

RESEARCH ARTICLE

Land use modulates resistance of grasslands against future climate and inter-annual climate variability in a large field experiment

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Abstract

Climate and land-use change are key drivers of global change. Full-factorial field experiments in which both drivers are manipulated are essential to understand and predict their potentially interactive effects on the structure and functioning of grassland ecosystems. Here, we present 8 years of data on grassland dynamics from the Global Change Experimental Facility in Central Germany. On large experimental plots, temperature and seasonal patterns of precipitation are manipulated by superimposing regional climate model projections onto background climate variability. Climate manipulation is factorially crossed with agricultural land-use scenarios, including intensively used meadows and extensively used (i.e., low-intensity) meadows and pastures. Inter-annual variation of background climate during our study years was high, including three of the driest years on record for our region. The effects of this temporal variability far exceeded the effects of the experimentally imposed climate change on plant species diversity and productivity, especially in the intensively used grasslands sown with only a few grass cultivars. These changes in productivity and diversity in response to alterations in climate were due to immigrant species replacing the target forage cultivars. This shift from forage cultivars to immigrant species may impose additional economic costs in terms of a decreasing forage value and the need for more frequent management measures. In contrast, the extensively used grasslands showed weaker responses to both experimentally manipulated future climate and inter-annual climate variability, suggesting that these diverse grasslands are more resistant to climate change than intensively used, species-poor grasslands. We therefore conclude that a lower management intensity of agricultural grasslands, associated with a higher plant diversity, can stabilize primary productivity under climate change.

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KEYWORDS

ANPP, climate change, community dynamics, Global Change Experimental Facility, grazing, land-use intensity, mowing, plant diversity

1 | INTRODUCTION

Grasslands cover more than one-third of the Earth's terrestrial surface and provide important ecosystem functions and services (Bengtsson et al., 2019). They store at least one-third of the terrestrial carbon (Bai & Cotrufo, 2022; White et al., 2000), are essential for food production (O'Mara, 2012), and can maintain exceptionally high biodiversity at a small spatial scale (Biurrun et al., 2021; Sabatini et al., 2022). Climate change and land-use intensification—two main constituents of anthropogenic global change—are major threats to the biodiversity and functioning of these important ecosystems (Gibson & Newman, 2019; Schils et al., 2022).

Over the last decades, global mean temperature has increased by about 1°C and is projected to increase by 1.5–4°C (2070–2100) depending on the emissions scenario (IPCC, 2021). In addition, seasonal precipitation patterns (e.g., intra- and inter-annual variability) have changed across the globe, a trend which is expected to continue in the future (IPCC, 2021). As a consequence, extreme climate events, such as droughts, have dramatically increased in frequency and extent over the last decades, and are expected to do so even more in the future (IPCC, 2021). Climate change experiments that monitor community responses can establish cause-effect relationships and can improve our mechanistic understanding of the consequences of anthropogenic climate change on community- and ecosystem-level responses.

Climate change can lead to changes in the phenology, demography, and abundance of plant species (Compagnoni et al., 2021; Morris et al., 2020; Piao et al., 2019), subsequently leading to alterations in interactions within and across trophic levels (Gornish & Tylianakis, 2013; Renner & Zohner, 2018), ultimately driving shifts in plant community attributes (Bellard et al., 2012; Parmesan, 2006). Meta-analyses of experimental studies have shown that climate change can cause alteration in biodiversity and productivity (Bastazini et al., 2021; Gruner et al., 2017; Korell et al., 2021; Song et al., 2019; Wu et al., 2011). There is an extensive number of studies that consider shifts in seasonal patterns of precipitation (see, e.g., review by Hajek & Knapp, 2022) but experimental quantification of how plant communities and ecosystems respond to these changes is still largely underappreciated (Hajek & Knapp, 2022; Jentsch et al., 2007; Korell et al., 2020). Even small changes in seasonal precipitation patterns can have profound effects on ecosystem processes such as productivity (Fay et al., 2003; Gherardi & Sala, 2019; Wilcox et al., 2015) and can lead to changes in the composition and diversity of plant communities (Knapp et al., 2020). Although anthropogenic climate change comprises simultaneous alterations in temperature and precipitation regimes, their combined effect has been rarely considered in experimental studies so far (Song et al., 2019; Wu et al., 2011). However, a predictive understanding of plant

community and ecosystem responses requires experiments that cover future climate scenarios (Korell et al., 2020), for example, manipulating changes in seasonal precipitation patterns in combination with alterations in temperature (Schädler et al., 2019).

Climate change is acting in concert with other components of global change (Komatsu et al., 2019; Sala et al., 2000; Speißer et al., 2022) such as land-use change. Historically, semi-natural grasslands in Central Europe have been created by human activities and their maintenance needs regular management, that is, mowing and/or grazing (Poschold et al., 2009). Grasslands at low management intensity (i.e., extensively used) are usually highly diverse (Tälle et al., 2016). Yet, many European grasslands have been converted to intensively used grasslands through high fertilizer input, higher mowing frequency and/or livestock density, and sowing of highly productive grass cultivars (Poschold et al., 2005). This land-use intensification has led to a conversion of comparatively unproductive and highly diverse, extensively used grasslands to highly productive but low diverse, intensively used grasslands (Beckmann et al., 2019; Gossner et al., 2016). Diversity is suggested to warrant resistance (i.e., less change in ecosystem responses, Pimm, 1984) against environmental perturbations (Isbell et al., 2015; Yachi & Loreau, 1999). Multiple biotic mechanisms associated with species' functional traits and asynchrony in their abundances are suggested to be key for the temporal stability and resistance of plant communities against environmental changes (de Bello et al., 2021; Luo et al., 2023; Xu et al., 2015). The few experimental studies available indicate that different aspects of land use (e.g., management frequency and fertilization) can modulate the resistance of grasslands to climate alterations (Bharath et al., 2020; Hallett et al., 2017; Stampfli et al., 2018; Vogel et al., 2012). However, it remains unclear how these factors as a whole affect the resistance of differently managed grasslands to climate change.

Ecosystem responses to chronic environmental changes involve species reordering, species loss, and immigration (Smith et al., 2009). Immigration is expected to lead to large changes in ecosystem properties such as aboveground productivity (Alexander et al., 2015; Smith et al., 2009). Land-use intensity in combination with climate change may affect how many species can potentially immigrate into grassland systems: For instance, a greater dieback of grass cultivars after severe drought can accelerate such immigrations, as grass cultivars typically sown in intensively used grassland are bred to maximize yield at the expense of drought tolerance (Kozioł et al., 2012; Lüscher et al., 2022).

Here, we present the results of 8 years (2015–2022) of realistic climate manipulations on the productivity, diversity, and composition of different grassland types. We made use of the Global Change Experimental Facility (GCEF), a large experimental platform located in Central Germany. Future temperature and seasonal precipitation

are experimentally manipulated based on regional climate model projections and factorially crossed with different realistic agricultural land-use scenarios, including intensively used meadows and extensively used meadows and pastures (Schädler et al., 2019). As background climate conditions varied considerably during our study period, including 3 years of extreme drought (Rakovec et al., 2022), we could also compare community responses to experimental climate manipulation with responses to inter-annual climate variability. Such high climate variability can be also considered a consequence of anthropogenic global change (Naumann et al., 2021).

Specifically, we asked the following questions: (1) How does future climate affect plant species diversity of differently managed grasslands? We expect that highly productive cultivars in intensively used grasslands may be less tolerant to summer droughts than resident species in extensively used grasslands. Greater dieback of these cultivars in intensively used grasslands may allow more species from the regional species pool to immigrate, resulting in a net increase in species richness under future climate conditions. (2) How does future climate affect the productivity of differently managed grasslands? Climate manipulation may lead to an overall decline in productivity and responses will be stronger in the intensively used grasslands due to less drought-tolerant cultivars. (3) What is the relative importance of inter-annual background climate variability and experimental climate change for changes in productivity, and how do grasslands differ in their resistance against background climate variability? We hypothesize that inter-annual climate variability, including extreme drought years, will have more drastic effects on productivity compared to effects of the climate manipulation, which includes wetter springs and falls that could counteract the negative effects of drier summer conditions. We expect intensively used grasslands to show a lower resistance to inter-annual climate variability than extensively used ones.

2 | MATERIALS AND METHODS

2.1 | Study site and experimental design

The experimental site is located at the Field Experimental Station of the Helmholtz-Centre for Environmental Research—UFZ in Bad Lauchstädt, Central Germany (51°22'60N, 11°50'60 E, 118 m a.s.l.). It is characterized by a sub-continental climate with a mean annual temperature of 8.9°C and a mean annual precipitation of 489 mm (1896–2013). During the study period (2015–2022), which included three drought years in a row (2018–2020), annual precipitation was on average 97 mm lower, and the annual temperature was 1.8°C warmer than the long-term mean (Figure S1). The nutrient-rich soil is a Haplic Chernozem upon carbonatic loess substrate with a high humus content as well as a high water holding capacity (for further details see Altermann et al., 2005).

The Global Change Experimental Facility (GCEF) was established on a former arable field in 2012. The experiment was set up using a two-factorial split-plot design (see Figure 1): 10 main plots of

80×24 m size, which have a minimum distance of 25 m to each other, were randomly assigned to one of two climate treatments (ambient climate vs. future climate). Each main plot was subdivided into five subplots of 16×24 m, which in turn were randomly assigned to one of five land-use treatments (organic farming, conventional farming, intensively used meadow, extensively used meadow, and extensively used pasture). This results in a total of 50 subplots with five replicates for each combination of climate and land use. In 2013, oat was sown on all plots in order to homogenize soil conditions including soil seed bank. In this study, we will consider the three grassland types only: the intensively used meadows (IM) were set up in fall 2013, and the extensively used meadows (EM) as well as the extensively used pastures (EP) were sown in early spring 2014. Climate manipulation started in the spring of 2014 for all land-use treatments (see Schädler et al., 2019 for details).

2.2 | Climate manipulation

Within the GCEF, the climate was manipulated according to projections of dynamic regional climate models for the period of 2070–2100. We used the mean projection of 12 simulations based on three models and four emission scenarios, which corresponds to an increase in temperature by 2°C and a changed seasonal pattern of precipitation, with about 10% increase in spring and fall and about 20% decrease in summer (see Schädler et al., 2019 for details). We superimposed the seasonal change in precipitation on the ambient precipitation pattern, thereby retaining the background climate variability. This was implemented by roof structures that were installed above each main plot representing future climate, equipped with translucent tarpaulins which closed every day from sunset to sunrise to achieve passive warming. We considered passive nighttime warming to be in accordance with the predicted asymmetry in global warming between day and night (Davy et al., 2017; Harvey, 1995). However, the resulting temperature increase was lower than projected: for example, mean daily temperature increased by 0.55°C at a height of 5 cm and by 0.24°C at a height of 70 cm (see Schädler et al., 2019 for details). In the summer months (June–August), roofs were additionally closed during daytime rain events to reduce summer precipitation by 20%. In spring (March–May) and fall (September–November) stored rainwater was added using an irrigation system to increase precipitation by 10%. Air and soil temperature as well as precipitation are continuously measured on the 10 main plots representing ambient and future climate treatments (Schädler et al., 2019). Plots of ambient climate were equipped with similar roof constructions, but without tarpaulins and irrigation systems, to mimic possible side effects (Kreyling et al., 2017).

2.3 | Land-use treatments

The three grassland types differ with respect to a range of factors, such as initial species composition, fertilization, management type,

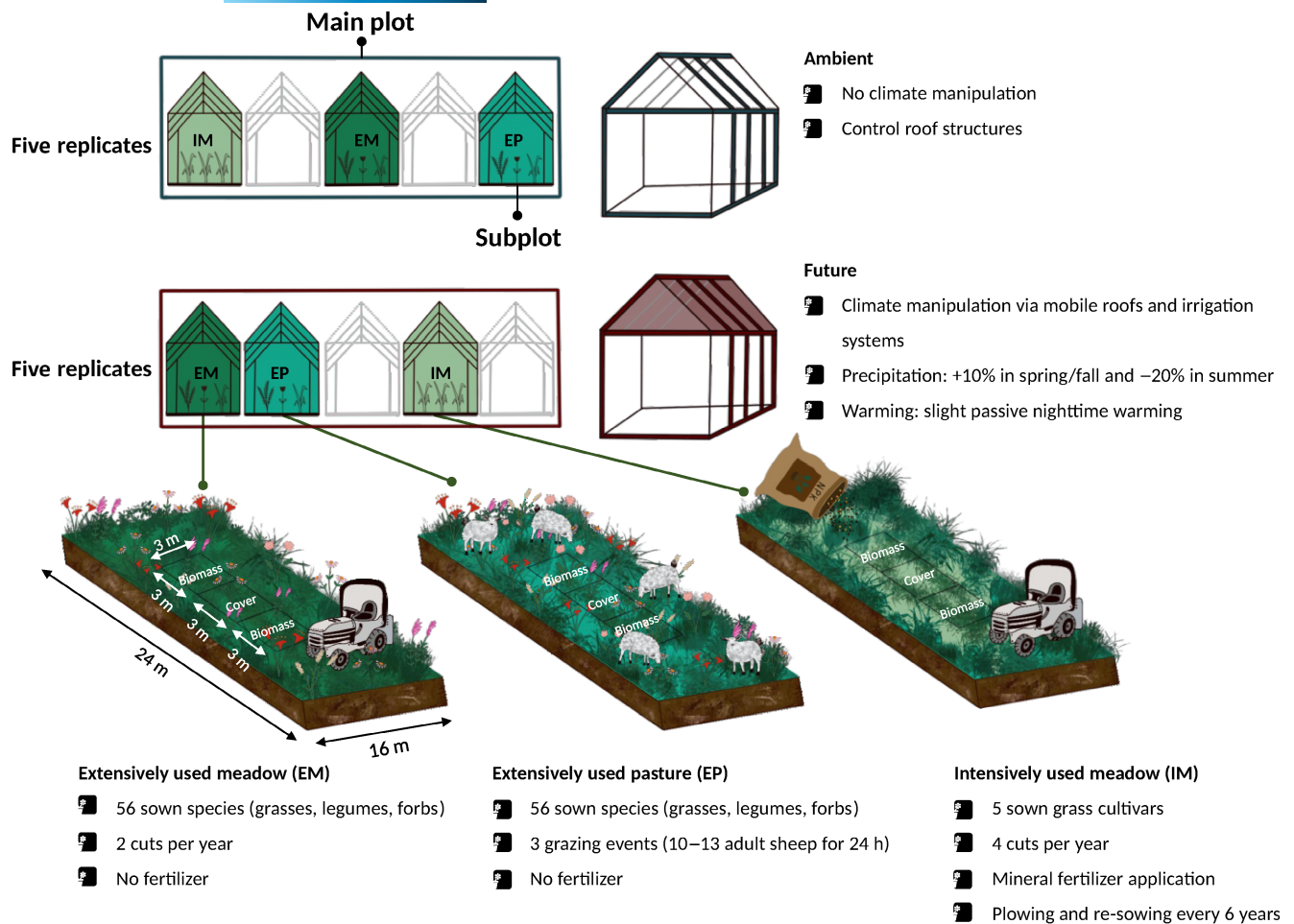


FIGURE 1 Most important features of the design and the treatment structure of the experiment. Based on a split-plot design, the main plots reflect the two climate scenarios (ambient climate and future climate). The future climate scenario is based on regional climate models that predict seasonal shifts in precipitation patterns and an increase in temperature. Climate manipulation is achieved via mobile roofs and irrigation systems. The subplots correspond to five different land-use types, of which only the three grasslands are considered in this manuscript (extensively used pastures, extensively used meadows, and intensively used meadows). The grasslands differ in management type, intensity as well as sown species diversity. Graphical illustration created by M. Milanović.

and management frequency. Considering the different management, we will refer to them as land-use types according to Schädler et al. (2019). For the extensively used meadows (EM) and extensively used pastures (EP), seeds of 56 native grassland species (14 grasses, 10 legumes, and 32 non-legume forbs; Table S1) from the regional species pool were sampled in one to six local populations per species. The selected species are typical for mesophilous to dry grasslands as well as steppe grasslands of Central Germany (Arrhenatherion, Cynosurion, Festucion valesiacae, and Cirsio-Brachypodium communities according to Schubert et al. 2010). In early March 2014, seeds were sown at a total density of c. 1600 seeds m^{-2} (2.2 g m^{-2}), which is within the range recommended for grassland restoration in the region (Kirmer & Tischew, 2006). A few poorly germinated forb species were re-sown in early October 2014. In summer of 2014, the first growing season after sowing, mowing was applied once to EM and EP in order to suppress weed establishment. Beginning in 2015, the year when vegetation sampling started, EM was mown twice every year (late spring, midsummer), except in 2018, 2019, and 2020,

when mowing had to be suspended in summer due to insufficient regrowth. EP was mown in late spring 2015 as well, and the first grazing by sheep was initiated in midsummer 2015. The lower grazing intensity at the beginning of the experiment was intended to facilitate the establishment of sown species. In 2016, grazing took place two times, in late spring and midsummer. Starting in 2017, grazing frequency was increased to three times per year (early spring, late spring, midsummer). In 2018, 2019, and 2020, however, grazing had to be reduced to two times each year, and in 2022 to one time, because of insufficient regrowth owing to summer drought. Grazing is conducted as short-time, high-intensity grazing with a group of 10–13 adult sheep and 10–20 lambs remaining on each EP subplot for 24 h. Such grazing management is recommended for nature conservation purposes (Landesamt für Landwirtschaft, 2010).

For the intensively used meadows (IM), species composition follows official recommendations of state authorities for drier sites (Landesanstalt für Landwirtschaft und Gartenbau Sachsen-Anhalt, 2020). The used seed mixture “RG8” contains five grass

cultivars: 10% of early-season *Lolium perenne* cv. "Nui," 10% of midseason *L. perenne* cv. "Toronto," 50% of "Festulolium" (*Festuca pratensis* × *Lolium multiflorum*) cv. "Felopa," 20% of *Dactylis glomerata* cv. "Lidacta," and 10% of *Poa pratensis* cv. "Balin," with a total sowing density of 3.0 g m⁻². The IM grassland was sown in fall of 2013 and mown three times in 2014 (midspring, early summer, and early fall). Starting in 2015, mowing frequency was increased to four times each year (midspring, late spring, midsummer, and mid-fall). Owing to dry summers, mowing frequency had to be reduced to two cuts each year in 2018, 2019, and 2020, and to three cuts in 2022. In the fall 2020, IM subplots were plowed and re-sown using the same seed mixture as before. This is part of the typical management of intensively used grasslands in Central Europe to re-establish the desired mixture of cultivars. According to agricultural practice, mineral fertilizer is applied every year at the start of the growing season (90 kg/ha N, 30 kg/ha P, and 110 kg/ha K) and after the first (80 kg/ha N), second (70 kg/ha N), and third cut (60 kg/ha N).

2.4 | Vegetation sampling and compilation of derived variables

2.4.1 | Species diversity

A 3 × 3 m permanent quadrat was established on each of the 30 grassland subplots (Figure 1). On this quadrat, percentage cover of each higher plant species was visually estimated two times each year on EM and EP (late spring and midsummer, before mowing or grazing) and four times each year on IM (midspring, late spring, midsummer, and midfall), except in 2015 and 2020 when IM was sampled three times per year only. Data on species cover were used to calculate total species richness, richness of sown species (hereafter referred to as "resident species"), richness of non-sown species (hereafter referred to as "immigrant species"), as well as average cover of each species per 9 m² sampling quadrat and year. As a measure of community evenness, we used a bias-corrected version (Chase et al., 2018) of the probability of interspecific encounter, PIE (Hurlbert, 1971). We used the average cover of species per year rather than the number of individuals and converted PIE into the effective number of species $SPIE = 1 / \sum_{i=1}^S p_i^2$, where S is the total number of species and p_i the proportion of each species i and it is equivalent to 1/Simpson's index (Hill, 1973; Jost, 2006).

2.4.2 | Species-specific aboveground biomass

To measure standing biomass of each plant species, aboveground biomass samples were taken just after cover estimation, that is, two times a year on EM and EP, and four times a year on IM. Aboveground biomass was cut with scissors at a height of about 2 cm within four 20 × 50 cm metal frames which were randomly

placed in two 3 × 3 m areas next to the area used for cover estimates within each grassland subplot (Figure 1). Biomass samples were then sorted by species and dead biomass, dried at 70°C for 48 h, and weighed. Only three biomass harvests took place on IM subplots in 2018 because there was no regrowth prior to the fourth occasion, and in 2020, because plots were plowed and re-sown. Species-specific dry masses of the four samples per subplot were averaged to one biomass value per species, harvest date, and subplot, and then used to calculate average biomass of resident and immigrant species per year for each subplot.

2.4.3 | Standing biomass and annual above-ground net primary production (ANPP)

For EM, EP, and IM subplots, we used the biomass data described above and calculated standing biomass for each harvest date by adding species-specific biomass and dead biomass. As EM and IM were completely mown on each occasion, standing above-ground biomass of subsequent harvest dates was considered to represent regrowth. To estimate ANPP, we added standing biomass of subsequent harvest dates of a given year (see Ruppert & Linstädter, 2014 for a method comparison). On EP subplots, an average of 66% of aboveground biomass remained after each grazing. Therefore, we applied the "moveable exclosures" method to estimate ANPP (McNaughton et al., 1996): Four cages of c. 1 m² area were randomly placed on each EP subplot to exclude vegetation underneath from grazing. Immediately after grazing, cages were removed and biomass was harvested within 20 × 50 cm metal frames as described above. Similar biomass samples were taken at four randomly chosen positions outside cages on each subplot. Samples were dried at 70°C for 48 h and weighed. Biomass values of the four samples inside cages and the four samples outside cages were averaged for each EP subplot to estimate standing biomass on each grazing event and remaining biomass after grazing, respectively. Re-growth between two grazing events was calculated as the difference in (grazed) biomass outside cages at time t and (ungrazed) biomass inside cages at time $t + 1$. ANPP was then calculated by adding standing biomass measured on the first grazing date and regrowth during the following grazing events in each year.

2.4.4 | Precipitation and temperature

To characterize climatic conditions, we measured precipitation and air temperature at a height of 1.5 m and 70 cm above the soil surface, respectively, on each main plot. We compiled precipitation sum and mean air temperature for each month, for the four seasons spring (March to May), summer (June to August), fall (September–November), and winter (December–February), and for each study year. Because precipitation and temperature were correlated ($r = -0.90$; $p < .01$), we used De Martonne's index dMI which combines the two measures (Andrade et al., 2021) to characterize

drought conditions for ambient and future climate treatments on an annual basis: $dMI = \text{precipitation [mm]} / (10 + \text{temperature [}^{\circ}\text{C]})$.

2.5 | Statistical analyses

2.5.1 | Species diversity and ANPP

Generalized linear mixed-effects models were fitted to the data using the procedure GLIMMIX in SAS v. 9.4 (© SAS Institute Inc., Cary, NC, USA; see supporting information B for SAS Code). For count data (total species richness, richness of residents, and richness of immigrants) we used models with Poisson distribution and log link function; for all biomass values (annual productivity, standing biomass, the biomass of residents, and biomass of immigrants) models with log-normal distribution and identity link function; and for proportional richness of immigrant species (richness of immigrants / total species richness) models with binomial distribution and logit link function (for the analyzed data see Korell et al., 2023). As proportional biomass of immigrants (biomass of immigrants / total living biomass) was not based on count data, we applied a logit-transformation to the data and used models with Gaussian distribution (Warton & Hui, 2011). We empirically applied a log transformation to S_{PIE} values and used a model with Gaussian distribution as well.

As we were interested in community dynamics across the experimental period, we considered the eight study years explicitly. Since measurements taken on the same experimental units across time are not independent, we applied repeated measurement analyses which differentiate between within-subject effects and between-subject effects (von Ende, 2001). According to the split-plot design of the experiment, the between-subject model included the fixed factor climate at the main-plot level and the random effect of the main plot nested within climate as the respective error term, while the factor land use and the climate \times land use interaction were considered as fixed effects at the subplot level. The within-subject model included the fixed effects of year and of the year \times climate interaction at the main-plot level, and the random effect of year \times main plot nested within climate as the respective error term, as well as the year \times land use and year \times climate \times land use interaction as fixed effects at the subplot level. We included a first-order autoregressive covariance structure, if the 95% confidence intervals showed a significant temporal autocorrelation or if the Akaike Information Criterion revealed an improved model fit. If appropriate, we explicitly accounted for heteroscedasticity among land-use types, and for over- or underdispersion by including a group-specific multiplicative dispersion parameter. In order to test a priori hypotheses of differences between the intensively used grassland and the two extensively used grasslands, we decomposed the land use effect into orthogonal contrasts. In order to test how land-use types differed in their response to climate manipulation, we “sliced” the climate \times land use interaction into the simple main effect (Woodward & Bonett, 1991) of climate on each level of land use. For graphical presentation, we extracted

the marginal means and their standard errors from the mixed-effect models.

2.5.2 | Effects of experimental manipulation versus effects of inter-annual climate fluctuation on ANPP

We calculated the log response ratios (LRR; Hedges et al., 1999) of annual aboveground productivity between each subplot under future climate and the closest subplot under ambient climate for each land-use type and each year. The LRR values per subplot were averaged across years, and the mean among the five replicates and its standard error were calculated for each land-use type. We then compiled the LRR between the driest year (2018) and the wettest year (2021) for each subplot of the ambient climate treatment, and compared the mean response of each land-use type with its response to the experimental climate manipulation (see Kröel-Dulay et al., 2022).

To investigate how ANPP of the three land-use types depended on inter-annual variability in climatic conditions, we applied an ANCOVA to mean ANPP, with treatment-specific annual dMI, land use, climate, and their interactions as fixed effects. Year was included as random effect because measurements taken within a year are not independent. To quantify the resulting temporal stability in productivity, we calculated the coefficient of variation (CV) of ANPP for each of the 30 climate \times land use subplots across the eight study years. We are aware of the disadvantages of CV as an inverse measure of stability (Reckling et al., 2021), however, the time frame of 8 years was too short to allow for the commonly recommended corrections (e.g., Döring & Reckling, 2018). We empirically applied a square root transformation to CV, and used a model with Gaussian distribution. According to the split-plot experimental design, climate was considered as fixed effect, and main plot nested within climate as random effect at the main-plot level, and land use as well as the climate \times land use interaction as fixed effects at the subplot level. To test our hypothesis that the extensively used grasslands are less variable in time (i.e., more stable) than intensively used grasslands, we decomposed the climate \times land use interaction into the respective contrasts.

3 | RESULTS

3.1 | Magnitudes of climate manipulations and of inter-annual climate fluctuations

Experimentally imposed climate change resulted on average in a 6.9 ± 0.7 mm increase (+11.0%) of precipitation during spring (March–May), in a 25.5 ± 4.6 mm reduction (−21.4%) during summer (June–August), a 5.5 ± 0.6 mm increase (+6.0%) during fall (September–November), and unintentionally in a 4.8 ± 1.0 mm decrease (−7.4%) in winter (December–February) relative to plots of ambient climatic conditions (means \pm standard error). Consequently,

annual precipitation was reduced by an average of 18.2 ± 4.0 mm (-5.2%) under future climatic conditions (Figure 2). The seasonal manipulation did hardly affect the CV of precipitation within years (ambient climate: $63.1\% \pm 5.3\%$, future climate: $59.0 \pm 3.8\%$) owing to

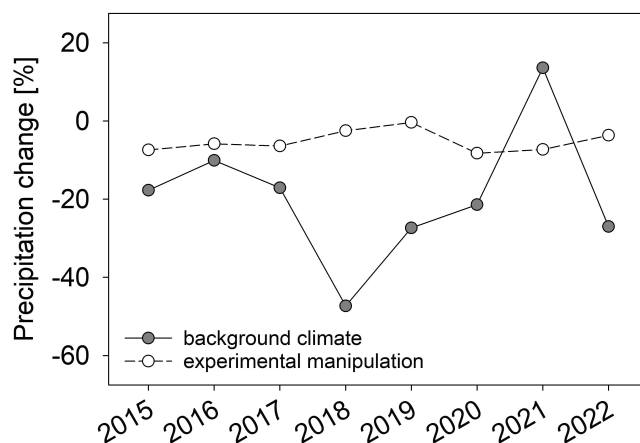


FIGURE 2 Effect of climate manipulation on annual precipitation (relative differences between future and ambient climate treatments), and inter-annual variation in background precipitation (relative differences between annual precipitation and the long-term mean 1896–2013) across the eight study years. Please note that the mean effect of climate manipulation does not reflect the seasonal change in precipitation pattern (increase in spring and fall, decrease in summer).

TABLE 1 Results of repeated measurements ANOVAs based on generalized linear mixed effects models for the effects of climate, land use, and year on total plant species richness, species richness of immigrants, annual above-ground net primary production (ANPP), and proportional contribution of immigrant species to total above-ground biomass.

	df	F ratio			
		Total richness	Richness of immigrants	ANPP	Proportional biomass of immigrants
Climate	1, 8	4.12 ⁺	3.84 ⁺	3.56 ⁺	0.58
Land use	2, 16	1029.59***	4.99*	705.80***	5.05*
Extensive vs. Intensive	1, 16	2027.29***	9.96**	1411.26***	0.16
EM vs. EP	1, 16	17.14***	0.18	68.46***	9.70**
Climate × Land use	2, 16	0.16	0.10	1.45	4.54*
Climate EM	1, 16	2.41	1.49	0.13	0.94
Climate EP	1, 16	1.16	1.58	4.89*	0.08
Climate IM	1, 16	1.62	3.36 ⁺	3.41 ⁺	4.81*
Year	7, 56	28.25***	27.69***	27.87***	10.14***
Year × climate	7, 56	2.82*	3.01**	1.14	1.55
Year × land use	14, 112	35.65***	27.01***	8.01***	22.59***
Year × climate × land use	14, 112	2.58**	1.63 ⁺	0.92	1.57 ⁺

Note: To test a-priori hypotheses, the main effect of land use is decomposed into orthogonal contrasts, and the climate × land use interaction is decomposed into simple main effects of climate on each land use type.

Abbreviations: *df*, numerator and denominator degrees of freedom; EM, extensively used meadows; EP, extensively used pastures; IM, intensively used meadows.

⁺*p* < .1;

p* < .05; *p* < .01; ****p* < .001.

the summer maximum of precipitation. Experimental climate change increased air temperature by on average $0.14 \pm 0.01^\circ\text{C}$ in spring, $0.21 \pm 0.01^\circ\text{C}$ in summer, $0.21 \pm 0.01^\circ\text{C}$ in fall, and $0.08 \pm 0.00^\circ\text{C}$ in winter, resulting in a mean annual increase of $0.16 \pm 0.01^\circ\text{C}$. During the study period, annual ambient precipitation ($328 \pm 26 \text{ mm year}^{-1}$) was on average 161 mm lower than the long-term mean of 489 mm. However, it varied considerably among study years (range: 209–460 mm) with 2018, 2019, 2020, and 2022 being exceptionally dry years (48%, 28%, 22%, and 27% less than the long-term mean, Figure 2). These droughts occurred mainly during the summer months, which was in synergy with the seasonal pattern of our experimental manipulation. Mean annual temperature ($10.8 \pm 0.2^\circ\text{C}$, range: 9.8°C to 11.3°C) was on average 1.9°C warmer than the long-term mean of 8.9°C .

3.2 | Effects of experimental climate change on plant diversity across study years

Intensively used meadows (IM) showed, on average, a lower species richness (13.7 ± 0.3 ; mean \pm standard error of 9 m² sampling plots across years) than the two extensively used grasslands. Among them, species richness was higher in the extensively used meadows (EM; 46.4 ± 0.6) compared with the extensively used pastures (EP; 43.1 ± 0.8 ; significant land use contrasts, Table 1). Species richness of EM and EP displayed rather small inter-annual

variability, with a decrease during the drought years and a slight recovery afterward. For IM, species richness increased substantially in the first years following establishment, declined in the first drought year 2018 but increased strongly in the second drought year 2019 (significant year \times land use interaction). The effect of experimental climate change on species richness differed among land-use types and among years (significant three-way interaction). While species richness of EM and EP showed only a minor, positive response to future climate during the first study years, the richness of IM responded more strongly (Figure 3a, significant three-way interaction). However, this response was not consistent across years: the richness of IM increased under future climatic conditions during the first study years but decreased in 2020 before re-sowing.

Consistent with differences in the numbers of species sown, the realized richness of residents was much lower on the intensively used

grassland (3.9 ± 0.0) than on the two extensively used grasslands. Among the two extensively used grasslands, richness of residents was larger on EM (36.1 ± 0.4) compared to EP (33.0 ± 0.5 ; Table S2). Furthermore, resident species richness showed larger temporal fluctuations on EM and EP compared to IM (significant year \times land use interaction) but weak response to climate treatments (Figure S2a).

A considerable number of non-sown species were recruited by immigration from the regional species pool or from the soil seed bank (EM: 10.3 ± 0.5 , EP: 10.1 ± 0.5 , IM: 9.8 ± 0.3). Species richness of immigrants showed a decline in EM and EP during the first study years but a strong increase in IM (significant year \times land use interaction; Table 1 and Figure 3b). After a general decline in the first year of drought, the number of immigrant species increased again during the following year in all three grassland types. In contrast to resident richness, the richness of immigrants was higher under future climate during the first study years but this effect vanished in subsequent

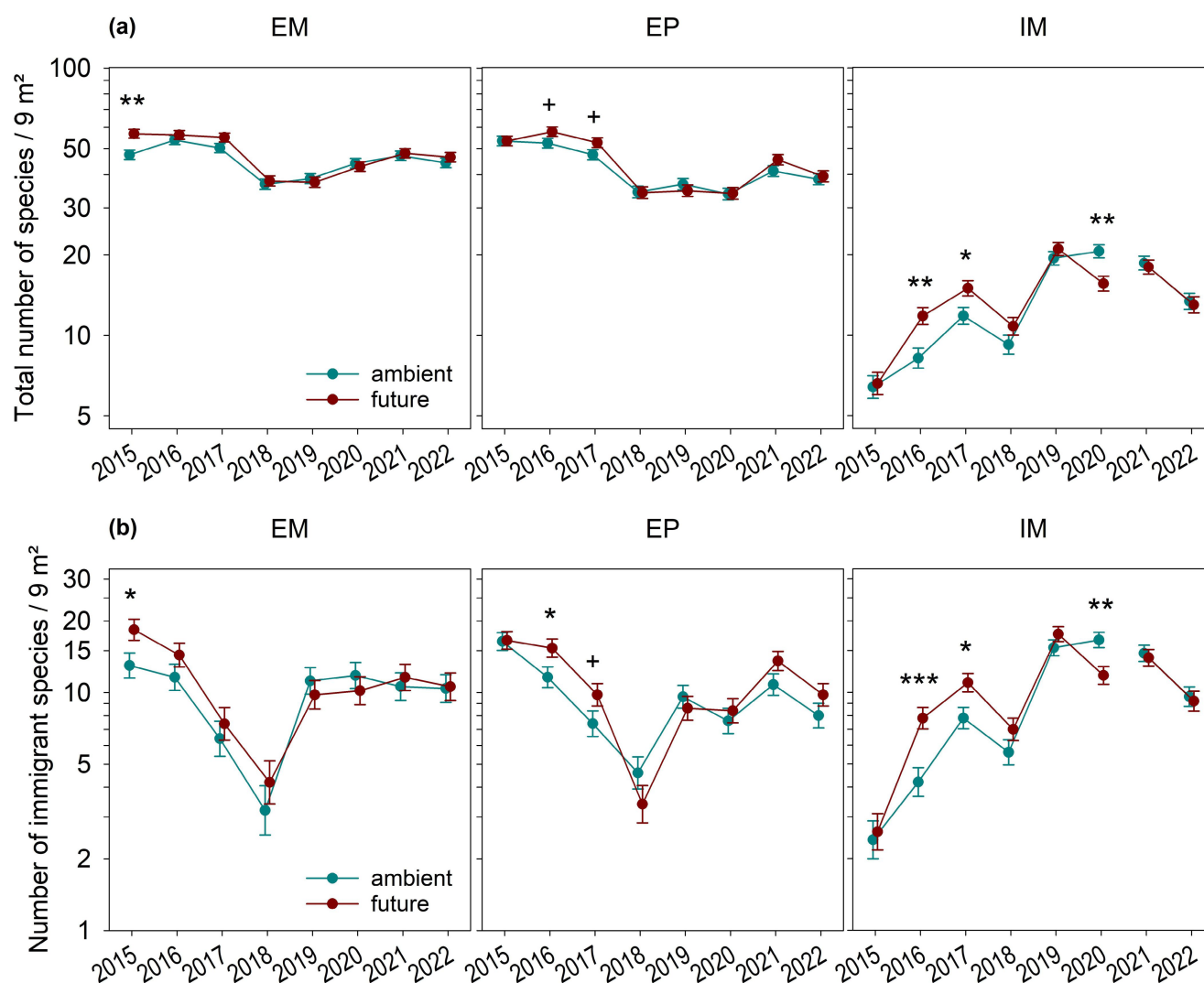


FIGURE 3 (a) Total plant species richness, and (b) species richness of immigrants of extensively used meadows (EM), extensively used pastures (EP) and intensively used meadows (IM) under ambient and future climatic conditions across eight study years, as measured on 9 m² sampling plots (y axes log scaled). Please note that IM was re-sown in fall 2020. (Marginal means and their standard errors extracted from generalized linear mixed effects models; significance of simple main effects of climate for each year and land-use type: + $p < .1$, * $p < .05$, ** $p < .01$, *** $p < .001$.)

years (significant year \times climate interaction; Table 1 and Figure 3b). The resulting proportional contribution of immigrants to total richness was much larger on IM than on EM and EP, but besides that, it mirrored their absolute numbers (Table S2 and Figure S2b).

The effective number of species, S_{PIE} , as a measure of evenness was on average higher on the two extensively used grasslands compared to the intensively used grassland, but there were also striking differences between them in the temporal dynamics of S_{PIE} (significant year \times land use interaction; Table S2 and Figure S2c). On EM and EP, S_{PIE} decreased during the first four to six study years, while on IM, a slight drop at the beginning was followed by a strong increase in S_{PIE} until plots were re-sown. The effect of experimental climate change on S_{PIE} depended on land use as well (significant climate \times land use interaction). On EM, S_{PIE} was on average higher under future climatic conditions compared to ambient conditions but did not significantly differ among climate treatments on EP and IM.

To summarize, species diversity in IM was on average lower than in EM or EP but showed both, a strong increase over time and a stronger response to experimentally imposed future climate. These responses of IM were associated with an increasing richness of immigrating species.

3.3 | Effects of experimental climate change on ANPP across study years

Annual aboveground net primary production (ANPP) of the intensively used grassland ($1015 \pm 21 \text{ g m}^{-2} \text{ year}^{-1}$ across the study period) was about twice as large as productivity of the two extensively used grasslands, and was higher on EM ($553 \pm 18 \text{ g m}^{-2} \text{ year}^{-1}$) than on EP ($405 \pm 14 \text{ g m}^{-2} \text{ year}^{-1}$; significant land use contrasts, Table 1). In addition, ANPP of IM showed a much steeper decline during the drought years and recovered only after re-sowing (significant year \times land use interaction; Figure 4a). Surprisingly, experimental climate change had only a minor, marginally significant effect on ANPP, and neither the climate \times land use interaction nor the three-way interaction with year were significant. However, when evaluating climate effects for each land-use type individually (Table 1), we found that ANPP on EP was on average lower under future than under ambient climate, while ANPP on IM was lower under future climate in the first study years but higher in the second year of drought (Figure 4a).

The proportional contribution of immigrant species to aboveground biomass did, on average, not significantly differ between intensively and extensively used grasslands, but was larger on EM than on EP (Table 1). However, proportional biomass of immigrants showed distinct temporal patterns according to land use (significant year \times land use interaction; Figure 4b): On EM and EP plots, it decreased until the first and the third year of drought, respectively, and recovered afterwards. On IM plots, proportional biomass of immigrants continuously increased until the plots were re-sown. This was driven by decreasing absolute biomass of residents during drought years and a continuously increasing immigrant biomass (Figure S3a,b and Table S2). While there was no significant effect of climate

manipulation on EM and EP, future climate led to an increase in the proportional biomass of immigrants on IM (significant climate \times land use interaction; Table 1 and Figure 4b).

To summarize, ANPP of IM was much higher than ANPP of EM or EP and showed stronger, but variable responses to climate manipulation as well as a stronger decline during drought years. These responses were accompanied by an increasing contribution of immigrant species to ANPP over time.

To evaluate whether the responses of ANPP to climate manipulation were related to the seasonal pattern of precipitation manipulation, we inspected intra-annual dynamics of standing biomass more closely (Table 2 and Figure S4). In all three grassland types, biomass reached its maximum in spring (first harvest on EM, first two harvests on EP and IM), during or just after experimentally increased precipitation under future climatic conditions. At that time, there was almost no difference in EM biomass between ambient and future climate and a marginally significant decrease of EP biomass under future conditions. Future climate had a weak positive effect on IM biomass in early spring, but a significantly negative effect in late spring. In midsummer, after a period of reduced precipitation, biomass of EM and IM was lower under future than under ambient conditions, while EP showed no difference between climate treatments. Only IM biomass was harvested in fall, when it was still lower under future conditions despite increased precipitation.

3.4 | Effects of inter-annual climate variability on ANPP

In the two extensively used grasslands, relative difference in ANPP (as quantified by log response ratio, LRR) between the driest year 2018, and the wettest year 2021 was close to zero, and even smaller in magnitude than the LRR to experimental climate manipulation (Figure S5). ANPP on IM plots showed a much larger response to the difference in background climatic conditions compared with its response to experimental climate manipulation. While ANPP varied independently of dMI on EM and EP, it increased strongly with increasing dMI, that is, with decreasing drought, on IM (Figure 5 and Table S3). There was no main or interactive effect of climate manipulation on the relationship between ANPP and treatment-specific dMI, indicating that climate manipulation affected ANPP in the same way as background climate fluctuations. Although the resulting CV of ANPP (as an inverse measure of stability) did not show a significant climate \times land use interaction (Table S4), a priori contrasts revealed that the coefficient of variation was significantly higher (i.e., stability was lower) on IM compared to the two extensively used grasslands which did not differ from each other (Figure 6). However, this effect was only evident under ambient climate, while there was no difference among land-use types under future climatic conditions. To prove that the higher variability of IM in ANPP was not caused by re-sowing, we repeated this analysis using the time span before re-sowing (2015–2020) but this did not change the results qualitatively.

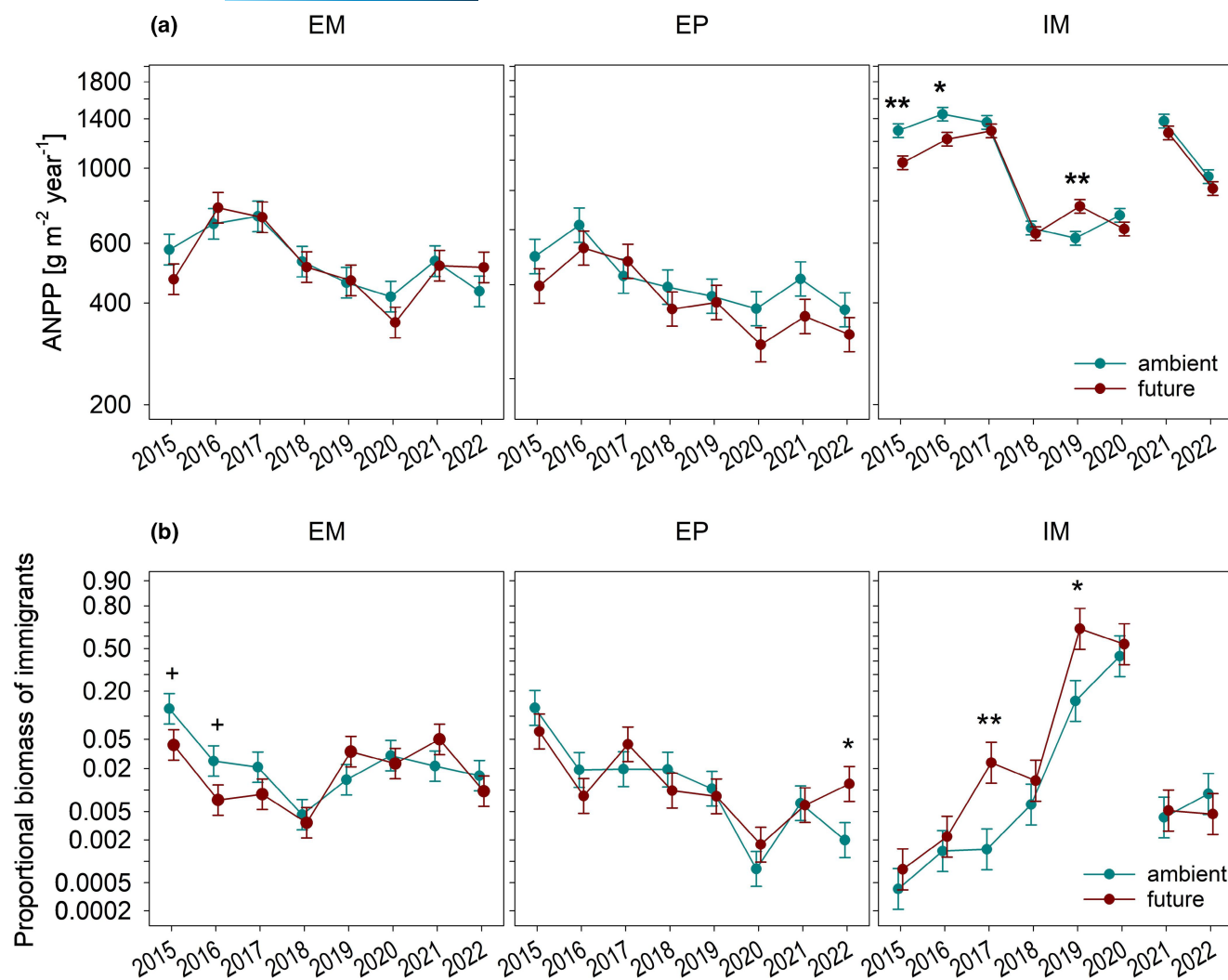


FIGURE 4 (a) Annual above-ground net primary production (ANPP, log scaled) and (b) proportional contribution of immigrant species to above-ground biomass (logit scaled) of extensively used meadows (EM), extensively used pastures (EP) and intensively used meadows (IM) under ambient and future climatic conditions across eight study years. Please note that IM was re-sown in fall 2020. (Marginal means and their standard errors extracted from generalized linear mixed effects models; significance of simple main effects of climate for each year and land-use type: + $p < .1$, * $p < .05$, ** $p < .01$)

To summarize, ANPP only depended on the background climatic conditions of a respective year in IM, and this response to inter-annual climate fluctuations was larger than the response to experimental climate manipulation.

4 | DISCUSSION

While climate and land-use change are expected to interactively affect ecosystems, this interaction is rarely considered (Oliver & Morecroft, 2014), especially in experimental studies. We found that the effects of inter-annual variability in background climate, including a series of extreme drought years, on the diversity and productivity of grasslands exceeded the effects of seasonal experimental climate manipulation that was superimposed onto background climate variability. Providing a higher diversity, extensively managed grasslands could better resist climate change compared to

intensively used grasslands composed of a few, but highly productive, grass cultivars.

The plant species diversity of the grasslands changed through time and weakly across experimental climate treatments. In line with our expectations, the diversity responses to climate manipulation and inter-annual climate variability were still stronger and more variable in intensively used grasslands. Initially, intensively used meadows were much less diverse than extensively used grasslands (meadows and pastures), as the former were sown with a few grass cultivars that are recommended for agricultural grasslands in drier regions in Central Germany (see Schädler et al., 2019 for more details). Changes in diversity were almost exclusively due to increases in the number of immigrant species, which may have entered from within (soil seed bank) or from outside (seed migration) the experiment. This is likely because more dieback of resident species occurred, particularly in drought years, creating opportunities for the establishment of drought-adapted immigrant species

TABLE 2 Results of repeated measurements ANOVAs based on generalized linear mixed effects models for the effects of climate, year, and harvest date on seasonal above-ground biomass.

	EM		EP		IM	
	df	F ratio	df	F ratio	df	F ratio
Climate	1, 8	2.94	1, 8	1.65	1, 8	32.28***
Year	7, 120	27.46***	7, 154	9.33***	7, 248	105.20***
Harvest	1, 120	2053.58***	2, 154	116.81***	3, 248	559.70***
Year×climate	7, 120	0.35	7, 154	0.54	7, 248	4.37***
Harvest×climate	1, 120	22.48***	2, 154	0.40	3, 248	14.24***
Year×harvest	7, 120	64.62***	11, 154	9.54***	19, 248	41.68***
Year×harvest×climate	7, 120	1.71	11, 154	0.67	19, 248	1.45

Note: Because of the different numbers of biomass harvests, separate models were compiled for each land use type.

Abbreviations: *df*, enumerator and denominator degrees of freedom; EM, extensively used meadows; EP, extensively used pastures; IM, intensively used meadows.

*** $p < .001$.

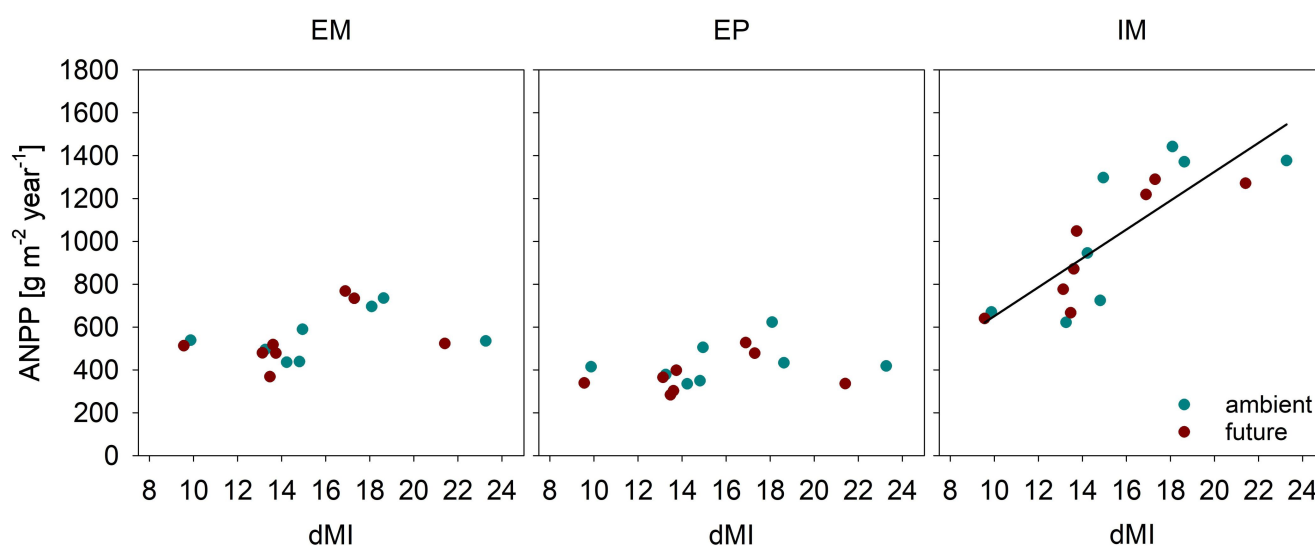


FIGURE 5 Effects of de Martonne's index (DMI) and climate manipulation on annual above-ground net primary production (ANPP) of extensively used meadows (EM), extensively used pastures (EP) and intensively used meadows (IM) under ambient and future climatic conditions. The de Martonne's index combines annual precipitation sum and mean annual temperature of each year and climate treatment, and increases with decreasing drought. According to ANCOVA, the climate×land use interaction is significant, but climate manipulation has no effect (see Table S2). Separate regression analyses for each land-use type reveal that productivity does not significantly depend on DMI on EM ($r^2 = .16$, $p = .13$) and EP ($r^2 = .11$, $p = .21$), while the relationship is significant for IM ($r^2 = .67$, $p < .0001$).

(see also Catford et al., 2020). Many other studies have also shown that less diverse communities are more likely to be invaded (e.g., Hector et al., 2001; Roscher et al., 2009). This pattern is often attributed to the higher number of unfilled niches compared to more diverse communities (Levine & D'Antonio, 1999; MacArthur, 1970). We would like to emphasize that the responses of our grasslands represent transitions of resident ecosystems in response to global change drivers, characterized by abundance shifts and immigration from the regional species pool (see Smith et al., 2009).

We found relatively weak effects of experimental climate on the aboveground net primary production (ANPP) of all grassland ecosystems. It should be noted that our climate manipulation retained the background inter-annual climate variability including the extremes.

The weak overall response of productivity to the climate manipulation might be explained by the seasonal nature of the climate manipulation (see also Denton et al., 2017; Hajek & Knapp, 2022; Heitschmidt & Vermeire, 2006), in which spring and fall are wetter and summer is drier, according to the climate model projections. In our grasslands, maximum growth occurs in spring, and the regrowth of plants during the summer contributes less to annual productivity. Thus, under future climate conditions, the slight increases in productivity in spring due to higher water availability can compensate for the decline in productivity during the dry summer. Interestingly, the productivity of intensively used meadows in fall was still reduced under future climate even though this treatment involves higher fall precipitation, indicating a reduced capacity of these grasslands to

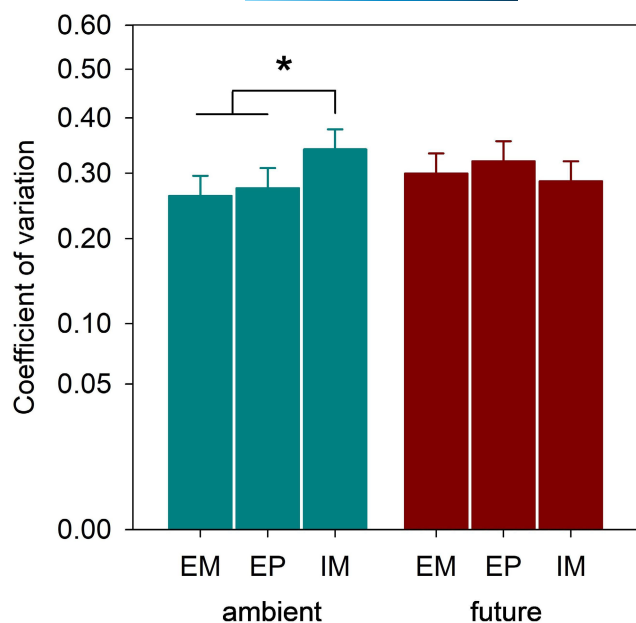


FIGURE 6 Coefficient of variation in annual above-ground net primary production (ANPP, square-root scaled) as an inverse measure of temporal stability of extensively used meadows (EM), extensively used pastures (EP) and intensively used meadows (IM) under ambient and future climatic conditions. (Marginal means and their standard errors extracted from generalized linear mixed effects models; contrast between the two extensively used grasslands and the intensively used grassland: $p < .05$.)

recover from summer drought. There is a clear need for more experimental research on factors that potentially mediate post-drought ecosystem recovery (Knapp et al., 2024) such as land-use intensity.

At the beginning of the experiment, the ANPP of intensively used grasslands was high, and the future climate caused a small decrease in ANPP. As time passed, immigrants contributed increasingly to ANPP, especially in the future climate treatment and after the drought years, and overall productivity declined. Our results are in line with other studies that have found that fertile grasslands primarily composed of fast-growing species showed a stronger response to climate change compared to infertile grasslands (Grime et al., 2000; Van Sundert et al. 2021, but see Stampfli et al., 2018). The declining productivity and increase of immigrants in intensively used grasslands have practical implications for farmers because these immigrant species have much lower forage values compared to the originally sown cultivars (forage values in 2020; sown: 8.67 ± 0.33 ; immigrants: 3.60 ± 0.52 ; mean \pm standard error; <https://wiki.ufz.de/biolflor/index.jsp>, Briemle et al., 2002; Klotz et al., 2002). The process of degradation, in which immigrant species replace the resident cultivars, is well known, and farmers expect to plow and re-sow their intensively used grasslands after some years (Bayerische Landesanstalt für Landwirtschaft, 2018). However, we show here that with climate change, this process of degradation will be accelerated, which may impose additional economic costs as a consequence of a faster-decreasing forage value and the need for more frequent management measures.

During the experiment, Central Europe experienced a series of consecutive droughts (years 2018, 2019, and 2020) that were

amongst the most severe since the beginning of records (Boergens et al., 2020; Hari et al., 2020; Rakovec et al., 2022). We therefore had the unique opportunity to quantify the stability of differently used grasslands during a period with large inter-annual climate variability. We found a clear signal of the drought years on ANPP, especially in the intensively used grasslands for which we found a clear positive relationship between ANPP and water availability (quantified as dMI). Accordingly, intensively used grasslands had a larger coefficient of variation (CV) under ambient climate conditions, suggesting lower stability in ANPP compared to extensively used grasslands.

Confirming our hypothesis, the results clearly show a lower resistance of intensively used grasslands to drought compared to the extensively used ones. However, we are not able to disentangle the pure effects of management intensity, diversity, and composition on the resistance of our grasslands because this study mimics realistic land-use scenarios of the study region that typically differ in many aspects of management and plant diversity. Multiple biotic mechanisms are suggested to play a role in community stability (de Bello et al., 2021) and may help to explain the higher resistance of the extensive grasslands against climate fluctuations. In our study, there is only limited overlap in the dominant plant species between the intensively and extensively used grasslands. Thus, differences in resource use and drought-tolerance traits between the dominant species could help to explain the different stability and resistance of the grassland systems (Hallett, Hsu, Clela et al., 2017). Furthermore, asynchrony in species' abundances is known to facilitate community stability and resistance against environmental perturbations (de Bello et al., 2021). Studies have shown that the asynchrony of species increases with species richness (Roscher et al., 2011) but declines with fertilization (Xu et al., 2015), two factors that differ between the extensively and intensively used grasslands in our study. The higher resistance of extensively used grasslands to inter-annual climate variability and climate manipulation could be therefore also partly explained by higher species' asynchrony (Xu et al., 2015; Zhang et al., 2019).

The stronger effects of inter-annual climate variability compared to experimental climate manipulation in our study might be due to the intensity of the drought events, which were unprecedented in their intensity (Rakovec et al., 2022) and likely exceeded a threshold of tolerance in water scarcity for most plants. Two meta-analyses also report stronger responses of plant communities to inter-annual climate variability compared to climate manipulation (Kröel-Dulay et al., 2022; Langley et al., 2018). Our seasonal climate manipulation was intended to correspond to a realistic future climate scenario and was not as extreme as many other experimental climate studies (Korell et al., 2020). Nevertheless, even when the magnitudes of experimental manipulation are stronger, weak responses of plant productivity to climate manipulations are quite common (Grime et al., 2000; Hoover et al., 2014; Jentsch et al., 2007, 2011). When considering below-ground processes, other published studies from the GCEF have demonstrated that future climate conditions reduced soil biological activity (Kostin et al., 2021; Siebert et al., 2019) and changed soil microbial communities (Bei et al. 2023). These alterations in belowground processes can feedback on aboveground processes

such as productivity (Bardgett & Van der Putten, 2014) and emphasize the need to jointly consider above- and belowground processes as well as multitrophic interactions in global change experiments in order to understand related ecosystem functions.

5 | CONCLUSIONS

Climate and land-use change are known to be major threats to biodiversity and the functioning of ecosystems, but how these global change drivers interact is less clear. Our study provides experimental evidence that land-use change, including alterations in management intensity and plant diversity, alters the response of grassland communities to climate change. A realistic scenario of climate change, simulating seasonal shifts of precipitation, had relatively small effects on diversity and productivity of grasslands which were most pronounced in intensively used grasslands composed of a few grass cultivars. Future climate accelerated the shift from these forage cultivars to less valuable plant communities composed increasingly of immigrating species, which will have economic consequences for farmers. Likewise, intensively used grasslands showed significantly lower resistance to inter-annual climate variability, including the most severe droughts since the beginning of records, even though seed mixtures included cultivars recommended for moderately dry regions. We therefore conclude that a lower management intensity, associated with a higher plant diversity is an important tool to stabilize primary production under the impact of climate change.

AUTHOR CONTRIBUTIONS

Lotte Korell: Conceptualization; formal analysis; investigation; writing – original draft; writing – review and editing. **Martin Andrzejak:** Investigation; writing – review and editing. **Sigrid Berger:** Data curation; investigation; writing – review and editing. **Walter Durka:** Investigation; methodology; writing – review and editing. **Sylvia Haider:** Investigation; methodology; writing – review and editing. **Isabell Hensen:** Investigation; writing – review and editing. **Yva Herion:** Investigation; writing – review and editing. **Johannes Höfner:** Investigation; writing – review and editing. **Liana Kindermann:** Investigation; writing – review and editing. **Tiffany M. Knight:** Investigation; writing – review and editing. **Stefan Klotz:** Funding acquisition; methodology; writing – review and editing. **Anja Linstädter:** Investigation; writing – review and editing. **Anna-Maria Madaj:** Investigation; writing – review and editing. **Ines Merbach:** Investigation; project administration; writing – original draft. **Stefan Michalski:** Investigation; writing – review and editing. **Carolin Plos:** Investigation; writing – review and editing. **Christiane Roscher:** Investigation; methodology; writing – review and editing. **Martin Schädler:** Methodology; project administration; writing – review and editing. **Erik Welk:** Investigation; methodology; writing – review and editing. **Harald Auge:** Conceptualization; data curation; formal analysis; funding acquisition; methodology; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at <https://doi.org/10.6084/m9.figshare.24960669>.

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