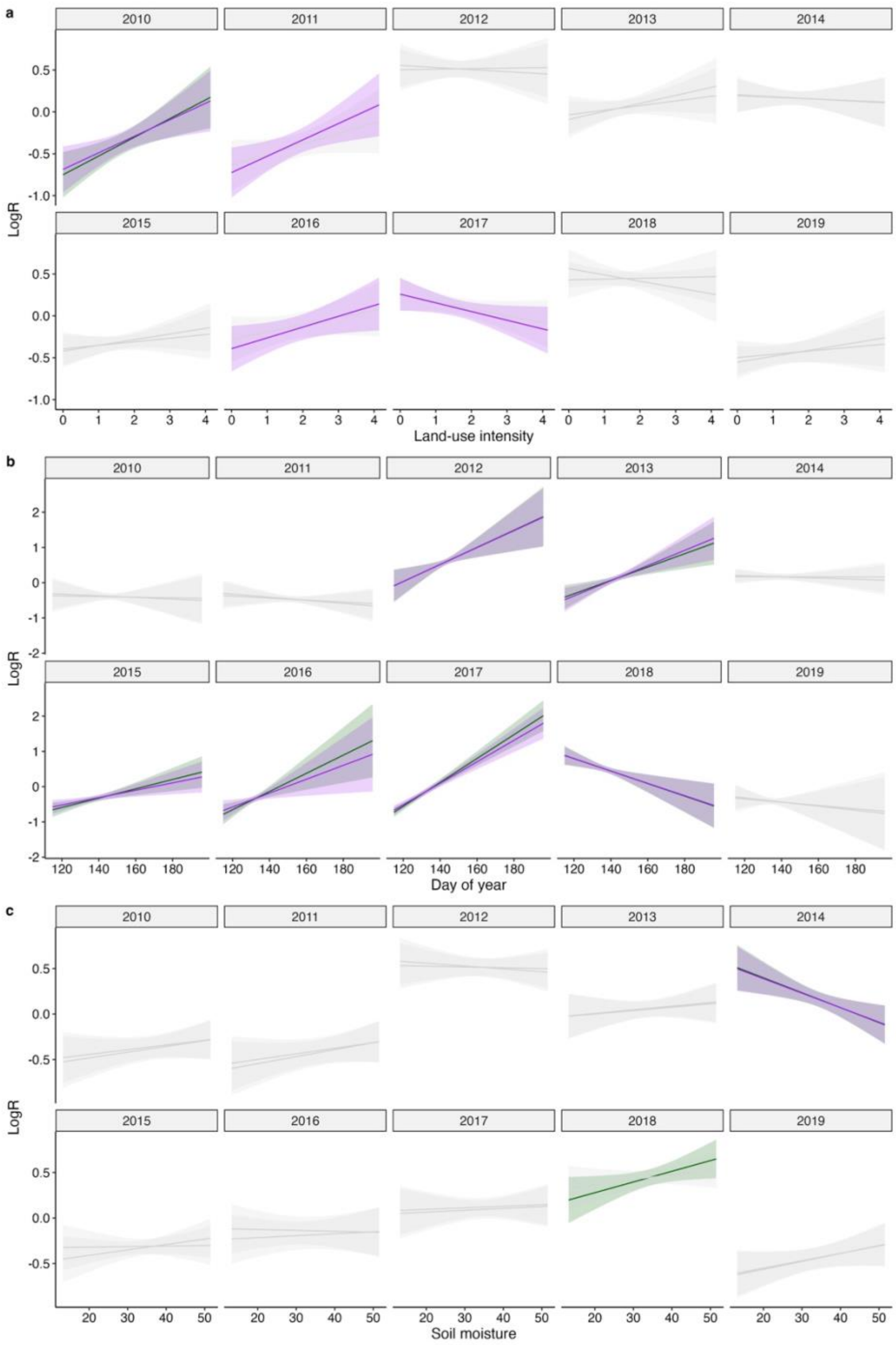

Figure A4.2 - Association between the LogR, land-use intensity (panel a), day of the year (i.e. day of biomass harvest, panel b) and soil moisture (panel c). Land-use intensity, day of year and soil moisture were included in both models including either the functional components (slow-fast continuum and functional diversity) or species richness. Statistically significant relationships are reported in green when detected in the model including the functional components, and in purple if detected in the model including species richness (not statistically significant relationships are reported in light grey).

Results for $LogR_{ref\text{-}plot}$ *(plot reference log ratio)*

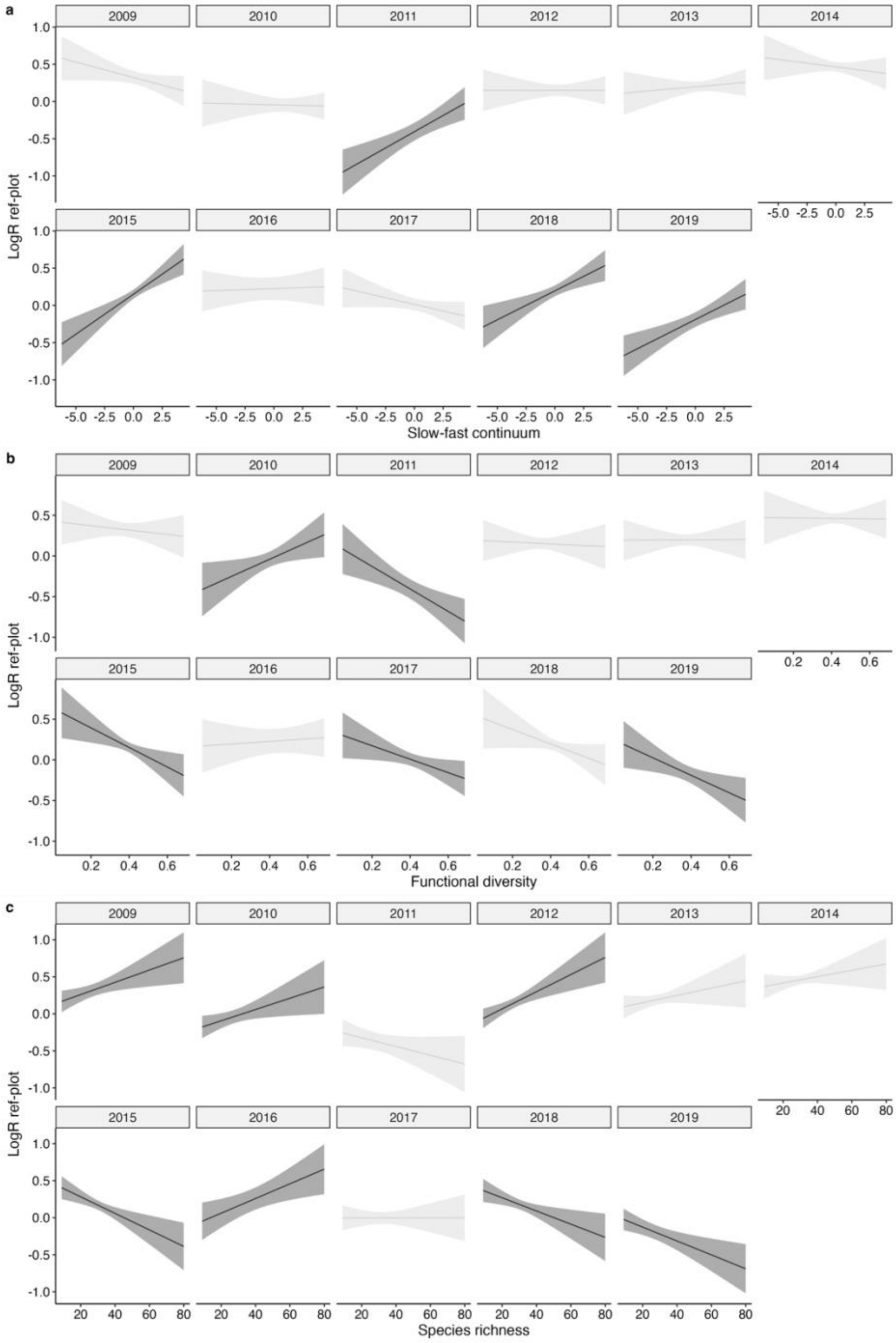

Figure A4.3 - Association between the $LogR_{ref\text{-}plot}$ and slow-fast continuum (panel a), functional diversity (panel b) and species richness (panel c). The relationships between the functional components (slow-fast continuum and functional diversity), species richness and the $LogR_{ref\text{-}plot}$ were analysed in separate models. Dark grey lines and ribbons highlight statistically significant relationships (not statistically significant relationships are reported in light grey).

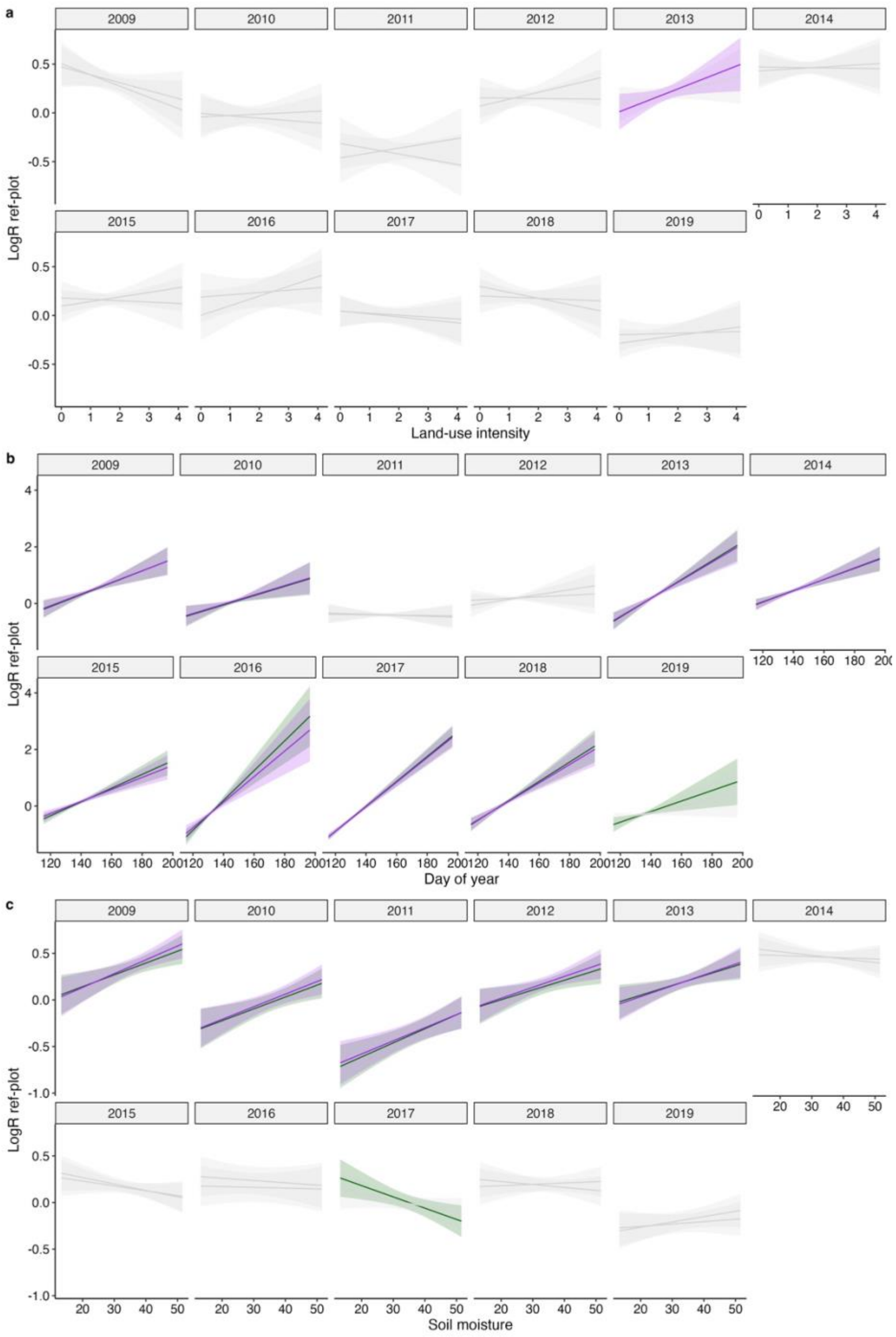

Figure A4.4 - Association between the $\text{LogR}_{\text{ref-plot}}$, land-use intensity (panel a), day of the year (i.e. day of biomass harvest, panel b) and soil moisture (panel c). Land-use intensity, day of year and soil moisture were included in both models including either the functional components (slow-fast continuum and functional diversity) or species richness. Statistically significant relationships are reported in green when detected in the model including the functional components, and in purple if detected in the model including species richness (not statistically significant relationships are reported in light grey).

Appendix A5 - Effect of the interaction between functional composition, functional diversity, species richness and SPEI on recovery

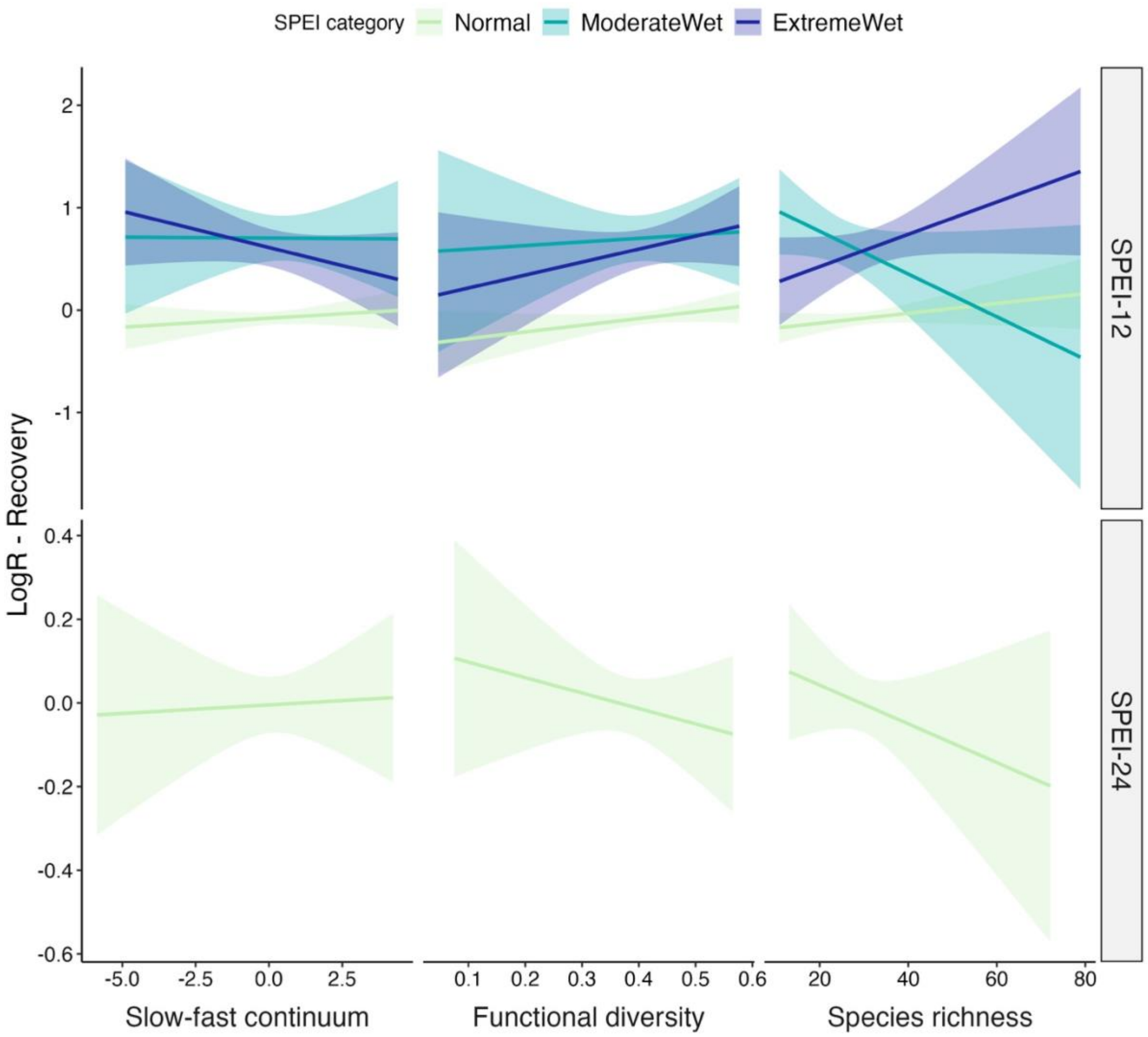

Figure A5.1 - Effect of the interaction between water availability (Standardised Precipitation-Evapotranspiration Index - SPEI categories: normal, moderate and extreme wet) and slow-fast continuum, functional diversity and species richness (columns) on recovery (LogR). Results are reported for the SPEI-12 (annual) and SPEI-24 (biannual) (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. Line colours represent different water availability conditions: from normal water budget (light green) to extreme (blue) wet. Bands represent 95% confidence intervals for conditional means.

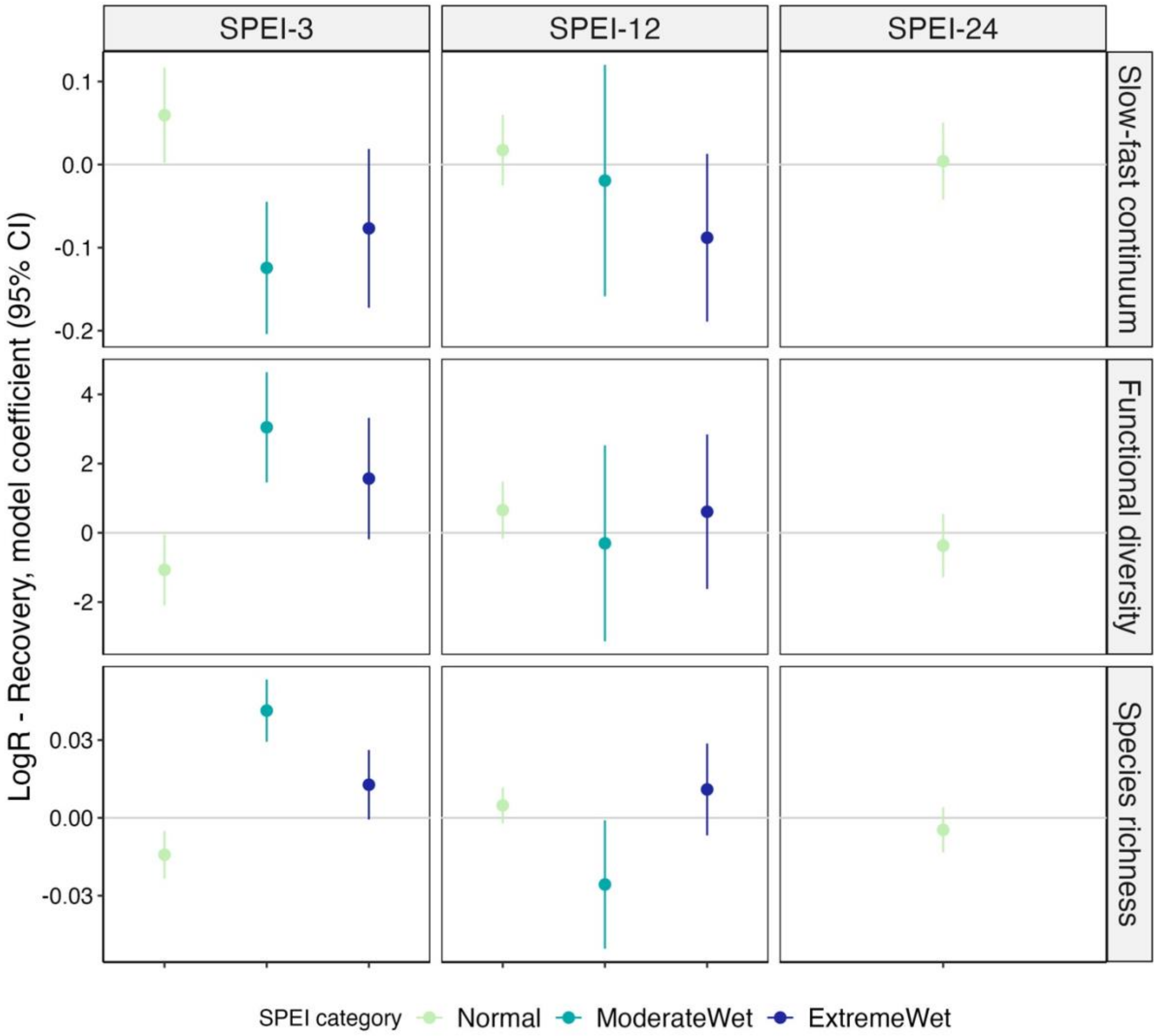

Figure A5.2 - Regression coefficients (and 95% confidence intervals for parameters) for models testing the interaction between slow-fast continuum, functional diversity, and species richness (rows) and the categorical Standardised Precipitation-Evapotranspiration Index (SPEI-3/-12/-24, columns) on recovery. 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.

Table A5.1 - 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: R-squared. Adj-R2: adjusted 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	-0.107 0.064 (0.094)	-0.228 0.052 (<0.001)	0.347 0.067 (<0.001)

ModerateWet	0.185 0.084 (0.029)	0.781 0.123 (<0.001)	-
ExtremeWet	0.076 0.118 (0.522)	0.682 0.099 (<0.001)	-
Central	-0.015 0.118 (0.896)	0.477 0.077 (<0.001)	-0.292 0.113 (0.011)
North-East	-0.137 0.082 (0.097)	-0.038 0.109 (0.728)	-0.777 0.108 (<0.001)
Slow-fast continuum	0.059 0.029 (0.042)	0.017 0.022 (0.420)	0.004 0.023 (0.862)
Functional diversity	-1.069 0.520 (0.041)	0.657 0.420 (0.119)	-0.369 0.464 (0.427)
Land-use intensity	0.002 0.055 (0.967)	0.041 0.052 (0.426)	-0.046 0.068 (0.495)
Day of the year	-0.006 0.006 (0.307)	-0.022 0.004 (<0.001)	0.016 0.008 (0.043)
Soil moisture	-0.002 0.004 (0.620)	0.005 0.005 (0.267)	0.008 0.005 (0.126)
ModerateWet:Slow-fast continuum	-0.124 0.040 (0.002)	-0.019 0.071 (0.786)	-
ExtremeWet:Slow-fast continuum	-0.077 0.049 (0.115)	-0.088 0.051 (0.087)	-
ModerateWet:Funct. diversity	3.048 0.809 (<0.001)	-0.303 1.441 (0.833)	-
ExtremeWet:Funct. diversity	1.568 0.891 (0.080)	0.610 1.135 (0.592)	-
Num. Obs.	293	440	148
R2	0.117	0.292	0.356
Adj-R2	0.076	0.270	0.324

Table A5.2 - 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: R-squared. Adj-R2: adjusted 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	-0.170 0.064 (0.009)	-0.219 0.050 (<0.001)	0.350 0.066 (<0.001)
ModerateWet	0.305 0.079 (<0.001)	0.617 0.140 (<0.001)	-
ExtremeWet	0.034 0.113 (0.767)	0.671 0.099 (<0.001)	-
Central	0.078 0.112 (0.489)	0.431 0.074 (<0.001)	-0.262 0.109 (0.017)
North-East	-0.074 0.095 (0.440)	0.005 0.113 (0.968)	-0.819 0.121 (<0.001)
Species richness	-0.014 0.005 (0.003)	0.005 0.003 (0.169)	-0.005 0.004 (0.296)
Land-use intensity	-0.020 0.053 (0.714)	0.070 0.049 (0.154)	-0.062 0.068 (0.367)
Day of the year	-0.007 0.006 (0.239)	-0.023 0.004 (<0.001)	0.016 0.008 (0.032)
Soil moisture	-0.003 0.004 (0.428)	0.002 0.005 (0.690)	0.007 0.005 (0.164)
ModerateWet:Species richness	0.041 0.006 (<0.001)	-0.026 0.013 (0.042)	-
ExtremeWet:Species richness	0.013 0.007 (0.061)	0.011 0.009 (0.225)	-
Num. Obs.	293	440	148
R2	0.179	0.290	0.358
Adj-R2	0.150	0.273	0.331

Table A5.3 - Models for recovery including slow-fast continuum and functional diversity. Analysis of variance table (Type II F-tests). 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). Sum sq.: sum of squares.

	SPEI-3			**SPEI-12**			**SPEI-24**		
	F	Df	p-value	F	Df	p-value	F	Df	p-value
SPEI	4.1097	2	*	50.8581	2	***	-	-	-
Slow-fast continuum	0.0128	1	n.s.	0.0946	1	n.s.	0.0304	1	n.s.
Functional diversity	0.0647	1	n.s.	3.2644	1	n.s.	0.6334	1	n.s.
Land-use intensity	0.0017	1	n.s.	0.6356	1	n.s.	0.4684	1	n.s.
Region	1.6927	2	n.s.	23.8118	2	***	26.3248	2	***
Day of the year	1.0488	1	n.s.	23.6855	1	***	4.1834	1	*
Soil moisture	0.2463	1	n.s.	1.2375	1	n.s.	2.3704	1	n.s.
SPEI:Slow-fast c.	4.8868	2	**	1.4780	2	n.s.	-	-	-
SPEI:Fun. div.	7.2721	2	***	0.1780	2	n.s.	-	-	-
Residuals (Sum sq.; Df)			63.10; 279			136.77; 426			23.77; 140

Table A5.4 - Models for recovery including species richness. Analysis of variance table (Type II F-tests). 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). Sum sq.: sum of squares.

	SPEI-3			**SPEI-12**			**SPEI-24**		
	F	Df	p-value	F	Df	p-value	F	Df	p-value
SPEI	4.5843	2	*	49.2529	2	***	-	-	-
Species richness	0.0107	1	n.s.	1.3792	1	n.s.	1.0985	1	n.s.
Land-use intensity	0.1343	1	n.s.	2.0401	1	n.s.	0.8174	1	n.s.
Region	0.9339	2	n.s.	18.4116	2	***	24.5290	2	***
Day of the year	1.3941	1	n.s.	27.3520	1	***	4.6851	1	*
Soil moisture	0.6303	1	n.s.	0.1593	1	n.s.	1.9575	1	n.s.
SPEI:Sp. richness	23.0523	2	***	2.9788	2	n.s.	-	-	-
Residuals (Sum sq.; Df)			58.65; 282			137.14; 429			23.69; 141

Appendix A6 - Effect of the interaction between functional composition, functional diversity, species richness and SPEI on resistance

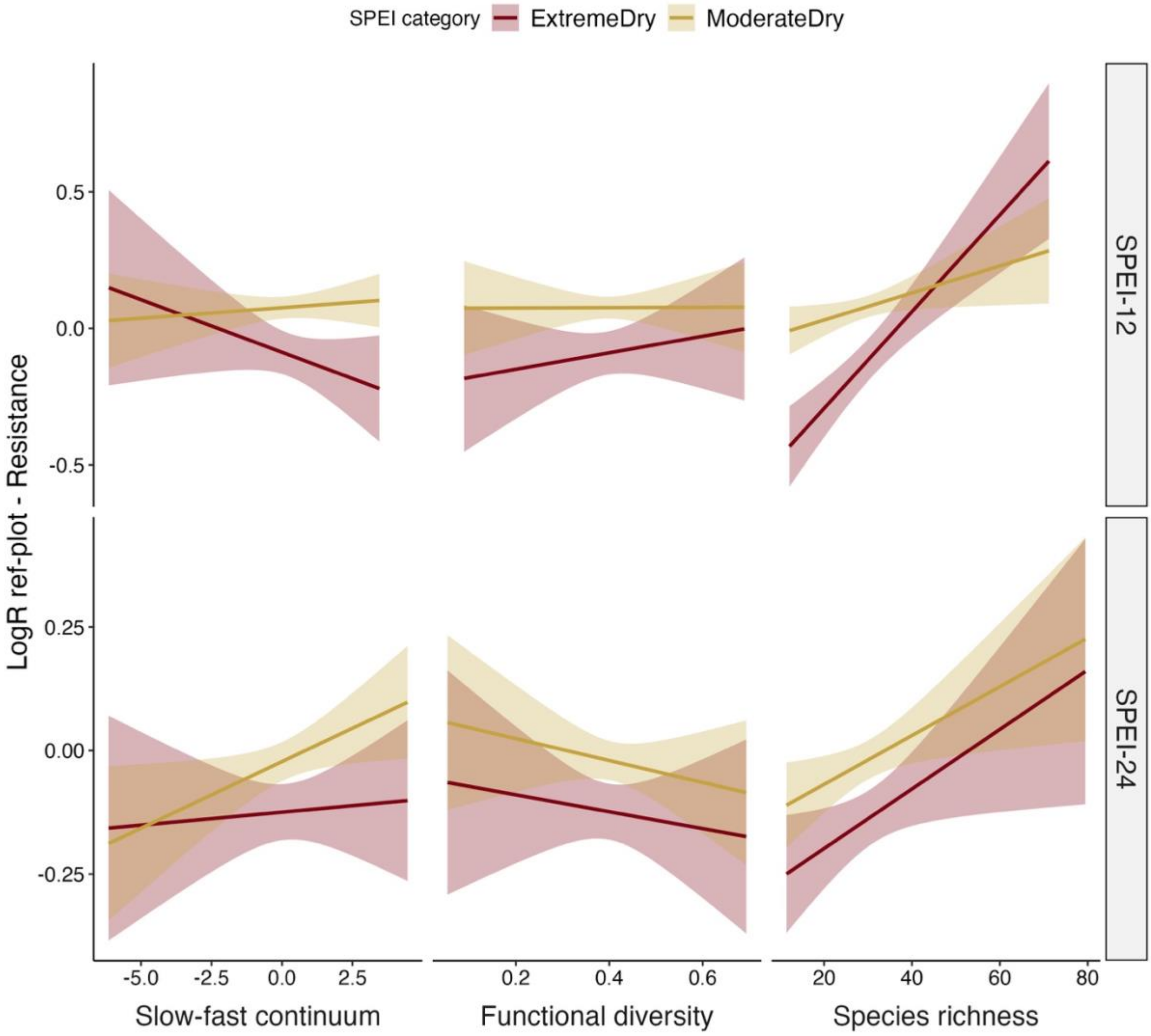

Figure A6.1 - Effect of the interaction between water availability (Standardised Precipitation-Evapotranspiration Index - SPEI categories: moderate and extreme dry) and slow-fast continuum, functional diversity and species richness (columns) on resistance ($\mathrm{LogR}_{\mathrm{ref\text{-}plot}}$). Results are reported for the SPEI-12 (annual) and SPEI-24 (biannual) (see rows) and pertain to models fitted on data from the years featuring either moderate or extreme drought. Line colours represent different water availability conditions: from extreme (reddish) to moderate (ochre) drought. Bands represent 95% confidence intervals for conditional means.

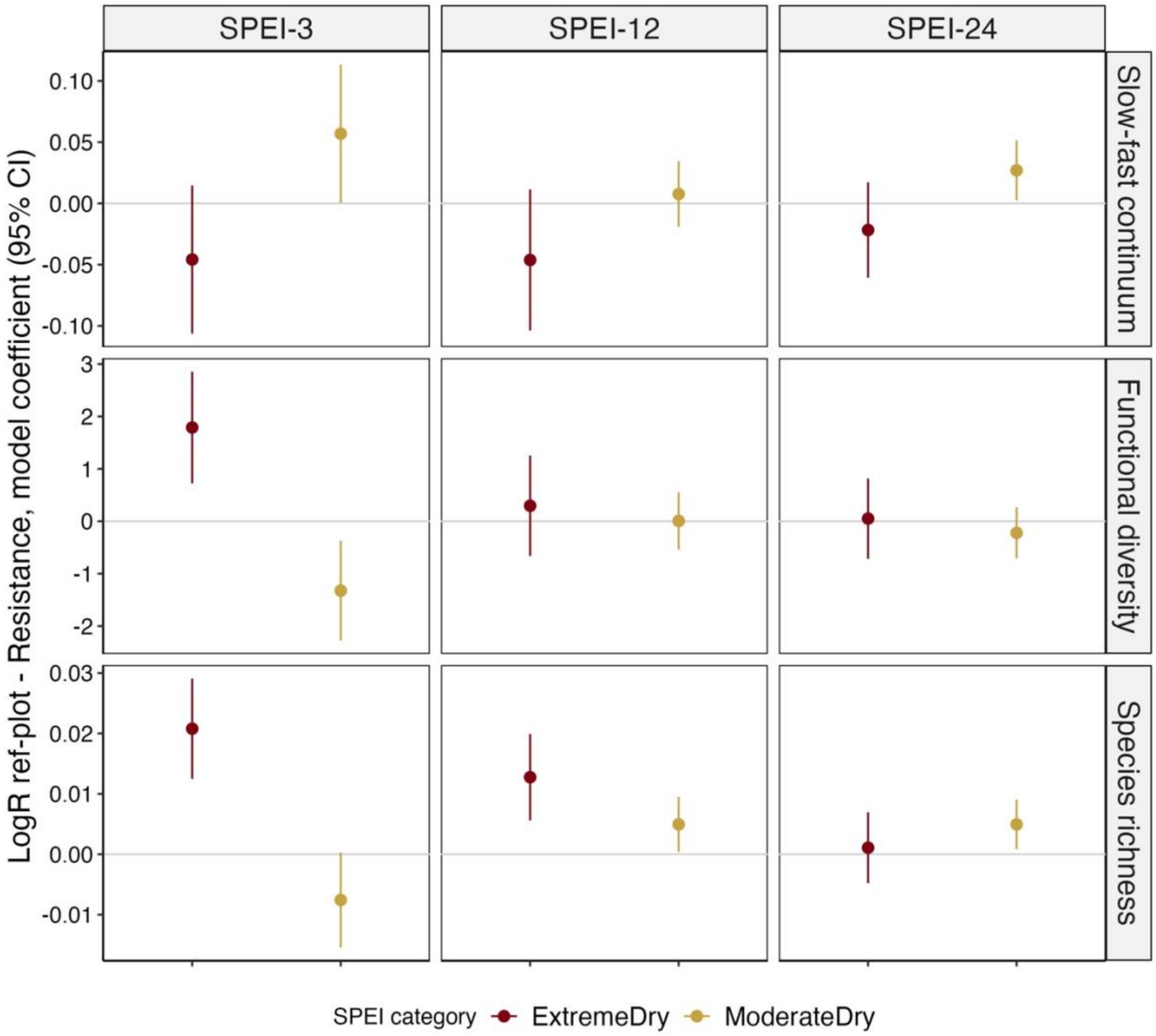

Figure A6.1 - Regression coefficients (and 95% confidence intervals for parameters) for models testing the interaction between slow-fast continuum, functional diversity, and species richness (rows) and the categorical Standardised Precipitation-Evapotranspiration Index (SPEI-3/-12/-24, columns) on resistance. 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.

Table A6.1 - 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: R-squared. Adj-R2: adjusted 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	-0.052 0.064 (0.414)	-0.031 0.034 (0.356)	-0.139 0.029 (<0.001)

ExtremeDry	-0.026 0.049 (0.599)	-0.166 0.048 (<0.001)	-0.103 0.038 (0.007)
Central	-0.025 0.056 (0.656)	0.097 0.049 (0.050)	0.199 0.045 (<0.001)
North-East	0.064 0.058 (0.270)	0.247 0.055 (<0.001)	0.203 0.046 (<0.001)
Slow-fast continuum	0.057 0.029 (0.048)	0.008 0.014 (0.574)	0.027 0.012 (0.030)
Functional diversity	-1.324 0.484 (0.006)	0.007 0.278 (0.981)	-0.222 0.250 (0.375)
Land-use intensity	0.076 0.036 (0.034)	0.029 0.033 (0.376)	0.046 0.028 (0.100)
Day of the year	0.015 0.002 (<0.001)	0.024 0.002 (<0.001)	0.026 0.002 (<0.001)
Soil moisture	0.004 0.003 (0.110)	-0.002 0.003 (0.574)	-0.001 0.002 (0.568)
ExtremeDry:Slow-fast continuum	-0.046 0.031 (0.137)	-0.046 0.029 (0.116)	-0.022 0.020 (0.274)
ExtremeDry:Funct. diversity	1.789 0.543 (0.001)	0.296 0.488 (0.545)	0.051 0.390 (0.897)
Num. Obs.	786	839	836
R2	0.134	0.241	0.254
Adj-R2	0.123	0.232	0.245

Table A6.2 - 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: R-squared. Adj-R2: adjusted 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	-0.117 0.061 (0.056)	-0.059 0.032 (0.064)	-0.167 0.028 (<0.001)

ExtremeDry	0.001 0.048 (0.978)	-0.194 0.047 (<0.001)	-0.119 0.038 (0.002)
Central	-0.054 0.052 (0.298)	0.101 0.045 (0.025)	0.206 0.043 (<0.001)
North-East	0.171 0.058 (0.003)	0.353 0.056 (<0.001)	0.306 0.048 (<0.001)
Species richness	-0.008 0.004 (0.059)	0.005 0.002 (0.032)	0.005 0.002 (0.018)
Land-use intensity	0.168 0.034 (<0.001)	0.088 0.032 (0.005)	0.117 0.027 (<0.001)
Day of the year	0.014 0.002 (<0.001)	0.023 0.002 (<0.001)	0.025 0.002 (<0.001)
Soil moisture	0.006 0.003 (0.023)	0.003 0.003 (0.339)	0.002 0.002 (0.465)
ExtremeDry:Species richness	0.021 0.004 (<0.001)	0.013 0.004 (<0.001)	0.001 0.003 (0.717)
Num. Obs.	786	839	836
R2	0.162	0.263	0.257
Adj-R2	0.153	0.256	0.250

Table A6.3 - Models for resistance including slow-fast continuum and functional diversity. Analysis of variance table (Type II F-tests). SPEI: categorical predictor representing the different SPEI categories for resistance models (ModerateDry and ExtremeDry). n.s.: not significant (i.e., p-value > 0.05). Sum sq.: sum of squares.

	SPEI-3			**SPEI-12**			**SPEI-24**		
	F	Df	p-value	F	Df	p-value	F	Df	p-value
SPEI	1.1700	1	n.s.	14.0853	1	***	7.6475	1	**
Slow-fast continuum	1.9339	1	n.s.	0.0022	1	n.s.	3.5304	1	n.s.
Functional diversity	0.0226	1	n.s.	0.1290	1	n.s.	0.9686	1	n.s.
Land-use intensity	4.5242	1	*	0.7833	1	n.s.	2.7070	1	n.s.
Region	1.7542	2	n.s.	10.5229	2	***	13.1350	2	***
Day of the year	66.4308	1	***	164.3991	1	***	159.6291	1	***
Soil moisture	2.5551	1	n.s.	0.3171	1	n.s.	0.3266	1	n.s.
SPEI:Slow-fast c.	2.2137	1	n.s.	2.4793	1	n.s.	1.1973	1	n.s.
SPEI:Fun. div.	10.8571	1	**	0.3670	1	n.s.	0.0169	1	n.s.
Residuals (Sum sq.; Df)			200.29; 775			200.27; 828			152.60; 825

Table A6.4 - Models for resistance including species richness. Analysis of variance table (Type II F-tests). SPEI: categorical predictor representing the different SPEI categories for resistance models (ModerateDry and ExtremeDry). n.s.: not significant (i.e., p-value > 0.05). Sum sq.: sum of squares.

	SPEI-3			**SPEI-12**			**SPEI-24**		
	F	Df	p-value	F	Df	p-value	F	Df	p-value
SPEI	1.0403	1	n.s.	18.4705	1	***	9.6967	1	**
Species richness	15.2472	1	***	14.8979	1	***	8.0703	1	**
Land-use intensity	24.3099	1	***	7.7512	1	**	19.0224	1	***
Region	9.1697	2	***	20.4849	2	***	23.4911	2	***
Day of the year	53.5676	1	***	159.2213	1	***	144.4189	1	***
Soil moisture	5.2270	1	*	0.9146	1	n.s.	0.5335	1	n.s.
SPEI:Sp. richness	24.1568	1	***	12.2257	1	***	0.1314	1	n.s.
Residuals (Sum sq.; Df)			193.98; 777			194.56; 830			152.02; 827