Restoration and management of abandoned, dry Continental heathland and sandy grassland communities

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Summary

Land-use changes and long-term abandonment are main drivers that change ecosystem functioning and cause biodiversity loss of many semi-natural habitats, such as heathlands and grasslands. Traditional management measures such as low-intensity grazing created these semi-open landscapes and maintained a high species richness. However, from the middle of the 19th century onwards, traditional management practices began to decline due to socio-economic changes, and large areas of heathlands and grasslands were subjected to succession and reverted to woodland.

Nowadays, dry heathlands as well as dry sandy grasslands are recognized as being of high conservation value and classified as "habitats of community interest" ("European dry heaths", habitat code 4030; "Xeric sand calcareous grasslands", habitat code *6120). Whereas heathlands in the Atlantic biogeographical region have been in the centre of interest, dry heathland communities in the Continental biogeographical region have been widely neglected, even though they comprise 30 % of all dry heaths as well as 89 % of all dry sandy grasslands, respectively, in Europe. Thereby, the conservation status of both habitat types is listed as unfavourable-bad across the Continental biogeographical region.

Surprisingly, no detailed studies are available on cost-efficient and sustainable restoration and management schemes to successfully restore and maintain highly degraded, long-abandoned Continental heaths and sandy grasslands, and thus, to counteract the poor conservation status of the habitat types. This shows the great need for research for the Continental biogeographical region (chapter I). Thus, the present thesis provides substantial knowledge about the population dynamics of the key plant species of dry heaths *Calluna vulgaris vulgaris* (L.) HULL (henceforth referred to as *Calluna*) by investigating key processes in the biology of the species as well as about the restoration and management of long-abandoned, dry Continental heathland and sandy grassland communities.

In order to better understand the process of successful Continental heathland restoration, I analysed the reproductive potential (seed production, soil seed bank, and germination ability of seeds) of degenerate *Calluna* stands as well as the effects of single and combined management options on the generative rejuvenation (i.e., recruitment and survival) of *Calluna* (chapter II). The results are based on a comprehensive three-year field experiment including the management options year-round, low-

intensity cattle and horse grazing, one-time mowing and one-time shallow soil disturbances combined with greenhouse investigations on the soil seed bank content and germination ability of *Calluna* seeds. The results showed that even after long-term abandonment, seed production of degenerate *Calluna* stands and the germination ability of seeds proved to be high, being similar to Atlantic heathlands, whereas the soil seed bank is considerably reduced probably due to the dry conditions in the Continental region. In addition, low-intensity grazing with free-ranging robust breeds and the combination with one-time mowing at the beginning of the restoration process is an effective means of supporting the generative rejuvenation of this key plant species in degraded Continental heaths.

The second study of this thesis (chapter III) focussed on the first-year establishment of *Calluna* in managed and unmanaged dry heaths and heaths in mosaics with dry sandy grasslands. The germination ability of seeds of different life-history phases of *Calluna* was analysed to determine if the predominance of the late life-history phase restricts the rejuvenation process of this key plant species. In addition, beside effects of management measures (year-round, low-intensity grazing, one-time mowing, one-time shallow soil disturbances) I analysed the most important safe site conditions that possibly influenced the germination and the first-year survival of *Calluna*. The results of the study combine field experiments with growth chamber investigations. I found that life-history phase of *Calluna* did not significantly affect seed germination and thus, the predominance of the degenerate life-history phase does not restrict the rejuvenation process. In addition, the results of my study revealed that grazing and thus trampling intensity must be temporarily and locally enhanced at the beginning of the restoration process of highly degraded heaths to increase safe site availability for successful *Calluna* establishment. Thereby, shadowing is the most important safe site condition that limit *Calluna* recruitment and survival in the first year in both degraded heaths as well as in mosaics with sandy grasslands, since seedlings receiving full sunlight die significantly more frequently than slightly or fully shaded seedlings.

In the third study (chapter IV), I investigated the impacts of year-round low-intensity cattle and horse grazing on the development of the highly competitive grass *Calamagrostis epigejos* (henceforth referred to as *Calamagrostis*), as well as the vegetation structure and plant species richness of long-abandoned but nutrient-poor dry heathland and sandy grassland communities, their mosaics and

Calamagrostis stands. Finally, I assessed the local conservation status of the habitat types after seven years of grazing in comparison to long-abandoned sites. The results are based on a comprehensive field study on two spatial scales (plot-level: 25 m², macroplot-level: 1 ha). I found that grazing successfully reduced the coverage and prevented the further spread of *Calamagrostis*, while simultaneously maintained or improved characteristic species richness and vegetation structure across the different nutrient-poor vegetation types over time, and thus enhanced the local conservation status of habitat types of community interest.

In conclusion, the results of my studies considerably improved the understanding of dry, Continental heathland and sandy grassland restoration and management. They provide evidence that even after long-term management abandonment, year-round low-intensity cattle and horse grazing is a suitable management tool for restoring, maintaining and even improving nutrient-poor heathland and sandy grassland communities. However, at the beginning of the restoration process, additional management measures are necessary to faster restore abandoned habitats, especially highly degraded heaths.

Chapter I

Restoration and management of abandoned, dry Continental heathland and

sandy grassland communities

– A general overview

General introduction

Dry heaths are widely distributed across Europe but belong essentially to the Atlantic biogeographical region (henceforth referred to as the Atlantic region), with mild winters, high rainfall and low annual temperature oscillation (Gimingham 1972, Loidi *et al.* 2010). Thus, they reach their ecological and geographical limits in more Continental climates with less favourable climatic conditions, for example in Eastern Germany, Poland or Czech. Besides the key species of dry heaths – *Calluna vulgaris* (L.) HULL (henceforth referred to as *Calluna*) – species with more eastern distributions and typical of dry sandy grasslands accompanying Continental heaths (Sedláková & Chytrý 1999), making these heathlands rich in species.

Therefore, dry heathlands as well as dry sandy grasslands are recognized as being of high conservation value and classified as "habitats of community interest" ("European dry heaths", habitat code 4030; "Xeric sand calcareous grasslands", habitat code *6120; Council Directive 92/43/EEC). They mainly originated from a long history of low-intensity grazing, often in combination with other land use practices (e.g. mowing, sod-cutting, burning; Bredenkamp, Spada & Kazmierczak 2002; Garcia *et al.* 2013; Dengler *et al.* 2014). Traditional management measures contributed to soil impoverishment, prevented succession to closed woodlands, created semi-open landscapes, and maintained a high species richness (Gimingham 1972; Webb 1998). Especially light-demanding, slow-growing and low-competitive species adapted to nutrient-poor soil conditions benefited from these management measures. From the middle of the 19th century onwards, traditional pastoralism began to decline due to socio-economic changes, and large areas of dry heaths and sandy grasslands were subjected to succession and reverted to woodland (Price 2003).

Some of these low-productive areas were used for military training activities, thus maintaining their open character, nutrient-poor soil conditions and species richness through a combination of heterogeneously distributed disturbances from military training activities and the exclusion of intensive agriculture or forestry (Warren *et al.* 2007; Jentsch *et al.* 2009). Today, military training areas represent some of the last large remnants of heathlands and sandy grasslands in Europe (Warren & Büttner 2014). However, political changes in the former Eastern bloc countries have led to the cessation of these activities in most areas (Cizek *et al.* 2013, Schumacher & Johst 2015). As a

consequence of the abandonment of both traditional management and military training activities, the conservation status of dry heathland and sandy grassland habitats is listed as unfavourable-bad across the Continental region of Europe (EEA 2015a, b).

The predominance of degenerate *Calluna* stands, the lack of earlier life-history phases of *Calluna* and the invasion of competitive grasses such as *Calamagrostis epigejos* (henceforth referred to as *Calamagrostis*) are the main degradation processes in abandoned dry heaths and sandy grasslands (Britton *et al.* 2000a; Dostálek & Frantík 2015) besides other successional changes such as shrub and tree encroachment (Gimingham 1992; Newton *et al.* 2009). Counteracting these processes is difficult in the current socio-economic situation in Europe and requires the development of scientifically based and cost-effective restoration schemes (Török *et al.* 2016a), based on a sound understanding of the effects of management on *Calluna* population dynamics and plant community interactions (Bullock & Pakeman 1996; Bullock *et al.* 2001; Soons & Bullock 2008).

The population dynamics of *Calluna vulgaris*

Essential indicators for predicting and evaluating the rejuvenation process of *Calluna* are the reproductive potential, i.e. the number of seeds produced, the soil seed bank and the seed germination ability, as well as the number of recruiting and surviving *Calluna* individuals (i.e. generative rejuvenation). Degenerate *Calluna* stands are characterized by a high proportion of woody or even dead *Calluna* biomass and a reduced proportion of flowering shoots (Miller & Miles 1970; Gimingham 1972). Reduced flowering with increasing age might result in a lower annual seed production in comparison to managed heaths where *Calluna* is more vigorous and early life-history phases are more prominent. This fact in its turn could lead to net losses in the seed bank (Ooi 2015). In addition, there is evidence that the soil seed bank of *Calluna* is smaller under drier, warmer site conditions in Atlantic heaths (Pakeman *et al.* 1999, Pywell *et al.* 2002). Therefore, the soil seed bank might be even smaller in Continental heaths with higher temperatures, less precipitation and drought periods leading to limited seedling recruitment (Ooi 2015). The less favourable climatic conditions in the Continental region compared to the Atlantic region could also lead to a greater probability of failed recruitment and higher seedling mortality since *Calluna* seedlings and juveniles are highly susceptible

to drought (Britton *et al.* 2003; Fagúndez 2012; Meyer-Grünefeldt *et al.* 2015). Drought events are more common in the Continental than in the Atlantic region, and it is predicted that climate change will lead to an increase in drought periods during the growing season (EEA 2008; Zacharias, Koppe & Mücke 2015). However, no detailed studies are available on the reproductive potential of degenerate *Calluna* in Continental heaths.

Rather than the absolute seed number, the availability of safe-sites determines the extent of future seedling recruitment and survival (Harper 1977; Maron & Gardner 2000). Safe sites are species-specific and characterized by several attributes which ensure a favourable microclimate, adequate soil structure and soil moisture (Uhl *et al.* 1981; Fowler 1988; Urbanska 1997) as well as light-availability. From Atlantic research it is well-known that *Calluna* is a light-demanding species requiring at least patches of bare soil for the germination of its small seeds (thousand-seed weight: 0.017 g; Bloemer 2014) and the survival of its slowly growing juveniles (Iason & Hester 1993; Quin *et al.* 2014). However, no information is available about specific safe site conditions for successful *Calluna* establishment under the less favourable Continental climate.

New restoration and management options

Nowadays, year-round large herbivore grazing is increasingly used to restore and maintain species-rich habitats as an alternative to the more costly traditional herding (Bokdam & Gleichman 2000; von Oheimb *et al.* 2006). Grazing has to be found to create safe sites by reducing aboveground biomass and creating bare soil patches (Oesterheld & Sala 1990). However, the suitability of this new grazing regime has not yet been investigated for long-abandoned, highly degraded but nutrient-poor heathland and sandy grassland communities and thus, is considered to be controversial (Newton *et al.* 2009).

In particular, it is unclear if large herbivore grazing is effective in enhancing *Calluna* rejuvenation, since at the beginning of the restoration process, degenerate *Calluna* stands might be largely neglected by the grazing animals due to the high proportion of woody biomass. Hence, grazing might not reduce the aboveground biomass and enhance bare-soil patch density sufficiently to increase generative *Calluna* rejuvenation. Therefore, degraded heaths are often mown before the re-introduction of grazing management to reduce vegetation density, support the vegetative rejuvenation of *Calluna* with

re-sprouting which subsequently enhances the fodder value (Pywell *et al.* 1995; Webb 1998). This, in turn, should help to enhance grazing pressure and the creation of bare soil patches. In regions where the re-introduction of livestock grazing is not viable due to socio-economic changes, mowing alone is considered to be a practical and affordable substitute (Adamowicz 2010; Diemont *et al.* 2013; Borghesio 2014). However, some studies showed that grazing creates a more open vegetation structure and reduces competing grasses (e.g., *Deschampsia flexuosa*, *Calamagrostis epigejos*, *Molinia caerulea*) more successfully than mowing, due to selective feeding (Borer *et al.* 2014; Pywell *et al.* 1995). Thus, the suitability of mowing as a substitute for livestock grazing in heaths remains uncertain.

In addition, it is still unclear if low-intensity, year-round grazing is effective in suppressing the further spread of highly competitive grasses such as *Calamagrostis* and simultaneously maintaining or improving characteristic plant species composition. There are major concerns regarding the unequal utilization of the pasture, with partial undergrazing potentially resulting in an increase of ruderal plant species, the further degeneration of *Calluna* (Putfarken *et al.* 2008), as well as the impairment of endangered plant species while partial overgrazing can also have negative effects such as damage of the *Calluna* canopy (Gimingham 1992). Therefore, repeated surveys over several years are urgently needed to determine the long-term and large-scale impacts of year-round grazing with large herbivores and therefore whether this type of grazing strategy is a suitable management tool.

Aims and outline of the thesis

Whereas Atlantic heathlands have been in the focus of restoration and management measurements (e.g. Gimingham 1972; Webb 1998), dry Continental heathland communities have been widely neglected (Sedláková & Chytrý 1999; Henning *et al.* 2017a, b), even though they comprise 30 % of all dry heaths as well as 89 % of all dry sandy grasslands, respectively, in Europe (EEA 2015a, b). However, much less is known about the suitability of cost-effective management schemes to successfully restore and maintain highly degraded, long-abandoned Continental heaths and sandy grasslands especially in situations where other traditional management measures, such as burning or

sod-cutting, are impossible because they are either too expensive, restricted due to environmental laws or prohibited due to the danger of unexploded ammunition in deeper soil layers as a result of the former military use.

Thus, the thesis aims to shed light on the population dynamics of *Calluna* in Continental climates by investigating key processes in the biology of the species as well as to provide substantial knowledge about the restoration and management of long-abandoned, dry Continental heathland and sandy grassland communities (Figure 1). The focus of the thesis lies on the rejuvenation process of *Calluna*, in particular under the consideration of the reproductive potential and the generative rejuvenation of *Calluna* (chapter II and III), and on the development of nutrient-poor plant communities by analysing management effects on plant species richness and species composition as well as on vegetation structure (chapter IV). For implementation into practice, I present new restoration and management strategies to successfully restore and maintain long-abandoned, dry Continental heathlands and sandy grasslands when traditional management options are no longer feasible (chapter II, III and IV).
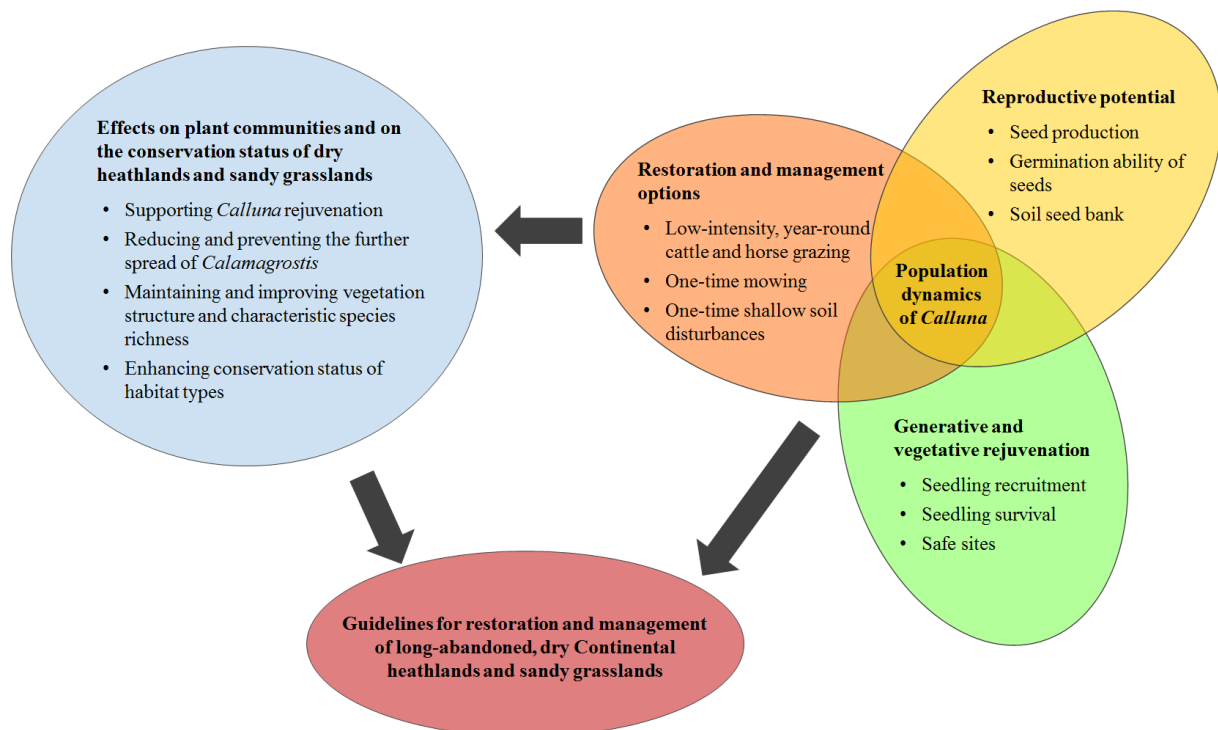

Figure 1: Outline of the thesis.

The essential contents of the three publications that form the basis for the present thesis are:

To systematically explore restoration options in abandoned, dry Continental heaths, **chapter II** (Henning *et al.* 2017a) presents the results of a three-year field experiment to assess the effects of single and combined management options (low-intensity grazing, one-time mowing, one-time shallow soil disturbance) on the generative rejuvenation process of *Calluna* in a large-scale heath, grazed year-round by Heck cattle and Konik horses. Moreover, the study is the first to determine the reproductive potential, i.e. seed production, the germination ability of seeds and the soil seed bank, of degenerate *Calluna* by using field studies and greenhouse investigations. I aim 1) to close the knowledge gap regarding the reproductive potential of degenerate *Calluna* stands in Continental heaths, and 2) to investigate suitable and cost-efficient management schemes to successfully restore and maintain highly degraded, long-abandoned Continental heaths in situations where other traditional management measures, such as burning or sod-cutting, are impossible.

Chapter III (Henning, von Oheimb & Tischew 2015) focuses on the first-year establishment of *Calluna* on managed dry Continental heaths and heaths in mosaics with dry sandy grasslands as well as on control sites. I analysed the germination ability of seeds of different life-history phases of *Calluna* to determine if the predominance of the late life-history phase restricts the rejuvenation process of *Calluna*. Furthermore, beside single management measures, I evaluated the importance of safe-site availability by analysing the most important safe site conditions that possibly influenced the germination and the first-year survival of *Calluna* and work out possible optimisation for future restoration and management measurements.

In **chapter IV** (Henning *et al.* 2017b) I systematically analyse the effects of low-intensity, year-round cattle and horse grazing on the development of the highly competitive grass *Calamagrostis epigejos*, as well as on the vegetation structure and plant species richness of long-abandoned but nutrient-poor dry heathland and sandy grassland communities, their mosaics and *Calamagrostis* stands. The results are based on a comprehensive seven-year field study on two spatial scales (plot-level: 25 m², macroplot-level: 1 ha). The study tries to give evidence, if low-intensity, year-round grazing is suitable

to suppress and to prevent the further spread of *Calamagrostis* while simultaneously maintaining or improving characteristic species richness and vegetation structure, and thus, to enhance the local conservation status of the habitat types. Based on our findings, I draw general conclusions for future restoration and management measurements of nutrient-poor dry heathland and sandy grassland communities.

General discussion

To my knowledge the present thesis is the first to systematically determine the reproductive potential (seed production, soil seed-bank content, germination ability of seeds) of degenerate *Calluna* stands and analyse the effects of single and combined management options on the generative rejuvenation of *Calluna* as well as on the importance of safe site conditions for successful *Calluna* establishment in dry, Continental heathlands. This thesis is also the first to assess the effects of low-intensity, year-round cattle and horse grazing on the development of the highly competitive grass *Calamagrostis epigejos,* as well as the vegetation structure and plant species richness of long-abandoned dry heathland and sandy grassland communities, their mosaics and *Calamagrostis* stands in the Continental biogeographical region. The results of the thesis shed light on the population dynamics of *Calluna* in Continental climates, provide substantial knowledge about suitable and cost-efficient management schemes, and enables us to formulate suggestions/guidelines for future restoration and management to successfully restore and maintain highly degraded, long-abandoned, dry Continental heathland and sandy grassland communities.

Reproductive potential of degenerate *Calluna* stands

In my study, annual seed production of degenerate *Calluna* stands of the long-abandoned, dry Continental heath as well as the germination ability of their seeds, being still high and similar to Atlantic heathlands (chapter II; Mallik, Hobbs & Legg 1984; Barclay-Estrup & Gimingham 1994; Vera 1997). Life-history phases did not significantly affect seed germination (chapter III), while

stratification significantly accelerated germination (chapter II and III), since stratification as well as fluctuating changes in temperature are beneficial to breaking the dormancy of *Calluna* seeds (Pons 1989; Miller & Cummins 2001; Måren & Vandvik 2009). As temperature fluctuations are more pronounced in the Continental than in the Atlantic region, *Calluna* germination could probably benefit from these climatic conditions on our site.

The long-term persistent soil seed bank enables *Calluna* to survive under unfavourable environmental conditions and to re-establish at a later date (Putwain & Gillham 1990; Bossuyt & Hermy 2003). Contrary to seed-bank densities of degenerate *Calluna* stands in the Atlantic region, our densities are three times lower than those investigated by Mallik, Hobbs & Legg (1984), whereas managed Atlantic heaths show even four to 15 times higher seed densities (chapter II; Legg, Maltby & Proctor 1992; Pywell *et al.* 2002). Soil seed-bank densities of our 20-year abandoned Continental heathland were similar to densities found in heaths that had been afforested by conifers 60 years ago (Pywell *et al.* 2002) or had undergone succession by birch and pine (Mitchell, Marrs & Auld 1998) for 49 years. This was an unexpected finding, since the above-mentioned abandonment was up to three times longer than in our investigated heath. Considering the climatic gradients, Pakeman *et al.* (1999) found lower seed-bank densities for *Calluna* stands on drier, warmer sites in the Atlantic region than on cooler, wetter sites. However, seed-bank densities in abandoned Atlantic heaths in the south of Great Britain were still five times higher than in our heathland (Mitchell, Marrs & Auld 1998). This confirms our assumption that seed-bank densities are generally lower under Continental conditions obviously reflecting a limited longevity of *Calluna* seeds in the soil due to differences in soil temperature and moisture (Ooi 2012).

However, since the seed production of our degenerate *Calluna* stands as well as the germination ability of *Calluna* seeds were still high, generative rejuvenation should not generally be restricted.

Generative rejuvenation of *Calluna*

Seedling recruitment, the importance of safe site conditions and survival in the first year
My study showed that both low-intensity grazing as well as one-time mowing alone did not result in a considerable increase in *Calluna* recruitment, whereas an additional one-time creation of bare soil

patches or the one-time creation of bare soil without subsequent management significantly facilitated seedling recruitment (chapter II). These results stress the importance of bare soil patches for successful *Calluna* establishment (Gimingham 1972; de Hullu & Gimingham 1984), especially in highly degraded heaths (chapter III). Thus, additional shallow soil disturbances enhanced the number of suitable safe sites for successful *Calluna* recruitment and first-year survival (chapter III) by reducing competition (Pywell *et al.* 2007) and litter accumulation (de Hullu & Gimingham 1984) as well as by improving light availability on the ground (Gimingham 1972). However, a light shadowing is most crucial for successful *Calluna* recruitment and survival in the first year in both degraded heaths as well as in mosaics with sandy grasslands, since seedlings receiving full sunlight die significantly more frequently than slightly or fully shaded seedlings (chapter III).

Nevertheless, the overall level of seedling recruitment in the field was considerably lower in comparison with Atlantic heaths (chapter II; de Hullu & Gimingham 1984; Bokdam & Gleichman 2000), despite the observed high seed production and germination ability of seeds. This might be related to the drier climatic conditions in the Continental region and the high susceptibility of *Calluna* juveniles to drought (Britton *et al.* 2003; Fagúndez 2012; Meyer-Grünefeldt *et al.* 2015) leading to a lower establishment success as was observed for drier sites in the Atlantic region by Britton *et al.* (2000b). Studies from the Continental region found similarly low seedling numbers to those observed in my study with no or very low *Calluna* recruitment on unmanaged sites (Sedláková & Chytrý 1999) and slightly higher numbers on grazed sites (Dostálek & Frantík 2015).

Survival of Calluna juveniles in the second and third year

Contrary to the seedling recruitment and first-year survival results, from the second year on, the positive effect of the creation of bare soil without subsequent management was no longer present (chapter II).

For survival in the second and third year, all sub-plots that included grazing showed higher survival rates than sub-plots without this treatment. The highest survival rate was observed on grazed and mown sub-plots (73 % survived until 2014 and 69 % until 2015, respectively), followed by grazing alone (72 % survived until 2014 and 65 % until 2015, respectively) and grazing in combination with

shallow soil disturbances (62 % survived until 2014 and 50 % until 2015, respectively). Thus, our results showed that grazing is crucial for successful survival of *Calluna* over the long-term.

Exclusively mown and experimentally disturbed sub-plots without grazing, as well as the combination of both, showed considerably lower *Calluna* survival after three years, since *Calamagrostis* encroached rapidly and suppressed the survival of *Calluna* (own unpubl. data). Thus, successful generative rejuvenation of *Calluna* cannot be achieved by the one-time creation of bare soil patches without subsequent management nor by an exclusively one-time mowing. The rapid encroachment of competitive grasses on exclusively mown heaths was also confirmed by other studies from Continental (Sedláková & Chytrý 1999) and Mediterranean heathlands (Calvo *et al.* 2007). This again stresses the importance of grazing for successful generative rejuvenation of *Calluna* by reducing competition from highly competitive grasses, such as *Calamagrostis* (chapter IV).

Development of *Calamagrostis*

My study showed for the first time that low-intensity year-round grazing with cattle and horses is very suitable to successfully reduce and prevent the further spreading of *Calamagrostis* within nutrient-poor, dry heathland and sandy grassland communities (chapter IV).

A significant reduction in the coverage of *Calamagrostis* was found on grazed *Calamagrostis* stands after seven years of grazing, while low coverages remained in grazed heaths, sandy grasslands and mosaics. Similar effects of mixed cattle and horse grazing or only horse grazing, respectively, within coastal dunes were found by de Bonte *et al.* (1999) and Cosyns *et al.* (2001). In addition, previous studies showed that *Calamagrostis* could also be reduced due to summer donkey and sheep grazing within sandy grasslands (Stroh *et al.* 2002; Schwabe, Süss & Storm 2013) as well as due to seasonally cattle grazing within fens (Williams, Wells & Wells 1974) and mesic semi-natural grasslands (Pykälä 2003).

On ungrazed sites, *Calamagrostis* coverage increased between 2008 and 2015 within each of the investigated vegetation types. *Calamagrostis* cover also increased or did not change on abandoned sites in other sandy grasslands (Süss *et al.* 2004; Schwabe, Süss & Storm. 2013). However, *Calamagrostis* may disappear spontaneously after 40 to 50 years in secondary grasslands such as

former vineyards, where a significant decrease was already visible after seven years without management (Háázi *et al.* 2011). In our study site, aerial photographs from the time immediately after abandonment of military use in 1992 indicated a lower proportion of tall grass vegetation compared to 2008 (own unpubl. data). Thus, a steady increase of *Calamagrostis* can be assumed since abandonment.

Vegetation structure

Under the influence of year-round mixed grazing, a more diversely structured vegetation developed over time in comparison to monospecific grazing, caused by the selective feeding preferences of the animal breeds (Olff *et al.* 1999; Adler, Raff & Lauenroth 2001). While horses are known to graze very selectively and closely to the ground (Lamoot, Meert & Hoffmann 2005; Köhler, Hiller & Tischew 2016), cattle are less selective since they wrap the forage with their tongue and graze most effective at a sward height of at least 15 cm (Jerrentrup *et al.* 2015; Tóth *et al.* 2016). Accordingly, both animal complement each other in their grazing behaviour, thus increasing the biodiversity of both plant and animal species (Loucougaray, Bonis & Bouzillé 2004). While litter cover and thickness significantly decreased, sites characterised by short vegetation and bare soil increased (chapter IV), supporting pioneer as well as low-competitive and bare soil-demanding species by enhancing light availability (Ausden *et al.* 2005, Schwabe, Süss & Storm 2013) and reducing interspecific competition.

Furthermore, my study showed that grazing led to an increase in herb cover and a significant decrease in grasses and ruderal indicators, which is in agreement with Köhler, Hiller & Tischew (2016) for year-round horse grazing in dry calcareous grasslands as well as with Süss & Schwabe (2007) for summer sheep and donkey grazing. Donkeys as well as horses are known for their graminoid foraging (Cosyns *et al.* 2001; Lamoot, Meert & Hoffmann 2005), thus they successfully reduce grass encroachment in grasslands (Catorci, Gatti & Cesaretti 2012) and heathlands (Lake, Bullock & Hartley 2001).

Contrary to our findings, some authors found no decrease in grass cover on cattle and horse grazed or on exclusively cattle grazed sites compared to ungrazed sites (Rupprecht, Gilhaus & Hölzel 2016; Bokdam & Gleichman 2000), but an increase in the cover of ruderal indicators (Rupprecht, Gilhaus &

Hölzel 2016; Sýkora *et al.* 2009), which might be related to a higher nutrient status and/or less complete biomass removal on these sits, probably due to insufficient grazing intensity.

Furthermore, *Calluna* cover distinctly decreased on ungrazed and marginally on grazed heaths with time, but slightly increased in grazed mosaics. It is generally assumed that low-intensity grazing enhances the coverage of *Calluna* (Welch & Scott 1995; Critchley *et al.* 2013). However, long-term abandonment led to heavy degenerate *Calluna* stands, a lack of generative rejuvenation and a die-back of this species in heaths at the beginning of our experiment (chapter II). During the first study years, these degenerate *Calluna* stands were largely neglected by the grazing animals (own unpubl. data) due to the high proportion of woody biomass and thus lower fodder quality (Pywell *et al.* 1995). Additional management measures, such as mowing, are suitable to facilitate the vegetative rejuvenation of *Calluna*, whereby the re-growth of young shoots subsequently improves the fodder quality of *Calluna* and thereby its attractiveness for grazing animals (Webb 1998). Consequently, grazing intensity was enhanced after the application of the one-time mowing, resulting in an increase in *Calluna* rejuvenation (chapter II and III; own unpubl. data).

Tree and shrub encroachment is a common problem concerning low-intensity (year-round) grazed heathlands and grasslands (Miles 1981; Cornelissen & Vulink 2001). Manual shrub cutting is not necessary if the overall degree of initial cover of woody species is less than 15 % (Köhler, Hiller & Tischew 2016). In this case, further shrub encroachment is limited due to winter browsing. However, if the overall initial cover of woody species is as high as it was in our case, manual shrub cutting is crucial to counter regrowth of woody species and thus maintain the open site character. Cattle and horses were not able to successfully counteract the regrowth of woody species, as shown by Bokdam & Gleichman (2002) for year-round cattle grazing in Atlantic heaths with less initial cover of woody species.

Species richness

While abandonment often leads to the development of species-poor, grass-dominated plant communities (Prach & Pysek 2001; Somodi, Virágh & Podani 2008), my study showed that year-round low-intensity grazing with cattle and horses led to a significant increase in total species number

and species richness across and within vegetation types over time (chapter IV). An increase in species richness by low-intensity grazing of dry grasslands and heathlands was also described by Bokdam & Gleichman (2000) and Kohyani *et al.* (2008). In addition, Török *et al.* (2016b) recommend a low- to medium-intensity cattle grazing to maintain a high cover of target species and high species diversity in dry low-productive grasslands. On the contrary, some authors reported negative impacts of large herbivore grazing on species richness and species composition on low productive sites (Olff & Ritchie 1998; Bakker *et al.* 2006). In my study, target species and subordinated target species were significantly favoured by the grazing regime as shown for year-round grazing in dry calcareous grasslands (Köhler, Hiller & Tischew 2016). Most species of dry heathland and sandy grassland communities are adapted to nutrient-poor site conditions (Bobbink, Hornung & Roelofs 1998; Bobbink *et al.* 2010), whereby grazing has been reported to decrease soil nutrient levels (Marrs 1993). Thus, I found a significant increase in N 1-3 and N 4-5 species (Ellenberg *et al.* 2001) after seven years of grazing, while no changes could be detected on ungrazed sites. In contrast, species associated with high nutrient values did not increase on grazed sites.

Moreover, my study showed that after seven years of grazing of *Calamagrostis* stands, the species number has doubled (from 17.3 to 37.0), obviously due to the increase in bare soil and the considerable decrease of *Calamagrostis* cover and litter layer, with especially target and subordinated target species re-establishing (chapter IV). Thus, grazed *Calamagrostis* stands developed towards the target habitat type sandy grasslands. In this context, grazing animals obviously serve as vectors for seed dispersal by their hooves, fur and dung (Olff & Ritchie 1998; Ozinga *et al.* 2009). However, it is necessary that seed sources or a sufficient soil seed-bank are still present on the site, otherwise the addition of seeds is a key factor in the restoration of long-abandoned heathland and sandy grassland communities (chapter II and III; Bossuyt & Hermy 2003).

Furthermore, sandy grasslands and mosaics benefited from the grazing regime by an increase of target species and subordinated target species over time, which agrees with the findings of Schwabe, Süss & Storm (2013) and Freund *et al.* (2014) in sandy grassland ecosystems.

The average lower total species number in heaths compared to sandy grasslands and mosaics is related to a reduced availability of suitable safe sites for species establishment, due to the high and dense

vegetation structure of degenerate *Calluna* stands (chapter II and III). In addition, the phytotoxic effects of *Calluna* litter can inhibit species germination (Gimingham 1972). However, both the total number of species and dry mesophilic grassland species significantly increased on grazed heaths between 2008 and 2015. In this context, the increase in mesophilic grassland species does not simultaneously imply an increase in the nutrient status of grazed heaths. Thus, species with low N-values significantly increased with grazing time, while species with moderate to high N-values did not significantly increase between 2008 and 2015. Moreover, total soil nitrogen content was still low in 2015, ranging between 0.1 % and 0.5 %. In addition, my study showed an increase, but not significantly, in target as well as subordinated target species, indicating a grazing induced shift between heaths and sandy grasslands (Olff *et al.* 1999), which could finally lead to a more pronounced mosaic structure over the whole study area.

Assessment of the conservation status

The assessment of the conservation status (CS) of habitat types serves as a suitable basis for the recognition of negative trends of the present management (Dimopoulos, Bergmeier & Fischer 2005). Thus, necessary adaptions in management can be early made, for example changes in the stocking rate or ratio between the animal breeds. In our study area, current grazing intensity is low with 0.2 livestock units ha^{-1}. However, grazing regime showed an improvement of both the vegetation structure as well as the species richness with simultaneous reduction of *Calamagrostis* cover in each vegetation type (chapter IV). Grazing in low stocking rates is considered to be proper to mimic natural grazing regimes in grasslands (Gilhaus, Stelzner & Hölzel 2013). Török *et al.* (2016b) found highest functional diversity under low-intensity grazing, while the highest cover of target species as well as the highest diversity was found under a medium grazing intensity in alkali steppes. Contrary, too high stocking rates could influence species richness negatively as it was shown in many other studies (e.g. Batáry, Báldi & Erdős 2007; Ambarlı & Bilgin 2014). Therefore, a constant monitoring is needed to track trends and changes in the CS of habitat types (Bergmeier & Fischer 2006), whereby the assessment of the CS can be performed in a few representative sites from which a generalization of the conservation status in the entire study area is possible. Thus, it is useful to use permanently marked

plots for the assessment of CS (Dimopoulos, Bergmeier & Fischer 2005), since changes in the cover or expansion of impairments such as highly competitive grasses, ruderal species or shrubs can be determined exactly after a defined period of time in contrast to unmarked areas.

In my study, the local CS of habitat types has changed with grazing time (chapter IV), whereby the CS of sandy grasslands and mosaics improved from a bad (value C) to a good (value B) CS after seven years of grazing, since habitat structure and species inventory improved, while impairments decreased. Moreover, *Calamagrostis* stands have developed towards the target habitat type sandy grasslands and can be classified as sandy grasslands with a total CS of C after seven years of grazing. A further improvement of *Calamagrostis* stands with grazing time can be expected, since shifts in species composition as well as general in plant communities are slow (Lorenz *et al.* 2013).

Although characteristic species increased, while impairments decreased on grazed heaths, the overall CS did not change over time and was still classified as B after seven years of grazing. This is due to the fact that the habitat structure is still bad, since the rejuvenation of *Calluna* is progressing only slowly (chapter II and III). Even if the cover of *Calluna* individuals in the degenerate phase is still high with over 70 %, all four *Calluna* phases were present on grazed sites and the coverage of bare soil was higher than on abandoned sites, which underline the steady improvement of the habitat type. To promote *Calluna* rejuvenation, additional management measures such as a one-time mowing management should be applied (chapter II and III) that has meanwhile been implemented on a larger-scale in the study area and showed positive results (own unpubl. data).

Conclusions and guidelines for restoration and management

My thesis revealed that year-round low-intensity cattle and horse grazing is a suitable management tool to restore and maintain long-abandoned, dry Continental heathland and sandy grasslands communities, and thus to enhance the local conservation status of habitats of community interest.

However, it is necessary that seed sources are still present in the area; otherwise the addition of seeds is a key factor in the restoration of species-rich heathlands and sandy grasslands, especially in long-abandoned sites. In addition, sufficient numbers of bare soil patches und thus suitable safe sites are

crucial for successful generative *Calluna* rejuvenation – the key species of dry heaths. This means, in practical terms, that grazing and thus trampling intensity must be temporarily and locally enhanced at the beginning of the restoration process. This can be achieved by placing mineral licks as a supplement for the animals' diet or installing temporary fencing in parts of the degraded heathland. Grazing intensity can also be enhanced by one-time mowing of degenerate *Calluna* as an initial restoration tool to remove the excessive woody or dead biomass, thus leading to increased vegetative rejuvenation of *Calluna,* whereby the re-growth of young shoots subsequently improves its fodder quality and thereby its attractiveness for grazing animals. This approach is particularly effective if mosaics of different habitats enable selective foraging, as it was shown for the study area Oranienbaumer Heide. In addition, mowing should be applied rotationally across the heathland to establish a mosaic of diverse structure.

I would like to stress that a higher grazing pressure at the beginning of the restoration process should not be achieved by increasing the overall stocking rate in the entire pasture because this would require supplementary feeding and thus a nutritional input into the nutrient-poor system. If the above-mentioned options are not feasible, the creation of bare soil and thus the creation of suitable safe sites can also be fostered by deep-set mowing which exposes the mineral soil in a patchy way; this type of mowing, however, requires a more or less even terrain and lack of stones.

In all cases, however, low-intensity grazing is essential for the successful survival and establishment of *Calluna* in the long-term as it prevents the re-growth and further spread of highly competitive grass species, such as *Calamagrostis*, and improves the vegetation structure, thus promoting slowly growing *Calluna* seedlings and juveniles, other target species as well as low-competitive and light-demanding species. However, manual shrub cutting should be considered if the initial cover of woody species (> 0.5 m) is as high as it was at our study site.

In addition, the maintenance costs of year-round grazing systems are low and can be covered by agri-environment schemes, making grazing management economically sustainable for the land user.

Future research needs

With my studies I contributed to the better ecological understanding of dry, Continental heathland and sandy grassland restoration and management.

As I observed a grazing induced shift between heaths and sandy grasslands, it would be highly interesting to study if these shifts would finally lead to a more pronounced mosaic structure of heathlands and sandy grasslands over the whole study area.

Further research is also needed on long-term browsing effects at sites with initially high woody plant cover, as it was obvious that the grazing animals were not able to sufficiently reduce the regrowth of woody species during the first years after the extensive shrub and tree clearance. Therefore, manual shrub cutting was necessary to maintain the open site character. However, it is expected that the constant browsing activity of the grazing animals will lead to a considerable reduction of the regrowth of woody species with ongoing time. In addition, more research is needed on the long-term browsing effects on invasive alien species, such as *Prunus serotina*, since biological invaders can cause biodiversity loss and changes in plant communities.

In order to assess the restoration success also in relation to fauna, the effects of year-round, low-intensity grazing on animal species serving as bioindicators, such as birds, should be studied. That would be highly interesting, especially as the abundance of common farmland birds has decreased dramatically since 1950 throughout Europe (EBCC 2017).

Finally, low-intensity, year-round grazing management with cattle and horses should be transferred to other dry heathlands and sandy grasslands within the Continental biogeographical region to verify our results.

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Overview of articles included in this cumulative Ph.D. thesis

(in accordance with the guideline for cumulative dissertations in Sustainability Science [January 2012], in the following termed "the guideline")

Title of PhD thesis: "Restoration and management of abandoned, dry Continental heathland and sandy grassland communities"

Papers included:

[1]   Henning, K., von Oheimb, G., Härdtle, W., Fichtner, A. & Tischew, S. (2017) The reproductive potential and importance of key management aspects for successful *Calluna vulgaris* rejuvenation on abandoned Continental heaths. Ecology and Evolution, 2017, 1-10.

[2]   Henning, K., von Oheimb, G. & Tischew, S. (2015) What restricts generative rejuvenation of *Calluna vulgaris* in continental, dry heathland ecosystems: seed production, germination ability or safe site conditions? Ecological Questions, 21, 25-28.

[3]   Henning, K., Lorenz, A., von Oheimb, G., Härdtle, W. & Tischew, S. (2017) Year-round cattle and horse grazing supports the restoration of abandoned, dry sandy grassland and heathland communities by supressing *Calamagrostis epigejos* and enhancing species richness. Journal for Nature Conservation, 40, 120-130.

Declaration of authorship

Authors' contributions to the articles and articles publication status (according to §16 of the guideline):

Article #	Short title	Specific contributions of all authors	Author status	WF	Publication status	Conference contributions
[1]	*Calluna* rejuvenation in abandoned Continental heaths	KH, ST, GvO, WH: experimental design KH: data collection, preparation and interpretation of data, literature review KH, AF: data analyses KH, ST: writing of the paper ST, GvO, WH: internal revision of the paper	Co-author with predominant contribution	1.0	Published in Ecology and Evolution (IF = 2.537)	9th SER 2014, 44th GfÖ 2014, FlorSoz 2015, NWK 2018
[2]	Restriction of the generative *Calluna vulgaris* rejuvenation	KH, ST, GvO: experimental design KH: data collection, preparation and analyses, data interpretation, literature review, writing of the paper	Co-author with predominant contribution	1.0	Published in Ecological Questions (ISI-ranked international peer-reviewed journal)	13th EHW 2013, Open Landscapes 2013, NWK 2018
[3]	Year-round grazing on abandoned sandy grasslands and heaths	ST, AL: experimental design KH, AL: data collection KH: data preparation, analyses and interpretation of data, literature review KH, ST: writing of the paper ST, GvO, WH: internal revision of the paper	Co-author with predominant contribution	1.0	Published in Journal for Nature Conservation (IF = 2.220)	14th EHW 2015, 10th SER 2016, NWK 2018, 11th SER 2018

WF = Weighting Factor; IF = ISI Web of Science – Impact Factor 2015

Specific contributions of all authors

KH [1,2] = Katrin Henning, GvO [3] = Goddert von Oheimb, ST [1] = Sabine Tischew, WH [2] = Werner Härdtle, AF [2] = Andreas Fichtner, AL [1] = Antje Lorenz

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Author status

According to §12b of the guideline:

Single author [Allein-Autorschaft] = Own contribution amounts to 100%.

Co-author with predominant contribution [Überwiegender Anteil] = Own contribution is greater than the individual share of all other co-authors and is at least 35%.

Co-author with equal contribution [Gleicher Anteil] = (1) own contribution is as high as the share of other co-authors, (2) no other co-author has a contribution higher than the own contribution, and (3) the own contribution is at least 25%.

Co-author with important contribution [Wichtiger Anteil] = own contribution is at least 25%, but is insufficient to qualify as single authorship, predominant or equal contribution.

Co-author with small contribution [Geringer Anteil] = own contribution is less than 20%.

Weighting factor

According to §14 of the guideline:

Single author [Allein-Autorschaft]	1.0
Co-author with predominant contribution [Überwiegender Anteil]	1.0
Co-author with equal contribution [Gleicher Anteil]	1.0
Co-author with important contribution [Wichtiger Anteil]	0.5
Co-author with small contribution [Geringer Anteil]	0.0

Conference contributions (acronym, society, date, venue, website)

[1]   13th EHW, European Heathland Network, 23.-28.06.2013, Denmark,

        http://publications.naturalengland.org.uk/publication/4672472104304640; Poster

[2]   Open Landscapes 2013, University of Hildesheim, 29.09.-02.10.2013, Hildesheim (Germany),

        http://open-landscapes2013.de; Talk

[3]   9th SER 2014, Society for Ecological Restoration, 03.-08.08.2014, Oulu (Finland),

        http://www.ser2014.org/; Talk

[4]   44th GfÖ Annual Meeting, The Ecological Society of Germany, Austria and Switzerland, 08.-

         12.09.2014, Hildesheim (Germany), http://www.gfoe.org/de/node/121; Talk

[5]   FlorSoz 2015, Floristisch-soziologische Arbeitsgemeinschaft e.V., 12.-15.06.2015, Bernburg

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[6]   14th EHW, European Heathland Network, 21.-27.06.2015, Poland,

        http://publications.naturalengland.org.uk/publication/4672472104304640; Talk

[7]   10th SER 2016, Society for Ecological Restoration, 22.-26.08.2016, Freising (Germany),

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[8]   NWK 2018, 19. Nachwuchswissenschaftlerkonferenz, 05-06.06.2018, Köthen (Germany),

        http://nwk2018.de/nwk2018/programm.html; Talk

[9]   11th SER 2018, Society for Ecological Restoration, 09.-13.09.2018, Reykjavik (Iceland),

        https://sere2018.org/program-2/; Talk

Declaration (according to §16 of the guideline)

I avouch that all information given in this appendix is true in each instance and overall.

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Katrin Henning

Magdeburg, den 14. August 2018

Chapter II

The reproductive potential and importance of key management aspects for successful *Calluna vulgaris* rejuvenation on abandoned Continental heaths

Katrin Henning, Goddert von Oheimb, Werner Härdtle, Andreas Fichtner & Sabine Tischew

Summary

1. The abandonment of traditional pastoralism as well as the use of heath areas for military purposes has had a major impact on dry heaths in the Continental biogeographical region of Europe, causing severe degradation of its key species *Calluna vulgaris* (L.) HULL. The reproductive potential of this species in a Continental climate is assumed to be low, although there is yet no observational or experimental evidence for this. More knowledge is also needed about cost-effective and sustainable measures to restore abandoned dry heaths in this biogeographical region, since traditional management options are often too expensive (e.g. sod-cutting) or restricted due to environmental laws and the danger of unexploded ammunition (e.g. burning).

2. Using as an example an 800 ha Continental heathland in Germany that has been abandoned for about two decades, we studied the reproductive potential (seed production, soil seed bank and germination ability) of degenerate *Calluna vulgaris* stands. In addition, we conducted a comprehensive field experiment to test the effects of low-intensity, year-round grazing by Heck cattle and Konik horses as well as one-time mowing and patchy exposure of bare soil on the generative rejuvenation (i.e. recruitment and survival) of degenerate *Calluna vulgaris* stands over three years. We used generalized linear mixed models for statistical analyses.

3. Seed production of degenerate *Calluna vulgaris* stands was high as well as the germination ability of their seeds, being similar to Atlantic heathlands. However, soil seed-bank densities were lower than those found in managed or abandoned Atlantic heaths.

4. Overall seedling recruitment in the field was considerably lower in comparison to Atlantic heaths. Low-intensity grazing or one-time mowing did not induce a substantial increase in *Calluna vulgaris* recruitment, whereas an additional one-time creation of bare soil patches or the one-time creation of bare soil without subsequent management significantly facilitated seedling recruitment and survival in the first year. However, from the second year on, the positive effect of the creation of bare soil without subsequent management was no longer present. In the third year, survival of juveniles was significantly supported by low-intensity grazing in combination with shallow soil disturbances as well as in combination with one-time mowing and shallow soil disturbances, whereas mowing alone resulted in marginally significant lower survival.

5. Synthesis and applications. After two decades of abandonment, seed production of degenerate *Calluna vulgaris* stands and the germination ability of seeds proved to be high, whereas the soil seed bank was considerably reduced probably due to the dry conditions in this Continental region. The extremely low seedling recruitment requires a careful choice of suitable management measures to promote the survival of sufficient numbers of *Calluna* individuals. Therefore, we recommend low-intensity grazing with free-ranging robust breeds and the combination of this with one-time mowing as an effective means of supporting generative rejuvenation of *Calluna vulgaris* in degraded heaths. However, at the beginning of the restoration process, the creation of bare soil patches for seedling recruitment is crucial. For implementation into practise, we present different strategies to enhance the proportion of bare soil after long-term abandonment of heaths when traditional management options are no longer feasible.

Keywords: Disturbance, Free-range grazing, Germination ability, Mowing, Seedling recruitment and survival, Seed production, Soil seed bank

Introduction

Heathlands are recognized as being of high conservation value throughout Europe and classified as "habitats of Community interest" (Council Directive 92/43/EEC). They are widely distributed across Europe, while dry heaths occurring within the Continental biogeographical region (henceforth referred to as the Continental region) account for 30% of all European dry heaths and cover a habitat area of 907.90 km² (EEA 2015). Nearly all dry heaths are semi-natural, having derived from woodland on dry and acidic sandy soils resulting from a long history of low-intensity grazing combined with rotational sod-cutting, mowing or burning (traditional heathland farming; Pywell *et al.* 1995; Webb 1998; García *et al.* 2013). The removal of the litter and humus layer as a result of these management measures led to nutrient removal and thus to soil impoverishment, which helped to support the generative rejuvenation of its key species *Calluna vulgaris* (L.) HULL (henceforth referred to as *Calluna*). *Calluna* is a light-demanding, low-competitive species requiring at least patches of bare soil for the germination of its small seeds (thousand-seed weight: 0.017 g; Bloemer 2014) and the survival of its slowly growing juveniles (Iason & Hester 1993; Quin *et al.* 2014). From the middle of the 19th century onwards, traditional heathland practices began to decline due to socio-economic changes, and large areas of the dry heaths reverted to woodland (Price 2003). During the 20th century, however, some of these low-productive areas were used for military training activities, thus maintaining the open nature of the landscape and the *Calluna*-dominated heaths (Wanner & Xylander 2003; Schröder, Balzer & Ellwanger 2008). More recently, political changes in the former Eastern bloc countries have led to the abandonment of the majority of military training areas in the Continental region (Schumacher & Johst 2015). In comparison to heaths in the Atlantic biogeographical region (henceforth referred to as the Atlantic region), Continental heaths are less threatened by high air-borne nitrogen inputs (Erisman *et al.* 2015). As a consequence especially of land-use changes, the conservation status of dry heath habitats is unfavourable-bad across Europe, with an ongoing deteriorating trend in the Continental region (EEA 2015). This challenging situation calls for scientifically based restoration schemes to counteract the abandonment of dry heaths in the Continental region, since well-known traditional measures, such as sod-cutting and burning, often cannot be applied because they are either too

expensive, restricted due to environmental laws or prohibited due to the danger of unexploded ammunition in deeper soil layers as a result of the former military use.

The predominance of degenerate *Calluna* stands and the invasion of competitive grasses are the main degradation processes in abandoned heaths (Britton *et al.* 2000a; Dostálek & Frantík 2015) besides other successional changes such as shrub and tree encroachment (Gimingham 1992; Newton *et al.* 2009). Counteracting these processes is difficult in the current socio-economic situation in Europe and requires the development of cost-effective restoration approaches, based on a sound understanding of the effects of management on *Calluna* population dynamics and plant community interactions (Bullock & Pakeman 1996; Bullock *et al.* 2001; Soons & Bullock 2008). The essential indicators for predicting and evaluating the rejuvenation process of *Calluna* are the reproductive potential, i.e. the number of seeds produced, the soil seed bank and the seed germination ability, as well as the number of recruiting and surviving *Calluna* individuals (i.e. generative rejuvenation). Degenerate *Calluna* stands are characterized by a high proportion of woody or even dead *Calluna* biomass and a reduced proportion of flowering shoots (Miller & Miles 1970; Gimingham 1972). Reduced flowering with increasing age might result in a lower annual seed production in comparison to managed heaths where *Calluna* is more vigorous and early life-history phases are more prominent. This fact in its turn could lead to net losses in the seed bank (Ooi 2015). In addition, there is evidence that the soil seed bank of *Calluna* is smaller under drier, warmer site conditions in Atlantic heaths (Pakeman *et al.* 1999, Pywell *et al.* 2002). Therefore, the soil seed bank might be even smaller in Continental heaths with higher temperatures, less precipitation and drought periods leading to limited seedling recruitment (Ooi 2015). The less favourable climatic conditions in the Continental region compared to the Atlantic region could also lead to a greater probability of failed recruitment and higher seedling mortality since *Calluna* seedlings and juveniles are highly susceptible to drought (Britton *et al.* 2003; Fagúndez 2012; Meyer-Grünefeldt *et al.* 2015). Drought events are more common in the Continental than in the Atlantic region, and it is predicted that climate change will lead to an increase in drought periods during the growing season (EEA 2008; Zacharias, Koppe & Mücke 2015). However, no detailed studies are available on the reproductive potential of degenerate *Calluna* in Continental heaths.

Another feature of abandoned heaths with degenerate *Calluna* is a high and dense vegetation structure and a lack of bare soil patches (Mitchell, Rose & Palmer 2008; Newton *et al.* 2009; van Wieren 2013). In recent years, year-round grazing by small numbers of free-ranging robust, large herbivores has replaced the traditional grazing practices in some regions and proved to be a profitable management tool in maintaining dry heaths (Bokdam & Gleichman 2000; Critchley *et al.* 2013). Large herbivores have been found to reduce aboveground biomass and create bare soil patches more efficiently than sheep (Mitchell, Rose & Palmer 2008). However, the suitability of this new grazing regime has not yet been investigated for long-abandoned heaths. At the beginning of the restoration process, degenerate *Calluna* stands might be largely neglected by the grazing animals due to the high proportion of woody biomass. Hence, grazing might not reduce the aboveground biomass and bare-soil patch density sufficiently to increase generative *Calluna* rejuvenation. Degraded heaths are often mown before the re-introduction of grazing management in order to reduce vegetation density, support the vegetative rejuvenation of *Calluna* with re-sprouting which subsequently enhances the fodder value (Pywell *et al.* 1995; Webb 1998). This, in turn, should help to enhance grazing pressure and the creation of bare soil patches. In regions where the re-introduction of livestock grazing is not viable due to socio-economic changes, mowing alone is considered to be a practical and affordable substitute (Adamowicz 2010; Diemont *et al.* 2013; Borghesio in press). However, some studies showed that grazing creates a more open vegetation structure and reduces competing grasses (e.g. *Deschampsia flexuosa, Calamagrostis epigejos, Molinia caerulea*) more successfully than mowing, due to selective feeding (Pywell *et al.* 1995; Borer *et al.* 2014). Thus, the suitability of mowing as a substitute for livestock grazing in heaths remains uncertain.

In order to systematically explore restoration options in abandoned, dry Continental heaths, we conducted a comprehensive 3-year field experiment to determine the effects of single and combined treatments (low-intensity grazing, one-time mowing, one-time shallow soil disturbance) on the generative rejuvenation of *Calluna* in a large-scale heath, grazed year-round by Heck cattle and Konik horses (*Bos taurus* and *Equus ferus caballus*, respectively). In addition, we investigated the seed production, the germination ability of seeds and the soil seed bank of degenerate *Calluna*. Our aim was 1) to close the knowledge gap regarding the reproductive potential of degenerate *Calluna* stands

in Continental heaths, and 2) to investigate suitable and cost-efficient management schemes to successfully restore and maintain highly degraded, long-abandoned Continental heaths in situations where other traditional management measures, such as burning or sod-cutting, are impossible. We asked:

1) Is the reproductive potential of degenerate Continental *Calluna* stands considerably lower than in the Atlantic region?

2) Which of the single and combined treatments best support the generative rejuvenation of *Calluna*?

Materials and Methods

Study site

The study site is located in the NATURA 2000 site Oranienbaumer Heide (Saxony-Anhalt, E Germany, 51° 46' N, 12° 21' E, 70 m a.s.l., 2.683 ha) within the Continental biogeographical region. The mean annual temperature is 9.2 °C. The climate is characterized by a mean annual precipitation of about 560 mm (climatologic station: Oranienbaum, period: 1961 to 1990, DWD 2015) and arid periods with negative climatic water balances in spring and summer (PIK 2009). Atmospheric N deposition is less than 10 kg ha^{-1} year^{-1} (Lorenz *et al.* 2013). The study site is characterized by acidic sandy soils (pH $_{H2O}$: 5.5, base saturation: 61.7 %). Grazing is said to have been a major land use practice in the area since the fourth century. From 1945 until 1989, the site was used for military training activities, thus maintaining large-scale open landscapes (John, Lorenz & Osterloh 2010). Nearly two decades of abandonment after this (1989 until 2008) led to rapid encroachment by Scots pine (*Pinus sylvestris*) and silver birch (*Betula pendula*). In addition, *Calamagrostis epigejos*, an indigenous but invasive grass, dominated parts of the area. "European dry heaths" dominated by *Calluna* (habitat code 4030; covering 330 ha) and "Xeric sand calcareous grasslands" (habitat code *6120; 135 ha) are the focus of current nature conservation activities. After pine and birch clearance, a permanent pasture was established at the end of 2008. The pasture encompasses 800 ha and is managed by year-round, low-intensity grazing with Heck cattle and Konik horses (stocking rate

approximately 0.2 livestock units ha^{-1}). In 2012, when this study started, 85 % of the *Calluna* stands were still in the degenerate life-history phase (age: 22 (mean), 33 (maximum) years; K. Henning, unpublished data) and *Calluna* had already died back in some places. Earlier life-history phases (pioneer phase, building phase, mature phase; Gimingham 1972) occurred only on patches where grazing pressure was higher due to the proximity of management facilities (mineral licks, watering places) or where *Calluna* was mixed with sandy grassland vegetation and thus more intensively grazed. Besides *Calluna, Calamagrostis, Festuca ovina, Agrostis capilaris, Euphorbia cyparissias,* as well as *Luzula campestris* occurred frequently in the field-layer. Rare heathland species such as *Genista pilosa*, *Genista germanica*, *Genista tinctoria*, *Carex ericetorum*, *Rumex acetosella* and *Pilosella officinarum* were less frequently present. The bottom layer of the degraded heathland was characterized by 60 % - 70 % of cryptogams, mainly mosses.

Experimental design and treatments

The experiment was established in areas dominated by heavily degenerate *Calluna*. We used a split-plot design with six randomly selected, replicated blocks to study the effects of different treatments (Table 1) on seed production, the soil seed bank and germination ability as well as on generative rejuvenation of *Calluna* over three years (2013 to 2015).

Table 1: Overview of the treatments.

Code	Management treatments and dates
C	Control (without management)
G	Grazing: low-intensity, year-round grazing with cattle and horses (0.2 livestock units ha^{-1})
M	Mowing once in November 2012
G+M	Grazing and mowing
D	Shallow soil disturbance once in November 2012
G+D	Grazing and soil disturbance
M+D	Mowing and soil disturbance
G+M+D	Grazing and mowing and soil disturbance

A block consisted of four 5 m x 5 m plots with ca. 15 m strips between plots. *Calluna* cover ranged from 70 to 90 %. The plots were covered by approximately 70 % litter in a 1-3 cm thick layer over a thin humus layer. Dominating vascular plant species as well as the cryptogam coverage were

mentioned above (see study site). Each block consisted of two grazed and two ungrazed plots (exclosures) as well as of two mown and two unmown plots. Grazing (G) and mowing (M) were the main treatments, with a soil disturbance treatment (D) included on half of each plot (i.e. sub-plots of 2.5 m x 5 m each). All possible combinations of these single treatments, including the control (C), resulted in eight different treatments (Figure 1). G treatment plots were grazed as described above (basic management measure in the study area). The ungrazed plots were set up before the implementation of grazing in 2008. For the M treatment, we cut *Calluna* with a brushcutter at a height of 3 to 10 cm above the ground in November 2012. The clipped material was removed from the plots. A total of 25 small-scale, shallow soil disturbances (10 cm x 10 cm x 3 cm) were randomly distributed over each D treatment sub-plot. These soil disturbances were supposed to mimic either higher grazing pressure (by imitating the trampling effects of grazers) or deep-set mowing which exposes bare soil, and were manually created by removing the litter and humus layer in November 2012.
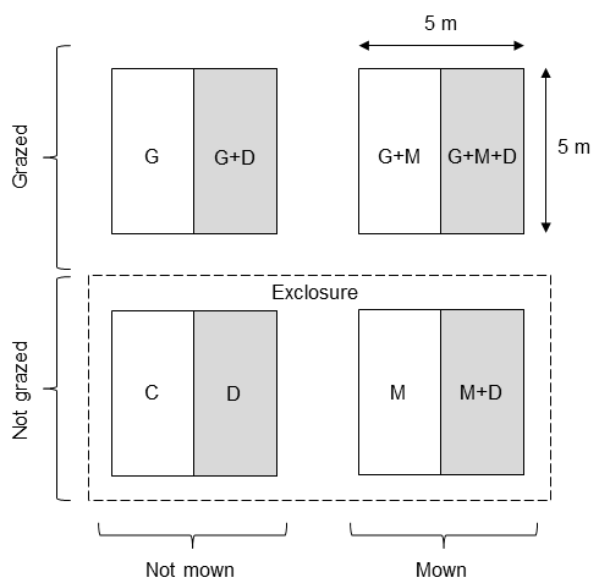

Figure 1: Experimental design: A block consists of four 5 m x 5 m plots containing the grazing (G) and mowing (M) treatments and the control (C). Soil disturbances (D treatment) were carried out on one half of each plot (i.e. on sub-plots of 2.5 m x 5 m each, grey shading). Each plot was separated by ca. 15 m buffer strips.

Data sampling

Seed production

Seed production was estimated at the plot level by collecting all flowering shoots of *Calluna* individuals on systematically selected 50 cm x 50 cm quadrats (northern right corner of each plot) at the time of highest seed maturity (end of October 2012) before mowing and soil disturbance were performed. The capsules and seeds of the 24 samples (six blocks with four plots each) were separated from the branches and leaves by hand-threshing. Because the seeds could not be completely separated from the capsules, the weight of each sample (seeds and capsules) was determined (total weight). A 0.1 g sub-sample of each sample was randomly selected and the fully developed seeds were counted. The total seed number was extrapolated to the total weight of the sample.

Soil seed bank

Soil samples were collected at the plot level at the end of March 2013, after natural stratification of the seeds had taken place in the field the previous winter. On each plot, 20 randomly positioned soil cores of 10 cm depth were sampled using a soil auger (diameter: 1.4 cm). After removal of the litter layer, the samples were subdivided into two depth layers: 0 - 2 cm and 2 - 10 cm. All samples from each plot and depth layer were mixed and spread in a 5 mm thin layer over horticultural perlite and sterile sand in plastic trays (60 cm x 40 cm x 6.5 cm), perforated for drainage. Trays were placed in an unheated greenhouse and watered daily for 12 months. Emerging *Calluna* seedlings were counted and removed every two to three weeks. Soils were stirred every eight weeks to expose buried seeds to light. The position of the trays was randomized every second week.

Germination ability (growth chamber experiment)

In order to determine the germination ability of seeds, we randomly took samples from patches in the degenerate life-history phase (Gimingham 1972) throughout the study site. Seeds were collected at the end of October 2012 from 50 randomly selected individuals of that life-history phase. Half of the seeds were stored dry at 5 °C for eight weeks in darkness (cold stratification) while the other half was stored dry at 15 °C. In January 2013, six times 100 randomly selected fully developed seeds of each

stratification type were sown on moist filter paper in plastic boxes with perforated plastic covers, yielding a total of 6 x 2 = 12 samples each with 100 seeds. The boxes were kept in a growth chamber at a day temperature of 20 °C and a night temperature of 10 °C with a photoperiod of 12 h light and 12 h darkness for 90 days. The seeds were regularly watered with tap water. Seeds were counted as germinated when radicles of 0.5 mm were observed. We counted the germinated seeds and rotated the boxes three times a week. The germination rates t_{10}, t_{50}, and t_{90} were determined as the time in days required to reach 10 %, 50 % and 90 % of the final germination percentage, respectively.

On-site generative rejuvenation of Calluna

On-site generative rejuvenation (i.e. recruitment and survival of *Calluna* seedlings / juveniles) was investigated by counting all seedlings at the sub-plot level in spring 2013 ("recruitment 2013"). The exact location of each seedling was documented on quadrille paper. These individuals were monitored again in autumn 2013 ("survival 2013"). The monitoring of the juveniles was repeated in autumn 2014 and autumn 2015 ("survival 2014" and "survival 2015", respectively).

Data analysis

We applied generalized linear mixed models (GLMM) to assess the impact of various treatments on the seed production, soil seed bank and generative rejuvenation of *Calluna*. To account for the hierarchical data structure and overdispersion, we used block as a random factor and a negative binomial error structure with a log-link function (Zuur *et al.* 2009). Given the large number of zero counts in the recruitment and survival data, we also accounted for zero-inflation in the recruitment (2013) and survival models (2013, 2014 and 2015). Analyses of seedling recruitment in spring 2013 and survival in autumn 2013, 2014 and 2015 were conducted at the sub-plot level; therefore, we used plot nested within block as random effects in these models.

Due to the sampling date, treatment in the seed production model included only grazing effects, while treatment in the soil seed bank model included grazing and mowing effects (i.e. control, G, M, G+M). To assess the importance of soil layer on the seed number, we also included soil depth (0 - 2 cm versus 2 - 10 cm) as a fixed effect in the soil seed bank model. Data from the seed production and the soil

seed bank sampling (based on the volume and area of soil sampled in the field and used in the trays) were transformed into seeds per square meter prior to analyses.

The influence of treatments on seedling recruitment and survival included grazing, mowing and soil disturbance as well as the combined effects of these treatments (see Table 1). Multiple comparisons among treatments were conducted using the Tukey HSD test ($P < 0.05$).

The germination ability of *Calluna* (growth chamber experiment) was analysed using percentage data, which were arcsine transformed to achieve normality prior to the ANOVAs and t-tests. Again, Tukey's HSD post hoc test was then run in the case of significant differences.

Data analyses were performed in R 3.2.3 (http://www.R-project.org) using the package glmmADMB (Fournier *et al.* 2012) and multcomp (Hothorn, Bretz, & Westfall 2008), and in SigmaPlot 11.0.

Results

Seed production

The number of seeds m^{-2} produced by degenerate *Calluna* ranged between 139 639 and 760 451 (mean: 345 118 seeds m^{-2}, SD: 141 205). However, the overall mean did not vary significantly between the G and C plots ($P = 0.27$).

Soil seed bank

A total of 140 641 and 133 495 seeds germinated from the 0 - 2 cm and the 2 - 10 cm soil depth layer samples, respectively, but differences in average seedling emergence between depth layers were not significant ($P = 0.22$). The highest average seedling emergence was observed in the control plots (4222 seeds m^{-2}, 2 - 10 cm depth layer), and the lowest seedling density in the G+M plots (1705 seeds m^{-2}, 2 - 10 cm depth layer, Table 2). However, the treatments did not significantly affect mean seedling emergence.

Table 2: Density of germinable *Calluna* seeds m^{-2} in the soil seed bank in relation to the soil depth layer (0 - 2 cm, 2 - 10 cm depth) and management treatments (grazing and mowing). C: control; G: grazing; M: mowing; G+M: grazing + mowing. Means ± SD are shown.

Soil layer / Management treatment	0-2 cm ($n = 6$)	2-10 cm ($n = 6$)
C	2977.4 (363.9)	4222.5 (865.8)
G	2977.4 (697.5)	2733.8 (829.5)
M	2869.1 (675.9)	2463.1 (624.8)
G+M	2896.2 (281.2)	1705.2 (294.1)

Germination ability (growth chamber experiment)

The mean germination rates of the growth chamber experiment ranged between 62.7 % ± 7.8 (with stratification) and 69.3 % ± 8.4 (without stratification; Figure 2). Stratified seeds reached t_{10} and t_{50}, respectively, in a shorter time than seeds without stratification ($P < 0.001$). For stratified seeds, t_{10} was achieved within 14 days, t_{50} within 19 days and t_{90} within 35 days.
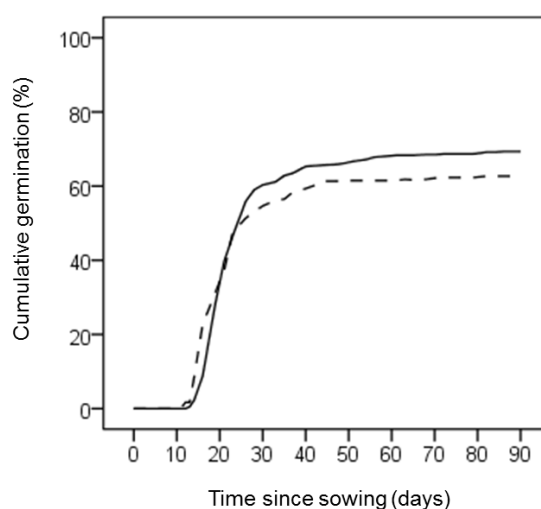
Figure 2: Percentage of cumulative germination over 90 days after sowing seeds collected from *Calluna* in the degenerate life-history phase. Seeds were subject to two stratification treatments (with cold period: dotted line; without cold period: solid line, $n = 6$).

Effects of treatments on generative rejuvenation of Calluna in the field

In spring 2013, a total of 1357 *Calluna* seedlings were recorded on all plots with 93.7 % surviving until autumn 2013, and 43.6 % and 25.8 % until autumn 2014 and 2015, respectively. Overall,

treatment had a significant effect on seedling recruitment 2013 ($P < 0.0001$) and on survival 2013, 2014 and 2015 ($P < 0.001$ for all years).

Seedling recruitment and survival 2013 were highest on sub-plots with the treatment combination G+M+D (Figure 3a, b). In addition, all other sub-plots with the D treatment showed a significantly higher seedling recruitment and survival 2013 than the controls (in the order G+D > M+D > D).

For survival 2014 and 2015, the positive effect of the D treatment was no longer present ($P = 0.16$ and 0.15, respectively), while *Calluna* survival was still higher in G+D, M+D and G+M+D plots than in C plots in 2014 ($P < 0.001$, $P = 0.01$, $P < 0.001$; Figure 3c). Survival was also higher in G+D and G+M+D than C plots in 2015 ($P < 0.01$, $P < 0.001$; Figure 3d). In addition, *Calluna* survival 2015 was marginally lower in M than in G+M+D plots ($P = 0.08$).

a)

b)

c)

d)
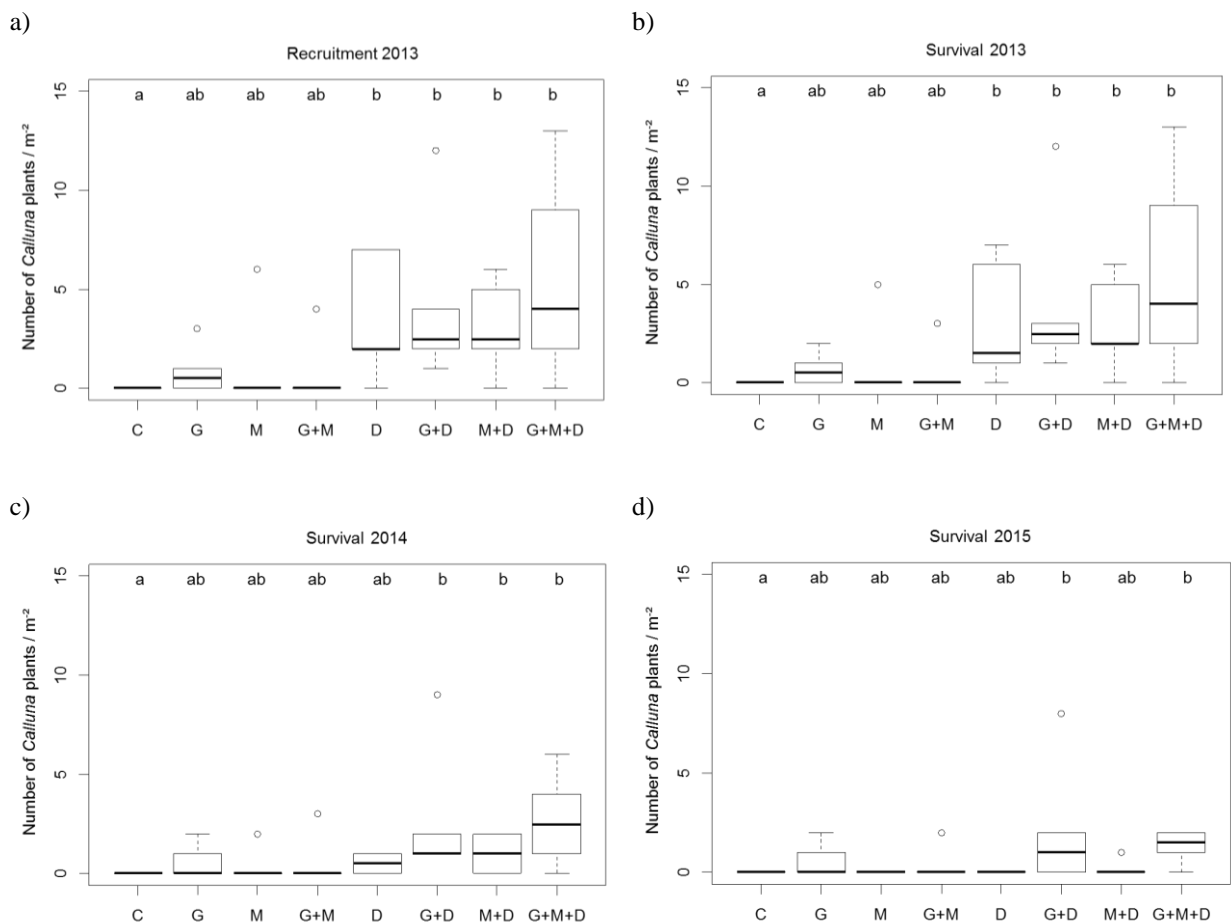
Figure 3: Treatment effects on *Calluna* recruitment in spring 2013 (a) and survival in autumn 2013 (b), 2014 (c) and 2015 (d). Lower case letters indicate significant differences between treatments (Tukey's HSD test; $P < 0.05$). C: control; G: grazing; M: mowing; G+M: grazing + mowing; D: soil disturbance; G+D: grazing + soil disturbance, M+D: mowing + soil disturbance; G+M+D: grazing + mowing + soil disturbance. ($n = 6$).

Discussion

1) Is the reproductive potential of degenerate Continental *Calluna* stands considerably lower than in the Atlantic region?

After nearly 20 years of abandonment, we still found a high annual seed production of degenerate *Calluna* stands in the investigated heathland. Seed production was as high as or even higher than reported for degenerate *Calluna* stands in the Atlantic region (Mallik, Hobbs & Legg 1984; Barclay-Estrup & Gimingham 1994). However, we are aware that seed production can display wide annual fluctuations depending on weather conditions (Gimingham 1972, Ooi 2012). Furthermore, we found high germination rates under controlled conditions (growth chamber) similar to studies from the Atlantic (Pons 1989; Vera 1997) and the Mediterranean region (Gonzàilez-Rabanal & Casal 1995). In our study, the seeds achieved 90 % of their final germination percentage within 35 days, independently of the stratification treatment. This coincides with findings of Gonzàilez-Rabanal & Casal (1995), whereas Vera (1997) determined a t_{90} of 90 to 120 days. However, the latter study was performed without changes in day and night temperature regime, which can lead to secondary dormancy (Pons 1989; Baskin & Baskin 1998). Fluctuating changes in temperature as well as stratification are beneficial to breaking the dormancy of *Calluna* seeds (Pons 1989; Miller & Cummins 2001; Måren & Vandvik 2009) as was also found in our study, where stratification significantly accelerated germination. As temperature fluctuations are more pronounced in the Continental than in the Atlantic region, *Calluna* germination could probably benefit from these climatic conditions on our site.

The long-term persistent soil seed bank enables *Calluna* to survive under unfavourable environmental conditions and to re-establish at a later date (Putwain & Gillham 1990; Bossuyt & Hermy 2003; Piessens, Honnay & Hermy 2005). Contrary to seed-bank densities of degenerate *Calluna* stands in the Atlantic region, our densities are three times lower than those investigated by Mallik, Hobbs & Legg (1984), whereas managed Atlantic heaths show even four to 15 times higher seed densities (Legg, Maltby & Proctor 1992; Pywell *et al.* 2002). Soil seed-bank densities of our 20 year abandoned Continental heathland were similar to densities found in heaths that had been afforested by conifers 60 years ago (Pywell *et al.* (2002) or had undergone succession by birch and pine (Mitchell, Marrs &

Auld 1998) for 49 years. This was an unexpected finding, since the above-mentioned abandonment was up to three times longer than in our investigated heath. Considering the climatic gradients, Pakeman *et al.* (1999) found lower seed-bank densities for *Calluna* stands on drier, warmer sites in the Atlantic region than on cooler, wetter sites. However, seed-bank densities in abandoned Atlantic heaths in the south of Great Britain were still five times higher than in our heathland (Mitchell, Marrs & Auld 1998). This confirms our assumption that seed-bank densities are generally lower under Continental conditions obviously reflecting a limited longevity of *Calluna* seeds in the soil due to differences in soil temperature and moisture (Ooi 2012).

However, since the seed production of our degenerate *Calluna* stands was still high and the germination of *Calluna* seeds is possible without cold stratification after seed setting in autumn, generative rejuvenation should not generally be restricted.

2) Which of the single and combined treatments best support the generative rejuvenation of *Calluna*?

Recruitment of Calluna seedlings in the first year

The highest seedling recruitment was found on sub-plots with the treatment combination grazing + one-time mowing + one-time soil disturbance. However, all other sub-plots that included additional experimental, shallow soil disturbances showed higher seedling numbers than sub-plots without this treatment. These results stress the importance of bare soil patches for successful *Calluna* establishment (Gimingham 1972; de Hullu & Gimingham 1984). These open patches may be created, for example, by grazing or other mechanical interventions (Bullock *et al.* 2001; Allison & Ausden 2006; Critchley *et al.* 2013). However, it turned out that low-intensity grazing alone did not result in a considerable increase in *Calluna* recruitment, showing that the intensity of disturbance is more important than the method of creating bare soil (Mitchell, Rose & Palmer 2008). Thus, additional shallow soil disturbances enhanced the number of microsites for successful *Calluna* recruitment by reducing competition (Pywell *et al.* 2007) and litter accumulation (de Hullu & Gimingham 1984) as well as by improving light availability on the ground (Gimingham 1972). Furthermore, we only found slightly higher seedling numbers on exclusively mown as well as on grazed + mown sub-plots in comparison

to control plots in the first study year, since both measures did not create sufficient amounts of suitable microsites for *Calluna* recruitment.

In contrast to Atlantic heaths (Miles 1974; de Hullu & Gimingham 1984; Bokdam & Gleichman 2000), the overall level of seedling recruitment was considerably lower on our study site despite the observed high seed production and germination ability of seeds. This might be related to the drier climatic conditions in the Continental region and the high susceptibility of *Calluna* juveniles to drought (Britton *et al.* 2003; Fagúndez 2012; Meyer-Grünefeldt *et al.* 2015) leading to a lower establishment success as was observed for drier sites in the Atlantic region by Britton *et al.* (2000b). Studies from the Continental region found similarly low seedling numbers to those observed in our study with no or very low *Calluna* recruitment on unmanaged sites (Sedláková & Chytrý 1999) and slightly higher numbers on grazed sites (Dostálek & Frantík 2015).

Survival of Calluna juveniles in the third year

Contrary to the seedling recruitment results, after three years, the highest number of surviving *Calluna* juveniles were found on grazed + soil disturbed sub-plots. In addition, all other sub-plots that included grazing showed higher survival rates than sub-plots without this treatment. The highest survival rate was observed on grazed + mown sub-plots (69 % survived until 2015), followed by grazing alone and grazing in combination with shallow soil disturbances (65 % and 50 % survived until 2015, respectively). Thus, our results showed that grazing is crucial for successful survival of *Calluna* over the long-term.

Exclusively mown and experimentally disturbed sub-plots without grazing, as well as the combination of both, showed considerably lower *Calluna* survival after three years, since *Calamagrostis* encroached rapidly and suppressed the survival of *Calluna* (K. Henning, unpublished data). Thus, successful generative rejuvenation of *Calluna* cannot be achieved by the one-time creation of bare soil patches without subsequent management nor by an exclusively one-time mowing. The rapid encroachment of competitive grasses on exclusively mown heaths was also confirmed by other studies from Continental (Sedláková & Chytrý 1999) and Mediterranean heathlands (Calvo *et al.* 2007). This

again stresses the importance of grazing for successful generative rejuvenation of *Calluna* by reducing competition from invasive grasses.

Implications for cost-efficient restoration schemes in Continental heaths

The restoration of long-abandoned Continental heaths using cost-efficient measures, such as low-intensity grazing with robust cattle and horse breeds, is realistic if sufficient numbers of viable *Calluna* seeds from the seed rain are present and if sufficient patches of bare soil can be created for generative *Calluna* rejuvenation. This means, in practical terms, that grazing and thus trampling intensity must be temporarily and locally enhanced at the beginning of the restoration process. This can be achieved by placing mineral licks as a supplement for the animals' diet or installing temporary fencing in parts of the degraded heathland. Grazing intensity in degraded heathlands can also be enhanced by one-time mowing as an initial restoration tool to remove the excessive woody or dead biomass, thus leading to increased vegetative rejuvenation of *Calluna* (K. Henning, unpublished data). The re-growth of young shoots subsequently improves the fodder quality of *Calluna* and thereby its attractiveness for the grazing animals. This approach is particularly effective if mosaics of different habitats enable selective foraging. Mowing should be applied rotationally across the heathland to establish a mosaic of diverse structure.

We would like to stress that higher grazing pressure at the beginning of the restoration process should not be achieved by increasing the overall stocking rate in the entire pasture because this would require supplementary feeding and thus a nutritional input into the nutrient-poor system. If the above-mentioned options are not feasible, the creation of bare soil can also be fostered by deep-set mowing which exposes the mineral soil in a patchy way; this type of mowing, however, requires a more or less even terrain and lack of stones.

In all cases, however, low-intensity grazing is essential for the successful survival and establishment of *Calluna* in the long-term to prevent the re-growth of highly competing grass species and thus facilitate slowly growing *Calluna* seedlings and juveniles. Furthermore, over the long-term, we expect changes in plant species composition, species number and species diversity due to management, particularly in favour of competitively weak and light needing plants and low-nutrient indicator

species (paper in preparation). In addition, we detected an increase in typical heathland species (paper in preparation). However, it is necessary that seed sources are still present on the site; otherwise the addition of seeds is a key factor in the restoration of species rich heathlands, especially in long-abandoned heaths.

Acknowledgements

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Chapter III

What restricts generative rejuvenation of *Calluna vulgaris* in continental, dry

heathland ecosystems: seed production, germination ability or safe site

conditions?

Katrin Henning, Goddert von Oheimb & Sabine Tischew

Abstract

A large-scale field experiment with different management options (free-range grazing, onetime cutting, additional disturbances and their interactions) was carried out in a continental, dry heathland. Within the framework of the experiment seed production and germination ability of over-aged *Calluna* individuals as well as specific safe site conditions were investigated to reveal restricting factors for the generative rejuvenation of *Calluna*. The calculated values of seed production and germination ability of over-aged Calluna individuals can be compared with those from literature or exceed the values reported there. Therefore, seed production and germination ability are not the limiting factors for the generative rejuvenation of *Calluna*. Free-range grazing with large herbivores combined with onetime cutting of over-aged *Calluna* stands supports the generative rejuvenation, especially due to the creation of specific safe sites, which are crucial for a successful survival of *Calluna* seedlings. Particularly a light shadowing seems to be the restricting factor for a successful generative rejuvenation of *Calluna* in continental, dry heathlands.

Keywords: disturbance, free-range grazing, germination, management, seedling establishment.

Introduction and study area

Heathlands at the edge of their ecological distribution (eastern, continental region) are often heavily degraded by an over-aging and the absent or limited generative rejuvenation of *C. vulgaris* (Sedláková & Chytrý 1999; Valbuena *et al*. 2000) due to land abandonment and changing environmental conditions. Still, there is a lack of knowledge of driving factors, which restrict and promote the generative rejuvenation of *Calluna* and regenerate over-aged heathlands in continental climates. Therefore, a large-scale field experiment in an abandoned former military training area in Eastern Germany (Oranienbaumer Heide) with free-ranging cattle and horses was implemented to test their effects on over-aged *Calluna* populations in heaths and mosaics with dry basophilic grasslands. In addition, combinations with a onetime cutting management and additional disturbances were tested. Furthermore, seed production and germination ability of over-aged *Calluna* individuals as well as essential safe site conditions were examined as potential limiting factors for the generative rejuvenation.

Research methods

The effects of grazing, cutting, disturbances as well as their interactions were investigated on 5 m x 5 m plots using a multi-factorial block experiment with an integrated split-plot design. Grazing was realized by the basic management in the study area. Cutting was done once with a brushcutter on a level of 3–5 cm over ground. The cutted material was removed from the plots. On the half of each plot (sub-plot) 25 randomly selected additional disturbances (10 cm x 10 cm) were applied by removing the litter and humus layer by hand. The disturbances imitate the trampling effects by cattle and horses and mimic a higher grazing pressure.

Seed production was estimated on sub-plot level by collecting all flowering shoots of the over-aged *Calluna* individuals within 96 quadrats (50 cm x 50 cm) at the time of the highest seed maturity. Germination ability of seeds was examined depending on different life cycle stages of *Calluna* and stratification in a growth chamber. The in situ germination and establishment of *Calluna* seedlings was investigated on sub-plot level twice a year on the basis of the following eight parameters: distance to

the nearest adult *Calluna* individual, shadowing, exposition, position, root competition, proportion of bare ground, soil without vegetation as well as coverage ratio of vegetation.

All data were processed and analysed using statistical package IBM SPSS statistics (version 19, IBM Corporation 2010) or R (version 3.0.2, R Development Core Team 2013), using the package lme4 (Bates *et al.* 2014). The measured data were tested for normality and homogeneity of variance using a one-sample Kolmogorov-Smirnov test and Levene's test. The statistical analysis of seed production and germination were carried out with one-sample t-tests or one-way analyses of variance (ANOVAs). Percentage data were arcsine transformed to achieve normality prior to the ANOVAs and t-tests being performed. The effects of treatments and safe site conditions on the survival of *Calluna* seedlings were analysed separately by using generalized linear mixed models (GLMMs) with a binomial error term, fitted by maximum likelihood. Grazing, onetime cutting, additional disturbances as well as safe site conditions were included as fixed effects. Plot was included as a random effect to account for the split-plot design of the experiment.

Results

Seed production per m2 of over-aged *Calluna* stands was extremely variable, ranging from 139 639 to 760 451 (mean: 340 770 seeds m-2, SD: 122 872.59). The mean germination rates depending on life cycle stage and stratification ranging between 62 % and 78 % but life cycle stages of *Calluna* did not affect seed germination significantly. The stratification had a significant effect on the germination of *Calluna*, showing higher germination rates for stratified seeds during the first 15 days.

In *Calluna* dominated stands highest seedling germination and establishment was observed on plots with the combination grazing, cutting and additional disturbances (Table 1). But also all other treatments that included additional disturbances (mimicking a higher grazing pressure) showed higher occurrences of *Calluna* seedlings than plots without these treatment. Additional disturbances and safe site conditions (i.e. light shadowing, high proportion of bare ground) significantly supported the survival of *Calluna* seedlings in *Calluna* dominated stands (Table 2).

Table 1: Mean values and standard deviations (in brackets) of seedlings and juveniles recorded per 12.5 m-² plot during one growing season. Significant differences for germination are indicated by an asterisk *p < 0.05, **p < 0.01. Treatments: G = Grazing, C = Cutting, D = Disturbances, 0 = Control.

Treatment	*Calluna*-dominated stands		Mosaics of heather and dry basophilic grasslands	
	seedlings	juveniles	seedlings	juveniles
G	8.2 *(12.3)*	6.7 *(9.2)*	2.2 *(2.6)*	2.2 *(2.6)*
G x C	8.7 *(17.4)*	8.2 *(17.2)*	7.2 *(12.3)*	5.7 *(9.6)*
G x D	50.3 *(51.9)* *	48.2 *(49.3)*	0.7 *(1.0)*	0.7 *(1.0)*
G x C x D	67.5 *(62.2)* *	65.0 *(60.2)*	1.2 *(1.6)*	1.2 *(1.6)*
C x D	38.4 *(30.1)* *	35.8 *(30.0)*	4.2 *(5.3)*	4.2 *(5.3)*
C	12.0 *(28.9)*	9.7 *(23.7)*	1.0 *(2.4)*	1.0 *(2.4)*
D	41.5 *(36.4)* *	40.2 *(36.5)*	1.2 *(1.6)*	0.7 *(0.8)*
0	0.0	0.0	4.7 *(6.9)*	3.5 *(5.2)*

Table 2: Generalized linear mixed models (GLMM's) for treatment and safe site condition effects on the survival of *Calluna* seedlings in *Calluna* dominated stands and mosaics of heather and dry basophilic grasslands during 1 growing season (n = 6). Significant differences for survival are indicated by an asterisk *p < 0.05, **p < 0.01, ***p < 0.001.

Treatments / Safe site conditions	*Calluna* dominated stands				Mosaics of heather and dry basophilic grasslands			
	Estimate	Std.Error	z-value	Pr(>|z|)	Estimate	Std.Error	z-value	Pr(>|z|)
(intercept)	3.13	0.65	4.79	< 0.001 ***	9.83	6.20	1,587	n.s.
Grazing	0.20	0.65	0.31	n.s.	-1.52	8.71	-0.18	n.s.
Cutting	-0.78	0.66	-1.18	n.s.	0.01	8.63	0.00	n.s.
Disturbances	0.80	0.25	3.25	< 0.01 **	-2.07	2.63	-0.79	n.s.
(intercept)	-0.87	1.66	-0.52	n.s.	19.37	25.67	0.75	n.s.
Shadowing	4.83	0.35	13.72	< 0.001 ***	5.91	2.62	2.26	< 0.05 *
Exposition	-0.22	0.07	-3.13	< 0.01 **	-0.36	0.26	-1.42	n.s.
Soil without vegetation	-0.03	0.01	-2.51	< 0.05 *	-0.02	0.17	-0.13	n.s.
Bare ground	0.05	0.03	2.12	< 0.05 *	-1.10	1.08	-1.02	n.s.
Position	-0.24	0.17	-1.46	n.s.	0.29	0.16	1.86	n.s.
Distance	0.01	0.02	0.88	n.s.	-0.66	2.27	-0.29	n.s.
Root competition	-0.11	0.17	-0.67	n.s.	1.47	1.28	1.14	n.s.
Vegetation coverage	0,013	0,01	1,168	n.s.	0.12	0.31	1.21	n.s.

Discussion

Seed production of over-aged *Calluna* individuals originating from the continental study area was comparable high as in Atlantic regions and was even as high as seed production found in earlier life cycle stages of *Calluna* or exceeded the values reported there (Cummins & Miller 2002; Piessens *et al*. 2005). The high percentage and rate of germination of *Calluna* seeds under controlled conditions is also in agreement with previous studies from Atlantic as well as continental sites (Pons 1989; Vera 1997).

Free-range grazing seems to be a suitable management tool to support *Calluna* rejuvenation due to the creation of safe sites for seedling establishment. Especially a light shadowing of *Calluna* seedlings supports the germination and the survival of them in continental regions. Therefore, it is essential to create and maintain a heterogeneous vegetation structure in dry heathlands, which is supported by grazing anyway (Bokdam & Gleichman 2000). A higher grazing pressure, mimicked by additional disturbances, lead to an increase creation of safe sites (Mitchell *et al*. 2008; Newton *et al.* 2009). In the naturally high presence of bare ground and light availability caused by lower vegetation cover, a low stocking rate is adequate to maintain patchy mosaics of heather and dry basophilic grasslands. In dense, over-aged *Calluna*-dominated stands a higher grazing pressure is necessary to increase the proportion of bare ground and light availability, which lead to a higher germination and survival of *Calluna* seedlings. Onetime cutting leads to a temporarily and locally higher grazing pressure due to the enhanced preference and digestibility of re-sprouted *Calluna* shoots by the grazing animals (Lake *et al.* 2001) and consequently supports the rejuvenation of *Calluna*.

Finally it can be stated, that even over-aged *Calluna* individuals are able to produce high quantities of seeds, which further show high germination rates. According to this, seed production and germination ability of seeds of over-aged *Calluna* stands are not the restricting factors for the generative rejuvenation. Safe site conditions are crucial and the limiting factor for the successful establishment and survival of *Calluna* seedlings.

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Chapter IV

Year-round cattle and horse grazing supports the restoration of abandoned, dry sandy grassland and heathland communities by supressing *Calamagrostis epigejos* and enhancing species richness

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Abstract

The spread of competitive grasses, changes in species composition and vegetation structure are direct consequences of grassland and heathland abandonment. As an alternative to more costly management measures such as traditional pastoralism, year-round low-intensity grazing with large herbivores is increasingly used to restore and maintain semi-open habitats. However, the suitability of this grazing regime has not yet been investigated for long-abandoned, highly degraded but nutrient-poor sandy grassland and heathland communities. In particular, it is unclear if year-round grazing is suitable for preventing the further spread of highly competitive grasses such as *Calamagrostis epigejos* while simultaneously maintaining or improving characteristic species richness and vegetation structure. Hence, we conducted a comprehensive field study on two spatial scales (plot-level: 25 m², macroplot-level: 1 ha) to analyse the impacts of year-round low-intensity cattle and horse grazing on the development of the highly competitive grass *Calamagrostis epigejos,* as well as the vegetation structure and plant species richness of long-abandoned but nutrient-poor dry sandy grassland and heathland communities, their mosaics and *Calamagrostis* stands within an 800 ha heathland between 2008 and 2015. Finally, we assessed the local conservation status of the habitat types after seven years of grazing in comparison to long-abandoned sites.

Grazing successfully reduced the coverage of *Calamagrostis epigejos*, whereby *Calamagrostis* stands developed towards species-rich sandy grasslands after seven years of grazing. In addition, the quality of the vegetation structure was improved by enhancing the proportion of bare soil, while litter and grass cover, litter thickness and height of the field layer as well as the coverage of ruderal indicators were significantly reduced on grazed sites in comparison to ungrazed sites in 2015. Moreover, we found an overall positive grazing effect on species richness: Total species number, number of target species as well as subordinated target species significantly increased within the vegetation types over time.

Thus, year-round low-intensity cattle and horse grazing is a suitable management tool for restoring, maintaining and even improving long-abandoned, nutrient-poor sandy grassland and heathland communities, and thus to enhance the local conservation status of the habitat types. However, if there is a high initial cover of woody species (e.g. shrubs, tree rejuvenation), then an extensive shrub and

tree clearance will be necessary, with manual shrub cutting being crucial to reduce the heavy regrowth of the woody species. In addition, a one-time mowing should be implemented in highly degraded heaths to facilitate the vegetative rejuvenation of degenerate stands of *Calluna vulgaris*, thus improving its attractiveness for the grazing animals.

Introduction

Dry sandy grassland and heathland communities are recognized throughout Europe as being of high conservation value and classified as "habitats of Community interest" ("Xeric sand calcareous grasslands", habitat code *6120; "European dry heaths", habitat code 4030; Council Directive 92/43/EEC). 89 % of the priority habitat type "Xeric sand calcareous grasslands" as well as 30 % of the habitat type "European dry heaths" are located in the Continental biogeographical region (EEA 2015a, b). They mainly originated from a long history of low-intensity grazing, often in combination with other land use practices (e.g. mowing, sod-cutting; Bredenkamp, Spada & Kazmierczak 2002; Garcia *et al.* 2013; Dengler *et al.* 2014). Traditional management measures created semi-open landscapes, prevented succession to closed woodlands and maintained a high species richness. From the middle of the 19th century onwards, traditional pastoralism such as sheep herding began to decline due to socio-economic changes, and large areas of sandy grasslands and heathlands were subjected to succession and reverted to woodland (Price 2003). Some of these low-productive areas were used for military training activities, thus maintaining their open character, nutrient-poor soil conditions and species richness through a combination of heterogeneously distributed disturbances from military training activities and the exclusion of intensive agriculture or forestry (Warren *et al.* 2007; Jentsch *et al.* 2009). Today, military training areas represent some of the last large remnants of sandy grasslands and heathlands in Europe (Warren & Büttner 2014). However, political changes in the former Eastern bloc countries have led to the cessation of these activities in most areas (Cizek *et al.* 2013). As a consequence of the abandonment of both traditional management and military training activities, the conservation status of sandy grassland and heathland habitats is listed as unfavourable-bad across the Continental region of Europe (EEA 2015a, b). Successional changes, in particular the spread of competitive grasses such as *Calamagrostis epigejos* (henceforth referred to as *Calamagrostis*), accompanied by a high litter accumulation, tree and shrub encroachment, the predominance of degenerate *Calluna vulgaris* (henceforth referred to as *Calluna*) stands as well as the lack of bare soil patches, are the main degradation processes in abandoned sandy grasslands and heathlands (Britton *et al.* 2000; Ödman *et al.* 2012). Counteracting these processes is difficult in the current socio-economic situation in Europe and requires the development of scientifically based and cost-efficient restoration

schemes (Török *et al.* 2016a). Nowadays, year-round large herbivore grazing is increasingly used to restore and maintain species-rich habitats as an alternative to the more costly traditional herding (Bokdam & Gleichman 2000; von Oheimb *et al.* 2006, Török *et al.* 2016b). For example, large herbivores have been found to reduce aboveground biomass and create bare soil patches more efficiently than sheep (Mitchell, Rose & Palmer 2008).

However, the suitability of year-round large herbivore grazing has not yet been investigated for long-abandoned, highly degraded but nutrient-poor sandy grassland and heathland communities and thus, is considered to be controversial (Newton *et al.* 2009). In particular, it is unclear if this grazing regime is effective in suppressing the further spread of highly competitive grasses such as *Calamagrostis* and simultaneously maintaining or improving the characteristic plant species composition. There are major concerns regarding the unequal utilization of the pasture, with partial undergrazing potentially resulting in an increase of ruderal plant species, the further degeneration of *Calluna* (Putfarken *et al.* 2008), as well as the impairment of endangered plant species while partial overgrazing can also have negative effects such as damage of the *Calluna* canopy (Gimingham 1992). Therefore, investigations are urgently needed to determine the long-term and large-scale impacts of year-round grazing with large herbivores and therefore whether this type of grazing strategy is a suitable management tool. Repeated surveys over several years are necessary to analyse the long-term trends in vegetation dynamics and changes in biodiversity (Silvertown *et al.* 2010; Critchley *et al.* 2013). However, most studies have investigated the effects of year-round grazing either only at one given time point (e.g. Rupprecht, Gilhaus & Hölzel 2016), focussed on other vegetation types (Köhler, Hiller & Tischew 2016 for calcareous grassland) or studied nutrient-richer heath habitats within the Atlantic region (Bokdam & Gleichman 2000). To representatively determine the grazing-dependent changes in vegetation structure of large-scale grazing systems, in addition to traditional vegetation surveys on small plots, investigations on larger plots might be supportive (Dimopoulos, Bergmeier & Fischer 2005). Due to wallowing and the creation of grazing lawns, large grazers cause disturbances at larger scales (Collins & Smith 2006; Turtureanu *et al.* 2014), which contributes to high spatial heterogeneity of the vegetation structure. Therefore, analysing disturbance-associated parameters (e.g. vegetation structure) on small scales might lead to inappropriate conclusions. Moreover, estimated parameters of

large-scale surveys can be used for a representative assessment of the conservation status of the habitat types (Dimopoulos, Bergmeier & Fischer 2005; Lorenz *et al.* 2013).

In this study, we report the findings of a comprehensive seven-year field study on two spatial scales, the plot-level (25 m²) and the macroplot-level (1 ha), to analyse the long-term effects of year-round low-intensity cattle and horse grazing on the development of the highly competitive grass *Calamagrostis,* the vegetation structure as well as the plant species richness of long-abandoned, nutrient-poor dry sandy grassland and heathland communities, their mosaics and *Calamagrostis* stands focusing on the following questions:

3) Is year-round grazing suitable to supress *Calamagrostis* and prevent its further spread into other vegetation types?

4) How does grazing management affect the vegetation structure?

5) Does grazing management improve species richness and composition towards to that of the target communities?

Finally, we assess the local conservation status of the habitat types after seven years of cattle and horse grazing in comparison to long-abandoned sites.

Material and methods

Study site

The study site is located in the NATURA 2000 site Oranienbaumer Heide (Saxony-Anhalt, E Germany, 51° 46' N, 12° 21' E, 70 m a.s.l., 2.683 ha). The continental climate is characterized by a mean annual temperature of 9.2 °C, mean annual precipitation of about 560 mm (climatologic station: Oranienbaum, period: 1961 to 1990, DWD 2015) and arid periods with negative climatic water balances in spring and summer (PIK 2009). Atmospheric N deposition is comparatively low with less than 10 kg ha^{-1} year^{-1} (Lorenz *et al.* 2013). The study site is characterised by Pleistocene sandy soils with topsoil pH$_{H2O}$ values between 4.9 and 5.8. Total soil nitrogen and carbon contents range between 0.1 % and 0.5 % and between 1.9 % and 6.9 %, respectively. Plant-available phosphorus and

potassium in the soil (mg per 100 g soil) range between 0.0 and 2.0 mg and between 3.3 and 12.1 mg, respectively. Grazing was a common land use practice on the site since the fourth century. From 1945 until 1989, the site was used for military training activities, thus maintaining large-scale open landscapes (John, Lorenz & Osterloh 2010). A nearly two decade cessation of military use, from 1989 to 2008, led to the rapid encroachment of woody species, mainly Scots pine (*Pinus sylvestris*) and silver birch (*Betula pendula*). In addition, *Calamagrostis* formed dense vegetation stands, accompanied by high litter accumulation in some parts of the area. Pine and birch were extensively cleared on 470 ha, with the regrowth of woody species > 0.5 m manually cut on approximately 90 ha every second year.

A permanent pasture was established at the end of 2008. The pasture encompasses 800 ha and is managed by year-round, low-intensity grazing with Heck cattle and Konik horses (stocking rate approximately 0.2 livestock units ha^{-1}). Supplementary food (1 kg hay/animal/day) is provided only in winter months with permanent snow cover. As a consequence of browsing and the manual cutting, the regrowth potential has decreased slowly with time (own unpubl. data). However, single trees and shrubberies were maintained as habitat structures for wildlife, in particular for birds. "Xeric sand calcareous grasslands" (habitat code *6120; 135 ha), "European dry heaths" dominated by *Calluna* (habitat code 4030; covering 330 ha) and mosaics of these habitat types (habitat code *6120/4030; 70 ha) are the focus of current nature conservation activities. Despite long-term abandonment, the study site is rich in species, with the frequent occurrence of *Armeria maritima, Calluna, Carex pilulifera, Dianthus deltoides*, *Euphorbia cyparissias, Festuca ovina, Fragaria viridis, Galium verum, Genista pilosa, Genista tinctoria, Koeleria macrantha, Pilosella officinarum, Potentilla neumanniana,*and *Thymus pulegioides*. Rare and endangered plant species such as *Botrychium lunaria, Botrychium matricariifolium, Carex ericetorum, Cuscuta epithymum, Genista sagittalis*, *Helichrysum arenarium*, *Peucedanum oreoselinum, Vicia cassubica* and *Viola rupestris* occur in some parts of the study site, with remarkably large populations in some areas.

Data sampling

Before grazing started, the study site was stratified based on mapping of the habitat types (Anhalt University of Applied Sciences 2007). Four vegetation types were selected for further analyses: sandy grasslands, heaths, mosaics of heath and sandy grassland, and *Calamagrostis*-stands. In 2008, six randomly selected 1 ha plots (100 m x 100 m, henceforth referred to as macroplots) were established in each of these four vegetation types, and distributed over the entire site (yielding a total of 6 x 4 = 24 macroplots). Half of the 24 macroplots were fenced to exclude cattle and horses (exclosures, used as control), while they were still accessible to wild herbivores such as roe deer or rabbits. At the macroplot-level, we estimated the cover of *Calamagrostis* as well as the vegetation structure (i.e. percentage cover of bare soil, cryptogams, litter layer, all grasses, all herbs, ruderal indicators (the two plant species *Tanacetum vulgare* and *Hypericum perforatum*), *Calluna* and other woody species < 0.5 m as well as the average vegetation height and thickness of the litter layer). Since woody species > 0.5 m are manually cut every second year (see above), we investigated only the cover of woody species < 0.5 m.

Data sampling was performed three times: in 2008, 2010, and 2015 in the sandy grasslands and *Calamagrostis* stands, and in 2008, 2010, and 2014 in the heaths and mosaics. A 25 m² plot (5 m x 5 m, henceforth referred to as plots) was placed in the centre of each macroplot to estimate the percentage cover of all vascular plant species using the extended Londo scale (Londo 1976). Furthermore, structural parameters, such as percentage cover of bare soil, cryptogams, field layer (i.e. all vascular plants < 0.5 m height) and the litter layer as well as the average vegetation height and litter layer thickness, were recorded on the plot-level. Data sampling in the plots was performed three times: in 2008, 2010, and 2015 in the sandy grasslands and *Calamagrostis* stands, and in 2008, 2011, and 2015 in the heaths and mosaics. Data collection within the vegetation types was split into two years due to shifts in project funding during the course of the study (i.e. 2010 and 2011 for plot-recording and 2014 and 2015 for macroplot-recording).

Data analyses

The species recorded were assigned to one of the following ecological groups: "target species", "subordinated target species", "dry mesophilic grassland species", "ruderal species" and "other species" (Table 1).

Table 1: Species allocation to ecological groups. Target species according to Schuboth & Frank (2010), Ludwig & Schnittler (1996) and Frank *et al.* (2004), affiliation to phytosociological groups according to Schubert (2001), Schubert, Hilbig & Klotz (2001) and BfN (2011).

Ecological group	Definition
Target species	Habitat code *6120 characterising species, phytosociological affiliation to Armerion elongatae communities: *Armeria maritima subsp. elongata*, *Centaurea stoebe*, *Dianthus deltoids*, *Festuca brevipila*, *Galium verum*, *Helichrysum arenarium*, *Koeleria macrantha*, *Peucedanum oreoselinum*
	Habitat code 4030 characterising species, phytosociological affiliation to Genistion pilosae communities: *Agrostis capillaris*, *Anthoxanthum odoratum*, *Calluna vulgaris*, *Carex pilulifera*, *Danthonia decumbens*, *Deschampsia flexuosa*, *Euphorbia cyparissias*, *Festuca ovina*, *Hypericum perforatum*, *Hypochoeris radicata*, *Luzula campestris*, *Pilosella officinarum*, *Rumex acetosella*
	Red List-species (status 0-3, extinct to vulnerable): *Aira caryophyllea*, *Botrychium lunaria*, *Botrychium matricariifolium*, *Carex ericetorum*, *Cuscuta epithymum*, *Luzula pallescens*, *Pilosella caespitosa*, *Pilosella setigera*, *Vicia cassubica*, *Viola rupestris*
Subordinated target species	Sandy grassland species: phytosociological affiliation to Armerion elongatae communities
	Heathland species: phytosociological affiliation to Genistion pilosae communities
Dry mesophilic grassland species	Phytosociological affiliation to Arrhenatheretalia elatioris communities
Ruderal species	Phytosociological affiliation to Artemisietea vulgaris, Epilobietea angustifolii, Stellarietea mediae or Plantaginetea majoris communities
Other species	All species not assigned to the other groups (i.e. woody species,

We defined as target species all species that are of conservation interest for one of the habitat types, "Xeric sand calcareous grasslands" or "European dry heaths" (Schuboth & Frank 2010), or are listed in the red lists of Germany (Ludwig & Schnittler 1996), or of Saxony-Anhalt (Frank *et al.* 2004). Subordinated target species are all species that are characteristic for the studied dry sandy grasslands or heathlands and show a phytosociological affiliation to Armerion elongatae communities or

Genistion pilosae communities, respectively (Schubert 2001, BfN 2011). Dry mesophilic grassland species are species that show a phytosociological affiliation to Arrhenatheretalia elatioris communities. Ruderal species belong to the Artemisietea vulgaris, Epilobietea angustifoliae, Stellarietea mediae or Planteginetea majoris communities (Schubert, Hilbig & Klotz 2001). Other species are all species not fulfilling the above mentioned criteria. Furthermore, Ellenberg indicator values for nitrogen (N-values) were assigned to each species (Ellenberg *et al.* 2001). For analyses, three subsets of species were created, i.e. mean number of species with low (N 1-3), moderate (N 4-5) and high (N 6-9) values. Indifferent species were excluded from the subsequent analyses. The complete list of species including their allocation to ecological groups and N-values are provided in Table S1.

Repeated measures analyses of variance (RM ANOVAs) were conducted on the macroplot- and plot-levels to show the development of species richness (i.e. total species number, species numbers within the ecological groups), N-values, cover of *Calamagrostis* and vegetation structure on grazed and ungrazed sites across and within the four vegetation types over time. Year of observation (plot-level: 2008, 2010/2011 and 2015, macroplot-level: 2008, 2010 and 2014/2015) was used as the within subject effect, while management (grazed vs. ungrazed) was used as the between subject effect. Species richness, N-values, cover of *Calamagrostis* and structural parameters served as the dependent variables. If Mauchly's test indicated that the assumption of sphericity had been violated, we applied the Greenhouse-Geisser test, which did not require sphericity. Moreover, we used paired *t*-tests to show the development of dependent variables after seven years of grazing (2008 vs. 2015) or abandonment on grazed as well as on ungrazed sites. Furthermore, *t*-tests were applied to determine whether the dependent variables differed between grazed and ungrazed sites in 2015. If necessary, the data were log- (i.e. ruderal species, height of the litter layer) or log + 1 (i.e. other species, coverage of bare soil, litter layer, field layer and *Calamagrostis*) transformed to achieve normality prior to the ANOVAs and *t*-tests. All analyses were performed using IBM SPSS Statistics 22.0 (IBM Corp. 2013). The local conservation status (CS) of the habitat types dry sandy grasslands and heathlands after seven years of grazing was evaluated on the basis of different structural parameters and species composition on the macroplots according to Table S3 (Schuboth & Frank 2010). Habitat structure, species

inventory and impairments serve as parameters for the assessment. Value categories for each of the three parameters were estimated and then combined to a total value (Table S3). Since there are no guidelines for the assessment of the CS of mosaics, we have combined various indicators regarding habitat structure, species inventory and impairments of sandy grasslands and heaths to evaluate the mosaics (Table S3).

Results

Development of Calamagrostis

A) Small-scale (plot-level) effects

In 2015, *Calamagrostis* cover was significantly lower on grazed than on ungrazed plots across the four vegetation types (Table 2), the result of substantial changes due to grazing over time (Figure 1a). Specifically, the grazing management significantly affected *Calamagrostis* coverage in sandy grasslands and *Calamagrostis* stands (Figure 1b and e). For example, *Calamagrostis* cover was significantly reduced from 45.8 to 2.0 % on grazed plots in *Calamagrostis* stands between 2008 and 2015 (Table 3). *Calamagrostis* cover within grazed sandy grasslands, heaths and mosaics did not change over time, and was still low in 2015 with average coverages between 0.2 and 1.5 %. In contrast, we found a significant increase in *Calamagrostis* cover on ungrazed plots in the mosaics and a marginal increase in the heaths between 2008 and 2015 (Figure 1c-d, Table 3). Significantly higher coverages were found on ungrazed plots compared to grazed plots in *Calamagrostis* stands in 2015, while the effect was marginal for the sandy grassland and mosaic plots after seven years of grazing (Table S2).

B) Large-scale (macroplot-level) effects

We found significant changes of the coverage of *Calamagrostis* over time across the four vegetation types (Figure 2a). Thus, *Calamagrostis* cover was significantly lower on grazed than on ungrazed macroplots in 2015 (Table 2). On grazed macroplots, *Calamagrostis* cover distinctly decreased from 25.3 to 8.5 % over time ($P = 0.000$), whereas it remained stable on ungrazed macroplots (from 28.5 to

33.5 %; P = 0.237). The RM ANOVAs showed a significant interaction effect of year and management for the sandy grasslands, mosaics and *Calamagrostis* stands (Figure 2b-e).

Table 2: Mean values (± SE) of species richness, N-values and structural parameters for grazed (G) and ungrazed (UG) plots and macroplots in 2015, seven years after the start of the experiment. Differences between grazing managements were determined by t-tests. X > Y indicates that the respective dependent variable was significantly greater under management X than under Y. Significant differences are marked as follows: * P < 0.05, ** P < 0.01, *** P < 0.001.

		P-value	Grazed	Ungrazed	
			$n = 12$	$n = 12$	
Plot-level (25 m²)					
Calamagrostis epigejos (%)	***	< 0.000	1.18 ± 0.25	19.71 ± 6.86	UG > G
Species richness					
Total species number	*	0.017	38.33 ± 2.32	28.92 ± 2.81	G > UG
Target species	*	0.019	10.75 ± 0.73	7.75 ± 0.94	G > UG
Subordinated target species	*	0.014	15.75 ± 1.27	10.25 ± 1.63	G > UG
Dry meso. grassland species	*	0.041	5.33 ± 0.67	3.58 ± 0.45	G > UG
Ruderal species		0.907	3.50 ± 0.44	3.58 ± 0.56	
Other species		0.484	3.00 ± 0.55	3.75 ± 0.90	
Ellenberg N-values					
N 1-3	*	0.018	21.50 ± 1.51	15.17 ± 1.98	G > UG
N 4-5	*	0.032	7.75 ± 0.92	5.08 ± 0.71	G > UG
N 6-9		0.256	3.92 ± 0.484	3.25 ± 0.31	
Macroplot-level (1 ha)					
Calamagrostis epigejos (%)	***	0.000	8.51 ± 3.75	33.51 ± 4.69	UG > G
Vegetation structure					
Bare soil (%)	***	0.000	3.52 ± 0.38	0.52 ± 0.12	G > UG
Cryptogams (%)	***	0.000	39.78 ± 3.72	72.50 ± 2.13	UG > G
Litter layer (%)	**	0.004	36.44 ± 4.92	62.77 ± 6.40	UG > G
Height of field layer (cm)	***	0.000	24.94 ± 2.77	53.23 ± 3.88	UG > G
Thickness of litter layer (cm)	**	0.007	0.59 ± 0.07	3.52 ± 0.89	UG > G
Grasses (%)	***	0.001	37.92 ± 4.55	61.29 ± 4.16	UG > G
Herbs (%)		0.114	32.56 ± 5.04	20.78 ± 5.16	
Calluna vulgaris (%)		0.495	24.91 ± 8.84	17.56 ± 5.84	
Ruderal indicators	*	0.049	1.62 ± 0.47	7.04 ± 2.56	UG > G
Woody species < 0.5 m (%)		0.588	0.70 ± 0.28	0.53 ± 0.13	

The strongest reduction (by 75%) in *Calamagrostis* cover was observed in grazed *Calamagrostis* stands after seven years of grazing (Table 3). In addition, *Calamagrostis* cover significantly decreased on grazed macroplots in the sandy grasslands between 2008 and 2015, while it did not change

significantly in grazed heaths and mosaics (Table 3). Simultaneously, coverage significantly increased in the ungrazed heaths, but did not differ in the ungrazed sandy grasslands, mosaics nor in the *Calamagrostis* stands (Table 3).

Table 3: Mean values (± SE) of *Calamagrostis* cover on grazed and ungrazed plots and macroplots within each vegetation type in 2008 and 2015. Differences between 2008 and 2015 were determined by paired *t*-tests. Significant differences are written in boldface.

	Grazed ($n = 3$)			Ungrazed ($n = 3$)		
	2008	2015	*P*-value	2008	2015	*P*-value
Plot-level (25 m²)						
Sandy grasslands	2.83 ± 2.33	0.23 ± 0.14	0.359	8.16 ± 3.16	17.50 ± 6.29	0.208
Heaths	1.66 ± 1.66	1.50 ±0.50	0.929	0.33 ± 1.66	2.66 ± 0.66	0.060
Mosaics	2.83 ± 1.16	1.00 ± 0.50	0.212	3.33 ± 2.12	5.33 ± 2.40	**0.020**
Calamagrostis stands	45.83 ± 8.70	2.00 ± 0.00	**0.037**	23.83 ± 18.11	53.33 ± 13.33	0.399
Macroplot-level (1ha)						
Sandy grasslands	12.08 ± 3.40	0.92 ± 0.39	**0.022**	24.58 ± 6.50	24.25 ± 6.62	0.977
Heaths	25.79 ± 16.6	17.58 ± 10.68	0.219	14.58 ± 2.81	39.50 ± 8.17	**0.038**
Mosaics	10.58 ± 6.68	2.90 ± 1.43	0.190	28.25 ± 11.02	27.67 ± 7.65	0.743
Calamagrostis stands	52.92 ± 8.81	12.63 ± 9.96	**0.029**	46.50 ± 17.54	42.63 ± 14.01	0.889

	F	P		F	P		F	P		F	P		F	P
Year	0.689	0.477		1.810	0.225		1.624	0.256		0.638	0.553		1.893	0.241
Grazing	2.284	0.145		11.901	0.026 *		1.746	0.257		1.168	0.341		16.550	0.015 *
Year * Grazing	14.581	< 0.000 ***		2.814	0.119		2.334	0.159		2.486	0.145		1.830	0.248

Figure 1: Repeated measurement ANOVA results of *Calamagrostis* coverage a) over the four vegetation types (n = 12), b) within sandy grasslands (n = 3), c) within heaths (n = 3), d) within mosaics (n = 3) and e) within *Calamagrostis* stands (n = 3) on permanent plots (25 m²); within subjects effect = year, between subjects effect = grazing. Means and ±1SE for grazed (solid line) and ungrazed (dotted line) plots are shown.

	F	P	F	P	F	P	F	P	F	P
Year	8.163	0.003 **	37.546	< 0.000 ***	1.429	0.298	6.116	0.024 *	8.071	0.044 *
Grazing	11.512	0.003 **	23.399	0.008 **	0.649	0.466	7.664	0.050 *	0.899	0.397
Year * Grazing	17.431	< 0.000 ***	37.099	< 0.000 ***	4.410	0.102	5.983	0.026 *	8.009	0.045 *

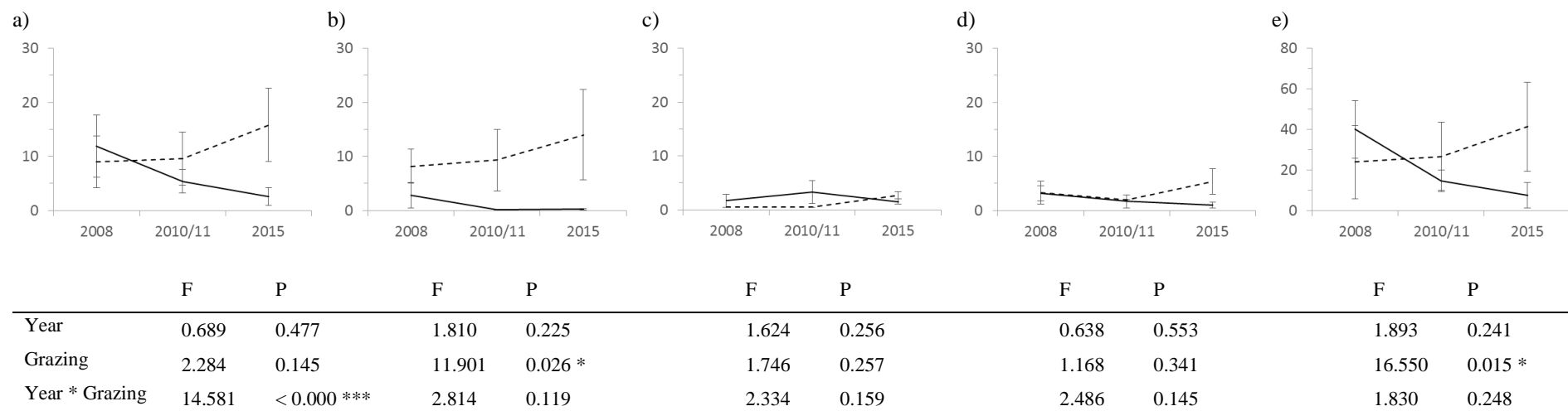Figure 2: Repeated measurement ANOVA results of *Calamagrostis* coverage a) over the four vegetation types (n = 12), b) within sandy grasslands (n = 3), c) within heaths (n = 3), d) within mosaics (n = 3) and e) within *Calamagrostis* stands (n = 3) on permanent macroplots (1 ha); within subjects effect = year, between subjects effect = grazing. Means and ±1SE for grazed (solid line) and ungrazed (dotted line) macroplots are shown.
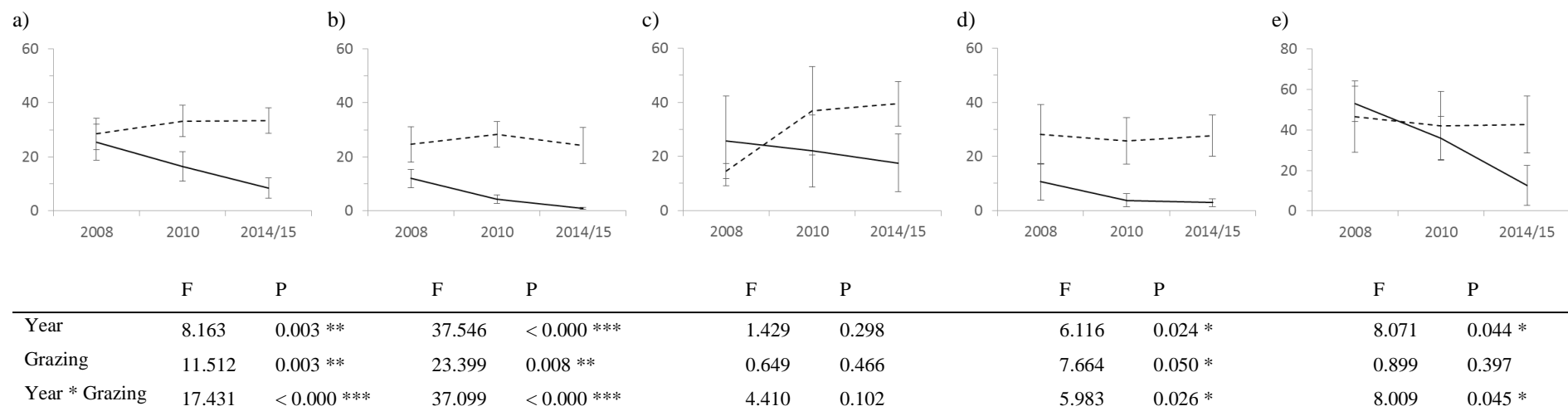
Vegetation structure

A) Across vegetation types

We found a significant interaction effect of year and grazing for the coverage of grasses, the litter layer and bare soil, as well as the litter layer thickness across the four vegetation types (Figure 3a-e), indicating different developments of these parameters on the grazed and ungrazed macroplots (1 ha) over time. Grass cover as well as coverage of the litter layer were significantly reduced from 52.9 ($\pm$ 6.5) to 37.9 % ($\pm$ 4.5) and from 57.8 ($\pm$ 7.1) to 36.4 % ($\pm$ 4.9), respectively, on grazed macroplots between 2008 and 2015 (P = 0.000 for both), while both parameters increased slightly, but not significantly, on ungrazed sites over time (Figure 3a and c). A significant decrease in cryptogam cover, woody species as well as the height of the field layer was observed on grazed sites over time (P = 0.000, P = 0.005 and P = 0.000, respectively), while these response variables did not change on ungrazed sites. In contrast, we found an increase in bare soil and herb cover on grazed macroplots (P = 0.000 and P = 0.003, respectively), while coverage of bare soil did not differ (P = 0.077) and herb cover significantly decreased (P = 0.027) on ungrazed sites across the vegetation types with time. Thus, coverage of cryptogams, grasses, ruderal indicators and the litter layer, as well as the height of the litter and field layers, were significantly lower, while the proportion of bare soil was significantly higher, on grazed than on ungrazed sites in 2015 (Table 2).

B) Within vegetation types

Grazing effects were also detected within each vegetation type. Plant height was significantly lower on grazed than ungrazed macroplots for each vegetation type (Table S2). In addition, after seven years of grazing, the proportion of bare soil was four to 15 times' higher in the sandy grasslands, heaths, mosaics and *Calamagrostis* stands than in ungrazed macroplots. Moreover, grass cover also significantly differed on grazed (42.9%) and ungrazed (77.1 %) macroplots within *Calamagrostis* stands in 2015 (Table S2). Furthermore, the height of the litter layer was 6.4 cm lower on grazed than on ungrazed *Calamagrostis* stands (Table S2). A significant decrease in *Calluna* cover from 76.6 % in 2008 to 43.8 % in 2015 was observed for ungrazed macroplots within heaths (P = 0.012), while a slight reduction was found on grazed macroplots (P = 0.062).

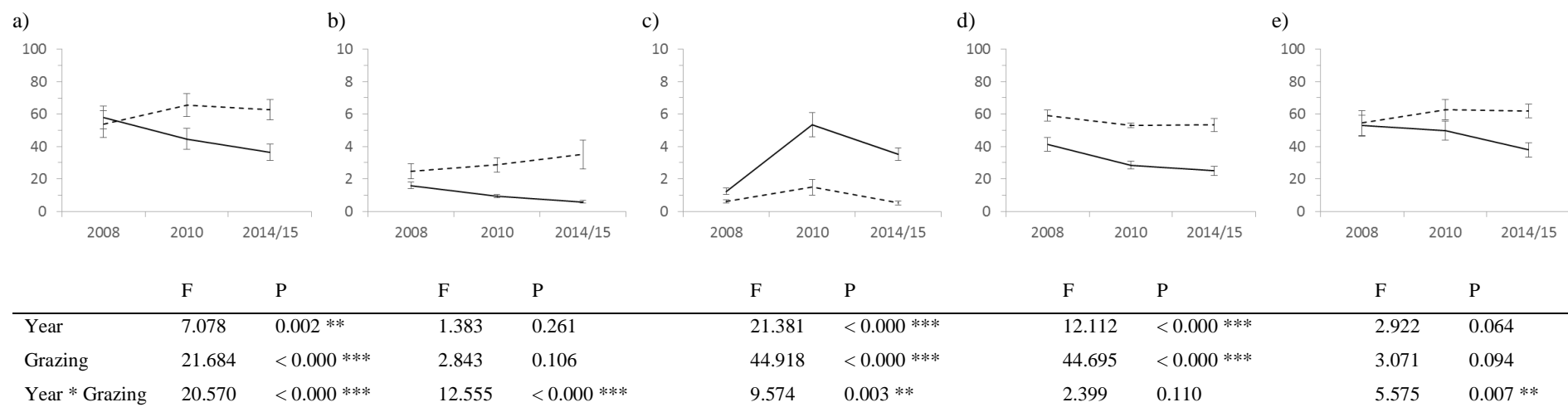|	F	P		F	P		F	P		F	P		F	P
Year	7.078	0.002 **		1.383	0.261		21.381	< 0.000 ***		12.112	< 0.000 ***		2.922	0.064
Grazing	21.684	< 0.000 ***		2.843	0.106		44.918	< 0.000 ***		44.695	< 0.000 ***		3.071	0.094
Year * Grazing	20.570	< 0.000 ***		12.555	< 0.000 ***		9.574	0.003 **		2.399	0.110		5.575	0.007 **

Figure 3: Repeated measurement ANOVA results of a) coverage of litter, b) height of the litter layer, c) coverage of bare soil, d) height of the field layer and e) coverage of grasses on permanent macroplots (1 ha); within subjects effect = year, between subjects effect = grazing. Means and ±1SE for grazed (solid line) and ungrazed (dotted line) macroplots are shown ($n = 12$).

Species richness

    A) Across vegetation types

In 2008, a total of 117 species, among them 26 target species and 41 subordinated target species, were recorded on all plots (25m²) across the investigated four vegetation types. In 2015, we found 140 species, among them 26 target species and 50 subordinated target species. While there were no significant differences in species richness between grazed and ungrazed plots in 2008, total species number, the number of target species as well as the number of subordinated target species and dry mesophilic grassland species were significantly higher in grazed than ungrazed vegetation types in 2015 (Table 2). Furthermore, we found a significant interaction effect of year and grazing for the target species, subordinated target species as well as mesophilic grassland species, indicating their increase on grazed plots with time, while they did not differ in the ungrazed plots (Figure 4b and c, and Figure 5a). Thus, the mean number of species increased significantly ($P = 0.000$) in the grazed plots from 24.8 to 38.3 between 2008 and 2015, while no significant differences could be detected in the ungrazed plots (27.5 and 28.9 species in 2008 and 2015, respectively; $P = 0.353$; Figure 4a). As a result of grazing, even red list species such as *Aira caryophyllea* and *Luzula pallescens* were able to establish within plots. In addition, the repeated measures ANOVA showed a significant time effect for ruderal species, whereas the mean number of ruderal species did not change significantly between the grazed and ungrazed plots (Figure 5b).

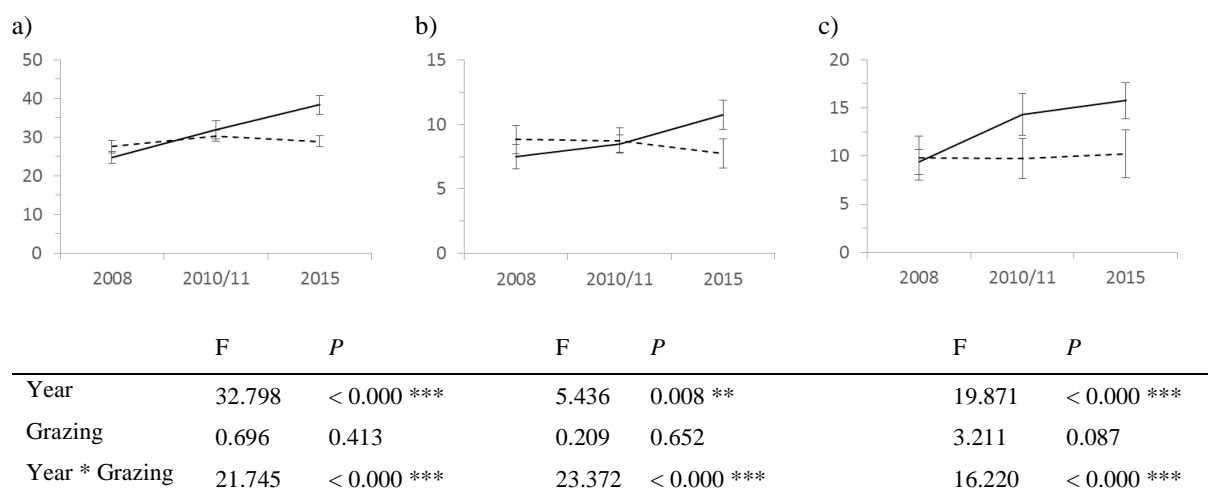|	F	P		F	P		F	P
Year	32.798	< 0.000 ***		5.436	0.008 **		19.871	< 0.000 ***
Grazing	0.696	0.413		0.209	0.652		3.211	0.087
Year * Grazing	21.745	< 0.000 ***		23.372	< 0.000 ***		16.220	< 0.000 ***

Figure 4: Repeated measurement ANOVA results of a) total species number, b) target species and c) subordinated target species on permanent plots (25 m²); within subjects effect = year, between subjects effect = grazing. Means and ±1SE for grazed (solid line) and ungrazed (dotted line) plots are shown ($n = 12$).

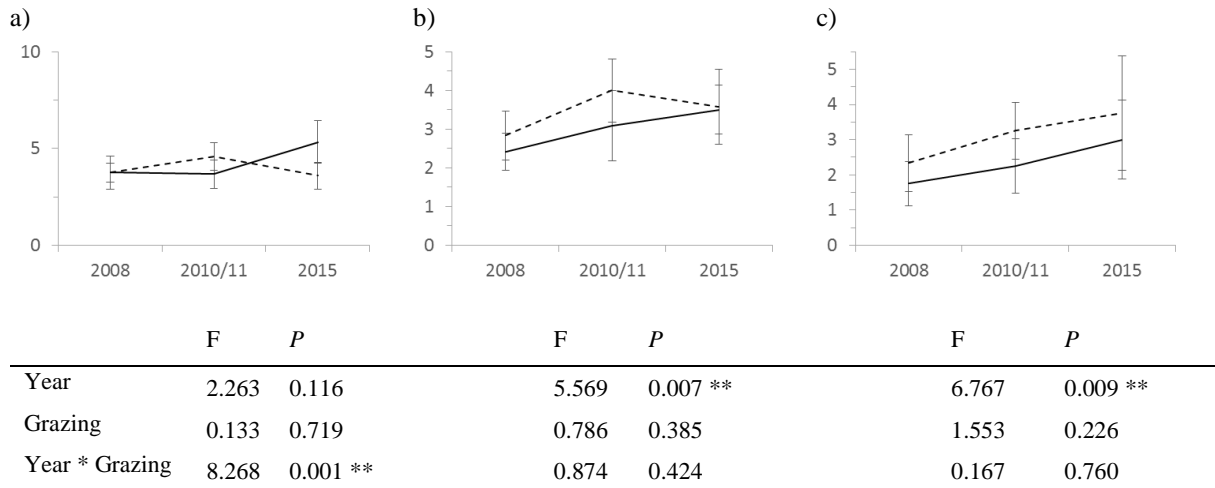|	F	P		F	P		F	P
Year	2.263	0.116		5.569	0.007 **		6.767	0.009 **
Grazing	0.133	0.719		0.786	0.385		1.553	0.226
Year * Grazing	8.268	0.001 **		0.874	0.424		0.167	0.760

Figure 5: Repeated measurement ANOVA results of a) dry mesophilic grassland species, b) ruderal species an c) other species on permanent plots (25 m²); within subjects effect = year, between subjects effect = grazing. Means and ±1SE for grazed (solid line) and ungrazed (dotted line) plots are shown ($n = 12$).

N-values differed significantly between grazed and ungrazed plots. Thus, we found a significant time effect for species associated with low and moderate nutrient values (N 1-3 species and N 4-5 species, respectively) as well as a significant interaction effect of year and grazing for N 1-3 and N 4-5 species as well as for species with high nutrient values (N 6-9 species; Figure 7). After seven years of grazing, N 1-3 and N 4-5 species were more abundant in grazed than in ungrazed plots, while no significant differences could be detected for N 6-9 species (Table 2).

B) Within vegetation types

Species richness significantly increased in the grazed plots between 2008 and 2015 within each vegetation type (Figure 6), while there were no significant differences in the sandy grasslands, heaths, mosaics as well as *Calamagrostis* stands ($P = 0.190$, $P = 0.464$, $P = 0.612$ and $P = 0.930$, respectively). The highest increase in species number, with 21 new species, was observed in the grazed *Calamagrostis* stands. Furthermore, we found a significant increase of subordinated target species on grazed plots in sandy grasslands, mosaics and *Calamagrostis* stands (Figure 6). In addition, the target species significantly increased in the grazed mosaics between 2008 and 2015, while significantly more mesophilic grassland species were found in the heaths as well as in the *Calamagrostis* stands (Figure 6). Ruderal species slightly increased from 2.3 to 4.7 species between

2008 and 2015 in grazed *Calamagrostis* stands, whereby especially low-growing herb species, such as *Veronica arvensis* or *Fragaria vesca*, were able to establish. However, the number of N 1-3 species has doubled to 20 after seven years of grazing in *Calamagrostis* stands (P = 0.058) and has significantly increased in mosaics (P = 0.023). In addition, there was a slight decrease in N 1-3 species on ungrazed plots in each of the four vegetation types with time.
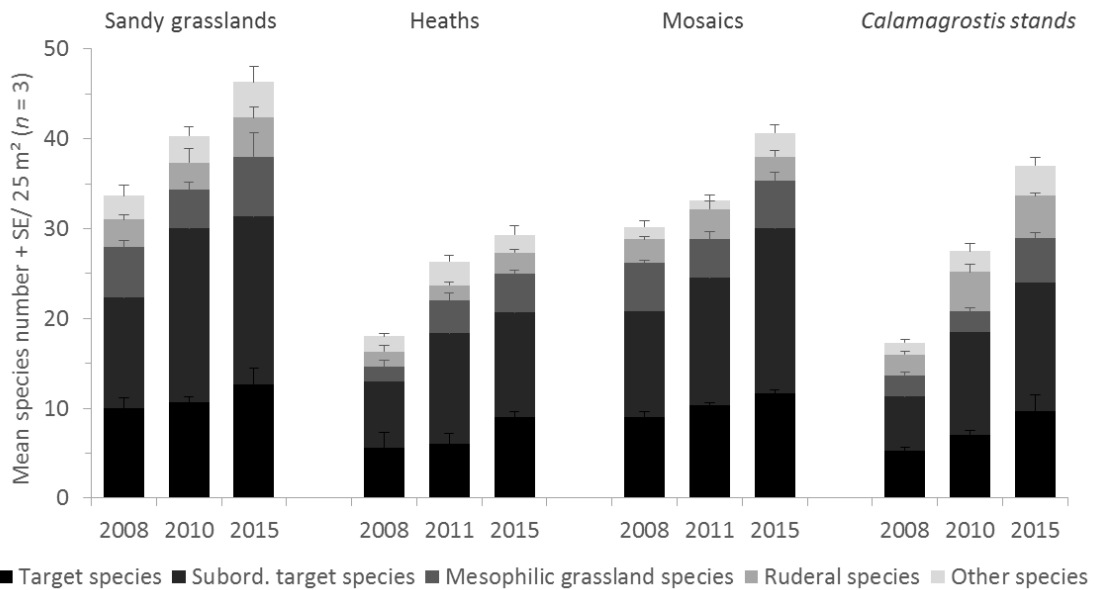
	Sandy grasslands		Heaths		Mosaics		*Calamagrostis* stands	
	T	*P*	T	*P*	T	*P*	T	*P*
Total	-5.429	0.032 *	-7.800	0.016 *	-5.547	0.031 *	-6.371	0.024 *
Target	-3.024	0.094	-2.774	0.109	-8.000	0.015 *	-2.457	0.133
SubTarget	-7.181	0.019 *	-2.457	0.133	-5.166	0.035 *	-13.868	0.005 **
Meso	-0.500	0.667	-8.000	0.015 *	0.000	1.000	-8.000	0.015 *
Ruderal	-1.512	0.270	-2.000	0.184	0.000	1.000	-7.000	0.020 *
Other	-2.000	0.184	-.277	0.808	-4.000	0.057	-3.464	0.074

Figure 6: Changes in ecological groups on permanent grazed plots (25 m²) within sandy grasslands, heaths, mosaics and *Calamagrostis* stands between 2008 and 2015 (paired *t*-test). Means and +1SE are shown (n = 3). Total: total species number, Target: target species, SubTarget: subordinated target species, Meso: dry mesophilic grassland species, Ruderal: ruderal species and Other: other species.
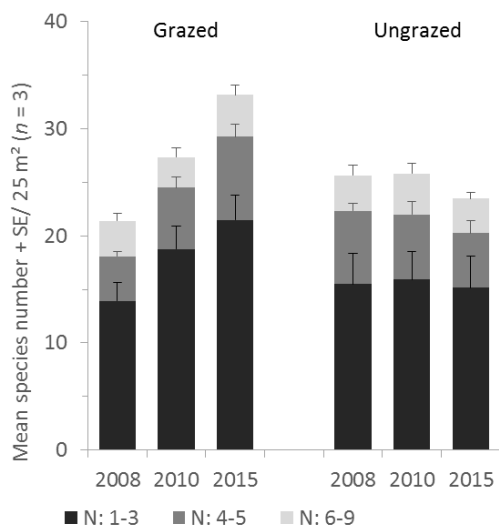
	N 1-3		N 4-5		N 6-9	
	F	*P*	F	*P*	F	*P*
Year	14.872	< 0.000 ***	9.916	< 0.000 ***	1.042	0.361
Grazing	1.396	0.250	0.417	0.525	0.000	1.000
Year * Grazing	16.694	< 0.000 ***	9.137	< 0.000 ***	4.608	0.015 *

Figure 7: Changes in Ellenberg N-values (N1-N9) on permanent grazed and ungrazed plots (25 m²) across all vegetation types between 2008 and 2015 (RM ANOVA: within subjects effect = year, between subjects effect = grazing). Means and +1SE are shown (n = 3). N 1-3: low-nutrient indicators, N 4-5: moderate-nutrient indicators, N 6-9: high-nutrient indicators.

Discussion

Development of Calamagrostis

Our study showed for the first time that low-intensity year-round grazing with cattle and horses is very suitable to successfully reduce and prevent the further spreading of *Calamagrostis* within nutrient-poor, dry sandy grassland and heathland communities. A significant reduction in the coverage of *Calamagrostis* by over 80 % was found on grazed plots in *Calamagrostis* stands after seven years of grazing, while low coverages between 0.2 and 1.5 % remained in grazed sandy grasslands, heaths and mosaics. De Bonte *et al.* (1999) and Cosyns *et al.* (2001) found similar effects of mixed cattle and horse grazing or only horse grazing, respectively, within coastal dunes. Horses are known to browse *Calamagrostis* more frequently than cattle (de Bonte *et al.* 1999). In addition, previous studies showed

that *Calamagrostis* could also be reduced due to summer donkey and sheep grazing within sandy grasslands (Stroh *et al.* 2002; Schwabe, Süss & Storm 2013) as well as due to seasonally cattle grazing within fens (Williams, Wells & Wells 1974) and mesic semi-natural grasslands (Pykälä 2003).

On ungrazed plots, *Calamagrostis* coverage increased between 2008 and 2015 within each of the investigated vegetation types. *Calamagrostis* cover also increased or did not change on abandoned sites in other sandy grasslands (Süss *et al.* 2004; Schwabe, Süss & Storm. 2013). However, *Calamagrostis* may disappear spontaneously after 40 to 50 years in secondary grasslands such as former vineyards, where a significant decrease was already visible after seven years without management (Házi *et al.* 2011). In our study site, aerial photographs from the time immediately after abandonment of military use in 1992 indicated a lower proportion of tall grass vegetation compared to 2008 (own unpubl. data). Thus, a steady increase of *Calamagrostis* can be assumed since abandonment.

Developments in *Calamagrostis* cover on grazed and ungrazed macroplots corresponded to the above-mentioned plot-level observations and thus substantiate our results. Like on the plot-level, the highest reduction of *Calamagrostis* cover, by over 75 %, was observed in *Calamagrostis* stands after seven years of grazing, while abandoned sites showed still high proportions of over 40 % in 2015. In addition, our investigations on the macroplot-level helped to evaluate the overall improvement of the conservation status of habitat types according to Schuboth & Frank (2010) (see also the next section). These evaluation procedures are not feasible on small-scale plots. Therefore, in the monitoring procedures of Schuboth & Frank (2010), a similar plot size of 1 ha was chosen.

Vegetation structure

Under the influence of year-round mixed grazing, a more diversely structured vegetation developed over time in comparison to monospecific grazing, caused by the selective feeding preferences of the animal breeds (Olff *et al.* 1999; Adler, Raff & Lauenroth 2001). While horses are known to graze very selectively and closely to the ground (Lamoot, Meert & Hoffmann 2005; Köhler, Hiller & Tischew 2016), cattle are less selective since they wrap the forage with their tongue and graze most effective at a sward height of at least 15 cm (Jerrentrup *et al*. 2015; Tóth *et al*. 2016). Accordingly, both animal

complement each other in their grazing behaviour, thus increasing the biodiversity of both plant and animal species (Loucougaray, Bonis & Bouzillé 2004). While litter cover and thickness significantly decreased, plots characterised by short vegetation and bare soil increased. Patches of bare soil are characteristic for dry grasslands and heaths as a result of the trampling and wallowing of the grazers, enhancing the probability for the regeneration and colonization of low-competitive species (Newton *et al.* 2009). After seven years of grazing, the coverage of bare soil was up to seven times higher than on ungrazed plots. Especially for pioneer species such as *Calluna vulgaris*, as well as for low-competitive species such as *Aira caryophyllea*, the exposure of bare soil and the simultaneous reduction of interspecific competition are crucial (Stroh *et al.* 2002; Henning *et al.* 2017). Our study showed that the average litter layer thickness was significantly reduced on grazed macroplots across all vegetation types, while it significantly increased on ungrazed plots. The strongest change in litter thickness was observed in *Calamagrostis* stands, indicated by a reduction of more than 70 % (to 0.6 cm) on grazed plots in 2015, but nearly a doubling of the litter layer thickness in ungrazed plots (to 7.0 cm). While a low to medium litter layer can promote seedling recruitment in dry grassland habitats, thick litter layers of more than 4 cm thickness can inhibit seedling recruitment (Grubb 1977; Loydi *et al.* 2013). Moreover, a reduction of the vegetation height, as well as the reduction of the tall grass *Calamagrostis* (see above), enhances light availability to the ground (Ausden *et al.* 2005, Schwabe, Süss & Storm 2013) and thus reduces the intensity of competition for light. Hence, light- and bare soil demanding species such as *Aira caryophyllea*, *Helichrysum arenarium*, and *Dianthus deltoides* were facilitated on grazed sites, which is in accordance with (Kooijman & Smit 2001; Schwabe, Süss & Storm 2013). Contrary to Rupprecht, Gilhuas & Hölzel (2016), cryptogam cover was significantly reduced after seven years of grazing in comparison to ungrazed plots. Cryptogam cover mainly consisted of mosses, while lichens were already rare before grazing started. Lake, Bullock & Hartley (2001) and Newton *et al.* (2009, review) in turn found a grazing-dependent increase in the cover of mosses, especially under low-intensity grazing.

Furthermore, grazing led to an increase in herb cover from 21.9 % to 32.7 % and a decrease in grasses from 52.9 % to 37.9 %, which is in agreement with Köhler, Hiller & Tischew (2016) for year-round horse grazing in dry calcareous grasslands as well as with Süss & Schwabe (2007) for summer sheep

and donkey grazing. Donkeys as well as horses are known for their graminoid foraging (Cosyns *et al.* 2001; Lamoot, Meert & Hoffmann 2005), thus they successfully reduce grass encroachment in grasslands (Catorci, Gatti & Cesaretti 2012) and heathlands (Lake, Bullock & Hartley 2001). Contrary to our findings, Rupprecht, Gilhaus & Hölzel (2016) and Bokdam & Gleichman (2000) found no decrease in grass cover on cattle and horse grazed or on exclusively cattle grazed sites compared to ungrazed sites, which is probably related to the less nutrient-rich conditions of our study site. In addition, our year-round grazing approach led to complete biomass removal at the end of the winter period, even under the relatively low stocking rate of 0.2 livestock units' ha^{-1}, which also supported the reduction of grasses and litter layer.

We also found a significantly lower cover of ruderal indicators on grazed than on ungrazed macroplots in 2015. This is in accordance with other studies of grazed dry habitats (Socher *et al.* 2012; Köhler, Hiller & Tischew 2016), while Rupprecht, Gilhaus & Hölzel (2016) as well as Sýkora *et al.* (2009) found an increase in the cover of ruderal species in other vegetation types on year-round grazed sites. The latter results might also be related with a higher nutrient status and/or less complete biomass removal on these sits, probably due to insufficient grazing intensity. A remarkable reduction in the cover of ruderal indicators was observed in grazed *Calamagrostis* stands, where the cover decreased from 17.3 % to 3.0 % between 2008 and 2015.

Calluna cover distinctly decreased on ungrazed and marginally on grazed heath macroplots with time, but increased from 36.3 % to 45.0 % in grazed mosaics. It is generally assumed that low-intensity grazing enhances the coverage of *Calluna* (Welch & Scott 1995; Critchley *et al.* 2013). However, long-term abandonment led to heavy degenerate *Calluna* stands, a lack of generative rejuvenation and a die-back of this species in heaths at the beginning of our experiment (Henning *et al.* 2017). During the first study years, these degenerate *Calluna* stands were largely neglected by the grazing animals (own unpubl. data) due to the high proportion of woody biomass (Gimingham 1972) and thus lower fodder quality (Pywell *et al.* 1995). Additional management measures, such as mowing, are suitable to facilitate the vegetative rejuvenation of *Calluna*, whereby the re-growth of young shoots subsequently improves the fodder quality of *Calluna* and thereby its attractiveness for grazing animals (Webb 1998). In areas in which grazing was complemented by a one-time mowing regime, the high

proportion of woody biomass was reduced. Consequently, grazing intensity was enhanced after the application of the one-time mowing, resulting in an increase in *Calluna* rejuvenation (Henning *et al.* 2017; own unpubl. data). However, this mowing treatment was not implemented on the plots investigated in the present study, and explains the different findings by Henning *et al.* (2017).

Tree and shrub encroachment is a common problem concerning low-intensity (year-round) grazed grasslands and heathlands (Miles 1981; Cornelissen & Vulink 2001). Manual shrub cutting is not necessary if the overall degree of initial cover of woody species is less than 15 % (Köhler, Hiller & Tischew 2016). In this case, further shrub encroachment is limited due to winter browsing. However, if the overall initial cover of woody species is as high as it was in our case, manual shrub cutting is crucial to counter regrowth of woody species and thus maintain the open site character. Cattle and horses were not able to successfully counteract the regrowth of woody species, as shown by Bokdam & Gleichman (2002) for year-round cattle grazing in Atlantic heaths with less initial cover of woody species. Nevertheless, we found no increase of woody species < 0.5 m on grazed macroplots, indicating a gradual decrease of woody species regrowth as well as increased browsing of the grazing animals (grazed plots) and wild herbivores such as roe deer and rabbits (ungrazed plots). However, further research is needed on long-term browsing effects at sites with initially high woody plant cover.

Species richness

Our study showed that year-round low-intensity grazing with cattle and horses led to a significant increase in total species number and species richness across and within vegetation types over time. An increase in species richness by low-intensity grazing of dry grasslands and heathlands was also described by Bokdam & Gleichman (2000) and Kohyani *et al.* (2008). In addition, Török *et al.* (2016b) recommend a low- to medium-intensity cattle grazing to maintain a high cover of target species and high species diversity in dry low-productive grasslands. On the contrary, some authors reported negative impacts of large herbivore grazing on species richness and species composition on low productive sites (Olff & Ritchie 1998; Bakker *et al.* 2006). In our study, target species and subordinated target species were significantly favoured by the grazing regime as shown for year-round grazing in dry calcareous grasslands (Köhler, Hiller & Tischew. 2016). Most species of dry, sandy

grassland and heathland communities are adapted to nutrient-poor site conditions (Bobbink *et al.* 1998; Bobbink *et al.* 2010), whereby grazing has been reported to decrease soil nutrient levels (Marrs 1993). Thus, we found a significant increase in N 1-3 and N 4-5 species (Ellenberg *et al.* 2001) after seven years of grazing, while no changes could be detected on ungrazed sites. In contrast, species associated with high nutrient values did not increase on grazed plots. In addition, the number of ruderal species only slightly increased on grazed sites by an average of one species to 3.5 species. Contrary to our results, Rupprecht, Gilhaus & Hölzel (2016) and Sýkora *et al.* (2009) found a stronger increase in ruderal species on grazed sites, probably due to insufficient grazing intensity and/or more nutrient-rich sites in the latter study.

Abandonment often leads to the development of species-poor, grass-dominated plant communities (Prach & Pysek 2001; Somodi, Virágh & Podani 2008). However, after seven years of grazing of *Calamagrostis* stands, the species number has doubled (from 17.3 to 37.0), obviously due to the increase in bare soil and the considerable decrease of *Calamagrostis* cover and litter layer, with especially target species, such as *Helichrysum arenarium*, *Peucedanum oreoselinum*, *Dianthus deltoides*, and subordinated target species such as *Euphrasia stricta*, *Jasione montana*, *Erigeron acris* and *Cerastium glutinosum*, re-establishing in the study area. Most of the immigrated species have low to moderate N-values. In this context, grazing has been reported to be beneficial to species preferring low soil nutrient conditions (Moog *et al.* 2002; Pykälä 2005). In addition, the number of species with low N-values may be useful to evaluate the restoration success. Thus, grazed *Calamagrostis* stands developed towards the target habitat type sandy grasslands. In this context, grazing animals obviously serve as vectors for seed dispersal by their hooves, fur and dung (Olff & Ritchie 1998; Ozinga *et al.* 2009). However, it is necessary that seed sources or a sufficient soil seed-bank are still present on the site, otherwise the addition of seeds is a key factor in the restoration of long-abandoned sandy grassland and heathland communities (Bossuyt & Hermy 2003). Furthermore, sandy grasslands and mosaics benefited from the grazing regime by an increase of target species and subordinated target species over time, which agrees with the findings of Schwabe, Süss & Storm (2013) and Freund *et al.* (2014) in sandy grassland ecosystems.

The average lower total species number in heaths compared to sandy grasslands and mosaics is related to a reduced availability of suitable safe sites for species establishment, due to the high and dense vegetation structure of degenerate *Calluna* stands (Henning, von Oheimb & Tischew 2015; Henning *et al.* 2017). In addition, the phytotoxic effects of *Calluna* litter can inhibit species germination (Gimingham 1972). However, both the total number of species and dry mesophilic grassland species significantly increased on grazed heaths between 2008 and 2015, in which *Campanula patula*, *Achillea millefoilum*, and *Plantaga lanceolata* were able to re-colonize. In general, grazing benefitted creeping and rosette-forming species (e.g. *Plantago lanceolata*, *Hypochaeris radicata* or *Hierarcium umbellatum*), which is in accordance with several studies (Loucougaray, Bonis & Bouzillé 2004; Gilhaus, Stelzner & Hölzel 2013; Török *et al.* 2014). However, the coverage of dry mesophilic grassland species increased only slightly, from 0.6 to 0.9 %, between 2008 and 2015. In this context, the increase in mesophilic grassland species does not simultaneously imply an increase in the nutrient status of grazed heaths. Thus, species with low N-values significantly increased with grazing time, while species with moderate to high N-values did not significantly increase between 2008 and 2015. Moreover, total soil nitrogen content was still low in 2015, ranging between 0.1 % and 0.5 %. In addition, we found an increase, but not significantly, in target species such as *Luzula pallescens* and *Hypochaeris radicata,* as well as subordinated target species such as *Festuca filiformis, Luzula multiflora* and *Hierarcium umbellatum*. This indicated a grazing induced shift between heaths and sandy grasslands (Olff *et al.* 1999), which could finally lead to a more pronounced mosaic structure over the whole study area and will be the subject of further investigations on our study site.

Assessment of the conservation status

The assessment of the conservation status (CS) of habitat types serves as a suitable basis for the recognition of negative trends of the present management (Dimopoulos, Bergmeier & Fischer 2005). Thus, necessary adaptions in management can be early made, for example changes in the stocking rate or ratio between the animal breeds.

In our study area, current grazing intensity is low with 0.2 livestock units ha^{-1}. However, grazing regime showed an improvement of both the vegetation structure as well as the species richness with

simultaneous reduction of *Calamagrostis* cover in each vegetation type. Grazing in low stocking rates is considered to be proper to mimic natural grazing regimes in grasslands (Gilhaus, Stelzner & Hölzel 2013). Török *et al.* (2016b) found highest functional diversity under low-intensity grazing, while the highest cover of subordinated target species as well as the highest diversity was found under a medium grazing intensity in alkali steppes. Contrary, too high stocking rates could influence species richness negatively as it was shown in many other studies (e.g. Batáry, Báldi & Erdös 2007; Ambarlı & Bilgin 2014). Therefore, a constant monitoring is needed to track trends and changes in the CS of habitat types (Bergmeier & Fischer 2006), whereby the assessment of the CS can be performed in a few representative sites from which a generalization of the conservation status in the entire study area is possible. Thus, it is useful to use permanently marked plots for the assessment of CS (Dimopoulos, Bergmeier & Fischer 2005), since changes in the cover or expansion of impairments such as highly competitive grasses, ruderal species or shrubs can be determined exactly after a defined period of time in contrast to unmarked areas.

Due to our applied grazing regime, the local conservation status (CS) of habitat types has changed with grazing time. Compared to ungrazed sites, habitat structure and species inventory improved from the value category C to B, while impairments decreased in sandy grasslands. Thus, the formerly bad CS of dry sandy grasslands has improved after seven years of grazing. Moreover, *Calamagrostis* stands have developed towards the target habitat type sandy grasslands, since we found five characteristic and one typical species of that habitat type and a considerable reduction in impairments. After seven years of grazing, they can be classified as sandy grasslands with a total CS of C. We expect a further improvement of *Calamagrostis* stands with grazing time, since shifts in species composition as well as general in plant communities are slow (Lorenz *et al.* 2013).

Although we found more characteristic species and less impairments on grazed than on ungrazed heaths and thus an improvement from the value category B to A, the overall local conservation status did not change over time and was still classified as B after seven years of grazing. This is due to the fact that the habitat structure is still bad, since the rejuvenation of *Calluna* is progressing only slowly and the cover of *Calluna* individuals in the degenerate phase is still over 70 %. To facilitate vegetative as well as generative *Calluna* rejuvenation, additional management measures such as a one-time

mowing management can be applied (see above; e.g. Webb 1998; Henning *et al.* 2017). However, all four *Calluna* phases were present on grazed sites and the coverage of bare soil was higher than on abandoned sites, which underline the steady improvement of the habitat type.

Since there are no guidelines for the assessment of the CS of mosaics, we used indicators and thresholds of both sandy grasslands and heaths (Table S3). The CS improved from a bad to a good CS (value B) after seven years of grazing. Habitat structure improved from the value category C to B in grazed mosaics, since we found a coverage of 27 % of grasses typical for sandy grasslands, and all four *Calluna* phases with less than 70 % of the degenerate phase. In addition, coverage of shrubs and trees, tall grasses (i.e. *Calamagrostis*) and ruderal species decreased with grazing time, thereby improving the value category of impairments from C to B.

Conclusions

Our study revealed that year-round low-intensity cattle and horse grazing is a suitable management tool to restore semi-open and species-rich sandy grassland and heathland communities, and thus to enhance the local conservation status of habitat types of community interest. Grazing improved both the vegetation structure and the overall species richness through the (re-)establishment of target species and subordinated target species with low N-values, which in turn was related to a concomitant successful reduction of *Calamagrostis* cover. In addition, the maintenance costs of year-round grazing systems are low and can be covered by agri-environment schemes, making grazing management economically sustainable for the land user.

However, *Calluna* cover slightly decreased within the heath sites in spite of grazing, indicating a further die-back and a lack of successful rejuvenation of this key species (Henning *et al.* 2017). Furthermore, the cover of degenerate *Calluna* within heaths is still high with over 70 % after seven years of grazing. Thus, combining grazing with other management measures that foster *Calluna* rejuvenation should be considered (e.g. a temporally and locally higher grazing pressure induced by a one-time mowing regime, Henning *et al.* 2017). In addition, manual shrub cutting should be taken into account if the initial cover of woody species (> 0.5 m) is as high as it was at our study site. However,

further research is needed to determine the long-term effects of cattle and horse browsing in initially highly encroached heaths and sandy grasslands as well as the effects of year-round grazing on highly competitive, invasive alien species, such as *Prunus serotina*. In addition, low-intensity, year-round grazing management with cattle and horses should be transferred to other dry sandy grasslands and heathlands within the Continental biogeographical region to verify our results.

Acknowledgements

Appendix A. Supplementary data

Table S1: List of 160 higher plant species recorded during the study period 2008 to 2015 on permanent plots (25 m²).

Table S2: Mean values (± SE) of species richness and structural parameters for grazed (G) and ungrazed (UG) plots and macroplots per vegetation type in 2015.

Table S3: Indicators and thresholds for the assessment of the local conservation status (CS) of the habitat type *6120 ("Xeric sand calcareous grasslands"), 4030 ("European dry heaths") and *6120 / 4030 (mosaics of dry sandy grasslands and heaths) in Germany.

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Appendix A. Supplementary data

Table S1: List of 160 higher plant species recorded during the study period 2008 to 2015 on permanent plots (25 m²). Species allocation to an ecological group is indicated by an "x". Target species and subordinated target species are assigned to sandy grassland species (SG) and heath species (H). N-values according to Ellenberg *et al.* (2001), Ind. = indifferent species.

	Target species	Subordinated target species	Dry mesophilic grassland species	Ruderal species	Other species	N-value
Red list species						
Aira caryophyllea	x					1
Botrychium lunaria	x					2
Botrychium matricariifolium	x					2
Carex ericetorum	x					2
Luzula pallescens	x					2
Pilosella caespitosa	x					3
Pilosella setigera	x					1
Vicia cassubica	x					3
Viola rupestris	x					2
Species with phytosociological affiliation to						
Achillea millefolium agg.			x			5
Achillea ptarmica					x	2
Acinos arvensis		SG				1
Agrostis capillaris	H					4
Agrostis vinealis		SG, H				1
Ajuga genevensis		SG, H				2
Allium oleraceum		SG				4
Anthericum ramosum		SG, H				3
Anthoxanthum odoratum	H					Ind.
Anthyllis vulneraria		SG				2
Arabidopsis thaliana		SG, H				4
Arabis hirsuta		SG				Ind.
Arenaria serpyllifolia		SG, H				Ind.
Armeria maritima subsp. Elongata	SG					2
Arrhenatherum elatius			x			7
Betula pendula					x	Ind.
Brachypodium pinnatum		SG				4
Calamagrostis epigejos				x		6
Calluna vulgaris	H					1
Campanula patula			x			5
Campanula rotundifolia		SG, H				2
Carex acutiformis					x	5
Carex caryophyllea		SG, H				2
Carex hirta					x	5

	Target species	Subordinated target species	Dry mesophilic grassland species	Ruderal species	Other species	N-value
Carex leporina		H				3
Carex pairae				x		6
Carex pilulifera	H					3
Carlina vulgaris		SG				2
Centaurea jacea		SG, H				Ind.
Centaurium erythraea		SG, H				6
Cerastium arvense		SG				4
Cerastium glutinosum		SG				2
Cerastium holosteoides			x			5
Cerastium semidecandrum		SG, H				Ind.
Cirsium arvense				x		7
Cirsium vulgare				x		8
Conyza canadensis				x		5
Crataegus agg.					x	Ind.
Dactylis glomerata			x			6
Danthonia decumbens	H					2
Daucus carota			x			4
Deschampsia flexuosa	H					3
Dianthus deltoides	SG					2
Draba verna		SG				2
Echium vulgare				x		4
Elymus repens				x		7
Epilobium angustifolium				x		8
Erigeron acris		SG				2
Euphorbia cyparissias	H					3
Euphorbia esula			x			Ind.
Euphorbia stricta					x	7
Euphrasia stricta		SG				2
Festuca brevipila	SG					2
Festuca filiformis		H				2
Festuca ovina	H					1
Festuca rubra			x			Ind.
Fragaria vesca				x		6
Fragaria viridis		SG, H				3
Galium album			x			Ind.
Galium boreale					x	2
Galium pumilum		H				2
Galium verum	SG					3
Galium x pomeranicum			x			Ind.
Genista tinctoria		SG, H				1
Helichrysum arenarium	SG					1
Helictotrichon pubescens		SG				4
Herniaria glabra		SG, H				Ind.
Hieracium lachenalii		H				2
Hieracium umbellatum		SG, H				2

	Target species	Subordinated target species	Dry mesophilic grassland species	Ruderal species	Other species	N-value
Holcus lanatus			x			5
Holcus mollis					x	3
Holosteum umbellatum		SG				Ind.
Hypericum perforatum	H					4
Hypochaeris radicata	H					3
Jasione montana		SG, H				2
Juncus conglomeratus					x	3
Juncus effusus					x	4
Koeleria macrantha	SG					2
Lathyrus pratensis			x			6
Lepidium campestre				x		6
Leucanthemum vulgare agg.			x			Ind.
Linaria vulgaris				x		5
Linum catharticum		SG, H				2
Lotus corniculatus		SG, H				3
Lotus pedunculatus					x	4
Luzula campestris	H					3
Luzula multiflora		SG, H				3
Lysimachia nummularia				x		Ind.
Moehringia trinervia				x		7
Molinia caerulea					x	2
Myosotis ramosissima		SG, H				1
Petrorhagia prolifera		SG				2
Peucedanum oreoselinum	SG					2
Pilosella officinarum	H					2
Pilosella piloselloides					x	2
Pimpinella saxifraga		SG, H				4
Pinus sylvestris					x	Ind.
Plantago lanceolata			x			Ind.
Plantago major				x		Ind.
Poa angustifolia		SG, H				3
Poa compressa		SG, H				3
Poa pratensis			x			6
Polygala vulgaris		SG, H				2
Populus tremula					x	Ind.
Potentilla argentea		SG, H				1
Potentilla cinerea subsp. Incana		SG, H				1
Potentilla heptaphylla		SG, H				2
Potentilla neumanniana		SG, H				2
Potentilla recta		SG				2
Potentilla reptans				x		5
Prunus serotina					x	Ind.
Pteridium aquilinum subsp. Pinetorum					x	Ind.
Quercus robur					x	Ind.
Rosa canina agg.					x	Ind.

	Target species	Subordinated target species	Dry mesophilic grassland species	Ruderal species	Other species	N-value
Rumex acetosa		SG, H				6
Rumex acetosella	H					2
Rumex thyrsiflorus					x	4
Salix caprea					x	7
Salix cinerea					x	4
Salix viminalis					x	Ind.
Saxifraga granulata		SG				3
Scleranthus polycarpos		SG				1
Senecio jacobaea				x		5
Spergularia rubra					x	4
Tanacetum vulgare				x		5
Taraxacum sect. Erythrosperma		SG, H				2
Taraxacum sect. Ruderalia			x			8
Thymus pulegioides		SG, H				1
Tragopogon dubius			x			4
Tragopogon minor				x		Ind.
Tragopogon orientalis			x			6
Tragopogon pratensis			x			Ind.
Trifolium alpestre					x	3
Trifolium arvense		SG, H				1
Trifolium campestre		SG, H				3
Trifolium dubium		SG				4
Trifolium pratense			x			Ind.
Trifolium repens			x			6
Turritis glabra				x		5
Valeriana officinalis					x	5
Verbascum lychnitis		SG, H				3
Veronica arvensis				x		Ind.
Veronica chamaedrys			x			Ind.
Veronica officinalis		SG, H				4
Vicia angustifolia					x	Ind.
Vicia hirsuta				x		4
Vicia tetrasperma				x		5
Viola arvensis				x		Ind.
Viola canina		SG, H				2
Viola riviniana					x	Ind.
Viola tricolor				x		Ind.

Table S2: Mean values (± SE) of species richness and structural parameters for grazed (G) and ungrazed (UG) plots and macroplots per vegetation type in 2015, seven years after the start of the experiment. Differences between grazing managements were determined by t-tests. X > Y indicates that the respective dependent variable was significantly greater under management X than under Y. Significant differences are marked as follows: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

		P-value	Grazed	Ungrazed	
			$n = 3$	$n = 3$	
Plot-level (25 m²)					
<u>Dry sandy grasslands</u>					
Calamagrostis epigejos (%)		0.050	0.23 ± 0.150	17.50 ± 6.29	
Species richness					
Total species number		0.215	46.33 ± 4.41	39.33 ± 1.76	
Target species		0.431	12.67 ± 1.86	10.67 ± 1.33	
Subordinated target species		0.433	18.67 ± 3.18	15.67 ± 1.33	
Dry mesophilic grassland species		0.574	6.67 ± 2.67	5.00 ± 0.57	
Ruderal species		0.292	4.33 ± 1.20	2.67 ± 0.67	
Other species		0.731	4.00 ± 1.73	5.33 ± 3.18	
Ellenberg N-values					
N 1-3		0.642	24.33 ± 2.91	22.33 ± 2.73	
N 4-5		0.386	10.33 ± 2.96	7.00 ± 1.73	
N 6-9		0.288	5.00 ± 1.53	3.00 ± 0.58	
<u>Heaths</u>					
Calamagrostis epigejos (%)		0.197	1.50 ± 0.50	2.67 ± 0.67	
Species richness					
Total species number		0.337	29.33 ± 2.40	23.00 ± 5.29	
Target species		0.081	9.00 ± 0.58	6.00 ± 1.15	
Subordinated target species		0.393	11.67 ± 2.73	7.00 ± 4.04	
Dry mesophilic grassland species		0.124	4.33 ± 0.33	2.00 ± 1.15	
Ruderal species		0.101	2.33 ± 0.33	3.33 ± 0.33	
Other species		0.163	2.00 ± 1.00	4.67 ± 1.20	
Ellenberg N-values					
N 1-3		0.239	16.67 ± 2.19	11.00 ± 3.47	
N 4-5		0.279	4.67 ± 0.67	3.00 ± 1.16	
N 6-9		0.288	3.00 ± 0.58	4.00 ± 0.58	
<u>Mosaics</u>					
Calamagrostis epigejos (%)		0.060	1.00 ± 0.50	5.33 ± 2.40	
Species richness					
Total species number	*	0.019	40.67 ± 2.05	30.83 ± 1.59	G > UG
Target species		0.238	11.67 ± 0.33	10.00 ± 1.15	
Subordinated target species	*	0.014	18.33 ± 0.73	11.83 ± 1.36	G > UG
Dry mesophilic grassland species		0.152	5.33 ± 0.88	3.67 ± 0.33	
Ruderal species		0.579	2.67 ± 0.67	3.33 ± 0.88	
Other species		0.561	2.67 ± 0.88	2.00 ± 0.57	

		P-value	Grazed	Ungrazed	
			n = 3	*n* = 3	
Ellenberg N-values					
N 1-3	*	0.020	25.33 ± 0.67	17.33 ± 2.03	G > UG
N 4-5		0.196	8.00 ± 1.16	6.00 ± 0.58	
N 6-9		0.621	3.33 ± 0.88	2.67 ± 0.88	
Calamagrostis stands					
Calamagrostis epigejos (%)	*	0.034	2.00 ± 0.00	53.33 ± 13.33	UG > G
Species richness					
Total species number		0.131	37.00 ± 3.61	22.50 ± 6.75	
Target species		0.060	9.67 ± 1.86	4.33 ± 0.88	
Subordinated target species		0.078	14.33 ± 0.67	6.50 ± 3.25	
Dry mesophilic grassland species		0.205	5.00 ± 0.58	3.67 ± 0.67	
Ruderal species		0.877	4.67 ± 0.33	5.00 ± 2.00	
Other species		0.859	3.33 ± 0.88	3.00 ± 1.53	
Ellenberg N-values					
N 1-3		0.118	19.67 ± 3.38	10.00 ± 3.51	
N 4-5		0.051	8.00 ± 0.00	4.33 ± 1.33	
N 6-9		0.251	4.33 ± 0.67	3.33 ± 0.33	
Macroplot-level (1 ha)					
Dry sandy grasslands					
Calamagrostis epigejos (%)	**	0.002	0.92 ± 0.40	24.25 ± 6.63	UG > G
Vegetation structure					
Bare soil (%)	*	0.023	4.21 ± 0.90	0.77 ± 0.34	G > UG
Cryptogams (%)	*	0.043	39.17 ± 9.61	67.50 ± 1.44	UG > G
Litter layer (%)	*	0.037	43.50 ± 5.30	71.50 ± 7.38	UG > G
Height of field layer (cm)	*	0.034	14.92 ± 3.44	38.33 ± 6.51	UG > G
Thickness of litter layer (cm)	*	0.024	0.43 ± 0.04	2.38 ± 1.10	UG > G
Grasses (%)	***	0.000	41.25 ± 1.25	59.17 ± 0.83	UG > G
Herbs (%)		0.288	49.58 ± 1.50	36.17 ± 10.86	
Calluna vulgaris (%)		0.950	2.10 ± 1.05	2.20 ± 1.04	
Ruderal indicators	*	0.016	0.23 ± 0.09	7.15 ± 3.84	UG > G
Woody species < 0.5 m (%)		0.326	0.13 ± 0.06	0.44 ± 0.28	
Heaths					
Calamagrostis epigejos (%)		0.154	17.58 ± 10.68	39.50 ± 8.20	
Vegetation structure					
Bare soil (%)	*	0.010	3.83 ± 0.72	0.43 ± 0.14	G > UG
Cryptogams (%)	**	0.002	27.50 ± 1.25	69.60 ± 5.79	UG > G
Litter layer (%)		0.239	24.33 ± 13.72	44.42 ± 10.37	
Height of field layer (cm)	*	0.011	33.33 ± 6.14	61.25 ± 0.72	UG > G
Thickness of litter layer (cm)		0.078	0.80 ± 0.16	2.92 ± 0.96	
Grasses (%)		0.488	34.00 ± 17.17	49.33 ± 10.44	
Herbs (%)		0.151	10.50 ± 3.84	3.63 ± 0.51	
Calluna vulgaris (%)		0.790	50.92 ± 23.66	43.75 ± 8.75	
Ruderal indicators		0.771	1.19 ± 0.72	1.57 ± 0.97	
Woody species < 0.5 m (%)		0.343	1.83 ± 0.83	0.871 ± 0.34	

		P-value	Grazed	Ungrazed	
			n = 3	n = 3	
<u>Mosaics</u>					
Calamagrostis epigejos (%)	*	0.014	2.90 ± 1.43	27.67 ± 7.65	UG > G
Vegetation structure					
Bare soil (%)		0.088	3.000 ± 1.00	0.70 ± 0.22	
Cryptogams (%)		0.051	50.83 ± 7.95	75.83 ± 4.41	
Litter layer (%)		0.109	29.58 ± 5.12	50.83 ± 9.02	
Height of field layer (cm)	**	0.002	30.00 ± 3.31	56.67 ± 1.10	UG > G
Thickness of litter layer (cm)	*	0.033	0.48 ± 0.08	1.75 ± 0.63	UG > G
Grasses (%)		0.075	33.50 ± 8.98	59.58 ± 6.14	
Herbs (%)		0.691	25.17 ± 4.56	28.75 ± 7.04	
Calluna vulgaris (%)		0.149	45.00 ± 9.21	22.25 ± 8.80	
Ruderal indicators	*	0.047	2.05 ± 0.98	15.42 ± 8.54	UG > G
Woody species < 0.5 m (%)		0.720	0.71 ± 0.08	0.66 ± 0.15	
<u>*Calamagrostis* stands</u>					
Calamagrostis epigejos (%)		0.102	12.63 ± 9.67	42.63 ± 14.01	
Vegetation structure					
Bare soil (%)	**	0.009	3.04 ± 0.58	0.20 ± 0.11	G > UG
Cryptogams (%)	**	0.001	41.63 ± 2.94	77.08 ± 3.41	UG > G
Litter layer (%)		0.083	48.33 ± 9.85	84.33 ± 12.17	
Height of field layer (cm)	*	0.039	21.50 ± 2.16	56.67 ± 11.46	UG > G
Thickness of litter layer (cm)	*	0.012	0.63 ± 0.14	7.04 ± 2.51	UG > G
Grasses (%)	*	0.018	42.92 ± 6.55	77.08 ± 5.83	UG > G
Herbs (%)		0.051	45.42 ± 4.81	14.58 ± 10.09	
Calluna vulgaris (%)		0.835	1.62 ± 1.02	2.04 ± 1.57	
Ruderal indicators		0.564	3.01 ± 1.14	4.03 ± 1.14	
Woody species < 0.5 m (%)		0.827	0.13 ± 0.05	0.15 ± 0.05	

Table S3: Indicators and thresholds for the assessment of the local conservation status (CS) of the habitat type *6120 ("Xeric sand calcareous grasslands"), 4030 ("European dry heaths") and *6120 / 4030 (mosaics of dry sandy grasslands and heaths) in Germany (Schuboth & Frank 2010).

Indicator	Good local CS		Bad local CS
	A – Excellent CS	B – Good CS	C – Moderate to low CS
Habitat type *6120			
Habitat structure	excellent characteristic	good characteristic	moderate to low characteristic
Cover of typical grasses [1]	> 50 %	25-50 %	< 25 %
Cover of bare soil	> 10 %	5-10 %	< 5 %
Species inventory	fully represented	largely represented	partly represented
Presence of characteristic species [2]	At least 6 characteristic species, 3 of them typical for that habitat type	At least 4 characteristic species, 2 of them typical for that habitat type	At least 1 species that is typical for that habitat type
Impairments	low	moderate	strong
Cover of shrubs and trees	0 %	< 10 %	10-70 %
Cover of tall grasses [3]	< 1 %	< 10 %	≥ 10 %
Cover of ruderal species [4]	< 1 %	< 10 %	≥ 10 %
Cover of invasive alien species [5]	0 %	1-2 %	> 2 %
Disturbances due to excessive use	No	Not substantial	Substantial
Habitat type 4030			
Habitat structure	excellent characteristic	good characteristic	moderate to low characteristic
Cover of *Calluna*	≥ 30 %	≥ 30 %	≥ 30 %
Age structure of *Calluna* [6]	All phases present and cover of degenerate phase is < 50 %	Not all phases present or cover of degenerate phase is between 50-70 %	Cover of degenerate phase is > 70 %
Cover of bare soil	> 10 %	5-10 %	< 5 %
Species inventory	fully represented	largely represented	partly represented
Presence of characteristic species [2]	*Calluna* and at least 8 characteristic species	*Calluna* and at least 5 characteristic species	*Calluna* and at least 1 characteristic species
Impairments	low	moderate	strong
Cover of shrubs and trees	< 10 %	10-30 %	> 30-70 %
Cover of tall grasses [3]	< 10 %	10-30 %	> 30-70 %
Cover of ruderal species [4]	< 10 %	10-30 %	> 30-70 %
Cover of invasive alien species [5]	0 %	≤ 10 %	> 10 %

Indicator	Good local CS		Bad local CS
	A – Excellent CS	B – Good CS	C – Moderate to low CS
Habitat type *6120 / 4030			
Habitat structure	excellent characteristic	good characteristic	moderate to low characteristic
Cover of typical grasses [1]	> 50 %	25-50 %	< 25 %
Cover of *Calluna*	< 30 %	< 30 %	< 30 %
Age structure of *Calluna* [6]	All phases present and cover of degenerate phase is < 50 %	Not all phases present or cover of degenerate phase is between 50-70 %	Cover of degenerate phase is > 70 %
Cover of bare soil	> 10 %	5-10 %	< 5 %
Species inventory	fully represented	largely represented	partly represented
Presence of characteristic species [2]	At least 6 characteristic species, 2 of them typical for habitat type *6120; *Calluna* and at least 8 characteristic species of habitat type 4030	At least 4 characteristic species, 2 of them typical for habitat type *6120; *Calluna* and at least 5 characteristic species of habitat type 4030	At least 1 species that is typical for habitat type *6120; *Calluna* and at least 1 characteristic species of habitat type 4030
Impairments	low	moderate	strong
Cover of shrubs and trees	0 %	< 10 %	10-70 %
Cover of tall grasses [3]	< 1 %	< 10 %	≥ 10 %
Cover of ruderal species [4]	< 1 %	< 10 %	≥ 10 %
Cover of invasive alien species [5]	0 %	1-2 %	> 2 %

[1] Typical grasses include: *Festuca brevipila, Festuca psammophila, Festuca polesica, Koeleria glauca, Koeleria macrantha*

[2] Characteristic and typical species of habitat type *6120 (typical species are underlined): *Alyssum montanum, Armeria elongata*, *Asperula cynanchica*, *Carex ligerica, Carex praecox, Centaurea stoebe, Chondrilla juncea, Dianthus deltoides, Festuca brevipila*, *Festuca polesica*, *Festuca psammophila*, *Galium verum, Helichrysum arenarium*, *Jurinea cyanoides*, *Koeleria glauca*, *Koeleria macrantha*, *Medicago minima*, *Peucedanum oreoselinum*, *Pseudolysimachion spicatum*, *Sedum rupestre*, *Silene otites*, *Thalictrum minus*, *Veronica prostrata*

Characteristic species of habitat type 4030: *Agrostis capillaris, Anthoxanthum odoratum, Calluna vulgaris, Carex pilulifera, Danthonia decumbens, Deschampsia flexuosa, Euphorbia cyparissias, Festuca ovina, Galium saxatile, Genista anglica, Genista pilosa, Helictotrichon pratense, Hieracium pilosella, Hypericum perforatum*, *Hypochaeris radicata, Luzula campestris, Potentilla erecta, Rumex acetosella, Vaccinium myrtillus*

[3] In particular: *Calamagrostis epigejos*

[4] In particular: *Tanacetum vulgare* or high covers of *Hypericum perforatum*

[5] In particular: *Prunus serotina*

[6] *Calluna* phases are: pioneer, building, mature and degenerate phase

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Curriculum vitae

Personal data _____

Name:	Katrin Henning
Address:	Gerwischer Straße 74, 39114 Magdeburg
Date and place of birth:	29.12.1988, Magdeburg
Nationality:	German

Education _____

Since 10/2012	PhD student at the Leuphana University Lüneburg (supported by the German Federal Environmental Foundation, DBU and by a scholarship under the Saxony-Anhalt Graduate Development Programme) Thesis: "Restoration and management of abandoned, dry Continental heathland and sandy grassland communities"
10/2010 – 09/2012	Studies in Nature Conservation and Landscape Planning, Anhalt University of Applied Sciences, Bernburg Master thesis: „Die Frischwiesen (LRT 6510) des Biosphärenreservates „Karstlandschaft Südharz" – Bodenkennwerte, Vegetationszusammensetzung und Futterwert" (Overall grade: 1.1)
10/2007 – 11/2010	Studies in Nature Conservation and Landscape Planning, Anhalt University of Applied Sciences, Bernburg Bachelor thesis: „Status quo einer Grünlandversuchsfläche im Wulfener Bruch – Bodenkennwerte und Vegetation" (Overall grade: 1.5)
08/2001 – 07/2007	Immanuel-Kant-Gymnasium, Magdeburg Graduation: Abitur (Overall grade: 2.4)

Professional experience _____

Since 04/2017	Research associate, Anhalt University of Applied Sciences, Bernburg Project: „Erhalt und Wiederherstellung großflächiger FFH-Offenlandlebensräume in der Oranienbaumer Heide durch extensive Ganzjahresbeweidung und ergänzende Maßnahmen unter besonderer Berücksichtigung der Heidelebensräume"
12/2014 – 09/2015 / 10/2011 – 12/2011	Research associate, Anhalt University of Applied Sciences, Bernburg Project: „Naturschutzfachliche Erfolgskontrolle von Managementmaßnahmen zum Erhalt und zur Entwicklung von FFH-Offenlandlebensräumen im NATURA 2000 Gebiet Mittlere Oranienbaumer Heide"

	Project: „Strategien zur ökologischen Optimierung des Grünlandmanagements für die Lebensraumtypen gemeinschaftlichen Interesses 6440, 6510 und 6520 in Sachsen-Anhalt"
01/2012 – 09/2012 / 02/2011 – 09/2011	Student assistant, Anhalt University of Applied Sciences, Bernburg Project: „Strategien zur ökologischen Optimierung des Grünlandmanagements für die Lebensraumtypen gemeinschaftlichen Interesses 6440, 6510 und 6520 in Sachsen-Anhalt"
11/2009 – 12/2010	Student assistant, Fugro Consult GmbH, Magdeburg

Skills

Language skills	German	native language
	English	very good knowledge in spoken and written
	Russian	good knowledge in spoken and written
	Latin	Latinum

Computer literacy	MS Office (Word, Excel, PowerPoint, Access), SPSS, SigmaPlot, ArcGIS
	R, AutoCAD, PCOrd – basic knowledge

Publications

Henning, K., Lorenz, A., von Oheimb, G., Härdtle, W. & Tischew, S. (2017) Year-round cattle and horse grazing supports the restoration of abandoned, dry sandy grassland and heathland communities by supressing *Calamagrostis epigejos* and enhancing species richness. Journal for Nature Conservation, 40, 120-130.

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Erklärungen und Versicherungen

Hiermit erkläre ich, dass ich mich noch keiner Doktorprüfung unterzogen oder mich um Zulassung zu einer solchen beworben habe.

Ich versichere, dass die Dissertation mit dem Titel „Restoration and management of abandoned, dry Continental heathland and sandy grassland communities" noch keiner Fachvertreterin bzw. Fachvertreter vorgelegen hat, ich die Dissertation nur in diesem und keinem anderen Promotionsverfahren eingereicht habe und, dass diesem Promotionsverfahren keine endgültig gescheiterten Promotionsverfahren vorausgegangen sind.

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Katrin Henning

Magdeburg, den 14. August 2018