Xerothermic grasslands in Central Germany: Vegetation changes, functional trait composition and plant-plant interactions

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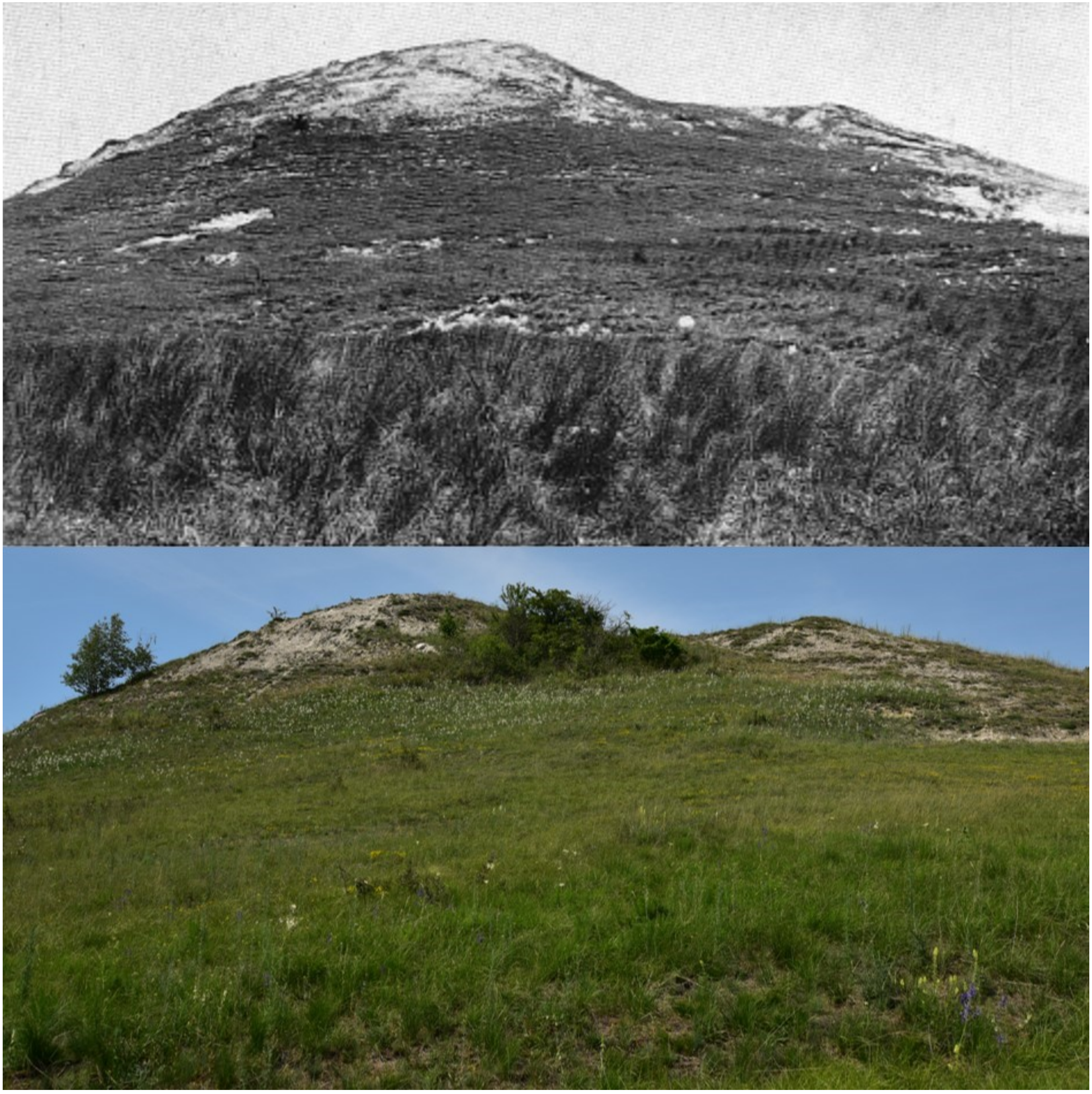

Vegetation on the southwest slope of the Dorl in the Kyffhäuser region in the 1930s (above; photo was taken from Meusel (1939)) and in 2019 (below; photo: Tim Meier, 04.06.2019).

„Darüber hinaus betrachten wir es aber als wichtigste Aufgabe, von den lokalen Beobachtungen ausgehend zu einem allgemeinen Gesamtbild vorzudringen. Denn so wesentlich jede zuverlässige Einzeluntersuchung für den Fortschritt der Forschung auch sein kann, so werden in der Vegetationskunde alle Teilbetrachtungen doch erst dann ins rechte Licht gesetzt, wenn man sie aus den großen, in der Natur allgemein zutage tretenden Grundlinien der Gestaltung zu verstehen trachtet.“

Hermann Meusel (1939): Die Vegetationsverhältnisse der Gipsberge im Kyffhäuser und im südlichen Harzvorland. – *Hercynia 4 (2)*: 1–372, p. 6.

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Attachment:

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Summary

Xerothermic grasslands contain various plant communities and can be divided mainly into two grassland types: Dry and semi-dry grasslands. These grasslands have a high biodiversity of both vascular plant and animal species and comprise a large proportion of rare and endangered species. But since the second half of the 20th century, xerothermic grasslands generally showed a dramatic loss of species caused by the processes of ongoing global change, such as global warming and atmospheric nitrogen deposition and resulting land use changes, whereby extreme weather events such as heat waves and droughts have recently become more frequent and intense, affecting the floristic and functional composition of xerothermic grasslands as well as plant interactions. For example, such processes have promoted the spread of different grass species, as they are often considered as strong competitors to forbs, so that they play a decisive role in the conversion of formerly species-rich plant communities into species-poorer ones. Particularly in Central Germany, the grass species *Bromus erectus* became increasingly dominant within xerothermic grasslands during the 20th century and could probably have a negative impact on their species richness in the future.

The general aim of my thesis is to reveal changes in the floristic and functional composition of xerothermic grasslands in Central Germany, as well as changes in plant-plant interactions, and to evaluate these results considering the processes of ongoing global change by also estimating future vegetation changes. A central aim is to investigate and evaluate the role of increasingly dominant grass species (e.g. abundance, intraspecific trait variability, plant-plant interactions), focusing on *Bromus erectus* within these grasslands, as the underlying mechanisms leading to such dominance are not fully understood. Other grasses such as *Brachypodium pinnatum*, *Festuca rupicola*, *Helictotrichon pratense* and *Stipa* sp. are also included in the investigations. Based on the results, recommendations for nature conservation will be made, as these grass species could possibly have a negative impact on the species richness of xerothermic grasslands in Central Germany. For this purpose, in the three study regions 1) Kyffhäuser, 2) Porphyry outcrops near Halle (Saale) and 3) Schafberg (lower Unstrut valley), I resurveyed vegetation relevés, took soil samples and measured functional traits. Additionally, a competition experiment was conducted in the Botanical Garden Halle (Saale) to investigate the plant-plant interactions of xerothermic grasses.

In the first two studies, so-called resurvey studies, I resurveyed vegetation relevés over a time period of more than 20 years to document temporal and spatial changes in the vegetation of xerothermic grasslands in Central Germany in the course of global change. In the first resurvey study, no changes in total species richness of dry and semi-dry grasslands in the regions Kyffhäuser and Porphyry outcrops near Halle (Saale) were found, whereas in the second resurvey study an overall decline of total species richness and within different xerothermic plant communities at the Schafberg in the lower Unstrut valley was recorded. Over time, in the first resurvey study, dry grasslands showed a higher floristic similarity than semi-dry grasslands. In contrast, the grasslands became more dissimilar in the second resurvey study, as species turnover in all four plant communities was on average 50%, while semi-dry grasslands showed higher species turnover than dry grasslands. However, in both studies, I revealed a decrease in typical, often threatened, xerothermic grassland species and an increase in annual species and in some dominant grass species. But in the first resurvey study, species number and cover of graminoids generally increased, while in the second resurvey study most of them decreased in presence and cover. Surprisingly, in both studies I found a significant increase in presence and cover of *Bromus erectus* in most of the investigated plant communities, whereas other dominant grasses (e.g. *Festuca rupicola*, *Helictotrichon pratense*) showed partly opposite trends. Furthermore, in the second resurvey study, I found a strong intercorrelation between the indicator values for moisture and nutrients.

In the third study, I conducted a functional approach for xerothermic grasslands in Central Germany by comparing both the functional trait composition of dry and semi-dry grasslands by calculating the community weighted mean (CWM) and by investigating the effect of different soil properties on the functional trait composition of both grassland types. Furthermore, I compared the functional traits and their intraspecific trait variability (ITV) of the five grasses *Bromus erectus*, *Brachypodium pinnatum*, *Festuca rupicola*, *Helictotrichon pratense* and *Stipa capillata*. There was only a small differentiation in the functional trait composition between dry and semi-dry grasslands regarding the CWM of leaf dry mass, leaf area, leaf nitrogen and leaf carbon concentration, while other traits (e.g. vegetative plant height, specific leaf area) did not differ between the two grassland types, but the functional structure was largely determined by the dominant grasses. Soil factors had minor effects on the functional trait composition of dry and semi-dry grasslands, although soil depth, carbonate content and carbon/nitrogen ratio had the highest influence on the CWM. I detected species-specific trait differences in the five grasses, but they showed relatively similar ITV and I concluded that *B. erectus* was not better adapted to changing environmental conditions than the other grasses.

In the fourth study, I experimentally investigated the growth performance and plant-plant interactions of *Bromus erectus* and the xerothermic grasses *Brachypodium pinnatum*, *Stipa capillata* and *Stipa tirsa* under nutrient addition and above-ground biomass removal or clipping. *Bromus erectus* showed the highest biomass production of all grasses under nutrient addition and was thus the most frequent winner under this treatment, but less so under the clipping treatment. Compared to the other grasses, the effect of intraspecific competition in *B. erectus* was slightly more intensive than interspecific competition. Finally, I revealed that the growth and competitive ability of *B. erectus* affected *S. capillata* and *S. tirsa* more negatively than *B. pinnatum*, which could lead to an increasing dominance of *B. erectus* under future increasing nitrogen enrichment, resulting to displacement of both species of *Stipa*.

Overall, I conclude from my results that all detected vegetation changes in xerothermic grasslands in Central Germany can be explained by global change, of which the main drivers in my thesis are, in this order: 1) global warming (especially severe drought events), 2) atmospheric nitrogen input and deposition, 3) changes in traditional land use. Generally, dry grasslands were less prone to successional processes than semi-dry grasslands, which was reflected in their site conditions (e.g. steeper slope, shallower soil depth, lower water and nutrient availability). In more than 20 years, a species turnover has taken place in which typical, partly rare and threatened xerothermic grassland species decreased and annuals and dominant grass species (especially *B. erectus*) increased. The replacement of habitat specialists by generalists, in this case dominant grasses, causes a functional homogenisation at the community level (main driver: severe drought). I confirmed this functional homogenisation of xerothermic grasslands, as both grassland types have become more functionally similar over time, in that increasingly dominant grasses (the most abundant species in the plots) have replaced the functions previously filled by other species in the grasslands with their own functions. Dominant grasses such as *B. erectus* are more resilient to drought and currently play an equivalent role in the ecosystem function of xerothermic grasslands, e.g. by maintaining biomass production under such disturbance. Nevertheless, xerothermic grasslands are subject to dynamic processes as environmental fluctuations caused changes in community composition, whereby such grasslands have the potential to regenerate spontaneously after years of heavy disturbance. Nowadays, *B. erectus* shows a high dominance in almost all investigated xerothermic plant communities in Central Germany and is the clear 'winner' of all investigated grasses under ongoing global change, which is attributed to its high regeneration potential after disturbance and its high competitive ability. *Bromus erectus* contributes most to the functional homogenisation of these xerothermic grasslands, but with negative effects on their phytodiversity, as the species may contribute to a conversion into species-poorer plant communities, whereas from a long-term perspective a prolonged drought could favour this conversion.

Finally, I assume that the xerothermic grasslands in Central Germany have lost part of its conservation value, for example as shown by the disproportionate loss of threatened species. Therefore, it is essential to continue or reintroduce traditional land use (e.g. grazing and mowing) to maintain and protect the biodiversity of these grasslands. The most advantageous opportunity of suppressing the increasing dominance of grasses such as *B. erectus* in the longer term is very early and intensive spring grazing with higher stocking rates of sheep. Unfortunately, I expect that in the near future some previously not yet threatened xerothermic species may have to be added to the Red Lists, while for other species their endangerment category will change in a negative sense. The loss of threatened species is irreversible, so that they could become locally extinct in xerothermic grasslands in the longer term despite appropriate management. Moreover, I expect a further increase of *B. erectus* within central German xerothermic grasslands in future, whereas their immigration in northern direction of Europe will dramatically continue. Although its competitive potential may not yet be fully achieved, the first negative effects of their dominance on the species richness of these grasslands are already noticeable.

Zusammenfassung

Xerothermrasen beinhalten vielfältige Pflanzengesellschaften und lassen sich hauptsächlich in zwei Graslandtypen einteilen: Trocken- und Halbtrockenrasen. Diese Grasländer weisen eine hohe Biodiversität sowohl an Gefäßpflanzen- als auch an Tierarten auf und umfassen einen großen Anteil an seltenen und gefährdeten Arten. Jedoch zeigte sich seit der zweiten Hälfte des 20. Jh. allgemein für Xerothermrasen ein dramatischer Artenverlust, verursacht durch die Prozesse des fortlaufenden „Globalen Wandels", wie Klimaerwärmung und atmosphärischer Stickstoffeintrag sowie damit verbundene Landnutzungsänderungen, wobei in jüngster Zeit auch extreme Wetterereignisse wie Hitzewellen und Dürren verstärkt und häufiger auftreten, was sich folglich auf die floristische und funktionelle Zusammensetzung von Xerothermrasen und auch auf die pflanzlichen Interaktionen auswirken. Solche Prozesse haben z. B. die Ausbreitung verschiedener Grasarten gefördert, da sie gegenüber Kräutern oft als die stärkeren Konkurrenten gelten, sodass sie eine entscheidende Rolle bei der Umwandlung von ehemals artenreichen in artenärmere Pflanzengemeinschaften spielen. Insbesondere in Mitteldeutschland hat im 20. Jh. die Grasart *Bromus erectus* innerhalb der Xerothermrasen zunehmend an Dominanz erlangt und könnte vermutlich einen negativen Einfluss auf deren Artenreichtum in Zukunft ausüben.

Das generelle Ziel meiner Arbeit ist es, Veränderungen in der floristischen und funktionellen Zusammensetzung von Xerothermrasen in Mitteldeutschland sowie Veränderungen in den pflanzlichen Interaktionen aufzuzeigen und diese Ergebnisse unter Berücksichtigung des fortlaufenden „Globalen Wandels" zu bewerten, indem auch zukünftige Vegetationsveränderungen abgeschätzt werden. Ein zentrales Ziel ist, die Rolle der zunehmend dominanten Grasarten zu untersuchen und zu bewerten (z. B. Abundanz, intraspezifische Merkmalsvariabilität, pflanzliche Interaktionen), fokussierend auf *Bromus erectus* in diesen Grasländern, da z. B. die zugrundeliegenden Mechanismen, die zu einer solchen Dominanz führen, nicht vollständig geklärt sind. Dabei werden andere Gräser, wie *Brachypodium pinnatum*, *Festuca rupicola*, *Helictotrichon pratense* und *Stipa* sp., auch in die Untersuchungen einbezogen. Anhand der Ergebnisse sollen Empfehlungen für den Naturschutz gegeben werden, da sich diese Grasarten eventuell negativ auf den Artenreichtum der Xerothermrasen in Mitteldeutschland auswirken könnten. Dafür habe ich in den drei Regionen 1) Kyffhäuser, 2) Porphyrkuppenlandschaft bei Halle (Saale) und 3) Schafberg (Unteres Unstruttal) frühere Vegetationsaufnahmen wiederaufgenommen, Bodenproben entnommen und funktionelle Merkmale erhoben. Zusätzlich wurde ein Konkurrenzexperiment im Botanischen Garten Halle (Saale) durchgeführt, um die pflanzlichen Interaktionen von xerothermen Gräsern zu untersuchen.

In den ersten beiden Studien, sogenannte Wiederholungsstudien, hatte ich über einen Zeitraum nach mehr als 20 Jahren Vegetationsaufnahmen wiederaufgenommen, um zeitliche und räumliche Veränderungen in der Vegetation der Xerothermrasen in Mitteldeutschland im Zuge des „Globalen

Wandels“ zu dokumentieren. In der ersten Wiederholungsstudie waren keine Veränderungen in der Gesamtartenzahl der Trocken- und Halbtrockenrasen für die Regionen Kyffhäuser und Porphyrkuppenlandschaft nachweisbar, wohingegen in der zweiten Wiederholungsstudie eine allgemeine Abnahme in der Gesamtartenzahl und innerhalb verschiedener xerothermer Pflanzengesellschaften am Schafberg im Unteren Unstruttal erfasst werden konnte. Über die Zeit wiesen in der ersten Wiederholungsstudie die Trockenrasen eine höhere floristische Ähnlichkeit als die Halbtrockenrasen auf. Dagegen wurden in der zweiten Wiederholungsstudie die Grasländer unähnlicher, da der Artenumsatz in allen vier untersuchten Pflanzengesellschaften durchschnittlich 50 % betrug, wobei die Halbtrockenrasen einen höheren Artenumsatz als die Trockenrasen aufwiesen. Trotzdem konnte ich in beiden Studien eine Abnahme von typischen, oftmals gefährdeten Xerothermrasenarten und eine Zunahme von annuellen Arten und einiger dominanter Grasarten nachweisen. Jedoch nahmen in der ersten Wiederholungsstudie die Artenzahl und Deckung der Graminoiden im Allgemeinen zu, während in der zweiten Wiederholungsstudie die meisten von ihnen in ihrer Stetigkeit und Deckung abnahmen. Überraschenderweise fand ich in beiden Studien eine signifikante Zunahme in der Stetigkeit und Deckung von *Bromus erectus* in fast allen untersuchten Pflanzengesellschaften, während andere dominante Gräser (z. B. *Festuca rupicola*, *Helictotrichon pratense*) teilweise gegenläufige Entwicklungen zeigten. Ferner konnte ich in der zweiten Wiederholungsstudie eine starke Interkorrelation zwischen den Zeigerwerten für Feuchtigkeit und Nährstoffe feststellen.

In der dritten Studie führte ich einen funktionellen Ansatz für die Xerothermrasen in Mitteldeutschland durch, indem ich sowohl die funktionelle Zusammensetzung der Trocken- und Halbtrockenrasen unter Berechnung des „gemeinschaftsgewichteten Mittelwertes“ (CWM) verglich als auch den Effekt unterschiedlicher Bodeneigenschaften auf die funktionelle Merkmalszusammensetzung beider Graslandtypen untersuchte. Weiterhin verglich ich die funktionellen Merkmale und deren intraspezifische Merkmalsvariabilität (ITV) der fünf Gräser *Bromus erectus*, *Brachypodium pinnatum*, *Festuca rupicola*, *Helictotrichon pratense* und *Stipa capillata*. Es zeigte sich nur eine geringe Differenzierung in der funktionellen Merkmalszusammensetzung zwischen Trocken- und Halbtrockenrasen hinsichtlich des CWM der Blatttrockenmasse, Blattfläche, Blattstickstoff- und Blattkohlenstoffkonzentration, während sich andere Merkmale (z. B. vegetative Wuchshöhe, spezifische Blattfläche) zwischen beiden Graslandtypen nicht unterschieden, jedoch die funktionelle Struktur weitestgehend durch die dominanten Gräser bestimmt wurde. Die Bodenfaktoren besaßen einen geringen Effekt auf die Merkmalszusammensetzung der Trocken- und Halbtrockenrasen, obwohl Gründigkeit, Carbonatgehalt und Kohlenstoff/Stickstoff-Verhältnis den höchsten Einfluss auf den CWM hatten. Ich konnte bei den fünf Gräsern zwar artspezifische Merkmalsunterschiede nachweisen, jedoch zeigten diese eine relativ ähnliche ITV, und ich schloss daraus, dass *B. erectus* nicht besser gegen verändernde Umweltbedingungen angepasst war als die anderen Gräser.

In der vierten Studie untersuchte ich experimentell die Wachstumsleistung sowie intra- und interspezifischen Interaktionen zwischen *Bromus erectus* und den xerothermen Gräsern *Brachypodium*

pinnatum, *Stipa capillata* und *Stipa tirsa* unter Nährstoffzugabe und oberirdischem Biomasseentzug bzw. Beschneidung. *Bromus erectus* zeigte von allen Gräsern die höchste Biomasseproduktion unter Nährstoffzugabe und war somit der häufigste Gewinner unter dieser Behandlung, wuchs aber weniger unter der Behandlung des Schnittes. Im Gegensatz zu den anderen Gräsern war der Effekt der intraspezifischen Konkurrenz bei *B. erectus* etwas stärker als die interspezifische Konkurrenz. Schließlich konnte ich nachweisen, dass sich das Wachstum und die Konkurrenzfähigkeit von *B. erectus* negativer auf *S. capillata* und *S. tirsa* als auf *B. pinnatum* auswirkten, was zu einer zunehmenden Dominanz von *B. erectus* bei einer zukünftig steigenden Stickstoffanreicherung führen könnte und die Verdrängung beider *Stipa*-Arten zur Folge hätte.

Insgesamt konnte ich anhand meiner Ergebnisse schließen, dass sich alle nachgewiesenen Vegetationsveränderungen der Xerothermrasen in Mitteldeutschland durch den „Globalen Wandel“ erklären lassen, deren Haupttreiber in meiner Arbeit in dieser Reihenfolge sind: 1) Klimaerwärmung (insbesondere schwere Dürreereignisse), 2) atmosphärischer Stickstoffeintrag und -deposition, 3) Veränderungen in der traditionellen Landnutzung. Generell waren Trockenrasen weniger anfällig für Sukzessionsprozesse als Halbtrockenrasen, was sich in ihren Standortbedingungen widerspiegelte (z. B. steilere Hangneigung, geringere Gründigkeit des Bodens, geringere Wasser- und Nährstoffverfügbarkeit). In mehr als 20 Jahren ist es zu einem Artenwechsel gekommen, indem typische, z. T. seltene und gefährdete Xerothermrasenarten abgenommen und Annuelle sowie dominante Grasarten (insbesondere *B. erectus*) zugenommen hatten. Der Ersatz von Habitatspezialisten durch Generalisten, in diesem Fall dominante Gräser, verursacht eine funktionelle Homogenisierung auf Gesellschaftsebene (Haupttreiber: schwere Dürre). Ich konnte diese funktionelle Homogenisierung der Xerothermrasen bestätigen, da beide Graslandtypen über die Zeit funktionell ähnlicher geworden sind, indem die zunehmend dominanten Gräser (die am häufigsten abundanten Arten in den Untersuchungsflächen) ihre eigenen Funktionen in diesen Grasländern durch die zuvor von anderen Arten ausgefüllten Funktionen ersetzt haben. Dominante Gräser, wie *B. erectus*, sind resilienter gegenüber Dürre und nehmen aktuell eine gleichwertige Rolle in der Ökosystemfunktion der Xerothermrasen ein, indem sie z. B. die Biomasseproduktion bei solchen Störungen aufrechterhalten können. Trotzdem unterliegen Xerothermrasen auch dynamischen Prozessen, da fluktuierende Witterungsbedingungen Veränderungen in der Zusammensetzung der Pflanzengesellschaften verursachen, wobei solche Grasländer das Potenzial haben, sich nach Jahren starker Störungen spontan regenerieren zu können. *Bromus erectus* zeigt mittlerweile in fast allen untersuchten xerothermen Pflanzengesellschaften in Mitteldeutschland eine hohe Dominanz und ist der klare „Gewinner“ von allen untersuchten Gräsern unter dem fortlaufenden „Globalen Wandel“, was auf das hohe Regenerationspotential nach Störung und die hohe Konkurrenzfähigkeit zurückzuführen ist. *Bromus erectus* trägt am meisten zur funktionellen Homogenisierung dieser Xerothermrasen bei, aber mit negativen Effekten auf deren Phytodiversität, da die Art zu einer Umwandlung in artenärmere

Pflanzengesellschaften beitragen kann, zumal aus langfristiger Sicht eine langanhaltende Trockenheit diese Umwandlung begünstigen könnte.

Letztlich gehe ich davon aus, dass die Xerothermrasen in Mitteldeutschland einen Teil ihres Naturschutzwertes eingebüßt haben, was sich z. B. anhand des überproportionalen Verlustes an gefährdeten Arten äußert. Deshalb muss unbedingt die traditionelle Landnutzung (z. B. Beweidung und Mahd) weitergeführt oder wiedereingeführt werden, um die Biodiversität dieser Grasländer zu erhalten und zu schützen. Die vorteilhafteste Möglichkeit, die zunehmende Dominanz von Gräsern, wie *B. erectus*, längerfristig zu verhindern, ist eine sehr frühe und intensive Frühjahrsbeweidung mit einer hohen Besatzstärke an Schafen. Leider erwarte ich in der nahen Zukunft, dass einige bisher noch nicht gefährdete Xerothermrasenarten in die Roten Listen aufgenommen werden müssen, während sich bei anderen Arten deren Gefährdungskategorie im negativen Sinne ändert. Der Verlust an gefährdeten Arten ist irreversibel, sodass sie längerfristig in den Xerothermrasen lokal aussterben könnten trotz eines angemessenen Managements. Außerdem erwarte ich zukünftig eine weitere Zunahme von *B. erectus* in den Xerothermrasen Mitteldeutschlands, wobei sich dessen Einwanderung in die nördliche Richtung Europas dramatisch fortsetzen wird. Obwohl das Konkurrenzpotenzial dieser Grasart scheinbar noch nicht vollends ausgeschöpft ist, sind bereits die ersten negativen Auswirkungen ihrer Dominanz auf den Artenreichtum dieser Grasländer spürbar.

Chapter 1

General introduction

Biodiversity of xerothermic grasslands

Palearctic grasslands cover about 10 million km^2 of earth's surface, i.e. 18% of their territory, constitute approximately 41% of the global proportion of grasslands (Dengler et al. 2020) and contain the most species-rich plant communities worldwide (Wilson et al. 2012, Chytrý et al. 2015). Thus, their relevance for various ecosystem functions (e.g. biomass production, evapotranspiration, decomposition) and ecosystem services (e.g. carbon sequestration, water regulation, soil erosion control) is undisputed (Petermann & Buzhdygan 2021). Grasslands are dominated mainly by graminoids of the families *Poaceae* and *Cyperaceae*, but also to a lesser extent by species of the family *Juncaceae*, and are generally characterised by a high cover of the herb layer (mostly above 10%), while woody species (dwarf shrubs, shrubs and trees) comprise a much smaller proportion than forbs (Dengler et al. 2020). Graminoids are anemogamous, whereas most forbs are pollinated by insects, which is essential for maintaining plant and pollinator communities (Ghazoul 2006, Ollerton et al. 2011).

Central European dry grasslands, often also referred to as xerothermic grasslands, can be divided into two main types: dry or xeric grasslands in a narrow sense, which can be considered near-natural or natural, and semi-dry or meso-xeric grasslands, which are semi-natural (Ellenberg & Leuschner 2010, Boch et al. 2020, Dengler et al. 2020). In this context, dry grasslands grow under drier conditions, are better adapted to extreme environmental changes (e.g. drought events, high solar radiation) (Partzsch 2000) and are therefore not or irregularly managed for their maintenance, while semi-dry grasslands grow under moderately dry conditions and are subject to a higher succession potential, so that traditional land use (e.g. grazing, mowing) is necessary to maintain species richness (Partzsch 2000, Ellenberg & Leuschner 2010, Kelemen et al. 2014). The plant communities of these two grassland types belong mainly to the classes *Festuco-Brometea* Br.-Bl. & Tx. ex Klíka & Hadač 1944 (basiphytic calcareous grasslands) and *Koelerio-Corynephoretea* Klika ap. Klika et Nowak 1941 (acid or siliceous and sandy grasslands) (Schubert et al. 1995, Boch et al. 2020).

Dry and semi-dry grasslands are a biodiversity hotspot of vascular plant species, bryophytes and lichens (Visconti et al. 2018) and comprise a large proportion of rare and endangered species (Veen et al. 2009, Dengler et al. 2014, 2020). In fact, semi-dry grasslands hold the most proportion of vascular plant species at small spatial scales (Wilson et al. 2012, Dengler et al. 2018, Biurrun et al. 2019). Additionally, grasslands represent very important habitats for other groups of taxa (not only faunistic generalists but also many specialists), such as birds (Nagy 2014), reptiles (Laufer et al. 2007), butterflies (van Swaay et al. 2006), grasshoppers (Hochkirch et al. 2016), spiders (Polchaninova et al. 2018) and mollusks (Neubert et al. 2019).

From an international conservation perspective, the protection and maintenance of biodiversity in xerothermic grasslands is a prerequisite (Janssen et al. 2016, Török & Dengler 2018). Due to their high conservation value, European grasslands are part of Natura 2000 sites and correspond to several EU priority habitat types (Ssymank et al. 2021). Traditional land use, such as grazing by sheep and goats, annual or biennial mowing, mulching, shrub encroachment and partly burning, are particularly considered appropriate management practices to maintain the biodiversity of these grasslands (Partzsch 2000, Kahmen et al. 2002, Klein 2013, Elias et al. 2018).

Threats to xerothermic grasslands by environmental and land use changes

The causes of biodiversity loss in grasslands are very diverse, but mainly human activities are responsible for it (Dengler et al. 2020). Since the second half of the 20th century, grasslands have been irreversibly damaged by fragmentation and isolation due to intensification or abandonment of land use (Lindborg et al. 2014, Deák et al. 2016, Visconti et al. 2018). Based on an analysed dataset of 7738 vegetation plots, more loser than winner species were found in Germany between 1927 and 2020 (Jandt et al. 2022), with more common species also showing significant declines (Eichenberg et al. 2021). These confirmed evidences reflect the current trend revealed by the German Red List of vascular plant species (Metzing et al. 2018). Thus, species richness of natural and semi-natural xerothermic grasslands has declined dramatically (Bruelheide et al. 2020), resulting in a replacement of species-rich by species-poor plant communities (Partzsch 2000, Donohue et al. 2000, Römermann et al. 2005, Enyedi et al. 2008), which in turn causes a homogenisation of these communities (Blüthgen et al. 2016, Visconti et al. 2018) and the loss of ecosystem multifunctionality (Soliveres et al. 2016).

Main drivers of species richness loss in xerothermic grasslands are processes of global change such as climate warming, soil acidification and atmospheric nitrogen deposition, as well as land use change (Bobbink et al. 2010, Dupré et al. 2010, Diekmann et al. 2019, Kübert et al. 2019). Although xerothermic grasslands are better adapted to heat and drought, their regeneration potential is low, so that climate warming seems to be the greatest future threat to its biodiversity (Petermann et al. 2007, Pörtner et al. 2021). Particularly in recent years, extreme weather events such as heat waves and droughts have intensified and become more frequent in Central Europe (Rousi et al. 2022), but also in Central Germany, where drought events in 2018 and 2019 were the most severe since weather records began (Boergens et al. 2020, European Drought Observatory 2021). For example, extreme temperatures and summer drought events combined with less precipitation can induce lethal effects in many perennial grassland species due to their reduced transpiration (Petřik et al. 2011, Fischer et al. 2020). Nowadays, mild winters and dry summers are increasing in Germany (Kreyling & Henry 2011), which can also affect land use practices in various ways (Schädler et al. 2019).

Atmospheric nitrogen deposition can lead to changes in nutrient and water cycling and soil conditions (Perring et al. 2018), destabilise primary production (Bharath et al. 2020) and increase the succession rate of abandoned xerothermic grasslands (Bohner et al. 2020), but nutrient uptake by plants is further hindered by water limitation (Ellenberg & Leuschner 2010), especially during drought events (Homyak et al. 2017). Diekmann et al. (2014) found increased nitrogen input over 70 years in north-western Germany, which led to the loss of typical small-sized grassland species (e.g. *Acinos arvensis*, *Trifolium campestre*), with limited soil water and phosphorus availability having an even greater impact on this species loss. Although the critical nitrogen loads for these grasslands lay between 14 and 25 kg $ha^{-1}a^{-1}$

(de Jong et al. 1998), nitrogen deposition, including fertilisation, promotes the growth performance of grass species becoming dominant (Bai et al. 2015, de Malach et al. 2017, Wang et al. 2021).
However, human-induced changes in traditional land use, such as cessation of grazing and mowing, currently have the greatest negative impacts on the species richness of xerothermic grasslands (Hülber et al. 2017, Visconti et al. 2018, Dengler et al. 2020). In contrast, intensive management such as overgrazing is an inappropriate opportunity as it also may negatively affect the biodiversity of these grasslands (Török et al. 2016). Abandonment favours shrub encroachment (Seither 2015), the immigration of ruderal and adventive species (Partzsch & Mahn 2001, Dostálek & Frantík 2008, Köhler et al. 2020) and, to a particular extent, the dominance of different grass species (Bobbink et al. 2010, Diekmann et al. 2014, 2019, Lemmer et al. 2021). Thereby, shade-intolerant or low-growing species are often replaced by taller grasses (Wesche et al. 2012, Bohner et al. 2019), as such grass species have high reproductive rates (Grime 2001) and can also spread and establish rapidly in response to environmental changes (Elias et al. 2018, Lemmer et al. 2021). Therefore, grasses are considered to be highly competitive compared to dicots (and other low-competitive monocots), inhibiting their development and displacing them (Goldberg et al. 2001, Del-Val & Crawley 2005, Partzsch et al. 2018). For example, grasses are more efficient at using available nitrogen from the soil and consequently exhibit higher biomass accumulation (Stevens & Gowing 2014), as higher layers of litter strongly reduce the availability of light for small forbs at ground level and increasingly suppress their growth (Foster & Gross 1998, Hegedušová & Senko 2011, Ridding et al. 2020). The increasing abundance of grasses is mainly a consequence of changes in traditional land use, so that they play a decisive role in the conversion of formerly species-rich to more species-poor xerothermic plant communities (Donohue et al. 2000, Partzsch 2000, Enyedi et al. 2008, Wesche et al. 2012, Rupprecht et al. 2016).

Increasing dominance of *Bromus erectus* in Central Germany

From a global perspective, an increasing spread of grass species has been documented in more than the last 100 years (Poschlod et al. 2005, Römermann et al. 2005, Chýlová & Münzbergová 2008). Several studies show that in xerothermic grasslands, the dominance of different grasses such as *Bromus erectus*, *Brachypodium pinnatum*, *Festuca* sp., *Helictotrichon* sp. and *Stipa* sp. has increased (Bobbink et al. 1998, Partzsch 2000, Bornkamm 2006, 2008, Klimaschewski et al. 2006, Meier & Partzsch 2018). They are better adapted to environmental changes because their competitive and stress-tolerant strategy enables a longer lifespan (Grime 2001).
During the 20th century, particularly in Central Germany, the grass species *Bromus erectus* has become increasingly widespread in xerothermic grasslands (Zündorf et al. 2006, Bornkamm 2006, 2008, Helmecke 2017). *Bromus erectus* is considered a character species of the order *Brometalia erecti* Br.Bl. 1936 (Schubert et al. 2001) and is listed as a neophyte in Germany for the federal states of Thuringia and Saxony-Anhalt due to its associated invasive character (Heinrich 2010, Frank & Schnitter 2016). This species migrates into neighbouring xerothermic plant communities, such as the *Festuco valesiacae-*

Stipetum capillatae (Libb. 1931) Mahn 1959 emend. Schub. 1995 (Bieringer & Sauberer 2001, Meier & Partzsch 2018), and can also occur on disturbed and ruderalised sites like roadsides or railway embankments (Bornkamm 2008). Interestingly, there were no confirmed occurrences of *B. erectus* in Thuringia before 1800 and the presumably oldest herbarium specimen of this species for Central Germany dates from 1827 at the Mittelberg near Auleben (Heinrich 2010). In Southern Lower Saxony, this grass also migrated into the xerothermic grasslands on a small scale through many individual occurrences about 100 years ago, before larger populations developed (Bornkamm 2008). Nevertheless, the species is undoubtedly benefitíng from the ongoing global change, as it originally comes from the south temperate zone of southern Central Europe and is successively migrating in a northern direction (Bornkamm 2008). Moreover, the decline in sheep and goat grazing and the subsequent reduction in grazing pressure promotes the abundance of *B. erectus* (Briemle 1999, Bornkamm 2008). In future, the dominance of this species could have a negative impact on the species richness of central German xerothermic grasslands, which has already been demonstrated for grasslands in Tuscany in Italy (Maccherini et al. 2000).

Plant functional traits, functional trait composition and intraspecific trait variability

Environmental and land use changes affect both the floristic and functional trait composition of xerothermic grasslands (Garnier et al. 2007, Lewis et al. 2014, Pichon et al. 2022). Plant functional traits are measurable morphological, physiological or phenological characteristics of an individual that indirectly affect their growth, reproduction and survival (Violle et al. 2007). They are essential key factors mediating both species and community responses or effects to environmental gradients (Lavorel et al. 2008, Shipley 2009, Garnier et al. 2016), implying strong effects on ecosystem stability and dynamic (Petchey & Gaston 2006) and can contribute to predict future community composition (Suding et al. 2008). Hence, functional traits are associated with e.g. biogeochemical cycles, disturbance, plant dispersal and competitiveness (Reich 2014, Funk & Wolf 2016), and thus influence ecosystem functions such as above-ground net primary productivity and litter decomposition rate (Garnier et al. 2007) as well as ecosystem services like climate and water regulation and soil stability (de Bello et al. 2010).

One of the most commonly used traits for detecting abiotic and biotic changes are plant height and leaf traits, particularly specific leaf area (SLA), leaf dry matter content (LDMC) and leaf nitrogen concentration (LNC), which are closely related to plant growth and fitness, such as resource acquisition and use, stress tolerance and competitive ability (Westoby et al. 2002, Freschet et al. 2010, Díaz et al. 2016, Garnier et al. 2016). Wright et al. (2004) described correlations between different leaf traits in the ‘leaf economics spectrum‘ (LES) by contrasting a gradient of resource conservation and resource turnover. For example, acquisitive fast-growing species (high SLA and LNC, low LDMC) have a higher relative growth rate and faster turnover of nutrients compared to conservative slow-growing species (low SLA and LNC, high LDMC), which have a longer leaf life but low turnover rate due to their investment in the conservation of nutrients (Wright et al. 2004, Shipley et al. 2006, Freschet et al. 2010, Reich 2014). In general, this reflects the functional comparison between grasses and forbs in xerothermic grasslands, as conservative grasses are often characterised by a higher LDMC but lower SLA and LNC than aquisitive forbs, indicating a long leaf life due to their higher proportion of scleromorphic tissue (Reich et al. 2003, Al Haj Khaled et al. 2005).

Moreover, the plant functional trait composition (i.e. the distribution of trait values in a community) largely determines ecosystem function such as productivity and nutrient cycling (Garnier et al. 2016, Funk et al. 2017). Hence, trait values of highly abundant species within a community have a greater influence on ecosystem function according to the 'mass ratio hypothesis' (Grime 1998). For this purpose, quantifying the functional trait composition, the community weighted mean (CWM) is calculated by weighting the traits of all individual species in a community (at the plot level) by their relative abundance (Garnier et al. 2004). CWM represents the dominant trait value and is commonly used to measure shifts among those values along different environmental conditions (Chelli et al. 2019) like climate and soil conditions (Ordoñez et a. 2009, Simpson et al. 2016). For example, species that are adapted to limited water and nutrient availability may be highly abundant in dry grasslands and therefore contribute more to their functional trait composition than to that of semi-dry grasslands (sensu Grime 1998). On the other hand, functional diversity (FD) describes the dissimilarity between traits of coexisting species within a community, reflecting their occupied niche space (Botta-Dukát 2005). Engel et al. (2023) found evidence on a global scale that the functional trait composition of grasslands is closely related to the resource economics and size traits of the dominant species. For plant communities in European habitats, climate-trait relationships could be assessed based on more than 300.000 vegetation plots by analysing CWMs of four functional traits (plant height, SLA, seed mass, specific root length), where macroclimate generally predicted trait distributions, but effects varied considerably between broadly and narrowly defined habitats due to local conditions (Kambach et al. 2023).

The variation of functional traits within species along environmental gradients should not be ignored, usually referred to as intraspecific trait variability (ITV) (Albert et al. 2010), which is the result of genetic differentiation and phenotypic plasticity (Nicotra et al. 2010, Albert et al. 2011). Soil properties and climatic conditions are considered the most important abiotic drivers of ITV change (Moles et al. 2014, Jager et al. 2015, Rosbakh et al. 2015). However, ITV also depends on species-specific responses and community structure (Whitlock et al. 2007, West et al. 2012, Jung et al. 2014), and has profound implications for species coexistence and ecosystem functions (Jung et al. 2010, Siefert et al. 2015), where variation within species (intraspecific) can differ considerably from variation between species (interspecific) (Jung et al. 2010, Albert et al. 2011, Kazakou et al. 2014, Herrera 2017). Nevertheless, intraspecific trait variation seems to be gaining importance for assessing habitat filtering in grassland communities, being higher in SLA and LNC than in LDMC (Jung et al. 2010). Siebenkäs et al. (2015) indicated that LDMC of xerothermic grasses have higher ITV than that of forbs in response to variation in nutrient and light availability, suggesting their stronger adaptation to environmental change.

Plant-plant interactions

The dramatic loss of species implies also changes in the interactions between coexisting species (Zobel 1992, Mariotte et al. 2013). Within a plant community, constituent plant species can interact in a variety of ways (Brooker et al. 2008). Thus, plant-plant interactions can be considered positive in the sense of facilitation or negative in the sense of competition, both intraspecifically (between individuals of the same species) and interspecifically (between individuals of different species) (Callaway & Walker 1997, Thorpe et al. 2011, Dohn et al. 2013, Liancourt & Dolezal 2021). Liancourt & Dolezal (2021) advocate the community-scale facilitative effect, in which facilitation not only take place between individual species, but is also a positive interaction in the entire plant community, which i.e. mitigates the effects of climatic changes on biodiversity (Cavieres et al. 2014, Michalet et al. 2014, Spasojevic et al. 2014) and enables coexistence in plant communities (Callaway 2007, Gross et al. 2015). In contrast, negative neighbour effects are generally more common, where individuals compete for limited resources such as light, water, nutrients, pollinators and space, and therefore weaken each other directly or indirectly (Del-Val & Crawley 2005, Brooker et al. 2008, Craine & Dybzinski 2013, Aschehoug et al. 2016). Due to changing abiotic conditions, plant-plant interactions between facilitation and competition can fluctuate on a temporal and spatial level (Kikvidze et al. 2006, Dickson & Foster 2011, Verwijmeren et al. 2013, Michalet et al. 2014). Moreover, interactions are fundamental determinants that can considerably influence the structure and dynamics of plant communities as well as ecosystem function (Le Bagousse-Pinguet et al. 2014, Tredennick et al. 2018). As mentioned before, various functional traits (e.g. plant height, SLA, LDMC, LNC, seed mass) are also linked with plant competitiveness (Funk & Wolf 2016). Again, in xerothermic grasslands, dominant grasses can outcompete forbs in various ways due to their greater competitive ability (Del-Val & Crawley 2005, Ridding et al. 2020). Thus, for example, it has been experimentally demonstrated that the presence of *Festuca rupicola* led to negative effects on the growth and fitness of typical threatened xerothermic grassland species, like e.g. *Biscutella laevigata* and *Campanula glomerata* (Bachmann et al. 2005, Faulhaber & Partzsch 2018, Partzsch 2019). But different studies also reported strong interspecific competitive effects between dominant grasses such as *Brachypodium pinnatum*, *B. rupestre*, *Bromus erectus* and *Arrhenatherum elatius* (Corcket et al. 2003, Liancourt et al. 2005). Although Meier et al. (2019) have shown that *B. erectus* and different species of *Stipa* are relatively similar in their functional traits, so that competitive exclusion may be the consequence of future environmental changes, the underlying plant-plant interactions between these grass species are still unknown.

Vegetation surveys as a tool for detecting vegetation changes

Vegetation surveys have been an essential tool in vegetation ecology for more than 100 years (Braun-Blanquet 1921) when documenting direct changes in vegetation over time (Bakker et al. 1996, Kudernatsch et al. 2016). On the other hand, vegetation surveys can also be used as a basis for further studies, e.g. for functional comparisons of plant communities by including the community weighted mean (Lauterbach et al. 2013, Helm et al. 2019, Meier et al. 2019). In particular, resurvey studies have become increasingly important in recent years due to the vegetation changes caused by global change (Jandt et al. 2022), in which previous vegetation relevés are compared with current ones after a certain time period (Hahn et al. 2013, Meier & Partzsch 2018, Bauer & Albrecht 2020, Mazalla et al. 2021, Schüle et al. 2023).

For resurveying, both quasi-permanent (or referred to as semi-permanent) and permanent plots are suitable for interpreting decadal changes in plant communities (Chytrý et al. 2014). However, there is a risk of pseudo-turnover when resurveying quasi-permanent plots, as the previous recorded plots are not marked and therefore only allow an approximate relocalisation, which can make temporal changes more difficult to disentangle than spatial ones (Fischer & Stöcklin 1997, Vymazalová et al. 2012, Kapfer et al. 2018). This problem can be avoided by studying permanent plots which have been previously marked (e.g. with coordinates and magnets), so that an accurate resurvey is possible (Chytrý et al. 2014). The disadvantage of these permanent plots is that they were hardly ever established by earlier authors and the spatial distribution of the different vegetation types is missing (Hédl et al. 2017). For this reason, nowadays, it is even more important to mark all vegetation relevés permanently to enable future biodiversity monitoring because assessing vegetation changes exclusively via vegetation databases should be carried out with extreme caution due to incorrect interpretations (Chytrý et al. 2014). In addition, possible observer errors cannot be avoided in a resurvey study, as each observer is trained differently in species identification (Verheyen et al. 2018, Boch et al. 2022). In grasslands, however, it has been shown that observer errors have only a relatively small influence on species diversity indices (Morrison et al. 2023) and that ecological indicator values are even robust to them (Boch et al. 2022).

Thesis objectives

The general aim of this thesis is to reveal changes in the floristic and functional trait composition of xerothermic grasslands in Central Germany, as well as changes in plant-plant interactions, and to evaluate these results considering the processes of ongoing global change by also estimating future vegetation changes. A central aim is to investigate and evaluate the role of increasingly dominant grass species (e.g. abundance, intraspecific trait variability, plant-plant interactions), focusing on *Bromus erectus* within these grasslands. As mentioned above, previous studies postulated an increasing dominance of *B. erectus* in different regions of Central Germany, but the underlying mechanisms leading to such dominance are not fully understood. It also needs to be ascertained into which plant communities the species is currently migrating. In this context, other xerothermic grasses, such as *Brachypodium pinnatum*, *Festuca rupicola*, *Helictotrichon pratense* and *Stipa* sp., are also highlighted and included in the investigations. From a nature conservation perspective, it is crucial to understand how to prevent the increasing spread of such grass species, especially *B. erectus*, as it could potentially have a negative impact on the species richness of xerothermic grasslands in Central Germany. For this purpose, in the three study regions 1) Kyffhäuser, 2) Porphyry outcrops near Halle (Saale) and 3) Schafberg (lower Unstrut valley), I resurveyed vegetation relevés over a time period of more than 20 years, took soil samples and measured functional traits (the study regions are characterised in the following two chapters regarding their climatic and edaphic conditions as well as their studied plant communities). Additionally, to investigate the plant-plant interactions of xerothermic grasses, I conducted a competition experiment in the Botanical Garden of Halle (Saale). Therefore, I addressed the following research questions:

(i) Which vegetation changes of xerothermic grasslands in Central Germany are evident in the course of ongoing global change over time and are there currently differences in the functional trait composition of these grasslands to reveal changes in their ecosystem function?

(ii) What is the current role of the increasingly dominant grasses, especially *Bromus erectus*, in the xerothermic grasslands of Central Germany?

(iii) Which future recommendations for nature conservation can be derived from the results?

The research questions of this thesis will be answered in the subsequent four chapters (see also Fig. 1):

In **chapter 2** and **chapter 3**, I document temporal and spatial changes in the vegetation of xerothermic grasslands in Central Germany over a time period of more than 20 years under ongoing climate warming, nitrogen deposition and land use changes. I present two resurvey studies that differ from each other both in their study sites and methodologically (in a total: 103 vegetation relevés). In **chapter 2**, I resurveyed 57 vegetation relevés of quasi-permanent plots in the regions Kyffhäuser (Thuringia) and Porphyry outcrops near Halle (Saale) (Saxony-Anhalt). I compared dry and semi-dry grasslands by floristic-ecological gradients, species richness and vegetation cover. Moreover, I divided functional groups into annuals, graminoids and forbs, compared them and investigated the increase and decrease of the different species belonging to these groups, focusing on the five grasses *Bromus erectus*, *Brachypodium pinnatum*, *Festuca rupicola*, *Helictotrichon pratense* and *Stipa capillata*. In **chapter 3**, I resurveyed 46 vegetation relevés of permanent plots at the Schafberg in the lower Unstrut valley (Saxony-Anhalt). I compared four plant communities (associations) of xerothermic grasslands by selecting a set of vegetation characteristics such as ecological indicator values, life forms, strategy types and species richness, and applied analyses to detect directional vegetation change, testing for floristic homogenisation. I also identified winners (increased species) and losers (decreased species) and particularly strived to highlight changes in short-lived plants and graminoids. In **chapter 2** and **chapter 3**, I assessed these vegetation changes in the background of changing environmental conditions (e.g. drought events, nitrogen deposition) and land use (**chapter 2**), as I expected that these factors to be the potentially strongest drivers of these vegetation changes over time. Furthermore, in both resurvey studies, I especially emphasised the role of increasing dominant grasses and expected an increase of *B. erectus* in different plant communities of xerothermic grasslands in Central Germany.

In **chapter 4**, I present a functional approach of xerothermic grasslands in Central Germany, focusing on functional differences both at the community and species level (i.e. dominant grasses). I compared the functional trait composition of dry and semi-dry grasslands using multi- and single-trait analyses. Building up on the vegetation relevés (in a total: 101 vegetation relevés) of the previous two chapters, I measured functional traits per individual of the most abundant species at the plot level in the field and subsequently calculated the community weighted mean (CWM). I analysed soil samples to assess the effects of different soil properties on the functional trait composition of these two grassland types. Moreover, I compared the functional traits of the five grasses *Bromus erectus*, *Brachypodium pinnatum*, *Festuca rupicola*, *Helictotrichon pratense* and *Stipa capillata* and analysed their extent of intraspecific trait variability (ITV) to reveal differences in their functional adaptation by changing environmental conditions. For *B. erectus*, I expected a stronger adaptation in functional traits to environmental changes than for the other four grasses.

In **chapter 5**, experimentally, I assess the growth performance and intra- and interspecific interactions of xerothermic grasses under nutrient addition and above-ground biomass removal. I conducted a competition experiment between *Bromus erectus* and the grasses *Brachypodium pinnatum*, *Stipa capillata* and *Stipa tirsa*, cultivating the species at two densities (9 individuals or 1 individual) and three different species compositions of nine plants in monoculture and mixtures (6:3, 3:6) under different nutrient conditions (nutrient-poor vs. nutrient-rich) and clipping treatments (unclipped vs. clipped). In two consecutive years, I measured vegetative (and generative) traits of all individuals. I asked whether these traits and also the plant-plant interactions between *B. erectus* and the other three grasses varied under different nutrient conditions and clipping treatments. Finally, I evaluated the interactive effects of *B. erectus* on the other three grasses.

In **chapter 6**, I summarise the key results and discuss the links between the different chapters. Additionally, I draw conclusions for the conservation of xerothermic grasslands in Central Germany, show limitations of my approach and future perspectives.

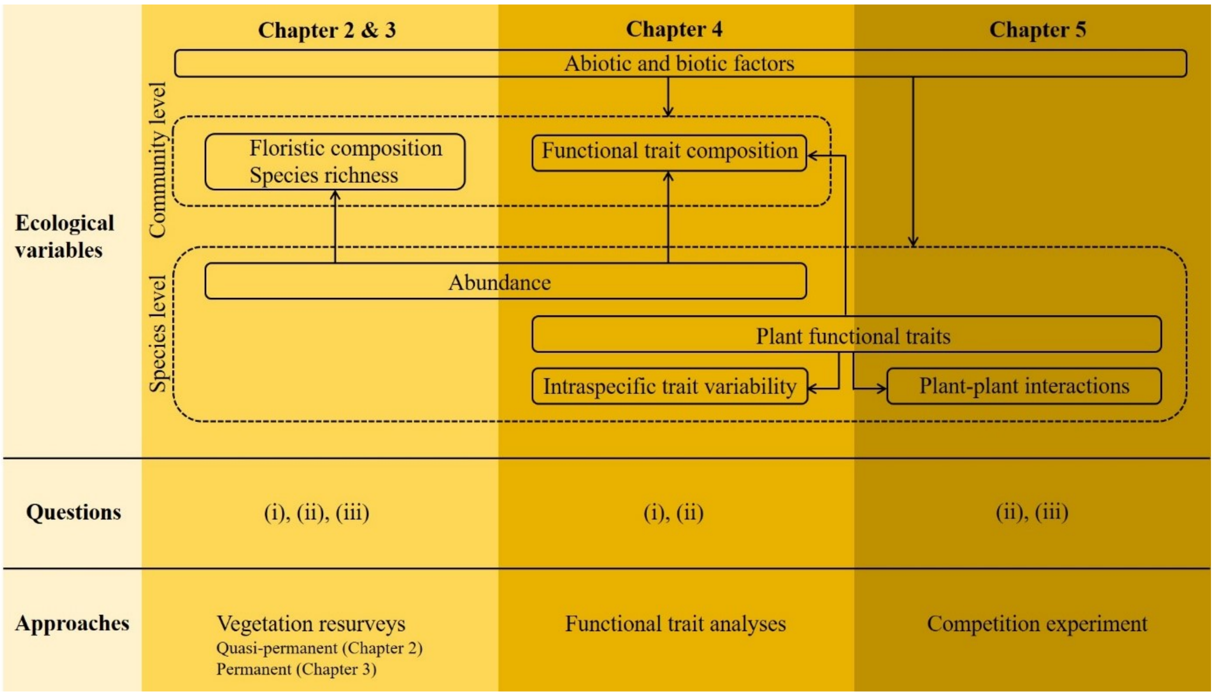

Fig. 1: Outline of this thesis. The chart depicts all main ecological variables, which are studied among the different chapters. Arrows indicate which variables have a considerable influence on the outcome of the other variables. Ongoing global change induces changes in abiotic and biotic factors, which in turn cause changes at community and species level. Research questions (see thesis objectives in the text) and approaches of the different chapters.

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Chapter 2

Floristic changes of xerothermic grasslands in Central Germany: A resurvey study based on quasi-permanent plots

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Floristische Veränderungen der Xerothermrasen in Mitteldeutschland: Eine Wiederholungsstudie basierend auf quasi-permanenten Dauerflächen

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Abstract

Biodiversity has declined in the dry and semi-dry grasslands of Central Germany over the past three decades, mainly as a result of 'Global Change', including changes to traditional land use practices. Such processes have promoted the spread of grass species such as *Bromus erectus*, which has become increasingly dominant within xerothermic grasslands. The aim of the study was to investigate changes in the vegetation of such grasslands over the last two decades by comparing previous and recent vegetation relevés (quasi-permanent plots) from two regions in Saxony-Anhalt and Thuringia (Saaletal northwest of Halle (Saale), Kyffhäuser). The floristic comparison was carried out between dry and semi-dry grasslands (by calculation of the Sørensen index) and within functional groups (annuals, graminoids, forbs). The following statistical analyses were performed: detrended correspondence analysis (DCA), paired t-tests, Wilcoxon signed-rank tests and Pearson correlations. Generally, there was no change in species number over time, but vegetation cover increased significantly. Dry grasslands showed a higher floristic similarity between the previous and recent relevés than semi-dry grasslands, indicating that plant communities in drier grasslands show relatively higher stability, which is likely due to local ecological conditions. Comparing the functional groups, annuals (e.g. *Hornungia petraea*) and graminoids (e.g. *B. erectus*) showed an increase and some new species were recorded over time (e.g. *Descurainia sophi*a, *Convolvulus arvensis*). In contrast, endangered forbs declined (e.g. *Asperula cynanchica*, *Euphrasia stricta*, *Silene otites*). While the dominant grasses *B. erectus* (highest increase in dry and semi-dry grasslands), *Festuca rupicola* and *Helictotrichon pratense* showed significant increases in coverage, species richness in the investigated plant communities was hardly affected as a result. We consequently concluded that an expansion of traditional land use measures may be required to halt the increasing spread of graminoids and to protect the biodiversity of the xerothermic grasslands in Central Germany.

Keywords: *Bromus erectus*, dominant grass species, *Festuco-Brometea*, functional group, global change, land use, nature conservation, Sørensen index, vegetation relevés

Erweiterte deutsche Zusammenfassung am Ende des Artikels

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1. Introduction

Dry and semi-dry grasslands in Europe are considered the most species-rich plant communities worldwide (Wilson et al. 2012, Chytrý et al. 2015, Dengler et al. 2020). Such xerothermic grasslands are characterized by their high biodiversity and large proportion of rare and (critically) endangered species (Korneck et al. 1996, van Swaay et al. 2006, Veen et al. 2009, Dengler et al. 2014), such that their protection is of the highest priority in nature conservation (Janssen et al. 2016, Frank et al. 2020).

Natural and semi-natural xerothermic grasslands have experienced dramatic declines in species richness in recent decades (Bruelheide et al. 2020), which is caused by increasing fragmentation and isolation of the landscape following agricultural intensification or abandonment (Lindborg et al. 2014, Deák et al. 2016, Janssen et al. 2016). Such land use change has led to declining biodiversity, even among more common species, in many regions of Germany (Diekmann et al. 2014, Peppler-Lisbach & Könitz 2017, Strubelt et al. 2017, Janssen et al. 2020, Eichenberg et al. 2021). The trend is of particular concern where species-rich xerothermic grasslands have been replaced by species-poor plant communities (Partzsch 2000, Römermann et al. 2005, Enyedi et al. 2008).

‘Global Change’ refers to diverse processes such as climate warming, soil acidification, increasing atmospheric nitrogen input and land use changes, which on grasslands leads to the dominance of grasses over dicotyledonous species and declining biodiversity (Willems 1987, Bobbink et al. 1998, 2010, Duprè et al. 2010, Wesche et al. 2012, Diekmann et al. 2014, Enright et al. 2014). In north-western Germany, increased atmospheric nitrogen input over 70 years led to the loss of typical xerothermic grassland species which was exacerbated by them being more limited by water and phosphorus availability in the soil (Diekmann et al. 2014). Not negligible is the nitrogen deposition, which on the one hand promotes the growth of grass species and on the other hand can lead to a change in nutrient cycles and thus to a change in species composition and soil conditions (Gilliam 2006, Perring et al. 2018). In addition, seasonal weather conditions can have different effects on grasslands (Petřík et al. 2011), in that extreme temperatures lead to lethal effects in many species, whereas higher precipitation in the previous vegetation period may support the germination and establishment of species in the following growing season (Fitter & Hay 2001).

Particular changes in traditional land use, such as grazing and mowing, cause declines in biodiversity in xerothermic plant communities (Poschlod & Wallis de Vries 2002, Hülber et al. 2017, Valkó et al. 2018). The lack of grazing promotes both the spread of dominant grass species and the immigration of ruderal and adventive species (Partzsch & Mahn 2001, Elias et al. 2018). In particular, grasses are considered to be stronger competitors than dicotyledonous species (del-Val & Crawley 2005, Partzsch et al. 2018), as they accumulate higher layers of litter, which can consequently reduce light availability at lower levels (Hegedušová & Senko 2011). Therefore, an increasing abundance of grasses is largely responsible for the conversion of formerly species-rich xerothermic grasslands into more species-poor plant communities (Donohue et al. 2000, Enyedi et al. 2008, Wesche et al. 2012). This is supported by several studies that found xerothermic grasslands to be increasingly dominated by various grass species such as *Bromus erectus*, *Brachypodium pinnatum*, *Festuca* sp., *Helictotrichon* sp. or *Stipa* sp. (Bobbink et al. 1998, Partzsch 2000, 2001, Pusch & Barthel 2003, Bornkamm 2006, 2008, Klimaschewski et al. 2006, Dostálek & Frantík 2008, Silantyeva et al. 2012, Meier & Partzsch 2018).

In Central Germany, the indigenous dominant grass species *Bromus erectus*, which is a characteristic species of the order *Brometalia erecti* (SCHUBERT et al. 2001), has become increasingly widespread across xerothermic grasslands (ZÜNDORF et al. 2006, BORNKAMM 2006, 2008, HELMECKE 2017) and therefore has an associated invasive character (VALÉRY et al. 2009). The species is classified as a neophyte in Germany in the federal states of Thuringia and Saxony-Anhalt (HEINRICH 2010, FRANK & SCHNITTER 2016). The increasing dominance of *B. erectus* is likely linked to a sharp decline in sheep and goat grazing and the consequent reduction in grazing pressure (BRIEMLE 1999, BORNKAMM 2008, DIEKMANN et al. 2014). In fact, *B. erectus* is now migrating into neighboring xerothermic plant communities, including *Stipa* grasslands (BIERINGER & SAUBERER 2001, MEIER & PARTZSCH 2018). As such, the question of the increasing dominance of grass species including *B. erectus* across the xerothermic grasslands of Central Germany and the underlying mechanisms of change in species composition is unresolved. From a nature conservation point of view, it is of crucial importance to understand how the increasing spread of dominant grass species occurs, especially for *B. erectus*, and how it can be prevented in order to counteract the decline of species of xerothermic grasslands.

In order to detect temporal and spatial changes in plant communities over time, many studies have compared previous and current vegetation relevés to determine any basis for 'Global Change' (e.g. JANTSCH et al. 2013, KUDERNATSCH et al. 2016). However, when recording quasi-permanent plots, there is a risk of pseudo-turnover, since changes over time (including fluctuations) are more difficult to record than spatial ones (FISCHER & STÖCKLIN 1997, VYMAZALOVÁ et al. 2012). Nevertheless, a renewed resumption of the vegetation by means of quasi-permanent plots should represent a more robust method for deriving and interpreting decadal changes in plant communities, although inaccurate plot sizes and observer errors cannot be neglected (ARCHAUX et al. 2006, VERHEYEN et al. 2018). Therefore, permanent marking of these plots with coordinates and magnets is a prerequisite for future accurate biodiversity monitoring (CHYTRÝ et al. 2014).

The aim of this study was to document temporal and spatial changes in the vegetation of sampled xerothermic grasslands in Central Germany over a more or less twenty-year period. An increase in grass species (especially *B. erectus*) was anticipated, and we set-out to assess the effects this would have on species composition among different plant communities of the dry and semi-dry grasslands. The approach involved a floristic comparison being undertaken between previous (1995–2002) and recent (2018/19) plots on vegetation relevés from two grassland locations in the dry region of Central Germany. A further aim of the study was to identify potential measures for applied nature conservation.

The study therefore set out to answer the following two questions: (1) Does the comparison of previous and recent relevés reveal changes in the floristic composition of plant communities of dry and semi-dry grasslands? (2) Does the comparison of previous and recent relevés reveal a change in the functional groups of species and is there an increasing dominance of grass species?

2. Material and Methods

2.1 Study areas

Seven study areas were selected from two regions in Central Germany that have pronounced occurrences of xerothermic grasslands: (1) Saaletal northwest of Halle (Saale) and (2) Kyffhäuser (Fig. 1, Supplement E1). The climate across the regions is characterized by low annual precipitation of around

Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

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Fig. 1. Overview map (created in ArcGIS 9) of the studied xerothermic grasslands in the Central German dry region (for abbreviations see Supplement E1). Detailed maps of the quasi-permanent plots and their respective coordinates are given in Supplement E2 and E5).

Abb. 1. Übersichtskarte (Erstellung in ArcGIS 9) der untersuchten Xerothermrasen im Mitteldeutschen Trockengebiet (Abkürzungen siehe Anhang E1). Detaillierte Karten der quasi-permanenten Flächen und deren jeweiligen Koordinaten sind in den Anhängen E2 und E5 angegeben.

450–550 mm and annual mean temperatures of 8.5–9.2 °C (DÖRING 2004). Typical soils belong mostly to the types protorendzina or rendzina and to partially degraded chernozem with different parent rocks (e.g. porphyry, limestone, gypsum) (MAHN 1965). The regions have been intensively studied and documented by various authors (see MEUSEL 1939, MAHN 1965, ANDRES 1994, HENSEN 1995, SCHNEIDER 1996, JANDT 1999, PARTZSCH 2000, 2001, RICHTER 2002, RICHTER et al. 2003, PUSCH & BARTHEL 2003, BECKER et al. 2011, HAHN et al. 2013, MEIER & PARTZSCH 2018 for detailed descriptions).

2.2 Plant communities

The xerothermic grasslands of Central Germany are characterized by their often quite rare plant communities, which are generally divided into the two classes *Koelerio-Corynephoretea* (acid or siliceous and sandy grasslands) and *Festuco-Brometea* (basiphytic calcareous grasslands). The investigated plant communities are included in the following system (according to SCHUBERT et al. 1995):

- Class: *Koelerio-Corynephoretea* Klika ap. Klika et Nowak 1941
  - Order: *Sedo-Scleranthetalia* Br.Bl. 1955
    - Suborder: *Alysso-Sedion* Oberd. et Th. Müll. ap. Th. Müll. 1961
      - Association: *Teucrio-Festucetum cinereae* Mahn 1959
  - Order: *Festuco-Sedetalia* R.Tx. 1951
    - Suborder: *Armerion elongatae* Krausch 1961
      - Association: *Filipendulo-Helictotrichetum pratensis* Mahn 1965
- Class: *Festuco-Brometea* Br.Bl. et R. Tx. 1943
  - Order: *Festucetalia valesiacae* Br.Bl. et R. Tx. 1943
    - Suborder: *Festucion valesiacae* Klika 1931
      - Association: *Festuco valesiacae-Stipetum capillatae* (Libb. 1931) Mahn 1959 emend.
    - Suborder: *Cirsio-Brachypodion* Hadač et Klika 1944
      - Association: *Stipetum stenophyllae* (Podp. 1930) Meusel 1938
      - Association: *Festuco rupicolae-Brachypodietum pinnati* Mahn 1959 emend.
  - Order: *Brometalia erecti* Br.Bl. 1936
    - Suborder: *Xerobromion* (Br.Bl. et Moor 1938) Moravec in Holub et al. 1967
      - Association: *Fumano-Seslerietum variae* W. Schub. 1963
    - Suborder: *Mesobromion erecti* (Br.Bl. et Moor 1938) R. Knapp 1942 ex Oberd. 1957
      - Association: *Onobrychido-Brometum erecti* Th. Müll. 1968
      - Association: *Gentiano-Koelerietum pyramidatae* Knapp 1942 ex Bornk. 1960

2.3 Vegetation relevés

A total of 57 previously sampled vegetation relevés were revisited in 2018 and 2019 including:

- 21 relevés of RICHTER (2002) from the porphyry landscape near Mücheln (Wettin);
- 30 relevés of SCHNEIDER (1996) from the Ochsenburg within the Kyffhäuser; and
- 6 relevés of PUSCH & BARTHEL (2003) from the Kyffhäuser area.

The vegetation relevés were assigned to the 8 associations listed above in Section 2.2.

The previous plots were identified using location sketches or vegetation maps prepared by the authors of the studies (SCHNEIDER 1996, RICHTER 2002). Using GoogleEarth (image overlay), the position for each plot could be relocated and its GPS coordinate specified, while GPS coordinates were already available in PUSCH & BARTHEL (2003). The new vegetation relevés were carried out using the same methodology as that adopted in the original study (including area size, recording time, cover-abundance values). Since the previous plots were not marked with magnets, a deviation of approx. 3 m from the newly created plots was assumed. These quasi-permanent plots allowed for an approximate resumption of the same position (CHYTRÝ et al. 2014).

The recent relevés were then marked out with magnets and the GPS coordinates were noted to facilitate monitoring in the future (CHYTRÝ et al. 2014). The field studies were then carried out during the same months as on the previous relevés, i.e. from the end of April to August in the years 2018 and 2019, and on two occasions, to ensure both early and late flowering species were recorded. Plot size varied from 9 to 25 m^2, due to paid attention to homogeneity. Geographical data such as height, exposition and inclination were documented. Coverage of the herb and cryptogamy layer (in %) as well as coverage of the plant species were determined using the 9-part Braun-Blanquet scale (REICHELT & WILMANNS 1973) (Supplement E3). The nomenclature of vascular plants was based on JÄGER (2017), that of the plant communities on SCHUBERT et al. (1995); cryptogams were not considered.

2.4 Data analysis

In the previous vegetation relevés by PUSCH & BARTHEL (2003), species coverage values followed the original 7-part Braun-Blanquet scale (BRAUN-BLANQUET 1964), such that the coverage levels for all other relevés had to be adjusted accordingly (including recent vegetation relevés). Correspondingly, the estimate values 2a (> 5–15% cover) and 2b (> 15–25% cover) of the 9-part Braun-Blanquet scale (REICHELT & WILMANNS 1973) were summarized as estimate value 2 (> 5–25% cover) of the 7-part Braun-Blanquet scale. In contrast, the estimated value 2m (many individuals, < 5% cover) given on the 9-part scale was converted into the estimate value 1 (> 1–5% cover) of the 7-part scale. The previous and recent vegetation relevés are presented in Supplement E3 and E4, including both the originally recorded and the adjusted coverage levels of the respective species. For all the other analyses, the adjusted coverage levels of the 7-part Braun-Blanquet scale were transformed as follows (according to DIERSCHKE 1994): r = 0.1%, + = 0.5%, 1 = 2.5%, 2 = 15%, 3 = 37.5%, 4 = 62.5%, 5 = 87.5%. The unweighted mean indicator values (ELLENBERG et al. 2001) for light, temperature, moisture, reaction and nutrients per plot (previous and recent relevés) were also calculated. Moreover, the plant communities were pooled into dry (*Teucrio-Festucetum*, *Festuco-Stipetum*, *Fumano-Seslerietum*) and semi-dry (*Filipendulo-Helictotrichetum*, *Stipetum stenophyllae*, *Festuco-Brachypodietum*, *Onobrychido-Brometum*, *Gentiano-Koelerietum*) grasslands.

Floristic-ecological gradients in the vegetation between previous and recent relevés were examined using detrended correspondence analysis (DCA). The data were logarithmically transformed (i.e. coverage levels (x+1)-logarithmized) in order to give less weighting to rarer species (DIERSCHKE & BECKER 2020). We applied DCA (function: decorana, gradient length of the first axis > 4) to investigate relationships between the mean indicator values and the dry and semi-dry grasslands. Explanatory variables (mean indicator values for light, temperature, moisture, reaction and nutrients) that significantly correlated ($p < 0.05$) with the axes of the ordination were post hoc fitted to the ordination diagram as vectors (function: envfit). The significance of these variables was checked using the Monte-Carlo test (9999 permutations). Additionally, a species ordination diagram was generated. DCA was carried out with the program R 3.6.0 (R CORE TEAM 2019), using the package vegan (OKSANEN et al. 2020).

To represent changes in the floristic composition of the dry and semi-dry grasslands, the similarity of the previous and recent vegetation relevés was calculated using the Sørensen index (SØRENSEN 1948), wherein more common species were more strongly weighted. The dimensionless index varied between 0 and 100, with values of over 75 indicating a high floristic similarity (MEIER & PARTZSCH 2018).

In addition, species number and vegetation cover (1) between the previous and recent relevés within the dry and semi-dry grasslands, and (2) between the previous and recent relevés within functional groups were studied. For the functional species group comparison, the species were previously divided into annuals, graminoids and forbs, and the cover of the five most common grasses was compared. Particular focus was placed on comparing the cover of *Bromus erectus* within the dry and semi-dry grasslands. The transformed data on the species number (log-transformed) and vegetation cover (arcsin-root-transformed) were checked for normal distribution using the Kolmogorov-Smirnov test. Using paired t-tests, it was possible to check for significant differences between the previous and recent relevés. The Pearson correlation coefficient was then used to calculate whether the increasing dominance of grass species had an effect on the species richness of the plant communities.

In order to investigate changes in the abundance of each species, species constancy (i.e. species occurrence in relation to the total number of vegetation relevés) between the previous and recent relevés was compared. The difference in constancy could then be used to show increases or decreases, with significant changes in constancy being determined using a Wilcoxon signed-rank test. Only species that appeared more than five times in the relevés were considered. To improve visualization, the different species were then listed according to their functional group. Finally, the percentage of changing species per functional group was calculated.

All statistical analyses were considered significant where $p < 0.05$. The statistical analyses (exception: DCA) were carried out using WinSTAT 2007.

3. Results

3.1 Floristic comparison of the dry and semi-dry grasslands

DCA did not reveal any changes between the previous and recent vegetation relevés (Fig. 2a). The indicator values for nutrients and moisture as well as vegetation cover were positively correlated with the first and second DCA-axes. The indicator values for light and temperature were also positively correlated, but they correlated negatively with those for nutrients and moisture. Thus, a clear differentiation between the nutrient-poorer, drier and more gappy dry grasslands and the more nutrient-rich and moist semi-dry grasslands was detected (Fig. 2a). The ordination species diagram supported the fact that there were differences in species composition between dry and semi-dry grasslands, as there tended to be a differentiation between dry grassland specialists and nutrient-depending species (Fig. 2b).

However, a comparison of the previous and recent relevés of the xerothermic grasslands based on the Sørensen index revealed significant differences ($F = 3.167$; $p = 0.003$) (Fig. 3). The dry grasslands were relatively stable (Sørensen index: 57), which indicates a higher floristic similarity between the previous and recent vegetation relevés compared to the semi-dry grasslands (Sørensen index: 49).

The comparison of the species numbers (previous relevés: in total 198 species; recent relevés: in total 210 species) of the dry and semi-dry grasslands did not show significant changes between the previous and recent relevés, but it revealed a significant increase in the vegetation cover (Fig. 4). The dry grasslands showed the highest increase of partly 50% in vegetation cover between the previous and recent relevés.

3.2 Floristic comparison of the functional groups of species

In the recent relevés, perennial forbs were the functional group with the highest number of species (mean: 20 species per relevé; total: 166 species), while the graminoids represented only a third of the total (mean: 7 species per relevé; total: 35 species), similar to the annuals (mean: 4 species per relevé; total: 38 species) (Fig. 5, Table 1). Annuals and graminoids were shown to have significantly increased in species number between the previous and recent relevés, while the number of forbs remained constant (Fig. 5). In the recent relevés, graminoids had a cover of approx. 75% and the forbs around 79%, while the small-grown and low-competitive annuals had a cover of approx. 7% (Fig. 5). The cover for graminoids and forbs therefore showed a significant increase between relevés while the annuals did not.

The comparison of constancy between the functional groups showed that 29% of the annuals and 49% of the graminoid species increased over time, while 23% of the forb species decreased (Table 1). In particular, annuals such as *Holosteum umbellatum*, *Draba verna* and *Hornungia petraea* increased significantly (Table 2). The dominant grass *Bromus erectus* increased significantly in presence, as did forbs such as *Euphorbia cyparissias*, *Falcaria vulgaris* and *Eryngium campestre*. The species *Descurainia sophia*, *Festuca csikhegyensis*, *Convolvulus arvensis* and *Polygala comosa* were all new to the recent relevés, while typical grasses and forbs of xerothermic grasslands including *Briza media*, *Euphrasia stricta*, *Asperula cynanchica*, *Silene otites* and *Allium lusitanicum* decreased significantly. *Linum catharticum* was the only annual species that showed a significant decrease. The species for which no significant increase or decrease could be detected are listed in the supplementary table (Supplement E6).

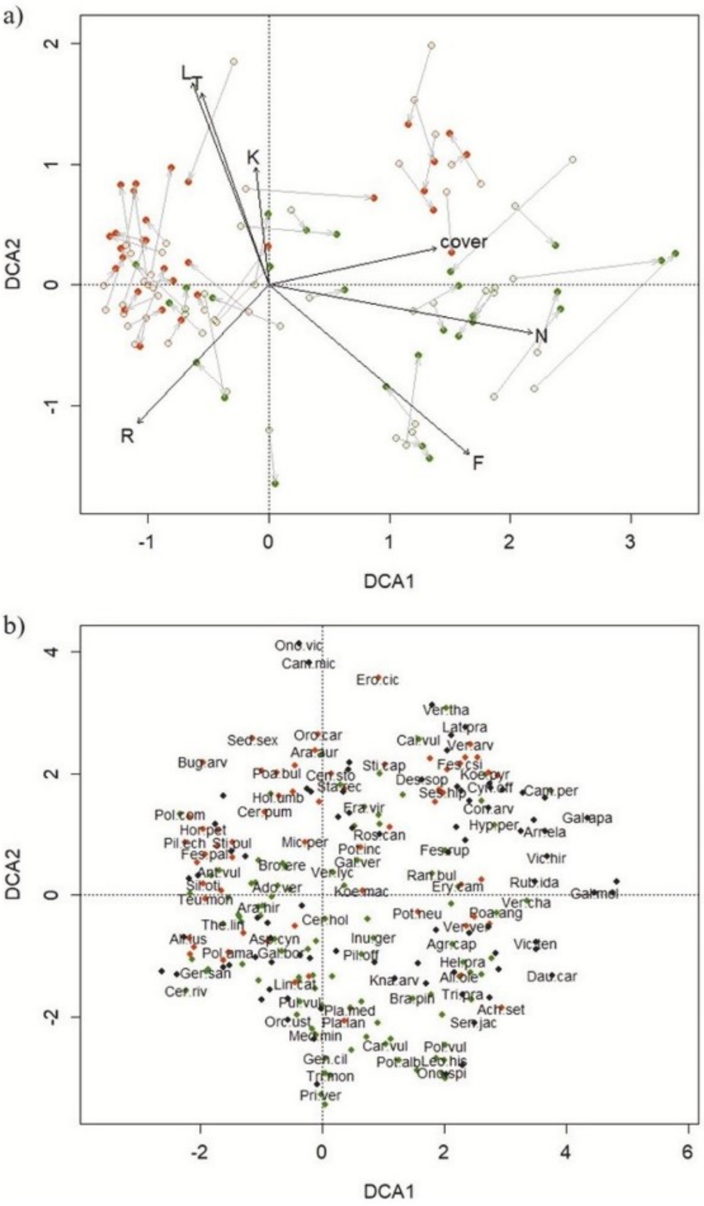

Fig. 2. Detrended Correspondence Analysis (DCA) of 57 quasi-permanent plots of the xerothermic grasslands in Central Germany. **a)** Diagram of the previous (1995–2002, empty symbols) and recent (2018/19, filled symbols) relevés for the dry grasslands (red) and semi-dry grasslands (green); relevé pairs are indicated by arrows. Ellenberg mean indicator values and vegetation cover, which are significantly correlated ($p < 0.05$) with the axes of the ordination, are shown as vector arrows. Eigenvalues: axis 1 = 0.588, axis 2 = 0.313; gradient length: axis 1 = 4.738, axis 2 = 3.627. **b)** Species diagram. Red: dry grassland species, green: semi-dry grassland species, black: other species).

Abb. 2. Detrended Korrespondenzanalyse (DCA) von 57 quasi-permanenten Dauerflächen der Xerothermrasen in Mitteldeutschland. **a)** Diagramm der früheren (1995–2002, leere Symbole) und aktuellen (2018/19, gefüllte Symbole) Vegetationsaufnahmen (insgesamt 114 Aufnahmeflächen) für die Trockenrasen (rot) und Halbtrockenrasen (grün); Aufnahmepaare sind durch Pfeile gekennzeichnet. Die mittleren Ellenberg´schen Zeigerwerte und die Vegetationsbedeckung, die signifikant mit den Achsen der Ordination korrelieren ($p < 0{,}05$), sind als Vektorpfeile dargestellt. Eigenvalues: Achse 1 = 0,588; Achse 2 = 0,313; Gradientenlängen: Achse 1 = 4,738; Achse 2 = 3,627. **b)** Diagramm der Arten. Rot: Trockenrasenarten, grüne: Halbtrockenrasenarten, schwarz: Sonstige).

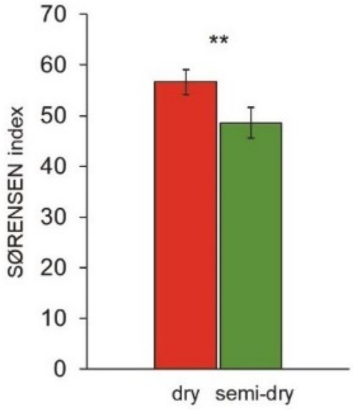

Fig. 3. Comparison of the Sørensen index (SØRENSEN 1948) between previous and recent vegetation relevés of the dry grasslands (n = 60) and semi-dry grasslands (n = 54) (mean + SE). Result of the t-test: ** $p < 0.01$.

Abb. 3. Vergleich des Sørensen-Index (SØRENSEN 1948) zwischen früheren und aktuellen Vegetationsaufnahmen der Trockenrasen (n = 60) und Halbtrockenrasen (n = 54) (Mittelwert + SE). Ergebnis des t-Tests: ** $p < 0{,}01$.

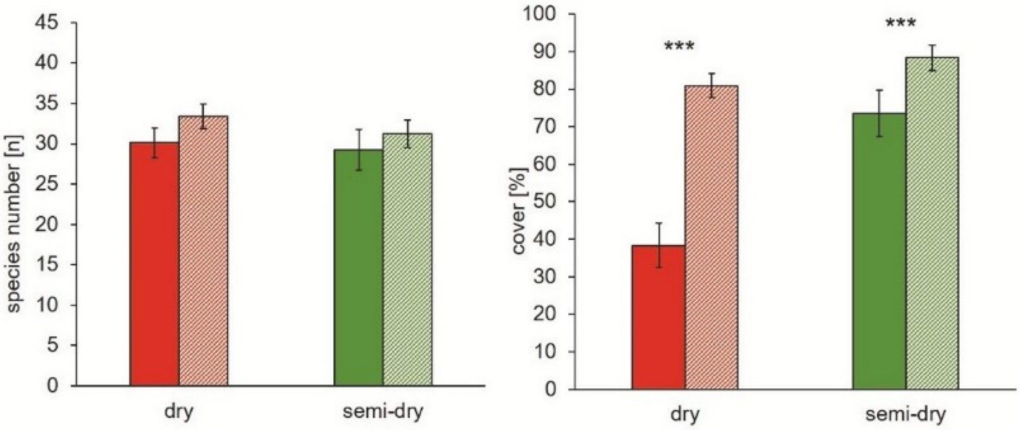

Fig. 4. Comparison of the species number (left) and vegetation cover (right) between the dry grasslands (n = 60) and semi-dry grasslands (n = 54). The filled bars represent the previous relevés; the hatched bars show the recent relevés (mean + SE). Significant differences between the previous and recent relevés show results from the paired t-tests: *** $p < 0.001$.

Abb. 4. Vergleich der Artenzahl und Vegetationsbedeckung zwischen den Trockenrasen (n = 60) und Halbtrockenrasen (n = 54). Die ausgefüllten Balken repräsentieren die früheren Aufnahmen, die schraffierten Balken die aktuellen Aufnahmen (Mittelwert + SE). Signifikante Unterschiede zwischen den früheren und aktuellen Aufnahmen sind als Ergebnisse der gepaarten t-Tests angegeben: *** $p < 0{,}001$.

The cover of the five most common dominant grasses varied between approx. 5% and 13% in the previous relevés and increased between approx. 8% and 33% in the recent relevés (Fig. 6). With the exception of *B. pinnatum* and *S. capillata*, the cover of grasses such as *B. erectus*, *F. rupicola* and *H. pratense* increased significantly by about 50% to 60%. *Bromus erectus* showed the highest cover and the greatest increase. While *B. erectus* did occur only with low percentages of presence in the dry and semi-dry grasslands, its cover increased significantly in the recent relevés (Fig. 7). *Bromus erectus* showed the strongest increase in semi-dry grasslands, especially in the *Onobrychido-Brometum* (from approx. 13% to approx. 52% cover).

The increasing dominance of grass species had an impact on the species richness of the plant communities in the case of *B. pinnatum* (r = -0.437, p = 0.033) and *S. capillata* (r = -0.442, p = 0.031) but not in the other grasses (*B. erectus*: r = 0.073, p = 0.344; *F. rupicola*: r = -0.210, p = 0.250; *H. pratense*: r = -0.085, p = 0.357).

Table 1. Total species number and percentage increase or decrease of the functional groups (annuals, graminoids, forbs) in their constancy between the previous (1995–2002) and recent relevés (2018/19).

Tabelle 1. Gesamtartenzahl und prozentualer Anteil zugenommener und abgenommener Arten der funktionellen Gruppen (Annuelle, Gräser, Kräuter) in der Stetigkeit zwischen den früheren (1995–2002) und aktuellen Aufnahmen (2018/19).

Functional group	Species number [*n*]	Increase [%]	Decrease [%]	No change [%]
annuals	38	29	8	63
graminoids	35	49	14	37
forbs	166	22	23	54

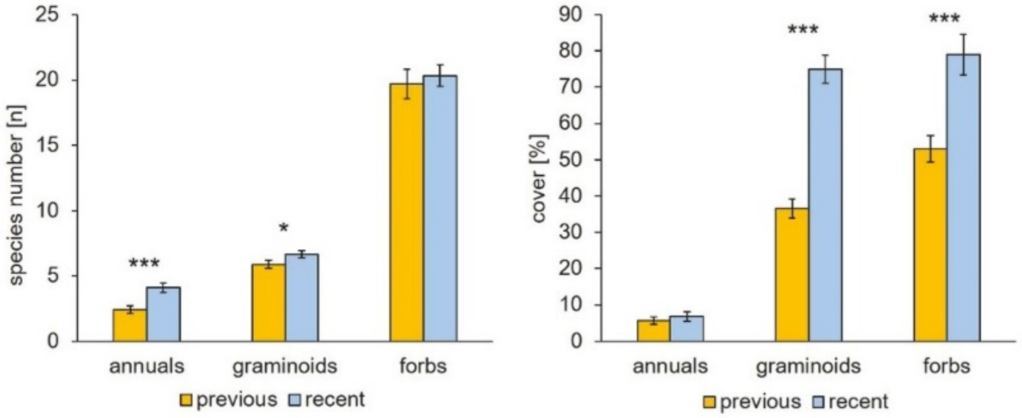

Fig. 5. Comparison of the species number (left) and vegetation cover (right) of the functional groups (annuals, graminoids, forbs) between previous ($n = 57$) and recent ($n = 57$) relevés (mean + SE). Significant differences between the previous and recent relevés show results from the paired t-tests: * $p < 0.05$, *** $p < 0.001$.

Abb. 5. Vergleich der Artenzahl (links) und Vegetationsbedeckung (rechts) der funktionellen Gruppen (Annuelle, Gräser, Kräuter) zwischen den früheren ($n = 57$) und aktuellen ($n = 57$) Aufnahmen (Mittelwert + SE). Signifikante Unterschiede zwischen den früheren und aktuellen Aufnahmen sind als Ergebnisse der gepaarten t-Tests angegeben: * $p < 0{,}05$; *** $p < 0{,}001$.

4. Discussion

Generally, a dramatic loss of species comparing the number of species between previous and recent vegetation relevés has not taken place over the last two decades for the xerothermic grasslands in Central Germany. The dry grasslands had a higher level of stability in terms of ecological site conditions than the semi-dry grasslands. Comparing functional groups, annuals and graminoids increased over time, while several endangered forbs showed a decline. The five most common dominant grasses increased in cover, which however did not affect species richness of forbs in the xerothermic grasslands in Central Germany.

4.1 Changes in dry and semi-dry grasslands

Based on the DCA, there were nearly no changes between the previous and recent floristic composition, which was also demonstrated in a resurvey study for the xerothermic grasslands of the ‘Badraer Lehde-Großer Eller’ in the area ‘Kyffhäuser’ (HAHN et al. 2013) and

Table 2. Species with increased or decreased constancy (presence/ absence) between previous (1995–2002) and recent (2018/19) vegetation relevés. The species are divided into functional groups (FG): annuals (A), graminoids (G), forbs (F). Within the functional groups, the species are sorted in descending order of difference. Only species with a significant change in constancy are shown. *P*-value: result of the Wilcoxon signed-rank test. Species without a significant change in constancy are shown in the Supplement E6. In addition, the status (0 – extinct or lost, 1 – threatened with extinction, 2 – critically endangered, 3 – endangered, D – insufficient data, V – warning list) according to the Red Lists (RL) of Saxony-Anhalt (SA; FRANK et al. 2020) and Thuringia (TH; KORSCH et al. 2011) as well as the legal protection status under the Federal Species Protection Regulation (S) are given.

Tabelle 2. Arten mit zunehmender und abnehmender Stetigkeit (Präsenz/ Absenz) zwischen den früheren (1995–2002) und aktuellen (2018/19) Vegetationsaufnahmen. Die Arten sind in funktionelle Artengruppen eingeteilt (FG): Annuelle (A), Gräser (G), Kräuter (F). Innerhalb der funktionellen Gruppen sind die Arten nach absteigender Differenz sortiert. Es sind nur Arten dargestellt, die eine signifikante Veränderung in der Stetigkeit aufweisen. *P*-Wert: Ergebnis des Wilcoxon-Signed-Rank-Tests. Arten ohne signifikante Veränderung in der Stetigkeit sind im Anhang E6. Außerdem sind der Gefährdungsstatus (0 – ausgestorben oder verschollen, 1 – vom Aussterben bedroht, 2 – stark gefährdet, 3 – gefährdet, D – Daten defizitär, V – Vorwarnliste) nach den Roten Listen (RL) von Sachsen-Anhalt (SA; FRANK et al. 2020) und Thüringen (TH; KORSCH et al. 2011) sowie der gesetzliche Schutz nach Bundesartenschutzverordnung (S) angegeben.

FG	RL		S	species	constancy		difference	*p*
	SA	TH			1995–2002	2018/19		
				increase of species				
A				*Holosteum umbellatum*	5	23	18	**< 0.001**
A				*Draba verna*	10	23	13	**0.003**
A	3	2		*Hornungia petraea*	2	12	10	**0.011**
A				*Microthlaspi perfoliatum*	2	12	10	**0.011**
A	D	2		*Buglossoides arvensis*	3	11	8	**0.025**
A	3	3		*Veronica praecox*	6	13	7	**0.018**
A				*Descurainia sophia*	0	6	6	**0.028**
G				*Bromus erectus*	23	33	10	**0.039**
G				*Festuca csikhegyensis*	0	5	5	**0.043**
F				*Euphorbia cyparissias*	44	56	12	**0.002**
F				*Falcaria vulgaris*	3	13	10	**0.005**
F				*Eryngium campestre*	13	22	9	**0.028**
F				*Convolvulus arvensis*	0	9	9	**0.008**
F	2			*Erysimum marschallianum*	5	12	7	**0.038**
F				*Vicia hirsuta*	1	7	6	**0.028**
F	3			*Polygala comosa*	0	5	5	**0.043**
F				*Daucus carota*	2	7	5	**0.043**
				decrease of species				
A	V			*Linum catharticum*	13	3	-10	**0.028**
G				*Agrostis gigantea*	6	0	-6	**0.028**
G	3			*Briza media*	18	6	-12	**0.005**
F				*Carlina vulgaris*	7	2	-5	**0.043**
F				*Knautia arvensis*	6	0	-6	**0.028**
F				*Teucrium montanum*	26	19	-7	**0.038**
F	3	3	§	*Allium lusitanicum*	12	5	-7	**0.041**
F	2	3		*Silene otites*	24	16	-8	**0.041**
F	3			*Asperula cynanchica*	25	15	-10	**0.028**
F				*Campanula rotundifolia*	14	4	-10	**0.019**
F	2			*Polygala amarella*	20	8	-12	**0.005**
F	V	3		*Euphrasia stricta*	17	1	-16	**< 0.001**

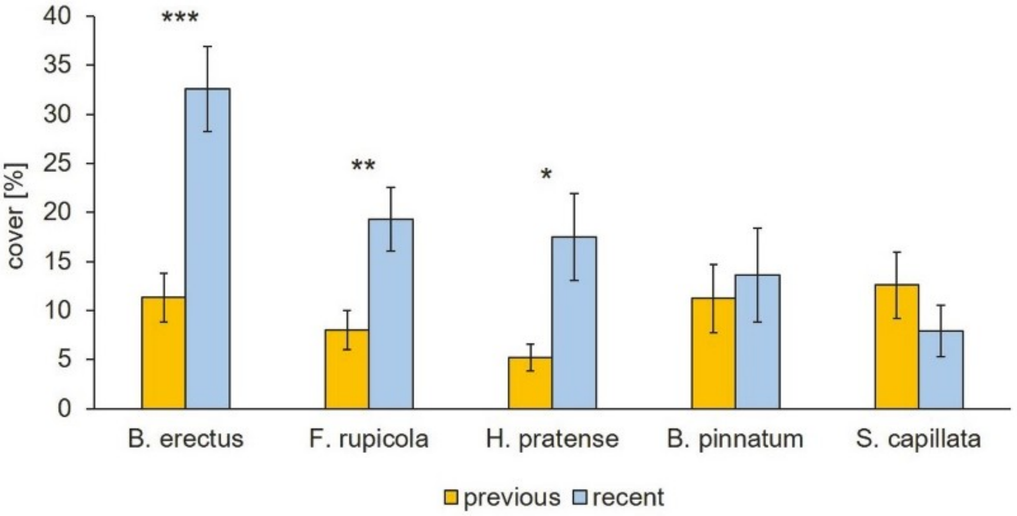

Fig. 6. Comparison of the cover of the dominant grasses between previous and recent relevés (mean + SE). Significant differences between the previous and recent relevés show results from the paired t-tests: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Abb. 6. Vergleich der Deckung der dominanten Grasarten zwischen den früheren und aktuellen Aufnahmen (Mittelwert + SE). Signifikante Unterschiede zwischen den früheren und aktuellen Aufnahmen sind als Ergebnisse der gepaarten t-Tests angegeben: * $p < 0,05$; ** $p < 0,01$; *** $p < 0,001$.

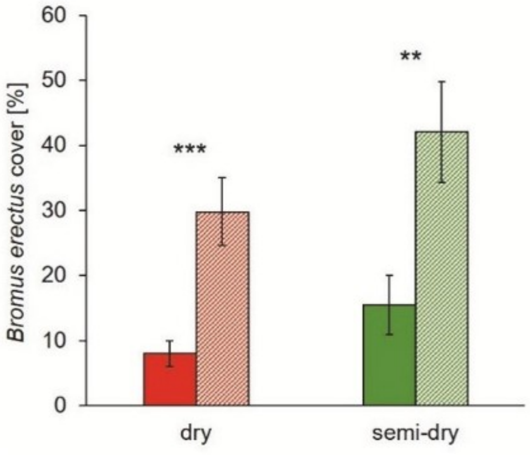

Fig. 7. Comparison of the *Bromus erectus* cover within the dry grasslands and semi-dry grasslands between previous (filled bars) and recent (hatched bars) relevés (mean + SE). Significant differences between the previous and recent relevés show results from the paired t-tests: ** $p < 0.01$, *** $p < 0.001$.

Abb. 7. Vergleich der Deckung von *Bromus erectus* innerhalb der Trockenrasen und Halbtrockenrasen zwischen den früheren (ausgefüllte Balken) und aktuellen (schraffierte Balken) Aufnahmen (Mittelwert + SE). Signifikante Unterschiede zwischen den früheren und aktuellen Aufnahmen sind als Ergebnisse der gepaarten t-Tests angegeben: ** $p < 0,01$; *** $p < 0,001$.

'Gabower Hänge' in Brandenburg (HÜLLBUSCH et al. 2016). Our DCA revealed positive correlations between the indicator values for nutrients and moisture, and negative correlations between the indicator values for light and temperature that have been proven by many studies of xerothermic grasslands (LÖBEL & DENGLER 2008, DÚBRAVKOVÁ et al. 2010, BECKER et al. 2011, HAHN et al. 2013, DIEKMANN et al. 2019), which indicates that water availability is the strongest driver for differentiation of the vegetation units (BECKER et al. 2011).

In general, the average number of species of the dry and semi-dry grasslands did not change significantly between the previous and recent relevés. This supports the assumption that phytodiversity did not decline at the local scale over time (VELLEND et al. 2013, GONZALEZ et al. 2016, CARDINALE et al. 2018). The results of a meta-analysis of xerothermic grasslands in Western and Central Europe demonstrated that particularly the number of xerothermic grassland specialists declined (DIEKMANN et al. 2019).

We found a higher floristic similarity of dry grasslands (Sørensen index: 57) compared to semi-dry grasslands (Sørensen index: 49) between both time windows. Due to their natural conditions (shallow soil depth, steep inclination, extreme drought and light, low land use), dry grasslands have a high level of stability in terms of site conditions (KRUMBIEGEL et al. 1998, PARTZSCH 2000, MEIER & PARTZSCH 2018). In contrast, semi-dry grasslands have higher water availability, which allows for higher nutrient uptake. As such, these grasslands are subject to succession by e.g. shrub encroachment, which can lead to a series of plant communities by changing the floristic composition over time (ELLENBERG & LEUSCHNER 2010). Also, higher water and nutrient availability are generally responsible for the higher vegetation cover of semi-dry grasslands in comparison to the more extreme dry grasslands. Furthermore, vegetation cover in general and cover values of different life forms could depend on weather conditions (PETŘÍK et al. 2011).

4.2 Changes in functional groups

In the last 20 years, the species number of annuals and graminoids significantly increased while that of forbs remained constant. When comparing the constancy of the species of the functional groups, a partially different pattern was found. While around 29% of the annuals and about 49% of the graminoids increased, 23% of the forbs decreased.

The change in biodiversity takes place differently in the species of the various functional groups due to the respective biological-ecological plant traits, caused by land use changes and possibly nutrient inputs or weather extremes. Many species can vary in density of individuals, which can generally be traced back to vegetation-dynamic processes such as fluctuation or succession (DIERSCHKE 1994, ELLENBERG & LEUSCHNER 2010). Annuals in particular can fluctuate strongly, as they are influenced by seasonal weather events or the availability of resources. Such non-competitive species occur more frequently in years with good germination or establishment conditions in the preceding autumn or winter (sufficient moisture, short periods of frost) (HAHN et al. 2013). Furthermore, these species are associated with open soil sections caused by disturbance such as grazing (BECKER et al. 2011). Livestock create small gaps by trampling, which can serve as regeneration niches for seedlings for low-competitive and light-demanding species, and the diaspore bank can be activated (BULLOCK et al. 1994, RUPRECHT et al. 2010, SCHWABE et al. 2013, FREUND et al. 2015, KÖHLER et al. 2016, ELIAS et al. 2018). We detected a significant increase in seven annuals, including *Hornungia petraea*, a critically endangered species (KORSCH et al. 2011). In contrast, rare *Linum catharticum* was the only annual species that decreased significantly, which was also reported by HAHN et al. (2013).

The grass *B. erectus* increased significantly in presence, which is in line with the analysis of DIEKMANN et al. (2019). Forbs that increased or newly appeared are mainly ruderal species (e.g. *Convolvulus arvensis*, *Falcaria vulgaris*). Due to nutrient inputs, these species can immigrate from adjacent arable fields and fallows into xerothermic grasslands (KRUMBIEGEL et al. 1998, BRANDES & PFÜTZENREUTER 2013), but their sporadic occurrence does not currently threaten the xerothermic grassland communities (MEIER & PARTZSCH 2018).

We found that within the last two decades, typical xerothermic species (e.g. *Asperula cynanchica*, *Euphrasia stricta*) significantly decreased. This agrees with the results of DIEKMANN et al. (2019), who observed that only grass specialists of dry grassland declined. These are usually small, light-demanding and evergreen species with smaller seeds and scleromorphic leaves (DIEKMANN et al. 2014). In a resurvey study on the xerothermic grasslands in southern England, the increase in *B. erectus* and the decrease in *A. cynanchica* and *L. catharticum* could also be recorded after 30 years (RIDDING et al. 2020).

A significant increase in cover was proven over time for the functional groups of graminoids, likely due to the increasing atmospheric nitrogen input and changes in land use. The aboveground phytomass of graminoids can be strongly promoted and their dominance over dicotyledons can be favoured under such conditions (DIEKMANN et al. 2014, BAI et al. 2015, DEMALACH et al. 2017).

As such, the importance of the five most common dominant grass species in the relevés was highlighted. *Bromus erectus*, *F. rupicola* and *H. pratense* had significantly increased their cover; but we found no changes for *B. pinnatum* (see DIEKMANN et al. 2014) and *S. capillata*. After 35 years, an increase in both presence and cover of dominant grass species (e.g. *B. erectus*, *B. pinnatum*, *F. rupicola*, *H. pratense*) could be detected for the xerothermic grasslands of 'Garchinger Heide' in Bavaria (BAUER & ALBRECHT 2020, BAUER et al. 2020). All five grasses have a highly competitive and stress-tolerant strategy type (CS) (GRIME 2001), which affords them greater adaptation (i.e. long life), even under changing abiotic conditions.

There was a special focus on the increasing dominance of *B. erectus* in the dry and semi-dry grasslands. Currently, the grass is found in almost all studied plant communities of the classes *Koeleria-Corynephoretea* and *Festuco-Brometea*. This is most likely a successive process, as it is also reported that this grass immigrated into the communities of the class *Sedo-Scleranthetea* Br.-Bl. 1955 em. Th. Müller 1961 (LÖHR-BÖGER & FÖRSTER 2013). It also occurs more frequently in disturbed and ruderalized communities, such as the *Convolvulo-Agropyrion* Görs 1966 (BORNKAMM 2008). The morphology of large tussocks with well-developed root systems (MARTI 1994, JÄGER 2017) is advantageous for the species to emigrate to new sites quickly (ZSCHOKKE et al. 2000), and as a non-deciduous species, it can continuously produce phytomass for a large part of the year (BORNKAMM 2006).

Cover of *B. erectus* in dry and semi-dry grasslands has tripled in the past two decades. This was already found for the *Festuco-Stipetum* (MEIER & PARTZSCH 2018), where the species currently reached higher coverage values above 30%. *Bromus erectus* showed a higher cover in the semi-dry grasslands than in the dry grasslands due to higher water and nutrient availability (ELLENBERG & LEUSCHNER 2010) and compared to other xerothermic grassland species (BIERINGER & SAUBERER 2001, RIDDING et al. 2020). Particularly in *Onobrychido-Brometum*, the grass achieved mean coverage values of over 50%, but other typical character species (e.g. *Onobrychis viciifolia*, *Orchis militaris*) were missed (HOPP & DENGLER 2015).

Nowadays, it seems that *B. erectus* is increasingly spreading in the xerothermic grasslands in Central Germany, although it has not yet fully achieved the potential of its competitive ability, as we have not yet been able to demonstrate any significant influence of the cover of this grass species on the biodiversity of the plant communities (the same applies to the dominant grass species *F. rupicola* and *H. pratense*). In contrast, in the grasslands of Tuscany in Italy, species richness decreased with increasing cover of *B. erectus* (MACCHERINI et al. 2000). The grass accumulates higher layers of litter, which significantly negatively affects the growth of surrounding smaller species (e.g. *Campanula glomerata*, *Pulsatilla vulgaris*) due to the reduced availability of light on the ground (WALKER & PINCHES 2011, RIDDING et al. 2020), which sooner or later could lead to a local loss of species (PARTZSCH 2000, WALKER et al. 2009). From our results, we did not find any typical xerothermic grassland species that were exclusively displaced by the increasing dominance of *B. erectus*.

However, the cover of *B. pinnatum* and *S. capillata* showed a significantly negative effect on the species richness of the plant communities. Cover of *B. pinnatum* may also favored by shading from surrounding shrubs that could suppress the growth of light-demanding species (BAIER & TISCHEW 2004). Although *S. capillata* has its main occurrence in the *Festuco-Stipetum* (SCHUBERT et al. 1995), the species is also able to grow in ruderalized communities (MAHN 1965, BRANDES & PFÜTZENREUTER 2013).

4.3 Nature conservation assessment

All investigated dry and semi-dry grassland communities are classified as endangered or critically endangered according to the Red List of Thuringia (HEINRICH et al. 2011) and Saxony-Anhalt (SCHUBERT et al. 2020). Moreover, many of the xerothermic grassland species we have recorded are also listed in the Red List of Thuringia (KORSCH et al. 2011) and Saxony-Anhalt (FRANK et al. 2020) as well as for Germany (METZING et al. 2018) as endangered or critically endangered. Hence, these rare and species-rich plant communities are subject to permanent biomonitoring (SSYMANK 1998), which, due to their high nature conservation value, are designated as priority habitats according to the Fauna-Flora-Habitat Directive, and they are subject to FFH-LRT 6210 ‘Semi-natural calcareous dry grasslands and their stages of shrub encroachment (*Festuco-Brometalia*) (* special stands with remarkable orchids)’ as well as FFH-LRT 6240* ‘Sub-Pannonian steppe dry grasslands’ (FRANK 2007, LANDESAMT FÜR UMWELTSCHUTZ SACHSEN-ANHALT 2014).

Indeed, endangered and critically endangered species such as *Allium lusitanicum*, *Polygala amarella* and *Silene otites*, decreased in abundance. Therefore, appropriate management measures, such as more traditional land use practices, are necessary to counteract the loss of xerothermic grassland specialists. However, there are also doubts that traditional land use in many sites is not sufficient (low grazing and mowing intensity, unfavorable timing of management) to stop the loss of typical xerothermic grassland species (DIEKMANN et al. 2019). Mowing alone, instead of grazing, does not seem to be a suitable solution, as this promotes the growth of *B. erectus* (DIEKMANN et al. 2019). According to our own studies, we saw that in summer the leaves of larger tussocks of *B. erectus* were partially grazed, which consequently allowed the leaves to quickly resprout again in autumn. This supports the assumption that *B. erectus* probably has a higher competitive ability than expected. For this reason, intensive spring grazing is an opportunity to suppress competitive grasses, as the freshly sprouting shoots provide higher amounts of nutrients for livestock and are not spurned (DOSTÁLEK & FRANTÍK 2012, ELIAS & TISCHEW 2016, ELIAS et al. 2018). In addition to sheep, goats should also be used in order to prevent increasing shrub cover (ELIAS et al. 2013, 2018). In the case of more gappy and steeper dry grasslands with valuable species inventory, it is recommended to pay attention to a lower stocking rate and grazing intensity (MANN & NECKER 2019). A one-year or two-year mowing, primarily in semi-dry grasslands and depending on the location, as well as mechanical cutting of shrubs, should be included as supplementary management measures (PUSCH verbal information). In order to preserve and protect the biodiversity of the species-rich xerothermic grasslands, traditional land use must be continued or reintroduced and can create a good balance between the competitive grasses and the often-endangered dicots.

Erweiterte deutsche Zusammenfassung

Einleitung – Trocken- und Halbtrockenrasen besitzen eine hohe Biodiversität und sind gekennzeichnet durch einen hohen Anteil an seltenen oder gefährdeten sowie stark gefährdeten Arten (DENGLER et al. 2014, FRANK et al. 2020). Jedoch zeichnet sich seit den letzten drei Jahrzehnten ein dramatischer Artenverlust ab (BRUELHEIDE et al. 2020, EICHENBERG et al. 2021), der vor allem durch die Prozesse des „Global Change“ und dem damit verbundenen Rückgang der traditionellen Landnutzung verursacht wird (DUPRÈ et al. 2010, DIEKMANN et al. 2014, HÜLBER et al. 2017, VALKÓ et al. 2018). Die ehemals artenreichen Xerothermrasen werden zunehmend von verschiedenen Grasarten dominiert, wie *Bromus erectus*, *Brachypodium pinnatum*, *Festuca* sp., *Helictotrichon* sp. oder *Stipa* sp. (BOBBINK et al. 1988, PARTZSCH 2000, 2001, PUSCH & BARTHEL 2003, BORNKAMM 2006, DOSTÁLEK & FRANTÍK 2008, SILANTYEVA et al. 2012, MEIER & PARTZSCH 2018). Besonders in Mitteldeutschland hat sich *B. erectus* zunehmend in den Xerothermrasen ausgebreitet (ZÜNDORF et al. 2006, BORNKAMM 2006, 2008, HELMECKE 2017). In dieser Studie sollte analysiert werden, ob es zu einer zeitlichen und räumlichen Veränderung in den mitteldeutschen Trocken- und Halbtrockenrasen innerhalb der letzten zwei Jahrzehnte gekommen ist und diese mit Veränderungen innerhalb der funktionellen Gruppen (Annuelle, Gräser, Kräuter) sowie mit einer eventuellen Zunahme der Grasarten einhergegangen ist. Die Ergebnisse sollten auch ermöglichen, eine naturschutzfachliche Bewertung hinsichtlich eines zukünftigen Pflegemanagements zur Erhaltung von artenreichen Xerothermrasen abzuleiten.

Material und Methoden – Für diese Studie wurde ein floristischer Vergleich zwischen früheren und aktuellen Vegetationsaufnahmen von Trocken- und Halbtrockenrasen herangezogen. Als Grundlage dienten 57 vorangegangene Vegetationsaufnahmen aus zwei Regionen des Mitteldeutschen Trockengebietes (Saaletal nordwestlich von Halle (Saale), Kyffhäuser), die nach ca. 20 Jahren noch annähernd genau lokalisiert werden konnten und erneut aufgenommen wurden. Um ein zukünftiges flächenbezogenes Biodiversitätsmonitoring zu gewährleisten, wurden die aktuellen Aufnahmeflächen mit Magneten dauerhaft markiert und GPS-Koordinaten erhoben. Die floristisch-ökologischen Gradienten in den Xerothermrasen zwischen den früheren und aktuellen Vegetationsaufnahmen wurden mit einer Detrended Korrespondenzanalyse (DCA) anhand der ungewichteten Zeigerwerte (ELLENBERG et al. 2001) und Vegetationsbedeckung nachgewiesen. Um Veränderungen in der floristischen Zusammensetzung der Trocken- und Halbtrockenrasen darzustellen, wurde die Ähnlichkeit der früheren und aktuellen Vegetationsaufnahmen mittels Sørensen-Index (SØRENSEN 1948) berechnet. Außerdem wurden die Artenzahl und Vegetationsbedeckung der Aufnahmen beider Zeitpunkte (1) innerhalb der Trocken- und Halbtrockenrasen und (2) innerhalb von funktionellen Artengruppen (Annuelle, Gräser, Kräuter) untersucht. Zur Überprüfung von zunehmenden und abnehmenden Arten wurde ein Stetigkeitsvergleich zwischen den funktionellen Artengruppen ausgeführt. Die Deckung der fünf dominierenden Gräser wurde zwischen den früheren und aktuellen Aufnahmen verglichen, wobei ein besonderer Fokus auf dem Vergleich der Deckung von *B. erectus* zwischen den Trocken- und Halbtrockenrasen lag. Es wurde geprüft, ob die zunehmende Dominanz der Grasarten einen Einfluss auf die Artenvielfalt der Pflanzengesellschaften hatte.

Ergebnisse – Anhand der DCA ergaben sich keine Unterschiede zwischen den früheren und aktuellen Vegetationsaufnahmen, jedoch eine klare Differenzierung zwischen Trocken- und Halbtrockenrasen. Der Sørensen-Index zeigte, dass die Trockenrasen eine signifikant höhere floristische Ähnlichkeit gegenüber den Halbtrockenrasen aufwiesen. Im Allgemeinen waren innerhalb der letzten 20 Jahre keine Veränderungen in der Gesamtartenzahl erkennbar, jedoch eine signifikante Zunahme in der Vegetationsbedeckung. Deshalb wurde ein Vergleich der funktionellen Artengruppen durchgeführt, der zeigte, dass die Zahl der Kräuter konstant blieb, die der Annuellen und Gräser signifikant zunahm. Hinsichtlich der Deckung nahm die der Gräser und Kräuter signifikant zu, jedoch nicht die der Annuellen. Dabei hatten die kurzlebigen Annuellen (z. B. *Holosteum umbellatum*, *Draba verna*, *Hornungia petraea*) innerhalb der letzten zwei Jahrzehnte eine hohe Zunahme in der Stetigkeit. Das dominante Gras *Bromus erectus* sowie krautige Arten mit ruderalem Charakter (z. B. *Convolvulus arvensis*, *Falcaria vulgaris*) nahmen ebenfalls in ihrer Stetigkeit signifikant zu bzw. traten neu auf. Im Gegensatz dazu wurde eine signifikante Abnahme typischer Xerothermrasenarten wie *Linum catharticum*, *Briza media*, *Asperula cynanchica*, *Euphrasia stricta* und *Silene otites* verzeichnet. Die dominanten Gräser *B. erectus* (höchste Zunahme), *Festuca rupicola* und *Helictotrichon pratense* nahmen innerhalb der letzten 20 Jahre in der Deckung signifikant zu, während sich bei *Brachyposium pinnatum* und *Stipa capillata* keine Änderung zeigte. Die Deckung von *B. erectus* hat mittlerweile in den Trocken- und Halbtrockenrasen sehr stark zugenommen. Trotzdem hatte die Deckung der dominanten Grasarten (außer *B. pinnatum* und *S. capillata*) keinen signifikanten Einfluss auf die Artenvielfalt der Pflanzengesellschaften.

Diskussion – Die Trocken- und Halbtrockenrasen zeigten ein unterschiedliches ökologisches Verhalten, was auf die Wasserverfügbarkeit der Standorte als stärksten Treiber für die Differenzierung dieser Vegetationseinheiten hindeutet (BECKER et al. 2011, HAHN et al. 2013, DIEKMANN et al. 2019). Außerdem zeigten die untersuchten Trockenrasen eine höhere Stabilität hinsichtlich ihrer klimatischen und edaphischen Standortsverhältnisse gegenüber den Halbtrockenrasen (KRUMBIEGEL et al. 1998, MEIER & PARTZSCH 2018). Die Gesamtartenzahl der mitteldeutschen Xerothermrasen hat sich innerhalb der letzten 20 Jahre nicht grundlegend geändert, sodass sich ein dramatischer Artenverlust (noch) nicht eingestellt hat (HÜLLBUSCH et al. 2016). Analysiert man die Arten nach ihren biologisch-ökologischen Merkmalen (funktionelle Artengruppen), zeigte sich, dass Annuelle und Gräser über die Zeit zunahmen, während typische Kräuter abnahmen (DIEKMANN et al. 2019), letztere gelten teilweise als gefährdet oder stark gefährdet (KORSCH et al. 2011, FRANK et al. 2020). Viele Arten können in ihrer Individuendichte schwanken, die sich allgemein auf vegetationsdynamische Prozesse, wie Fluktuation zurückführen lassen (DIERSCHKE 1994, ELLENBERG & LEUSCHNER 2010). Vor allem Annuelle können durch Beweidung gefördert werden, da die Trittbelastung der Weidetiere kleine Vegetationslücken schafft, die als Regenerationsnischen von Keimlingen für konkurrenzschwache und lichtliebende Arten sowie zur Aktivierung der Diasporenbank dienen können (SCHWABE et al. 2013, KÖHLER et al. 2016, ELIAS et al. 2018). Besonders die Deckung der dominierenden Gräser hatte zugenommen (vgl. BAUER et al. 2020); diese sind durch einen konkurrenzstarken und stresstoleranten Strategietypen (CS) (GRIME 2001) gekennzeichnet. Dies ermöglicht ihnen eine stärkere Anpassung (u.a. hohe Lebensdauer) auch unter verändernden abiotischen Bedingungen (z. B. erhöhte Stickstoffeinträge) (BOBBINK et al. 2010, BAI et al. 2015). Die Zunahme von *Bromus erectus* in fast allen untersuchten Pflanzengesellschaften ist offenbar ein sukzessiv verlaufender Prozess (BORNKAMM 2008). Trotzdem scheint das Potenzial der Konkurrenzkraft noch nicht vollständig erreicht zu sein, da die Deckung bisher kaum einen direkten Einfluss auf die Artenvielfalt der mitteldeutschen Xerothermrasen hatte. Durch die traditionelle Landnutzung kann eine gute Balance zwischen den konkurrenzkräftigen Gräsern und den häufig gefährdeten dikotylen Arten hergestellt werden, so dass ein entsprechendes Pflegemanagement auch in der Zukunft wichtig für die Erhaltung der artenreichen Xerothermrasen ist.

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Author contributions

TM conducted field work, performed statistical analyses and wrote the manuscript. MP supported the data analysis and helped writing the manuscript. IH helped with the final writing of the manuscript. IH and MP supervised the research work of TM.

Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Regions and their study areas (see Fig. 1).

Anhang E1. Regionen und ihre Untersuchungsgebiete (vgl. Abb. 1).

Supplement E2. Detailed map of the quasi-permanent plots in the individual study areas. The relevé number refers to the recent vegetation relevés in Supplement E3. Coordinates are given in Supplement E5. **a)** near Mücheln (Wettin); **b)** Mittelberg (41) and Badraer Lehde (40) (Kyffhäuser); **c)** Ochsenburg (Kyffhäuser); **d)** Kosakenberg (24, 39), Grauer Berg (25) and Hämling (23) (Kyffhäuser).

Anhang E2. Detaillierte Karten der quasi-permanenten Aufnahmeflächen der einzelnen Untersuchungsgebiete. Die Aufnahmenummer bezieht sich auf die aktuellen Vegetationsaufnahmen in Anhang E3. Koordinaten sind in Anhang E5 angegeben **a)** bei Mücheln (Wettin); **b)** Mittelberg (41) und Badraer Lehde (40) (Kyffhäuser); **c)** Ochsenburg (Kyffhäuser); **d)** Kosakenberg (24, 39), Grauer Berg (25) und Hämling (23) (Kyffhäuser).

Supplement E3. Comparison of the previous (1995–2002) and recent (2018/19; bold) vegetation relevés of the dry and semi-dry grasslands in Central Germany (original coverage of the species). The plant communities are classified according to SCHUBERT et al. (1995). In the recent relevés, the coverage of the species was estimated using the 9-part Braun-Blanquet scale (REICHELT & WILMANNS 1973) (for adjusted coverage see Supplement E4).

Anhang E3. Vergleich der früheren (1995–2002) und aktuellen (2018/19; fett gedruckt) Vegetationsaufnahmen der Trockenrasen und Halbtrockenrasen in Mitteldeutschland (originale Deckungsgrade der Arten). Die Einteilung der Pflanzengesellschaften erfolgt nach SCHUBERT et al. (1995). Bei den aktuellen Aufnahmen wurden die Deckungsgrade der Arten nach der 9-teiligen Braun-Blanquet-Skala (REICHELT & WILMANNS 1973) geschätzt (angepasste Deckungsgrade siehe Anhang E4).

Supplement E4. Comparison of the previous (1995–2002) and recent (2018/19; bold) vegetation relevés of the dry grasslands and semi-dry grasslands in Central Germany with adjusted coverages of the species. Explanations and abbreviations see Supplement E3.

Anhang E4. Vergleich der früheren (1995–2002) und aktuellen (2018/19; fett gedruckt) Vegetationsaufnahmen der Trockenrasen und Halbtrockenrasen in Mitteldeutschland mit angepassten Deckungsgraden der Arten. Erläuterungen und Abkürzungen siehe Supplement E3.

Supplement E5. Coordinates for the 57 quasi-permanent plots. The relevé number refers to the recent vegetation relevés in Supplement E3.

Anhang E5. Koordinaten für die 57 quasi-permanenten Aufnahmeflächen. Die Aufnahmenummer bezieht sich auf die aktuellen Vegetationsaufnahmen in Anhang E3.

Supplement E6. Species with increased or decreased constancy (presence/ absence) between previous (1995–2002) and recent (2018/19) vegetation relevés. The species are divided into functional groups (FG): annuals (A), graminoids (G), forbs (F). Within the functional groups, the species are sorted in descending order of difference. Species without a significant change in constancy are shown. Only species that appeared more than five times in the relevés were considered.

Anhang E6. Arten mit zunehmender und abnehmender Stetigkeit (Präsenz/ Absenz) zwischen den früheren (1995–2002) und aktuellen (2018/19) Vegetationsaufnahmen. Die Arten sind in funktionelle Artengruppen eingeteilt (FG): Annuelle (A), Gräser (G), Kräuter (F). Innerhalb der funktionellen Gruppen sind die Arten nach absteigender Differenz sortiert. Es sind Arten dargestellt, die keine signifikante Veränderung in der Stetigkeit aufweisen. Dabei werden nur Arten berücksichtigt, die mehr als fünfmal in den Aufnahmen vorkamen.

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Chapter 3

Are recent climate change and airborne nitrogen deposition responsible for vegetation changes in a central German dry grassland between 1995 and 2019?

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Are recent climate change and airborne nitrogen deposition responsible for vegetation changes in a central German dry grassland between 1995 and 2019?

Sind der aktuelle Klimawandel und Stickstoffeinträge aus der Luft für die Vegetationsveränderungen in einem mitteldeutschen Trockenrasen zwischen 1995 und 2019 verantwortlich?

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This article is dedicated to the botanical conservationist Albert Keding, Naumburg (Saale), who protected the Schafberg from being converted into a vineyard in the 1980s by assessing the site as unsuitable for viticulture in order to preserve the dry grasslands.

Abstract

Temperate dry grasslands are adapted to heat and drought and may therefore be resilient to global warming. We investigated vegetation changes in a dry grassland comprising three xeric associations (*Carici-Seslerietum*, *Festuco-Stipetum*, *Trinio-Caricetum*) and one meso-xeric association (*Gentiano-Koelerietum*) in the dry region of Central Germany (lower Unstrut valley) between 1995 and 2019 by one-time repetition of 46 permanent 1 m² plots distributed along a 244 m line. During this period, the mean summer temperature in the region has increased by 3.1 °C, and the frequency and intensity of heat waves and drought events have increased strongly. Because there was also persistent airborne N deposition, we hypothesized both environmental factors as major causes of potential vegetation changes. We found a significant change in vegetation composition indicated by a 50% species turnover based on the presence/absence of species. However, the mean indicator value for nutrients did not increase and the mean indicator value for moisture did not decrease. This result contradicts to our prediction, but can be explained by the fact that both indicator values were strongly intercorrelated, i.e. eutrophication and drought compensated for each other in their indicator values. In addition, a sharp decline in the proportion of meso-xerophilic plant species (as opposed to that of xerophilic species) clearly indicated increasing drought. Another indication of the now drier conditions was the strong increase in winter annuals, which was presumably due to the drought-induced lower competition from perennial plants. In addition, many graminoids and all of the few summer annuals declined sharply, probably due to drought, while sub-ruderal biennials increased, probably due to the combination of eutrophication and drought. Among graminoids, only the xerophilic *Stipa capillata* and the xero-tolerant *Bromus erectus* increased, probably due to the drier summers (*S. capillata*) and due to milder

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winters (*B. erectus*). These increased Mediterranean climate conditions were also indicated by a decreased continentality indicator value. The positive correlation of the NMDS axis of vegetation change and the mean Ellenberg indicator value for nutrients indicated eutrophication (airborne N deposition) as a reason of vegetation change. However, N deposition without increasing drought would have resulted in denser and more mesophilic grasslands, i.e. the opposite pattern than we observed. Therefore, we assume that climate change (mainly summer drought, but also mild winters) was the main cause for the observed changes. This assessment is also supported by the fact that the grasslands became floristic more heterogeneous (because prevailing eutrophication would have led to homogenisation). With 29 loser species and 9 winner species, and 18.2% decline in species richness and 30% decline in the number of threatened species, we conclude that the conservation value of our grassland has decreased significantly. Overall, we conclude that dry grasslands in the dry area of Central Germany, are already affected by climate change (especially increased drought) in addition to N deposition, and that climate change is very likely the greatest threat to these grasslands.

Keywords: Atmospheric nitrogen deposition, *Bromus erectus*, drought, eutrophication, *Festuco-Brometea*, global warming, monitoring, permanent plot, plant functional types, xeric grassland

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Central European dry grasslands are particularly species-rich, but their occurrences have declined sharply in size and number. Therefore, they are considered to be particularly valuable and highly endangered (VEEN et al. 2009, WILSON et al. 2012, JANSSEN et al. 2016, DENGLER et al. 2020). Their significant reduction (POSCHLOD & WALLIS DE VRIES 2002, ENYEDI et al. 2008) and fragmentation (LINDBORG et al. 2014, DEÁK et al. 2016) was caused by intensification or abandonment of land use, starting with the use of artificial fertilizers since the beginning of the 20th century and especially after World War II. A current threat to dry grassland is airborne or atmospheric nitrogen deposition and an assumed future threat is climate change. Dry grasslands are adapted to heat and drought and may therefore be resilient to climate change which is generally considered to be the greatest future threat to biodiversity (MOSBRUGGER et al. 2012, PÖRTNER et al. 2021). Both positive and negative effects of climate change on dry grasslands are possible. A positive effect would be if climate change compensates for nitrogen inputs due to drought and thus also slows down the rate of succession of dry grasslands. Irreversible heat and drought damage would be negative. Because of their generally precarious situation and their low regeneration potential, PETERMANN et al. (2007) attested dry grasslands a high sensitivity to climate change. A feature of climate change is that extreme weather events such as heat waves and droughts have increased in frequency and intensity, currently particularly in Western and Central Europe (ROUSI et al. 2022). In Central Germany, the heat waves and drought events of 2003, 2015, 2018 and 2019 (as well as 2020 and 2022 following our study), were particularly extreme (BOERGENS et al. 2020, EDO 2021) and are considered the most severe in 2000 years (BÜNTGEN et al. 2021). Especially the 2018 drought (the year before our resurvey) was severe, while the 2019 drought was less so, but soils had a higher water deficit because the deep-water storage was greatly reduced in 2018 and not refilled in winter 2018–2019 (BOERGENS et al. 2020). Drought events are mainly caused by less precipitation, but also by higher temperature leading to increased evapotranspiration. In the town Artern, close to our study area and with comparable climate, annual precipitation in 2018 was only 273 mm, 58% of the average of 1961–1990 (WETTERKONTOR 2022). The mean spring temperature in Artern in 2018 was 10.8 °C and the mean summer temperature 20.8 °C, i.e. 2.7 °C and

3.8 °C above the average, respectively, and the sunshine duration in 2018 was 34% above the average. Altogether, in Artern, over the period 2015–2019 (which is expected to be most relevant here), annual temperature and sunshine duration increased by 2.0 °C (from 8.5 °C to 10.5 °C) and 20% (from 1457 h to 1749 h), respectively, and annual precipitation decreased by 9% (from 475 mm to 430 mm), compared with 1961–1990 (WETTERKONTOR 2022). However, mean values over several years must not adequately reflect weather extremes such as drought events (BENISTON et al 2007). Another feature of climate change in Central Europe has been mild winters since decades (KREYLING & HENRY 2011). Mild winters and dry summers are expected to increase and increasingly influence ecosystems (SCHÄDLER et al. 2019).

Airborne nitrogen deposition (hereafter referred simply as N deposition), in contrast, have been effective for longer time. Eutrophication effects due to N deposition are known from many regions in Central Europe, especially from nutrient-poor habitats such as heathlands (BOBBINK et al. 1992), acid grasslands (DUPRÈ et al. 2010, MAZALLA et al. 2021) and meso-xeric calcareous grasslands (DIEKMANN et al. 2014). Studies of N deposition in true xeric grasslands are largely missing, but in xeric grasslands, eutrophication is certainly suppressed by water-limitation hindering nutrient uptake by the plants (ELLENBERG & LEUSCHNER 2010). Deposition of nitrogen has the potential to change nutrient-poor grasslands fundamentally (BOBBINK et al. 1998, PAYNE et al. 2017). It favours nitrophilic plants but also mesophilic plants, as nitrogen compensates for dryness (ELLENBERG & LEUSCHNER 2010: 929). In addition, N deposition may increase successional speed of abandoned dry grasslands (BOHNER et al. 2020). Current N deposition rates of 10–16 kg ha^{-1} y^{-1} in the study area (SCHAAP et al. 2018) are at the level of the critical loads for dry grasslands (8–15 kg ha^{-1} y^{-1}) (BOBBINK & HETTELINGH 2011). N deposition is also often leading to floristic homogenisation of the community, mainly by replacement of many less-competitive loser species by few competitive winner species (MCKINNEY & LOCKWOOD 1999). Floristic heterogenisation, in contrast, is often driven by disturbance (MORI et al. 2018). Homogenisation was often found in forests (KEITH et al. 2009, NAAF & WULF 2010, REINECKE et al. 2014) and rarely in grasslands (DIEKMANN et al. 2019; for positive examples see ROSS et al. 2012 and HANSEN et al. 2021).

Dry grasslands in a broader sense can be divided into dry (xeric) types in a narrow sense and semi-dry (meso-xeric) types being considered near-natural/natural and semi-natural, respectively (ELLENBERG & LEUSCHNER 2010, DENGLER et al. 2020). Meso-xeric grasslands grow under moderately dry conditions and can only be maintained by cyclic disturbance, i.e. biomass must regularly be removed by moderate grazing or mowing for maintaining high species richness (PETRAITIS et al. 1989, KELEMEN et al. 2014). Xeric grasslands, in contrast, grow under drier conditions thus having lower successional potential and therefore need to be managed at most irregularly for maintenance (ELLENBERG & LEUSCHNER 2010). Within xeric and meso-xeric grasslands, various further dry grassland types can be distinguished representing ecological entities. This makes them particularly suitable for studying the effects of habitat differences on vegetation change. A key species group within dry grasslands are graminoids mainly from the *Poaceae* family but also *Cyperaceae* species. Because these matrix species often produce the main biomass, they affect the community in different ways, including above- and below-ground competition, nutrient cycling due to differences in litter decomposition rates, and influence vegetation structure and thus microclimatic conditions for e.g. insects (STEVENS & GOWING 2014, PONIATOWSKI et al. 2018). Many graminoids have clear ecological preferences regarding nutrient and water supply and can therefore be used as ecological indicators (ELLENBERG 1986). Short-lived plants, on the other hand, need open soil patches with low competition for germination and recruitment thus being ruderal strategists and therefore indicators for disturbance e.g. by trampling of livestock or even drought events (FISCHER et al. 2020, MEIER et al. 2021). In addition, graminoids and short-lived plants have high reproduction rates and high dispersal potential and therefore can establish rapidly (GRIME 2001), allowing them to respond quickly to environmental changes.

In order to detect changes in dry grassland vegetation over time, several studies have compared previous and current vegetation on semi-permanent plots (e.g. PARTZSCH 2000, BENNIE et al. 2006, TOROK & SZITAR 2010, NEWTON et al. 2012, HAHN et al. 2013, DIEKMANN et al. 2014, 2019, BAUER & ALBRECHT 2020, RIDDING et al. 2020, CHARMILLOT et al. 2021, MEIER et al. 2021, MAZALLA et al. 2022, SCHÜLE et al. 2022), while resurvey studies based on permanent plots are still largely missing. Of these studies, to our knowledge, only MAZALLA et al. (2022) found evidence of climate change effects on meso-xeric calcareous grasslands so far. Furthermore, climate change impacts on acidic sand grassland (SCHÜLE et al. 2022) and alpine calcareous grasslands (KUDERNATSCH et al. 2016) have been identified.

We studied vegetation changes in dry grasslands in Central Germany (which are often referred to as xerothermic grasslands). After 24 years, we repeated 46 permanent 1 m² plots along a 244 m long transect line that passed through four associations. We selected a set of species traits and vegetation characteristics that have been widely used to measure vegetation change in dry grasslands but focused on variables likely to indicate nutrient input and climate change, such as drought, which we expect to be the main drivers of potential change. In detail, we focus on ecological indicator values, life forms especially of short-lived plants, CSR strategies, graminoids and species richness. We applied ordination analysis for detecting directional vegetation change and tested for taxonomic homogenisation. In particular, we expected an increased mean indicator value for temperature and nutrients and a decreased mean indicator value for moisture. We further expected a decrease of meso-xerophytic plants and an increase of short-lived plants and SR strategists because both species groups normally do profit from drought, especially in combination with nutrient input (GRIME 2001). We also expected a decrease in species richness. Regarding homogenisation, we were ambiguous: we either expected an increase due to possibly increased competition due to N deposition or a decrease (i.e. heterogenisation) due to disturbance by drought events. In order to draw sound conclusions, we were particularly interested in the possible mechanisms of the assumed changes. Our hypotheses are summarized in Table 1.

2. Study site and system

The study was conducted at the Schafberg in the lower Unstrut valley nearby the village Zscheiplitz (Saxony-Anhalt, Central Germany) (Fig. 1). The Schafberg is located at the southern edge of the tectonic limestone plate Querfurter Platte which steeply drops down to the Unstrut river around Freyburg. The Schafberg, on the other hand, has gentler slopes (about 20° inclination) especially in south-western (210°) exposure. At the top of the hill (206 m a.s.l.), the Lower Muschelkalk outcrops, while below frost debris layers form the substrate (for soil profiles see BECKER 1998a). At the foot of the hill (135 m a.s.l.), these gravel and loam layers can be 1 m thick.

The macroclimate at the Schafberg site is distinctly dry and warm in summer, but the microclimate is significantly drier due to the southwest-exposed slope and, according to data logger measurements from June to August 2019, about 3 °C warmer than the macroclimate (T. Meier, unpublished data; for temperature, evaporation and humidity patterns over the day at the Schafberg, see BECKER 1998a). Between 1991 and 2020, the mean annual precipitation in Laucha, about 3 km away, was 542 mm and the mean annual temperature in Querfurt, about 20 km away, was 9.3 °C (July mean 18.6 °C) (DWD 2022).

The weather of the first year of recording (1995) was average overall. Spring (March to May, the most important season for development of our xeric grassland) and summer (June to August) were 0.5 °C and 1.4 °C warmer and slightly wetter (106% precipitation) and slightly drier (92% precipitation), respectively, than the 1960–1990 means of the Artern climate station about 30 km west of the study area with comparable climate (WETTERKONTOR 2022). The weather in the resurvey year 2019 was also ± average in spring (+0.3 °C, 100% precipitation), but warmer and drier than average in summer (+2.2 °C, 56% precipitation) compared to the more recent comparison period 1991–2020 (which was already 1.2 °C warmer and 1% wetter in the area than the period 1961–1990) (WETTERKONTOR 2022).

During the first survey, the dry grasslands on the Schafberg were assigned to four associations within the class *Festuco-Brometea* Br.-Bl. & Tx. ex Klíka & Hadač 1944 (BECKER 1998a, b). The association names used at that time are still current with the exception of *Teucrio-Seslerietum* Volk 1937, which was renamed *Carici humilis-Seslerietum* Zlatník 1928 in the EuroVegChecklist for priority reasons (cf. BERGMEIER 2020). Only the higher syntaxonomic levels of our associations have partially changed (cf. BERGMEIER 2020). The meso-xeric grassland on the north-east exposed back of the hill was assigned to the *Gentiano-Koelerietum pyramidatae* Knapp 1942 ex Bornk. 1960 as xeric-calcareous subassociation *teucrietosum* Möseler 1989 (hereafter abbreviated as *Koeleria* grassland). The xeric grassland on the south-western slope was divided into three associations: The dry grassland on the uppermost south-western slope on raw, flat soil was assigned to *Carici humilis-Seslerietum albicantis* Zlatník 1928 (*Sesleria* grassland). The dry grassland on the middle and lower south-western slope on more or less flat ground was assigned to the *Trinio-Caricetum humilis* Volk ex Br.-Bl. et Moor 1938 as meso-xeric subassociation *cirsietosum* Becker 1998 (*Carex humilis* grassland). The dry grassland on the lower central south-western slope on shallow clay soil was assigned to *Festuco valesiacae-Stipetum capillatae* (Libbert 1931) Mahn 1959 as calcareous subassociation *teucrietosum* Becker 1998 (*Stipa* grassland). The order of associations along the transect from the back of the hilltop across the hilltop along the large SW slope to the base of the hill was *Gentiano-Koelerietum* → *Carici-Seslerietum* → *Trinio-Caricetum* → *Festuco-Stipetum* → *Trinio-Caricetum* (BECKER 1998a, b).

The Schafberg with its approximately 25 ha of dry grassland is a hotspot of rare and endangered plant species and thus has eminent nature conservation value. It is part of the Natura 2000 site "Schafberg und Nüssenberg bei Zscheiplitz" (EU FFH code: DE 4736-305, federal code: FFH0148, 211 ha) (JENTZSCH & REICHHOFF 2013). During the study period from 1995 to 2019, the Schafberg dry grassland was continuously grazed by sheep, with interruptions in individual years. However, due to the nutrient-poor soils and the xeric conditions, the Schafberg dry grassland is very less productive and therefore less susceptible to succession.

Fig. 1. Aerial view of the 244 m long transect (yellow line) on the Schafberg. The transect ranged from the north slope (upper right) across the crest of the hill (small white gap) to the foot of the large south-west slope (lower left). The upper photo **a)** dates from 2000 and the lower one **b)** from 2020. The light shimmering areas in the lower photo show the less productive (sparser) vegetation due to drought. The degree of shrub cover has hardly changed. The old-growth *Pinus nigra* forest (above centre left cut) on the plateau largely died during the 2018 drought. The complex of shrubland and limestone heaps on the right indicates a former quarry (Images from Google Earth, a) 01.06.2000, b) 11.09.2020).

Abb. 1. Luftbild des 244 m langen Transekts (gelbe Linie) am Schafberg. Der Transekt reicht vom Nordhang (oben rechts) über die Kuppe (kleine weiße Blänke) zum Fuß des großen Südwesthangs (unten links). Das obere Luftbild **a)** stammt aus dem Jahr 2000 und das untere **b)** aus dem Jahr 2020. Die hell schimmernden Flächen auf dem unteren Foto zeigen die dürrebedingt weniger produktive (schütterere) Vegetation. Der geringe Verbuschungsgrad ist dagegen fast unverändert. Der in der Bildmitte oben links angeschnittene ältere Schwarzkiefernforst ist während der Dürre 2018 weitgehend abgestorben. Der Komplex aus Gebüschen und Schutthalden rechts auf dem Plateau zeigt einen ehemaligen Steinbruch (Luftbilder aus Google Earth, Aufnahmedatum a) 01.06.2000, b) 11.09.2020).

According to the German Red List, the communities are classified as endangered (*Gentiano-Koelerietum* and *Carici-Seslerietum*) or critically endangered (*Festuco-Stipetum* and *Trinio-Caricetum*) (RENNWALD & MITARB. 2000). In Saxony-Anhalt, all communities are classified as endangered (SCHUBERT & MITARB. 2020). The *Gentiano-Koelerietum* corresponds to the EU priority habitat type 6210 (Near-natural dry grasslands and shrubs on calcareous substrates (*Festuco-Brometalia*), important orchid sites), the *Festuco-Stipetum* to the priority habitat type 6240 (Sub-Pannonian steppe dry grasslands) and the *Trinio-Caricetum* shows a mixture of the priority habitat types 6210 and 6240 (SSYMANK et al. 2021). The *Carici-Seslerietum* corresponds to the non-priority habitat type 6210 (Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*).

The lower Unstrut valley is a main area of dry grasslands in Central Germany with high supra-regional nature conservation value (BECKER 2000). Here, the combination of dry climate and calcareous substrate leads to a distinctive mixture of plants with continental and sub-Mediterranean distribution, which is the main characteristic of the dry grasslands of the lower Unstrut valley (BECKER 1998b). The dry grasslands of the lower Unstrut valley as a whole (an approx. 20 km long valley section) were studied by BECKER (1998b). A detailed study was carried out on the Schafberg, focusing on microclimatic and edaphic factors for community differentiation (BECKER 1998a). In addition, several studies on life strategies in individual communities have been carried out in this area (BÖTTNER et al. 1997, HENSEN 1997, MEIER & PARTZSCH 2018, MEIER et al. 2019). All this knowledge, gained mainly by us authors, was used here as background for the interpretation of the results and for conclusions. Figures 2–3 show the grassland areas in 1995.

3. Methods

3.1 Vegetation survey and resurvey

The first survey was carried out on 25–27 June and 3 July 1995. 46 plots of 1 m² were distributed along a 244 m long linearly line running from the north-exposed back of the hill (running metres 1–21) to the foot of the southwest-exposed front of the hill (running metres 22–243) (BECKER 1998a). Along this line the plots were distributed more or less regularly, with the aim to cover all important grassland types with a larger number of samples. The beginning and the end of this transect were permanently marked with a buried magnet, while the position of the plots was measured in running metres from the starting point with a tape measure. Plots were delineated with a 1 × 1 m wooden frame, and vascular plant species were recorded per plot with their cover according to the standard Braun-Blanquet scale, with cover class 2 divided into 2a (5–15% cover) and 2b (>15–25% cover).

The resurvey was carried out on 5 and 21 June 2019 in the same way as the first survey, i.e. the buried magnets at the beginning and end were found again with a detector, and the plots were found again with a tape measure and based on their distances from the beginning. Both data sets were merged and species names were harmonised according to the Checklist of Vascular Plants of Germany (HAND et al. 2022). The micro species *Achillea pannonica* and *A. millefolium* s. str. were aggregated to *A. millefolium* agg.; no further aggregation was necessary. During the re-survey, all plots were permanently marked with a buried magnet in their centre (plot no. 1: N 51° 12' 58.62" E 11° 43' 17.10", no. 46: N 51° 12' 58.14" E 11° 43' 16.44"). We consider the plots to be permanent, but the newly surveyed plots can be moved slightly (up to about 1 m).

Fig. 2. First record of the *Carex humilis* grassland (*Trinio-Caricetum*) on the middle SW slope of the Schafberg. In late June 1995, a climatically average summer at the time, the vegetation was still without severe water deficit. The 244 m long red transect line along which the plots were distributed is visible. *Brachypodium pinnatum* in flower (Photo: T. Becker, 26.06.1995).

Abb. 2. Erstaufnahme des Erdseggen-Trockenrasens (*Trinio-Caricetum*) am mittleren Südwesthang des Schafbergs. Ende Juni 1995, einem damals klimatisch durchschnittlichen Sommer, zeigte die Vegetation noch keinen stärkeren Wassermangel. Sichtbar ist die rote Transektschnur entlang der die 46 Aufnahmeflächen lagen. *Brachypodium pinnatum* in Blüte (Foto: T. Becker, 26.06.1995).

3.2 Vegetation variables

The following variables were calculated from the vegetation data per plot in each year (cf. Supplement E1): 1) Mean unweighted ecological indicator values for light, temperature, continentality, moisture, soil reaction and nutrients according to ELLENBERG et al. (2001). 2) Proportion and number of xerophilic or meso-xerophilic plants (summarised as moisture types or moisture behaviour, respectively) as an additional measure for dryness. Xerophilic plants were defined as those that were diagnostic for xeric grassland types (assocs. *Festuco-Stipetum* and *Carici-Seslerietum*, and subassocs. *Trinio-Caricetum stipetosum* and *festucetosum pallentis*, and rock-ledge communities of the class *Sedo-Scleranthetea*) according the survey by BECKER (1998b). Meso-xerophilic plants were defined as those that were diagnostic of meso-xeric grassland types (assoc. *Gentiano-Koelerietum* and subassoc. *Trinio-Caricetum cirsietosum*). The meso-xerophilic species showed a significantly higher mean indicator value for moisture than the xerophilic species (3.5 ± 0.14 *vs.* 2.4 ± 0.15, $p < 0.001$). 3) Proportions of the general Raunkiaer life forms chamaephytes, hemicryptophytes and therophytes (annuals) according to ELLENBERG et al. (2001) and numbers of special life forms of short-lived plants, i.e. summer and winter annuals as well as biennials (monocarpic perennials) according to standard books and own observations. 4) Proportions of the CSR strategy types CS, CSR and SR according to KLOTZ et al. (2002) (other strategy types and life forms proved negligible and were therefore not taken into account). 5) Occurrence of graminoids and short-lived plants as product of presence × ordinal-transformed cover (r = 1, + = 2, 1 = 3, etc.). 6) Richness of vascular plant species (α-diversity). 7) Number of threatened vascular plant species (including critically endangered, endangered and near threatened (Vorwarnliste) species according to the German Red List; METZING et al. 2018). 8) Temporal species turnover

(Bray-Curtis dissimilarity, β-diversity) was calculated pairwise for old and new plots based on species presence/absence and species cover. 9) Total β-diversity of associations was calculated for plot collectives and compared between years based on species presence/absence and species cover. Total β-diversity was used as a measure of homogenisation (decreasing β-diversity over time) or heterogenisation (increasing β-diversity). β-diversity (species turnover/dissimilarity) was bounded between 0 and 1, where 0 means that the two samples have the same composition (that they have all species in common) and 1 means that the two sites have no species in common.

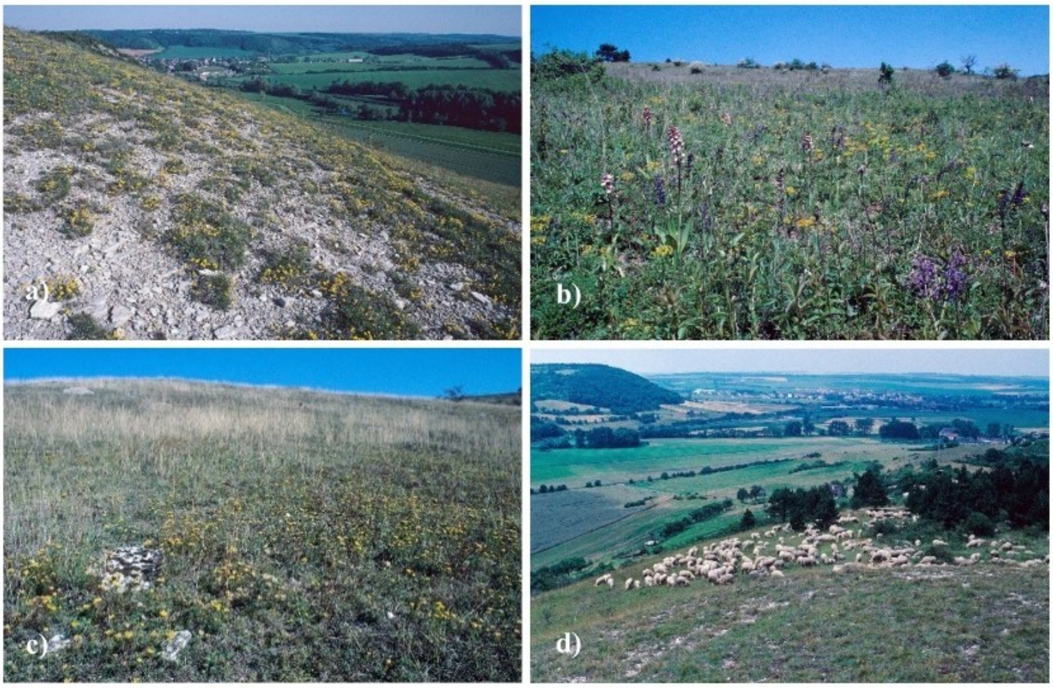

Fig. 3. a) *Sesleria* grassland (*Carici-Seslerietum*) in the transect area on the Schafberg hilltop during the flower of *Helianthemum canum* in May 1995. Of the four associations, the *Carici-Seslerietum* had changed the least. **b)** Fresh green *Carex humilis* grassland (*Trinio-Caricetum*) in the transect area of the middle SW slope of the Schafberg. In mid-June 1995, *Euphorbia cyparissias*, *Orchis purpurea* and *Salvia pratensis* were in flower. In front: *Inula hirta* vegetatively. **c)** *Carex humilis* grassland (*Trinio-Caricetum*) at the middle SW slope of the Schafberg in the transect area in 1995. Back then, the vegetation was still green in September. *Galatella linosyris* in flower. The dried grass flower shoots belong to *Brachypodium pinnatum*. **d)** Grazing sheep in the *Sesleria* grassland (*Carici-Seslerietum*) on the Schafberg hilltop in July 1995. Even in midsummer, the vegetation was green during that time. On the right the village of Weischütz and in the background the small town of Laucha (Photos: T. Becker).

Abb. 3. a) Blaugras-Trockenrasen (*Carici-Seslerietum*) im Bereich des Transekts an der Schafberg-Kuppe im Mai 1995 zur Blüte von *Helianthemum canum*. Von den vier Assoziationen hatte sich das *Carici-Seslerietum* am wenigsten verändert. **b)** Frisch grüner Erdseggen-Trockenrasen (*Trinio-Caricetum*) im Bereich des Transekts am mittleren Südwesthang des Schafbergs. Mitte Juni 1995 blühten hier *Euphorbia cyparissias*, *Orchis purpurea* und *Salvia pratensis*. Im Vordergrund: *Inula hirta* vegetativ. **c)** Erdseggen-Trockenrasen (*Trinio-Caricetum*) im Bereich des Transekts am mittleren Südwesthang des Schafbergs im September 1995. Die Vegetation war damals noch im September grün. *Galatella linosyris* in Blüte. Die vertrockneten Grasblütentriebe gehören zu *Brachypodium pinnatum*. **d)** Schafbeweidung im Blaugras-Trockenrasen (*Carici-Seslerietum*) auf der Schafberg-Kuppe im Juli 1995. Auch im Hochsommer war die Vegetation damals noch grün. Rechts angeschnitten das Dorf Weischütz und hinten die Kleinstadt Laucha (Fotos: T. Becker).

3.3 Statistical analyses

Prior to statistical analyses, Braun-Blanquet coverage values were converted to the mean percentage of the corresponding class as follows: r = 0.1%, + = 0.5%, 1 = 2.5%, 2a = 10%, 2b = 20%, 3 = 37.5%, 4 = 62.5%, 5 = 87.5%. For indicator species analysis (ISA) and non-metric multi-dimensional scaling (NMDS), the cover values were then log(x + 1) transformed to avoid the processes being dominated by a few very abundant species. For the cover turnover analysis (Bray-Curtis), the cover values were left untransformed (to test for maximum cover effects). ISA (DUFRÊNE & LEGENDRE 1997) was used to identify species characteristic of the associations in either 1995 (loser species) or 2019 (winner species). The ecological indicator values obtained were tested for significance by Monte Carlo permutation tests with 9999 runs. NMDS (MCCUNE & GRACE 2002) with Bray-Curtis as distance metric was used to extract floristic dimensions (gradients). A Monte Carlo permutation test revealed highly significant ($p < 0.01$) low stress. The final stress for the two-dimensional NMDS solution was 11.8. The relationships between NMDS axis 2 and the variables of environmental conditions, including the climate variables of the two years (see introduction), and the proportions of xerophilic and meso-xerophilic plants were analysed using Pearson correlation. The same was done for the analysis of the relationship between the Ellenberg indicator values for moisture and nutrients. Pair-wise temporal turnover between old and new plots (BRAY & CURTIS 1957) was used to assess changes in species composition, and overall turnover of plots within associations and years was used to assess homogenisation or heterogenisation of vegetation. Both tests were applied with solely presence/absence data and untransformed cover data each. To obtain sound diagnostic species within the previous data and current data a Fisher's exact test was defined with JUICE 7.0 (TICHÝ 2002). Mean values of Ellenberg indicator values, life forms, CSR strategies, and moisture types were compared between previous and recent plots with pairwise *t* test or one-way ANOVA with subsequent Tukey post-hoc tests. The normal distribution of the residuals of all variables was visually checked and confirmed using histograms. ISA, NMDS and *β-diversity* calculation were performed with PC-ORD 6.0 (MCCUNE & MEFFORD 2011), and Pearson correlation, *t* test and ANOVA with SPSS 22 (IBM CORP. RELEASED 2013).

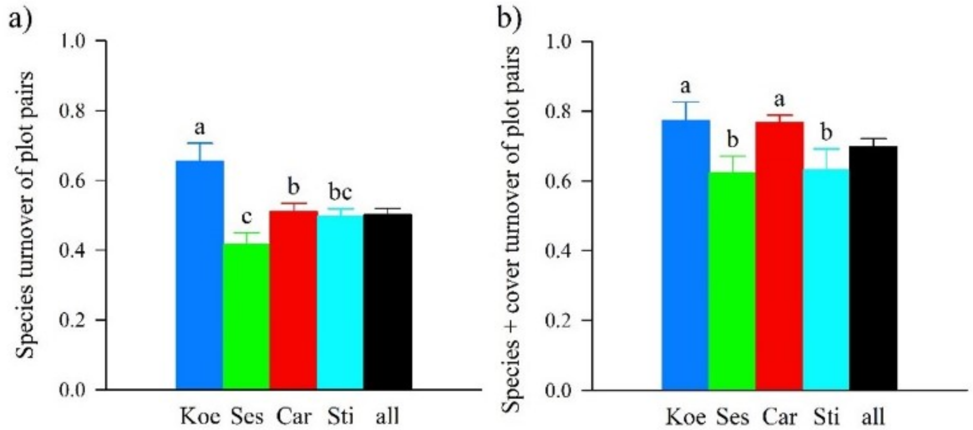

Fig. 4. Species turnover (Bray-Curtis *β*-diversity) of plot pairs 1995/2019 based on **a)** presence/absence and **b)** cover. A value of 1 indicates 100% species turnover. Four dry grassland associations separately and together: *Car – Carex humilis* grassland, *Koe – Koeleria* grassland, *Ses – Sesleria* grassland, *Sti – Stipa* grassland. Mean values and 1 SE. Mean values with different letters differ significantly at $p < 0.05$.

Abb. 4. Artumsatz (Bray-Curtis *β*-Diversität) der Aufnahmepaare 1995/2019 nach **a)** Präsenz/Absenz und **b)** Deckung der Arten. Ein Wert von 1 bedeutet einen Artumsatz von 100 %. Vier Trockenrasen-assoziationen einzeln und zusammen (die Bedeutung der Kürzel geht aus der englischen Abbildungs-unterschrift her). Mittelwerte und einfache Standardfehler. Mittelwerte mit unterschiedlichen Buchstaben unterscheiden sich signifikant bei $p < 0,05$.

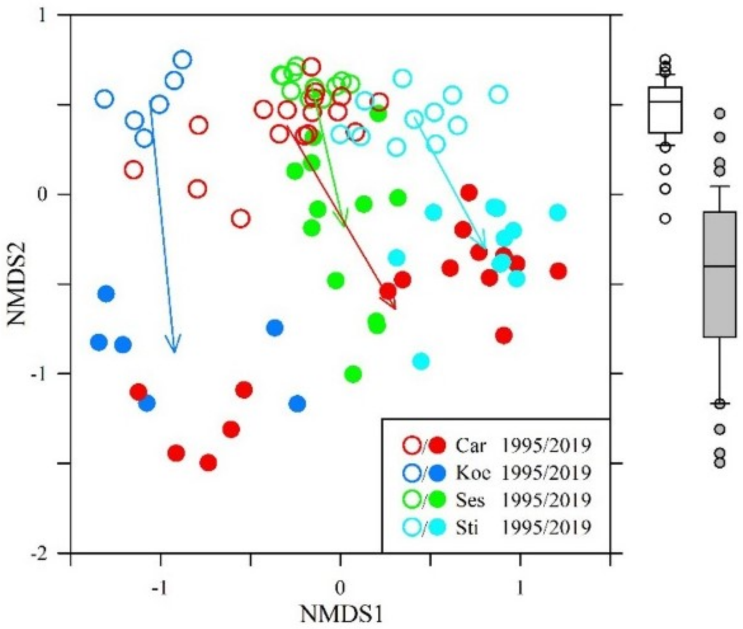

Fig. 5. NMDS of four dry grassland associations in 1995 (empty circles) and 2019 (filled circles). *Car* – *Carex humilis* grassland, *Koe* – *Koeleria* grassland, *Ses* – *Sesleria* grassland, *Sti* – *Stipa* grassland. Minimal stress of axis 2 is 11.8. Vectors between 1995/2019 centroids indicate direction and change extent of each association along the first two NMDS axes. Box whisker plots show score variance 1995 (empty boxes and circles) and 2019 (grey boxes and circles) along axis 2.

Abb. 5. NMDS von vier Trockenrasenassoziationen in den Jahren 1995 (leere Kreise) und 2019 (gefüllte Kreise). Die Bedeutung der Kürzel der Assoziationen geht aus der englischen Abbildungsunterschrift hervor. Der minimale Stresswert von Achse 2 beträgt 11,8. Vektoren zwischen den Zentroiden 1995/2019 zeigen die Richtung und den Umfang der Veränderung der einzelnen Assoziationen entlang der ersten beiden NMDS-Achsen an. Die Kastengraphiken zeigen die Varianz der Werte aus 1995 (leere Kästen und Kreise) und 2019 (graue Kästen und Kreise) entlang Achse 2.

4. Results

Most of the associations were still present after 24 years. Only the *Gentiano-Koelerietum* on the back of the hill had become a ruderalised *Onobrychido-Brometum* (Scherrer 1925) Th. Müller 1966, and the *Trinio-Caricetum* could no longer be assigned to the slightly mesoxeric subassociation *cirsietosum*, but developed into the more xeric subassociation *typicum*. However, the former diagnostic species groups of the associations have thinned out considerably and to a lesser extent new diagnostic species groups have formed (Supplement E2).

The species turnover (Bray-Curtis dissimilarity) of the 1995/2019 plot pairs based on presence/absence in all associations was 0.502, which means that on average 50.2% of the species were replaced at plot level during the study period. Replacement was highest in the *Koeleria* grassland (65.4%) and lowest in the *Sesleria* grassland (41.6%) (Fig. 4a). This order corresponded to the ratio of winner/loser species, reflecting the ranking of associations by decreasing change: *Gentiano-Koelerietum* → *Trinio-Caricetum* → *Festuco-Stipetum* → *Carici-Seslerietum* (Table 2). Species turnover of plot pairs based on species cover was higher than based on presence/absence of species (69.8% replaced species in all associations), indicating that cover has also changed (Fig. 4b).

Table 1. Expected and observed changes in 12 individual characteristics due to climate change (winter mildness and summer drought) and N deposition. Up-pointing arrows "↑" indicate positive and down-pointing arrows "↓" negative relationships. Symbols and arrow numbers indicate the relative strength of the expected relationships: Hyphens "–" no change was expected, arrows in brackets "(↑/↓)" weak change, simple arrows "↑/↓" strong change, double arrows "↑↑/↓↓" even stronger change. Question marks "?" indicate ambiguous expectations (positive or negative relationship). CC = climate change [differentiated according to winter mildness ($_{w}$) and summer drought ($_{s}$) or both together ($_{ws}$)] and ND = N deposition indicate the assumed causes for the observed vegetation change. CC→ND indicates that both factors presumably play a role but that N deposition only can let to the pattern under given climate change. p = ***, $p < 0.001$, ** $p < 0.01$, * $p < 0.05$ ($n = 46$).

Tabelle 1. Erwartete und festgestellte Veränderung von 12 Einzelmerkmalen bei Klimawandel (Wintermilde und Sommerdürre) und Stickstoffeinträgen. Pfeile nach oben "↑" oder unten "↓" zeigen positive oder negative (erwartete oder beobachtete) Effekte des Klimawandels bzw. der N-Depositionen auf die untersuchten Einzelmerkmale an. Die Symbole bzw. Anzahl der Pfeile zeigen die relative erwartete Stärke der erwarteten Zusammenhänge: – = keine Veränderung, (↑/↓) = schwache Veränderung, ↑/↓ = starke Veränderung, ↑↑/↓↓ = noch stärkere Veränderung. Unentschiedene Erwartungen (positiver oder negativer Zusammenhang) sind mit Fragezeichen „?" gekennzeichnet. CC = Klimawandel [unterschieden nach Wintermilde ($_{w}$) und Sommerdürre ($_{s}$) oder Beides zusammen ($_{ws}$)] und ND = N-Depositionen geben die mutmaßlichen Gründe der beobachteten Vegetationsänderung an. CC→ND bedeutet, dass beide Faktoren eine Rolle spielen aber der zweite nur unter dem ersten das beobachtete Ergebnis erklären kann. Die Stärke der festgestellten Veränderungen ist nicht angegeben. *** $p < 0{,}001$, ** $p < 0{,}01$, * $p < 0{,}05$ ($n = 46$).

	Expected change due to:			Detected change	Detected change explained by:
	Solely climate change	Solely N deposition	Both climate change and N deposition		
Indicator values and moisture types					
Light (L)	↑	↓	–	↑ *	CC_s
Temperature (T)	↑	–	↑	↑ **	CC_w
Continentality (K)	↓	–	↓	↓ ***	CC_w
Moisture (F)	↓	(↑)	?	–	CC_s 1)
Nutrients (N)	(↓)	↑	?	–	ND 1)
% xerophilic species	↑	(↓)	(↑)	↑ ***	CC_s
% meso-xerophilic species	↓	–	(↓)	↓ ***	CC_s
Life forms and strategy types					
Winter annuals	↑	↓	↑↑	↑ ***	CC_{ws}→ND
Summer annuals	↓	–	↓	↓ *	CC_s
Biennials	(↑)	(↑)	↑↑	↑ *	CC_{ws}→ND
SR strategy	↑	–	↑↑	↑ **	CC_{ws}→ND
Increased graminoids					
Bromus erectus	↑	↑	↑↑	↑ ***	CC_w→ND
Stipa capillata	↑	–	↑	↑ ***	CC_s→ND
Species richness	↓	↓	↓	↓ ***	CC_s
Homogenisation	↓	↑	?	↓ ***	CC_s

1) Considering that F and N were intercorrelated, the non-significant change in the two indicator values can be interpreted as an indication of actually drier and more nutrient-rich conditions.

The NMDS revealed directional floristic changes in all associations along axis 2 (Fig. 5). This axis was positively correlated with time (and all time-related binary climate variables mentioned in the introduction for climate change evidence) and the mean Ellenberg indicator value for nutrients, and negatively correlated with the mean indicator values for continentality and soil reaction (Table 3). In a direct comparison between 1995 and 2019, the mean Ellenberg indicator values of all plots together changed as follows: The indicator values for light and temperature increased and the indicator value for continentality decreased, while the indicator values for moisture, soil reaction and nutrients did not change significantly (Fig. 6a). However, the indicator values for moisture and nutrients were strongly positively intercorrelated (Fig. 6b). The proportion of meso-xerophilic species decreased, while the proportion of xerophilic species increased (Fig. 6c). These changes were due to a decrease in meso-xerophilic species rather than an increase in xerophilic species (Fig. 6d).

In terms of life forms, chamaephytes and hemicryptophytes decreased, while therophytes (annual plants) increased (Fig. 7a). These changes were more pronounced in the *Sesleria* and *Carex humilis* grasslands than in the *Koeleria* and *Stipa* grasslands. Among short-lived plants, winter annuals increased and summer annuals decreased (Fig. 7b). Biennial plants were generally rare but increased. Within plant strategy types, competitive stress (CS) and competitive ruderal strategists (CSR) decreased, but stress ruderals (SR) increased (Fig. 8). This pattern was very clear in the *Sesleria* and *Carex humilis* grasslands, while there was only a weak trend in the *Koeleria* and *Stipa* grasslands.

A total of 38 species (36% of all species) increased or decreased significantly in at least one association (Table 2). Within these species, nine winners (species that increased) faced 29 losers (species that decreased). Winners included five xerophilic winter annuals (e.g. *Cerastium pumilum* s. str., *Draba verna*, *Hornungia petraea*), one xerophilic biennial (*Centaurea stoebe*), two graminoids (*Bromus erectus*, *Stipa capillata*, the first with indifferent moisture behaviour within dry grasslands, the other xerophilic) and one shrub (*Prunus spinosa*) with indifferent moisture behaviour.

Among loser species were nine graminoids of which six were meso-xerophilic, one xerophilic, and two moisture indifferent (Fig. 9a, and see below), eight meso-xerophilic hemicryptophytes (e.g. *Asperula cynanchica*, *Pimpinella saxifraga*) and three xerophilic hemicryptophytes (e.g. *Potentilla incana*, *Seseli hippomarathrum*) and three moisture indifferent hemicryptophytes (e.g. *Euphorbia cyparissias*, *Hippocrepis comosa*), three xerophilic chamaephytes (e.g. *Helianthemum canum*, *Teucrium montanum*) and one moisture indifferent chamaephyte (*Thymus praecox*), and two summer annuals (the meso-xerophilic *Linum catharticum* and the moisture indifferent *Cuscuta epithymum*). The increase and decrease of short-lived plants such as annual and biennial winter and summer flowers is summarised in Figure 9b.

Sixty-three species (64%) did not change significantly in all associations together or in any single association, many of which were too rare to detect any possible change (Supplement E3). Most graminoids decreased in frequency/abundance (Fig. 9b). *Carex humilis*, *Sesleria caerulea* and *Brachypodium pinnatum* (in that order) decreased the most. *Helictochloa pratensis* disappeared from the plots, while *Bromus erectus* and *Stipa capillata* increased. Especially in the *Koeleria* and *Carex humilis* plots, *B. erectus* increased significantly (Table 2).

Table 2. Vascular plant species in four dry grassland associations separately and together after winner and loser. *Car* – *Carex humilis* grassland (*Trinio-Caricetum*), *Koe* – *Koeleria* grassland (*Gentiano-Koelerietum*), *Ses* – *Sesleria* grassland (*Carici-Seslerietum*), *Sti* – *Stipa* grassland (*Festuco-Stipetum*). Frequencies (constancies) in percent and mean percent cover values in uppercase. Bold type indicates at least marginal significant changes: ↑ – increase, ↓ – decrease. *** $p < 0.001$, ** $p < 0.01$*, $p < 0.05$, + $p < 0.1$. Normal type indicates no significant changes at $p < 0.1$. p values derive from ISA. Line symbols indicate that a species did not occur in the association neither in 1995 nor in 2019. For constant species or species that are too rare for assessing change see Supplement E3.

Tabelle 2. Gefäßpflanzenarten in vier Trockenrasenassoziationen einzeln und zusammen nach Gewinnern und Verlierern. *Car* – *Carex humilis*-Trockenrasen (*Trinio-Caricetum*), *Koe* – *Koeleria*-Halbtrockenrasen (*Gentiano-Koelerietum*), *Ses* – *Sesleria*-Trockenrasen (*Carici-Seslerietum*), *Sti* – *Stipa*-Trockenrasen (*Festuco-Stipetum*). Prozentstetigkeiten und mittlere Prozentdeckungen (hochgestellt). Fettgedruckte Werte zeigen zumindest marginal-signifikante Veränderungen an: ↑ – Zunahme, ↓ – Abnahme. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, + $p < 0.1$. Werte ohne Signifikanzsymbol unterscheiden sich nicht-signifikant bei $p < 0.1$. Die p-Werte stammen aus ISA. Striche (–) kennzeichnen nicht vorkommende Arten. Konstante Arten sowie Arten, welche zu selten sind, um ihre Veränderung zu bemessen, s. Beilage E3.

	Koe ($n = 6$)			*Ses* ($n = 12$)			*Car* ($n = 17$)			*Sti* ($n = 11$)			all ($n = 46$)		
	1995	2019	*p*	1995	2019	*p*	1995	2019	*p*	1995	2019	*p*	1995	2019	*p*
Winner species															
Graminoids															
Bromus erectus	**17^{3}**	**100^{46}**	↑ **	**0^{-}**	**92^{14}**	↑ ***	**12^{3}**	**47^{32}**	↑ *	**0^{-}**	**55^{16}**	↑ *	**7^{3}**	**67^{25}**	↑ ***
Stipa capillata	–	–		–	–		**35^{2}**	**65^{36}**	↑ *	**91^{19}**	**100^{42}**	↑ *	**35^{13}**	**48^{39}**	↑ *
Herbs															
Centaurea stoebe	–	–		–	–		**0^{-}**	**$35^{0.8}$**	↑ *	0^{-}	$27^{0.5}$		**0^{-}**	**$20^{0.7}$**	↑ **
Cerastium pumilum s. str.	–	–		**0^{-}**	**42^{1}**	↑ *	**$6^{0.5}$**	**47^{1}**	↑ *	36^{3}	$64^{0.8}$		**11^{2}**	**43^{1}**	↑ **
Cerastium semidecandrum	**0^{-}**	**$67^{0.4}$**	↑ +	**0^{-}**	**$50^{0.8}$**	↑ *	**0^{-}**	**59^{1}**	↑ ***	**0^{-}**	**64^{2}**	↑ **	**0^{-}**	**59^{1}**	↑ ***
Draba verna	**0^{-}**	**67^{1}**	↑ +	**0^{-}**	**83^{1}**	↑ ***	**0^{-}**	**$65^{0.9}$**	↑ ***	55^{3}	$64^{0.5}$		**13^{3}**	**$70^{0.9}$**	↑ ***
Hornungia petraea	–	–		**0^{-}**	**92^{2}**	↑ ***	**0^{-}**	**82^{1}**	↑ ***	55^{3}	91^{2}		**13^{3}**	**76^{1}**	↑ ***
Microthlaspi perfoliatum	–	–		**0^{-}**	**$33^{0.4}$**	↑ +	0^{-}	24^{2}		–	–		**0^{-}**	**17^{1}**	↑ **
Woody species															
Prunus spinosa juv.	–	–		–	–		**6^{3}**	**41^{4}**	↑ *	–	–		**2^{3}**	**15^{4}**	↑ *
Loser species															
Graminoids															
Brachypodium pinnatum	0^{-}	$50^{0.4}$		50^{10}	67^{13}		**94^{17}**	**47^{11}**	↓ ***	36^{18}	18^{1}		**57^{15}**	**46^{9}**	↓ *
Carex caryophyllea	**83^{3}**	**0^{-}**	↓ *	–	–		–	–		–	–		**11^{3}**	**0^{-}**	↓ +
Carex humilis	100^{15}	100^{11}		**100^{17}**	**100^{14}**	↓ +	**76^{38}**	**71^{8}**	↓ +	100^{17}	100^{12}		**91^{23}**	**89^{11}**	↓ **
Festuca csikhegyensis	$17^{0.5}$	0^{-}		100^{6}	92^{5}		**71^{2}**	**$35^{0.7}$**	↓ **	**100^{2}**	**$18^{0.1}$**	↓ ***	**78^{4}**	**41^{3}**	↓ ***
Festuca rupicola	**100^{11}**	**$17^{0.5}$**	↓ **	–	–		**65^{5}**	**18^{8}**	↓ **	9^{3}	0^{-}		**39^{7}**	**9^{6}**	↓ ***
Helictochloa pratensis	**83^{3}**	**0^{-}**	↓ *	**67^{3}**	**0^{-}**	↓ ***	**88^{3}**	**0^{-}**	↓ ***	**36^{2}**	**0^{-}**	↓ +	**70^{2}**	**0^{-}**	↓ ***
Koeleria macrantha	33^{3}	0^{-}		25^{2}	0^{-}		**59^{2}**	**$18^{0.2}$**	↓ **	**73^{3}**	**$9^{0.1}$**	↓ ***	**50^{2}**	**$9^{0.2}$**	↓ ***
Koeleria pyramidata	**67^{3}**	**0^{-}**	↓ +	**33^{2}**	**0^{-}**	↓ +	$6^{0.5}$	0^{-}		–	–		**20^{2}**	**0^{-}**	↓ **
Sesleria caerulea	**100^{39}**	**0^{-}**	↓ **	**100^{22}**	**58^{20}**	↓ **	–	–		–	–		**39^{27}**	**15^{20}**	↓ **

	Koe (n = 6)			*Ses* (n = 12)			*Car* (n = 17)			*Sti* (n = 11)			all (n = 46)		
	1995	2019	p	1995	2019	p	1995	2019	p	1995	2019	p	1995	2019	p
Herbs															
Adonis vernalis	–	–		25^{2}	8$^{0.5}$		47^{2}	35$^{0.6}$		36^{3}	18$^{0.3}$		**33**^{2}	**20**$^{0.5}$	↓*
Anthyllis vulneraria	**100**^{13}	**67**^{3}	↓*	8^{3}	0^{-}		–	–		–	–		15^{12}	9^{3}	
Asperula cynanchica	**100**^{4}	**0**$^{-}$	↓**	**67**^{3}	**0**$^{-}$	↓**	**53**^{3}	**0**$^{-}$	↓**	**55**^{2}	**0**$^{-}$	↓*	**63**^{3}	**0 -**	↓***
Cuscuta epithymum	–	–		25^{3}	0^{-}		**71**^{2}	**29**$^{0.5}$	↓**	**36**^{2}	**0**$^{-}$	↓+	**41**^{2}	**11**$^{0.5}$	↓***
Euphorbia cyparissias	50^{3}	17^{3}		58^{4}	92$^{0.8}$		**100**^{4}	**82**^{2}	↓***	36^{3}	64$^{0.7}$		**67**^{4}	**72**^{1}	↓+
Helianthemum canum	**100**^{23}	**33**^{10}	↓**	**100**^{16}	**75**^{9}	↓**	**88**^{13}	**71**^{3}	↓**	**100**^{11}	**100**^{4}	↓+	**96**^{15}	**74**^{5}	↓***
Hippocrepis comosa	33^{3}	0^{-}		**58**^{2}	**17**$^{0.5}$	↓*	**59**^{4}	**24**^{4}	↓*	0^{-}	9$^{0.1}$		**41**^{3}	**15**^{2}	↓**
Linum catharticum	**100**^{3}	**0**$^{-}$	↓**	8^{3}	0^{-}		12^{3}	0^{-}		–	–		**20**^{3}	**0**$^{-}$	↓**
Lotus corniculatus	50^{3}	33$^{0.5}$		17^{3}	0^{-}		12^{3}	0^{-}		–	–		**15**^{3}	**4**$^{0.5}$	↓*
Pimpinella saxifraga	**83**^{6}	**0**$^{-}$	↓*	8$^{0.5}$	0^{-}		**59**^{2}	**0**$^{-}$	↓***	–	–		**35**^{3}	**0**$^{-}$	↓***
Potentilla heptaphylla	**67**^{3}	**0**$^{-}$	↓+	8$^{0.5}$	8$^{0.5}$		**35**^{2}	**0**$^{-}$	↓*	9^{3}	0^{-}		**26**^{2}	**2**$^{0.5}$	↓***
Potentilla incana	–	–		**83**^{3}	**58**^{1}	↓*	**59**^{3}	**29**$^{0.9}$	↓*	55^{4}	36$^{0.9}$		**57**^{3}	**35**^{1}	↓**
Potentilla verna	**100**^{3}	**50**^{2}	↓+	25^{3}	0^{-}		24^{2}	0^{-}		–	–		**28**^{2}	**7**^{2}	↓**
Salvia pratensis	–	–		**0**$^{-}$	**33**$^{0.4}$	↑+	**94**^{6}	**71**^{1}	↓***	36^{3}	73^{1}		43^{6}	52^{1}	
Sanguisorba minor	83^{3}	67^{11}		75^{3}	67^{2}		**53**^{2}	**29**$^{0.9}$	↓*	27^{2}	0^{-}		**57**^{2}	**37**^{4}	↓+
Seseli hippomarathrum	17^{3}	17$^{0.1}$		100^{2}	92^{3}		**71**^{5}	**41**^{2}	↓**	73^{3}	73^{4}		**72**^{3}	**59**^{3}	↓+
Taraxacum sect. *Erythrosperma*	33^{3}	0^{-}		8^{3}	0^{-}		24^{2}	0^{-}		**45**^{3}	**0**$^{-}$	↓*	**26**^{2}	**0**$^{-}$	↓***
Teucrium montanum	67^{3}	17^{10}		100^{4}	75^{12}		**71**^{6}	**41**^{1}	↓**	**73**^{17}	**36**^{6}	↓+	**78**^{7}	**46**^{7}	↓***
Teucrium chamaedrys	**100**^{8}	**17**$^{0.5}$	↓**	**100**^{17}	**75**^{15}	↓+	88^{9}	94^{8}		**64**^{8}	**100**^{6}	↑+	87^{11}	80^{9}	
Thymus praecox	33^{11}	67^{1}		92^{8}	75^{4}		**100**^{28}	**24**^{1}	↓***	**91**^{22}	**18**$^{0.5}$	↓***	**87**^{20}	**41**^{2}	↓***
Winner/loser ratio	3/13 = 0.23			7/9 = 0.78			8/19 = 0.42			4/9 = 0.44			9/26 = 0.35		

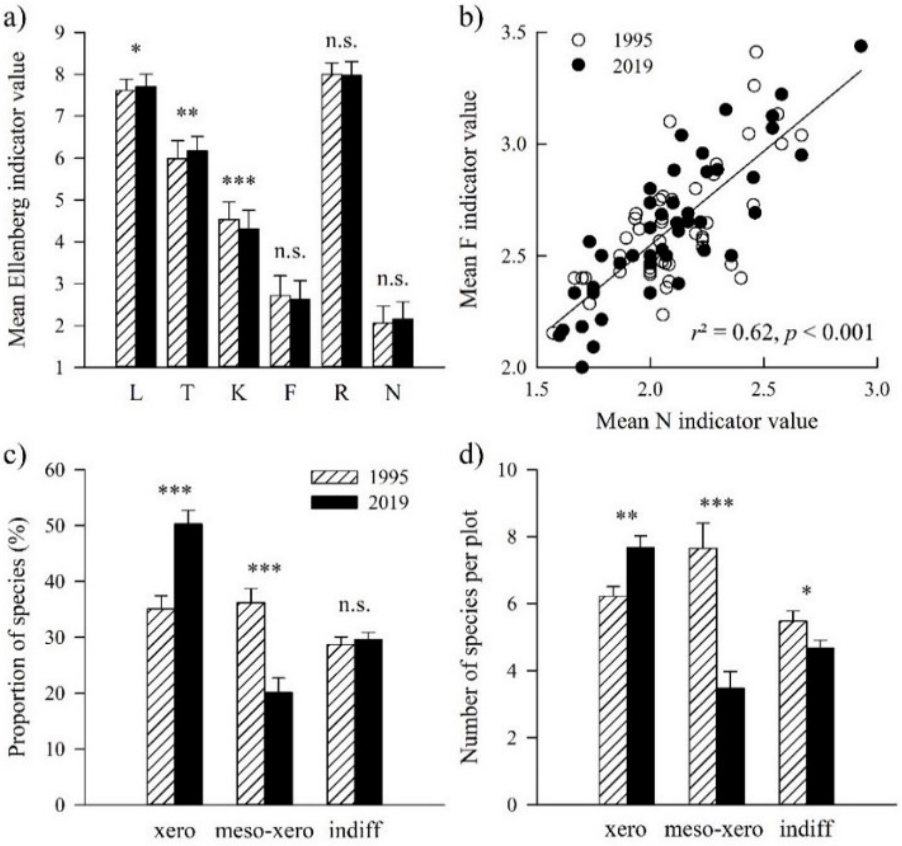

Fig. 6. a) Mean Ellenberg indicator values for L – light, T – temperature, K – continentality, F – moisture, R – soil reaction and N – nutrients, **b)** relationship between the mean N and F indicator value, **c)** proportions and **d)** numbers of xerophilic (*xero*), meso-xerophilic (*meso-xero*) and moisture indifferent (*indiff*) species in the dry grasslands. Mean values and 10 SE (in a) and 1 SE (in c, d). *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, *n.s.* not significant.

Abb. 6. a) Mittlere Ellenberg-Zeigerwerte für L – Licht, T – Temperatur, K – Kontinentalität, F – Feuchte, R – Bodenreaktion und N – Nährstoff, **b)** Zusammenhang zwischen dem mittleren N- und F-Zeigerwert, **c)** Anteil und **d)** Anzahl der xerophilen (*xero*), meso-xerophilen (*meso-xero*) und Feuchte-indifferenten (*indiff*) Arten in den Trockenrasen. Mittelwerte und 10-fache (in a) bzw. 1-fache (in c, d) Standardfehler. *** $p < 0,001$, ** $p < 0,01$, * $p < 0,05$, *n.s.* nicht signifikant.

The species richness of the plots decreased significantly by 18.2% in all associations (from 19.3 to 15.8 species) (Fig. 10a). In the *Koeleria* grassland, species richness decreased by 41% (from 24.5 to 14.3 species) and in the *Carex humilis* grassland by 24% (from 22.9 to 17.5 species). In the *Sesleria* grassland and the *Stipa* grassland, species richness did not change significantly. Species richness of threatened plants decreased by 30% across all associations (from 12.0 to 8.4 species) (Fig. 10b). Again, *Koeleria* grassland and *Carex humilis* grassland showed higher losses (61.4% and 31.5%, respectively), but *Sesleria* grassland and *Stipa* grassland were also affected by losses of threatened plants (20.9% and 17.5%, respectively). The (cumulative) total number of species has developed as follows: 85 vascular plant species were found in all 1995 plots, compared to 75 species in all 2019 plots (Table 2). 26 species disappeared and 16 newly appeared in the plots. Among the species that disappeared were 11 threatened species and among the new species that appeared, five

Table 3. Pearson correlations between NMDS axis 2 and time (1995/2019), mean Ellenberg indicator values (EIV), and the proportions of xerophilic and meso-xerophilic plant species. Significant relationships in bold face.

Tabelle 3. Pearson-Korrelationen zwischen NMDS-Achse 2 und der Zeit (1995/2019) sowie mittleren Ellenberg-Zeigerwerten (EIV) und den Anteilen xerophiler und meso-xerophiler Pflanzenarten. Signifikante Zusammenhänge sind fettgedruckt.

	r	p
Year (and all binary climatic variables 1995 *vs.* 2019)	**-0.81**	**< 0.001**
EIV for light (L)	0.03	0.799
EIV for temperature (T)	0.18	0.093
EIV for continentality (K)	**-0.26**	**0.012**
EIV for moisture (F)	0.14	0.187
EIV for soil reaction (R)	**-0.39**	**< 0.001**
EIV for nutrients (N)	**0.49**	**< 0.001**
Proportion of xerophilic plants	-0.17	0.104
Proportion of meso-xerophilic plants	**0.21**	**0.045**

were threatened (Supplement E1). Most of the newly emerged species were annuals or biennials. In total, 45 threatened vascular plant species were found in the 1995 plots and 39 threatened species in the 2019 plots (Supplement E1).

Homogenisation of vegetation was only observed in the *Stipa* grassland, where the Bray-Curtis dissimilarity of species cover slightly decreased between 1995 and 2019 (Fig. 11b). Only the *Stipa* grassland showed no change in species turnover based on species presence/absence. In contrast, three out of four associations (*Koeleria*, *Sesleria*, and *Carex humilis* grassland) and all associations together showed heterogenisation in both species' presence/absence and species cover. When cover was considered in the analysis, species turnover was higher both within and between plots when only species presence was considered (Fig. 11a), indicating that not only species composition but also species cover changed. The NMDS also showed heterogeneity of associations through higher variance of 2019 values compared to 1995 values along axis 2 (Fig. 5). The condition of the grassland in 2018/2019 is shown in Figures 12–14.

5. Discussion

5.1 Changes in ecological indicator values and plant moisture types

Following our hypothesis that N deposition and climate change (especially summer drought but also mild winters) were the main drivers of vegetation change, we were surprised that only the mean indicator value for temperature increased but not that for nutrients (N), and that the indicator value for moisture (F) did not decrease. However, the nutrient value was still correlated with NMDS axis 2, the axis of vegetation change. The fact that the moisture value and nutrient value did not decrease or increase significantly (the F value decreased from 2.72 to 2.63, $p = 0.175$, and the N value increased from 2.06 to 2.16, $p = 0.096$) can be explained by their strong intercorrelation i.e., increasing nutrients (eutrophication) and decreasing moisture (drought) compensated each other in their indicator values which is in accordance to the farmer's theorem "nitrogen replaces water" (ELLENBERG 1986). Therefore, the fact that the moisture value did not decrease and the nutrient value did not increase can be taken as an indication of increased dryness and nutrients. – Intercorrelated indicator values are not uncommon and cannot be easily mathematically disentangled within resurvey studies. The indicator values for nutrients and soil reaction (R) seem to be particularly often positively intercorrelated, which can then lead to increasing R values in the case of eutrophication, although the pH values remained constant (Van Calster et al. 2007, Seidling & Fischer 2008, Reinecke et al. 2014) or even decreased significantly (Litza & Diekmann 2017). For N and F values, we are not (further) aware of such an intercorrelation in resurvey studies.

Independently from the indicator value for moisture, in our study, increased dryness was clearly indicated by the decreased proportion of meso-xerophilic plants, in contrast to the proportion of xerophilic plants that increased. However, there were some meso-xerophilic plants with storage taproots or rhizomes (e.g. *Anthericum ramosum*, *Cirsium acaulon*, *Peucedanum cervaria*) that declined only little, probably because these organs store water.

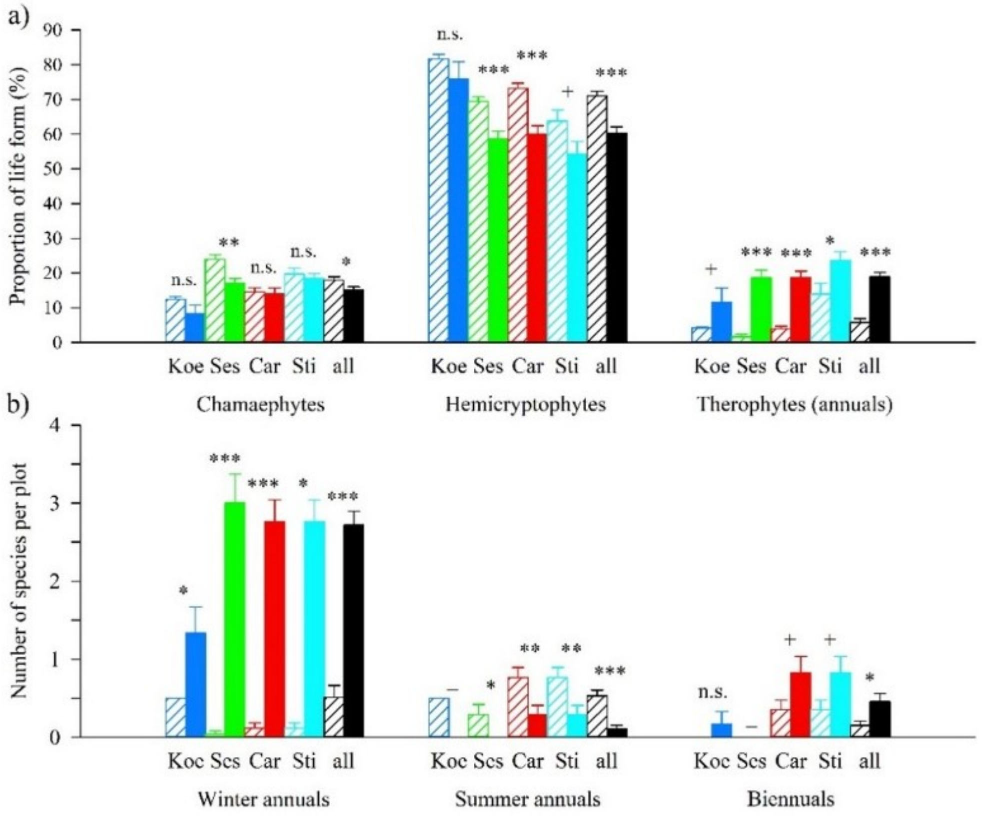

Fig. 7. a) Proportions of three general life forms and **b)** number of species of three special life forms of short-lived plant species in four dry grassland associations separately and together: *Car* – *Carex humilis* grassland, *Koe* – *Koeleria* grassland, *Ses* – *Sesleria* grassland, *Sti* – *Stipa* grassland. Hatched bars: 1995, filled bars: 2019. Mean values and 1 SE. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, + $p < 0.1$, *n.s.* not significant.

Abb. 7. a) Anteile von drei allgemeinen Lebensformen und **b)** Anzahl der Arten von drei speziellen Lebensformen kurzlebiger Pflanzenarten in vier Trockenrasenassoziationen getrennt und zusammen. Die Bedeutung der Kürzel geht aus der englischen Abbildungsunterschrift hervor. Schraffierte Balken: 1995, gefüllte Balken: 2019. Mittelwerte und einfache Standardfehler. *** $p < 0,001$, ** $p < 0,01$, * $p < 0,05$, + $p < 0,1$, *n.s.* nicht signifikant.

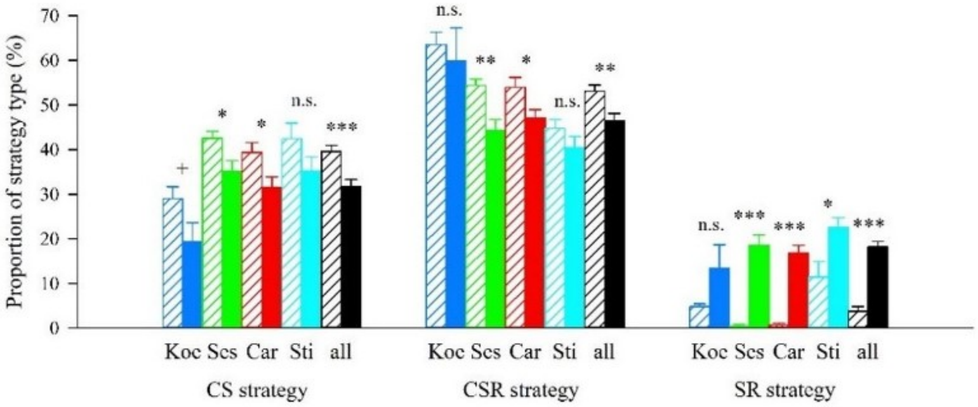

Fig. 8. Proportions of the plant strategy types CS – competition-stress, CSR – competition-stress-ruderal, and SR – stress-ruderal in four dry grassland associations separately and together: *Car* – *Carex humilis* grassland, *Koe* – *Koeleria* grassland, *Ses* – *Sesleria* grassland, *Sti* – *Stipa* grassland. Hatched bars: 1995, filled bars: 2019. Mean values and 1 SE. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, + $p < 0.1$, *n.s.* not significant.

Abb. 8. Anteile der Strategietypen CS – Konkurrenz-Stress-Strategie, CSR – Konkurrenz-Stress-Ruderal-Strategie und SR – Stress-Ruderal-Strategie in vier Trockenrasenassoziationen getrennt und zusammen. Die Bedeutung der Kürzel geht aus der englischen Abbildungsunterschrift hervor. Schraffierte Balken: 1995, gefüllte Balken: 2019. Mittelwerte und einfache Standardfehler. *** $p < 0{,}001$, ** $p < 0{,}01$, * $p < 0{,}05$, $p + < 0{,}1$, *n.s.* nicht signifikant.

The reaction value probably did not decrease because possible acidic compounds from deposition were buffered by the calcareous soil. The decreased continentality value indicates a shift in climate from more continental to more Mediterranean (not suboceanic, which is what low K values are supposed to indicate), i.e. winters became mild and humid but summers hot and arid. In fact, six winner species with sub-Mediterranean distribution (five winter annuals and *Bromus erectus*) faced one winner species with continental distribution (*Stipa capillata*) (*Centaurea stoebe* is sub-Mediterranean-continentally distributed). The increased light value can be explained by the sparser vegetation due to drought influence.

5.2 Changes in life forms and plant strategy types

Perhaps the most striking change in vegetation in our study was the large increase in winter annuals, which are considered SR strategists (GRIME 2001), resulting in an increase in SR strategy. Of the four associations, in 1995, the winter annuals were restricted to the *Stipa* grassland, where they colonised open gaps between *S. capillata* tussocks (BECKER 1998a, b). These open gaps were the result of strong competition for water in summer. The absence of winter annuals in the dense *Koeleria* and *Carex humilis* grasslands in 1995 was probably due to strong light competition from perennial plants. The restriction of winter annuals to *Stipa* grassland has been highlighted (and documented) by many authors for different periods (for the lower Unstrut valley e.g. MEUSEL 1937, MAHN 1965, HENSEN 1997, BECKER 1998b) indicating a stable pattern over many decades. In 2019, however, winter annuals occurred in large numbers in all associations. In the *Koeleria* and *Carex humilis* grasslands, this change was most likely due to severe droughts in previous years, which led to a decline in perennial plant vegetation and thus to open gaps. An increase of winter annuals after drought events was also observed in other German regions, e.g. in Rhein Hesse and in the Rhenish Massif

(T. Becker, pers. observation). But an increase in winter annuals due to trampling by sheep, as found by MEIER et al. (2021) for the Kyffhäuser mountains, is unlikely in our study. This is because the Schafberg was regularly grazed over the entire period and the grazing intensity was not significantly increased, and because the dry grasslands in the lower Unstrut valley occur on cohesive shell limestone soils with a loamy texture, whereas in the Kyffhäuser mountains they occur on unstable gypsum soils with a sandy texture. This means that the soils on the steep slopes of the Kyffhäuser mountains are much more affected by trampling than in the Unstrut valley, especially not on the gentle slope of the Schafberg. Thus, we conclude that trampling was not the cause of the increased occurrence of winter annuals in our study.

Annual fluctuation effects due to merely favourable (wet and mild) or unfavourable (dry and cold) previous winters (PETŘÍK et al. 2011, FISCHER et al. 2020) are also unlikely to be causes of the increase in winter annuals, as the winter of 1994–95 was climatically average and the restriction of winter annuals to *Stipa* grassland has been a constant pattern at least since 1994. In fact, however, winters have become wetter and milder (i.e. more Mediterranean), which, in addition to open vegetation, probably permanently favours winter annuals. In the Czech dry grasslands, recent summer drought events also led to the death of perennial plants and favoured short-lived and fast-growing annual plants (FISCHER et al. 2020).

Only the colonisation of the *Sesleria* grassland by winter annuals cannot be plausibly necessarily explained by drought. The *Sesleria* grasslands both on the Schafberg and in the entire Unstrut valley already had open vegetation in 1995, but no winter annuals (cf. Table 8 in BECKER 1998b). In the decades before our study, winter annuals were still almost completely absent from xeric *Sesleria* grasslands on Muschelkalk in the entire Unstrut valley (SCHUBERT 1963) and adjacent regions (SCHMIDT 2000). We therefore assume that the colonisation of the *Sesleria* grasslands by winter annuals was mainly caused by a nutrient input due to airborne N deposition. This means that the probable reason for the absence of annuals in the *Sesleria* grassland in 1995 was nutrient limitation, as the soil was heavily eroded and skeletal (cf. Fig. 3a). This is because annual plants need sufficient nutrients (at least some humus enrichment) for their seed production. In general, airborne N deposition for the area was reported to be up to 10 kg per ha^{-1} × year^{-1}, which is close to the critical nitrogen load of 14 and 25 kg ha^{-1} × year^{-1} for nutrient-poor grassland reported by DE JONG et al. (1998) and BOBBINK & HETTELINGH (2011). However, nitrogen inputs were high especially in the 1990s and have recently declined (FÖRSTER et al. 2017). The fact that winter annuals did not appear when N deposition was highest, but only when N deposition declined, can be explained by nutrient accumulation and by a threshold that nutrients first had to cross. We conclude that in the *Koeleria* and *Carex humilis* grasslands, winter annuals were mainly promoted by drought events and on the *Sesleria* grasslands by N deposition.

The increase in biennials, which are mainly sub-ruderals (cf. BRANDES & PFÜTZENREUTER 2013), was probably due to both factors, increased nutrients and stronger drought. However, the number of biennials in our study was low (only five species in total, of which only *Centaurea stoebe* was common), so the corresponding results are unreliable.

Summer annuals such as *Linum catharticum* or *Cuscuta epithymum* declined strongly in our study. This can be explained by the germination/establishment phase of summer annuals in early summer, when drought is often already severe. A strong decline of summer annuals in dry grasslands was also found by HAHN et al. (2013), RIDDING et al. (2020) and MEIER et al. (2021). In the Swiss Jura mountains, CHARMILLOT et al. (2021) found that *Linum catharticum* was the species with the greatest decline in meso-xeric grasslands.

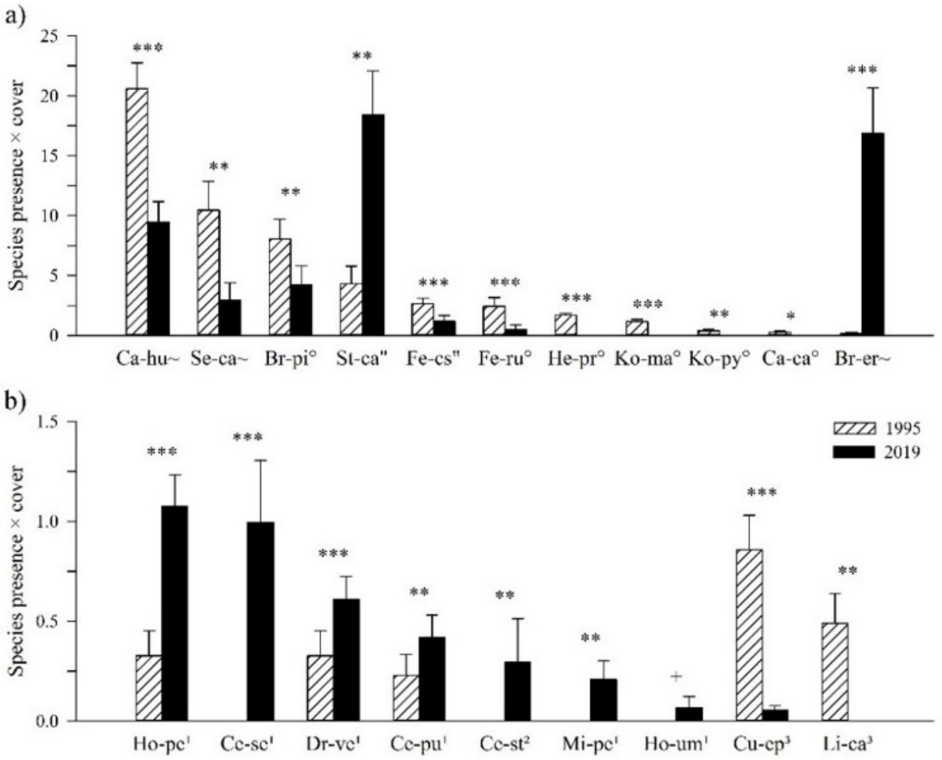

Fig. 9. The main **a)** short-lived species (^{1} – winter annuals, ^{2} – biennials, ^{3} – summer annuals) and **b)** graminoids (° – meso-xerophilic, " – xerophilic, and ~ – indifferent species) in the dry grasslands (all associations together) in 1995 and 2019 ($n = 46$, each). Mean values of presence × cover and 1 SE (for cover, the median percentage of the corresponding Braun-Blanquet class was taken). **a)** *Ce-pu – Cerastium pumilum* s. str., *Ce-se – Cerastium semidecandrum*, *Ce-st – Centaurea stoebe*, *Cu-ep – Cuscuta epithymum*, *Dr-ve – Draba verna*, *Ho-pe – Hornungia petraea*, *Ho-um – Holosteum umbellatum*, *Li-ca – Linum catharticum*, *Mi-pe – Microthlaspi perfoliatum*. **b)** *Br-er – Bromus erectus*, *Br-pi – Brachypodium pinnatum*, *Ca-ca – Carex caryophyllea*, *Ca-hu – Carex humilis*, *Fe-cs – Festuca csikhegyensis*, *Fe-ru – Festuca rupicola*, *He-pr – Helictochloa pratensis*, *Ko-ma – Koeleria macrantha*, *Ko-py – Koeleria pyramidata*, *Se-ca – Sesleria caerulea*, *St-ca – Stipa capillata*. Order of species according decreasing presence × cover values in 1995, each. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, + $p < 0.1$.

Abb. 9. Die wichtigsten **a)** kurzlebigen Arten (^{1} – Winterannuelle, ^{2} – Bienne, ^{3} – Sommerannuelle) und **b)** Grasartigen (° – meso-xerophile, " – xerophile und ~ – indifferente Arten) in den Trockenrasen (alle Assoziationen zusammen) in den Jahren 1995 und 2019 (jeweils $n = 46$). Mittelwerte der Präsenz × Deckung mit einfachem Standardfehler (als Deckung diente in der Rechnung der Median des Prozentsatzes des entsprechenden Braun-Blanquet-Deckungsgrads). Die Bedeutung der Art-Kürzel geht aus der englischen Abbildungsunterschrift hervor. Die Arten sind jeweils nach abnehmender Präsenz × Deckung im Jahr 1995 sortiert. *** $p < 0{,}001$, ** $p < 0{,}01$, * $p < 0{,}05$, + $p < 0{,}1$.

5.3 Changes in graminoids

Most graminoids decreased, especially meso-xerophilic species like *Brachypodium pinnatum* but also xerophilic species like *Festuca csikhegyensis* and moisture indifferent (but xero-tolerant) species like *Carex humilis* and *Sesleria caerulea*. The somewhat meso-xerophilic *Helictochloa pratensis*, which was present in 70% of the plots in 1995, disappeared completely from the plots. The most likely reason for the general decline of graminoids is again severe summer drought. Although xerophilic graminoids are generally well protected against drought, e.g. by small rolled-up leaves with wax coatings, these species seem to be more sensitive to drought in the root zone than many dicots, as they do not have thick storage roots protected by a periderm. Especially small-growing graminoids like *Koeleria macrantha* do not root deeply (Kutschera & Lichtenegger 1982) and are therefore vulnerable to drought. In contrast, graminoids with deep roots did not decline in our study. Theoretically rooting up to 280 cm deep, *Stipa capillata* (Kutschera & Lichtenegger 1982) increased mainly in cover, but also in abundance. *Stipa capillata* is both xerophilic and to some extent nitrophilic, which is why the species was probably promoted by N deposition in combination with drought. Nevertheless, drought seemed to be the determining factor, as nutrient supply alone tends to disadvantage *S. capillata* by increasing competition from mesic plants.

However, the main winner in our study was *Bromus erectus*, whose abundance increased by 933% (from 3 to 31 occupied plots) and whose coverage increased by 733% (on average from 3% to 25% coverage). *Bromus erectus* is currently invading many xeric and meso-xeric grasslands in Central Germany (Bornkamm 2006, 2008, Heinrich 2010, Meier et al. 2021). On the Schafberg, its invasion has apparently started from the upper and lower edge. Here, in 1995, single tussocks of *B. erectus* grew scattered mainly in the *Koeleria* grassland at the back of the hill and in the *Carex humilis* grassland at the foot of the hill (cf. relevés in Becker 1998b). The likely reasons for the success of the species are, in our opinion, in this order: The evergreen, sub-Mediterranean species benefits from climate change towards sub-Mediterranean climatic conditions mainly through (1) milder winters, which allow it to extend the growing season (Bornkamm 2006), and (2) drier summers, which the species can cope with using its deep roots (up to at least 90 cm according to Kutschera &

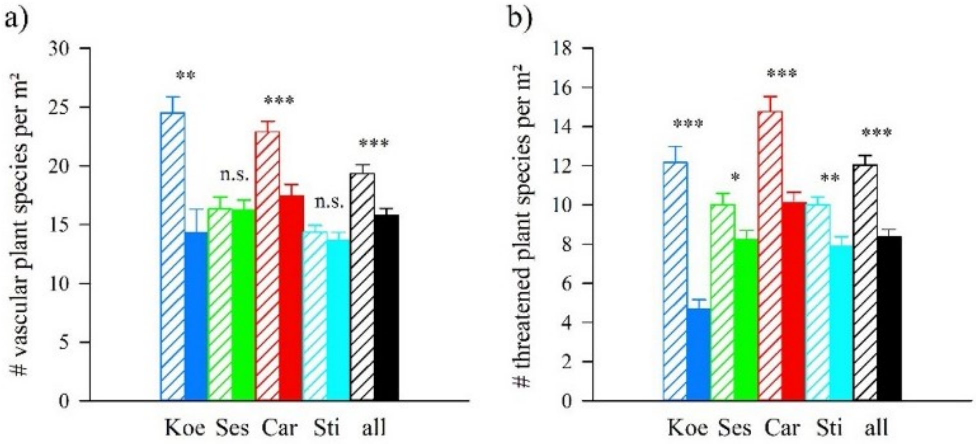

Fig. 10. Species richness (α diversity) of **a)** vascular plants and **b)** threatened vascular plants in four dry grassland associations separately and together: *Car* – *Carex humilis* grassland, *Koe* – *Koeleria* grassland, *Ses* – *Sesleria* grassland, *Sti* – *Stipa* grassland. Hatched bars: 1995, filled bars: 2019. Mean values and 1 SE. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, *n.s.* not significant.

Abb. 10. Artenreichtum (α-Diversität) von **a)** allen Gefäßpflanzen und **b)** gefährdeten Gefäßpflanzen in vier Trockenrasenassoziationen einzeln und zusammen. Die Bedeutung der Kürzel geht aus der englischen Abbildungsunterschrift hervor. Schraffierte Balken: 1995, gefüllte Balken: 2019. Mittelwerte und einfache Standardfehler. *** $p < 0{,}001$, ** $p < 0{,}01$, * $p < 0{,}05$, *n.s.* nicht signifikant.

LICHTENEGGER 1982). Drought damage can also be easily regenerated due to the high regeneration potential of the species (PÉREZ-RAMOS et al. 2013). Apart from climate change, it is (3) nutrient input due to N deposition or low nutrient output due to low management intensity that enable the species (which is considered a CS strategist according to GRIME 2001) to reach full competitiveness when being dominant (ELLENBERG 1986: 655, WILLEMS 1987, NOWAK & SCHULZ 2002). On the other hand, historical reasons for the success of *B. erectus*, such as late recolonisation after a possible earlier extinction in the Pleistocene (HEINRICH 2010, SUTKOWSKA et al. 2013), are implausible, as common graminoids like *B. erectus* can usually build up high seed pressure and are therefore unlikely to be severely restricted in their dispersal. Following LEMMER et al. (2021) we therefore assume that in our study the main factor for the invasion of *B. erectus* is indeed climate change (i.e. drier summers and milder winters), while eutrophication also plays a role but is of secondary importance. If the tall species is dominant, it contributes to higher vegetation, which reduces the species richness of plants (MEIER et al. 2021, SPLITH et al. 2021) and insects (e.g. leafhoppers) (PONIATOWSKI et al. 2018). Overall, we expect *B. erectus* in particular to continue to increase on the Schafberg.

5.4 Changes in species richness and conservation value

In the 24 years covered by our study, all plots together lost 11.8% of their cumulative plant species richness and 13.3% of their cumulative number of threatened plant species. At the plot level, 18.1% of vascular plant species and 30.3% of threatened vascular plant species were lost. This indicates a disproportionate loss of threatened plants. The grassland had thus lost part of its conservation value. Other grassland resurvey studies also found disproportionate losses in threatened vascular plants, but no overall decline in species richness (e.g. DIEKMANN et al. 2019, MEIER et al. 2021, SCHÜLE et al. 2022). Only in the study by HAHN et al. (2013) from the neighbouring Kyffhäuser Mountains did threatened plant species increase, presumably because the Kyffhäuser grasslands had regenerated after decades of over-intensive use through grazing. In meso-xeric grasslands in north-western Germany, declining species richness was observed on south-exposed slopes after intense drought events between 2008 and 2019, while no negative trends were observed for ruderal species (MAZALLA et al. 2022).

5.5 Changes in homogenisation

While floristic homogenisation was found in forests in most resurvey studies (KEITH et al. 2009, REINECKE et al. 2014, HEINRICHS & SCHMIDT 2017), the results for dry grasslands are ambiguous. Accordingly, no general trend was found in the meta-analysis by DIEKMANN et al. (2019) which includes six resurvey studies mainly on meso-xeric grassland. In our study, in three out of four associations (and in all associations combined) species dissimilarity of plot collectives increased over time, indicating reduced homogenisation and thus heterogenisation. This is a clear indication that the vegetation changes in our study were not primarily caused by N deposition or lower management intensity, but by increasing drought. N deposition and lower management intensity usually promote competitive species, leading to a lesser dissimilarity, i.e. homogenisation of vegetation, while disturbance by drought events usually leads to greater dissimilarity, i.e. heterogenisation (MCKINNEY & LOCKWOOD 1999).

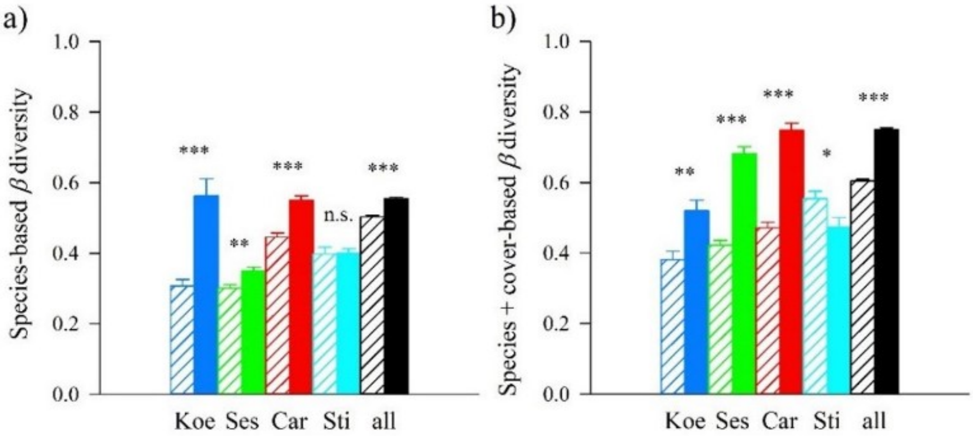

Fig. 11. Development of taxonomic β-*diversity* (Bray-Curtis) in four dry grassland associations alone and together over time (1995/2019). Decreased β-*diversity* means homogenisation and increased β-*diversity* heterogenisation. **a)** Species-based and **b)** species plus cover-based β-*diversity*. *Car – Carex humilis* grassland, *Koe – Koeleria* grassland, *Ses – Sesleria* grassland, *Sti – Stipa* grassland. Hatched and filled bars indicate β-*diversity* in 1995 and 2019, respectively. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, *n.s.* non-significant at $p < 0.05$.

Abb. 11. Entwicklung der taxonomischen β-Diversität (Bray-Curtis) von vier Trockenrasenassoziationen einzeln und zusammen über die Zeit (1995/2019). Abnehmende β-Diversität bedeutet Homogenisierung und zunehmende β-Diversität Heterogenisierung. **a)** Artbasierte und **b)** art- plus deckungsbasierte β-Diversität. Ein β-Diversitätswert von 1 bedeutet eine Unterschiedlichkeit von 100 %. Die Bedeutung der Kürzel geht aus der englischen Abbildungsunterschrift hervor. Mittelwerte und einfache Standardfehler. Schraffierte und gefüllte Balken zeigen die β-Diversität der Vegetation in 1995 bzw. 2019 an. *** $p < 0{,}001$, ** $p < 0{,}01$, * $p < 0{,}05$, *n.s.* nicht-signifikant bei $p < 0{,}05$.

This conclusion that management intensity has not decreased is consistent with our finding that the Schafberg has been adequately managed throughout the period, so management cannot be the reason for the change in vegetation. Another indication that management intensity has not decreased is that fringe species such as *Peucedanum cervaria* or *Inula hirta* have not increased; both species often become dominant in the Unstrut valley when the dry grasslands are abandoned (BECKER 1998b). The fact that dissimilarity increased is all the more remarkable as *Bromus erectus* became the dominant species in several plots and probably competes strongly with other species. This again indicates that the increasing dryness must have been the most important factor for the observed vegetation changes. Only the *Stipa* grassland was slightly homogenised. One possible explanation is that the *Stipa* grassland was already extremely dry in the past and contained many winter annuals, so that the corresponding tipping point could already have been reached before the first survey. We also found only weak heterogenisation in the *Sesleria* grassland. This can be explained by the extreme habitat conditions of the skeletal soil and the competitive, stress-tolerant species such as *Sesleria caerulea*, which may have prevented heterogenisation. Another explanation could be that this association in particular was heavily invaded by the competitive *Bromus erectus*, which may have counteracted heterogenisation.

Fig. 12. a) *Sesleria* grassland (*Carici-Seslerietum*) on the upper SW slope of the Schafberg in the transect area during the drought event 2018. In July, the vegetation was largely desiccated with exception of *Carex humilis*. This stand has been invaded by *Bromus erectus* (see dried flower shoots). **b)** The southwest slope of the Schafberg from the west. The transect went over the hilltop, in a direct line down along to the right of the single black pine to the foot of the hill (Photos: T. Meier, a) 10.07.2018, b) 08.07.2015).

Abb. 12. a) Blaugras-Trockenrasen (*Carici-Seslerietum*) am oberen Südwesthang des Schafbergs im Bereich des Transekts während der Dürre 2018. Mit Ausnahme von *Carex humilis* war die Vegetation im Juli weitgehend vertrocknet. *Bromus erectus* (siehe die vertrockneten Blütenstände) hat den Bestand invadiert (Foto: T. Meier, 08.07.2015). **b)** Der Südwesthang des Schafbergs von Westen aus. Der Transekt verlief über die Kuppe, rechts von der einzelnen Schwarzkiefer entlang in direkter Line nach unten (Fotos: T. Meier, a) 10.07.2018, b) 08.07.2015).

5.6 Treating associations individually or together

A special feature of our study is that we divided our grassland into four associations and analysed them both individually and together. Overall, the four associations differed greatly in their floristic composition. Of the total 38 species that changed significantly in at least one association after ISA, only seven species (19.4%) decreased in three or four associations, while 29 species (80.6%) changed in only one or two associations (two species changed only when all four associations were considered together). On the other hand, associations have often changed in parallel for common species. Only *Salvia pratensis* and *Teucrium chamaedrys* changed in opposite ways, i.e. they decreased in one association and increased in another. One could therefore argue that a distinction between associations would not have been necessary to detect most species changes. However, there were clear differences in the results of the individual associations. Evidence of eutrophication resulting, for example, from the colonisation of *Sesleria* grassland by winter annuals would not have been found if this grassland type had not been differentiated. The stronger changes in the meso-xeric *Koeleria* grassland correspond to results of MEIER et al. (2021) from the Kyffhäuser mountains where meso-xeric grasslands also changed more than xeric grasslands. We therefore conclude that distinguishing community types like associations, in addition to combining them, can be a suitable tool to obtain both detailed and general results on vegetation change.

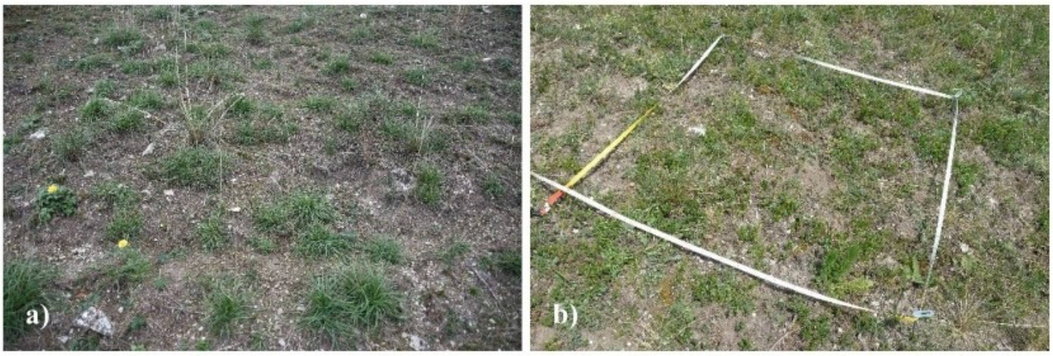

Fig. 13. a) Detail of the *Carex humilis* grassland (*Trinio-Caricetum*) on the upper SW slope of the Schafberg in October 2018 after severe drought. *Bromus erectus* (most tussocks) has already regenerated well despite the late season. **b)** Resurvey plot no. 20 in the *Carex humilis* grassland (*Trinio-Caricetum*) on the Schafberg SW middle slope in June 2019. More plants than expected survived the severe drought in previous year but vegetation was severely thinned. Visible are the dwarf shrubs *Teucrium chamaedrys* and *T. montanum* (in flower), the graminoids *Carex humilis* and *Stipa capillata* and the herbs *Adonis vernalis* and *Salvia pratensis*. Meso-xerophilic species like *Helictochloa pratensis* and *Hippocrepis comosa* had disappeared. This plot was still not invaded by *Bromus erectus* (Photos: T. Meier).

Abb. 13. a) Detail des Erdseggen-Trockenrasens (*Trinio-Caricetum*) am oberen Südwesthang des Schafbergs im Oktober 2018 nach schwerer Dürre. *Bromus erectus* (die meisten Horste) hat sich trotz fortgeschrittener Jahreszeit bereits gut regeneriert. **b)** Wiederholungsaufnahmefläche Nr. 20 im Erdseggen-Trockenrasen (*Trinio-Caricetum*) am mittleren Südwesthang des Schafbergs im Jahr 2019. Mehr Arten als erwartet hatten die schwere Dürre im Vorjahr überlebt, aber die Vegetation war stark ausgedünnt. Zu sehen sind die Zwergsträucher *Teucrium chamaedrys* und *T. montanum* (in Blüte), die Gräser *Carex humilis* und *Stipa capillata* und die Kräuter *Adonis vernalis* and *Salvia pratensis*. Meso-xerophile Arten wie *Helictochloa pratensis* und *Hippocrepis comosa* waren verschwunden. Diese Fläche war noch nicht von *Bromus erectus* invadiert (Fotos: T. Meier).

5.7 Study characteristics and limitations

Our study differs from other resurvey studies in four methodological points: the plot size was small, the plots were set up along a transect line, the study area was small, and the plots were relocated almost exactly (permanent plots). In general, very small plots are not necessarily representative. However, our 1 m² plots from 1995 contained an average of 20 vascular plant species, i.e. 63% of the number of species of the regular 20 m² plots recorded in the same year in the transect area on the Schafberg (cf. BECKER 1998b). We therefore conclude that our plots were sufficiently representative. Furthermore, we do not expect any negative effects of the transect approach. The 244 m transect encompassed the entire sequence of xeric and meso-xeric grassland types of the region compensating for the small study area, and the Schafberg dry grasslands were typical developed and thus representative. This is because the Schafberg was never used for viniculture/agriculture, i.e. the soil was never disturbed by terracing/ploughing, so that the dry grassland was ancient and completely preserved (BECKER 2010). The grassland was also managed throughout the study period and was in a good status of management during both surveys. However, local studies like ours are always associated with limitations related to the small size of the study area. *Helictochloa pratensis* and *Koeleria macrantha*, for example, declined at the Schafberg, but were constant in the Kyffhäuser Mountains between 1996 and 2018/2019

Fig. 14. *Carex humilis* grassland (*Trinio-Caricetum*) on the middle SW slope of the Schafberg in the transect area during the drought 2018. In August, with exception of *Vincetoxicum hirundinaria*, the above-ground vegetation was nearly completely dead (Photo: T. Meier).

Abb. 14. Erdseggen-Trockenrasen (*Trinio-Caricetum*) am mittleren Südwesthang des Schafbergs am Ende der Dürre 2018. Mit Ausnahme von *Vincetoxicum hirundinaria* war die Vegetation oberflächlich fast vollständig tot (Foto: T. Meier).

(MEIER et al. 2021). The same was found for *H. pratensis* on the Porphyry outcrops near Halle (Saale) between 2002 and 2018/2019 (MEIER et al. 2021). Furthermore, our approach of permanent plots led to a high data quality, i.e. pseudo-turnover by semi-permanent plots according to KAPFER et al. (2018) and VERHEYEN et al. (2018) were largely avoided. The high data quality also compensated for the relatively low number of plots in individual associations. We can also largely exclude out observer errors, which often result from the absence of inconspicuous species (MORRISON et al. 2020). At the beginning of our survey and resurvey, both observers were excellently trained by, among other things, recording many regular plots on the Schafberg. The absence of winter annuals in the non-*Stipa* grassland plots was also observed in the standard plots on the Schafberg in spring 1995, when these species were fully developed. Finally, in merging our data, taxonomic concepts were thoroughly harmonised and the error-prone division of taxa was avoided. We therefore conclude that our data was of high quality and our results were clear, consistent and plausible.

6. Conclusions

Our study shows that climate change (i.e. mild winters but especially the hot and dry summers since about 2015) as well as airborne nitrogen deposition are most likely the main drivers behind vegetation changes in a central German dry grassland between 1995 and 2019. At the same time, we were surprised by the strength of the changes after only 24 years, i.e. we had expected fewer changes. In fact, most of our changes were shifts within existing species, which can happen relatively quickly. Annual plants, for example, can increase quickly due to their rapid reproduction, and perennials can die quickly during drought. However, the increase in *Stipa capillata* and *Bromus erectus* was not a short-term pattern, suggesting that climate change has been affecting the grassland for some time but was not properly recognised.

The observed vegetation changes were probably caused mainly by climate change, but partly also in interaction with N deposition. However, it is very likely that climate change has almost always been the driving force behind our patterns, because without climate change, N deposition would have led to more mesophilic grassland, i.e. the opposite pattern we have observed. For example, the increase in annual and biennial plants due to N deposition was only possible because drought had damaged the perennial plants, leaving open gaps. Only the colonisation of the *Sesleria* grassland by winter annuals can be attributed to N deposition alone, as this community already had many open gaps during the first survey but no winter annuals.

While MAZALLA et al. (2022) found evidence of climate change impacts for semi-dry (meso-xeric) grassland (i.e. a decline in species richness on south-facing slopes for all species groups except ruderal species), our study suggests for the first time, to our knowledge, such complex floristic changes for dry and semi-dry grassland that can be attributed to climate change. In our study, however, the mean indicator values for moisture and nutrients did not reflect any change in the factors concerned, which was due to their intercorrelation, i.e. mutual compensation. Such intercorrelation effects show limitations of indicator values which need to be taken more into account in resurvey studies.

Erweiterte deutsche Zusammenfassung

Einleitung – Trockenrasen haben durch Nutzungsintensivierung und -aufgabe einen starken Rückgang erfahren und zählen daher zu den wertvollsten Habitaten in Mitteleuropa (JANSSEN et al. 2016). Selbst in Schutzgebieten wird ihr Naturschutzwert jedoch durch inadäquate Pflege, atmosphärische Stickstoffeinträge (BOBBINK et al. 1998) und Fragmentierung (COUSINS 2009) weiter reduziert. Eine neue Gefahr für Trockenrasen bildet der Klimawandel. Da Trockenrasen grundsätzlich an Hitze und Trockenheit angepasst sind, könnte man eine gewisse Resilienz gegenüber Temperaturerhöhung und zunehmender Trockenheit erwarten; konkret sind sowohl positive als auch negative Effekte denkbar. Positiv wäre es, wenn der Klimawandel durch Trockenheit die Stickstoffdepositionen kompensieren und so auch die Sukzession der Bestände verlangsamen würde (ELLENBERG & LEUSCHNER 2010: 949). Negativ wären irreversible Hitze- und Trockenschäden. Die Faktoren (Treiber), welche Vegetationsveränderungen bewirken, können mit Hilfe von ökologischen Zeigerwerten sowie Zeigerarten detektiert werden. Winterannuelle zeigen in Trockenrasen z. B. starke Sommertrockenheit an, die zu Vegetationslücken führt, welche die konkurrenzschwachen Wintereinjährigen benötigen. Grasartige dagegen haben in Trockenrasen als aufbauende Arten eine Bedeutung und sind gleichzeitig oftmals ökologisch eng eingenischt und daher oft gute Indikatoren. Die relativ wenigen vorliegenden Studien zu Vegetationsveränderungen in Trockenrasen fanden oft eine Abnahme seltener und gefährdeter Arten, seltener eine Abnahme der Gesamtartenzahl, sowie eine Zunahme an Nährstoffzeigern und teilweise auch eine Abnahme an Störungszeigern (z. B. PARTZSCH 2000, HAHN et al. 2013, DIEKMANN et al. 2014, 2019, CHARMILLOT et al. 2021, MEIER et al. 2021). Halbtrockenrasen hatten sich meist stärker verändert als Volltrockenrasen (z. B. MEIER et al. 2021). Lediglich MAZALLA et al. (2022) beobachteten in Halbtrockenrasen negative Effekte von Dürre auf den Artenreichtum. Wir untersuchten Vegetationsveränderungen in einem Trockenrasen am Schafberg im unteren Unstruttal über einen Zeitraum von 24 Jahren (1995–2019). In dieser Zeit gab es v. a. zum Ende hin vier schwere Dürren (BOERGENS et al. 2020), welche mit dem Klimawandel in Verbindung gebracht werden. Daher fragen wir, ob bzw. wie sich die Trockenrasen zwischen 1995 und 2019 durch diese klimawandelassoziierten Dürren aber auch den Temperaturanstieg sowie Stickstoffdepositionen verändert haben. Zur Beantwortung dieser Fragen untersuchten wir neben Veränderungen in der Gesamtartenkombination eine Reihe von Merkmalen, die in der Vegetationsanalyse erprobt und verbreitet sind und speziell auf veränderte Trockenheit oder Nährstoffversorgung reagieren: Ökologische Zeigerwerte nach Ellenberg, Anteile xerophiler und meso-xerophiler Pflanzenarten, Raunkiaer-Lebensformen, CSR-Strategietypen und die β-Diversität der Vegetation als Maß für eine mögliche Homogenisierung. Innerhalb der Arten fokussierten wir uns besonders auf kurzlebige Pflanzenarten und Graminoide. Tabelle 1 fasst unsere einzelnen Hypothesen zusammen.

Untersuchungsgebiet – Die Studie wurde am Schafberg bei Zscheiplitz im unteren Unstruttal (Sachsen-Anhalt) durchgeführt (Abb. 1). Der Untergrund besteht hier aus Unterem Muschelkalk und das Klima war mit ca. 550 mm Jahresniederschlag immer schon sehr trocken (BECKER 1998b). Bei der Erstaufnahme im Jahr 1995 wuchs am Nordhang des Schafbergs ein *Gentiano-Koelerietum* und an dem großen Südwesthang auf Steinböden ein *Carici-Seslerietum*, auf mittelgründigen Lehmböden ein *Trinio-Caricetum humilis* und auf flachgründigen Lehmböden ein *Festuco-Stipetum* (BECKER 1998a). Abbildung 2–3 zeigt die Rasen im Jahr der Erstaufnahme und Abbildung 12–14 im Jahr der Wiederaufnahme.

Methoden – Bei der Erstaufnahme im Jahr 1995 wurden entlang einer 244 m-Transektlinie von der Rückseite des Berges (Nordhang) über den Südwesthang bis zum Bergfuß 46 Dauerflächen von je 1 m² eingemessen und aufgenommen (BECKER 1998b). Die Wiederaufnahme erfolgte im Juni 2019 in gleicher Weise. Aus den Vegetationsdaten wurden folgende Variablen pro Fläche und Jahr berechnet: (1) Artumsatz in den Aufnahmepaaren nach Bray-Curtis, (2) mittlere Zeigerwerte nach Ellenberg, (3) Anteile und Summen der xerophilen und meso-xerophilen Arten, (4) Anteile der Lebensformen nach Raunkiaer einschließlich winter- und sommerannueller sowie bienner Arten, (5) Anteile der wichtigsten CSR-Strategietypen, (6) Veränderung der wichtigsten Grasartigen als Produkt ihrer Präsenz und ihres ordinal-transformiertem Deckungsgrades, (7) Artenreichtum (α-Diversität) und Anzahl gefährdete Arten, (8) Homogenisierung/Heterogenisierung als Veränderung der β-Diversität der Vegetation. Unterschiede in den Mittelwerten der Variablen nach Assoziationen getrennt und zusammen wurden mit *t*-Tests und Unterschiede zwischen Assoziationen mit einfaktorieller ANOVA und anschließendem Tukey-post-hoc-Test analysiert. Arten mit signifikanter Zu- (Gewinner) oder Abnahme (Verlierer) wurden mit Hilfe von Zeigerartanalyse (ISA) determiniert. Eine Ordinationsanalyse (NMDS) diente zur Extraktion und Visualisierung des floristischen Gradienten der Veränderung. Zusammenhänge zwischen diesem Gradienten und Umweltvariablen wurden mithilfe von Pearson-Korrelationen analysiert.

Ergebnisse – Die meisten Assoziationen waren bei ihrer Wiederaufnahme noch erkennbar vorhanden. Lediglich das *Gentiano-Koelerietum* am Nordhang hatte sich in ein *Onobrychido-Brometum* gewandelt und das *Trinio-Caricetum humilis* entsprach nicht mehr der meso-xerischen Subassoziation *cirsietosum*, sondern eher der xerischen Subassoziation *typicum* (Anhang E1). Der Artumsatz innerhalb der Flächenpaare auf Basis der Präsenz/Absenz der Arten betrug über alle vier Assoziationen 50 % (Abb. 4). In der NMDS-Ordination wurde die Vegetation der beiden Jahre entlang der zweiten Achse voneinander getrennt, die mit der Zeit korrelierte (Abb. 5). Der mittlere Ellenberg-Zeigerwert für Temperatur nahm zu und der für Kontinentalität ab, während die Zeigerwerte für Nährstoffe und Feuchte keine signifikante Veränderung zeigten (Abb. 6a). Die Ellenberg-Zeigerwerte für Nährstoff und Feuchte waren eng miteinander korreliert (Abb. 6b). Der Anteil meso-xerophiler Arten nahm ab und der Anteil xerophiler Arten zu (Abb. 6c). Winterannuelle hatten stark zugenommen, die wenigen Sommerannuellen dagegen stark abgenommen und die ebenfalls wenigen Biennen zugenommen (Abb. 7). CS- und CSR-Strategen hatten ab- und SR-Strategen zugenommen (Abb. 8). Insgesamt standen neun Gewinnerarten 29 Verliererarten gegenüber (Tabelle 2). 31 % der Verliererarten waren Grasartige, darunter die dominanten *Carex humilis*, *Sesleria caerulea* und *Brachypodium pinnatum*. Auch typische kleinwüchsige Horstgräser (z. B. *Festuca csikhegyensis*) hatten abgenommen oder waren verschwunden (*Helictochloa pratensis*) (Abb. 9a). *Stipa capillata* und vor allem *Bromus erectus* hatten dagegen zugenommen. Der Gesamtartenreichtum pro Quadratmeter hatte von 19,3 auf 15,8 (-18 %) und der Artenreichtum gefährdeter Arten von 12,0 auf 8,4 abgenommen (-30 %) (Abb. 10). Die Vegetation war insgesamt heterogener geworden (Abb. 11).

Diskussion – Vor dem Hintergrund unserer Hypothese bzw. anderen Ergebnissen, dass der Klimawandel und atmosphärische Stickstoffdepositionen die wichtigsten Treiber der Vegetationsveränderungen waren, waren wir überrascht, dass der mittlere Zeigerwert für Nährstoffe (N-Wert) nicht signifikant zu- und insbesondere der für Feuchte (F-Wert) nicht signifikant abnahm. Dies kann durch die starke Interkorrelation der beiden Zeigerwerte erklärt werden, die dazu führte, dass zunehmende Trockenheit den Anstieg der N-Werte und Eutrophierung das Absinken der F-Werte verhindert hat – obwohl Eutrophierung und Austrocknung tatsächlich stattfanden. Vor diesem Hintergrund interpretieren wir die nicht signifikant veränderten N- und F-Werte als Anzeichen für stärkere Trockenheit und Eutrophierung. Ein weiteres Indiz für stärkere Trockenheit war die Zu- bzw. Abnahme der Anteile der xerophilen bzw. meso-xerophilen Arten, was v. a. durch die überproportionale Abnahme meso-xerophiler Arten bedingt war, die offenbar vertrocknet waren. Der verringerte Zeigerwert für Kontinentalität kann als Indiz für ein weniger kontinentales und stärker mediterranes (nicht ozeanisches) Klima gewertet werden. Tatsächlich standen sechs Gewinnerarten mit submediterraner Verbreitung zwei Gewinnerarten mit kontinentaler Verbreitung gegenüber. Unter den Ersteren waren fünf Winterannuelle (u. a. *Cerastium pumilum* s. str., *C. semidecandrum*, *Hornungia petraea*), die in der Erstaufnahme noch auf die *Stipa*-Rasen (*Festuco-Stipetum*) beschränkt waren, wo sie in Vegetationslücken wuchsen, während sie in den anderen Rasentypen aus Mangel an Vegetationslücken fehlten. Bei der Wiederaufnahme in 2019 waren die Winterannuellen dann in allen Assoziationen häufig vertreten, was wir auf mildere Winter aber v. a. die Ausdünnung der Vegetation durch die Sommerdürren zurückführen (vgl. Abb. 12a und 14). Nur in den *Sesleria*-Rasen (*Carici-Seslerietum*) griff diese Erklärung nicht, da es dort früher schon zahlreiche Vegetationslücken gab, aber keine Winterannuellen. Hier nehmen wir an, dass die Winterannuellen früher aus Nährstoffmangel fehlten, der dann durch die Stickstoffdepositionen überwunden wurde. Die starke Abnahme der Sommerannuellen wie *Linum catharticum* oder *Cuscuta epithymum* lässt sich dagegen durch deren Keim- und Etablierungsphase im Frühsommer erklären, wenn oftmals bereits Dürre herrscht. Auch den starken Rückgang der Graminoiden führen wir auf die jetzt stärkere Trockenheit zurück. Denn obwohl sich xerophytische Graminoide grundsätzlich vor Trockenheit schützen können, reagieren sie auf andauernde tiefe Bodentrockenheit anscheinend empfindlicher als viele Dikotylen mit ihren Speicherwurzeln mit Periderm. Dies gilt v. a. für kleinwüchsige Gräser wie *Koeleria*- oder *Festuca*-Arten, die eher flach wurzeln (KUTSCHERA & LICHTENEGGER 1982). Graminoide mit tiefreichenden Wurzeln wie *Stipa capillata* und *Bromus erectus* hatten dagegen zugenommen. Letzterer hatte die Rasen regelrecht invadiert. Hauptgrund dieser Invasion dürfte ebenfalls der Klimawandel sein, der mit trockeneren Sommern (welche die Art toleriert bzw. deren Schäden sie schneller als andere Arten regeneriert) und v. a. milderen Wintern (in denen die Art effektiv produziert) die Klimaansprüche der submediterranen Art bedient (LEMMER et al. 2021). Unterstützend dürften aber auch Stickstoffdepositionen gewirkt haben, welche die wuchskräftig-konkurrenzstarke Art insgesamt fördern (LEMMER et al. 2021). Insgesamt haben sich die Trockenrasen des Schafbergs während nur 24 Jahren nicht nur deutlich verändert, sondern auch einen Teil ihres Naturschutzwertes eingebüßt, wie die abgenommene Artendiversität und der überproportional starke Rückgang der gefährdeten Arten zeigen. Andere Wiederholungsstudien im Grasland fanden ebenfalls über-proportionale Verluste gefährdeter Arten, aber keinen generellen Rückgang des Artenreichtums (z. B. DIEKMANN et al. 2019, MEIER et al. 2021, SCHÜLE et al. 2022). Insgesamt bewerten wir in unserer Studie den Klimawandel mit v. a. Sommerdürren aber auch milden Wintern als die treibende und Stickstoffdepositionen als untergeordnete (aber dennoch wichtige) Kraft. Denn ohne den Einfluss des Klimawandels hätten die Stickstoffdepositionen zu entgegengesetzten Ergebnissen führen müssen, nämlich einer mehr mesophilen und dichteren Vegetation. Nutzungsänderungen als Grund für unsere Vegetationsveränderungen können wir weitgehend ausschließen; in beiden Jahren war der Pflegezustand der Rasen gut und es gab keine Anzeichen einer Verbrachung. Unseres Wissens zeigt unsere Studie erstmals die beginnenden Auswirkungen des Klimawandels auf Trockenrasen auf breiter Ebene. Außer der Studie von MAZALLA et al. (2022) sind uns überhaupt keine weiteren Untersuchungen bekannt, die wie wir die Vegetationsveränderungen in Trocken- oder Halbtrockenrasen mit dem Klimawandel in Zusammenhang bringen können.

Schlussfolgerung – Unsere Ergebnisse indizieren, dass mitteleuropäische Trockenrasen gegen den Klimawandel nicht resilient, sondern teilweise davon in vielfältiger Weise bereits betroffen und dadurch gefährdet sind.

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Author contribution statement

The vegetation was surveyed by T.B. and resurveyed by T.M. within his PhD project supervised by I.H. and M.P. T.B. and T.M. performed data analysis and drafted the manuscript. All authors revised the draft and agreed with the final manuscript for publication.

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Supplements

Additional supporting information may be found in the online version of this article.
Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Biological/ecological characteristics of studied species.
Anhang E1. Biologisch-ökologische Eigenschaften der untersuchten Arten.

Supplement E2. Synoptic table of the dry grassland communities in 1995 und 2019.
Anhang E2. Übersichtstabelle der Trockenrasengesellschaften in den Jahren 1995 und 2019.

Supplement E3. (Table 2 continued) Constant vascular plant species or species that are too rare for assessing their change.
Anhang E3. (Fortsetzung Tabelle 2) Konstante Gefäßpflanzenarten oder Arten, die zu selten sind, um ihre Veränderung zu bemessen.

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Chapter 4

Functional approach to xerothermic grasslands in Central Germany: Trait composition, dominant grasses and soil factors

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Preslia (in revision)

Functional approach to xerothermic grasslands in Central Germany: Trait composition, dominant grasses and soil factors

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Abstract

Functional traits mediate how species and community respond (or effect) to environmental gradients. These are impacted by 'Global Change', which has led to e.g. climate change and land use change, affecting soil conditions, species richness and functional diversity in, among others, xerothermic (respectively dry or semi-dry) grasslands. Within the last decades, the dominance of grass species like *Bromus erectus* has increased in such grasslands in Central Germany, but factors driving their intraspecific trait variability (ITV) are not yet well understood. The aim of our study was, on the one hand, to compare the functional trait composition of two grassland types, namely dry and semi-dry, using multi- and single-trait approaches and to assess the effects of soil properties on these traits, and, on the other hand, to reveal differences in functional traits and their ITV between the five dominant grasses *B. erectus*, *Brachypodium pinnatum*, *Festuca rupicola*, *Helictotrichon pratense* and *Stipa capillata*. Based on vegetation relevés, functional traits (PH - vegetative plant height, LDM - leaf dry mass, LA - leaf area, SLA - specific leaf area, LDMC - leaf dry matter content, LNC - leaf nitrogen concentration, LCC - leaf carbon concentration, leaf C/N ratio) were measured and soil factors (soil depth, pH value, $CaCO_3$ content, soil N and C content, soil C/N ratio) analysed. For each plot, the community weighted mean (CWM) of all functional traits were calculated to determine differences between the two grassland types, and the coefficient of variation for interpreting differences in the ITV between the five grasses. There were minor differences between dry and semi-dry grasslands in the CWM of the functional traits LDM, LA, LNC and LCC, while other traits did not differ between the two grassland types. Soil factors had little effects on the trait composition of dry and semi-dry grasslands, although soil depth, $CaCO_3$ content and C/N ratio had the highest influence on CWM and were potentially the strongest drivers for differentiation. The five grasses had species-specific trait distributions but showed relatively similar ITV, so we conclude that *B. erectus* was not more adapted to changing environmental conditions than the other grasses. Generally, we only found minor changes in the functional trait composition of dry and semi-dry grasslands in Central Germany and thus the environmental gradient was too small to derive clear differences in the ecosystem function between both grassland types, although the functional structure was largely determined by the dominant grasses.

Keywords: *Bromus erectus*, community weighted mean, dry grassland, functional traits, intraspecific trait variability, semi-dry grassland, soil factors

Introduction

Ongoing 'Global Change' (including climate warming, rising atmospheric nitrogen deposition, soil acidification, land use change) does not only affect the species composition of grasslands (Bobbink et al. 2010, Dupré et al. 2010, Wesche et al. 2012, Diekmann et al. 2014, 2019), but also their functional trait composition (Garnier et al. 2007, Wellstein et al. 2013, Lewis et al. 2014, Helm et al. 2019, Pichon et al. 2022). Within the last decades, an increasingly dramatic loss of species (Bruelheide et al. 2020, Jandt et al. 2022, Meier et al. 2022a) and changes in functional diversity (Bernhardt-Römermann et al. 2011, Socher et al. 2012) have been found for species-rich, often endangered and protected xerothermic (dry or semi-dry, respectively) grasslands (Dengler et al. 2020).

Functional traits are defined as any measurable morphological, physiological or phenological characteristic of an individual that indirectly affects individual fitness (Violle et al. 2007). In particular, they are considered to reliably mediate species and community responses or effects to environmental gradients (Lavorel et al. 2008, Shipley 2009, Garnier et al. 2016) and thus influence ecosystem services, e.g. climate and water regulation, soil stability and protection from disturbance (de Bello et al. 2010). Vegetative plant height (VPH) and leaf traits are important key traits linked to plant resource acquisition and use, stress tolerance and competitive ability (Westoby et al. 2002, Díaz et al. 2016, Garnier et al. 2016). In this context, some leaf traits, such as specific leaf area (SLA), leaf dry matter content (LDMC) and leaf nitrogen concentration (LNC) are closely associated with leaf water and nutrient availability, photosynthetic rate, relative growth rate, leaf longevity and soil water content (Reich et al. 1999, Garnier et al. 2001, Wright et al. 2004, McGill et al. 2006). These three traits represent important components of the 'leaf economics spectrum', which captures relationships between several leaf traits and describes a gradient between traits of resource conservation and those of an acquisitive strategy, i.e. quick resource uptake and turnover (Wright et al. 2004). Fast-growing plants of nutrient-rich sites are characterised by high SLA and LNC but lower LDMC, resulting in faster turnover of nutrients, while slow-growing plants of nutrient-poor sites have low SLA and LNC but higher LDMC and are investing in conservation of nutrients (Díaz et al. 2004, Wright et al. 2004, Shipley et al. 2006).

The 'mass ratio hypothesis' (Grime 1998) states that trait values of the dominant species of a community (those that contribute most to the biomass) have a higher influence on ecosystem functions. Therefore, to calculate the functional composition of a community, the trait values of the single species are multiplied by their relative abundance and then summed up, resulting in the community weighted mean (CWM) (Garnier et al. 2004). Environmental changes can cause not only a shift in the abundance of species, but also a shift in their intraspecific trait variability, leading to a new functional composition of a community (Lepš et al. 2011).

Intraspecific trait variability (ITV) usually describes the variability of functional traits of individuals within a species (Albert et al. 2010) but can also be studied between and within populations (Jung et al. 2010, Pakeman 2013, Mitchell & Bakker 2014). This variability can, for example, have implications for species coexistence and ecosystem functions (Jung et al. 2010, Siefert et al. 2015) and represents the result of genetic differentiation and phenotypic plasticity (Nicotra et al. 2010, Albert et al. 2011). In particular, phenotypic plasticity, i.e. the emergence of multiple phenotypes from a single genotype (Miner et al. 2005, Violle et al. 2012), allows the plant to respond to changing environmental conditions by morphological and physiological adaptations throughout its life span (Stark et al. 2017).

Dry grasslands are characterised by a steeper slope, shallower soil depth and lower water and nutrient availability than semi-dry grasslands and are therefore subject to slower successional processes (Ellenberg & Leuschner 2010), causing differences in species composition (Meier et al. 2021) and probably functional trait composition between both grassland types. Thus, drought-adapted species may have a higher abundance in dry grasslands, which implies a stronger influence on their functional trait composition (sensu Grime 1998), whereby, for example, the same species could have a lower VPH and SLA in dry grasslands due to a higher water limitation than in semi-dry grasslands.

In xerothermic grasslands, competitive grasses produce more biomass than dicotyledonous species (Del-Val & Crawley 2005) and can thus contribute considerably to the functional composition of these communities, which has already been demonstrated for *Stipa* grasslands (Meier et al. 2019). In addition, the increasing abundance of dominant grasses is promoted by nitrogen inputs and the loss in traditional land use (e.g. grazing or mowing) (Diekmann et al. 2014, Lemmer et al. 2021), so that they are mainly responsible for the conversion of previously species-rich to species-poor grassland communities due to increasing competition effects (Wesche et al. 2012).

Within the last three decades, various studies revealed an increasing dominance of grass species in xerothermic grasslands, such as *Bromus erectus*, *Brachypodium pinnatum*, *Festuca rupicola*, *Helictotrichon pratense* and *Stipa* sp. (Bobbink et al. 1998, Bornkamm 2006, 2008, Meier et al. 2021, 2022a), which often co-occur in different plant communities (Meier & Partzsch 2018, Meier et al. 2021, 2022a). Particularly for Central Germany, in more than two decades, there was a significant increase in the presence of *B. erectus*, which tripled to quintupled in cover in the dry and semi-dry grasslands, depending on the different study regions (Meier et al. 2021, 2022a). Moreover, *B. erectus* and *Stipa* species are relatively similar in their functional traits (Meier et al. 2019). Accordingly, it has been experimentally shown that under nutrient addition the growth performance and competitive ability of *B.*

erectus had negative effects on *S. capillata* and *S. tirsa*, which could lead to the displacement of both *Stipa* species in the future (Meier et al. 2022b).

To predict the outcome of environmental changes on xerothermic grasslands, the underlying mechanisms of plant adaptation based on functional traits are an important prerequisite (Wellstein et al. 2013). In particular, soil properties (e.g. soil depth, pH value, $CaCO_3$ content, C/N ratio) cause strong changes in functional traits (Jager et al. 2015). The aim of our study was, on the one hand, to compare the functional trait composition (CWM) of dry and semi-dry grasslands in Central Germany based on published vegetation relevés (Meier et al. 2021, 2022a) using multi- and single-trait approaches and to assess the effects of the abiotic conditions on these traits using different soil properties (cf. Le Bagousse-Pinguet et al. 2014). On the other hand, functional differences between the dominant grasses *B. erectus*, *B. pinnatum*, *F. rupicola*, *H. pratense* and *S. capillata* should be revealed, as these could negatively influence the species richness of xerothermic grasslands due to their competitive and stress-tolerant strategy type (CS) (Grime 2001). We expected a higher ITV for *B. erectus* compared to the other grasses, as this species benefits from climate change and nitrogen depositions (Meier et al. 2022a, Meier et al. 2022b).

We asked the following questions: (i) Does the functional trait composition of dry grasslands clearly differ from that of semi-dry grasslands? (ii) What is the effect of soil factors on the functional trait composition and which ones have the largest influence? (iii) Do the five dominant xerothermic grasses differ in their functional traits? (iv) Does *Bromus erectus* show a higher adaptation in functional traits to environmental changes compared to the other grasses?

Material and methods

Study areas

The study region is in Central Germany within the federal states of Saxony-Anhalt and Thuringia. Vegetation relevés, soil samples and functional traits of the xerothermic grasslands of the Kyffhäuser, the Porphyry outcrops near Halle (Saale) and the Saale-Unstrut-Triasland were investigated in 2018 and 2019. The vegetation relevés were published in Meier et al. (2021) and Meier et al. (2022a) (see there for detailed information), while species abundance was used for functional trait analyses. Most of the sites were grazed (with varying grazing intensity), while only a few sites were abandoned (Porphyry outcrops). The proportion of grazed plots and the grazing intensity were similar among dry and semi-dry grasslands. A total of 101 relevés were included in this analysis, whereas the plant communities belong to the class *Festuco-Brometea* and were here classified into dry and semi-dry grasslands. The same classification was already used by Meier et al. (2021) assigning different plant communities to these grassland types (see further information in that study). In contrast, the different plant communities *Gentiano-Koelerietum*, *Carici-Seslerietum*, *Trinio-Caricetum*, *Festuco-Stipetum* were not subdivided into dry and semi-dry grasslands in Meier et al. (2022a), so we assigned these plant communities to the two grassland types based on the EuroVegChecklist (cf. Bergmeier 2020): The *Carici-Seslerietum*, *Trinio-Caricetum* and *Festuco-Stipetum* were classified here as dry grassland and the *Gentiano-Koelerietum* as semi-dry grassland. To draw clearer conclusions about the functional adaptation of *B. erectus*, additional functional traits were collected for this species in 2019. Therefore, 93 existing vegetation relevés of the Kyffhäuser (Leonhardt 2019) were revisited and only functional traits of *B. erectus* were sampled.

Soil analyses

For each plot, the soil depth [cm; SD] was measured with the help of a metal rod, with five punctures per plot. Moreover, a mixed sample of the mineral topsoil (A-horizon) was taken from each plot with five punctures and the soil samples were dried in the laboratory at room temperature. Subsequently, the pH_{H_2O} value (Microprocessor pH-Meter (pH537 WTW), Schütt Labortechnik GmbH), C content [%], N content [%], C/N ratio (C/N analyser; vario EL cube, Elementar Analysensysteme GmbH) and $CaCO_3$ content [%] (Scheibler apparatus) were measured.

Measurement of functional traits

In all plots, functional traits of the most abundant species were studied, which together accounted for 80% of the biomass present in each community (Grime 1998, Garnier et al. 2004). For an overview on measured functional traits and their ecological functions see Tab. 1. From ten individuals per species, vegetative plant height [cm; VPH] was measured, which is defined as the distance between the highest photosynthetic organ and the base of the plant (Weiher et al. 1999). Compared to upright growing plants, the plant height of rosette plants was measured directly on the leaves of the rosette. The leaf traits were investigated according to a standardised protocol (Perez-Harguindeguy et al. 2013). If possible, attention was paid to the fact that the leaf traits were studied on the same individuals on which the plant height was also measured. A total of ten leaves were harvested for each species per plot, i.e. one leaf per individual (preferably the highest young but fully developed leaf). However, if fewer individuals were present, two leaves per individual were harvested (minimum five individuals). Only intact, fully developed leaves were taken, which were oriented preferably towards the sunlight. The leaf samples were kept moist with water in plastic bags and stored in a cool box for further analyses. In the laboratory, the leaves were scanned with a flatbed scanner with a resolution of 300 dpi and their leaf areas [mm^2; LA] were analysed using WinFOLIA Pro S, version 2004a. If some leaves were too large, they were cut up and the cumulative area of all parts was determined. Then, the leaves were freshly weighed individually, dried in a drying cabinet at 80 °C for 24 h and weighed again to determine the leaf dry mass [mg; LDM]. Based on these parameters, SLA (ratio between leaf area and leaf dry mass in mm^2/mg) and LDMC (ratio between leaf dry mass and water-saturated fresh mass of the leaf in mg/g) were calculated. Afterwards, a C and N analysis of the leaves was performed. For this purpose, the leaf samples were milled beforehand (Vibratory Mill MM 400, Retsch GmbH) and then transferred to the

C/N analyser. Only mixed leaf samples were analysed, i.e. one sample for each species per plot. However, an exception was made for the five dominant grasses *B. erectus*, *B. pinnatum*, *F. rupicola*, *H. pratense* and *S. capillata*, where single leaf samples were analysed (ten samples per plot). Resulting from this analysis, LCC [%] and LNC [%] as well as the C/N ratio could be determined. The functional traits were deliberately collected on the plot-level in the field, as trait values from databases do not take ITV into account (Cordlandwehr et al. 2013).

Data analysis

Statistical analyses were performed in R 3.6.0 (R Core Team 2019). The soil factors and functional traits that represented the dependent variables, were checked graphically for normal distribution and homoscedasticity, and were all logarithmically transformed to achieve normality for subsequent analyses. For each relevé, the CWM (log-transformed data) was calculated for all functional traits: $CWM = \sum_{i=1}^{S}(p_{ic} \text{ x } t_{ic})$. Here, the mean value of trait *t* of species *i* was weighted by the relative species abundance *p* in the community *c*, with a total of *S* species (Garnier et al. 2004). Therefore, the relative abundances of the species (transformed Braun-Blanquet coverage values) of both vegetation datasets were harmonised, whereby the estimate values 2a and 2b were previously combined into estimate value 2 (cf. Meier et al. 2021). The packages dplyr (Wickham et al. 2021) and tidyr (Wickham 2021) and the function ‘weighted.mean’ were used to help calculating the CWM.

A principal component analysis (PCA) should reveal functional gradients between communities of dry and semi-dry grasslands. For this purpose, the CWM values were scaled to zero mean and unit variances, and the results were presented graphically in a biplot over the trait composition. As a complement to PCA, multivariate analysis of variance (MANOVA) with Pillai’s trace as a test statistic was used for directly testing the difference between all functional traits together as response variables and the grassland type as a predictor. Mean values of the CWM (log-transformed values were back-transformed) of different functional traits were compared between dry and semi-dry grasslands with paired t-tests. To determine gradients between functional traits (CWM) and soil factors (see variables above), a redundancy analysis (RDA) was performed and tested for significance using a Monte-Carlo test (9999 permutations). Forward selection was performed using the ‘ordistep’ function to reduce the number of soil factors of the RDA which contribute significantly to explaining the functional trait composition. The results were visualized in a triplot together with the trait composition and the soil factors. All multi-trait analyses were performed using the package vegan (Oksanen et al. 2020).

Furthermore, the package corrplot (Wei & Simko 2021) was used to generate a correlation matrix of the pairwise correlations of all functional traits, which was calculated across the most common species of the dry and semi-dry grasslands (Tab. S1). In addition, mean functional traits were calculated for the functional groups of grasses and forbs.

Tab. 1: Summary of all investigated functional traits with their definitions and ecological functions that were used as predictor for community weighted mean (CWM) and intraspecific trait variability (ITV).

Functional trait	**Abbreviation**	**Unit**	**Definition**	**Ecological function**
vegetative plant height	VPH	cm	distance between highest photosynthetic organ and base of the plant	light interception, competitive ability
leaf dry mass	LDM	mg	dry weight of an individual leaf	relative growth rate, metabolic rate
leaf area	LA	mm^2	one-sided projected surface area of an individual leaf	relative growth rate, metabolic rate
specific leaf area	SLA	mm^2/mg	ratio of fresh leaf area to leaf dry mass	relative growth rate, photosynthesis rate
leaf dry matter content	LDMC	mg/g	ratio of leaf dry mass to leaf fresh mass	metabolic rate, biomass production
leaf nitrogen concentration	LNC	%	total amount of N per unit of leaf dry mass	relative growth rate, resource acquisition and use
leaf carbon concentration	LCC	%	total amount of C per unit of leaf dry mass	relative growth rate, resource acquisition and use
leaf carbon/nitrogen ratio	C/N	-	ratio of C per unit of leaf dry mass to N per unit of leaf dry mass	resource acquisition and use

Analysis of covariance (ANCOVA), conducted with the package car (Fox & Weisberg 2019), was used to investigate the effect of each soil factor on each functional trait (CWM) between the dry and semi-dry grasslands. The CWMs of each functional trait represented the response variables, while the soil factors and the grassland type (dry and semi-dry) were the fixed factors. In addition, interactions between metric and categorical predictors were included in the models (soil factor × grassland type), but model simplification was performed if there were no significant interactions. To avoid pseudoreplication, the nested random effect of the vegetation plot was included in the models, as many species were sampled over several plots and within a plot several individuals of a species had different trait values. These results were visualised by using the package ggplot2 (Wickham 2016).

To characterise the ITV of the five dominant grasses, the coefficient of variation (CV) was calculated (Everitt 1998). Higher CV values indicate that species have a high ITV and thus their traits are more strongly influenced by environmental factors (according to Wellstein et al. 2013 a very high variability if $CV > 0.51$). We applied one-way analysis of variance (ANOVA) with subsequent Tukey's post-hoc test using the multcomp package (Hothorn et al. 2008) to determine differences in both the unweighted functional traits (normally distributed data) and their CV between the five dominant grasses and additionally for *B. erectus* between dry and semi-dry grasslands. All statistical analyses were considered significant if $p < 0.05$.

Results

Functional trait composition of dry and semi-dry grasslands

The first two axes of the PCA explained ~72% of the variation and revealed a strong positive covariation between the traits VPH, LDM and LA, resulting in a slight differentiation of CWMs between dry and semi-dry grasslands (Fig. 1). In addition, SLA and LNC were positively correlated with each other, negatively with CN and to a lesser degree with LDMC and LCC. MANOVA revealed significant differences between all functional traits together and the grassland type (Tab. S2). The semi-dry grasslands had significantly higher LDM and LA, but significantly lower LNC and LCC compared to the dry grasslands (Fig. 2). There were no significant differences in VPH, SLA, LDMC and C/N between the two grassland types. Comparing functional groups, grasses had higher VPH, LDMC and LCC than forbs (Tab. S1). Across all species, functional traits showed both strong significantly negative (e.g. LNC and C/N, SLA and C/N) and positive (e.g. LDM and LA, LDMC and C/N) correlations (Fig. S1).

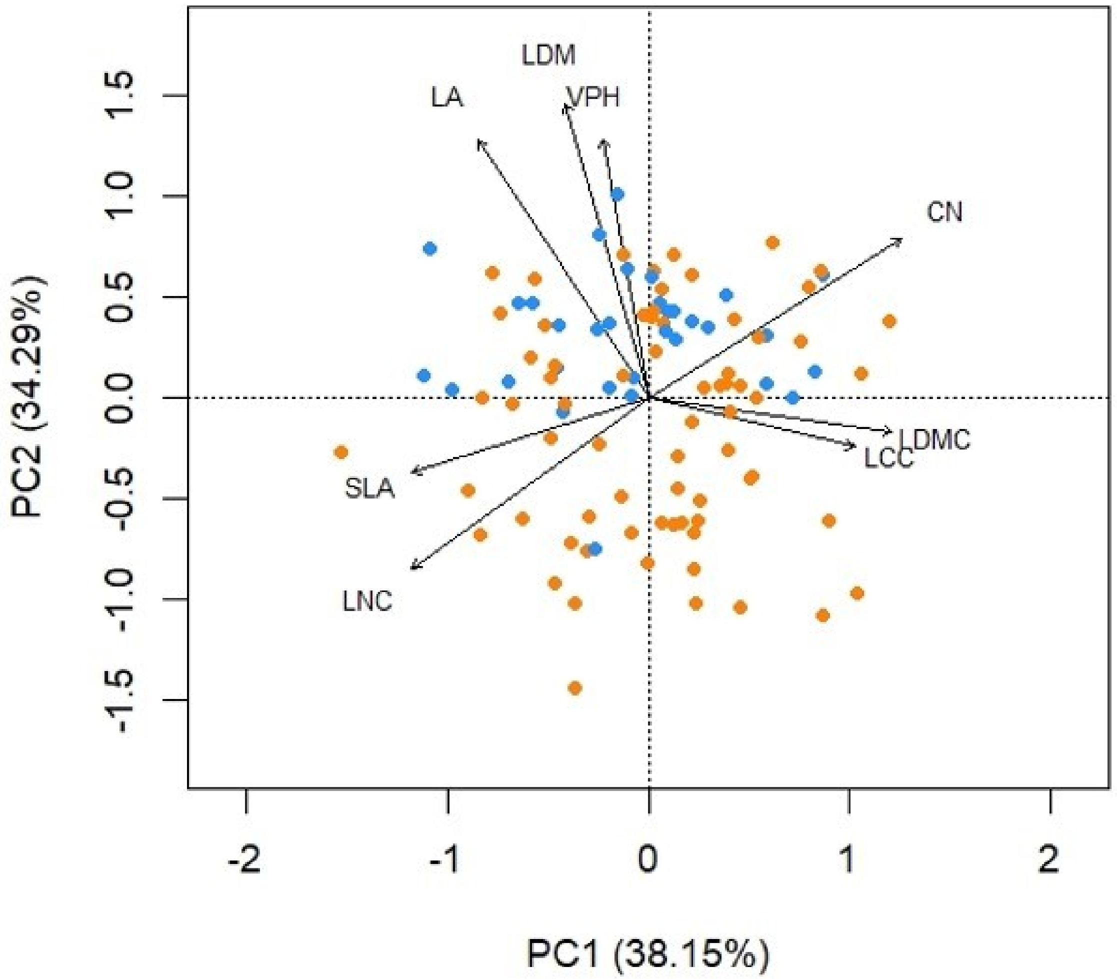


Fig. 1: Principal component analysis (PCA) of the distribution of the community weighted mean (CWM) within the dry (orange symbols) and semi-dry (blue symbols) grasslands (in a total of 101 relevés). Functional traits (VPH, LDM, LA, SLA, LDMC, LNC, LCC, C/N; abbreviations cf. Tab. 1) are shown as vectors. The proportions of declared variability are given on the axes.

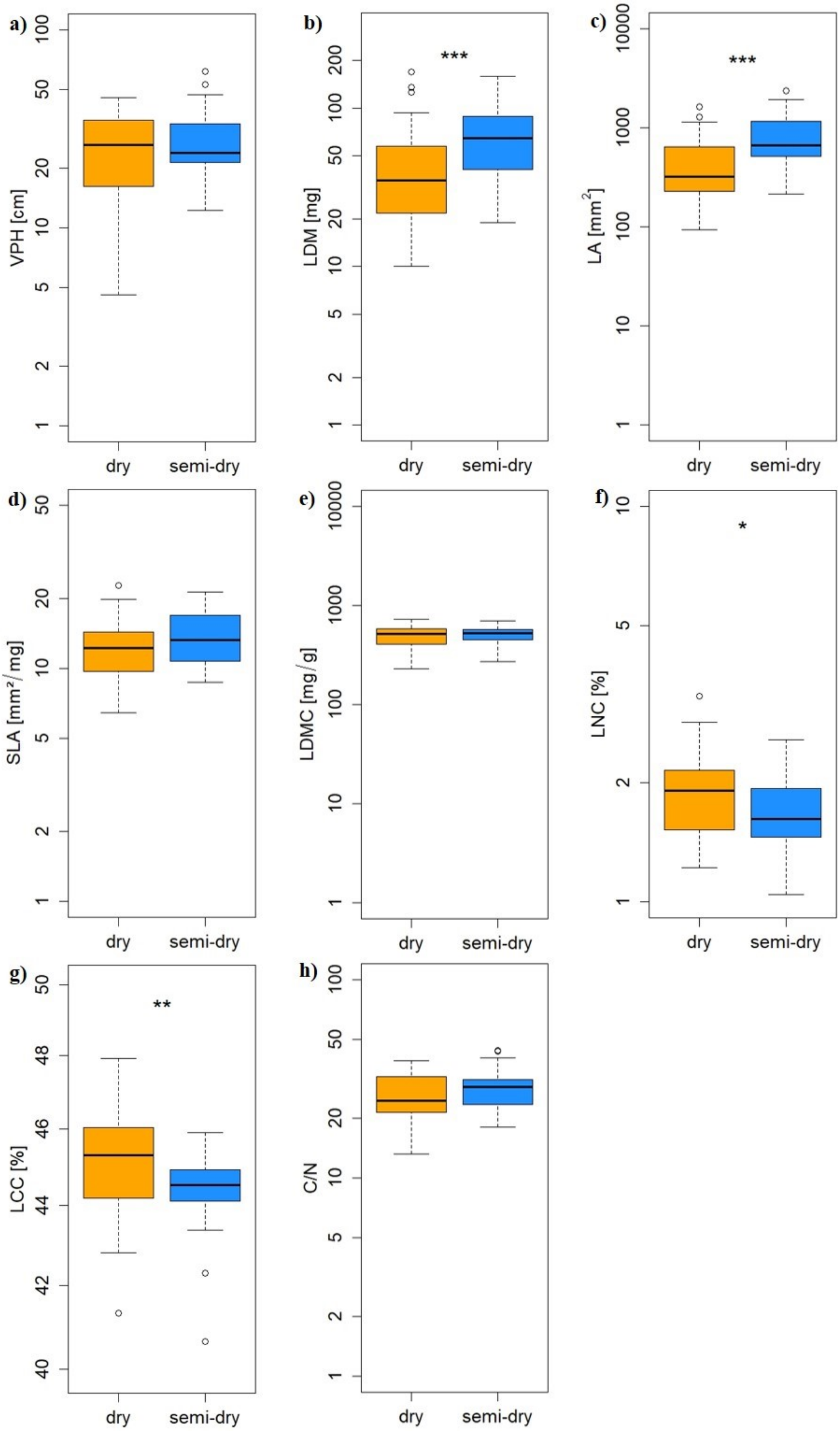

a)
VPH [cm]
1
2
5
10
20
50
100
dry
semi-dry
b)
***
LDM [mg]
1
2
5
10
20
50
100
200
dry
semi-dry
c)
***
LA [mm^2]
1
10
100
1000
10000
dry
semi-dry
d)
SLA [mm²/mg]
1
2
5
10
20
50
dry
semi-dry
e)
LDMC [mg/g]
1
10
100
1000
10000
dry
semi-dry
f)
*
LNC [%]
1
2
5
10
dry
semi-dry
g)
**
LCC [%]
40
42
44
46
48
50
dry
semi-dry
h)
C/N
1
2
5
10
20
50
100
dry
semi-dry

Fig. 2: Community weighted mean (CWM) for each functional trait (abbreviations cf. Tab. 1) between dry and semi-dry grasslands: a) VPH, b) LDM, c) LA, d) SLA, e) LDMC, f), LNC, g) LCC, h) C/N. Results of the t-test: * $0.01 \leq p < 0.05$, ** $0.001 \leq p < 0.1$, *** $p < 0.001$.

Influence of soil factors on functional traits of dry and semi-dry grasslands

Only ~20% of the declared variability could be explained by soil factors on the first two axes of the RDA, while SO, $CaCO_3$ content and the C/N ratio of the soil were significantly correlated (Fig. 3). Most of the CWMs had a low variability with respect to soil factors, and there were no differences between dry and semi-dry grasslands.

In general, ANCOVA revealed only weak effects of the soil factors on the CWM values of dry and semi-dry grasslands and few significant differences in their interactions (Tab. S3, Fig. 4 - 8, Fig. S2 - S4). Thus, no significant differences were found in the interaction between SO, soil N as well as soil C content and the grassland types regarding their CWMs (Tab. S3). VPH, LDM and LA showed a significant increase with increasing SO (Fig. 4a, S2a, S3a). Moreover, VPH and leaf C/N ratio of the grassland type decreased significantly with increasing $CaCO_3$ content (4c, 8c). We found a significant interaction between pH and grassland type on SLA (Tab. S3), whereby the slope was negative in dry grasslands and positive in semi-dry grasslands (Fig. 5b). However, there were particularly significant differences in the interactions between $CaCO_3$ content and grassland type on the response variables LDM, LA, SLA and LDMC (Tab. S3). With increasing $CaCO_3$ content, LDM and LA decreased in dry grasslands, although significantly different slopes between the two grassland types were found (Fig. S2c, S3c). Instead, SLA showed different patterns with increasing $CaCO_3$ content, with a negative slope in dry grasslands but a positive slope in semi-dry grasslands (Fig. 5c). There were significant effects on LDM, LA, SLA, LNC and LCC of the grassland type regarding soil N content, whereas a significant difference in the interaction between soil C/N ratio and grassland type was found for LDMC (Tab. S3). Regarding to LDMC, the slope was positive in dry grasslands and negative in semi-dry grasslands with increasing $CaCO_3$ content and soil C/N ratio (Fig. 6c, 6f).

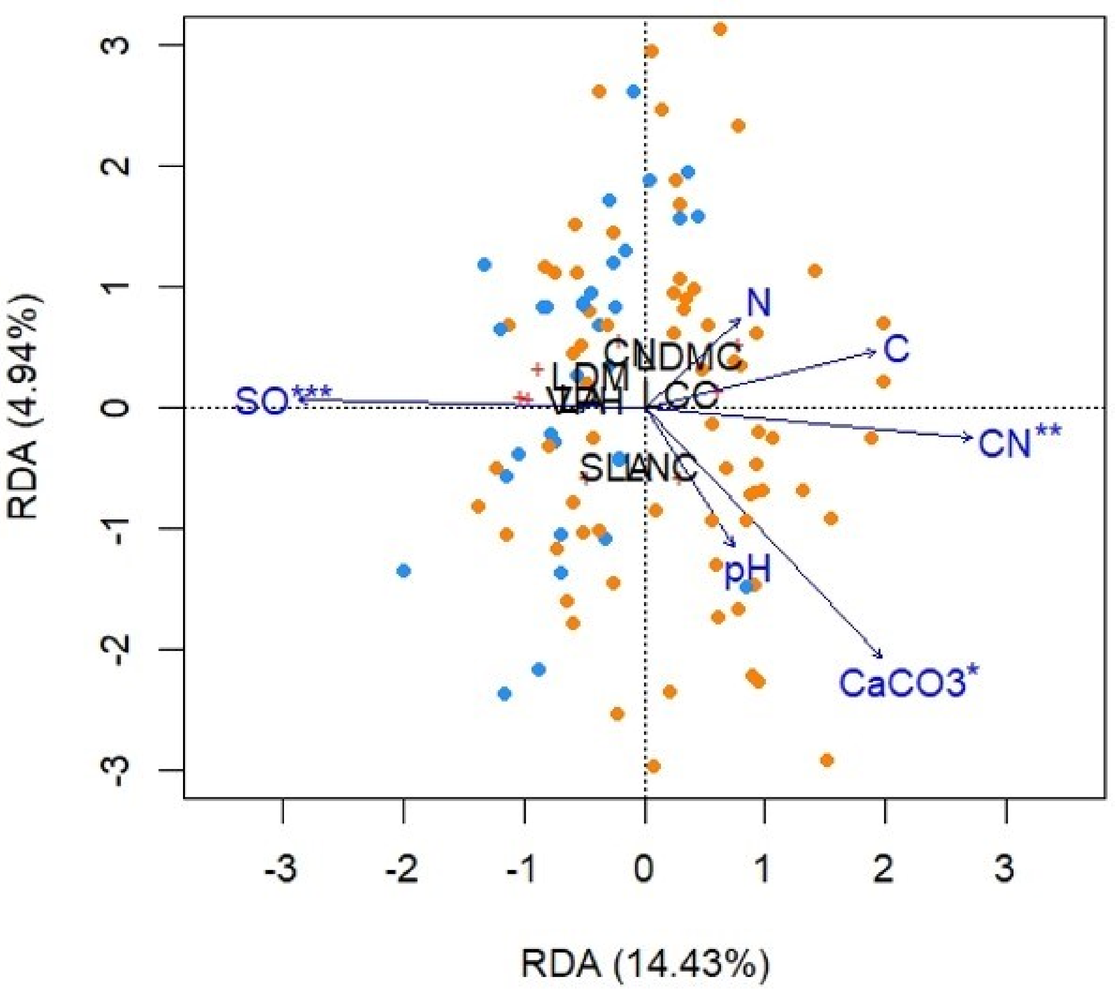


Fig. 3: Redundancy analysis (RDA) of soil factors on the community weighted mean (CWM) within the dry (orange symbols) and semi-dry (blue symbols) grasslands (in a total of 101 relevés). Soil factors (SO – soil depth, pH – pH-value, CaCO3 – $CaCO_3$ content, N – nitrogen content, C – carbon content, CN – C/N ratio) are shown as vector arrows (darkblue colour) and functional traits (VPH, LDM, LA, SLA, LDMC, LNC, LCC, C/N; abbreviations cf. Tab. 1) are represented as centroids. Soil factors which are significantly correlated with the axes of the RDA after forward selection: * $0.01 \leq p < 0.05$, ** $0.001 \leq p < 0.1$, *** $p < 0.001$. The proportions of declared variability are given on the axes and the whole model was significant (9999 permutations, $p < 0.001$).

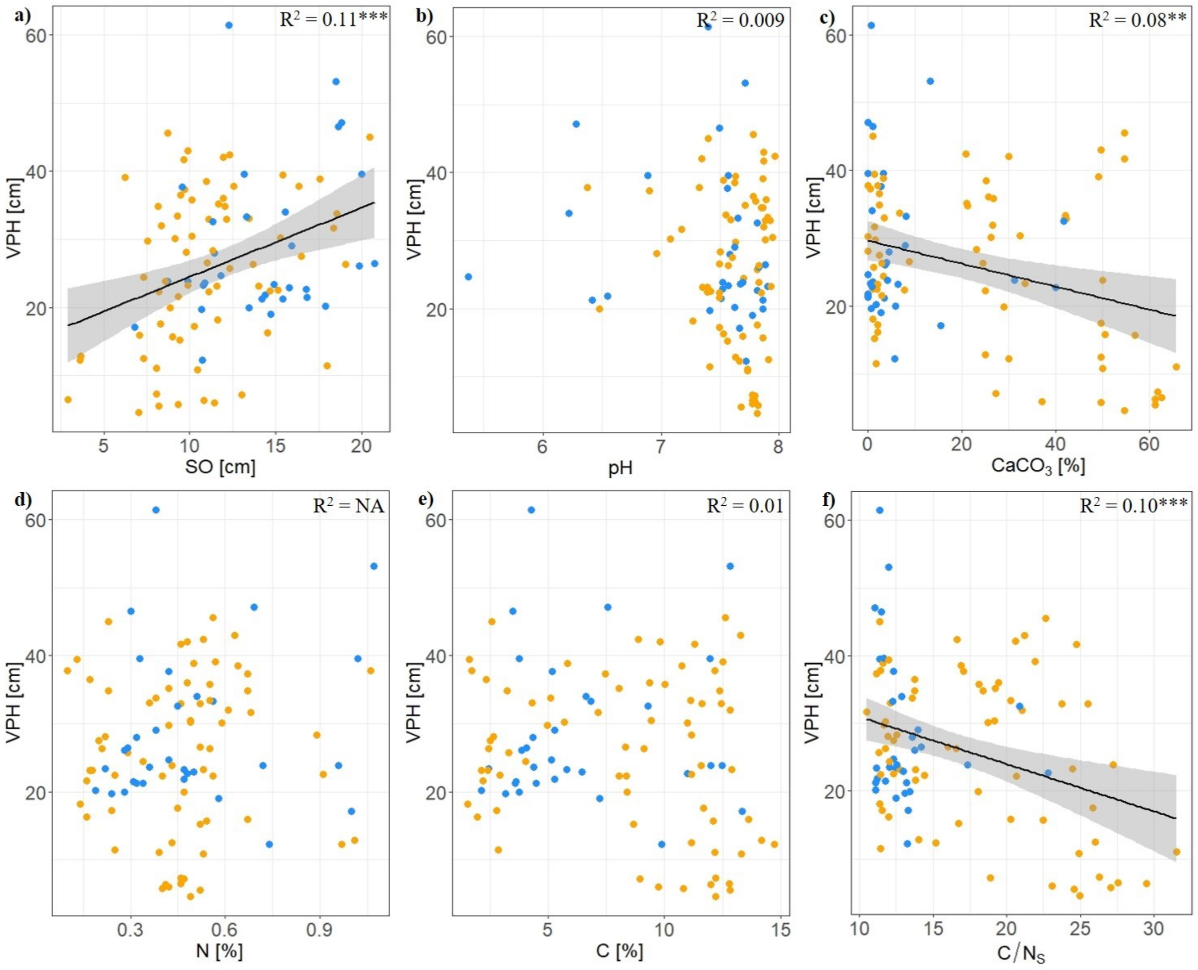


Fig. 4: Relationships between the community weighted mean of the vegetative plant height (VPH) of dry (orange colour) and semi-dry grasslands (blue colour) to soil factors: a) SO – soil depth, b) pH – pH-value, c) $CaCO_3$ – $CaCO_3$ content, d) N – nitrogen content, e) C – carbon content, f) C/N_s – soil C/N ratio. Adjusted R^2 and significance are given (** $0.001 \leq p < 0.1$, *** $0.001 < p$, NA – not available). Visualisation based on the results of the ANCOVAs (cf. Tab. S3) as follows: significant main effect, but no interaction effect: one regression line with 95% confidence level; no significant main effect and interaction effect: without regression line.

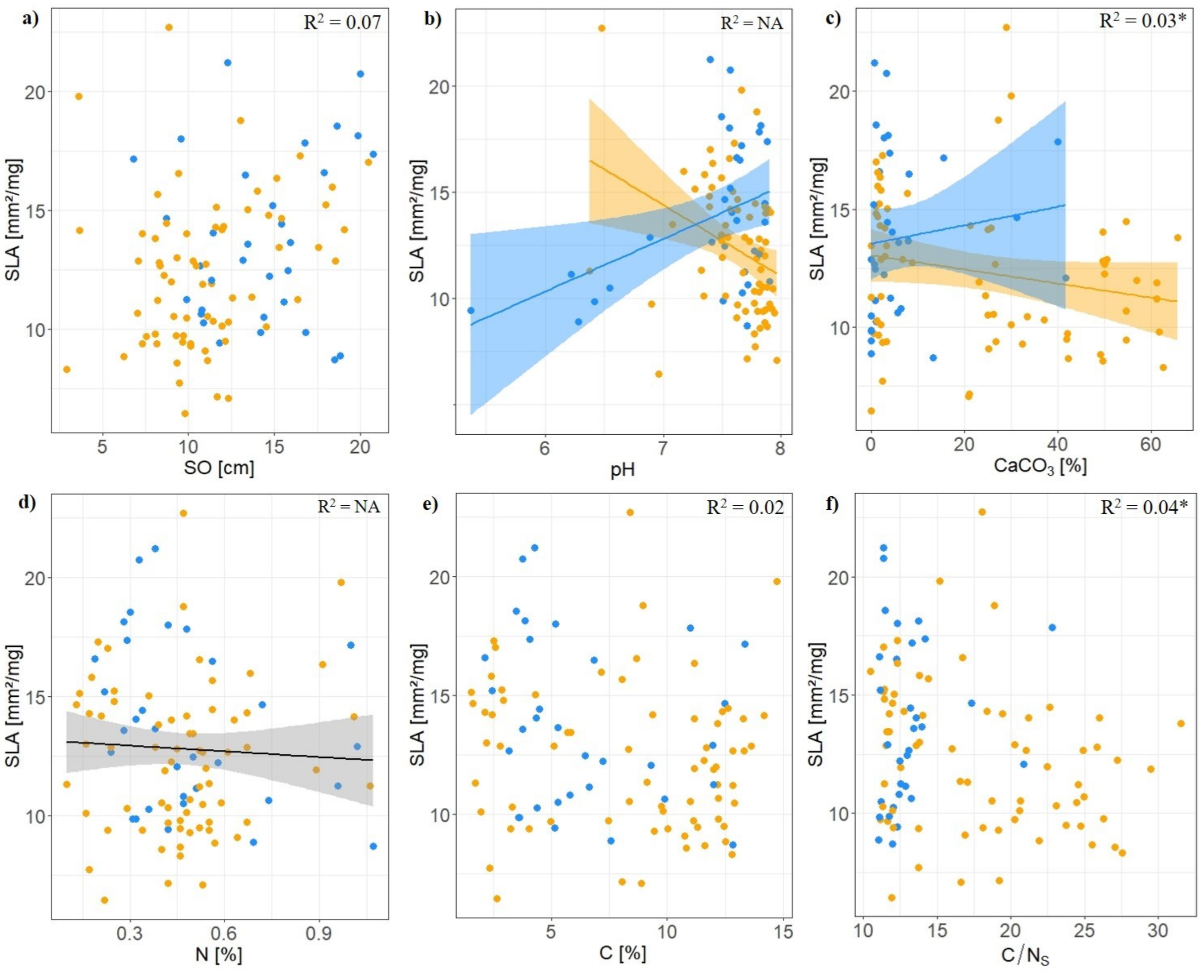


Fig. 5: Relationships between the community weighted mean of the specific leaf area (SLA) of dry (orange colour) and semi-dry grasslands (blue colour) to soil factors: a) SO, b) pH, c) CaCO$_3$, d) N, e) C, f) C/N$_s$ (abbreviations cf. Fig. 4). Adjusted R^2 and significance are given (* $0.01 \le p < 0.05$, NA – not available). Visualisation based on the results of the ANCOVAs (cf. Tab. S3) as follows: significant interaction effect: two regression lines with 95% confidence level; significant main effect, but no interaction effect: one regression line with 95% confidence level; no significant main effect and interaction effect: without regression line.

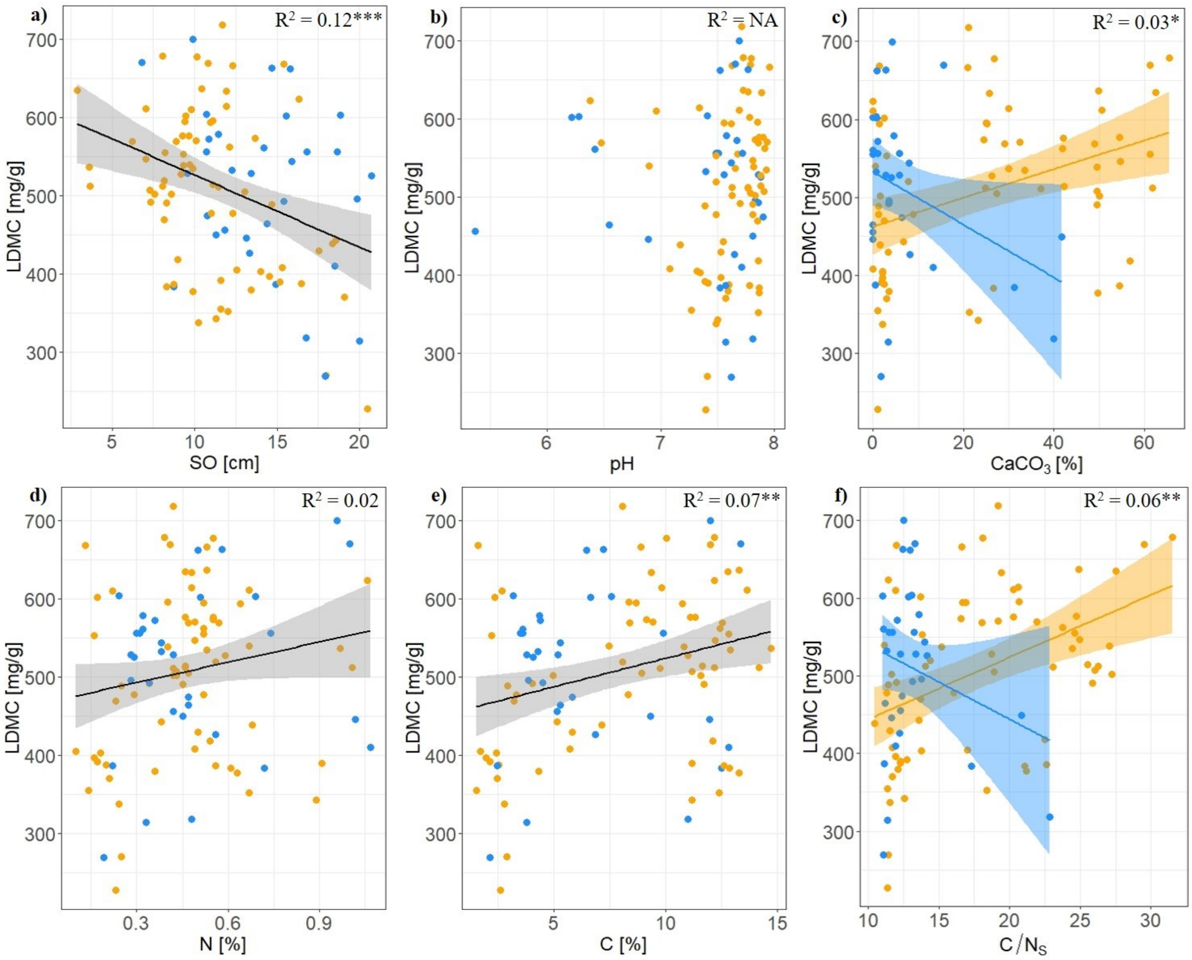


Fig. 6: Relationships between the community weighted mean of the leaf dry matter content (LDMC) of dry (orange colour) and semi-dry grasslands (blue colour) to soil factors: a) SO, b) pH, c) $CaCO_3$, d) N, e) C, f) C/N_s (abbreviations cf. Fig. 4). Adjusted R^2 and significance are given (* $0.01 \leq p < 0.05$, ** $0.001 \leq p < 0.1$, *** $p < 0.001$, NA – not available). Visualisation based on the results of the ANCOVAs (cf. Tab. S3) as follows: significant interaction effect: two regression lines with 95% confidence level; significant main effect, but no interaction effect: one regression line with 95% confidence level; no significant main effect and interaction effect: without regression line.

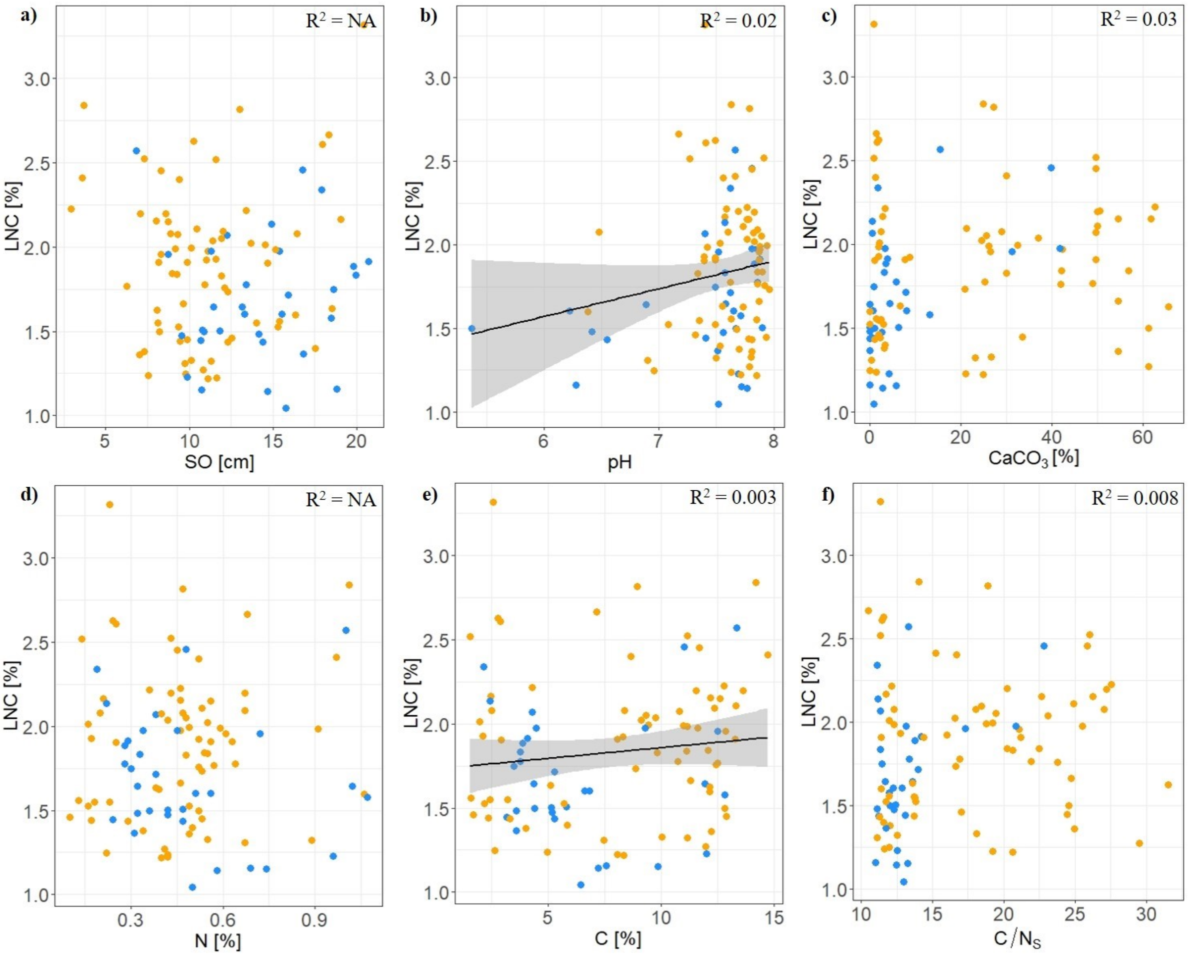


Fig. 7: Relationships between the community weighted mean of the leaf nitrogen concentration (LNC) of dry (orange colour) and semi-dry grasslands (blue colour) to soil factors: a) SO, b) pH, c) $CaCO_3$, d) N, e) C, f) C/N_s (abbreviations cf. Fig. 4). Adjusted R^2 is given (NA – not available). Visualisation based on the results of the ANCOVAs (cf. Tab. S3) as follows: significant main effect, but no interaction effect: one regression line with 95% confidence level; no significant main effect and interaction effect: without regression line.

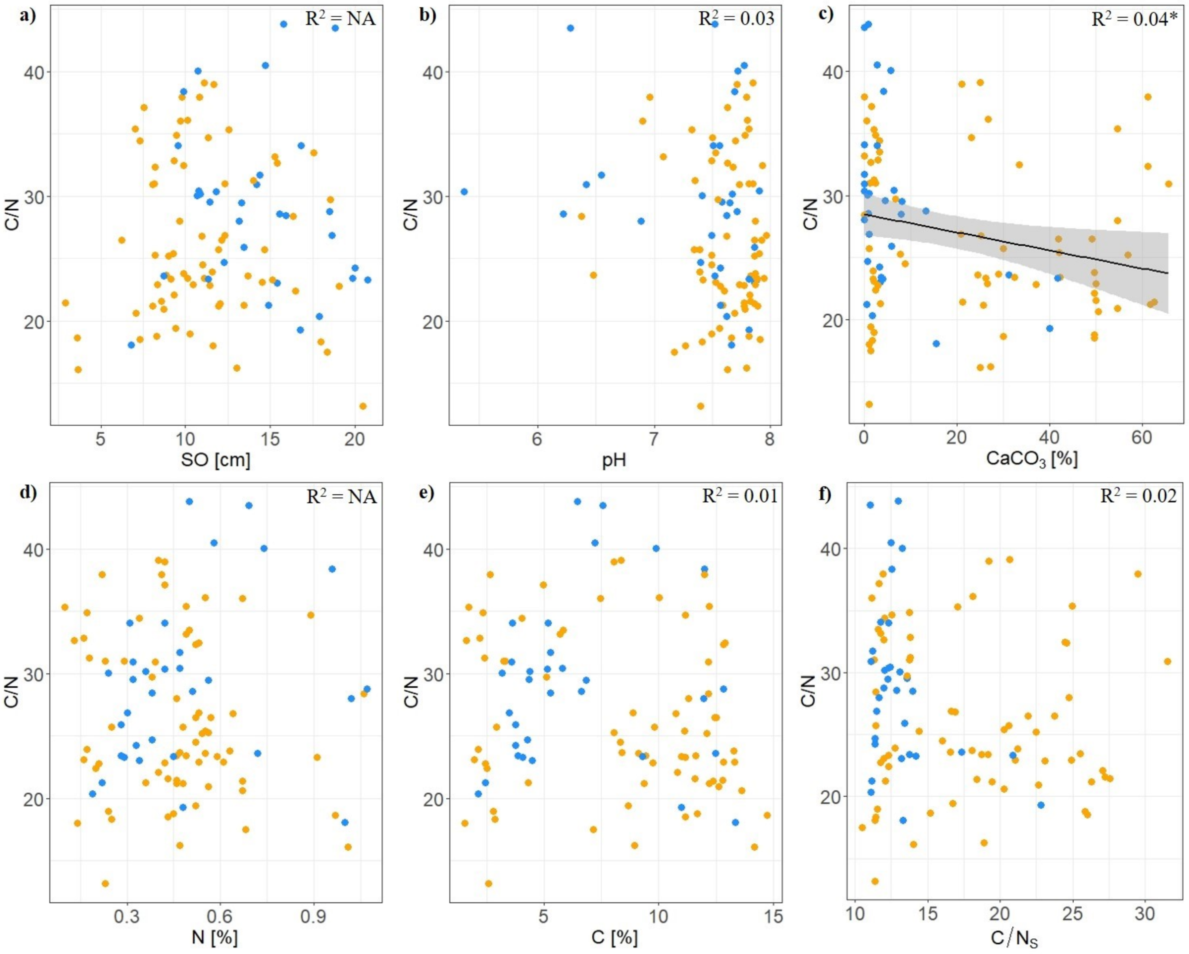
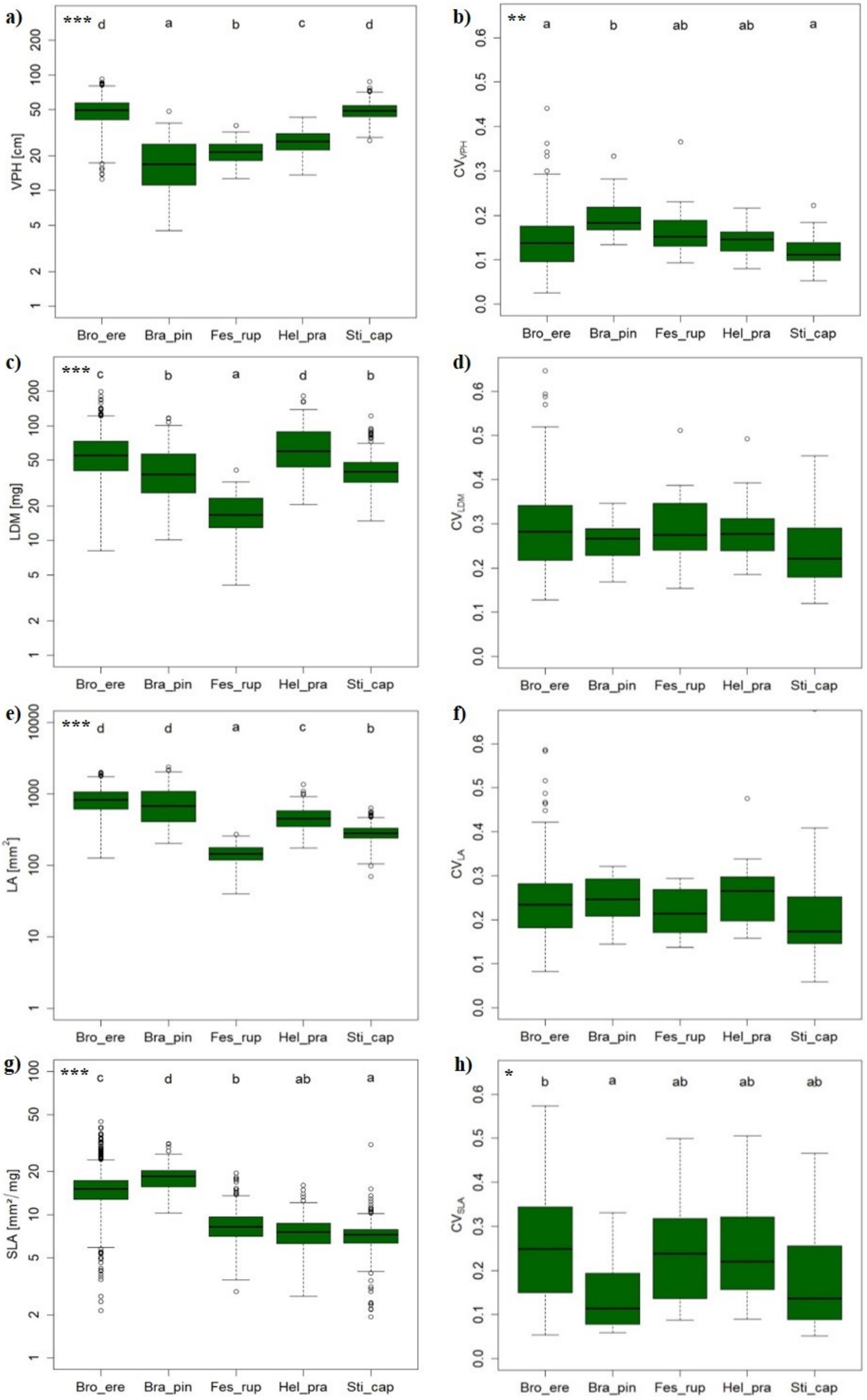


Fig. 8: Relationships between the community weighted mean of the leaf C/N ratio (C/N) of dry (orange colour) and semi-dry grasslands (blue colour) to soil factors: a) SO, b) pH, c) $CaCO_3$, d) N, e) C, f) C/N_s (abbreviations cf. Fig. 4). Adjusted R^2 and significance is given (* $0.01 \leq p < 0.05$, NA – not available). Visualisation based on the results of the ANCOVAs (cf. Tab. S3) as follows: significant main effect, but no interaction effect: one regression line with 95% confidence level; no significant main effect and interaction effect: without regression line.

Functional traits and intraspecific trait variability of xerothermic grasses

In general, we found significant differences between the five grasses in terms of their functional traits and intraspecific trait variability (Fig. 9). *Bromus erectus* and *S. capillata* had the highest and *B. pinnatum* the lowest VPH (Fig. 9a). In contrast, *B. pinnatum* had the highest, whereas *B. erectus* and *S. capillata* the lowest CV_{VPH} (Fig. 9b). LDM was highest in *H. pratense* and LA in *B. erectus* and *B. pinnatum*, while both traits were lowest in *F. rupicola* (Fig. 9c, 9e). Nevertheless, no significant differences were found between the five grasses regarding CV_{LDM} and CV_{LA} (Fig. 9d, 9f). The highest SLA was recorded for *B. pinnatum*, whereas *S. capillata* had the lowest SLA, which was not significantly different from *H. pratense* (Fig. 9g). For CV_{SLA}, only significant differences between *B. erectus* and *B. pinnatum* were observed (Fig. 9h). *Bromus erectus* and *H. pratense* had the lowest LDMC values (Fig. 9i). LNC was highest in *B. erectus*, *B. pinnatum* and *S. capillata* and lowest in *F. rupicola* and *H. pratense* (Fig. 9k). The CV_{LDMC} and CV_{LNC} of *S. capillata* was significantly different to *B. erectus* and *F. rupicola* (Fig. 9j, 9l). The highest LCC values were recorded for *S. capillata* and the lowest values for *B. erectus* and *H. pratense* (Fig. 9m). The CV_{LCC} was higher for *F. rupicola* than for *B. erectus* and *S. capillata* (Fig. 9n). All species differed among each other in their C/N, with *F. rupicola* having the highest and *B. erectus* the lowest C/N ratio (Fig. 9o). The $CV_{C/N}$ values for *F. rupicola* were higher than for *H. pratense* and *S. capillata*, but there were also significant differences between *S. capillata* and *B. erectus*, and between *B. pinnatum* and *H. pratense* (Fig. 9p).

The trait values for VPH, LDM, LA, LDMC and C/N of *B. erectus* were significantly higher in semi-dry grasslands than in dry grasslands (Fig. S5a, S5c, S5e, S5i, S5o), while the trait values for LNC and LCC were significantly higher in dry grasslands than in semi-dry grasslands (S5k, S5m). No significant differences were found for SLA (S5g). Regarding CV, there were no significant differences between the two grassland types.


a)
*** d a b c d
VPH [cm]
1 2 5 10 20 50 100 200
Bro_ere Bra_pin Fes_rup Hel_pra Sti_cap
b)
** a b ab ab a
CV_{VPH}
0.0 0.1 0.2 0.3 0.4 0.5 0.6
Bro_ere Bra_pin Fes_rup Hel_pra Sti_cap
c)
*** c b a d b
LDM [mg]
1 2 5 10 20 50 100 200
Bro_ere Bra_pin Fes_rup Hel_pra Sti_cap
d)
CV_{LDM}
0.0 0.1 0.2 0.3 0.4 0.5 0.6
Bro_ere Bra_pin Fes_rup Hel_pra Sti_cap
e)
*** d d a c b
LA [mm^2]
1 10 100 1000 10000
Bro_ere Bra_pin Fes_rup Hel_pra Sti_cap
f)
CV_{LA}
0.0 0.1 0.2 0.3 0.4 0.5 0.6
Bro_ere Bra_pin Fes_rup Hel_pra Sti_cap
g)
*** c d b ab a
SLA [mm²/mg]
1 2 5 10 20 50 100
Bro_ere Bra_pin Fes_rup Hel_pra Sti_cap
h)
* b a ab ab ab
CV_{SLA}
0.0 0.1 0.2 0.3 0.4 0.5 0.6
Bro_ere Bra_pin Fes_rup Hel_pra Sti_cap

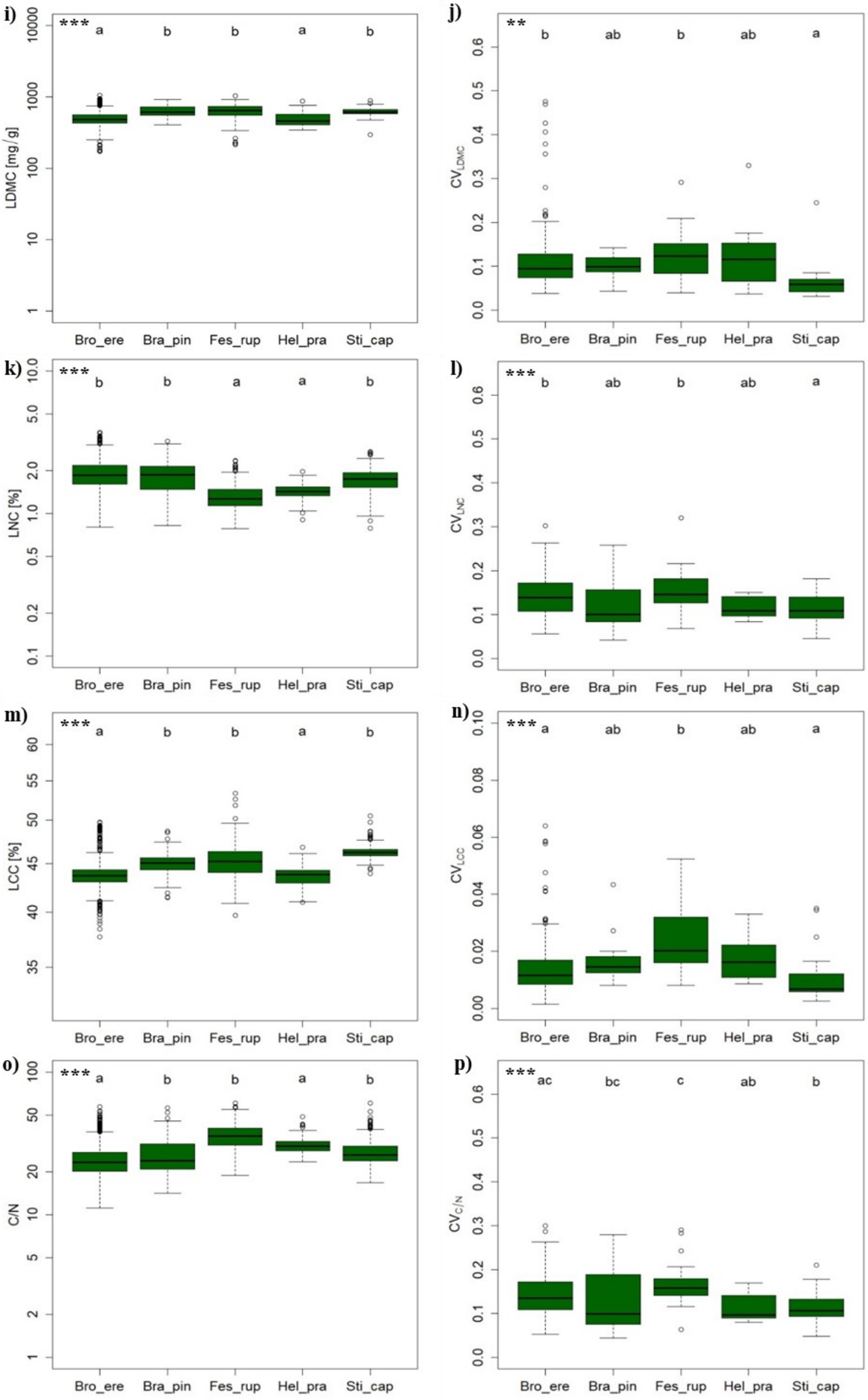

i)
***
a b b a b
LDMC [mg/g]
1
10
100
1000
10000
Bro_ere Bra_pin Fes_rup Hel_pra Sti_cap
j)
**
b ab b ab a
CV_{LDMC}
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Bro_ere Bra_pin Fes_rup Hel_pra Sti_cap
k)
***
b b a a b
LNC [%]
0.1
0.2
0.5
1.0
2.0
5.0
10.0
Bro_ere Bra_pin Fes_rup Hel_pra Sti_cap
l)
***
b ab b ab a
CV_{LNC}
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Bro_ere Bra_pin Fes_rup Hel_pra Sti_cap
m)
***
a b b a b
LCC [%]
35
40
45
50
55
60
Bro_ere Bra_pin Fes_rup Hel_pra Sti_cap
n)
***
a ab b ab a
CV_{LCC}
0.00
0.02
0.04
0.06
0.08
0.10
Bro_ere Bra_pin Fes_rup Hel_pra Sti_cap
o)
***
a b b a b
C/N
1
2
5
10
20
50
100
Bro_ere Bra_pin Fes_rup Hel_pra Sti_cap
p)
***
ac bc c ab b
$CV_{C/N}$
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Bro_ere Bra_pin Fes_rup Hel_pra Sti_cap

Fig. 9: Functional traits and their coefficient of variation (CV) of the five dominant grasses (Bro_ere – *Bromus erectus*, Bra_pin – *Brachypodium pinnatum*, Fes_rup – *Festuca rupicola*, Hel_pra – *Helictotrichon pratense*, Sti_cap – *Stipa capillata*): a) VPH, b) CV_{VPH}, c) LDM, d) CV_{LDM}, e) LA, f) CV_{LA}, g) SLA, h) CV_{SLA}, i) LDMC, j) CV_{LDMC}, k) LNC, l) CV_{LNC}, m) LCC, n) CV_{LCC}, o) C/N, p) $CV_{C/N}$ (abbreviations cf. Tab. 1). Results of the one-way ANOVA (* $0.01 \leq p < 0.05$, ** $0.001 \leq p < 0.01$, *** $p < 0.001$) and calculated Tukey's post hoc-test (different letters indicate significant differences at $p < 0.05$).

Discussion

In this study, we confirmed only a small differentiation in functional trait composition between dry and semi-dry grasslands (i). Soil factors had only minor effects on the trait composition of both grassland types, although soil depth, C/N ratio and $CaCO_3$ content had the highest influence on this composition (ii). The five dominant xerothermic grasses differed in their vegetative plant height and leaf traits (iii), but contrary to our question, all grasses showed a relatively similar ITV, so that we can conclude that *B. erectus* was not more adapted to changing environmental conditions (iv).

Functional comparison of dry and semi-dry grasslands

We have found a slight differentiation in functional trait composition between dry and semi-dry grasslands. The semi-dry grasslands had significantly higher LDM and LA than the dry grasslands, likely indicating higher relative growth rates of the species (Garnier et al. 2016). Indeed, based on PCA, we detected a gradient between taller semi-dry grassland species with larger leaves and small dry grassland species with smaller leaves. Especially small and evergreen dry grassland species with scleromorphic leaves decreased within the last two decades in West and Central Europe (Diekmann et al. 2019), but we assume that such species with a smaller VPH, LDM and LA might be better equipped for dry years that have occurred multiple times in previous years (e.g. 2015, 2018, 2019). For dry grasslands in Slovenia, it was shown that threatened species richness decreased significantly with increasing VPH and SLA, whereby the influence of tall and competitive species should be considered (Pipenbaher et al. 2013). The dry grasslands had a significantly higher LNC and LCC, so that they were able to accumulate more nitrogen and carbon in their tissues, which may be associated with thicker leaves to maintain stomatal transpiration under drought stress (Hultine & Marshall 2000, Siefert 2012). Nevertheless, no differences were found in VPH, SLA, LDMC and C/N between dry and semi-dry grasslands. This can probably be attributed to the different management practices of these grasslands. Grazing can regulate the functional trait composition of grasslands through ITV and species turnover (Niu et al. 2016), which in our case can lead to a shift from less conservative to more conservative species (i.e. that these species tend to be less variable in their traits) as such species develop grazing-avoidance strategies (Adler et al. 2004, Zheng et al. 2015). These are particularly slow-growing, conservative perennial grasses whose traits are adapted by grazing (Wang et al. 2023). However, we measured functional traits on both grazed (and therein with different grazing intensities) and abandoned sites, suggesting that the observed effects may have overlapped. Unfortunately, as we were not primarily interested in comparing different management practices on the functional trait composition of our dry and semi-dry grasslands, this aspect was not investigated and would require clarification in a further study.

However, both grassland types are characterised by a large proportion of grasses, which in our study had higher VPH, LDMC and LCC than forbs. Grasses have a higher percentage of structural tissue and relative cover (Reich et al. 2003, Al Haj Khaled et al. 2005, Pichon et al. 2022). The dominant grasses (e.g. *B. erectus*) were the most abundant species in our investigated dry and semi-dry grasslands (cf. Meier et al. 2021: increasing cover of all grasses of ~40% within the last two decades; see also Tab. S1) and we assume that the functional composition and structure of these grasslands is largely determined by these species (cf. Lepš et al. 2011), supporting the biomass ratio hypothesis (Grime 1998). Moreover, the functional traits of dominant grasses have important implications for ecosystem function (e.g. primary production) of natural and restored grasslands (de Vries et al. 2011, Baer et al. 2016). Otherwise, due to the extreme summer droughts in 2018/2019 in Central Germany (Boergens et al. 2020, European Drought Observatory 2021), nutrient uptake by the plants was likely suppressed by water limitation (Ellenberg & Leuschner 2010, Meier et al. 2022a), so that in both dry and semi-dry grasslands many species could only acquire few resources via the soil and thus a longer-term storage of e.g. nitrogen in the leaves might have been necessary.

Functional changes in dry and semi-dry grasslands caused by soil factors

The soil factors had minor effects on CWM of dry and semi-dry grasslands, which is in line with Meier et al. (2019), who found no effects of soil properties on the functional traits of *Stipa* grasslands in Central Germany. Conversely, Li et al. (2017) postulated that quantitative functional traits, but not functional diversity, are directly associated to soil properties and play therefore an important role in plant-soil interactions, but we could not prove this fact.

In our study, soil depth, $CaCO_3$ content and soil C/N ratio were the strongest drivers of CWM differentiation between dry and semi-dry grasslands and had consequently the highest influence on their functional trait variability. Regarding the $CaCO_3$ content, there was a significant decrease in LDM and LA, while soil C/N ratio showed a similar trend (no interaction between soil factor and grassland type). Dry grassland communities are characterised by many calcareous species (Schubert et al. 2001). In the dry grasslands over lower shell limestone in the Saale-Unstrut-Triasland (Becker 1998), a significant decrease in species richness due to increasing drought and additional nitrogen deposition was detected after more than two decades (Meier et al. 2022a), but not for the regions Kyffhäuser and Porphyry outcrops (Meier et al. 2021). We therefore assume that calcareous species in particular have suffered from these extreme environmental changes, in that they were only able to form a lower VPH, LDM and LA and probably stored more nitrogen and carbon in the leaves.

Furthermore, LDM and LA increased with increasing soil depth (in relation to chapter 4.1 especially for semi-dry grasslands) and decreased with increasing soil N and C content, although no significant differences in the interaction between soil parameters and grassland type could be revealed. Species on sites with deeper soils can have higher relative growth rates, but despite higher soil nutrient levels, their uptake of nitrogen and carbon may be limited by a stressed water availability, likely due to extreme drought events (Ellenberg & Leuschner 2010). These species will likely need to invest in the conservation and protection of their resources in the longer term as part of the 'leaf economics spectrum' (Wright et al. 2004).

Functional comparison of xerothermic grasses

To our knowledge, our study is the first to provide a direct functional comparison across xerothermic grasses and their ITV. As in our study, *B. erectus* and *B. pinnatum,* for example, were investigated functionally, but in terms of different management practices (Targetti et al. 2013) or to show several strategy types (Fort et al. 2012), while their ITV was not considered in detail.

In our functional comparison, all five dominant grasses showed species-specific responses. Generally, they are conservative species with low SLA but high LDMC, corresponding to longer leaf lives, denser leaf tissues and lower growth rates to better protect their resources from abiotic (e.g. extreme temperatures, intense sunlight, drought events) and biotic stress (e.g. herbivory) (Wright et al. 2004, Hodgson et al. 2005, Kleyer et al. 2008). For example, *B. erectus* showed high VPH, SLA and LNC, but lower LDMC, while *B. pinnatum* had the highest SLA (cf. Arredondo & Schnyder 2003 and Targetti et al. 2013 for trait values of *B. erectus* and *Brachypodium rupestre*, which have a similar ecological behaviour to *B. pinnatum*). In particular, species with significantly higher VPH and SLA often grow on moister (or rather less dry) soils (Wellstein et al. 2013, Garnier et al. 2016). Such species can have a competitive advantage to species with opposite trait characteristics (Poorter et al. 2009, Lauterbach et al. 2013). Both *B. erectus* and *B. pinnatum* produced larger and heavier leaves than *F. rupicola* and *S. capillata*, which can be related to the results of Bohner et al. (2019) by showing that generally larger, broad-leaved grasses displace medium-sized, fine-leaved grasses. In fact, it was experimentally verified that *B. erectus* under nutrient addition produced more biomass and negatively affected the grasses *S. capillata* and *S. tirsa*, which could lead to the displacement of these rare species in the future (Meier et al. 2022b). As a competitive species, *B. erectus* can quickly access additional resources (Hautier et al. 2009) and is more stress-tolerant to drought and disturbance (Liancourt et al. 2005, Targetti et al. 2013), which we confirmed by their increased LNC and LCC in dry grasslands. Moreover, such species invest in vessel sclerification to maintain water uptake and transport during dry conditions (Fort et al. 2012). Nevertheless, besides *B. erectus*, *S. capillata* also showed increased VPH and LNC. Both species are deep-rooting, whereby *B. erectus* develops up to 90 cm and *S. capillata* theoretically up to 280 cm deep roots (Kutschera & Lichtenegger 1982) and can therefore assimilate resources in deeper soil layers. Their growth was probably promoted by nitrogen deposition in combination with drought, which has led to an increasing abundance of both species within the last two decades (Meier et al. 2022a). *Helictotrichon pratense* could rather be considered as a functional intermediate between the other species in our study.

Nevertheless, all grasses had low variation in their trait values (except for slightly increased CV_{SLA} values) and in contrast to our initial question (iv), *B. erectus* is not more adapted to environmental conditions in its functional traits than the other grasses as previously expected. Indeed, even the CV values for *B. erectus* between dry and semi-dry grasslands did not differ significantly from each other. However, SLA of all grasses showed higher CV values, which was consistent with other studies on ITV indicating that SLA is a highly variable functional trait at different spatial scales (Wellstein et al. 2013, Siefert et al. 2015, Mitchell et al. 2017). The five dominant grasses had a relatively similar ITV, thus they likely exhibit a high degree of habitat specialisation and may have a relative fitness advantage at preferred sites (Sultan 2000, Sides et al. 2014). Species with low ITV occupy narrower niches, are associated with relatively homogeneous environmental conditions and play an important role in stabilising plant communities (Umaña et al. 2015, He et al. 2018).

Conclusions

There were few differences (LDM, LA, LNC, LCC) in the functional trait composition of dry and semi-dry grasslands in Central Germany. Soil properties also had only a minor influence on the trait composition of both grassland types. Therefore, we assume that the environmental gradient was too moderate to derive clear differences in the ecosystem function between these two grassland types. Rather, the functional structure of the grasslands was determined by the dominant grass species (most abundant species, particularly *B. erectus*) and our results suggest that such grasslands have a relatively similar primary production (vegetative plant height as proxy). Contrary, it has been shown over time that environmental changes (e.g. climate change, nitrogen deposition) cause a loss of species richness of dry and semi-dry grasslands (Bruelheide et al. 2020, Jandt et al. 2022, Meier et al. 2022a), which should not be confused with the measurements of functional traits.

Although a shift in abundance was already detected in the dominant grasses (Meier et al. 2021, Meier et al. 2022a), our results showed that there were no obvious differences in their ITV during the time of sampling, which is particularly true for *B. erectus*. In future, this species will increase in abundance due to increasing nitrogen deposition and climate warming (Meier et al. 2022a, 2022b), but presumably the adaptation of its functional traits to environmental conditions is independent of the grassland type, as currently no differences between dry and semi-dry grasslands are detectable in its ITV.

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Supplement

Tab. S1: Mean frequencies and covers of the most common species and their functional traits (VPH – vegetative plant height, LDM – leaf dry mass, LA – leaf area, SLA – specific leaf area, LDMC – leaf dry matter content, LNC – leaf nitrogen concentration, LCC – leaf carbon concentration, C/N – leaf carbon/nitrogen ratio; mean and SD). Additionally, these parameters are given at the end of the table for the functional groups of grasses and forbs.

species	**fre [%]**	**cov [%]**	**VPH [cm]**		**LDM [mg]**		**LA [mm^2]**		**SLA [mm^2/mg]**		**LDMC [mg/g]**		**LNC [%]**		**LCC [%]**		**C/N**	
			Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Achillea pannonica	2.97	0.32	26.04	10.17	74.06	85.76	881.75	861.06	14.78	5.08	342.70	102.97	1.87	0.69	40.16	7.33	22.92	7.62
Acinos arvensis	6.93	0.77	8.76	3.48	2.44	0.73	49.58	9.67	21.90	7.19	398.26	126.30	1.60	0.46	47.49	1.49	31.60	8.03
Agrimonia eupatoria	7.92	0.89	18.17	5.84	308.61	142.30	3691.67	1623.01	13.01	5.35	324.88	63.68	2.09	0.35	46.46	0.51	22.81	3.84
Alyssum montanum	10.89	0.99	8.23	2.30	1.61	1.21	25.14	14.43	19.53	12.33	505.86	184.93	1.83	0.45	36.17	3.18	20.93	5.60
Anthericum liliago	10.89	1.91	25.24	7.94	74.53	38.26	804.89	304.43	11.92	3.98	232.56	39.63	3.15	0.83	44.37	0.61	15.08	4.16
Anthericum ramosum	1.98	0.17	20.82	10.63	25.45	5.66	292.52	73.71	11.78	3.11	292.13	59.87	2.58	0.74	45.69	0.55	18.53	5.54
Anthyllis vulneraria	7.92	0.89	13.91	6.03	33.45	17.19	545.37	251.28	17.74	6.21	336.76	192.19	2.32	0.43	38.78	1.45	17.12	2.49
Arrhenatherum elatius	4.95	1.66	62.50	11.82	32.12	11.25	781.13	258.40	25.28	7.10	613.02	125.69	2.42	0.33	45.39	0.31	18.99	2.47
Artemisia campestris	2.97	0.32	27.93	8.98	12.72	7.04	176.48	87.17	14.80	5.53	301.59	71.48	3.56	0.27	45.10	0.71	12.73	0.95
Astragalus danicus	4.95	0.59	9.81	4.83	15.71	5.69	286.42	125.60	19.10	7.01	389.95	64.00	2.36	0.83	41.43	5.88	18.81	4.82
Brachypodium pinnatum	15.84	4.63	18.73	8.86	42.66	22.21	794.01	466.26	18.37	3.87	629.05	110.50	1.89	0.54	45.01	1.11	26.01	8.15
Bromus erectus	56.44	18.13	44.83	13.50	53.49	25.21	708.54	300.09	14.27	5.02	541.69	139.99	1.91	0.54	44.51	1.61	25.42	8.21
Carex humilis	56.44	8.81	9.04	3.69	8.35	4.28	115.59	57.87	14.60	4.75	588.72	134.16	1.98	0.51	45.83	1.39	24.86	6.89
Centaurea scabiosa	10.89	1.11	22.00	13.94	183.76	110.80	2615.60	1767.28	15.52	7.26	211.61	49.47	3.01	0.69	44.61	1.37	15.56	3.63
Centaurea stoebe	7.92	1.26	64.71	24.10	67.39	58.96	939.45	799.46	14.90	4.73	298.12	91.42	2.79	0.69	45.29	1.40	17.15	4.25
Cervaria rivini	6.93	0.89	10.05	4.07	279.66	164.76	2497.36	1210.63	11.16	8.55	403.92	37.05	2.13	0.54	45.54	1.17	22.60	5.83
Dianthus carthusianorum	2.97	0.07	21.52	7.80	9.33	3.41	109.89	27.99	12.72	3.94	456.80	91.32	2.03	0.19	44.81	0.40	22.15	2.32
Eryngium campestre	7.92	0.45	18.68	4.99	531.00	354.40	3030.80	1433.60	7.71	5.77	447.42	104.40	1.54	0.37	44.98	1.01	31.07	8.99
Erysimum crepidifolium	2.97	0.20	15.97	6.06	21.63	9.84	209.41	99.93	10.06	2.75	393.79	50.25	2.61	0.35	43.71	0.31	16.95	2.18
Euphorbia cyparissias	18.81	0.84	14.66	4.80	0.84	0.49	17.22	9.59	25.30	20.02	476.57	186.50	2.72	0.67	45.01	2.62	17.49	4.62
Falcaria vulgaris	3.96	0.35	26.19	9.30	253.77	175.20	2457.87	1404.31	13.31	10.25	366.27	41.90	1.82	0.50	42.23	1.20	24.49	6.16
Festuca csikhegyensis	16.83	2.33	11.46	6.31	20.42	9.90	122.93	55.67	6.42	1.81	588.67	114.77	1.58	0.36	45.05	1.12	30.19	7.62
Festuca rupicola	22.77	5.37	21.79	4.87	17.97	6.64	145.98	46.46	8.60	2.55	645.74	138.88	1.32	0.30	45.35	2.04	35.78	7.50
Filipendula vulgaris	10.89	2.75	21.08	7.31	143.41	62.53	1544.38	581.80	11.11	1.81	469.32	48.57	1.90	0.47	45.47	2.03	24.81	3.91
Fragaria viridis	2.97	0.32	11.41	3.35	136.38	51.31	1403.50	509.58	11.48	5.27	475.69	58.85	1.74	0.24	44.93	3.23	26.29	5.33

Galatella linosyris	8.91	0.35	12.71	9.38	2.89	1.30	44.03	21.94	18.69	14.13	432.72	175.51	2.31	0.51	45.74	1.67	20.81	5.35
Galium boreale	3.96	0.35	16.70	4.85	2.29	0.76	53.08	14.08	24.48	6.63	373.85	169.17	2.36	0.48	45.41	0.41	19.96	4.64
Galium mollugo	1.98	0.30	53.85	6.84	2.16	1.18	35.83	10.30	21.53	11.60	460.30	151.35	1.43	0.22	44.25	0.84	31.45	5.50
Galium verum	6.93	0.54	22.24	7.47	1.14	0.46	18.11	8.80	17.97	9.19	519.02	177.38	2.16	0.71	46.37	1.59	23.33	6.58
Gypsophila fastigiata	10.89	1.11	11.94	6.56	13.42	6.54	174.42	63.69	14.25	5.30	255.86	117.51	2.33	0.56	37.09	2.03	16.72	3.87
Helianthemum canum	15.84	1.51	4.22	2.08	4.51	1.95	48.04	15.09	12.55	7.61	463.79	158.92	1.98	0.58	44.76	1.01	24.51	7.42
Helianthemum nummularium	15.84	1.71	10.63	3.30	4.83	2.06	81.58	28.16	18.26	5.68	392.72	151.58	2.31	0.65	44.91	1.19	20.71	4.93
Helictotrichon pratense	11.88	3.56	27.14	6.24	66.85	30.65	490.42	212.16	7.73	2.25	486.50	98.01	1.44	0.19	43.64	1.02	30.92	4.43
Hippocrepis comosa	11.88	2.10	12.27	4.09	29.52	14.69	444.91	211.49	15.94	3.96	282.12	63.30	3.97	0.57	44.32	1.07	11.39	1.66
Hypochaeris maculata	1.98	0.74	18.12	6.26	309.61	118.15	4419.56	1302.76	15.15	3.76	169.39	14.33	2.43	0.82	40.98	0.35	17.88	6.14
Inula hirta	2.97	0.32	17.16	4.28	41.98	19.87	528.08	126.10	14.77	5.60	388.28	97.52	2.34	0.93	45.59	0.17	22.51	11.44
Koeleria macrantha	6.93	0.79	18.87	3.64	18.46	9.95	207.24	97.88	12.35	4.79	598.06	94.34	1.81	0.20	44.19	1.33	24.77	3.16
Medicago falcata	1.98	0.30	30.61	16.92	7.38	2.33	170.79	81.02	24.35	11.26	453.10	131.49	2.42	2.17	37.05	8.59	23.05	17.17
Pilosella officinarum	2.97	0.07	3.58	1.40	20.96	5.39	288.27	132.01	13.46	4.44	371.95	164.95	2.05	0.19	45.68	0.66	22.42	2.00
Plantago media	3.96	0.10	6.48	2.48	98.28	47.84	1401.19	746.92	14.67	5.11	189.49	46.08	1.72	0.29	40.69	3.17	23.99	2.11
Poa angustifolia	3.96	0.69	27.67	7.78	11.78	5.90	135.36	56.15	12.75	4.18	692.89	127.01	1.37	0.04	43.27	1.12	31.70	0.09
Polygonatum odoratum	1.98	0.74	36.13	4.52	78.41	23.67	1632.84	425.95	21.13	1.72	201.89	27.22	2.63	0.41	43.75	1.03	16.88	3.01
Potentilla incana	3.96	0.79	7.49	1.31	80.05	21.62	722.10	236.75	9.00	1.43	478.28	76.61	1.62	0.20	46.21	1.01	28.89	4.12
Prunella grandiflora	2.97	0.20	7.17	1.48	24.71	7.71	432.40	92.95	18.62	5.61	212.19	34.59	1.80	0.35	44.08	0.56	25.06	4.21
Pulsatilla vulgaris	1.98	0.52	11.94	2.57	100.83	24.81	1213.24	310.93	12.65	3.99	259.95	32.42	2.29	0.13	44.91	0.45	19.63	1.31
Rosa rubiginosa	2.97	0.20	45.87	20.93	59.45	35.05	635.14	330.70	11.22	2.22	427.45	37.18	2.52	0.34	44.20	0.22	17.80	2.54
Salvia pratensis	15.84	1.61	18.95	7.07	272.67	105.91	3433.52	1422.64	13.15	4.79	237.99	41.71	2.17	0.54	42.96	3.73	20.63	4.35
Sanguisorba minor	2.97	0.32	5.32	1.58	39.36	18.75	380.41	166.60	10.11	2.46	547.21	63.77	1.34	0.17	45.45	0.67	34.11	3.76
Scabiosa canescens	21.78	2.57	12.99	6.30	29.37	11.05	412.83	151.98	14.36	2.65	243.60	62.82	1.99	0.69	44.43	2.75	24.03	6.04
Scabiosa ochroleuca	1.98	0.30	4.83	4.55	25.45	13.01	260.35	114.22	10.75	1.57	434.97	89.02	1.04	0.18	41.93	0.47	41.05	7.93
Seseli hippomarathrum	8.91	0.84	6.38	4.04	47.36	22.47	353.51	168.10	7.77	1.80	445.80	110.56	1.99	0.50	45.39	1.66	24.06	5.93
Sesleria caerulea	9.90	1.78	10.36	6.14	34.78	17.37	332.11	173.19	9.60	2.02	498.49	70.99	1.49	0.37	44.90	0.91	31.73	7.49
Silene otites	6.93	0.30	23.78	8.30	13.07	5.61	199.21	68.86	16.12	3.97	228.54	54.85	3.12	0.56	44.37	1.40	14.69	3.06
Stipa capillata	26.73	10.10	49.39	9.21	42.88	16.39	292.68	88.30	7.25	2.28	623.52	69.70	1.73	0.34	46.32	0.82	27.98	6.52
Stipa pennata	1.98	0.40	54.78	10.30	125.64	46.03	533.69	171.63	4.66	1.97	679.59	87.46	1.47	0.20	46.12	0.38	32.00	4.62
Stipa pulcherrima	9.90	2.25	57.03	16.70	122.76	58.13	574.83	224.07	5.29	2.06	686.59	142.68	1.54	0.37	45.86	1.03	31.47	7.68

Stipa tirsa	2.97	1.61	47.46	7.50	37.87	9.55	227.56	55.07	6.30	1.95	782.65	65.98	1.26	0.36	43.72	3.08	38.34	14.20
Teucrium chamaedrys	27.72	4.16	6.15	2.53	6.43	2.64	85.23	24.43	14.43	4.16	467.70	90.61	2.19	0.68	45.96	3.81	23.40	8.99
Teucrium montanum	11.88	2.08	5.13	1.99	2.49	1.04	32.18	16.92	13.08	4.54	530.77	175.78	1.65	0.38	48.52	2.11	31.09	7.99
Thalictrum minus	7.92	1.36	23.00	10.27	158.89	80.04	2090.00	1177.09	15.25	12.36	308.68	112.10	2.64	1.03	47.05	3.75	20.77	9.61
Thesium linophyllon	5.94	0.50	8.77	2.49	4.11	1.77	47.34	15.33	12.96	5.39	548.32	165.53	2.13	0.32	43.75	3.60	21.19	4.86
Thymus praecox	5.94	0.40	2.70	1.44	0.87	0.51	13.88	6.63	21.45	12.69	510.61	236.66	1.51	0.38	48.09	1.48	33.43	7.69
Vicia hirsuta	2.97	0.32	29.17	5.48	36.71	11.81	593.70	177.11	17.37	7.96	417.50	39.98	3.58	0.65	43.58	0.60	12.43	2.19
Vincetoxicum hirundinaria	9.90	1.09	33.83	13.61	55.16	26.07	1154.03	437.53	22.06	5.30	243.77	77.33	3.72	0.67	44.18	0.79	12.26	2.50
grasses	17.68	4.44	32.93	8.32	45.43	19.53	390.15	161.66	10.96	3.33	618.23	108.58	1.66	0.33	44.94	1.23	29.30	6.36
forbs	7.37	0.86	17.91	6.45	75.00	38.63	859.58	386.03	15.31	6.10	372.44	96.25	2.27	0.53	44.08	1.79	21.98	5.18

Tab. S2: MANOVA for directly testing the difference between all functional traits together as response variables and the grassland type as a predictor (above). Univariate ANOVAs for testing the effect of the grassland type on the CWMs of each functional trait (VPH, LDM, LA, SLA, LDMC, LNC, LCC, C/N; abbreviations cf. Tab. 1) as response variables (below). Degrees of freedom (df), Pillai's trace, F-values and error probabilities (* $0.01 \le p < 0.05$, ** $0.001 \le p < 0.1$, *** $p < 0.001$, ns = not significant).

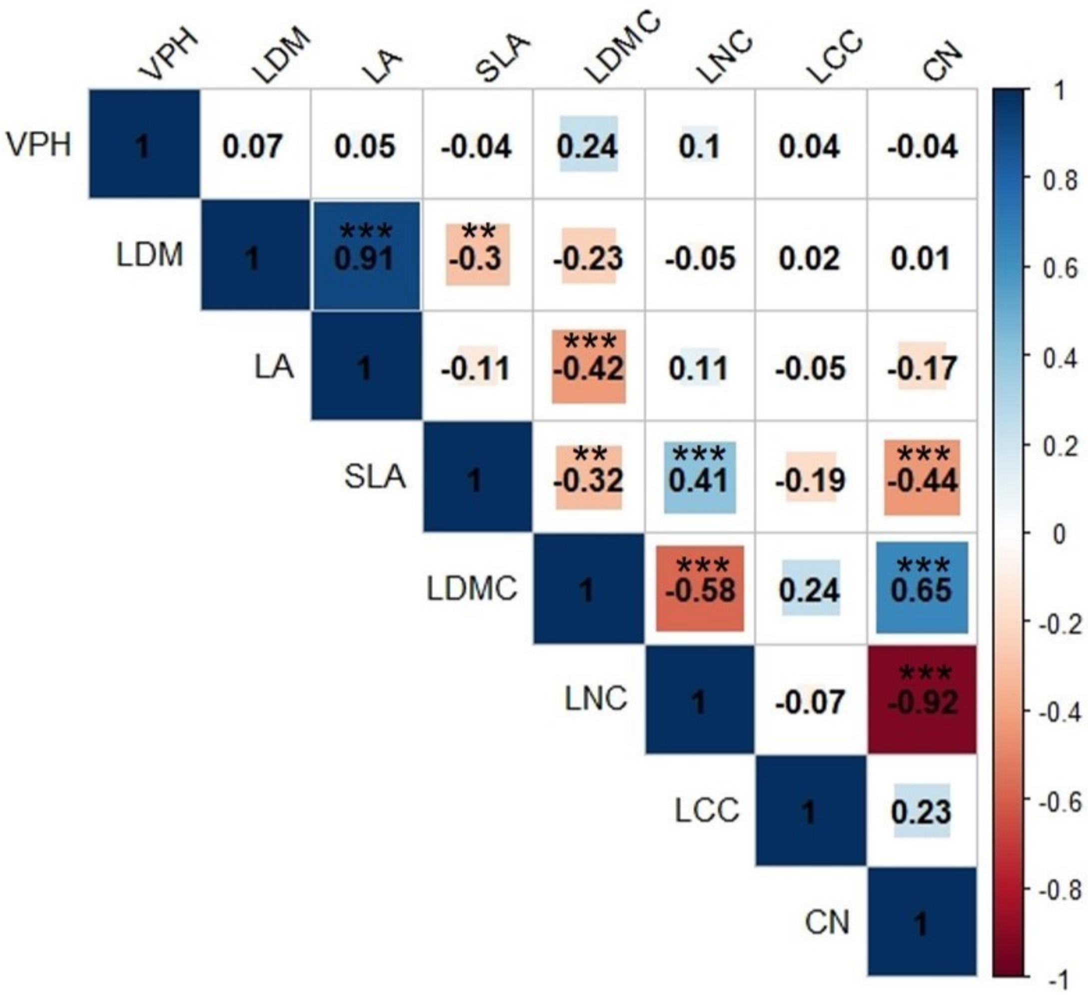
Source of variation	df	Pillai	F	p
Grassland type	1	0.36	6.53	***
Residuals	99			

Source of variation		**VPH**		**LDM**		**LA**		**SLA**		**LDMC**		**LNC**		**LCC**		**C/N**	
	df	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p
Grassland type	1	1.57	ns	12.22	***	20.35	***	4.29	ns	0.03	ns	5.40	*	9.91	**	3.70	ns
Residuals	99																

Tab. S3: ANCOVA after model simplification for testing the effect of soil factors on functional traits (CWM) between dry and semi-dry grasslands. The CWMs of each functional trait (VPH, LDM, LA, SLA, LDMC, LNC, LCC, C/N; abbreviations cf. Tab. 1) represent the response variables, while the soil factors (SO, pH, $CaCO_3$, N, C, C/N; abbreviations cf. Fig. 3) and the grassland type (dry and semi-dry) were the fixed factors. Degrees of freedom (df) and error probabilities (* $0.01 \le p < 0.05$, ** $0.001 \le p < 0.1$, *** $p < 0.001$, ns = not significant).

Source of variation	**VPH**		**LDM**		**LA**		**SLA**		**LDMC**		**LNC**		**LCC**		**C/N**	
	df	p	df	p	df	p	df	p	df	p	df	p	df	p	df	p
1) Influence of soil depth on CWM																
Intercept	1	***	1	***	1	***	1	***	1	***	1	***	1	***	1	***
SO	1	***	1	***	1	***	1	ns	1	***	1	ns	1	ns	1	ns
grassland	1	ns	1	*	1	**	1	ns	1	ns	1	*	1	*	1	ns
SO x grassland																
Residuals	98		98		98		98		98		98		98		98	
2) Influence of pH-value on CWM																
Intercept	1	**	1	ns	1	*	1	***	1	***	1	ns	1	***	1	***

pH	1	ns	1	ns	1	ns	1	*	1	ns	1	ns	1	ns	1	ns
grassland	1	ns	1	***	1	***	1	***	1	ns	1	*	1	**	1	ns
pH x grassland							1	***								
Residuals	98		98		98		97		98		98		98		98	
3) Influence of $CaCO_3$ on CWM																
Intercept	1	***	1	***	1	***	1	***	1	***	1	***	1	***	1	***
$CaCO_3$	1	*	1	**	1	**	1	ns	1	*	1	*	1	ns	1	*
grassland	1	ns	1	ns	1	**	1	ns	1	ns	1	ns	1	*	1	ns
$CaCO_3$ x grassland			1	*	1	*	1	*	1	*						
Residuals	98		97		97		97		97		98		98		98	
4) Influence of soil N on CWM																
Intercept	1	***	1	***	1	***	1	***	1	***	1	***	1	***	1	***
N	1	ns	1	**	1	*	1	ns	1	*	1	ns	1	ns	1	ns
grassland	1	ns	1	***	1	***	1	*	1	ns	1	*	1	**	1	ns
N x grassland																
Residuals	98		98		98		98		98		98		98		98	
5) Influence of soil C on CWM																
Intercept	1	***	1	***	1	***	1	***	1	***	1	***	1	***	1	***
C	1	ns	1	**	1	**	1	ns	1	***	1	ns	1	*	1	ns
grassland	1	ns	1	***	1	***	1	ns	1	ns	1	*	1	**	1	ns
C x grassland																
Residuals	98		98		98		98		98		98		98		98	
6) Influence of soil C/N on CWM																
Intercept	1	***	1	***	1	***	1	***	1	***	1	ns	1	***	1	***
C/N	1	***	1	**	1	**	1	ns	1	***	1	ns	1	**	1	ns
grassland	1	ns	1	*	1	**	1	ns	1	*	1	ns	1	ns	1	ns
C/N x grassland									1	*						
Residuals	98		98		98		98		97		98		98		98	



	VPH	LDM	LA	SLA	LDMC	LNC	LCC	CN
VPH	1	0.07	0.05	-0.04	0.24	0.1	0.04	-0.04
LDM		1	*** 0.91	** -0.3	-0.23	-0.05	0.02	0.01
LA			1	-0.11	*** -0.42	0.11	-0.05	-0.17
SLA				1	** -0.32	*** 0.41	-0.19	*** -0.44
LDMC					1	*** -0.58	0.24	*** 0.65
LNC						1	-0.07	*** -0.92
LCC							1	0.23
CN								1

Fig. S1: Correlation matrix of pairwise correlations of all functional traits (VPH, LDM, LA, SLA, LDMC, LNC, LCC, C/N; abbreviations cf. Tab. 1). Calculation was done across the most common species of the dry and semi-dry grasslands (see Tab. S1). Correlation coefficients (range from -1 to 1) and error probabilities (** $0.001 \leq p < 0.1$, *** $p < 0.001$). Colours are used to visualise a positive (blue colours) or negative (red colours) correlation, and the size of the squares indicate the strength of the correlation.

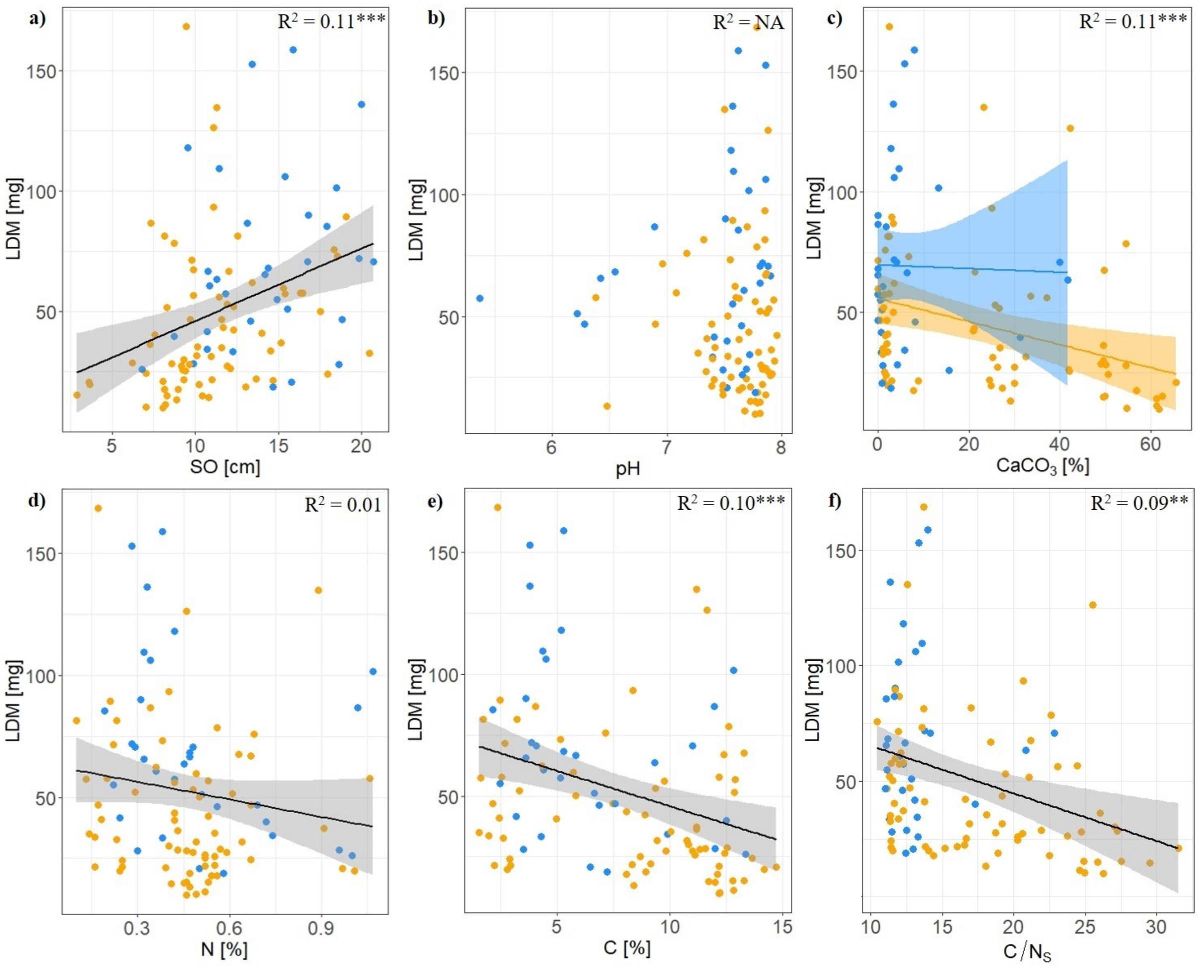


Fig. S2: Relationships between the community weighted mean of the leaf dry mass (LDM) of dry (orange colour) and semi-dry grasslands (blue colour) to soil factors: a) SO, b) pH, c) CaCO$_3$, d) N, e) C, f) C/N$_s$ (abbreviations cf. Fig. 4). Adjusted R^2 and significance are given (** $0.001 \leq p < 0.1$, *** $0.001 < p$, NA – not available). Visualisation based on the results of the ANCOVAs (cf. Tab. S3) as follows: significant interaction effect: two regression lines with 95% confidence level; significant main effect, but no interaction effect: one regression line with 95% confidence level; no significant main effect and interaction effect: without regression line.

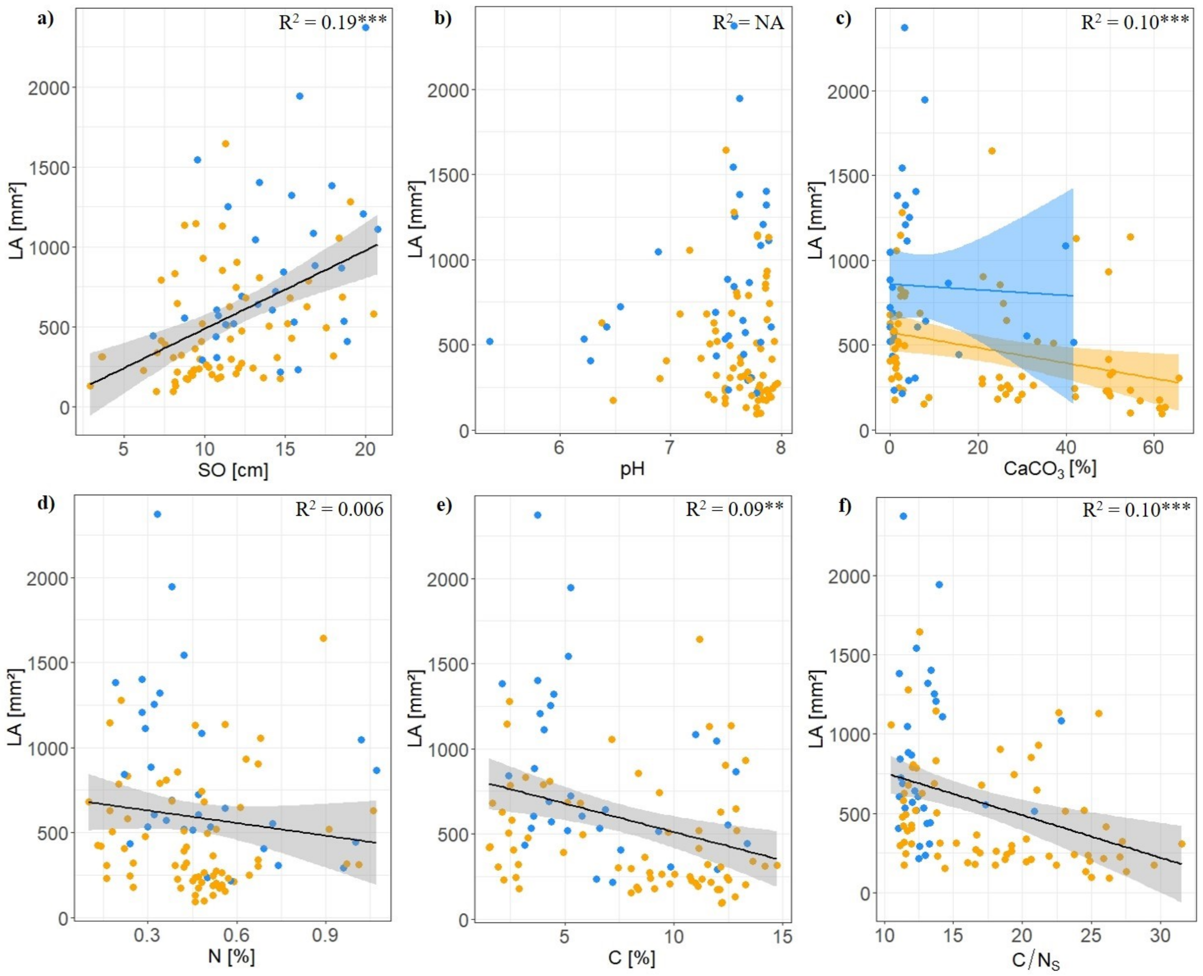


Fig. S3: Relationships between the community weighted mean of the leaf area (LA) of dry (orange colour) and semi-dry grasslands (blue colour) to soil factors: a) SO, b) pH, c) $CaCO_3$, d) N, e) C, f) C/N_s (abbreviations cf. Fig. 4). Adjusted R^2 and significance are given (** $0.001 \leq p < 0.1$, *** $0.001 < p$, NA – not available). Visualisation based on the results of the ANCOVAs (cf. Tab. S3) as follows: significant interaction effect: two regression lines with 95% confidence level; significant main effect, but no interaction effect: one regression line with 95% confidence level; no significant main effect and interaction effect: without regression line.

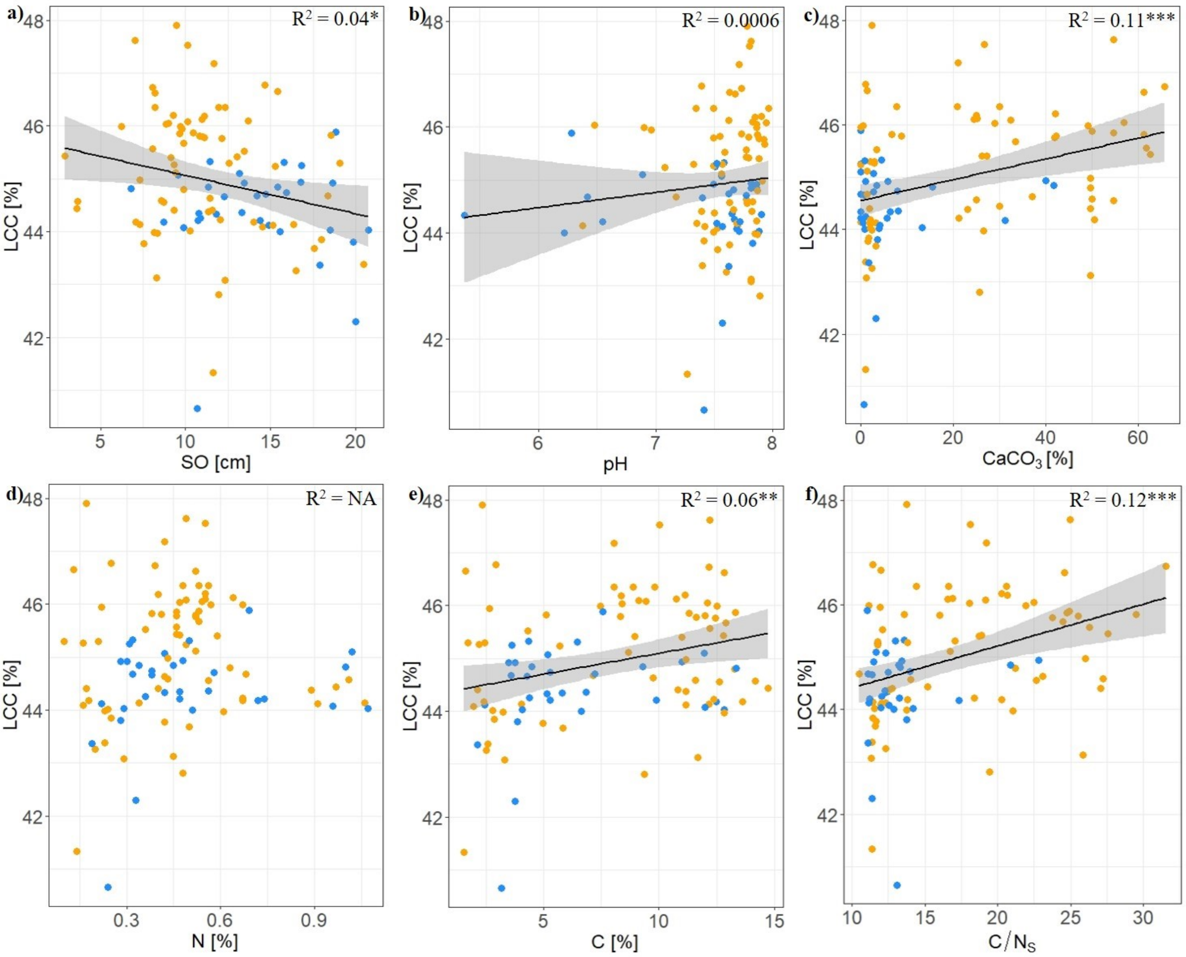
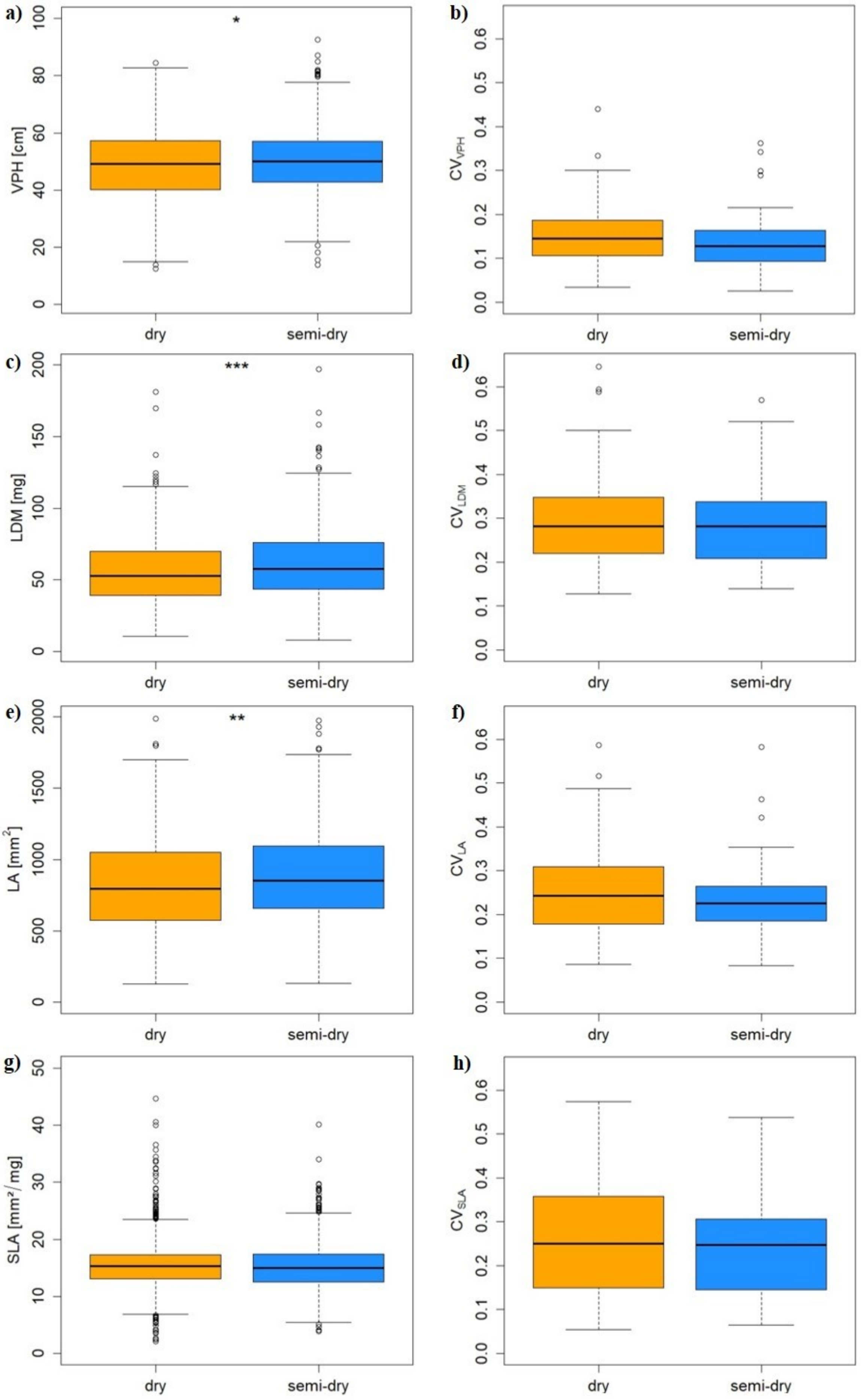


Fig. S4: Relationships between the community weighted mean of the leaf carbon concentration (LCC) of dry (orange colour) and semi-dry grasslands (blue colour) to soil factors: a) SO, b) pH, c) $CaCO_3$, d) N, e) C, f) C/N_s (abbreviations cf. Fig. 4). Adjusted R^2 and significance are given (* $0.01 \leq p < 0.05$, ** $0.001 \leq p < 0.1$, *** $0.001 < p$, NA – not available). Visualisation based on the results of the ANCOVAs (cf. Tab. S3) as follows: significant main effect, but no interaction effect: one regression line with 95% confidence level; no significant main effect and interaction effect: without regression line.


a)
VPH [cm]
0
20
40
60
80
100
*
dry
semi-dry
b)
CV$_{VPH}$
0.0
0.1
0.2
0.3
0.4
0.5
0.6
dry
semi-dry
c)
LDM [mg]
0
50
100
150
200
***
dry
semi-dry
d)
CV$_{LDM}$
0.0
0.1
0.2
0.3
0.4
0.5
0.6
dry
semi-dry
e)
LA [mm^2]
0
500
1000
1500
2000
**
dry
semi-dry
f)
CV$_{LA}$
0.0
0.1
0.2
0.3
0.4
0.5
0.6
dry
semi-dry
g)
SLA [mm²/mg]
0
10
20
30
40
50
dry
semi-dry
h)
CV$_{SLA}$
0.0
0.1
0.2
0.3
0.4
0.5
0.6
dry
semi-dry

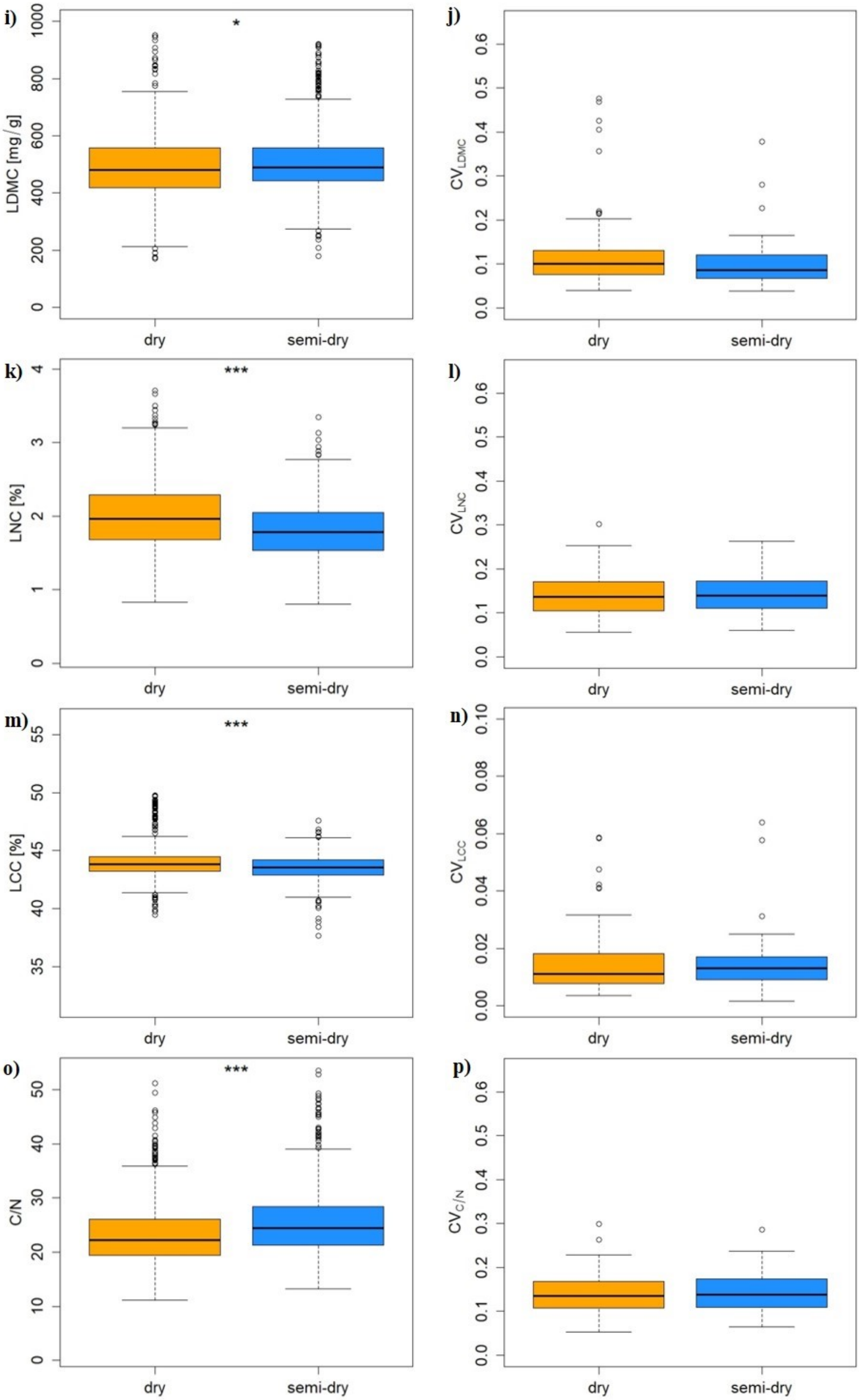

i)
LDMC [mg/g]
0
200
400
600
800
1000
*
dry
semi-dry
j)
CV_{LDMC}
0.0
0.1
0.2
0.3
0.4
0.5
0.6
dry
semi-dry
k)
LNC [%]
0
1
2
3
4
***
dry
semi-dry
l)
CV_{LNC}
0.0
0.1
0.2
0.3
0.4
0.5
0.6
dry
semi-dry
m)
LCC [%]
35
40
45
50
55
***
dry
semi-dry
n)
CV_{LCC}
0.00
0.02
0.04
0.06
0.08
0.10
dry
semi-dry
o)
C/N
0
10
20
30
40
50
***
dry
semi-dry
p)
$CV_{C/N}$
0.0
0.1
0.2
0.3
0.4
0.5
0.6
dry
semi-dry

Fig. S5: Functional traits and their coefficient of variation (CV) of *Bromus erectus* within dry and semi-dry grasslands: a) VPH, b) CV_{VPH}, c) LDM, d) CV_{LDM}, e) LA, f) CV_{LA}, g) SLA, h) CV_{SLA}, i) LDMC, j) CV_{LDMC}, k) LNC, l) CV_{LNC}, m) LCC, n) CV_{LCC}, o) C/N, p) $CV_{C/N}$ (abbreviations cf. Tab. 1). Results of the t-test: * $0.01 \leq p < 0.05$, ** $0.001 \leq p < 0.01$, *** $p < 0.001$.

Chapter 5

Effects of nitrogen addition and above-ground biomass removal on the growth and interactions between species of xerothermic grasses

Tim Meier, Isabell Hensen, Monika Partzsch

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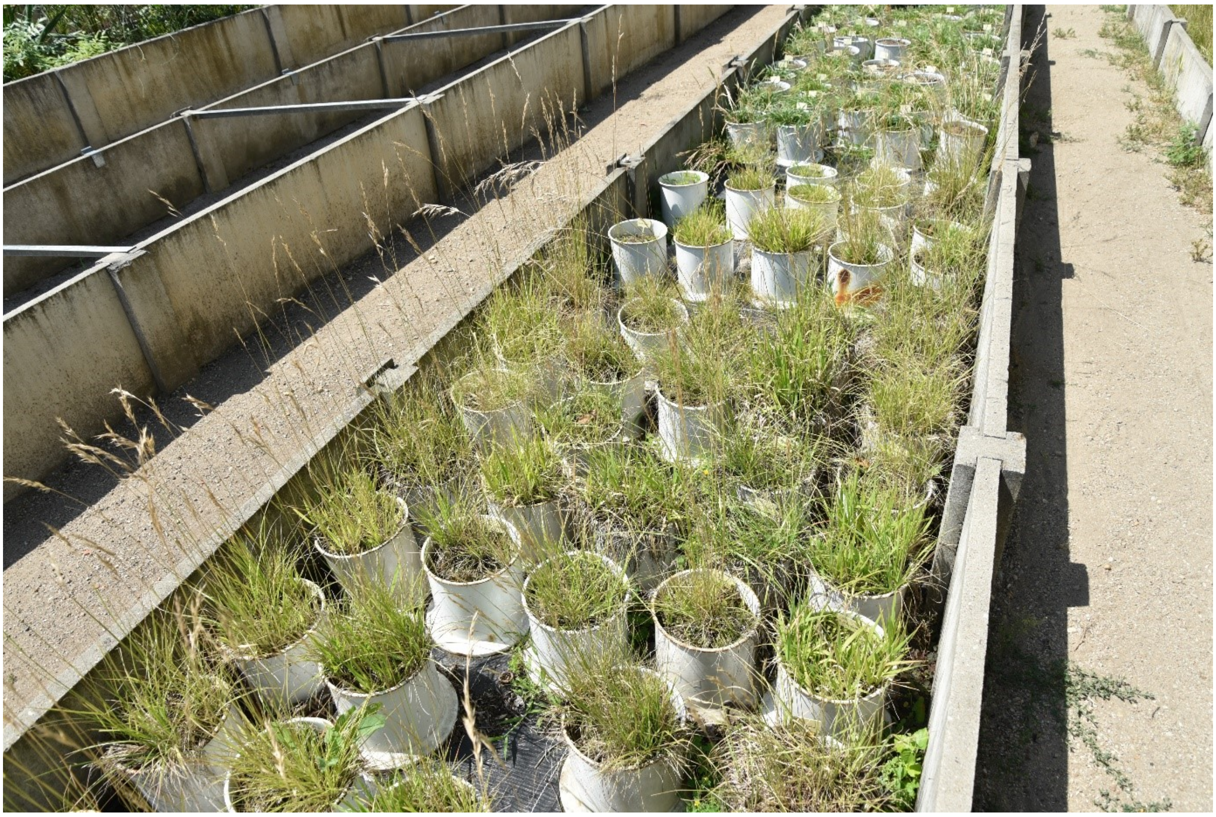

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Preslia

Effects of nitrogen addition and above-ground biomass removal on the growth and interactions between species of xerothermic grasses

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Abstract: Aspects of global change, such as increasing atmospheric nitrogen deposition and changes in land use, promote the increasing dominance of grass in xerothermic grasslands. It is assumed that nutrient addition and land use affect interactions between the expanding *Bromus erectus* and other co-occurring xerothermic species of grass in central Germany. The plant-plant interactions are key factors in the regulation of species composition, productivity, structure and dynamics of plant communities as well as the functioning of ecosystems. A competition experiment between *B. erectus* and the grasses *Brachypodium pinnatum*, *Stipa capillata* and *Stipa tirsa* was carried out using a replacement design, with species cultivated at two densities (9 individuals or 1 individual per pot) and three different species compositions of nine plants in monoculture and mixtures (6:3, 3:6), to study the effect of *B. erectus* on the other three grasses. Treatments included nutrient addition (nutrient-poor vs. nutrient-rich) and above-ground biomass removal (unclipped vs. clipped). Over two consecutive years, each species' growth was documented by measuring both vegetative traits (i.e. above-ground biomass, plant height, specific leaf area (SLA), leaf nitrogen concentration (LNC)) and generative traits (panicle length, number of inflorescences, seed mass). Plant-plant interactions were assessed by calculating the Relative Interaction Index (RII). *Bromus erectus* increases at the detriment of the other three species because of its highest biomass production when nutrients are added. When *B. erectus* was grown alone, biomass production significantly increased when nutrients were added. The effect of intraspecific competition in *B. erectus* was slightly more intensive than interspecific competition, in contrast to the other grasses. Also, *B. erectus* was dominant when nutrients were added, but less so when clipped. As a result, the growth and competitive ability of *B. erectus* affected *S. capillata* and *S. tirsa* more negatively than *B. pinnatum*, which can result an increasing dominance of *B. erectus* under future increasing nitrogen enrichment, leading to displacement of the two rare species of *Stipa*.

Keywords: *Bromus erectus*, *Brachypodium pinnatum*, clipping, functional traits, land-use change, nitrogen addition, growth performance, plant-plant interaction, Relative Interaction Index, *Stipa capillata*, *Stipa tirsa*

Introduction

Global change in terms of deposition of atmospheric nitrogen and changes in land use can affect species richness in xerothermic grasslands (Bobbink et al. 2010, Duprè et al. 2010, Diekmann et al. 2014, Hülber et al. 2017, Kübert et al. 2019). For such grasslands, critical

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nitrogen loads range between 14 and 25 kg/ha per year (de Jong et al. 1998) and nitrogen uptake by plants is likely to decline due water stress associated with drought (Homyak et al. 2017), resulting in an increase in plant mortality (Kübert et al. 2019). Human-caused eutrophication has led to changes in nutrient and water cycling and soil conditions (Perring et al. 2018), destabilized primary production in grasslands (Bharath et al. 2020) and losses of typical species of xerothermic grassland in recent decades (Bruelheide et al. 2020), all of which point to changes in the interactions between grass species (Mariotte et al. 2013). In contrast, nitrogen over-fertilization can result in certain grass species becoming dominant (de Malach et al. 2017, Wang et al. 2021) and promote their above-ground biomass production (Bai et al. 2015). Grasses have the competitive advantage of being able to use available nitrogen more efficiently (Hautier et al. 2009, Stevens & Gowing 2014) and produce a lot of litter (Foster & Gross 1998), which inhibits the growth of smaller species along with reducing the amount of light that reaches ground level (Hegedušová & Senko 2011, Ridding et al. 2020). Thus, an increase in the amount of litter can strongly inhibit seed germination and seedling survival (Donath & Eckstein 2010).

In addition to nitrogen input, changes in traditional land use (e.g. grazing by sheep and goats, annual or biennial mowing in order to prevent encroachment by shrubs) may have an adverse effect on the biodiversity of xerothermic grassland and promote the dominance of certain grass species (Bobbink et al. 2010, Diekmann et al. 2014, 2019, Elias et al. 2018, Bohner et al. 2019, Lemmer et al. 2021). Grasses produce more biomass in xerothermic grasslands than dicotyledonous plants (Del-Val & Crawley 2005, Partzsch et al. 2018) and following changes in land use, their increase has resulted in the conversion of previously species-rich to species-poor grassland communities (Partzsch 2000, Wesche et al. 2012, Rupprecht et al. 2016). Selective defoliation caused by traditional land use induces grasses to produce compensatory growth and partially or completely replace all the lost biomass (Agrawal 2000, Stevens & Gowing 2014). Moreover, the timing of grazing can have an important effect on the competitive ability of grasses, since e.g. with extensive late summer grazing, competitive grasses are less likely to be grazed due to their reduced nutritional value (Dostálek & Frantík 2012, Hejcmanová et al. 2016).

Over the last few centuries, there has been an increase in the dominance of grasses such as *Bromus erectus*, *Brachypodium pinnatum*, *Festuca rupicola*, *Helictotrichon pratense* and species of *Stipa* in xerothermic grasslands (Bobbink et al. 1998, Bornkamm 2006, 2008, Meier & Partzsch 2018, Meier et al. 2021), which seems to be a global phenomenon (Chýlová & Münzbergová 2008). In central Germany, within the last two decades the presence of *B. erectus* has significantly increased and its cover in dry and semi-dry grasslands has tripled, while that of *B. pinnatum* and *S. capillata* has remained constant (Meier et al. 2021). These grasses have a longer lifespan than others and are therefore more resistant to environmental changes, and have a competitive and stress-tolerant strategy type (CS) (Grime 2001). Furthermore, *B. erectus*, *B. pinnatum* and species of *Stipa* often occur together in xerothermic grasslands (Bieringer & Sauberer 2001, Meier & Partzsch 2018, Meier et al. 2021) and have been the subject of various experiments on plant-plant interactions, e.g. under nitrogen addition, drought and changes in land use (Corcket et al. 2003, Wang et al. 2021).

Plant-plant interactions can be both positive in the sense of facilitation and negative in the sense of competition between individuals of one species (intraspecific) or individuals of different species (interspecific) (Callaway & Walker 1997, Brooker et al. 2008, Freckleton et al. 2009, Thorpe et al. 2011, Dohn et al. 2013, Liancourt & Doležal 2021). These interactions depend on environmental conditions and species-specific plant traits (Callaway & Walker 1997, Holmgren et al. 1997, Callaway 2007, Seifan et al. 2010) and are important factors determining the regulation of species composition, productivity, structure and dynamics of plant communities and function of ecosystems (Brooker 2006, Thorpe et al. 2011, Le Bagousse-Pinguet et al. 2014, Tredennick et al. 2018). Also, commonness and status of the plants play an important role. So, rare native plants are less competitive than non-native plants or common native plants (Zhang & van Kleunen 2019). Functional traits such as plant height, specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen concentration (LNC) and seed mass are linked to resource use and competitiveness of plants (Reich 2014, Garnier et al. 2016). However, there are no reports of the interactions between xerothermic species of grass in combination with nutrient supply and above-ground biomass removal and previous studies on the competitive ability of *B. erectus* are rather limited to long-term observations (Bornkamm 1961, 1974, 2006).

The aim of this study is therefore to determine whether *B. erectus*, in particular, becomes more competitive when grown with other species of xerothermic grass when nutrients are added and traditional land use decreases, such as grazing or mowing. Such effects could result in changes in dominance ratios and eventually to a decline in species diversity in xerothermic plant communities, especially since *B. erectus* and species of *Stipa* (e.g. *S. capillata*, *S. tirsa*) are relatively similar in their functional traits, so that competitive exclusion can occur if abiotic conditions change (Meier et al. 2019). In the present study, clipping experiments were used to study the effects of land use on grasses, where the above-ground biomass of a plant is trimmed to stubble height (Kimball & Schiffman 2003), but excluding the influence of livestock trampling and excrement (Li et al. 2015). In order to investigate growth and interactions between *B. erectus* and the grasses *B. pinnatum*, *S. capillata* and *S. tirsa*, we simulated nutrient addition and clipping in a replacement design competition experiment (de Wit 1960) and measured several functional traits.

The objective of this study was to answer the following questions: (i) How do the vegetative traits of *B. erectus* and the other three grasses differ in the nutrient conditions and clipping treatments? (ii) Do the generative traits of *B. erectus* differ in monoculture and mixtures subject to different nutrient conditions and clipping treatments? (iii) How does *B. erectus* interact with the other three grasses when subjected to different nutrient conditions and clipping treatments?

Materials and methods

Study species

Bromus erectus Huds. (*Poaceae*) is a 30–90 cm tall perennial hemicryptophyte that produces tussocks with slightly ciliate leaf blades and 10–25 cm long panicles (Jäger 2017). The average specific leaf area is 165.7 cm^2/g (Splith et al. 2021), while mean seed mass is 4.4 mg and seed length about 10.9 mm (Klotz et al. 2002).

Brachypodium pinnatum (L.) P. Beauv. (*Poaceae*) is a perennial hemicryptophyte with a creeping rhizome. It is 60–100 cm tall and has 4–25 cm long inflorescences that are always upright (Jäger 2017) and a mean seed mass of 3.8 mg and seed length of 9.8 mm (Klotz et al. 2002). The specific leaf area is about 183.7 cm^2/g (T. Meier, unpubl. data).

Stipa capillata L. and *S. tirsa* Steven (*Poaceae*) are deciduous, perennial hemicryptophytes that produces tussocks and reach a height of 30–100 cm. *Stipa capillata* usually has folded leaf blades, while *S. tirsa* has very thin, thread-like and always folded leaf blades that extend into a long bristle-shaped tip. *Stipa capillata* is hairless, while *S. tirsa* has hairy feathered awns up to 50 cm long that form on caryopses (Jäger 2017). Whereas *S. capillata* has a mean seed mass of 9.6 mg and seed length of 11.4 mm, *S. tirsa* has a mean seed mass of 17.8 mg and seed length of 17.4 mm. Their specific leaf areas varied between 72.5 cm^2/g and 63 cm^2/g (T. Meier, unpubl. data). There are slight local differences in the occurrence of these two species (Meier & Partzsch 2018).

Competition experiment

To study the effect of *B. erectus* on *B. pinnatum* as well as *S. capillata* and *S. tirsa* we used a replacement design wherein the proportion of species within mixtures was varied maintaining a constant density throughout (de Wit 1960). In this experiment, addition of nutrients and above-ground removal were simulated. In summer 2017, we collected mature seeds of the target species from different populations in xerothermic grasslands in Saxony-Anhalt, Germany. The seeds were pooled and the seeds of *S. capillata* and *S. tirsa* were cold-stratified for 10 days to break dormancy (as reported for other species of *Stipa* (Ronnenberg et al. 2008)). In October 2017, seeds of all these grass species were sown in plastic pots containing a compost-sand mixture (3:2, pH value 7.0) and cultivated in a greenhouse.

In April 2018, juvenile plants at the stage of the first primary leaves were transferred to Mitscherlich-pots (diameter 22 cm; height 19 cm) filled with the same substrate (the soil was pretreated with steam to preclude the emergence of other seedlings). All pots were placed outdoors in the Botanical Garden of Halle (Saale). The plants were planted at two density levels of either 9 individuals per pot or 1 individual per pot and in three different species compositions for the 9 plants per pot: monoculture or two mixtures with either a ratio of 6:3 or 3:6. The plants were arranged in three rows of three per pot (plants of the same species placed in one horizontal row). Within the mixtures, the proportion of the two species varied, with the less abundant species being placed in the middle row. In addition, single individuals of each species were planted in order to calculate the plant-plant interaction indices. All monocultures, mixtures and single individuals were grown with and without additional nutrients. Unfertilized pots simulated nutrient-poor conditions, while fertilized pots simulated nutrient-rich conditions by adding 1 g (per pot) of NPK (nitrogen, phosphorus, potassium) slow-release granule fertilizer (Basacote Plus 9M, 15% N, manufactured by COMPO GmbH & KG, Münster, Germany).

The following 14 density-composition levels were used: (i) monocultures: Be9 (*B. erectus*, 9 individuals), Bp9 (*B. pinnatum*, 9 individuals), Sc9 (*S. capillata*, 9 individuals), St9 (*S. tirsa*, 9 individuals); (ii) mixtures: Be6Bp3 (*B. erectus*, 6 individuals and *B. pinnatum*, 3 individuals), Be3Bp6 (*B. erectus*, 3 individuals and *B. pinnatum*, 6 individuals), Be6Sc3 (*B. erectus*, 6 individuals and *S. capillata*, 3 individuals), Be3Sc6 (*B. erectus*, 3 individuals and *S. capillata*, 6 individuals), Be6St3 (*B. erectus*, 6 individuals and *S. tirsa*, 3 individuals), Be3St6 (*B. erectus*, 3 individuals and *S. tirsa*, 6 individuals);

(iii) low-density level: Be1 (*B. erectus*, 1 individual), Bp1 (*B. pinnatum*, 1 individual), Sc1 (*S. capillata*, 1 individual), St1 (*S. tirsa*, 1 individual). Each density-composition level was replicated 16-times (448 pots: 224 unfertilized, 224 fertilized; total of 3008 individuals) and all pots were located randomly, with their positions changed every 2–3 weeks throughout the vegetation period. The plants in the pots were watered as required and any weeds removed.

In July 2018, the following growth and fitness traits were measured per individual: plant height [cm], leaf area [mm^2], leaf dry mass [mg], SLA [$mm^2 \cdot mg^{-1}$], LDMC [$mg \cdot g^{-1}$], leaf carbon concentration (LCC) [%], leaf nitrogen concentration (LNC) [%] and C/N ratio. These traits were quick and easy to measure and are closely linked to resource utilization and competitiveness (Garnier et al. 2016). Plant height was measured as the distance between the highest photosynthetic organ and the base of the plant (Weiher et al. 1999); thus, inflorescences were not considered. One well-developed leaf of each individual per pot was taken and kept moist in plastic bags with water and stored in a cool box for further analysis (Pérez-Harguindeguy et al. 2013). In the laboratory, the leaves were then scanned (resolution: 300 dpi) and their areas analysed using the program WinFOLIA Pro (S). They were weighed, then dried at 80 °C for 24 h and weighed again to determine their leaf dry mass. The data were used to calculate SLA (ratio between leaf area and leaf dry mass) and LDMC (ratio between leaf dry mass and water-saturated fresh mass of the leaf). Afterwards, the leaf samples were milled (Vibratory Mill MM 400, Retsch GmbH) and transferred to a C/N analyser (vario EL cube, Elementar Analysensysteme GmbH). Only mixed leaf samples were examined, i.e. one sample for each species per pot (monocultures: one sample, mixtures: two samples). As a result, LCC and LNC can be determined and the C/N ratio analysed.

Subsequently (end of July 2018), to simulate above-ground removal, plants from eight replications of each nutrient condition per density-composition level were clipped (clipping time for nutrient-poor grasslands at the beginning of July or later; Briemle 2004). The individuals were clipped at 3–5 cm above the soil surface to avoid any damage to the meristem (standard cutting height of 5 cm in agriculture; lower cutting height possible for grasses; Löbbert 1998). The above-ground biomass [g] was dried at 80 °C for 24 h and then weighed. As a control, the plants from the other eight replications of each nutrient condition per density level remained unclipped. Therefore, the following four treatments (112 pots per treatment) of the 14 density-composition levels were carried out: (i) unclipped, no fertilizer; (ii) unclipped, with fertilizer; (iii) clipped, no fertilizer; (iv) clipped, with fertilizer. One year later, in July 2019 (without further application of fertilizer and clipping), the same parameters were recorded and, additionally for *B. erectus*, the generative traits per individual: panicle length [cm], number of inflorescences [n] and seed mass [mg]. To determine the seed mass, 10 seeds were taken from each individual, weighed separately and the mean value calculated. After the end of the experiment (end of July 2019), the above-ground biomass produced in all treatments (unclipped and clipped) was harvested (biomass in the second year was cut at the same level as in half of the pots in the first year) and dry weighed. The experiment was run over two consecutive years, as the combined effects of nutrient addition and clipping could only be investigated in the second year and growth performance and plant-plant interactions can change over time (Kikvidze et al. 2006).

Data analysis

In order to assess plant-plant interactions between the xerothermic grasses, the Relative Interaction Index (RII) was calculated (Armas et al. 2004): RII = $(P_{+N} - P_{-N}) / (P_{+N} + P_{-N})$. P_{+N} is the performance of a target plant in the presence of neighbouring plants (≙ individuals of the monocultures or mixtures), while P_{-N} is the performance of a target plant in the absence of neighbouring plants (≙ single individual (low-density level); data shown in Supplementary Table S1). The RII values are in the range –1 to +1; positive values correspond to facilitation and negative values to competition. We only calculated the RII for above-ground biomass per individual as a measure of growth performance.

All the plant parameters recorded were checked for normality and variance homogeneity (Crawley 2007) and transformed logarithmically for the subsequent analyses. With the help of the Bartlett test, it was confirmed that there were no serious deviations from the assumption of an analysis of variance (ANOVA). Using two-way ANOVA, it was possible to check for differences and interactions in the first-year growth performance between the three species compositions (9, 6:3, 3:6) and nutrient conditions (without nutrients (N–) and with nutrients (N+)). Three-way ANOVA were carried out to determine differences and interactions in the second-year growth performance between species compositions, nutrient conditions and clipping treatments (unclipped and clipped). Finally, for all grasses, a general comparison was performed between the two nutrient conditions, comparing the biomass of single individuals (without interaction), and plant interactions (intraspecific = species composition in monocultures (9); interspecific = species composition in mixtures (6:3, 3:6)) using RII. Therefore, first- and second-year above-ground biomass data were pooled without differentiating between clipped and unclipped treatments in the second year, while species compositions (6:3, 3:6) were pooled for interspecific interactions. Mean values of species above-ground biomass were compared between nutrient-poor and nutrient-rich conditions using pairwise t-tests (single individuals) or two-way ANOVA with subsequent Tukey post-hoc tests (plant interactions). The various plant parameters are the dependent variables. The different species compositions and nutrient conditions as well as effects of clipping (second year) were treated as independent variables. The probability of error (P) of the independent variables was checked using an F-test, where $P < 0.05$ was considered significant. Statistical analyses were performed using R 3.6.0 (R Core Team 2019).

Results

Vegetative performance of plants

Generally, the biomass of *B. erectus* was greater in monocultures and mixtures than that of the other three species of grass in the first and second year. In the second year, there were significant differences recorded for *B. erectus* in the clipping treatment, nutrient condition and species composition (exception: mixtures with *B. pinnatum*) (Fig. 1, Table 1). In mixtures with *S. capillata* and *S. tirsa*, *B. erectus* had the significantly highest increase in biomass in the nutrient addition and unclipped treatments Be3Sc6 and Be3St6. The biomass of *B. pinnatum* was significantly higher in the monoculture in the nutrient addition and unclipped treatments, whereas for *S. capillata* there were only significant differences

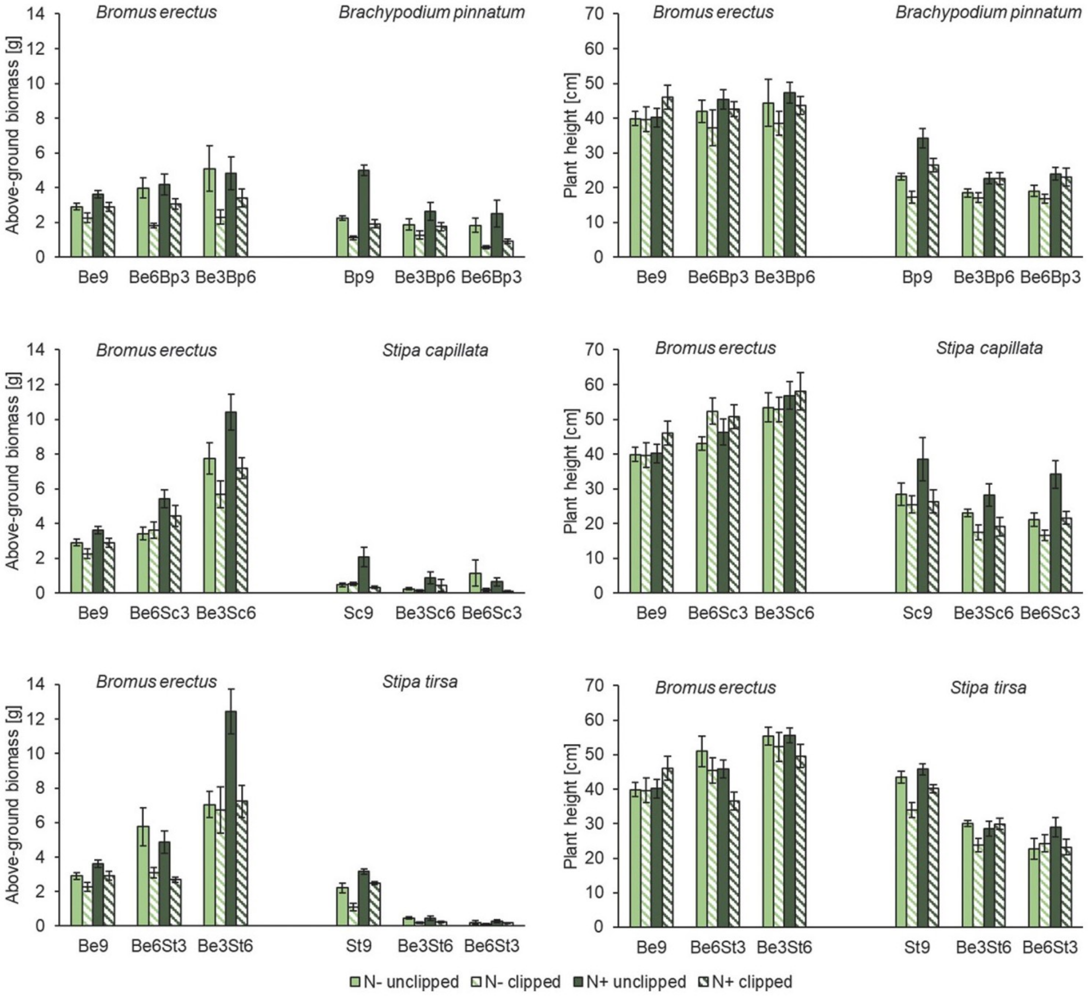

Fig. 1. Second-year performance in terms of the above-ground biomass (left) and plant height (right) per individual of *Bromus erectus* in combination with *Brachypodium pinnatum* (above), *Stipa capillata* (middle) and *S. tirsa* (below). The different coloured bars (mean+SE) represent the different species compositions (9, 6:3, 3:6) in the different combinations of nutrient conditions and clipping treatments. Using three-way ANOVA for testing mean differences (see Table 1).

between clipping treatment and species composition, Sc9 and Be3Sc6. The monocultures of *S. tirsa* produced a significantly higher biomass than the mixtures Be3St6 and Be6St3 in all nutrient conditions and clipping treatments. *Bromus erectus* reached the highest plant height in monoculture and mixtures. In Be3Bp6, *B. erectus* was significantly taller in the nutrient addition and unclipped treatments (Fig. 1, Table 1), while in mixtures with *S. capillata* and *S. tirsa*, it significantly increased in plant height with decrease in density in the pots. For the other three grasses, no significant differences resulting from the clipping, nutrient and species composition treatments were detected. The plants in monocultures Bp9, Sc9 and St9 were taller, especially in the nutrient addition and unclipped treatments. The SLA of *Brachypodium pinnatum* was higher than that of the other species and there were no significant differences in the SLAs of all the grasses, except for *B. erectus* in the mixture with *S. tirsa*, when its SLA was significantly higher in the nutrient and clipping treatments (Fig. 2, Table 1). The four grasses had a relatively similar LNCs, and

Table 1. Results of the three-way ANOVA of above-ground biomass, plant height, SLA, LNC and RII in the competition experiment: *Bromus erectus* in combination with (1) *Brachypodium pinnatum*, (2) *Stipa capillata* and (3) *S. tirsa* in the second year (clipping treatment: unclipped/clipped; nutrient condition: nutrient poor/nutrient rich; species composition: 9, 6:3, 3:6). Degrees of freedom (df), F-values and error probabilities (* $P < 0.05$, ** $P < 0.1$, *** $P < 0.001$) are given. Abbreviations: CT = clipping treatment; NC = nutrient condition; SC = species composition; E = error; ns = not significant.

Source of variation	Biomass [g]			Plant height [cm]			SLA [mm^2/mg]			LNC [%]			RII		
	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P
1. *B. erectus* in combination with *B. pinnatum*															
B. erectus															
CT	1	20.31	***	1	0.91	ns	1	2.57	ns	1	0.66	ns	1	22.16	***
NC	1	8.66	**	1	5.54	*	1	0.10	ns	1	2.13	ns	1	8.67	**
SC	2	0.67	ns	2	0.21	ns	2	0.45	ns	2	5.44	**	2	1.98	ns
CT × NC	1	2.39	ns	1	0.90	ns	1	3.92	ns	1	0.69	ns	1	46.77	***
CT × SC	2	0.69	ns	2	1.10	ns	2	0.75	ns	2	0.48	ns	2	0.87	ns
NC × SC	2	0.01	ns	2	0.13	ns	2	0.59	ns	2	0.79	ns	2	0.21	ns
CT × NC × SC	2	0.43	ns	2	0.18	ns	2	1.48	ns	2	1.24	ns	2	1.07	ns
E	84			84			83			83			84		
B. pinnatum															
CT	1	36.18	***	1	9.75	**	1	0.44	ns	1	1.81	ns	1	50.37	***
NC	1	12.36	***	1	42.38	***	1	3.16	ns	1	2.06	ns	1	61.21	***
SC	2	14.53	***	2	7.82	***	2	3.06	ns	2	2.21	ns	2	11.71	***
CT × NC	1	0.33	ns	1	0.45	ns	1	1.05	ns	1	0.92	ns	1	35.62	***
CT × SC	2	1.81	ns	2	2.66	ns	2	0.47	ns	2	0.27	ns	2	3.57	*
NC × SC	2	1.40	ns	2	1.28	ns	2	0.31	ns	2	0.76	ns	2	4.40	*
CT × NC × SC	2	1.00	ns	2	0.02	ns	2	3.20	*	2	3.52	*	2	2.40	ns
E	83			83			82			82			83		
2. *B. erectus* in combination with *S. capillata*															
B. erectus															
CT	1	13.81	***	1	2.42	ns	1	1.24	ns	1	2.17	ns	1	97.94	***
NC	1	21.43	***	1	1.74	ns	1	0.98	ns	1	0.04	ns	1	12.38	***
SC	2	78.53	***	2	15.27	***	2	1.42	ns	2	0.16	ns	2	65.70	***
CT × NC	1	0.36	ns	1	0.12	ns	1	1.32	ns	1	0.00	ns	1	40.05	***
CT × SC	2	1.41	ns	2	0.91	ns	2	1.12	ns	2	0.65	ns	2	2.18	ns
NC × SC	2	0.13	ns	2	0.25	ns	2	1.17	ns	2	0.07	ns	2	0.80	ns
CT × NC × SC	2	0.56	ns	2	0.69	ns	2	2.62	ns	2	4.13	*	2	2.14	ns
E	84			84			83			83			84		
S. capillata															
CT	1	11.06	**	1	14.93	***	1	0.44	ns	1	2.30	ns	1	21.84	***
NC	1	0.73	ns	1	6.45	**	1	0.21	ns	1	2.62	ns	1	5.77	**
SC	2	8.61	***	2	6.11	***	2	1.25	ns	2	4.56	*	2	8.25	***
CT × NC	1	3.32	ns	1	0.87	ns	1	0.37	ns	1	0.82	ns	1	2.26	ns
CT × SC	2	0.67	ns	2	0.40	ns	2	0.20	ns	2	1.13	ns	2	0.19	ns
NC × SC	2	0.05	ns	2	1.28	ns	2	1.12	ns	2	0.18	ns	2	0.55	ns
CT × NC × SC	2	0.24	ns	2	0.11	ns	2	0.66	ns	2	2.05	ns	2	0.58	ns
E	75			75			75			71			75		
3. *B. erectus* in combination with *S. tirsa*															
B. erectus															
CT	1	30.93	***	1	3.18	ns	1	8.29	**	1	0.05	ns	1	42.54	***
NC	1	5.54	*	1	0.53	ns	1	1.86	ns	1	1.92	ns	1	22.86	***
SC	2	74.16	***	2	14.10	***	2	0.37	ns	2	2.31	ns	2	56.67	***
CT × NC	1	0.77	ns	1	0.00	ns	1	2.69	ns	1	0.32	ns	1	23.78	***
CT × SC	2	1.55	ns	2	2.76	ns	2	0.84	ns	2	1.59	ns	2	4.99	**
NC × SC	2	4.47	*	2	2.79	ns	2	1.42	ns	2	0.57	ns	2	2.68	ns
CT × NC × SC	2	1.14	ns	2	1.04	ns	2	0.95	ns	2	4.35	*	2	0.07	ns
E	84			84			83			83			84		
S. tirsa															
CT	1	18.93	***	1	11.05	**	1	0.35	ns	1	5.13	*	1	4.67	*
NC	1	11.87	***	1	7.26	**	1	2.35	ns	1	15.77	***	1	660.91	***
SC	2	100.68	***	2	48.64	***	2	3.15	*	2	1.88	ns	2	308.83	***
CT × NC	1	1.06	ns	1	0.58	ns	1	0.12	ns	1	0.01	ns	1	0.00	ns
CT × SC	2	1.64	ns	2	1.06	ns	2	0.52	ns	2	1.04	ns	2	0.57	ns
NC × SC	2	2.29	ns	2	0.03	ns	2	2.39	ns	2	3.91	*	2	124.89	***
CT × NC × SC	2	0.68	ns	2	4.18	**	2	0.10	ns	2	7.59	**	2	1.65	ns
E	73			73			73			73			71		

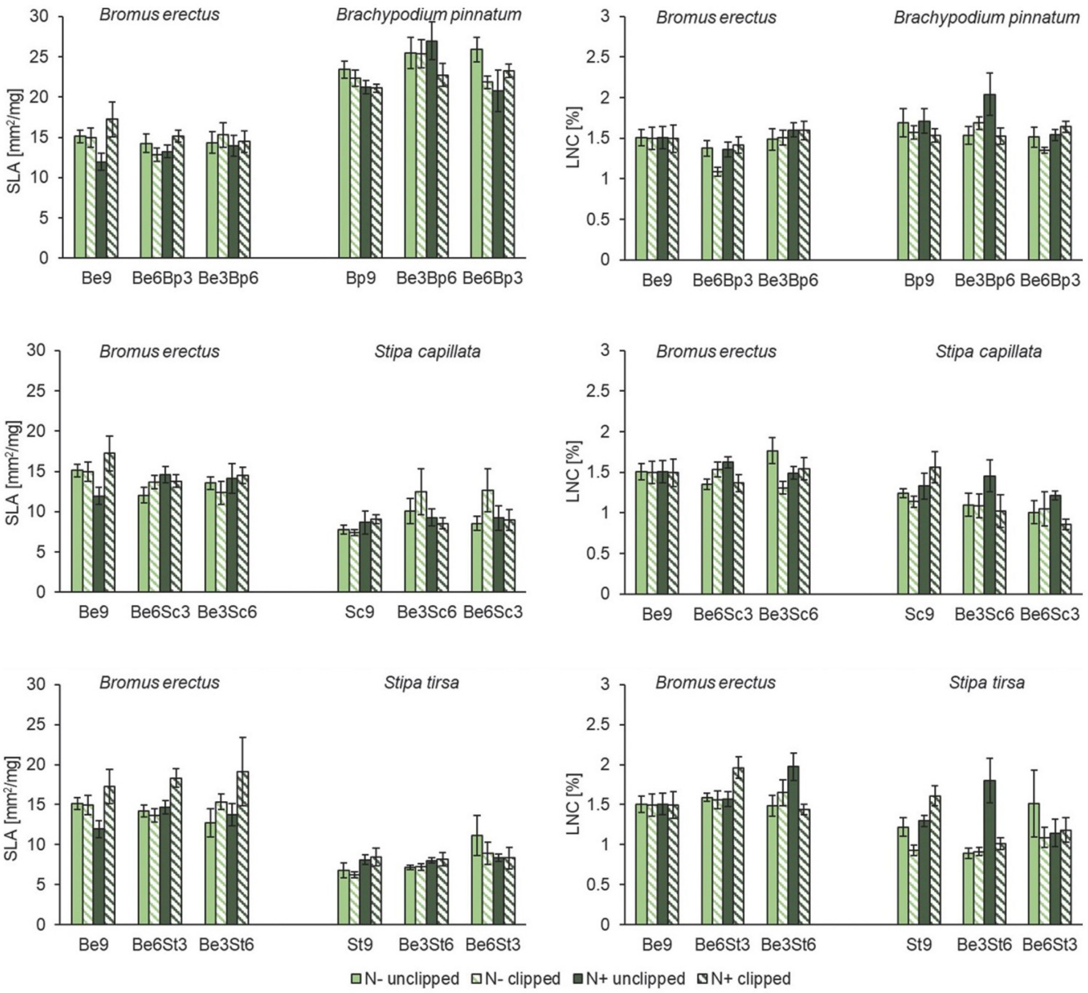

Fig. 2. Second-year performance in terms of SLA (left) and LNC (right) per individual of *Bromus erectus* in combination with *Brachypodium pinnatum* (above), *Stipa capillata* (middle) and *S. tirsa* (below). The different coloured bars (mean+SE) represent the species compositions (9, 6:3, 3:6) in the different combinations of nutrient conditions and clipping treatments. Using three-way ANOVA for testing mean differences (see Table 1).

significant differences were only recorded for *S. tirsa* in the nutrient and clipping treatments (Fig. 2, Table 1). Moreover, *B. erectus* and *B. pinnatum* had higher leaf areas and leaf dry masses than *S. capillata* and *S. tirsa* (Supplementary Fig. S1). Nevertheless, both species of *Stipa* had a higher LDMC and C/N ratio than *B. erectus* (Supplementary Fig. S2). For these grasses, significant differences in the C/N ratio between the monocultures and mixtures were detected (Supplementary Table S2). There were no pronounced differences in the effects of species composition and nitrogen addition recorded in the first and second year, so the results for the first year are shown in the supplement (Supplementary Fig. S3–S6, Supplementary Table S3, S4).

Generative performance of plants

Bromus erectus produced flowers in the second year, but the other three grasses did not. In general, the seed mass of *B. erectus* was highest in the monocultures in the clipped

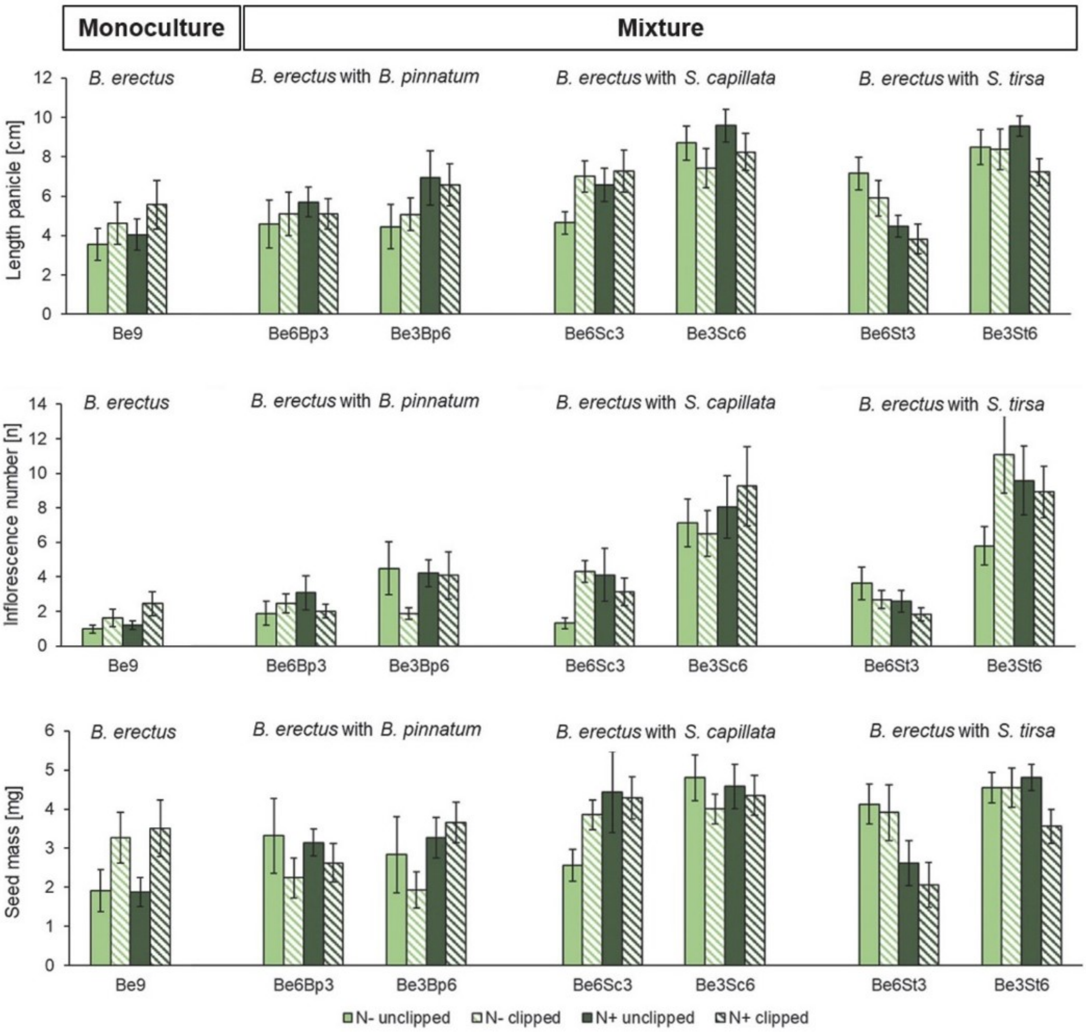

Fig. 3. Second-year performance in terms of panicle length (above), number of inflorescences (middle) and seed mass (below) per individual for the monoculture of *Bromus erectus* and in combination with *Brachypodium pinnatum*, *Stipa capillata* and *S. tirsa*. The different coloured bars represent the species compositions (9, 6:3, 3:6) in the different combinations of nutrient conditions and clipping treatments (mean+SE). Using three-way ANOVA for testing mean differences (see Table 2).

treatment, while the number of inflorescences increased significantly with decrease in the number of individuals of *B. erectus* in the pots (Fig. 3, Table 2). In the mixture with *B. pinnatum*, the only significant differences in the nutrient conditions were panicle length and seed mass associated with the interaction between clipping and species composition treatments. In contrast to the monoculture, panicle length and seed mass significantly increased in the mixtures Be3Sc6 and B3St6. Seed mass decreased significantly under nutrient addition in the mixture Be6St3 (interaction nutrient condition × species composition), especially when there were higher numbers of individuals of *B. erectus*.

Plant-plant interactions

The value of RII was significantly the lowest for the monoculture of *B. erectus* in the first year and nutrient addition resulted in a reduction in RII (Fig. 4, Supplementary Table S3).

Table 2. Results of the three-way ANOVA of the panicle length, number inflorescence and seed mass for *Bromus erectus* in the competition experiment: *B. erectus* in combination with (1) *Brachypodium pinnatum*, (2) *Stipa capillata* and (3) *S. tirsa* in the second year (clipping treatment: unclipped/clipped; nutrient condition: nutrient poor/ nutrient rich; species composition: 9, 6:3, 3:6). Degrees of freedom (df), F-values and error probabilities (* P < 0.05, ** P < 0.1, *** P < 0.001) are given. Abbreviations: CT = clipping treatment; NC = nutrient condition; SC = species composition; E = error; ns = not significant.

Source of variation	Panicle length [cm]			Inflorescence number [n]			Seed mass [mg]		
	df	F	P	df	F	P	df	F	P
1. *B. erectus* in combination with *B. pinnatum*									
CT	1	0.87	ns	1	0.07	ns	1	0.89	ns
NC	1	4.23	*	1	2.10	ns	1	3.14	ns
SC	2	2.02	ns	2	6.48	**	2	0.81	ns
CT × NC	1	0.71	ns	1	0.37	ns	1	0.00	ns
CT × SC	2	0.19	ns	2	1.11	ns	2	3.37	*
NC × SC	2	0.17	ns	2	0.04	ns	2	0.72	ns
CT × NC × SC	2	0.11	ns	2	0.90	ns	2	0.33	ns
E	84			84			74		
2. *B. erectus* in combination with *S. capillata*									
CT	1	0.75	ns	1	2.71	ns	1	5.09	*
NC	1	2.03	ns	1	1.17	ns	1	0.94	ns
SC	2	17.70	***	2	32.00	***	2	13.68	***
CT × NC	1	0.36	ns	1	1.12	ns	1	0.56	ns
CT × SC	2	1.48	ns	2	1.43	ns	2	3.07	ns
NC × SC	2	0.05	ns	2	0.06	ns	2	0.58	ns
CT × NC × SC	2	0.19	ns	2	1.18	ns	2	0.46	ns
E	84			84			81		
3. *B. erectus* in combination with *S. tirsa*									
CT	1	0.31	ns	1	0.55	ns	1	0.11	ns
NC	1	0.59	ns	1	0.02	ns	1	3.58	ns
SC	2	18.54	***	2	40.48	***	2	11.46	***
CT × NC	1	0.28	ns	1	0.57	ns	1	1.17	ns
CT × SC	2	1.71	ns	2	1.08	ns	2	5.27	**
NC × SC	2	3.35	*	2	1.22	ns	2	3.29	*
CT × NC × SC	2	0.10	ns	2	0.17	ns	2	0.02	ns
E	84			84			82		

In all mixtures, the RII values of *B. erectus* were (significantly) slightly lower in the nutrient addition treatment. Nutrient addition resulted in the strongest reduction in RII in the monocultures and the mixtures with *B. pinnatum*, but weakest for *S. capillata* in mixtures with *B. erectus*. Interestingly, the monoculture of *S. capillata* had positive RII values in the nutrient addition treatment. The monoculture of *S. tirsa* had negative RII values similar to their mixtures, but nutrient addition resulted in an increase in RII.

In terms of RII, similar to the first year, in the second year high negative interactions between all species of grass were recorded, with significant differences in clipping, nutrient and species composition treatments (Fig. 4, Table 1). In particular, the RII recorded for the monoculture of *B. erectus* was more negative and varied less than those recorded in the mixtures. In contrast to *B. pinnatum*, the RII values were generally lower for *B. erectus* under the nutrient addition and unclipped treatments and there were strong negative interactions between *B. erectus* and both species of *Stipa*. *Stipa capillata* had the significantly lowest RII in the nutrient addition and clipped treatments, but in the monocultures with and without the nutrient addition and clipped treatments, the RII values were positive. *Stipa tirsa* had the significantly lowest RII values in the without nutrient addition treatment in both the monocultures and the mixtures, whereas in the monoculture, positive RII values were recorded in the nutrient addition treatment.

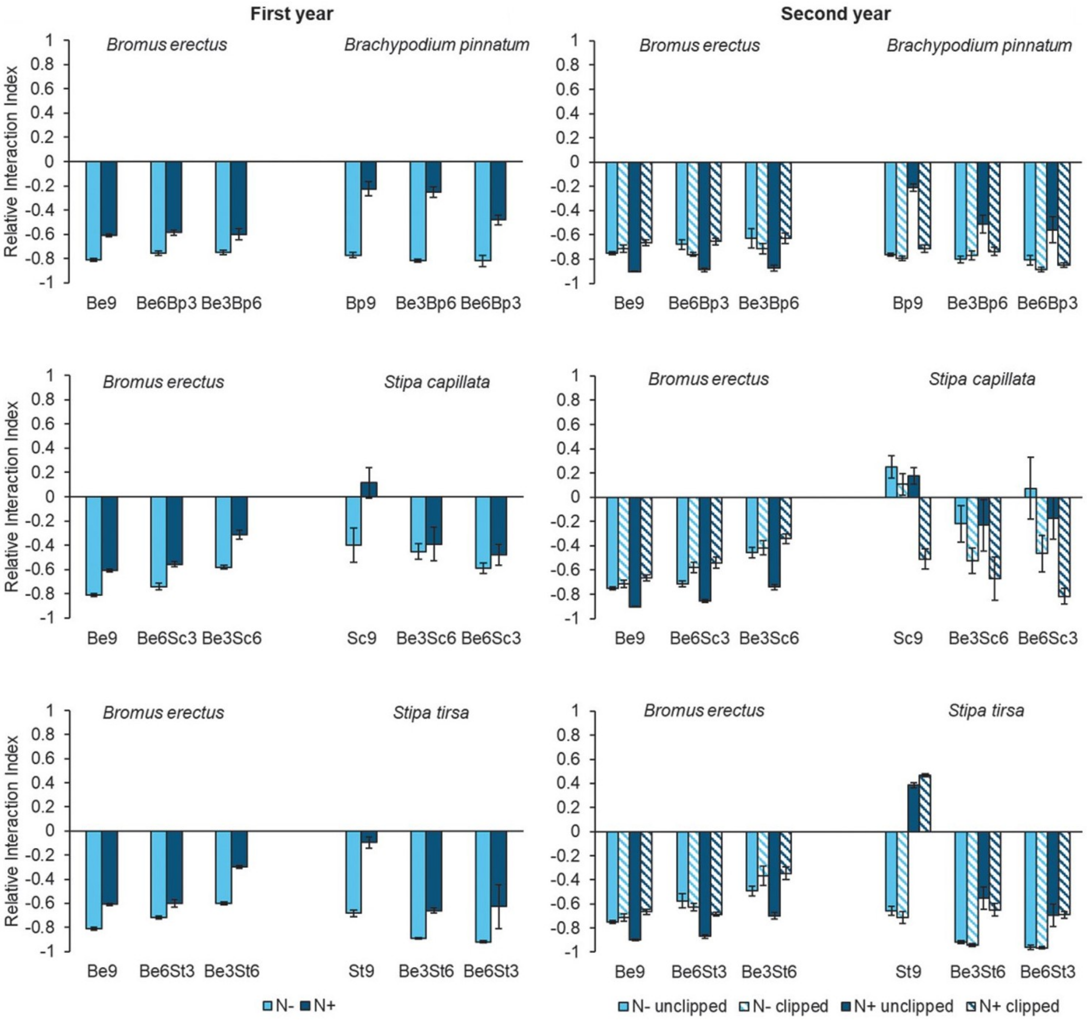

Fig. 4. First-year performance (left) and second-year performance (right) in terms of the Relative Interaction Index (calculated using above-ground biomass) of *Bromus erectus* in combination with *Brachypodium pinnatum* (above), *Stipa capillata* (middle) and *S. tirsa* (below). Positive values correspond to facilitation and negative values to competition. The different coloured bars (mean+SE) represent the species compositions (9, 6:3, 3:6) in the different combinations of nutrient conditions (left) and the combination of different nutrient conditions and clipping treatments (right). Two-way ANOVA (first-year performance) and three-way ANOVA (second-year performance) were used to test mean differences (see Table 1, Supplementary Table S2).

In general, the biomass of single individuals and interactions between the four grasses differed significantly in the different nutrient conditions (Fig. 5, Table 3). Nutrient addition resulted in a significant increase in biomass of *B. erectus* when grown alone and affected both its intra- and interspecific competitive ability, with the former interaction being more negative. On the other hand, a different pattern was identified for *B. pinnatum* and *S. tirsa*: the biomass of single individuals was significantly higher in the without nutrient addition treatment, and both intra- and interspecific competition was significantly higher than in the nutrient addition treatment. Moreover, for *S. tirsa* there was a slight intraspecific facilitation in the nutrient addition treatment. For the biomass of single individuals of *S. capillata* only a small significant increase in the nutrient addition

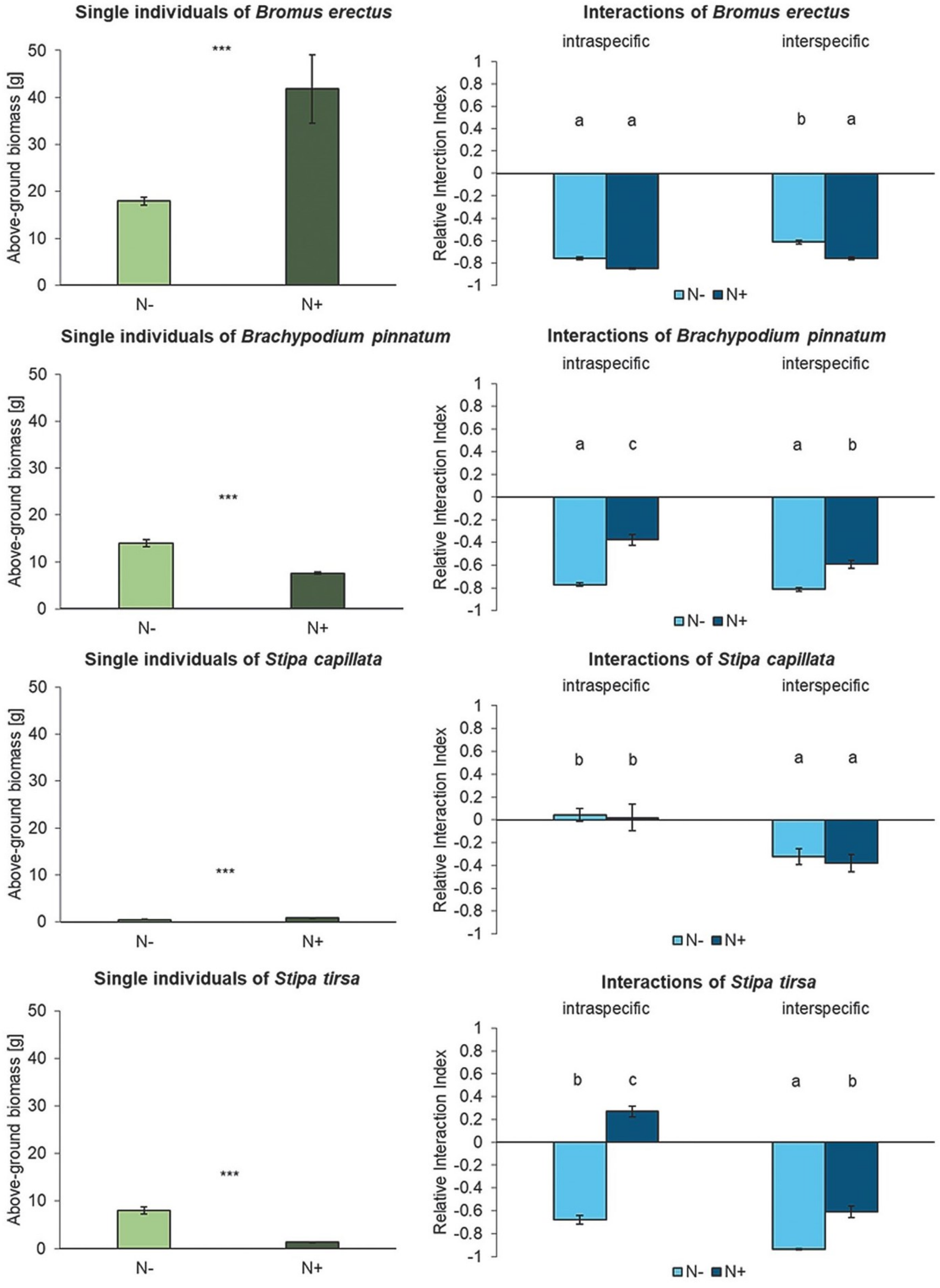

Fig. 5. General comparison of the above-ground biomass produced by single individuals (left) and plant interactions (intraspecific = species composition in monocultures (9); interspecific = species composition in mixtures (6:3, 3:6)) calculated using the Relative Interaction Index (right) of the four grasses in terms of the above-ground biomass. Relation based on the Relative Interaction Index: positive values correspond to facilitation and negative values to competition. The different coloured bars (mean+SE) represent the different nutrient conditions. The data for the first- and second-year performances in terms of above-ground biomass were pooled (no differentiation between clipped and unclipped treatments in the second year; for interspecific interaction, the species compositions (6:3, 3:6) were pooled). Results of the t-test (single individuals): *** $P < 0.001$. Results of the two-way ANOVA (see also Table 3) and calculated Tukey's post hoc-test (plant interactions): different letters indicate significant differences at $P < 0.05$.

Table 3. Results of the two-way ANOVA of the combined effects of the nutrient poor/ nutrient rich and interspecific/ intraspecific treatments for the four grasses in terms of above-ground biomass. The data for the first year and second year above-ground biomasses were pooled (see chapter: data analysis). Degrees of freedom (df), F-values and error probabilities (** $P < 0.1$, *** $P < 0.001$) are given. Abbreviations: NC = nutrient condition; PI = plant interaction; E = error; ns = not significant.

Source of variation	*B. erectus*			*B. pinnatum*			*S. capillata*			*S. tirsa*		
	df	F	P	df	F	P	df	F	P	df	F	P
NC	1	62.26	***	1	80.90	***	1	0.17	ns	1	195.38	***
PI	1	21.91	***	1	15.55	***	1	18.84	***	1	174.91	***
NC × PI	1	1.18	ns	1	7.13	**	1	0.04	ns	1	53.99	***
E	220			91			87			83		

treatment was recorded, but it had no significant effect on the interactions between plants. Unfortunately, the effects on the generative traits of *B. erectus* could not be studied as only a few individuals produced flowers so it was not possible to calculate its RII.

Discussion

The four species of xerothermic grass responded differently to nitrogen addition and above-ground biomass removal. Compared to the other three grasses, the growth of *B. erectus* in terms of its vegetative traits was the greatest. The greater growth and competitive ability of *B. erectus* affected *S. capillata* and *S. tirsa* more negatively than *B. pinnatum*. *Bromus erectus* was often dominant in the nutrient addition treatment, but less so in the clipping treatment, which had the strongest effect on its intraspecific competition and slightly weaker effect on its interspecific competitive ability. It is likely that in the future *B. erectus* will become increasingly dominant in xerothermic grasslands in central Germany and displace both species of *Stipa*.

Vegetative performance of the four xerothermic grasses

In the first and second year, species-specific responses in growth performance in the monocultures and mixtures and nutrient conditions and clipping treatments were detected for the four species of grass, with *B. erectus* being most frequently dominant. In general, there was a clear significant effect of the presence of neighbouring plants in the different species compositions on above-ground biomass, whereas there were only slight (none significant) effects on other vegetative traits. The vegetative traits of *B. erectus* (highest biomass production and tallest) and *B. pinnatum* (highest SLA) increased significantly better than those of *S. capillata* and *S. tirsa*.

There were few interactive effects between nutrient addition, clipping and species composition for all the grasses studied. Grasses are strongly nitrogen-limited (Ellenberg et al. 2001), which was particularly evident as the growth of *B. erectus* and *B. pinnatum* in the first year was enhanced by the addition of nitrogen; although LNC also increased in all grasses under the same conditions. Nitrogen addition can lead to increased LNC in grasses, as a richly branched root system enable the rapid uptake of nutrients from soil (You et al. 2017).

Bromus erectus was the tallest and produced the most biomass of all the species, even in the second year, with lower numbers of individuals in the mixtures with both species of *Stipa* in the nutrient addition and unclipped treatments. This indicates a trend towards overcompensation in the production of above-ground biomass (Stevens & Gowing 2014), as in the second year, nitrogen addition resulted in the above-ground growth of *B. erectus* being even higher, as competitive species can quickly obtain additional resources (Hautier et al. 2009). Meier et al. (2021) report that leaves of large tussocks of *B. erectus* are partially grazed in summer and rapidly resprout in autumn. Nitrogen inputs and abandonment can favour an increase in the dominance of *B. erectus* (Bornkamm 2008) such that this species becomes a major contributor to the above-ground biomass in plant communities (Steinger et al. 2007). Nevertheless, *B. pinnatum* had a higher SLA than *B. erectus*, indicating a presumably higher mass-based light-saturated photosynthetic rate (Wright et al. 2004).

Differences in growth are also associated with the morphology of the species. Taller, more broad-leaved grasses generally outcompete more medium-sized, fine-leaved grasses (Bohner et al. 2019), which was verified by the results for the mixtures of *B. erectus* (higher SLA) and *S. capillata* or *S. tirsa* (lower SLA). In this context, light plays a crucial role, as plants that use light more efficiently and position their leaves between neighbouring plants have a greater or faster growth rate (Farrer & Goldberg 2011, Craine & Dybzinski 2013). Thus, the increased biomass accumulation of *B. erectus* growing in pots may reduce the light available to both species of *Stipa* and consequently inhibit their growth.

Generative performance of Bromus erectus

The likelihood of *B. erectus* flowering in the second year was significantly enhanced by decreasing numbers of individuals in the pots at all three species composition levels. This indicates intraspecific competition in the mixtures. In the clipping treatment, seed mass significantly increased in the monoculture. The production of heavier and larger seeds can be beneficial for seedling establishment and survival (Leishman & Westoby 1994, Moles & Westoby 2006) and clipping may have a positive effect on the fitness of *B. erectus*. Lemmer et al. (2021) experimentally demonstrate that under current climatic conditions, population growth of *B. erectus* is higher in mowed than in grazed plots, while under future climatic conditions, population growth rates are similar in both types of management. Thus, population growth rates of *B. erectus* can respond quickly to environmental conditions and their interactions (Compagnoni & Adler 2014, Prevéy & Seastedt 2015), but this may be considered to be problematic for conservation as it could enable this grass to become more abundant in the future compared to other xerothermic grassland species.

Plant-plant interactions of the four xerothermic grasses

We revealed very strong intraspecific competition for *B. erectus*, as the significantly lowest RII values were recorded for the monoculture of this species in the nutrient addition treatment (see Splith et al. 2021) and intraspecific competition was evident for *B. pinnatum* in nutrient poor conditions. Similar results are well documented experimentally for *Festuca rupicola*, in that this species is more negatively affected by high intraspecific competition and, consequently, it suppresses itself (Schulze et al. 2014, Faulhaber & Partzsch

2018, Partzsch 2019). As such, increased self-limitation may occur with increase in numbers of individuals of the same species in pots (see e.g. Blank 2010, Müller et al. 2016), which was also confirmed for *B. erectus* (Splith et al. 2021). Such self-limitation induced by intraspecific competition is consistent with the theory of species coexistence, which assumes that competition inevitably results in a decline in biodiversity (Aschehoug & Callaway 2015). Hence, the effect of intraspecific competition should be stronger than that of interspecific competition in order to provide a stabilizing mechanism for regulating species abundance and coexistence (Chesson 2000, Silvertown 2004).

Conversely, in the second year, both species of *Stipa* showed facilitative effects in the monocultures, but with different responses to the respective nutrient conditions and clipping treatments. Here, the biomass of *S. capillata* was higher under nutrient-poor conditions (although the general comparison based on the pooled data revealed no differences between the nutrient conditions for the plant interactions), while that of *S. tirsa* was promoted under nutrient-rich conditions. This indicates the best conditions for both species, with *S. capillata* occurring mainly in continental dry and *S. tirsa* in continental semi-dry grassland communities, which have higher nutrient and water supply (Schubert et al. 1995, Meier & Partzsch 2018). Moreover, intraspecific competition was recorded for *S. capillata* in nutrient addition and clipping treatments. It is generally known that this species is intolerant of mowing (mowing tolerance 2; Klotz et al. 2002) and, probably based on our simulated above-ground removal, only single individuals of the monoculture were able to resprout in the second year.

Then again, strong interspecific competition occurred in mixtures, which favoured *B. erectus*. Neighbouring species compete for essential resources from a common finite pool (Aschehoug et al. 2016), which was simulated by the limited amount space in the pots in our experiment. While *B. erectus* is more sensitive than *B. pinnatum* to competition, it is more stress tolerant with regard to drought and disturbance (Corcket et al. 2003, Liancourt et al. 2005). Furthermore, *B. erectus* develops very extensive root systems of up to at least 90 cm (Kutschera & Lichtenegger 1982), which outcompete *B. pinnatum* with its shallow rooting system and elongated rhizomes (Bornkamm 2006). Plants with deeper root systems are also able to obtain water from deeper soil layers and thus reduce the water available for competitors (Violle et al. 2009). However, site-specific aspects cannot be neglected in the field, where the cover of *B. erectus* may decrease due to being shaded by surrounding shrubs (Dierschke 2006) and the cover of *B. pinnatum* may increase (Baier & Tischew 2004).

The lowest RII values were recorded for the functionally similar species *S. capillata* and *S. tirsa* in the presence of *B. erectus* in the clipping treatment. In accordance with the results of Meier et al. (2019), this could lead to the competitive exclusion of both species of *Stipa* in the field if abiotic conditions change in the future (e.g. global warming and/or eutrophication) and *B. erectus* becomes increasingly more competitive. Indeed, *B. erectus* is spreading more and more into *Stipa* grasslands, which is considered to be consequence of succession (Bieringer & Sauberer 2001, Meier & Partzsch 2018, Meier et al. 2021). Functionally similar dominant species of grass play an equivalent role in ecosystem function (Joner et al. 2011) and are key drivers of plant community dynamics (Smith & Knapp 2003, Smith et al. 2020).

Conclusions

Based on our results, the growth and competitive ability of *B. erectus* affected *S. capillata* and *S. tirsa* more negatively than *B. pinnatum*. In particular, the growth of *B. erectus* was greater in the nutrient addition treatment, but slightly less in above-ground removal treatment. This species is taller and benefits from both nitrogen deposition and climate warming (Meier et al. 2022), and is favoured by low levels of management (Lemmer et al. 2021). We also found the same pattern, when *B. erectus* grew alone as its biomass production was boosted by the addition of nitrogen. *Bromus erectus* is spreading in xerothermic grassland and is therefore classified as a neophyte in the federal states of Thuringia and Saxony-Anhalt in Germany (Heinrich 2010, Frank & Schnitter 2016). Currently, the average cover values for *B. erectus* are between 30% and 40% in xerothermic grasslands in central Germany, but its competitive potential may not yet be fully achieved (Meier et al. 2021). In the future, tall-growing species like *B. erectus* may become more dominant, affecting the community through high competition and structural changes, resulting in a lower species diversity (Meier et al. 2021, 2022). Zhang & van Kleunen (2019) report that high intrinsic growth rates are the main drivers of the highly competitive ability of common alien plants with strong intraspecific competition and thus play an essential role in the invasion success of a species, which indicates the superiority of *B. erectus*.

Compared to clipping or annual mowing, grazing had a more positive effect in the conservation of grasslands by promoting gradual but continuous biomass removal as well as more openness throughout the growing season, which reduces competition between species (Tälle et al. 2016). In practice, additional intensive spring grazing may be required to suppress highly competitive grasses (Elias et al. 2018), as mowing late in the season can promote the spread of grasses (Nowak & Schulz 2002, Briemle 2004).

Supplementary materials

Fig. S1. – Second-year performance in terms of leaf area and leaf dry mass of *Bromus erectus* in combination with *Brachypodium pinnatum*, *Stipa capillata* and *S. tirsa*.

Fig. S2. – Second-year performance in terms of LDMC and C/N ratio of *Bromus erectus* in combination with *Brachypodium pinnatum*, *Stipa capillata* and *S. tirsa*.

Fig. S3. – First-year performance in terms of above-ground biomass and plant height of *Bromus erectus* in combination with *Brachypodium pinnatum*, *Stipa capillata* and *S. tirsa*.

Fig. S4. – First-year performance in terms of of SLA and LNC of *Bromus erectus* in combination with *Brachypodium pinnatum*, *Stipa capillata* and *S. tirsa*.

Fig. S5. – First-year performance in terms of the leaf area and leaf dry mass of *Bromus erectus* in combination with *Brachypodium pinnatum*, *Stipa capillata* and *S. tirsa*.

Fig. S6. – First-year performance in terms of LDMC and C/N ratio of *B. erectus* in combination with *Brachypodium pinnatum*, *Stipa capillata* and *S. tirsa*.

Table S1. – First-year and second-year performance in terms of above-ground biomass of *Bromus erectus*, *Brachypodium pinnatum*, *Stipa capillata* and *S. tirsa* in the different nutrient conditions and clipping treatments.

Table S2. – Results of the three-way ANOVA of leaf area, leaf dry mass, LDMC, C/N ratio and RII in the competition experiment.

Table S3. – Results of the two-way ANOVA of above-ground biomass, plant height, SLA, LNC and RII in the competition experiments.

Table S4. – Results of the two-way ANOVA of leaf area, leaf dry mass, LDMC, C/N ratio and RII in the competition experiment.

Supplementary materials are available at www.preslia.cz

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Vliv přidání živin a odstranění nadzemní biomasy na interakce mezi druhy xerotermních trav

Aspekty globální změny, jako jsou zvyšující se atmosférická depozice dusíku a změny ve využívání půdy, podporují nárůst dominance trav v xerotermních travních porostech. Předpokládá se, že zvýšený obsah živin a změny ve využívání krajiny ovlivňují interakce mezi expandujícím sveřepem vzpřímeným (*Bromus erectus*) a dalšími xerotermními druhy trav ve středním Německu. Interakce mezi rostlinami jsou klíčovým faktorem regulace druhového složení, produktivity, struktury a dynamiky rostlinných společenstev i fungování ekosystémů. Provedli jsme kompetiční pokus s *B. erectus* a dalšími druhy trav (*Brachypodium pinnatum*, *Stipa capillata* a *S. tirsa*). Abychom zjistili vliv *B. erectus* na ostatní trávy, pěstovali jsme všechny druhy ve dvou hustotách (9 jedinců nebo 1 jedinec na květináč) a ve třech různých druhových složeních devíti rostlin v monokultuře a směsi (6:3, 3:6). Ošetření zahrnovala přídavek živin (prostředí chudé vs. bohaté na živiny) a odstranění nadzemní biomasy (nestříhané vs. stříhané). Během dvou po sobě následujících let byl růst každého druhu dokumentován měřením vegetativních (nadzemní biomasa, výška rostlin, specifická listová plocha – SLA, koncentrace dusíku v listech – LNC) a generativních znaků (délka lat, počet květenství, hmotnost semen). Interakce mezi rostlinami byly hodnoceny pomocí relativního interakčního indexu (RII). *Bromus erectus* prospíval na úkor ostatních tří druhů, při přidání živin měl nejvyšší produkci biomasy. Vliv vnitrodruhové kompetice na *B. erectus* byl intenzivnější než vliv kompetice mezidruhové. *Bromus erectus* měl při mezidruhové kompetici větší negativní vliv na *Stipa capillata* a *S. tirsa* než na *B. pinnatum*, takže v budoucnosti předpokládaná rostoucí dominance *B. erectus* v důsledku zvýšeného obohacování dusíkem může vést k vytlačení obou vzácných druhů rodu *Stipa*.

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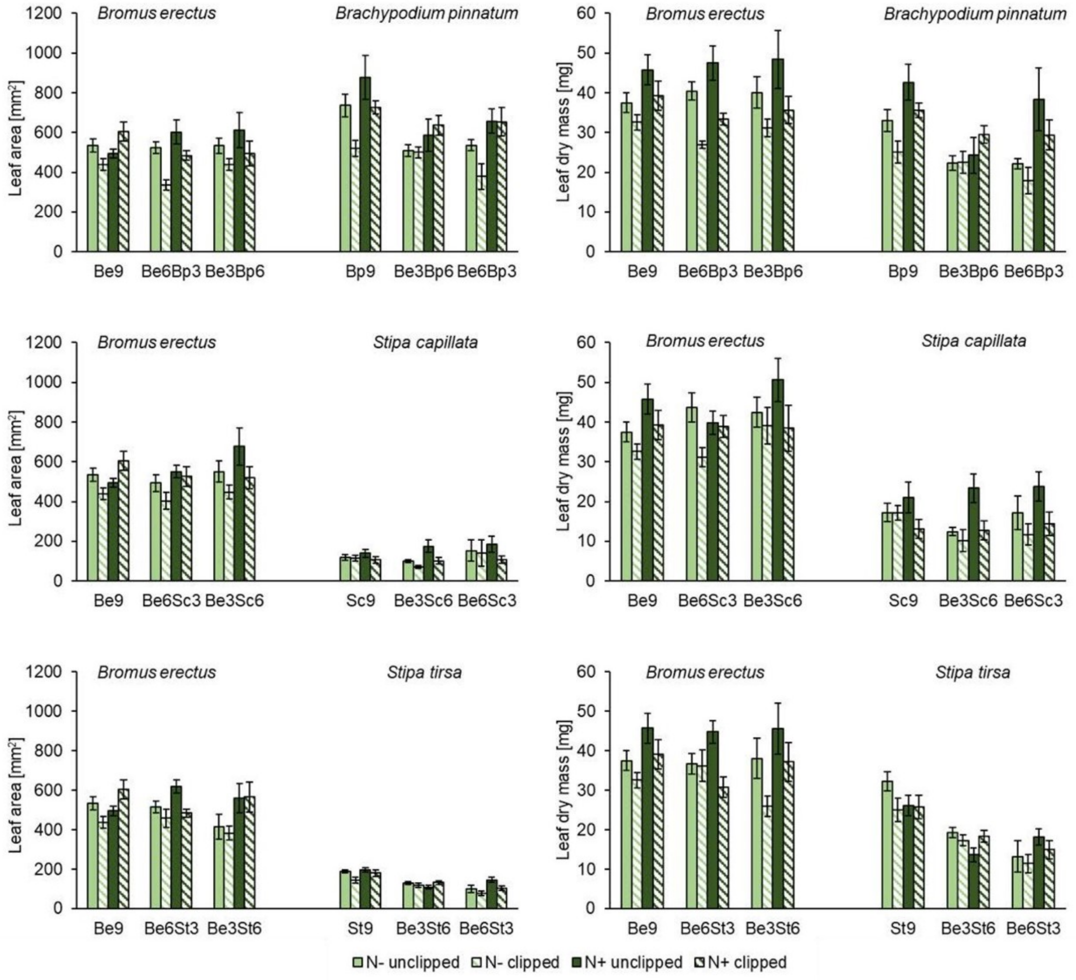
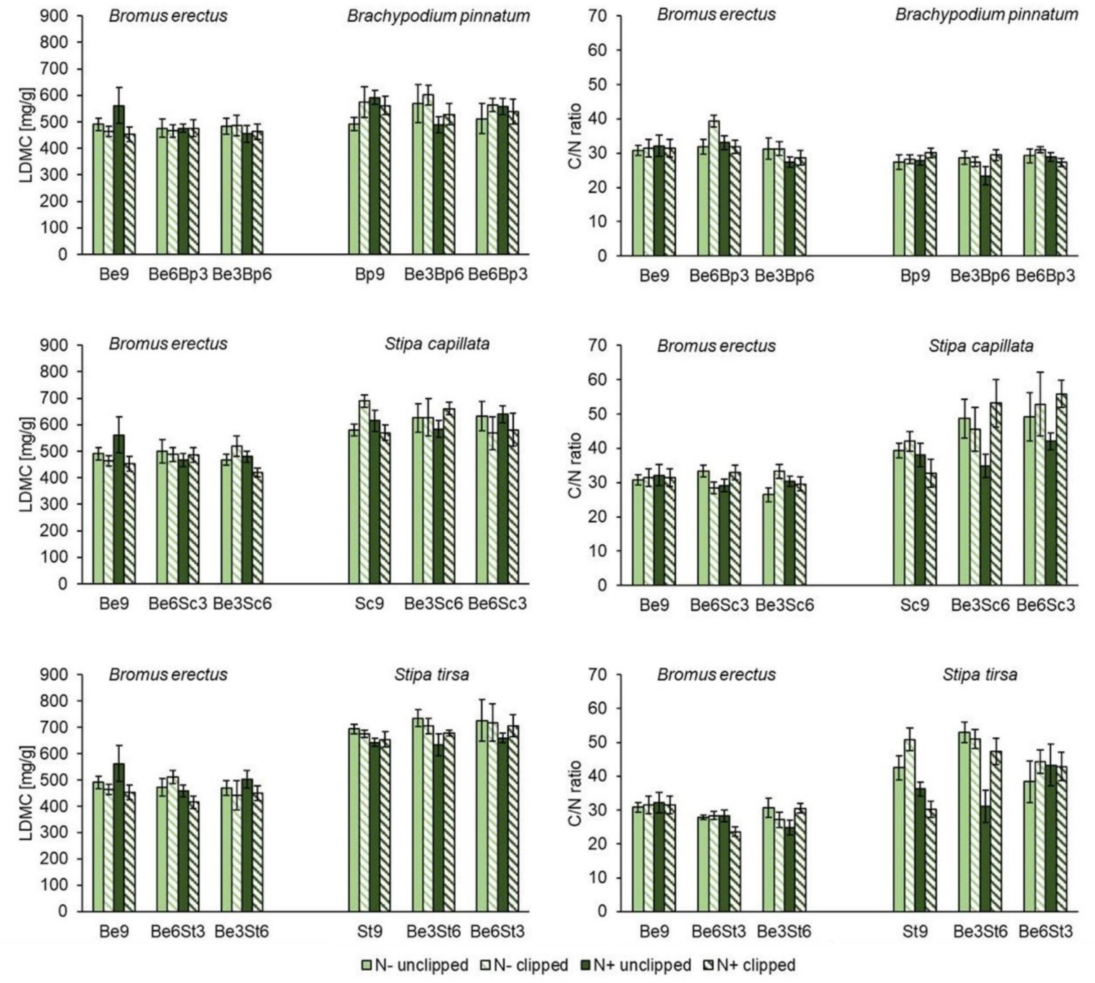
Supplementary Fig. S1. – Second year performance in terms of leaf area (left) and leaf dry mass (right) per individual of *Bromus erectus* in combination with *Brachypodium pinnatum* (above), *Stipa capillata* (middle) and *S. tirsa* (below). The different coloured bars (mean + SE) represent the different species compositions (9, 6:3, 3:6) in the different combinations of nutrient conditions and clipping treatments. Using three-way ANOVA for testing mean differences (see Table S2).



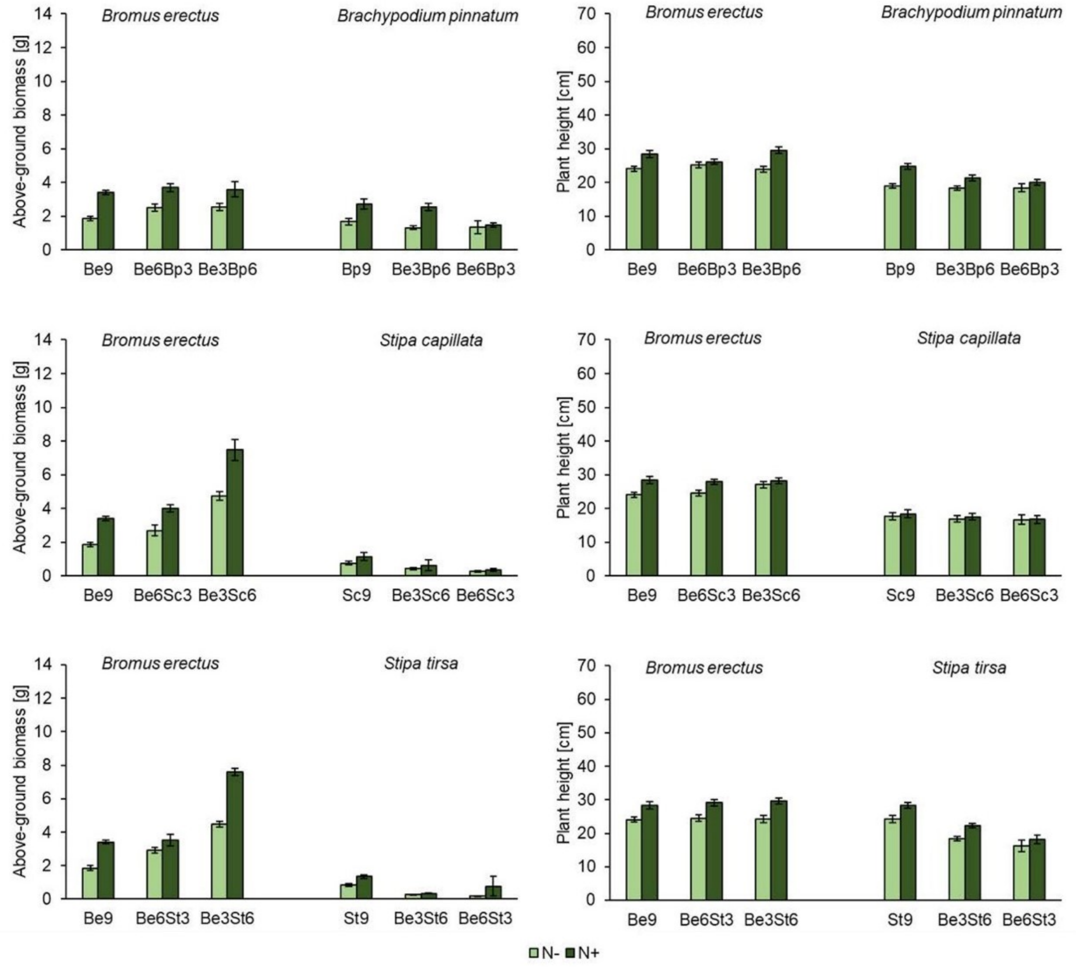
Meier T., Hensen I. & Partzsch M. (2022) Effects of nitrogen addition and above-ground biomass removal on the growth and interactions between species of xerothermic grasses. – Preslia 94: 607–629.

Supplementary Fig. S2. – Second year performance in terms of LDMC (left) and C/N ratio (right) per individual of *Bromus erectus* in combination with *Brachypodium pinnatum* (above), *Stipa capillata* (middle) and *S. tirsa* (below). The different coloured bars (mean + SE) represent the different species compositions (9, 6:3, 3:6) in the different combinations of nutrient conditions and clipping treatments. Using three-way ANOVA for testing mean differences (see Table S2).



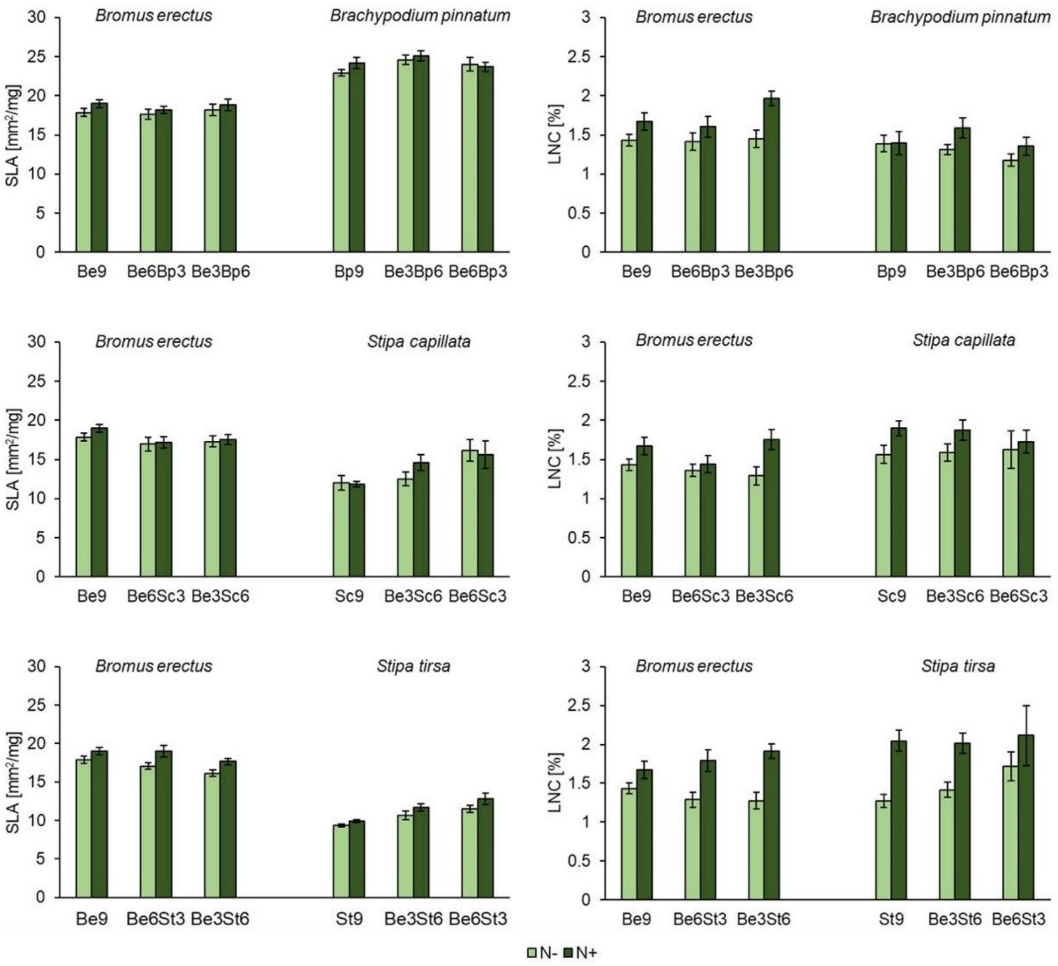
Meier T., Hensen I. & Partzsch M. (2022) Effects of nitrogen addition and above-ground biomass removal on the growth and interactions between species of xerothermic grasses. – Preslia 94: 607–629.

Supplementary Fig. S3. – First year performance in terms of above-ground biomass (left) and plant height (right) per individual of *Bromus erectus* in combination with *Brachypodium pinnatum* (above), *Stipa capillata* (middle) and *S. tirsa* (below). The different coloured bars (mean + SE) represent the different species compositions (9, 6:3, 3:6) in the different nutrient conditions. Using two-way ANOVA for testing mean differences (see Table S3).



Meier T., Hensen I. & Partzsch M. (2022) Effects of nitrogen addition and above-ground biomass removal on the growth and interactions between species of xerothermic grasses. – Preslia 94: 607–629.

Supplementary Fig. S4. – First year performance in terms of of SLA (left) and LNC (right) per individual of *Bromus erectus* in combination with *Brachypodium pinnatum* (above), *Stipa capillata* (middle) and *S. tirsa* (below). The different coloured bars (mean + SE) represent the different species compositions (9, 6:3, 3:6) in the different nutrient conditions. Using two-way ANOVA for testing mean differences (see Table S3).



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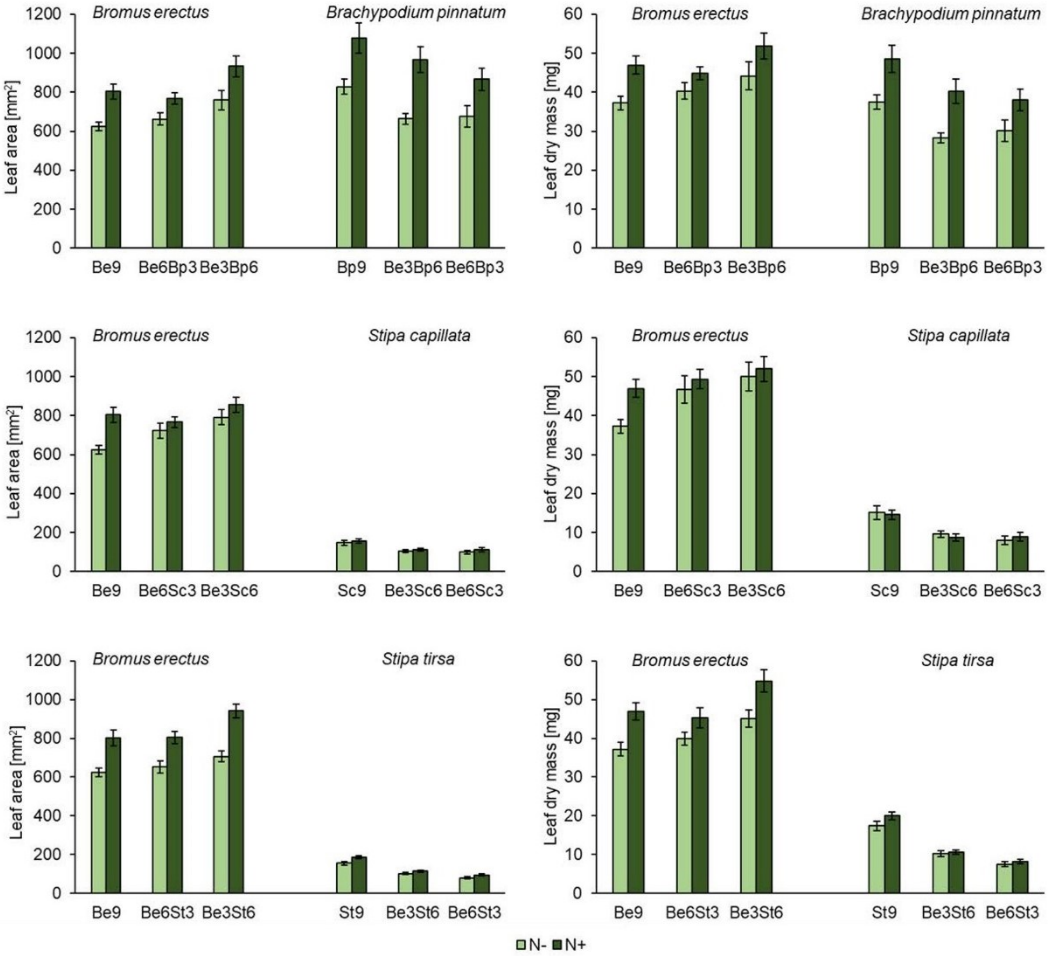
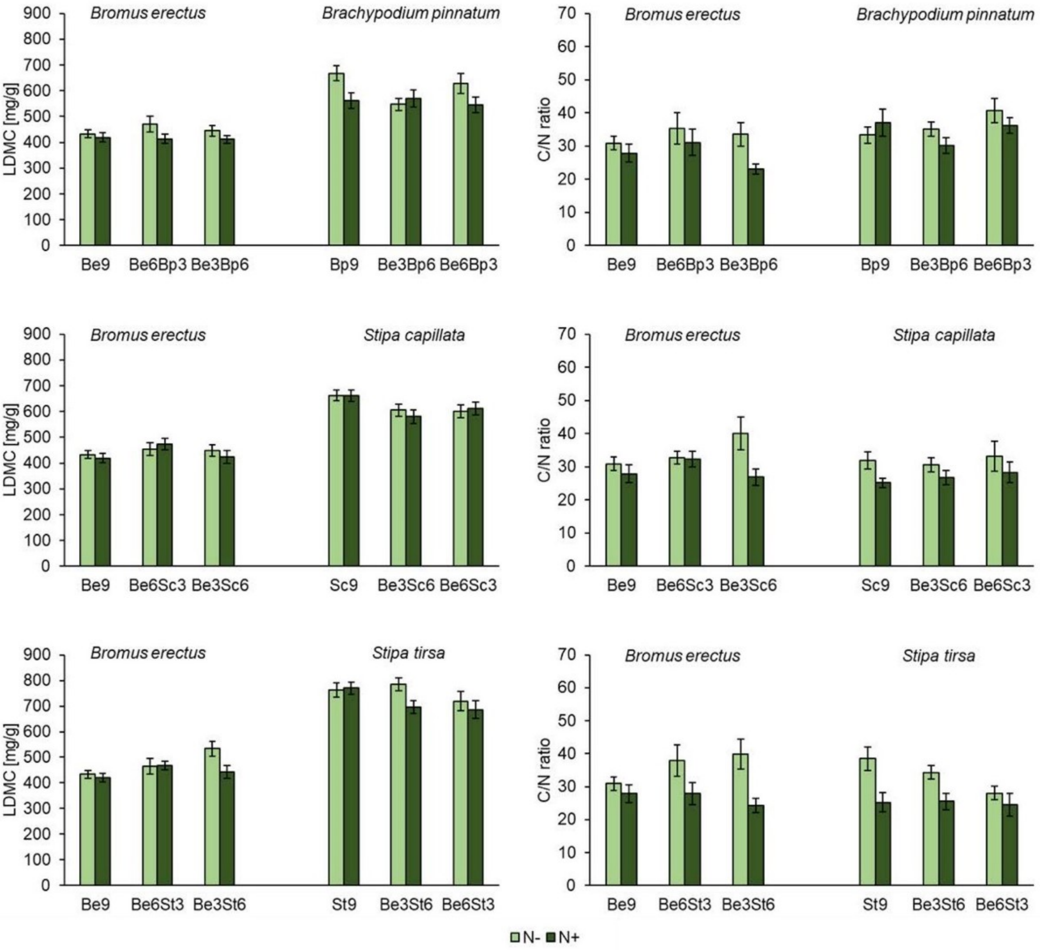
Supplementary Fig. S5. – First year performance in terms of the leaf area (left) and leaf dry mass (right) per individual of *Bromus erectus* in combination with *Brachypodium pinnatum* (above), *Stipa capillata* (middle) and *S. tirsa* (below). The different coloured bars (mean + SE) represent the different species compositions (9, 6:3, 3:6) in the different nutrient conditions. Using two-way ANOVA for testing mean differences (see Table S4).



Meier T., Hensen I. & Partzsch M. (2022) Effects of nitrogen addition and above-ground biomass removal on the growth and interactions between species of xerothermic grasses. – Preslia 94: 607–629.

Supplementary Fig. S6. – First year performance in terms of LDMC (left) and C/N ratio (right) per individual of *Bromus erectus* in combination with *Brachypodium pinnatum* (above), *Stipa capillata* (middle) and *S. tirsa* (below). The different coloured bars (mean + SE) represent the different species compositions (9, 6:3, 3:6) in the different nutrient conditions. Using two-way ANOVA for testing mean differences (see Table S4).



Meier T., Hensen I. & Partzsch M. (2022) Effects of nitrogen addition and above-ground biomass removal on the growth and interactions between species of xerothermic grasses. – Preslia 94: 607–629.

Supplementary Table S1. – First-year and second year performance in terms of above-ground biomass of *Bromus erectus*, *Brachypodium pinnatum*, *Stipa capillata* and *S. tirsa* in the different nutrient conditions and clipping treatments.

	B. erectus	***B. pinnatum***	***S. capillata***	***S. tirsa***
first year				
N-	17.80 ± 3.47	12.79 ± 2.19	1.06 ± 0.38	4.43 ± 1.07
N+	13.97 ± 2.71	4.15 ± 1.54	0.93 ± 0.46	1.58 ± 0.33
second year				
N-, unclipped	20.27 ± 4.92	16.73 ± 2.63	0.24 ± 0.08	10.58 ± 1.74
N-, clipped	13.33 ± 2.11	9.56 ± 1.59	0.37 ± 0.11	6.40 ± 1.31
N+, unclipped	69.48 ± 9.85	7.55 ± 1.86	0.73 ± 0.18	1.39 ± 0.62
N+, clipped	14.39 ± 3.58	11.34 ± 1.97	0.91 ± 0.17	0.90 ± 0.32

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Supplementary Table S2. – Results of the three-way ANOVA of leaf area, leaf dry mass, LDMC, C/N ratio and RII in the competition experiment: *Bromus erectus* in combination with 1) *Brachypodium pinnatum*, 2) *Stipa capillata* and 3) *S. tirsa* in the second year (clipping treatment: unclipped/ clipped; nutrient condition: nutrient poor/ nutrient rich; species composition: 9, 6:3, 3:6). Degrees of freedom (df), F-values and error probabilities (* p < 0.05, ** p < 0.1, *** p < 0.001) are given. Abbreviations: CT = clipping treatment; NC = nutrient condition; SC = species composition; E = Error; ns = not significant.

Source of variation	**leaf area [mm^2]**			**leaf dry mass [mg]**			**LDMC [mg/g]**			**C/N ratio**		
	df	F	p	df	F	p	df	F	p	df	F	p
1) *B. erectus* in combination with *B. pinnatum*												
B. erectus												
CT	1	11.50	**	1	22.38	***	1	1.11	ns	1	0.84	ns
NC	1	8.31	*	1	9.30	**	1	0.01	ns	1	2.41	ns
SC	2	1.07	ns	2	0.33	ns	2	0.35	ns	2	4.19	*
CT x NC	1	3.97	*	1	0.01	ns	1	0.19	ns	1	1.16	ns
CT x SC	2	2.92	ns	2	1.38	ns	2	1.17	ns	2	0.48	ns
NC x SC	2	0.84	ns	2	0.09	ns	2	0.54	ns	2	0.78	ns
CT x NC x SC	2	1.32	ns	2	0.08	ns	2	0.51	ns	2	1.15	ns
E	83			83			83			83		
B. pinnatum												
CT	1	7.00	*	1	3.12	ns	1	1.49	ns	1	2.76	ns
NC	1	23.44	***	1	21.07	***	1	0.00	ns	1	0.59	ns
SC	2	9.73	***	2	9.21	***	2	0.14	ns	2	1.58	ns
CT x NC	1	4.94	*	1	1.34	ns	1	2.51	ns	1	0.64	ns
CT x SC	2	2.93	ns	2	2.99	ns	2	0.10	ns	2	0.67	ns
NC x SC	2	1.34	ns	2	1.82	ns	2	2.27	ns	2	1.18	ns
CT x NC x SC	2	0.53	ns	2	0.18	ns	2	0.45	ns	2	2.92	ns
E	82			82			82			82		
2) *B. erectus* in combination with *S. capillata*												
B. erectus												
CT	1	5.34	*	1	10.71	**	1	1.28	ns	1	0.46	ns
NC	1	8.40	**	1	3.61	ns	1	0.73	ns	1	0.03	ns
SC	2	1.06	ns	2	0.89	ns	2	0.32	ns	2	0.53	ns
CT x NC	1	2.12	ns	1	0.05	ns	1	2.10	ns	1	0.01	ns
CT x SC	2	1.21	ns	2	0.10	ns	2	1.29	ns	2	0.98	ns
NC x SC	2	0.15	ns	2	0.46	ns	2	0.99	ns	2	0.01	ns
CT x NC x SC	2	1.23	ns	2	2.05	ns	2	1.39	ns	2	4.28	*
E	83			83			83			83		
S. capillata												
CT	1	8.42	**	1	10.29	**	1	0.01	ns	1	1.23	ns
NC	1	3.38	ns	1	3.28	ns	1	0.11	ns	1	2.11	ns
SC	2	0.65	ns	2	1.36	ns	2	0.33	ns	2	4.14	*
CT x NC	1	1.23	ns	1	1.17	ns	1	0.06	ns	1	1.00	ns
CT x SC	2	0.60	ns	2	0.58	ns	2	1.81	ns	2	1.10	ns
NC x SC	2	1.06	ns	2	2.40	ns	2	0.61	ns	2	0.70	ns
CT x NC x SC	2	0.04	ns	2	0.20	ns	2	1.83	ns	2	2.17	ns
E	75			75			75			71		
3) *B. erectus* in combination with *S. tirsa*												
B. erectus												
CT	1	1.37	ns	1	12.98	***	1	3.66	ns	1	0.06	ns
NC	1	12.91	***	1	6.71	*	1	0.06	ns	1	1.03	ns
SC	2	2.43	ns	2	1.03	ns	2	0.82	ns	2	4.49	*
CT x NC	1	0.74	ns	1	0.37	ns	1	2.03	ns	1	0.25	ns
CT x SC	2	1.19	ns	2	0.40	ns	2	0.82	ns	2	0.93	ns
NC x SC	2	1.63	ns	2	1.19	ns	2	2.08	ns	2	0.47	ns
CT x NC x SC	2	1.54	ns	2	1.48	ns	2	0.45	ns	2	3.99	*
E	83			83			83			83		
S. tirsa												
CT	1	5.95	*	1	0.62	ns	1	0.14	ns	1	3.77	ns
NC	1	7.25	**	1	0.47	ns	1	4.06	*	1	14.59	***
SC	2	31.05	***	2	24.61	***	2	0.52	ns	2	1.75	ns
CT x NC	1	1.86	ns	1	1.35	ns	1	1.59	ns	1	0.01	ns
CT x SC	2	1.99	ns	2	0.66	ns	2	0.11	ns	2	1.07	ns
NC x SC	2	3.68	*	2	4.13	*	2	0.32	ns	2	4.26	*
CT x NC x SC	2	1.35	ns	2	1.33	ns	2	0.17	ns	2	5.80	**
E	73			73			73			73		

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Supplementary Table S3. – Results of the two-way ANOVA of above-ground biomass, plant height, SLA, LNC and RII in the competition experiments: *Bromus erectus* in combination with 1) *Brachypodium pinnatum*, 2) *Stipa capillata* and 3) *S. tirsa* in the first year (nutrient condition: nutrient poor/ nutrient rich; species composition: 9, 6:3, 3:6). Degrees of freedom (df), F-values and error probabilities (* $p < 0.05$, ** $p < 0.1$, *** $p < 0.001$) are given. Abbreviations: NC = nutrient condition; SC = species composition; E = Error; ns = not significant.

Source of variation	biomass [g]			plant height [cm]			SLA [mm^2/mg]			LNC [%]			RII		
	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p
1) *B. erectus* in combination with *B. pinnatum*															
B. erectus															
NC	1	28.05	***	1	25.70	***	1	2.65	ns	1	9.44	**	1	81.90	***
SC	2	1.67	ns	2	0.05	ns	2	0.54	ns	2	1.55	ns	2	1.69	ns
NC x SC	2	1.41	ns	2	3.69	*	2	0.10	ns	2	1.21	ns	2	0.61	ns
E	42			90			90			90			42		
B. pinnatum															
NC	1	17.90	***	1	23.06	***	1	0.75	ns	1	1.50	ns	1	217.68	***
SC	2	7.14	**	2	5.39	**	2	2.05	ns	2	1.42	ns	2	7.98	**
NC x SC	2	1.15	ns	2	1.87	ns	2	0.57	ns	2	0.93	ns	2	5.01	*
E	42			90			90			86			42		
2) *B. erectus* in combination with *S. capillata*															
B. erectus															
NC	1	37.75	***	1	17.83	***	1	1.03	ns	1	7.10	**	1	133.22	***
SC	2	37.31	***	2	1.93	ns	2	2.84	ns	2	0.85	ns	2	70.93	***
NC x SC	2	0.43	ns	2	1.79	ns	2	0.26	ns	2	1.79	ns	2	1.89	ns
E	42			90			90			90			42		
S. capillata															
NC	1	0.49	ns	1	0.28	ns	1	0.47	ns	1	6.65	*	1	6.35	*
SC	2	12.19	***	2	0.97	ns	2	6.72	**	2	0.38	ns	2	6.97	**
NC x SC	2	0.36	ns	2	0.02	ns	2	1.25	ns	2	0.19	ns	2	2.66	ns
E	41			89			89			77			41		
3) *B. erectus* in combination with *S. tirsa*															
B. erectus															
NC	1	89.51	***	1	39.79	***	1	12.68	***	1	21.39	***	1	242.00	***
SC	2	117.63	***	2	0.31	ns	2	4.74	*	2	0.19	ns	2	145.19	***
NC x SC	2	8.71	***	2	0.23	ns	2	0.23	ns	2	1.91	ns	2	15.93	***
E	42			90			90			90			42		
S. tirsa															
NC	1	5.04	*	1	14.02	***	1	7.54	**	1	26.84	***	1	40.43	***
SC	2	34.05	***	2	27.88	***	2	18.36	***	2	1.52	ns	2	19.58	***
NC x SC	2	0.17	ns	2	0.03	ns	2	0.25	ns	2	1.20	ns	2	3.61	*
E	40			83			83			72			40		

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Supplementary Table S4. – Results of the two-way ANOVA of leaf area, leaf drymass, LDMC, C/N ratio and RII in the competition experiment: *Bromus erectus* in combination with 1) *Brachypodium pinnatum*, 2) *Stipa capillata* and 3) *S. tirsa* in the first year (nutrient condition: nutrient poor/ nutrient rich; species composition: 9, 6:3, 3:6). Degrees of freedom (df), F-values and error probabilities (* p < 0.05, ** p < 0.1, *** p < 0.001) are given. Abbreviations: NC = nutrient condition; SC = species composition; E = Error; ns = not significant.

Source of variation	**leaf area [mm^2]**			**leaf dry mass [mg]**			**LDMC [mg/g]**			**C/N ratio**		
	df	F	p	df	F	p	df	F	p	df	F	p
1) *B. erectus* in combination with *B. pinnatum*												
B. erectus												
NC	1	24.13	***	1	13.96	***	1	4.68	*	1	8.17	**
SC	2	6.45	**	2	2.27	ns	2	0.23	ns	2	1.28	ns
NC x SC	2	0.40	ns	2	0.50	ns	2	0.51	ns	2	0.93	ns
E	90			90			90			90		
B. pinnatum												
NC	1	21.98	***	1	18.66	***	1	5.10	*	1	1.07	ns
SC	2	4.86	**	2	6.72	**	2	1.67	ns	2	2.06	ns
NC x SC	2	0.32	ns	2	0.13	ns	2	2.22	ns	2	1.18	ns
E	90			90			90			86		
2) *B. erectus* in combination with *S. capillata*												
B. erectus												
NC	1	12.51	***	1	6.30	*	1	0.20	ns	1	6.99	*
SC	2	5.56	**	2	4.84	*	2	1.71	ns	2	1.05	ns
NC x SC	2	2.14	ns	2	1.25	ns	2	0.85	ns	2	2.14	ns
E	90			90			90			90		
S. capillata												
NC	1	1.00	ns	1	0.00	ns	1	0.11	ns	1	5.84	*
SC	2	11.38	***	2	14.71	***	2	4.83	*	2	0.13	ns
NC x SC	2	0.01	ns	2	0.31	ns	2	0.30	ns	2	0.18	ns
E	89			89			89			77		
3) *B. erectus* in combination with *S. tirsa*												
B. erectus												
NC	1	51.64	***	1	19.69	***	1	2.65	ns	1	18.36	***
SC	2	6.81	**	2	7.32	**	2	3.32	*	2	0.23	ns
NC x SC	2	0.43	ns	2	0.65	ns	2	2.56	ns	2	1.85	ns
E	90			90			90			90		
S. tirsa												
NC	1	17.23	***	1	4.78	*	1	2.08	ns	1	23.75	***
SC	2	69.72	***	2	80.78	***	2	2.59	ns	2	1.77	ns
NC x SC	2	0.32	ns	2	0.34	ns	2	1.42	ns	2	1.03	ns
E	83			83			83			72		

Chapter 6

Synthesis

In this thesis, I studied vegetation changes of xerothermic grasslands in Central Germany at the community and species level under changing environmental conditions and land use practices over a time period of more than 20 years by resurveying of vegetation relevés. I analysed functional traits to detect differences in the functional trait composition between dry and semi-dry grasslands to reveal changes in the ecosystem function, and how this functional composition is influenced by soil conditions. In particular, I focused on the abundance, functional traits and their intraspecific trait variability and plant-plant interactions of xerothermic grass species, especially of *Bromus erectus*, to gain a better understanding of the current role of dominant grasses within these grasslands. In the following, I summarise the key results of this thesis and discuss the links across the different chapters.

Summary of results

In **chapter 2** and **chapter 3**, I examined floristic and ecological changes of different xerothermic plant communities and looked at changes in the abundance of grasses, forbs and short-lived plants over time. I found no changes in total species richness of dry and semi-dry grasslands in the regions Kyffhäuser and Porphyry outcrops near Halle (Saale) over time (**chapter 2**), while I confirmed an overall decline of total species richness (-18.2%) and within different xerothermic plant communities at the Schafberg in the lower Unstrut valley (**chapter 3**). In the Kyffhäuser and Porphyry outcrops, dry grasslands showed a higher floristic similarity than semi-dry grasslands over time (**chapter 2**). But at the Schafberg, the grasslands became more dissimilar, as species turnover based on presence/absence of species was 50% across all four investigated associations, while semi-dry grasslands indicated higher species turnover (**chapter 3**). Furthermore, I showed in **chapter 3** that the mean indicator value for temperature increased and that for continentality decreased, whereas the indicator values for nutrients and moisture did not change, but rather were strongly intercorrelated. The proportion of meso-xerophilic species decreased and the proportion of xerophilic species increased (**chapter 3**). In **chapter 2** and **chapter 3**, I revealed a decline of threatened xerothermic species (e.g. *Asperula cynanchica*, *Linum catharticum*, *Teucrium montanum*) and an increase of annual species (e.g. *Draba verna*, *Hornungia petraea*, *Microthlaspi perfoliatum*). While species number and cover of graminoids generally increased (**chapter 2**), most of them decreased in their presence and cover (e.g. *Festuca csikhegyensis*, *Koeleria macrantha*, *Sesleria caerulea*) (**chapter 3**). Surprisingly, in **chapter 2** and **chapter 3**, I found a dramatically significant increase in presence and cover of *Bromus erectus* in most of all investigated plant communities. Other dominant grasses showed partly opposite developments, depending on the study regions: *Brachypodium pinnatum*: no change (**chapter 2**), significant decrease (**chapter 3**); *Festuca rupicola*: significant increase (**chapter 2**), significant decrease (**chapter 3**); *Helictotrichon pratense*: significant increase (**chapter 2**), disappearance (**chapter 3**); *Stipa capillata*: no change (**chapter 2**); significant increase (**chapter 3**).

In **chapter 4**, I compared the functional trait composition between dry and semi-dry grasslands, analysed the impact of soil properties on these grasslands and investigated the intraspecific trait variability of the five dominant grasses *Bromus erectus*, *Brachypodium pinnatum*, *Festuca rupicola*, *Helictotrichon pratense* and *Stipa capillata*. First, I found only a small differentiation in functional trait composition between dry and semi-dry grasslands. The community weighted mean (CWM) of leaf dry mass and leaf area of semi-dry grasslands was significantly higher than those of dry grasslands, likely indicating higher relative growth rates of the species. Second, soil factors had minor effects on the functional trait composition of dry and semi-dry grasslands, but soil depth, soil $CaCO_3$ content and soil C/N ratio had the highest influence on CWM and were the strongest drivers for differentiation. Third, I revealed that the five dominant grasses had species-specific trait differences. For example, *B. erectus* and *S. capillata* showed high vegetative plant height and LNC, while *B. pinnatum* had the highest SLA. Furthermore, all five dominant grasses showed a relatively similar intraspecific trait variability (ITV). Interestingly, *B. erectus* was not better adapted to changing environmental conditions than the other grasses, and even its ITV did not differ between dry and semi-dry grasslands.

In **chapter 5**, I experimentally investigated the growth performance and plant-plant interactions of *Bromus erectus* and the three xerothermic grasses *Brachypodium pinnatum*, *Stipa capillata* and *S. tirsa* under nutrient addition and above-ground biomass removal by conducting a competition experiment. I found that the growth of *B. erectus* was highest in terms of its vegetative traits (e.g. plant height) compared to the other grasses. *Bromus erectus* showed the highest biomass production of all species both in the monocultures and in the mixtures when nutrients were added. The biomass production of *B. erectus* was even doubled by the addition of nutrients when the species was grown alone as single individuals. Moreover, I detected that only *B. erectus* developed generative traits, whereby, for example, its seed mass increased in the monocultures under above-ground removal. Although *B. erectus* was often the most frequent winner after nutrient addition and thus dominant in this treatments, it was less so in the above-ground removal treatment in the mixtures. Compared to the other three grasses, the effect of intraspecific competition in *B. erectus* was slightly more intensive than interspecific competition. Nevertheless, I revealed that the growth and competitive ability of *B. erectus* affected *S. capillata* and *S. tirsa* more negatively than *B. pinnatum*.

General discussion

(i) Which vegetation changes of xerothermic grasslands in Central Germany are evident in the course of ongoing global change over time and are there currently differences in the functional trait composition of these grasslands to reveal changes in their ecosystem function?

In more than 20 years, I found considerable vegetation changes in xerothermic grasslands of Central Germany (**chapter 2, chapter 3**), which can clearly be explained by global change (cf. Dengler et al. 2020). In my thesis, I found that the main drivers are, in this order: 1) climate warming, i.e. mild winters and extremely frequent and intensively hot and dry summers (especially severe drought during my study years 2018/2019), 2) atmospheric nitrogen input and deposition, 3) changes in land use practices. Total species richness depended on the study region, as it did not decrease at the local scale in the Kyffhäuser and Porphyry outcrops, but it did at the Schafberg. However, it is likely that there was no change in total species richness in the Kyffhäuser and Porphyry outcrops, as the loss of one species was compensated by individuals of a newly appeared species (Ellis et al. 2012, Vellend et al. 2013).

In both resurvey studies, I revealed a general species turnover, which was lower in dry grasslands than in semi-dry grasslands (**chapter 2**, **chapter 3**), as the latter are more prone to successional processes (Partzsch 2000, Ellenberg & Leuschner 2010). The species turnover was characterised by 1) a disproportionate decrease and loss in, usually threatened, xerothermic grassland specialists, 2) an increase in winter annuals and 3) an increase in dominant grasses, particularly *Bromus erectus*. My results are consistent with various resurvey studies on xerothermic grasslands, but with changing total species richness. In Germany, for example, no change in species richness was found for the calcareous grasslands of the 'Badraer Lehde-Großer Eller' in the Kyffhäuser area (Hahn et al. 2013), the 'Gabower Hänge' in Brandenburg (Hüllbusch et al. 2016) and the 'Garchinger Heide' in Bavaria (Bauer & Albrecht 2020), while an increase in species richness was recorded for the acidic sandy grasslands of the 'Märkische Schweiz' in Brandenburg (Schüle et al. 2023). Mazalla et al. (2022) found a declining species richness on south-facing slopes for the semi-dry grasslands in north-western Germany. In Europe, for example, an increase in species richness has been documented for the alpine calcareous grasslands in the Northern Alps (Schwaiger et al. 2022) and those of the Vinschgau in South Tyrol (Lübben & Erschbamer 2021), but a decrease in species richness for the calcareous grasslands of southern England (Ridding et al. 2020), semi-dry grasslands of the Swiss Jura Mountains (Charmillot et al. 2021), acidic dry grasslands in southwestern and central Moravia (Harásek et al. 2023) and for the subalpine grasslands of the 'Hrubý Jeseník Mountains' in the Eastern Sudetes of Czech Republic (Klinkovská et al. 2023). Independently of the study region, grassland type and total species richness, it can be generalised: Over time, there was a species turnover, determined by 1) a decrease in typical, often threatened, dry and semi-dry grassland species (resp. character species), so-called habitat specialists, 2) an increase in short-lived (or ruderal) annuals and 3) an increase of some graminoids, which are becoming more dominant.

The replacement of habitat specialists by generalists, in this case dominant grasses, causes a functional homogenisation at the community level, which can have an alternating effect on ecosystem functions (Clavel et al. 2011). I clearly confirmed this functional homogenisation (should not be confused with the taxonomic homogenisation (or floristic similarity) in **chapter 3**) for the xerothermic grasslands of Central Germany, as there were currently hardly any differences in the functional trait composition between dry and semi-dry grasslands at local scale and thus no clear differences in ecosystem function between the two grassland types (**chapter 4**). The functional structure of these grasslands was largely determined by the dominant grasses (mainly *B. erectus*), i.e. more conservative species, suggesting, for example, a relatively similar above-ground biomass production and litter accumulation between dry and semi-dry grasslands (**chapter 4**). It is very likely that global change (especially severe drought) and the resulting species turnover have led to an increasing functional similarity of both grassland types over time (cf. Olden 2006), in that such increased dominant grasses have replaced the functions previously filled by other species in the grasslands with their own functions. Such species are characterised by higher LDMC values, which can be considered the more stable species within a plant community over time (Conti et al. 2022). Consequently, dominant grasses, although exhibiting species-specific trait differences (**chapter 4**), play an equivalent role in the ecosystem function (Joner et al. 2011) of these xerothermic grasslands, and can be considered functionally redundant as they may have a positive effect on the stability of plant communities (Biggs et al. 2020).

In the following, it is therefore necessary to focus on the stability of xerothermic grasslands because the term 'stability' is rather ambiguous, as it often encompasses different properties like constancy, resistence or resilience (Grimm & Wissel 1997). Constancy is the temporal invariability of a system independent of disturbances (Orians 1974) and thus may not contribute to the stability per se, but is rather to be considered as a consequence of that (Van Meerbeek et al. 2021). Communities that have been constant over time can yet be strongly affected by disturbances (Justus 2007), which is the case for the xerothermic grasslands in Central Germany, as most of the investigated dry and semi-dry grassland communities were still recognisable after more than 20 years despite species turnover due to environmental changes (**chapter 2**, **chapter 3**). On the other hand, resistance describes the ability of a specific state variable of an ecosystem to remain during a disturbance (Stuart-Haentjens et al. 2018), while resilience refers to the ability of a specific state variable of an ecosystem to recover after a disturbance (Hodgson et al. 2015). Therein, state variables describe the structure or functioning of an ecosystem (Justus 2007), for example abundance, biomass production or species composition (Standish et al. 2014, Weise et al. 2020), and it is also important to distinguish between 'press' disturbances, continuous changes over time, and 'pulse' disturbances, acute and discrete events that lead to a more or less rapid change in an ecosystem (Jentsch & White 2019). Grazing and climate change can be considered as a 'press' disturbance, while an extreme climate event like a severe summer drought, as pointed out in this thesis, is a 'pulse' disturbance (Sasaki et al. 2015), which can be a source of resilience in xerothermic grasslands.

Generally, xerothermic grasslands are low resistant but high resilient to drought (Hoover et al. 2014, Mackie et al. 2019, Hossain et al. 2023), evidenced, e.g., by a shift in species composition after such 'pulse' disturbance, whereby the proportion of xerophilic species increased and that of meso-xerophilic species decreased (**chapter 3**). However, heat waves and severe summer droughts have increased in frequency and intensity in recent years (Rousi et al. 2022), so that xerothermic grasslands only regenerate more slowly in their species composition after disturbance due to limited resource availability (Stuart-Haentjens et al. 2018), which in turn underlines the fact that a conversion from less conservative to more conservative species (dominant grasses) has taken place over time within both grassland types (**chapter 4**).

Moreover, Oliver et al. (2015) defined the concept of 'functional resilience', which describes the magnitude and frequency of an ecosystem function to resist or recover quickly from environmental disturbances. Dominant grasses, particularly *B. erectus*, are more resilient to drought by maintaining ecosystem function like above-ground biomass production (high LDMC values) of xerothermic grasslands despite such disturbances (**chapter 4**), allowing this ecosystem function to regenerate more quickly. In other words: Regarding the state variable biomass production, dominant grasses can have a positive effect on the 'stability' of the xerothermic grassland communities (see above).

Indeed, some studies revealed that resilience was not considerable affected by species richness of grassland communities (van Ruijven & Berendse 2010, Isbell et al. 2015) and thus the ecosystem probably becomes more resistant to future severe drought events (Xu et al. 2021). However, the investigated grasslands are already affected by climate change and could possibly become less resilient in the course of long-term changes with increasing extreme heat and drought, as the first signals of a negative change in species richness were currently noticeable (**chapter 3**). As the central German xerothermic grasslands are already vulnerable to climate change, adaptive mechanisms need to be implemented, i.e. when the threat is generally known but management can still be adjusted over time (cf. Weise et al. 2020), like varying grazing intensities (see question *(iii)*). Probably, grazing ('press') can mitigate the strength of the drought effect ('pulse') on the ecosystem function of xerothermic grasslands, which could lead to a compensation of grass dominance.

I strongly assume that the increasing drought events are the main drivers for the resulting functional homogenisation of these grasslands, as drought- and stress-tolerant grasses like *B. erectus* can benefit from such conditions (see question *(ii)*). This inevitably leads to the question if weather conditions are not generally the strongest drivers for all vegetation changes in xerothermic grasslands of Central Germany. For example, the increase of winter annuals (**chapter 3**) is mainly caused by fluctuating environmental conditions, as previous milder and wetter winters are beneficial for their successful establishment in early spring, and otherwise, the thinning of vegetation due to summer drought events and partly in interaction with nitrogen deposition leaving open gaps for a new seedling recruitment (Petřík et al. 2011, Fischer et al. 2020), contributing to a large proportion of primary production (Wilcox et al. 2020). Hence, xerothermic grasslands are subject to dynamic processes as environmental fluctuations caused changes in community composition (Adler et al. 2006, Dostálek & Frantík 2011), whereby such grasslands have the potential to regenerate spontaneously after years of heavy disturbance (Labadessa et al. 2023). For this reason, it is crucial to consider temporal variation in environmental conditions, as the predictive power of abiotic factors and functional traits can vary over time, which in turn affects ecosystem function (van der Plas et al. 2020, Huxley et al. 2023). Al Haj Khaled et al. (2005) revealed that SLA and LDMC can fluctuate between the seasons, e.g. grasses developed a significantly higher LDMC in spring than in summer. Conceivably, decadal dynamics due to unpredictable weather conditions, for example, instead of severe drought events, higher amounts of precipitation during the summer months, could probably lead to a regressive succession and thus reduced functional homogenisation (i.e. functional heterogenisation) of xerothermic grasslands.

From a long-term perspective, prolonged drought could lead to a strong conversion of (often species-poorer) dry and semi-dry grassland communities in Central Germany, as dominant grasses have a highly competitive and stress-tolerant strategy type (Grime 2001) and can therefore outcompete other (usually low-competitive) species (Del-Val & Crawley 2005). However, it is rather unlikely that the vegetation units will merge and there will no longer be any independent plant communities, as dry and semi-dry grasslands differ in their site conditions (e.g. slope, soil moisture, light availability) (Ellenberg & Leuschner 2010), which could be mediated in **chapter 2** by differentiating the grassland types on the basis of their indicator values. On the other hand, the mean indicator values for nutrients and moisture did not change, which can be explained by their strong intercorrelation, i.e. increasing drought and eutrophication compensated for each other in their indicator values (**chapter 3**).

Moreover, soil properties such as soil depth, carbonate content and soil C/N ratio had the highest influence on the functional trait composition of these grasslands (**chapter 4**). Becker et al. (2007) indicated that soil depth, carbonate content and pH value have a strong positive and C/N ratio a negative influence on the species richness of xerothermic grasslands. I have only tested the relationships between soil properties and the CWMs and revealed a significant decrease in CWM of leaf dry mass and leaf area, particularly with increasing carbonate content, suggesting that calcareous species suffered from extreme environmental changes by having lower leaf dry mass and leaf area in dry grasslands and thus having to store and maintain their resources in the longer term (Wright et al. 2004). In xerothermic grasslands, there are more calcareous than calcifying species (Ewald 2003), corresponding to the 'species pool concept', in which local species richness is mainly defined by species pool size (Grubb 1987). Pärtel (2002) showed from an evolutionary-historical perspective for the European flora that calcareous soils with a high pH value dominated and therefore revealed a positive correlation between species richness and pH value. Contrary to this, in **chapter 3**, the xerothermic grasslands occur on lower shell limestone and there was a significant decrease in local species richness, so that it cannot be excluded that nowadays soil properties such as carbonate content and pH value may considerably contribute to changing ecosystem functions of these grasslands, which has to be clarified in a further study.

(ii) What is the current role of the increasingly dominant grasses, especially Bromus erectus, in the xerothermic grasslands of Central Germany?

Considering different aspects, such as abundance (**chapter 2**, **chapter 3**), functional traits and their intraspecific trait variability (**chapter 4**) and plant-plant interactions (**chapter 5**), I assessed the current role of the increasingly dominant grasses, especially *Bromus erectus*, within xerothermic grasslands in Central Germany. Depending on the study regions, there were partly opposite results regarding the presence and cover of the grasses *Brachypodium pinnatum*, *Festuca rupicola*, *Helictotrichon pratense* and *Stipa capillata*, presumably due to the edaphic conditions. Especially, soils at the Schafberg are very shallow, often have a high skeletal proportion and a very high carbonate content compared to the other regions (Kugler & Schmidt 1988, Becker 1999, own observations). During severe drought, calcareous soils have the tendency to dry out more rapidly (cf. Amelung et al. 2018), resulting in a possibly negative effect on plant growth. The five grasses differ in their moisture behaviour: *B. pinnatum*, *F. rupicola* and *H. pratense* are meso-xerophilic, while *S. capillata* is xerophilic (partly nitrophilic) and *B. erectus* indifferent (Becker 1998). *Stipa capillata* and *B. erectus* develop an extensively deep root system (Kutschera & Lichtenegger 1982) and are basically better protected against drought than the other shallow-rooted grasses, as they gain water more efficiently in deeper soil layers, reflecting e.g. in their higher vegetative plant height (**chapter 4**). Therefore, *B. pinnatum*, *F. rupicola* and *H. pratense* showed a decrease and *S. capillata* an increase only at the Schafberg (**chapter 3**), but not in the other regions (**chapter 2**). As reported in **chapter 3**, the growth of *S. capillata* is promoted in combination with nitrogen deposition and drought, whereas increased nutrient supply alone might be rather unfavourable because biomass production was higher under nutrient-poor conditions (**chapter 5**).

But over a time period of more than 20 years, only *B. erectus* showed dramatically increasing presence and cover in most of all investigated dry and semi-dry grassland communities of the class *Festuco-Brometea* (**chapter 2**, **chapter 3**). Several resurvey studies documented an increase of at least one of these five grass species (Bauer & Albrecht 2020, Ridding et al. 2020, Lübben & Erschbamer 2021, Mazalla et al. 2022, Klinkovská et al. 2024), whereby *B. erectus* increased considerably in almost all of these studies. In fact, for Central Germany, my results are undisputed and consistent with former authors (Bornkamm 2006, 2008, Heinrich 2010, Helmecke 2017) that *B. erectus* is currently becoming increasingly dominant and truly invading the xerothermic grasslands. Further grass species should also be mentioned here, some of them are becoming increasingly dominant, particularly in Germany or in different parts of Europe in partially other vegetation types (e.g. *Molinio-Arrhenatheretea*) and are also benefiting from ongoing global change: *Arrhenatherum elatius* (Dostálek & Frantík 2012, Holub et al. 2012, Charmillot et al. 2021, Harásek et al. 2023, Klinkovská et al. 2024), *Calamagrostis epigejos* (Süß et al. 2004, Somodi et al. 2008, Hejda et al. 2021), *Dactylis glomerata* (Schüle et al. 2023, Klinkovská et al. 2024).

Primary drivers of the increasing dominance of tall-growing and deep-rooting *B. erectus* are climate change leading to milder winters and drier summers (following its sub-Mediterranean preferences) in combination with airborne nitrogen input and deposition, and secondary drivers are insufficient management practices (e.g. late grazing), which in turn favour its competitiveness (Bornkamm 2006, Lemmer et al. 2021). Therefore, *B. erectus* is clearly the winner of all investigated grass species under ongoing global change, which is attributed to its 1) high regeneration potential after drought damage and disturbance (Corcket et al. 2003, Liancourt et al. 2005, Craine & Dybzinski 2013, Pérez-Ramos et al. 2013, Targetti et al. 2013) and 2) its high competitive ability (Grime 2001, Lemmer et al. 2021). The ability for drought stress tolerance was also revealed in its leaf traits, with *B. erectus* showing significantly higher LNC and LCC but significantly lower vegetative plant height in dry grasslands than in semi-dry grasslands (**chapter 4**). During dry conditions, this species can tolerate better dehydration by transporting and storing of essential resources into its vessels, thereby maintaining leaf turgor and prevent leaf senescence (Pérez-Ramos et al. 2013). Interestingly, Madaj et al. (2023) found no effect of drought on the genetic trait structure of the multivariate phenotype in *B. erectus*.

Once *B. erectus* has established at a site and becoming dominant, it invests in higher biomass production and therefore influences the plant community by competing strongly with other species, leading to lower species richness (Poniatowski et al. 2018, Ridding et al. 2020). Probably, as a consequence of increasing dryness, *B. erectus* may have contributed to the conversion of the *Gentiano-Koelerietum* into an *Onobrychido-Brometum* (**chapter 3**), highlighting the general behaviour of increasing dominant grasses during successional processes (Partzsch 2000, Wesche et al. 2012). Particularly, in an experimental way, *B. erectus* exerted a strong interspecific competition on the three grasses *B. pinnatum*, *S. capillata* and *S. tirsa* under nutrient addition and above-ground removal, leading to competitive exclusion of both species of *Stipa* in future (**chapter 5**). This result is supporting the 'limiting similarity hypothesis' (McArthur & Levins 1967), as these species occupy similar temporal and spatial sites, which intensifies competition for the same resources and can lead to displacement of subordinate species. Thus, in **chapter 5**, the biomass production not only of *B. erectus* individuals growing alone, but also of individuals of this species in the mixtures with the other three grasses was significantly boosted by nutrient addition, suggesting a tendency to overcompensation (cf. Stevens & Gowing 2014) by efficiently using of additional resources (Aschehoug et al. 2016). Indeed, *B. erectus* was the only grass species that showed a high vegetative plant height both in the field and in the experiment (**chapter 4**, **chapter 5**). Likely, *B. erectus* invasion success can also be explained by its highly competitive ability with strong intraspecific competition, mainly driven by high growth rates (cf. Zhang & van Kleunen 2019) and the presence of the 'storage effect' (Adler et al. 2006), meaning that favourable fluctuating environmental conditions can lead to an increase in abundance of a particular species, which after a certain time is limited by intraspecific competition and thus has a stabilising effect on the regulation of species coexistence and community diversity (Chesson 2008, Wilson 2011).

In **chapter 4**, intraspecific trait variability (ITV) of *B. erectus* did not differ fundamentally from those of the grasses *B. pinnatum*, *F. rupicola*, *H. pratense* and *S. capillata*, and even for *B. erectus* not between dry and semi-dry grasslands, indicating a similar adaptation of their functional traits to environmental conditions, which in turn emphasises their equivalent role in stabilising these grasslands (He et al. 2018). However, I only investigated selected vegetative traits (plant height and leaf traits) at an adult life stage of the individuals and other traits were not measured in the field (**chapter 4**). Although vegetative traits for some grasses and additionally generative traits for *B. erectus* were investigated experimentally, I did not consider ITV as it was not the focus of the study in **chapter 5**. Siebenkäs et al. (2015) found that grasses had a low ITV in their leaf traits and plant height but a high ITV in their root traits. Presumably, a higher ITV for *B. erectus* could be shown in its root traits compared to the other grasses because this species is able to cope with increasing summer drought by assimilating resources from deeper soil layers via its extended root system and thus e.g. exerts a strong root competition against *B. pinnatum* (Corcket et al. 2003, Liancourt et al. 2005, Bornkamm 2006). Nevertheless, my overall results only indicate a shift in abundance between the dominant grasses over time, but with no differences in their variability of their vegetative traits (plant height and leaf traits) to environmental conditions during the time of sampling.

But *B. erectus* also might exhibit higher variability in its life-history traits (e.g. plant lifespan, plant persistence, reproductive strategy, growth rate, lateral spread) (Weiher et al. 1999, in' t Zandt et al. 2022), which are associated with the ecological functions such as plant longevity, space-holding ability and disturbance tolerance (Weiher et al. 1999). From my own observations, I definitely noticed that *B. erectus* showed a faster growth rate, as it re-sprouted quickly after clipping and was the only grass species which developed generative traits in the second year of the experiment (**chapter 5**). In' t Zandt et al. (2022) assume that the colonisation success of a species on open soil patches in a grassland community is determined by its life-history traits, which might probably true for *B. erectus*. Despite all dominant grasses being perennial species, it is obvious that *B. erectus*, besides its high disturbance tolerance, also has a higher longevity compared to the other grasses. Therefore, it would be useful to divide perennial plants into longevity categories following the assumption of Weiher et al. (1999). Further evidence for a higher variability in life-history traits of *B. erectus* could be provided by the fact that in the field this species extends its vegetation period by a large part of the year (even in winter) (**chapter 3**), whereby even higher temperatures in early spring can promote successful germination, as the seedlings have a higher frost tolerance (Kahlert et al. 2005, Moser et al. 2011).

Finally, among all dominant grasses, *B. erectus* contributed the most to the functional homogenisation of the xerothermic grasslands of Central Germany (see question *(i)*), but with negative effects on phytodiversity. A similar trend was assumed for the semi-dry grasslands of the 'Diemel Valley' between the federal states of North Rhine-Westphalia and Hesse of Germany by comparing plots in presence and absence of *B. erectus*, but without a resurvey of permanent or quasi-permanent plots and measuring any vegetative traits (Poniatowski et al. 2018).

(iii) Which future recommendations for nature conservation can be derived from the results?

The xerothermic grasslands of Central Germany have lost part of its conservation value as many habitat specialists, including many threatened species, have declined or disappeared in more than 20 years (**chapter 2**, **chapter 3**). My investigated study sites in protected areas were mainly extensively grazed with sheep and goats, while only a few plots were abandoned (Porphyry outcrops; **chapter 2**). Thus, traditional land use have to be continued or reintroduced to maintain and protect the biodiversity of xerothermic grasslands (Török et al. 2016, Benthien et al. 2018, Elias et al. 2018) primarily to counteract the loss of such specialised species and to prevent the increasing dominance of grasses, which in turn could lead to an reduced functional homogenisation, i.e. the ecosystem functions (e.g. primary production) of both grassland types would become more dissimilar.

However, I advocate that grazing is more beneficial for grassland conservation than mowing as it 1) reduces competition between species (i.e. changes in dominance ratios) by a continuous biomass removal during the vegetation period (Tälle et al. 2016) as well as selective defoliation (Stevens & Gowing 2014), 2) creates open soil patches for sufficient seedling recruitment by trampling (Köhler et al. 2016), 3) transports seeds by epi- and endozoochoric dispersal (Benthien et al. 2016), and 4) promotes nutrient uptake by low-competitive species through increased accumulation of excrements (Li et al. 2015). Grazing depends on local site conditions (Tóth et al. 2016), so I recommend a lower grazing intensity for dry grasslands due to their drier site conditions, steeper slope and more sparse vegetation, underlying lower species turnover (**chapter 2**, **chapter 3**). Instead, a higher grazing intensity is required on semi-dry grasslands due to the higher potential for succession to maintain species richness. Therefore, mechanical cutting is also useful to prevent shrub encroachment (Masson et al. 2015), while annual or biennial mowing should be practised as a supplementary measure to grazing (Kahmen et al. 2002).

A current management problem is to suppress highly competitive grasses, especially *B. erectus*, within the xerothermic grasslands of Central Germany. *Bromus erectus* has a high regeneration potential after disturbance (Corcket et al. 2003, Liancourt et al. 2005), which is consistent with own observations in **chapter 2** and **chapter 3**, whereby the leaves of larger tussocks after summer grazing rapidly re-sprouted in autumn. Another hint was noticed when the species re-sprouted vigorously only a few weeks later after an experimental clipping at the end of July, although its growth suffered slightly from above-ground removal (**chapter 5**). These findings definitely reveal that less a low but rather an unfavourable timing of land use promotes the spread of such tall-sized grasses, enabling its higher competitive ability (Nowak & Schulz 2002, Dostálek & Frantík 2012, Lemmer et al. 2021). The most advantageous opportunity of suppressing the increasing dominance of grasses such as *B. erectus* in the longer term is very early and intensive spring grazing with higher stocking rates of sheep (preferably starting at the end of March, or even earlier if the winters are milder and wetter) because the freshly sprouting shoots of such grasses have a higher nutritional value for grazing animals (Elias & Tischew 2016, Elias et al. 2018, Poniatowski et al. 2018). In fact, *B. erectus* has a higher fodder value than *B. pinnatum*, *H. pratense* and *S. capillata* for livestock (Klapp et al. 1953, Klotz et al. 2002), indicating it is likely not spurned as a juvenile plant. Solely mowing is not sufficient, as it favours the growth of *B. erectus* but suppresses those of *B. pinnatum*, whereas burning has the opposite effect on these species (Moog et al. 2002, Kahlert et al. 2005). However, burning is often controversially discussed, as it can remove high levels of litter and promote the recruitment of seedlings (Barnkoth 2013, Klein 2013), but can also considerably alter the species composition of these grasslands (Kahmen et al. 2002).

Nevertheless, Klinkovská et al. (2024) revealed a loss of species richness and a disproportionate decline of habitat specialists and Red List species within xerothermic grasslands in more than four decades, not only in non-protected, but surprisingly also in protected areas of the Central Moravian Carpathians in Czech Republic. Despite a sufficient conservation management in protected areas, the loss of biodiversity seems to be irreversible due to ongoing global change, which has been shown by other resurvey studies (Timmermann et al. 2015, Diekmann et al. 2019, Bauer & Albrecht 2020, Kindermann et al. 2024). Supporting this assumption and based on my results, it is very alarming that traditional land use in protected areas of Central Germany in the course of climate warming (i.e. in particular increasing drought events) and eutrophication obviously can only slows down but not stop the loss of often rare and threatened, xerothermic grassland specialists (and probably the increase of *B. erectus*), leading to a time-delayed extinction of such species at local scale (cf. Klinkovská et al. 2024). For this reason, it is nowadays absolutely necessary to push ahead appropriate grassland restoration (Lyons et al. 2023) because e.g. the creation of adequate restoration sites can improve the functional connectivity of fragmented grassland patches (Deák et al. 2021). Further opportunities for species reintroduction can be direct sowing from a native species pool (Kiehl et al. 2010, Kiss et al. 2021) or targeted planting of pre-cultivated species, which was successfully realised e.g. for the threatened species *Jurinea cyanoides* (Tischew & Kommraus 2009) and *Scorzonera purpurea* (Kienberg et al. 2013). Problematically, such projects usually depend on funding from responsible policy initiatives (Löfqvist & Ghazoul 2019).

Conclusion, study limitations and future perspectives

My results contribute considerably to the understanding of vegetation changes in xerothermic grasslands of Central Germany. In dry and semi-dry grasslands, a species turnover has taken place in more than two decades and the vegetation became more dissimilar, primarily driven by increasingly severe drought events. Currently, there are no fundamental differences in the functional trait composition of both grassland types. Therefore, for the first time, the functional homogenisation of xerothermic grasslands in Central Germany was revealed. Moreover, novel insights into the current role of dominant grasses within central German xerothermic grasslands were obtained, particularly with the grass species *B. erectus* being the clear winner of all species under ongoing global change due to its high regeneration potential after drought and disturbance and high competitive ability. Thus, traditional land use practices are essential for the protection of the biodiversity of these grasslands and for the suppression of highly competitive grasses.

However, it should be considered that studies at local scale cannot reflect global trends (Vellend et al. 2013, Blowes et al. 2019) and Chase et al. (2019) highlighted that species richness can change across different spatial scales, which should definitely be taken into account when considering biodiversity changes. But resurvey studies are essential for the assessment of future vegetation changes (Jandt et al. 2022). I detected similar results by resurveying both quasi-permanent and permanent plots (e.g. decrease of xerothermic grassland specialists, increase of annuals and *B. erectus*), confirming that both resurvey methods are adequate and valid for studying vegetation changes of xerothermic grasslands over time (Chytrý et al. 2014). So, I marked all plots with magnets, which enables a future biodiversity monitoring. As described in **chapter 1**, relocalisation problems and obersever errors cannot be avoided (Kapfer et al. 2018, Boch et al. 2022), but I have tried to minimise these factors as much as possible, even if I may have overlooked (e.g. annuals) or misidentified single species during the resurvey. Additionally, two plots out of a total of 103 resurveyed plots could not be functionally investigated because the sites were grazed on the day of the vegetation survey. Nevertheless, the functional traits were only investigated at the time of sampling in 2018/2019 during periods of extreme droughts (**chapter 4**). For this reason, it would be advisable to measure functional traits again on the same plots to check whether decadal changes in weather conditions lead to a decreasing or increasing functional homogenisation of xerothermic grasslands. Here, the effect of land use could also be included (grazed vs. mowed vs. abandoned sites), as e.g. grazing can have different effects on the functional trait composition of these grasslands (Niu et al. 2016). Of course, covering not only three regions but also as many other study areas in Central Germany as possible would be beneficial to allow more general conclusions about this xerothermic grasslands. Furthermore, further functional traits (e.g. root traits) could have been investigated in the competition experiment (**chapter 5**) (see question *(ii)*), as it is known that *B. erectus* has a strong root competition with other species (Bornkamm 2006). However, such an experiment requires a different study design with plant tubes (see methods in Davrinche & Haider 2023, but it was only conducted for trees and is possibly transferable to perennial grasses).

In the near future, I strongly expect that some previously not yet threatened xerothermic species may have to be added to the Red Lists of the federal states of Thuringia, Saxony-Anhalt or probably even for Germany, while for other species their endangerment category will change in a negative sense (theoretically, these lists should be revised annually). The loss of threatened species is irreversibly, leading to the assumption that these species may truly become locally extinction in the longer term within xerothermic grasslands. Particularly, the decline or disappearance of *Asperula cynanchica* and/or *Linum catharticum* has already been reported by many authors (Hahn et al. 2013, Ridding et al. 2020, Charmillot et al. 2021, Harásek et al. 2023, Klinkovská et al. 2024). Understanding species rarity for conservation, a novel approach could be to investigate how functional trait architecture differs between threatened and common xerothermic grassland species to find out which functional traits are associated with the extinction of habitat specialists. Similarly, one study has already been conducted for species in Czech Republic, but it was not directly focused on the comparison between dry and semi-dry grasslands (Gabrielová et al. 2013). Indeed, probably an evidence of a functional gradient between taller semi-dry grassland species with heavier and larger leaves and small dry grassland (often calcareous) species with lighter and smaller leaves could be detected (**chapter 4**). Presumably, species with a smaller vegetative plant height, leaf dry mass and leaf area could decline more rapidly than species with opposite characteristics. Mariotte (2014) stated that species with smaller leaves are less able to capture light and are therefore less common than species with larger leaves.

Seemingly, *B. erectus* has a fitness advantage compared to other dominant xerothermic grasses, as it was the only species to develop generative traits already in the second year of the competition experiment (**chapter 5**), suggesting a more efficient establishment and reproduction in the field on new sites. Early flowering of *B. erectus* in spring allows it to reproduce before hot and dry summer conditions arise, which could have an advantage compared to other species under future climatic conditions (Andrzejak et al. 2023). Therefore, a germination experiment would be conceivable by testing germination rates of *B. erectus* (and other dominant grasses) in combination between different temperature conditions (ambient vs. future temperatures) and land use practices (e.g. seed origins from grazed vs. mowed plots). In addition, so-called 'early seedling traits' should definitely be investigated, as only a few studies have so far dealt with functional traits of seedlings (cf. Larson & Funk 2016, Harrison & LaForgia 2019) offering new insights into the seedling establishment of dominant grasses.

Moreover, herbarium specimens are becoming more important in global change research (Lang et al. 2019, Kozlov et al. 2021). A novel approach is to compare earlier with current leaf nutrient concentrations by using herbarium specimens (cf. Gritcan et al. 2016), as such comparison could potentially be used to derive the increasing dominance of *B. erectus* over time. If possible, the preferably former locations of this grass should be revisited, leaves collected and then both herbarium and current leaf samples investigated using C/N analysis or in a non-destructive way via Near-Infrared Spectroscopy (NIRS) (cf. Kühn et al. 2024).

Based on my results, I expect a further increase of *B. erectus* within central German xerothermic grasslands in future, whereas its immigration in northern direction of Europe will dramatically continue (cf. Bornkamm 2008). In the course of climate warming, this grass could colonise new sites in previously colder regions, suggesting the validity of the 'law of relative site constancy', which states that species compensate for their regional differences in climatic conditions by choosing relatively similar sites and adjusting their topographical position (Walter & Walter 1953). Genetic studies may be a supporting approach to gain a better understanding of the new immigration trends of this species. In fact, based on ISSR-PCR fingerprinting, the genetic stock of the German *B. erectus* populations probably originates from Moravia and Bohemia, where such species survived the last glacial maximum (Sutkowska et al. 2013). Although the competitive potential of *B. erectus* may not yet be fully achieved (or the 'tipping point' is not yet attained), the first negative effects of its dominance on the species richness of these grasslands are already noticeable. Nevertheless, the increased drought was a stronger driver than the increase in competition from *B. erectus* on the resulting dissimilarity of the vegetation. However, I advocate a new project that is currently being realised in Central Germany, in which different management practices are tested on selected sites dominated by *B. erectus*: grazing with different livestock (cattle, horses, sheep, goats), mowing, shrub cutting, burning and abandonment (Offenlandinfo n.d.). Among the grazing variants, respectively, it would be useful to differentiate not only between the animal species, but also between stocking rates and timing (e.g. spring vs. summer grazing). The prioritised aim of this project is to identify effective countermeasures and the most appropriate management practice to successfully prevent the expansion of *B. erectus* at an early stage and also to sensibilise land owners towards this issue. A good idea would be here to include not only vegetation surveys but also functional traits.

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Appendix

List of electronic supplements

Chapter 2:

Supplement E1. Regions and their study areas (see Fig. 1).

Anhang E1. Regionen und ihre Untersuchungsgebiete (vgl. Abb. 1).

Supplement E2. Detailed map of the quasi-permanent plots in the individual study areas. The relevé number refers to the recent vegetation relevés in Supplement E3. Coordinates are given in Supplement E5. a) near Mücheln (Wettin); b) Mittelberg (41) and Badraer Lehde (40) (Kyffhäuser); c) Ochsenburg (Kyffhäuser); d) Kosakenberg (24, 39), Grauer Berg (25) and Hämling (23) (Kyffhäuser).

Anhang E2. Detaillierte Karten der quasi-permanenten Aufnahmeflächen der einzelnen Untersuchungsgebiete. Die Aufnahmenummer bezieht sich auf die aktuellen Vegetationsaufnahmen in Anhang E3. Koordinaten sind in Anhang E5 angegeben a) bei Mücheln (Wettin); b) Mittelberg (41) und Badraer Lehde (40) (Kyffhäuser); c) Ochsenburg (Kyffhäuser); d) Kosakenberg (24, 39), Grauer Berg (25) und Hämling (23) (Kyffhäuser).

Supplement E3. Comparison of the previous (1995 - 2002) and recent (2018/19; bold) vegetation relevés of the dry and semi-dry grasslands in Central Germany (original coverage of the species). The plant communities are classified according to SCHUBERT et al. (1995). In the recent relevés, the coverage of the species was estimated using the 9-part Braun-Blanquet scale ((REICHELT & WILMANNS 1973) (for adjusted coverage see Supplement E4). The coordinates for the recent relevés are listed in Supplement E5. Abbreviations: 1) Author: BR - Babette Richter, KS - Katrin Schneider, JP - Jürgen Pusch, TM - Tim Meier; 2) Plant community: TeF - *Teucrio-Festucetum*, FeS - *Festuco-Stipetum*, FuS - *Fumano-Seslerietum*, FiH - *Filipendulo-Helictotrichetum*, Sts - *Stipetum stenophyllae*, FeB - *Festuco-Brachypodietum*, OnB - *Onobrychido-Brometum*, GeK - *Gentiano-Koelerietum*; 3) Study site: MCH - Mücheln, MBA - Mittelberg, BDL - Badraer Lehde, OCH - Ochsenburg, KKB - Kosakenberg, GBF - Grauer Berg, HLU - Hämling; 4) Bedrock: por - porphyry, gps - gypsum, ahy - anhydrite, kak - limestone.

Anhang E3. Vergleich der früheren (1995–2002) und aktuellen (2018/19; fett gedruckt) Vegetationsaufnahmen der Trockenrasen und Halbtrockenrasen in Mitteldeutschland (originale Deckungsgrade der Arten). Die Einteilung der Pflanzengesellschaften erfolgt nach SCHUBERT et al. (1995). Bei den aktuellen Aufnahmen wurden die Deckungsgrade der Arten nach der 9-teiligen Braun-Blanquet-Skala (REICHELT & WILMANNS 1973) geschätzt (angepasste Deckungsgrade siehe Anhang E4). Die Koordinaten für die aktuellen Aufnahmen sind in Anhang E5 aufgeführt. Abkürzungen: 1) Autor: BR – Babette Richter, KS – Katrin Schneider, JP – Jürgen Pusch, TM -Tim Meier; 2) Pflanzengesellschaft: TeF - *Teucrio-Festucetum*, FeS - *Festuco-Stipetum*, FuS - *Fumano-Seslerietum*, FiH - *Filipendulo-Helictotrichetum*, Sts - *Stipetum stenophyllae*, FeB - *Festuco-Brachypodietum*, OnB - *Onobrychido-Brometum*, GeK - *Gentiano-Koelerietum*; 3) Gebiet: MCH - Mücheln, MBA - Mittelberg, BDL - Badraer Lehde, OCH - Ochsenburg, KKB - Kosakenberg, GBF - Grauer Berg, HLU - Hämling; 4) Ausgangsgestein: por - Porphyr, gps - Gips, ahy - Anhydrit, kak - Kalkstein.

Supplement E4. Comparison of the previous (1995–2002) and recent (2018/19; bold) vegetation relevés of the dry grasslands and semi-dry grasslands in Central Germany with adjusted coverages of the species. Explanations and abbreviations see Supplement E3.

Anhang E4. Vergleich der früheren (1995–2002) und aktuellen (2018/19; fett gedruckt) Vegetationsaufnahmen der Trockenrasen und Halbtrockenrasen in Mitteldeutschland mit angepassten Deckungsgraden der Arten. Erläuterungen und Abkürzungen siehe Supplement E3.

Supplement E5. Coordinates for the 57 quasi-permanent plots. The relevé number refers to the recent vegetation relevés in Supplement E3.

Anhang E5. Koordinaten für die 57 quasi-permanenten Aufnahmeflächen. Die Aufnahmenummer bezieht sich auf die aktuellen Vegetationsaufnahmen in Anhang E3.

Supplement E6. Species with increased or decreased constancy (presence/ absence) between previous (1995–2002) and recent (2018/19) vegetation relevés. The species are divided into functional groups (FG): annuals (A), graminoids (G), forbs (F). Within the functional groups, the species are sorted in descending order of difference. Species without a significant change in constancy are shown. Only species that appeared more than five times in the relevés were considered. P-value: result of the Wilcoxon signed-rank test. In addition, the status (0 - extinct or lost, 1 - threatened with extinction, 2 - critically endangered, 3 - endangered, D - insufficient data, V - warning list) according to the Red Lists (RL) of Saxony-Anhalt (SA; FRANK et al. 2020) and Thuringia (TH; KORSCH e tal. 2011) as well as the legal protection status under the Federal Species Protection Regulation (S) are given.

Anhang E6. Arten mit zunehmender und abnehmender Stetigkeit (Präsenz/ Absenz) zwischen den früheren (1995–2002) und aktuellen (2018/19) Vegetationsaufnahmen. Die Arten sind in funktionelle Artengruppen eingeteilt (FG): Annuelle (A), Gräser (G), Kräuter (F). Innerhalb der funktionellen Gruppen sind die Arten nach absteigender Differenz sortiert. Es sind Arten dargestellt, die keine signifikante Veränderung in der Stetigkeit aufweisen. Dabei werden nur Arten berücksichtigt, die mehr als fünfmal in den Aufnahmen vorkamen. P-Wert: Ergebnis des Wilcoxon-Signed-Rank-Tests. Außerdem sind der Gefährdungsstatus (0 - ausgestorben oder verschollen, 1 - vom Aussterben bedroht, 2 - stark gefährdet, 3 - gefährdet, D - Daten defizitär, V - Vorwarnliste) nach den Roten Listen (RL) von Sachsen-Anhalt (SA; FRANK et al. 2020) und Thüringen (TH; KORSCH et al. 2011) sowie der gesetzliche Schutz nach Bundesartenschutzverordnung (S) angegeben.

Chapter 3:

Supplement E1. Biological/ecological characteristics of studied species. Threat categories according to the RL G – Red List of Germany (METZING et al. 2018) and RL SA – Red List of Saxony-Anhalt (FRANK et al. 2020): 1 – critically endangered, 2 – endangered, 3 – vulnerable, V – near-threatened. § – protected after national species protection ordinance. Life forms (LF) according to ELLENBERG et al. (2001): C – herbaceous chamaephyte, G – geophyte, H – hemicryptophyte, N – nano-phanerophyte, P – phanerophyte, T – therophyte. Sublife forms of short-lived species according to KLOTZ et al. (2002) and own observations: sum – summer annuals, win – winter annuals, bien – biennials (monocarpic-perennial). CSR strategy types according to KLOTZ et al. (2002): CS – competition/stress strategy, CSR – competition/stress/ruderal strategy, SR – stress/ruderal strategy. Moisture behaviour types according to BECKER (1998b): xero – xerophilic, meso-xero – meso-xerophilic, × – indifferent behaviour. Mean Ellenberg indicator values according to ELLENBERG et al. (2001) for: L – light, T – temperature, K – continentality, F – moisture, R – soil reaction, N – nutrients.

Anhang E1. Biologisch-ökologische Eigenschaften der untersuchten Arten. Gefährdung nach der RL G – Roten Liste Deutschlands (METZING et al. 2018) und RL SA – Roten Liste Sachsen-Anhalts (FRANK et al. 2020). Die Gefährdungskategorien sind: 1 – vom Aussterben bedroht, 2 – stark gefährdet, 3 – gefährdet, V – Vorwarnliste. § – geschützt nach Bundesartenschutzverordnung. Lebensformen (LF) nach ELLENBERG et al. (2001): C – krautige Chamaephyten, G – Geophyten, H – Hemikryptophyten, N – Nano-Phanerophyten, P – Phanerophyten, T – Therophyten. Sub-Lebensformen kurzlebiger Arten nach KLOTZ et al. (2002) und eigenen Beobachtungen: sum – sommer-annuell, win – winter-annuell, bien – zweijährig (mehrjährig-monokarp). CSR-Strategietypen nach KLOTZ et al. (2002): CS – Konkurrenz/Stress-Stratege, CSR – Konkurrenz/Stress/Ruderal-Stratege, SR – Stress/Ruderal-Stratege. Feuchteverhalten nach BECKER (1998b): xero – xerophil, meso-xero – meso-xerophil, × – indifferentes Verhalten. Mittlere Ellenberg-Zeigerwerte nach ELLENBERG et al. (2001): L – Licht, T – Temperatur, K – Kontinentalität, F – Feuchte, R – Bodenreaktion, N – Nährstoff.

Supplement E2. Synoptic table of the dry grassland communities in 1995 und 2019. Species are primary arranged according their association indication in 1995 und secondary according their association indication in 2019. Associations are: Bro – Bromus grasslands (*Onobrychido-Brometum*), Car – *Carex humilis* grassland (*Trinio-Caricetum*), Koe – Koeleria grassland (*Gentiano-Koelerietum*), Ses – Sesleria grassland (*Carici-Seslerietum*), Sti – Stipa grassland (*Festuco-Stipetum*). Percent constancies with mean percent cover in upper case. Species with fidelity degree ϕ > 0.25 in one or several associations after a Fisher's exact test are highlighted in grey. Within the groups, species are arranged according to decreasing constancy. Species that are diagnostic for more than one unit are sorted within the unit with the higher phi -value. Significant winner species (W) or loser species (L) – over all associations – are indicated by W/L symbols. W/L symbols in bold indicate new or disappeared winner or loser species.

Anhang E2. Übersichtstabelle der Trockenrasengesellschaften in den Jahren 1995 und 2019. Die Arten sind primär nach ihrer Assoziationsindikation in 1995 und sekundär nach ihrer Assoziationsindikation in 2019 sortiert. Die Assoziationen sind: Bro – Bromus-Halbtrockenrasen (*Onobrychido-Brometum*), Car – *Carex humilis* -Trockenrasen (*Trinio-Caricetum*), Koe – Koeleria-Halbtrockenrasen (*Gentiano-Koelerietum*), Ses – Sesleria-Trockenrasen (*Carici-Seslerietum*), Sti – Stipa-Trockenrasen (*Festuco-Stipetum*). Prozentstetigkeiten mit hochgestellter mittlerer Prozentdeckung. Hochtreue Arten der Assoziationen mit $\phi > 0,25$ nach einem Fisher's exact-Test sind grau hinterlegt. Innerhalb der Differentialartengruppen sind die Arten nach abnehmender Stetigkeit sortiert. Die Position derjenigen Arten, die für mehrere Einheiten diagnostisch sind, richtet sich nach der derjenigen Einheit, in der die Arten ihren höchsten ϕ -Wert aufweisen. Signifikante Gewinner-(W) oder Verliererarten (L) – über alle Assoziationen – sind mit W/L-Symbolen gekennzeichnet. Fettgedruckte W/L-Symbole zeigen neue oder verschwundene Gewinner- oder Verliererarten an.

Supplement E3. Constant vascular plant species or species that are too rare for assessing their change. Frequencies (constancies) in percent and mean percent cover values in uppercase. All comparisons shown are not significant (n.s.) at $p > 0.1$.

Anhang E3. Konstante Gefäßpflanzenarten oder Arten, die zu selten sind, um ihre Veränderung zu bemessen. Prozentstetigkeiten und mittlere Prozentdeckungen (hochgestellt). Alle gezeigten Vergleiche sind nicht signifikant (n.s.) bei $p > 0,1$.

Unpublished original data. Vegetation relevés of 1995 and 2019 of the dry grassland communities at the Schafberg.

Unpublizierte originale Daten. Vegetationsaufnahmen von 1995 und 2019 der Trockenrasengesellschaften am Schafberg.

Betreuerbestätigung

Bestätigung des Betreuers der Dissertation von Herrn Tim Meier

Hiermit bestätige ich als Betreuer/in der o. g. Dissertation, dass die gemeinsame Arbeit mehrerer Personen an der Arbeit durch den Forschungsgegenstand gerechtfertigt ist.

Mit freundlichen Grüßen,

Datum: 23.04.2024

…………………………………………….

Prof. Dr. Isabell Hensen

Author contributions

Deklaration der Beiträge von Autoren zur kumulativen Arbeit (entsprechend §7 (5) der Promotionsordnung der Naturwissenschaftlichen Fakultäten I, II und III der MLU).

Chapter 2: Tim Meier, Isabell Hensen, Monika Partzsch (2021), "Floristic changes of xerothermic grasslands in Central Germany: A resurvey study based on quasi-permanent plots", *Tuexenia*, 41, 203–226. DOI 10.14471/2021.41.009

	Tim Meier [%]	**Isabell Hensen [%]**	**Monika Partzsch [%]**
Design	60	20	20
Implementation	100	0	0
Analysis	80	0	20
Writing	60	20	20

Chapter 3: Tim Meier, Isabell Hensen, Monika Partzsch, Thomas Becker (2022), "Are recent climate change and airborne nitrogen deposition responsible for vegetation changes in a central German dry grassland between 1995 and 2019?", *Tuexenia*, 42, 165–200. DOI 10.14471/2022.42.011

	Tim Meier [%]	**Isabell Hensen [%]**	**Monika Partzsch [%]**	**Thomas Becker [%]**
Design	40	20	20	20
Implementation	100	0	0	0
Analysis	50	0	0	50
Writing	40	10	10	40

Chapter 4: Tim Meier, Isabell Hensen, Ingolf Kühn, "Functional approach to xerothermic grasslands in Central Germany: Trait composition, dominant grasses and soil factors", *Preslia* (in revision).

	Tim Meier [%]	**Isabell Hensen [%]**	**Ingolf Kühn [%]**
Design	50	20	30
Implementation	100	0	0
Analysis	70	0	30
Writing	60	10	30

Chapter 5: Tim Meier, Isabell Hensen, Monika Partzsch (2022), “Effects of nitrogen addition and above-ground biomass removal on the growth and interactions between species of xerothermic grasses“, *Preslia 94(4)*, 607–629. DOI 10.23855/preslia.2022.607

	Tim Meier [%]	**Isabell Hensen [%]**	**Monika Partzsch [%]**
Design	50	20	30
Implementation	100	0	0
Analysis	80	0	20
Writing	60	20	20

Datum: 23.04.2024

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Tim Meier Prof. Dr. Isabell Hensen

Curriculum vitae

Tim Meier

Education

10/2017 - present: PhD student
Institute of Biology/ Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg
PhD thesis: „Xerothermic grasslands in Central Germany: Vegetation changes, functional trait composition and plant-plant interactions“
Supervisor: Prof. Dr. Isabell Hensen
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10/2013 - 09/2017: Master of Science Biology
Martin Luther University Halle-Wittenberg
Master thesis: „Abiotische Faktoren und funktionelle Merkmale von *Stipa* dominierten Xerothermrasen in Mitteldeutschland“
Supervisors: Prof. Dr. Isabell Hensen, Prof. Dr. Ingolf Kühn

10/2010 - 12/2013: Bachelor of Science Biology
Martin Luther University Halle-Wittenberg
Bachelor thesis: „Keimung, Keimlingsetablierung und Wachstumsentwicklung von drei dikotylen Graslandarten in *Festuca rupicola*-Beständen mit unterschiedlicher Dichte“
Supervisors: Prof. Dr. Isabell Hensen, Dr. Monika Partzsch

09/2003 - 08/2009: Abitur: Käthe-Kollwitz-Gymnasium, Halberstadt

Professional experience

11/2023 - 01/2024: Research assistant
Helmholtz Centre for Environmental Research (UFZ), Department of Community Ecology, Halle (Saale)
Supervisor: Dr. Lotte Korell
Projects: „BugNet“, „Plant Demography“, „RegioDiv“

03/2023 - 10/2023: Research assistant
Institute for Ecology and Evolution, Plant Biodiversity Group, Friedrich Schiller University Jena
Supervisors: Prof. Dr. Christine Römermann, Matthias Körschens
Project: „PhenEye - Having an eye on the fingerprint of global change: observing phenology using automated monitoring“

12/2022 - 09/2023: Technical assistant
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07/2017 - 09/2017:	Research assistant Institute of Geobotany and Botanical Garden, Plant Ecology Group, Martin Luther University Halle-Wittenberg Supervisor: Prof. Dr. Isabell Hensen
09/2009 - 08/2010:	Voluntary Ecological Year (FÖJ) Museum Heineanum, Halberstadt Topics: ornithology, ecology, nature conservation

Teaching and supervision

2024:	Markus Splith. Master thesis: „Population ecology studies on three *Helianthemum* species in Central Germany: environmental factors and functional traits“ Main supervisor: Prof. Dr. Isabell Hensen
2021:	Markus Splith. Bachelor thesis: „Intra- und interspezifische Interaktionen bei *Bromus erectus* und *Linum austriacum*“ Main supervisor: Prof. Dr. Isabell Hensen
2021:	Sandro Dreilich. Bachelor thesis: „Einfluss von *Bromus erectus* auf die Keimung und Etablierung von zwei dikotylen Xerothermrasenarten“ Main supervisor: Prof. Dr. Isabell Hensen
06/2019:	Master student course: „Field Ecology“, Institute of Biology/ Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg

09/2017, 09/2019:	Practical course for students in the Müritz Nationalpark, Institute of Biology/ together with Geobotany and Botanical Garden and Molecular Ecology, Martin Luther University Halle-Wittenberg
2018 - 2023 (annual):	Bachelor student excursions: „Vegetation of alluvial forests“, „Vegetation of ruderal sites“, „Vegetation of xerothermic grasslands“, Institute of Biology/ Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg

Participation in courses

06/2016:	Graduate Course: 'Species traits: a functional approach to biodiversity, from organisms to ecosystems (6th edition).' University of South Bohemia, České Budějovice, Czech Republic

Scientific memberships

since 2021:	Botanischer Verein Sachsen-Anhalt e.V.
since 2021:	Floristisch-soziologische Arbeitsgemeinschaft e.V.

Scholarships and awards

Scholarship of the federal state Saxony-Anhalt (10/2017 - 03/2021): Funding of my PhD studies.

Award of the Floristic-Sociological Working Group (FlorSoz) for young authors: **Meier, T.**, Hensen, I., Partzsch, M. (2021): Floristic changes of xerothermic grasslands in Central Germany: A resurvey study based on quasi-permanent plots. – *Tuexenia 41*: 203–226. (20.08.2021, Rostock, Germany)

Halle (Saale), 23.04.2024 ....

Tim Meier

List of publications

Publications of this thesis

Meier, T., Hensen, I., Kühn, I.: Functional approach to xerothermic grasslands in Central Germany: Trait composition, dominant grasses and soil factors. – *Preslia* (in revision)

Meier, T., Hensen, I., Partzsch, M. (2022): Effects of nitrogen addition and above-ground biomass removal on the growth and interactions between species of xerothermic grasses. – *Preslia 94(4)*: 607–629. DOI: 10.23855/preslia.2022.607

Meier, T., Hensen, I., Partzsch, M., Becker, T. (2022): Are recent climate change and airborne nitrogen deposition responsible for vegetation changes in a central German dry grassland between 1995 and 2019? – *Tuexenia 42*: 165–200. DOI: 10.14471/2022.42.011

Meier, T., Hensen, I., Partzsch, M. (2021): Floristic changes of xerothermic grasslands in Central Germany: A resurvey study based on quasi-permanent plots. – *Tuexenia 41*: 203–226. DOI: 10.14471/2021.41.009

Other publications of the author

Meier, T., Rußwurm, N., Wegener, U.: Phytocoenology, growth and fitness of *Pulsatilla pratensis* subsp. *nigricans* (STÖRCK) ZÄMELIS in the northern foothills of the Harz Mountains (Saxony-Anhalt, Germany). (in preparation)

Meier, T. (2023): *Aster alpinus* L. an den Kleinen Rabenklippen oberhalb der Rappbodetalsperre nördlich von Trautenstein (Landkreis Harz). – *Mitteilungen zur floristischen Kartierung in Sachsen-Anhalt (Halle) 28*: 49–54. DOI: 10.21248/mfk.436

Meier, T. (2022): Ökologische Untersuchungen an *Iris aphylla* L. im Osthuy nordwestlich von Halberstadt (Landkreis Harz). – *Mitteilungen zur floristischen Kartierung in Sachsen-Anhalt (Halle) 27*: 105–112. DOI: 10.21248/mfk.14

Meier, T. (2021): *Scorzonera purpurea* L. am Taubenberg bei Sargstedt (Landkreis Harz). – *Mitteilungen zur floristischen Kartierung in Sachsen-Anhalt (Halle) 26*: 93–97. DOI: 10.21248/mfk.29

Splith, M., Hensen, I., Partzsch, M., **Meier, T.** (2021): Intra- und interspezifische Interaktionen in Xerothermrasen zwischen dem dominanten Gras *Bromus erectus* und der dikotylen Art *Linum austriacum*. – *Hercynia N. F. 54(2)*: 157–179.

Meier, T., Hensen, I., Kühn, I. (2019): Federgras-Bestände in Mitteldeutschland. - Teil II. Funktionelle Merkmale. – *Hercynia N. F. 52(2)*: 129–163.

Meier, T., Partzsch, M. (2018): Federgras-Bestände in Mitteldeutschland. - Teil I. Aktuelle Situation und Bestandsentwicklung. – *Hercynia N. F. 51(2)*: 113–154.

Partzsch, M., Faulhaber, M., **Meier, T.** (2018): The effect of the dominant grass *Festuca rupicola* on the establishment of rare forbs in semi-dry grasslands. – *Folia Geobotanica 53*: 103–113. DOI: 10.1007/s12224-017-9298-8

Book reviews of the author

Meier, T. (2023): Sundin, A. (2023): Farne – Vielfalt und Geschichte einer der ältesten Pflanzengruppen. – *Hercynia N. F. 56*: 29–31.

Meier, T. (2023): Schönfelder, I., Schönfelder, P. (2023): Der Kosmos Heilpflanzenführer – Über 600 Heil- und Giftpflanzen Europas. – *Hercynia N. F. 56*: 27–28.

Meier, T. (2022): Succow, M., Jeschke, L. (2022): Deutschlands Moore – Ihr Schicksal in unserer Kulturlandschaft. – *Hercynia N. F. 55*: 69–71.

Meier, T. (2022): Laux, H. E. (2022): Der große Kosmos Pilzführer – Alle Speisepilze mit ihren giftigen Doppelgängern. – *Hercynia N. F. 55*: 67–68.

Meier, T. (2021): Griebl, N., Presser, H. (2021): Orchideen-Europas. – *Hercynia N. F. 54(2)*: 181–182.

Meier, T. (2020): Wegener, U. (2017): Bewegte Zeiten in zwei Gesellschaftssystemen - Naturschutz im Wandel. – *Hercynia N. F. 53(2)*: 390–392.

Meier, T. (2020): Hauck, M., Leuschner, C., Homeier, J. (2019): Klimawandel und Vegetation - Eine globale Übersicht. – *Hercynia N. F. 53(2)*: 386–389.

Conference contributions

Meier, T. (2018): Die von *Stipa* dominierten Xerothermrasen in Mitteldeutschland. Frühjahrstagung Botanischer Verein Sachsen-Anhalt e. V., Halle (Saale), 03.03.2018. (talk)

Partzsch, M., Faulhaber, M., **Meier, T.** (2017): The stages of establishment of rare semi-dry grassland forbs are differently affected by vegetation density and seed size. – 30th Conference of the Plant Population Biology Section of the Ecological Society of Germany, Austria and Switzerland. "POPBIO 2017 Population Biology in a Changing World". 18. -20.05.2017, Halle (Saale), Germany. (poster)

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Bromus erectus. Moreover, I thank the whole team for the family atmosphere I enjoyed during my fieldwork while staying there.

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I would also like to thank Birgit Müller for her indispensable support with field and laboratory work. Also, I acknowledge Tim Walther for his guidance with the C/N analysis, Gunnar Seidler for creating the maps of the study areas, Sebastian Leonhardt for providing vegetation data and Danny McCluskey for various language corrections of the manuscripts.

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My PhD studies were supported by a graduate stipend of the federal state of Saxony-Anhalt. After my scholarship ended, I worked in different institutions to get financial support. There, I had the opportunity to learn a variety of working methods and to acquire or intensify new scientific knowledge. Representatively, I would like to mention the following people who were particularly involved in giving me temporary employment: Prof. Dr. Isabell Hensen (Martin Luther University Halle-Wittenberg, Institute of Geobotany and Botanical Garden, Working Group Plant Ecology), Prof. Dr. Christine Römermann (Friedrich Schiller University Jena, Institute of Ecology and Evolution with Botanical Garden and Herbarium Haussknecht, Working Group Plant Biodiversity), Prof. Dr. Nico Eisenhauer and Anna-Maria Madaj (University Leipzig, German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Working Group Experimental Interaction Ecology), Dr. Lotte Korell (Helmholtz Centre for Environmental Research (UFZ), Department Community Ecology). I am deeply grateful to all of them.

Finally, I warmly thank my parents and grandparents for their unlimited support and motivation during all the years since I started my study.

Eigenständigkeitserklärung

Hiermit erkläre ich, dass ich die vorliegende Doktorarbeit mit dem Titel „Xerothermic grasslands in Central Germany: Vegetation changes, functional trait composition and plant-plant interactions“ 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.

Halle (Saale), 23.04.2024 ....

Tim Meier

Supplement E1. Regions and their study areas (see Fig. 1).

Anhang E1. Regionen und ihre Untersuchungsgebiete (vgl. Abb. 1).

region	**abbreviation**	**study area**
Saaletal	MCH	Mücheln (Wettin)
Kyffhäuser	MBA	Mittelberg, Auleben
Kyffhäuser	BDL	Badraer Lehde, Badra
Kyffhäuser	OCH	Ochsenburg, Steinthaleben
Kyffhäuser	KKB	Kosakenberg, Bad Frankenhausen
Kyffhäuser	GBF	Grauer Berg, Bad Frankenhausen
Kyffhäuser	HLU	Hämling, Udersleben

Supplement E2. Detailed map of the quasi-permanent plots in the individual study areas. The relevé number refers to the recent vegetation relevés in Supplement E3. Coordinates are given in Supplement. E5. **a)** near Mücheln (Wettin); **b)** Mittelberg (41) and Badraer Lehde (40) (Kyffhäuser); **c)** Ochsenburg (Kyffhäuser); **d)** Kosakenberg (24, 39), Grauer Berg (25) and Hämling (23) (Kyffhäuser).

Anhang E2. Detaillierte Karten der quasi-permanenten Aufnahmeflächen der einzelnen Untersuchungsgebiete. Die Aufnahmenummer bezieht sich auf die aktuellen Vegetationsaufnahmen in Anhang E3. Koordinaten sind in Anhang E5 angegeben **a)** bei Mücheln (Wettin); **b)** Mittelberg (41) und Badraer Lehde (40) (Kyffhäuser); **c)** Ochsenburg (Kyffhäuser); **d)** Kosakenberg (24, 39), Grauer Berg (25) und Hämling (23) (Kyffhäuser).

Supplement E3. Comparison of the previous (1995 - 2002) and recent (2018/19; bold) vegetation relevés of the dry and semi-dry grasslands in Central Germany (original coverage of the species). The plant communities are classified according to SCHUBERT et al. (1995). In the recent relevés, the coverage of the species was estimated using the 9-part Braun-Blanquet scale ((REICHELT & WILMANNS 1973) (for adjusted coverage see Supplement E4). The coordinates for the recent relevés are listed in Supplement E5. Abbreviations: 1) Author: BR - Babette Richter, KS - Katrin Schneider, JP - Jürgen Pusch, TM - Tim Meier; 2) Plant community: TeF - *Teucrio-Festucetum*, FeS - *Festuco-Stipetum*, FuS - *Fumano-Seslerietum*, FiH - *Filipendulo-Helictotrichetum*, Sts - *Stipetum stenophyllae*, FeB - *Festuco-Brachypodietum*, OnB - *Onobrychido-Brometum*, GeK - *Gentiano-Koelerietum*; 3) Study site: MCH - Mücheln, MBA - Mittelberg, BDL - Badraer Lehde, OCH - Ochsenburg, KKB - Kosakenberg, GBF - Grauer Berg, HLU - Hämling; 4) Bedrock: por - porphyry, gps - gypsum, ahy - anhydrite, kak - limestone.

Anhang E3. Vergleich der früheren (1995 - 2002) und aktuellen (2018/19; fett gedruckt) Vegetationsaufnahmen der Trockenrasen und Halbtrockenrasen in Mitteldeutschland (originale Deckungsgrade der Arten). Die Einteilung der Pflanzengesellschaften erfolgt nach SCHUBERT et al. (1995). Bei den aktuellen Aufnahmen wurden die Deckungsgrade der Arten nach der 9-teiligen Braun-Blanquet-Skala (REICHELT & WILMANNS 1973) geschätzt (angepasste Deckungsgrade siehe Anhang E4). Die Koordinaten für die aktuellen Aufnahmen sind in Anhang E5 aufgeführt. Abkürzungen: 1) Autor: BR - Babette Richter, KS - Katrin Schneider, JP - Jürgen Pusch, TM - Tim Meier; 2) Pflanzengesellschaft: TeF - *Teucrio-Festucetum*, FeS - *Festuco-Stipetum*, FuS - *Fumano-Seslerietum*, FiH - *Filipendulo-Helictotrichetum*, Sts - *Stipetum stenophyllae*, FeB - *Festuco-Brachypodietum*, OnB - *Onobrychido-Brometum*, GeK - *Gentiano-Koelerietum*; 3) Gebiet: MCH - Mücheln, MBA - Mittelberg, BDL - Badraer Lehde, OCH - Ochsenburg, KKB - Kosakenberg, GBF - Grauer Berg, HLU - Hämling; 4) Ausgangsgestein: por - Porphyr, gps - Gips, ahy - Anhydrit, kak - Kalkstein.

	dry grasslands																																																											semi-dry grasslands																																																					
Sequential number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114
Relevé number	1a	1b	2a	2b	3a	3b	4a	4b	5a	5b	6a	6b	7a	7b	8a	8b	9a	9b	10a	10b	11a	11b	12a	12b	13a	13b	14a	14b	15a	15b	16a	16b	17a	17b	18a	18b	19a	19b	20a	20b	21a	21b	22a	22b	23a	23b	24a	24b	25a	25b	26a	26b	27a	27b	28a	28b	29a	29b	30a	30b	31a	31b	32a	32b	33a	33b	34a	34b	35a	35b	36a	36b	37a	37b	38a	38b	39a	39b	40a	40b	41a	41b	42a	42b	43a	43b	44a	44b	45a	45b	46a	46b	47a	47b	48a	48b	49a	49b	50a	50b	51a	51b	52a	52b	53a	53b	54a	54b	55a	55b	56a	56b	57a	57b
Year	1995	2018	1995	2019	1995	2018	1999	2018	1999	2018	1999	2019	2001	2019	2001	2019	2001	2019	1995	2018	1995	2019	1995	2018	1995	2019	1995	2018	1995	2019	1995	2018	1995	2019	1995	2018	1995	2019	1995	2018	1995	2019	1995	2019	2002	2018	2002	2019	2002	2018	1995	2019	1995	2018	1995	2018	1995	2019	1995	2019	2001	2018	2001	2019	2001	2019	2001	2018	2001	2019	2001	2019	2001	2018	2001	2018	1999	2018	2001	2019	2001	2019	2001	2019	2000	2018	2001	2018	2001	2018	2001	2019	1995	2018	1999	2019	1995	2018	1995	2019	1995	2018	1995	2019	1995	2018	1995	2019	1995	2018	1995	2018	1995	2019
Author	KS	TM	KS	TM	KS	TM	BR	TM	BR	TM	BR	TM	BR	TM	BR	TM	BR	TM	KS	TM	KS	TM	KS	TM	KS	TM	KS	TM	KS	TM	KS	TM	KS	TM	KS	TM	KS	TM	KS	TM	KS	TM	KS	TM	JP	TM	JP	TM	JP	TM	KS	TM	KS	TM	KS	TM	KS	TM	KS	TM	BR	TM	BR	TM	BR	TM	BR	TM	BR	TM	BR	TM	BR	TM	BR	TM	JP	TM	JP	TM	JP	TM	BR	TM	BR	TM	BR	TM	BR	TM	BR	TM	BR	TM	BR	TM	KS	TM	KS	TM	KS	TM	KS	TM	KS	TM	KS	TM	KS	TM	KS	TM	KS	TM
Plant community	TeF	TeF	TeF	TeF	TeF	TeF	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FuS	FuS	FuS	FuS	FuS	FuS	FuS	FuS	FuS	FuS	FiH	FiH	FiH	FiH	FiH	FiH	FiH	FiH	FiH	FiH	FiH	FiH	FiH	FiH	FiH	FiH	Sts	Sts	Sts	Sts	Sts	Sts	FeB	FeB	FeB	FeB	FeB	FeB	FeB	FeB	FeB	FeB	FeB	FeB	FeB	FeB	OnB	OnB	OnB	OnB	OnB	OnB	OnB	OnB	OnB	OnB	OnB	OnB	OnB	OnB	GeK	GeK	GeK	GeK
Study site	OCH	OCH	OCH	OCH	OCH	OCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	HLU	HLU	KKB	KKB	GBF	GBF	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	KKB	KKB	BDL	BDL	MBA	MBA	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH
Plot size [m²]	25	25	16	16	25	25	16	16	16	16	16	16	9	9	9	9	9	9	25	25	16	16	16	16	25	25	25	25	25	25	25	25	20	20	25	25	25	25	20	20	25	25	25	25	9	9	20	20	16	16	16	16	16	16	25	25	16	16	25	25	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	25	25	16	16	16	16	9	9	9	9	9	9	9	9	9	9	9	9	9	9	25	25	25	25	25	25	16	16	25	25	25	25	25	25	16	16	25	25
Altitude (m ü. NN)	214	214	194	194	193	193	108	108	110	110	112	112	110	110	110	110	110	110	224	224	209	209	182	182	217	217	204	204	207	207	256	256	201	201	222	222	194	194	175	175	176	176	197	197	232	232	215	215	235	235	183	183	188	188	178	178	188	188	256	256	115	115	117	117	117	117	115	115	115	115	107	107	107	107	117	117	199	199	237	237	197	197	112	112	115	115	115	115	100	100	100	100	101	101	103	103	174	174	195	195	180	180	184	184	174	174	212	212	227	227	211	211	207	207
Exposition	sso	sso	so	so	sso	sso	ssw	ssw	s	s	sw	sw	sw	sw	sw	sw	sw	sw	so	s	so	so	wsw	wsw	so	so	w	w	sw	sw	s	s	wsw	wsw	so	so	w	w	w	w	w	w	wsw	wsw	s	s	s	s	s	s	sw	sw	wsw	wsw	so	so	sso	sso	s	s	w	w	so	so	so	so	w	w	w	w	nw	nw	nw	nw	so	so	ssw	ssw	s	s	s	s	-	-	-	-	-	-	nw	nw	nw	nw	nw	nw	nw	nw	w	w	so	so	so	so	so	so	wsw	wsw	nw	nw	ssw	ssw	nw	nw	nw	nw
Inklination [°]	45	45	35	35	45	45	20	20	25	25	30	30	15	15	15	15	25	25	10	25	30	30	25	25	25	25	60	60	50	50	15	15	70	70	5	5	50	50	15	15	25	25	75	75	30	30	60	5	35	35	30	30	40	40	25	25	30	30	15	15	15	15	20	20	30	30	15	15	15	15	60	60	60	60	15	15	25	25	10	10	10	10	0	0	0	0	0	0	35	35	45	45	30	30	40	40	10	10	55	55	35	35	35	35	20	20	10	10	10	10	2	2	10	10
Bedrock	gps	gps	gps	gps	gps	gps	por	por	por	por	por	por	por	por	por	por	por	por	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	kak	kak	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	por	por	por	por	por	por	por	por	por	por	por	por	por	por	por	por	gps	gps	gps	gps	gps	gps	por	por	por	por	por	por	por	por	por	por	por	por	por	por	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps
Cover shrub layer [%]									10				5																			1	1	3	1				1													1			1		1	1							5	7				2																		2												1	5	3	1	1		3	3	5					
Cover herb layer [%]	10	60	3	40	15	75	90	95	85	95	75	95	95	98	87	95	90	95	15	85	15	50	20	95	15	85	15	75	10	70	15	90	60	60	40	90	40	90	30	95	15	90	10	40	95	90	30	90	85	90	15	85	15	90	20	85	25	85	15	50	87	90	92	95	90	90	85	85	83	90	97	100	100	100	95	95	90	90	95	95	90	99	98	98	100	100	100	100	95	90	92	50	98	95	95	95	40	90	20	75	15	90	20	85	20	95	20	20	90	99	60	99	20	70
Cover cryptogams [%]		20		1		15		5		5	5	5		2	3	5		2		10	1	45		2		10		1		2		1		10		5		3		2		5		10		1		1		2	1	10		1		10		10	3	45	8	8	3	3	5	2	8	8	10	10	1					3		1		1		1		2					3	10	3	50		5		5		1		10		2	25	10		1				1		1	50	30
Species number of vascular plants	31	31	31	29	33	42	22	20	15	21	12	32	15	32	14	28	15	29	40	34	35	32	30	32	25	33	23	31	22	31	30	26	42	37	46	43	42	46	48	42	43	50	38	20	29	30	28	29	33	24	30	38	21	41	42	44	37	49	31	25	23	32	32	37	33	39	22	24	18	24	9	19	8	20	9	27	49	49	19	28	27	37	18	24	12	29	19	26	27	24	26	27	39	29	29	26	26	18	49	43	41	38	42	45	39	22	32	44	44	41	44	36	53	35
Sørensen-Index		67.7		73.3		66.7		42.9		50		40.9		51.1		38.1		45.5		64.9		74.6		51.6		65.5		59.3		60.4		67.9		63.3		58.4		72.7		62.2		51.6		44.8		30.5		31.6		45.6		61.8		51.6		62.8		55.8		85.7		61.8		49.3		63.9		47.8		52.4		14.3		14.3		27.8		73.5		59.6		31.3		42.9		19.5		35.6		47.1		56.6		47.1		65.5		50		58.7		63.3		64.4		55.7		39.5		61.2		52.5		56.8

Festucion valesiacae
Stipa capillata
Stipa pulcherrima
Festuca csikhegyensis
Seseli hippomarathrum
Cirsio-Brachypodion
Thesium linophyllon
Astragalus danicus
Adonis vernalis
Scabiosa ochroleuca
Stipa tirsa
Onobrychis arenaria
Festucetalia valesiacae
Potentilla incana
Silene otites
Stipa pennata
Scorzonera purpurea
Achillea setacea
Xerobromion erecti
Helianthemum nummularium
Teucrium montanum
Sesleria caerulea
Polygala amarella
Teucrium chamaedrys
Fumana procumbens
Mesobromion erecti
Cirsium acaule
Carlina vulgaris
Medicago lupulina
Ranunculus bulbosus
Gentianopsis ciliata
Ononis spinosa
Orchis ustulata
Nonea erecta
Onobrychis viciifolia
Ononis repens
Ophrys insectifera
Koelerio-Phleoin phleoidis
Koeleria macrantha
Festuca valesiaca
Brometalia erecti
Bromus erectus
Helictotrichon pratense
Dianthus carthusianorum
Hippocrepis comosa
Arabis hirsuta
Anthyllis vulneraria
Pulsatilla vulgaris
Koeleria pyramidata
Scabiosa columbaria
Festuco-Brometea
Brachypodium pinnatum
Festuca rupicola
Euphorbia cyparissias
Galium verum
Carex humilis
Salvia pratensis
Thymus praecox
Centaurea scabiosa
Sanguisorba minor
Asperula cynanchica
Filipendula vulgaris
Eryngium campestre
Galatella linosyris
Poa angustifolia
Centaurea stoebe
Phleum phleoides
Bothrichloa ischaemum
Pimpinella saxifraga
Prunella grandiflora
Potentilla neumanniana
Potentilla heptaphylla
Asparagus officinalis
Veronica spicata
Stachys recta
Polygala comosa
Allium oleraceum
Trifolium montanum
Orobanche caryophyllacea
Campanula glomerata
Odontites luteus
Nardo-Callunetea
Cuscuta epithymum
Luzula campestris
Polygala vulgaris
Calluna vulgaris
Carex pilulifera
Sedo-Scleranthetea
Achillea pannonica
Gypsophila fastigiata
Holosteum umbellatum
Acinos arvensis
Alyssum montanum
Cerastium pumilum
Draba verna
Festuca pallens
Arenaria serpyllifolia
Veronica praecox
Artemisia campestris
Taraxacum sect. *Erythrosperma*
Hornungia petraea
Allium lusitanicum
Microthlaspi perfoliatum
Myosotis stricta
Buglossoides arvensis subsp. *sibthorpiana*
Cerastium semidecandrum
Poa bulbosa
Erodium cicutarium
Erysimum crepidifolium
Veronica arvensis
Arabis auriculata
Valerianella dentata
Helichrysum arenarium
Pilosella echioides
Sedum acre
Trifolium campestre
Sedum sexangulare
Potentilla argentea
Veronica verna
Arabidopsis thaliana
Corynephorus canescens
Myosotis ramosissima
Thymus serpyllum
Saxifraga tridactylites
Hylotelephium telephium
Molinio-Arrhenatheretea
Dactylis glomerata
Carduus nutans
Taraxacum sect. *Ruderalia*
Plantago lanceolata
Convolvulus arvensis
Linum catharticum
Vicia angustifolia
Knautia arvensis
Trifolium pratense
Silene latifolia
Galium boreale
Agrostis gigantea
Saxifraga granulata
Arrhenatherum elatius
Senecio jacobaea
Leucanthemum vulgare
Cerastium holosteoides
Galium mollugo
Vicia cracca
Serratula tinctoria
Helictotrichon pubescens
Genista tinctoria
Lathyrus pratensis
Leucojum aestivum
Lolium perenne
Rumex acetosa
Tragopogon pratensis
Vicia hirsuta
Veronica hederifolia
Galium aparine
Lathyrus hirsuta
Picris hieracioides
Vicia tetrasperma
Glechoma hederacea
Urtica dioica
widespread grassland species
Pilosella officinarum
Plantago media
Briza media
Lotus corniculatus
Agrostis capillaris
Thymus pulegioides
Leontodon hispidus
Centaurea jacea
Hypochoeris radicata
herbaceous fringe species
Scabiosa canescens
Vincetoxicum hirundinaria
Anthericum liliago
Agrimonia eupatoria
Thalictrum minus
Hypericum perforatum
Viola rupestris
Fragaria viridis
Cervaria rivini
Verbascum lychnitis
Campanula rotundifolia
Erysimum marschallianum
Hypochoeris maculata
Epipactis atrorubens
Bupleurum falcatum
Galium glaucum
Medicago falcata
Hypericum elegans
Polygonatum odoratum
Inula hirta
Viola hirta
Geranium sanguineum
Medicago minima
Veronica chamaedrys
Potentilla alba
Hieracium sabaudum
Inula germanica
Campanula bononiensis
Geum urbanum
Primula veris
Verbascum thapsus
Origanum vulgare
Anthericum ramosum
Dictamnus albus
Campanula persicifolia
Centaurium erythraea
Hieracium umbellatum
Laserpitium latifolium
Lithospermum officinale
Ranunculus auricomus
Scorzonera hispanica
Silene nutans
Trifolium alpestre
Vicia tenuifolia
other species
Euphrasia stricta
Echium vulgare
Falcaria vulgaris
Daucus carota
Viola arvensis
Verbascum densiflorum
Descurainia sophia
Cerastium arvense
Lamium amplexicaule
Brassica napus
Bromus inermis
Sonchus asper
Reseda lutea
Bromus hordeaceus
Camelina microcarpa
Lactuca serriola
Papaver argemone
Veronica agrestis
Bromus sterilis
Bromus tectorum
Tragopogon dubius
Artemisia vulgaris
Lappula squarrosa
Capsella bursa-pastoris
Cynoglossum officinale
Lamium maculatum
Senecio vernalis
Triticum aestivum
Carduus acanthoides
Caucalis platycarpos
Consolida regalis
Linaria vulgaris
Torilis japonica
Valerianella locusta
woody species
Quercus robur juv.
Rosa rubiginosa juv.
Rosa canina juv.
Crataegus monogyna juv.
Prunus spinosa juv.
Frangula alnus juv.
Populus tremula juv.
Cornus sanguinea juv.
Pinus sylvestris juv.
Betula pendula juv.
Rubus idaeus juv.
Cotoneaster integerrimus juv.
Prunus avium juv.
Prunus cerasus juv.
Rosa corymbifera
Rhamnus cathartica
Rosa elliptica juv.
Cornus mas juv.
Corylus avellana juv.
Prunus serotina juv.
Quercus petraea juv.
Prunus fruticosa
Syringa vulgaris juv.

Supplement E4. Comparison of the previous (1995 - 2002) and recent (2018/19; bold) vegetation relevés of the dry grasslands and semi-dry grasslands in Central Germany with adjusted coverages of the species. Explanations and abbreviations see Supplement E3.

Anhang E4. Vergleich der früheren (1995 - 2002) und aktuellen (2018/19; fett gedruckt) Vegetationsaufnahmen der Trockenrasen und Halbtrockenrasen in Mitteldeutschland mit angepassten Deckungsgraden der Arten. Erläuterungen und Abkürzungen siehe Anhang E3.

	dry grasslands																													
Sequential number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Relevé number	1a	1b	2a	2b	3a	3b	4a	4b	5a	5b	6a	6b	7a	7b	8a	8b	9a	9b	10a	10b	11a	11b	12a	12b	13a	13b	14a	14b	15a	15b
Year	1995	2018	1995	2019	1995	2018	1999	2018	1999	2018	1999	2019	2001	2019	2001	2019	2001	2019	1995	2018	1995	2019	1995	2018	1995	2019	1995	2018	1995	2019
Author	KS	TM	KS	TM	KS	TM	BR	TM	BR	TM	BR	TM	BR	TM	BR	TM	BR	TM	KS	TM	KS	TM	KS	TM	KS	TM	KS	TM	KS	TM
Plant community	TeF	TeF	TeF	TeF	TeF	TeF	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS
Study site	OCH	OCH	OCH	OCH	OCH	OCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH
Plot size [m²]	25	25	16	16	25	25	16	16	16	16	16	16	9	9	9	9	9	9	25	25	16	16	16	16	25	25	25	25	25	25
Altitude (m ü. NN)	214	214	194	194	193	193	108	108	110	110	112	112	110	110	110	110	110	110	224	224	209	209	182	182	217	217	204	204	207	207
Exposition	sso	sso	so	so	sso	sso	ssw	ssw	s	s	sw	sw	sw	sw	sw	sw	sw	sw	so	s	so	so	wsw	wsw	so	so	w	w	sw	sw
Inklination [°]	45	45	35	35	45	45	20	20	25	25	30	30	15	15	15	15	25	25	10	25	30	30	25	25	25	25	60	60	50	50
Bedrock	gps	gps	gps	gps	gps	gps	por	por	por	por	por	por	por	por	por	por	por	por	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps
Cover shrub layer [%]									10				5																	
Cover herb layer [%]	10	60	3	40	15	75	90	95	85	95	75	95	95	98	87	95	90	95	15	85	15	50	20	95	15	85	15	75	10	70
Cover cryptogams [%]		20		1		15		5		5	5	5		2	3	5		2		10	1	45		2		10		1		2
Species number of vascular plants	31	31	31	29	33	42	22	20	15	21	12	32	15	32	14	28	15	29	40	34	35	32	30	32	25	33	23	31	22	31
Sørensen-Index		67.7		73.3		66.7		42.9		50		40.9		51.1		38.1		45.5		64.9		74.6		51.6		65.5		59.3		60.4
Festucion valesiacae																														
Stipa capillata	.	.	.	.	.	+	3	3	3	3	2	3	2	1	3	2	2	2	1	+	2	+	1	.	.	.	.	2	+	+
Stipa pulcherrima	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	1	.	2	3	1	1	1	+
Festuca csikhegyensis	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	1	.	2	.	.	.	.	.	.	.	.	.	.	.	.
Seseli hippomarathrum	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cirsio-Brachypodion																														
Thesium linophyllon	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	1	1	+	1	+	1	+
Astragalus danicus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Adonis vernalis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Scabiosa ochroleuca	.	.	.	.	.	.	.	1	.	+	.	.	1	1	1	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Stipa tirsa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Onobrychis arenaria	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Festucetalia valesiacae																														
Potentilla incana	1	+	1	.	1	.	1	3	.	1	.	3	.	1	.	1	1	.	1	+	1	.	.	+	.	1	.	.	.	.
Silene otites	1	+	1	+	1	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	1	1	1	1	1	1	1	1	1
Stipa pennata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	.
Scorzonera purpurea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
Achillea setacea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

	dry grasslands																													
Sequential number	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Relevé number	16a	16b	17a	17b	18a	18b	19a	19b	20a	20b	21a	21b	22a	22b	23a	23b	24a	24b	25a	25b	26a	26b	27a	27b	28a	28b	29a	29b	30a	30b
Year	1995	2018	1995	2019	1995	2018	1995	2019	1995	2018	1995	2019	1995	2019	2002	2018	2002	2019	2002	2018	1995	2019	1995	2018	1995	2018	1995	2019	1995	2019
Author	KS	TM	KS	TM	KS	TM	KS	TM	KS	TM	KS	TM	KS	TM	JP	TM	JP	TM	JP	TM	KS	TM	KS	TM	KS	TM	KS	TM	KS	TM
Plant community	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FeS	FuS	FuS	FuS	FuS	FuS	FuS	FuS	FuS	FuS	FuS
Study site	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	HLU	HLU	KKB	KKB	GBF	GBF	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH
Plot size [m²]	25	25	20	20	25	25	25	25	20	20	25	25	25	25	9	9	20	20	16	16	16	16	16	16	25	25	16	16	25	25
Altitude (m ü. NN)	256	256	201	201	222	222	194	194	175	175	176	176	197	197	232	232	215	215	235	235	183	183	188	188	178	178	188	188	256	256
Exposition	s	s	wsw	wsw	so	so	w	w	w	w	w	w	wsw	wsw	s	s	s	s	s	s	sw	sw	wsw	wsw	so	so	sso	sso	s	s
Inklination [°]	15	15	70	70	5	5	50	50	15	15	25	25	75	75	30	30	60	5	35	35	30	30	40	40	25	25	30	30	15	15
Bedrock	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	kak	kak	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps
Cover shrub layer [%]	1	1	3	1				1														1			1		1	1		
Cover herb layer [%]	15	90	60	60	40	90	40	90	30	95	15	90	10	40	95	90	30	90	85	90	15	85	15	90	20	85	25	85	15	50
Cover cryptogams [%]		1		10		5		3		2		5		10		1		1		2	1	10		1		10		10	3	45
Species number of vascular plants	30	26	42	37	46	43	42	46	48	42	43	50	38	20	29	30	28	29	33	24	30	38	21	41	42	44	37	49	31	25
Sørensen-Index		67.9		63.3		58.4		72.7		62.2		51.6		44.8		30.5		31.6		45.6		61.8		51.6		62.8		55.8		85.7
Festucion valesiacae																														
Stipa capillata	.	+	2	1	.	.	.	.	.	.	.	.	1	+	+	2	+	.	.	+	r	1	.	.	.	.	.	1	.	.
Stipa pulcherrima	1	.	2	2	1	.	2	3	1	+	1	.	1	.	.	.	2	2	+	2	.	.	.	4	.	.	.	1	.	.
Festuca csikhegyensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Seseli hippomarathrum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cirsio-Brachypodion																														
Thesium linophyllon	1	.	.	.	.	.	1	+	1	1	1	1	1	.	.	.	.	.	.	.	1	1	1	+	r	+	1	+	1	r
Astragalus danicus	.	.	.	.	+	+	.	.	1	+	.	r	.	.	.	.	.	.	.	.	.	r	.	.	1	1	.	.	.	.
Adonis vernalis	.	.	.	.	.	.	1	r	+	+	1	+	+	.	.	.	.	.	.	.	+	+	.	.	.	.	.	+	.	.
Scabiosa ochroleuca	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Stipa tirsa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Onobrychis arenaria	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Festucetalia valesiacae																														
Potentilla incana	1	.	.	.	1	+	1	.	1	1	1	+	.	.	.	+	+	.	+	+	.	+	.	1	1	1	1	1	.	+
Silene otites	.	.	1	1	.	.	1	1	.	2	1	.	1	.	.	.	+	.	+	.	1	1	1	1	1	.	1	1	.	.
Stipa pennata	.	3	.	.	1	.	.	1	.	1	.	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	.	.
Scorzonera purpurea	.	.	1	r	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Achillea setacea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

	semi-dry grasslands																													
Sequential number	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
Relevé number	31a	31b	32a	32b	33a	33b	34a	34b	35a	35b	36a	36b	37a	37b	38a	38b	39a	39b	40a	40b	41a	41b	42a	42b	43a	43b	44a	44b	45a	45b
Year	2001	2018	2001	2019	2001	2019	2001	2018	2001	2019	2001	2019	2001	2018	2001	2018	1999	2018	2001	2019	2001	2019	2001	2019	2000	2018	2001	2018	2001	2018
Author	BR	TM	BR	TM	BR	TM	BR	TM	BR	TM	BR	TM	BR	TM	BR	TM	JP	TM	JP	TM	JP	TM	BR	TM	BR	TM	BR	TM	BR	TM
Plant community	FiH	FiH	FiH	FiH	FiH	FiH	FiH	FiH	FiH	FiH	FiH	FiH	FiH	FiH	FiH	FiH	Sts	Sts	Sts	Sts	Sts	Sts	FeB	FeB	FeB	FeB	FeB	FeB	FeB	FeB
Study site	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH	KKB	KKB	BDL	BDL	MBA	MBA	MCH	MCH	MCH	MCH	MCH	MCH	MCH	MCH
Plot size [m²]	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	25	25	16	16	16	16	9	9	9	9	9	9	9	9
Altitude (m ü. NN)	115	115	117	117	117	117	115	115	115	115	107	107	107	107	117	117	199	199	237	237	197	197	112	112	115	115	115	115	100	100
Exposition	w	w	so	so	so	so	w	w	w	w	nw	nw	nw	nw	so	so	ssw	ssw	s	s	s	s	-	-	-	-	-	-	nw	nw
Inklination [°]	15	15	20	20	30	30	15	15	15	15	60	60	60	60	15	15	25	25	10	10	10	10	0	0	0	0	0	0	35	35
Bedrock	por	por	por	por	por	por	por	por	por	por	por	por	por	por	por	por	gps	gps	gps	gps	gps	gps	por	por	por	por	por	por	por	por
Cover shrub layer [%]					5	7				2																			2	
Cover herb layer [%]	87	90	92	95	90	90	85	85	83	90	97	100	100	100	95	95	90	90	95	95	90	99	98	98	100	100	100	100	95	90
Cover cryptogams [%]	8	8	3	3	5	2	8	8	10	10	1					3		1		1		1		2					3	10
Species number of vascular plants	23	32	32	37	33	39	22	24	18	24	9	19	8	20	9	27	49	49	19	28	27	37	18	24	12	29	19	26	27	24
Sørensen-Index		61.8		49.3		63.9		47.8		52.4		14.3		14.3		27.8		73.5		59.6		31.3		42.9		19.5		35.6		47.1
Festucion valesiacae																														
Stipa capillata	.	.	.	.	.	+	.	.	.	r	.	.	.	.	.	.	1	+	.	.	.	.	.	.	.	.	.	.	.	.
Stipa pulcherrima	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	.	.	.	.	.	.	.	.	.	.	.
Festuca csikhegyensis	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Seseli hippomarathrum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cirsio-Brachypodion																														
Thesium linophyllon	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Astragalus danicus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	.	.	.	+	.	.	.	.	.	.	.	.
Adonis vernalis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	1	.	.	.	.	.	.	.	.	.
Scabiosa ochroleuca	r	.	.	.	.	1	.	.	r	.	.	.	+	.	.	.	.	.	.	.	.	.	1	+	.	r	+	1	.	.
Stipa tirsa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	3	4	4	3	4	.	.	.	.	.	.	.	.
Onobrychis arenaria	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Festucetalia valesiacae																														
Potentilla incana	1	1	1	1	2	1	1	+	1	+	.	.	.	.	.	2	1	.	.	.	.	1	.	.	.	.	.	.	+	.
Silene otites	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
Stipa pennata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	+	.	.	.	.	.	.	.	.	.
Scorzonera purpurea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Achillea setacea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.

	semi-dry grasslands																							
Sequential number	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114
Relevé number	46a	46b	47a	47b	48a	48b	49a	49b	50a	50b	51a	51b	52a	52b	53a	53b	54a	54b	55a	55b	56a	56b	57a	57b
Year	2001	2019	1995	2018	1999	2019	1995	2018	1995	2019	1995	2018	1995	2019	1995	2018	1995	2019	1995	2018	1995	2018	1995	2019
Author	BR	TM	BR	TM	BR	TM	KS	TM	KS	TM	KS	TM	KS	TM	KS	TM	KS	TM	KS	TM	KS	TM	KS	TM
Plant community	FeB	FeB	FeB	FeB	FeB	FeB	OnB	OnB	OnB	OnB	OnB	OnB	OnB	OnB	OnB	OnB	OnB	OnB	OnB	OnB	GeK	GeK	GeK	GeK
Study site	MCH	MCH	MCH	MCH	MCH	MCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH	OCH
Plot size [m²]	9	9	9	9	9	9	25	25	25	25	25	25	16	16	25	25	25	25	25	25	16	16	25	25
Altitude (m ü. NN)	100	100	101	101	103	103	174	174	195	195	180	180	184	184	174	174	212	212	227	227	211	211	207	207
Exposition	nw	nw	nw	nw	nw	nw	w	w	so	so	so	so	so	so	wsw	wsw	nw	nw	ssw	ssw	nw	nw	nw	nw
Inklination [°]	45	45	30	30	40	40	10	10	55	55	35	35	35	35	20	20	10	10	10	10	2	2	10	10
Bedrock	por	por	por	por	por	por	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps	gps
Cover shrub layer [%]											1	5	3	1	1		3	3	5					
Cover herb layer [%]	92	50	98	95	95	95	40	90	20	75	15	90	20	85	20	95	20	20	90	99	60	99	20	70
Cover cryptogams [%]	3	50		5		5		1		10		2	25	10		1				1		1	50	30
Species number of vascular plants	26	27	39	29	29	26	26	18	49	43	41	38	42	45	39	22	32	44	44	41	44	36	53	35
Sørensen-Index		56.6		47.1		65.5		50		58.7		63.3		64.4		55.7		39.5		61.2		52.5		56.8
Festucion valesiacae																								
Stipa capillata	.	.	.	.	.	.	.	.	.	+	.	r	.	.	.	.	.	.	.	.	.	.	.	.
Stipa pulcherrima	.	.	.	.	.	.	.	.	.	1	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Festuca csikhegyensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Seseli hippomarathrum	.	r	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cirsio-Brachypodion																								
Thesium linophyllon	.	.	.	.	.	.	.	.	1	1	1	.	1	1	1	.	1	+	.	+	.	.	1	+
Astragalus danicus	.	.	+	.	.	.	1	.	1	.	1	1	1	1	1	r	1	+	1	+	1	2	1	.
Adonis vernalis	.	.	.	.	.	.	.	r	1	.	.	.	.	+	1	+	1	.	.	.	+	.	.	.
Scabiosa ochroleuca	.	+	+	2	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Stipa tirsa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Onobrychis arenaria	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.
Festucetalia valesiacae																								
Potentilla incana	1	.	.	.	.	.	.	.	1	.	1	+	1	1	1	.	1	+	.	.	.	.	1	.
Silene otites	.	.	.	.	.	.	.	.	1	1	1	.	.	r	+	.	.	.	.	.	.	.	1	.
Stipa pennata	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	1	.	.	.	.
Scorzonera purpurea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	+	.	.	.	.	.	+
Achillea setacea	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Supplement E5. Coordinates for the 57 quasi-permanent plots. The relevé number refers to the recent vegetation relevés in Supplement E3.

Anhang E5. Koordinaten für die 57 quasi-permanenten Aufnahmeflächen. Die Aufnahmenummer bezieht sich auf die aktuellen Vegetationsaufnahmen in Anhang E3.

Relevé number	Coordinates
1	N51°23'10.08"; E11°2'12.66"
2	N51°23'8.59"; E11°2'12.58"
3	N51°23'10.44"; E11°2'16.62"
4	N51°34'44.76"; E11°49'32.28"
5	N51°34'44.76"; E11°49'32.82"
6	N51°34'45.18"; E11°49'31.92"
7	N51°34'45.84"; E11°49'29.4"
8	N51°34'46.08"; E11°49'28.56"
9	N51°34'46.44"; E11°49'27.66"
10	N51°23'11.7"; E11°2'14.64"
11	N51°23'10.71"; E11°2'14.94"
12	N51°23'8.52"; E11°2'9.78"
13	N51°23'10.57"; E11°2'11.04"
14	N51°23'10.68"; E11°2'9.72"
15	N51°23'9.90"; E11°2'22.50"
16	N51°23'12.24"; E11°2'27.9"
17	N51°23'12.30"; E11°2'8.59"
18	N51°23'10.98"; E11°2'12.84"
19	N51°23'13.15"; E11°2'7.73"
20	N51°23'10.56"; E11°2'7.56"
21	N51°23'12.97"; E11°2'6.17"
22	N51°23'15.49"; E11°2'6.12"
23	N51°23'7.22"; E11°9'38.34"
24	N51°22'2.4"; E11°4'44.46"
25	N51°21'51.12"; E11°6'30.24"
26	N51°23'9.60"; E11°2'8.99"
27	N51°23'9.24"; E11°2'9.72"
28	N51°23'7.44"; E11°2'13.2"
29	N51°23'9.35"; E11°2'14.86"
30	N51°23'13.31"; E11°2'36.14"
31	N51°34'46.26"; E11°49'31.38"
32	N51°34'44.28"; E11°49'42.24"
33	N51°34'44.1"; E11°49'41.88"
34	N51°34'46.08"; E11°49'31.32"
35	N51°34'45.9"; E11°49'31.26"
36	N51°34'49.92"; E11°49'28.62"
37	N51°34'49.8"; E11°49'28.5"
38	N51°34'44.22"; E11°49'42.06"
39	N51°22'5.16"; E11°4'37.2"
40	N51°24'22.54"; E10°59'59.46"
41	N51°25'23.95"; E10°58'13.87"
42	N51°34'43.08"; E11°49'48.42"
43	N51°34'43.14"; E11°49'49.8"
44	N51°34'43.26"; E11°49'49.44"
45	N51°34'44.26"; E11°49'39.09"
46	N51°34'44.54"; E11°49'39.25"
47	N51°34'44.91"; E11°49'39.74"
48	N51°34'44.76"; E11°49'39.40"
49	N51°23'13.38"; E11°2'5.64"
50	N51°23'10.25"; E11°2'15.76"
51	N51°23'8.16"; E11°2'14.1"
52	N51°23'7.98"; E11°2'13.09"
53	N51°23'8.4"; E11°2'9"
54	N51°23'19.36"; E11°2'14.35"
55	N51°23'11.58"; E11°2'12.78"
56	N51°23'17.52"; E11°2'9.54"
57	N51°23'20.70"; E11°2'15.99"

Supplement E6. Species with increased or decreased constancy (presence/ absence) between previous (1995 - 2002) and recent (2018/19) vegetation relevés. The species are divided into functional groups (FG): annuals (A), graminoids (G), forbs (F). Within the functional groups, the species are sorted in descending order of difference. Species without a significant change in constancy are shown. Only species that appeared more than five times in the relevés were considered. P-value: result of the Wilcoxon signed-rank test. In addition, the status (0 - extinct or lost, 1 - threatened with extinction, 2 - critically endangered, 3 - endangered, D - insufficient data, V - warning list) according to the Red Lists (RL) of Saxony-Anhalt (SA; FRANK et al. 2020) and Thuringia (TH; KORSCH et al. 2011) as well as the legal protection status under the Federal Species Protection Regulation (S) are given.

Anhang E6. Arten mit zunehmender und abnehmender Stetigkeit (Präsenz/ Absenz) zwischen den früheren (1995 - 2002) und aktuellen (2018/19) Vegetationsaufnahmen. Die Arten sind in funktionelle Artengruppen eingeteilt (FG): Annuelle (A), Gräser (G), Kräuter (F). Innerhalb der funktionellen Gruppen sind die Arten nach absteigender Differenz sortiert. Es sind Arten dargestellt, die keine signifikante Veränderung in der Stetigkeit aufweisen. Dabei werden nur Arten berücksichtigt, die mehr als fünfmal in den Aufnahmen vorkamen. P-Wert: Ergebnis des Wilcoxon-Signed-Rank-Tests. Außerdem sind der Gefährdungsstatus (0 - ausgestorben oder verschollen, 1 - vom Aussterben bedroht, 2 - stark gefährdet, 3 - gefährdet, D - Daten defizitär, V - Vorwarnliste) nach den Roten Listen (RL) von Sachsen-Anhalt (SA; FRANK et al. 2020) und Thüringen (TH; KORSCH et al. 2011) sowie der gesetzliche Schutz nach Bundesartenschutzverordnung (S) angegeben.

FG	RL		S		constancy		difference	*p*
	SA	TH		species	1995-2002	2018/19		
				increase of species				
A	D			*Cerastium pumilum*	12	18	6	0.126
A	V			*Arabis hirsuta*	19	24	5	0.139
A				*Arenaria serpyllifolia*	10	15	5	0.221
A				*Cerastium semidecandrum*	6	7	1	0.735
G				*Brachypodium pinnatum*	16	23	7	0.112
G	V	3	§	*Stipa capillata*	16	23	7	0.062
G	V			*Carex humilis*	33	40	7	0.112
G				*Dactylis glomerata*	10	16	6	0.215
G				*Festuca rupicola*	26	31	5	0.287
G	V	2		*Poa bulbosa*	3	8	5	0.139
G	2	2		*Koeleria macrantha*	31	36	5	0.314
G	3	3	§	*Stipa pennata*	5	9	4	0.262
G	V	3		*Festuca valesiaca*	11	15	4	0.262
G				*Arrhenatherum elatius*	2	6	4	0.208
G				*Poa angustifolia*	13	16	3	0.424
G				*Agrostis capillaris*	7	9	2	0.529
G	2	3	§	*Stipa pulcherrima*	14	15	1	0.790
G	V	2		*Bothrichloa ischaemum*	7	8	1	0.317
G	V			*Helictotrichon pratense*	19	20	1	0.820
F				*Sanguisorba minor*	19	28	9	0.101
F	V	3		*Filipendula vulgaris*	15	23	8	0.060
F				*Centaurea stoebe*	9	17	8	0.060
F				*Dianthus carthusianorum*	22	29	7	0.087
F				*Lotus corniculatus*	7	13	6	0.126
F				*Hypericum perforatum*	9	15	6	0.187
F		3		*Taraxacum sect. Erythrosperma*	5	9	4	0.308
F		3		*Artemisia campestris*	9	13	4	0.308
F	1	2	§	*Scorzonera purpurea*	2	6	4	0.068
F				*Fragaria viridis*	5	9	4	0.142
F				*Viola arvensis*	1	5	4	0.142
F	3	2		*Viola rupestris*	9	12	3	0.374
F	V			*Hippocrepis comosa*	23	26	3	0.374
F	2	2		*Hypochoeris maculata*	6	9	3	0.225
F				*Pimpinella saxifraga*	5	8	3	0.310
F				*Viola hirta*	2	5	3	0.310
F				*Erysimum crepidifolium*	4	7	3	0.225
F				*Carduus nutans*	7	10	3	0.463
F	3	3	§	*Inula hirta*	3	5	2	0.361
F				*Scabiosa ochroleuca*	9	11	2	0.575
F	3	3		*Galatella linosyris*	15	17	2	0.529
F				*Plantago lanceolata*	6	8	2	0.463
F				*Agrimonia eupatoria*	14	16	2	0.529
F				*Verbascum densiflorum*	3	5	2	0.361
F				*Medicago falcata*	5	6	1	0.735
F				*Salvia pratensis*	28	29	1	0.735
F				*Galium verum*	36	37	1	0.767
F	V			*Centaurea scabiosa*	26	27	1	0.686
F				*Potentilla heptaphylla*	4	5	1	0.686
				decrease of species				
A				*Erodium cicutarium*	5	2	-3	0.225
A	V			*Acinos arvensis*	22	18	-4	0.346
G		3		*Festuca pallens*	23	20	-3	0.374
G				*Sesleria caerulea*	20	17	-3	0.310
G	3	3		*Phleum phleoides*	13	9	-4	0.262
F				*Achillea pannonica*	24	23	-1	0.721
F	3	3	§	*Adonis vernalis*	11	10	-1	0.767
F	3	3		*Astragalus danicus*	14	13	-1	0.735
F		3		*Potentilla incana*	30	29	-1	0.861
F	2	3	§	*Pulsatilla vulgaris*	5	4	-1	0.686
F				*Teucrium chamaedrys*	10	9	-1	0.686
F	V	2		*Helianthemum nummularium*	28	27	-1	0.735
F				*Myosotis stricta*	6	5	-1	0.767
F	V			*Thymus pulegioides*	5	4	-1	0.593
F	3	3		*Scabiosa canescens*	32	31	-1	0.767
F				*Vincetoxicum hirundinaria*	23	22	-1	0.735
F				*Verbascum lychnitis*	12	11	-1	0.767
F				*Bupleurum falcatum*	7	6	-1	0.767
F	V	3		*Galium glaucum*	7	6	-1	0.767
F	D			*Anthyllis vulneraria*	15	13	-2	0.660
F	3	3	§	*Gypsophila fastigiata*	23	21	-2	0.463
F	V			*Galium boreale*	7	5	-2	0.463
F	2	2		*Fumana procumbens*	9	7	-2	0.463
F	3	3		*Thalictrum minus*	15	13	-2	0.463
F	D			*Thymus praecox*	30	27	-3	0.496
F	V			*Cirsium acaule*	19	16	-3	0.424
F	3			*Prunella grandiflora*	8	5	-3	0.310
F				*Pilosella officinarum*	22	19	-3	0.600
F				*Vicia angustifolia*	6	2	-4	0.142
F	1	3		*Hypericum elegans*	8	4	-4	0.208
F	3	2		*Thesium linophyllon*	22	18	-4	0.208
F				*Epipactis atrorubens*	9	5	-4	0.208
F				*Echium vulgare*	9	5	-4	0.262
F	3	3	§	*Alyssum montanum*	26	21	-5	0.182
F				*Taraxacum sect. Ruderalia*	10	4	-6	0.126

Supplement E1. Biological/ecological characteristics of studied species. Threat categories according to the RL G – Red List of Germany (METZING et al. 2018) and RL SA – Red List of Saxony-Anhalt (FRANK et al. 2020): 1 – critically endangered, 2 – endangered, 3 – vulnerable, V – near-threatened. § – protected after national species protection ordinance. Life forms (LF) according to ELLENBERG et al. (2001): C – herbaceous chamaephyte, G – geophyte, H – hemicryptophyte, N – nano-phanerophyte, P – phanerophyte, T – therophyte. Sub-life forms of short-lived species according to KLOTZ et al. (2002) and own observations: sum – summer annuals, win – winter annuals, bien – biennials (monocarpic-perennial). CSR strategy types according to KLOTZ et al. (2002): CS – competition/stress strategy, CSR – competition/stress/ruderal strategy, SR – stress/ruderal strategy. Moisture behaviour types according to BECKER (1998b): *xero* – xerophilic, *meso-xero* – meso-xerophilic, × – indifferent behaviour. Mean Ellenberg indicator values according to ELLENBERG et al. (2001) for: L – light, T – temperature, K – continentality, F – moisture, R – soil reaction, N – nutrients.

Anhang E1. Biologisch-ökologische Eigenschaften der untersuchten Arten. Gefährdung nach der RL G – Roten Liste Deutschlands (METZING et al. 2018) und RL SA – Roten Liste Sachsen-Anhalts (FRANK et al. 2020). Die Gefährdungskategorien sind: 1 – vom Aussterben bedroht, 2 – stark gefährdet, 3 – gefährdet, V – Vorwarnliste. § – geschützt nach Bundesartenschutzverordnung. Lebensformen (LF) nach ELLENBERG et al. (2001): C – krautige Chamaephyten, G – Geophyten, H – Hemikryptophyten, N – Nano-Phanerophyten, P – Phanerophyten, T – Therophyten. Sub-Lebensformen kurzlebiger Arten nach KLOTZ et al. (2002) und eigenen Beobachtungen: sum – sommer-annuell, win – winter-annuell, bien – zweijährig (mehrjährig-monokarp). CSR-Strategietypen nach KLOTZ et al. (2002): CS – Konkurrenz/Stress-Stratege, CSR – Konkurrenz/Stress/Ruderal-Stratege, SR – Stress/Ruderal-Stratege. Feuchteverhalten nach BECKER (1998b): *xero* – xerophil, *meso-xero* – meso-xerophil, × – indifferentes Verhalten. Mittlere Ellenberg-Zeigerwerte nach ELLENBERG et al. (2001): L – Licht, T – Temperatur, K – Kontinentalität, F – Feuchte, R – Bodenreaktion, N – Nährstoff.

	Threat and protection			Raunkiaer life form	Short-lived life form	CSR strategy	Moisture behaviour	Ellenberg indicator value					
	RL G	RL SA	§					L	T	K	F	R	N
Graminoids													
Agrostis gigantea	–	–	–	H	–	C	meso-xero	7	5	3	8	7	6
Avenula pubescens	–	–	–	H	–	C	meso-xero	5	×	3	3	×	4
Bothriochloa ischoemum	3	V	–	H	–	CSR	xero	9	7	6	3	8	3
Brachypodium pinnatum	–	–	–	G, H	–	CS	meso-xero	6	5	5	4	7	4
Briza media	–	3	–	H	–	CSR	meso-xero	8	×	3	×	×	2
Bromus erectus	–	–	–	H	–	CS	×	8	5	2	3	8	3
Carex caryophyllea	V	–	–	G, H	–	CSR	meso-xero	8	×	3	4	×	2
Carex humilis	V	V	–	H	–	CSR	×	7	6	5	2	8	3
Dactylis glomerata	–	–	–	H	–	C	meso-xero	7	×	3	5	×	6
Festuca csikhegyensis	3	–	–	H	–	CS	xero	9	7	4	2	8	1
Festuca rupicola	V	–	–	H	–	CS	meso-xero	9	7	7	3	8	2
Festuca valesiaca	3	V	–	H	–	CSR	xero	8	7	7	2	7	2
Helictochloa pratensis	V	V	–	H	–	CS	meso-xero	7	6	4	3	×	2
Koeleria macrantha	V	–	–	H	–	CS	meso-xero	7	6	7	3	8	2
Koeleria pyramidata	V	–	–	H	–	CS	meso-xero	7	6	4	4	7	2
Poa badensis	2	3	–	H	–	CSR	xero	8	7	4	3	8	1
Sesleria caerulea	–	–	–	H	–	CS	×	7	3	2	4	9	3
Stipa capillata	3	V	§	H	–	CS	xero	8	7	8	2	8	2
Stipa pulcherrima	2	2	§	H	–	CS	xero	9	8	7	1	8	1
Herbs													
Achillea millefolium agg.	V	–	–	H	–	CS	×	7	7	6	3	6	2
Adonis vernalis	3	3	§	H	–	CSR	meso-xero	7	6	7	3	7	2
Agrimonia eupatoria	–	–	–	H	–	C	meso-xero	7	6	4	4	8	4
Allium lusitanicum	3	3	§	G	–	CSR	xero	9	×	5	2	6	2
Anthericum ramosum	V	3	§	H	–	CSR	meso-xero	7	5	4	3	7	3
Anthyllis vulneraria	–	–	–	H	–	CSR	meso-xero	8	6	3	3	7	2
Arabis hirsuta	V	V	–	H	bien	CSR	meso-xero	7	5	3	4	8	×
Arenaria serpyllifolia	–	–	–	H, T	sum/win	R	xero	8	×	×	4	7	×
Asparagus officinalis	–	–	–	G	–	CS	×	6	6	7	3	×	4
Asperula cynanchica	V	3	–	H	–	CSR	meso-xero	7	×	5	3	8	3
Astragalus danicus	3	3	–	H	–	CSR	meso-xero	8	7	7	3	9	2
Bupleurum falcatum	V	–	–	H	–	CSR	meso-xero	6	6	6	3	9	3
Campanula rotundifolia	–	–	–	H	–	CSR	meso-xero	7	5	×	×	×	2
Carlina acaulis subsp. *simplex*	V	3	§	H	–	CSR	meso-xero	9	×	4	4	×	2
Carlina vulgaris	–	–	–	H, T	bien	CSR	meso-xero	7	5	3	4	7	3
Centaurea scabiosa	–	–	–	H	–	C	meso-xero	7	×	3	3	8	4
Centaurea stoebe	–	–	–	H, T	bien	CSR	xero	8	7	6	2	8	3
Cerastium pumilum s. str.	–	–	–	T	win	SR	xero	8	7	4	2	8	2
Cerastium semidecandrum	–	–	–	T	win	R	xero	8	6	3	3	6	×
Cirsium acaulon	V	V	–	H	–	CSR	meso-xero	9	5	4	3	8	2
Cuscuta epithymum	3	3	–	T	sum	-	×	×	×	5	×	×	2
Daucus carota	–	–	–	H	–	CR	meso-xero	8	6	5	4	×	4
Draba verna	–	–	–	T	win	SR	xero	8	6	3	×	×	2
Echium vulgare	–	–	–	H	bien	CR	xero	9	6	3	4	8	4
Eryngium campestre	V	–	–	H	–	CS	×	9	7	5	3	8	3
Euphorbia cyparissias	–	–	–	H	–	CSR	×	8	×	4	3	×	3
Falcaria vulgaris	–	–	–	H	–	CS	xero	7	7	6	3	9	×
Filipendula vulgaris	3	V	–	H	–	CSR	meso-xero	7	6	5	3	8	2
Fragaria viridis	–	–	–	H	–	CSR	meso-xero	7	5	5	3	8	3
Galatella linosyris	3	3	–	H	–	CSR	xero	8	7	5	2	8	2
Galium glaucum	V	V	–	H	–	CSR	xero	8	7	6	2	9	2
Galium verum	–	–	–	H	–	CS	meso-xero	7	6	×	4	7	3
Globularia bisnagarica	3	3	§	H	–	CSR	xero	8	6	5	2	9	2
Helianthemum canum	3	3	§	C	–	CS	xero	8	7	4	2	9	1
Hieracium pilosella	–	–	–	H	–	CSR	meso-xero	7	×	3	4	×	2
Hippocrepis comosa	V	V	–	C, H	–	CSR	×	7	5	2	3	7	2
Holosteum umbellatum	–	–	–	T	win	SR	xero	8	6	5	3	×	2
Hornungia petraea	2	3	–	T	win	SR	xero	8	7	2	2	9	1
Hypericum elegans	2	1	–	H	–	CS	xero	7	7	6	3	9	2
Hypericum perforatum	–	–	–	H	–	C	meso-xero	7	6	5	4	6	4
Inula hirta	3	3	–	H	–	CS	xero	7	6	6	3	8	3
Linum catharticum	–	V	–	T	sum	SR	meso-xero	7	×	3	×	7	2
Lotus corniculatus	–	–	–	H	–	CSR	meso-xero	7	×	3	4	7	3
Medicago falcata	–	–	–	H	–	CS	×	8	6	7	3	9	3
Medicago lupulina	–	–	–	H	–	CSR	meso-xero	7	5	×	4	8	×
Microthlaspi perfoliatum	–	–	–	T	win	SR	xero	8	6	5	4	8	2
Ononis spinosa agg.	–	–	–	C, H	–	CS	meso-xero	8	6	5	4	7	3
Orchis purpurea	V	3	§	G	–	CSR	meso-xero	5	7	4	4	8	3
Peucedanum cervaria	V	3	–	H	–	CS	×	7	6	4	3	7	3
Pimpinella saxifraga	–	–	–	H	–	CS	meso-xero	7	×	5	3	×	2
Plantago lanceolata	–	–	–	H	–	CSR	meso-xero	6	×	3	×	×	×
Plantago media	–	–	–	H	–	CSR	meso-xero	7	×	7	4	7	3
Potentilla heptaphylla	V	–	–	H	–	CSR	meso-xero	7	5	4	3	9	2
Potentilla incana	V	–	–	H	–	S	xero	9	7	6	1	8	1
Potentilla verna	–	–	–	H	–	CSR	meso-xero	8	6	4	3	7	2
Prunella grandiflora	V	3	–	H	–	CSR	meso-xero	7	×	5	3	8	3
Pulsatilla vulgaris	3	2	§	H	–	CSR	meso-xero	7	6	5	2	7	2
Reseda lutea	–	–	–	H	bien	CSR	xero	7	6	3	3	8	5
Salvia pratensis	V	–	–	H	–	CSR	×	8	6	4	3	8	4
Sanguisorba minor	–	–	–	H	–	CSR	meso-xero	7	6	5	3	8	2
Scabiosa canescens	3	3	–	H	–	CSR	xero	7	7	6	3	8	3
Scabiosa ochroleuca	3	–	–	H	–	CSR	meso-xero	8	5	2	3	8	3
Securigera varia	–	–	–	H	–	C	meso-xero	7	6	5	4	9	3
Seseli hippomarathrum	2	3	–	H	–	CS	xero	9	8	6	2	9	1
Silene latifolia	–	–	–	H	–	C	meso-xero	8	6	×	4	×	7
Stachys recta	V	V	–	H	–	CSR	xero	7	6	4	3	9	2
Taraxacum sect. *Erythrosperma*	–	–	–	H	–	CSR	×	8	6	5	3	7	2
Teucrium chamaedrys	–	–	–	C	–	CSR	xero	7	6	4	2	8	1
Teucrium montanum	V	–	–	C	–	CSR	xero	8	5	4	1	9	1
Thesium linophyllon	3	3	–	G	–	CSR	meso-xero	8	7	5	2	8	1
Thymus praecox	–	3	–	C, H	–	CSR	×	8	6	5	3	8	1
Trifolium pratense	–	–	–	H	–	C	meso-xero	7	×	3	5	×	×
Veronica praecox	V	3	–	T	win	SR	xero	8	8	5	2	8	1
Veronica spicata	3	3	§	H	–	CSR	meso-xero	7	7	6	3	7	2
Vincetoxicum hirundinaria	–	–	–	H	–	CS	×	6	5	5	3	7	3
Viola hirta	–	–	–	H	–	CSR	meso-xero	6	5	5	3	8	3
Viola rupestris	2	3	–	H	–	CSR	meso-xero	6	5	7	3	8	2
Woody plants													
Cornus sanguinea juv.	–	–	–	N	–	C	×	7	5	4	5	7	×
Prunus spinosa juv.	–	–	–	N	–	C	×	7	5	5	4	7	×
Rosa canina juv.	–	–	–	N	–	C	×	8	5	3	4	×	×
Rosa elliptica juv.	3	–	–	N	–	C	×	8	6	4	3	8	3
Rosa rubiginosa juv.	–	–	–	N	–	C	×	7	6	2	3	8	3

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Supplement E2. Synoptic table of the dry grassland communities in 1995 und 2019. Species are primary arranged according their association indication in 1995 und secondary according their association indication in 2019. Associations are: Bro – Bromus grasslands (*Onobrychido-Brometum*), Car – *Carex humilis* grassland (*Trinio-Caricetum*), Koe – Koeleria grassland (*Gentiano-Koelerietum*), Ses – Sesleria grassland (*Carici-Seslerietum*), Sti – Stipa grassland (*Festuco-Stipetum*). Percent constancies with mean percent cover in upper case. Species with fidelity degree $\phi > 0.25$ in one or several associations after a Fisher's exact test are highlighted in grey. Within the groups, species are arranged according to decreasing constancy. Species that are diagnostic for more than one unit are sorted within the unit with the higher *phi*-value. Significant winner species (W) or loser species (L) – over all associations – are indicated by W/L symbols. W/L symbols in bold indicate new or disappeared winner or loser species.

Anhang E2. Übersichtstabelle der Trockenrasengesellschaften in den Jahren 1995 und 2019. Die Arten sind primär nach ihrer Assoziationsindikation in 1995 und sekundär nach ihrer Assoziationsindikation in 2019 sortiert. Die Assoziationen sind: Bro – Bromus-Halbtrockenrasen (On*obrychido-Brometum*), Car – *Carex humilis*-Trockenrasen (*Trinio-Caricetum*), Koe – Koeleria-Halbtrockenrasen (*Gentiano-Koelerietum*), Ses – Sesleria-Trockenrasen (*Carici-Seslerietum*), Sti – Stipa-Trockenrasen (*Festuco-Stipetum*). Prozentstetigkeiten mit hochgestellter mittlerer Prozentdeckung. Hochtreue Arten der Assoziationen mit $\phi > 0,25$ nach einem Fisher's exact-Test sind grau hinterlegt. Innerhalb der Differentialartengruppen sind die Arten nach abnehmender Stetigkeit sortiert. Die Position derjenigen Arten, die für mehrere Einheiten diagnostisch sind, richtet sich nach der derjenigen Einheit, in der die Arten ihren höchsten ϕ-Wert aufweisen. Signifikante Gewinner- (W) oder Verliererarten (L) – über alle Assoziationen – sind mit W/L-Symbolen gekennzeichnet. Fettgedruckte W/L-Symbole zeigen neue oder verschwundene Gewinner- oder Verliererarten an.

		1995				**2019**			
		Koe	***Ses***	***Car***	***Sti***	***Bro***	***Ses***	***Car***	***Sti***
Local assoc. diagnostics in 1995									
L	*Anthyllis vulneraria*	100^{12}	$8^{2.5}$	.	.	$67^{2.6}$	.	.	.
L	*Potentilla verna*	$100^{2.5}$	$25^{2.5}$	$24^{2.0}$	.	$50^{1.8}$	.	.	.
L	*Asperula cynanchica*	$100^{3.5}$	$67^{2.5}$	$53^{2.5}$	$55^{2.2}$	.	.	.	.
L	*Linum catharticum*	$100^{2.5}$	$8^{2.5}$	$12^{2.5}$	.	.	.	.	.
	Briza media	$100^{9.4}$	.	$18^{6.7}$	$9^{2.5}$	$67^{6.6}$	.	$12^{2.5}$	$9^{2.5}$
L	*Festuca rupicola*	100^{10}	.	$65^{4.5}$	$9^{2.5}$	$17^{0.5}$	.	$18^{7.1}$	.
L	*Scabiosa canescens*	83^{15}	$17^{2.5}$	$29^{5.8}$	$9^{0.5}$	50^{15}	.	$47^{4.2}$	.
L	*Carex caryophyllea*	$83^{2.5}$	.	.	.	.	.	.	.
L	*Pimpinella saxifraga*	$83^{5.0}$	$8^{0.5}$	$59^{2.1}$	.	.	.	.	.
L	*Plantago media*	67^{11}	$8^{2.5}$	$6^{2.5}$	.	$67^{1.5}$	.	.	.
	Achillea millefolium agg.	$67^{2.5}$	.	$18^{2.5}$	.	$17^{2.5}$	.	$24^{1.0}$	.
	Scabiosa ochroleuca	$67^{5.6}$	.	$24^{2.0}$	.	50^{13}	.	$24^{2.5}$	.
L	*Koeleria pyramidata*	$67^{2.5}$	$33^{2.0}$	$6^{0.5}$	.	.	.	.	.
L	*Potentilla heptaphylla*	$67^{2.5}$	$8^{0.5}$	$35^{1.5}$	$9^{2.5}$	.	$8^{0.5}$	.	.
	Avenula pubescens	$50^{2.5}$	.	.	.	.	.	.	.
L	*Lotus corniculatus*	$50^{2.5}$	$17^{2.5}$	$12^{2.5}$	.	$33^{0.5}$	.	.	.
	Cirsium acaulon	$50^{4.6}$	$17^{5.6}$	$18^{2.5}$	.	$50^{4.6}$	$25^{1.0}$	$12^{0.1}$	.
L	*Taraxacum* sect. *Erythrosperma*	$33^{2.5}$	$8^{2.5}$	$24^{2.0}$	$45^{2.5}$	.	.	.	.
	Veronica spicata	$33^{1.5}$	.	.	.	$17^{0.1}$	.	.	.
	Campanula rotundifolia	$33^{1.5}$	.	.	.	.	.	.	.
	Agrostis gigantea	$17^{2.5}$	.	.	.	.	.	.	.
	Daucus carota	$17^{2.5}$	.	.	.	.	.	.	.
	Plantago lanceolata	$17^{0.5}$	.	.	.	.	.	.	.
	Medicago lupulina	$17^{2.5}$	.	.	.	.	.	.	.
	Astragalus danicus	$17^{2.5}$	.	.	.	50^{20}	.	.	.
	Medicago falcata	$17^{2.5}$	.	$6^{2.5}$	.	.	.	.	.
	Fragaria viridis	$17^{2.5}$	.	$6^{8.8}$	.	$17^{0.5}$	.	.	.
	Carlina acaulis subsp. *simplex*	$17^{2.5}$	$8^{0.5}$	.	.	.	.	.	.
L	*Sesleria caerulea*	100^{38}	100^{21}	.	.	.	58^{19}	.	.
L	*Seseli hippomarathrum*	$17^{2.5}$	$100^{2.0}$	$71^{4.9}$	$73^{3.0}$	$17^{0.1}$	$92^{2.7}$	$41^{1.6}$	$73^{3.6}$
L	*Festuca csikhegyensis*	$17^{0.5}$	$100^{5.9}$	$71^{2.2}$	$100^{2.1}$	.	$92^{4.6}$	$35^{0.7}$	$18^{0.1}$
L	*Teucrium montanum*	$67^{2.5}$	$100^{4.1}$	$71^{5.4}$	73^{16}	$17^{8.8}$	75^{12}	$41^{1.1}$	$36^{6.1}$
L	*Potentilla incana*	.	$83^{3.1}$	$59^{2.5}$	$55^{3.8}$	.	$58^{1.1}$	$29^{0.9}$	$36^{0.9}$
	Rosa rubiginosa juv.	.	$42^{4.2}$	$35^{4.3}$	$18^{0.5}$	$17^{0.1}$	$33^{0.9}$	$18^{1.7}$	$27^{1.0}$
	Hieracium pilosella	$33^{2.5}$	$33^{2.5}$	$24^{2.5}$	.	$50^{1.2}$	$33^{1.5}$	.	.
L	*Euphorbia cyparissias*	$50^{2.5}$	$58^{3.4}$	$100^{3.8}$	$36^{2.5}$	$17^{2.5}$	$92^{0.8}$	$82^{1.5}$	$64^{0.7}$
L	*Salvia pratensis*	.	.	$94^{5.4}$	$36^{2.5}$	.	$33^{0.4}$	$71^{1.5}$	$73^{1.0}$
L	*Brachypodium pinnatum*	.	$50^{9.0}$	94^{15}	36^{20}	$50^{0.4}$	67^{13}	$47^{10.8}$	$18^{1.3}$
L	*Helictochloa pratensis*	$83^{2.5}$	$67^{2.5}$	$88^{2.5}$	$36^{1.8}$	.	.	.	.
L	*Cuscuta epithymum*	.	$25^{2.5}$	$71^{2.0}$	$36^{1.8}$	.	.	$29^{0.5}$	.
	Peucedanum cervaria	.	$8^{0.5}$	$47^{5.3}$	$9^{2.5}$	.	$17^{0.3}$	$47^{5.1}$	27^{19}
L	*Adonis vernalis*	.	$25^{1.8}$	$47^{1.8}$	$36^{2.5}$	.	$8^{0.5}$	$35^{0.6}$	$18^{0.3}$
	Galatella linosyris	.	$8^{0.5}$	$41^{5.7}$	.	.	$33^{1.0}$	$35^{2.2}$	.
	Thesium linophyllon	.	$8^{2.5}$	$41^{2.5}$	.	.	$33^{10.3}$	$35^{2.2}$	.
	Rosa canina juv.	.	.	$29^{0.5}$	.	.	.	$6^{2.5}$	.
	Prunella grandiflora	.	.	29^{16}	.	.	.	$18^{2.5}$	.
	Anthericum ramosum	.	$25^{4.6}$	$29^{2.1}$	.	.	$33^{3.6}$	$29^{1.1}$	$9^{0.1}$
	Galium verum	.	.	$24^{2.5}$	.	.	.	$29^{1.7}$	$9^{2.5}$
	Eryngium campestre	.	.	$24^{8.1}$	.	.	.	$6^{2.5}$	$9^{2.5}$
	Bupleurum falcatum	.	.	$18^{3.9}$	.	.	.	$12^{0.3}$	.
	Centaurea scabiosa	.	.	$18^{3.9}$	.	.	.	$18^{0.9}$	.
	Rosa elliptica juv.	.	$8^{0.5}$	$18^{1.2}$	.	.	.	.	.
	Stachys recta	.	.	$12^{2.5}$	.	.	.	$18^{1.0}$	.
	Inula hirta	.	.	$12^{1.5}$	.	.	.	$18^{3.9}$	.
	Viola hirta	.	.	$12^{1.5}$	.	.	.	.	.
W	*Stipa capillata*	.	.	$35^{4.5}$	91^{18}	.	.	65^{36}	100^{41}
W	*Draba verna*	.	.	.	$55^{2.5}$	$67^{1.0}$	$83^{1.1}$	$65^{0.9}$	$64^{0.5}$
W	*Hornungia petraea*	.	.	.	$55^{2.5}$	.	$92^{1.8}$	$82^{1.1}$	$91^{1.5}$
W	*Cerastium pumilum* s. str.	.	.	$6^{0.5}$	$36^{2.5}$	.	$42^{1.2}$	$47^{1.0}$	$64^{0.8}$
	Bothriochloa ischoemum	.	.	$18^{2.5}$	$18^{5.6}$	.	.	$12^{2.5}$	$27^{2.5}$
	Arenaria serpyllifolia	.	.	.	$18^{2.5}$	.	.	.	.
	Veronica praecox	.	.	.	$9^{0.5}$	.	.	.	.
Local assoc. diagnostics in 2019									
W	*Bromus erectus*	$17^{2.5}$	.	$12^{2.5}$	.	100^{45}	92^{13}	47^{32}	55^{16}
	Securigera varia	.	.	$6^{8.8}$	.	50^{26}	.	.	.
	Agrimonia eupatoria	.	.	$6^{2.5}$	.	$33^{1.3}$	.	.	.
	Poa badensis	.	.	.	.	$17^{2.5}$	$8^{2.5}$	.	.
	Trifolium pratense	.	.	.	.	$17^{0.5}$	.	.	.
	Pulsatilla vulgaris	.	.	.	.	$17^{0.1}$	.	.	.
	Echium vulgare	.	.	.	.	$17^{0.1}$	.	$6^{2.5}$	.
L	*Thymus praecox*	33^{116}	$92^{7.0}$	100^{26}	91^{24}	$67^{1.0}$	$75^{3.7}$	$24^{1.0}$	$18^{0.5}$
L	*Sanguisorba minor*	$83^{2.5}$	$75^{2.5}$	$53^{2.3}$	$27^{1.8}$	$67^{9.7}$	$67^{1.8}$	$29^{0.9}$	.
W	*Microthlaspi perfoliatum*	.	.	.	.	.	$33^{0.4}$	$24^{0.2}$	.
	Viola rupestris	$17^{2.5}$	.	$6^{2.5}$	.	.	$8^{0.1}$	.	.
W	*Prunus spinosa* juv.	.	.	$6^{2.5}$	.	.	.	$41^{3.4}$	.
W	*Centaurea stoebe*	.	.	.	.	.	.	$35^{0.8}$	$27^{0.5}$
	Arabis hirsuta	.	.	$24^{2.0}$	$9^{2.5}$	.	.	$35^{0.2}$	$18^{0.1}$
	Vincetoxicum hirundinaria	.	.	$6^{2.5}$	.	$17^{0.1}$	.	$29^{0.4}$	$9^{0.1}$
L	*Koeleria macrantha*	$33^{2.5}$	$25^{1.8}$	$59^{2.3}$	$73^{2.5}$	.	.	$18^{0.2}$	$9^{0.1}$
	Falcaria vulgaris	.	.	.	.	.	.	$6^{0.1}$	.
	Silene latifolia	.	.	.	.	.	.	$6^{0.1}$	.
L	*Teucrium chamaedrys*	$100^{7.3}$	100^{16}	$88^{8.5}$	$64^{7.5}$	$17^{0.5}$	75^{15}	$94^{7.6}$	$100^{5.7}$
L	*Helianthemum canum*	100^{22}	100^{15}	88^{12}	100^{11}	$33^{9.6}$	$75^{8.4}$	$71^{2.7}$	$100^{3.6}$
	Holosteum umbellatum	.	.	.	.	.	.	.	$27^{1.0}$
	Filipendula vulgaris	.	.	.	.	.	.	$6^{0.1}$	$18^{0.5}$
	Asparagus officinalis	.	.	$6^{2.5}$	.	.	.	.	$9^{0.1}$
Non-diagnostic species									
L	*Carex humilis*	100^{14}	100^{16}	76^{38}	100^{14}	100^{10}	100^{14}	$71^{7.3}$	100^{11}
L	*Hippocrepis comosa*	$33^{2.5}$	$58^{2.2}$	$59^{3.8}$	.	.	$17^{0.5}$	$24^{3.6}$	$9^{0.1}$
	Carlina vulgaris	.	.	$12^{1.5}$	.	.	.	.	.
	Allium lusitanicum	.	$8^{2.5}$	.	.	.	.	.	.
	Galium glaucum	.	.	$6^{2.5}$	.	.	.	.	.
	Dactylis glomerata	.	.	$6^{0.5}$	.	.	.	.	.
	Festuca valesiaca	.	.	$6^{2.5}$	.	.	.	.	.
	Hypericum elegans	.	.	$6^{2.5}$	.	.	.	.	.
	Hypericum perforatum	.	.	$6^{2.5}$	.	.	.	.	.
	Orchis purpurea	.	.	$6^{2.5}$	.	$17^{0.1}$	.	.	$9^{0.5}$
W	*Cerastium semidecandrum*	.	.	.	.	$67^{0.4}$	$50^{0.8}$	$59^{1.3}$	$64^{1.6}$
	Stipa pulcherrima	.	.	.	.	.	$17^{1.3}$	$6^{0.5}$	.
	Cornus sanguinea juv.	.	.	.	.	$17^{0.5}$	.	.	.
	Reseda lutea	.	.	.	.	.	.	$6^{0.5}$	$9^{0.1}$
	Globularia bisnagarica	.	.	.	.	.	.	.	$9^{0.1}$
	Ononis spinosa agg.	.	.	.	.	.	.	$6^{0.5}$	.

Supplement E3. Constant vascular plant species or species that are too rare for assessing their change. Frequencies (constancies) in percent and mean percent cover values in uppercase. All comparisons shown are not significant (*n.s.*) at $p > 0.1$.

Anhang E3. Konstante Gefäßpflanzenarten oder Arten, die zu selten sind, um ihre Veränderung zu bemessen. Prozentstetigkeiten und mittlere Prozentdeckungen (hochgestellt). Alle gezeigten Vergleiche sind nicht signifikant (*n.s.*) bei $p > 0,1$.

	Koe **(*n* = 6)**			***Ses*** **(*n* = 12)**			***Car*** **(*n* = 17)**			***Sti*** **(*n* = 11)**			***all*** **(*n* = 46)**		
	1995	**2019**		**1995**	**2019**		**1995**	**2019**		**1995**	**2019**		**1995**	**2019**	
Graminoids															
Agrostis gigantea	17^{3}	0^{-}	*n.s.*	–	–		–	–		–	–		2^{3}	0^{-}	*n.s.*
Bothriochloa ischoemum	–	–		–	–		18^{3}	12^{3}	*n.s.*	18^{6}	27^{3}	*n.s.*	11^{4}	11^{3}	*n.s.*
Briza media	100_{10}	67^{7}	*n.s.*	–	–		18^{8}	12^{3}	*n.s.*	9^{3}	9^{3}	*n.s.*	22^{8}	15^{5}	*n.s.*
Dactylis glomerata	–	–		–	–		$6^{0.5}$	0^{-}	*n.s.*	–	–		$2^{0.5}$	0^{-}	*n.s.*
Festuca valesiaca	–	–		–	–		6^{3}	0^{-}	*n.s.*	–	–		2^{3}	0^{-}	*n.s.*
Avenula pubescens	50_{3}	0^{-}	*n.s.*	–	–		–	–		–	–		7^{3}	0^{-}	*n.s.*
Poa badensis	0_{-}	17^{3}	*n.s.*	0^{-}	8^{3}	*n.s.*	–	–		–	–		0^{-}	4^{3}	*n.s.*
Stipa pulcherrima	–	–		0^{-}	17^{1}	*n.s.*	0^{-}	$6^{0.5}$	*n.s.*	–	–		0^{-}	7^{1}	*n.s.*
Herbs															
Achillea millefolium agg.	67_{3}	17^{3}	*n.s.*	–	–		18^{3}	24^{1}	*n.s.*	–	–		15^{3}	11^{1}	*n.s.*
Agrimonia eupatoria	0_{-}	33^{1}	*n.s.*	–	–		6^{3}	0^{-}	*n.s.*	–	–		2^{3}	4^{1}	*n.s.*
Allium lusitanicum	–	–		8^{3}	0^{-}	*n.s.*	–	–		–	–		2^{3}	0^{-}	*n.s.*
Anthericum ramosum	–	–		25^{5}	33^{4}	*n.s.*	29^{2}	29^{1}	*n.s.*	0^{-}	$9^{0.1}$	*n.s.*	17^{3}	22^{2}	*n.s.*
Arabis hirsuta	–	–		–	–		24^{2}	$35^{0.2}$	*n.s.*	9^{3}	$18^{0.1}$	*n.s.*	11^{2}	$17^{0.2}$	*n.s.*
Arenaria serpyllifolia	–	–		–	–		–	–		18^{3}	0^{-}	*n.s.*	4^{3}	0^{-}	*n.s.*
Asparagus officinalis	–	–		–	–		6^{3}	0^{-}	*n.s.*	0^{-}	$9^{0.1}$	*n.s.*	2^{3}	$2^{0.1}$	*n.s.*
Astragalus danicus	17_{3}	50^{20}	*n.s.*	–	–		–	–		–	–		2^{3}	7^{20}	*n.s.*
Bupleurum falcatum	–	–		–	–		18^{4}	$12^{0.3}$	*n.s.*	–	–		7^{4}	$4^{0.3}$	*n.s.*
Campanula rotundifolia	33^{2}	0^{-}	*n.s.*	–	–		–	–		–	–		4^{2}	0^{-}	*n.s.*
Carlina acaulis	17^{3}	0^{-}	*n.s.*	$8^{0.5}$	0^{-}	*n.s.*	–	–		–	–		4^{2}	0^{-}	*n.s.*
Carlina vulgaris	–	–		–	–		12^{2}	0^{-}	*n.s.*	–	–		4^{2}	0^{-}	*n.s.*
Centaurea scabiosa	–	–		–	–		18^{4}	$18^{0.9}$	*n.s.*	–	–		7^{4}	$7^{0.9}$	*n.s.*
Cirsium acaulon	50^{5}	50^{5}	*n.s.*	17^{6}	25^{1}	*n.s.*	18^{3}	$12^{0.1}$	*n.s.*	–	–		17^{4}	17^{2}	*n.s.*
Daucus carota	17^{3}	0^{-}	*n.s.*	–	–		–	–		–	–		2^{3}	0^{-}	*n.s.*
Echium vulgare	0^{-}	$17^{0.1}$	*n.s.*	–	–		0^{-}	6^{3}	*n.s.*	–	–		0^{-}	4^{1}	*n.s.*
Eryngium campestre	–	–		–	–		24^{9}	6^{3}	*n.s.*	0^{-}	9^{3}	*n.s.*	9^{9}	4^{3}	*n.s.*
Falcaria vulgaris	–	–		–	–		0^{-}	$6^{0.1}$	*n.s.*	–	–		0^{-}	$2^{0.1}$	*n.s.*
Filipendula vulgaris	–	–		–	–		0^{-}	$6^{0.1}$	*n.s.*	0^{-}	$18^{0.5}$	*n.s.*	0^{-}	$7^{0.4}$	*n.s.*
Fragaria viridis	17^{3}	$17^{0.5}$	*n.s.*	–	–		6^{10}	0^{-}	*n.s.*	–	–		4^{6}	$2^{0.5}$	*n.s.*
Galatella linosyris	–	–		$8^{0.5}$	33^{1}	*n.s.*	41^{6}	35^{2}	*n.s.*	–	–		17^{5}	22^{2}	*n.s.*
Galium glaucum	–	–		–	–		6^{3}	0^{-}	*n.s.*	–	–		2^{3}	0^{-}	*n.s.*
Galium verum	–	–		–	–		24^{3}	29^{2}	*n.s.*	0^{-}	9^{3}	*n.s.*	9^{3}	13^{2}	*n.s.*
Globularia bisnagarica	–	–		–	–		–	–		0^{-}	$9^{0.1}$	*n.s.*	0^{-}	$2^{0.1}$	*n.s.*
Hieracium pilosella	33^{3}	50^{1}	*n.s.*	33^{3}	33^{2}	*n.s.*	24^{3}	0^{-}	*n.s.*	–	–		22^{3}	15^{1}	*n.s.*
Holosteum umbellatum	–	–		–	–		–	–		0^{-}	27^{1}	*n.s.*	0^{-}	7^{1}	*n.s.*
Hypericum elegans	–	–		–	–		6^{3}	0^{-}	*n.s.*	–	–		2^{3}	0^{-}	*n.s.*
Hypericum perforatum	–	–		–	–		6^{3}	0^{-}	*n.s.*	–	–		2^{3}	0^{-}	*n.s.*
Inula hirta	–	–		–	–		12^{2}	18^{4}	*n.s.*	–	–		4^{2}	7^{4}	*n.s.*
Medicago falcata	17^{3}	0^{-}	*n.s.*	–	–		6^{3}	0^{-}	*n.s.*	–	–		4^{3}	0^{-}	*n.s.*
Medicago lupulina	17^{3}	0^{-}	*n.s.*	–	–		–	–		–	–		2^{3}	0^{-}	*n.s.*
Ononis spinosa agg.	–	–		–	–		0^{-}	$6^{0.5}$	*n.s.*	–	–		0^{-}	$2^{0.5}$	*n.s.*
Orchis purpurea	0^{-}	$17^{0.1}$	*n.s.*	–	–		6^{3}	0^{-}	*n.s.*	0^{-}	$9^{0.5}$	*n.s.*	2^{3}	$4^{0.3}$	*n.s.*
Peucedanum cervaria	–	–		$8^{0.5}$	$17^{0.3}$	*n.s.*	47^{6}	47^{5}	*n.s.*	9^{3}	27^{19}	*n.s.*	22^{5}	28^{8}	*n.s.*
Plantago lanceolata	$17^{0.5}$	0^{-}	*n.s.*	–	–		–	–		–	–		$2^{0.5}$	0^{-}	*n.s.*
Plantago media	67^{11}	67^{2}	*n.s.*	8^{3}	0^{-}	*n.s.*	6^{3}	0^{-}	*n.s.*	–	–		13^{8}	9^{2}	*n.s.*
Prunella grandiflora	–	–		–	–		29^{17}	18^{3}	*n.s.*	–	–		11^{17}	7^{3}	*n.s.*
Pulsatilla vulgaris	0^{-}	$17^{0.1}$	*n.s.*	–	–		–	–		–	–		0^{-}	$2^{0.1}$	*n.s.*
Reseda lutea	–	–		–	–		0^{-}	$6^{0.5}$	*n.s.*	0^{-}	$9^{0.1}$	*n.s.*	0^{-}	$4^{0.3}$	*n.s.*
Scabiosa canescens	83^{16}	50^{17}	*n.s.*	17^{3}	0^{-}	*n.s.*	29^{6}	47^{5}	*n.s.*	$9^{0.5}$	0^{-}	*n.s.*	28^{9}	24^{8}	*n.s.*
Scabiosa ochroleuca	67^{6}	50^{14}	*n.s.*	–	–		24^{2}	24^{3}	*n.s.*	–	–		17^{4}	15^{7}	*n.s.*
Securigera varia	0^{-}	50^{26}	*n.s.*	–	–		6^{10}	0^{-}	*n.s.*	–	–		2^{10}	7^{26}	*n.s.*
Silene latifolia	–	–		–	–		0^{-}	$6\ 0.^{1}$	*n.s.*	–	–		0^{-}	$2^{0.1}$	*n.s.*
Stachys recta	–	–		–	–		12^{3}	18^{1}	*n.s.*	9^{3}	0^{-}	*n.s.*	7^{3}	7^{1}	*n.s.*
Thesium linophyllon	–	–		8^{3}	33^{10}	*n.s.*	41^{3}	35^{2}	*n.s.*	–	–		17^{3}	22^{5}	*n.s.*
Trifolium pratense	0^{-}	$17^{0.5}$	*n.s.*	–	–		–	–		–	–		0^{-}	$2^{0.5}$	*n.s.*
Veronica praecox	–	–		–	–		–	–		$9^{0.5}$	0^{-}	*n.s.*	$2^{0.5}$	0^{-}	*n.s.*
Veronica spicata	33^{2}	$17^{0.1}$	*n.s.*	–	–		–	–		–	–		4^{2}	$2^{0.1}$	*n.s.*
Vincetoxicum hirundinaria	0^{-}	$17^{0.1}$	*n.s.*	–	–		6^{3}	$29^{0.4}$	*n.s.*	0^{-}	$9^{0.1}$	*n.s.*	2^{3}	$15^{0.3}$	*n.s.*
Viola hirta	–	–		–	–		12^{2}	0^{-}	*n.s.*	–	–		4^{2}	0^{-}	*n.s.*
Viola rupestris	17^{3}	0^{-}	*n.s.*	0^{-}	$8^{0.1}$	*n.s.*	6^{3}	0^{-}	*n.s.*	–	–		4^{3}	$2^{0.1}$	*n.s.*
Woody species															
Cornus sanguinea juv.	0^{-}	$17^{0.5}$	*n.s.*	–	–		–	–		–	–		0^{-}	$2^{0.5}$	*n.s.*
Rosa canina juv.	–	–		–	–		$29^{0.5}$	6^{3}	*n.s.*	–	–		$11^{0.5}$	2^{3}	*n.s.*
Rosa elliptica juv.	–	–		$8^{0.5}$	0^{-}	*n.s.*	18^{1}	0^{-}	*n.s.*	–	–		9^{1}	0^{-}	*n.s.*
Rosa rubiginosa juv.	0^{-}	$17^{0.1}$	*n.s.*	42^{5}	$33^{0.9}$	*n.s.*	35^{5}	18^{2}	*n.s.*	–	–		28^{4}	24^{1}	*n.s.*