

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

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23

24 **Abstract**

25

26 1. How biodiversity underpins ecosystem resistance (i.e., ability to withstand environmental perturbations) and recovery  
27 (i.e., ability to return to a pre-perturbation state) and thus stability under extreme climatic events is a timely question in  
28 ecology. To date, most studies have focused on the role of taxonomic diversity, neglecting how community functional  
29 composition and diversity beget stability under exceptional climatic conditions. In addition, land use potentially  
30 modulates how biodiversity and ecosystem functions respond to extreme climatic conditions.

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

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

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

43 **Running title:** grassland stability under extreme drought

44 **Keywords:** resistance, recovery, plant biomass, standardised precipitation-evapotranspiration index, land-use  
45 intensity, extreme climatic events, ecosystem function and services.

## 46 1. Introduction

47

48 A growing effort has been devoted to understanding how ecosystems respond to *extreme climatic events* (hereafter ECE)  
49 such as heat waves and/or droughts (De Boeck et al. 2018). The frequency, magnitude, and impact of ECE will increase  
50 in the near future (EEA 2017), so determining the capacity of ecosystems to respond to these phenomena is a pressing  
51 task (Smith 2011; De Boeck et al. 2018). Extreme climatic events can strongly impact the stability of ecosystem functions  
52 or nature contributions to people (Diaz et al. 2018; Xu et al. 2019; Bastos et al. 2020; Xu et al. 2020; Domeisen et al.  
53 2022). Ideally, to withstand ECE, ecosystems should be able to (i) maintain their properties under strong environmental  
54 perturbations (i.e., show high resistance), and to (ii) quickly recover their functioning after environmental perturbations  
55 (i.e., show high recovery) (Isbell et al. 2015; de la Riva et al. 2017; Neilson et al. 2020). Ecosystems with low resistance  
56 and recovery are expected to be more vulnerable to the effect of ECE (Oliver et al. 2015). Which biological features make  
57 ecosystems resist to and recover from ECE is, however, still a subject of research (Mahecha et al. 2022).

58

59 Under average climate, biodiversity should stabilise ecosystem functions over time, although the paradigm  
60 ‘biodiversity begets stability’ has long been debated (Lepš et al. 1982; McCann 2000; Diaz & Cabido 2001; Tilman et al.  
61 2006; Li et al. 2022). In principle, biodiversity can support stability via several mechanisms related to species richness,  
62 abundance, and temporal fluctuation of population sizes. More diverse communities can be more stable because they  
63 can harbour species with different responses to environmental fluctuations, which insures ecosystems against loss of  
64 functions (i.e., ‘insurance effect’; Ives et al. 2000; McCann 2000; Diaz & Cabido 2001). However, in line with the ‘mass  
65 ratio hypothesis’ (Grime 1998), species’ contribution to stability is proportional to their relative abundance, so that few  
66 but abundant species can determine stability (i.e., ‘dominant species effect’; Lisner et al. 2022). Apart from community  
67 composition, asynchronous fluctuations of individual species’ population sizes can also stabilise ecosystem functions  
68 (Allan et al. 2011; Lepš et al. 2019). Empirical and experimental studies found that taxonomic diversity has a positive  
69 (Tilman et al. 1994, Isbell et al. 2015), negative (Pfisterer et al. 2002; Fischer et al. 2016), or no effect (Caldeira et al.  
70 2005; Dormann et al. 2017; Kreyling et al. 2017; De Boeck et al. 2018) on resistance, recovery, or both under ECE.  
71 Somewhat surprisingly, the role of community functional composition and diversity has been poorly investigated in the  
72 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.  
73 2017). Yet, accounting for it may explain how biodiversity begets stability under ECE, as functional traits, namely any  
74 biological feature measurable at the individual level (Violle et al. 2007), can reveal a mechanistic link between ecosystem  
75 functioning and environmental variability (Diaz & Cabido 2001; Suding et al. 2008; Polley et al. 2013; Cadotte 2017).

76

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

92 traits, i.e. traits producing an impact on ecosystem processes (Diaz & Cabido 2001; de Bello et al. 2021). Nevertheless,  
93 both measures of trait composition and diversity can be important predictors of ecosystem resistance and recovery under  
94 ECE (Griffin-Nolan et al. 2019).

95  
96 Here we analysed how multiple biodiversity components (functional composition, functional diversity and  
97 taxonomic diversity) support the resistance and recovery of plant biomass of managed grasslands undergoing extreme  
98 drought. Specifically, by measuring year-to-year changes in plant aboveground biomass, we derived yearly estimates of  
99 resistance and recovery, which we related to the functional and taxonomic characteristics of plant communities. We  
100 tested this in a gradient of land-use intensity representing realistic management conditions of central European  
101 grasslands. Our aims were to: (i) assess how functional composition, functional diversity, and taxonomic diversity  
102 mediate plant biomass fluctuation along a gradient of land-use intensity; (ii) test whether the association between  
103 biodiversity, biomass and land use changes under exceptional climatic conditions (i.e., moderate-to-extreme drought,  
104 hereafter also collectively referred to as severe drought); and (iii) investigate whether and how biodiversity-related  
105 mechanisms mediated by functional traits, such as dominant species and insurance effects, support ecosystem resistance  
106 and recovery during and after severe drought. To this end, we analysed an 11-year grassland time-series of field-collected  
107 plant biomass, biodiversity and land-use data from Germany.

## 108 **2. Materials and methods**

### 109 **2.1. Data from the Biodiversity Exploratories**

110  
111 We gathered data on vegetation characteristics and land-use intensity from the German Biodiversity Exploratories, a  
112 long-term project aiming at exploring and monitoring the relationships among land use, biodiversity, and ecosystem  
113 functioning (Fischer et al. 2010). The Biodiversity Exploratories (hereafter BE) consist of a network of permanent plots  
114 in three regions, which cover a wide latitudinal extent: Schorfheide-Chorin (hereafter North-East; North-East Germany:  
115 52°470 to 53°130N; 13°230 to 14°090E); Hainich-Dün (hereafter Central; Central Germany: 50°940 to 51°380N;  
116 10°170 to 10°780E); and Schwäbische Alb (hereafter South-West; South-West Germany: 48°340 to 48°530N; 9°180 to  
117 9°600E) (Figure 1; also see Fisher et al. 2010 for a thorough description of the three regions). The BE regions span a wide  
118 range of altitude (South-West: 460-860 m; Central: 285-550 m; North: 3-140 m), as well as a considerable range of  
119 precipitation (South-West: 700-1000 mm; Middle: 500-800 mm; North-East: 500-600 mm) and temperature (South-  
120 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  
121 were randomly placed within larger management units and have been surveyed yearly since 2008 to measure  
122 aboveground plant biomass (from 2009), and collect data on several biotic (e.g., plant composition based on estimated  
123 cover), abiotic (e.g., soil moisture) and anthropogenic (e.g., land-use intensity) variables.

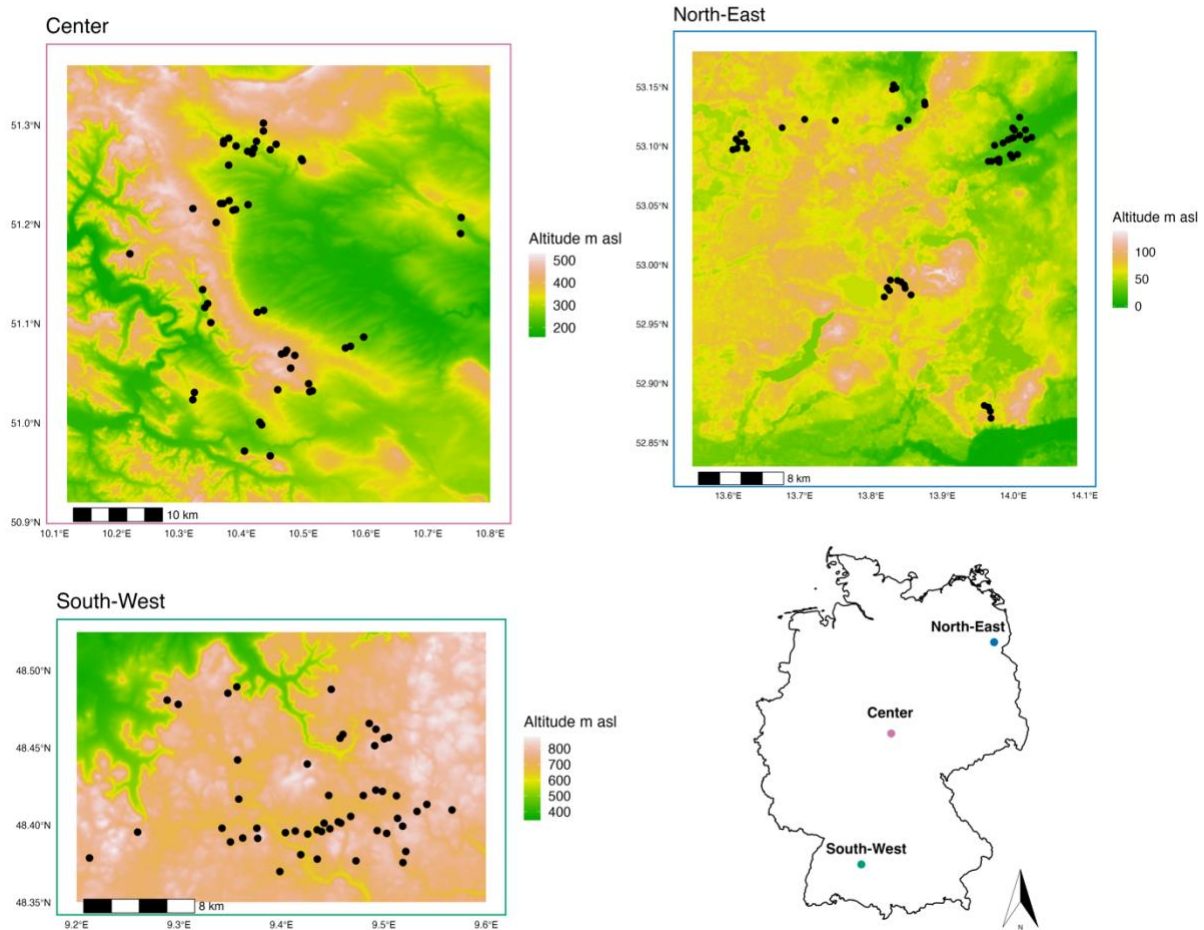


Figure 1 - Study area. Panels show the location of grassland plots in each region of the Biodiversity Exploratories overlaid to an altitude layer (m asl: metres above the sea level).

### 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: 142<sup>nd</sup>, 138<sup>th</sup>-147<sup>th</sup> in South-West; 137<sup>th</sup>, 134<sup>th</sup>-141<sup>st</sup> in Central; 141<sup>st</sup>, 137<sup>th</sup>-145<sup>th</sup> 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:

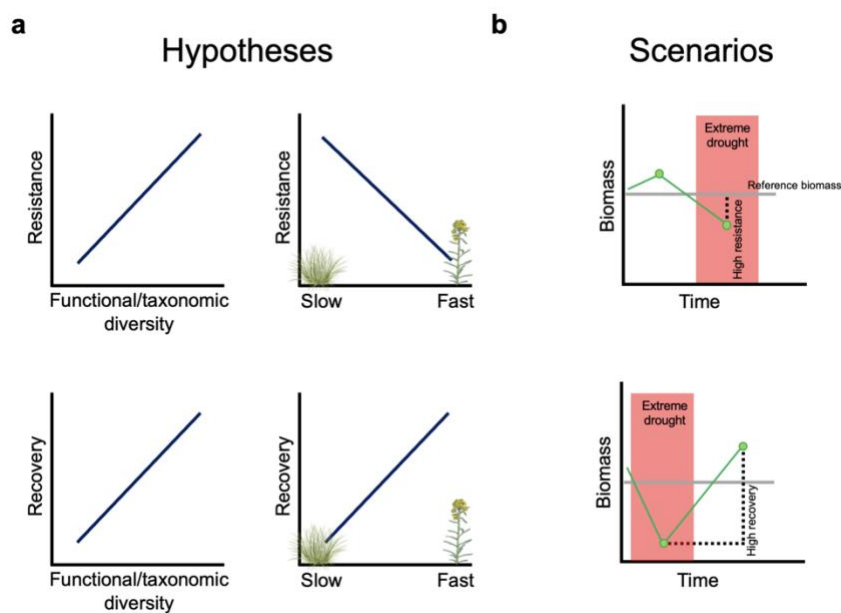
$$\text{LogR} = \ln\left(\frac{\text{biomass}_{\text{plot } i, \text{year } t}}{\text{biomass}_{\text{plot } i, \text{year } t-1}}\right),$$

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

153  
 154 
$$\text{LogR}_{\text{ref-plot}} = \ln\left(\frac{\text{biomass}_{\text{plot } i, \text{year } t}}{\text{median biomass}_{\text{plot } i}}\right),$$

155  
 156 where  $\text{median biomass}_{\text{plot } i}$  is the median value of the biomass collected in  $\text{plot } i$ , over the time-series. This measure was used  
 157 to quantify the year specific biomass budget of  $\text{plot } i$  with respect to the plot reference value (i.e.,  $\text{median biomass}_{\text{plot } i}$ ).  
 158 When focusing on years featuring severe drought, we used the  $\text{LogR}_{\text{ref-plot}}$  (hereafter also referred to as **plot reference**  
 159 **log ratio**) to measure grassland resistance.

160  
 161 See Figure 2 for the hypothesised association between biomass recovery, resistance, biodiversity and slow- vs. fast-  
 162 growing strategies, and for scenarios of recovery and resistance arising under extreme drought.  
 163



164  
 165  
 166 Figure 2 - Hypotheses about the association between biomass recovery, resistance, biodiversity and slow- vs. fast-growing strategies  
 167 (panel a), and scenarios of recovery and resistance under extreme drought (panel b). Plant icons (*Festuca* spp. on the 'slow side' and  
 168 *Euphorbia esula* on the 'fast' side) by Tracey Saxby (Integration and Application Network, ian.umces.edu/media-library), CC BY-SA  
 169 4.0 DEED. No changes were made to the original icons.

170  
 171 **2.1.2. Plant community characteristics**

172 We calculated several characteristics of grassland communities:

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

175 **Functional traits.** We used multiple above-ground traits to summarise the functional composition and  
 176 diversity of grassland communities. These were: plant height (m); leaf dry matter content (mg/g); specific leaf area  
 177 (m<sup>2</sup>/kg); seed mass (mg); leaf nitrogen and leaf phosphorus content (mg/g). Plant height is associated with  
 178 competitiveness for light and the overall plant fecundity; specific leaf area (hereafter SLA), leaf dry matter content  
 179 (hereafter LDMC), leaf nitrogen and leaf phosphorus content are related to resource acquisition, growth and

180 photosynthetic rate; seed mass is associated with plant persistence and dispersal capacity (Perez-Harguindeguy et al.  
181 2013). Data on SLA and LDMC are from both the BE and TRY datasets, while data for all the other traits are from the  
182 TRY database (Kattge et al. 2020). We preferred measured values from the BE (available for SLA and LDMC, and for a  
183 total of 317 species; Breitschwerdt et al. 2018; Prati et al. 2021) and, when these were not available, we filled the gaps  
184 with trait data from TRY, cleaned and aggregated at the species level (Neyret & Manning 2023).

185 **Functional composition.** As a measure of functional composition, for each plot, we computed the (year-  
186 specific) community weighted mean of each of the above-ground plant traits, and performed a principal component  
187 analysis (PCA) on their correlation matrix. We used the first axis of the PCA, which explained 48% of the variance, as a  
188 proxy of the leaf-economic spectrum (hereafter *slow-fast continuum*) (see Figure A1, Appendix A1 for supplementary  
189 information on the PCA). Positive values of the slow-fast continuum were associated with plant communities  
190 dominated by species with acquisitive strategies (fast-growing species), whereas negative values represented plant  
191 communities characterised by species with conservative strategies (slow-growing species). Note that, to compute  
192 community weighted means, trait values were weighted by species cover, which we measured (on a percentage scale) in  
193 the same 4 m x 4 m sub-quadrats where we also recorded species richness.

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

205

### 206 2.1.3. Land-use intensity and soil moisture

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

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

221

## 222 2.2. Data on annual drought

223 To analyse the response of grasslands to different drought severities, we gathered data from the Global SPEI database  
224 (SPEIbase, version 2.6; Vicente-Serrano et al. 2010). We downloaded the **Standardised Precipitation-  
225 Evapotranspiration Index** (hereafter **SPEI**; data available until 2018), which is a multiscalar, site-specific drought

226 indicator of deviations from average water balance. In contrast to other drought indices (e.g., the Standardised  
227 Precipitation Index), the SPEI not only accounts for precipitation, but also incorporates the influence of temperature  
228 on drought severity (see Vicente-Serrano et al. 2010). The SPEI has been used in several studies assessing the effect of  
229 drought on plant biomass and ecosystem stability (Isbell et al. 2015; Ivits et al. 2016; Slette et al. 2019; Matos et al. 2020;  
230 Chen et al. 2022). Also, it is expressed in z-scores, which facilitates the classification of drought events of different  
231 magnitude (see Isbell et al. 2015). For example, an annual value of SPEI equal to (or lower than) -1.28 indicates that the  
232 associated annual drought event (or a more extreme one if lower than -1.28) is likely to occur once every 10 years.

233 We considered SPEI aggregating data on cumulative water balance over 3, 12 and 24 months (hereafter SPEI-  
234 3/-12/-24) before the peak of biomass growth (i.e., May). This allowed analysing resistance and recovery from drought  
235 measured at multiple time-scales, and, in turn, to assess biomass response to short- and long-term drought. The SPEI  
236 values for all time-scales were obtained for each year of the time-series (see Figure A2, Appendix A2 for SPEI-3/-12/-24  
237 temporal trend). Data on SPEI were gathered as raster layers of 0.5 degrees resolution from which we extracted, separately  
238 for each region, the index value at the geographical centroid of the ensemble of vegetation plots in a region.

239 Following Isbell et al. (2015), continuous SPEI-3/-12/-24 were categorised to extreme drought (SPEI < -1.28);  
240 moderate drought (-1.28 <= SPEI <= -0.67); normal water balance (-0.67 < SPEI < 0.67); moderate wetness (0.67 <=  
241 SPEI <= 1.28); extreme wetness (SPEI > 1.28). Table A2 (Appendix A2) provides the numbers of dry (or wet) years in  
242 each time series and BE region.

243

## 244 2.3. Analysis of grassland resistance and recovery

245

### 246 2.3.1. Time-series analysis of plant biomass change

247 Using generalised least squares models, we analysed how the LogR and LogR<sub>ref-plot</sub> related to land-use intensity, slow-fast  
248 continuum, functional diversity, day of the year (day of biomass harvest), soil moisture and plant species richness over  
249 the time-series. Also, we included a categorical variable with three levels, each representing one of the three BE regions,  
250 to account for mean region-specific differences. Species richness was correlated with slow-fast continuum (mean Pearson  
251 correlation computed over the time-series: -0.43), functional diversity (0.51), and land-use intensity (-0.40). Therefore,  
252 we analysed species richness separately, i.e. repeating analyses including species richness in the models and excluding  
253 slow-fast continuum and functional diversity.

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

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

269 We fitted generalised least squares models using the *nlme* R package (Pinheiro et al. 2021). All numeric (non-  
270 categorical) predictors were centred before fitting the models. Models' predictions on the association between the log  
271 response ratios *vs.* slow-fast continuum, functional diversity, species richness and land-use intensity were compared with



272 the observed relationship between these predictors and biomass. This allowed determining whether the former  
273 predictors related differently to overall biomass and biomass change (here measured by the two log response ratios).  
274 Models' predictions were computed using the *effects* R package (Fox & Weisberg 2018, 2019).

275

### 276 **2.3.2. Effect of functional composition, functional and taxonomic diversity on resistance and recovery**

277 To test for the effect of community functional composition and diversity, and taxonomic diversity on resistance and  
278 recovery under drought, we fitted linear models including the statistical interaction between the functional and  
279 taxonomic components and the categorical SPEI. To analyse recovery (models for the annual log ratio, LogR), we used  
280 observations from the year immediately after one or more consecutive events of either moderate or extreme drought.  
281 This way we assessed whether and how functional composition, and functional and taxonomic diversity of plant  
282 communities support recovery of plant biomass after severe droughts, and we tested this under different conditions of  
283 water availability (from normal water budget to extreme wetness). For the resistance analysis (models for the plot  
284 reference log ratio,  $\text{LogR}_{\text{ref-plot}}$ ), we focused on observations from years of moderate or extreme drought, which allowed  
285 us to examine the role of functional composition, functional and taxonomic diversity in buffering grasslands under water  
286 shortage.

287 We fitted separate models for the different SPEI time-scales, i.e. SPEI-3/-12/-24. As done in 2.3.1. analyses  
288 were carried out separately for functional composition and diversity, and for species richness. Land-use intensity, day of  
289 the year, soil moisture and region were included as predictors in the model but were excluded from the interaction with  
290 the categorical SPEI. By including region as a predictor in the models, we allowed for mean region-specific differences  
291 to be accounted for. At the same time, we assumed that the interaction between biodiversity components and drought  
292 intensity, as well as the association between recovery, resistance and the other predictors, was the same within each  
293 region. This way we focused on the overall trend of the relationship between recovery, resistance, biodiversity and  
294 drought. Note that according to the categorical SPEI-24, events of moderate or extreme drought were followed only by  
295 years of normal water budget conditions. Therefore, recovery was analysed under a lower number of water availability  
296 conditions than for SPEI-3 and -12. All numeric (non-categorical) predictors were centred before fitting the models.  
297 Model assumptions of normality, linearity and homoscedasticity were assessed using the *performance* R package  
298 (Lüdecke & Mattan 2021). Models' predictions were computed using the *effects* R package (Fox & Weisberg 2018,  
299 2019).

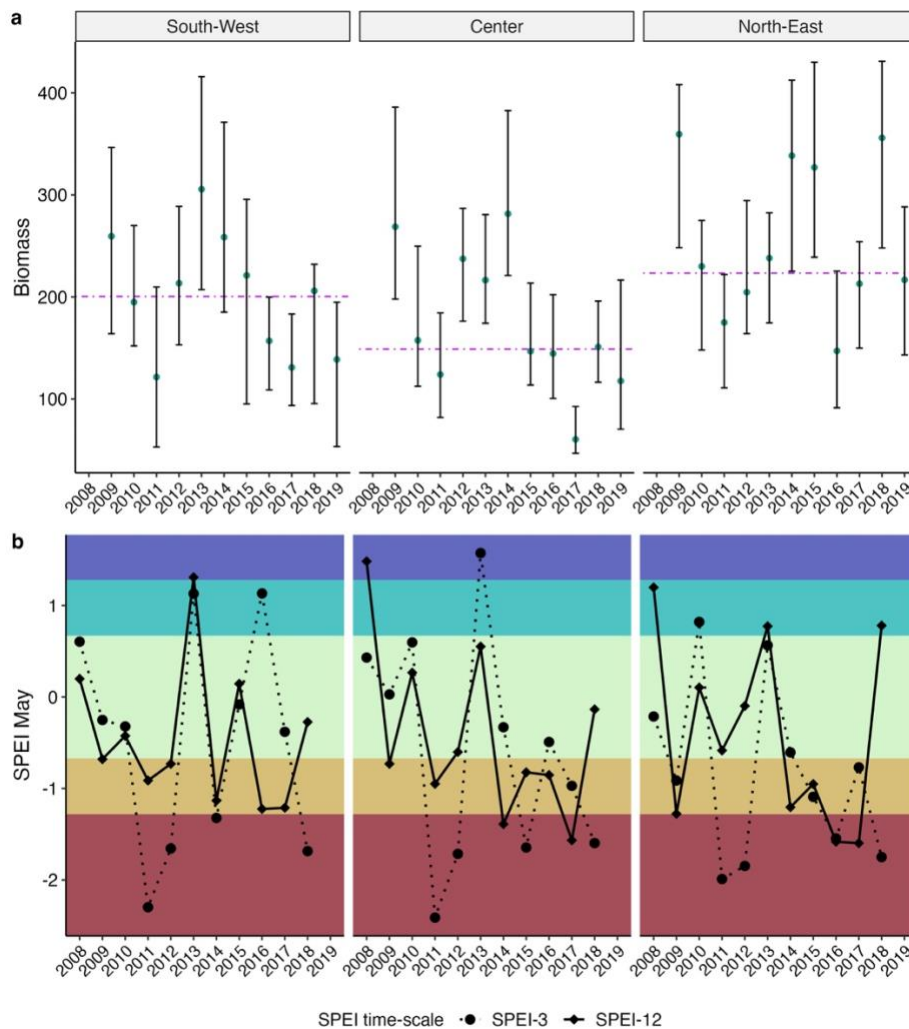
300

## 301 **3. Results**

302

303 The three regions showed similar temporal trends in plant biomass production, which, overall, was higher in South-West  
304 and North-East than in Central Germany over the time-series (Figure 3a). In Central and North-East Germany plant  
305 biomass production was highest in 2009 and 2014, while in the South-West it was highest in 2013. According to all SPEI  
306 time-scales, 2009, 2013 and 2014 either featured or were preceded by average or above average water budgets in all regions  
307 (Figure 3b, Figure A2, Appendix A2). Biomass production was lower than the overall trend in all regions in 2011 and  
308 2017 (Figure 3a), both years which featured severe droughts at different time-scales (Figure 3b, Figure A2, Appendix  
309 A2).

310



311  
 312 Figure 3 - Temporal trends in biomass (panel a) and Standardised Precipitation-Evapotranspiration Index (panel b) in the three  
 313 regions of the Biodiversity Exploratories. Panel a) Green points represent median biomass collected in each year in each region (South-  
 314 West, Center and North-East). Bars delimit the interquartile range of biomass values and the purple dotted lines represent the regional  
 315 median biomass across the time-series. Panel b) Temporal trend of 3- and 12-months SPEI. Temporal trend for SPEI-24 is reported  
 316 in Appendix A2 (Figure A2). Colours of horizontal bands are associated with water budget conditions, with ochre and reddish colours  
 317 representing moderate and extreme drought, respectively (following the classification of continuous SPEI values into categories of  
 318 water availability conditions reported in 2.2.).

319  
 320 **3.1. Association between biomass, biomass change, biodiversity and land use over time**

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

327 The sign of the relationships between  $\text{LogR}$  as well as  $\text{LogR}_{\text{ref-plot}}$  and the predictors varied across the years. In  
 328 particular, in the years 2009, 2010, 2012 and 2016 (Figures A4.1,3, Appendix A4), the two log response ratios exhibited  
 329 an opposite relationship with the slow-fast continuum, functional diversity and species richness to the overall  
 330 relationship observed for biomass (Figure A3.1, Appendix A3). This means that the three biodiversity components  
 331 affected biomass change in these years differently than overall biomass growth.

332 Results for the annual (LogR) and plot reference log ratio ( $\text{LogR}_{\text{ref-plot}}$ ) suggest that grasslands with different  
333 functional composition, functional diversity and species richness responded differently to drought. Concerning the  
334 LogR, both species rich and functionally diverse communities produced more biomass in 2012, which featured (and  
335 was preceded by) extremely dry conditions in all three regions according to the SPEI-3, while having an overall normal  
336 water budget according to SPEI-12 (Figure 3b). In 2017, which featured severe droughts in all regions according to all  
337 SPEI time-scales, land-use intensity negatively affected the LogR (although significantly only in the model including  
338 species richness), indicating that communities subject to low land-use intensity produced more (or lost less) biomass in  
339 that year than in the previous year. Overall, vegetation plots harvested later in the sampling season were predicted to have  
340 higher LogR values (Figure A4.2, Appendix A4), while soil moisture seemed not to consistently affect the LogR.

341 In 2009, 2010, 2012 and 2016, the  $\text{LogR}_{\text{ref-plot}}$  correlated positively with species richness, indicating that species  
342 rich communities produced more (or lost less) biomass (with respect to the plot reference median biomass) than species  
343 poor communities (Figure A4.3, Appendix A4). According to SPEI-12, all regions experienced moderate drought in  
344 2009, while they all undergone extreme drought in 2012 (according to SPEI-3) and moderate-to-extreme drought in  
345 2016 (according to SPEI-12) (Figure 3b). Land-use intensity significantly (and positively) affected the  $\text{LogR}_{\text{ref-plot}}$  only  
346 in 2013, and exclusively in the model including species richness. As observed for the LogR, vegetation plots harvested  
347 later in the sampling season were predicted to have higher  $\text{LogR}_{\text{ref-plot}}$  values (Figure A4.4, Appendix A4). Finally, soil  
348 moisture positively affected the  $\text{LogR}_{\text{ref-plot}}$  from 2009 to 2013, meaning that vegetation plots located in wetter areas  
349 produced more (or lost less) biomass (with respect to the plot reference median biomass) in these years.

350  
351

### 352 **3.2. Effect of the interaction between functional composition, functional and taxonomic diversity and SPEI** 353 **on resistance and recovery**

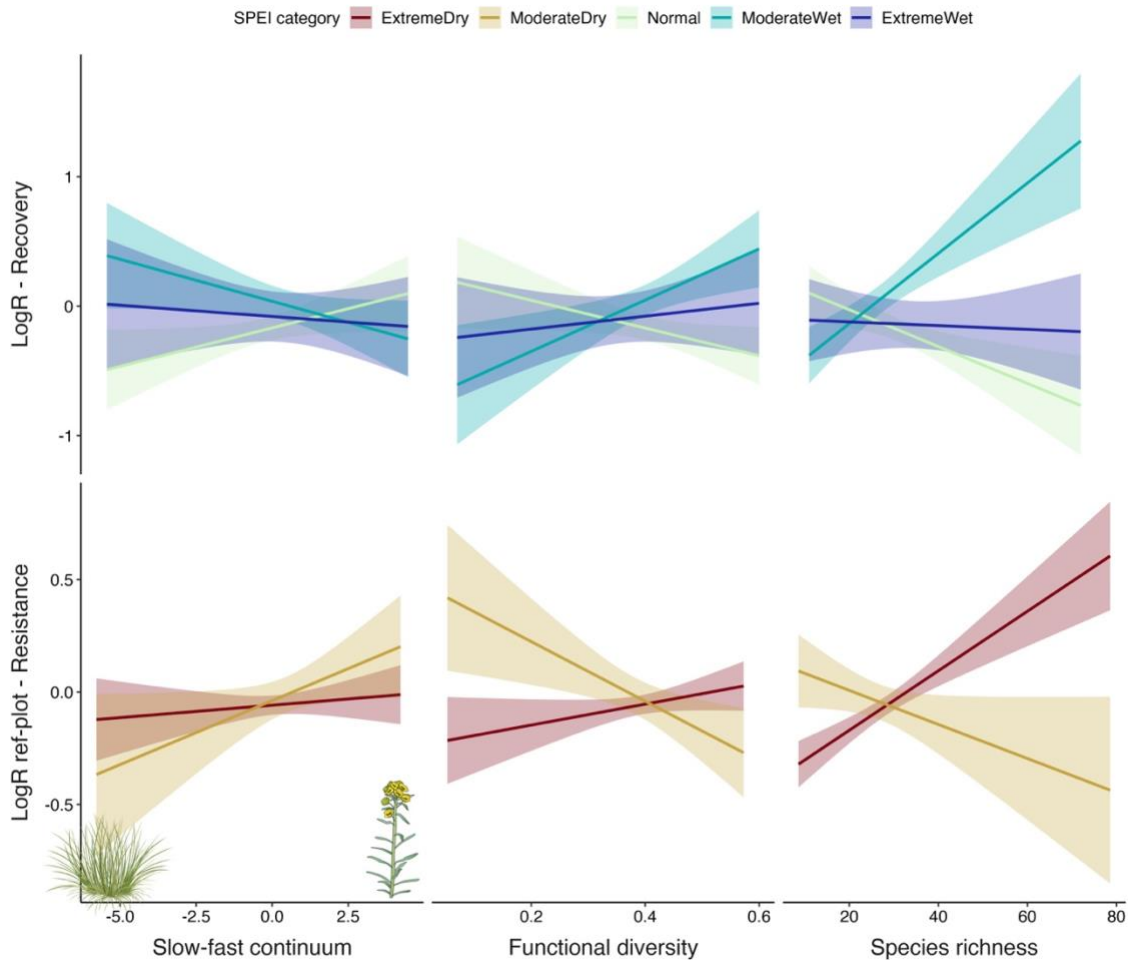
354 At SPEI-3, the effect of slow-fast continuum and functional diversity on plant community recovery depended on water  
355 availability after drought (i.e., SPEI categories: normal, moderate and extreme wet) (slow-fast continuum:  $F = 4.89$ ,  $p$ -  
356 value  $< 0.05$ ; functional diversity:  $F = 7.27$ ,  $p$ -value  $< 0.05$ ), while there was no evidence of such an interaction at SPEI-  
357 12 (full summary of Type II analysis of variance reported in Table A5.3, Figures A5.1,2, Appendix A5). In particular,  
358 functionally poor and fast-growing plant communities showed a more pronounced plant biomass growth (i.e., higher  
359 recovery) when drought was followed by normal water conditions, whereas more functionally diverse and slow-growing  
360 communities seemed favoured when drought was followed by moderate wetness (Figures 4, A5.2, Appendix A5).

361 Concerning taxonomic diversity, at SPEI-3 species poor communities produced more biomass when drought  
362 was followed by normal water budgets, while species rich communities exhibited higher recovery capabilities when  
363 drought was followed by moderate wetness ( $F = 23.05$ ,  $p$ -value  $< 0.05$ ) (Figures 4, A5.2, Appendix A5). On the contrary,  
364 at SPEI-12 species poor communities were predicted to produce more biomass when drought was followed by moderate  
365 wetness, although the interaction between species richness and water availability after drought was only marginally  
366 significant ( $F = 2.98$ ,  $p$ -value = 0.05) (Figures A5.1,2; full summary of Type II analysis of variance reported in Table  
367 A5.4, Appendix A5). We found no evidence of an association between functional composition, functional diversity,  
368 species richness and recovery at SPEI-24, according to which severe drought was followed only by normal water budget  
369 (Figure A5.1,2, Tables A5.3, A5.4, Appendix A5).

370

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

378 Species richness interacted with drought intensity in affecting resistance at SPEI-3 and -12 (Table A6.4,  
 379 Appendix A6). At both time-scales, species rich communities had a more pronounced biomass growth (or lower biomass  
 380 loss) than species poor communities under extreme drought (Figures 4, A6.1,2, Appendix A6). We found no statistical  
 381 interaction between species richness and drought intensity at SPEI-24 (Table A6.4, Appendix A6).  
 382



383 Figure 4 - Effect of the interaction between slow-fast continuum, functional diversity, and species richness (columns) and the  
 384 categorical 3-months Standardised Precipitation Evapotranspiration Index (SPEI-3: from extreme drought, in reddish, to extreme  
 385 wet, in blue) on recovery (upper panel) and resistance (bottom panel). Bands represent 95% confidence intervals for conditional  
 386 means. An example of a slow-growing species (*Festuca* spp.) is located at the leftmost end of the slow-fast continuum, while an example  
 387 of a fast-growing species (*Euphorbia esula*) is located at the rightmost end of the spectrum. Plant icons by Tracey Saxby (Integration  
 388 and Application Network, [ian.umces.edu/media-library](http://ian.umces.edu/media-library/)), CC BY-SA 4.0 DEED. No changes were made to the original icons.  
 389

390  
 391 **4. Discussion**  
 392

393 When focusing on short-term water budgets (i.e., SPEI-3), we found that functionally and taxonomically diverse  
 394 communities buffered extreme droughts better, whereas species-poor, fast-growing communities had higher recovery  
 395 capabilities when severe drought was followed by normal water conditions. This shows that mechanisms such as  
 396 insurance (Diaz & Cabido 2001) and dominant species effect (Lisner et al. 2022) support resistance and recovery of  
 397 grasslands experiencing unfavourable environmental conditions.  
 398

399 **4.1. Community composition and land use vs. temporal fluctuation of biomass**

400 Our results suggest that land use is the main determinant of grassland biomass production, likely through direct  
401 management (e.g., fertilisation) that influences community functional and taxonomic composition (Socher et al. 2012;  
402 Blüthgen et al. 2016). In this regard, we observed that species poor plant communities with fast-growing species, low  
403 functional diversity (Figure A3.1, Appendix A3), and subject to high land-use intensity (Figure A3.1,2, Appendix A3),  
404 produced more biomass. On the contrary, species rich plant communities with abundant slow-growing species and high  
405 functional and taxonomic diversity were less productive (Figure A3.1, Appendix A3). These findings are in line with  
406 Allan et al. (2015) and Májeková et al. (2016), who previously described such a relationship in grasslands.

407 However, we found that the association between biodiversity and plant biomass fluctuation (i.e., LogR and  
408  $\text{LogR}_{\text{ref-plot}}$ ) had opposite signs to those found for biomass in several years with severe drought (2009, 2012 and 2016; see  
409 Figure 3b). This supports the idea that biodiversity mediates the response of grassland biomass to drought. Under average  
410 climatic conditions, land use determines plant community composition, with intense land use shifting vegetation  
411 towards fast-growing competitive species, and thus highly productive but functionally poor communities (Laliberté &  
412 Tylianakis 2012; Májeková et al. 2016). However, in dry years functionally and species rich communities produce more  
413 (or lose less) biomass than functionally and species poor communities, thus pointing to high biodiversity as a factor  
414 promoting long-term stability of ecosystem functions (Isbell et al. 2017; Craven et al. 2018 and references therein).

415

#### 416 **4.2. Community composition and diversity vs. resistance and recovery**

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

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

446 compensatory growth (Hoover et al. 2014; Stampfli et al. 2018; Wilcox et al. 2020). Thus, the effect of (functional)  
447 diversity should be always considered together with the effect of functional composition, particularly the effect of the  
448 strategies of dominant species – in our case, represented by the slow-fast continuum.

449 In line with Oram et al. (2020), at SPEI-3 we found that species rich, slow-growing communities recovered  
450 better than species poor, fast communities when drought was followed by moderate wetness. This can be ascribed to  
451 conservative species being usually tolerant to stressful environmental conditions. On the contrary, we found that species  
452 poor communities recovered better under moderate wetness at SPEI-12. Such a contrasting association between species  
453 richness and recovery under wet conditions measured at different SPEI time-scales was also reported by Isbell et al.  
454 (2015). However, our results for recovery under above-average wetness should be interpreted with caution due to the  
455 low number of moderate and extreme events at all SPEI time-scales in our time-series (Table A2, Appendix A2).

456

#### 457 **4.3. Generality over SPEI time-scales**

458 We found that functional components of biodiversity mediated the response of biomass to drought only at SPEI-3,  
459 which in our study quantified water availability right before and at the peak of biomass growth. On the contrary, we  
460 observed that species richness and resistance were positively associated at all SPEI time-scales (although they negatively  
461 correlated under moderate short-term drought). Similarly, species richness affected recovery of biomass under both  
462 short- (SPEI-3) and long-term (SPEI-12) drought, although the interaction between species richness and SPEI was only  
463 marginally significant in the latter case. Our results thus suggest that biodiversity mechanisms mediated by functional  
464 traits and taxonomic diversity may operate at different temporal scales: functional traits, which are more mechanistically  
465 linked to plants ecophysiological response to water shortage (Fatichi et al. 2016), may be better at capturing vegetation  
466 response to short-term drought (e.g., right before the biomass peak), whereas taxonomic diversity may also catch  
467 vegetation response to long-term droughts. We acknowledge that our results do not prove that there is an interaction  
468 between drought duration (i.e., press *vs.* pulse drought) and biodiversity facets, and this is worth a more targeted study  
469 in the future.

470

#### 471 **5. Conclusion**

472

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

482

#### 483 **Authors contribution**

484

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

487

#### 488 **Data availability statement**

489

490 This work is based on data elaborated by several projects of the Biodiversity Exploratories program (DFG Priority  
491 Program 1374). The datasets are publicly available in the Biodiversity Exploratories Information System

492 (<http://doi.org/10.17616/R32P9Q>), (Breitschwerdt et al. 2018; Bolliger et al. 2021; Prati et al. 2021; Lorenzen et  
493 al. 2022; Wöllauer et al. 2022; Hinderling et al. 2023; Neyret & Manning 2023).

494

#### 495 **Code availability statement**

496

497 Data and R code for reproducing the results presented in this manuscript can be found at:  
498 <https://github.com/ManueleBazzichetto/ResistRecoverDrought> (or at: <https://doi.org/10.5281/zenodo.10518333>).

499

#### 500 **Conflict of interest statement**

501

502 Authors have no conflict of interest to declare.

503

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505

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520

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