

**The impact of species' range type
on the responses of congeneric plant species
to different climate conditions, biotic interactions and land use**

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Summary

A long-standing field of research in biology is phytogeography, which includes the study on geographical plant distributions or plant ranges and the underlying causes of these distribution patterns. The classification of species according to their geographical distribution patterns into distribution types, so-called geographic range types, is a traditional topic within phytogeography. Often, the definition of range-type groups is done with reference to climatic zones in which the distribution centers of the corresponding species are located. Examples include meridional, temperate, boreal, or planar, montane and alpine as well as continental and oceanic range types.

Due to this obvious connection of species distributions with climate zones, it was initially assumed that the distribution of species is determined predominantly by physiologically limited climatic tolerances of the species, and thus, directly driven by climate. However, numerous studies have shown that climatic conditions often have only an indirect effect on plant distributions. For example, climatic conditions influence interspecific competition or habitat conditions in a way that positively or negatively affects the occurrence probability or performance of a plant species. Further studies have also shown that also land use has a significant influence on geographical distribution patterns, at least at the local level. Within this complex system, the relative importance of these individual factors in limiting species distributions is not yet well understood.

It has been often pointed out that the effect of biotic interactions or land use on plant distributions is limited to the local or fine geographic scales. However, there is evidence that at least biotic interactions can also influence plant geographic patterns at larger scales. Recent theories assume that the effect of climate varies along climatic stress gradients. Thereby, with increasing climatic stress, e.g. where drought, frost or heat occur more frequently, climate should have a stronger limiting influence on plant ranges, while under lower climatic stress, i.e. under more favourable climatic conditions, negative biotic interactions should become more important. Negative biotic interactions include, for example, interspecific competition, predation/herbivory or disease/parasitism. Climatic stress gradients can occur, along altitudinal, latitudinal or longitudinal gradients. The latter is particularly pronounced in Europe and known as the continentality-oceanity gradient, in which the continental eastern end is climatically more stressful due to colder winters, hotter summers and lower annual precipitation.

Within the framework of this thesis, three experiments were conducted to investigate the importance of the three factors climate, biotic interactions and land use on the geographic distribution of plants. For this purpose, plant species with contrasting range types (continental vs. oceanic) were selected and exposed to different climates along a continentality-oceanity gradient,

different biotic interactions (competition, mollusk herbivory) and different land use conditions (different grassland management types).

Firstly, it was tested whether species survive and grow better under more "familiar" climatic conditions according to their climatic origin. Secondly, it was assumed that species that are predominantly distributed in regions with favorable climatic conditions cope better with negative biotic interactions than species from regions with more stressful climatic conditions. Thirdly, the extent to which different types of grassland management affect species with different distributions was investigated.

A consistent result of the study was that plant performance increased in principle and independently of the range type under less stressful climatic conditions. Thus, the species did not show climatic preferences that corresponded to their range type. However, the species showed different sensitivities to competition and mollusk herbivory, with continental species showing greater reductions in performance than oceanic species. In contrast, oceanic species even showed compensatory responses, suggesting some adaptation to negative biotic interactions and thus an advantage over continental species under benign climatic conditions. This suggests that species with distribution centers in more stressful climates are less adapted to negative biotic interactions and may therefore be increasingly excluded under more benign climatic conditions. The distribution of these species there is thus determined less by the climate itself, but rather indirectly by negative biotic interactions. Regarding the different types of grassland management, a mixed picture emerged, as the species of different range types showed inconsistent preferences in the respective experiments, which, however, could also be due to the experimental implementation. There is therefore a need for further investigation, e.g. by extending the duration of the experiments.

In general, the approach of selecting target species according to range type classification was successful and should be used more frequently in further experimental studies investigating distribution patterns of species. In this way, it is possible to achieve more generalizable results than from single-species studies, yet without disproportionately increasing the technical effort and time expenditure. In this context, the here presented study represents a valuable contribution to the research in the field of experimental phytogeography and provides suggestions for improvement for future investigations of geographical distribution patterns.

Zusammenfassung

Der Einfluss des Arealtyps auf die Reaktion von Pflanzenarten auf unterschiedliche Klimabedingungen, biotische Wechselwirkungen und Landnutzung

Eine langwährende Forschungsrichtung in der Biologie ist die Phytogeographie bzw. Arealkunde, von welcher geographische Pflanzenverbreitungen dokumentiert und die den Verbreitungsmustern zugrunde liegenden Ursachen erforscht werden. Die Klassifizierung von Arten anhand ihrer geographischen Verbreitungsmuster in Verbreitungstypen, so genannte Arealtypen, ist ebenso ein traditionelles Arbeitsfeld innerhalb der Phytogeographie. Meist erfolgt die Definition und Abgrenzung von Arealtypengruppen mit Bezug auf klimatische Zonen, in welchen sich die Verbreitungsschwerpunkte der entsprechenden Arten befinden. Beispiel dafür sind meridionale, temperate, boreale oder aber planare, montane und alpine sowie kontinentale und ozeanische Arealtypen.

Aufgrund dieses offensichtlichen Zusammenhangs von Artverbreitungen mit klimatischen Zonierungen wurde lange Zeit angenommen, dass die Verbreitung von Arten hauptsächlich durch begrenzte physiologische Klimatoleranzen der Arten und somit direkt durch das Klima bestimmt werden. Mittlerweile haben allerdings zahlreiche Studien gezeigt, dass klimatische Bedingungen sich oftmals nur indirekt auf Pflanzenverbreitungen auswirken. Beispielsweise werden durch klimatische Bedingungen Konkurrenzverhältnisse oder bestimmte Habitatbedingungen beeinflusst, die sich wiederum positiv oder negativ auf das Vorkommen bzw. die Leistung einer Pflanzenart auswirken. In weiteren Studien hat sich außerdem gezeigt, dass auch die Landnutzung zumindest auf lokaler Ebene einen erheblichen Einfluss auf geographische Verbreitungsmuster hat. Innerhalb dieses komplexen Systems ist die relative Bedeutung der einzelnen Faktoren für die Begrenzung von Artverbreitungen aber bislang nur unzureichend geklärt.

Oftmals ist darauf verwiesen worden, dass sich die Auswirkung biotischer Interaktionen oder Landnutzung auf die Pflanzenverbreitung nur auf die lokale bzw. kleinräumige geographische Ebene beschränkt. Es gibt allerdings Hinweise darauf, dass zumindest biotische Interaktionen

auch auf größeren Skalenebenen Einfluss auf pflanzengeographische Muster aufweisen können. In neueren Theorien wird davon ausgegangen, dass die Wirkung des Klimas entlang von klimatischen Stressgradienten variiert. Dabei nimmt man an, dass bei zunehmendem klimatischem Stress das Klima einen stärkeren limitierenden Einfluss auf die Verbreitung von Pflanzenarten hat, während unter geringerem klimatischem Stress, also unter günstigen klimatischen Bedingungen, negative biotische Interaktionen eine größere Bedeutung zukommt. Zu negativen biotischen Interaktionen werden beispielsweise zwischenartliche Konkurrenz, Fressfeinde/Herbivorie oder Krankheiten/Parasitismus gezählt. Klimatische Stressgradienten können beispielsweise entlang von Höhengradienten oder in Richtung der Breiten- und Längengrade auftreten. Letzterer ist vor allem in Europa stark ausgeprägt und bekannt als Kontinentalitäts-Ozeanitätsgradient, bei welchem die kontinentalen östlichen Regionen mit kalten Wintern, heißen Sommern und geringen Gesamtniederschlägen als pflanzenphysiologisch stressvoller sind.

Im Rahmen dieser Studie wurde mit Hilfe dreier Experimente untersucht, welche relative Bedeutung den Faktoren Klima, biotische Interaktionen und Landnutzung auf die Verbreitung von Pflanzen zukommt. Dafür wurden Pflanzenarten mit kontrastierenden Arealtypen ausgewählt (kontinental vs. ozeanisch) und verschiedenen Klimaten entlang eines Kontinentalitäts-Ozeanitätsgradienten, biotischen Interaktionen (Konkurrenz, Schneckenherbivorie) und Landnutzung (verschiedene Grünlandnutzungstypen) ausgesetzt. Einerseits wurde getestet, ob die Arten entsprechend ihrer klimatischen Herkunft besser im gewohnten Klima überleben und wachsen. Andererseits sollten die Arten, die überwiegend in Regionen mit günstigen klimatischen Bedingungen verbreitet sind, besser in der Lage sein, mit negativen biotischen Interaktionen umzugehen als Arten aus Regionen mit stressigeren klimatischen Bedingungen. Drittens wurde geprüft, inwieweit sich unterschiedliche Grünland-Nutzungsformen auf verschieden verbreitete Arten auswirken.

Ein konsistentes Ergebnis der Studie war, dass die Leistung der Pflanzen prinzipiell und unabhängig vom Arealtyp unter weniger stressreichen klimatischen Bedingungen anstieg. Die Arten wiesen somit keine klimatischen Präferenzen auf, die mit ihrem Verbreitungstyp übereinstimmten. Jedoch zeigten die Arten unterschiedliche Sensitivitäten gegenüber Konkurrenz und Schneckenherbivorie, wobei die kontinentalen Arten stärkere Leistungsminderungen aufwiesen als die ozeanischen Arten. Im Gegensatz dazu wiesen die ozeanischen Arten sogar kompensatorische Reaktionen auf, die auf eine gewisse Anpassung an negative biotische Interaktionen deuten und somit ein Vorteil gegenüber kontinentalen Arten unter günstigen klimatischen Bedingungen darstellen. Dies deutet darauf hin, dass Arten mit Verbreitungsschwerpunkten in stressvolleren Klimaten weniger an negative biotische Interaktionen angepasst sind und womöglich deswegen nicht unter günstigeren klimatischen

Bedingungen vorkommen. Die Verbreitung dieser Arten ist somit weniger durch das Klima selbst, sondern eher indirekt durch negative biotische Interaktionen bestimmt. Hinsichtlich der verschiedenen Grünlandnutzungstypen ergibt sich ein gemischtes Bild, da die verschiedenen Arealtypen in den jeweiligen Experimenten uneinheitliche Präferenzen aufwiesen, was jedoch auch auf die experimentelle Durchführungsweise zurückzuführen sein könnte. Dazu besteht also weiterer Untersuchungsbedarf; u. a. mit verlängerter Versuchsdauer.

Generell zeigte sich, dass der Ansatz, Arten verschiedener Verbreitungsklassen zu verwenden, Erfolg zeigte und auch in weiterführenden experimentellen Studien zur Untersuchung von Verbreitungsmustern von Arten stärker zur Anwendung kommen sollte. Auf diesem Wege ist es möglich, stärker generalisierbare Aussagen als aus Einzelartstudien zu treffen, ohne jedoch dabei den technischen und zeitlichen Aufwand unverhältnismäßig zu erhöhen. In diesem Zusammenhang liefert die hier vorgestellte Studie einen wertvollen Beitrag für die Forschung im Bereich der experimentellen Phytogeographie und Hinweise für Erweiterungsmöglichkeiten und Verbesserungen der Untersuchung geographischer Verbreitungsmuster.

Chapter 1

General Introduction

Geographic range limits and their relationship to environmental niche limits

The range or geographic distribution of a plant species is an area or a set of individual areas that comprises the sum of all geographic locations where populations of the species occur. Central goals of ecological science are to study geographic distribution patterns and identify limiting factors that shape the range of species. Since Darwin and Humboldt (especially for elevation gradients), geographic patterns of distribution have been systematically linked to environmental conditions to find relationships and regularities. First distribution maps of certain clades or taxa were compiled in the 19th century (e.g. Schouw 1823; Grisebach 1838). The approach of relating geographic distributions to environmental conditions was considerably improved with the development of the niche concept, in which distributions in geographic space were translated into environmental space (Grinnell 1917; Elton 1927).

Hutchinson (1957) extended this concept by distinguishing between a species' fundamental and realized niche. Thereby, the fundamental niche is defined as the sum of all suitable environmental (abiotic) factors that enable the survival and persistence of the species, spanning a multidimensional hypervolume, i.e. macroecological space. The realized niche is considered to be the projection of the observable geographic species range into macroecological space (Sexton et al. 2009). Here it usually comprises only a subset of the fundamental niche, which results for example from limitations to dispersal (physical barriers, time lags, etc.) and through biotic interactions (competition, facilitation, herbivory, mutualism, etc.). In that regard, the relative role of dispersal, biotic and abiotic factors for limiting distribution ranges is constantly debated (e.g. Wiens 2011; Cahill et al. 2014; Alexander et al. 2016; Early & Keith 2019; Sirén & Morelli 2020), though a number of correlative and experimental studies indicate that geographic range limits can be considered to be niche limits (see reviews by Hargreaves et al. 2014; Lee-Yaw et al. 2016).

Range types based on current species distribution

Every species has its own specific and unique geographical distribution. Nevertheless, similarities in the extent, shape and location of the geographic distribution suggest the existence of geographic species groups (Meusel et al. 1965; Jäger 1968; Walter & Straka 1970; Preston & Hill 1997; Finnie et al. 2007). These groupings are called range types (the term 'geoelements' is sometimes used as synonym) or, in the case of plants, floristic elements. Assignment to range types is made at the species level and usually based on the current eco-geographical distribution of the species, while assignments to floristic elements might also take migration history into account. In the present thesis only the concept of range types will be used. Range types may include, for example, species with similar geographic distributions along altitudinal gradients (lowland, montane, alpine

species), along latitudinal gradients (Mediterranean, temperate, boreal, arctic species) or longitudinal gradients (oceanic, continental species). However, it must be noted that despite the assignment to range types, the distributions of species within range types, and thus range boundaries, vary to some extent, with the result that range boundaries rarely match exactly. Because of the similarities in geographical patterns, range types indicate corresponding environmental limitations (Preston & Hill 1997).

Climate as range limiting factor at the broad scale

A large number of mostly correlative studies have shown that geographic species distributions are predominantly shaped by climatic conditions (Grace 1987; Woodward 1987; Pearson & Dawson 2003). For example, Iversen (1944) observed in one of the earliest studies (but see Johnston 1924), that *Ilex aquifolium* occurs only in regions with mild winters, where mean winter temperatures do usually not fall below -1 °C in mean monthly temperature. Additionally, postglacial range shifts during the Holocene (Davis & Shaw 2001) and current range shifts to higher latitudes and elevations (Parmesan 2006; Walther 2010; Pecl et al. 2017) could be attributed to changing climatic conditions, indicating again the high importance of climate in shaping the geographic distribution of species.

Some climate factors may have direct effects: for example frost, drought and heat can cause lethal damage to tissues and reduce leaf unfolding, flowering, seed production and germination rates (e.g. Loehle 1998; Muffler et al. 2016; Adams et al. 2017; Szymańska et al. 2017). Direct effects are mainly found in regions with generally stressful environmental conditions. However, recent research on species distributions also points to the importance of indirect climate effects through the modulation of other limiting factors, such as biotic interactions, resource availability, soil conditions or land use (Sexton et al. 2009; Thomas 2010; Wisz et al. 2013; Alexander et al. 2016). The relative impact of climate on setting range limits varies along climatic gradients, with increased importance under stressful climate conditions (Louthan et al. 2015; Freeman et al. 2018). As a common pattern, climate becomes harsher or more stressful towards highest elevations or latitudes due to lower temperatures.

Another important, yet much less studied, climatic gradient is the continentality-oceanity gradient in the Northern Hemisphere, which is defined not only by a change in thermal, but also in hygric conditions (Crawford 2000; Berg et al. 2017). The 'continental end' of this gradient is considered to be more stressful, in the sense of a harsher climate, due to a higher average annual temperature range with very cold winters and hot summers in combination with lower annual precipitation and thus more pronounced arid conditions. In contrast, the 'oceanic end' is characterized by more benign climate with less distinct temperature and precipitation seasonality and humid conditions

(Crawford 2000; Berg et al. 2017). Since the continentality-oceanity gradient is strongly based on seasonality, continentality cannot be defined for the tropics. In the context of eco-geographical classifications of species distributions into range types (see above), it is also possible to use range positions along this continentality-oceanity gradient to define range types (Meusel et al. 1965; Jäger 1968). Transferring the observed results from studies along altitudinal or latitudinal gradients to the continentality-oceanity gradient, an increase in the relative impact of climatic factors on shaping distribution patterns can be expected with increasing continentality.

The role of biotic interactions in setting range limits

Analyses of current climate change-related range dynamics showed shifts of partly unexpected direction and magnitude, indicating that factors other than climate have significant impacts on regional range limits (Lenoir et al. 2010; Chen et al. 2011; Freeman et al. 2018). In this context, it has been suggested that biotic interactions are accountable for the majority of such variances (Araújo & Luoto 2007; Ettinger & HilleRisLambers 2017; Early & Keith 2019). Recent considerations on range-limit theories include the shifting impact of climate vs. biotic interactions along climate-stress gradients. It has been discussed that under less stressful climatic conditions productivity and biodiversity increases, and therefore, negative biotic interactions (competition, herbivory or parasitism) become more important for setting range limits (Hargreaves et al. 2014; Louthan et al. 2015; Sirén & Morelli 2020). However, other studies showed that biotic interactions, such as competition, can push species realized niches towards marginal, harsher climatic conditions (Freeman et al. 2018; Armitage & Jones 2020; Shepard et al. 2021). and thus, may have not only impacts on local but also at broader geographic scales. In this regard, it is important that biotic interactions were found to vary in strength, depending on the species involved and their characteristics (Ettinger & HilleRisLambers 2017; Early & Keith 2019; Briscoe Runquist et al. 2020).

One of the most studied biotic interactions is competition (Morales-Castilla et al. 2015). Especially, interspecific competition is often suggested to shape species distributions and community assemblages not only at the local but also at the regional and even global scales (Wisz et al. 2013). The outcome of competitive effects seems to vary in dependence of the species' competitive ability, yet also on their stress tolerance (Liancourt et al. 2005). Along stress gradients it was found that the relative competitive ability of stress-tolerant species increased with increasing stress, while that of stress-intolerant species decreased (Qi et al. 2018; Tang et al. 2018). For example, both Crain (2008) and Engels & Jensen (2010) showed that the competitive ability of stress-tolerant salt-marsh species varied along environmental gradients. Stress-tolerant species may be ultimately outcompeted under less stressful conditions due to a general lower competitive

ability compared to less stress-tolerant species. Hence it might be assumed that local competitive ability or vulnerability to competition varies with stress levels and that stress levels vary relative to the species' geographic distribution. In this context, plant competitiveness can be viewed as a trade-off between active growth performance (e.g. through increased resource acquisition) and passive tolerance (e.g. frost or drought tolerance). At the broad geographic scale, this might result in range limits for stress-tolerant species under increasingly benign conditions, because of the greater competitive ability of the resident species (Grime 1988; Liancourt et al. 2005).

In addition to competition, also herbivory has been identified to affect distribution limits of species (Bruehlheide & Scheidel 1999; Baer & Maron 2018; Benning et al. 2019). Several studies indicate that herbivory intensity varies along climate-stress gradients, with increasing relative herbivore impact observed under more favorable climate conditions (e.g. Louthan et al. 2018; Lynn et al. 2019; Pepi & Karban 2021). However, other studies revealed that the impact of herbivory is more species-specific i.e. that the variability of herbivory intensity along climate-stress gradients strongly depends on the ecological requirements and stress-tolerances of the specific herbivore (Early & Keith 2019). Nevertheless, the stress-gradient effect described above might apply to less stress-tolerant herbivores, which commonly occur under benign climate conditions. For example, slugs have been demonstrated to be sensitive to drought and high temperatures (Nicolai & Ansart 2017). Despite their small body size compared to rodents, slugs and snails can cause high amounts of feeding damage, which can lead to reduced seedling establishment or plant fitness (Buschmann et al. 2005; Korell et al. 2016). The potential of slugs to influence range limitations along an altitudinal gradient was already demonstrated in the late 1990s (Bruehlheide & Scheidel 1999). However, studies considering the role of slugs or other climate-sensitive herbivores in shaping the geographical distribution of plant species along larger climate-stress gradients are still lacking.

Land-use impacts on species ranges

The outcome of correlative approaches of climate-based species distribution analyses are assumed to be scale-dependent. Among environmental variables, climate is the predominant driver at the continental level, while land use, land cover or soil properties become more important at regional and local scales (Jäger 1992; Gaston 2003; Pearson & Dawson 2003). For example, integrating land-use variables into species distribution models has been shown to improve predictions of plant species distribution at the regional scale (Pompe et al. 2008; Tyler et al. 2018). Land-use variables mostly consist of very coarse land-use categories, such as 'forest', 'grassland', 'agricultural land' or 'urban area'. However, each land-use category comprises a wide variety of land-use types. Often land-use types are defined in regard to the respective intensity of

human impact (e.g. Blüthgen et al. 2012). However, differences in plant species composition can even be found, for example, within extensively or moderately used grasslands (Mayel et al. 2021). Often land-use types are representing certain agricultural management practices. For instance, in permanent grassland, mowing, grazing or combinations of both can lead to significant differences in floristic composition and community structure (Römermann et al. 2009; Tälle et al. 2016). In these cases, such differences can be explained mainly by varying tolerances of grassland species towards effects of cutting, grazing and trampling (Briemle et al. 2002; Stammel et al. 2003; Scheidel & Bruelheide 2004; Moog et al. 2009). Due to the simultaneous biomass removal connected with mowing, meadows tend to be more homogeneous in vegetation structure and nutrient content (Mayel et al. 2021). In contrast, pastures are generally more heterogeneous due to selective grazing and disturbance by trampling, which creates a high number of microsites (Tälle et al. 2016). In general, intensely grazed sites are frequently more open and exposed with disturbed vegetation, and thus, pastures might represent physically and microclimatically more stressful habitats than meadows, which in turn would imply that stress-intolerant species have a disadvantage in pastures. In consequence, different land-use types might impact local species performance, and in consequence, also distribution patterns (Newbold et al. 2015). However, studies addressing possible land-use impacts at coarse scale on species distributions are lacking. This is probably based on the spatial mismatch between fine-grained land-use patterns and generally much coarser broad-scale macroclimatic patterns rendering consistent information at the same spatial resolution and scale unavailable for both drivers.

Research gaps and aims of the study

It can be summarized that in addition to climatic constraints, biotic interactions, land use or other factors should also be considered when investigating species distribution limits. Previous findings suggest that the importance of these non-climatic factors may vary along climate-stress gradients. A common tool for range-wide studies to species geographic distributions and limitations are niche-based species distribution models (SDMs), where occurrence data (often together with absence data) are correlated with corresponding environmental variables (Guisan & Zimmermann 2000; Guisan & Thuiller 2005). Therefore, various techniques exist which use different algorithms for their calculations (Araújo et al. 2019). However, the derived insights might be limited due to unfulfilled assumptions (environmental equilibrium), methodological issues (variable selection, spatial autocorrelation of predictors, etc.) and unrecognized causalities behind correlative signals (Dormann et al. 2018; Willi & van Buskirk 2019).

Experimental tests at the plot level along climatic gradients or beyond range boundaries provide an appropriate alternative tool to evaluate the relative impact of range-limiting factors (Lee-Yaw

et al. 2016). However, most experimental approaches only study single or a few species since such empirical studies are logistically extremely challenging. A possible solution is to compare plant species with distinctly different geographic range types to connect local-scale processes with broad-scale pattern. The rationale behind this is that otherwise similar species with distinctly different macroclimatic niches may vary in general stress tolerance and might respond differently to certain biotic interactions or land-use types. Then, the question is whether plant species of contrasting range types respond differently to specific local processes under varying climatic conditions, such as the above described oceanic-continental gradient.

As suggested above, common garden or transplant experiments provide a possibility to reveal a deeper understanding in underlying mechanisms, as individual factors can be independently manipulated and direct species responses can be evaluated (Bruehlheide 1999; Gaston 2003). The validity of such experimental studies is, however, limited due to difficulties in controlling for phylogenetic constraints (evolutionary history) and the generally small geographic scale. The use of congeneric species pairs with similar habitat requirements but contrasting geographical distributions is a suitable way to create a manageable, practicable approach for transferring local studies to a broader scale. Such contrasting distributions should ideally span climatic-stress gradients, which would allow for a direct comparison with the stress tolerance of the considered species. For this purpose, congeneric species which represent contrasting range types, such as continental vs. oceanic, can be particularly suitable.

The thesis presented here aims at filling the gap between both, broad-scale correlative SDMs and local-scale experimental setups, by using three independent field experiments with phytometer species across large spatial scales covering the continentality-oceanity climate gradient in Germany. In these experiments, the responses of phytometer species with contrasting range types to ambient and manipulated climate conditions, manipulated negative biotic interactions (competition, herbivory) and certain land-use types (grassland management practices) were investigated. The findings of each experiment resulted in separate publications, presented in Chapters II, III and IV.

General hypotheses and study design

The experiments described in this thesis were designed to evaluate if local species responses to certain environmental factors are related to the geographical distributions, i.e. range types of the respective species. To answer this question, the following hypotheses were tested:

H1 Climate as main driver of species distribution: Species perform best under the climate conditions that correspond best to their main native distribution.

H2 Biotic interactions as potential drivers of species distribution limits: Species from more stressful environments are locally more susceptible to negative biotic interactions.

H3 Land-use impacts on species distribution: Species with distinctly different geographic distribution respond differentially to varying land-use types.

These hypotheses were addressed in different settings in the three studies presented in Chapters 2-4 within this thesis. An overview of which hypothesis was tested in which setting can be found in Table 1-1. All experiments have in common that phytometer species were used as a measure of plant species responses to various environmental factors. To account for phylogenetic constraints, I used pairs of congeneric plant species with similar growth forms that have similar habitat preferences, yet contrasting geographical distributions as phytometers. Within each species pair, one phytometer species was selected to represent the 'oceanic', the other the 'continental' range type. Assignment to range types were made according to the geographical distribution along the continentality-oceanity gradient of the respective species, compared to the other species within each species pair. In particular, the relative longitudinal position of their distribution boundary towards increasingly oceanic and thus less stressful climatic conditions was taken into account. Table 1-1 presents an overview of the included plant species and their assignments to range types within species pairs for each experiment. Overall, in the three experiments 4864 individuals of 16 different plant species were planted as phytometers.

All experiments were arranged along the continentality-oceanity climate gradient in Germany. Along this gradient, temperature seasonality as well as precipitation varies, whereby continentality with much colder winters, distinctly warmer summers and lower annual precipitation, and thus increasing climatic stress, was expected to increase in direction to the East of Germany. In this regard, two different systems were used to study the climate gradient: Botanical Gardens and the German Biodiversity Exploratories (Table 1-1, Figure 1-1).

Table 1-1 General overview of the experimental approaches presented in Chapters 2-4.

Publication	Chapter 2 Welk et al. 2014 -PLoS ONE Biotic interactions overrule plant responses to climate, depending on the species' biogeography	Chapter 3 Bütof et al. 2012 -Global Change Biology The responses of grassland plants to experimentally simulated climate change depend on land use and region	Chapter 4 Welk et al. 2019 -Ecology Plant species' range type determines local responses to biotic interactions and land use
Tested hypotheses	H1 and H2	H1 and H3	H1, H2 and H3
Time frame	June 2008-Oktober 2009	June 2008-April/May 2009	April/May 2009-August 2010
Used framework	Botanical Gardens	Biodiversity Exploratories	
Phytometer			
Congeneric species pairs (designated range type within species pairs: <i>oceanic</i> / <i>continental</i>)	<i>Carlina vulgaris</i> / <i>Ca. biebersteinii</i> <i>Centaurea scabiosa</i> / <i>Ce. stoebe</i> <i>Dianthus deltoides</i> / <i>D. carthusianorum</i> <i>Inula conyzae</i> / <i>I. hirta</i> <i>Koeleria pyramidata</i> / <i>K. macrantha</i> <i>Scabiosa columbaria</i> / <i>S. ochroleuca</i> <i>Silene nutans</i> / <i>S. otites</i>	<i>Achillea millefolium</i> / <i>A. pannonica</i> <i>Centaurea scabiosa</i> / <i>Ce. stoebe</i> <i>Dianthus deltoides</i> / <i>D. carthusianorum</i>	<i>Carlina vulgaris</i> / <i>Ca. biebersteinii</i> <i>Centaurea scabiosa</i> / <i>Ce. stoebe</i> <i>Dianthus deltoides</i> / <i>D. carthusianorum</i> <i>Koeleria pyramidata</i> / <i>K. macrantha</i> <i>Scabiosa columbaria</i> / <i>S. ochroleuca</i> <i>Silene nutans</i> / <i>S. otites</i>
Total number of planted individuals	1824	520	2520
Experimental setup			
Climate gradient (Locations/Regions ordered from most oceanic to most continental climate conditions)	Osnabrück Münster Bonn Braunschweig Mainz Jena Halle Frankfurt a. M. Potsdam	Schwäbische Alb Hainich-Dün Schorfheide-Chorin	
Land-use types (ambient grassland management)	/	Meadows Mown Pastures Pastures	
Climate-manipulation treatment	/	Rain shelters in summer and subsequent open top chambers in spring vs. control	/
Biotic-interaction treatments (crossed)	Competition (removal vs. sown <i>Festuca rubra</i>) & herbivory (slug enclosure vs. control) (4 replicates)	/	Competition (removal vs. ambient competitors) & herbivory (slug enclosure vs. control) (2 replicates)
Number of subplots	9 locations x 16 subplots = 144 subplots	3 regions x 15 plots x 2 subplots = 90 subplots	3 regions x 15 plots x 8 subplots = 360 subplots

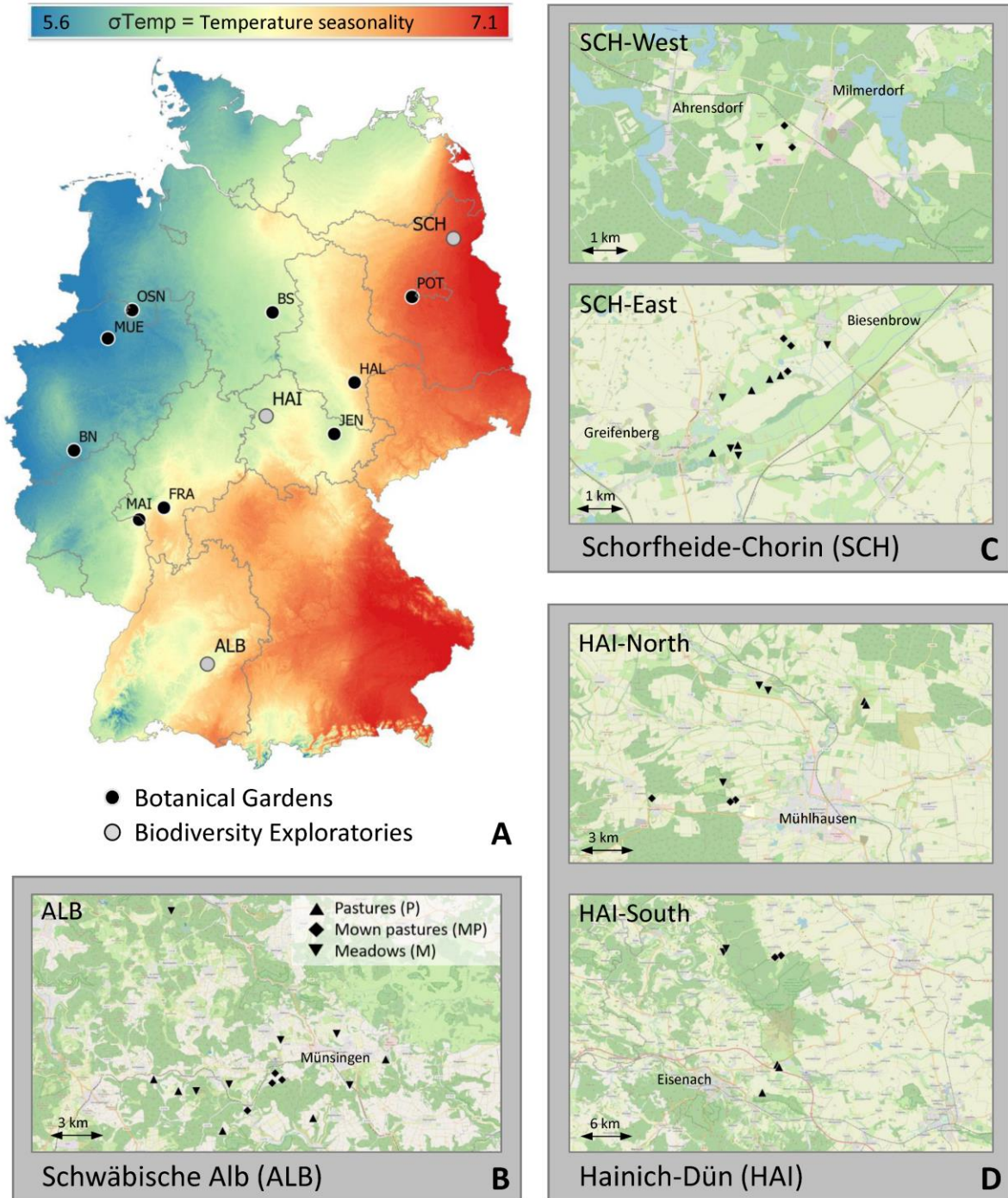


Figure 1-1 Study locations within Germany along the continentality-oceanity gradient. **A.** The overview map of Germany shows in the color-coded mean standard deviation of the monthly mean temperatures, i.e., the mean temperature seasonality (WorldClim 2, BIO4, Fick & Hijmans 2017), which indicates climatic continentality. However, note that climate continentality is also characterized by drier conditions, warmer summers and higher frequencies of frost events, which are not illustrated here but do show a comparable pattern. Locations within the framework of the Botanical Gardens are indicated by black dots (BN – Bonn, BS – Braunschweig, FRA – Frankfurt a. M., HAL – Halle, JEN – Jena, MAI – Mainz, MUE – Münster, OSN – Osnabrück, POT – Potsdam). For the Biodiversity-Exploratory regions (ALB – Schwäbische Alb, HAI – Hainich-Dün, SCH – Schorfheide-Chorin), centroids are shown as grey dots. **B–D.** Within each Biodiversity-Exploratory region, 15 study plots were established, comprising different land-use types, in particular meadows (▲), mown pastures (◆) and pastures (▼). The locations of these plots are illustrated in the respective site maps (grey boxes) for each exploratory.

Chapter 2 presents a common garden experiment in nine Botanical Gardens spanning the continentality gradient in Germany (locations ordered from oceanic to continental: Osnabrück, Münster, Bonn, Braunschweig, Mainz, Jena, Halle, Frankfurt a. M. and Potsdam; see map in Figure 1-1.). Making use of Botanical Gardens offered the advantage of evaluating manipulation treatment effects more accurately, as other influencing factors such as plant community composition could be controlled more effectively. Within this experimental setup, competition and herbivory were manipulated with a presence/absence approach (Table 1-1). For this purpose, a factorial crossed treatment design was used, with competition as absent (regular removing of upcoming plants) or present (sown *Festuca rubra*) in combination with slug and snail herbivory as absent (exclusion with slug fences) or present (no slug fences). With the experiment conducted in Botanical gardens, hypotheses H1 and H2 were tested.

On the other hand, for the two other experiments the framework of the German Biodiversity Exploratories was used (see <http://www.biodiversity-exploratories.de>; Fischer et al. 2010). There, experimental plots are arranged in three distant study regions across a south-west to north-east climate gradient in Germany: Schwäbische Alb, Hainich-Dün and Schorfheide-Chorin (Figure 1-1). In every exploratory region, several experimental plots are located in different agriculturally used grasslands comprising different grassland-management practices. This enabled analyzing impacts of certain land-use types (meadow, mown pasture, pasture) in interaction with varying climate conditions (Table 1-1, Figure 1-1). Here, the performance of phytometers was studied in long-established permanent grasslands, which improves potential transferability to general patterns.

Both experimental set-ups in the framework of the Exploratories included the same number and combination of plots but differed in the duration of implementation and subplot manipulation. In the experiment presented in **Chapter 3**, not only the impact of the ambient climate conditions, but also of manipulated climate conditions were investigated. Climate manipulations included a combination of simulated summer drought (rain shelters in summer) and an increase in next year's spring temperature (open top chambers in spring; see also Dormann et al. 2017). This provided the opportunity to test for a stronger climatic stress level than that provided by the climatic differences between the exploratory regions alone. In this experiment, biotic interactions were not manipulated. Hence, the second experiment addressed hypotheses H1 and H3 regarding climate and land-use impacts.

In contrast to the other two experiments, the third experiment, which is presented in **Chapter 4**, was designed to evaluate all three hypotheses (H1, H2 and H3). Therefore, biotic interactions were manipulated in the same plots used in the experiment presented in Chapter 3. Manipulations of biotic factors were very similar to those implemented in the botanical-garden experiment (Chapter 2). However, the absence of competition was controlled by removing ambient

competitors in a 10 cm diameter around the planted phytometer while in the competition-presence treatment ambient competitors were retained. Herbivory was manipulated in the same way. With this set-up it was possible to test not only for biotic-interaction effects, but also simultaneously for climate and land-use effects.

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Chapter 2

Biotic interactions overrule plant responses to climate, depending on the species' biogeography

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Biotic Interactions Overrule Plant Responses to Climate, Depending on the Species' Biogeography

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Abstract

This study presents an experimental approach to assess the relative importance of climatic and biotic factors as determinants of species' geographical distributions. We asked to what extent responses of grassland plant species to biotic interactions vary with climate, and to what degree this variation depends on the species' biogeography. Using a gradient from oceanic to continental climate represented by nine common garden transplant sites in Germany, we experimentally tested whether congeneric grassland species of different geographic distribution (oceanic vs. continental plant range type) responded differently to combinations of climate, competition and mollusc herbivory. We found the relative importance of biotic interactions and climate to vary between the different components of plant performance. While survival and plant height increased with precipitation, temperature had no effect on plant performance. Additionally, species with continental plant range type increased their growth in more benign climatic conditions, while those with oceanic range type were largely unable to take a similar advantage of better climatic conditions. Competition generally caused strong reductions of aboveground biomass and growth. In contrast, herbivory had minor effects on survival and growth. Against expectation, these negative effects of competition and herbivory were not mitigated under more stressful continental climate conditions. In conclusion we suggest variation in relative importance of climate and biotic interactions on broader scales, mediated via species-specific sensitivities and factor-specific response patterns. Our results have important implications for species distribution models, as they emphasize the large-scale impact of biotic interactions on plant distribution patterns and the necessity to take plant range types into account.

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Introduction

Understanding the causes of species geographical distributions is a major research goal in ecology, often driven by the desire to model future species distributions in a world undergoing climate change. Soberón [1] summarized the main determinants of species distribution, which apart from a species' dispersal capacity comprise the physiological niche and biotic interactions. Depending on the species' physiological niche [2,3], a fundamental range of environmental, and in particular climatic conditions, defines the suitable range for growth, reproduction and establishment of populations [4]. This fundamental range of environmental conditions is usually modified by biotic interactions, for example owing to constricted tolerances in the presence of competitors or herbivores [1,5]. The result is the species' ecological [2,3] or realized niche [6], which is the environmental range of conditions under which a species does occur in nature.

Correlative species distribution models are based on the central assumption that on broad geographic scales, species' spatial distributions are in equilibrium with climate, while biotic interactions are of minor importance [7]. At the same time, it has been emphasized that biotic interactions are important at local scales, e.g. for presence and abundance in communities [1,8]. However, it has been recognized that detrimental biotic interac-

tions, such as competition and herbivory, have the potential to limit plant distribution also on large spatial scales [9,10]. For instance, Bruelheide & Scheidel [11] demonstrated that the altitudinal distribution of a montane plant species is restricted to higher elevations because of increasing slug herbivory in the lowlands.

Impacts of biotic interactions on plant performance have been demonstrated to change along climate gradients as for example was proposed by the stress gradient hypothesis for competition [12,13]. Thereby, competition should gain in relative importance under benign climate conditions. For example, Loehle [14] suggested that the northern range limits of North American tree species are limited by cold tolerance, while competitive ability should determine the southern range limits. This has also been demonstrated with examples of increasing competition with decreasing altitude [15]. Similarly, other biotic interactions might vary with climate conditions. For example, slug herbivore pressure was shown to increase with decreasing altitude [16].

In addition to altitudinal and latitudinal climate gradients, environments in Europe are also structured by a distinct longitudinal differentiation in climate. A strong gradient exists from oceanic climate in Western Europe, with relatively narrow annual temperature ranges and constantly humid conditions, to continental climate in Eastern Europe, with large temperature

seasonality and low annual precipitation. Along this gradient, the general physiological growth conditions for plants get harsher with increasing continentality. The strong impact of this continentality gradient on plant distribution is also evident in phytogeographical classification systems that classify plant species according to their geographic distribution along this gradient into oceanic and continental plant range types [17,18].

Species populations are expected to increase in performance, the closer their locations' growth conditions is to the species' climate optimum [19]. Under the general assumption that species' geographic distributions reflect their environmental requirements, species should do better under conditions which are climatically less peripheral. Testing this assumption for North American tree species, Purves [20] found distinct differences in growth and demographic rates between northern and southern peripheral range sections when compared with the core area. Accordingly, oceanic and continental plant species should perform better in oceanic and continental climates respectively. On the other hand, this view has recently been challenged as glasshouse experiments revealed no clear differences between responses of oceanic and continental species in respect to soil moisture levels and frost hardness [21,22]. However, multiple species field tests on plant range type-specific adaptations are still missing.

If closely related plant species tend to be similar in their fundamental niche requirements, differences in geographical distribution patterns might be caused by dispersal limitation, biogeographical history and biotic interactions. Differences in biotic characteristics are probably responsible for the large amount of unexplained interspecific variation in periphery-core comparisons of species performance [20]. As predicted by the stress-gradient-hypothesis, plant-plant interactions can turn from competition to facilitation with increasing abiotic stress [15]. Thus, competition should be less intense in continental compared to oceanic regions. Similarly, mollusc herbivory might also be reduced in continental regions as slugs (e.g. Arionidae) show clear preferences to more benign climate conditions [16]. Hence, species distributed in continental regions may be less adapted to negative biotic interactions and more vulnerable to biotic stress. This mismatch might be disadvantageous in the climatically more favourable oceanic regions. In consequence, detrimental biotic interactions should have a different impact depending on the species' plant range type.

Based on these considerations a transplant experiment was set up in nine Botanic Gardens along a continentality gradient in Germany (Fig. 1), where the relative impact of biotic interactions (competition and mollusc herbivory) and climate was tested with congeneric plant species of contrasting plant range types. Such transplant experiments have been used before and demonstrated a strong climatic impact on the transplants' survival, growth and reproduction [23–25].

The following hypotheses were tested: H1) There is an interactive effect between climate and biotic treatments on plant performance. In particular, we expected the effect of competition and herbivory to become weaker with increasing climatic continentality. H2) At the oceanic end of the gradient, species with general oceanic distribution should perform better than species with general continental distribution range and vice versa, indicating range type-specific adaptation. H3) Depending on the plant range type, biotic treatments affect species differently, as the continental plant species should be more susceptible to competition and herbivory. Furthermore, assuming that the relative importance of herbivory and competition decreases with increasingly continental climate, the negative biotic effects on continental species should decrease with increasing continentality. Testing

these hypotheses aims at improving the mechanistic understanding of species distribution patterns.

Material and Methods

Ethics statement

The authorities that issued the permit to use the Botanical Gardens were the scientific or technical directors of the gardens. As they also assigned the piece of land to us, carrying out the experiment without this permit would not have been possible. Seeds for the experiment were collected from public land and all regulations concerning protected or endangered species were respected.

Climate gradient

To establish a climatic gradient for common garden locations, we made use of the network of Botanical Gardens, as they provide excellent conditions for reproducibility, and generally have similar soil conditions, i.e. fertile garden soils (hortisols). Additionally, these gardens usually suffer from high mollusc densities, which motivated us to manipulate mollusc herbivory as a negative biotic impact. Using the geographic coordinates of 66 major Botanical Gardens in Germany we extracted the mean values for mean minimum temperatures of the coldest month and mean annual precipitation for the last 50 years, using the WORLDCLIM dataset [26]. We chose 12 gardens located along a gradient from oceanic (mild winter and high precipitation) to continental (cold winter and low precipitation) climate conditions. Out of these, nine gardens responded positively to our request for conducting an experiment (Fig. 1, Table 1).

For the study period (June 2008–October 2009), monthly mean data for temperature and precipitation were obtained from the nearest official meteorological stations. Table 1 shows mean temperatures as well as accumulated temperature and precipitation sums at the nine study sites for the investigation period. To analyze the weather conditions during the study period, the climate data of all nine Botanical Gardens were subjected to a principal component analysis (PCA, prcomp procedure; R 2.15.2, R Development Core Team 2012). In the PCA, the Botanical Gardens were ordered along a clear gradient related to temperature on the first, and precipitation variables on the second axis (explaining 53% and 28% of the overall variance in climate conditions, respectively). Summer temperature of 2009 had the highest loading and was positively correlated with the first PCA axis scores (Table 1). The remaining temperature variables for the vegetation period were also highly positively correlated with the first PCA axis while precipitation variables and minimum temperature were negatively correlated with this axis (Table 1). Regarding the second PCA axis, summer precipitation in 2009 had the highest loading and was negatively correlated with the respective axis scores (Table 1). The Botanical Gardens were arranged from Osnabrück (OSN) to Frankfurt (FRA) and from Frankfurt (FRA) to Braunschweig (BS) along PCA axis 1 and 2, respectively (Table 1).

Transplants and measurements

Fourteen herbaceous species were included in the experiment, two from each of seven genera. The two congeneric species are of similar growth form, have similar habitat preferences (Table S1), but differ in their geographical distribution range, in particular with respect to the longitudinal positions of their western range boundary (Figure S1). The following species were included in this transplant experiment (taxonomy according Jäger & Werner [27], plant range type as follows: oceanic-continental): *Carlina vulgaris*

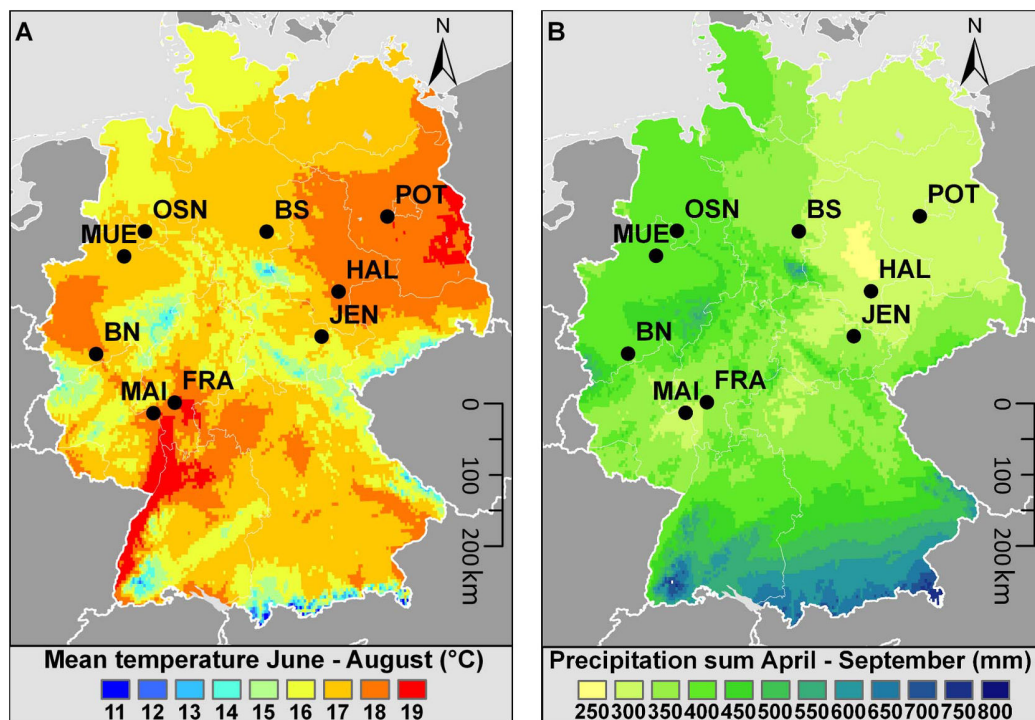


Figure 1. Locations of the Botanical Gardens in the transplant experiment showing the main gradients in climatic differences. A) Sum of the monthly mean temperature in summer (June-August), B) Precipitation of the vegetation period in mm. Climate data were obtained from [26] and refer to the same periods as used in Table 1, but refer to long-term averages. For abbreviations of locations see Table 1. doi:10.1371/journal.pone.0111023.g001

- *Ca. biebersteimii*, *Centaurea scabiosa* - *Ce. stoebe*, *Dianthus deltooides* - *Di. carthusianorum*, *Inula conyzae* - *I. hirta*, *Koeleria pyramidata* - *K. macrantha*, *Scabiosa columbaria* - *Sc. ochroleuca* and *Silene nutans* - *Si. oites*. The species are perennial plants which are all native to Europe (see distribution maps in Figure S1) and occur mainly in dry to semidry open grasslands [27]. All species had already been investigated in other glasshouse [21,22] and field experiments [28].

Seeds of all species were collected in summer 2007 in Central Germany, using large populations to avoid negative effects of low genetic diversity (for geographical coordinates of the sampling localities see Table S1). Seedlings of all species were raised under controlled standardized glasshouse conditions in spring 2008. In June 2008, the young seedlings were transplanted into the plots. To ensure initial establishment, plants were watered regularly for one month. There were some species for which not enough seedlings were available, resulting in three species pairs that could not be planted in all gardens. These missing species pairs were randomly assigned to all gardens, except for those at the ends of the climate gradient which received all seven genera. We made sure that no more than one species pair was missing in any of the nine gardens.

At the beginning of the experiment, the leaf number of every transplant was counted to calculate relative growth rates according to Hunt [29]. At the end of the experiment, in October 2009, survival, flowering status, number of leaves, number of flowering units, plant height, specific leaf area (SLA) and the proportion of consumed leaf area (visually assessed) were recorded. Additionally, aboveground biomass was harvested and weighed after drying at 70°C for 48 hours.

All data are available at http://data.idiv.de/repo/data_Welk_etal_PlosOne.xls.

Experimental setup

In every garden one study plot consisting of 16 subplots of one by one metre area each was established (Figure S2). Each subplot was divided in four rows and four columns, resulting in 16 planting positions (Figure S2). One individual per plant species was planted in every subplot at randomly chosen positions resulting in a maximum of 14 transplants (and two empty positions) per subplot. For the competition treatment, seeds of *Festuca rubra* (cultivar *Wilma*, RUDLOFF Feldsaaten GmbH, Bad Schwartau, Germany) were sown (5 g/m²) on eight subplots at the time of planting of the transplants (Figure S2). All subplots were regularly weeded except for *Festuca rubra* in the competition subplots. For the mollusc enclosure we regularly applied a mollusc repellent (Ferramol, W. Neudorff GmbH KG, Emmerthal) on eight of the subplots. In spring 2009, these plots were additionally equipped with metal frame fences to exclude molluscs (IRKA, R+M Gartenbedarf, Rehling, www.der-schneckenzaun.de). The competition and mollusc enclosure treatments were fully crossed and all treatment combinations were replicated four times per Botanical Garden (Figure S2), resulting in a total of 144 subplots and 1824 transplant individuals.

Statistical analyses

All response variables (survival, incidence of flowering, RGR of leaf number, aboveground biomass, plant height, number of flowering units, SLA and proportion of consumed leaf area biomass) were analysed with separate generalized linear mixed effect models (GLMM, `proc glimmix`, type III SS, SAS 9.2, SAS Institute Inc. 2008). For survival and incidence of flowering, a logit-link function and binomial error distribution were used, while the GLMM for all other response variables had an identity-link

Table 1. Climatic conditions of the Botanical Gardens and results from the principal component analysis (PCA).

Climate variable	Botanical garden											Loadings PCA1		Loadings PCA2	
	FRA	MAI	HAL	POT	BS	JEN	BN	MUE	OSN						
Sum of the monthly mean temperature in summer 2009 (June-August) in °C	57.9	56.6	54.4	54.4	53.6	53.2	53.5	52.9	52.7			0.422	-0.227		
Sum of the monthly mean temperature of the vegetation period 2008 (August-October) in °C	42.8	42.0	41.6	41.0	41.4	40.6	40.9	41.0	40.5			0.412	-0.186		
Sum of the monthly mean temperature of the vegetation period 2008 and 2009 in °C	147.0	144.4	138.5	138.2	137.1	135.5	136.8	136.1	135.2			0.411	-0.258		
Sum of the monthly mean temperature of the vegetation period 2009 (April-September) in °C	104.2	102.4	96.9	97.2	95.7	94.9	95.9	95.1	94.7			0.404	-0.269		
Precipitation in summer 2009 (June-August) in mm	205.5	163.2	151.1	152.1	139.2	173.3	182.9	209.3	198.1			-0.140	-0.592		
Precipitation of the vegetation period 2009 (April-September) in mm	334.6	281.6	302.2	278.0	240.4	362.8	368.0	332.0	316.0			-0.149	-0.399		
Minimum of monthly mean temperature 2008-2009	-1.9	-1.8	-2.1	-1.9	-0.7	-2.6	-0.8	-0.5	-0.2			-0.279	-0.097		
Precipitation of the vegetation period 2008 (August-October) in mm	168.9	169.1	152.0	178.4	169.9	159.3	171.7	223.7	280.2			-0.316	-0.244		
Precipitation of the vegetation period 2008 and 2009 in mm	503.5	450.7	454.2	456.4	410.3	522.1	539.7	555.7	596.2			-0.317	-0.443		
First axis scores of the PCA (=PCA1)	3.32	2.76	0.99	0.45	0.32	-0.98	-1.35	-2.20	-3.30						
Second axis scores of the PCA (=PCA2)	-2.66	-0.13	1.25	1.41	2.50	0.42	-0.54	-1.11	-1.13						

Climate variables are arranged according to their loadings on the first PCA axis. Botanical gardens included in this study are sorted according to their scores of the first PCA axis. Scores and loadings of the Principal Component Analysis (PCA) are shown in italics. The three variables with highest absolute loadings per PCA axis are shown in bold letters. Botanical garden abbreviation: BN – Bonn, BS – Braunschweig, FRA – Frankfurt am Main, HAL – Halle (Saale), JEN – Jena Isserstedt, MAI – Mainz, MUE – Münster, OSN – Osnabrück, POT – Potsdam.
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function and Gaussian error distribution. To identify the most relevant climatic drivers of the different response variables we included the scores of the first and second PCA axes as covariates in the models. Fixed categorical factors in all models were plant range type (oceanic, continental), competition (presence/absence) and herbivory (presence/absence). All possible two and three-way interactions of fixed factors and covariates were included. Subplot identity (nested in the interaction of garden identity, herbivory and competition treatment) and species identity (nested in plant range type) entered the models as crossed random factors.

Unbiased least square means (LS means) and standard errors were calculated using the LSMEANS statements in SAS 9.2 (SAS Institute Inc. 2008) and used to produce graphs. Tukey post-hoc tests were calculated for contrasts between treatment combinations. All graphs were produced with R 2.15.2 (R Development Core Team 2012).

Results

Main effects of climate, competition and herbivory

The climate gradient significantly affected survival, aboveground biomass, plant height, number of flowering units, SLA and proportion of leaf area consumed (Table 2). While temperature, which was captured by the first PCA axis, had no significant effect on any response variable, precipitation, with high loadings on the second PCA axis, played a major role. Survival ($p = 0.005$), plant height ($p = 0.013$) and number of flowering units ($p < 0.001$) decreased with decreasing precipitation (i.e. increasing PCA2 scores), while proportion of consumed leaf area increased ($p = 0.020$). Additionally, there were significant interactions of both PCA axes for survival ($p = 0.002$), aboveground biomass ($p = 0.005$), plant height ($p = 0.038$), number of flowering units ($p < 0.001$) and specific leaf area ($p = 0.042$, Table 2).

The competition and mollusc exclusion treatments had strong effects on all response variables except survival (Table 2). This demonstrates that our experimental subplot manipulation of biotic interactions was effective and that these two biotic factors were key determinants of plant performance across all species. Competition significantly reduced the incidence of flowering (by -7.1% , referring to LSmeans estimates from the GLMM, $p < 0.001$), RGR of leaf number (by -59.2% , $p < 0.001$), aboveground biomass (by -40.8% , $p < 0.001$) and number of flowering units (by -35.5% , $p < 0.001$). Furthermore, there was an increase in SLA (by $+6.2\%$, $p = 0.022$) and proportion of consumed leaf area (by $+50.1\%$, $p < 0.001$) when competitors were present. Mollusc exclusion resulted in increased plant height (by $+3.5\%$, $p = 0.031$) and lower proportions of consumed leaf area (by -29.7% , $p < 0.001$). Additionally, proportions of consumed leaf area showed a significant interaction effect of competition with herbivory ($p = 0.004$): While the mollusc exclusions reduced the amount of consumed leaf area by -10.3% in absence of competition, the reduction was -40.5% in presence of competition.

Interaction of climate with impacts of competition and herbivory

In general, the climate gradient had no effects on the outcome of the biotic subplot manipulations for most response variables (Table 2). Along the first PCA axis (temperature) the competition effect on number of flowering units changed ($p = 0.043$, Table 2). With increasing temperature (i.e. increasing PCA1 scores), the number of flowering units increased when competitors were absent, while the number of flowering units remained unchanged when competitors were present. The effect of mollusc exclusion changed along the second PCA axis (precipitation) for incidence of

flowering ($p = 0.027$, Table 2). With decreasing precipitation (i.e. increasing PCA2 scores) flowering was observed less frequently when molluscs were excluded, while flowering increased in frequency in the presence of mollusc herbivory.

Effects of plant range type and the interactions of plant range type with climate, competition and herbivory

No significant main effects of plant range type were observed for any of the response variables (Table 2). This also applied to SLA, showing that the two representatives for plant range types did not differ in basic functional traits. However, significant interactions indicated that species of different plant range types responded differently along the climate gradient and to the subplot treatments (Table 2).

Survival, incidence of flowering, aboveground biomass and number of flowering units were significantly affected by the interaction of plant range type with competition (Table 2). The plants of the oceanic range type survived slightly better in presence of competitors ($+1.6\%$), whereas those of the continental range type had clearly lower survival rates (-9.0%) when competitors were present ($p = 0.025$, Fig. 2A). Similarly, plants with continental range type flowered less frequently in presence of competitors (-7.7%), whereas flowering of oceanic plants remained nearly unaffected by competition (-0.9% , $p = 0.030$, Fig. 2B). In contrast, aboveground biomass (oceanic -47.9% , continental -32.6% , $p = 0.008$) and number of flowering units (oceanic -40.5% , continental -27.0% , $p = 0.017$) were generally negatively affected by competition, with stronger negative effects on plants with oceanic than on continental range type (Fig. 2C,D).

With respect to the herbivory treatment, plant range type was important for the incidence of flowering ($p = 0.007$) and proportion of consumed leaf area ($p = 0.027$, Table 2). Plants of the continental range type showed a decrease in the proportion of flowering individuals (-4.8%) in the presence of molluscs while those of the oceanic range type displayed a slight increase ($+0.6\%$, Fig. 2E). Without mollusc exclusion, plants of the oceanic range type were consumed more frequently than plants of the continental range type (Fig. 2F).

There were also threefold significant interactions of competition, herbivory and plant range type. The plant range types displayed contrasting response patterns to herbivory and competition in survival ($p = 0.028$, Fig. 3A,B), plant height ($p = 0.023$, Fig. 3C,D) and number of flowering units ($p = 0.022$, Fig. 3E,F, Table 2). Survival and plant height of continental plants were strongly negatively affected by the single effects of herbivory and competition (Fig. 3B,D). These effects had the same magnitude and were not additive when mollusc herbivory occurred in combination with competition. Survival and plant height of oceanic plants remained unaffected by the biotic treatments (Fig. 3A,C). The contrasting pattern was observed for the number of flowering units, where oceanic plants were strongly affected by biotic interactions (Fig. 3E), while continental plants were not (Fig. 3F). In oceanic plants, herbivory and competition had opposing effects on number of flowering units. While herbivory alone caused a significant increase in number of flowering units, competition alone had no significant effect. However, when competitors were present in addition to herbivores, the number of flowering units of oceanic plants strongly decreased (Fig. 3E). Neither RGR of leaf number nor the proportion of consumed leaf area showed significantly different effects for the contrasting range types in the presence or absence of herbivores or competition (Table 2).

The responses to the climatic variables of plants of contrasting range types differed for incidence of flowering (PCA2, $p = 0.018$,

Table 2. The effect of climatic covariates (PCA axes 1 and 2, representing temperature and precipitation effects, respectively), competition, herbivory and plant range type on the different variables of plant performance measured in the Botanical Gardens.

Effect	Survival rates		Incidence of flowering		RGR of leaf number		Aboveground biomass		Plant height		Number of flowering units		Specific leaf area (SLA)		Proportion of consumed leaf area					
	DF _{num}	DF _{den}	F	DF _{den}	F	DF _{den}	F	DF _{den}	F	DF _{den}	F	DF _{den}	F	DF _{den}	F					
PCA1	1	1638	0	1500	2.78	1243	1.04	1225	0.13	1449	0.46	1499	2.5	1172	0.5	1237	0.16			
PCA2	1	1638	7.84	**	1500	0.15	1243	2.03	1225	2.04	1449	6.20	*	1499	16.72	***	1237	5.40	*	
PCA1×PCA2	1	1638	10.06	**	1500	1.41	1243	1.23	1225	8.08	**	1449	4.30	*	1499	19.61	***	1172	4.13	*
Competition (C)	1	129	0.28	130	13.52	***	130	16.26	***	128	53.13	***	130	3.02	130	28.58	***	130	5.37	*
C×PCA1	1	1638	0.25	1500	1.15	1243	0.01	1225	0	1449	0.65	1499	4.12	*	1172	0.07	1237	0.48		
C×PCA2	1	1638	2.21	1500	0.23	1243	0.47	1225	1.19	1449	0.04	1499	0.23	1172	0.60	1237	0.35			
C×PCA1×PCA2	1	1638	0.32	1500	1.37	1243	1.17	1225	0.77	1449	0.15	1499	7.76	**	1172	0.67	1237	0.88		
Herbivory (H)	1	129	0.87	130	1.72	130	0.66	128	0.04	130	4.78	*	130	0.44	130	2.41	130	14.40	***	
H×PCA1	1	1638	0	1500	2.11	1243	0.09	1225	0.01	1449	0.68	1499	0.34	1172	0.11	1237	0			
H×PCA2	1	1638	0.26	1500	4.90	*	1243	0.39	1225	0.03	1449	0.72	1499	1.38	1172	0	1237	1.66		
H×PCA1×PCA2	1	1638	0.01	1500	0.47	1243	0.50	1225	0	1449	0.46	1499	1.29	1172	0.02	1237	0.38			
C×H	1	129	0.08	130	0.25	130	0.64	128	0.19	130	0.06	130	2.32	130	0.20	130	8.47	**		
C×H×PCA1	1	1638	1.63	1500	0.17	1243	0.76	1225	0.07	1449	0.01	1499	0	1172	0.07	1237	0.05			
C×H×PCA2	1	1638	0.35	1500	2.47	1243	1.15	1225	1.11	1449	0.30	1499	0.17	1172	0.48	1237	2.74			
Range type (R)	1	12	1.49	12	0.50	12	2.50	12	0.02	12	0.07	12	0.63	12	1.13	12	0.37			
R×PCA1	1	1638	0.06	1500	1.67	1243	0.80	1225	0.02	1449	2.01	1499	0.80	1172	0.03	1237	0.45			
R×PCA2	1	1638	0.56	1500	5.64	*	1243	0	1225	0.54	1449	6.65	*	1499	0.51	1237	0.88			
R×PCA1×PCA2	1	1638	2.29	1500	0.78	1243	0.40	1225	0.39	1449	0.53	1499	3.19	1172	2.42	1237	0.03			
C×R	1	1638	5.07	*	1500	4.71	*	1243	1.09	1225	6.97	**	1449	5.74	*	1172	0.07	1237	1.59	
C×R×PCA1	1	1638	2.23	1500	0.01	1243	0.23	1225	0.44	1449	3.42	1499	0.62	1172	0.48	1237	0.11			
C×R×PCA2	1	1638	0.84	1500	3.96	*	1243	1.38	1225	4.57	*	1449	1.51	1172	2.64	1237	1.27			
H×R	1	1638	0.44	1500	7.76	**	1243	0.03	1225	0.95	1449	1.26	1499	0.08	1172	0.02	1237	4.91	*	
H×R×PCA1	1	1638	0.05	1500	2.36	1243	0.12	1225	0.50	1449	0.50	1499	1.22	1172	0.13	1237	0.01			
H×R×PCA2	1	1638	0.18	1500	0.02	1243	0.02	1225	0.01	1449	0.82	1499	0.99	1172	0.06	1237	0.03			
R×C×H	1	1638	4.85	*	1500	2.94	1243	3.31	1225	0.20	1449	5.18	*	1499	5.29	*	1172	0.50	1237	0.12

The table shows degrees of freedom for the numerator and denominator (DF_{num} and DF_{den}) respectively as well as F values from a type III Anova based on generalized linear models. Bold F values indicate significant effects. ***p<0.001, **p<0.01, *p<0.05.
doi:10.1371/journal.pone.0111023.t002

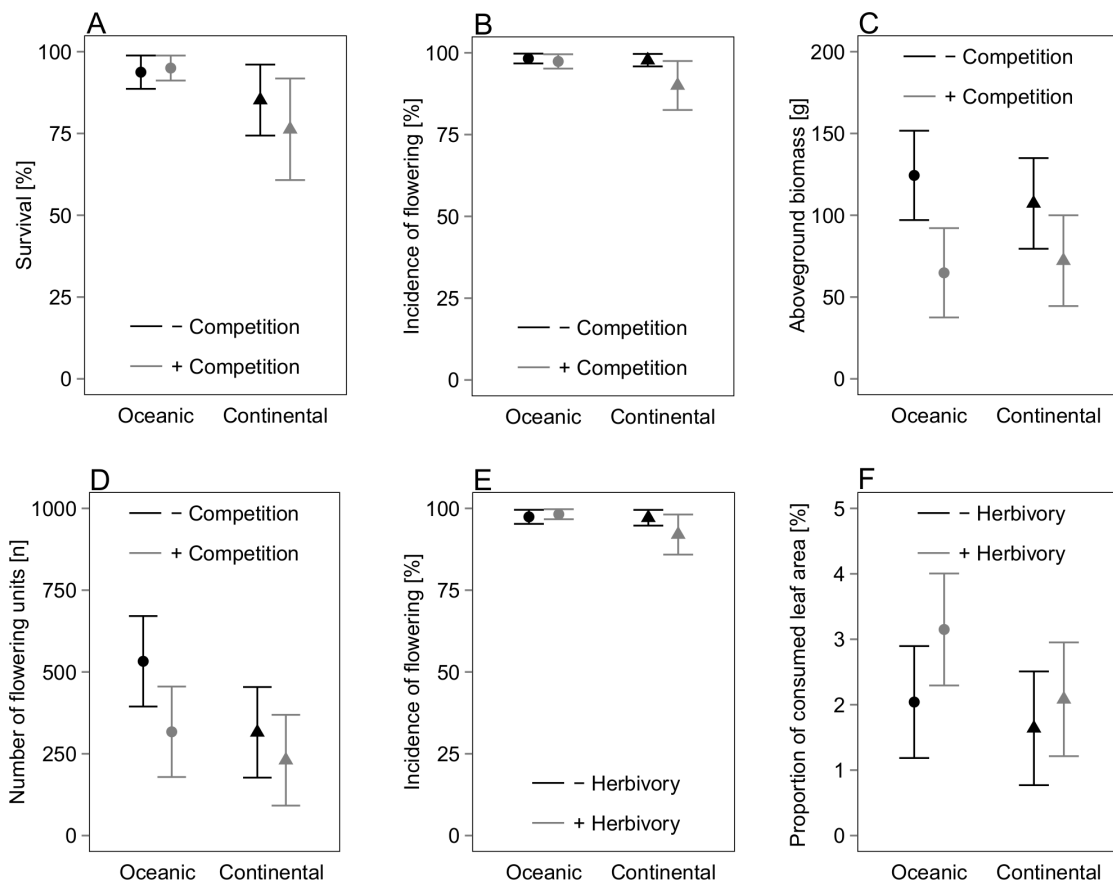


Figure 2. Significant interactive effects of plant range type with competition on A) survival, B) incidence of flowering, C) aboveground biomass and D) number of flowering units, and interactive effects of plant range type with herbivory on E) incidence of flowering and F) proportion of consumed leaf area. Graphs are plotted with LSmeans estimates and standard errors derived from the GLMM's. For statistical details see Table 2. doi:10.1371/journal.pone.0111023.g002

Fig. 4A) and plant height (PCA2, $p=0.010$, Fig. 4B, Table 2). Incidence of flowering of continental plants decreased with decreasing precipitation (i.e. increasing PCA2 scores) while that of oceanic plants increased (Fig. 4A). Similarly, plant height of continental plants decreased with decreasing precipitation but remained constant in oceanic plant species (Fig. 4B). At the moist end of the gradient, plants of the continental range type flowered more frequently and were taller than oceanic ones, while on the dry end the pattern was reversed (Fig. 4A,B).

Furthermore, along the precipitation gradient, the effect of competition differed between range types for incidence of flowering (PCA2, $p=0.047$, Fig. 4C) and aboveground biomass (PCA2, $p=0.033$, Fig. 4D, Table 2). For both response variables, oceanic plants showed changed climate responses when competition was manipulated. Incidence of flowering and aboveground biomass strongly increased with decreasing precipitation (i.e. increasing PCA2 scores) when competitors were absent (Fig. 4C). In the presence of competition, oceanic plants showed only a slight increase in incidence of flowering (Fig. 4C) and a decrease in aboveground biomass with decreasing precipitation (i.e. increasing PCA2 scores, Fig. 4D). In contrast, plants with continental plant range type showed almost no changes in their climate responses when competition was manipulated. With decreasing precipitation (i.e. increasing PCA2 scores) incidence of flowering and above-

ground biomass of continental plants decreased, both in the absence and presence of competitors (Fig. 4C,D).

Discussion

The climate conditions in our transplant experiment were characterized by a distinct gradient from oceanic to continental climate. Across all species included in our study, temperature was less important for performance variation than precipitation. Plants benefited from higher precipitation in terms of higher survival, taller growth and increasing number of flowering units. Additionally, plant growth and reproduction were strongly negatively affected by competition and partly by mollusc herbivory, indicating that competition was more detrimental than herbivory. Biotic interactions affected all response variables except plant survival. This indicates that the relative importance of biotic interactions and climate differed among the different response variables.

Effects of climate on biotic interactions

In our first hypothesis, we expected that the negative effect of competition and herbivory is mitigated under the more stressful continental climate conditions. This was not the case for survival and plant growth. Biotic interactions only changed the response along the climate gradient in the case of variables related to

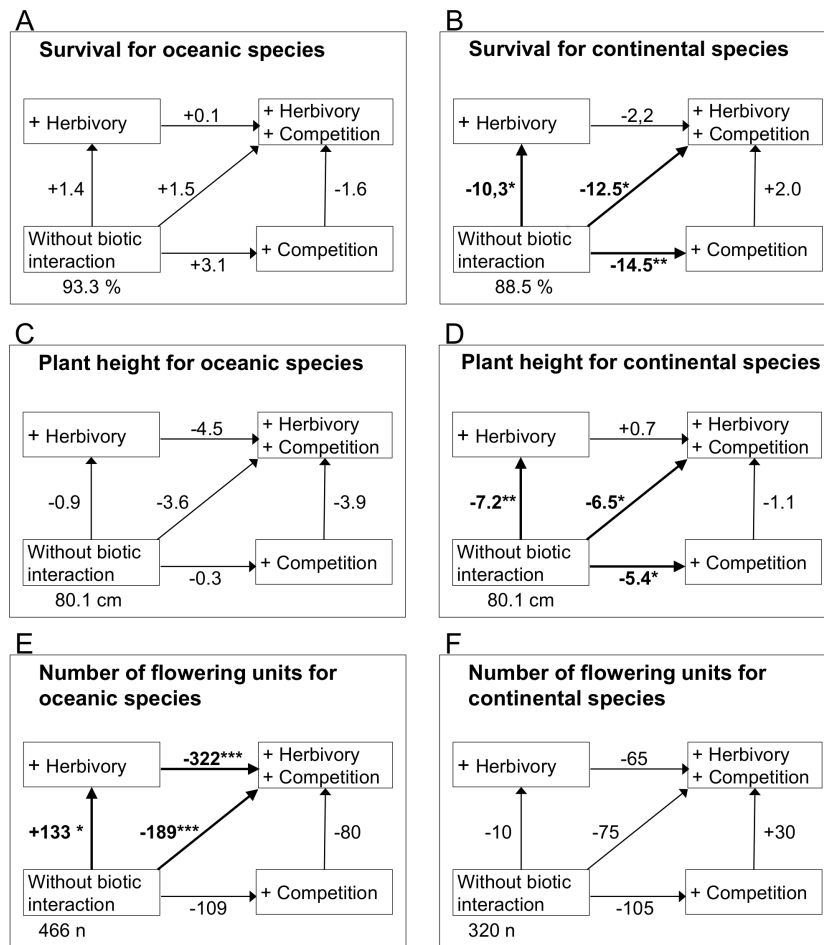


Figure 3. Summary of interactive effects of competition and herbivory on species with different plant range types for survival (A,B), plant height (C,D) and number of flowering units (E,F). Effects for the oceanic species are illustrated on the left side (A,C,E), for continental on the right side (B,D,F). The values in the bottom left corner are LSmeans estimates calculated from the GLMM for the treatment without biotic interactions. The values on the arrows are differences in the LSmeans estimates of this treatment-combination indicating the direction and strength of the relation. Units are percentage (A,B), cm (C,D) and numbers (E,F). Bold arrows indicate significant effects according to the Tukey post hoc-test. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. doi:10.1371/journal.pone.0111023.g003

flowering. Competition generally reduced aboveground biomass and growth, irrespective of climate. Restrictions in water supply at the dry end of the climatic gradient did not aggravate the effect of competition, probably because target plants and competitors were affected likewise. However, we also have to consider that the fertile garden soils used in our experiment have affected the interaction of climate and competition. While competition is expected to become more pronounced under fertile conditions, drought effects might have been reduced. In contrast to competition, mollusc herbivory had no impact on biomass production and was independent of the climate conditions in our experiment, except for incidence of flowering. This does not confirm the results of a recent global meta-analysis of Rodríguez-Castañeda [30], who found that the effect of general herbivory on plant performance increased in moister ecosystems. Bruehlheide & Scheidel [11] described increased slug herbivory with decreasing altitude, which was reflected in increasing temperatures, and overall, more benign growth conditions. A potential explanation for this mismatch to our results might be that the climate gradient used in our study was not steep enough to evoke climate-dependent herbivory effects on plant performance. Additionally, the generally high slug

abundances in Botanical gardens might have uncoupled the climate-herbivory relationship, which emphasises the need for assessing mollusc densities in future studies. Given the large distance between the experimental sites, we were not able to count molluscs during rain events or to quantify mollusc activity [11,16].

Interaction of climate with plant range type

We secondly hypothesised that the changing climate conditions in our study have a different impact on the transplants with respect to their range type. The expectation that species of the oceanic plant range type perform better at the oceanic end of the climate gradient and those of the continental plant range type at the continental end of the climate gradient was not confirmed. Instead, we even found opposing patterns with increased incidence of flowering, plant height and aboveground biomass for continental plants under moister conditions and for oceanic plants under drier conditions. These results support the outcome of previous experiments in the field and the greenhouse, where analyses with the same species set revealed similar responses to manipulated climate change [28] or altered soil moisture conditions [21,22]. Nevertheless, at least for the continental species, we expected a

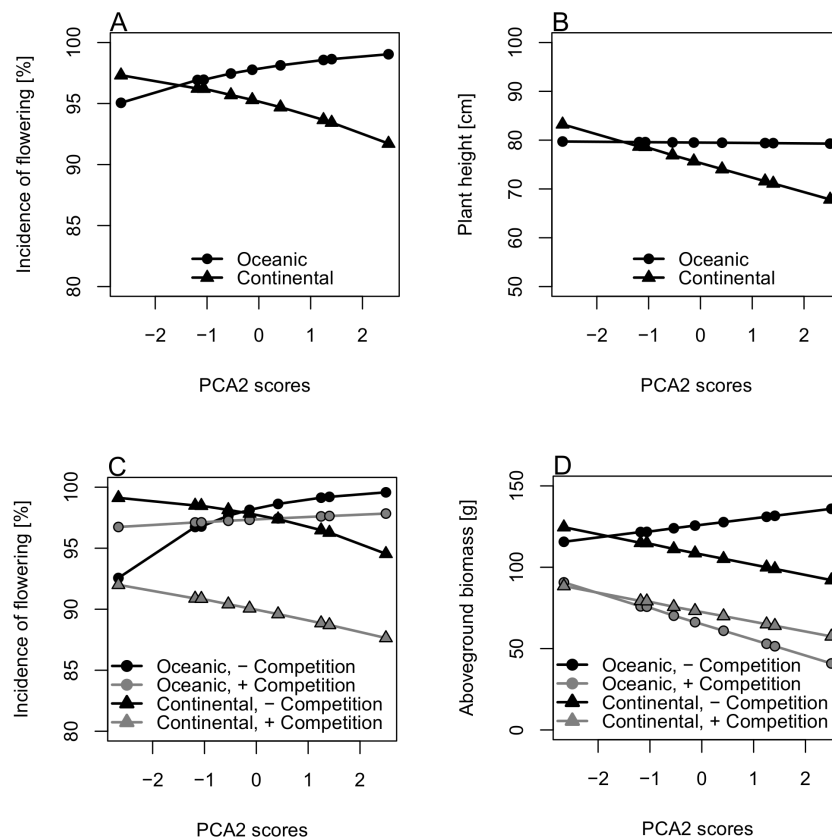


Figure 4. Significant effects of the climate gradient (climate covariate) on plants with different plant range types for A) incidence of flowering and B) plant height, and in interaction with competition for C) incidence of flowering and D) aboveground biomass. Climate covariates are PCA 2 scores which are negatively correlated with precipitation sums of the vegetation period during the experiment (Table 1). Graphs are plotted with LSmeans estimates derived from the GLMM's. For statistical details see Table 2. doi:10.1371/journal.pone.0111023.g004

poorer performance in the more oceanic climate since the experimental setup covered an area extending beyond their western distribution limit (Figure S1). However, the general impression was that plants of the continental range type responded stronger to the climatic gradient than those of the oceanic range type, especially with plant height. In contrast to our findings, numerous transplant experiments have described a decreased fitness beyond a species' current range [31]. However, most of these species' range boundaries were studied along latitudinal or altitudinal climate gradients [32,33], where temperature is the dominant driver. In contrast, the climate gradient covered in our experiment is less simple as higher temperatures that favour growth rates are counteracted by increasing drought risk. Consistent with our results, Stanton-Geddes et al. [34] observed fitness declines towards the northern range edge but not to the western range edge of *Chamaecrista fasciculata*, a widespread annual legume from North America. However, we also have to consider that short-term experiments, as presented here, might perhaps not be able to detect clear home-site advantages. For example, in a transplant experiment monitored over 30 years Bennington [35] encountered increasingly stronger home-site advantages for ecotypes of two arctic plant species with time. Our study design also did not allow for assessing the impact of climate on population demography as we did not focus on recruitment. Given that our species are almost all long-lived, although some of them are hapaxanth (Table S1), a 2 years-study period is certainly not sufficient to estimate the impact of climate

on long-term survival and demography. This clearly underlines the need for long-term studies.

Interaction of competition and herbivory with plant range type

When climatic factors failed to explain species range limitation, biotic interactions have often been made accountable for directly limiting distribution ranges [31,36]. For example, Engels & Jensen [37] found that plant species from salt marshes performed similarly well in both freshwater and saltwater marshes, when competition was excluded. Similarly, in our experiment, plants with continental range type survived much better in absence of competition than those with oceanic plant range type. In addition, continental plants flowered more frequently when competitors or herbivores were removed or excluded, respectively. This sensitivity to competition and herbivory of continental plants was not modified by climate. This indicates that the geographic distribution of continental plants is not directly limited by climate conditions but by other factors, such as competition. However, biotic interactions might act on different spatial scales. In a tundra study system Le Roux et al. [38] found that small scale species distribution was shaped by horizontal biotic interactions (i.e. competition) rather than by vertical interactions (i.e. herbivory). Similarly, our experimental evidence on survival and incidence of flowering supports our third hypothesis stating that continental plants are more vulnerable to competition and herbivory than

oceanic plants. However, oceanic plants were stronger negatively affected by competition in biomass and flower production than continental plants. Regarding these inconsistent results, the third hypothesis that continental plants are more susceptible to competition or herbivory has to be rejected.

Although individuals of both plant range types suffered from biotic stress, they showed different strategies to cope with that. Particularly, the combined effect of competition and herbivory caused different plant responses with respect to plant range type. Only plants of continental range type displayed lower survival rates and smaller plant height in presence of competitors and herbivores. In contrast, oceanic plants were significantly affected in their flower production by herbivory alone and in combination with competition. The reduced flower production of the oceanic plants might be an effect of the compensatory response to herbivory and demonstrates a shift in resource allocation to enhanced plant growth [39]. Further reproductive traits such as number of seeds, seed mass and seed dispersal mode, have also profound effects on plant persistence [40] but could not be assessed in our experiment. Nevertheless, survival of plant individuals is ecologically essential to maintain a population. A synthesis of all our results indicates, that continental plants run a higher risk to suffer from competition and herbivory than oceanic plants, particularly if they are subjected to the combination of both competition and herbivory.

Conclusion

From the results of our experiment we can conclude that, at the geographical scale of Germany, the continentality gradient is of minor direct importance for species of the considered plant range types compared to negative biotic interactions. Competition and herbivory affected particularly the performance of individuals of continental plant range type. There was only weak evidence for the assumption that the impact of competition and herbivory should vary with climate. In consequence, predictions of future geographic range dynamics of plants species have to be considered with caution, especially when based solely on occurrence data and climatic variables. Mechanistic models would be more suitable, but to devise such models a better understanding of plant ecology is needed [41]. Consequentially, Wisz et al [42] recommended targeted long-term field monitoring approaches. Such long-term field experiments should not only include species of different plant range types but also measure demographic rates, which requires the assessment of sexual and vegetative recruitment.

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Supporting Information

Figure S1 Distribution maps of the congeneric species pairs used in the study. A – *Carlina*, B – *Centaurea*, C – *Dianthus*, D – *Inula*, E – *Koeleria*, F – *Scabiosa*, G – *Silene*. Species which were assigned to oceanic range types are coloured in blue, continental are coloured in red. Violet colour indicates range overlap of the two species. The Botanical Gardens where the experimental sites were located are shown as black dots. Details on the compilation of the data for these distributions maps are given in Hofmann et al. (2013). (DOCX)

Figure S2 Plot scheme of the experimental design in every Botanical Garden. All treatments were randomly assigned to subplots and plants were randomly assigned to planting positions. All species were planted into subplots. Symbols: - C = absence of competitors (regular weeding), + C = presence of competitors (*Festuca rubra*), - H = slug herbivore exclusion (subplot with metal frame and slug repellents), + H = without slug herbivore exclusion (subplot without metal frame). (DOCX)

Table S1 Species characteristics (Jäger & Werner 2005) and coordinates of the localities where seeds were collected. Growth form: eg = evergreen, sg = summergreen, hc = hemicryptophyte, p = perennial. (DOCX)

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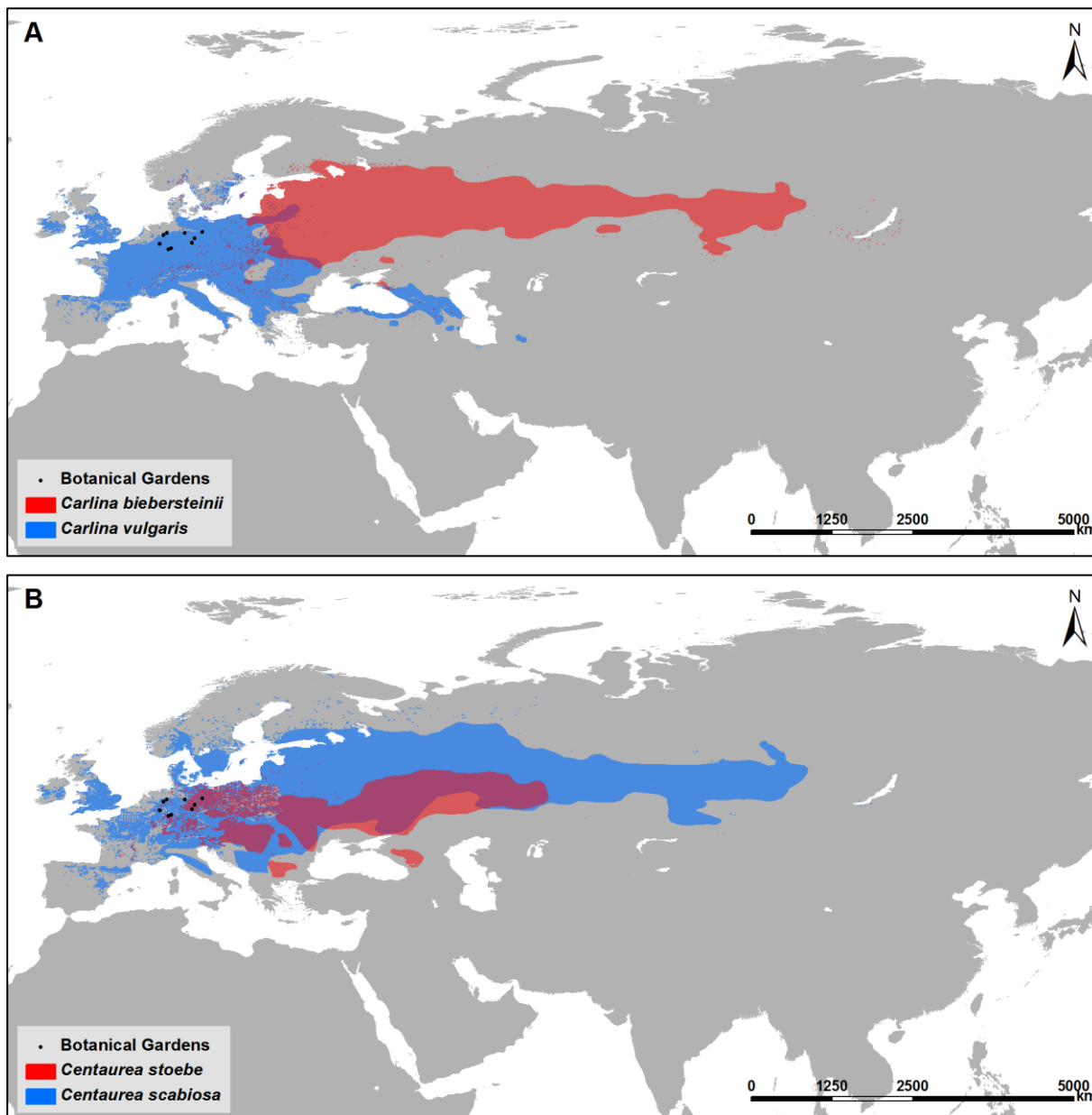
Author Contributions

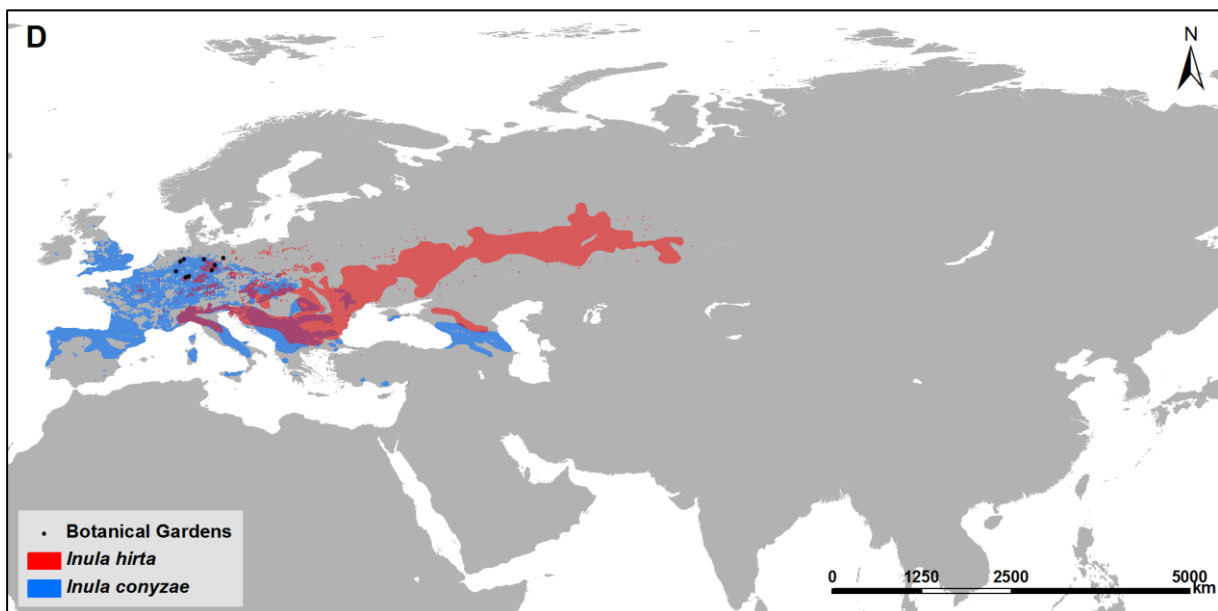
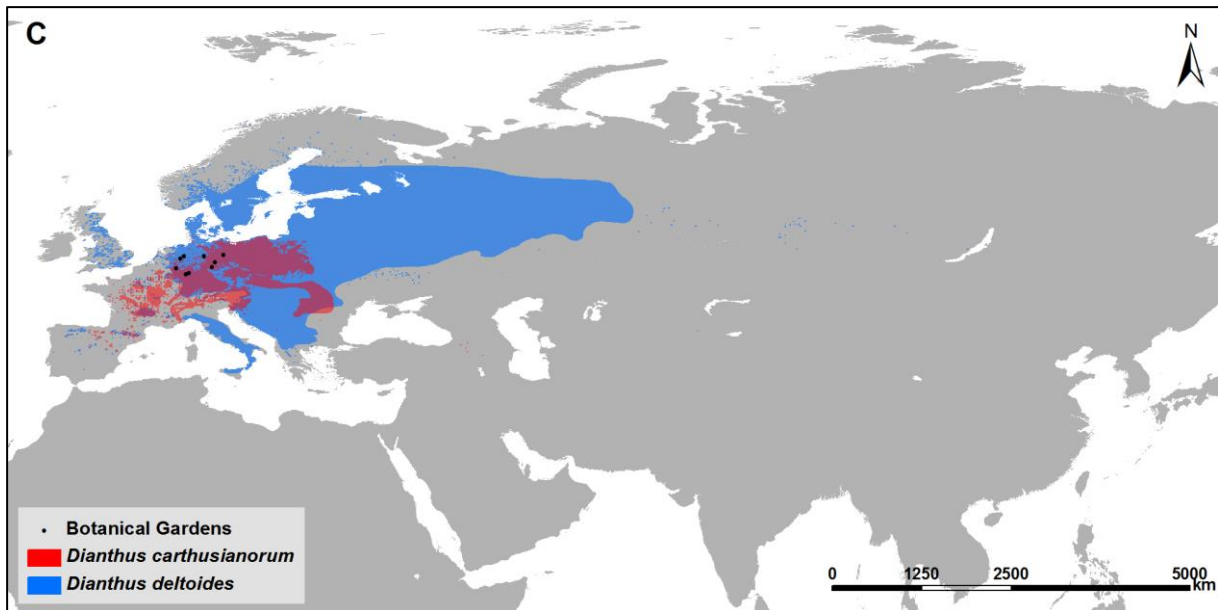
Conceived and designed the experiments: AW EW HB. Performed the experiments: AW. Analyzed the data: AW EW HB. Contributed reagents/materials/analysis tools: AW EW HB. Wrote the paper: AW EW HB.

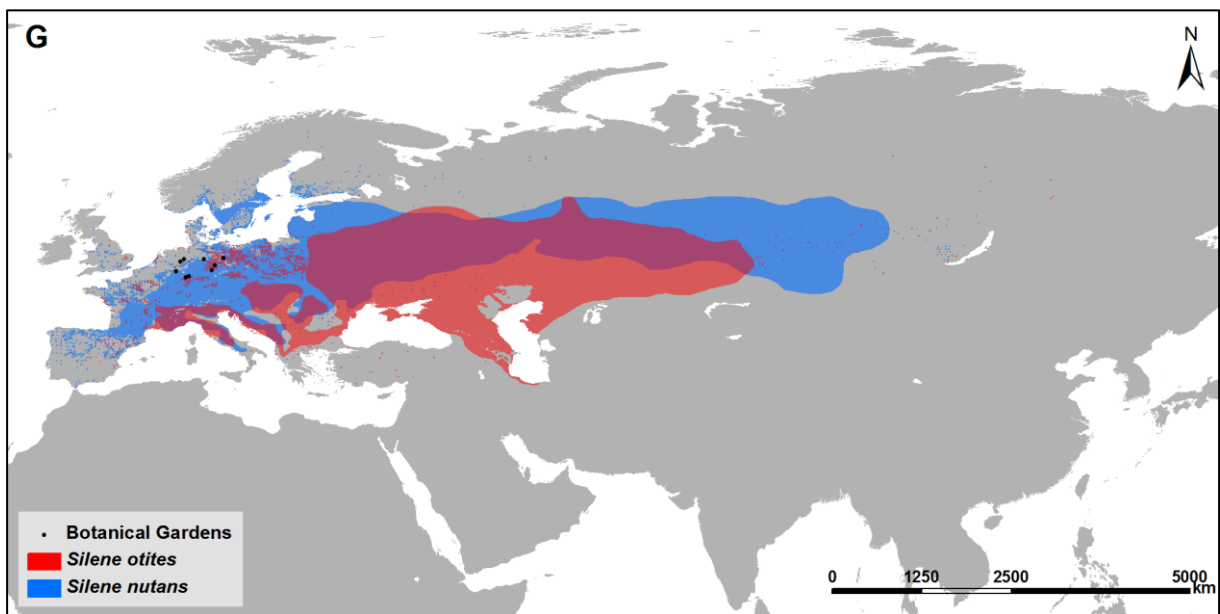
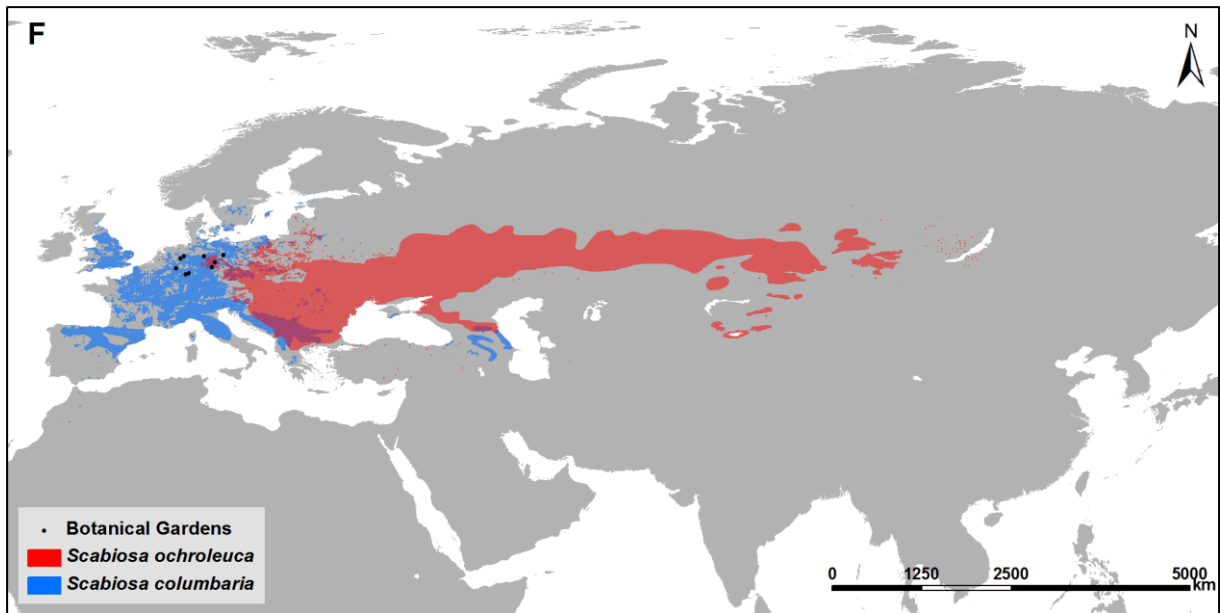
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Supporting Information Chapter 2

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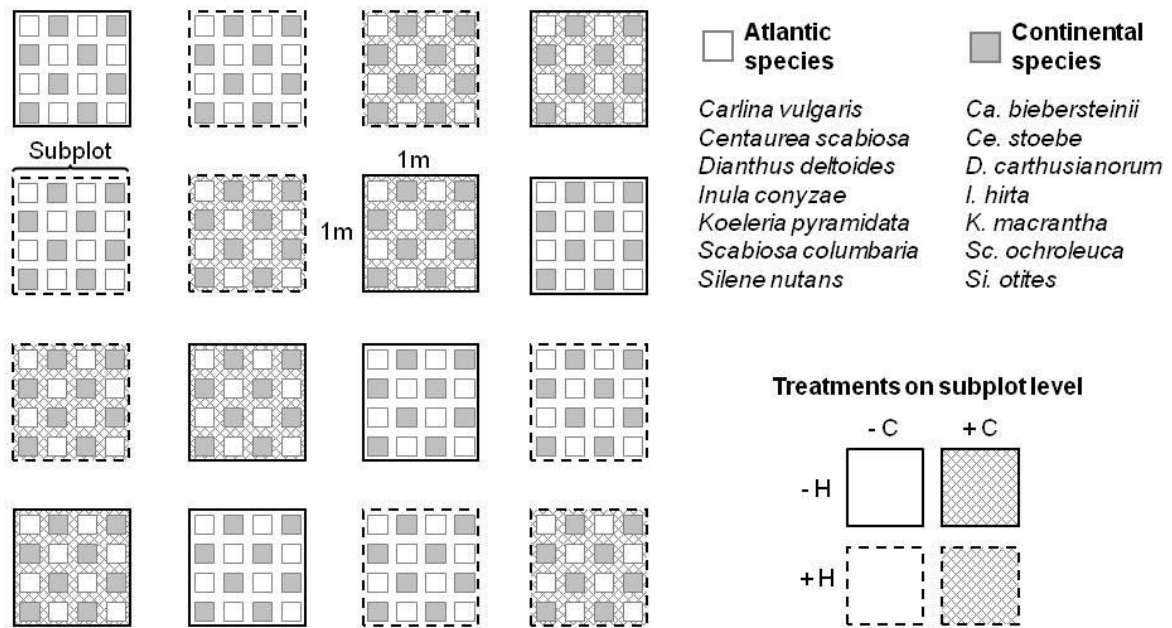


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Table S1 Species characteristics (Jäger & Werner 2005) and coordinates of the localities where seeds were collected. Growth form: eg=evergreen, sg=summergreen, hc= hemicryptophyte, p= perennial.

Genus	Species	Range-type	Growth form	Habitat (in Germany)	Seed origin	
					Latitude	Longitude
<i>Carlina</i>	<i>vulgaris</i>	Oceanic	eg, semi-rosulate, hc, hapaxanth	silicate and semidry grasslands, montane - subalpine meadows, cleared forests	51.547828° N	11.946354° E
	<i>biebersteinii</i>	Continental	eg, semi-rosulate, hc, hapaxanth	silicate and semidry grasslands, dry – moderately dry ruderal area, cleared forests and forest edges	48.805876° N	16.646231° E
<i>Centaurea</i>	<i>scabiosa</i>	Oceanic	sg, semi-rosulate, hc, p	calcareous dry and semidry grasslands, dry meadows and shrubland	51.528795° N	11.889641° E
	<i>stoebe</i>	Continental	eg, semi-rosulate, hc, biennial, hapaxanth	dry and sandy, partly ruderal xerothermic grasslands	51.503299° N	11.945023° E
<i>Dianthus</i>	<i>deltoides</i>	Oceanic	semi-eg, semi-rosulate, p	xerothermic grasslands, dry slopes and edges of forests	52.510644° N	11.180309° E
	<i>carthusianorum</i>	Continental	eg, no rosulate, chamaephyt/hc, p	dry and sandy grasslands, rare in arid environments	51.533204° N	11.981404° E
<i>Inula</i>	<i>conyzae</i>	Oceanic	eg, semi rosulate, biennial, hapaxanth/short-lived	semidry grasslands, dry shrubland, forests and their edges	50.963212° N	11.596487° E
	<i>hirta</i>	Continental	sg, no rosulate, hc, p	xerothermic grasslands, dry slopes and borders of forests	51.534788° N	11.902825° E
<i>Koeleria</i>	<i>pyramidata</i>	Oceanic	sg, hc, p	dry and semidry grasslands, dry ruderal areas, cleared pine-forests	51.592711° N	9.949324° E
	<i>macrantha</i>	Continental	sg, hc/ geophyt, p	dry and semidry grasslands, dry ruderal areas, dry meadows, cleared pine-forests	51.532948° N	11.914366° E
<i>Scabiosa</i>	<i>columbaria</i>	Oceanic	eg, semi-rosulate, hc, short-lived, p	calcareous dry and semidry grasslands, meadows and shrubland	51.592711° N	9.949324° E
	<i>ochroleuca</i>	Continental	eg, semi-rosulate, hc, p	continental, dry and semidry grasslands	51.533204° N	11.981404° E
<i>Silene</i>	<i>nutans</i>	Oceanic	sg, semi-rosulate, hc, p	silicate dry grasslands, dry shrubland, dry forests and their edges	51.592302° N	9.948576° E
	<i>otites</i>	Continental	eg, semi-rosulate, hc, short-lived, p	calcareous, silicate and sandy dry grasslands, dry pine-forests	51.527867° N	11.890091° E

Jäger EJ, Werner K, editors (2005) Werner Rothmaler: Exkursionsflora von Deutschland. 10. edition. München: Elsevier (Spektrum)

Chapter 3

The responses of grassland plants to experimentally simulated climate change depend on land use and region

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The responses of grassland plants to experimentally simulated climate change depend on land use and region

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Abstract

Macroclimatic niche properties derived from species distribution ranges are fundamental for projections of climate change impacts on biodiversity. However, it has been recognized that changes in regional or local distribution patterns also depend on interactions with land use. The reliability and transferability of large scale geographic predictions to small scale plant performance need to be tested experimentally. Thus, we asked how grassland plant species pairs with different macroclimatic niche properties respond to increased spring temperature and decrease summer precipitation in three different land-use types. An experiment was carried out in the framework of the German Biodiversity Exploratories simulating climate change in 45 experimental plots in three geographical regions (Schorfheide-Chorin, Hainich-Dün, Schwäbische Alb) and three grassland management types (meadow, pasture, mown pasture). We planted six plant species as phytometers, each two of them representing congeneric species with contrasting macroclimatic niches and recorded plant survival and growth over 1 year. To quantify the species macroclimatic niches with respect to drought tolerance, the species' distribution ranges were mapped and combined with global climate data. The simulated climate change had a general negative effect on plant survival and plant growth, irrespective of the macroclimatic niche characteristics of the species. Against expectation, species with ranges extending into drier regions did not generally perform better under drier conditions. Growth performance and survival was best in mown pastures, representing a quite intensive type of land use in all study regions. Species with higher macroclimatic drought tolerance were generally characterized by lower growth rates and higher survival rates in land-use types with regular mowing regimes, probably because of reduced competition in the growing season. In conclusion, plant species with similar climatic niche characteristics cannot be expected to respond consistently over different regions owing to complex interactions of climate change with land use practices.

Keywords: Biodiversity Exploratories, climate change, field experiment, grassland management, plant distribution

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Introduction

The ongoing global climatic change might force many plant species to shift their geographical distribution ranges (Parmesan & Yohe, 2003; Walther *et al.*, 2005; Thuiller, 2007; Loarie *et al.*, 2009; Walther, 2010). Species distribution models (SDM) that predict future range shifts or species extinctions under climate change scenarios are built on the assumption that climate is the main driver of species distribution (Huntley *et al.*, 1995; Guisan & Zimmermann, 2000; Thomas *et al.*, 2004; Thuiller *et al.*, 2005; Hijmans & Graham, 2006; McKenney *et al.*, 2007). The reliability of such models has been repeatedly challenged (e.g. Dormann, 2007) and the

necessity to integrate interactions between global change factors has been stressed (Pereira *et al.*, 2010).

Since species responses to climatic changes are ultimately dependent on the fitness and performance of populations at much smaller spatial scales, the transferability of SDM predictions to local scales can be expected to be much more reliable when land-use variables are taken into account (Tubiello *et al.*, 2007; de Chazal & Rounsevell, 2009). Reliability is not only an issue in SDMs but also on models based on SDMs such as stacked SDMs, used to predict species richness in climate change scenarios. For instance, Pompe *et al.* (2008) could highly improve purely bioclimatic models of species richness in Germany by including land-use variables. Commonly, such models work with coarse land-use categories such as forest, grassland, agricultural land or urban area. However, these categories themselves comprise highly variable types of land use.

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Especially in grasslands, certain management practices can lead to significant differences in floristic and functional structure (Römermann *et al.*, 2009), since species have different tolerances to cutting, grazing and trampling (Briemle *et al.*, 2002; Stammel *et al.*, 2003; Scheidel & Bruelheide, 2004; Moog *et al.*, 2009). If such tolerances are linked to a species' macroclimatic niche characteristics, purely climatic SDMs will only be valid in certain land-use types. Different management regimes facilitate certain species with certain traits and affect species. For example, Kühner & Kleyer (2008) described a positive relationship of highly fertilized and frequently disturbed grassland habitats with species characterized by high specific leaf area and canopy height. Thus, species' local responses to climate change cannot be inferred from macroclimatic SDM alone but requires taking land use into account. As land-use patterns generally have a much finer grain than macroclimatic patterns, the problem arises that consistent information on both factors is not available at the same spatial scale. Actually, this difference in scale is the reason why macroecological approaches have rarely addressed land use so far. One obvious approach to bridge the different scales is experimental testing at the plot scale. Since such empirical studies are lacking so far we asked if and how different grassland management practices, like mowing, cutting or a combination of both, in interaction with regional climate change will affect plant species that differ in their macroclimatic niches.

Following regional climate changes predictions for Europe (Spekat *et al.*, 2006; Christensen & Christensen, 2007), two variables can be expected to have a paramount impact on the primary producers. One is the increase in spring temperatures, resulting in prolonged vegetation periods, which is an already observed phenomenon (Menzel *et al.*, 2006; IPCC, 2007). The other is a decline in summer precipitation involving more severe and prolonged drought periods (Christensen & Christensen, 2007; Knapp *et al.*, 2008). These two aspects of climate change have already been addressed in manipulative field experiments in grasslands. For example, earlier spring will result in earlier snow melt, which has been shown to reduce aboveground biomass of three common dwarf shrub species in a snow removal experiment in the Swiss Alps (Wipf *et al.*, 2009). Rain shelter (RS) experiments have shown that drought affects important ecosystem processes, such as productivity (Kahmen *et al.*, 2005; Engel *et al.*, 2009; Heisler-White *et al.*, 2009; Miranda *et al.*, 2009) and nutrient cycling (Sardans *et al.*, 2006).

So far most climate change experiments have only been carried out at single locations. Given the naturally limited number of treatment combinations between climate and land use, such single-site experiments will

not provide insight how land use will affect plant responses in different climates. One exception is a 7 years experimental warming project in shrublands along a north–south gradient in Europe (Peñuelas *et al.*, 2007) which found that the magnitude of responses depended greatly on the climatic differences between the six sites. Similarly, Heisler-White *et al.* (2009) detected differences in aboveground net primary productivity changes as response to altered precipitation events between three different grassland types in the Central Plains Region of North America. In contrast, in the International Tundra Experiment Walker *et al.* (2006) encountered similar responses of the plant community to increased temperatures between 11 experimental sites. The experiences from these experiments point out the value of manipulating climate simultaneously at different locations, but also show that the interaction with land use has to be addressed.

Experimental analyses of effects that are confined to the extant community have the disadvantage that comparisons with nonresident species, which have the potential to take over the role of the current residents in the future, are precluded. In field studies, such questions can only be addressed with phytometer approaches. Phytometers (*sensu* Gibson, 2002) can be chosen in a way to anticipate the putative effects of global change, i.e. by comparing species with macroclimate niches that either better match the ambient or the manipulated climate regime. Using phytometers in replicated global change experiments distributed along climatic gradients also allows for evaluating site effects in a space-for-time approach.

Herein we make use of such a space-for-time approach, by carrying out highly replicated climate change experiments, covering three regions in Germany that differ in climate and three different types of land use in each region. Planting seedlings of species with contrasting distribution ranges and analysing their macroclimatic niches, we carried out a climate change experiment with increased spring temperatures and reduced summer precipitation in a total of 45 field greenhouses.

With this setup we tested the following hypotheses: (H1) The effects of simulated warming and drought on plant performance are similar to the effects of regional climatic differences among the study regions. More specifically, we tested whether or not the climatic differences between study regions result in effects are comparable to the climate change manipulations within each study region. (H2) The effects of climate change on plant performance are influenced by grassland land-use types. In particular, we tested whether climate change effects are mitigated or intensified in certain land-use types. Finally (H3) differences in the species'

performance in the experiment can be predicted from their macroclimatic niches, at least after having accounted for effects of region and land use. Testing this hypothesis is particularly important for global change research as it asks for the reliability and transferability of large scale geographic predictions to small scale plant performance.

Methods

Studied species and distribution data

Three pairs of species of contrasting distribution range were included in the study, each consisting of congeneric species,

one with a more oceanical and one with a more continental range (Table 1). All six species are native to European grasslands. Regarding habit and growth form, they are supposed to be intermediate in their grazing and mowing tolerance (Briemle *et al.*, 2002). In addition, the species pairs can be regarded to represent largely identical plant functional types (Box, 1996; Díaz & Cabido, 1997). The distribution data of the species were obtained from published range maps (Meusel *et al.*, 1965; Hultén & Fries, 1986; Meusel & Jäger, 1992) and updated with national and regional floristic data and internet databases. Climatic variables (mean temperature in April, precipitation in July) were extracted from the WORDCLIM dataset (Hijmans *et al.*, 2005) in a 2.5 arc minutes grid for the distribution ranges of all six species. As a proxy for macroclimatic summer drought tolerance we calculated the first

Table 1 Characteristics of the study species and description of the collection localities

Genus	Species	Minimum precipitation in July (mm)	Maximum aridity (growing season)	Maximum temperature in April (°C)	Growth form	Habitat type (in Central Germany)	Locality of collected seeds	
							Latitude	Longitude
<i>Achillea</i>	<i>millefolium</i>	7	0.25	16.9	Sg semirosulate, pl-polycarpic	Calcareous dry and semidry grasslands, dry meadows and shrubland	52.510644°N	11.180309°E
	<i>pannonica</i>	22	1.16	12.4	Eg semirosulate, pl-monocarpic	Dry and sandy, partly ruderal or rocky xerothermic grasslands	51.527867°N	11.890091°E
<i>Centaurea</i>	<i>scabiosa</i>	39	1.19	11.4	Sg semirosulate, pl-polycarpic	Calcareous dry and semidry grasslands, dry meadows and shrubland	51.528795°N	11.889641°E
	<i>stoebe</i>	35	1.56	11.6	Eg semirosulate, pl-monocarpic	Dry and sandy, partly ruderal or rocky xerothermic grasslands	51.528795°N	11.889641°E
<i>Dianthus</i>	<i>deltoides</i>	33	2.02	11.6	Eg erosulate, pl-polycarpic	Dry and sandy grasslands, rare in arid environment	52.510644°N	11.180309°E
	<i>carthusianorum</i>	50	3.42	10.7	Semi-eg semirosulate, pl-polycarpic	Xerothermic grasslands, dry slopes and borders of forests	51.534788°N	11.902825°E

Minimum precipitation in July, maximum aridity in the growing season, and mean temperature of April have been derived from a species macroclimatic niche analysis (see text). Growth form and habitat type are listed according Jäger & Werner (2005). Sg, summergreen; eg, evergreen; pl, plurennial.

Table 2 Overview about the geographical location and the climate of the three study regions

Study region	Latitude	Longitude	Altitude (m)	a.s.l.	Temperature in April (°C)			Summer precipitation (mm)		
					Mean	2009	Predicted	Mean	2008	Predicted
Schorfheide-Chorin	52°47'24.8"–53°13'26.0"N	13°23'27"–14°8'52.7"E	3–140		8.1	12.9	10.5	180	100	163
Hainich-Dün	50°56'14.5"–51°22'43.4"N	10°10'24.0"–10°46'45.0"E	285–550		7.1	11.5	9.8	215	136	175
Schwäbische Alb	48°20'60.0"–48°32'3.7"N	9°12'13.0"–9°34'48.9"E	460–860		6.8	10.2	9.4	290	316	270

Climate data are representative mean values for each region, derived from the WorldClim dataset (means between 1930 and 1990, Hijmans *et al.*, 2005; <http://www.worldclim.org>). Values for summer precipitation (June–August) in 2008 and mean temperature in April in 2009 were provided by local climate stations (Angermünde, Mühlhausen-Görmar, Münsingen-Apfelstetten). Predicted values refer to the period 2021–2050 according to the SRES-A1b climate change scenario from the CIAT database (Ramirez & Jarvis, 2008; <http://gisweb.ciat.cgiar.org/GCMPPage>).

percentile of July precipitation encountered throughout the distribution range. Alternatively, we estimated values for maximum drought in the growing season (mean monthly temperature >5 °C), by calculating monthly values of aridity (Trabucco & Zomer, 2009) to quantify precipitation availability over atmospheric water demand. Niche values for warm spring temperatures were calculated as the 99th percentile of mean April temperature values throughout the range.

Experimental sites (Exploratories, land use)

The experiment was set up in the framework of the German Biodiversity Exploratories (see <http://www.biodiversity-exploratories.de>; Fischer *et al.*, 2010). In three distant study regions in Germany (Schorfheide-Chorin, Hainich-Dün, Schwäbische Alb, for details see Table 2 and Fischer *et al.*, 2010), 45 experimental plots were used for this study, comprising three different grassland land-use types (meadows, pastures, mown pastures). Schorfheide-Chorin is located in NE Germany, Hainich-Dün is close to Germany's geographical centre and the Schwäbische Alb is located in SW Germany. The difference in current summer precipitation and spring temperature between the three regions is about two times larger than the expected changes according to the A1F1 climate change scenario (Table 2). In all three regions, each of the three land-use types was replicated five times (except in Schwäbische Alb: six pastures and four mown pastures). Meadows were mown twice or three times per year, and in addition, received fertilizer. Mown pastures were grazed and mown once per year and additionally fertilized in Hainich-Dün and Schwäbische Alb. Pastures were only grazed and received no additional fertilization.

Climate change manipulation

Since current regional climate change predictions for Central Europe (Spekat *et al.*, 2006) assume an earlier start of the growing season, as an effect of increasing spring temperatures, and prolonged summer drought periods, we decided to

simulate these two particular aspects of climate change. Two subplots were established in each plot, one was manipulated by placing open top chambers (OTCs) in spring (April 2009) and RSs in summer (July 2008), increasing temperatures in spring and drought in summer, the other subplot was used as nonmanipulated control.

The OTCs measured 2 m × 3 m, had a height of 1.4 m and were made of a PVC tube construction with a 0.2 mm thick greenhouse plastic (UV 5 coex-foil made of ethylene vinyl acetate copolymers; folitec Agrarfolien-Vertriebs GmbH, Westerbürg, Germany) enclosing all four sides. The same tube construction was used for the RSs, removing the greenhouse plastic from the sides and using it as a top cover. Soil moisture and temperature (aboveground and at 10 cm soil depth) were measured every half an hour by moisture sensors (ECH2O, type EC-5; Decagon Devices, Inc., Pullman, WA, USA) and temperature sensors (Thermochron® iButton; Maxim Integrated Products, Inc., Sunnyvale, CA, USA) in three plots per exploratory region and recorded by a data logger (Em5b; Decagon Devices, Inc.). Differences between the control and climate change plots were tested for significance with pair wise *t*-tests.

Phytometers

Seeds of all species were collected in summer 2007 in Central Germany (for sampling locations, see Table 1) and seedlings were raised under controlled standardized conditions in a glasshouse in spring 2008. We refrained from accounting for putative intra-specific variation in species responses because evidence for different responses in provenance at this geographic scale has been found to be of minor importance (Weißhuhn *et al.*, 2011). Instead we aimed at using a single provenance of each species that was sampled from closely adjacent sites, thus avoiding the additional complexity of differences in local adaptations of target species. Accordingly, the seeds were sampled in climatically very similar lowland sites in Saxony-Anhalt, covering two adjacent soil-climate-regions (Roßberg *et al.*, 2007). The climate data from the two meteorological station closest to the respective sampling sites

(ca. 20 km) only differ by 7 mm in monthly precipitation (SD 5.42) and by 0.075 K in monthly mean temperature (SD 0.28).

In June 2008, the raised individuals had reached an age of 16 weeks and were planted in the plots (one individual per species in each subplot) and watered once to ensure initial establishment. At the time of planting, eight individuals of each plant species were harvested to obtain initial dry biomass data for calculating relative growth rates (RGR). Roots and shoots were separated and dried for 42 h at 70 °C. The same procedure was carried out for each planted individual at the end of the experiment in May 2009. Survival of each individual plant, RGR according to Hunt (1990) and shoot–root ratios were used for further statistical analyses.

Statistics

The data (survival, RGR of total biomass and shoot–root ratio) were analysed with generalized linear mixed effect models (GLMM). For survival, a logit-link function and binomial error distribution were used, while the GLMM for all other response variables had an identity-link function and Gaussian error distribution. The fixed factors were study region (Alb, Hainich, Schorfheide), climate change treatment (climate change, control) and land use (meadow, pasture, mown pasture). Minimum July precipitation, maximum monthly aridity in the growing season and maximum April temperature as obtained from the species' macroclimatic niche served as continuous covariable in separate models. Plot identity (nested within study region and land-use type) and genus entered the models as random factors. In a first step, linear mixed effect models were fitted that included the following interactions according to our hypotheses: study regions \times climate change manipulation (Hypothesis 1), land use \times study region and land use \times climate change manipulation (Hypothesis 2), and the interaction of the minimum July precipitation, maximum monthly aridity and the maximum April temperature as derived from the macroclimatic niche analysis with climate change, study region and land use (Hypothesis 3). In a second step, each model was optimized by removing insignificant interactions. Optimization was based on maximum-likelihood parameter estimation and continued until the lowest Akaike Information Criterion value was reached or when only the

main effects remained in the model (Zuur *et al.*, 2009). The probabilities and estimates of the final models were then calculated using restricted maximum likelihood estimation, as recommended by Zuur *et al.* (2009). All statistical analyses were computed in SAS 9.1 (proc glimmix; SAS Institute Inc., 2002, Cary, NC, USA). Graphs were produced with R 2.10.1 (R Development Core Team 2009, Vienna, Austria), using the least square estimates and standard errors from proc glimmix.

Results

Climate change manipulation

The OTCs in spring 2009 increased soil and air temperature between 0.2 and 0.69 K (Table 3). Soil moisture was merely affected (Hainich-Dün and Schorfheide-Chorin) or even slightly increased on the climate change plots (Schwäbische Alb).

The treatment effect of the RSs in summer 2008 was much more pronounced and also resulted in larger differences between the study regions (Table 3). Soil moisture reduction on the climate change plots ranged between 14.1 and 3.7 percentage points in water content (i.e. percentage soil water content in the control minus percentage soil water content in the climate change treatment) in the Schwäbische Alb and Hainich-Dün, respectively. In the Schwäbische Alb, the RSs also increased soil and air temperature at a higher level than the OTC's in spring 2009 (Table 3).

Plant responses

Table 4 shows all effects of the optimized models for survival, RGR of total biomass and shoot–root ratio, using region, climate change treatment, land use and the first percentile of July precipitation in the species' distribution range as predictors. In general, the models based on maximum monthly aridity instead of summer drought (mean first percentile of July precipitation)

Table 3 Mean differences between plots with simulated climate change and control plots

Manipulation	Study region	Temperature (in K)		Moisture (in Δ vol.%)
		Air (10 cm height)	Soil (10 cm depth)	Soil (10 cm depth)
Increased spring temperature (OTC)	Alb	0.69 \pm 0.06***	0.45 \pm 0.02***	1.7 \pm 0.6*
	Hainich	0.39 \pm 0.01***	0.30 \pm 0.01***	0.8 \pm 0.5
	Schorfheide	0.36 \pm 0.01***	0.20 \pm 0.01***	–0.2 \pm 0.8
Summer drought (RS)	Alb	1.15 \pm 0.06***	0.84 \pm 0.04***	–14.1 \pm 1.5***
	Hainich	0.32 \pm 0.06***	–0.03 \pm 0.01	–3.7 \pm 0.5**
	Schorfheide	0.53 \pm 0.06***	0.08 \pm 0.01*	–6.3 \pm 2.9*

Moisture refers to the difference in per cent soil water content between the climate change and the control treatment. Significant differences are indicated as follows: *** P < 0.001, ** P \leq 0.01, * P \leq 0.05.

OTC, open top chamber; RS, rain shelter.

Table 4 Results of the generalized mixed models for survival (with logit-link function and binomial error distribution) as well as relative growth rate (RGR) of total biomass ($\text{g g}^{-1} \text{ week}^{-1}$) and shoot–root ratio (g g^{-1}) (with identity-link function and Gaussian error distribution), based on REML parameter estimation

Source of variation	df	RGR total Shoot– biomass root ratio		
		Survival F-value	F-value	F-value
Region	2	15.10***	1.95	0.30
Climate change	1	25.52***	4.71*	0.46
Region \times climate change	2	11.30***	0.92	–
Land use	2	3.35*	3.97*	0.91
Region \times land use	4	2.57†	1.23	–
Climate change \times land use	2	–	3.62*	–
Region \times climate change \times land use	3	–	2.71*	–
JulyPrec	1	3.39†	34.07***	18.33***
Region \times JulyPrec	1	–	–	–
Climate change \times JulyPrec	1	–	–	–
Land use \times JulyPrec	1	4.06*	–	–

Plot (nested in study region and land-use type) and genus were considered random factors in the models. Significant effects are indicated as follows: *** $P < 0.001$, * $P \leq 0.05$, † $P \leq 0.1$.

JulyPrec, first percentile of July precipitation in the species' distribution range; REML, restricted maximum likelihood.

gave nearly identical results (minor differences in a few significance values), as both variables were strongly correlated ($r = 0.864$, $P = 0.026$). The inclusion of spring warmth (mean maximum April temperature) revealed even smaller differences in the model results since the

correlation with July drought ($r = -0.915$, $P = 0.011$) is even higher.

Thus, in Table 4 and in the following discussion only the results based on tolerated macroclimatic summer drought (minimum July precipitation) as macroclimatic niche property are given.

Survival

The survival of the plants differed strongly between study region and climate change treatment (Table 4). Survival in the Alb with a mean survival rate of 81.9% was about two times larger than in the Schorfheide (38.9%) and four times larger than in the Hainich (18.8%; Fig. 1a). The climate change treatment had an overall negative impact on survival compared to the control, reducing survival rates to more than half (Fig. 1b). However, the effect differed between study regions, indicated by a significant interaction of study region with climate change (Table 4). At the coldest and wettest site (Alb), survival rates were highest and did not differ between climate change treatments, whereas summer drought and spring warming had negative effects at the other sites, in particular in the Hainich, where only a few individuals survived in the climate change treatment (Fig. 1c).

Survival also differed between land-use types (Table 4). Most individuals survived in mown pastures (53.5%) compared to uniform land use in pure pastures (42.6%) or meadows (43.8%). In contrast, summer drought resistance, measured as the first percentile of July precipitation in the geographical distribution range, had only marginal effects on the species' survival rate, but showed significant interactions with land use (Table 4). Species that had niches extending into drier areas survived better in land-use types with a regular mowing regime, i.e. in meadows and mown

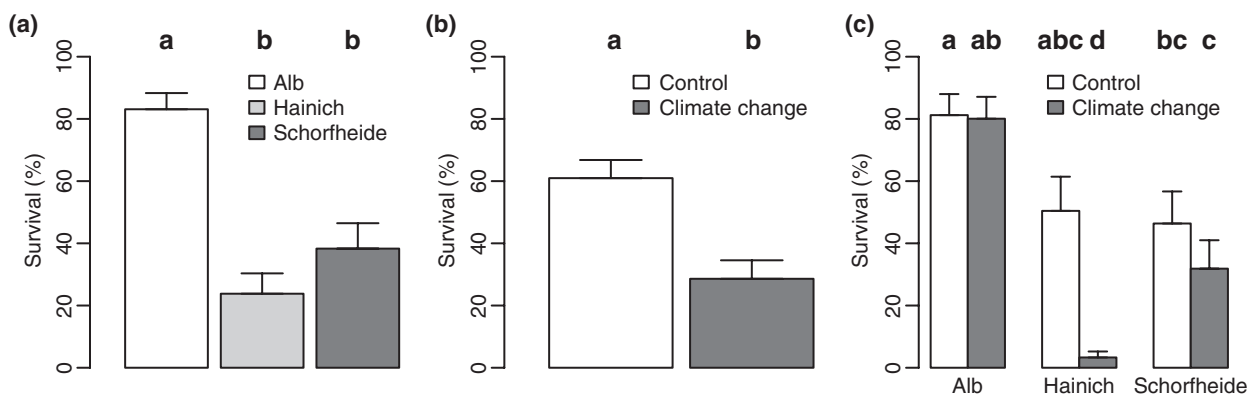


Fig. 1 Survival rates (\pm SE) of the transplanted species (a) in the three different study regions, (b) under simulated climate change and in the control plots and (c) under simulated climate change and in the control plots, separately by regions. Small letters indicate significant differences according to the Tukey *post hoc* test. For statistical details, see Table 4.

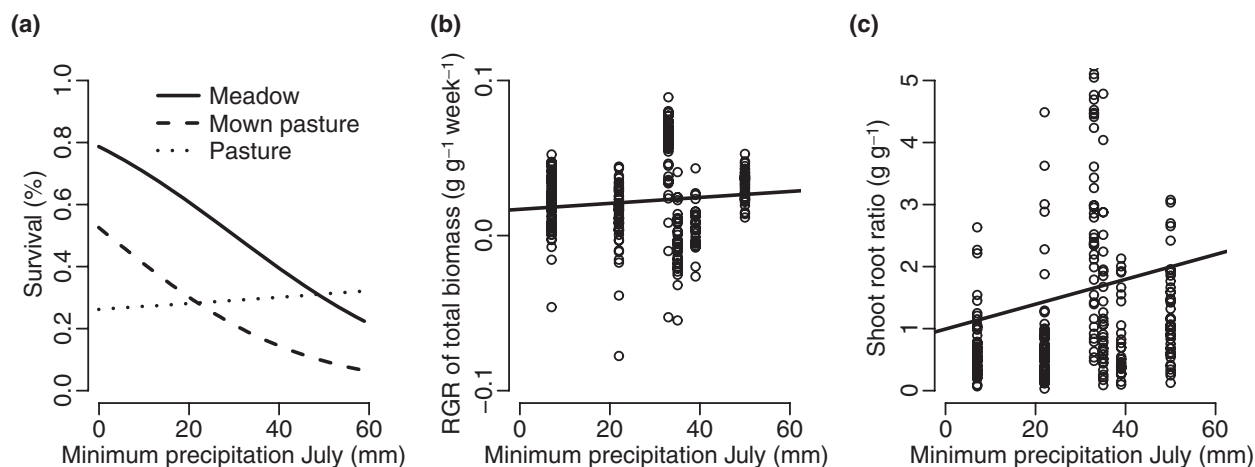


Fig. 2 Effect of the species' macroclimatic drought tolerance, expressed as the first percentile of July precipitation in the species' geographical distribution, on (a) plant survival rates in the three different land-use types, as estimated by the generalized linear mixed model with logit-link function, (b) relative growth rates (RGR) of total biomass and (c) shoot-root ratio of the phytometer species, showing raw data and regression lines as estimated by the generalized linear mixed model with identity-link function. For statistical details, see Table 4.

pastures (Fig. 2a). In contrast, macroclimatic summer drought tolerance seemed not to play any role for survival in pastures (Fig. 2a).

Growth performance

Study region was not decisive for growth performance of the plants (Table 4). Similar to the results for survival, the climate change manipulation was detrimental and reduced RGR of total biomass to about 21.1% compared to the control. Furthermore, type of land use resulted in differences in RGR of total biomass (Table 4). The RGR of total biomass of the survived plants was significantly higher in mown pastures (mean \pm SE, 0.0298 ± 0.0031 g g⁻¹ week⁻¹) compared to pastures (0.0201 ± 0.0025 g g⁻¹ week⁻¹) and meadows (0.0171 ± 0.0029 g g⁻¹ week⁻¹). In addition, the effect of the climate change manipulation on RGR of total biomass differed between land-use types (Table 4; Fig. 3a). The relative reduction in growth caused by the climate change manipulation was lowest in mown pastures (-9.2%) compared to pastures (-34.4%) and meadows (-26.9%). However, the amount of growth reduction caused by simulated climate change was different in the three study regions with respect to land-use types (Table 4). In the Alb, the largest growth reduction was recorded for meadows (Fig. 3b). In contrast, in the Hainich and the Schorfheide, growth reduction caused by the climate change manipulation was highest in pastures (Fig. 3c and d).

Among all response variables, the species' macroclimatic drought tolerance, derived from minimum July precipitation in the species distribution range, was

found to have the largest general effect on RGR (Table 4). The RGR of total biomass decreased with increasing macroclimatic drought tolerance (Fig. 2b). This relationship between growth performance of species and macroclimatic drought tolerance did not differ between study regions, land-use types or climate change treatments, as seen in the absence of significant interactions in Table 4. For example plant growth responses to experimental climate change simulation were quite species specific (Fig. S1).

Allocation pattern

Shoot-root ratios did not differ between study regions, land-use types or climate change treatments (Table 4). The species differed solely in shoot-root ratio in relation to macroclimatic drought tolerance measured as minimum July precipitation encountered in their distribution range (Table 4). Species with a higher macroclimatic drought tolerance showed smaller shoot-root ratios than species that were macro-climatically less drought tolerant (Fig. 2c). As for RGR of total biomass, there were no significant interactions with regions, land-use types or the climate change treatments (Table 4).

Discussion

The survival of phytometer plants was affected by both the climatic differences between the three exploratory regions and the climate change treatment effects. As assumed in the first hypothesis, both treatments had similar effects on the plants, as survival rates decreased

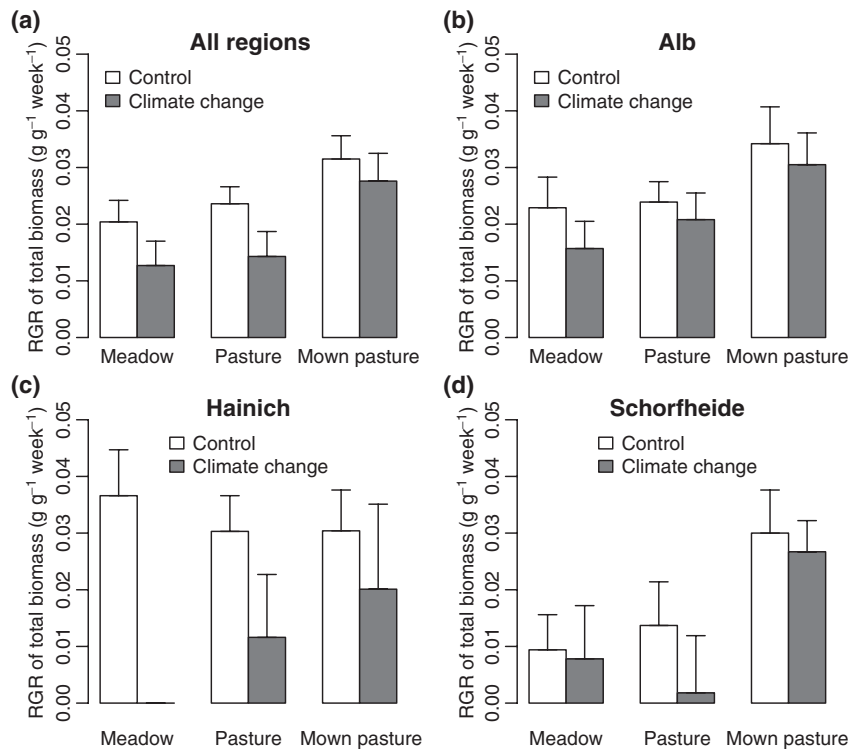


Fig. 3 Relative growth rates of total biomass (\pm SE) as a function of land use and climate change treatment for (a) all regions, (b) Schwäbische Alb, (c) Hainich-Dün, and (d) Schorfheide-Chorin. For statistical details, see Table 4.

with increasing mean annual temperature and decreasing precipitation in the three study regions (control plots) as well as under manipulated climate change resulting in summer drought. Hence, this is a justification for space-for-time approaches, complementing manipulative climate change experiments. However, as hypothesized we detected regional differences in effect sizes of the climate change treatments. While the climate change treatment had no effect on survival at the wettest site (Schwäbische Alb), there was a significant reduction at the other two sites. As all planted species naturally occur in mesic to semidry grasslands (Jäger & Werner, 2005), the consistently higher mortality cannot be attributed to the species' particular sensitivity. On the contrary, from the results we can conclude that increasing summer drought in regions with low precipitation might present a risk also to populations of rather drought tolerant plant species. Although the effects of manipulated climate change on the abiotic environment (soil moisture and temperature) were greatest in the Schwäbische Alb, it can be assumed that the general moister conditions have buffered the impact of the experimental drought.

Overall, these results point out the necessity to consider regional variation of climate change effects below the spatial scale of biomes, for which already strongly

different responses have been reported (Parmesan, 2006; IPCC, 2007). Ecoregion- or even landscape-specific response patterns have also been reported by Heisler-White *et al.* (2009) from three different grassland sites in the Central Plains Region of North America. The authors showed that changes in aboveground net primary productivity as response to simulated extreme rainfall regimes differed between study sites according to differences in the sites' mean annual precipitation. Our findings also explain contrasting findings in monitoring studies on climate change effects. For example, while Vittoz *et al.* (2009) found comparably low impacts of climate change on subalpine grasslands in the Swiss Northern Alps, Pauli *et al.* (2007) showed rapid range shifts of plant species in Tyrol in Austria. According to our results, changes in species survival, and thus in occurrence, can be expected to be more rapid and to occur to a greater extent even in climatically slightly stressful regions. As we have shown, this does not only apply to extreme biomes such as alpine or desert habitats (Brown *et al.*, 1997; IPCC, 2007; Pauli *et al.*, 2007; Kelly & Goulden, 2008), but also to regional differences within mesophilous grasslands. However, the overall survival rate was not lowest at the driest site, which shows that there is some variation not accounted for by region alone, such as for example variation in soil

properties or differences in land-use intensity within regions.

The planted phytometers showed also differences in survival and growth rates between land-use types. As hypothesized, we encountered interactive effects of land-use management with manipulated climate change. Across all regions plants grew better in mown pastures and additionally, in this land-use type the negative effect of simulated climate change was lower than in grasslands that were uniformly managed as meadows or pastures.

Among all studied land-use types mown pastures receive the highest management intensity as they were mown, grazed and additionally fertilized. Fertilization might have partly compensated for the negative climate change effects. In a warming experiment Sardans *et al.* (2008) have shown that warming by 1 °C decreased N leaf concentrations of shrub species by 25%. The underlying causes were not altered allocation patterns but probably changes in soil N availability. Consequently, the comparably high N supply in mown pastures might mitigate climate warming effects. Although the meadows in the three study regions received even higher levels of fertilizers than the mown pastures, they might have provided less favourable conditions for the phytometers due to stronger competition effects from a higher and denser stand structure. In contrast, disturbance in pastures was higher and biomass removal was more selective than in mown pastures. Higher disturbances can not only lead directly to plant mortality but overgrazed microsites are also more susceptible to drought (Ryser, 1993). This might be particularly problematic in very intensively grazed sites with high stocking rates (Kemp & Michalk, 2007).

As both, grazing and mowing are combined in mown pastures, the discussed negative effects for herb species survival might have been less detrimental compared to plots with a uniform management. Probably the mitigating effect of mown pastures has been the combination of resource supply with lower competition intensity and lower physical disturbance. In consequence, if mown pastures provided a more balanced habitat for mesophilous grassland species, this land-use type might be generally more able to buffer climate change effects. In contrast, for pastures and meadows, local aspects might play a more important role in mitigating climate change impacts. Climate change effects were better buffered in meadows in the Schorfheide-Chorin and in pastures in the Schwäbische Alb. In conclusion, for conservation strategies concerning changing climatic conditions, potential land-use changes between grassland management types should be considered very carefully.

In contrast to our third hypothesis, the measured plant species responses along the environmental gradient of the exploratory regions and under simulated climate change were not clearly predictable from their macroclimatic niche properties. No evidences were found that species with a higher summer drought tolerance in their geographical range performed better under drier conditions and *vice versa*. Consequently, we have to conclude that species' local responses to changing climate cannot by default be derived from their macroclimatic niche characteristics but might be strongly affected by further drivers in a complex manner. Macroclimatic niche properties seemed to be related to some extent to general growth performance patterns. Species with a higher summer drought tolerance in their geographic range did not only show lower growth rates and lower shoot-root ratios but also performed better in land-use types with a regular mowing regime. Drought-adapted species have often been shown to allocate more resources to belowground biomass (Jackson *et al.*, 1996; Schulze *et al.*, 1996), especially in early developmental stages (Padilla *et al.*, 2007, 2009). In addition, being stress tolerators, these species also display lower growth rates, thus representing inferior competitors *sensu* Grime (1977). In grasslands with regular cuts, strong herbaceous competitors are less frequent. Consequently, drought tolerant species might take advantage of reduced competition, which in this study seem to be reflected in higher survival rates in meadows and mown pastures. In contrast, the more randomly occurring disturbances in form of trampling and grazing in pastures may have led to the observed overall average survival rates of both, geographically drought tolerant and drought sensitive species. In consequence, our results indicate that on smaller spatial and temporal scales, the competitive and probably compensative abilities of species might play a more important role for survival and growth under climate change than the macroclimatic niche properties of a plant species.

Conclusion

Macroclimatic niche properties were found to be related to general growth patterns, but were not sufficient to directly predict plant responses to global climate change. Depending on ecoregion, landscape, or even management practices, species might show strongly varying, yet partly contrary local responses. Consequentially, anticipatory conservation and management strategies require improved climate change predictions with stronger model regionalization and consideration of interactions with land use variables.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Effect of the climate change treatment to relative growth rates of total biomass. Am, *Achillea millefolium*; Ap, *Achillea pannonica*; Csc, *Centaurea scabiosa*; Cst, *Centaurea stoebe*; Dc, *Dianthus carthusianorum*; Dd, *Dianthus deltoides*. For species characteristic, see Table 1.

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Supporting Information Chapter 3

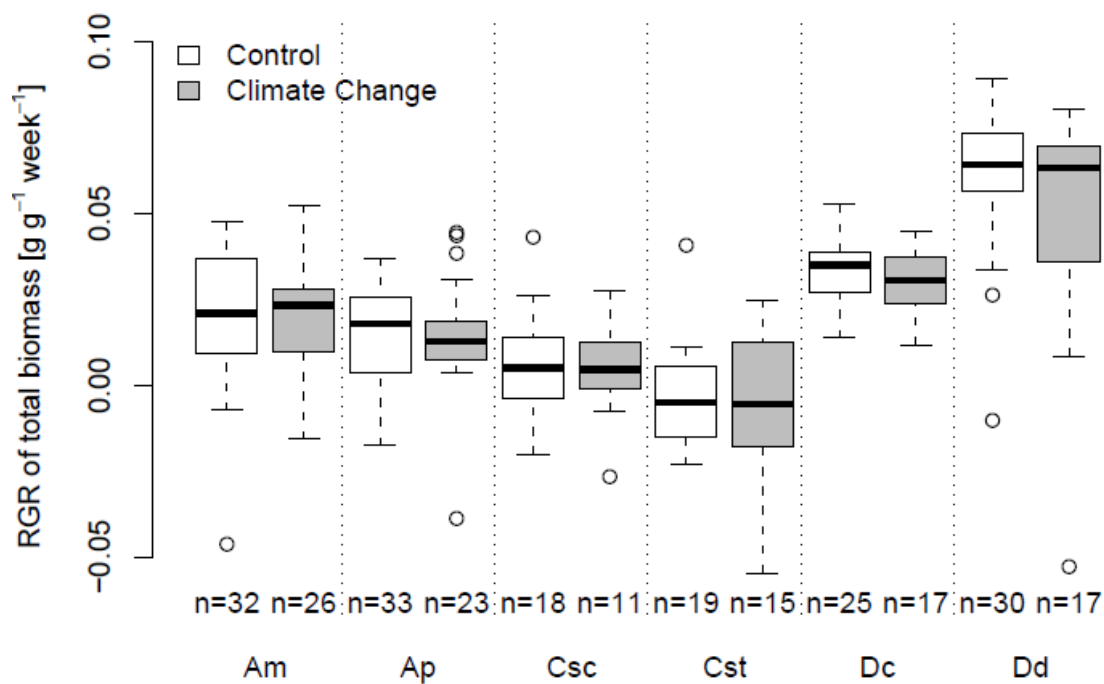


Figure S1 Effect of the climate change treatment to relative growth rates of total biomass. Am – *Achillea millefolium*, Ap – *A. pannonica*, Csc – *Centaurea scabiosa*, Cst – *C. stoebe*, Dc – *Dianthus carthusianorum*, Dd – *D. deltoides*. For species characteristic see Table 1.

Chapter 4

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

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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, Gavilán 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 m²),

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, Emmersthal, 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 deltooides*/*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: *** $P < 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$. 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

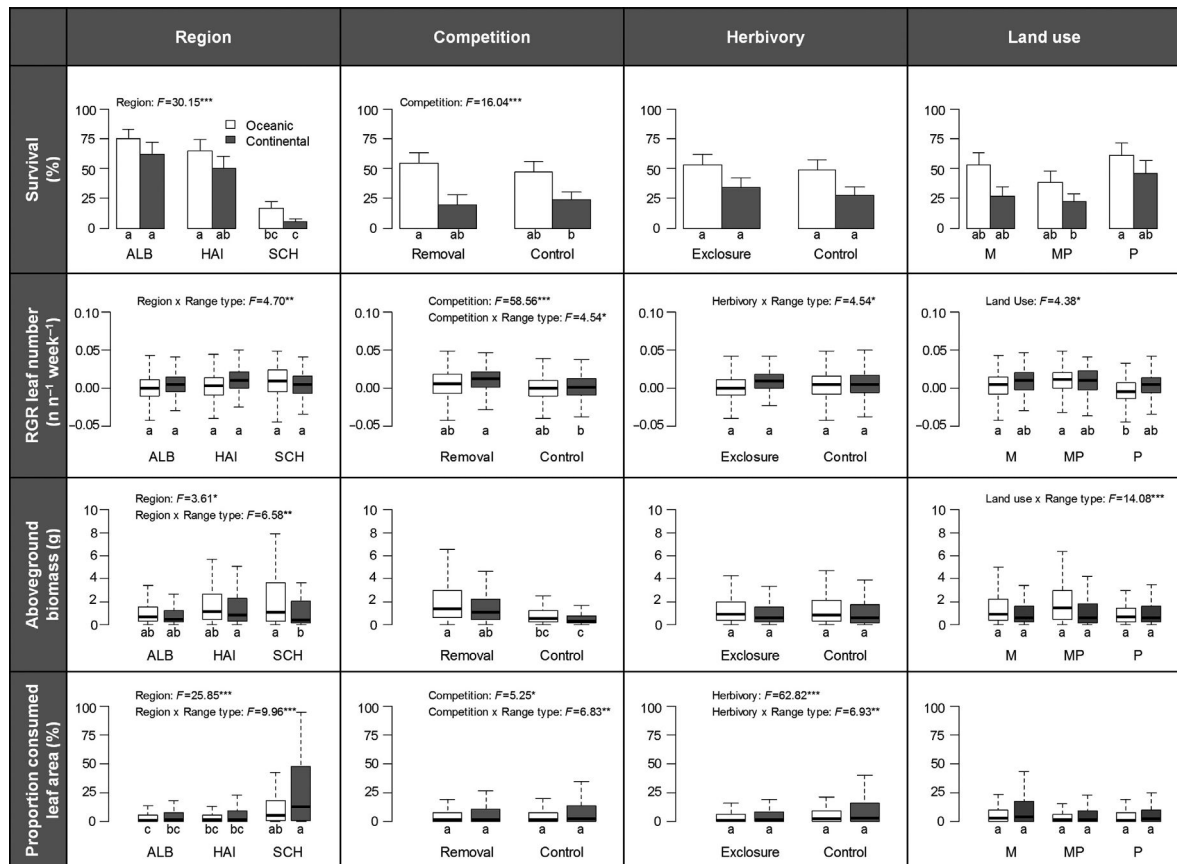


FIG. 1. Survival, RGR (relative growth rate) of leaf number, aboveground biomass, and proportion of consumed leaf area as a function of the interactive effects of range type with study region, range type with competition, range type with herbivory, and range type with land use. Data for oceanic and continental 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>

Supporting Information Chapter 4

APPENDIX S1: Plot design and treatments on subplot level.

Fig. S1 Map of the three study regions.

Fig. S2 Plot scheme.

Fig. S3 Competition removal.

Table S1 List of the most frequent plant species in the 45 plots.

Fig. S4 Mollusk exclosure.

Fig. S5 Mollusk abundance assessment.

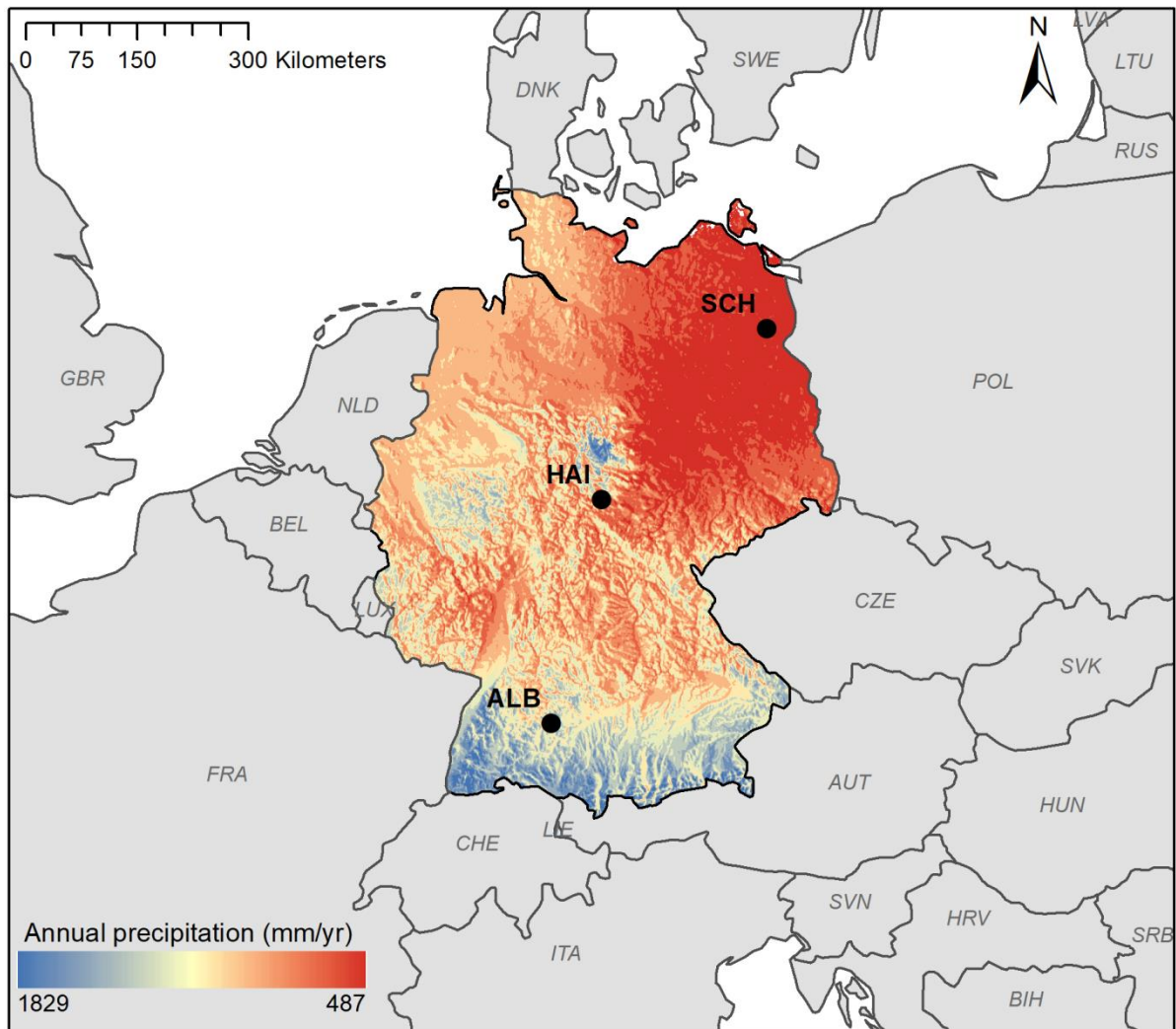


Fig. S1 **Map of the three study regions** located in Germany (Central Europe): Schorfheide-Chorin in Brandenburg (= SCH, north-east Germany) is the most continental study region, Hainich in Thuringia (= HAI, central Germany) takes an intermediate position and Schwäbische Alb in Baden-Württemberg (= ALB, south-west Germany) is the least continental study region (for details see Fischer et al. 2010). They are located along a climate gradient, which is here presented by the mean annual precipitation (high precipitation in blue, low precipitation in red). In each study region, 15 plots were established in grasslands of three different land-use types, each replicated five times per study region, resulting in a total of 45 plots.

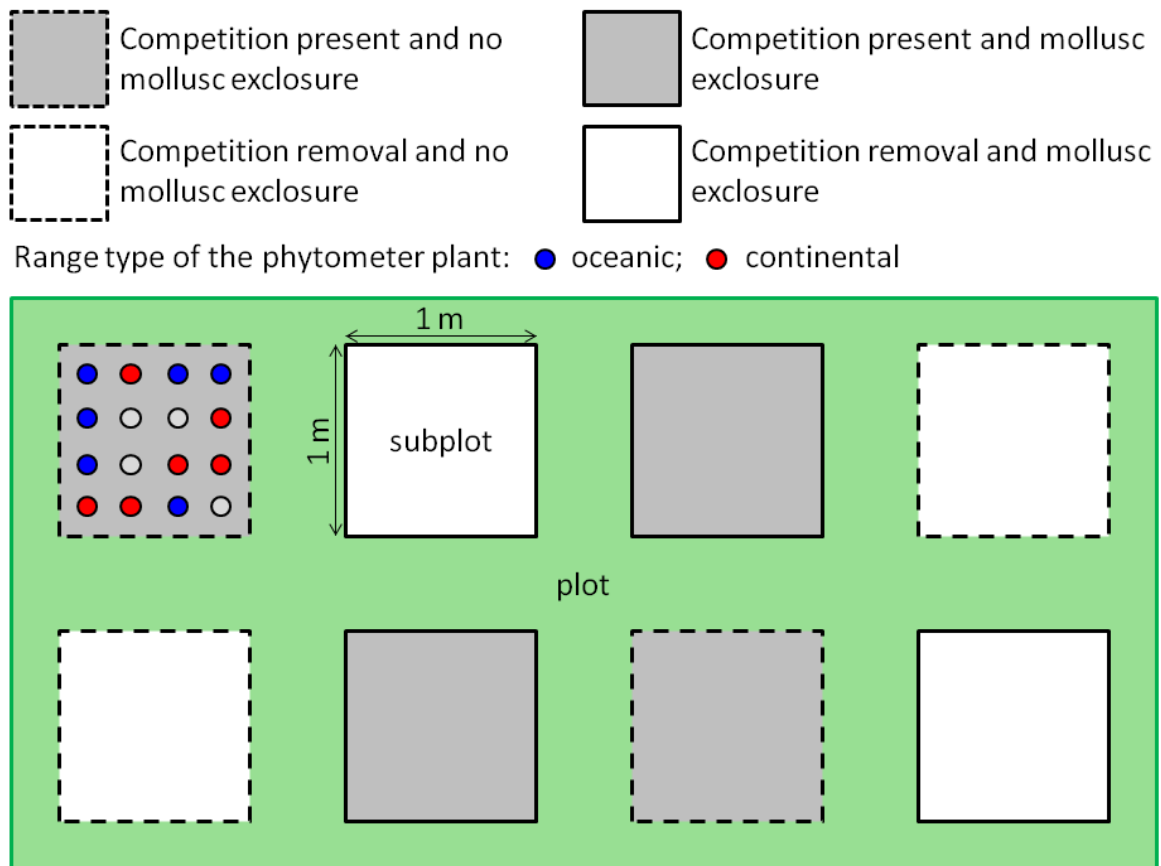


Fig. S2 Plot scheme. Each plot (signed in green) consists of eight subplots with four treatment combinations, each replicated two times, respectively. Subplots were sized one by one meter with half meter in between. Subplots with ambient competitors are signed in grey. Subplots, where competitors in a 10 cm radius of the phytometer were removed, are signed in white. Continuous lines of the subplot represent metal frames to exclude mollusk herbivores. Subplots without metal frames are bordered with dashed lines. The subplots are arranged in 16 planting positions. At maximum, one individual of each species was planted into the subplots, resulting in 12 phytometer plants per subplot.



Fig. S3 **Competition removal.** To manipulate competition intensity, we extracted a cylindrical soil core (diameter 10 cm, height 10 cm) at all planting positions in all subplots. Then we removed the aboveground biomass on the top of this cylindrical soil core and turned it upside-down before putting it back into the ground. Subsequently, one phytometer plant was planted into each soil core on the respective planting position.

Table S1 List of the most frequent plant species in the 45 plots.

Species Name	Frequency (Number of plots with occurrences)
<i>Trifolium repens</i>	35
<i>Poa trivialis</i>	34
<i>Poa pratensis</i>	33
<i>Cerastium holosteoides</i>	32
<i>Dactylis glomerata</i>	32
<i>Taraxacum</i> Sec. <i>Ruderalia</i>	28
<i>Lolium perenne</i>	24
<i>Plantago lanceolata</i>	24
<i>Elymus repens</i>	23
<i>Trifolium pratense</i>	23
<i>Festuca pratensis</i>	22
<i>Alopecurus pratensis</i>	21
<i>Heracleum sphondylium</i>	20
<i>Ranunculus repens</i>	20
<i>Veronica arvensis</i>	20
<i>Arrhenatherum elatius</i>	15
<i>Bromus hordeaceus</i>	15
<i>Galium mollugo</i>	15
<i>Anthriscus sylvestris</i>	14
<i>Plantago major</i>	14
<i>Ranunculus acris</i>	14
<i>Trisetum flavescens</i>	14
<i>Crepis biennis</i>	13
<i>Phleum pratense</i>	13
<i>Rumex acetosa</i>	13
<i>Achillea millefolium</i>	12
<i>Agrostis stolonifera</i>	12
<i>Cirsium arvense</i>	12
<i>Pimpinella saxifraga</i>	12
<i>Veronica chamaedrys</i>	12
<i>Ranunculus bulbosus</i>	11
<i>Rumex crispus</i>	11
<i>Taraxacum</i> species	11

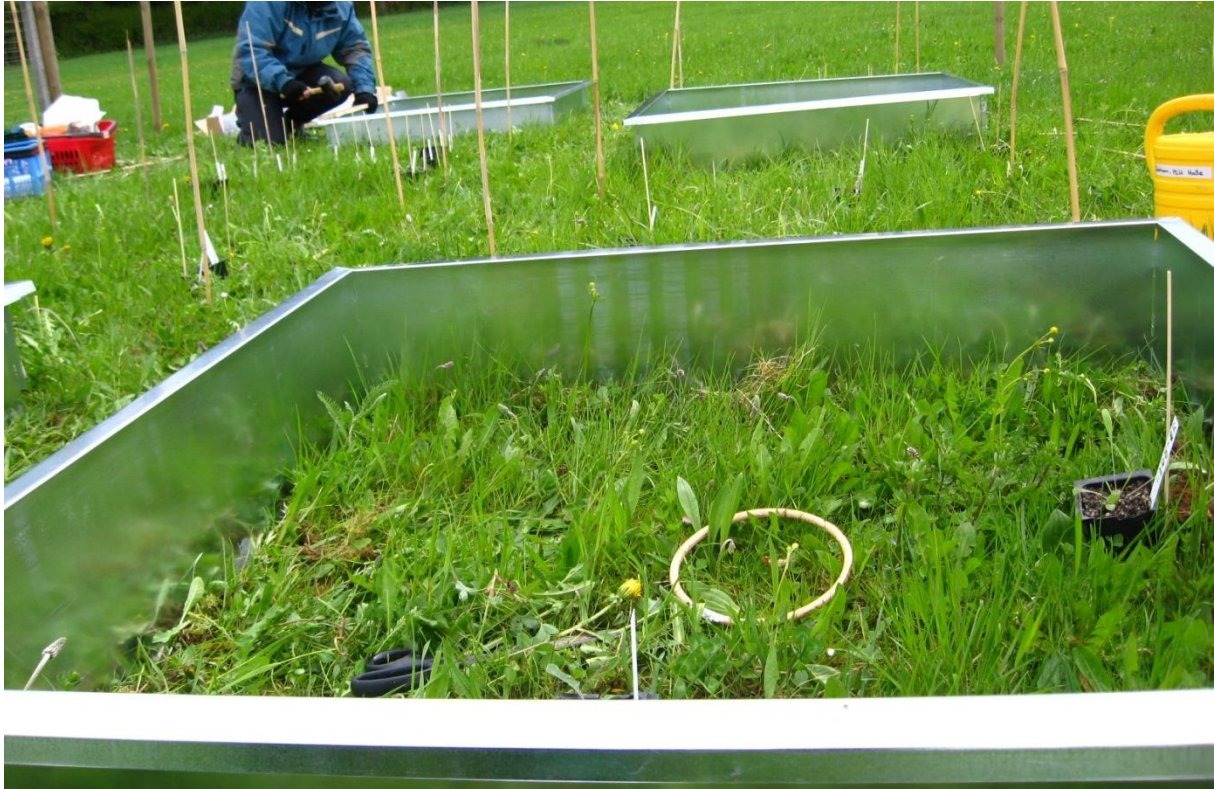


Fig. S4 Mollusk enclosure. To exclude mollusks, four subplots were fenced with metal frames (IRKA, Typ 1, R+M Gartenbedarf, Rehling, Germany). Additionally, mollusk repellent was applied at these plots (Ferramol, W. Neudorff GmbH KG, Emmerthal, Germany).



Mown Pasture in the ALB

Meadow in the ALB

Fig. S5 Mollusk abundance assessment. To assess herbivory pressure, we exposed two tiles sprinkled with coal powder for one night on each plot. In the centre of each tile, a petri dish with oats and beer was placed as lure. On the next day the number of mollusk trails were recorded.

APPENDIX S2: Phytometer plants.

Table S1	Species characteristics.
Fig. S1	Distribution maps of <i>Carlina biebersteinii</i> and <i>C. vulgaris</i> .
Fig. S2	Distribution maps of <i>Centaurea stoebe</i> and <i>C. scabiosa</i> .
Fig. S3	Distribution maps of <i>Dianthus carthusianorum</i> and <i>D. deltoides</i> .
Fig. S4	Distribution maps of <i>Koeleria macrantha</i> and <i>K. pyramidata</i> .
Fig. S5	Distribution maps of <i>Scabiosa ochroleuca</i> and <i>S. columbaria</i> .
Fig. S6	Distribution maps of <i>Silene otites</i> and <i>S. nutans</i> .
Table S2	Planting scheme for experimental plots.

Table S1 Species characteristics (Jäger 2017) and coordinates of the localities where seeds were collected. Abbreviations for growth form: eg=evergreen, sg=summergreen; hc= hemicryptophyte. Assignment to the oceanic and continental range type was done by the degree to which the species' distribution range extends into the oceanic climate regions of Europe.

Genus	Species	Range type	Growth form*	Habitat (in Germany)*	Seed origin	
					Latitude	Longitude
<i>Carlina</i>	<i>vulgaris</i>	Oceanic	Eg, semi-rosulate, hc, hapaxanth	Silicate and semidry grasslands, montane - subalpine meadows, cleared forests	51.547828° N	11.946354° E
	<i>biebersteinii</i>	Continental	Eg, semi-rosulate, hc, hapaxanth	Silicate and semidry grasslands, dry – moderately dry ruderal area, cleared forests and forest edges	48.805876° N	16.646231° E
<i>Centaurea</i>	<i>scabiosa</i>	Oceanic	Sg, semi-rosulate, hc, perennial	Calcareous dry and semidry grasslands, dry meadows and shrubland	51.528795° N	11.889641° E
	<i>stoebe</i>	Continental	Eg, semi-rosulate, hc, biennial, hapaxanth	Dry and sandy, partly ruderal xerothermic grasslands	51.503299° N	11.945023° E
<i>Dianthus</i>	<i>Deltoides</i>	Oceanic	Semi-eg, semi-rosulate, hc, perennial	Xerothermic grasslands, dry slopes and edges of forests	52.510644° N	11.180309° E
	<i>Carthusianorum</i>	Continental	Eg, no rosulate, chamaeophyt/hc, perennial	Dry and sandy grasslands, rare in arid environments	51.533204° N	11.981404° E
<i>Koeleria</i>	<i>Pyramidata</i>	Oceanic	Sg, hc, perennial	Dry and semidry grasslands, dry ruderal areas, cleared pine-forests	51.592711° N	9.949324° E
	<i>Macrantha</i>	Continental	Sg, hc/geophyt, perennial	Dry and semidry grasslands, dry ruderal areas, dry meadows, cleared pine-forests	51.532948° N	11.914366° E
<i>Scabiosa</i>	<i>columbaria</i>	Oceanic	Eg, semi-rosulate, hc, short-lived, perennial	Calcareous dry and semidry grasslands, meadows and shrubland	51.592711° N	9.949324° E
	<i>ochroleuca</i>	Continental	Eg, semi-rosulate, hc, perennial	Continental, dry and semidry grasslands	51.533204° N	11.981404° E
<i>Silene</i>	<i>nutans</i>	Oceanic	Sg, semi-rosulate, hc, perennial	Silicate dry grasslands, dry shrubland, dry forests and their edges	51.592302° N	9.948576° E
	<i>otites</i>	Continental	Eg, semi-rosulate, hc, short-lived, perennial	Calcareous, silicate and sandy dry grasslands, dry pine-forests	51.527867° N	11.890091° E

*Jäger EJ, editor (2017) Rothmaler - Exkursionsflora von Deutschland. Gefäßpflanzen: Grundband. 21. edition. Springer Berlin Heidelberg.

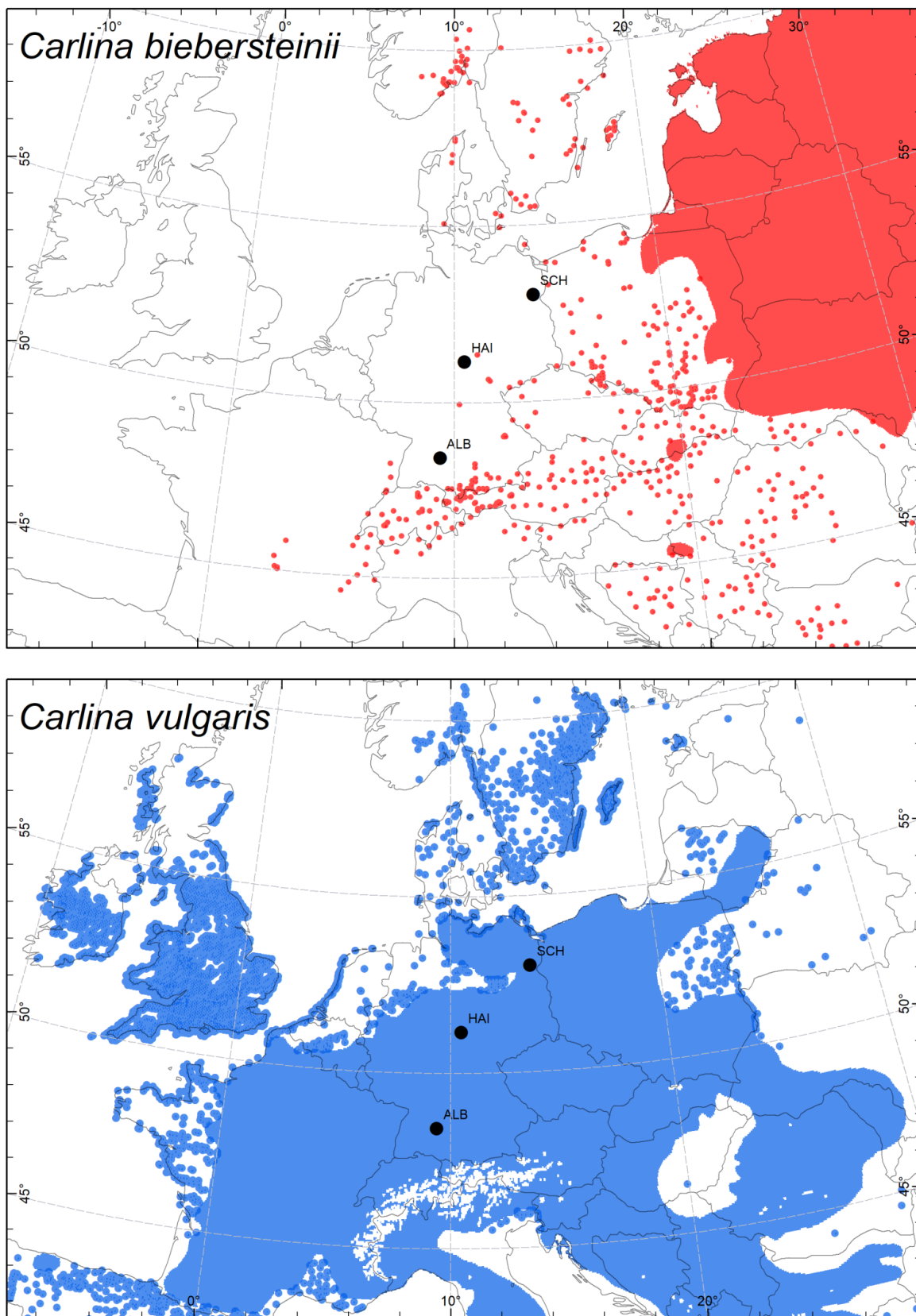


Fig. S1 Distribution maps of *Carlina biebersteinii* and *C. vulgaris*. The geographic range of the continental species is shown in red, that of the oceanic species in blue.

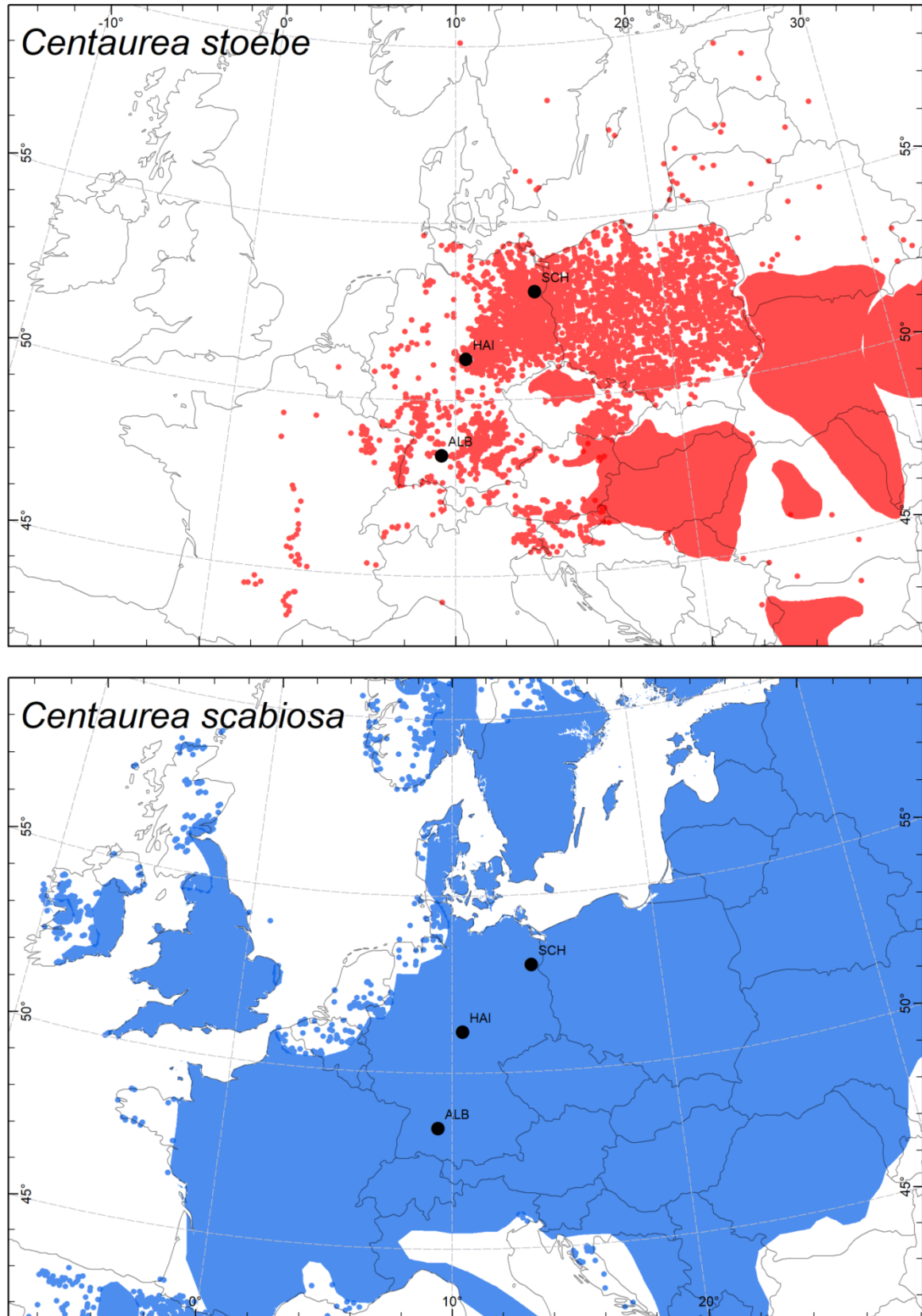


Fig. S2 Distribution maps of *Centaurea stoebe* and *C. scabiosa*. The geographic range of the continental species is shown in red, that of the oceanic species in blue.

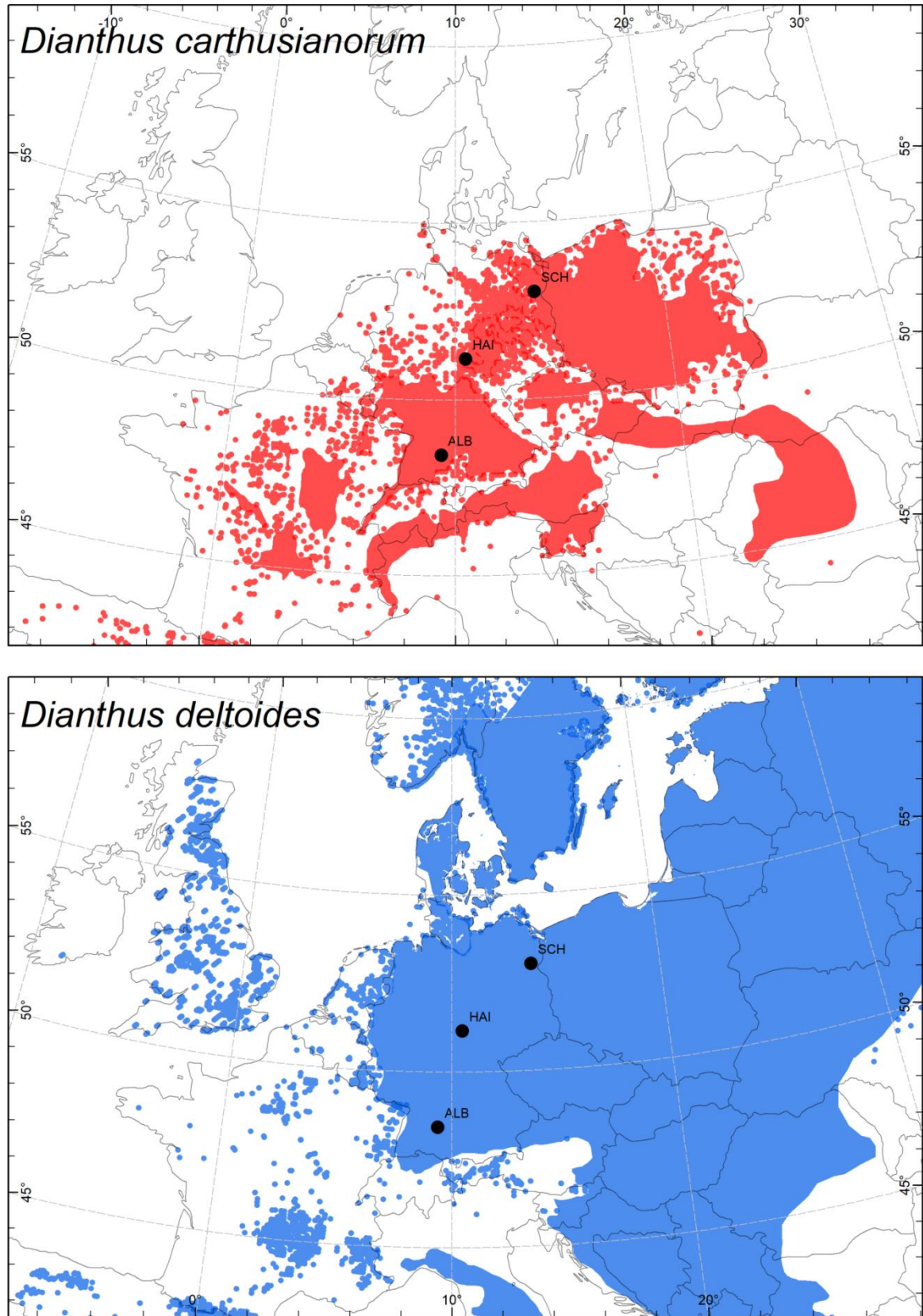


Fig. S3 Distribution maps of *Dianthus carthusianorum* and *D. deltoides*. The geographic range of the continental species is shown in red, that of the oceanic species in blue.

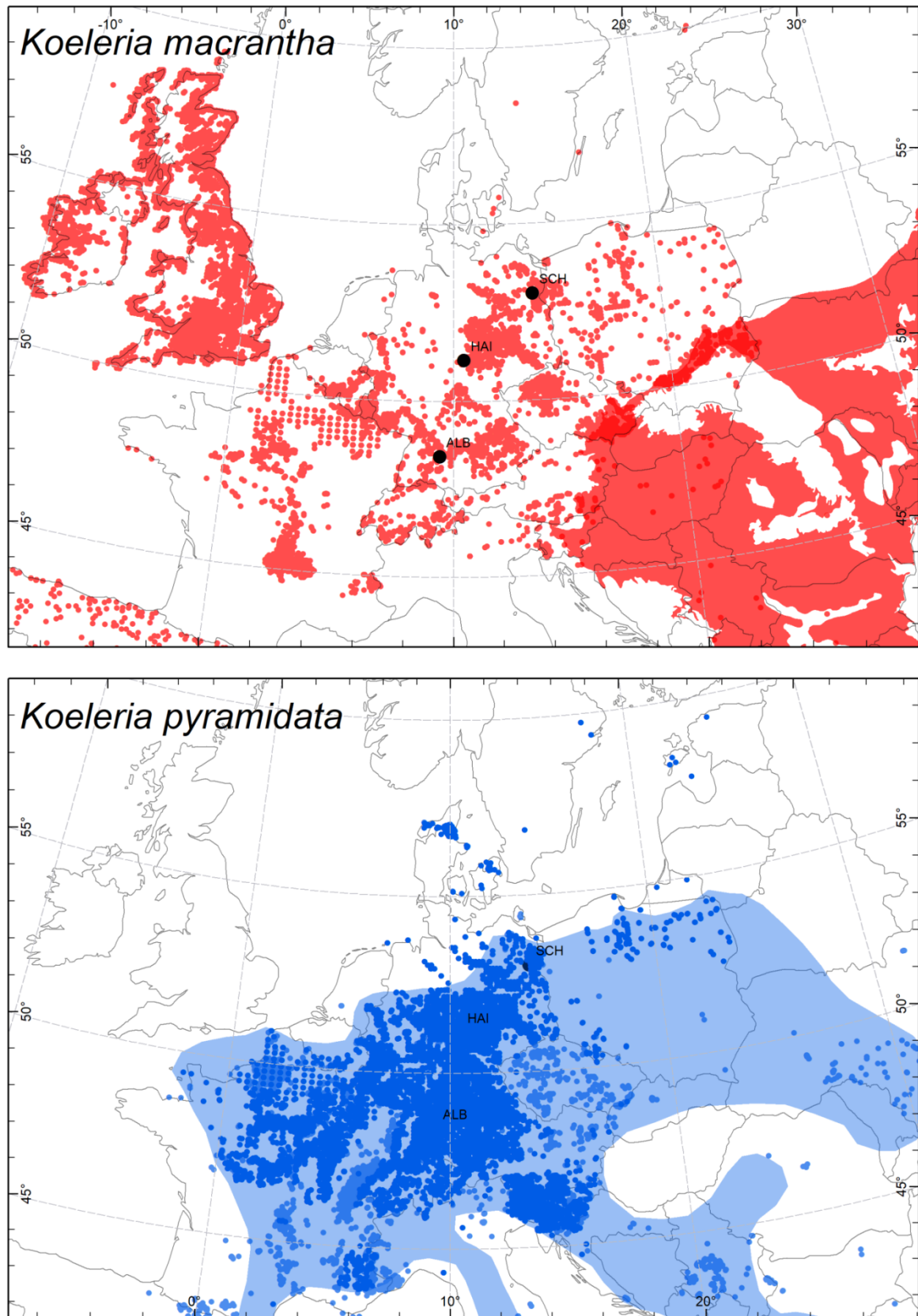


Fig. S4 Distribution maps of *Koeleria macrantha* and *K. pyramidata*. The geographic range of the continental species is shown in red, that of the oceanic species in blue.

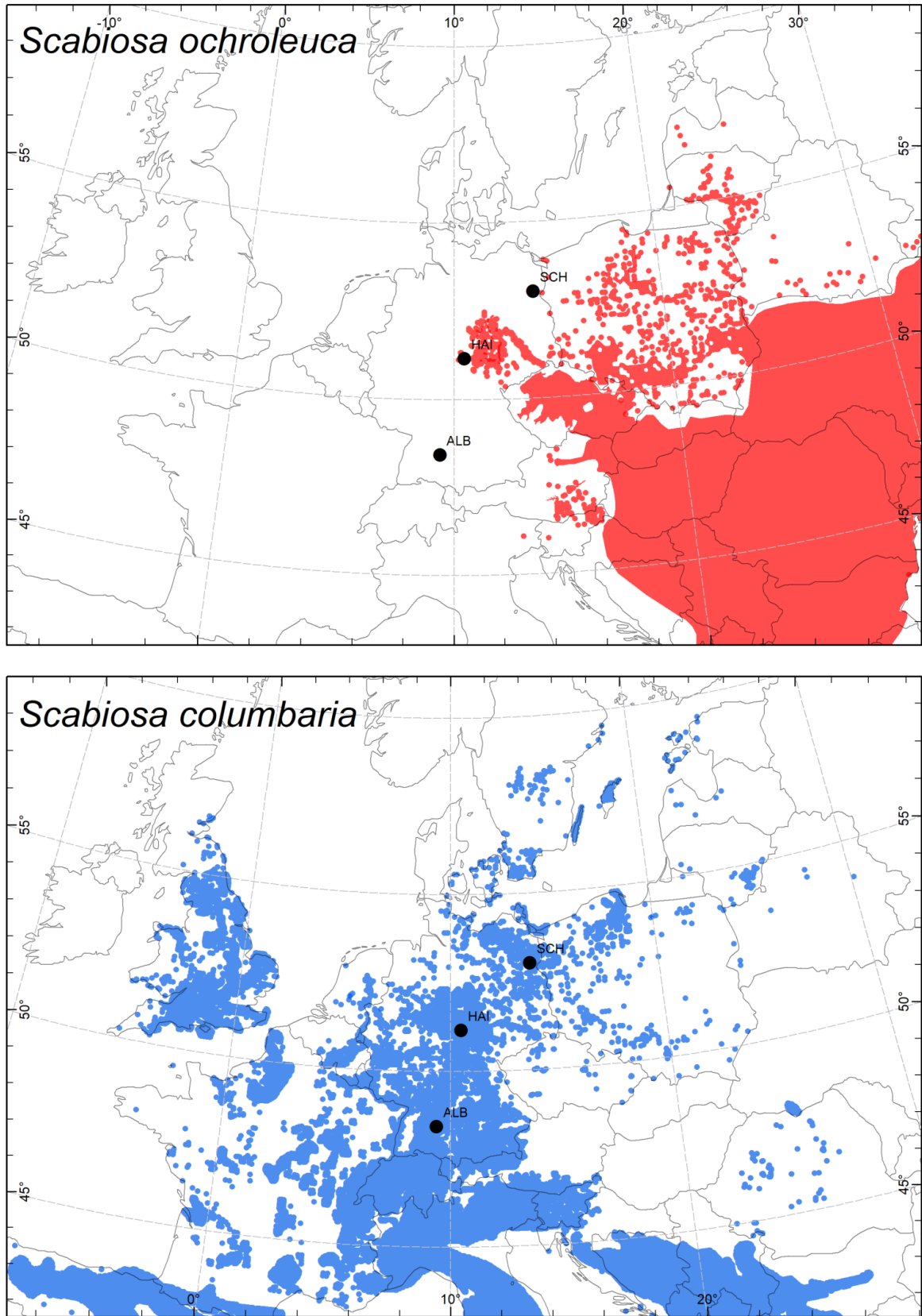


Fig. S5 Distribution maps of *Scabiosa ochroleuca* and *S. columbaria*. The geographic range of the continental species is shown in red, that of the oceanic species in blue.

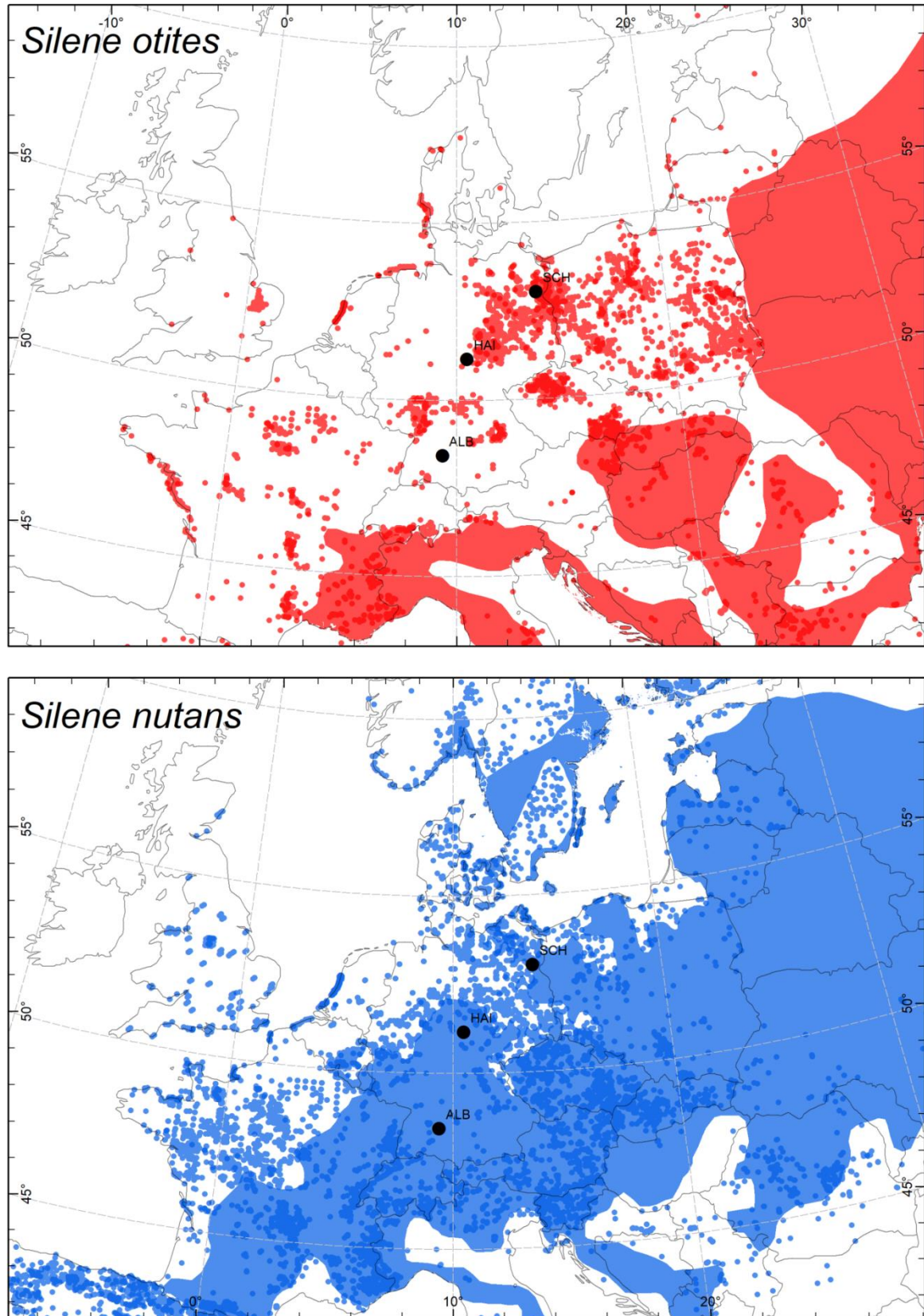


Fig. S6 Distribution maps of *Silene otites* and *S. nutans*. The geographic range of the continental species is shown in red, that of the oceanic species in blue.

Table S2 **Planting scheme for experimental plots**, which was the same for all 45 plots in the whole experiment. Each row represents one subplot with the stated treatment combination. ● indicates that one individual each of both species of the genus was transplanted as phytometer into this subplot.

Subplot treatment	Replicate	Congeneric species pair					
		<i>Carlina</i>	<i>Centaurea</i>	<i>Dianthus</i>	<i>Koeleria</i>	<i>Scabiosa</i>	<i>Silene</i>
Control	1 st	●	●	●	●	●	●
Control	2 nd		●	●			●
Slug enclosure	1 st		●	●	●		●
Slug enclosure	2 nd		●	●			●
Competition removal	1 st		●	●			●
Competition removal	2 nd		●	●			●
Competition removal × slug enclosure	1 st		●	●			●
Competition removal × slug enclosure	2 nd		●	●			●
Total number of planted phytometer over all 45 plots (in the maximum)		90	720	720	180	90	720

APPENDIX S3: Detailed summaries of all calculated GLMMs.

Fig. S1	PCA of the data with the response variables used in the final GLMMs.
Table S1	Matrix for pairwise regression diagnostics.
Table S2	Detailed summary of the GLMM for survival.
Table S3	Detailed summary of the GLMM for relative growth rate of leaf number.
Table S4	Detailed summary of the GLMM for plant height.
Table S5	Detailed summary of the GLMM for aboveground biomass.
Table S6	Detailed summary of the GLMM for belowground biomass.
Table S7	Detailed summary of the GLMM for total biomass.
Table S8	Detailed summary of the GLMM for number of flowering units.
Table S9	Detailed summary of the GLMM for specific leaf area.
Table S10	Detailed summary of the GLMM for proportion of consumed leaf area in autumn 2009.
Table S11	Summary of all GLMMs on survival and plant growth with data only including the three genera <i>Centaurea</i> , <i>Dianthus</i> and <i>Silene</i> .
Table S12	Summary of all GLMMs on plant response including all possible two-way interactions.

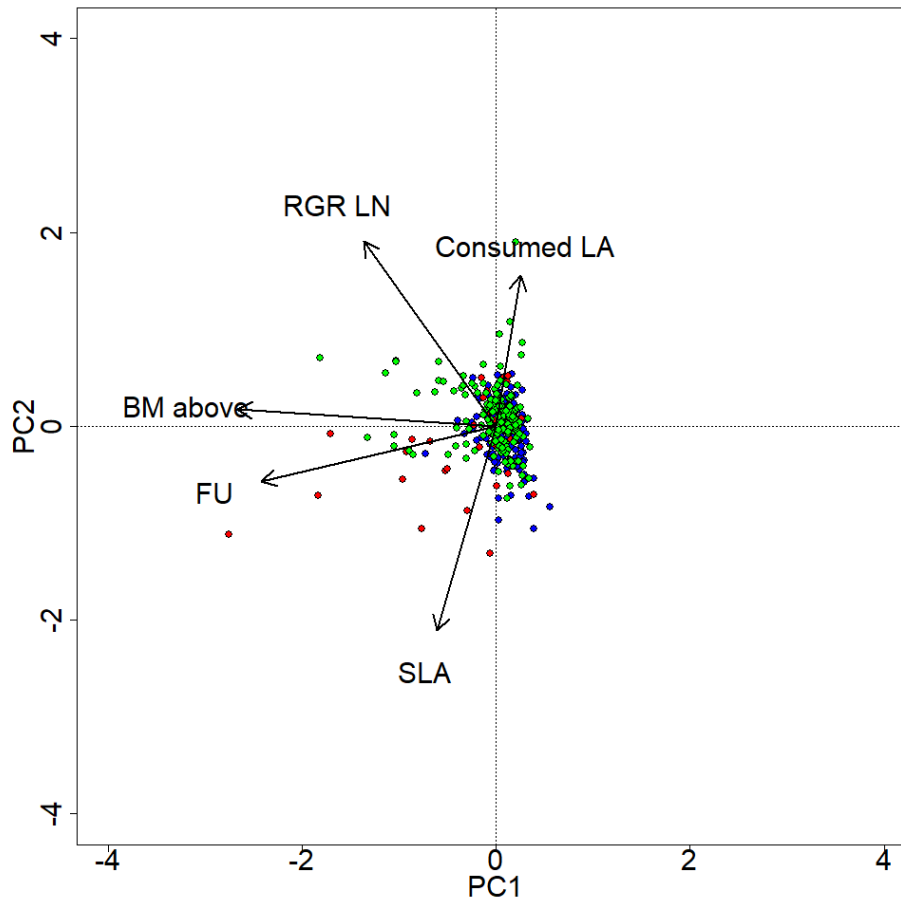


Fig. S1 PCA of the data with the response variables used in the final GLMMs (except survival). PC1 and PC2 with Eigenvalues > 1, cumulative proportion of explained variance 55.48%. Different colors indicate the three study regions with Schorfheide in red, Hainich in green and Schwäbische Alb in blue. Abbreviations of the response variables are used as follows: RGR LN – RGR leaf number; Height – Plant height; BM above – Aboveground biomass; FU – Number flowering units; SLA – Specific leaf area; Consumed LA – Proportion of consumed leaf area.

Table S1 Matrix for pairwise regression diagnostics for the response variables used in the final GLMMs (except survival). Lower left part shows pairwise variable correlation (Adjusted R^2) and upper right part regression diagnostics i.e., correlation (Pearson's r) between observed residuals and expected residuals under normality.

	RGR LN	BM above	FU	SLA	Consumed LA
RGR LN		0.979	0.988	0.989	0.988
BM above	0.131		0.798	0.930	0.745
FU	0.004	0.379		0.732	0.668
SLA	0.022	0.005	0.030		0.925
Consumed LA	0.006	0.003	-0.002	0.008	

Table S2 Detailed summary of the GLMM for the effects of study region, competition, herbivory, land-use type and species' range type on **survival** of phytometer plants. Given are degrees of freedom (Df) for the numerator (Num) and the denominator (Den), F-values and p-values. Significant effects are in bold. Estimates for the random terms are presented at the end of the table.

Survival				
Observations used: 2335				
Effect	Df _{Num}	Df _{Den}	F-value	p-value
Study region	2	38.45	30.15	<.0001
Competiton	1	303.50	16.04	<.0001
Herbivory	1	352.40	3.35	0.0679
Land-use type	2	36.59	3.17	0.0540
Range type	1	11.30	4.00	0.0702
Range type × Study region	2	2321	2.68	0.0688
Range type × Competiton	1	2321	3.20	0.0739
Range type × Herbivory	1	2321	0.23	0.6281
Range type × Land-use type	2	2321	1.89	0.1509
Covariance Parameter		Estimate	Standard error	
Plot Identity(Study region × Land use type)		1.0117	0.2770	
Subplot Identity(Plot Identity × Study region × Competition × Herbivory × Land use type)		0.1757	0.08780	
Species(Range type)		0.4810	0.2507	

Table S3 Detailed summary of the GLMM for the effects of study region, competition, herbivory, land-use type and species' range type on **relative growth rate of leaf number** (number number⁻¹ week⁻¹) of phytometer plants. Given are degrees of freedom (Df) for the numerator (Num) and the denominator (Den), F-values and p-values. Significant effects are in bold. Estimates for the random terms are presented at the end of the table.

Relative growth rate of leaf number				
Observations used: 1049				
Effect	Df _{Num}	Df _{Den}	F-value	p-value
Study region	2	42.63	1.34	0.2735
Competiton	1	211.9	58.56	<.0001
Herbivory	1	248.9	0.92	0.3393
Land use type	2	35.04	4.38	0.0200
Range type	1	9.863	0.22	0.6501
Range type × Study region	2	942	4.70	0.0093
Range type × Competiton	1	918	4.54	0.0334
Range type × Herbivory	1	912.7	7.75	0.0055
Range type × Land-use type	2	901.3	16.39	<.0001
Covariance Parameter		Estimate	Standard error	
Plot Identity(Study region × Land use type)		0.000049	0.000015	
Subplot Identity(Plot Identity × Study region × Competition × Herbivory × Land use type)		7.816E-6	6.646E-6	
Species(Range type)		0.000039	0.000023	
Residual		0.000213	0.000011	

Table S4 Detailed summary of the GLMM for the effects of study region, competition, herbivory, land-use type and species' range type on **plant height** (cm) of phytometer plants. Given are degrees of freedom (Df) for the numerator (Num) and the denominator (Den), F-values and p-values. Significant effects are in bold. Estimates for the random terms are presented at the end of the table.

Plant height				
Observations used: 1019				
Effect	Df _{Num}	Df _{Den}	F-value	p-value
Study region	2	53.8	3.17	0.0500
Competiton	1	249	67.91	<.0001
Herbivory	1	290.1	0.26	0.6078
Land use type	2	40.63	2.69	0.0799
Range type	1	20.96	1.69	0.2076
Range type × Study region	2	942.9	1.54	0.2147
Range type × Competiton	1	910.8	4.44	0.0353
Range type × Herbivory	1	893.2	0.54	0.4643
Range type × Land-use type	2	907.3	6.23	0.0021
Covariance Parameter		Estimate	Standard error	
Plot Identity(Study region × Land use type)		51.3265	13.9865	
Subplot Identity(Plot Identity × Study region × Competition × Herbivory × Land use type)		3.3308	3.8293	
Species(Range type)		14.8780	7.8113	
Residual		153.59	7.6702	

Table S5 Detailed summary of the GLMM for the effects of study region, competition, herbivory, land-use type and species' range type on **aboveground biomass** (g) of phytometer plants. Given are degrees of freedom (Df) for the numerator (Num) and the denominator (Den), F-values and p-values. Significant effects are in bold. Estimates for the random terms are presented at the end of the table.

Aboveground biomass				
Observations used: 1071				
Effect	Df _{Num}	Df _{Den}	F-value	p-value
Study region	2	43.96	3.61	0.0354
Competiton	1	1025	54.33	<.0001
Herbivory	1	1002	0.45	0.5022
Land use type	2	36.83	0.14	0.8676
Range type	1	16.11	2.94	0.1057
Range type × Study region	2	1041	6.58	0.0014
Range type × Competiton	1	1023	0.11	0.7351
Range type × Herbivory	1	1001	0.13	0.7137
Range type × Land-use type	2	1038	14.08	<.0001
Covariance Parameter		Estimate	Standard error	
Plot Identity(Study region × Land use type)		1.7859	0.5220	
Subplot Identity(Plot Identity × Study region × Competition × Herbivory × Land use type)		0	.	
Species(Range type)		0.7266	0.3668	
Residual		7.6977	0.3423	

Table S6 Detailed summary of the GLMM for the effects of study region, competition, herbivory, land-use type and species' range type on **belowground biomass** (g) of phytometer plants. Given are degrees of freedom (Df) for the numerator (Num) and the denominator (Den), F-values and p-values. Significant effects are in bold. Estimates for the random terms are presented at the end of the table.

Belowground biomass				
Observations used: 348				
Effect	Df _{Num}	Df _{Den}	F-value	p-value
Study region	2	57.26	3.55	0.0352
Competiton	1	171.4	3.60	0.0596
Herbivory	1	193.1	0.95	0.3315
Land use type	2	46.94	0.10	0.9094
Range type	1	21.17	2.31	0.1430
Range type × Study region	2	315.6	3.15	0.0441
Range type × Competiton	1	324	0.00	0.9490
Range type × Herbivory	1	309.3	0.59	0.4444
Range type × Land-use type	2	310.4	6.68	0.0014
Covariance Parameter		Estimate	Standard error	
Plot Identity(Study region × Land use type)		0.008628	0.006196	
Subplot Identity(Plot Identity × Study region × Competition × Herbivory × Land use type)		0.01780	0.008505	
Species(Range type)		0.009781	0.006177	
Residual		0.08478	0.007914	

Table S7 Detailed summary of the GLMM for the effects of study region, competition, herbivory, land-use type and species' range type on **total biomass** (g) of phytometer plants. Given are degrees of freedom (Df) for the numerator (Num) and the denominator (Den), F-values and p-values. Significant effects are in bold. Estimates for the random terms are presented at the end of the table.

Total biomass				
Observations used: 348				
Effect	Df _{Num}	Df _{Den}	F-value	p-value
Study region	2	64.84	1.55	0.2208
Competiton	1	162.6	1.12	0.2921
Herbivory	1	179.4	0.59	0.4422
Land use type	2	52.71	0.32	0.7276
Range type	1	32.96	5.00	0.0323
Range type × Study region	2	314.7	4.23	0.0154
Range type × Competiton	1	322.6	0.64	0.4240
Range type × Herbivory	1	298.7	0.01	0.9142
Range type × Land-use type	2	309.2	5.65	0.0039
Covariance Parameter		Estimate	Standard error	
Plot Identity(Study region × Land use type)		1.5012	0.6346	
Subplot Identity(Plot Identity × Study region × Competition × Herbivory × Land use type)		1.7189	0.7551	
Species(Range type)		0.4195	0.3003	
Residual		7.2219	0.6767	

Table S8 Detailed summary of the GLMM for the effects of study region, competition, herbivory, land-use type and species' range type on **number of flowering units** of phytometer plants. Given are degrees of freedom (Df) for the numerator (Num) and the denominator (Den), F-values and p-values. Significant effects are in bold. Estimates for the random terms are presented at the end of the table.

Number of flowering units				
Observations used: 401				
Effect	Df _{Num}	Df _{Den}	F-value	p-value
Study region	2	35.8	0.59	0.5609
Competiton	1	80.85	1.91	0.1706
Herbivory	1	69.38	1.03	0.3130
Land use type	2	28.58	0.10	0.9008
Range type	1	15.16	1.86	0.1923
Range type × Study region	2	261.6	8.90	0.0002
Range type × Competiton	1	268.7	1.75	0.1872
Range type × Herbivory	1	237.9	0.58	0.4462
Range type × Land-use type	2	262.3	2.11	0.1238
Covariance Parameter		Estimate	Standard error	
Plot Identity(Study region × Land use type)		1207.72	468.20	
Subplot Identity(Plot Identity × Study region × Competition × Herbivory × Land use type)		504.63	459.06	
Species(Range type)		476.84	295.78	
Residual		3279.67	422.69	

Table S9 Detailed summary of the GLMM for the effects of study region, competition, herbivory, land-use type and species' range type on **specific leaf area** (g cm⁻²) of phytometer plants. Given are degrees of freedom (Df) for the numerator (Num) and the denominator (Den), F-values and p-values. Significant effects are in bold. Estimates for the random terms are presented at the end of the table.

Specific leaf area				
Observations used: 1022				
Effect	Df _{Num}	Df _{Den}	F-value	p-value
Study region	2	40.75	16.28	<.0001
Competiton	1	42.08	0.40	0.5286
Herbivory	1	45.55	3.02	0.0889
Land use type	2	34.75	0.37	0.6914
Range type	1	13.15	2.20	0.1617
Range type × Study region	2	545.2	5.74	0.0034
Range type × Competiton	1	424.7	0.95	0.3315
Range type × Herbivory	1	430.5	1.58	0.2094
Range type × Land-use type	2	386.3	3.24	0.0402
Covariance Parameter		Estimate	Standard error	
Plot Identity(Study region × Land use type)		553.10	183.40	
Subplot Identity(Plot Identity × Study region × Competition × Herbivory × Land use type)		630.36	297.24	
Species(Range type)		715.07	334.09	
Residual		1737.11	148.41	

Table S10 Detailed summary of the GLMM for the effects of study region, competition, herbivory, land-use type and species' range type on **proportion of consumed leaf area in autumn 2009** (%) of phytometer plants. Given are degrees of freedom (Df) for the numerator (Num) and the denominator (Den), F-values and p-values. Significant effects are in bold. Estimates for the random terms are presented at the end of the table.

Proportion of consumed leaf area in autumn 2009				
Observations used: 1860				
Effect	Df _{Num}	Df _{Den}	F-value	p-value
Study region	2	36.95	25.85	<.0001
Competiton	1	1810	5.25	0.0220
Herbivory	1	1812	62.82	<.0001
Land use type	2	36.06	2.39	0.1060
Range type	1	12.6	0.80	0.3871
Range type × Study region	2	1806	9.96	<.0001
Range type × Competiton	1	1807	6.83	0.0090
Range type × Herbivory	1	1807	6.93	0.0085
Range type × Land-use type	2	1810	2.72	0.0662
Covariance Parameter		Estimate	Standard error	
Plot Identity(Study region × Land use type)		26.5119	7.5575	
Subplot Identity(Plot Identity × Study region × Competition × Herbivory × Land use type)		0	.	
Species(Range type)		81.8863	37.0771	
Residual		213.82	7.1438	

Table S11 Summary of all GLMMs on survival and plant growth with data only including the three genera *Centaurea*, *Dianthus* and *Silene*. Given are F-values. Significant effects are shown in bold and indicated as follows: ***: $p < 0.001$, **: $p \leq 0.01$, *: $p \leq 0.05$.

Source of variation	Survival	RGR leaf number	Plant height	Aboveground biomass	Belowground biomass	Total biomass	Number flowering units	Specific leaf area	Proportion consumed leaf area
	F-value	F-value	F-value	F-value	F-value	F-value	F-value	F-value	F-value
Study region (= region)	26,77 ***	1,21	3,97 *	3,48 *	3,60 *	1,33	0,57	12,29 ***	24,49 ***
Competition (= comp)	14,07 ***	49,57 ***	69,21 ***	42,44 ***	2,14	0,69	1,33	0,72	5,90 *
Herbivory (= herb)	3,71	1,35	0,31	0,36	0,76	0,32	1,29	2,36	59,78 ***
Land-use type (= use)	3,59 *	4,49 *	2,27	0,04	0,01	0,06	0,08	0,32	3,02
Range type (= range)	1,94	1,00	0,92	0,91	1,89	2,42	1,28	3,51	1,17
Range × region	3,32 *	3,43 *	2,27	5,36 **	2,52	2,84	10,21 ***	7,20 **	9,59 ***
Range × comp	2,81	3,43	5,56 *	0,08	0,56	0,11	1,84	1,00	8,19 **
Range × herb	0,39	7,87 **	0,50	0,14	0,47	0,02	0,38	1,59	6,60 *
Range × use	1,68	15,97 ***	6,26 **	13,59 ***	4,80 **	4,93 **	2,32	2,88	3,96 *

Table S12 Summary of all GLMMs on plant response including all possible two-way interactions. Values are error probabilities. Significant effects are shown in bold and indicated as follows: ***: $p < 0.001$, **: $p \leq 0.01$, *: $p \leq 0.05$.

Source of variation	Survival	RGR leaf number	Plant height	Aboveground biomass	Belowground biomass	Total biomass	Number flowering units	Specific leaf area	Proportion consumed leaf area
Study region (= region)	< 0.001 ***	0.210	0.065	0.018 *	0.271	0.466	0.352	< 0.001 ***	< 0.001 ***
Competition (= comp)	< 0.001 ***	< 0.001 ***	< 0.001 ***	< 0.001 ***	0.273	0.450	0.397	0.083	0.048 *
Herbivory (= herb)	0.016 *	0.126	0.541	0.402	0.753	0.928	0.007 **	0.003 **	< 0.001 ***
Land-use type (= use)	0.066	0.007 **	0.345	0.485	0.236	0.582	0.202	0.289	0.101
Range type (= range)	0.066	0.675	0.195	0.083	0.363	0.070	0.115	0.124	0.387
Range × region	0.068	0.013 *	0.200	< 0.001 ***	0.054	0.018 *	< 0.001 ***	0.001 **	< 0.001 ***
Range × comp	0.096	0.025 *	0.061	0.706	0.812	0.634	0.142	0.425	0.011 *
Range × herb	0.515	0.004 **	0.370	0.607	0.175	0.872	0.836	0.167	0.008 **
Range × use	0.171	< 0.001 ***	0.003 **	< 0.001 ***	0.004 **	0.008 **	0.039 *	0.034 *	0.066
Region × comp	0.636	0.520	0.465	0.013 *	0.784	0.956	0.897	< 0.001 ***	0.702
Region × herb	0.176	0.254	0.453	0.978	0.676	0.798	0.077	0.001 **	0.111
Region × use	0.044 *	0.168	0.339	0.074	0.211	0.311	0.013 *	0.134	0.176
Comp × herb	0.190	0.964	0.009 **	0.051	0.080	0.103	0.097	0.069	0.528
Comp × use	0.641	0.053	0.295	0.423	0.570	0.615	0.885	0.100	0.269
Herb × use	0.123	0.192	0.585	0.665	0.265	0.503	0.833	0.096	0.614

APPENDIX S4: Summary of LS-Means estimated from GLMMs.

Table S1	Summary of the LS-Means estimated from the GLMMs for survival as well as relative growth rate of leaf number and plant height.
Table S2	Summary of the LS-Means estimated from the GLMMs for aboveground biomass as well as number of flowering units and specific leaf area.
Table S3	Summary of the LS-Means estimated from the GLMMs for proportion of consumed leaf area.

Table S1 Summary of the LS-Means estimated from the GLMMs for survival (%) as well as relative growth rate (RGR) of leaf number (number number⁻¹ week⁻¹) and plant height (cm) with sample sizes (n) for each treatment. Categories of the main effects are given in bold. Thereafter the separated LS-Means of the range types for the categories are listed which is equivalent to the interactive effect of range type with the other main effects. Bold letters after the LS-Means indicate assignments to Tukey groupings. Thereby, capital letters correspond assignments to Tukey groupings within the main effects, small letters to the Tukey groupings within the respective interaction effect. Categories with same letters are not significantly different according to tukey post-hoc tests.

Source	Survival			RGR of leaf number			Plant height		
	n	LS-means ± SE		n	LS-means ± SE		n	LS-means ± SE	
Study region									
Alb	835	69.1 ± 7.4	A	509	0.004 ± 0.003	A	513	13.4 ± 2.3	A
Alb – oceanic	419	75.4 ± 7.7	a	295	0.003 ± 0.003	a	294	13.1 ± 2.6	a
Alb – continental	416	62.0 ± 9.7	a	214	0.005 ± 0.003	a	219	13.7 ± 2.7	a
Hainich	815	57.6 ± 8.4	A	440	0.008 ± 0.003	A	441	18.7 ± 2.3	A
Hainich – oceanic	415	64.9 ± 9.3	a	264	0.006 ± 0.003	a	265	17.8 ± 2.6	a
Hainich – continental	400	50.2 ± 10.2	ab	176	0.009 ± 0.003	a	176	19.5 ± 2.7	a
Schorfheide	685	9.3 ± 3.1	B	100	0.003 ± 0.004	A	65	22.1 ± 3.6	A
Schorfheide – oceanic	359	16.6 ± 5.9	bc	79	0.008 ± 0.004	a	54	17.5 ± 3.3	a
Schorfheide – continental	326	5.0 ± 2.3	c	21	-0.002 ± 0.005	a	11	26.7 ± 5.4	a
Competition									
Present	1248	34.9 ± 6.1	B	519	0.000 ± 0.002	B	502	14.5 ± 1.9	B
Present – oceanic	637	47.5 ± 8.5	ab	326	0.002 ± 0.003	ab	313	13.5 ± 2.2	c
Present – continental	611	24.1 ± 6.4	b	193	0.001 ± 0.003	b	189	15.5 ± 2.7	bc
Removal	1087	46.3 ± 6.8	A	530	0.009 ± 0.002	A	517	21.6 ± 1.9	A
Removal – oceanic	556	54.5 ± 8.6	a	312	0.008 ± 0.003	ab	300	18.9 ± 2.2	ab
Removal – continental	531	38.3 ± 8.4	ab	218	0.009 ± 0.003	a	217	24.4 ± 2.7	a
Slug herbivory									
Present	1341	37.8 ± 6.3	A	587	0.004 ± 0.002	A	569	17.8 ± 1.9	A
Present – oceanic	688	48.9 ± 8.4	a	359	0.006 ± 0.003	ab	345	15.6 ± 2.2	a
Present – continental	653	27.8 ± 6.9	a	228	0.001 ± 0.003	b	224	19.9 ± 2.8	a
Exclosure	994	43.2 ± 6.8	A	462	0.006 ± 0.002	A	450	18.3 ± 2.0	A
Exclosure – oceanic	505	53.1 ± 8.8	a	279	0.005 ± 0.003	ab	268	16.7 ± 2.3	a
Exclosure – continental	489	33.8 ± 8.1	a	183	0.006 ± 0.003	a	182	19.9 ± 2.7	a
Land-use type									
Meadow	777	39.1 ± 8.3	AB	350	0.006 ± 0.003	AB	347	16.3 ± 2.6	A
Meadow – oceanic	393	53.2 ± 10.3	b	219	0.007 ± 0.003	a	213	14.2 ± 2.9	a
Meadow – continental	384	26.7 ± 8.3	b	131	0.005 ± 0.004	ab	134	18.4 ± 3.3	a
Mown Pasture	769	29.6 ± 7.2	B	271	0.009 ± 0.003	A	302	15.7 ± 2.5	A
Mown Pasture – oceanic	412	38.5 ± 9.6	ab	175	0.013 ± 0.003	a	168	15.8 ± 2.8	a
Mown Pasture – continental	385	22.0 ± 7.2	b	96	0.005 ± 0.004	ab	90	15.6 ± 3.1	a
Pasture	761	53.7 ± 8.9	A	428	0.001 ± 0.003	B	414	22.2 ± 2.7	A
Pasture – oceanic	388	61.3 ± 10.0	a	244	-0.003 ± 0.003	b	232	18.4 ± 2.8	a
Pasture – continental	373	46.0 ± 10.7	ab	184	0.003 ± 0.004	ab	182	25.9 ± 3.3	a

Table S2 Summary of the LS-Means estimated from the GLMMs for aboveground biomass (g) as well as number of flowering units (no) and specific leaf area (g cm⁻²) with sample sizes (n) for each treatment. Categories of the main effects are given in bold. Thereafter the separated LS-Means of the range types for the categories are listed which is equivalent to the interactive effect of range type with the other main effects. Bold letters after the LS-Means indicate assignments to tukey groupings. Thereby, capital letters correspond assignments to Tukey groupings. Thereby, capital letters correspond assignments to Tukey groupings within the main effects, small letters to the Tukey groupings within the respective interaction effect. Categories with same letters are not significantly different according to tukey post-hoc tests.

Source	Aboveground biomass			Number of flowering units			Specific leaf area		
	n	LS-means ± SE		n	LS-means ± SE		n	LS-means ± SE	
Study region									
Alb	512	0.95 ± 0.46	A	174	2.6 ± 13.9	A	499	141.5 ± 10.4	B
Alb – oceanic	294	1.16 ± 0.53	ab	93	-9.0 ± 16.4	b	287	151.2 ± 13.1	bc
Alb – continental	218	0.74 ± 0.55	ab	81	14.2 ± 17.2	ab	212	131.7 ± 13.0	bc
Hainich	452	2.25 ± 0.46	A	186	17.9 ± 13.1	A	420	118.1 ± 10.4	B
Hainich – oceanic	267	2.21 ± 0.54	ab	96	14.7 ± 16.2	ab	261	121.2 ± 13.1	bc
Hainich – continental	185	2.28 ± 0.55	a	90	21.2 ± 15.8	ab	159	115.0 ± 13.0	c
Schorfheide	107	0.93 ± 0.61	A	41	1.9 ± 21.4	A	103	188.6 ± 12.9	A
Schorfheide – oceanic	83	2.27 ± 0.62	a	31	54.4 ± 31.5	a	81	211.3 ± 14.4	a
Schorfheide – continental	24	-0.42 ± 0.87	b	10	-50.7 ± 31.5	ab	22	165.8 ± 17.8	ab
Competition									
Present	521	0.71 ± 0.38	B	207	2.1 ± 12.4	A	455	150.8 ± 9.3	A
Present – oceanic	326	1.18 ± 0.46	bc	109	10.1 ± 14.8	a	275	161.2 ± 12.1	a
Present – continental	195	0.23 ± 0.51	c	96	-5.9 ± 17.2	a	180	140.3 ± 12.6	a
Removal	550	2.04 ± 0.38	A	196	12.8 ± 11.7	A	567	148.0 ± 9.3	A
Removal – oceanic	318	2.58 ± 0.47	a	111	30.0 ± 14.2	a	354	161.3 ± 12.2	a
Removal – continental	232	1.51 ± 0.52	ab	85	-4.4 ± 16.0	a	213	134.7 ± 12.6	a
Slug herbivory									
Present	596	1.44 ± 0.37	A	139	11.1 ± 11.8	A	523	153.2 ± 9.4	A
Present – oceanic	364	1.91 ± 0.45	a	84	26.1 ± 14.2	a	312	167.0 ± 12.1	a
Present – continental	232	0.97 ± 0.45	a	55	-3.9 ± 16.0	a	211	139.4 ± 12.4	a
Exclosure	475	1.31 ± 0.39	A	262	3.8 ± 12.2	A	499	145.6 ± 9.2	A
Exclosure – oceanic	280	1.85 ± 0.47	a	136	14.0 ± 14.7	a	317	155.5 ± 12.3	a
Exclosure – continental	195	0.77 ± 0.53	a	126	-6.4 ± 16.8	a	182	135.6 ± 12.8	a
Land-use type									
Meadow	359	1.13 ± 0.50	A	119	8.7 ± 15.6	A	344	144.1 ± 11.1	A
Meadow – oceanic	223	2.11 ± 0.55	a	65	29.4 ± 17.5	a	220	154.6 ± 13.4	a
Meadow – continental	136	0.48 ± 0.64	a	54	-12.0 ± 20.8	a	124	133.6 ± 14.3	a
Mown Pasture	276	1.55 ± 0.48	A	98	10.9 ± 14.6	A	266	152.7 ± 10.8	A
Mown Pasture – oceanic	175	2.40 ± 0.56	a	64	22.6 ± 17.0	a	172	160.9 ± 13.4	a
Mown Pasture – continental	101	0.71 ± 0.60	a	34	-0.9 ± 18.9	a	94	144.5 ± 13.6	a
Pasture	436	1.27 ± 0.50	A	184	2.9 ± 15.8	A	412	151.3 ± 11.1	A
Pasture – oceanic	246	1.14 ± 0.57	a	91	8.1 ± 17.5	a	237	168.2 ± 13.5	a
Pasture – continental	190	1.41 ± 0.62	a	93	-2.4 ± 19.9	a	175	134.4 ± 14.1	a

Table S3 Summary of the LS-Means estimated from the GLMMs for proportion of consumed leaf area (%) with sample sizes (n) for each treatment. Categories of the main effects are given in bold. Thereafter the separated LS-Means of the range types for the categories are listed which is equivalent to the interactive effect of range type with the other main effects. Bold letters after the LS-Means indicate assignments to Tukey groupings. Thereby, capital letters correspond assignments to Tukey groupings within the main effects, small letters to the Tukey groupings within the respective interaction effect. Categories with same letters are not significantly different according to tukey post-hoc tests.

Source	Proportion of consumed leaf area	
	n	LS-means \pm SE
Study region		
Alb	713	3.6 \pm 2.9 B
Alb – oceanic	365	3.1 \pm 3.8 c
Alb – continental	348	4.1 \pm 3.8 bc
Hainich	773	5.6 \pm 2.8 B
Hainich – oceanic	400	4.3 \pm 3.8 bc
Hainich – continental	373	7.0 \pm 3.8 bc
Schorfheide	374	18.3 \pm 2.9 A
Schorfheide – oceanic	237	13.5 \pm 3.9 ab
Schorfheide – continental	137	23.1 \pm 3.9 a
Competition		
Present	1043	10.0 \pm 2.6 A
Present – oceanic	565	6.8 \pm 3.4 a
Present – continental	478	13.1 \pm 3.6 a
Removal	817	8.4 \pm 2.6 B
Removal – oceanic	437	7.1 \pm 3.7 a
Removal – continental	380	9.7 \pm 3.6 a
Slug herbivory		
Present	969	12.1 \pm 2.6 A
Present – oceanic	525	8.9 \pm 3.6 a
Present – continental	444	15.3 \pm 3.6 a
Exclosure	891	6.2 \pm 2.7 B
Exclosure – oceanic	477	5.0 \pm 3.7 a
Exclosure – continental	414	7.5 \pm 3.7 a
Land-use type		
Meadow	626	10.9 \pm 2.9 A
Meadow – oceanic	342	7.6 \pm 3.8 a
Meadow – continental	284	14.2 \pm 3.8 a
Mown Pasture	594	6.5 \pm 2.9 A
Mown Pasture – oceanic	319	5.2 \pm 3.8 a
Mown Pasture – continental	275	7.8 \pm 3.8 a
Pasture	640	10.1 \pm 2.9 A
Pasture – oceanic	341	8.0 \pm 3.9 a
Pasture – continental	299	12.2 \pm 3.8 a

APPENDIX S5: Figures of significant main effects and significant interactions with range type.

- Fig. S1 Effect of the study region.
- Fig. S2 Effect of the competition treatment.
- Fig. S3 Effect of the mollusk-herbivory treatment.
- Fig. S4 Effect of the land-use types.
- Fig. S5 Interacting effects of study region with range type.
- Fig. S6 Interacting effects of competition with range type.
- Fig. S7 Interacting effects of herbivory with range type.
- Fig. S8 Interacting effects of land-use type with range type.

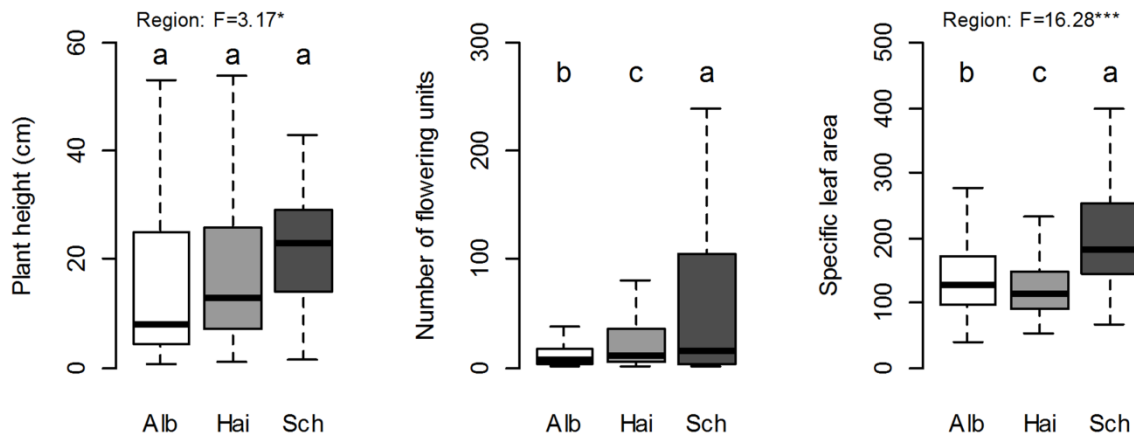


Fig. S1 Effect of the study region on plant height, number of flowering units and specific leaf area. Abbreviations for study regions: Alb – Schwäbische Alb, Hai – Hainich, Sch – Schorfheide. Significant single effects as result from the GLMMs are mentioned with F-value and asterisks (** $p < 0.01$, * $p \leq 0.05$). Different small letters indicate statistically significant differences according to a Tukey post-hoc test, using the full model of Table 1 and Appendix S4.

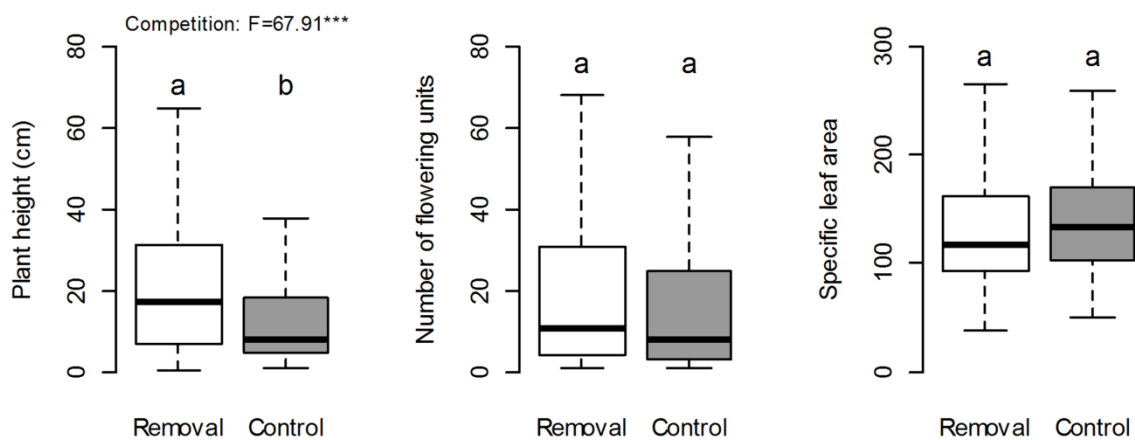


Fig. S2 Effect of the competition treatment on plant height, number of flowering units and specific leaf area. Significant single effects as result from the GLMMs are mentioned with F-value and asterisks (** $p < 0.01$, * $p \leq 0.05$). Different small letters indicate statistically significant differences according to a Tukey post-hoc test, using the full model of Table 1 and Appendix S4.

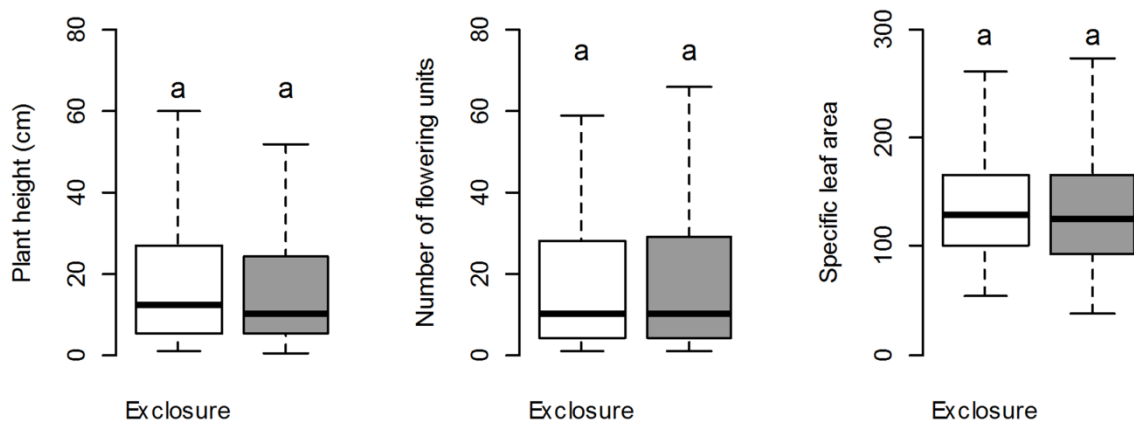


Fig. S3 Effect of the mollusk-herbivory treatment on plant height, number of flowering units and specific leaf area. Significant single effects as result from the GLMMs are mentioned with F-value and asterisks

(*** $p < 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$). Different small letters indicate statistically significant differences according to a Tukey post-hoc test, using the full model of Table 1 and Appendix S4.

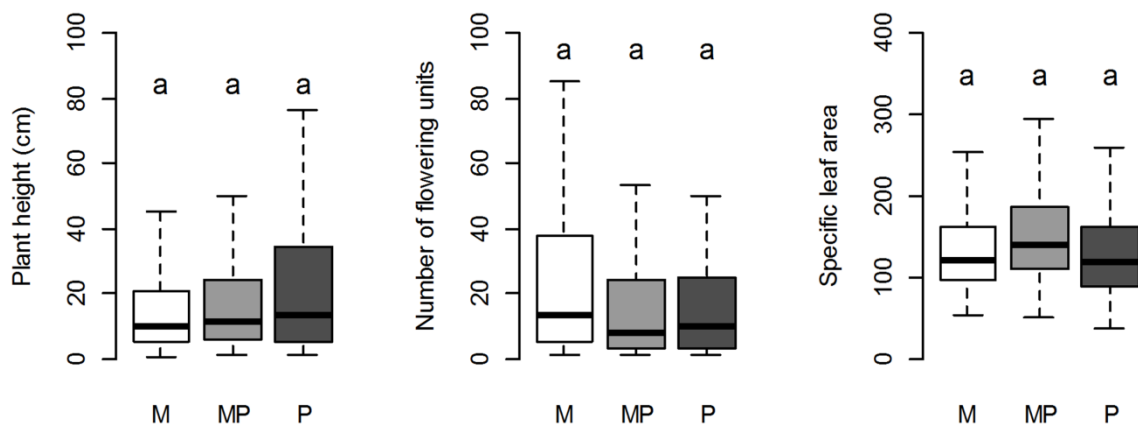


Fig. S4 Effect of the land-use types on plant height, number of flowering units and specific leaf area. Abbreviations for land-use types: M – meadow, MP – mown pasture, P – pasture. Significant single effects as result from the GLMMs are mentioned with F-value and asterisks

(*** $p < 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$). Different small letters indicate statistically significant differences according to a Tukey post-hoc test, using the full model of Table 1 and Appendix S4.

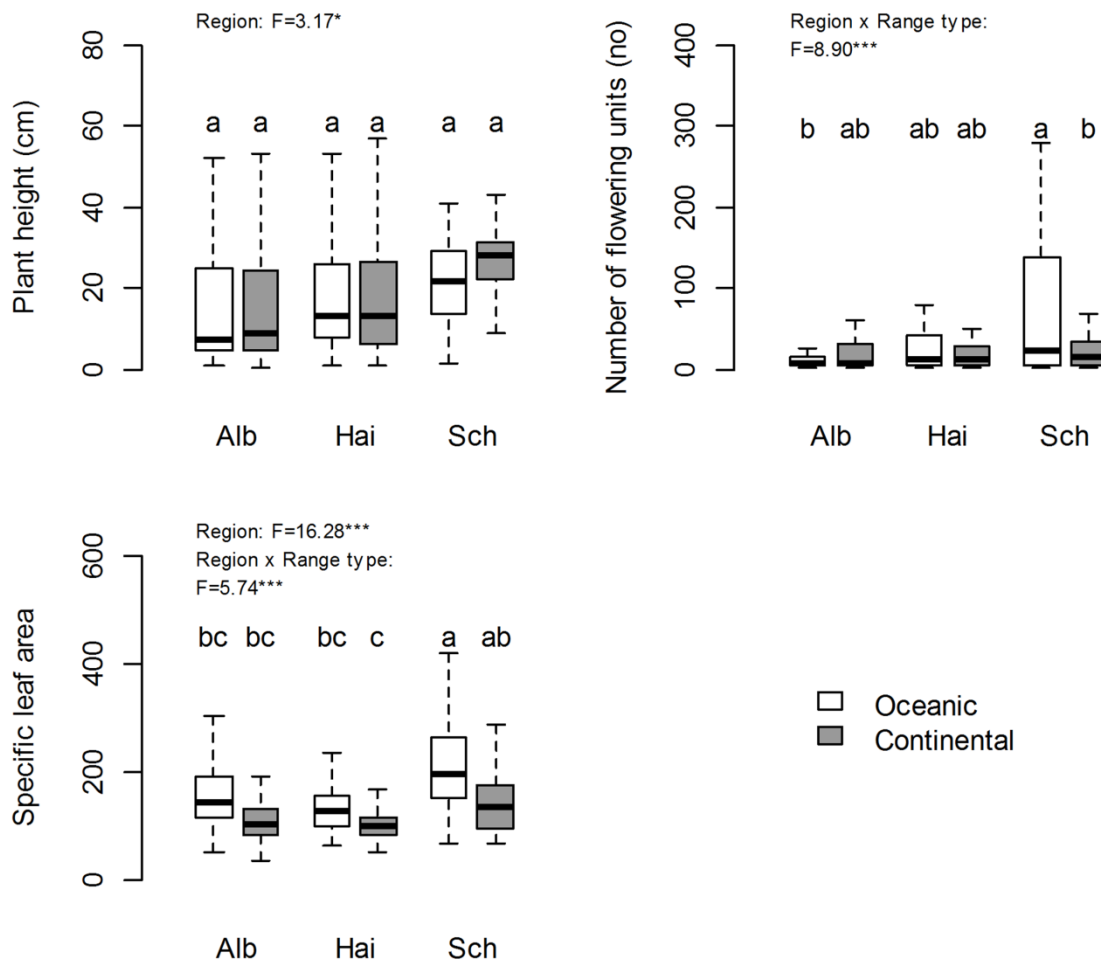


Fig. S5 Interacting effects of study region with range type on plant height, number of flowering units and specific leaf area. Oceanic and continental species are shown in white and grey, respectively. Abbreviations for study regions: Alb – Schwäbische Alb, Hai – Hainich Dün, Sch – Schorfheide-Chorin. Significant single or interactive effects as result from the GLMMs are mentioned with F-value and asterisks (** $p < 0.01$, *** $p < 0.001$, * $p \leq 0.05$). Different small letters indicate statistically significant differences according to a Tukey post-hoc test, using the full model of Table 1 and Appendix S4.

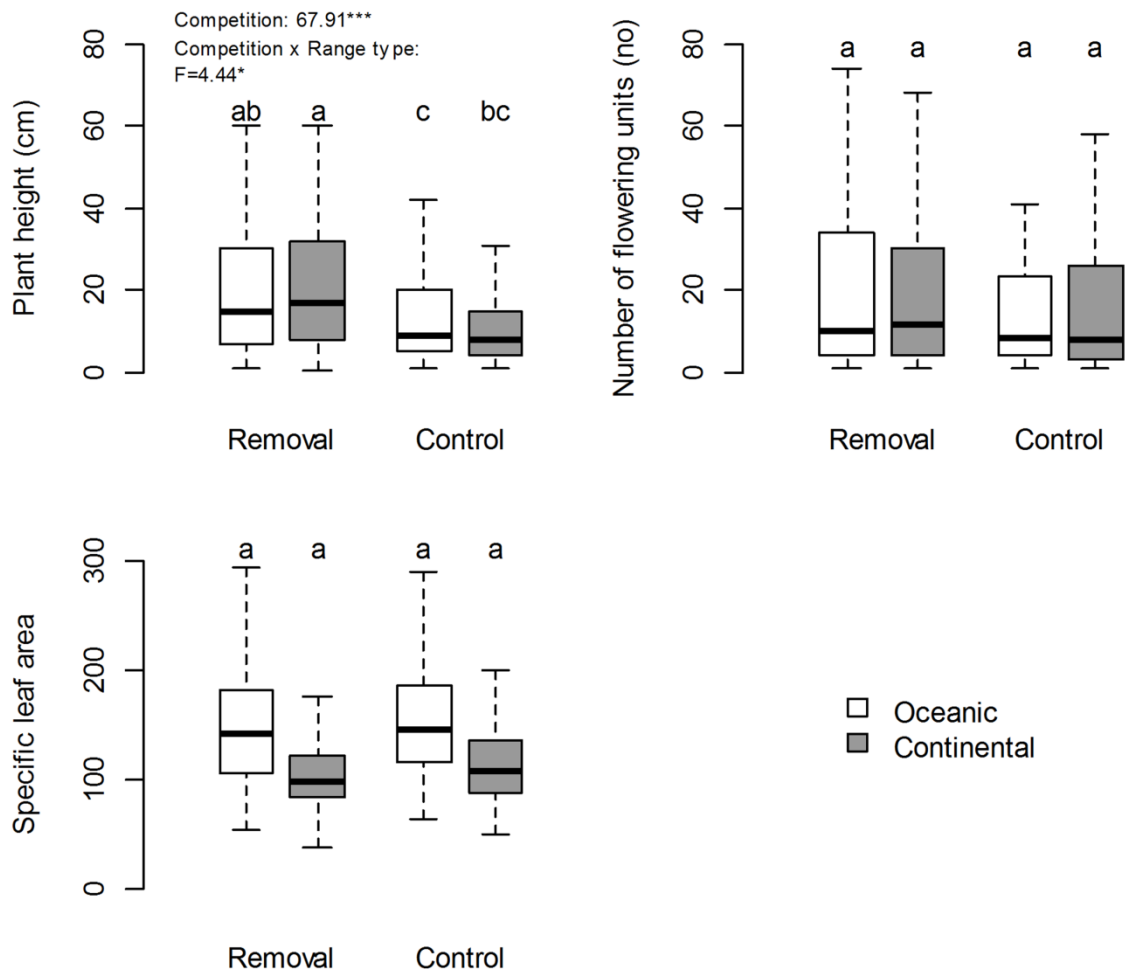


Fig. S6 Interacting effects of competition with range type on plant height, number of flowering units and specific leaf area. Oceanic and continental species are shown in white and grey, respectively. Significant single or interactive effects as result from the GLMMs are mentioned with F-value and asterisks (** $p < 0.01$, *** $p < 0.001$, * $p \leq 0.05$). Different small letters indicate statistically significant differences according to a Tukey post-hoc test, using the full model of Table 1 and Appendix S4.

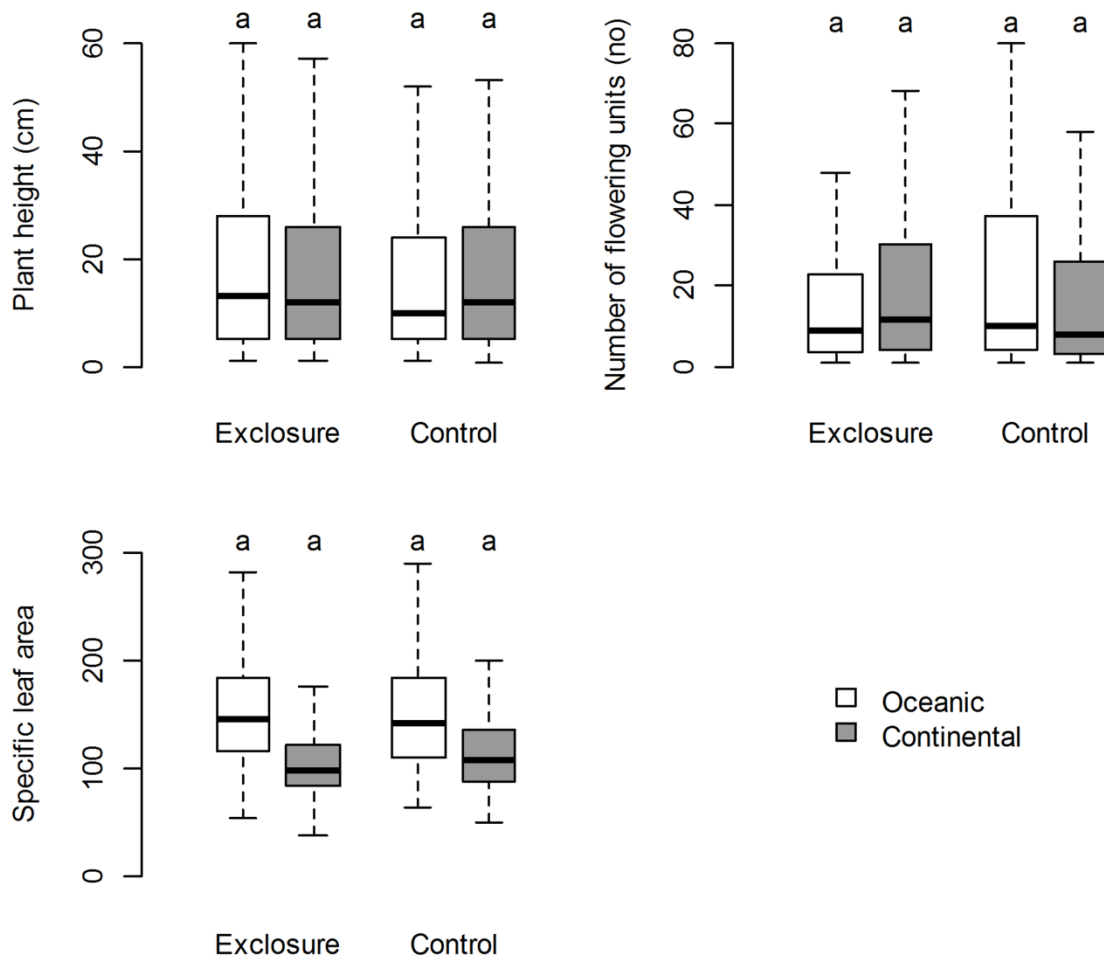


Fig. S7 Interacting effects of herbivory with range type on plant height, number of flowering units and specific leaf area. Oceanic and continental species are shown in white and grey, respectively. Significant single or interactive effects as result from the GLMMs are mentioned with F-value and asterisks (** $p < 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$). Different small letters indicate statistically significant differences according to a Tukey post-hoc test, using the full model of Table 1 and Appendix S4.

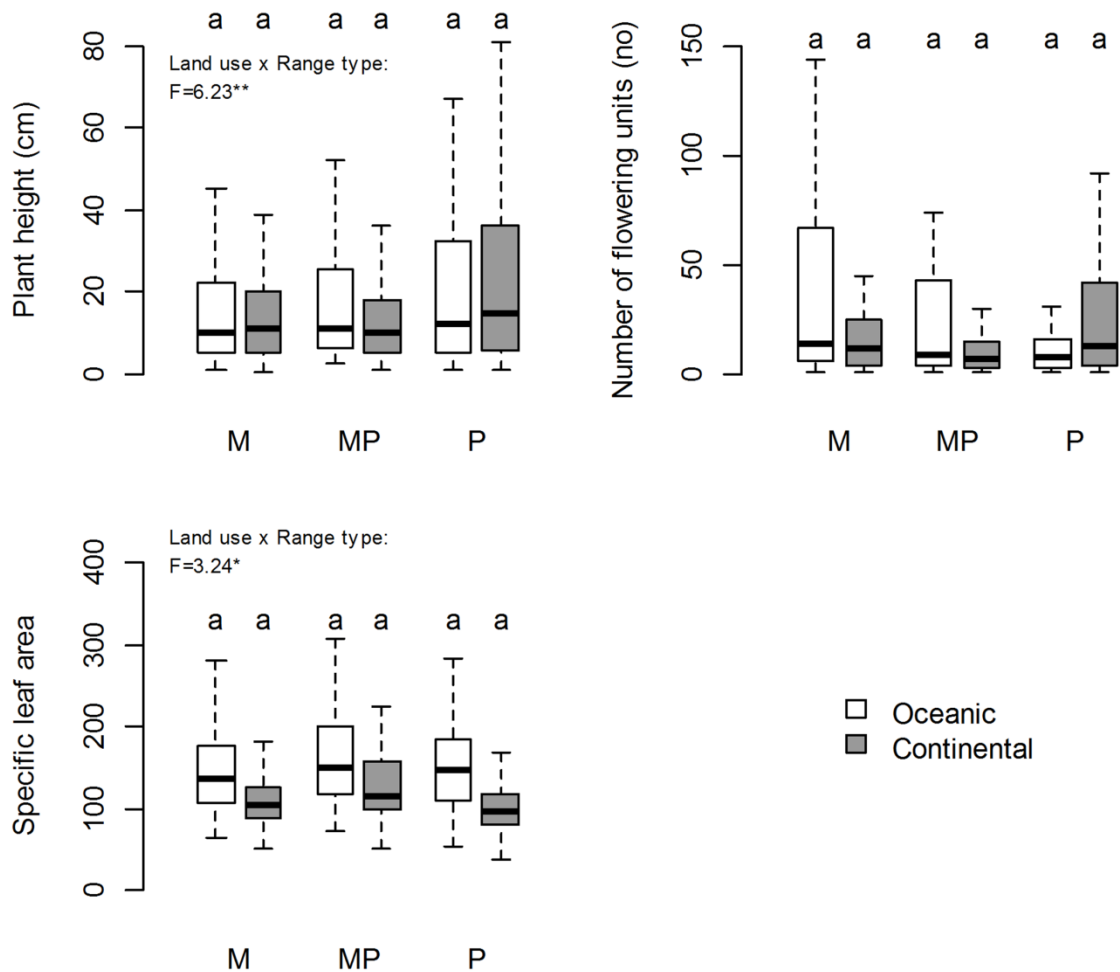


Fig. S8 Interacting effects of land-use type with range type on plant height, number of flowering units and specific leaf area. Oceanic and continental species are shown in white and grey, respectively. Abbreviations for land use: M – meadow, MP – mown pasture, P – pasture. Significant single or interactive effects as result from the GLMMs are mentioned with F-value and asterisks (** $p < 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$). Different small letters indicate statistically significant differences according to a Tukey post-hoc test, using the full model of Table 1 and Appendix S4.








Chapter 5

Synthesis

Main results

The idea behind this experimental approach was to test if and to what extent geographical range characteristics influence plant species' local responses to environmental conditions. Therefore, the present thesis focused on the separate and interacting effects of varying climate conditions along climatic stress gradients as well as negative biotic interactions, in particular competition and slug herbivory, and different land-use types on plant species with divergent macroclimatic characteristics. To this end, three independent experiments were conducted which are presented in Chapter 2-4 of this thesis. In the following, the main results of the experiments are presented referring to the hypotheses introduced at the end of chapter 1. Table 5-1 provides an overview of these hypotheses and the corresponding results from the three studies in this thesis.

Table 5-1 Overview of the hypotheses and the corresponding confirmations in the respective experiments

Publication	Chapter 2 Welk et al. 2014 - PLoS ONE Biotic interactions overrule plant responses to climate, depending on the species' biogeography	Chapter 3 Bütof et al. 2012 - Global Change Biology The responses of grassland plants to experimentally simulated climate change depend on land use and region	Chapter 4 Welk et al. 2019 - Ecology Plant species' range type determines local responses to biotic interactions and land use
H1 Species perform best under the <u>climate conditions</u> that correspond best to their native distribution.			
H2 Species from more stressful environments are locally more susceptible to negative <u>biotic interactions</u> .		Not tested	
H3 Species with divergent geographic distribution respond differentially to variable <u>land-use</u> types. ¹	Not tested		

¹ The results derived from this experiment were not consistent in their direction and the corresponding hypothesis can therefore only be accepted with some reservation. The answers were therefore put in brackets.

The experiment presented in **Chapter 2** was implemented in nine Botanical Gardens in Germany across a considerable climatic continentality-oceanity gradient, with increasing temperature and decreasing precipitation towards more continental climate in the summer 2009. In general, the

climate conditions during the experiment had an impact on the performance of the phytometer. However, in contrast to hypothesis H1, it could not be confirmed that species responses along the climate gradient consistently corresponded to their range type. Moreover, it was observed that species of the continental range type showed increased growth under oceanic, more benign climatic conditions, while species of the oceanic range type did not similarly benefit from the 'better' climatic conditions. Species with different range types also showed general differences in their sensitivity to biotic interactions. According to hypothesis H2, the continental species showed lower survival rates and lower height growth in the presence of both, competitors and herbivores, while these treatments had almost no impact on oceanic species. Interestingly, I found that the effect of the competition treatment varied along the climate gradient in dependence of the species range type. At the dry end of the climate gradient, oceanic species had higher aboveground biomass in absence of competitors, while continental species did so in presence of competitors. In summary, as a result of the first experiment in Botanical Gardens, hypothesis H1 had to be rejected, while hypothesis H2 could be confirmed (Table 5-1).

The second experiment, presented in **Chapter 3**, examined the impact of climate and land-use (ambient grassland management: meadow, mown pasture or pasture) on species with different macroclimatic niche characteristics. For this purpose, plots were established at sites of the Biodiversity Exploratories, which are located in three distant study regions with significantly different climatic conditions. Additionally, climate was manipulated at the plot-level with increased summer drought and increased spring temperature. For each of the six species included in the study, selected macroclimatic niche characteristics obtained from distribution data and corresponding climate data regarding drought resistance and tolerance to warm spring temperatures were used for the statistical analyses. Both ambient and manipulated climate conditions had significant effects on plant growth and survival. However, as in the first experiment, species responses to varying climatic conditions were found not to be in accordance with their macroclimatic niche characteristics. In particular, species distributed in drier regions did not perform best in tolerating dry conditions. However, these species displayed overall lower growth rates of total biomass and a lower shoot-root-ratio compared to species of more humid climates. Survival rates in the different land-use types depended on the macroclimatic drought tolerance of the species. In meadows and mown pastures, survival rates strongly decreased with decreasing drought tolerance, whereas in pastures survival rates were independent of the species' macroclimatic drought tolerance. In summary, hypothesis H1 was again rejected, while hypothesis H3 was confirmed (Table 5-1).

The third experiment, presented in **Chapter 4**, was also carried out in the framework of the Biodiversity Exploratories, on the same plots as the second experiment, but one year later. There, the responses of congeneric species with contrasting range types to the differences of the

climatic conditions between the study regions, biotic interactions and, additionally, different land use types were tested. Phytometer responses to climate conditions differed in dependence to their range type. However, the direction of the phytometer responses was not as expected in hypothesis H1. Again, the continental species did not generally perform best in the continental region. Within the biotic treatments, the effect of competition was much stronger than that of herbivory. However, for both biotic treatments, phytometer responses were found to be consistently different in dependence of their range type. As hypothesized in H2, the continental species were more affected by the presence of competitors and slug herbivores than the oceanic species. The oceanic species instead showed even higher growth rates in the presence of slug herbivores. Only for continental species it was also found that leaf damage from herbivory was higher when competitors were present, while such an interactive effect was not encountered for oceanic species. Species also differed in their performance between land-use type in dependence of their respective range type. While the same plots were used as in the second experiment presented in Chapter 3, the response directions differed compared to the former experiment. In the third experiment, species with continental range type performed better in pastures than species with oceanic range type, while the opposite pattern was encountered in meadows and mown pastures. Because this result partly stands in contrast with the outcome of the second experiment, the third hypothesis H3 can be accepted for both experiments only to a limited extent. Hypothesis H1 could, however, again not be confirmed, while hypothesis H2 could be accepted (Table 5-1).

To summarize, in none of the three experiments the species' responses to varying climate conditions differed simply according to their geographic distribution (H1). In contrast, in both experiments that tested for biotic interactions, continental species were found to be more affected by competition and slug herbivory than oceanic species (H2). Finally, species with contrasting range types showed also differing responses to land-use types (H3), however, the results of the two experiments differed partly in their direction, allowing only for cautious general conclusions.

Plant species responses to climate conditions

Both gradients studied were characterized by differing temperature and precipitation, also during the experiments. The results of all three experiments showed that the survival and growth responses of phytometer plant species were influenced by climate conditions. However, in none of the studies the species responded simply in correspondence to range types or climate niche characteristics. Continental (Chapter 2 and 4) as well as drought tolerant species (Chapter 3) grew better under more benign climate conditions. In particular, the species assigned to the

continental distribution type were transplanted towards oceanic conditions they encounter at their distribution limits. Consequently, here one would have expected decreasing performance, assuming that the distribution of a species corresponds to the respective climatic requirements and tolerances rendering marginal conditions less favorable (Brown 1984; Pearson & Dawson 2003; Soberón 2007). Additionally, drought resistance and frost hardiness experiments with nearly the same set of plant species found no relationship between species responses and macroclimatic niches (Bütöf & Bruelheide 2011; Hofmann et al. 2013). This shows that the local responses of the investigated species to climate conditions cannot be predicted solely from corresponding macroclimatic niche properties derived from the geographic distribution.

One possible explanation is that species performance within ranges does not vary according to a simple Gaussian response curve (Hirzel & Le Lay 2008). Similarly, Brewer et al. (2016) argued for ecologically more plausible plateau responses. Other studies that focused on the relationship between niche position and species abundance reported similar results. For example, in a comparison of a large vegetation data set with species distribution models for about 500 European vascular plant species, Sporbert et al. (2020) did not find a clear relationship between local species abundances in vegetation plots and predicted climatic suitability of these plots. Moreover, geographical distribution limits were sometimes located near the center of the corresponding macroclimatic niche. In consequence, peripheral sites may not in general represent unfavorable climate conditions for the respective species.

In a review of transplant experiments beyond range boundaries, Hargreaves et al. (2014) found that in 75% of cases performance declined beyond the range. The authors suggested that niche constraints (i.e., decline in habitat quality) were responsible for these results. Most performance declines beyond range limits were, however, attributed to limits along elevational gradients, and there they occurred more frequently and to a greater extent towards high elevation limits. It is discussed that especially low temperatures are the predominant climatic driver of elevational range limitation. In contrast, the climate gradient studied in this thesis is not as simple. Along the continentality-oceanity gradient, precipitation decreases towards more continental climate, but temperature, especially that during the growing season, increases. The higher temperature, which generally enhances plant growth, might have counteracted the lower precipitation at the 'continental' sites, where moreover, no limiting arid conditions occurred. Consistent with the results of the here presented experiments, a drought experiment with 40 temperate grassland species also revealed no clear relationship between fundamental drought resistance and species distribution across moisture gradients (Jung et al. 2020). Similarly, also other experimental studies failed to detect any effect of climate relationships to distribution patterns across less steep climatic gradients or towards more favorable climatic conditions (e.g. Stanton-Geddes et al. 2012; Ettinger & HilleRisLambers 2013; but see Cahill et al. 2014).

In general, plant performance not only comprises survival and plant growth, but also successful reproduction in terms of flower development, seed production, seed germination and seedling establishment. The duration of the experiments presented in this thesis covered a maximum of two growing seasons each, and therefore, were too limited in time to study the entire life cycle of the species included. The results can, therefore, only be interpreted to a limited extent and may not be suitable to identify explicit home-site advantages. For example, in a transplantation experiment with two Arctic species over 30 years, home sites advantages became increasingly evident with increasing duration of the experiment (Bennington et al. 2012). Accordingly, several recommendations for conducting transplant experiments to investigate distribution limits contain the need to design them as long-term studies that also consider recruitment (Hargreaves et al. 2014; Lee-Yaw et al. 2016; Willi & van Buskirk 2019).

The impact of biotic interactions in dependence of range type

The impact of negative biotic interactions on species responses were tested in two of the three experiments (Chapter 2 and 4). There, biotic interactions in terms of competition and slug herbivory were manipulated along the two climate gradients presented in Chapter 1. In both experiments, competition as well as slug herbivory affected species responses, with the impact of competition generally being greater than that of slug herbivory. In addition, the species responses to biotic interactions were found to be range type-dependent. As hypothesized in H2, continental species, and thus, species experiencing more stressful climate conditions in their general range, were found to be more sensitive to detrimental biotic interactions than their oceanic congeners. They showed stronger decreases in survival and growth in both experiments. In consequence, it can be concluded that local responses to certain biotic interactions are range type-specific. Since the continental range type is connected with more stressful climate conditions, the respective species should, therefore, be more stress-tolerant. In consequence, the results of the two experiments support that stress-tolerant species are more vulnerable to negative biotic interactions (Louthan et al. 2015; Jones & Gilbert 2016).

This sensitivity of continental species might be a result of adaptation processes that are coupled with evolved trade-offs between stress-tolerance and the ability to cope with negative biotic interactions. In the study presented here, this means that species that are distributed in regions with more stressful climate conditions and lower intensities of competition and slug herbivory may be less adapted to these negative biotic interactions. For example, another transplant study found that fitness declines beyond range margins were the result of negative biotic interactions, in particular herbivory (Benning et al. 2019). Consequently, variations of biotic interactions along climate gradients may lead to lower fitness or abundance and may finally create range

limits that differ from expectations based solely on climatic tolerances of the species (Early & Keith 2019).

Although climate conditions during the experiments differed clearly between the study sites, in contrast to expectation, the impacts of the biotic treatments did not vary along the studied climate gradient (Chapter 2 and 4). However, in several other studies, such patterns could be found. For instance, Lynn et al. (2019) reported from their study along a number of elevational gradients that the negative impact of biotic interactions in terms of herbivory and competition increased towards lower altitudes. Especially plants from the upper sites suffered more from higher plant cover and foliar herbivory damage at lower sites which resulted in lower abundances. Similarly, an experimental approach across an aridity gradient in a semiarid African savanna detected stronger declines in population growth caused by negative biotic interactions in less stressful mesic areas than in more stressful arid sites (Louthan et al. 2018). Probably, the climate gradient investigated within this thesis was not stressful enough at the 'continental end' to cause such effects. Despite these methodological limitations, the detected range type-dependent effects (Chapter 2 and 4) of competition and herbivory on species responses support relevant assumptions on the potential of biotic interactions in limiting broad-scale plant distribution ranges.

However, the underlying mechanisms for these outcomes are still not clear. For instance, slug herbivory was detected to act as limiting factor for the distribution of *Arnica montana*, a species typical of montane meadows (Bruelheide & Scheidel 1999). In a transplant experiment along an elevational gradient, herbivory damage was observed to increase towards lower elevation with generally more benign climate conditions, which caused reduced fitness and higher mortality of the focal species. However, such observations provide no clear evidence for a putative stress tolerance – herbivory resistance trade-off. Another experiment that compared the palatability and feeding preferences of slugs between several Asteraceae species found that species restricted to higher altitudes, and thus more stressful habitats, were not generally preferred by slugs (Scheidel et al. 2003). Furthermore, it has been suggested that species that have to cope with stressful environments in terms of water balance are less prone to slug herbivory because of a harder leaf texture and a higher content of secondary metabolites which is mostly correlated with lower growth rates (Grime et al. 1968; Grime et al. 1996).

In the here presented experiments, relative herbivory damage ratios between oceanic and continental species were not consistent, since in the Botanical Gardens the oceanic species showed higher increases in proportion of consumed leaf area (Chapter 2), while the opposite was observed in the Biodiversity Exploratories (Chapter 4). However, in both experiments I found that oceanic species showed better compensatory responses to biotic interactions. In the Botanical Gardens, particularly when competitors and herbivores were present, number of

flower units of oceanic species decreased, which might be a response to changed resource allocation patterns with a switch to increased vegetative growth (Rosenthal & Kotanen 1994). This suggestion is supported by the observation in the Exploratories (Chapter 4), where oceanic species showed slightly increased growth rates in presence of herbivores. Hence, the higher sensitivity of continental and thus stress-tolerant species to slug herbivory does not seem to be based on a generally higher palatability due to a lack of defense adaptations, but rather to a lower capacity to compensate for herbivore damage.

In summary, I found range type-specific responses to both biotic interaction types, which however were not modified by climate conditions. In the literature, the assumption that biotic interactions become more important towards benign climate conditions is repeatedly discussed, but experimental evidences are rare (Louthan et al. 2015; Lee-Yaw et al. 2016). Support for this hypothesis was mostly derived from observational studies or from the fact that climatic causes for range limitations could not be identified. Experiments such as those performed for this thesis, in which the impact of different controlled biotic interactions on multiple species are investigated simultaneously along climate gradients, are highly recommended by several authors, but rarely carried out, perhaps because of the high effort involved.

Land-use effects on species responses

In the framework of the Biodiversity Exploratories, it was possible to test if species responses differ between certain land-use types, in particular different grassland management practices (H3). Two experiments were carried out using the same combination of plots in three Exploratory regions (Chapter 3 and 4). Within each Exploratory, 15 plots were established in commercially managed grasslands, representing either meadows, mown pastures or pastures. In both experiments, the species of the contrasting range types differed in their responses to land-use types. However, the direction of the results was not consistent. In the second experiment (Chapter 3), species with a higher macroclimatic drought tolerance, derived from the species geographical distribution, survived better in meadows, followed by mown pastures and pastures. The opposite was found in the third experiment, albeit not for survival, but for response variables related to plant growth.

Because of these mixed results I have to reject the third hypothesis (H3). Although the set of species included in the studies differed in number, at least two thirds of the species from the second experiment (Chapter 3) were also included in the third experiment (Chapter 4). In addition, according to Briemle et al. (2002), all included species have similar, i.e. intermediate tolerances to mowing, grazing and trampling. The different outcomes with respect to the species' range type might be due to context-specific effects of land use on survival and growth,

which could not be accounted for in the study design. The duration and time frame of the experiments differed slightly. While the second experiment ran from summer 2008 to spring 2009, the third experiment ran from spring 2009 to summer 2010 (see Table 1-1, Chapter 1). Because the phytometers of the last experiment (Chapter 4) experienced two summer periods, and therefore, also more cutting and mowing events, they probably have shown higher differences in growth performance but no survival differences between the land-use types. Conversely, the available period for phytometer growth in the second experiment (Chapter 3) was too short to obtain response differences related to plant growth, since they were planted in summer and harvested in the following spring. In turn, the differences in survival in the second experiment (Chapter 3) developed possibly because the phytometer planting took place in summer 2008 just before the rain shelters were installed. In summer, the more dense and homogenous vegetation matrix of mown grasslands might have provided facilitative effects for the individuals that were planted shortly before. However, these facilitative effects were most pronounced for species with a continental range type. Conversely, the disturbance in purely grazed plots may have had higher impacts on survival when planting occurred in summer in experiment 2, compared to planting in spring in experiment 3. Indeed, survival in the second experiment (Chapter 3) was overall lower in pastures compared to the other land-use types, while in the third experiment (Chapter 4) no differences in survival were found between land-use types.

Another possible explanation is that the contrasting directions in the responses of continental or more drought-tolerant species and, conversely, oceanic or less drought-tolerant species are caused by context-specific sensitivities to mowing and grazing impacts on survival and plant growth. While higher disturbance in pastures may cause higher mortality in younger life stages of more drought-tolerant species (Chapter 3), plant growth should be stronger affected by competition in mown grasslands (Chapter 4). In contrast, the oceanic, i.e., less drought tolerant species, showed no clear differences in survival between the land-use types (Chapter 3 and 4) but much higher plant growth in meadows and mown pastures compared to pastures (Chapter 4). This could indicate that not mowing or grazing per se affected the survival of oceanic species, but that disturbance in pure pastures resulted in decreased plant growth of these species.

Disturbance in pastures does not only increase the risk of plants being damaged by grazing and trampling, but also exposing them to more stressful microclimatic conditions with higher surface temperature or topsoil drought in open sites, which might favor stress- or disturbance-tolerant species (Deléglise et al. 2015). Similarly, Busch et al. (2019) found that species differed in their growth responses to mowing and grazing with respect to their ecological strategy type, and thus, their sensitivity to disturbance in pastures and competition in meadows. For example, mowing, especially at higher frequencies, favored fast-growing, competitive species. Similar

results were not only found in temperate but also in sub-Mediterranean grasslands, for example in a comparison of karst meadows and karst pastures in the North Adriatic Karst (Pipenbaher et al. 2011). In accordance with these studies, in the present thesis, the oceanic or less drought-tolerant species, which were found to be less affected by competition (Chapter 2 and 4) and to have overall higher growth rates than continental species (Chapter 3), grew better in land-use types with a regular mowing regime (Chapter 4).

In summary, plant responses to different land-use types were found to be range type-specific in both experiments. Interestingly, response patterns for survival and plant growth differed in direction, indicating, that sensitivities to grazing and mowing may vary during different stages of plant life cycle. Other transplantation studies with grassland species also found contrasting outcomes for several response variables (Herz et al. 2017; Breitschwerdt et al. 2019). Additionally, clearer conclusions about the impact of different land-use types can only be drawn from long-term studies, since effects of different grassland-management practices can sometimes become apparent only after several years (Koncz et al. 2020). Especially, information on recruitment patterns and reproduction in the different land-use types would be needed to draw valid conclusions if responses to land use show range type-specific patterns. Fertilization effects may further increase differences in plant responses on grazing and mowing and should therefore be taken into account in future studies (Tälle et al. 2016). Overall, the comparative discussion of the presented results is limited because similar research is lacking in the literature, except for studies dealing with effects on plants of different ecological strategy types. Nevertheless, the findings of the present thesis highlight the importance of different land-use types that affect local species responses in several ways. Consequently, plant responses to actual land use or land-use change can be assumed to be context-specific and not uniform. This may apply in particular to plant species that occur predominantly in semi-natural habitats, such as grassland, whose conservation is strongly dependent on human use or maintenance (Veen et al. 2009).

Conclusion and Outlook

An important conclusion from the results of the experiments presented here is that local plant performance cannot be predicted simply from the species' macroclimatic realized niche characteristics. However, species were found to have locally different sensitivities to negative biotic interactions depending on their range type. These different sensitivities could be due to different selection pressures and adaptations in species' main climatic niche conditions. Such processes are conceivable as a trade-off between higher competitive ability combined with better compensatory abilities to herbivory, and lower tolerance to stressful abiotic

environmental conditions. Conversely, higher tolerance of stressful abiotic conditions is linked to lower overall growth performance and lower compensatory or competitive ability. The findings on the different sensitivities of plant species to negative biotic interactions in dependence on their range type support recent findings on the changing effects of climate and biotic interactions in defining distribution boundaries along stress gradients. There, it is assumed that climate becomes less and biotic interactions more important with more benign climatic conditions.

The experiments also showed that land-use effects, such as different grassland management practices, can have different impacts on species responses at the local scale, which are strongly context specific. This indicates that – as already known for different ecological strategy types – species of the same type do not generally respond in the same way to grazing or mowing, here in the case of different geographical range types. However, due to the inconsistent results, further research is needed to clarify the influence of species' geographical distribution on plant responses to certain land-use types.

The main finding of this work is that the inclusion of a priori classifications of species based on their geographical distribution, such as range types, provides a useful framework for experimental studies of species distribution differences. Of course, it is important to be aware of the criteria that are to be used to group species into the appropriate range types and that these criteria should also fit the research question and the factors addressed in the study. Examples of such classifications apart from the range type studied here (continental vs. oceanic) are qualitative classifications, such as cold vs. warm (Hofmann et al. 2013), or quantitative classifications, such as endemic vs. wide-spread (Lavergne et al. 2004), or rare vs. common (Kempel et al. 2020). Similarly, a categorization or grouping of species considering their climate niche properties may also be useful (e.g. climatic niche groups, see Bilton et al. 2016; Liu et al. 2018). Such categorizations provide a way to generalize conclusions about mechanisms concerning certain groups of species from experimental approaches with only using subsets of species of these groups, which makes such experiments feasible. In addition, using a priori classifications helps testing macroecological hypotheses or developing hypotheses within experimental approaches.

In general, the experiments presented here have revealed important results that help to understand some underlying mechanisms of the causes of geographic plant distributions. However, some limitations were found that might be optimized in further experiments.

Firstly, the length of the experiments should ideally include also the plants' reproductive phase and seedling establishment to investigate plant performance over a full life cycle. Secondly, further experiments should make use of longer gradients to include also the climatic niche margins. However, finding comparable field sites at broader scales, which differ solely or mainly

in the factors of interest becomes more difficult at larger distances. Furthermore, the risk of confounding effects which are correlated with the respective study sites increases. Therefore, carefully designed, simultaneously implemented manipulations are essential, which involve a high logistic effort. A good opportunity would be an approach similar to the experimental set-up presented in Chapter 2 using Botanical Gardens, but then also including sites outside Germany, across countries or even continents. As Botanical Gardens have the advantage to be mostly connected to academic research facilities, it should be easier to obtain and install equipment there, and there usually staff is available to support the treatments and measurements. Since experiments at larger geographical and temporal scales require considerably more logistic effort and time, well designed and coordinated distributed experiments (see Fraser et al. 2013) seem to be the most promising approach.

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Appendices

Author contributions

Chapter 2

AW, EW and HB developed the study concept. AW prepared and carried out the field work and data collection. The statistical analyses were also carried out by AW with the help of HB. AW wrote the first draft of the manuscript. EW and HB contributed to writing the final version of the manuscript. Contribution of AW 90 %.

Chapter 3

The concept of the climate change treatment within the Exploratories was developed by CD and MSL. AB (AW), HB and EW conceived the phytogeographical study question and the species selection. LvR carried out the field work for the experimental setup, including phytometer planting. The harvest and data collection concerning the phytometers were conducted by AB (AW). Statistical analyses were carried out by AB (AW), whereby EW helped by calculating the species' macroecological niche and HB gave helpful comments to concepting the R-codes for the generalized mixed models. AB (AW) wrote the first draft of the manuscript. EW and HB contributed to the writing of the manuscript. CD and MSL gave helpful comments. Contribution of AB (AW) 80 %.

Chapter 4

EW and HB developed the study concept. The experimental set up, field work and data collection were prepared and coordinated solely by AW. MB, JB and AW carried out the field work and data collection equally. The statistical analyzes were conducted by AW, whereby HB helped to develop the SAS-syntax. AW wrote the first draft of the manuscript and EW and HB contributed to writing the final version. Contribution of AW 80 %.

Curriculum Vitae

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2000 – 2007 Studies in biology, Martin-Luther-University Halle-Wittenberg
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- 2010 Franziska Reitmajer: „Bedeutung abiotischer und biotischer Einflüsse auf den Diasporenansatz und die Diasporenqualität verschieden verbreiteter Grünlandarten“
Bachelor-Thesis
- 2010 Nicole Stahl: „Einfluss von Temperatur und Bodenfeuchte auf das Wachstum unterschiedlich verbreiteter Arten der Trocken- und Halbtrockenrasen“
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List of publications

Publications of this thesis:

Bütof, A., von Riedmatten, L.R., Dormann, C.F., Scherer-Lorenzen, M., Welk, E., & Bruelheide, H. 2012. The responses of grassland plants to experimentally simulated climate change depend on land use and region. *Global Change Biology* 18: 127–137.

Welk, A., Welk, E., Baudis, M., Böckelmann, J., & Bruelheide, H. 2019. Plant species' range type determines local responses to biotic interactions and land use. *Ecology* 100: e02890.

Welk, A., Welk, E., & Bruelheide, H. 2014. Biotic interactions overrule plant responses to climate, depending on the species' biogeography. *PLoS ONE* 9: e111023.

Other publications by the author:

Bütof, A., & Bruelheide, H. 2011. Effects of an unspecialized soil pathogen on congeneric plant species with different geographic distributions. *Preslia* 83: 205–217.

Hofmann, M., **Bütof, A.**, Welk, E., & Bruelheide, H. 2013. Relationship between fundamental and realized niches with respect to frost and drought resistance. *Preslia* 85: 1–17.

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Eigenständigkeitserklärung

Hiermit erkläre ich, dass ich die vorliegende Doktorarbeit mit dem Titel „The impact of species' range type on the responses of congeneric plant species to different climate conditions, biotic interactions and land use“ eigenständig und ohne fremde Hilfe verfasst sowie keine anderen als die im Text angegebenen Quellen und Hilfsmittel verwendet habe. Textstellen, welche aus verwendeten Werken wörtlich oder inhaltlich übernommen wurden, wurden von mir als solche kenntlich gemacht.

Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe. Die vorliegende Doktorarbeit wurde bis zu diesem Zeitpunkt weder bei der Naturwissenschaftlichen Fakultät I – Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt.

Astrid Welk, Halle (Saale), 16.11.2021