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Climate change and grassland management interactively influence the population dynamics of *Bromus erectus* (Poaceae)

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Abstract

Climate and land management are important environmental drivers that affect the structure of terrestrial plant communities worldwide. Demographic studies allow a mechanistic understanding of the pathways in which environmental factors change population size. Climate and land management might interactively influence vital rates and growth rates of populations, however, demographic studies have not heretofore considered both factors in combination. We used the Global Change Experimental Facility as a platform to study the effect of climate (ambient climate conditions vs. future climate conditions) and land management (sheep grazing vs. mowing) on the demography of the common grass, *Bromus erectus* growing in semi-natural grassland communities. We found positive population growth rates for *B. erectus* under all treatment combinations, and an interactive effect of climate and land management. Under ambient climate conditions, population growth of *B. erectus* was higher in mowed than grazed grassland plots, while population growth rates were similar across both management types under future climatic conditions. This interaction was primarily due to changes across treatments in seedling recruitment, a vital rate the population growth rate was particularly sensitive to changes in. The interaction found in this study highlights the importance of considering multiple environmental drivers in demographic studies, to better predict future plant population dynamics and ultimately changes in community structure.

Keywords: integral projection model, life table response experiment, grazing, mowing, grassland management, climate change experiment, plant population dynamics, elasticity analysis

Introduction

Grasslands cover 40% of the Earth's ice-free terrestrial surface (Blair, Nippert & Briggs 2014), and provide vital ecosystem services, such as housing high biodiversity and producing fodder for animals (Sala & Paruelo 1997). Grasslands are threatened by habitat loss, management intensification, and land abandonment (Hejcman, Ceskova, Schellberg & Paetzold 2010; Janssens, Peeters, Tallowin, Bakker, Bekker et al. 1998; Klimek, Richter gen. Kemmermann, Hofmann & Isselstein 2007; Socher, Prati, Boch, Mueller, Klaus et al. 2012; Wesche, Krause, Culmsee & Leuschner 2012). The composition of plants in semi-natural grasslands (moderately used in agricultural landscapes that contain high biodiversity) is largely influenced by management practices (Cousins & Eriksson 2001; Tscharntke, Klein, Kruess, Steffan-Dewenter & Thies 2005). Mowing management with low to moderate frequencies is linked to high biodiversity through releasing subdominant species from competition and facilitating germination and seedling recruitment (Foster & Gross 1998; Hansson & Fogelfors 2000; Klein, Harte & Zhao 2004; Talle, Deak, Poschlod, Valko, Westerberg et al. 2016). Grazing management can similarly promote biodiversity, but creates more heterogeneous disturbances through preferential biomass removal and soil disturbances by animals (Klimek et al. 2007; Olff & Ritchie 1998).

Semi-natural grasslands will be altered by climate change, as climate has strong influences on the demographic vital rates of plants that ultimately determine plant population dynamics and the structure and function of terrestrial plant communities. Global surface temperature and precipitation are projected to change in the next 30 years (IPCC 2014; Stocker, Qin, Plattner, Tignor, Allen et al. 2013). In Europe, an increase in temperature of 0.8 to 1.3 °C is predicted for the next 30 years, with the strongest warming occurring in winter and autumn (Wagner et al. 2013). These increases in temperature will be accompanied by a decrease in summer precipitation, and an increase in spring and fall precipitation (Rajczak, Pall & Schaer 2013; Schaedler, Buscot, Klotz, Reitz, Durka et al. 2019).

It is still poorly understood how climate and land management will affect plant populations in European grasslands (Ehrlén 2019; Maron & Crone 2006). Management practices are known to strongly influence plant demography and population growth. Seedling germination and establishment increase in grasslands that are grazed and mowed (Brys, Jacquemyn, Endels, Blust & Hermy 2004; Ehrlén, Syrjänen, Leimu, Begona Garcia & Lehtilä 2005; Lennartsson & Oostermeijer 2001), whereas reproduction is decreased by repeated removal of above-ground biomass by grazing and mowing (Lennartsson et al. 2001), particularly when it occurs early in the season (Brys et al. 2004). Climate change and management might interactively influence plant demography (Klein et al. 2004; Martorell 2007), but the effects cannot be easily predicted (Bütof, von Riedmatten, Dormann, Scherer-Lorenzen, Welk et al. 2012). On one hand, these treatment combinations might lead to high combined pressure for plants, and have additive or multiplicative effects on plant vital rates (Selwood, McGeoch & Mac Nally 2015). On the other hand, appropriate management might stabilize grassland communities facing climate change and buffer plant vital rates from change (Post 2013).

Structured population models such as Matrix Projection Models and Integral Projection Models are commonly used methods to link the demography of plant and animal species to their asymptotic (long-term) population growth rate (λ)(Caswell 2001; Easterling, Ellner & Dixon 2000). A mechanistic understanding on the effects of treatments (e.g. climate change and land management) can be gained using Life Table Response Experiments (LTREs, which decompose the role of individual vital rates on the observed difference in λ across treatments. Vital rates that have a high contribution to the observed change will be those that change dramatically between treatments and/or those that λ is sensitive to changes in.

We quantified the interplay of climate and management on the demography and population dynamics of the common grass, *Bromus erectus*, in a full-factorial experiment. Our experiment platform, the Global Change Environmental Facility, is unique in that it experimentally manipulates realistic future climates for our region (Korell, Auge, Chase, Harpole & Knight 2020a; Korell, Auge, Chase, Harpole & Knight 2020b) in combination with different land management types (Schaedler et al. 2019). To our knowledge, we perform the first demographic study that experimentally quantifies the interaction of these two important environmental drivers on plant population dynamics. Before the start of our study, *B. erectus* was more abundant in mowed than in grazed extensively-used grassland communities and thus, we hypothesized that population growth rates under ambient climate would mirror this pattern. As *B. erectus* is a drought-tolerant species (Perez-Ramos, Volaire, Fattet, Blanchard & Roumet 2013), we hypothesized that its population growth rate might increase under future climate treatments. Specifically, we asked the following questions: (1) How do the treatment combinations of climate change and grassland management affect the vital rates and population growth rates of *B. erectus*? (2) Which changes in vital rates is the population growth rate of *B. erectus* most sensitive to? (3) Which life stages contribute most to the differences in population growth rates of *B. erectus* across climate and grassland management treatments?

Methods

Study species

Bromus erectus Huds. (Poaceae, Syn. *Bromopsis erecta* (Huds.) Fourr.) is a common grass of nutrient poor calcareous grasslands (Ellenberg 1996). It became increasingly common across Europe since the Modern Age (Poschlod & WallisDeVries 2002). *Bromus erectus* grows well in mown sites (Moog, Poschlod, Kahmen & Schreiber 2002; Wells 1968, but see Catorci, Ottaviani, Ballelli & Cesaretti 2011) and while its young shoots are grazed by sheep, older individuals are avoided (Wedl & Meyer). *Bromus erectus* can contribute a large share to the above-ground community biomass (Steinger, Stephan & Schmid 2007) and is thus economically important for extensively used meadows and pastures. This species can cope with high rates of dehydration, has a comparatively high survival after severe droughts (Perez-Ramos et al. 2013) and is considered a stress-tolerant competitor (Grime, Hodgson & Hunt 2014). This erect brome is a perennial and polycarpic grass species which forms no persistent seed bank (Thompson & Grime 1979). *B. erectus* is wind pollinated and self-incompatible (Zeiter & Stampfli 2008). It can reproduce vegetatively via rhizomes, but it predominantly grows in small tussocks consisting of clumping ramets. We defined a tussock that is comprised of one genet as an individual, and we did not observe the split of such a unit.

Study site

We carried out this study at the Global Change Experimental Facility (GCEF). This climate change experiments was established in 2014 and is part of the field station of the Helmholtz Centre for Environmental Research – UFZ, at Bad Lauchstädt, Central Germany (51°23’29.47”N, 11°52’27.76”E). The study site is a former arable field with temperate climate and mean annual precipitation of 489 mm a^{-1} and mean annual temperature of 8.9 °C (Schaedler et al. 2019). The experimental setup of the GCEF follows a split-plot design in which climate (ambient vs. future) is a main plot factor and land use (including extensively used grasslands) is a subplot factor (Schaedler et al. 2019). The experiment comprises ten main plots with a size of 80 x 24 m, half of which were randomly chosen to be subjected to current local climate conditions (henceforth called “ambient climate”). The remaining five plots are subjected to a future climate scenario for the years 2070 – 2100 based on regional dynamic climate models (henceforth called “future climate”). In future climate plots, a combination of changes in the precipitation pattern and increases in temperature are applied. Spring and autumn precipitation is increased by ~10% via irrigation systems, and summer precipitation is partially blocked to decrease precipitation by ~20%. The predicted surface temperature increase is realized through automated roofs and side panels. Passive night-time warming increases mean temperature by ~0.55°C (Schaedler et al. 2019). Nested within each main plot, we considered two grassland management treatments, each spanning 24 x 16m. Non-intensive meadows were mown in June 2018 and 2019 and non-intensive pastures were grazed in late April / early May and in June 2018 and 2019. In total we had five replicates per climate x grassland management treatment combination.

Demographic data collection

In 2018, we established a nine-meter transect in each extensively used grassland plot (meadows vs pastures) nested within the 10 main plots exposed to an experimental climate treatment (ambient vs. future climate) (2 climate x 2 land management x 5 replicates = ∑ 20 transects). Along each transect we established six to eight permanent subplots of 0.25 m^2. Three subplots were located at predefined intervals, the remaining subplots were established at areas with higher abundances of the focal species. We surveyed individuals within subplots and, when sample sizes were not sufficient, we tagged additional individuals outside of subplots, but within the transects. Tags consisted of small plastic labels with numbered IDs that were secured to the ground with needles of 4 cm length. In all transects we surveyed at least 10 individuals of *B. erectus* (tussocks consisting of one genet) with more than three shoots. We established this as the minimum appropriate sample size (N > 50 individuals per treatment) to parameterize the IPM.

We performed all measurements in the years 2018 and 2019. In April 2018, we recorded the XY-location of each individual within each subplot. We defined *B. erectus* plants with less than 3 shoots as seedlings (Fig. 1). Before the first grazing event in 2018 and 2019, we measured the longest side of individuals (length), and the longest side perpendicular to the longest side (width) with a measuring stick. Our measure of individual size was basal area, calculated as length x width. Individuals present in April 2018 but not April 2019 were marked as dead, and all new individuals in subplots were recorded and measured. To quantify reproduction, we estimated the number of seeds produced per individual. To do so, we first counted the number of fruiting ramets per individual before and after every management event (four times a year). Then, we sampled two fully developed fruiting ramets of *B. erectus* just outside of each transect and counted the number of seeds per ramet. We estimated the number of seeds produced per individual by multiplying the mean number of seeds per ramet in the according treatment combination to the number of fruiting ramets per individual. Finally, we counted seedlings in the first three subplots of each transect in April 2018 and 2019 before the first management event, and in November 2018, as germination of *B. erectus* occurs in autumn and spring (Zeiter et al. 2008).

Life-cycle stages and vital rates

We modeled the year-to-year life-cycle of *Bromus erectus* as comprised of one continuous, and one discrete stage class. The continuous class is represented by "plants" and the discrete class is represented by "spring seedlings" (Fig. 1). *B. erectus* has a short-lived transient seed bank, thus we treated seeds from year *t* as either germinated or dead in year *t* +1.

We modeled the vital rates associated with the continuous stage class as a function of the natural logarithm of individual size by fitting generalized linear models. Plant survival, $S_{i,t+1}$ described whether an individual plant (*i*) observed in year *t* was alive or dead in year *t* + 1. We modeled survival as a Bernoulli process with probability of survival $\hat{S}_{t+1}$ (Table 1, Eq. 1). We modeled the probability of survival as a function of log size in year *t*, using a logit link function (Eq. 2),

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

$$[2] \qquad logit\left(\hat{S}_{t+1}\right) = \alpha_t^S + \beta^S \, log_e(size_t)$$

where α^S is the intercept, β^S is the slope (the effect of size), and the superscripts, *S*, are not an exponent, but refer to survival.

Plant growth, $G_{i,t+1}$ describes the normally distributed change in log transformed size of a surviving individual plant (*i*) from year *t* to year *t* + 1 (Eq. 3). We modeled log size at year *t*+1 as a linear function of plant log size in year *t*, with intercept α^G, slope β^G (Eq. 4) and standard deviation σ_G (Eq. 3):

[3] $$G_{i,t+1} \sim Normal\left(\hat{G}_{t+1}, \sigma_G\right)$$

[4] $$\hat{G}_{i,t+1} = \alpha_t^G + \beta^G \, log_e(size_t).$$

The reproduction probability $P_{i,t}$ described whether an individual plant (*i*) observed in year *t* produced flowers in year *t*. We modeled reproduction probability as a Bernoulli process (Eq. 5) dependent on log transformed plant size in year *t*, with intercept α^P and slope β^P using a logit link function (Eq. 6),

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

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

Seeds per reproductive plant, $F_{i,t}$, described the number of seeds produced by a reproductive plant (i) in year *t*. We calculated the number of seeds by rounding the product of multiplying the number of fruiting ramets $F_{i,t}$ by the mean number of seeds per fruiting ramet of the according treatment combination $L_{i,t}$ (Eq. 7). We modeled the product as a Poisson distributed process via a linear function of plant size in year *t* with intercept α^F and slope β^F (Eq. 8),

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

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

Fall ($\theta_{f,j,t}$) and spring ($\theta_{s,j,t}$) recruitment described the proportion of emergent seedlings per total number of seeds produced at the subplot level, where θ is recruitment, *f* is fall, *s*, is spring, *j* is the transect, and *t* refers to 2018. We calculated the seeds produced per subplot as $F_{j,t} = \sum_1^n F_{i,t}$, where *i* refers to all the individuals that produced seeds in subplot *j* in year *t*. We divided the number of emerging seedlings in the subsequent fall 2018 ($Rf_{j,k,t}$) and spring 2019 ($Rs_{j,t+1}$) by the number of seeds per subplot:

[9] $$\theta_{f,t} = \hat{R}f_t / F_t.$$

[10] $$\theta_{s,t+1} = \hat{R}s_{t+1} / F_t.$$

We calculated seedling survival at the subplot level. Seedling survival, $B_{,k}$, was the proportion of seedlings emerged in year *t* in subplot j, $Rsum_{j,t}$, that survived to year *t+1*,$Rsum_{j,t+1}$. We calculated the number of emerging seedlings at time t, in subplot j, $Rsum_{j,t}$, by summing the fall, $Rf_{j,t}$, and spring, $Rs_{j,t}$, recruitment in year *t*. Hence:

[11] $$B_{b,j} = Rsum_{j,t+1}/Rsum_{j,t}$$

Finally, we modeled the log size distribution of new plants, η, as the normally distributed size of surviving seedlings entering the continuous plant stage in year *t* + 1 (Eq. 14). We calculated the mean ($log_e(\hat{\eta}_{t+1})$) and standard deviation (σ_η) of this size distribution:

[12] $$log_e(\eta_{i,t+1}) \sim Normal\ \left(log_e(\hat{\eta}_{t+1}), \sigma_\eta\right)$$

Effects of treatments on vital rates

We fit these vital rate models to identify substantial differences between treatments using a model selection approach. First, we fit baseline models on plant survival, growth, reproduction probability and seeds per reproductive plant which only included plant size at year *t* (fixed factor). Then, we fit more complicated models including climate (ambient vs. future; fixed factor) and management (meadow vs. pasture; fixed factor) and their interactions. We fit a total of five models for each vital rate, and we compared them using Akaike Information Criterion (AIC, Burham & Anderson 2002). We used corrected AIC weights to select the best among these 5 models.

Integral projection model

We used an Integral Projection Model (IPM) to quantify the influence of the treatments on the population dynamics of *B. erectus.* IPMs are used to project populations whose structure contains at least one continuous trait in discrete time (Easterling et al. 2000; Ellner, Childs & Rees 2016; Metcalf, McMahon, Salguero-Gómez & Jongejans 2013). In our case, the IPM describes the dynamics of two stages: one continuous stage (plants), and one discrete stage (seedlings, Fig. 1). From now on, we follow the notation suggested by Ellner et al. (2016). When describing the dynamics of the continuous stage, this IPM considers all possible transitions from size z at time t, to size z' at time t+1. The change in the number of plants from one year to the next is described by:

$$[15] \qquad n(z',t+1) = M(t)B\eta(z') + \int_L^U S(z)G(z',z) + P(z)F(z)\theta_f B\eta(z')n(z,t)dz$$

The vector *n*(*z'*, *t* + 1) describes the number of plants at size *y* at time *t* + 1. The first term represents recruitment of spring seedlings to the size distribution of adult plants, based on the number of spring seedlings at time *t*, *M*(*t*), the seedling survivorship, *B*, and the size distribution of new plants $\eta(z')$. The second term is a kernel (or a surface) that describes the transition from plants of size z at time t, *n(z,t)*, to plants of size z' at time t+1, *n(z',t+1)*. This kernel is an integral defined between the lowest, L, and upper, U, size observed in our population. We evaluated this integral across 200 equally spaced size bins using the midpoint rule as a 200 x 200 matrix. The integral describes size-dependent plant survivorship *S*(*z*), plant growth *G*(z',*z*), reproduction probability *P*(*z*), seeds per reproductive plant *F(z),* fall recruitment θ_f, seedling survivorship *B,* and the size distribution of new plants $\eta(z')$. Note that in this IPM, we assume survivorship, *B*, is the same for both fall and spring seedlings. The recruitment of spring seedlings from one year to the next is described by:

$$M(t+1) = \int_L^U P(z)F(z)\theta f n(z,t)dz. \quad [16]$$

Effects of climate and grassland management on the population dynamics of *B. erectus*

We created four IPMs, one for each treatment combination of management and climate, to test the effects of treatments on the population dynamics of *B. erectus*. We first tested the effect of treatments on asymptotic population growth rate (λ). Then, we quantified the relative contribution of separate vital rates to these differences via elasticity analysis, and a life table response experiment (LTRE). Our treatment combinations were grazing – ambient, grazing – future, mowing – ambient, and mowing – future. We built these four IPMs, using four separate datasets, each referring to one of the four treatment combinations. Moreover, to quantify the uncertainty in these estimates, we created 1000 replicate IPMs using a bootstrap procedure We randomly drew data referred to one individual at a time, with replacement, for as many times as the number of individuals included in the original dataset (grazing – ambient: 95, grazing – future: 80, mowing – ambient: 88, mowing – future: 88). These 1000 IPMs allowed us to produce 95% confidence intervals around the response variables of our tests. We tested whether differences in λ between pairwise treatment combinations were significant using a permutation (randomization) test (N=1000 permutations).

Life table response experiments

To further understand the influence of each life-cycle stage (Table 1, survival, growth, reproduction, recruitment and establishment) on the observed difference in population growth rates between pairwise treatment combinations, Life Table Response Experiments (LTREs) were conducted with all treatment combinations (mowing ambient – mowing future, grazing ambient – grazing future, mowing ambient – grazing ambient and mowing future – grazing future). We calculated differences in population growth rates as:

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

Where $\Delta\lambda^{treatment}$ estimates the effect of the climate or management treatment on the population growth rate of two populations that share the other treatment (management or climate consecutively). The contribution of each vital rate to the $\Delta\lambda^{treatment}$ was calculated as:

[18] $$\widetilde{\delta}^{\,treatment} = \sum_i^{14}(\alpha_i^{treatment\ combination\ 1} - \alpha_i^{treatment\ combination\ 2})\ \frac{\partial\lambda}{\partial\alpha_i}$$

where α_i is one of the fourteen vital rates included in the IPMs, and the term $\frac{\partial\lambda}{\partial\alpha_i}$ describes the sensitivity of the population growth rate to each vital rate. Vital rates that strongly influence differences in population growth rates between treatments are those that display great change between treatments and / or those that λ is sensitive to. We calculated this LTRE with respect to five demographic processes which combined the effect of multiple parameters: survival, growth, reproduction, recruitment, and establishment. The LTRE results on survival and growth represented the combined effects of the intercept and slope of survival and growth, respectively. Reproduction combined the parameters of reproduction probability and seeds per reproductive plants. Recruitment combined the parameters of fall and spring recruitment and thus describes total seedling recruitment. Establishment summarizes the seedling survival and the size distribution of newly established plants. We aggregated LTRE results at the level of these demographic processes to facilitate the biological interpretation of our results. Finally, to display the proportional influence of each life-cycle stage on the difference between population growth rates, we scaled $\widetilde{\delta}^{\,treatment}$ to 1. This allowed us to interpret the results referring to each vital rates as the percent contribution of each life-cycle stage to the change in λ.

Data and code availability

All analyses and visualizations were performed in R (version 3.5.1; R Core Team 2018). The data and code that produce the results of this study are available in GitHub (https://github.com/Martin19910130/Bromus_IPM_publication.git).

Results

Treatment effects on vital rates

Vital rates were all influenced by plant size at time *t* and best described by models that included climate (Table A.1; Fig. 2; plant survival), management (plant growth and seeds per reproducing plant) or the interaction of both (reproduction probability). However, additive models of climate and management for plant survival, growth and seeds per reproductive plant and interactive models for plant growth had similarly high weighted AICc as the best model (Table A.1). Visualization of vital rates differences between all treatment combinations show that vital rates respond in different directions (Fig. 3). For example, under ambient climate, the intercept of reproduction probability (P) was higher in the grazed treatment, whereas the slope of reproduction probability (P), seedling survivorship (B) and Fall (θ_f) and spring (θ_s) recruitment were all higher in the mowing treatment (Fig. 3).

Treatment effects on population growth rates

Population growth rates (and lower confidence intervals) of *B. erectus* were above one for all treatment combinations, implying a positive population growth (Fig. 4). Climate and management interactively influence the population growth rate of *B. erectus* (Fig. 4): under ambient conditions population growth rates were higher in mown compared to grazed grassland communities ($\lambda = 2.66$ vs. $\lambda = 1.55$; permutation test, *p*=0.026), whereas under future climate conditions population growth rates did not differ between management regimes.

In all treatments, population growth rates of *B. erectus* were most sensitive to reproduction, establishment and particularly recruitment (Fig. 5). While relative differences in fall and spring recruitment between treatments were large (up to 6-fold change), differences in absolute values were very small (Fig. 3). *B. erectus* population growth in all treatments was relatively insensitive to changes in survival and growth (Fig. 5).

Life table Response experiments

The LTREs show that in all pairwise treatment comparisons, differences in population growth rates were primarily due to changes across treatments in reproduction, recruitment and / or establishment of new individuals (Fig. 6). For example, in ambient climate, higher population growth rates of *B. erectus* in the mowed compared to the grazed treatment were primarily explained by higher reproduction, recruitment and establishment (Fig. 6a). In future climate, increases in the reproduction of plants in the mowing treatment were counteracted by higher recruitment and establishment rates of grazed population (Fig. 6b).

Discussion

As expected, population growth rates of *B.* erectus under ambient climatic conditions were higher in mown vs. grazed grassland communities (increase by 64%) and thus mirrored current abundances. Population growth rates were significantly growing under both ambient and future climatic conditions, which we expected as *B. erectus* is a drought-tolerant species. The population growth rate of *B. erectus* was particularly sensitive to reproduction, recruitment and establishment of new individuals. These sensitive parameters responded differentially to the climate and grassland management treatments, creating a significant interactive effect of these treatments on population growth rates. Specifically, under ambient climate conditions the higher population growth rate of *B. erectus* in mown compared to grazed grassland communities was mainly explained by higher rates of reproduction, recruitment and establishment in meadows. In contrast, under future climate conditions, higher rates of reproduction were counteracted by lower rates of recruitment and establishment in mown compared to grazed treatments.

Spring and fall seedling recruitment, the vital rates to which the population growth rate was most sensitive to, declined under future compared to ambient climate conditions in both management regimes. This could have been due to reduced germination rates under future climate conditions if temperatures exceeded the optimum conditions for germination (Lonati, Moot, Aceto, Cavallero & Lucas 2009). Drought events are known to negatively affect germination of *B. erectus* (Moser, Fridley, Askew & Grime 2011). Mowing might have benefitted fall and spring seedling recruitment through lower above-ground competition, as vegetation cover was lower in mown compared to grazed grassland communities (mean vegetation cover including dead and living biomass in August 2018: mowing 64% vs. grazing 82% , unpublished data).

Grazing tended to increase the establishment (in particular, the seedling survival) of *B. erectus* under future climate conditions. Seedlings of *B. erectus* that germinate in spring and fall are highly sensitive to drying out (Bertiller, Zaixso, Irisarri & Brevedan 1996; Soriano & Sala 1986). As precipitation is increased in spring and fall under future climate conditions, this treatment should be generally beneficial for seedlings. However, the positive effect of future climate conditions on establishment was much smaller in mown compared to grazed grasslands, which might be due to other limiting resources such as light and nutrients (Liu, Mao, Wang & Han 2008, Newingham, Vidiella & Belnap 2007). Compared to mowing, grazing results in lower vegetation density in early summer (mean vegetation cover of living biomass in June 2018: mowing 96% vs grazing 73%), which has been shown to positively influence seedling survival (Newingham, Vidiella & Belnap 2007). Furthermore, sheep manure may provide increased nutrient availability to seedlings.

So far, most demographic studies are observational and investigate the impact of climate on population growth rates by comparing the effects of inter-annual climate variations (Bialic-Murphy & Gaoue 2018; Martorell 2007) or through transplant experiments along climate gradients (Topper, Meineri, Olsen, Rydgren, Skarpaas et al. 2018). There are only a handful of studies that experimentally change climate and follow changes in the population growth rate of focal species (Compagnoni & Adler 2014; Gornish 2014; Prevey & Seastedt 2015; Williams, Wills, Janes, Schoor, Newton et al. 2007). Climate change experiments have the advantage of altering specific environmental parameters while all others remain constant – thus they can disentangle the effects of certain climate drivers from other environmental conditions. In contrast to many other climate change experiments the climate treatment in the GCEF is based on realistic, region specific model projections (Korell et al. 2020a; Schaedler et al. 2019) and is combined with different land-use scenarios, including the extensively used grasslands (Schaedler et al. 2019), allowing a better understanding of our future ecosystems based on realistic climate change and management scenarios.

Several demographic studies have considered the effect of grazing or herbivory (García & Ehrlén 2002; Martorell 2007; Rydgren, De Kroon, Okland & Van Groenendael 2001), competition (Fréville & Silvertown 2005) and burning (Emery & Gross 2005; Hoffmann 1999; Kesler, Trusty, Hermann & Guyer 2008) on population growth rates, and these studies consider biotic and abiotic changes that are comparable to those altered by our management treatments. Grazing typically has negative effects on population growth rates of other grassland species (Hansen and Wilson 2006; Jacquemyn, Brys, Davison, Tuljapurkar and Jongejans 2012, van der Meer, Dahlgren, Milden and Ehrlen 2014). Two other studies have found that the effect of grazing on plant population growth will depend on climate (Martorell 2007), suggesting that interactions between climate and management might be a common phenomenon. Population growth rates of the genus *Bromus* are known to be responsive to many environmental gradients and their interactions, including warming, precipitation, and management (Compagnoni et al. 2014; Prevey et al. 2015; Zelikova, Hufbauer, Reed, Wertin, Fettig et al. 2013). These results, combined with ours, highlights the importance of considering multiple environmental drivers in future demographic studies (see also Williams et al. 2007).

Non-intensive grazing and mowing are important management regimes of grasslands in Europe that help conserve species richness. While *B. erectus* is already common in nutrient poor, calcareous grasslands it might become even more dominant in non-intensively used pastures. Because older *B. erectus* individuals are avoided by grazers, climate change could decrease the grazing value of these grasslands. Additionally, non-intensively used grasslands are important biodiversity hotspots in Europe and an increased dominance of *B. erectus* could pose a threat to species with a lower competitive ability (Poniatowski, Hertenstein, Raude, Gottbehuet, Nickel et al. 2018).

Conclusion

Our results support the idea that the impact of climate change depends on the management regime (Ehrlén 2019). To our knowledge, this study is the first one to provide experimental evidence of an interactive effect of climate change and grassland management on the population growth rate of a common grassland species, *Bromus erectus*. This interaction was mainly caused by differences in reproduction, seedling recruitment and establishment, which are sensitive stages in the life-cycle of our population. Demographic studies are an underutilized tool that can provide a mechanistic understand of treatment effects and can project how populations will develop under future conditions. Our results show that under ambient climate conditions, the abundance of *B, erectus* can be regulated via changes in the management regime.

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Figure legends

Fig. 1: Life-cycle diagram of *Bromus erectus* with all parameters included in the IPM and their abbreviations.

Fig. 2: Visualization of parameter estimates of all vital rates included in the IPMs based on the original data. Logistic (a & c) and linear (b) and poisson (d) functions describe individual based and size-dependent processes, while bar charts (e – g) show the mean and standard error for plot-based calculations, and the boxplot (h) displays the median and the size distribution of new plants, an individual-based, non-size-dependent vital rate.

Fig. 3: Differences in vital rates between pairwise treatment combinations. Displayed are the changes in mean, intercept (Int), slope and standard deviation (SD) to vital rates caused by the management treatment under (a) ambient and (b) future climatic conditions and changes caused by the climate treatment in (c) mowing and (d) grazing. The direction of bars indicate higher vital rates in the according climate or management treatment. For abbreviations and according vital rates see Tab. 2.

Fig. 4: Mean population growth rates of *Bromus erectus* under ambient and future climate treatments in mown (triangle) or grazed grasslands (dots). Error bars encompass bootstrapped 95% confidence intervals.

Fig. 5: Sensitivity of pairwise treatment combinations to all vital rates included in the IPM.

Fig. 6: Life table response experiments (LTREs) showing the percentagewise effect of the five life-cycle stages on differences between pairwise treatments in population growth rate. LTREs were calculated for pairwise comparisons of treatment combinations: management influence under (a) ambient and (b) future climatic conditions and climate influence under (c) mowing and (d) grazing management conditions. To obtain the total impact of a life-cycle stage on the population growth rate LTRE results of vital rates that contribute to the same life-cycle stage were summed. The direction of the bars indicates the direction of the contribution of the according climate or management treatment for each life-cycle stage.

Figures

Fig. 1

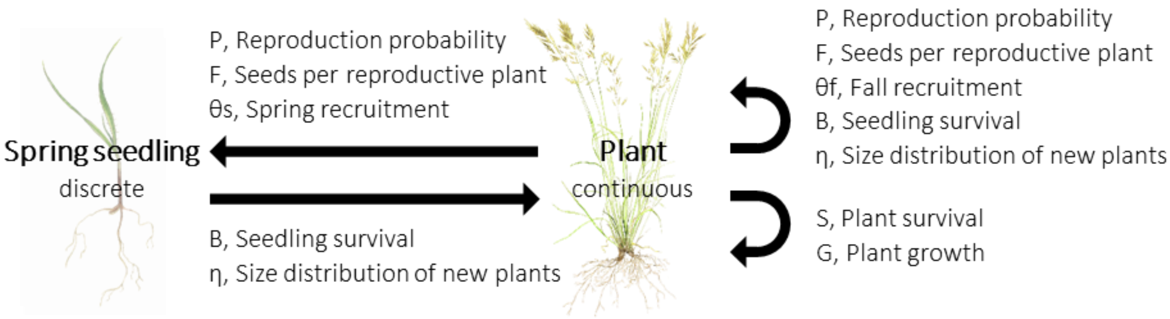
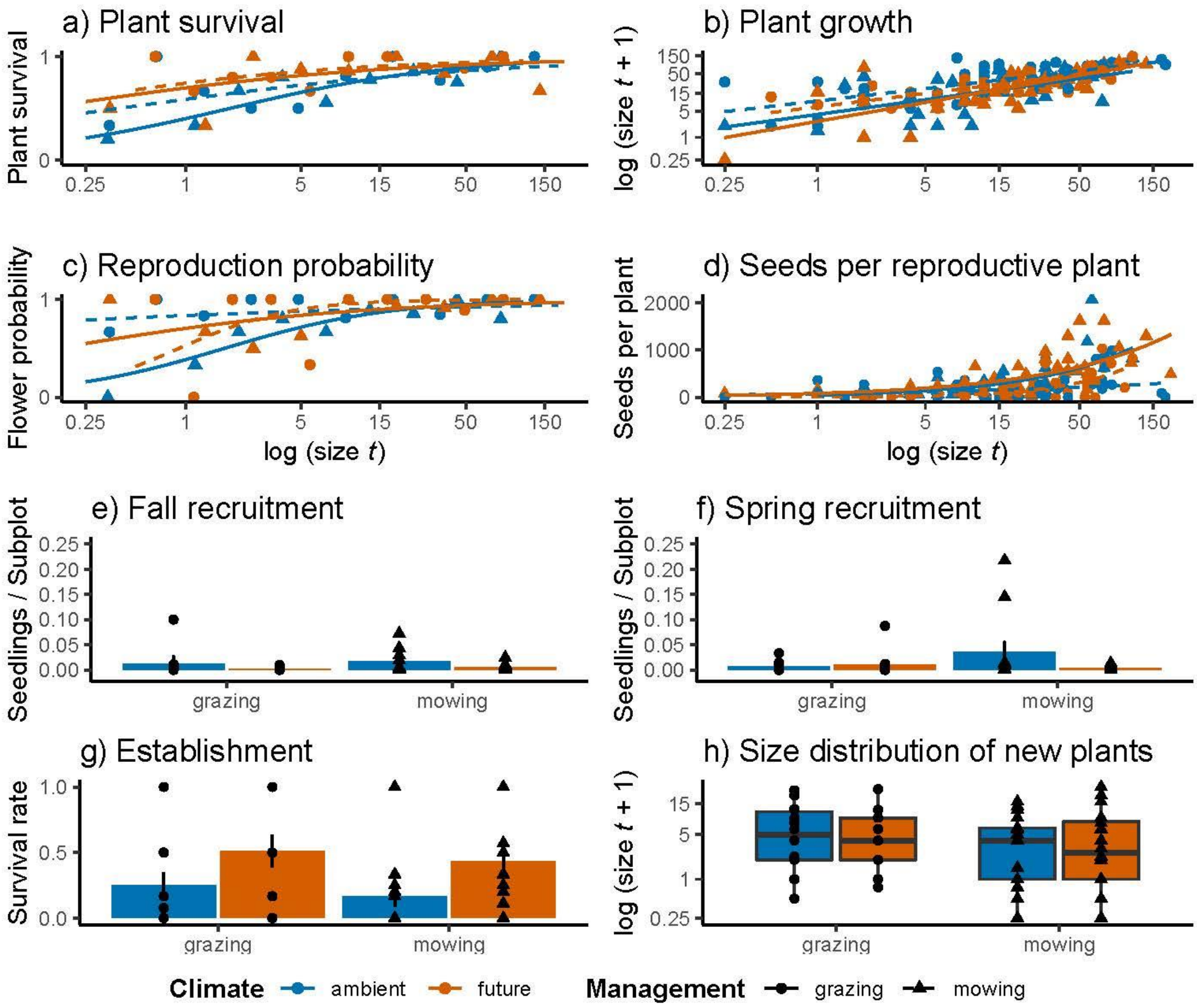


Fig. 2



a) Plant survival
Plant survival
1
0
0.25
1
5
15
50
150
b) Plant growth
log (size t + 1)
150
50
15
5
1
0.25
c) Reproduction probability
Flower probability
log (size t)
d) Seeds per reproductive plant
Seeds per plant
2000
1000
0
e) Fall recruitment
Seedlings / Subplot
0.25
0.20
0.15
0.10
0.05
0.00
grazing
mowing
f) Spring recruitment
g) Establishment
Survival rate
1.0
0.5
0.0
h) Size distribution of new plants
Climate
ambient
future
Management
grazing
mowing

Fig. 3

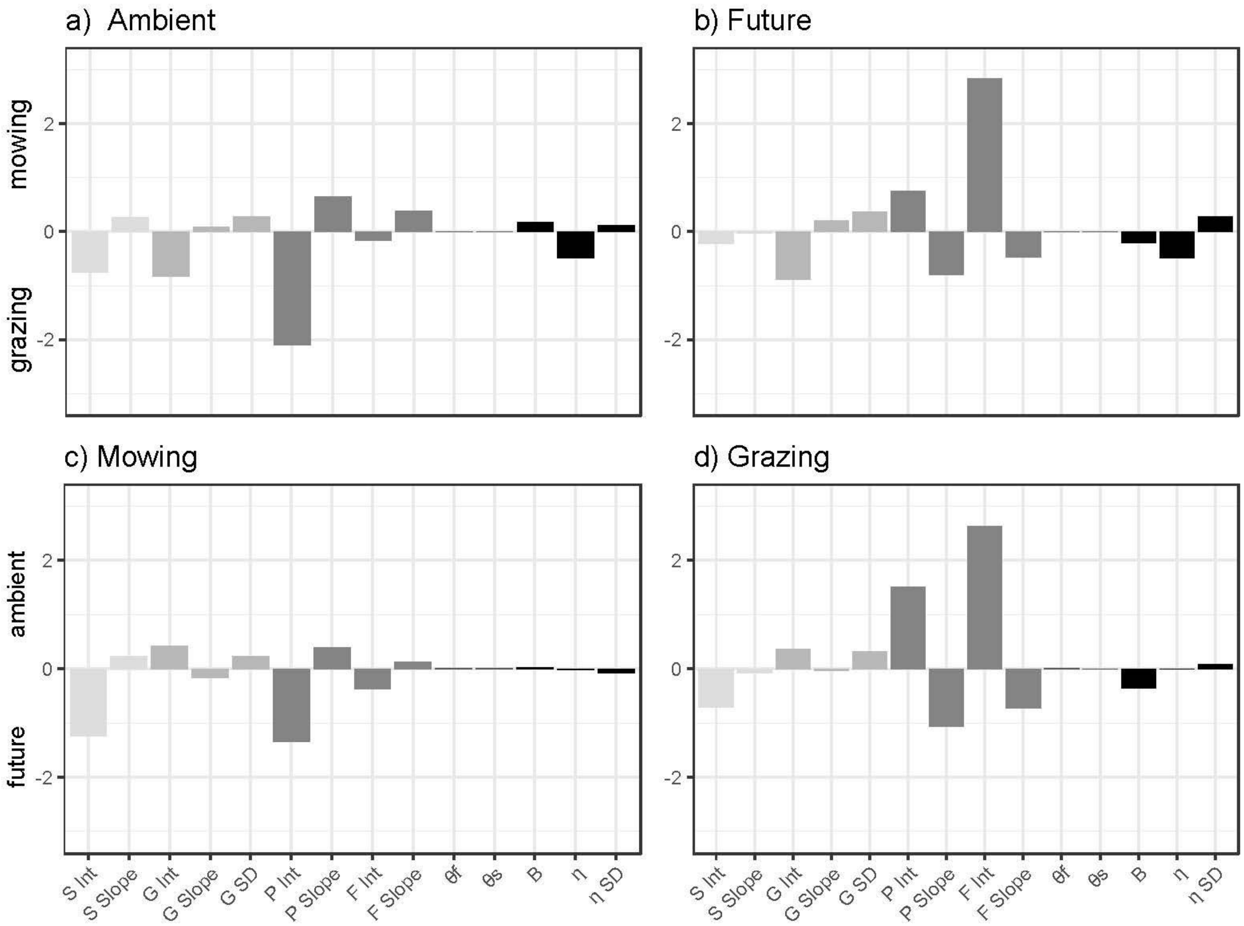
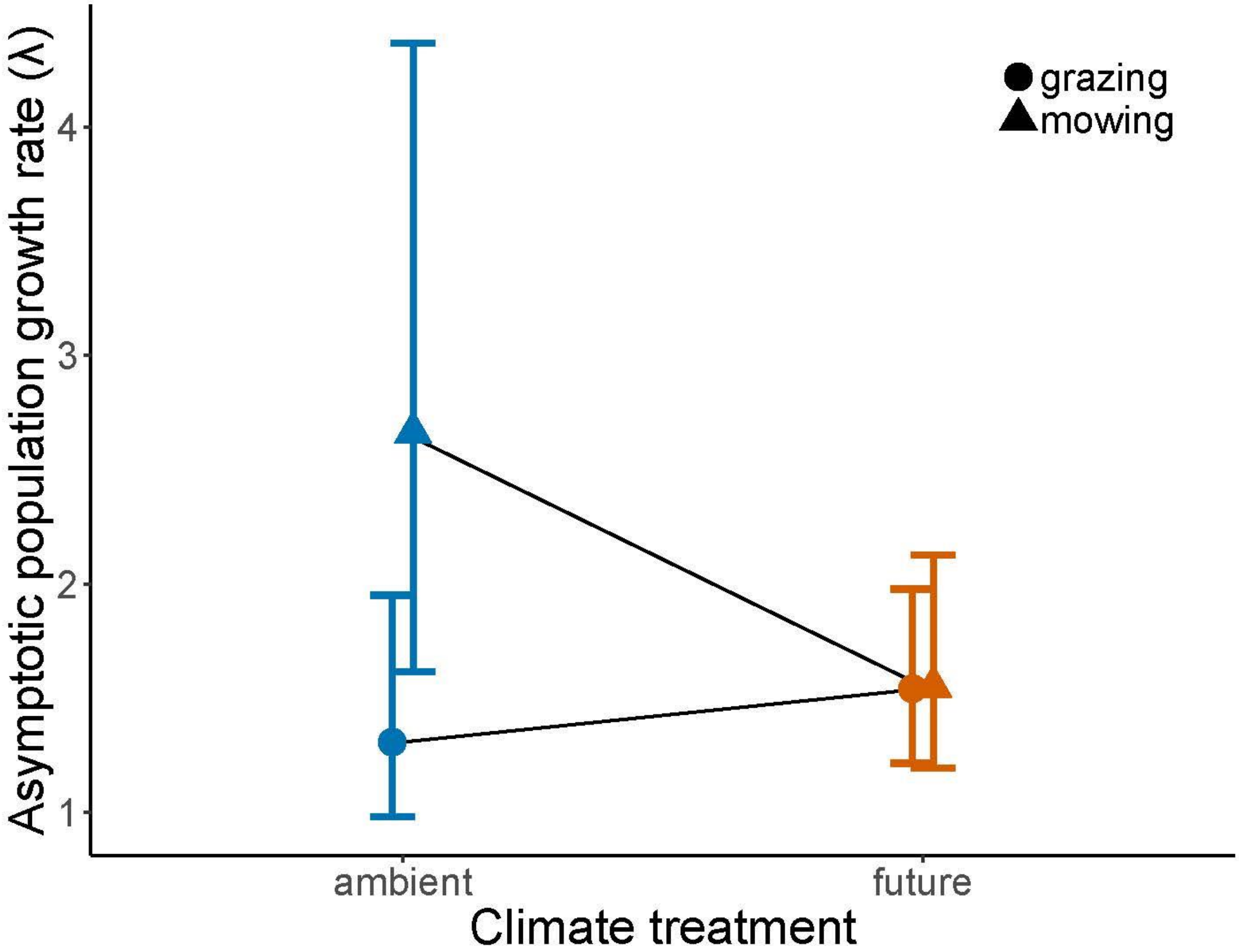

a) Ambient
b) Future
c) Mowing
d) Grazing
mowing
grazing
ambient
future
2
0
-2
S Int
S Slope
G Int
G Slope
G SD
P Int
P Slope
F Int
F Slope
θf
θs
B
η
η SD

Fig. 4

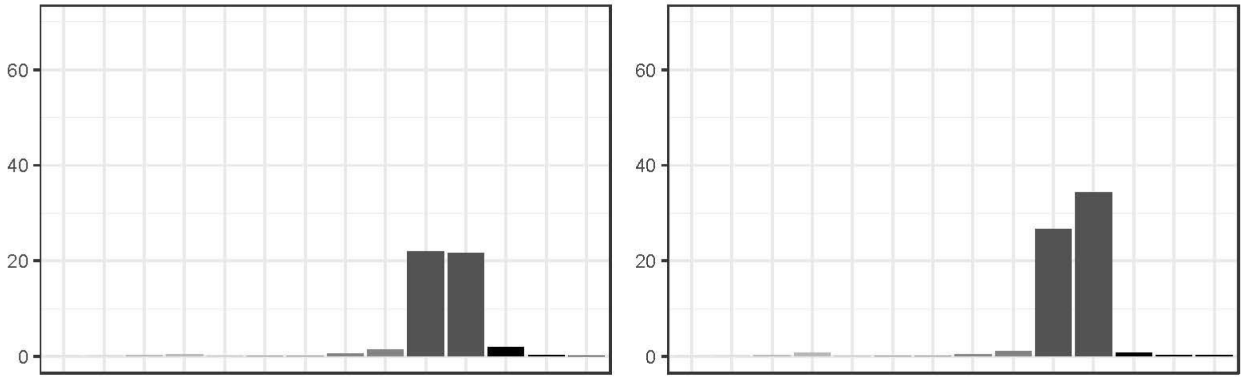


Asymptotic population growth rate (λ)
4
3
2
1
ambient
future
Climate treatment
● grazing
▲ mowing

Fig. 5

a) Mowing ambient * grazing ambient

b) Grazing future * mowing future



c) Mowing ambient * mowing future

d) Grazing ambient * grazing future

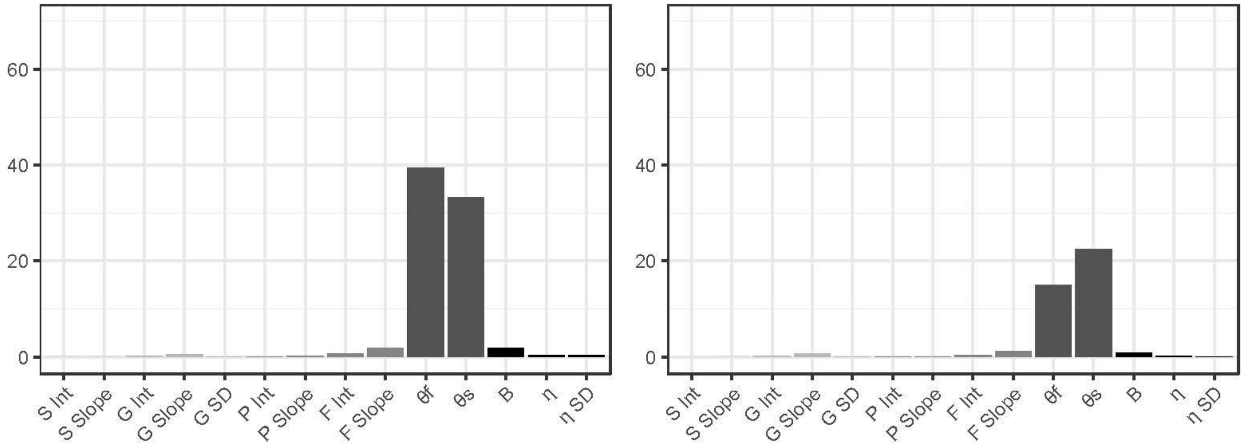


Fig. 6

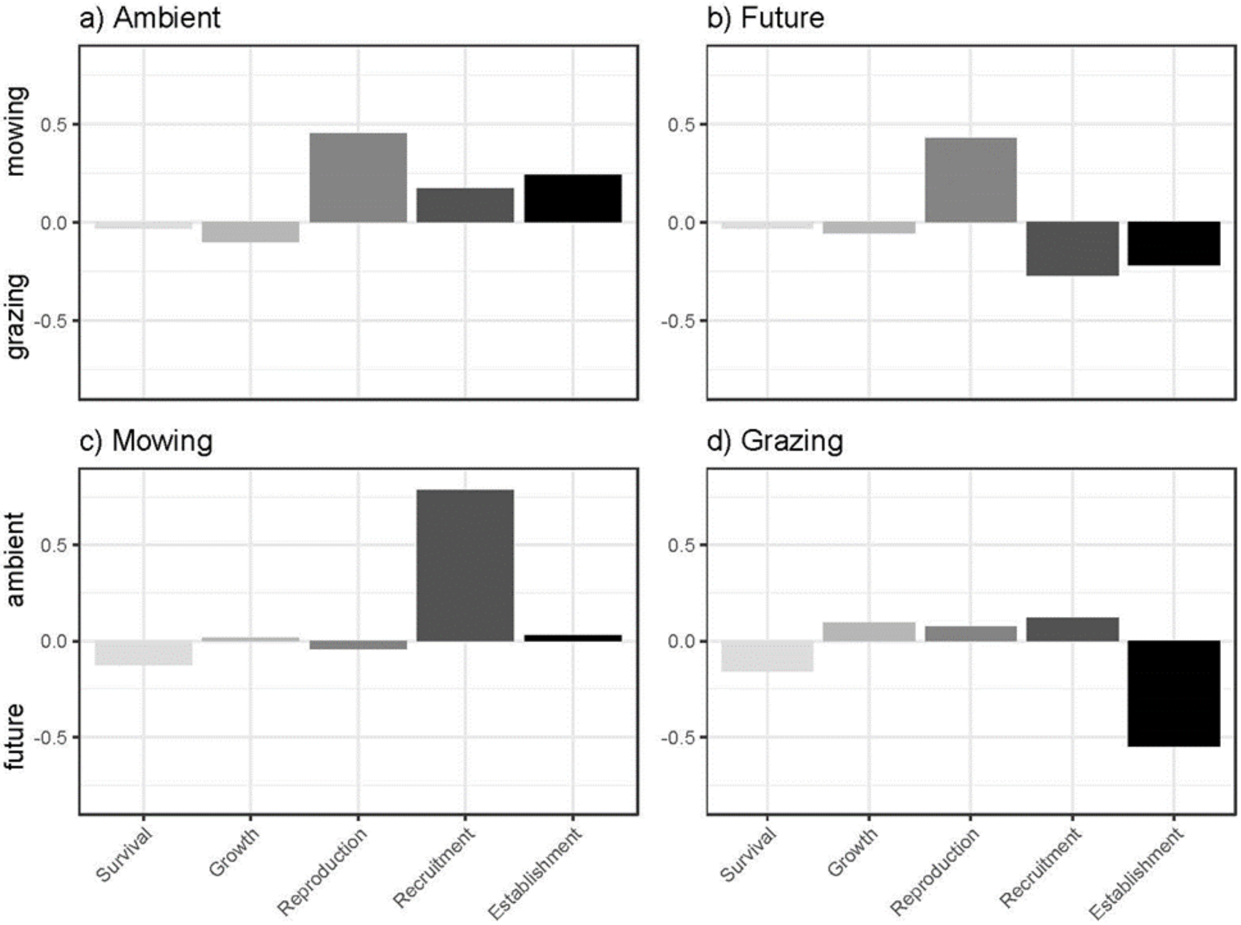

a) Ambient
b) Future
c) Mowing
d) Grazing
mowing
grazing
ambient
future
0.5
0.0
-0.5
Survival
Growth
Reproduction
Recruitment
Establishment

Table Legends

Table 1: Parameters of vital rates included in the IPM and their abbreviations and distributions. Recruitment stands for the number of seedlings per seeds in November or April.

Table A.1: Corrected Akaike Information Criterion (AICc) weights for size dependent parameters included in the IPM. Tested were the Null-model with log size at t as the only explaining variable, effects of the climate treatment, management treatment, their interactive effects, and their additive effects. Larger numbers indicate a better fit.

Tables

Table 1

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

Table A.1

Parameter	Null-model	Climate	Management	Climate * Management	Climate + Management
Plant survival	0.093	0.506	0.047	0.092	0.262
Plant growth	0.001	0.001	0.473	0.219	0.307
Reproduction probability	0.151	0.092	0.386	0.128	0.243
Seeds per reproductive plant	0.000	0.000	0.000	0.974	0.026