



# 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. Using an integral projection model, 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 between-treatment changes in seedling recruitment, a vital rate to which the population growth rate is particularly sensitive. 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.

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**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 (Hejman, Ceskova, Schellberg & Paetzold 2010; Janssens et al. 1998; Klimek, Richter, Hofmann & Isselstein 2007; Socher et al. 2012; Wesche, Krause, Culmsee & Leuschner 2012). The composition of

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plants in grasslands is largely influenced by management practices. In Europe, semi-natural grasslands with high biodiversity can be sustainably managed with ‘extensive grassland management’, which involves low intensity mowing or grazing and no nutrient inputs (Cousins & Eriksson 2001; Tschamtkke, 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 et al. 2016). Grazing management can similarly promote biodiversity, but creates more heterogeneous disturbances through preferential biomass removal and soil disturbances by animals (Klimek, Richter, Hofmann & Isselstein 2007; Olff & Ritchie 1998).

The composition of semi-natural grasslands is also determined by climate, 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 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 fall (Wagner, Berg, Schädler & Kunstmann 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; Schädler 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 extensively managed 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 & Oostermeijer 2001), particularly when it occurs early in the season (Brys, Jacquemyn, Endels, Blust & Hermy 2004). Climate change and management might interactively influence plant demography (Klein, Harte & Zhao 2004; Martorell 2007), but the effects cannot be easily predicted (Bütof 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 (IPMs) are commonly used methods to link the demography of plant and animal species to their asymptotic (long-term) population growth rate ( $\lambda$ ) (Caswell 2001; Easterling, Ellner & Dixon 2000). A

mechanistic understanding of 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  $\lambda$  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  $\lambda$  is sensitive to.

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 experimental 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 (Schädler 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-managed 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?

## Materials and 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 2003). *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, Volaire, Fattet, Blanchard & Roumet 2013) and is considered a stress-tolerant competitor (Grime, Hodgson & Hunt 2014). The erect brome is a perennial and

polycarpic grass species which forms a non-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 experiment 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<sup>-1</sup> and mean annual temperature of 8.9°C (Schädler et al. 2019). *Bromus erectus* is the third most dominant species of all 56 sown grassland plant species with a mean cover (across all treatments and years) of about 10% (Auge et al., unpublished data). Seed material of all sown species originated from several, regional source populations (Schädler et al. 2019) and for *B. erectus* five source populations successfully established in the GCEF (Madaj, Michalski & Durka 2020). The experimental setup of the GCEF follows a split-plot design in which climate (ambient vs. future) is a main plot factor and land management (including extensively managed with grazing and extensively managed with mowing) is a subplot factor (Schädler et al. 2019). The experiment comprises ten main plots with a size of 80×24 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 is applied. Spring and fall 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 (Schädler et al. 2019). Nested within each main plot, we considered two land management treatments, each spanning 24×16 m. Subplots in the mowing treatment were mown in June 2018 and 2019 and subplots in the grazing treatment were grazed by sheep 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 subplot nested within the 10 main plots exposed to an experimental

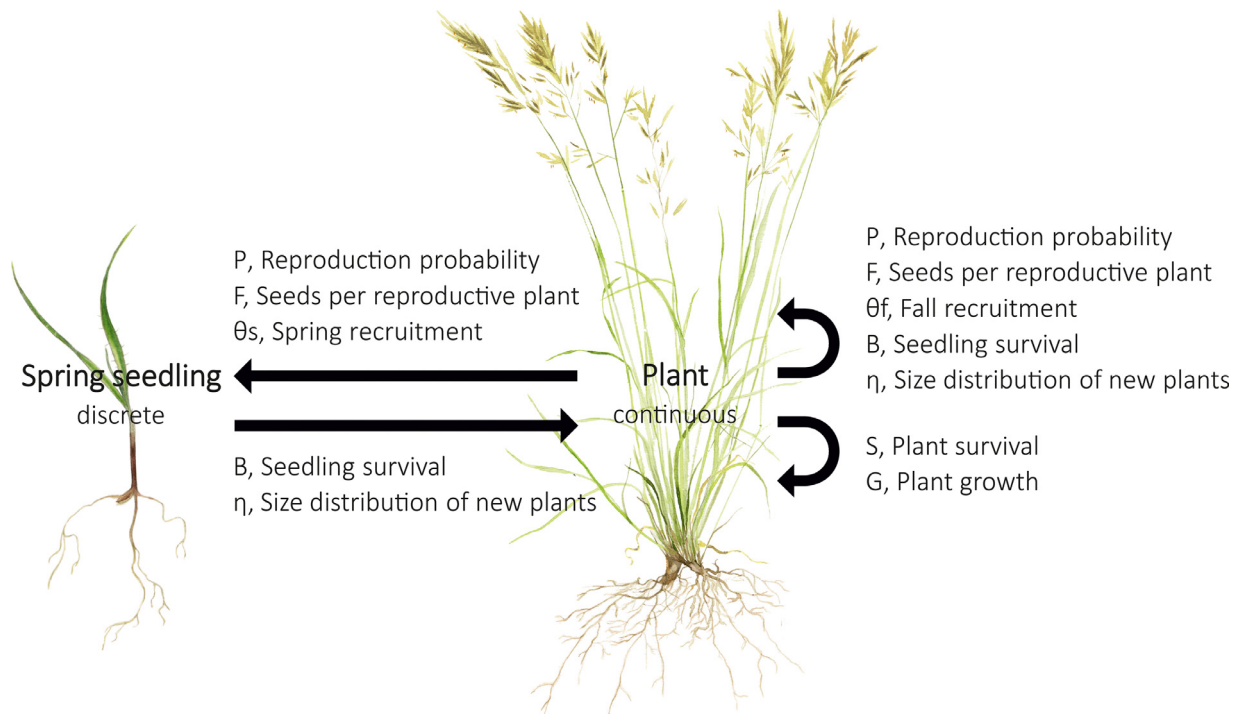
climate treatment (ambient vs. future climate) (2 climate x 2 land management x 5 replicates =  $\sum$  20 transects). Along each transect we established six to eight permanent quadrats of 0.5×0.5 m. Three quadrats were located at predefined intervals, the remaining quadrats were established at areas with higher abundances of the focal species. We surveyed individuals within quadrats and, when sample sizes were not sufficient, we tagged additional individuals outside of quadrats, 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 combination) 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 quadrat. We defined *B. erectus* plants with less than 3 shoots as seedlings (Fig. 1). Before the first grazing event in 2018 and 2019, we calculated basal area for each individual as the product of genet length and width. Length was measured as the longest lateral dimension of each plant, and width was measured perpendicular to length. Individuals present in April 2018 but not April 2019 were marked as dead, and all new individuals in quadrats 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 by the number of fruiting ramets per individual. Finally, we counted seedlings in the first three quadrats of each transect in April 2018 and 2019 before the first management event, and in November 2018, as germination of *B. erectus* occurs in fall and spring (Zeiter & Stampfli 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 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



**Fig. 1.** Life-cycle diagram of *Bromus erectus* with all parameters included in the integral projection model (IPM) and their abbreviations. Paintings by Myriam Kind.

a function of log size in year  $t$ , using a logit link function (Eq. 2),

$$S_{i,t+1} \sim \text{Bernoulli}(\hat{S}_{t+1}) \quad (1)$$

$$\text{logit}(\hat{S}_{t+1}) = \alpha^S + \beta^S \log_e(\text{size}_t) \quad (2)$$

where  $\alpha^S$  is the intercept,  $\beta^S$  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  $\alpha^G$ , slope  $\beta^G$  (Eq. 4) and standard deviation  $\sigma^G$  (Eq. 3):

$$G_{i,t+1} \sim \text{Normal}(\hat{G}_{t+1}, \sigma^G) \quad (3)$$

$$\hat{G}_{t+1} = \alpha^G + \beta^G \log_e(\text{size}_t) \quad (4)$$

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  $\alpha^P$  and slope  $\beta^P$  using a logit link function (Eq. 6),

$$P_{i,t} \sim \text{Bernoulli}(\hat{P}_t) \quad (5)$$

**Table 1.** Parameters of vital rates included in the integral projection model (IPM) and their abbreviations and distributions. Recruitment stands for the number of seedlings per seeds in November or April.

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	$\theta_f$	Recruitment	Mean	Poisson
Spring recruitment	$\theta_s$	Recruitment	Mean	Poisson
Seedling survival	$B$	Establishment	Mean	Bernoulli
Size distribution of new plants	$\eta$	Establishment	Mean, SD	Normal



$$\text{logit}(\hat{P}_t) = \alpha_t^P + \beta^P \log_e(\text{size}_t) \quad (6)$$

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 reproductive plant 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  $\alpha F$  and slope  $\beta F$  (Eq. 8),

$$F_{i,t} \sim \text{Poisson}(\hat{F}_t) \quad (7)$$

$$\hat{F}_t = \alpha^F + \beta^F \log_e(\text{size}_t) \quad (8)$$

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 quadrat level, where  $\theta$  is recruitment,  $f$  is fall,  $s$ , is spring,  $j$  is the quadrat, and  $t$  refers to 2018. We calculated the seeds produced per quadrat as  $F_{j,t} = \sum F_{i,t}$ , where  $i$  refers to all the individuals that produced seeds in quadrats  $j$  in year  $t$ . We divided the number of emerging seedlings in the subsequent fall 2018 ( $R_{f,j,t}$ ) and spring 2019 ( $R_{s,j,t+1}$ ) by the number of seeds per quadrat:

$$\theta_{f,j,t} = \hat{R}_{f,j,t} / F_{j,t} \quad (9)$$

$$\theta_{s,j,t+1} = \hat{R}_{s,j,t+1} / F_{j,t} \quad (10)$$

We calculated seedling survival at the quadrat level. Seedling survival,  $B_j$ , was the proportion of emerging seedlings in year  $t$  in quadrat  $j$ ,  $R_{sum,j,t}$ , that survived to year  $t+1$ ,  $R_{sum,j,t+1}$ . Hence:

$$B_j = R_{sum,j,t+1} / R_{sum,j,t} \quad (11)$$

$R_{sum,j,t}$  is the sum of fall,  $R_{f,j,t}$ , and spring,  $R_{s,j,t}$ , recruitment in year  $t$ .

Finally, we modeled the log size distribution of new plants,  $\eta$ , 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 ( $\sigma_\eta$ ) of this size distribution:

$$\log_e(\eta_{i,t+1}) \sim \text{Normal}(\log_e(\hat{\eta}_{t+1}), \sigma_\eta) \quad (12)$$

## Effects of treatments on vital rates

We fit 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 five 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, Childs and Rees \(2016\)](#). 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:

$$n(z', t+1) = M(t)B\eta(z') + \int_L^U S(z)G(z', z) + P(z)F(z)\theta_f B\eta(z')n(z, t)dz \quad (13)$$

The vector  $n(z, t+1)$  describes the number of plants at size  $z$  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  $200 \times 200$  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  $\theta_f$ , 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:

$$M(t+1) = \int_L^U P(z)F(z)\theta_f s(z, t)dz \quad (14)$$

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

We created four IPMs, one for each treatment combination of land 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

( $\lambda$ ). Then, we calculated sensitivities and elasticities of  $\lambda$  to kernel element perturbations for each treatment combination (Fig A1). Finally, we quantified the relative contribution of separate vital rates to these differences in  $\lambda$  for each pairwise treatment combination using 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 bootstrapped estimates for each parameter in the model (for each treatment combination) by resampling with replacement from the original raw data set (resampling individuals plants for most parameters, resampling quadrats for recruitment and establishment), then ran the IPM once for each bootstrapped parameter set. We tested whether differences in  $\lambda$  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 – grazing ambient, mowing future – grazing future, mowing ambient – mowing future, grazing ambient – grazing future). The contribution of each vital rate to the difference in  $\lambda$  between two different treatment combinations was calculated as:

$$\tilde{\delta}^{treatment} = \sum_i^{14} (\alpha_i^{treatment\ combination\ 1} - \alpha_i^{treatment\ combination\ 2}) \frac{\partial \lambda}{\partial \alpha_i} \quad (15)$$

where  $\alpha_i$  is one of the fourteen vital rates included in the IPMs, and the term  $\frac{\partial \lambda}{\partial \alpha_i}$  is 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  $\lambda$  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 plant. 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 vital rate on the difference between population growth rates, we scaled  $\tilde{\delta}^{treatment}$  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  $\lambda$ .

All analyses and visualizations were performed in R (version 3.5.1; R Core Team 2018).

## Results

### Treatment effects on vital rates

Vital rates of plants were all influenced by plant size at time  $t$  and best described by models that included climate (Table 2; Fig. 2; plant survival), management (plant growth and reproduction probability) or the interaction of both (seeds per reproductive plant). 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 2). Vital rates respond in different directions to the treatments (Table 3). For example, under ambient climate, the intercept of reproduction probability ( $P$ ) was higher in the grazing treatment, whereas the slope of reproduction probability ( $P$ ) and mean seedling survivorship ( $B$ ), mean fall ( $\theta_f$ ) and spring ( $\theta_s$ ) recruitment were all higher in the mowing treatment (Table 3).

### Population growth rates, sensitivity and elasticity analysis

Population growth rates (and lower confidence intervals) of *B. erectus* were above one for all treatment combinations,

**Table 2.** Corrected Akaike Information Criterion (AICc) weights for size dependent parameters included in the integral projection model (IPM). Tested were the Null-model with log size at  $t$  as the only explaining variable, effects of the climate treatment (C), management treatment (M), their interactive effects, and their additive effects. Larger numbers indicate a better fit.

Parameter	Null-model	Climate (C)	Management (M)	C x M	C + M
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

implying a positive population growth (Fig. 3). Climate and management interactively influence the population growth rate of *B. erectus* (Fig. 3): under ambient conditions population growth rates were higher in mown compared to grazed grassland communities ( $\lambda = 2.51$  vs.  $\lambda = 1.30$ ; permutation test,  $p=0.024$ ), whereas under future climate conditions population growth rates did not differ between land management treatments ( $\lambda$  future mowing = 1.56 vs.  $\lambda$  future grazing = 1.54).

In all treatments, population growth rates of *B. erectus* were most sensitive to reproduction, establishment and particularly recruitment (Fig. 4, Fig. A1). *B. erectus* population growth in all treatments was relatively insensitive to changes in survival and growth (Fig. 4, Fig. A1).

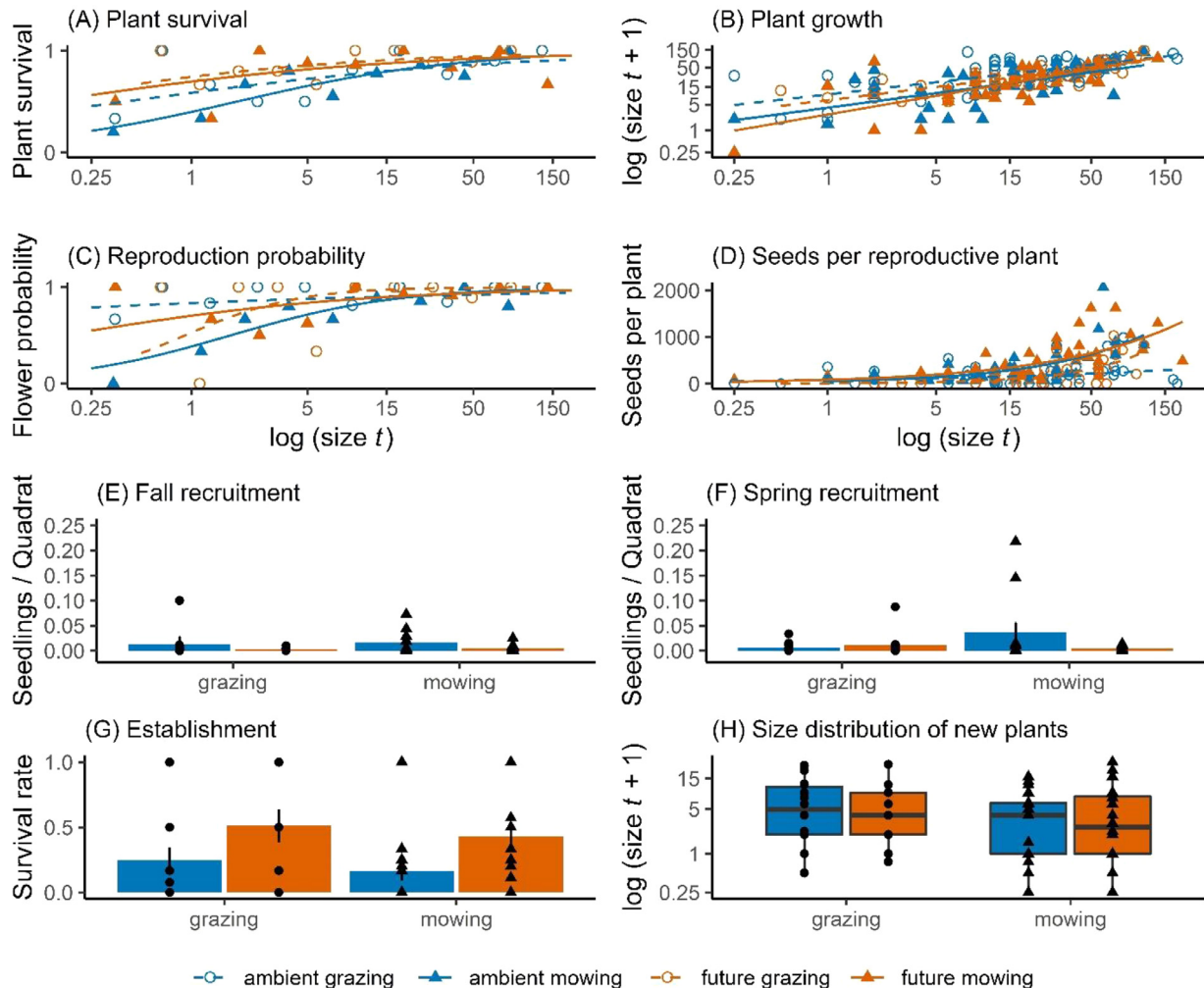
### Life table response experiments

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. 5 A-D). 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. 5A). In future climate, increases in the reproduction of plants in the mowing treatment were contrasted by higher recruitment and establishment rates of grazed populations (Fig. 5B).

### Discussion

As expected, population growth rates of *B. erectus* under ambient climatic conditions were higher in mown vs. grazed grassland communities (increase by 93%) 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-



**Fig. 2.** Visualization of parameter estimates of all vital rates included in the integral projection models (IPMs) based on the original data. Logistic (A & C), 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.

**Table 3.** Bootstrapped mean and standard error the parameters of vital rates included in the integral projection model (IPM).

Vital rate	Parameter	Ambient grazing		Ambient mowing		Future grazing		Future mowing	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE
Survival ( <i>S</i> )	Intercept	0.367	0.017	-0.438	0.016	1.109	0.116	0.800	0.094
	Slope	0.382	0.006	0.688	0.008	0.639	0.511	0.538	0.064
Growth ( <i>G</i> )	Intercept	2.215	0.011	1.398	0.012	1.852	0.006	0.999	0.016
	Slope	0.481	0.003	0.564	0.004	0.521	0.002	0.719	0.005
	SD	0.731	0.002	1.002	0.003	0.425	0.002	0.769	0.004
Reproduction probability ( <i>P</i> )	Intercept	1.845	0.033	-0.522	0.016	-0.893	0.168	0.787	0.040
	Slope	0.200	0.017	0.938	0.010	4.507	0.417	0.560	0.015
Seeds per reproductive plant ( <i>F</i> )	Intercept	4.244	0.013	3.883	0.013	1.769	0.021	4.366	0.010
	Slope	0.280	0.004	0.643	0.004	1.012	0.006	0.539	0.003
Fall recruitment ( $\theta_f$ )	Mean	0.011	<0.001	0.012	<0.001	0.003	<0.001	0.006	<0.001
Spring recruitment ( $\theta_s$ )	Mean	0.008	<0.001	0.026	<0.001	0.009	<0.001	0.005	<0.001
Seedling survival ( <i>B</i> )	Mean	0.276	0.004	0.679	0.009	0.789	0.01	0.388	0.003
Size distribution of new plants ( $\eta$ )	Mean	1.437	0.008	0.913	0.008	1.432	0.009	0.957	0.008
	SD	1.166	0.004	1.295	0.003	1.070	0.005	1.364	0.004

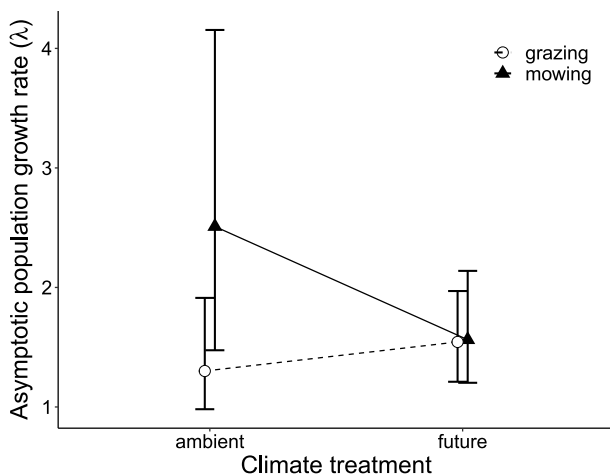
tolerant species. The population growth rate of *B. erectus* was particularly sensitive to reproduction, recruitment and establishment of new individuals. These sensitive parameters responded differentially to the climate and grassland management treatments, creating a significant interactive effect 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 for which the population growth rate was most sensitive, 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%; Auge et al., unpublished data).

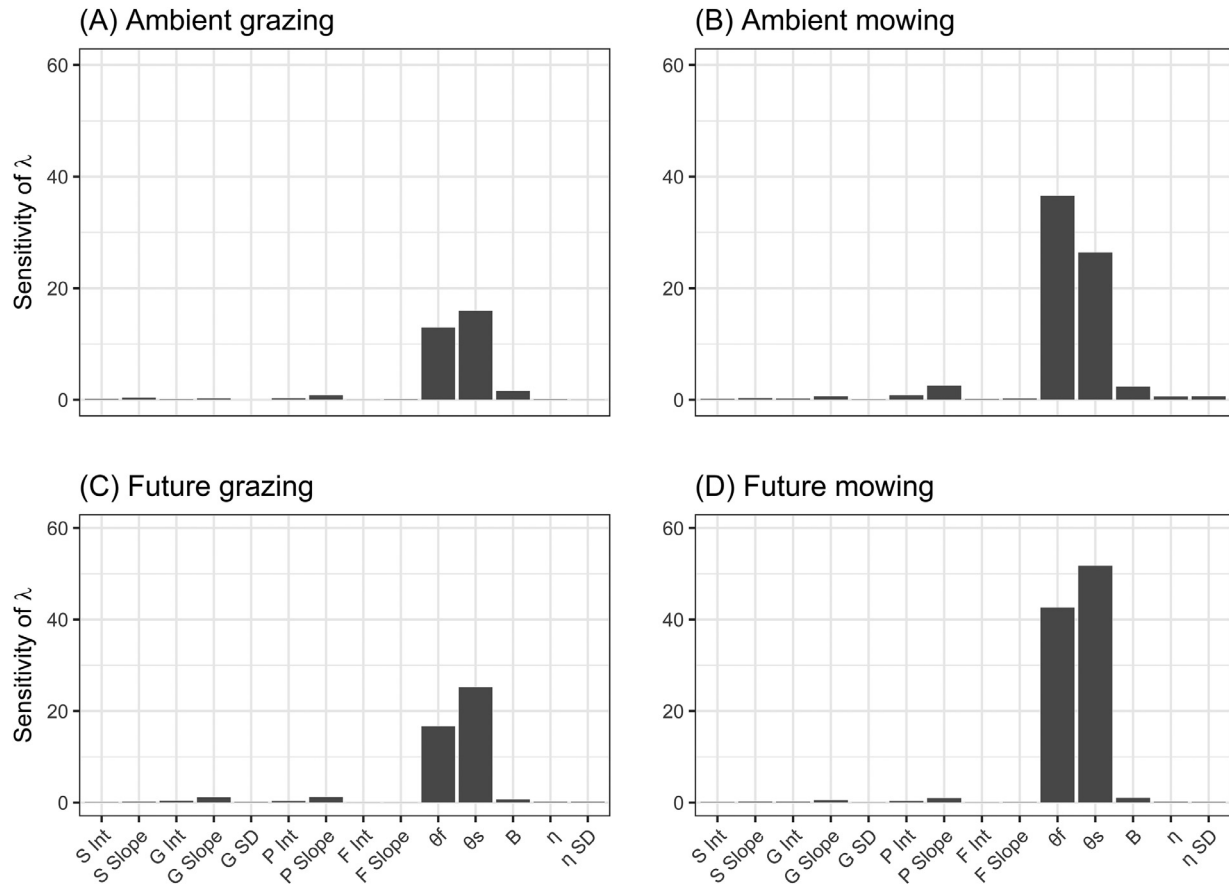
Grazing tended to increase the establishment (in particular, the seedling survival) of *B. erectus* under future climate conditions. Seedlings of *B. erectus* that germinate in spring and fall are highly sensitive to drying out (Bertiller, Zaixso, Irisarri & Brevedan 1996; Soriano & Sala 1986). As precipitation 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%; Auge et al., unpublished data), 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 simulate climate change and



**Fig. 3.** 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.



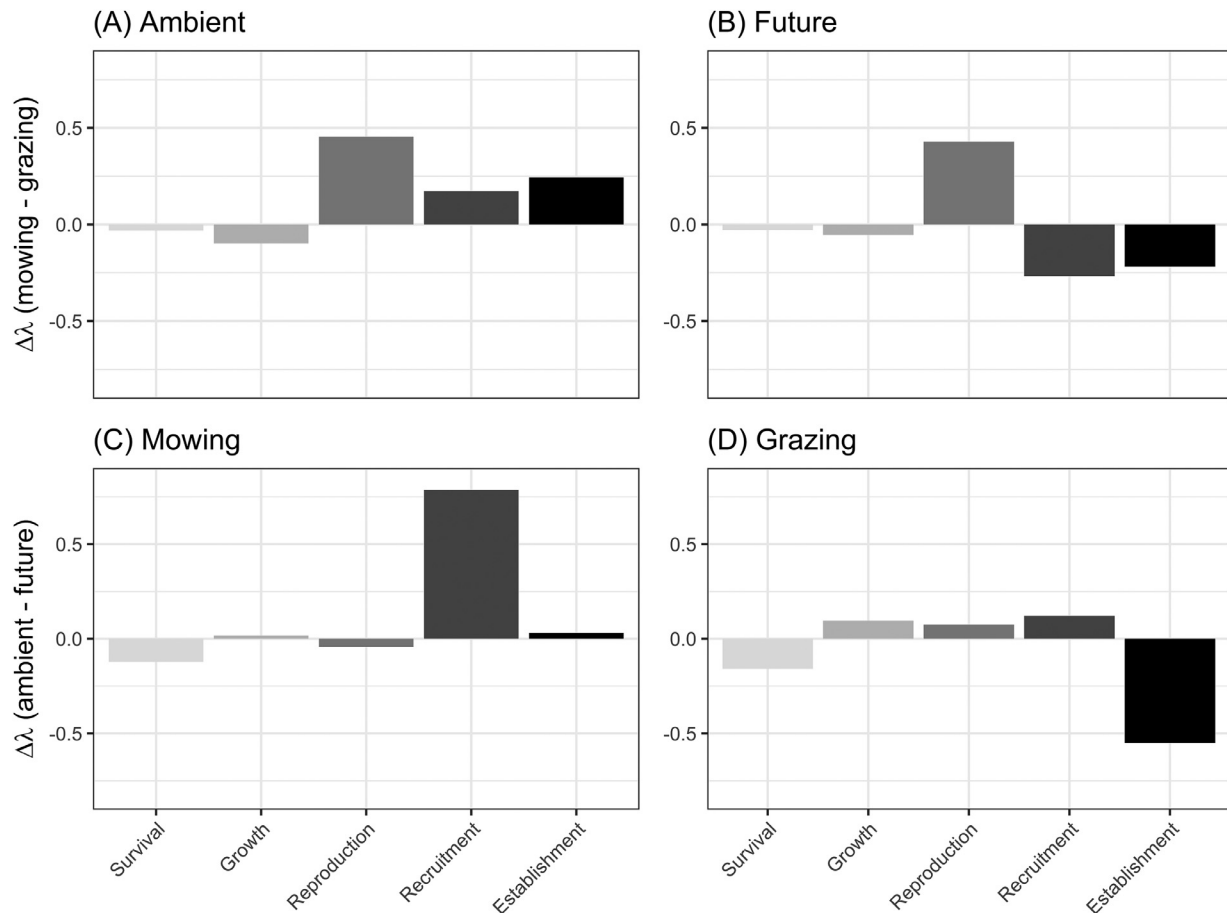


**Fig. 4.** Sensitivity of pairwise treatment combinations to all vital rates included in the integral projection model (IPM).

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, Auge, Chase, Harpole & Knight 2020a; Schädler et al. 2019) and is combined with different land-use scenarios, including the extensively used grasslands (Schädler 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 & Wilson 2006; Jacquemyn, Brys, Davison, Tuljapurkar & Jongejans 2012; van der Meer, Dahlgren, Mil-den & Ehrlén 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 & Adler 2014; Prevey & Seastedt 2015; Zelikova et al. 2013). These results, combined with ours, highlight 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 et al. 2018).



**Fig. 5.** Life table response experiments (LTREs) showing the relative contribution of the five life-cycle stages on pairwise differences between treatment combinations in the population growth rate ( $\Delta\lambda$ ). Panels show contributions of life cycle stages to  $\Delta\lambda$  in the treatment combinations (A) ambient mowing and ambient grazing, (B) future mowing and future grazing, (C) ambient mowing and future mowing, and (D) ambient grazing and future grazing. The direction of the bars indicates the direction of the contribution of each life cycle stage to the pairwise differences in the population growth rate ( $\Delta\lambda$ ).

## Conclusion

Our results support the idea that climate and land management interactively influence plant population dynamics (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 understanding 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.

## Data and code availability

The data and code that produce the results of this study are available in GitHub ([https://github.com/Martin19910130/Bromus\\_IPM\\_publication.git](https://github.com/Martin19910130/Bromus_IPM_publication.git)).

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2021.06.012.

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