Effects of climate change and grassland management on plant population dynamics are mediated by changes in reproductive success

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Abstract

1. Climate change is one of the largest threats to grassland plant species, which can be modified by land management. Although climate change and land management can separately and interactively influence plant demography this has been rarely considered within one experimental set-up.
2. We used a large-scale experiment to quantify the effects of grassland management, climate change and their joint effect on the demography and population growth rate of 11 native plant species. We parameterized integral projection models with four years of demographic data to project the population growth rate. We hypothesized, plants would perform better in ambient than in the future climate treatment that creates hotter and drier summer conditions and that plant performance in grazing vs. mowing would vary across species and depend on their traits.

3. Due to extreme drought events, over half of our study species went quasi extinct. Of the persistent species, only one supported our expectations, and the rest either had higher population growth rates in the future climate treatment or showed no significant difference in population growth between climate treatments. Species with shorter flowering durations performed better in the mowing treatment while those with longer flowering durations performed better in the grazing treatment. The population growth rates of these species were sensitive to changes in vital rates related to reproduction and recruitment.
4. Our study highlights how extreme climate events, can influence long term experimental results. Depending on the species we found effects of land management and climate change on population growth rates but we did not find strong support for interactive effects among both factors.
5. Experiments combined with measuring plant demographic responses provide a way to isolate the effects of different drivers on the long-term persistence of species, and to identify the demographic vital rates that are critical to manage in the future. Our study suggests that it will become increasingly difficult to maintain species with preferences for moister soil conditions, that traits such as flowering duration might predict responses to management, and that vital rates such as reproduction and recruitment are disproportionately important.

Keywords

Integral projection model, life table response experiment, sheep grazing, mowing, grassland management, climate change experiment, plant population dynamics, elasticity analysis

Introduction

Grasslands cover approximately 40% of the Earth's surface (Bardgett et al., 2021) and provide important ecosystem services to society, such as food for livestock and humanity, pollination and biodiversity (Biurrun et al., 2021; Feurdean et al., 2018). In Central Europe, semi-natural grasslands were historically managed using low-intensity (i.e. extensive) mowing or grazing, which prevents their succession into forests (Poschlod et al., 1998; Tälle et al., 2015). These different types of management affect which types of plants can persist. For example, grazing favors plants with traits related to higher grazing resistance (e.g. hairiness) or grazing tolerance (e.g. resprouting capacity) (Bernhardt-Römermann et al., 2011; Evju et al., 2009; Kahmen et al., 2002). Anthropogenic climate change may modify the effects that management has on the demography and persistence of plant species (Bardgett et al., 2021; Kariyeva et al., 2012; Redlich et al., 2022). For example, individuals that currently avoid loss of reproduction from mowing by flowering before or after mowing events might shift in their phenology in the future due to climate change, which could lead to mismatches between flowering timing and mowing events that harm plant reproductive success (Cleland et al., 2006; Gordo & Sanz, 2010).

In central Europe, temperature is projected to increase and it is projected to become wetter in spring and fall and drier in summer (Döscher et al., 2002; Jacob & Podzun, 1997; Rockel et al.,

2008; Wagner et al., 2013). Drought-tolerant species should be best able to survive the drier summers expected in the future (Belovsky & Slade, 2021). Species that flower earlier and across a longer time period might be favored in the future, because they can take best advantage of the wet spring conditions and because the long flowering duration might buffer their populations from complete reproductive failure during periods of extreme weather. This leads to the expectation that drought-tolerant plants with an early flowering start combined with a long flowering period should be best able to avoid losing reproductive success under future climate conditions in the presence of grazing and mowing land management types.

In order to understand population dynamics of plant species, demographic studies quantify vital rates such as survival, growth and reproductive output across the entire life cycle of the plant and project long-term population growth rate using structured population models (Caswell, 2000; Crone et al., 2011; Easterling et al., 2000). A common approach to analyzing plant demographic data are Integral Projection models (IPMs), which consider a relationship between continuous plant size and vital rates and can also incorporate discrete development stages (Childs et al., 2003; Jacquemyn et al., 2010; Yule et al., 2013). Retrospective analyses of IPMs, such as life table response experiments, decompose the contribution of individual vital rates to the changes in population growth rate between treatments. Vital rates that are more responsible for the change are those that, either change dramatically between the treatments and/or those that the population growth rate is sensitive to changes in (Rees & Ellner, 2009).

Many demographic studies have been conducted to assess how the demography of species responds to climate (Ehrlen, 2019; Ehrlén et al., 2016; Ehrlén & Morris, 2015; Lemmer et al., 2021; Morris et al., 2020). Most studies focus on natural variation across space and time in

87 climate conditions and measure plant demographic responses (Compagnoni et al., 2021). Such
88 observational studies are limited in their ability to assess cause and effect relationships, as
89 there are often other important factors that co-vary with climate. A few studies have
90 experimentally assessed how climate affects plant demography (Compagnoni & Adler, 2014;
91 Lemmer et al., 2021; Lyu & Alexander, 2022; Töpper et al., 2018; Williams et al., 2007).
92 However, most climate change experiments consider extreme manipulations of temperature
93 and precipitation, making it hard to predict how plants might respond under realistic future
94 climate change scenarios (Korell et al., 2020).

95 We have a unique opportunity to study how a realistic future climate scenario as well as two
96 different grassland management types (extensive grazing vs. mowing) influence the
97 demography and population dynamics of plants using the Global Change Experimental Facility
98 (GCEF) in Germany. Our study builds on the research of Lemmer and colleagues (Lemmer et al.,
99 2021), which discovered that land management types and climate change interactively affected
100 the population growth rate of the drought-tolerant grass, *Bromus erectus* L., and that this
101 interaction was primarily due to higher seedling recruitment of plants under the future climate
102 and mowing management treatment combination. Lemmer et al. (2020) measured the
103 demography across a short time period (1transition, two years) and concentrated on a single
104 species. In this study, we expand the scope to understand the demography and population
105 responses to climate and land management types across multiple transitions along a longer
106 time period and multiple plant species. Demographic data was collected over the course of five
107 years (2018 – 2022) for eleven (Table 1) grassland plant species that represent a range of
108 different plant statures (tall vs. small), life forms (grasses, herbs) and life histories (biennials vs

perennials). In general, we expected i) the effects of land management types will vary across species and depend on their traits, ii) plants show higher population growth rates under ambient compared to future climate conditions and iii) the effects of climate treatments and land management types on the population growth rate will be interactive.

Methods

Study site

We conducted our research in the Global Change Experimental Facility (GCEF), which was established in 2013. The experiment is part of the research station Bad Lauchstädt (51°22060 N, 11°50060 E, 118 m a.s.l.). It is designed to simulate a realistic future climate scenario combined with the manipulation of different land management types, including extensively managed grasslands. The future climate treatment is based on a mean of 12 regional climate models for the region (Schädler et al., 2019).

The GCEF consists of 10 main units, five with ambient climate and five with future climate conditions. Precipitation in the future climate treatment is manipulated seasonally: increases in precipitation by +10 % compared to the ambient climate in spring and fall and reduced precipitation by -20 % compared to the ambient climate in summer (for more details see Schädler et al. 2019). The minimum temperature in the future climate treatment is increased by about +1.5°C by passive nighttime warming (Schädler et al. 2019).

Each main unit is divided into five subunits that are 16m x 24m in size, each representing a different land management. Each subunit has 14m x 19.5m available for measurements and the remainder is left as an edge area, where no experiments or measurements can be undertaken (Appendix 1, Fig. A1). Our study was established in two of the five land managements, the extensive meadow (mown one or two times per year) and the extensive pasture (grazed by 20 sheep for 24 hours twice to three times per year). These two land management types were initially sown in 2013 with 56 plant species native to Germany (Schädler et al., 2019). This design leads to the following treatment combinations in our experiment: (1) ambient grazing, (2) ambient mowing, (3) future grazing and (4) future mowing.

Study species

In 2018, we chose eleven different species (Table 1) for our demographic study based on the criteria that they were abundant enough for demographic data collection (minimum number of individuals in 2018 was 50 per treatment combination), and that they were species that are typically associated with mesic or dry grasslands. The species covered a range of growth forms, plant families and life histories (biennial vs. perennial). Every plant species in this study is native to Germany and was sown into the GCEF experiment when it was established.

Table 1 Description of each plant species in the study. Life histories are: p = perennial and iteroparous, b = biennial, h = pluriennial-hapaxanthic (https://wiki.ufz.de/biolflor/index.jsp). Ellenberg wetness values (indicator of drought tolerance, (Ellenberg et al., 1991): 3 = species is more common at dry sites, avoids wet habitats (indicator for dry habitats), 4 = usually more on dry habitats, however able to grow on wet sites, 5 = prefers intermediate locations, missing on very dry and very wet locations, 6 = prefers semi wet to wet locations, 7 = prefers wet locations, without waterlogging. Ind = indifferent can grow in dry

150 and wet conditions. In 2020 we recorded the starting month and ending month of flowering for each
151 species in the GCEF. Flowering duration is the number of months we found an individual flowering
152 (difference between the end and start month of flowering). Unit of measurement describes how plant
153 size was measured for each species: basal area (length and width of an individual was recorded and area
154 was calculated), number of leaves. The grazing resistance of each species was based on the Biolflor
155 database's index of grazing resistance: 2 = intolerant to sensitive to grazing, 4 = sensitive to moderately
156 tolerant to grazing, 5 = moderately tolerant to grazing and 6 = moderately tolerant to well tolerant to
157 grazing, NA = no information available. The mowing resistance of each species was based on the Biolflor
158 database's index of mowing resistance: 3 = sensitive to mowing, 4 = sensitive to moderately tolerant to
159 mowing, 5 = moderately tolerant to mowing, 6 = moderately to well tolerant to mowing, 7 = well
160 tolerant to mowing.

Species name	Growth form	Plant family	Life history	Ellenberg	Start of flowering	End of flowering	Duration of flowering	Unit of measure	Grazing resistance	Mowing tolerance
Anthoxanthum odoratum L.	Grass	Poaceae	p	ind	April	April	1	Basal	5	7
Bromus erectus Huds.	Grass	Poaceae	p	3	May	June	2	Basal	4	5
Crepis biennis L.	Forb	Asterace	b	6	June	August	3	Number	2	6
Dianthus carthusianorum L.	Forb	Caryoph	p	3	May	October	6	Basal	4	3
Lotus corniculatus L.	Legume	Fabacea	p	4	June	July	2	Basal	4	6
Lychnis flos-cuculi L.	Forb	Caryoph	p	7	NA	NA	NA	Basal	2	4
Medicago falcata (L.) Arcang	Legume	Fabacea	p	3	June	July	2	Basal	2	5
Plantago lanceolata L	Forb	Plantagi	p	ind	May	July	3	Number	6	7
Scabiosa ochroleuca L.	Forb	Dipsacac	p	3	June	October	5	Basal	NA	NA
Tragopogon orientalis L.	Forb	Asterace	h	5	June	August	3	Number	NA	NA
Trifolium pratense L.	Legume	Fabacea	p	5	May	May	1	Basal	4	7

Demographic data collection

In April 2018, we established one transect on all our study subunits resulting in 20 transects (five replicates per treatment combination). Our goal was to find a minimum of 10 individuals per transect, to reach a minimum of 50 individuals per treatment combination for every species. Along each transect, 50 x 50 cm subplots were established. We assigned three of the subplots to a fixed positions along each transect (0– 0.50 m; 3 – 3,50 m; 6-6.50 m). The location of other subplots were chosen along the transect at strategic locations to capture individuals of species that were needed to achieve our target of 50 individuals per species and transect. Following this procedure, most transects had eight subplots. This leads to a different overall subplot number for each species, with rarer species having more subplots than common species. Each subplot was marked with a land marking (pipe with red plastic top) in the bottom left and a nail with a white plastic ring the top right corner.

In April 2018, we measured the size of each individual target species in each subplot using either basal area or number of leaves (Table 1). Basal area (cm^2) measured as the product of the horizontal width and length at the base of each individual. Length was measured as the longest lateral dimension of each plant, and width was measured perpendicular to the length. For rosette species (e.g. *Plantago lanceolata, Tragopogon orientalis*), we used the number of leaves as proxy for their size. We recorded the location of each individual within the 50 x 50 cm subplot, using an XY-coordinate system so that individuals could be followed over the years. In rare cases if we spotted individuals of our rarer species just outside of our subplot, we would measure those individuals and track their position relative to the subplot (one of the coordinates would exceed 50 cm).

From 2019 until 2022, we went to the field five times a year. In April, we re-located individuals from the previous year and measured their size, identified new individuals and measured their size, and counted the number of new seedlings (for details on how we identified seedlings see Appendix 3, Table A2). Depending on the phenology of the species and the management events (see Table 1, Table A1), we counted flowers and seed heads of all reproductive individuals in each transect. Further we collected two seed heads per subunit and species from individuals that were outside of our transects but within the same subunits. Number of seeds in each seed head were counted in the lab. In late autumn (October/November), we counted the number of seedlings in our subplots, as seedlings of these species can germinate in spring or in fall.

From 2019 onwards, we decided to mark individuals of the very abundant species *Bromus erectus* with ID's as that helped separating and finding individuals. To mark the individuals, we used rings made of wire with a tag with a running number on it and put it around the base of the individual. We left enough space for the individual to grow. Special care was taken to not harm any of the vegetation during that process.

The multiple droughts Germany experienced during several of the years of this study prevented more frequent mowing and grazing than would otherwise be incorporated into the treatment plan (Schädler et al., 2019). During the time of our experiment, the extensive meadows were mown once per year in early summer time from 2018 – 2020 and two times (early and late summer) in 2021. The extensively grazed subplots were grazed twice per year in spring and early summer from 2018-2020, and three times in 2021 (spring, early and late summer). For a detailed look at the management timing, see Appendix 2, Table A1.

204 For information on traits for our species, we used Ellenberg values (Ellenberg et al., 1991), the
205 Bioflor database (https://wiki.ufz.de/biolflor/index.jsp) and our own measurements of
206 phenology. For drought tolerance, we used categorical Ellenberg values (Ellenberg et al., 1991,
207 Table 1). For grazing and mowing resistance, we used categorical values from the Bioflor
208 database (Table 1). In 2020, we collected phenology data on our target species in the GCEF
209 between April and December within the central 3 x 3 m vegetation survey plot of each subunit
210 where no experiments or other disturbances (besides the management events) occur. This
211 provides information on the month in which flowering began and the month it ended, taking all
212 individuals inside the central vegetation plot into account.

213

214 **Quasi extinction**

215 Some of the species declined so significantly over the course of our demographic study, that we
216 considered them quasi extinct and no longer continued to collect demographic data. We
217 defined quasi extinction from a treatment combination as fewer than 25 individuals total and
218 fewer than 10 flowering individuals, thus those species treated the species as quasi extinct.

219

220 **Life cycle stages and vital rates**

221 For all species, we modeled a year-to-year life cycle (April to April) with two stage classes. A
222 discrete class for seedlings and a continuous class for plants (Fig. 1). Most of our species do not
223 form long lasting seed banks, and thus we do not have a seed bank class. *Plantago lanceolata*

does have a long-lived seed bank (Chen, 2018), but most of the seeds of this species germinate immediately and therefore demographic studies on this species do not typically incorporate the seed bank stage (e.g., www.plantpopnet.com).

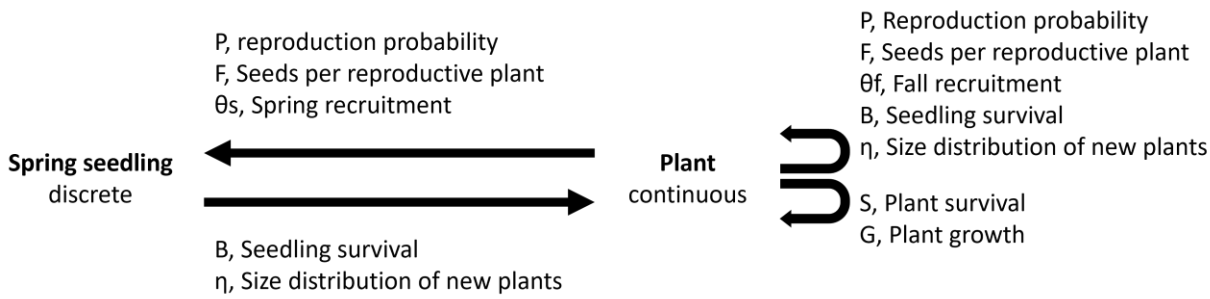

Fig. 1 Life cycle diagram of the study species. The diagram shows every vital rate incorporated in the integral projection model (IPM) and the abbreviation used.

We modeled each continuous state of the IPM as a function of the natural logarithm of the size of an individual. We used generalized linear models to fit all continuous variables. Survival is a function of whether or not an individual (i) was still alive at t1, dependent on its log transformed size (z) at t0 (Eq. 1), modeled as a Bernoulli process with probability of survival S_{t1} (Eq. 2).

[1] $$S_{i,t1} \sim Bernoulli\left(\hat{S}_{t1}\right)$$

[2] $$logit\left(\hat{S}_{t1}\right) = \alpha + \beta\, log_e(z)$$

In this function α is the intercept and β the slope of the curve.

Growth of plants $G_{i,\,t1}$ is described as the normally distributed change in z and log transformed size at t1 (z') of a surviving individual plant (i) (Eq. 3). It was modeled as a linear function of z' of

surviving individuals depending on z, where the intercept is defined as α^G, the slope as β^G (Eq. 4) and the standard deviation as σ_G (Eq. 3).

[3] $$G_{i,t1} \sim Normal\left(\hat{G}_{t1}, \sigma_G\right)$$

[4] $$\hat{G}_{i,t1} = \alpha^G + \beta^G \, log_e(z)$$

Similar to survival, we modeled reproduction probability ($P_{i,\,t0}$) as Bernoulli process (Eq. 5). Here we tested how the probability an individual i reproduces at time t0 depends on z. The intercept is defined as α_t^P and the slope as β^P using a logit link function (Eq. 6)

[5] $$P_{i,to} \sim Bernoulli\left(\hat{P}_t\right)$$

[6] $$logit\left(\hat{P}_{to}\right) = \alpha_t^P + \beta^P \, log_e(z).$$

For every reproductive plant, we calculated the number of seeds it produced (Eq. 7). The number of seeds produced by an individual I at t0 was a function of z, modeled as a Poisson distribution. The intercept was defined as α_t^F and slope β^F (Eq. 8)

[7] $$F_{i,t0} \sim Poisson\left(\hat{F}_{t0}\right)$$

[8] $$\hat{F}_t = \alpha_t^F + \beta^F \, log_e(z).$$

Recruitment, the emerged seedlings per total number of seeds, was separated into fall - ($\theta_{f,\,j,\,t0}$) and spring recruitment ($\theta_{s,\,j,\,t0}$). To calculate recruitment, we summed the total number of seeds per subplot ($S_{j,t}$, Eq. 9). Where $S_{i,t1}$ is the total number of seeds produced by one individual (n) in a subplot at time t1.

[9] $$S_{j,t} = \sum_1^n S_{i,t1}.$$

We then divided the result of Eq. 9 by the number of seedlings found in that subplot in fall t0 ($Rf_{j,\,to}$, Eq. 10) and spring t1 ($Rs_{j,t1}$, Eq. 11).

[10] $$\theta_{f,j,t} = \hat{R}f_{j,to} / S_{j,t}.$$

[11] $$\theta_{s,j,t+1} = \hat{R}s_{j,t1} / S_{j,t}.$$

Establishment (B_j) is the proportion of seedlings that survive to become plants from t0 to t1 in each subplot j. We calculated the sum of seedlings in spring and fall t0 ($Rsum_{j,\,t0}$) of a subplot and divided that number by the number of new individuals at t1 ($Ni_{j,\,t1}$) in the same subplot.

[12] $$B_j = Ni_{j,t1} / Rsum_{j,t0}$$

We calculated the log size distribution of new plants η which is defined as the normally distributed size of individuals that entered the continuous plant stage in year t1 (Eq. 12). We used the mean ($log_e(\hat{\eta}_{t1})$) and standard deviation (σ_η) of this size in our final parametrization of the IPM.

[13] $$log_e(\eta_{i,t1}) \sim Normal\ \left(log_e(\hat{\eta}_{t1}), \sigma_\eta\right)$$

Effects of treatments on vital rates

For each vital rate (survival, growth, reproduction probability, number of seeds, recruitment, establishment, size distribution of new plants), we generated three independent pipelines. The first pipeline differentiated between the climate treatment and thus we calculated the

parameters for ambient and future climate, respectively (Table 2). The second pipeline differentiated between land management types (mowing and grazing). In the third pipeline, we differentiated between all four treatment combinations to also account for possible interactions among treatments. In each of those models, we dropped year, to make the models more robust (but see Appendix 5 for the “yearly” models).

Table 1. Vital rates included in integral projection model (IPM), its abbreviation, the parameters used and the according distribution, and which life table response experiment LTRE stage class it was part of.

Vital rates	Abbreviation	Life-cycle stage	Parameters	Distribution	LTRE stage
Plant survival	S	Survival	Intercept (Int), Slope	Bernoulli	Survival
Plant growth	G	Growth	Intercept (Int), Slope, SD	Normal	Growth
Reproduction probability	P	Reproduction	Intercept (Int), Slope	Bernoulli	Reproduction
Number of seeds per reproductive plant	F	Reproduction	Intercept (Int), Slope	Poisson	Reproduction
Fall recruitment	θf	Recruitment	Mean		Recruitment
Spring recruitment	θs	Recruitment	Mean		Recruitment
Seedling establishment	B	Establishment	Mean		Establishment
Size distribution of new plants	η	Establishment	Mean, SD		Establishment

Integral projection model (IPM)

For each species and pipeline, we created an IPM to calculate the influence of climate and management on the long-term population growth (λ). In every IPM, we calculate all possible transitions from z to z' at. The change in number of plants from one year to the other is described by:

[14] $$n(z',t1) = M(t0)B\eta(z') + \int_L^U S(z)G(z',z) + P(z)F(z)\theta_f B\eta(z')n(z,t0)dz$$

Where the vector n(z', t1) is the number of plants at size z' at time t1. In this function, the first term represents the recruitment of spring seedlings entering the adult plant class. This is based on the number of spring seedlings at t0, M(t0), the seedling establishment, B, and the size distribution of new plants η(z'). The second kernel (or surface) describes the growth and survival of plants from t0, n(z, t0) to t1, n(z', t1). It is defined as an integral with in the upper limit U, which is the biggest size observed and the lowest size L, observed for the species in our study. The integrals were evaluated across 200 equally spaced size bins using the midpoint rules as a 200 x 200 matrix.

The recruitment of spring seedlings from one year to the next is described by:

[15] $$M(t+1) = \int_L^U P(z)F(z)\theta_s dz.$$

As we did not distinguish the new plants we see in April as those that were seedlings from fall vs. spring, we use the same establishment estimate for seedlings (B) twice in the model.

Effects of treatments on population growth rate

To determine the effect of the climate treatment on λ, we calculated λ for the ambient and future treatments and then calculated an effect size by subtracting λ ambient from λ future. Positive values show a species´ preference for ambient climate conditions whereas negative values show a species´ preference for future climate conditions. Likewise, for land management types, we subtracted λ grazed from λ mowing to calculate an effect size. Here, positive values

show a species preference for the grazing treatment whereas negative values show a species favors the mowing treatment.

To test whether traits influenced the effect size of land management types on λ, we ran simple linear models using the effect size as response variable and the following traits as explanatory variable: flowering start month, duration of flowering, grazing resistance and mowing resistance. Because flowering time, start and end could differ between treatments due to the effect of the land management type we decided to not calculate a mean across those.

To quantify uncertainty in estimates of λ, we bootstrapped our data a thousand times and calculated the λ each time. To test for significant differences in λ between treatments and treatment combinations, we used permutation (randomization) tests (N = 1000 permutations). For each treatment combination, we calculated sensitivities and elasticities of λ to kernel element perturbations.

Life table response experiment (LTRE)

In order to decompose the influences of vital rates on the difference in λ, across treatment combinations, we conducted Life Table Response Experiments (LTRE) for each pairwise treatment combination. The difference in λ, $\Delta\lambda$, is:

[17] $$\Delta\lambda = \lambda^{treatment\ combination\ 1} - \lambda^{treatment\ combination\ 2}$$

The contribution of each vital rate to Δλ, $\tilde{\delta}^{\alpha i}$, is:

[18] $$\tilde{\delta}^{\alpha i} = \sum_i^{14} (a_i^{treatment\ combination\ 1} - a_i^{treatment\ combination\ 2}) \frac{\partial\lambda}{\partial\alpha_i}$$

Here α_i is one of the fourteen vital rates that are included in the IPMs, while the sensitivity of λ to each vital rate is defined as $\frac{\partial \lambda}{\partial \alpha_i}$. Vital rates will have a strong contribution to the observed difference in λ between treatment combinations if the vital rates change strongly in magnitude between the two treatment combinations and/or if λ is sensitive to changes in that vital rate. To facilitate the understandability, we combined the vital rates with respect to six demographic processes: survival, growth, reproduction, recruitment, establishment (Table 2). After this we scaled $\widetilde{\delta}^{\alpha_i}$ to 1 (to display proportional influence).

Analysis

All analysis were carried out in R (R Core Team, 2022). Figures were made using the ggplot2 package (Wickham, 2016). The integral projection model was run and calculated using the ipmr packages (Levin et al., 2021). Other packages used were: openxlsx (Schauberger & Walker, 2021) to load the xlsx files into R, dplyr (Wickham et al., 2022) for structuring data and piping and the package parallel (R Core Team, 2022) to decrease the running time of R scripts. The R code can be found at GitHub:

Martin19910130/Effect_of_climate_and_land_use_on_population_growth_rate

and the data is supplied at figshare:

https://figshare.com/account/home#/projects/157925.

Results

Quasi extinction

The following six species went quasi extinct over the course of the experiment: *Anthoxanthum odoratum, Crepis biennis*, *Lotus corniculatus*, *Lychnis flos-cuculi* and *Trifolium pratense*. While there is too small of a sample size (N=11 species) for statistical analysis, it is notable that the species that went quasi extinct were also the ones that were less drought tolerant based on their Ellenberg values (Table 1) and that the first few years of our study were extraordinarily dry for our region (Boergens et al., 2020).

Management effects on population growth rate

Tragopogon orientalis had significantly higher λ in mowing compared to grazing management (permutation test $p = 0.042$, Fig. 2E), whereas all other species did not show a significant main effect of management on λ (Fig. 2A-D).

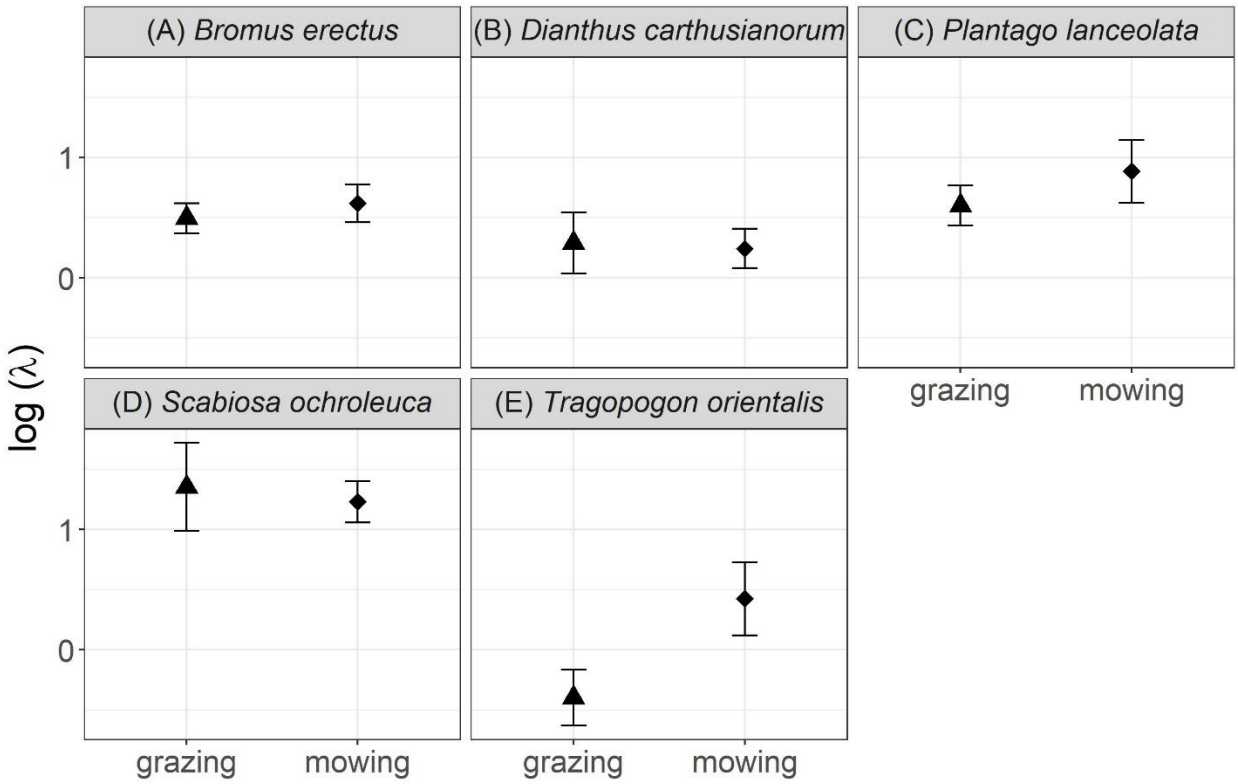

Fig. 2 Log population growth rate (λ) for each of the five study species (A-E) considering the two different land management types (grazing and mowing). Displayed is the mean ± one standard deviation.

Traits related to grazing resistance and mowing resistance did not explain the effect size of land management type on λ (Appendix 4, Fig. A2). However, flowering duration was positively related to the effect size of land management type on λ; species with lower flowering duration (i.e. *Plantago lanceolata, Bromus erectus, Tragopogon orientalis*) performed better in the mowing treatment while those with longer flowering duration (*Dianthus carthusianorum*, *Scabiosa ochroleuca*) performed better in the grazing treatment ($t = 6.087$, $p < 0.001$, $r^2 = 0.8$; Fig. 3A). The start of flowering was a poor predictor of management preferences (Fig. 3B, $t = -0.206$, $p = 0.842$, $r^2 = -0.1191$).

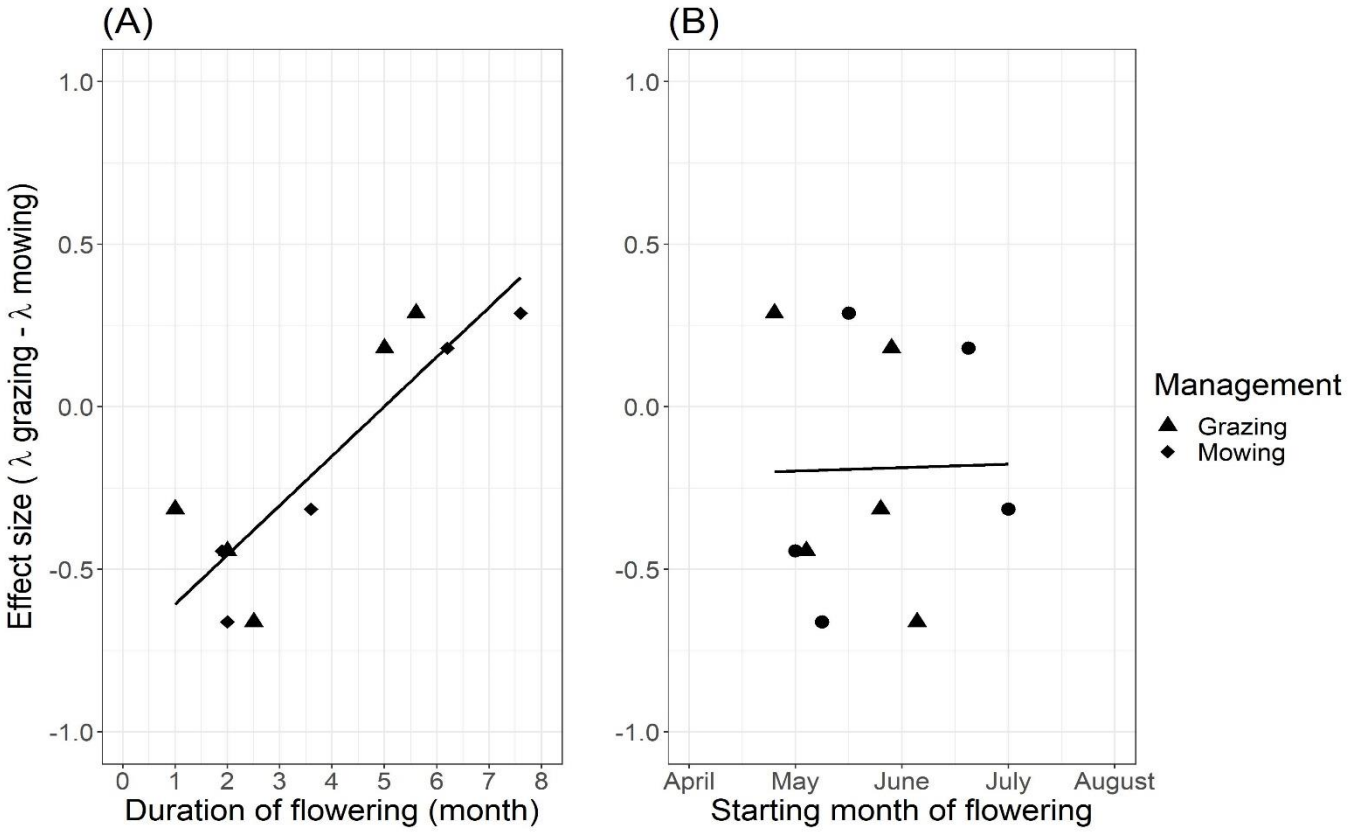

Fig. 3 Relationship between the effect size of management on population growth rate (λ grazing – λ mowing) plotted against A) The mean duration of flowering for each species and B) the mean beginning of flowering for each species. The line indicates the trend from the linear model. Symbols show the management treatment in which phenology was measured.

Climate effects on population growth rate

B. erectus had a significantly higher λ in future compared to ambient climate (permutation test, p = 0.023, Fig. 4A), and the other four species did not show significant differences in λ with regard to the climate treatment (Fig. 4B-E).

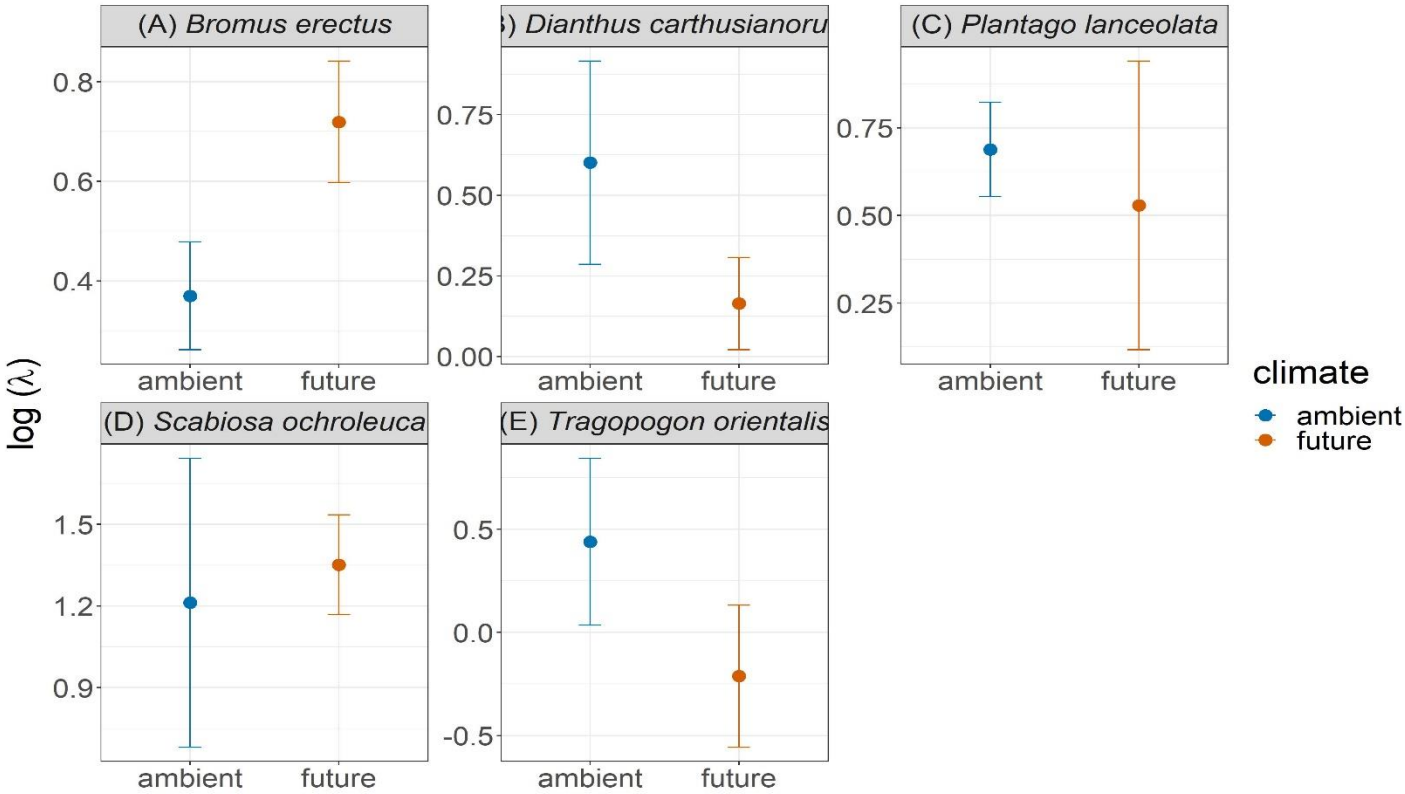

Fig. 4 Bootstrapped logged λ plotted against the two climate treatments (ambient and future) for the five different study species (A-E). Displayed is the mean logged λ of the 1000 repetitions, with the standard deviation.

Effect of climate and land management type on population growth rate

In *S. ochroleuca,* λ was significantly higher in future compared to ambient climate in the mowing land management type (future mowing > ambient mowing; permutation test, $p = 0.011$) but not in grazing land management (permutation test, $p > 0.05$, Fig. 5D). The λ of *T. orientalis* was significantly higher in ambient compared to future climate only in the grazing management treatment (ambient grazing > future grazing; permutation test, $p = 0.006$) and λ was higher in mowing compared to grazing management only in future climate (permutation test, $p = 0.026$, Fig. 5E). For all other species (*B. erectus*, *D. carthusianorum* and *P. lanceolata*) the lines in the interaction plots crossed but they were not significantly different from each other due to the large variability around the mean (Fig. 5A-C).

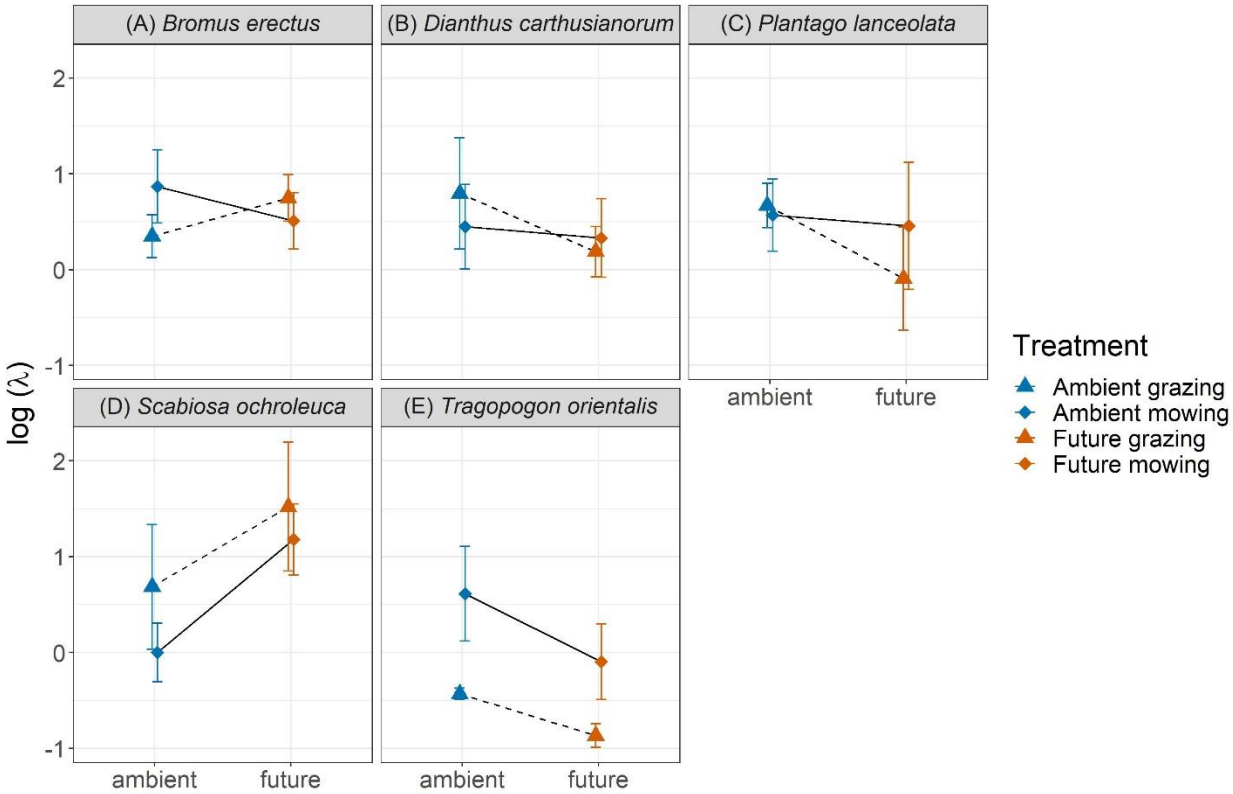

Fig. 5 Effect of climate (ambient and future) and land management type (grazing and mowing) on population growth rate (λ) of the five study species (A-E). Displayed is the mean and the standard deviation.

Sensitivity

Across all species and treatments, λ was most sensitive to changes in reproduction parameters (Fig. 6). While the magnitude differed between treatments and species (e.g. *S. ochroleuca* highest in grazing and future *D. carthusianorum* highest in ambient).

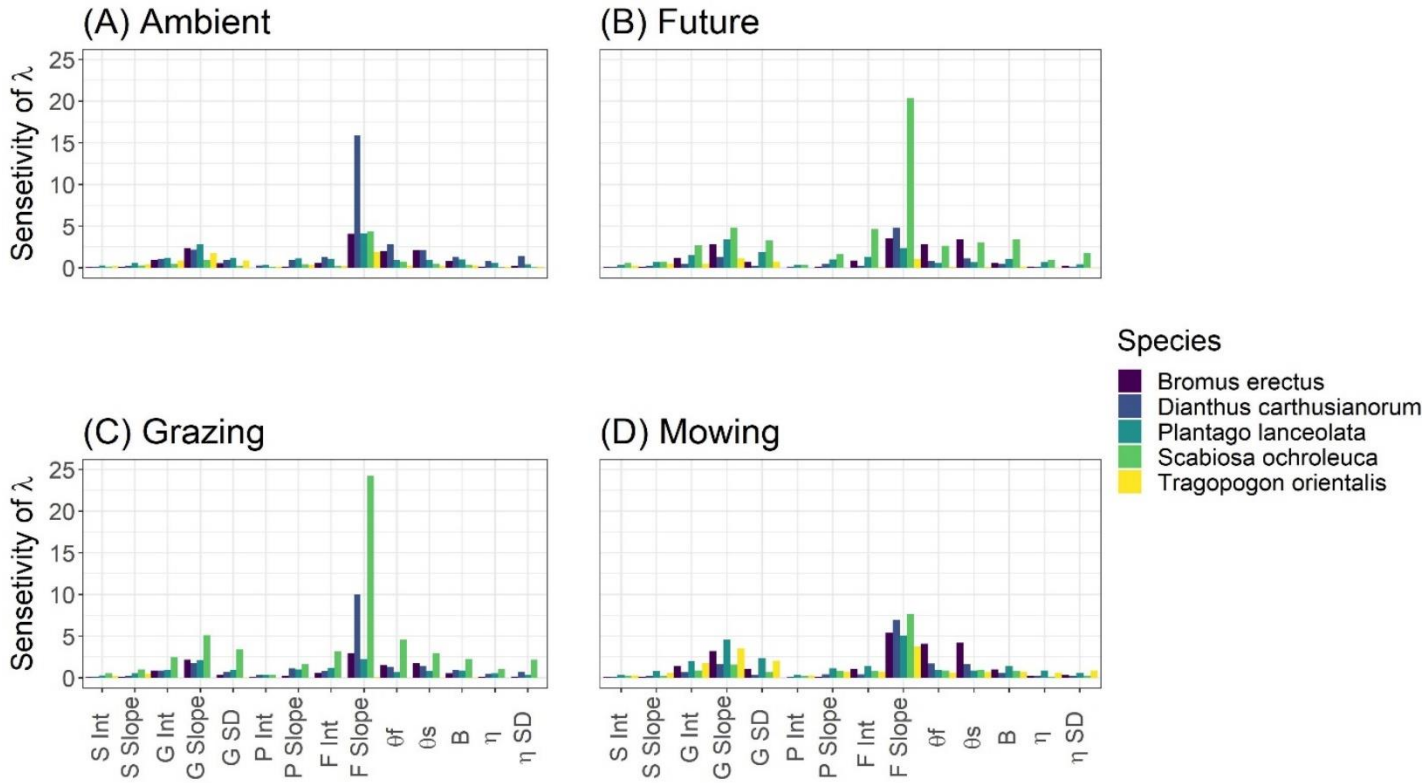

Fig. 6 Sensitivity of pairwise treatment combinations for every vital rate included in the IPM. Each species is color-coded.

Life Table Response Experiment

The higher λ of *B. erectus* in future compared to ambient climate was primarily due to increases in reproduction and recruitment of this species under future climate (Fig. 7C and 7D). The higher λ of *S. ochroleuca* in future compared to ambient climate in the mowing management treatment was primarily due to increases in the reproduction of this species in the future mowing treatment (Fig. 7D). The higher λ of *T. orientalis* in ambient compared to future climate in the grazing management treatment was primarily due to increases in plant survivorship (Fig.

7C), whereas the higher λ in this species in mowing compared to grazing in future climate treatment was due to higher survival and reproduction (Fig. 7B).

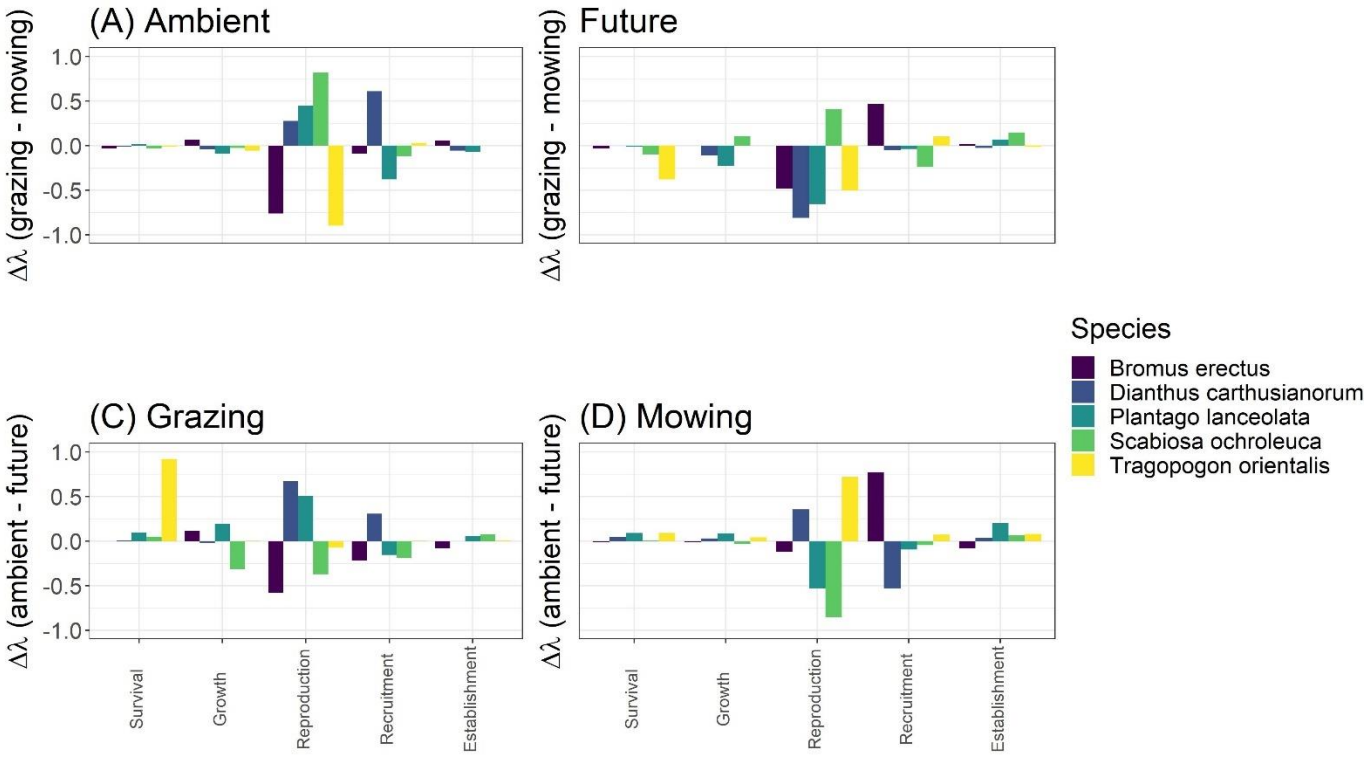

Fig. 7 Results for the Life Table Response Experiment (LTRE). Each species is displayed in a different color. A) Ambient climate treatment and the effect of the two land management types on the parameters. B) Future climate treatment and the effect of the two land management types on the parameters. C) Grazing land management type and the effect of climate on the parameters. D) Mowing land management type and the effect of climate on the life stages. For a better overview, we summed the parameters according to their corresponding live stage.

434 **Discussion**

435 Our study aimed to examine whether plant species interactively respond to climate and land
436 management types in their demography and population dynamics. However, in the early years
437 of our study, six of our eleven focal species went quasi extinct from the experiment, likely due
438 to the extreme drought conditions that occurred in our region in 2018 and 2019. This is
439 becoming an increasing phenomenon in experimental global change research—even the
440 control treatments experience extreme climate events because these are now more common in
441 our rapidly changing world (IPCC, 2014; Jentsch et al., 2007; Orlowsky & Seneviratne, 2012;
442 Tebaldi et al., 2006). Of the remaining five species, we found that flowering duration is an
443 important trait that predicts responses to land management types, with shorter duration
444 species having higher λ in mowing management and longer duration species having higher λ in
445 grazing management. In contrast to our expectation that plants would perform better in
446 ambient compared to future climate conditions, we found that two species (*B. erectus* and *S.*
447 *ochroleuca*) have higher λ in the future climate treatment and only *T. orientalis* shows the
448 expected higher λ in ambient climate. We suggest this is likely due to the high drought
449 tolerance of *B. erectus* and *S. ochroleuca*. We did not find strong support that the effects of
450 climate and land management types were interactive for our study species, and it is unclear if
451 this is because these interactive effects do not occur or because we have low power to detect
452 them.

453 We expected that plants species in the study region (Central Germany) would perform best in
454 ambient climate, as they would have difficulty dealing with the dry conditions expected in the
455 summer under future climate. However, our results do not support this hypothesis. The first

year of our demographic study, 2018, coincided with the driest summer for Germany since start of recording (Schuldt et al., 2020). This drought had dramatic and long-lasting effects on the plant communities across the entire GCEF experiment. Many of the species that went extinct were those that are indicative of moist soil conditions. Four of the five species that remained are indicative of drier habitat conditions and commonly occur in semi-dry or dry meadows (*B. erectus*, *D. carthusianorum* and *S. ochroleuca*) or are known to be highly generalized with regards to the moisture of the habitat (*P. lanceolata*). *B. erectus* and *S. ochroleuca* were also the two species that performed better in future experimental climate conditions. This result matches previous experimental studies (Lemmer et al., 2021; Moser et al., 2011; Poniatowski et al., 2018) that show high performance of *B. erectus* in hot and dry summer conditions. Our LTRE results revealed that the higher λ of *B. erectus* in future climate was due primarily to the higher reproduction and recruitment in this treatment (see also Lemmer et al. 2021). The earlier flowering of *B. erectus* compared to other species could explain its relative advantage in future climate conditions; *B. erectus* is able to take advantage of the additional water resources in spring and reproduce before the hot and dry summer conditions in the future climate treatment.

Only one of our remaining species, *T. orientalis,* is indicative of moist to moderately dry soil conditions (Sebald et al., 1990; Ellenberg et al., 1991; Bomble, 2013) and managed to persist in our study. This species did indeed show the expected higher performance in the ambient compared to future climate treatment. We suggest that we may have found more support for our hypothesis if we had been able to study the demography of more typical species from moister grassland communities as we initially planned. Our study highlights the importance of

historical legacies in shaping experimental results and support projections that communities may shift towards more drought tolerant species under future climate conditions (Belovsky & Slade, 2021; Craine et al., 2013).

Surprisingly, most of our study species did not show strong differences in their population growth across land management types. The only exception was the biennial species, *T. orientalis*, which performed significantly better in the mowing compared to grazing management treatment, primarily due to higher survival and reproduction in the mowing treatment. The vegetative parts of *T. orientalis* are relatively soft and easy for sheep to chew (personal observation) and the large flower heads may attract sheep. We also observed that the flower buds were eaten by other wild animals, such as rabbits (personal observation). This species adds to several studies that showed that grazing has a negative effect on plant population dynamics (Hansen & Wilson, 2006; Jacquemyn et al., 2012; van der Meer et al., 2014). For example, in *Primula veris*, grazing was found to decrease population growth rate, primarily through its negative effect on reproduction (Jacquemyn et al., 2012).

Our results show that the effect of management on λ depended on flowering duration. Plants that flowered a relatively short duration showed higher λ in mowing (e.g. *T. orientalis*), whereas those flowering across a longer duration showed higher λ in the grazing management. This could be because plant populations that flower across a long time period are buffered from losing all of their reproductive success from disturbances that occur in a short time interval, such as grazing. However, we have to be cautious when interpreting these results as in our study years the management was mostly applied in a lower frequency than usual; most years had one mowing and two grazing events. This was because mowing and grazing were not

500 possible when there was too little biomass regrowth, which occurred during the dry study
501 years. Other studies have also shown that low frequency (once a year) and late season mowing
502 benefits the reproduction of plants (Jantunen et al., 2007; Johansen et al., 2019). Across all of
503 our study species, we found that the population growth rates were most sensitive to
504 reproduction. Thus, it may be a general finding that management treatments should be timed
505 to interfere as little as possible with peak flowering and fruiting (Nakahama et al., 2016; Reisch &
506 Poschlod, 2009).
507 We expected that interaction effects of treatments on λ would be common in our study and
508 that each species would have a treatment combination that was most optimal for λ. However,
509 we had little power to test for these interactions due to the high variation across individuals in
510 the sensitive vital rates of seed production and recruitment. For example, the high variation in λ
511 of *S. ochroleuca* in the ambient-grazing treatment combination is likely due to very high seed
512 production (>2000 seeds) of three individuals in this treatment combination (Appendix 6).
513 Similarly, the high variation in λ in the ambient treatment for *D. carthusianorum* is likely due to
514 high seed production of a few individuals in the ambient mowing treatment (Appendix 6) and
515 high recruitment of new spring seedlings in a few plots in the ambient grazing treatment
516 (Appendix 7). Finally, while *P. lanceolata* appears overall have higher λ in ambient compared to
517 future climate treatments, high variance in the future-mowing treatment combination, which is
518 likely due to two reproductive individuals with outlier high seed production, may prevent the
519 detection of an effect.

520 In demographic studies of both plants and animals, reproductive output is known to be skewed
521 across individuals, with only a few individuals producing many offspring (van Daalen & Caswell,

522 2020). The ability to distinguish deterministic treatments effects from stochasticity among
523 individuals would require much higher sample sizes than is available in our GCEF experiment.
524 While there are many advantages of conducting multi-species demographic studies like this one
525 and of conducting demographic research in a controlled experimental setting, one distinct
526 disadvantage is the effort and sample size required to adequately detect small changes in
527 sensitive vital rates (McMahon et al., 2019).

528 It was surprising to find in our LTRE that changes in reproduction and recruitment often
529 contributed most to the observed responses of λ to management and climate. Usually in longer
530 lived species, λ is highly sensitive to changes in survival (Weppler, Stoll and Stöcklin, 2006; Kuss
531 et al., 2008) and thus even small changes in survival across treatments should contribute
532 significantly to changes in λ. In our case, we find that λ is highly sensitive to recruitment. This
533 might be due to the relatively high λ of our perennial species; species with high λ are often
534 more sensitive to reproduction and recruitment than to survivorship (Franco & Silvertown, 2004;
535 Ramula et al., 2008). Further, many of our species were able to maintain their survival across
536 treatments, but had high changes in their reproduction and recruitment.

537 **Conclusions**

538 Our study is a first step towards answering important yet unanswered question on how climate
539 change affects population dynamics of grassland species and how this effect is modified by
540 different land management types (Ehrlen, 2019). Our results are optimistic for our four more
541 drought-tolerant species characteristic for dry or semi-dry grasslands, showing persistent or
542 growing populations in both management types (grazing vs. mowing) and under future climate

conditions as well as after natural extreme drought events. However, less drought-tolerant species either went quasi extinct early in the study or were projected to decline in the future, indicating that populations cannot persist in the presence of future climate conditions. Our results suggest that it will be more difficult to create and maintain especially mesophilic grasslands composed of species with preference for moister soil conditions in the future. Furthermore, we suggest that management in future climate should carefully be timed outside of peak flowering and fruiting, so that as many species as possible can reproduce and persist in managed grasslands.

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Conflict of interest

No Author has a conflict of interest

Data availability statement

Data (Size data and reproduction data, as well as number of seed data):

https://figshare.com/account/home#/projects/157925

Author contributions

The study was designed by LK (leading) and MA and TMK (supporting). Fieldwork was designed and carried out by LK and MA (both leading). The data for the phenology of plants was collected by CP (leading). Analysis was carried out by MA (leading) with support of the other co-authors. The manuscript was written by MA (leading) and TMK and LK (supporting). All authors commented and improved the manuscript.

References

Bardgett, R. D., Bullock, J. M., Lavorel, S., Manning, P., Schaffner, U., Ostle, N., Chomel, M., Durigan, G., L. Fry, E., Johnson, D., Lavallee, J. M., le Provost, G., Luo, S., Png, K., Sankaran, M., Hou, X., Zhou, H., Ma, L., Ren, W., … Shi, H. (2021). Combatting global grassland degradation. *Nature Reviews Earth and Environment*, *2*(10), 720–735. https://doi.org/10.1038/s43017-021-00207-2

Belovsky, G. E., & Slade, J. B. (2021). Climate change and primary production: Forty years in a bunchgrass prairie. *PLoS ONE*, *15*(12 December). https://doi.org/10.1371/journal.pone.0243496

Bernhardt-Römermann, M., Gray, A., Vanbergen, A. J., Bergès, L., Bohner, A., Brooker, R. W., De Bruyn, L., De Cinti, B., Dirnböck, T., Grandin, U., Hester, A. J., Kanka, R., Klotz, S., Loucougaray, G., Lundin, L., Matteucci, G., Mészáros, I., Oláh, V., Preda, E., … Stadler, J. (2011). Functional traits and local environment predict vegetation responses to disturbance: A pan-European multi-site experiment. *Journal of Ecology*, *99*(3), 777–787. https://doi.org/10.1111/j.1365-2745.2011.01794.x

Biurrun, I., Pielech, R., Dembicz, I., Gillet, F., Kozub, Ł., Marcenò, C., Reitalu, T., Van Meerbeek, K., Guarino, R., Chytrý, M., Pakeman, R. J., Preislerová, Z., Axmanová, I., Burrascano, S., Bartha, S., Boch, S., Bruun, H. H., Conradi, T., De Frenne, P., … Dengler, J. (2021). Benchmarking plant diversity of Palaearctic grasslands and other open habitats. *Journal of Vegetation Science*, *32*(4). https://doi.org/10.1111/jvs.13050

Boergens, E., Güntner, A., Dobslaw, H., & Dahle, C. (2020). Quantifying the Central European Droughts in 2018 and 2019 With GRACE Follow-On. *Geophysical Research Letters*, *47*(14). https://doi.org/10.1029/2020GL087285

Bomble, W. F. (2013). *Tragopogon-Bocksbart (Asteraceae) in Nordrhein-Westfalen*.

Caswell, H. (2000). *Matrix population models (Vol.1)* (Vol. 1).

Chen, S. (2018). *Modelling plant populations - do clonality and seed ecology matter?* .

Childs, D. Z., Rees, M., Rose, K. E., Grubb, P. J., & Ellner, S. P. (2003). Evolution of complex flowering strategies: An age- and size-structured integral projection model. *Proceedings of the Royal Society B: Biological Sciences*, *270*(1526), 1829–1838. https://doi.org/10.1098/rspb.2003.2399

Cleland, E. E., Chiariello, N. R., Loarie, S. R., Mooney, H. A., & Field, C. B. (2006). Diverse responses of phenology to global changes in a grassland ecosystem. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(37), 13740–13744. https://doi.org/10.1073/pnas.0600815103

Compagnoni, A., & Adler, P. B. (2014). Warming, competition, and Bromus tectorum population growth across an elevation gradient. *Ecosphere*, *5*(9). https://doi.org/10.1890/ES14-00047.1

Compagnoni, A., Levin, S., Childs, D. Z., Harpole, S., Paniw, M., Römer, G., Burns, J. H., Che-Castaldo, J., Rüger, N., Kunstler, G., Bennett, J. M., Archer, C. R., Jones, O. R., Salguero-Gómez, R., & Knight, T. M. (2021). Herbaceous perennial plants with short generation time have stronger responses to climate anomalies than those with longer generation time. *Nature Communications*, *12*(1). https://doi.org/10.1038/s41467-021-21977-9

Craine, J. M., Ocheltree, T. W., Nippert, J. B., Towne, E. G., Skibbe, A. M., Kembel, S. W., & Fargione, J. E. (2013). Global diversity of drought tolerance and grassland climate-change resilience. *Nature Climate Change*, *3*(1), 63–67. https://doi.org/10.1038/nclimate1634

Crone, E. E., Menges, E. S., Ellis, M. M., Bell, T., Bierzychudek, P., Ehrlén, J., Kaye, T. N., Knight, T. M., Lesica, P., Morris, W. F., Oostermeijer, G., Quintana-Ascencio, P. F., Stanley, A., Ticktin, T., Valverde, T., & Williams, J. L. (2011). How do plant ecologists use matrix population models? *Ecology Letters*, *14*(1), 1–8. https://doi.org/10.1111/j.1461-0248.2010.01540.x

Döscher, R., Willén, U., Jones, C., Rutgersson, A., Meier, H. E. M., Hansson, U., & Graham, L. P. (2002). The development of the regional coupled ocean-atmosphere model RCAO. *Boreal Environment Research*, *7*(3), 183–192.

Easterling, M. R., Ellner, S. P., & Dixon, P. M. (2000). Size-Specific Sensitivity: Applying a new sturctured population model. *Ecology*, *81*(3), 694–708.

Ehrlen, J. (2019). Climate change in grasslands - demography and population dynamics. In D. J. Gibson & J. A. Newman (Eds.), *Grasslands and climate change* (pp. 172–187).

Ehrlén, J., & Morris, W. F. (2015). Predicting changes in the distribution and abundance of species under environmental change. In *Ecology Letters* (Vol. 18, Issue 3, pp. 303–314). https://doi.org/10.1111/ele.12410

Ehrlén, J., Morris, W. F., von Euler, T., & Dahlgren, J. P. (2016). Advancing environmentally explicit structured population models of plants. *Journal of Ecology*, *104*(2), 292–305. https://doi.org/10.1111/1365-2745.12523

Ellenberg, H., Weber, H. E., Düll, R. , Wirth, V., Werner, & W. Paulissen, D. (1991). *Zeigerwerte von Pflanzen in Mitteleuropa* (3rd ed.). Erich Goltze KG.

Evju, M., Austrheim, G., Halvorsen, R., & Mysterud, A. (2009). Grazing responses in herbs in relation to herbivore selectivity and plant traits in an alpine ecosystem. *Oecologia*, *161*(1), 77–85. https://doi.org/10.1007/s00442-009-1358-1

Feurdean, A., Ruprecht, E., Molnár, Z., Hutchinson, S. M., & Hickler, T. (2018). Biodiversity-rich European grasslands: Ancient, forgotten ecosystems. *Biological Conservation*, *228*(May), 224–232. https://doi.org/10.1016/j.biocon.2018.09.022

Franco, M., & Silvertown, J. (2004). A Comparative Demography of Plants Based upon Elasticities of Vital Rates. In *Source: Ecology* (Vol. 85, Issue 2).

Gordo, O., & Sanz, J. J. (2010). Impact of climate change on plant phenology in Mediterranean ecosystems. *Global Change Biology*, *16*(3), 1082–1106. https://doi.org/10.1111/j.1365-2486.2009.02084.x

Hansen, M. J., & Wilson, S. D. (2006). Is management of an invasive grass Agropyron cristatum contingent on environmental variation? *Journal of Applied Ecology*, *43*(2), 269–280. https://doi.org/10.1111/j.1365-2664.2006.01145.x

IPCC. (2014). IPCC, 2014: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. *IPCC*, *Geneva, Sw*, 151.

Jacob, D., & Podzun, R. (1997). Sensitivity studies with the regional climate model REMO. *Meteorology and Atmospheric Physics*, *63*(1–2), 119–129. https://doi.org/10.1007/BF01025368

Jacquemyn, H., Brys, R., Davison, R., Tuljapurkar, S., & Jongejans, E. (2012). Stochastic LTRE analysis of the effects of herbivory on the population dynamics of a perennial grassland herb. *Oikos*, *121*(2), 211–218. https://doi.org/10.1111/j.1600-0706.2011.19774.x

Jacquemyn, H., Brys, R., & Jongejans, E. (2010). Size-dependent flowering and costs of reproduction affect population dynamics in a tuberous perennial woodland orchid. *Journal of Ecology*, *98*(5), 1204–1215. https://doi.org/10.1111/j.1365-2745.2010.01697.x

Jantunen, J., Saarinen, K., Valtonen, A., & Saarnio, S. (2007). Flowering and seed production success along roads with different mowing regimes. *Applied Vegetation Science*, *10*(2), 285. https://doi.org/10.1658/1402-2001(2007)10[285:faspsa]2.0.co;2

Jentsch, A., Kreyling, J., & Beierkuhnlein, C. (2007). A new generation of climate-change experiments. *Frontiers in Ecology and the Environment*, *5*, 365–374.

Johansen, L., Westin, A., Wehn, S., Iuga, A., Ivascu, C. M., Kallioniemi, E., & Lennartsson, T. (2019). Traditional semi-natural grassland management with heterogeneous mowing times enhances flower resources for pollinators in agricultural landscapes. *Global Ecology and Conservation*, *18*, e00619. https://doi.org/10.1016/j.gecco.2019.e00619

Kahmen, S., Poschlod, P., & Schreiber, K. F. (2002). Conservation management of calcareous grasslands. Changes in plant species composition and response of functional traits during

25 years. *Biological Conservation*, *104*(3), 319–328. https://doi.org/10.1016/S0006-3207(01)00197-5

Kariyeva, J., van Leeuwen, W. J. D., & Woodhouse, C. A. (2012). Impacts of climate gradients on the vegetation phenology of major land use types in Central Asia (1981-2008). *Frontiers of Earth Science*, *6*(2), 206–225. https://doi.org/10.1007/s11707-012-0315-1

Korell, L., Auge, H., Chase, J. M., Harpole, S., & Knight, T. M. (2020). We need more realistic climate change experiments for understanding ecosystems of the future. *Global Change Biology*, *26*(2), 325–327. https://doi.org/10.1111/gcb.14797

Kuss, P., Rees, M., Ægisdóttir, H. H., Ellner, S. P., & Stöcklin, J. (2008). Evolutionary demography of long-lived monocarpic perennials: A time-lagged integral projection model. *Journal of Ecology*, *96*(4), 821–832. https://doi.org/10.1111/j.1365-2745.2008.01374.x

Lemmer, J., Andrzejak, M., Compagnoni, A., Knight, T. M., & Korell, L. (2021). Climate change and grassland management interactively influence the population dynamics of Bromus erectus (Poaceae). *Basic and Applied Ecology*, *56*, 226–238. https://doi.org/10.1016/j.baae.2021.06.012

Levin, S. C., Childs, D. Z., Compagnoni, A., Evers, S., Knight, T. M., & Salguero-Gómez, R. (2021). ipmr: Flexible implementation of Integral Projection Models in R. *Methods in Ecology and Evolution*, *12*(10), 1826–1834. https://doi.org/10.1111/2041-210X.13683

Lyu, S., & Alexander, J. M. (2022). Competition contributes to both warm and cool range edges. *Nature Communications*, *13*(1), 1–9. https://doi.org/10.1038/s41467-022-30013-3

McMahon, S. M., Arellano, G., & Davies, S. J. (2019). The importance and challenges of detecting changes in forest mortality rates. *Ecosphere*, *10*(2). https://doi.org/10.1002/ecs2.2615

Morris, W. F., Ehrlén, J., Dahlgren, J. P., Loomis, A. K., & Louthan, A. M. (2020). *Biotic and anthropogenic forces rival climatic/abiotic factors in determining global plant population growth and fitness*. *117*(2), 1107–1112. https://doi.org/10.5061/dryad.95x69p8fm

Moser, B., Fridley, J. D., Askew, A. P., & Grime, J. P. (2011). Simulated migration in a long-term climate change experiment: Invasions impeded by dispersal limitation, not biotic resistance. *Journal of Ecology*, *99*(5), 1229–1236. https://doi.org/10.1111/j.1365-2745.2011.01841.x

Nakahama, N., Uchida, K., Ushimaru, A., & Isagi, Y. (2016). Timing of mowing influences genetic diversity and reproductive success in endangered semi-natural grassland plants. *Agriculture, Ecosystems and Environment*, *221*, 20–27. https://doi.org/10.1016/j.agee.2016.01.029

Orlowsky, B., & Seneviratne, S. I. (2012). Global changes in extreme events: Regional and seasonal dimension. *Climatic Change*, *110*(3–4), 669–696. https://doi.org/10.1007/s10584-011-0122-9

Poniatowski, D., Hertenstein, F., Raude, N., Gottbehüt, K., Nickel, H., & Fartmann, T. (2018). The invasion of Bromus erectus alters species diversity of vascular plants and leafhoppers in calcareous grasslands. *Insect Conservation and Diversity*, *11*(6), 578–586. https://doi.org/10.1111/icad.12302

Poschlod, P., Kiefer, S., Tränkle, U., Fischer, S., & Bonn, S. (1998). Plant species richness in calcareous grasslands as affected by dispersability in space and time. *Applied Vegetation Science*, *1*(1), 75–91. https://doi.org/10.2307/1479087

R Core Team. (2022). *R: A language and environment for statistical computing. R Foundation for Statistical Computing.* https://www.r-project.org/

Ramula, S., Knight, T. M., Burns, J. H., & Buckley, Y. M. (2008). General guidelines for invasive plant management based on comparative demography of invasive and native plant populations. *Journal of Applied Ecology*, *45*(4), 1124–1133. https://doi.org/10.1111/j.1365-2664.2008.01502.x

Redlich, S., Zhang, J., Benjamin, C., Dhillon, M. S., Englmeier, J., Ewald, J., Fricke, U., Ganuza, C., Haensel, M., Hovestadt, T., Kollmann, J., Koellner, T., Kübert-Flock, C., Kunstmann, H., Menzel, A., Moning, C., Peters, W., Riebl, R., Rummler, T., … Steffan-Dewenter, I. (2022). Disentangling effects of climate and land use on biodiversity and ecosystem services—A multi-scale experimental design. *Methods in Ecology and Evolution*, *13*(2), 514–527. https://doi.org/10.1111/2041-210X.13759

Rees, M., & Ellner, S. P. (2009). Integral projection models for populations in temporally varying environments. In *Ecological Monographs* (Vol. 79, Issue 4).

Reisch, C., & Poschlod, P. (2009). Land use affects flowering time: Seasonal and genetic differentiation in the grassland plant scabiosa columbaria. *Evolutionary Ecology*, *23*(5), 753–764. https://doi.org/10.1007/s10682-008-9270-4

Rockel, B., Will, A., & Hense, A. (2008). The regional climate model COSMO-CLM (CCLM). *Meteorologische Zeitschrift*, *17*(4), 347–348. https://doi.org/10.1127/0941-2948/2008/0309

Schädler, M., Buscot, F., Klotz, S., Reitz, T., Durka, W., Bumberger, J., Merbach, I., Michalski, S. G., Kirsch, K., Remmler, P., Schulz, E., & Auge, H. (2019). Investigating the consequences of climate change under different land-use regimes: a novel experimental infrastructure. *Ecosphere*, *10*(3). https://doi.org/10.1002/ecs2.2635

Schauberger, P., & Walker, A. (2021). *Openxlsx: Read, Write and Edit xlsx Files.* (4.2.5).

Schuldt, B., Buras, A., Arend, M., Vitasse, Y., Beierkuhnlein, C., Damm, A., Gharun, M., Grams, T. E. E., Hauck, M., Hajek, P., Hartmann, H., Hiltbrunner, E., Hoch, G., Holloway-Phillips, M., Körner, C., Larysch, E., Lübbe, T., Nelson, D. B., Rammig, A., … Kahmen, A. (2020). A first assessment of the impact of the extreme 2018 summer drought on Central European forests. *Basic and Applied Ecology*, *45*, 86–103. https://doi.org/10.1016/j.baae.2020.04.003

Sebald, O., Seybold, S., & Philippi, G. (1990). *Die Farn- und Blütenpflanzen Baden-Württembergs* (Vol. 1). E. Ulmer.

Tälle, M., Fogelfors, H., Westerberg, L., & Milberg, P. (2015). The conservation benefit of mowing vs grazing for management of species-rich grasslands: A multi-site, multi-year field experiment. *Nordic Journal of Botany*, *33*(6), 761–768. https://doi.org/10.1111/njb.00966

Tebaldi, C., Hayhoe, K., Arblaster, J. M., & Meehl, G. A. (2006). Going to the extremes: An intercomparison of model-simulated historical and future changes in extreme events. In *Climatic Change* (Vol. 79, Issues 3–4, pp. 185–211). Springer Netherlands. https://doi.org/10.1007/s10584-006-9051-4

Töpper, J. P., Meineri, E., Olsen, S. L., Rydgren, K., Skarpaas, O., & Vandvik, V. (2018). The devil is in the detail: Nonadditive and context-dependent plant population responses to increasing temperature and precipitation. *Global Change Biology*, *24*(10), 4657–4666. https://doi.org/10.1111/gcb.14336

van Daalen, S. F., & Caswell, H. (2020). Variance as a life history outcome: Sensitivity analysis of the contributions of stochasticity and heterogeneity. *Ecological Modelling*, *417*. https://doi.org/10.1016/j.ecolmodel.2019.108856

van der Meer, S., Dahlgren, J. P., Mildén, M., & Ehrlén, J. (2014). Differential effects of abandonment on the demography of the grassland perennial Succisa pratensis. *Population Ecology*, *56*(1), 151–160. https://doi.org/10.1007/s10144-013-0400-7

Wagner, S., Berg, P., Schädler, G., & Kunstmann, H. (2013). High resolution regional climate model simulations for Germany: Part II-projected climate changes. *Climate Dynamics*, *40*(1–2), 415–427. https://doi.org/10.1007/s00382-012-1510-1

Weppler, T., Stoll, P., & Stöcklin, J. (2006). The relative importance of sexual and clonal reproduction for population growth in the long-lived alpine plant Geum reptans. *Journal of Ecology*, *94*(4), 869–879. https://doi.org/10.1111/j.1365-2745.2006.01134.x

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag.

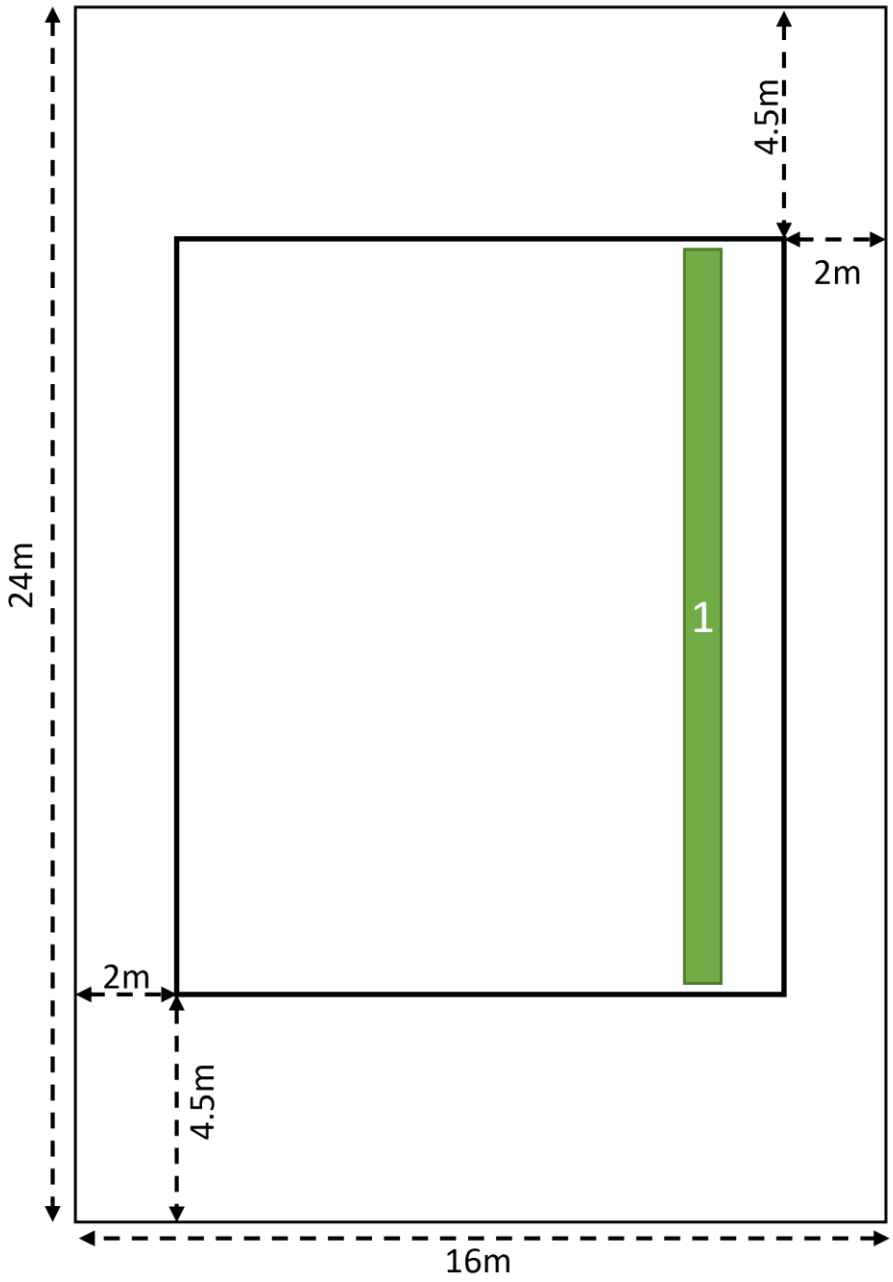
Wickham, H., François, R., Henry, L., & Müller, K. (2022). *dplyr: A Grammar of Data Manipulation* (1.0.9).

Williams, A. L., Wills, K. E., Janes, J. K., vander Schoor, J. K., Newton, P. C. D., & Hovenden, M. J. (2007). Warming and free-air CO2 enrichment alter demographics in four co-occurring grassland species. *New Phytologist*, *176*(2), 365–374. https://doi.org/10.1111/j.1469-8137.2007.02170.x

Yule, K. M., Miller, T. E. X., & Rudgers, J. A. (2013). Costs, benefits, and loss of vertically transmitted symbionts affect host population dynamics. *Oikos*, *122*(10), 1512–1520. https://doi.org/10.1111/j.1600-0706.2012.00229.

Appendix 1

Fig. A1 Layout of every GCEF plot. 1 indicates where the transect was situated at each GCEF subunit. Displayed is the overall size of the GCEF subunits and the inner subunit where experiments take place.



Appendix 2

Table A1 Given are the dates of the management events. Sheep graze one plot for 24 hours and thus the management took place over the course of 10 days. The sheep were let on one plot in the morning of the day and the next day they moved to the next plot. Mowing was done in one day.

Management event	Year	Date
Grazing	2018	30.04 - 11.05
Grazing	2018	11.06 - 22.06
Mowing	2018	11.06
Grazing	2019	6.05 - 17.05
Grazing	2019	10.06 - 21.06
Mowing	2019	11.06
Grazing	2020	11.05 - 22.5
Grazing	2020	22.06 - 03.07
Mowing	2020	08.06
Grazing	2021	10.05 - 21.05
Grazing	2021	14.06 - 25.06
Mowing	2021	14.06
Mowing	2021	06.09.2023
Grazing	2021	06.09 - 17.09

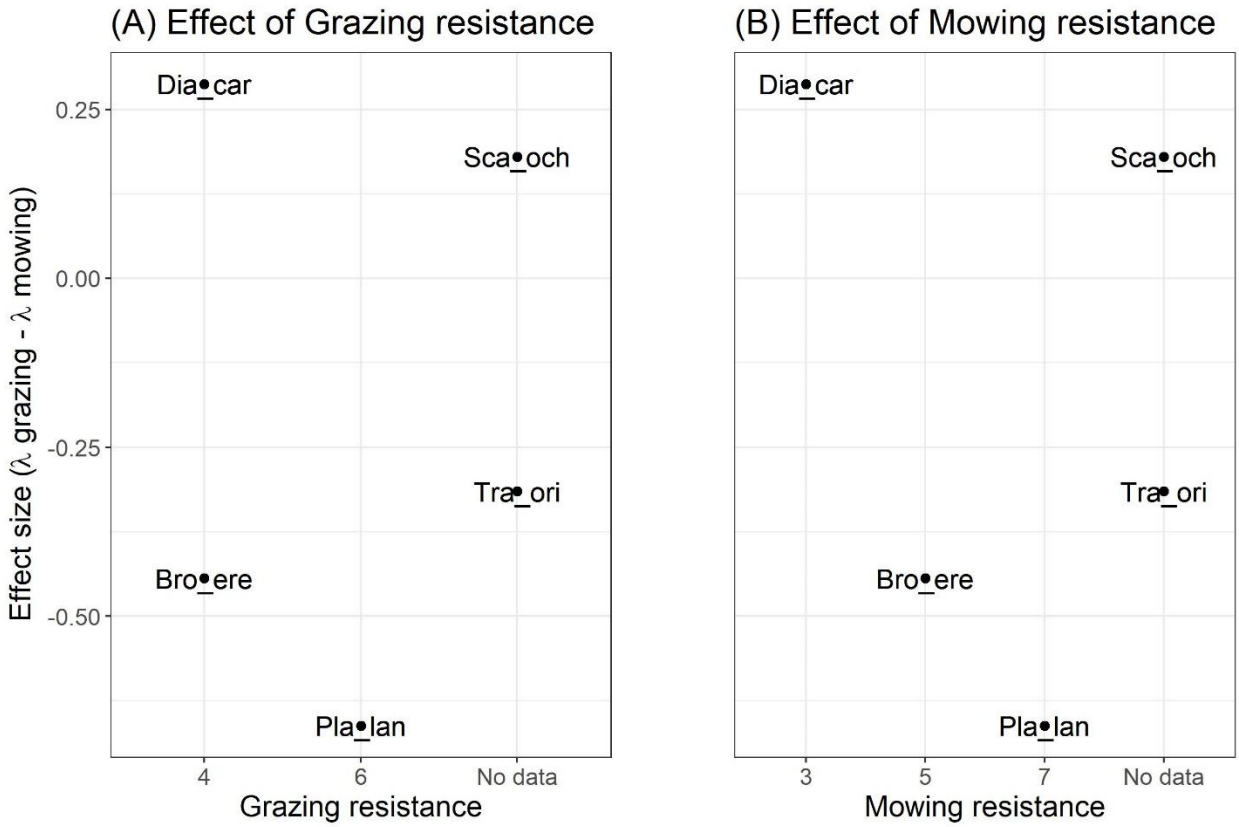
Appendix 3

Table A2 Information on how we identified seedlings. Mostly that stage class was size dependent and if an individual plant didn't grow to a certain size, it was identified as seedling. Some *Bromus erectus* individuals flowered after they developed 4 leafs but still were smaller then 0.25 cm^2 which is why we classified every individual with three or more leafs as adult.

Species	Maximum size as a seedling
Anthoxanthum odoratum	< 4 leafs
Bromus erectus	1 ramet with maximum 3 leafs
Crepis bunnies	1 ramet with maximum 3 leafs
Dianthus carthusianorum	Size of rosette <0.25cm^2
Lotus corniculatus	Size of rosette <0.25cm^2
Lychnis flos-cuculi	Didn't find seedling
Medicago falcata	Size of rosette <0.25cm^2
Plantago lanceolata	1 ramet with maximum 3 leafs
Scabiosa ochroleuca	1 ramet with maximum 2 leafs
Tragopogon orientalis	Maximal 3 leafs
Trifolium pratense	1 individual with maximum 2 leafs

Appendix 4

Fig. A2 Grazing and mowing resistance plotted against the effect size of λ. Negative values indicate that the species has a higher λ in the mowing treatment. Panel A.) shows the effect of grazing resistance on the effect size and panel B.) shows the effect of mowing resistance on the effect size.



Appendix 5

Fig. A3 Bootstrapped λ of each species over the study years for the management treatment (mowing, grazing). Displayed is the mean λ and the standard deviation. Each year on the x axis stands for a transition: 2018 = 2018–2019, 2019 = 2019–2020, 2020 = 2020–2021, 2021 = 2021–2022. For the transition 2021 we were not able to calculate a lambda for *T. orientalis* in the grazing land management treatment due to lack of data points.

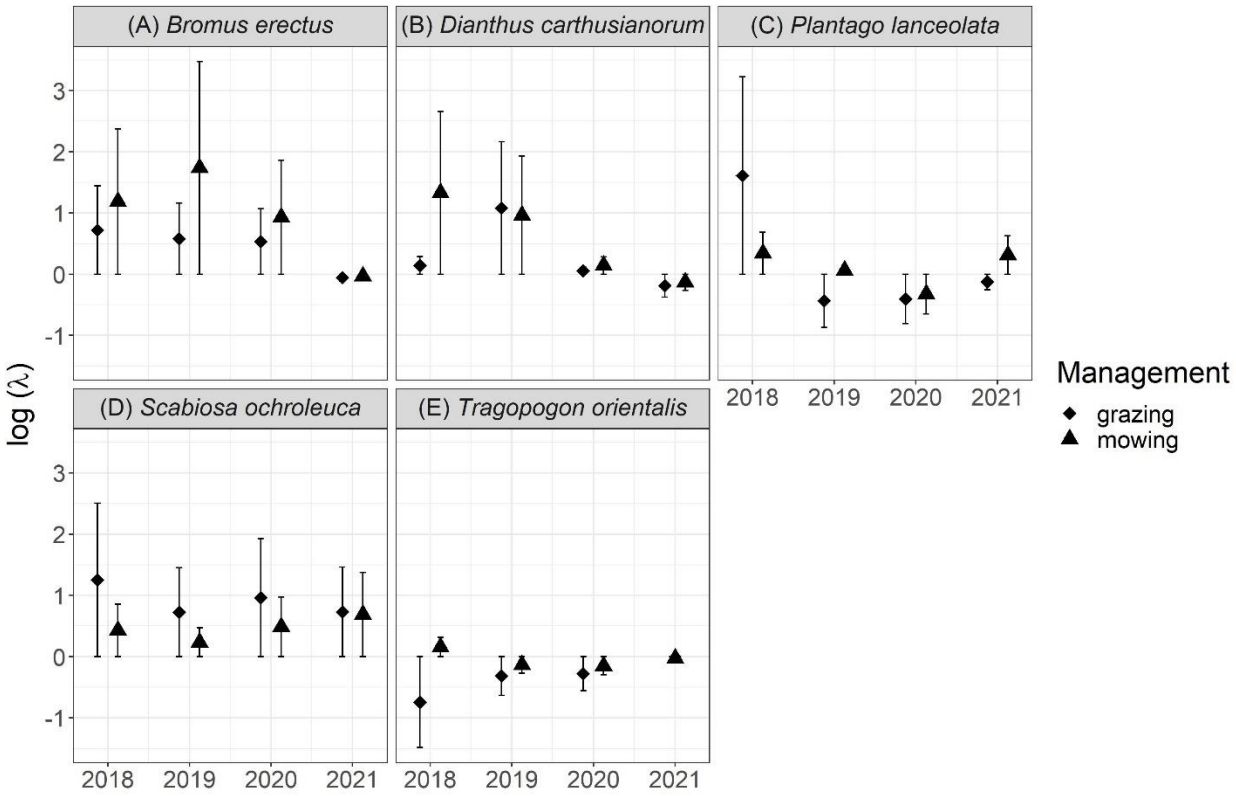


Fig. A4 Bootstrapped λ of each species over the study years for the climate treatment (ambient, future). Displayed is the mean λ and the standard deviation. Each year on the x axis stands for a transition: 2018 = 2018 – 2019, 2019 = 2019 – 2020, 2020 = 2020 – 2021, 2021 = 2021 – 2022. S. ochroleuca in 2019 and T. orientalis did not have enough data points in order for us to calculate the population growth rate.

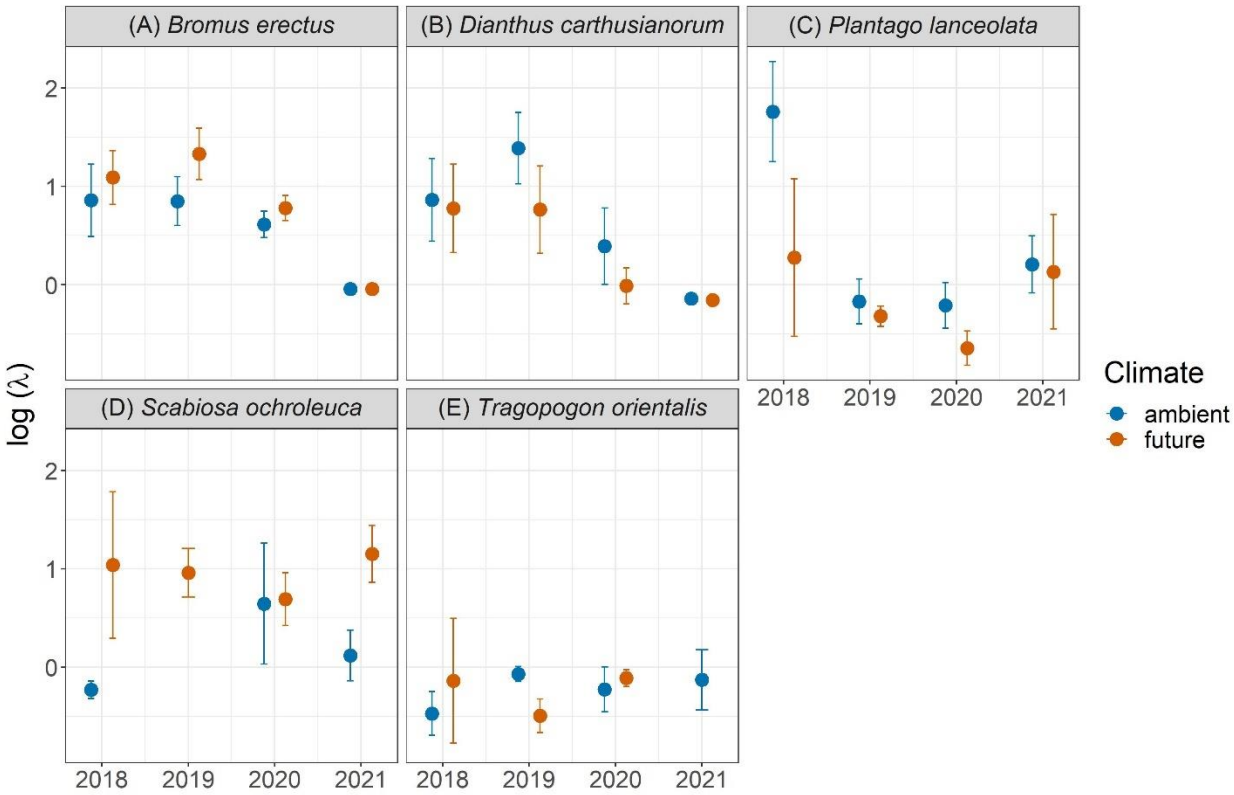
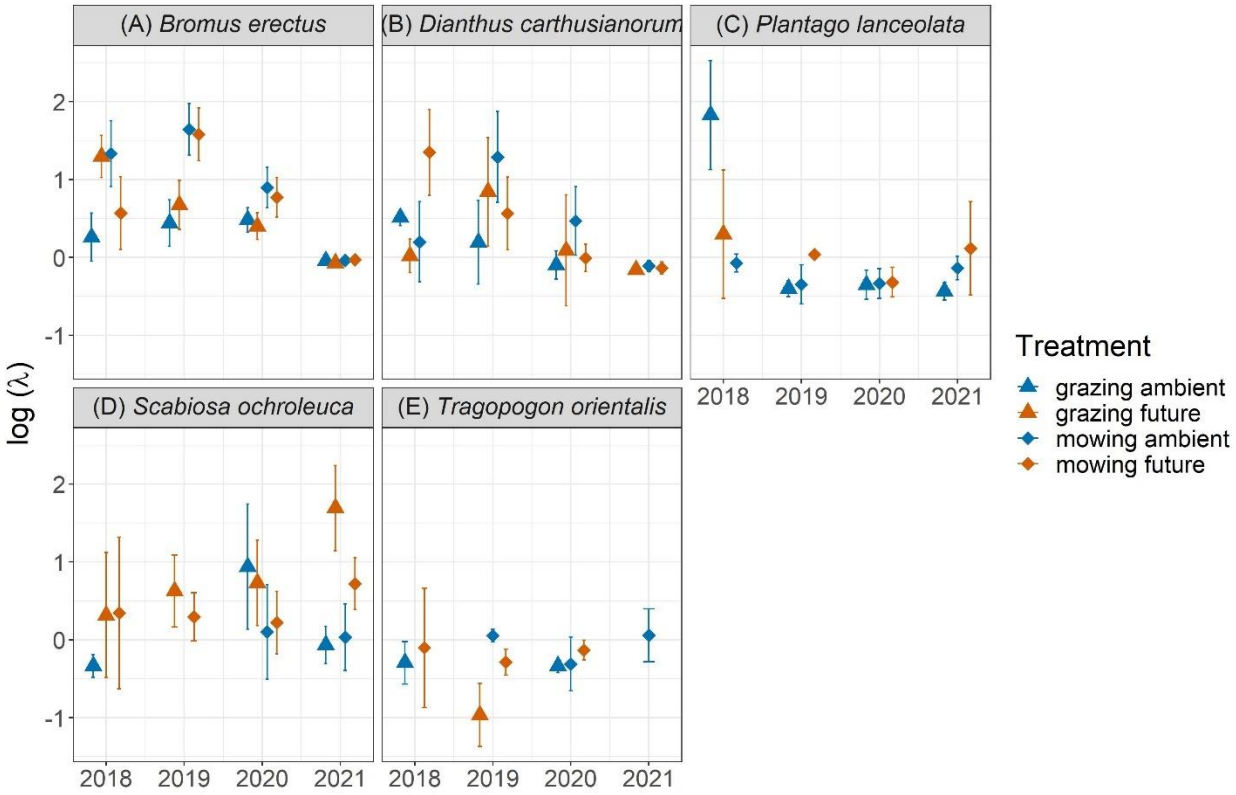
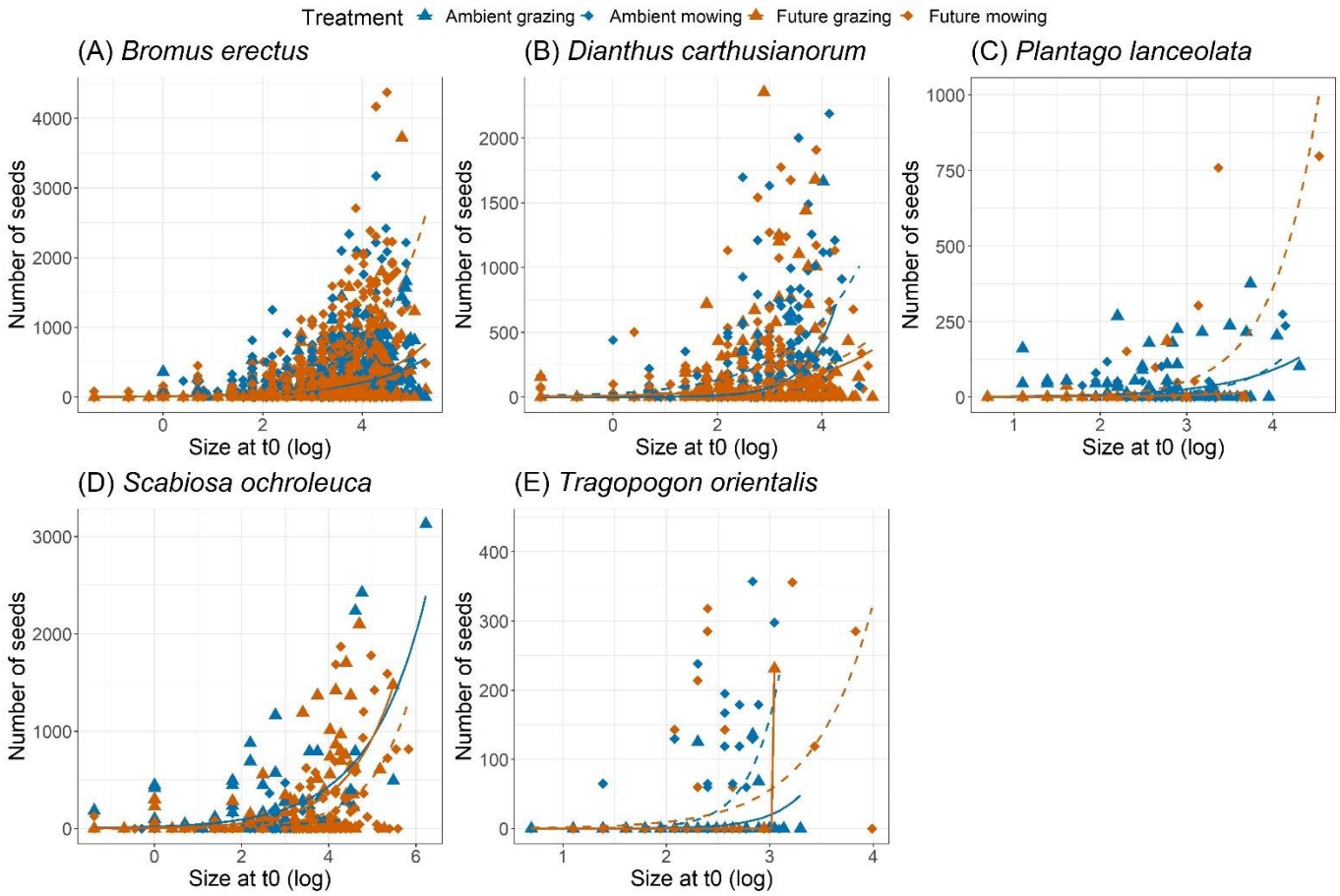


Fig. A5 The effect of the treatment combinations (management and climate) over the years of the study on λ. Displayed is the mean λ and the standard deviation. Each year on the x axis stands for a transition: 2018 = 2018 – 2019, 2019 = 2019 – 2020, 2020 = 2020 – 2021, 2021 = 2021 – 2022. Missing points are due to lack of data points to calculate the population growth rate.



Appendix 6

Fig. A6 Number of seeds plotted against the size of each reproductive individual for the species (A) *Bromus erectus,* (B) *Dianthus carthusianorum*, (C) *Plantago lanceolata*, (D) *Scabiosa ochroleuca* and (E) *Tragopogon orientalis*. Different treatments are indicated with different shapes and colors.



Appendix 7

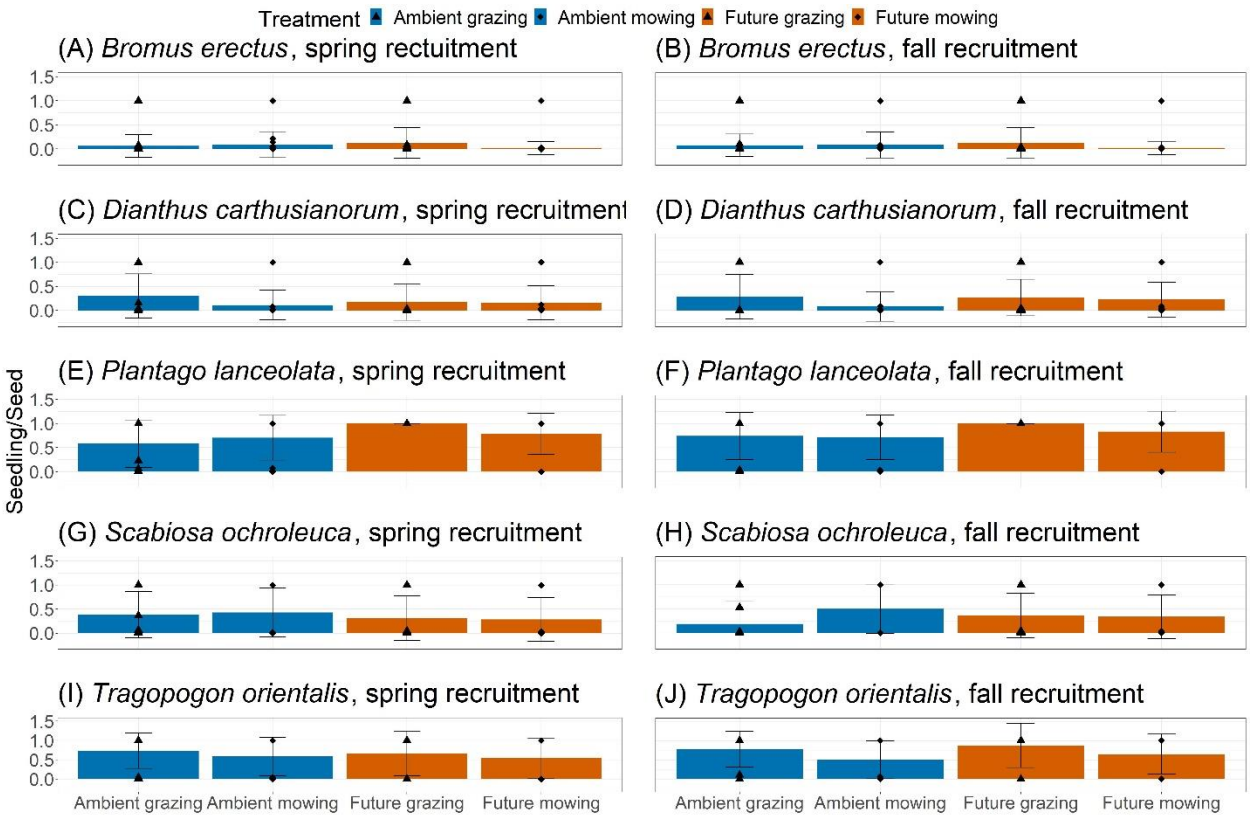



Fig. A7 Turnover from seeds to seedling in the different treatments for (A) *Bromus erectus*, spring recruitment (B) *Bromus erectus*, fall recruitment (C) *Dianthus carthusianorum*, spring recruitment (D) *Dianthus carthusianorum*, fall recruitment (E) *Plantago lanceolata*, spring recruitment (F) *Plantago lanceolata*, fall recruitment (G) *Scabiosa ochroleuca*, spring recruitment (H) *Scabiosa ochroleuca*, fall recruitment (I) *Tragopogon orientalis*, spring recruitment (J) *Tragopogon orientalis*, fall recruitment.