



Plant species' range type determines local responses to biotic interactions and land use

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Abstract. Geographic plant distribution is often assumed to be predominantly limited directly by the climatic tolerances of species. However, the role of climate is now known to be mainly an indirect one mostly mediating dispersal and establishment, species interactions, or habitat characteristics, which all are often modified by human land use. In these complex systems, negative biotic interactions are predicted to increase in relative importance toward benign climatic conditions. We tested this hypothesis experimentally by exposing plant species with different geographic distribution ranges to different climates, biotic interactions, and land use. Thereby, species predominantly distributed in regions with benign climatic conditions were expected to be better able to cope with negative biotic interactions than species from regions with environmentally stressful climatic conditions. **We present results of a fully crossed two-year transplantation field experiment replicated in 45 plots in three study regions along a precipitation gradient across Germany. We manipulated biotic interactions (presence/absence of competition and mollusk herbivory) in grasslands of different management regimes (meadows, mown pastures, pastures).** The transplanted phytometers consisted of six congeneric species pairs, each representing one oceanic and one distinctly more continental range type. The oceanic range type is predominantly distributed in benign climatic conditions in Western Europe, while the more continental type is distributed in regions with more stressful climatic conditions in Eastern Europe. This experimental setting allowed us to study the impact of negative biotic interactions along an abiotic stress gradient under realistic land-use conditions. Under competition and mollusk herbivory, growth performance was more strongly reduced in continental compared to oceanic species. Range types also differed in their responses to grassland management. Differences in survival between the congeneric species were found to be region-specific and largely unaffected by biotic interactions and land use. In consequence, our results suggest that local responses to biotic interactions and land-use practices of otherwise very similar plant species can differ strongly depending on species' large-scale geographical distribution. Regionally differing responses to biotic interactions also show that local conditions can drastically change responses expected from macroecological theory.

Key words: biogeography; biotic interactions; competition; grassland plants; land use; mollusk herbivory; phytometers; plant growth; plant species distribution; range type; survival; transplant experiment.

INTRODUCTION

Exploring the processes that shape species' range limits becomes increasingly important for predicting distribution dynamics in response to climate change (Sax et al. 2013, Parmesan and Hanley 2015) or range expansions of invasive species (Alexander and Edwards 2010). Initially, it was assumed that at large spatial scales, vegetation, and plant species ranges are directly limited by climatic conditions (e.g., De Saussure 1779, Grisebach

1838). Later, this relationship was described with correlative (Shreve 1914, Iversen 1944, Grace 1987) and niche modeling approaches (Lee-Yaw et al. 2016). Current research on plant ranges showed a much more indirect impact of climate by mediating further determinants such as biotic interactions, land use, or soil conditions (Sexton et al. 2009, Hargreaves et al. 2014). Particularly, biotic interactions received increasing attention in the last few years, because of their perceived potential to affect species' range dynamics under climate change (HilleRisLambers et al. 2013, Afkhami et al. 2014, Hernández et al. 2019). In particular, the role of competition and negative trophic interactions, such as herbivory or parasitism, has already been pointed out to

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affect local population performance and, ultimately, geographic range limits (Bruehlheide and Scheidel 1999, Soberón 2007, Benning et al. 2019).

Different subsets of a species' range may be limited by different factors. The effect of biotic interactions on limits of geographic ranges is predicted to increase in importance relative to abiotic limitations with improving resource availability and, thus, under more benign climatic conditions (Cahill et al. 2014, Louthan et al. 2015). Darwin (1859) suggested an increasingly "... directly injurious action of climate ..." toward northern environments. Further studies related to plant distribution in this context were published by Tansley (1917) and Loehle (1998). Ettinger et al. (2011) and Hargreaves et al. (2014) showed that biotic factors are more important at low elevations as compared to high-elevation range limits. However, also in this spatial context, a recent meta-analysis by Freeman et al. (2018) showed that there is no signature of climate to become a more directly controlling factor toward harsher (higher) elevation limits. Another review suggests that the strength of biotic interactions varies not only with climatic conditions but also in dependence of the species included and the species' characteristics (Early and Keith 2019).

The competitive ability of a species is always relative to others. For stress-tolerant species, competitive ability is expected to decrease toward less stressful conditions (Tang et al. 2018). This might ultimately result in range restrictions under more benign conditions, where interspecific competition should be stronger, because of the greater competitive ability of the resident less stress-tolerant species (Grime 1988, Liancourt et al. 2005). In a similar context, Crain (2008) as well as Engels and Jensen (2010) showed that interactions of stress-tolerant salt marsh species vary depending on environmental gradients. Similarly, in contrast to plant species from stressful continental areas, species from benign regions with more favorable, yet also more competitive, environments may be more tolerant to interspecific competition. In this context, the competitive ability of plants should be regarded as a combination of active growth performance (e.g., by increased resource acquisition) and passive tolerance (e.g., shade tolerance).

Certain herbivores, especially snails and slugs, have clear preferences for benign climatic conditions (Barker 2002, Willis et al. 2006, Hof 2011). Particularly slugs, which are not protected by hard shells, are very sensible to drought stress and heat and thus are of minor importance in areas with low precipitation and pronounced heat events (Nicolai and Ansart 2017). This in turn, lets them come into question as potential drivers of range limitations. Slugs can be important herbivores as have been shown for seedling herbivory (Hanley 1998), for mountain grassland species in Germany (Scheidel and Bruehlheide 2005), for community diversity in experimental grasslands (Buschmann et al. 2005), or for rare plant restoration success in Hawaii (Joe and Daehler 2008). Plant species common in regions with benign climatic

conditions would be expected to be better adapted to higher mollusk herbivory pressure and should show a tendency of being more tolerant to mollusk herbivory (Bruehlheide and Scheidel 1999, Hensgen et al. 2011). Such higher tolerance of plants to herbivory in benign, resource-rich environments has been postulated as the compensatory continuum hypothesis (CCH; Wise and Abrahamson 2005). As a consequence, species from more stressful environments might be less successful in regions with benign climatic conditions because of stronger effects of negative interactions, in particular competition and mollusk herbivory.

Land use, such as different grassland management practices, have been shown to affect species diversity and species composition (Socher et al. 2012, White et al. 2014, Tälle et al. 2016). Long-term grassland management practices in temperate regions vary geographically and temporally (Peeters 2015). For example, in Europe, a higher proportion of mown grasslands (meadows) occur in the more densely populated West and an increasing proportion of grazed grasslands (pastures) in the continental East (Ahlenius 2006). In consequence, grassland species of contrasting regions might also be differently adapted to these two main types of management practice in grasslands.

In Europe, plant species' longitudinal distribution limits often occur along the distinct gradient from oceanic climate in the west to continental climate in the east (Jäger 1968, Gavián 2005). This gradient is characterized particularly by increasing temperature amplitudes and decreasing precipitation from west to east (Peel et al. 2007). In terms of strength and duration of cold and dry periods, the climatic conditions of oceanic Western Europe can be considered much more benign for plant growth than those in continental Eastern Europe (Peel et al. 2007). According to their range border positions along this climate gradient, European plant species can be grouped in different climatic range types, which can be seen as a kind of climatic niche grouping as described by Bilton et al. (2016). Gaston (2003: Chapter 2.2) summarizes the knowledge and evidence for the shift in relative roles of abiotic vs. biotic factors, which are dealt with in terms of (northern hemisphere) northern range edges, range centers, and southern range limits. In this context, eastern range limits of oceanically distributed plant species are often thought to be determined by unfavorable climatic conditions, while conversely, western range limits of continentally distributed species are less easily explained, with antagonistic biotic interactions being the most often invoked causes (Gaston 2003, Bütof and Bruehlheide 2011, Pigot and Tobias 2013).

In summary, beside climatic limitations, possible alternative processes shaping range boundaries of continental species in Western Europe may be a higher susceptibility to competition intensity, to mollusk herbivory and to mowing in oceanic regions. This leads to the main question if otherwise very similar species of contrasting range types (e.g., species with oceanic vs. continental

distribution tendency) might differ in their local responses to climate differences and biotic interactions.

Here, we present results from a large field transplant experiment over a wide range of grassland field sites. The sites are spread across three regions in Germany that are arranged along a 600-km climatic continentality gradient in mean temperature and annual precipitation, thus reflecting more favorable conditions for either oceanically or continentally distributed species. Plant species are usually best adapted to local climatic conditions that resemble those of their main geographical distribution. While the climatic conditions are the main difference between the three study regions, they are not the only ones, as the regions also differ in geology and land-use history. Thus, we have to consider that differences between regions may not be caused by climate alone. Experimental plots were implemented on farm grasslands with either mowing, grazing, or a combination of both, resulting in three different land-use types. In a split-plot design, the intensity of competition and mollusk herbivory was manipulated. The impact of these treatments on plants with contrasting geographical distribution ranges (oceanic vs. continental) was tested by transplanting individuals of congeneric plant species along this gradient.

In particular, we tested the following hypotheses: (H1) Responses of species with oceanic vs. continental distribution tendency should differ per se between the sites, with the respective optima in terms of highest survival, plant growth and reproductive capability at sites where the experienced climatic conditions are most similar to the average native range climate. For example, species of the continental range types characterized by harsher climatic conditions should also be better adapted to harsher site conditions. Such adaptation would be expected for growth but also for traits, e.g., by having lower values for specific leaf area (SLA). (H2) Since interspecific competition is expected to be generally more intense in oceanic regions, oceanic species are hypothesized to tolerate competition better than the more continental climate range types, which should result in higher survival, plant growth and reproductive capability. (H3) Likewise, oceanic species should be better adapted to mollusk herbivory than the more continental ones, and thus, suffer less when being exposed to mollusks. (H4) Species are differently adapted to types of land-use management, with a better survival and

plant growth of oceanic range-type species in meadows and of continental range-type species in pastures.

MATERIAL AND METHODS

Study regions and land-use types

The study made use of experimental plots established in permanently used grasslands in the German Biodiversity Exploratories (Fischer et al. 2010). This platform consists of three distant study regions arranged along a 600-km climatic, and thus continentality gradient (Appendix S1: Fig. S1) with decreasing mean annual temperature and increasing mean annual precipitation from northeast to southwest (Table 1; Appendix S1: Fig. S1). From north to south, the regions were Schorfheide in Brandenburg (SCH, northeast Germany), Hainich in Thuringia (HAI, central Germany), and Schwäbische Alb in Baden-Württemberg (ALB, southwest Germany; for details see Fischer et al. 2010). Along the whole European continentality gradient, Schorfheide (SCH) can be characterized by semi-continental climate, the Alb (ALB) by semi-oceanic climate, and the Hainich (HAI) by intermediate climatic conditions.

A total of 45 experimental plots (15 per study region) were selected on separate grassland sites, comprising three different grassland land-use types: meadows, pastures, and mown pastures. Land-use types were replicated five times per study region (except in ALB: six pasture sites and four mown pasture sites). Meadows were mown two to three times per year and received additional fertilizer. Mown pastures were grazed and mown once per year and additionally fertilized in Hainich and Schwäbische Alb. Pastures were grazed only and received no additional fertilization. Information concerning the particular land-use practices for each plot was collected by interviewing the farmers and land owners.

Experimental design

We studied the effect of biotic interactions by removal of competitors and mollusk exclosures. Plant responses to these treatments were assessed by monitoring phytometer individuals of 12 plant species, which were transplanted into the experimental plots. On each of the 45 selected experimental grassland plots, a 3.5×6.5 m section was divided into eight square subplots (1 m^2),

TABLE 1. Geographical locations and climatic conditions of the three study regions (Fischer et al. 2010).

Study region	Latitude	Longitude	Altitude (m above sea level)	Mean temperature (°C)	Annual mean precipitation (mm)
Schorfheide	52°47'24.8"– 53°13'26.0" N	13°23'27"– 14°8'52.7" E	3–140	8.0–8.5	500–600
Hainich	50°56'14.5"– 51°22'43.4" N	10°10'24.0"– 10°46'45.0" E	285–550	6.5–8.0	500–800
Schwäbische Alb	48°20'60.0"– 48°32'3.7" N	9°12'13.0"– 9°34'48.9" E	460–860	6.0–7.0	700–1,000

separated by margins of 0.5 m (Appendix S1: Fig. S2). On each subplot, a maximum number of 16 planting positions were available with a minimum distance of 20 cm between the phytometer plants. The subplots were subjected to different treatments. On four of the eight subplots, plants were released from competition by removing neighbor plants and from herbivory by excluding mollusks. Both treatments were fully crossed, resulting in four treatment combinations with two replicates each. Treatment combinations were assigned randomly to subplots. The whole experiment lasted over two vegetation periods from April 2009 to August 2010.

In the competition treatment, plant biomass in a 10 cm radius around the phytometer was removed. To minimize disturbances of the soil structure that might have resulted in fertilization effects, we extracted a cylindrical soil core of 10 cm length and 10 cm depth, removed the above-ground biomass of this soil core, and put it back upside-down (see Appendix S1: Fig. S3). Then one phytometer plant was planted into the center of the soil core. Although this treatment involved some minor soil disturbance it kept the immediate neighborhood of the target plants free from competitors for several months. Since all plots were established in managed grassland sites of similar productivity with fully closed vegetation cover, competition intensity was comparable among plots. The most common resident species are listed in the Appendix S1: Table S1. To exclude mollusks, four subplots were fenced with metal frames (IRKA, Typ 1, R+M Gartenbedarf, Rehling, Germany; Appendix S1: Fig. S4). Additionally, mollusk repellent was applied within these plots (Feramol, W. Neudorff GmbH KG, Emmerthal, Germany).

We inspected the experimental plots regularly every eight weeks (except in winter) and maintained the treatments by manually removing newly upcoming competitors in the 10 cm radius of the phytometer plants or applying new mollusk repellent, respectively. To assess herbivory pressure, we exposed tiles sprinkled with coal powder for one night on each plot and on the next day recorded the number of mollusk trails (Appendix S1: Fig. S5). Since the method failed in several plots, we are not able to present reliable data for mollusk presence for all plots. However, we additionally assessed the percentage of consumed area for each plant, which can be considered as phytometer response for mollusk herbivory pressure.

Phytometer plants and measurements

To study the impact of the species' range type on plant survival and growth in interaction with land-use practices, competition, and herbivory, we used six congeneric species pairs. The species of each pair differed in geographical distribution range, with one species representing the oceanic and one the continental range type (Appendix S2: Table S1). Assignment to the oceanic and continental range type was based on the degree to which the species' distribution range extends into the oceanic climate regions of Western Europe (distribution maps of

the species can be found in Appendix S2: Fig. S1–S6). Accordingly, the following plant species pairs were used in the experiment (oceanic/continental): *Carlina vulgaris*/*C. biebersteinii*, *Centaurea scabiosa*/*C. stoebe*, *Dianthus deltoides*/*D. carthusianorum*, *Koeleria pyramidata*/*K. macrantha*, *Scabiosa columbaria*/*S. ochroleuca*, and *Silene nutans*/*S. otites* (details of species characteristics in Appendix S2: Table S1).

In the global context, the geographic range of all species is neither strictly oceanic nor continental, since all have an overall West-Eurasian distribution, which generally excludes the fully oceanic Northwest of Europe as well as the highly continental Inner Asia. However, as mentioned above, the two species within one genus show different distribution limits especially in Central Europe with different tendencies to more oceanic or more continental climate. All species are native to European grasslands and share mostly similar growth forms and habitat preferences (Jäger 2017). Additionally, they are characterized by intermediate grazing and mowing tolerance (Briemle et al. 2002).

Seeds of all species were collected in 2007 in Central Germany (Appendix S2: Table S1). Starting in February 2009, phytometer plants were cultivated under common conditions in a greenhouse at the Botanical Garden in Halle (Saale). In April/May 2009, at the seedling stage without cotyledons (about six to eight weeks after germination), the phytometers were simultaneously planted in all three study regions. This was achieved by several planting teams, who planted all seedlings in one region in two to three weeks. Within each study site, the plot order of planting was random and independent of the land-use type. A maximum of 12 phytometer plants with one individual per species was planted into each subplot. As some species showed low germination rates, there were not enough plant individuals for every subplot (Appendix S2: Table S2). Here, we divided the number of planted individuals per species equally among the 45 experimental plots, first leaving out the subplot replicates, then the competition treatment. Species of each pair were planted in equal amounts. Overall, we planted 2,520 phytometer individuals.

All planted phytometers were watered once after transplantation to ensure initial establishment. At the time of planting, the number of leaves was counted for calculating relative growth rates (RGR) of leaf number according to Hunt (1990). To test the effectiveness of the mollusk enclosure treatment we estimated the proportion of consumed leaf area of all phytometers in autumn 2009. Damaged leaves of each plant were counted and then the percentage of consumed leaf areas of five randomly chosen damaged leaves were visually estimated in following classes: from 1% to 5% in 1% steps, from 5% to 95% in 5% steps.

In August 2010, we harvested above- and below-ground biomass, counted leaf number, and measured plant height of all phytometers. As a measurement for reproductive capability, we counted the flowering units of each flowering phytometer. At the same time, we also

sampled one middle-aged and, if possible, undamaged leaf per individual for determinations of specific leaf area (SLA). As it was not possible to scan the fresh leaves, we dried them in the field between papers sheets and later scanned the dried leaves in the laboratory. This might result in a slight bias in leaf area because of shrinkage. However, since the measurements were handled in the same way for all phytometers, the SLA values are comparable with each other. The biomass of shoots, roots, and leaf samples was determined after drying for 48 h at 70°C in a laboratory oven.

Statistical analyses

We utilized a principal component analysis (PCA on scaled variables) to test for collinearity between the different response variables. This resulted in removing total and belowground biomass from all further analysis (which also had a lower number of replicates), while retaining aboveground biomass. We analyzed the data for survival, relative growth rates of leaf number, biomass, number of flowering units, and SLA with generalized linear mixed effects models (GLMM) in SAS 9.2 (PROC GLIMMIX; SAS Institute, Cary, North Carolina, USA). Survival was analysed using a logit-link function and binomial error distribution, while the GLMMs for all other response variables had an identity-link function and Gaussian error distribution.

The fixed factors were study region (Alb, Hainich, Schorfheide), competition (absence, presence), herbivory (without mollusk enclosure, with mollusk enclosure), land-use type (meadow, pasture, mown pasture), and range type of the phytometer species (oceanic, continental). To evaluate our hypotheses, we included all possible two-way interactions that included range type. As we planted all phytometer species into every subplot, and applied all treatments within every plot, species were independent from plot or subplot effects. We accounted for independence by using both species identity and subplot (nested in plot) as separate (i.e., crossed) random effects. To obtain the correct degrees of freedom in denominator tests, plot identity was nested within land-use type and study region, subplot identity was nested within land-use type, study region, competition and herbivory treatment and species identity was nested within range type.

We accounted for the incomplete occupancy of species among the different treatment combinations by calculating type III SS and adjusted the degrees of freedom according to Kenward-Rogers. Tukey post hoc tests were applied to test for significant differences between the treatment combinations. Graphs were plotted with R 3.5.2 (R Development Core Team), using raw data and the least square estimates from PROC GLIMMIX (LSMEANS statements, SAS 9.2, SAS Institute). The data set generated and analyzed during this study is available in the Biodiversity Exploratories Information System (BEXIS; Welk et al. 2019; see Data Availability).

RESULTS

The principal component analysis (Appendix S3: Fig. S1, PC1 and PC2 with eigenvalues > 1, cumulative proportion of explained variance 55.48%) shows that aboveground biomass and other growth variables such as RGR of leaf number and height as well as the number of flowering units were only weakly related. The leaf area consumed was negatively correlated with specific leaf area (SLA). In the following, we present the results on these response variables, while those on belowground and total biomass as well as results on plant height are listed in Appendix S3: Table S4, S6, and S7.

Main effects on phytometer survival and growth

The study region had a general impact on plant survival, plant height, aboveground biomass, SLA and proportion of consumed leaf area (Table 2). The Schorfheide region with a more continental climate differed strongly from the other two regions, displaying very low plant survival rates as well as high values of specific leaf area and proportion of consumed leaf area (Appendix S4: Table S1–S3; Appendix S5: Fig. S1). On average, competition removal resulted in a 11% increase in survival rates, an eightfold increase in RGR of leaf number, higher aboveground biomass (+187%) and a 16% decrease in proportion of consumed leaf area compared to the control treatment (Table 2; Appendix S4: Table S1–S3; Appendix S5: Fig. S2). In contrast, herbivory enclosure caused no generally significant effects for survival and plant growth. However, the proportion of consumed leaf area was highly significantly reduced by 49% when slugs were excluded, showing the effectiveness of our method to modify mollusk herbivory pressure (Table 2; Appendix S4: Table S1–S3; Appendix S5: Fig. S3). A significant main effect of the land-use types was only encountered for RGR of leaf number (Table 2), with plants showing lowest and highest values in pastures and mown pastures, respectively (Appendix S4: Table S1; Appendix S5: Fig. S4).

Range-type-dependent effects on phytometer survival and growth

Species' range type had no significant main effects on the responses of phytometer plants (Table 2). However, except for survival, there were significant interactions of range type with study region, land-use type, competition, or mollusk herbivory for all other response variables.

Depending on the range type, differences between the study regions were detected for most response variables. However, the direction of the responses contradicts our first hypothesis. For example, continental species reached highest aboveground biomass in Hainich and lowest in the Schorfheide (Fig. 1), although the Schorfheide should be the site with the most continental climate. Conversely, oceanic species showed highest aboveground biomass in

TABLE 2. Statistical results of all GLMMs on survival, plant growth, and traits.

Source of variation	Survival <i>F</i>	Relative growth rate of leaf number <i>F</i>	Aboveground biomass <i>F</i>	Number of flowering units <i>F</i>	Specific leaf area <i>F</i>	Proportion consumed leaf area <i>F</i>
Study region (Reg)	30.15*** (A,H > S)	1.34	3.61* (A,H,S)	0.59	16.28*** (A,H > S)	25.85*** (S > A,H)
Competition (Comp)	16.04*** (-C > +C)	58.56*** (-C > +C)	54.33*** (-C > +C)	1.91	0.40	5.25* (+C > -C)
Herbivory (Herb)	3.35	0.92	0.45	1.03	3.02	62.82*** (+H > -H)
Land-use type (Use)	3.17	4.38* (MP ≥ M ≥ P)	0.14	0.10	0.37	2.39
Range type (Range)	4.00	0.22	2.94	1.86	2.20	0.80
Range × Reg	2.68	4.70**	6.58**	8.90***	5.74**	9.96***
Range × Comp	3.20	4.54*	0.11	1.75	0.95	6.83**
Range × Herb	0.23	7.75**	0.13	0.58	1.58	6.93**
Range × Use	1.89	16.39***	14.08***	2.11	3.24*	2.72

Notes: Values given are *F* values. Details on the degrees of freedom and *P* values are presented in Appendix S3. Significant effects are shown in boldface type and indicated as follows: *** *P* < 0.001, ** *P* ≤ 0.01, * *P* ≤ 0.05. For the significant main effects, the direction is presented in brackets with the following abbreviations: study regions are A, Alb; H, Hainich; S, Schorfheide; competition treatments are -C, competition removal; +C, competitors present; herbivory treatments are -H, mollusk herbivore exclusion; +H, mollusk herbivores present; for land uses are M, meadow; MP, mown pasture; P, pasture.

the Schorfheide, and lowest in the Alb, the site with the most oceanic climate (Fig. 1). The same direction of responses was observed for RGR of leaf number (Fig. 1) and number of flowering units (Table 2; Appendix S4; Table S1, S2; Appendix S5; Fig. S5).

Plants of contrasting range types showed significant differences in RGR of leaf number as response to competition removal and mollusk herbivory exclusion (Table 2). As hypothesized, continental species were more sensitive to biotic interactions than oceanic species. In comparison to oceanic species, continental species showed a stronger decrease in relative growth rate (RGR) of leaf number in presence of competitors (compared to competitor removal: oceanic -0.006 leaves·leaf⁻¹·week⁻¹ vs. continental -0.008 leaves·leaf⁻¹·week⁻¹) or mollusks (compared to mollusk exclusion: oceanic $+0.001$ leaves·leaf⁻¹·week⁻¹ vs. continental -0.005 leaves·leaf⁻¹·week⁻¹; Fig. 1, Appendix S4; Table S1, S2). Oceanic species even showed slightly higher RGRs in the presence than in the absence of mollusk herbivores, which might indicate that they were able to compensate mollusk herbivory by producing more leaves. The leaf area consumed was also differentially affected by competitors and mollusk herbivores (Table 2) since continental species were damaged more when competitors (oceanic 6.8% vs. continental 13.1%) or mollusks (oceanic 8.9% vs. continental 15.3%) were present (Fig. 1; Appendix S4; Table S3).

Additionally, species with contrasting range types differed strongly in response to land use (Table 2). In accordance with our third hypothesis, oceanic species in meadows and mown pastures displayed higher aboveground biomass (meadow, +1.63 g; mown pastures, +1.69 g) and higher RGR of leaf number (meadow, +0.002 leaves·leaf⁻¹·week⁻¹; mown pastures, +0.008 leaves·leaf⁻¹·week⁻¹) than continental species, whereas

the opposite pattern was encountered in pastures (aboveground biomass, -0.27 g; RGR leaf number, -0.006 leaves·leaf⁻¹·week⁻¹; Fig. 1). Other response variables, such as plant height and SLA, were also affected and showed a pattern similar to that of aboveground biomass (Table 2; Appendix S4; Table S1, S2; Appendix S5; Fig. S8).

DISCUSSION

Growth and survival of the 12 phytometer species in our study showed no direct and consistent increase in individual performance in regional macroclimates that were more similar to their respective main range conditions. Thus, we have to reject the first hypothesis. These results are consistent with those of Bütof et al. (2012) and Welk et al. (2014) who also did not find evidence for a direct link between climate range type and performance for a similar set of grassland species in a climate manipulation experiment and a transplant study in Botanical Gardens in Germany, respectively.

At first, this simply shows that expectations based on macroclimatic similarities do not directly translate into predictable local responses. Within-range variation in individual performance does not necessarily follow the assumption of simple, monotonous gradient response curves (Hirzel and Le Lay 2008). Additionally, there is an important parallel between our experimental findings and the mixed results of large meta-analyses with respect to empirical research about niche-position–species-abundance relationships, which have also only revealed equivocal relationships between predicted large scale environmental suitability and local abundance (Weber et al. 2017, Dallas and Hastings 2018).

Concerning hypotheses 2 and 3, we can summarize that the biotic interactions that were manipulated across

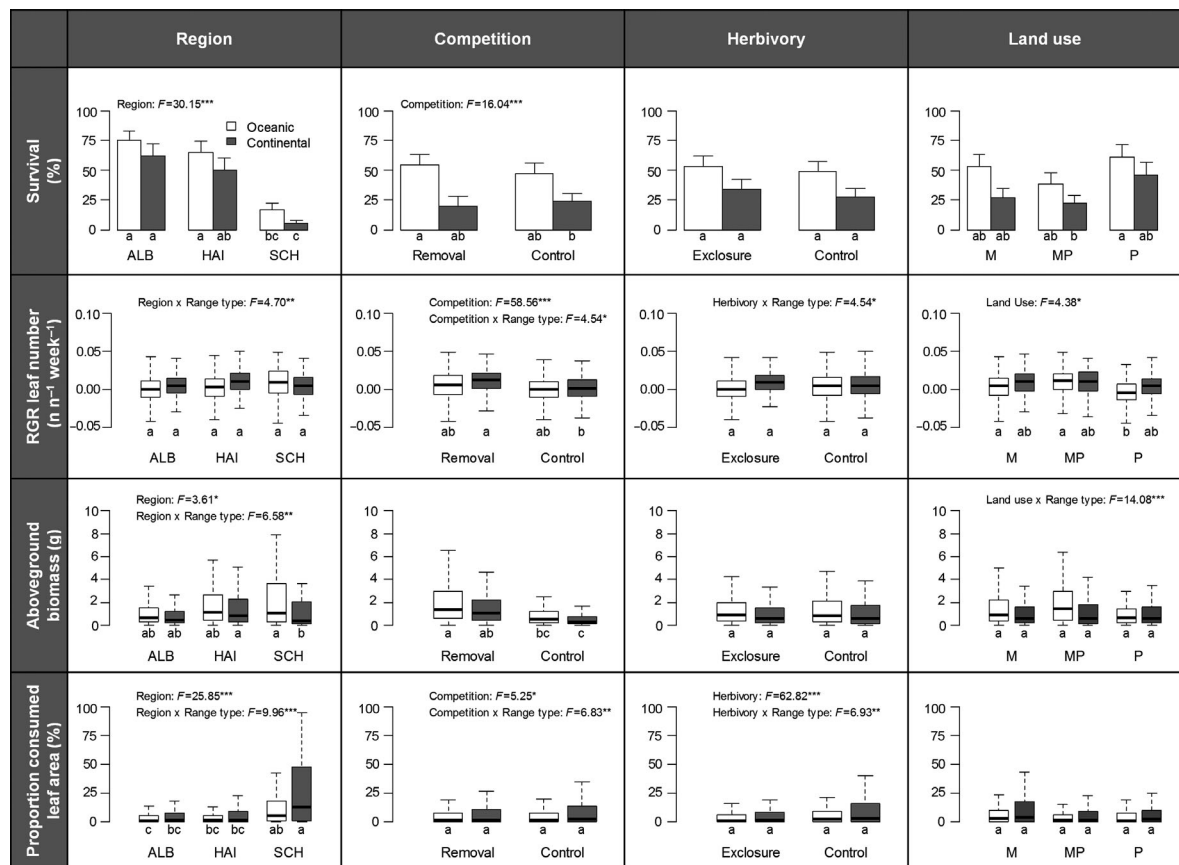


FIG. 1. Survival, RGR (relative growth rate) of leaf number, aboveground biomass, and proportion of consumed leaf area as a function of the interactive effects of range type with study region, range type with herbivory, range type with land use, and range type with land use. Data for oceanic and continental species are shown in white and gray, respectively. Box plot components are the minimum, the 25th percentile, the median, the 75th percentile, and the maximum. Abbreviations for study regions are ALB, Schwäbische Alb (most oceanic conditions); HAI, Hainich Dün (intermediate conditions); SCH, Schorfheide-Chorin (most continental conditions). Abbreviations for land use are M, meadows; MP, mown pastures; P, pastures. Significant main or interactive effects are mentioned with F value and asterisks indicating P values (** $P < 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$). Different lowercase letters indicate statistically significant differences according to a Tukey post hoc test, using the full model of Table 2 and Appendix S3.

multiple sites in climatically different study regions revealed consistent differences between species of the two contrasting range types. As hypothesized, continental species were more sensitive to detrimental biotic interactions than oceanic ones. Our results show that species of the more continental climate range type responded consistently to more intense biotic stress (here competition and mollusk herbivory) with stronger decreases in growth than their respective congeners of the oceanic range type. This indicates that species responses to environmentally controlled biotic interactions might be range-type-specific, a pattern hitherto neglected in climate-change-related projections.

Assuming that continental species have evolved under more stressful environmental conditions and lower relative intensity of competition and mollusk herbivory, our result support the compensatory continuum hypothesis (Wise and Abrahamson 2005). This would imply that

there is not only a direct environmental, but also an indirect, possibly evolutionary, constraint on herbivory impact mediated via differences in climate range type.

The different grassland land-use types in climatically different study regions provided an additional, anthropogenic, stress gradient of land-use intensity (Blüthgen et al. 2012, Socher et al. 2013). While meadows represent a relatively benign environment for most grassland plants in terms of disturbance, their comparatively high productivity involves high competition intensity for light. In contrast, in pastures, grazing activities result in higher levels of disturbance but lower aboveground competition intensity while, in terms of competition intensity, mown pastures take an intermediate position. As hypothesized, the species of the continental range type performed less well in the benign but more competitive meadow situations than congeneric species of the oceanic range type. In the pastures, the opposite pattern was encountered. Possibly,

oceanic species are more sensitive to these rather physical stress components of land use that render pastures to experience a more exposed, “continental-like” microclimate (Jantunen 2003, Koncz 2014, Tälle et al. 2016). This range-type-specific response to land-use practices is similar to the process described as “xerophytization” by Russian vegetation ecologists (Ramenskiy et al. 1956), which, however, has not yet been considered in global change projections of range dynamics.

For practical reasons, our work was limited in several aspects. We only monitored the phytometers over two years, which is short given the inevitably high interannual variability in plant growth (Breitschwerdt et al. 2018). Thus, it is difficult to compare to expected responses based on long-term averaged climate data (Buckley et al. 2010, Dahlgren et al. 2014). In addition, we only studied individual plant survival and growth but did not quantify vital rates of population dynamics that may result from such differences. However, since consistent range type \times biotic interaction effects were already detected with our short-term approach, we consider our results a valuable contribution to more long-term field studies as suggested by Louthan et al. (2015).

One has also to consider that plants experience varied environmental conditions through their range and are often locally adapted accordingly. On the one hand, by collecting all seeds in the same region (central Germany), we avoided such provenance issues. On the other hand, since our species should in general be relatively well adapted to the experimental regions and sites, we thus might have found less pronounced interspecific differences than would potentially be derived from the overall, “true” species average. A further methodological issue might be seen in the reduced competition treatment since this also involved soil disturbance, which may have enhanced mineralization, and in consequence, growth of the phytometers. However, since this treatment was identical for all plants at all sites and in all regions, we can exclude any range-type-specific bias.

Another issue is that the three study regions represent very different geomorphological settings in Central Europe. Thus, regional environmental characteristics such as geology, soil properties or the resident species pool may have obscured more consistent differences in growth between the regions, as was reported by Klaus et al. (2013). However, in another phytometer experiment in the same study regions, growth and root exudate patterns of phytometer plants were almost unaffected by different soil variables (Herz et al. 2017, Dietz et al. 2019).

CONCLUSION

We conclude that the relationship between local plant performance and macroclimate seems to be under strong influence from short-term interactions with local-scale factors causing significant deviations from expectations based on macroscale data. The results presented here suggest that land use is another factor, in addition to

competition intensity and mollusk herbivory, which might be responsible for locally differing success of plant species with contrasting range types. However, our results also point out that local-scale impacts on growth and abundance are not random, but follow large scale patterns owing to microclimatic similarities in combination with differently evolved environmental tolerances of species.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2890/supinfo>

DATA AVAILABILITY

Data are available from the Biodiversity Exploratories Information System (BEXIS) database at <https://doi.org/10.25829/bexis.19166-1.2.9>