



**Managing open habitats for species conservation: the role of wild ungulate grazing, small-scale disturbances, and scale**

**Institut für Biochemie und Biologie**  
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**Managing open habitats for species conservation: the role of  
wild ungulate grazing, small-scale disturbances, and scale**

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## Abstract

During the last decades, the global change of the environment has caused a dramatic loss of habitats and species. In Central Europe, open habitats are particularly affected. Currently, grazing by wild megaherbivores is intensively discussed in nature conservation practice as a tool to manage endangered open habitats. Being a method that is inexpensive and of high public acceptance, management by wild megaherbivores is very likely to be a frequently adopted method in the future. However, there is yet little experimental evidence showing that this method is superior to other management methods. Therefore, the main objective of this thesis was to experimentally test the suitability of wild megaherbivore grazing as a conservation tool to manage open habitats.

We studied the effect of wild ungulates in a 160 ha game preserve in NE Germany in three successional stages (i) *Corynephorus canescens*-dominated grassland, (ii) ruderal tall forb vegetation dominated by *Tanacetum vulgare* and (iii) *Pinus sylvestris*-pioneer forest over three years. In each successional stage, six paired 4 m<sup>2</sup>-monitoring plots of permanently grazed vs. ungrazed plots were arranged in three random blocks, leading to a total number of 18 plots. Removal of grazing was introduced de novo for the study. In each plot, percentage cover of each plant species and mean cover of woody plants was recorded.

Our results demonstrate that wild megaherbivores considerably affected species composition and delayed successional pathways in open habitats. Grazing effects differed considerably between successional stages: species richness was higher in grazed ruderal and pioneer forest plots, but not in the *Corynephorus* sites. Species composition changed significantly in the *Corynephorus* and ruderal sites. Grazed ruderal sites had turned into sites with very short vegetation dominated by *Agrostis* spp. and the moss *Brachythecium albicans*, most species did not flower. Woody plant cover was significantly affected only in the pioneer forest sites. Young pine trees were severely damaged and tree height was considerably reduced, leading to a “*Pinus*-macchie”-appearance.

Ecological patterns and processes are known to vary with spatial scale. Since grazing by megaherbivores has a strong spatial component, the scale of monitoring success of grazing may largely differ among and within different systems. However, the knowledge of the relevant scale would allow choosing appropriate monitoring scales.

Thus, the second aim of this thesis was to test whether grazing effects are consistent over different spatial scales, and to give recommendations for appropriate monitoring scales. For this purpose, we studied grazing effects on plant community structure using multi-scale plots that included three nested spatial scales (0.25 m<sup>2</sup>, 4 m<sup>2</sup>, and 40 m<sup>2</sup>). Percentage of open soil and woody species, and presence-absence data for each plant species was censused at all scales.

Over all vegetation types, the scale of observation directly affected grazing effects on woody plant cover and on floristic similarity, but not on the proportion of open soil and species richness. Grazing effects manifested at small scales regarding floristic similarity in pioneer forest and ruderal sites and regarding species richness in ruderal sites. The direction of scale-effects on similarity differed between vegetation types: Grazing effects on floristic similarity in the *Corynephorus* sites were significantly higher at the medium and large scale, while in the pioneer forest sites they were significantly higher at the smallest scale.

Disturbances, be they natural or artificial, initiate vegetation changes by creating gaps and affecting colonization and extinction rates. The third intention of the thesis was to investigate the effect of small-scale disturbances on the species-level. In a sowing experiment, we studied early establishment probabilities of *Corynephorus canescens*, a key species of open sandy habitats. Applying two different regimes of mechanical ground disturbance (disturbed and undisturbed) in the three successional stages mentioned above, we focused on the interactive effects of small-scale disturbances, successional stage and year-to-year variation.

Disturbance led to higher emergence in a humid and to lower emergence in a very dry year. Apparently, when soil moisture was sufficient, the main factor limiting *C. canescens* establishment was competition, while in the dry year water became the limiting factor. Survival rates were not affected by disturbance. In humid years, *C. canescens* emerged in higher numbers in open successional stages while in the dry year, emergence rates were higher in late stages, suggesting an important role of late successional stages for the persistence of *C. canescens*.

We conclude that wild ungulate grazing is a useful tool to slow down succession and to preserve a species-rich, open landscape, because it does not only create disturbances, thereby supporting early successional stages, but also at the same time efficiently controls woody plant cover. However, wild ungulate grazing considerably changed the

overall appearance of the landscape. Additional measures like shifting exclosures might be necessary to allow vulnerable species to flower and reproduce.

We further conclude that studying grazing impacts on a range of scales is crucial, since different parameters are affected at different spatial scales. Larger scales are suitable for assessing grazing impact on structural parameters like the proportion of open soil or woody plant cover, whereas species richness and floristic similarity are affected at smaller scales. Our results further indicate that small-scale disturbances promote germination of *C. canescens*. The optimal strategy for promoting *C. canescens* is to apply disturbances just before seed dispersal and not during dry years. Further, at the landscape scale, facilitation by late successional species may be an important mechanism for the persistence of protected pioneer species.

## Zusammenfassung

In den letzten Jahrzehnten führte der globale Wandel zu einem drastischen Habitat- und Artenschwund, von dem in Mitteleuropa offene Lebensräume besonders stark betroffen sind. Zu ihrem Erhalt wird gegenwärtig die Beweidung durch Wildtiere intensiv diskutiert. Da es sich um eine kostengünstige Methode handelt, die in der Öffentlichkeit auf hohe Akzeptanz stößt, ist es sehr wahrscheinlich, dass Wildtierbeweidung in Zukunft eine häufig angewandte Methode sein wird. Bisher gibt es jedoch kaum experimentelle Belege dafür, dass die Wildtierbeweidung anderen Managementverfahren überlegen ist. Das Hauptziel dieser Arbeit war es deshalb, experimentell zu untersuchen, ob Wildtierbeweidung eine geeignete Methode für das Offenlandmanagement ist.

Der Einfluss von Wildtieren wurde über drei Jahre in einem 160 ha großen Wildtiergehege im NO Deutschlands in drei Sukzessionsstadien untersucht: (i) *Corynephorus canescens*-dominierte Kurzgrasrasen, (ii) durch *Tanacetum vulgare* dominierte ruderalen Staudenfluren und (iii) *Pinus sylvestris*-Vorwälder. In jedem Sukzessionsstadium wurden sechs gepaarte (beweidete vs. unbeweidete) 4 m<sup>2</sup>-Flächen in drei Blöcken angelegt (insgesamt 18 Flächen). In jeder Fläche wurde die Deckung aller Arten sowie die Gehölzdeckung aufgenommen.

Die Ergebnisse zeigen, dass Wildtiere die Artenzusammensetzung offener Habitats entscheidend beeinflussen und die Sukzession verzögern. Zwischen den Sukzessionsstadien unterschieden sich die Beweidungseffekte deutlich: die Artenzahl war in den beweideten Ruderal- und Vorwaldflächen deutlich höher als in den unbeweideten, nicht jedoch in den *Corynephorus*-Flächen. Die Artenzusammensetzung wurde in den *Corynephorus*- und den Ruderal-Flächen verändert. Ruderal-Flächen entwickelten sich durch die Beweidung zu einem durch *Agrostis* spp. und das Moos *Brachythecium albicans* dominierten Vegetationstyp mit niedriger Vegetationshöhe, in dem die meisten Arten nicht zur Blüte kamen. Die Gehölzdeckung wurde nur in den beweideten Vorwaldflächen signifikant reduziert; junge Kiefern wurden stark geschädigt und in ihrer Wuchshöhe reduziert, was zu einem „*Pinus*-Macchien“-artigen Eindruck führte.

Analyse und Interpretation einer Untersuchung sind abhängig vom Beobachtungsmaßstab. Da die Beweidung durch Megaherbivore eine starke räumliche

Komponente besitzt, kann der geeignete Beobachtungsmaßstab innerhalb und zwischen verschiedenen Systemen variieren. Um eine geeignete Beobachtungsmaßstabsebene auszuwählen, ist es deshalb notwendig, die relevante Beobachtungsskala zu kennen. Daher war das zweite Ziel dieser Arbeit, zu testen, ob Beweidungseffekte über verschiedene räumliche Skalen konsistent sind, sowie Empfehlungen für geeignete Monitoring-Maßstäbe zu geben. Zu diesem Zweck wurde der Effekt von Wildtierbeweidung auf die Vegetation dreier Sukzessionsstadien mittels genesteter Dauerflächen untersucht, die drei verschiedene Flächengrößen umfassten: 0.25 m<sup>2</sup>, 4 m<sup>2</sup>, und 40 m<sup>2</sup>. Auf allen Maßstabsebenen wurden der Anteil offenen Bodens und der Gehölze sowie die Presence-absence-Daten für jede Art erhoben.

Betrachtet man alle Vegetationstypen zusammen, so beeinflusste der Beobachtungsmaßstab den Beweidungseffekt auf die Gehölzdeckung sowie auf die floristische Ähnlichkeit, aber nicht auf den Anteil offenen Bodens und die Artenzahl. Betrachtet man die Vegetationstypen getrennt, so zeigte sich der Beweidungseffekt auf kleinen Skalen in den Vorwaldflächen und den ruderalen Flächen hinsichtlich der Ähnlichkeit und in den ruderalen Flächen hinsichtlich der Artenzahl. Die Richtung der Skaleneffekte auf die floristische Ähnlichkeit unterschied sich zwischen den Vegetationstypen: Während sich beweidete und unbeweidete *Corynephorus*-Flächen auf der mittleren und der großen Skala signifikant voneinander unterschieden, war dies im Kiefernvorwald auf der kleinsten Skala der Fall.

Störungen, natürliche ebenso wie künstliche, führen zu Vegetationsveränderungen, welche die Einwanderungs- und Aussterberaten von Arten beeinflussen. Das dritte Ziel dieser Arbeit war es, den Effekt kleinräumiger Störungen auf der Art-Ebene zu untersuchen sowie deren Interaktion mit dem Sukzessionsstadium und der jährlichen Variabilität. In einem Aussaatexperiment wurde das Etablierungsverhalten von *Corynephorus canescens*, einer Schlüsselart sandiger Offenhabitats, die in allen untersuchten Vegetationstypen vorkommt, in drei Sukzessionsstadien und unter zwei Störungsregimes (gestört vs. ungestört) untersucht.

In einem feuchten Jahr führten Störungen zu höheren Keimraten, in einem trockenen Jahr dagegen zu niedrigeren Keimraten. Solange die Bodenfeuchtigkeit hoch genug war, war Konkurrenz der wichtigste limitierende Faktor für die Etablierung von *C. canescens*, während im trockenen Jahr Wasser zum entscheidenden Faktor wurde. Auf die Überlebensraten hatten Störungen keinen Einfluss.



In feuchten Jahren waren die Keimraten in offenen Sukzessionsstadien höher, während sie im trockenen Jahr im späten Sukzessionsstadium höher waren. Dies ist ein Hinweis darauf, dass spätere Sukzessionsstadien für die Persistenz von *C. canescens* eine wichtige Rolle spielen können.

Da Wild sowohl Störungen verursacht und dadurch frühe Sukzessionsstadien fördert, als auch die Gehölzdeckung reduziert, schlussfolgern wir, dass Wildtierbeweidung eine besonders geeignete Maßnahme ist, um artenreiche, offene Landschaften zu erhalten. Da die Beweidung mit Wildtieren zu teilweise drastischen Veränderungen der Landschaft führen kann, können jedoch zusätzliche Maßnahmen wie wechselnde Auskoppelungen notwendig sein, um ein reiches Mosaik verschiedener Sukzessionsstadien mit einer hohen Gesamtartenzahl zu erhalten.

Weiterhin zeigt die vorliegende Arbeit, dass die Untersuchung von Beweidungseffekten auf verschiedenen Maßstabsebenen von großer Bedeutung ist, da verschiedene Parameter auf unterschiedlichen Skalen beeinflusst werden. Größere Skalen sind geeignet, um den Beweidungseinfluss auf Strukturparameter wie den Anteil offener Bodens oder der Gehölzdeckung zu erfassen, während für die Erfassung der Veränderung des Artenreichtums und der floristischen Ähnlichkeit kleinere Skalen besser geeignet sind. Unsere Ergebnisse zeigen außerdem, dass kleinräumige Störungen die Keimung von *C. canescens* fördern. Die optimale Strategie um *C. canescens* zu fördern ist es, Störungen direkt vor der Samenausbreitung und nicht in trockenen Jahren durchzuführen. Auf Landschaftsebene kann die Förderung durch Arten späterer Sukzessionsstadien ein wichtiger Mechanismus für die Persistenz geschützter Pionierarten sein.

# Synopsis

## **1. Introduction**

During the last decades, the global change of the environment has caused a dramatic loss of habitats and species (Soulé 1986, Forman 1996, Fahrig 1997). In Central Europe, open habitats are particularly affected (Jentsch & Beyschlag 2003, Gharadjedaghi et al. 2004).

Open habitats are defined as areas that are neither intensively agriculturally used, nor covered with buildings, forests nor waters (Wallschläger & Wiegler 2000). According to the FFH-directory of the EU (Directive 92/43/EWG) and the Convention on Biodiversity (Rio 1992) open habitats are especially protected within the EU (Szymank et al. 1998). The importance of open habitats for nature conservation has been studied and proved by many authors (e.g. DLR 1992, Garcia 1992, Wallschläger 1997).

In Central Europe, spacious open landscapes are currently found only on former and active military training areas, post-mining areas and in some nature reserves. However, these remaining open landscapes are threatened by afforestation and succession. Therefore there is an urgent need for strategies in nature conservation to conserve such landscapes, since many endangered plant and animal species are specifically adapted to the ecological conditions of these nutrient poor habitats (Burkart et al. 2004, Finck et al. 2002).

Traditional concepts such as biotope management and contract nature conservation are cost-intensive. Therefore, on the long run they are unlikely to be suitable to protect all open habitats that need to be protected (Riecken et al. 1998, Finck et al. 2002). As an alternative, the use of grazing by megaherbivores in open habitat management has become increasingly popular (Wallis de Vries et al. 1988, Bokdam 2003). Large herbivores are considered a group of key species in ecosystems, having a major impact on vegetation structure and composition and hence on the biological appearance of the landscape (Baerselman 2002). In most cases, domestic life-stock is used (e.g. Delescaille 2002, Tsaryk & Tsaryk 2002, Kämmer 2002). Often, traditional herding has been replaced by continuous year-round grazing by free-ranging livestock within fenced areas. The arguments for these changes are to increase naturalness and biodiversity and to lower operational costs (Piek 1998). Currently, habitat management by wild megaherbivores is intensively discussed in nature conservation practice and adopted in

different projects, e.g. the Dutch project „Oostvaardersplassen“ (Krüger 1999), projects with red deer in Germany (Petraik 1992) and the Swiss national park „Ofenpaß/Il Fuorn“ (Krüsi et al. 1998, Schütz et al. 1999). The Europe-wide increasing importance of megaherbivore grazing is evident in the foundation of the “Large Herbivore Initiative” by WWF International (Baerselman 2002). However, experimental evidence to settle the question of the suitability of wild megaherbivore grazing in Europe is rare, and even though there is an urgent need for assessing appropriate grazing management techniques for specific aims, only few attempts have been made to gain this type of knowledge (Hester et al. 2000).

Therefore, a central aim of this thesis was to increase the knowledge about wild megaherbivore impact in different successional stages of open and semi-open habitats, focusing on the community level as well as on the landscape level. As a case study we chose a game reserve in NE Germany on a former military training area. The site is characterized by a mosaic of open areas with *Corynephorus canescens*, ruderal tall forb vegetation and dry pine and pioneer forests. Our approach is novel since we have studied wild ungulate grazing at different successional stages (Corynephorus site, ruderal site, pioneer forest site), which allowed evaluating wild ungulate grazing effects over a large spatial scale and different habitat conditions.

The second aim of this thesis was to study grazing impacts at different spatial scales. In ecology, “scale” is a term that has gained great currency during the past decades (Wiens 1989, Levin 1992, Ehleringer and Field 1993, Horne and Schneider 1995, Peterson and Parker 1998, Gardner et al. 2001), although the problem of defining the appropriate scale for measuring and studying ecological processes has long been recognized (e.g. Mercer and Hall 1911, Greig-Smith 1952), Levin (1992) emphasized that there is no single natural scale at which ecological phenomena should be studied, since systems generally show characteristic variability on a range of spatial, temporal and organizational scales.

The efficiency of grazing by domestic animals as a conservation tool has been shown in several studies (e.g. Redecker et al. 2002), and there is some evidence for the suitability of wild megaherbivores as well (Kuiters & Slim 2002, Virtanen et al. 2002, Schütz et al. 2003). However, little attention has been paid on the dependence of grazing effects on the scale of observation (but see Sala 1988, Brown & Allen 1989, Landsberg et al. 2002), and only few studies included community patterns at different scales within

single sites (Fuhlendorf & Smeins 1999, Wagner et al. 2000, Crawley and Herral 2001). This is regrettable, since the scales at which grazing can be successfully monitored may largely differ among and within different systems. Moreover, knowledge of the relevant scale would allow choosing a relevant monitoring scale. In our experimental study on scale effects we chose three different scales (0,25 m<sup>2</sup>, 4 m<sup>2</sup>, 40 m<sup>2</sup>) to study whether grazing effects are consistent over scale and how scale dependence may vary over different vegetation types.

The third intention of the thesis was to investigate the effect of small-scale disturbances on the species level. Disturbances, be they artificial or created by megaherbivores, initiate vegetation changes by creating gaps and affecting colonization and extinction rates (Connell and Slatyer 1977, Olff and Ritchie 1998). For the purpose of nature conservation it is important to know the degree to which the species in a system depend on specific forms of disturbance. Further, in a mosaic landscape, as it is represented by our study site, it is important to know how the role of disturbance varies between different vegetation types. We chose *Corynephorus canescens*, a key species of sandy open habitats that occurred in all investigated vegetation types, to study the effects of small-scale disturbances on early establishment probabilities. We focused on their interactions with successional stage and temporal environmental variation.

The thesis combines a community-level approach and a species-level approach, using univariate as well as multivariate methods. Combining these two allows exploring a wide range of questions concerning open habitat management.

## **2. Thesis objectives and organization**

This thesis consists of three main chapters that can be read independently and that are linked by short text sections. Summarized in these chapters, the objectives of the thesis were

- (i) to experimentally test for the suitability of grazing by wild megaherbivores as a management tool to conserve open habitats in three different vegetation types (*Corynephorus*-dominated site, ruderal site, pioneer forest) (chapter 1)
- (ii) to test whether the impact of grazing by megaherbivores on the vegetation is scale-dependent (chapter 2)
- (iii) to test the effect of small-scale disturbances on the key species *Corynephorus canescens* (chapter 3)

The three chapters are written as independent manuscripts each one showing an autonomous contribution into ecological research. This approach results, inevitably, in a certain repetition of some parts of the manuscripts, especially the introduction and methods sections. All chapters are, partly in slightly different versions, previewed for submission to scientific journals in cooperation with co-authors. Co-authors are my advisors Prof. D. Wallschläger and Prof. K. Tielbörger and Dr. M. Burkart. Owing to the idea of publishing every single chapter this thesis has been written in the first person plural.

## **3. Key Results**

### **Management of open habitats by wild ungulate grazing. A case-study in North-Eastern Germany (chapter 1)**

We tested the effect of wild megaherbivore grazing in three vegetation types (*Corynephorus*-dominated site, ruderal site and pioneer forest). Our results showed that wild megaherbivores considerably affected species composition and retarded successional pathways. This influence became manifest through alteration of abundances of only a few species.

Grazing effects differed considerably between successional stages: grazing led to higher species richness in grazed ruderal and pioneer forest sites, but not in the *Corynephorus* sites. Species composition changed significantly in the *Corynephorus* and ruderal sites. Grazed ruderal sites had turned into sites characterized by very short vegetation

dominated by *Agrostis* spp. and the moss *Brachythecium albicans*. Most species did not flower. Woody plant cover was affected only in the pioneer forest sites. Young pine trees were severely damaged and tree height was considerably reduced, leading to a “*Pinus-macchie*”-appearance.

### **Scale-dependence of wild ungulate grazing (chapter 2)**

We tested the scale-dependence of grazing effects in three vegetation types (*Corynephorus*-dominated site, ruderal site and pioneer forest). Over all vegetation types, the scale of observation directly affected grazing effects on woody plant cover and on floristic similarity, but not on the proportion of open soil and species richness. Regarding vegetation types separately, scale dependence of grazing effects on woody plant cover was more pronounced in the *Corynephorus* sites than in the pioneer forest sites. Further, the direction of scale-effects was different for the different vegetation types studied. While in the *Corynephorus* sites floristic similarity was significantly higher at the medium and large scale, in the pioneer forest sites it was significantly highest at the smallest scale. Species richness was strongest affected at the smallest scale in the ruderal sites.

### **The role of successional stage and small-scale disturbance for the establishment of the pioneer grass *Corynephorus canescens* (chapter 3)**

We experimentally studied early establishment probabilities of *C. canescens* in three successional stages (*Corynephorus*-dominated site, ruderal site and pioneer forest) by a seed-addition experiment under two different regimes of mechanical ground disturbance (disturbed and undisturbed). In average humid and humid years, emergence rates in undisturbed plots were significantly higher in the *Corynephorus* sites (early successional stage) than in the pioneer forest and ruderal sites (later successional stages). In a dry year, emergence rates were highest in the pioneer forest site. Disturbance led to higher emergence in a rather humid year and to lower emergence in a very dry year. Disturbance had no effect on survival rates.

In an average humid year, survival rates were significantly higher in the pioneer forest sites than in the two other sites, while in a humid year, survival rates did not differ between successional stages. In the average humid first year establishment probabilities were almost equal in *Corynephorus* and pioneer forest sites, due to high emergence rates and low survival rates in the *Corynephorus* sites and low emergence rates but high survival rates in the pioneer forest site.

#### **4. Discussion**

Our results demonstrate that wild megaherbivores considerably affected successional pathways and species composition in open habitats. We found that grazing by wild megaherbivores increased species richness in later successional stages whereas succession was retarded mainly in earlier stages (chapter 1). Since species richness usually increases in the course of succession, reaching a maximum at intermediate stages and because the early stages are less attractive to grazers, grazing is likely to have no effect in early stages. This is supported by earlier studies, that found that grazing favours local species richness in productive habitats, but decreases species richness when productivity is low (Austrheim and Eriksson 2001, Virtanen et al. 2002). Grazing effects on species composition and succession became manifest through alteration of abundances of only a few species. Our findings confirm results of Bullock et al. (2001) who found grazing-induced community changes to be manifested as increases or decreases in abundance of the dominant species.

Since experimental data on wild ungulate grazing are rare, our results considerably improve the knowledge about its suitability for managing open habitats. This is of high importance, since the problem of habitat management is temporarily acute and will be even more in future times. Being a method that is cheap and of high acceptance (Prochnow 2001, Tschöpe et al. 2004) management by wild ungulates is very likely to be a frequently adopted method in the future.

Studying wild ungulate grazing and browsing impact on three different spatial scales (chapter 2), we found complex scale-effects in the study system. Over all vegetation types, the scale of observation directly affected grazing effects on woody plant cover and on similarity, but not on the proportion of open soil and species richness. Further, the direction of scale-effects was different for the different vegetation types studied. Our results confirm earlier studies (e.g. Thompson and McGarigal 2002) that found that scale dependence is often specific for both the object under study and for the processes considered.

Scale dependence of grazing effects on woody plant cover was more pronounced in the *Corynephorus* sites, where trees were distributed patchily, than in the pioneer forest sites, where trees were distributed more regularly. This convincingly demonstrates the importance of observational scale when the ecosystem is spatially heterogeneous (Jentsch 2001).

Grazing effects manifested at small scales for floristic similarity in pioneer forest and ruderal sites (but not in *Corynephorus* sites) and for species richness in ruderal sites. This confirms studies by Bakker (2003) and Allcock & Hik (2003) who also found higher grazing effects at smaller scales. Grazing-induced disturbances facilitate the immigration of unpalatable or competitively inferior species, thereby affecting local extinction and immigration rates at small spatial scales. This led to differences between small disturbed spots and small undisturbed spots at small scales with more pronounced differences for similarity than for species richness. Considering that our data were presence-absence data, these small-scale differences average out over larger scales (Wiens 1989, Glenn-Lewin & van der Maarel 1992), because the probability that grazing-sensitive species survive in grazed plots, or competitively inferior species in ungrazed plots, increases with scale, while at the same time the species pool limits the number of potential immigrant species (Pärtel et al. 1996). As a result, average composition and species richness changed little at larger scales.

The grazing effect on species richness showed no direct scale-dependence. One reason for the consistency of grazing effects on species richness across scales may be that each small-scale sample quadrat (0.25m<sup>2</sup>, 4m<sup>2</sup>) sampled a reasonably high proportion (>45%) of the species pool of the next higher scale (4 m<sup>2</sup>, 40 m<sup>2</sup>).

The grazing effect on similarity was significantly higher at the medium and large scale in the *Corynephorus* sites, and significantly higher at the smallest scale in the pioneer forest sites. These differences in the scale on which grazing is most pronounced are probably due to the high proportion of frequent and unpalatable species in the *Corynephorus* sites (Stroh et al. 2002, Garcia et al. 2003), whereas grazing-sensitive species are less frequent, and therefore are detectable only at larger scales.

The study of the effect of small-scale disturbance on the key species *Corynephorus canescens* (chapter 3) revealed that the importance of small-scale disturbances for the emergence of *C. canescens* differed considerably between successional stages and year types, indicating complex interactions of environmental factors for the establishment of *C. canescens*.

Apparently, when soil moisture was sufficient, the main factor limiting *C. canescens* establishment was competition. However, low emergence rates in the dry year indicated that water became the overriding factor limiting establishment probabilities. This



finding is crucial for habitat management, since it highlights the importance of the correct timing of the disturbance for promoting early successional species. Disturbances, when applied in dry years, may have unwanted detrimental effects on the species' establishment. In addition to between-year timing of disturbance, within year timing has to be taken into consideration, too. Our findings suggest that survival rates were not affected by disturbance, while emergence rates showed a very strong response. This highlights that the optimal strategy for promoting *C. canescens* is to apply disturbances just before seed dispersal and not during dry years.

Our overall findings are furthermore intriguing in that they suggest an important role of late successional stages for the establishment of *C. canescens*. Specifically in years where water was not limiting, *C. canescens* emerged in higher numbers in open successional stages, while in the dry year higher success in the late stages suggests facilitation of *Corynephorus* by late successional species. Thus, as predicted by the stress gradient hypothesis (Callaway & Walker 1997), the outcome of biotic interactions shifted from competition during wet years to facilitation during dry years.

Our findings oppose the general assumption that the establishment of early successional species is poor in late successional stages. Namely given sufficient seed-availability, the pioneer-forest must be considered a beneficial habitat for *C. canescens*.

Studying effects in single vegetation types as well as over different vegetation types together, all experiments link the community and the landscape scale. This approach does not only illustrate that different vegetation types respond differently to the grazing regime. It also demonstrates that as the size of the observation unit increases, a greater proportion of the spatial heterogeneity of the system is contained and is lost to our resolution (Wiens 1989). For example, grazing affected species richness in the pioneer forest and ruderal sites, but the grazing effect over all successional stages was not significant. While at the same time, finer scales of observation let systems become more variable (Wiens 1989), this again highlights the importance of scale.

In this thesis, the knowledge about the suitability of wild ungulate grazing as a conservation tool to manage open habitats and the role of small-scale disturbances in particular has been noticeably improved. In summary, the sowing experiment (chapter 3) demonstrated that disturbances create micro-sites that promote germination and early establishment of early pioneer species and that pioneer forests may facilitate these

processes during dry years. Our results from the grazing experiment (chapter 1 and 2), revealed that grazing by wild ungulates considerably affected vegetation structure at different scales and was capable of controlling woody plant cover. This indicates that the importance of pioneer forests is not only temporarily, since grazing was able to arrest the pioneer forest in the pioneer stage. Because wild animals do not only create disturbances, thereby supporting early successional stages, but at the same time control woody plant cover, they are superior to domestic animals for open habitat management purposes.

## **5. Overall conclusions**

- (i) Wild ungulate grazing is a useful tool to slow down succession and to preserve a species-rich, open landscape.
- (ii) However, wild ungulate grazing considerably changed the overall appearance of the landscape. Additional measures like shifting exclosures might be necessary to allow vulnerable species to flower and reproduce.
- (iii) Our results confirm the importance of assessing grazing impacts on a range of scales, since different parameters are affected at different spatial scales.
- (iv) Larger scales are suitable to assess the grazing impact on structural parameters like the proportion of open soil or woody plant cover, whereas species richness and similarity are affected at smaller scales.
- (v) Late successional stages may be of great importance for the persistence of pioneer species during stressful years. Thus, management measures should not simply concentrate on grasslands dominated by *C. canescens*, but should include adjacent pioneer forests with *C. canescens* in the ground layer.
- (vi) Management strategies should explicitly consider small-scale disturbances. However, if artificial disturbance is adopted as a measure for restoration of *Corynephorus*-grasslands, extremely dry years should be avoided or pioneer forests should be subjected to disturbances, where applicable followed by artificial seeding

## **6. Declaration of my own contribution to the presented manuscripts**

I designed the experiments of all three studies, collected the field data, performed the statistical analysis of the data and wrote the major part of the manuscripts by myself, using relevant literature. While conducting the research I was advised by Prof. Dr. K. Tielbörger, who contributed to advanced drafts and final stages of the manuscripts as a co-author.

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# Chapter 1: Management of open habitats by wild ungulate grazing. A case study in North-Eastern Germany.



# Management of open habitats by wild ungulate grazing. A case study in North-Eastern Germany.<sup>1</sup>

## 1. Abstract

A major goal of nature conservation in Central Europe is to ensure the protection and the maintenance of open habitats and their unique diversity. Our study was designed to investigate the suitability of grazing by wild ungulates for the conservation of open habitats.

The effect of wild ungulate grazing was studied in three successional stages: (i) *Corynephorus canescens*-dominated grassland, (ii) ruderal tall forb vegetation dominated by *Tanacetum vulgare* and (iii) *Pinus sylvestris*-pioneer forest. The study was conducted over three years. In each successional stage, six paired 4 m<sup>2</sup>-monitoring plots of permanently grazed vs. ungrazed plots were arranged in three random blocks, leading to a total number of 18 plots. Removal of grazing was introduced de novo for the study. In each plot, percentage cover of each plant species and mean cover of woody plants was recorded.

Our results demonstrate that wild ungulates considerably affected successional pathways and species composition in open habitats. This influence became manifest through alteration of abundances of only a few species. Grazing effects differed considerably between successional stages: species richness was higher in grazed ruderal and pioneer forest plots, but not in the *Corynephorus* sites. Woody plant cover was affected only in the pioneer forest sites. Although the study period was too short to observe drastic changes in species richness and woody plant cover in all successional stages, changes in species composition took place in all stages.

We conclude that wild ungulate browsing is a useful tool to inhibit encroachment of woody vegetation and to preserve a species-rich, open landscape.

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Tschöpe, O., Tielbörger, K., Burkart, M. & Wallschläger, D.: Management of open habitats by wild ungulate grazing. A case-study in North-Eastern Germany. Restoration Ecology.



## **2. Introduction**

In contrast to the widely forested natural landscape of Central Europe, Central European lowland has been poorly forested for many centuries due to human land use (Lang 1994, Ellenberg 1986). This has led to the formation of distinct, species-rich plant and animal communities which are characteristic for open habitats and which have adapted to a unique set of habitat conditions. However, open habitats have become rare over the last few decades due to abandonment, afforestation, nitrogen deposition and changing land use (Heinken 1990, Jentsch and Beyschlag 2003).

It is well known that open landscapes are endangered by succession (Sukopp 1976, Kaule 1991). Since late successional stages are often relatively species-poor, a major goal of nature conservation has been to ensure the protection and the maintenance of open habitats and their unique diversity (Riecken et al. 1998, Redecker et al. 2002).

Traditional conservation practices of open habitats include clearing, mowing, extensive grazing with domestic animals, and the use of fire. More recently, the “new wilderness concept” claims that free-ranging wild herbivore assemblages can create open, nutrient-poor habitats as part of shifting successional mosaics (Vera 2000, Finck et al. 2002, Svenning 2002, Bokdam 2003). This concept is founded on theories about the appearance of the landscape since the tertiary, according to which Central Europe has been a mosaic of forest and open landscape created by megaherbivores (Geiser 1992, Hofmann and Scheibe 1997, Hofmann et al. 1998, Vera 2000, Bunzel-Drücke et al. 2002). Following this idea, the interest of managers in wild ungulate browsing has considerably increased in the past few years, as it is considered a “natural” method (Finck et al. 2002, Green 2002, Bokdam 2003). Also, it has been suggested that due to the special behavior of wild ungulates (e.g. browsing, fraying, bark stripping), game like elk, red deer, fallow deer and moufflon, with their different feeding types (Hofmann et al. 1998, Vila et al. 2004), are especially suitable to prevent tree encroachment. Since it is an inexpensive method of high public acceptance (Prochnow 2001, Tschöpe et al. 2004) management by wild ungulates is very likely to be a frequently adopted method in the future. Unfortunately, there is yet little experimental evidence showing that this practice is superior to other methods (but see Peart 1989, Virtanen et al. 2002). With this study, we aim at filling this gap.

Grazing reduces live vegetation (Grubb 1986, Mitchley & Willems 1995, Archer 1996, Vallentine 2001) and litter (Knapp & Seastedt 1986, Menke 1992) and disturbs the soil by trampling (Collins & Glenn 1988). Domestic grazing has been shown to both increase (Bakker 1989, Putman et al. 1991, Hill et al. 1992, Pucheta et al. 1998, Barbaro et al. 2001) and decrease species richness (Bullock et al. 2001, Lacey & Van Poolen 1981, Looman 1983) and to reduce the cover of woody plants (e.g. Bullock & Pakeman 1997, Carmel & Kadmon 1999). However, little is known about the differences between effects of wild versus domestic grazers.

In particular, the impact on different successional stages and on successional pathways has been rarely studied. This is surprising given that grazing may have opposite effects on woody plant encroachment in different successional stages (Noy-Meir et al. 1989, Oesterheld & Sala 1990, Bullock et al 1995).

Our study was designed to investigate the suitability of grazing by wild ungulates for the conservation of open habitats in a former military training area in Germany, where a monitoring programme was established in 2001. Our main aim was to evaluate the use of the current management in preserving the characteristic communities of open landscapes and preventing shrub and tree encroachment. We studied wild ungulate grazing at three successional stages and thus evaluated wild ungulate grazing effects over a large spatial scale and different habitat conditions.

In particular, we tested the following hypotheses:

1. Wild ungulate grazing preserves communities of open habitats by preventing woody plant encroachment and retarding the progression from one successional stage to the next.
2. Wild ungulate grazing increases species richness in late successional stages.

### **3. Methods**

#### **3.1 Study Site**

The study was conducted between 2001 and 2003 in the 160 ha game reserve “Wildgehege Glauer Tal”, which is located on a former military training area SW of Berlin, NE-Germany (UTM-coordinates: 3U 3373300 (E), 5787300 (N); 334700 (E), 5788800 (N)). The site is characterized by a mosaic of different successional stages,

such as open areas with the pioneer grass *Corynephorus canescens*, ruderal tall forb vegetation and dry pine and pioneer forests in varying percentages.

The substrate is sandy, acidic and poor in nutrients and carbonate, though it may be locally enriched where the ground moraine affects soil properties (Hinrichsen et al. 2004). Mean annual precipitation is 550 mm, mean annual temperature is 8.6°C. In the study years 2001-2003, total rainfall amounted to 573 mm, 734 mm and 372 mm, respectively (Deutscher Wetterdienst).

Successional pathways in the study area go from *C. canescens* dominated sites to *Pinus sylvestris* pioneer forests on dry sands and from annual ruderal vegetation to ruderal forb communities followed by *Pinus sylvestris* pioneer forests on more loamy soils (Fig. 1).

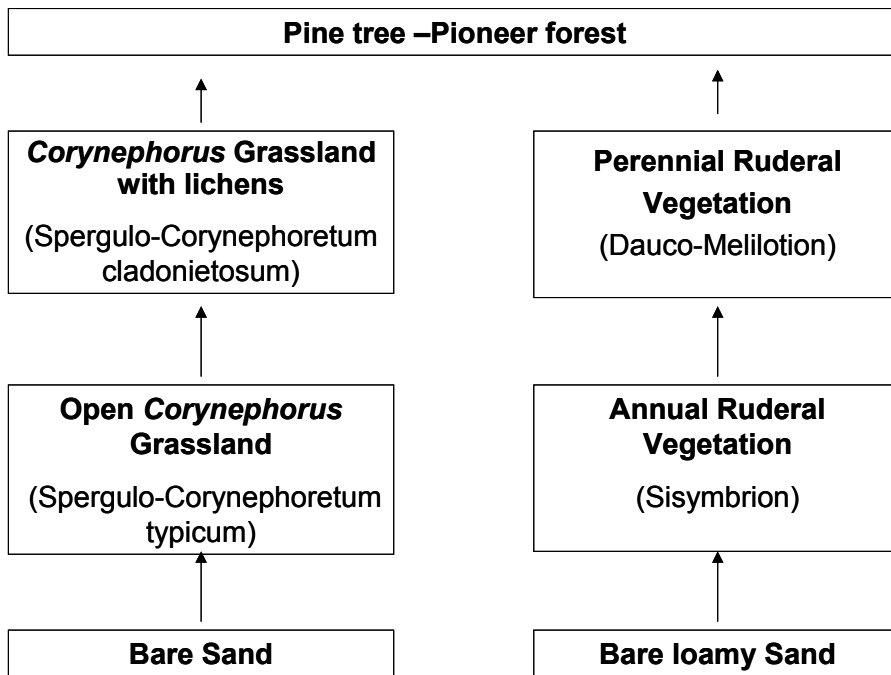


Fig. 1: Successional pathways in the study area (Burkart et al. 2004)

Until the first half of the 20<sup>th</sup> century the area was agricultural land. Since the beginning of the 1930s it was used as military training area. Since the abandonment of military utilisation in 1992, large pioneer forests, mainly of pine trees (*Pinus sylvestris*) have formed (Decruppe, unpub. 1996). In 1998, a local non-governmental initiative (Landschafts-Förderverein Nuthe-Nieplitz e.V.) founded the game enclosure with the aim to retard succession via grazing and browsing.

Permanent stocking rates in 2001 in the game enclosure were 142 individuals, including moufflon, red and fallow deer, and horses per 160 ha. The stocking rate increased to 165 animals in 2003 (Table 1).

**Table 1: Population development in the game preserve „Glauer Tal“**

	1999	2000	2001	2002	2003
<b>Fallow deer</b>	33	44	54	59	52
<b>Red deer</b>	20	28	38	45	45
<b>Moufflon</b>	30	38	47	57	65
<b>Horse</b>	3	3	3	3	3

Total number of animals in 2001: 142

Total number of animals in 2003: 165

### 3.2 Experimental design

The effect of wild ungulate grazing was studied for three successional stages: (i) an early successional stage dominated by the pioneer short-grass *C. canescens* (Cory site), (ii) a later stage dominated by ruderal forbs like *Tanacetum vulgare*, *Artemisia* spp. and *Echium vulgare* (Rud site) and (iii) a late stage characterized by a pioneer forest of *Pinus sylvestris* (PF site). The two former successional stages are listed in the red list of endangered plant communities of Germany (Jedicke 1997). The three successional stages differ in vegetation cover and aboveground biomass of herbaceous plants ranging from 63.7 g/m<sup>2</sup> at the Cory site, 83.9 g/m<sup>2</sup> at the Rud site to 274.9 g/m<sup>2</sup> at the PF site (Tschöpe, unpubl. data). From 2001 to 2003 a total of 132 vascular plant species and 24 moss and lichen species were recorded. Successional stages were distributed mosaic-like across the study area. Each successional stage was studied in three independent sites.

All areas have been grazed by wild ungulates since 1999, and exclosures were established in March 2001. Exclosures excluded moufflons, horses, red deer and fallow deer from grazing, while smaller animals like hares were able to pass through the meshes. Since patchiness in the study area was very small (ranging from a few m<sup>2</sup> to 1

ha), a plot size of 4 m<sup>2</sup> was chosen. In each successional stage, six paired 4 m<sup>2</sup>-monitoring plots of permanently grazed vs. ungrazed plots (exclosures) were arranged in three blocks (one per site), leading to a total number of 18 plots.

### 3.3 Data collection

In each plot, percentage cover of each plant species, including mosses and lichens, and mean cover of woody plants was recorded as percentage cover following Londo (1984). Recording took place in June and July in 2001 (i.e. three months after establishing of exclosures) and 2003 and in May and June in 2002, because the vegetation period started earlier in that year. The sampling time allowed including early annuals.

Nomenclature follows Wisskirchen & Haeupler (1998), Wirth (1995) and Frahm & Frey (2004). *Tragopogon pratensis*, *Achillea millefolium* and *Vicia tetrasperma* were identified to the aggregate level.

### 3.4 Data analysis

Univariate data were analyzed with the software package SPSS for windows (version 12.0, SPSS inc.). Nested ANOVAs were constructed with the dependent variables woody plant cover and mean number of species. The last year differences were analysed using the first year data as covariate, to account for potential initial differences. However, it should be noted that the first year densities were already affected by grazing for three months and thus do not exactly represent pre-treatment conditions. Treatment (grazed vs. ungrazed) was the within-subject factor and successional stage the between-subject factor, with block nested within stage and between-plot variation as error term. Post-hoc tests (SNK) were used to evaluate the specific differences in the dependent variables between years and successional stages. Data fulfilled the assumptions of ANOVA without transformation.

To investigate community-level response to grazing we used an ordination approach. Principle response curves (PRC, Van den Brink & Ter Braak, 1998, 1999) were calculated and created as described in Lepš & Šmilauer (2003, p. 224 ff.). PRC represent temporal trajectories of community composition for different treatments. PRCs were supplemented by the species scores on the corresponding RDA-axis. The value read from a PRC for a particular time and treatment can be combined with the species score by calculating the exponential transformation of their multiple. The

resulting value predicts the relative abundance of that species in comparison to the control at the same time. The vertical scores of PRC are based on the scores of environmental variables from a RDA, where the years was used as covariates and the interactions between the treatment levels and sampling times stand as environmental variables (Lepš & Šmilauer 2003). The species data set was log-transformed and analyzed separately for each successional stage.

To assess successional changes in the community structure, RDAs were constructed for the different vegetation types under grazing and non-grazing regime with year as the environmental variable. RDA was chosen because the length of gradient from a CCA was  $< 3$  (ter Braak & Šmilauer 2002), indicating that the underlying species-environment relationship was linear rather than unimodal (Lepš & Šmilauer 2003). Species data were log-transformed and centered by species. A Monte Carlo test with 499 unrestricted permutations was performed.

## 4. Results

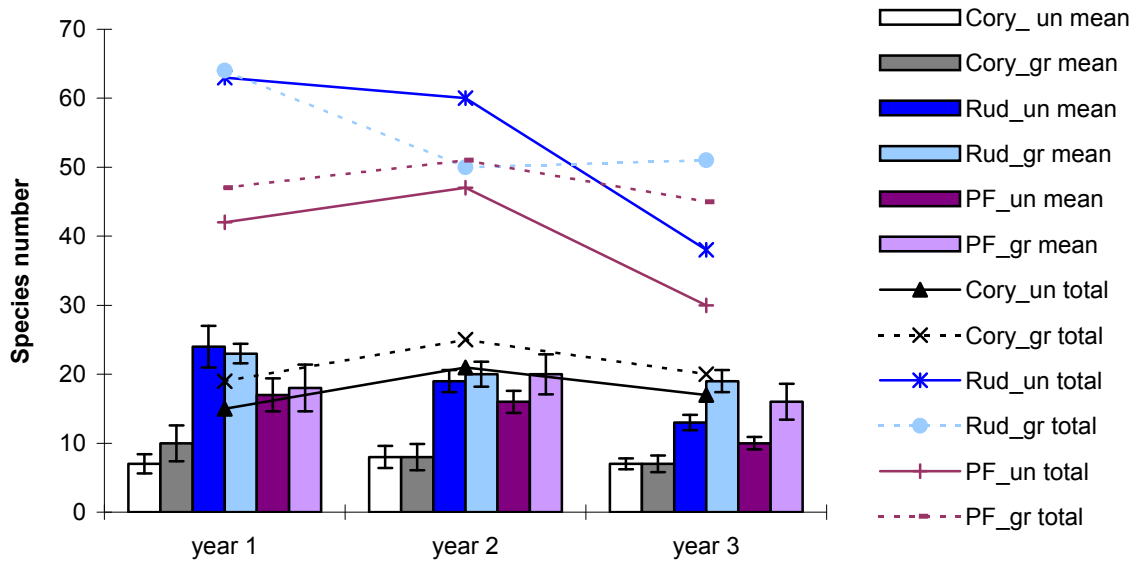
### Structural parameters and species richness

Mean species number was lowest in grazed and ungrazed *Corynephorus* sites and highest in grazed ruderal sites and grazed pioneer forest sites (Fig. 2). The proportion of woody plants was low in the *Corynephorus* and the ruderal sites and significantly higher in the pioneer forest sites (Fig. 3).

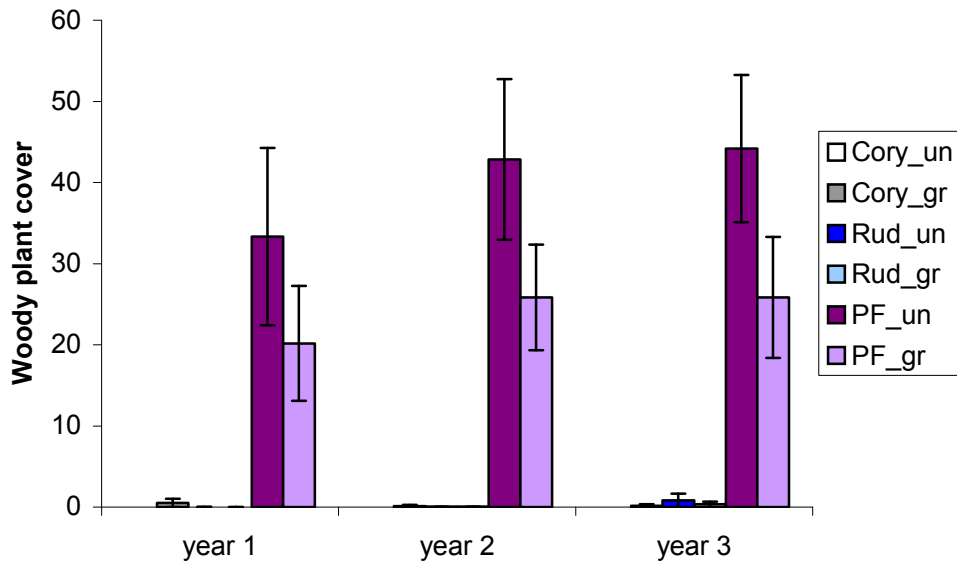
The ANOVA results showed no significant overall treatment effect on species richness and woody plant cover (Table 2). However, there was a strong trend that species richness in the third year was higher in grazed ruderal and pioneer forest sites than in ungrazed (Fig. 2) and woody plant cover was lower in grazed pioneer forest sites (Fig. 3).

**Table 2: F-values obtained in nested ANOVAs of 3<sup>rd</sup> year data with first year data used as covariate. \*:  $p < 0.05$**

Effect (df)	Mean no of species	Mean cover of woody plants
Treat (1)	2.21	0.23
Treat*site (2)	3.58	0.15
Treat*block (6)	1.12.	0.18.
Site (2)	4.60*	4.76*
Block (6)	1.42.	5.26*.



**Fig. 2: Mean species number (+ SE) and total species number in three sites under two grazing treatments in three years.** Cory: *Corynephorus* site, Rud: ruderal site, PF: pioneer forest site; \_un: ungrazed, \_gr: grazed; mean: mean species number, total: total species number.



**Fig. 3: Mean cover of woody plants (+SE) in the three successional stages in three years under two grazing treatments.** Cory: *Corynephorus* site, Rud: ruderal site, PF: pioneer forest site; \_un: ungrazed, \_gr: grazed.

The total number of species strongly declined in ungrazed ruderal and pioneer forest sites until the third year (Fig. 2). Most of the species that disappeared from the first to

the third year in ungrazed plots were annual and biennial species (ungrazed ruderal sites: 69%, compared to 19% perennials and 12% cryptogams; ungrazed pioneer forest sites: 92%, compared to 8% perennials). In grazed sites, the loss of species (ruderal sites: 44% annuals and biennials, 24% perennials, 32% cryptogams; pioneer forest sites: 60% annuals, 20% perennials, 20% cryptogams) was accompanied by a gain of species (ruderal sites: 58% annuals, 33% perennials, 9% cryptogams; pioneer forest: 56% annuals and biennials, 44% perennials) from the first to the third year. As there were no new species in ungrazed plots, the net result was an increase in species under the grazing treatment.

### Species composition

The principle response curves (Fig. 4 a-c) correspond to the first RDA axis. They show the extent and direction of the vegetation response to the grazing treatment over time, compared to the ungrazed control which is represented by the zero-line. The PRCs corresponding to the second RDA axis were not significant ( $p > 0.05$ , Monte Carlo test with 499 permutations).

The grazing treatment over three years led to significant differences in species compositions between grazed plots and ungrazed controls in the *Corynephorus* ( $F=3.94$ ,  $p=0.048$ ) and ruderal sites ( $F=8.33$ ,  $p=0.004$ ), but not in the pioneer forest sites ( $F=2.31$ ,  $p=0.400$ ). In all sites, abundances of annuals and clonal plants were higher in grazed plots, whereas in ungrazed plots erect forbs and herbs had higher abundances.

In the ***Corynephorus* sites**, 11.6% of the species variability was explained by the first ordination axis, i.e. the grazing treatment over time. Species that had their abundance well explained, i.e. species well fitted by the sample scores on the first ordination axis, were *Cladonia rei*, whose cover was 28% lower in grazed compared to ungrazed plots and “organic crusts” whose covers were 37% lower in ungrazed plots (Fig. 4a).

In the **ruderal sites**, 21.7 % of the species variability was explained by the grazing treatment over time. Species that had their abundance well explained by the grazing treatment over time were *Agrostis capillaris* (cover increased by 32% under grazing), *Calamagrostis epigejos* (25% increase) and *Agrostis stolonifera* (22%). In ungrazed plots, erect forbs like *Artemisia vulgaris* and *Tanacetum vulgare* had much higher covers (Fig. 4b). After three years, the cover of *Tanacetum vulgare* decreased by 32%



in exclosures compared to ungrazed plots and became the dominant plant with covers up to 70 %. As a result of three years of grazing, the ruderal sites were not recognizable as ruderal sites but had turned into sites with short vegetation (10.3 cm, compared to 48.3 in ungrazed plots) and a high cover of the moss *Brachythecium albicans* (30%) and *Agrostis* spp. (19%). Most species in grazed ruderal plots did not flower. It should be noted that because grazing started only 2 years before establishment of exclosures, vegetation outside the exclosures had not yet reached a relatively stable state.

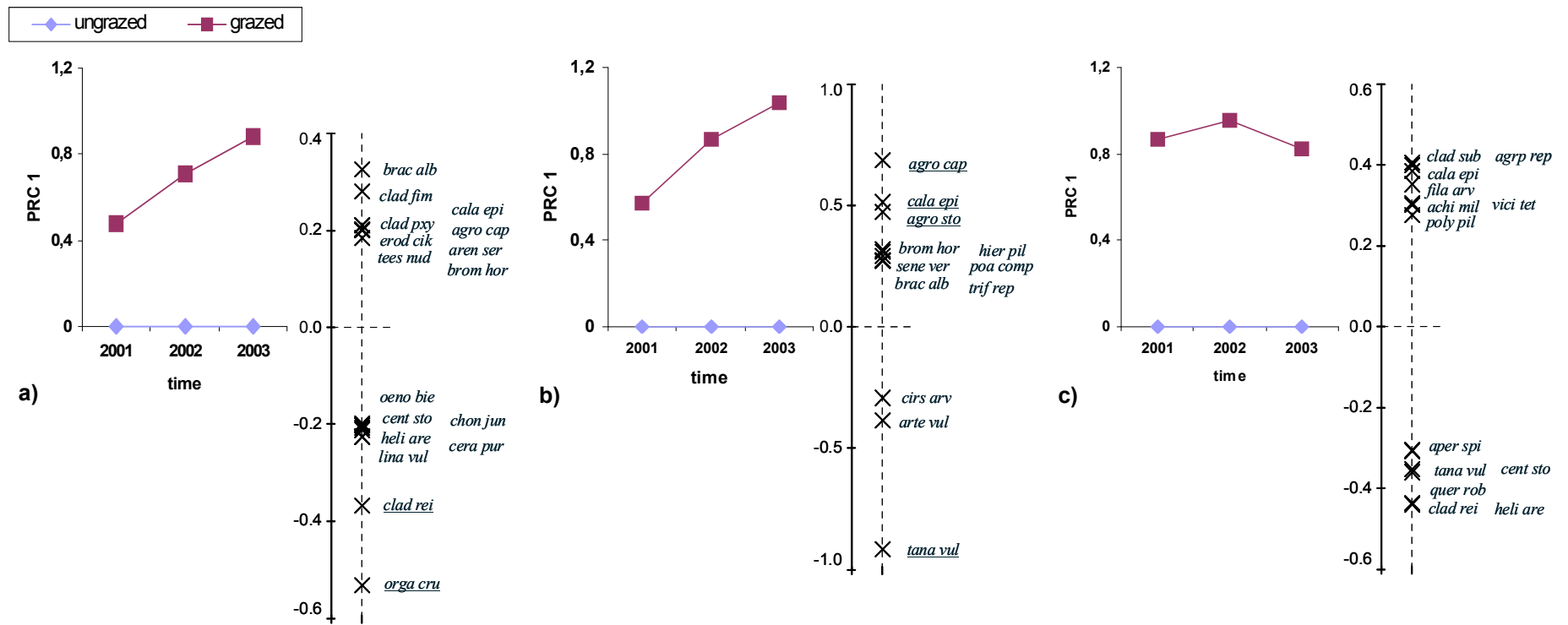
Although the treatment effect on species composition was not significant in the **pioneer forest sites**, there were higher numbers of *Quercus robur* seedlings inside exclosures than outside (Fig. 4c). The most striking effect of wild ungulate grazing in this site was that in grazed plots there was hardly any pine tree without injury. Pine trees were severely browsed, frayed and bark-stripped and tree height was considerably reduced (ungrazed plots: mean height 200 cm, maximum height 280 cm, grazed plots: mean height 100 cm, maximum height 210 cm), leading to a “*Pinus-macchie*”-appearance. Other woody plants like *Cytisus scoparius* and *Prunus serotina* emerged in grazed plots in single years, but were not able to establish.

### Successional pathways

Table 3 gives the results of permutation tests, which tested for differences between years in species composition within the different successional stages and treatments. In ungrazed ruderal and *Corynephorus* plots differences between years were significant, indicating that there were natural differences between years. In the corresponding grazed plots there was no significant difference between years, indicating that succession was delayed. In the pioneer forest plots, there were no differences between years in both grazed and ungrazed plots, which indicates a slower succession from pioneer forest to pine forest.

**Table 3: F- and p-values obtained in RDA with Monte Carlo permutation tests (499 permutations) for the effect of year on species composition**

Plots	F	p
<i>Corynephorus</i> ungrazed	3.36	0.012
<i>Corynephorus</i> grazed	0.91	0.422
Ruderal ungrazed	3.20	0.002
Ruderal grazed	1.81	0.094
Pioneer forest ungrazed	0.69	0.634
Pioneer forest grazed	0.82	0.544



**Fig. 4: Principle response curves of the grazing treatment over three years in three sites, supplemented by the accompanying diagrams showing the species scores on the corresponding RDA axis. a) *Corynephorus* site, b) Ruderal site, c) Pioneer forest site. Species well explained by the grazing treatment are underlined. A value read from a PRC can be combined with a species score to predict the relative cover at a particular time and treatment by calculating the exponential transformation of their multiple.**

## **5. Discussion**

Our overall results demonstrate that wild ungulates may considerably affect successional pathways and species composition in open habitats. The grazing effects differed considerably between successional stages: While wild grazers affected species numbers and woody plant cover mainly in later stages, succession was affected mainly in earlier stages.

In the *Corynephorus* sites grazing had no effect on species richness and woody plant cover. This was not surprising, since the proportion of woody plants was very low, and species richness usually increases in the course of succession and reaches a maximum at intermediate stages. Thus, grazing is likely to have no or even negative effects in early stages. In addition, as a result of the low biomass and low nutritious value of the dominant species (Kratochwil et al. 2002, Garcia et al. 2003), the *Corynephorus* sites were less attractive than the other successional stages to ungulate grazers (Stroh et al. 2002, personal observation) and were therefore visited less frequently.

However, succession was significantly retarded in grazed *Corynephorus* sites and species composition was significantly affected. This could be attributed mainly to the decrease of *Cladonia rei* and organic crusts in grazed plots, which are sensitive to trampling (Belnap 2002). Thus, the major impact of wild ungulates in this community was due to trampling, rather than grazing. Since succession was retarded rather than promoted in this community, the crust had probably a positive effect on vascular plant establishment, such as was found in previous studies (Pluis 1994, Lukesova 2001, Hoppert et al. 2004).

In contrast to the *Corynephorus* sites, grazing increased species richness in year three in the ruderal and pioneer forest sites, though this effect was not significant. The decline of the total number of species in the ungrazed ruderal and pioneer forest sites was mainly due to the loss of annual species and was associated with a decline in open soil (unpubl. data) and the resulting lack of safe sites (sensu Harper et al. 1965) for establishment of annual species. This confirms basic plant ecological theory about the loss of early successional species in increasingly dense vegetation (Begon et al. 2006).

Succession was significantly retarded in grazed ruderal sites, where grazing led to a drastic change from a tall ruderal forb community into a rather homogenous vegetation type with very short canopy height, dominated by *Agrostis* spp. and *Brachythecium*

*albicans*. A similar result was found by Schütz et al. (2003), who reported the disappearance of tall herb and meadow communities in subalpine grasslands due to red deer grazing. Gill (1992) stated that browsing by deer usually causes a decrease in shrub and herbaceous plant biomass in the ground vegetation and an increase in grasses, ferns and mosses. In our case, the structural changes could be attributed to the increase of clonal grasses and the reduction of *Tanacetum vulgare*. Being dominant in ungrazed plots, *T. vulgare* was reduced to covers below 5 % in grazed plots in the third year. This is in accordance with Bullock et al. (2001) who found that community changes due to grazing were manifest mostly as increases or decreases in abundance of the dominant species.

Since tall ruderal forbs like *T. vulgare* are sensitive to grazing (Dierschke & Briemle 2002), we conclude that continuous grazing will support grassland communities at the cost of tall ruderal vegetation. Being a red list community, a total loss of ruderal tall forb vegetation would be an unwanted effect.

Contrary to the *Corynephorus* and the ruderal sites, changes in community structure in the pioneer forest sites over time were slow irrespective of grazing. However, grazing resulted in the maintenance of open pine pioneer forests and *Pinus sylvestris* was severely damaged. Wild megaherbivores are known to damage woody plants (Putman and Moore 1998, Moore et al. 2000), and trees once browsed are likely to be browsed again (Moore et al. 2000), thereby getting increasingly damaged. Several studies have shown that large ungulates affect successional development by arresting or retarding height development of woody plants (Davidson 1993, Jefferies et al. 1994, Hester et al. 2000). The reason for the successful control of *Pinus sylvestris* is that young pine trees are particularly vulnerable to browsing, fraying and bark stripping (Putman & Moore 1998, Wagenknecht 2000, Vila et al. 2004).

Although disturbance is known to increase the availability of safe sites (Johnstone 1986; Hobbs & Huenneke 1992) and grazing may promote seedling establishment in a variety of environments (Oesterheld & Sala 1990), establishing rates of woody plants were not increased by grazing in the ruderal sites. We interpret this finding as the result of direct negative effects of browsing on tree seedlings, which concurs with the observations of Putman and Moore (1998) and Virtanen et al. (2002) who found reduced woody plant cover owing to deer impact. This highlights the usefulness of wild megaherbivores for conserving open habitats (Petraik 1992).

Although our study revealed significant wild ungulate impact, our results suggest that the three-year study-period was too short to finally evaluate wild megaherbivores grazing as a conservation tool. Rooney & Waller (2003) stated that ungulate effects on herbaceous communities might be quantified within a few decades, while effects on forest dynamics may require an even longer time to be detected. For example, although grazing in *Corynephorus* sites did not affect mean species richness in the study period, we predict that on the long run, species richness in exclosures will decline, since the increasing cover of organic crust as well as future tree establishment will affect species richness. Stampfli (1992) argued that permanent studies over three years may be too short to differentiate successional trends from fluctuations, since there is evidence that year-to-year fluctuations in plant communities can be large (Ward & Jennings 1990, Dodd et al. 1995). This was also true for our system where rainfall varied up to 49 % among years. Clearly, for distinguishing the signal (i.e. grazing) from the noise (i.e. environmental variation), a longer study period would be better. It is therefore remarkable that despite this limitation, we did detect a change in species composition already after three years.

Our overall findings therefore point to the usefulness of wild ungulate grazing as an appropriate management tool for preserving open landscapes. However, wild ungulate grazing considerably changed the overall appearance of the landscape. This was due to the creation of a “Pinus-Macchie”, characterised by very short pine-trees and the loss of ruderal forb communities, as well as the fact that many species in grazed plots did not flower.

However, since grazing had differential effects in different successional stages, we suggest that three-field rotation exclosures may be the best measure to conserve a rich mosaic of different successional stages with a high total number of species.

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## Link to the proceeding chapter

In the last chapter I investigated the suitability of grazing by wild ungulates for the conservation of open habitats. My results indicated a considerable effect on successional pathways and species composition in open habitats. However, ecological patterns and processes may vary with spatial scale (e.g. Wiens et al. 1987<sup>1</sup>, Fischer et al. 2004<sup>2</sup>) and conclusions appropriate to one scale may be inappropriate when transferred to another scale (Addicott et al. 1987<sup>3</sup>). Whether this is true for grazing impacts of wild megaherbivores in the studied system is subject of chapter 2.

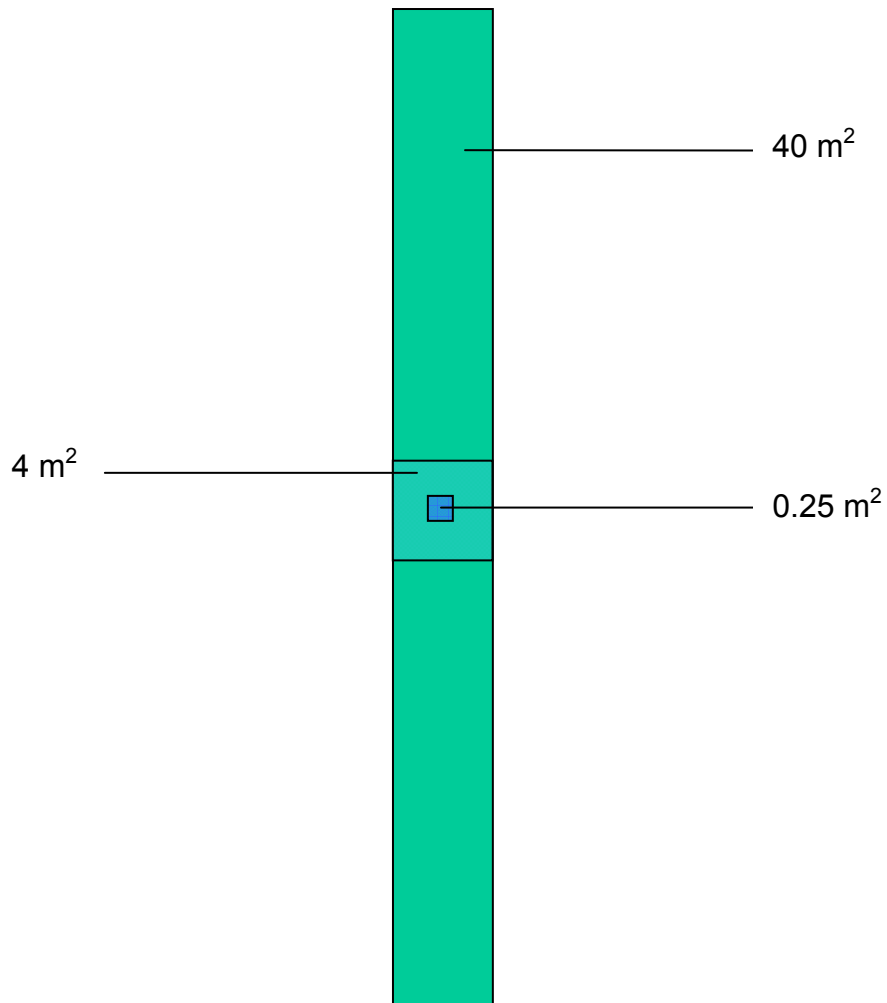
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<sup>1</sup> Wiens J.A., Rotenberry J.T. & Van Horne B. (1987): Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. *Oikos* 48: 132–147.

<sup>2</sup> Fischer J., Lindenmayer D.B. & Cowling A. (2004): The challenge of managing multiple species at multiple scales: reptiles in an Australian grazing landscape. *Journal of Applied Ecology* 41: 32–44.

<sup>3</sup> Addicott J.F., Aho J.M., Antolin M.F., Padilla D.K., Richardson J.S. & Soluk D.A. (1987): Ecological neighbourhoods: scaling environmental patterns. *Oikos* 49: 240-346.

## Chapter 2: Scale dependence of wild ungulate grazing effects



Multi-scale plot including three nested spatial scales

# Scale dependence of wild ungulate grazing effects<sup>1</sup>

## 1. Abstract

The importance of scale for ecological patterns and processes and the probability of detecting them are central problems in ecological research. An important ecological process affecting vegetation dynamics, which has a strong spatial component, is grazing by megaherbivores. Here, we tested the hypothesis that for different successional stages there are different appropriate scales for testing the efficiency of grazing for management purposes.

We experimentally studied grazing effects on plant community structure using multi-scale plots that included three nested spatial scales (0.25 m<sup>2</sup>, 4 m<sup>2</sup>, and 40 m<sup>2</sup>) in three different vegetation types (*Corynephorus canescens*-dominated short grass, ruderal tall forb vegetation, pine pioneer forest).

Over all sites, the scale of observation directly affected the probability of detecting grazing effects on woody plant cover and on floristic similarity, but not on the proportion of open soil and species richness. Grazing effects on similarity were manifested at small scales in pioneer forest and ruderal sites and on species richness in ruderal sites. The direction of scale-effects on similarity differed between vegetation types. While the grazing effect on floristic diversity was significantly higher at medium and large scales in the *Corynephorus* sites, in the pioneer forest sites it was significantly higher at the smallest scale.

We conclude that grazing effects on vegetation should be studied across a range of spatial scales for each response variable. Larger spatial scales are suitable for assessing grazing impact on structural parameters like proportion of open soil or woody plant cover, whereas species richness and similarity are affected at smaller scales.

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<sup>1</sup> This chapter is previewed for submission as:

Tschöpe, O., Tielbörger, K. & Burkart, M.: Scale dependence of wild ungulate grazing effects. Basic and Applied Ecology.

## **2. Introduction**

During the last decades, ecologists have emphasized the importance of scale for a variety of ecological processes and the probability of detecting them (e.g. Wiens 1989, Levin 1992, Ehleringer & Field 1993, Peterson & Parker 1998, Gardner, Kemp, Kennedy, & Petersen 2001). Therefore, an understanding of how ecological patterns and processes vary with spatial scale, and how the scale of investigation influences both analysis and interpretation of results has become a central question in ecological research (Morris 1987, Levin 1992, Meentemeyer & Box 1987, Fischer, Lindenmayer, & Cowling 2004). The importance of scale dependence has been recently highlighted by Ren, Niu, Zhang, & Ma (2006) who have considered the documentation of scale dependence across different systems “the major challenge to contemporary ecology and biogeography”.

An important ecological process affecting vegetation dynamics, which has a strong spatial component, is grazing by megaherbivores. Grazing is a widespread conservation tool for managing open habitats and their unique flora and fauna (Vera 2000, Svenning 2002, Finck, Riecken, & Schröder 2002, Bokdam 2003). In particular, grazing by wild ungulates has been used to prevent tree encroachment in early successional vegetation and to preserve species richness (Petrak 1992, Tschöpe, Beier, Burkart, Hinrichsen, Katscher et al. 2004, Burkart 2006). Although many studies have shown the effectiveness of grazing for nature conservation, little is known about how grazing effects depend on the scale of observation (but see Sala 1988, Brown & Allen 1989, Landsberg, James, Maconochie, Nicholls, Sol et al. 2002), and only few studies included community patterns on different scales within single sites (Fuhlendorf & Smeins 1999, Wagner, Wildi, & Ewald 2000, Crawley & Harral 2001). This is regrettable since the scale of monitoring success of grazing may largely differ among and within different systems. Also, knowledge of the relevant scale would allow choosing appropriate monitoring scales. Therefore, it has been suggested that the precise description of vegetation dynamics and grazing effects requires a multiple-scale approach (Brown & Allen 1989, Costanza & Maxwell 1994, Fuhlendorf & Smeins 1996, 1999, Jonsson & Moen 1998).

Grazing affects the vegetation by both the consumption of plant tissue and the creation of small-scale disturbances due to trampling (Archer 1996). Heterogeneous patterns (e.g. small-scale disturbances) are more likely to be detected at larger scales than at

small scales, because grain size needs to be large enough to include disturbed patches. On the other hand, the ability to detect homogeneous patterns should be the same over different scales. Herbivores have also been found to have a positive influence on diversity at small spatial scales, because they create small-scale disturbances that alter immigration and extinction rates, but to reduce diversity at larger scales because of a strong selection for grazing-tolerant species within the species pool (Olf & Ritchie 1998). Therefore, depending on the size and distribution of disturbed patches, or the size of a target organism, (e.g. tree vs. herbaceous plant) the degree of resolution will be critical (Jentsch 2001) for the probability of detecting grazing effects.

In a mosaic landscape, the optimal resolution to detect grazing effects may also vary between vegetation types that differ in heterogeneity. For example, trees are less frequent and more heterogeneously distributed in early successional stages sites than in later stages, requiring a larger sampling unit in the former to detect grazing effects on trees.

Our study was designed to investigate whether grazing effects on plant community structure are consistent over different spatial scales. Furthermore, based on our findings, we attempted to evaluate the appropriate scale of monitoring grazing effects as a function of vegetation type and response variable. As a case study we selected a game preserve which offered the opportunity to study wild ungulate grazing at different scales in different vegetation types.

In particular, we tested the following hypotheses:

1. There is a grazing x scale interaction, i.e. the grazing impact differs between scales.
2. Scale-dependence differs between vegetation types. Therefore, the optimal spatial scale at which grazing effects can be detected differs between vegetation types.

### **3. Methods**

#### **3.1 Study site**

The study was conducted in the 160 ha game reserve “Wildgehege Glauer Tal”, which is located on a former military training area in the Federal State of Brandenburg, North-

East Germany (UTM-coordinates: 3U 3373300(E), 5787300(N); 3374700(E), 5788800 (N)). The site is characterized by a mosaic of open areas with *Corynephorus canescens*, ruderal tall forb vegetation and pine and pioneer forests at dry sites.

The substrate is sandy, acidic and poor in nutrients and carbonate, though it may be locally enriched where the ground moraine affects soil properties (Hinrichsen, Anders, Beier, van Dorsten, Oehlschlaeger, et al. 2004). The regional climate is intermediate between the western, oceanic and the eastern continental climate. It is characterised by warm summers and moderately cold winters. Mean annual temperature (1961-1990) is 8.5°C and average rainfall amounts to 550 mm (Deutscher Wetterdienst). In the study years 2001-2003, total rainfall amounted to 573 mm, 734 mm and 371.8 mm, respectively. The growing season lasts from April to October.

Permanent stocking rate in the game enclosure in 2001 was 142 individuals, including red and fallow deer, moufflon and horses. It increased to 165 animals in 2003. The animals grazed the whole area of 160 ha. Additional winter-feeding has taken place.

### 3.2 Experimental design

The effect of wild ungulate grazing was studied in three successional stages (sites): (i) *Corynephorus canescens*-dominated grassland (Cory site) which can be considered a pioneer stage, (ii) ruderal tall forb vegetation dominated by *Tanacetum vulgare* (Rud site) and (iii) *Pinus sylvestris*-pioneer forest (PF sites), which are later successional stages on loamy and sandy substrates, respectively. Successional stages were distributed mosaic-like across the study area. Each successional stage was studied in three independent sites. In each successional stage, six paired monitoring plots of permanently grazed vs. ungrazed plots (exclosures) were arranged in three random blocks, resulting in a total number of 18 plots. The study was conducted over three years (2001-2003). All areas have been grazed by wild ungulates since 1999, and the experiment started with establishing exclosures in March 2001. To record dynamics at different scales, nested plots (0.25 m<sup>2</sup> – 4 m<sup>2</sup> – 40 m<sup>2</sup>) were used. Presence-absence data for each plant species was censused at all scales. Percentage of open soil, of woody species and the number of species were estimated separately for all plot sizes.

### 3.3 Data analysis

For each pair (grazed vs. ungrazed) of plots, a new variable, “relative grazing effect” (RGE) was calculated for year 1 and year 3 separately. The RGE for year 1 was



calculated to be used as a co-variable to account for initial differences between plots. RGE was calculated as

$$\text{RGE} = (X_{\text{ungrazed}} - X_{\text{grazed}}) / \text{maximum of } X_{\text{ungrazed}} \text{ and } X_{\text{grazed}}, \text{ respectively,}$$

with X being the dependent response variable (percentage of open soil, woody plant cover, species richness). The resulting value lies between -1 and +1 and is zero when the grazing effect is zero. Bonferroni-adjusted t-tests were used to test whether the RGE values were significantly different from zero.

The data were analyzed with the software package SPSS for windows (version 12.0, SPSS inc.). Repeated measures ANOVAs were calculated for the RGE of year 3. Scale was the within-subject factor and successional stage the between-subject factor in this model, with block nested within successional stage and between-plot variation as error term. The RGE of year 1 was used as co-variable. Post-hoc tests (SNK) were used to evaluate the specific differences between scales.

To investigate the community-level response to grazing, a Sørensen-coefficient (i.e. similarity between grazed and ungrazed plots) was calculated for each scale. Pairwise differences were evaluated using post-hoc tests (SNK).

#### **4. Results**

Over all sites, the factor scale had a significant impact on the RGE on the proportion of woody plants, but not on the proportion of open soil, mean species numbers and on the floristic similarity measured by the Sørensen-Index (Table1, Fig.1). However, for the Sørensen-index the scale\*site interaction was significant, indicating that the scale effect differed between sites. Post-hoc tests indicated that scale significantly affected the grazing effect on similarity between grazed and ungrazed plots in the *Corynephorus* and pioneer forest sites, but not in the ruderal sites ( $p < 0.05$ , SNK-test, Fig. 1d). The sites did not only differ in their scale-sensitivity to the grazing effect, but also in the direction by which scale influenced the grazing effect. In the *Corynephorus* sites the grazing effect was significantly lower (resulting in higher floristic similarity between grazed and ungrazed plots) at the 0.25 m<sup>2</sup> scale than at the 4 m<sup>2</sup> scale, in the pioneer forest sites it was significantly higher at the 0.25 m<sup>2</sup> scale than at the 4 m<sup>2</sup> and 40 m<sup>2</sup> scale. Comparing the different sites with respect to the species that grazed and ungrazed plots have in common, the proportion of shared species increased with scale in the ruderal

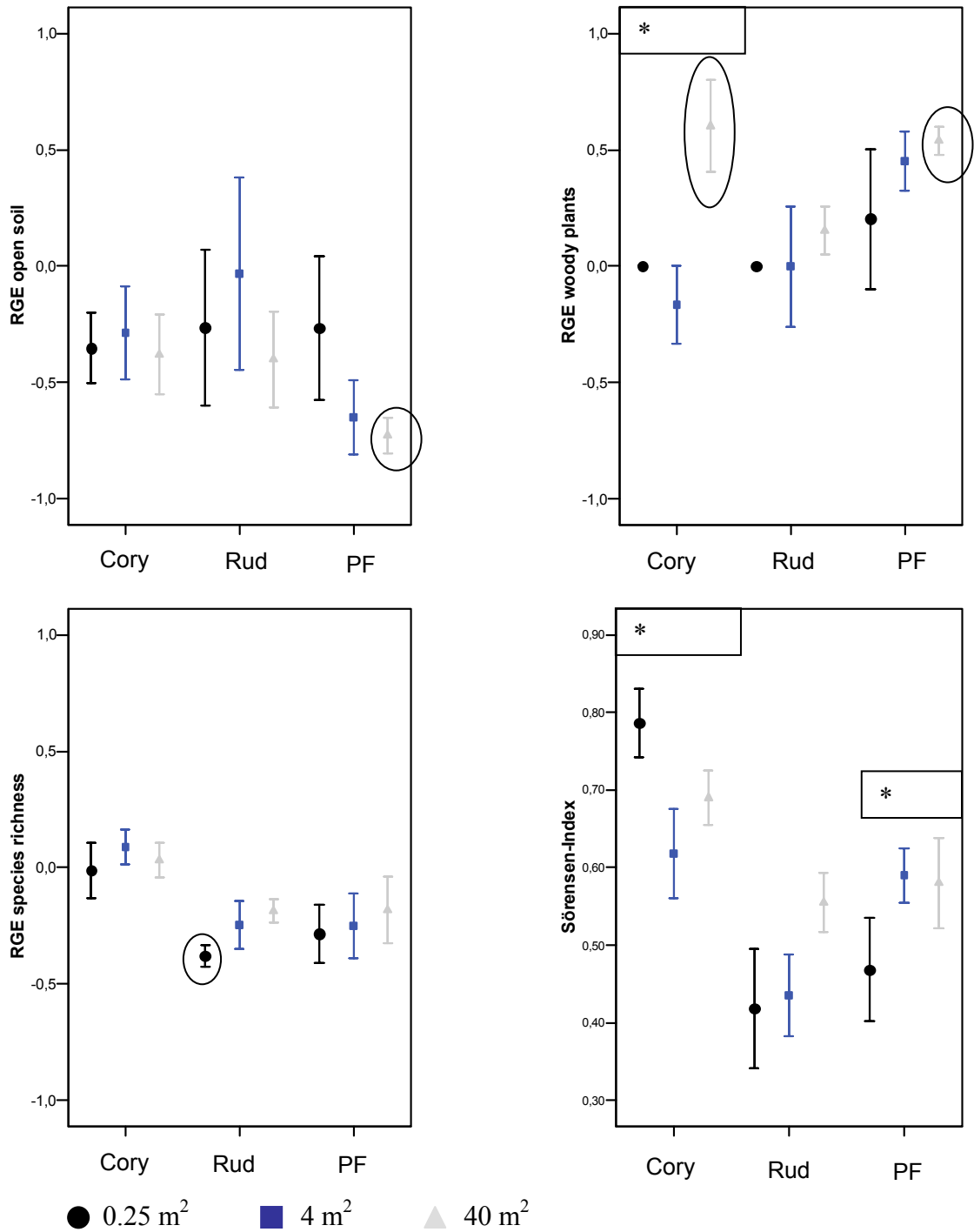
and pioneer forest sites, whereas it decreased with scale in the *Corynephorus* sites (Fig. 2).

There was also a significant scale effect of grazing on woody plants in the *Corynephorus* sites in the third year, where the grazing effect was significantly higher at the 40 m<sup>2</sup> scale (Fig 1b). However, this effect disappeared when the first year data was used as a co-variable.

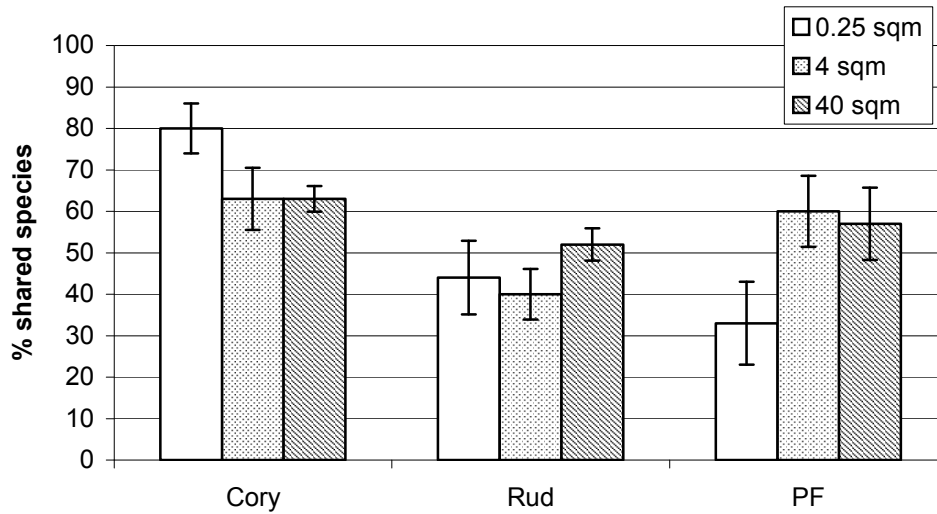
Though scale had no direct significant effect on woody plant cover and open soil in the pioneer forest site, there was a trend towards increasingly strong grazing effects with increasing spatial scale (Fig 1a, 1b). This was confirmed by additional Bonferroni-adjusted t-tests, that showed that the values of RGE most different from zero were those at the 40 m<sup>2</sup> scale. There was also a trend towards a higher grazing effect on species richness at the smallest scale in the ruderal site (Fig. 1 c), which was also confirmed by Bonferroni-adjusted t-tests.

**Table 1: Results (F-values) of repeated measurements ANOVAs constructed to test for the effect of scale (0.25 m<sup>2</sup>, 4 m<sup>2</sup>, 40 m<sup>2</sup>), site (Cory, Rud, PF) and block (random factor) on RGE on percentage of open soil, woody plants, mean species number per scale, and on floristic similarity (Sørensen-index). n. s.: non significant, \*: p<0.05.**

Effect (df)	RGE of % open soil	RGE of % woody plants	RGE of mean species no.	Sørensen-Index
Scale (2)	2.60 n.s.	11.97*	2.35 n.s.	2.04 n.s.
Site (2)	15.24**	1.59 n.s.	6.15*	28.37***
Block (6)	35.97***	0.13 n.s.	1.43 n.s.	6.36**
Scale*site (4)	1.06 n.s.	0.99 n.s.	0.51 n.s.	4.54*
Scale*block (12)	2.82 n.s.	0.30 n.s.	0.84 n.s.	1.75 n.s.



**Fig. 1: Scale dependence of grazing effects in three successional stages on a) the proportion of open soil, b) woody plant cover, c) species richness, d) floristic similarity (Sørensen-Index).** Note that for the ANOVA analysis of the scale effect, the first year data was used as a covariate. Asterisks indicate significant scale effects, circles indicate RGE significantly different from zero (Bonferroni-adjusted t-tests). Note the different scaling in Fig. 1d.



**Fig. 2: Percentage (+SE) of shared species in grazed and ungrazed plots in three successional stages measured at three spatial scales.** Cory: *Corynephorus* site, Rud: ruderal site, PF: pioneer forest site

## 5. Discussion

Our overall results indicate that there were considerable differences between scales in the direction and intensity of grazing effects on plant community structure. However, these effects were quite complex and differed between vegetation types. For example, over all vegetation types, the scale of observation directly affected grazing effects on woody plant cover and on floristic similarity, but not on the proportion of open soil and species richness. Our data thus indicated that grazing controls vegetation patterns at different scales and that scale dependence is often specific for both the object under study and for the processes considered, a result also found by Thompson and McGarigal (2002).

For managing purposes, the encroachment of **woody species** into open habitats has been a major point of concern. Therefore, it is useful to evaluate the relevant scale for detecting grazing effects on woody plant cover. Not surprisingly, there were no effects at the smallest scale, since the target organisms were too large and too heterogeneously distributed to detect significant effects (Harper 1977). More interestingly, the scale dependence of woody plant cover was more pronounced in the *Corynephorus* sites, where trees were distributed patchily, than in the pioneer forest sites, where trees were distributed more regularly. This demonstrates the importance of observational scale when the ecosystem is spatially heterogeneous (Jentsch 2001).

Grazing effects on the proportion of **open soil** showed no direct scale-dependence in our study, indicating a homogenous distribution of open soil. This does not meet our expectations, since animal disturbances are known to lead to spatial patchiness and to be created on small spatial scales (Adler 2001, Jentsch 2001, Allcock & Hik 2003). However, there was a trend towards an increasing grazing effect with increasing scale in the pioneer forest site, which may indicate patchy trampling not detectable at small scales. The effect was most pronounced in the pioneer forest sites, because the pioneer forests were more intensively grazed than the *Corynephorus* sites, but had less fast-growing species that would cover gaps than the ruderal sites.

Grazing effects on **similarity** were manifested at small scales (low Sørensen-index) in pioneer forest and ruderal sites (but not in *Corynephorus* sites) as well as on **species richness** in ruderal sites. While grazing leads to local extinctions of grazing-sensitive species, grazing-induced disturbances facilitate the immigration of unpalatable or competitively inferior species with the ability to exploit rare and unpredictable resources (Archer 1996, Briske 1996). Thus, grazers affect local extinction and immigration rates at small spatial scales, leading to differences between small disturbed spots and small undisturbed spots. However, these differences were more pronounced for similarity than for species richness. Our interpretation of this finding is that since our data were presence-absence data, small-scale differences average out over larger scales (Glenn-Lewin & van der Maarel 1992, Wiens 1989). This is because the probability that grazing-sensitive species survive in grazed plots or competitively inferior species in ungrazed plots increases with scale, while at the same time the species pool limits the number of potential immigrant species (Zobel 1997). As a result, average composition and species richness changed little at larger scales. Similar to our results, Bakker (2003) found that cattle grazing had a positive influence on species richness at smaller scales, while this effect disappeared at the largest scale of measurement. Also, Allcock & Hik (2003) could not find a significant scale-dependence of grazing effects on richness in Australian woodlands, although their grazing effect was higher at small scales. They argued that grazers remove biomass and create gaps at very small scales and thus increase small-scale heterogeneity (Adler 2001). However, this explanation does not hold for our case, since our results did not reveal a higher proportion of gaps at small scales.

The direction of scale-effects on **similarity** differed between vegetation types. While the Sørensen-index was significantly lower (i.e. grazing led to higher differences in species composition) at the medium and large scale in the *Corynephorus* sites, it was significantly highest at the smallest scale in the pioneer forest sites. In the ruderal sites the grazing effect was highest at the smallest and medium scale, although the difference was not significant. These differences in the scale on which grazing is most pronounced are probably due to the high proportion of unpalatable species in the *Corynephorus* sites (Stroh, Storm, Zehm, & Schwabe 2002, Garcia, Carrere, Soussana, & Baumont 2003). Grazing-sensitive species are less frequent in these sites, and therefore, they can be detected only at larger scales.

The grazing effect on **species richness** did not show any direct scale-dependence, but there was a clear trend that species richness was strongest affected at the smallest scale in the ruderal sites. One reason for the consistency of grazing effects on species richness across scales may be that each small-scale sample quadrat (0.25 m<sup>2</sup>, 4 m<sup>2</sup>) sampled a reasonably high proportion (>45%) of the species pool of the next larger scale (4 m<sup>2</sup>, 40 m<sup>2</sup>). The grazing effect, manifested at the smallest scale, was largest in the ruderal sites because these possess the largest proportion of palatable species and were therefore most intensively grazed.

To summarize, we found some interesting scale effects, but the overall trends were not consistent across vegetation types and response variables. However, although our objective was to investigate a range of spatial scales, it should be noted that the variety of scales investigated was limited to what Wiens et al. (1987) have called local scales. A wider range of spatial scales might lead to more pronounced differences between scales. In general, our findings support previous results, which have highlighted the general importance of measuring grazing effects at different spatial scales (Kuiters and Slim 2003, White, Feller, & Bayley 2003). We could further confirm that a proper analysis requires that the scale of measurements and that of the organisms' response fall within the same domain (Wiens 1989) and that the evaluation of disturbance effects varies with the level of resolution (Allen & Star 1982, White & Pickett 1985, Pickett, Kolasa, Armesto, & Collins 1989).

Our results highlight the importance of assessing grazing impacts on a range of scales, since different parameters are affected at different spatial scales. Our data indicate that for assessing grazing impact on structural parameters like the proportion of open soil or woody plant cover larger scales are more appropriate, whereas species richness and similarity are affected at smaller scales.

## **6. Acknowledgements**

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## Link to the proceeding chapter

In the last chapter, I investigated the suitability of wild ungulate grazing as a tool to conserve open habitats on the community level. In the following chapter, the effects of small-scale disturbances as a conservation measure for open habitats are studied on the species-level.

Disturbances initiate vegetation changes by creating gaps and affecting colonization and extinction rates (Olf and Ritchie 1998<sup>1</sup>). They can occur as natural disturbances, e.g. browsing and trampling by herbivores (Sousa 1984<sup>2</sup>, Huntly 1991<sup>3</sup>) or as artificial disturbances applied for conservation purposes. In the following chapter, mechanisms explaining the maintenance of an open-habitat species are investigated, illustrated by *Corynephorus canescens*, a key species of dry acidic open habitats.

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<sup>1</sup> Olf, H. & Ritchie, M.E. (1998): Effects of herbivores on grassland plant diversity. *Trends in Ecology and Evolution* 13: 261-265.

<sup>2</sup> Sousa, W.P. (1984): The role of disturbances in natural communities. *Annual Review of Ecology and Systematics* 15: 353-391

<sup>3</sup> Huntly, N.J. (1991): Herbivores and the dynamics of communities and ecosystems. *Annual Review of Ecology and Systematics* 22: 477-503.

### Chapter 3: The role of successional stage and small-scale disturbance for the establishment of pioneer grass *Corynephorus canescens*



Replicate of the sowing experiment in a *Corynephorus* site.

# The role of successional stage and small-scale disturbance for the establishment of pioneer grass *Corynephorus canescens*<sup>1</sup>

## 1. Abstract

Persistence and coexistence of species in plant communities are often explained by competition-colonization tradeoffs. This study investigates mechanisms that explain the maintenance of the protected pioneer grass *Corynephorus canescens* in a mosaic landscape.

We studied early establishment probabilities of *C. canescens* in three successional stages (*Corynephorus canescens*-dominated site, ruderal forb site and pioneer forest) under two different regimes of mechanical ground disturbance (disturbed and undisturbed), focusing on the interactive effects of small-scale disturbances, successional stage and year-to-year variation.

Disturbance led to higher emergence in a humid year and to lower emergence in a very dry year. Apparently, when soil moisture was sufficient, the main factor limiting *C. canescens* establishment was competition, while in the dry year water became the limiting factor. Survival rates were not affected by disturbance.

In humid years, *C. canescens* emerged in higher numbers in open successional stages while in the dry year, emergence rates were higher in late stages, suggesting an important role of late successional stages for the persistence of *C. canescens*.

Our results suggest that small-scale disturbances promote germination of *C. canescens*. However, disturbances should be carefully planned. The optimal strategy for promoting *C. canescens* is to apply disturbances just before seed dispersal and not during dry years. Further, on the landscape scale facilitation by late successional species may be an important mechanism for the persistence of protected pioneer species.

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<sup>1</sup> This chapter is previewed for submission as:  
Tschöpe, O. & Tielbörger, K.: The role of successional stage and small-scale disturbance for the establishment of the pioneer grass *Corynephorus canescens*. Plant Ecology.

## **2. Introduction**

The past decades have experienced an unprecedented loss of species in many ecosystems (Korneck and Sukopp 1988, Waldhardt et al. 2003). In Central Europe, species of open nutrient-poor landscapes are particularly vulnerable to extinction (Ellenberg 1986, Schumacher 1996). Due to human land use these landscapes have become one of the most threatened habitat types. Namely eutrophication has promoted the invasion of tall forbs and woody plant species (Riecken et al. 1998). Therefore, the protection of the remaining nutrient- and wood-poor open habitats and their unique fauna and flora is one of the major challenges for European nature conservation (Riecken 2003, Burkart et al. 2004).

To look at management effects for all focal plant and animal species and their interactions is highly time-consuming and work-intensive. Therefore, when studying ways of protecting certain habitat types and their component species, a commonly adopted approach is to focus on the response of a key species, which is indicative for the functioning of the whole system (Hunt 2001, Dyer 2002). In central European lowlands, such a key species for open acidic grasslands is grey hairgrass *Corynephorus canescens* (L.) P.B., one of the earliest pioneers in the system. *C. canescens* is a typical pioneer of sandy acidic soils that used to be widespread on European coastal and inland sand dunes. It is a tufted perennial of variable life span that regenerates by seeds (Marshall 1967, Jentsch and Beyschlag 2003). Dry acidic grasslands dominated by *Corynephorus canescens* are protected by the Fauna Flora Habitat directive by the EU (Directive 92/43/EEC). Currently they are more endangered by habitat destruction and eutrophication than bogs or calcareous grasslands (Rennwald 2000, Jentsch and Beyschlag 2003).

Mechanical soil disturbances have been demonstrated to be very effective conservation measures for dry acidic grasslands (Jentsch 2001, Jentsch et al. 2002). Disturbance is defined as any relatively discrete event in time that disrupts ecosystems, community or population structure and changes resources, substrate availability, or the physical environment (White and Pickett 1985). Disturbances can create bare substrate in otherwise closed vegetation (Klinkhamer and de Jong 1988, Peart 1989), thereby creating potential niches for the establishment of *Corynephorus canescens*, and may alter resource availability and reduce the intensity of competition (Grime 1979, Bazzaz 1983).

However, little is known about the optimal timing of the disturbance event and the effects of disturbances have been studied only in very early successional stages of sandy open habitats (Jentsch et al. 2002). Often, management concepts preserve only a limited spectrum of successional stages, and the restoration of diverse forest-open habitat transitions are rarely addressed (Riecken 2003).

In addition, traditional management concepts often regard late successional stages such as tall forb vegetation or forests as detrimental for the persistence of species of open habitats. Yet, when frequent small-scale disturbance occurs in such closed vegetation, these stages may still contain many of the species of open habitats. In a mosaic landscape, different successional stages or communities are part of a network of communities linked by dispersal, thereby representing a metacommunity (Hanski and Gilpin 1991, Wilson 1992). Coexistence in metacommunities is usually explained by competition-colonization tradeoffs (Tilman 1994, Yu and Wilson 2001). However, in some systems, facilitation rather than competition may be the important mechanism for persistence in communities (Bruno et al. 2003). This is especially the case in habitats with strong environmental stress (Bertness and Callaway 1994). Thus, when temporal variations in the environment, such as frequent droughts, lead to occasionally stressful conditions in the open spaces, higher vegetation should be able to facilitate plant species of open habitats via shading.

Species can also be favoured in some habitats and disfavoured in others, and thus coexist locally as a result of source-sink relationships (Amareske and Nisbet 2001, Mouquet and Loreau 2002, 2003). Unfortunately, the value of open space has been usually advocated per se (Klinkhamer and de Jong 1988, Milton et al. 1997) without considering the context and the importance of later successional stages for the long-term persistence of early successional species.

Seedling establishment is a crucial bottleneck for vegetation dynamics (Jentsch et al. 2002). Therefore, focusing on early seedling establishment is both critical for understanding persistence and dynamics of *C. canescens*, as well as for developing an optimal timing of potential conservation measures. In this study, we focused on the interactive effects of small-scale mechanical ground disturbances and successional stage and temporal environmental variation on early establishment probabilities of the key species *C. canescens*. The goal of this study was to investigate mechanisms that explain

the maintenance of an endangered species in a mosaic landscape under land use change. The study was conducted on two different levels: the community and the landscape.

In particular, we tested the following hypotheses:

1. Establishment of *C. canescens* depends on the availability of open space. Therefore:
  - germination and survival are poor in late successional stages, because the proportion of open soil is lower than in early successional stages
  - small-scale disturbances increase germination and survival rates in late successional stages, but not in early stages
2. Under dry conditions, late successional stages may facilitate the establishment of the early successional species *C. canescens*

### **3. Methods**

#### **3.1 Study Site**

The study was conducted in the game reserve “Wildgehege Glauer Tal”(UTM-coordinates: 3U 3373300(E), 5787300(N); 337400(E), 5788800 (N)), which is located on a former military training area SW of Berlin, in the Federal State of Brandenburg, NE-Germany. The site is characterised by a mosaic of open areas with *Corynephorus canescens*, ruderal tall forb vegetation and dry pine and pioneer forests. The mean vegetation covers in the different successional stages are given in Table 1. Successional pathways go from an early successional stage dominated by *Corynephorus canescens* on sandy substrate to a late stage characterised by a *Pinus sylvestris* pioneer forest, with *Corynephorus canescens* in the herb layer. Where the soil is loamier, the successional pathways go from annual ruderal vegetation over ruderal tall forb vegetation to pioneer forests (Burkart et al. 2004).

The substrate is sandy, acidic and poor in nutrients and carbonate, though it may be locally enriched where the ground moraine affects soil properties (Hinrichsen et al. 2004). The climate of the study region is intermediate between the western, oceanic and the eastern continental climate in Germany. It is characterised by warm summers and moderately cold winters. Mean annual temperature is 8.5°C and average rainfall amounts to 550 mm (1961-1990) (Deutscher Wetterdienst). In the study years 2001-

2003, total rainfall amounted to 573 mm, 734 mm and 371.8 mm, respectively. Thus, the first study year can be considered as an average humid year, the second as a humid and the third as an extremely dry year.

**Table 1: Mean proportion of open soil (%) and vegetation cover (%) in the three successional stages.** Cory: *Corynephorus* site, Rud: ruderal tall forb site, PF: pioneer forest site.

	<b>Cory</b>	<b>Rud</b>	<b>PF</b>
<b>Open soil</b>	63.8	11.1	26.0
<b>Cryptogams</b>	24.5	13.7	13.7
<b>Herbaceous plants</b>	11.1	27.4	27.4

The growing season lasts from April to October. Caryopses of *Corynephorus canescens* germinate in autumn, fruit ripening takes place in June/July (Frey and Hensen 1995). Most relevant for emergence rates is the rainfall during the emergence period, i.e. September and October. In 2001 it amounted to 163.3 mm, in 2002 to 111.6 and in 2003 to 75.9 mm.

### 3.2 Experimental design

To examine the effect of temporal environmental variation on *C. canescens* establishment, the study was conducted over three years. Emergence under natural conditions was studied from 2001 to 2003, and disturbance was applied over two years (2001-2002 and 2002-2003, respectively).

Diaspores of *Corynephorus canescens* were gathered each year at the study site when ripe, i.e. July, and stored at room temperature until sowing. Each year seeds ripened in the corresponding summer were sown. The viability of laboratory-stored, air-dry seed is maintained at a high level for at least 5 years (Marshall 1967). To measure emergence rates in the field, 100 diaspores were scattered evenly over 10 x 10 cm-plots in three successional stages (*Corynephorus* site, ruderal site, pioneer forest site). Sowing took place in October 2001, 2002 and 2003, respectively. Results of earlier experiments indicated that it was necessary to fence plots with plastic sheets to prevent the diaspores from getting blown away by the wind. The effect of the fencing on natural emergence was evaluated by using fenced control plots into which no diaspores were sown. Each replicate consisted of one plot into which 100 diaspores were sown and a control plot. In the first year, diaspores were sown directly in the natural vegetation of the particular



successional stage. In the second and third year, disturbance was introduced as an additional factor. Each replicate consisted of two plot-pairs: One pair with the vegetation completely removed, one with natural vegetation cover of the particular successional stage. Into one plot of each pair, 100 diaspores were sown, the other plot served as a control. In each successional stage, blocks and plots were chosen at random. In each successional stage, 12 replicates were established in three random blocks in a factorial design. Each year, new plots were created in the immediate vicinity of the previous year plots.

The cover of open soil, herbs and cryptogams was estimated for all plots to the nearest 5%. Emergence was interpreted as the appearance of the cotyledon.

After first emergence, seedlings were counted regularly in all plots. Natural emergence in the control plots gave information about the amount of diaspores in the soil. Emergence rates were estimated as the difference in seedling numbers in control and sowing plots, divided by the number of supplemented seeds.

Survival rates were assessed by counting survivors in the following spring. Emergence rates of the ruderal sites in the third year were not taken into account, because wild boar had destroyed all sowing quadrats.

The viability of seeds was determined each year in three climatic chambers at alternating light and temperatures (12 h dark, 10°C, 12 h light, 18°C) to test whether emergence rates were consistent over years. Each climate chamber contained 10 petri dishes with 50 diaspores. Petri dishes were controlled daily within the first 2 weeks and then weekly. Germinated diaspores were removed. In the first year, 67.3 % of the seeds germinated, 52.1 % in the second year, and 55.1% in the third year. Thus, germination rates in the laboratory were significantly higher in the first year than in the second and third year (Pairwise comparisons with Bonferroni adjustment, ER\_1 vs. ER\_2:  $T = 5.05$ ,  $p < 0.001$ , ER\_1 vs. ER\_3:  $T = 3.87$ ,  $p = 0.001$ , ER\_2 vs. ER\_3:  $T = -1.0$ ,  $p = 0.32$ ).

### **3.3 Data analysis**

Data were analysed with the software package SPSS for windows (version 11.5, SPSS inc.).

Nested ANOVAs were constructed with the dependent variables emergence rate and survival rate. Year (3 years) and successional stage were the fixed factors, with block nested within stage and between-plot variation as error term. To analyse the effect of

disturbance, similar ANOVA models were constructed with the dependent variables emergence rate and survival rate, and treatment (disturbed vs. undisturbed) as additional fixed factor. Post-hoc tests and pairwise comparisons (t-test for paired and unpaired samples, respectively) with Bonferroni correction were used to evaluate the specific differences in demographic parameters between years and successional stages.

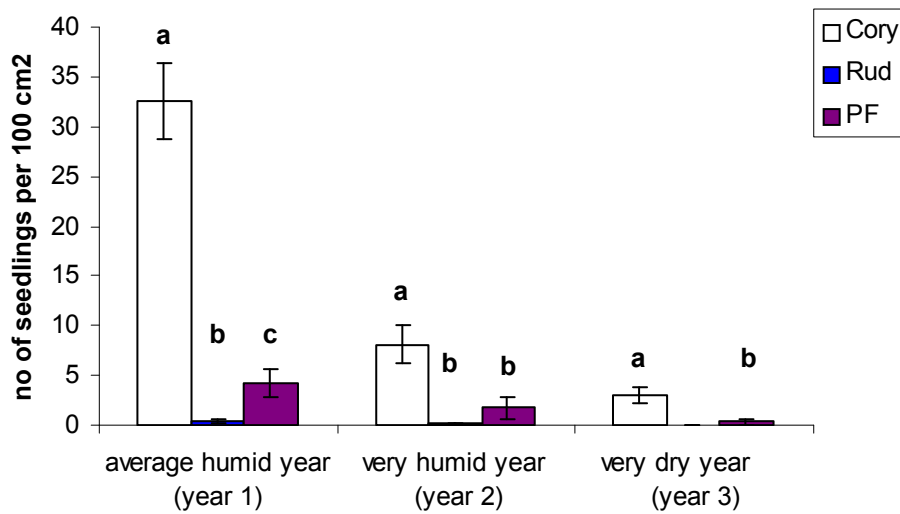
Emergence rates in the climate chambers were compared between years by means of mixed-model ANOVA with year as fixed effect and chamber as random effect.

## **4. Results**

### **Natural Emergence Densities**

Natural emergence densities in control plots (no diaspores sown) were highest in the *Corynephorus* site and lowest in the ruderal sites (Fig.1). Consequently, successional stage had a significant effect in the ANOVAs, as well as year and the year x successional stage interaction (Table 2). In the first year, emergence densities differed significantly between all three successional stages, being highest in the *Corynephorus* site and lowest in the ruderal sites. In the second, humid year, emergence densities were significantly higher in the *Corynephorus* site than in the other two successional stages. In the third, very dry year, they were significantly higher in the *Corynephorus* site than in the pioneer forest site (ruderal site missing) (Fig. 1).

In the *Corynephorus* site, natural emergence density differed significantly between all three years (post-hoc test with Bonferroni correction). In the pioneer forest site, natural emergence densities differed significantly between the average humid first and the very dry third year. In both successional stages, the highest emergence density occurred in the first year, the lowest in the third, corresponding with the precipitation pattern directly during and after sowing.



**Fig. 1: Mean number of seedlings (natural emergence densities) (+ SE) in unmanipulated control plots for *Corynephorus canescens* in 3 years and 3 successional stages.** Cory: *Corynephorus* site, Rud: ruderal site, PF: Pioneer forest site. Different letters indicate significant differences in emergence rates between successional stages within each year (post hoc test with Bonferroni correction,  $p < 0.01$ ). Note that data for the Rud site are missing in year 3.

**Table 2: F-values obtained in 2-way ANOVA for the effect of year and successional stage on natural emergence rates** \*\*\* $p < 0,001$ , \*\*  $p < 0,01$ , \*  $p < 0,05$ .

Effect (df)	Natural Emergence Rate
Successional stage (2)	15.17*
Year (2)	25.87**
Block (2)	7.03**
Year x Successional stage (4)	11.08**
Year x Block (4)	3.24*
Successional stage x block (4)	9.44***
Year x Successional stage x Block (8)	5.19***

### Emergence rates in undisturbed sowing quadrats

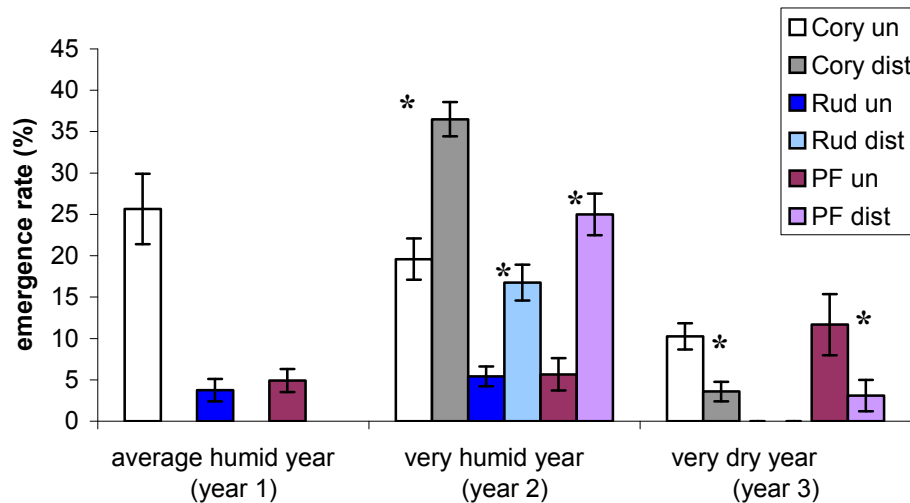
Mean emergence rates in undisturbed sowing quadrats showed patterns similar to natural emergence densities: Emergence rates were highest in the *Corynephorus* site and lower in the pioneer forest sites and in the ruderal sites (Fig 2), resulting in a significant effect of successional stage in the ANOVAs (Table 3). However, significant interactions between successional stage and year (Table 3) indicated that emergence rates decreased through the years in the *Corynephorus* sites, but increased in the two later successional stages (Fig. 2).

In the average humid first and the very humid second year, emergence rates in the *Corynephorus* site were significantly higher than those in the ruderal and pioneer forest site, while in the dry third year, emergence rates did not differ significantly between successional stages.

### Disturbance effects

Similar to the undisturbed plots, successional stage significantly affected emergence rates in disturbed plots, being higher, on the average, in the early successional stages. However, between-stage differences were not significant in the third dry year. Significant differences in emergence rates between disturbed and undisturbed plots with generally higher emergence in open spaces were obtained in all three successional stages in both years (Fig. 2).

A significant interaction between treatment and year (Table 4) indicated that in the third year, disturbances had an opposite effect than in the second: while in the second, humid year, emergence rates were significantly higher in disturbed plots, they were significantly lower in disturbed plots in the dry third year (Fig. 2).



**Fig.2: Mean emergence rates (+ SE) of *Corynephorus canescens* in 3 years in 3 successional stages under 2 disturbance regimes.** Cory: *Corynephorus*-site, Rud: ruderal site, PF: Pioneer forest-site. un: without disturbance, dist: with disturbance. Asterisks indicate significant differences between disturbances regimes ( $p < 0.05$ ). Note that data for the Rud site are missing in year 3 and there was no disturbance treatment in the first year.

**Table 3: F-values obtained in nested ANOVA for the effects of successional stage and year on emergence-rates in undisturbed plots.** Block was treated as nested within stage. \*\*\*  $p < 0,001$ , \*\*  $p < 0,01$ , \*  $p < 0,05$ , n.s.: not significant.

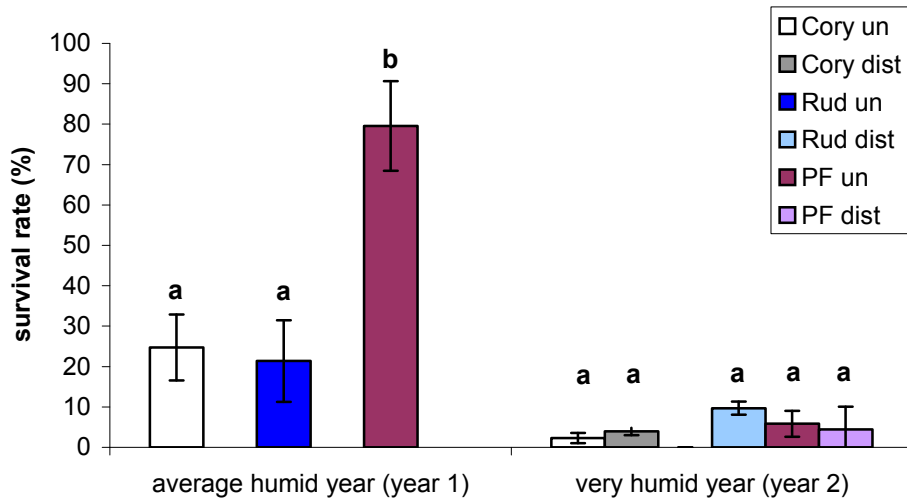
Effect (df)	Emergence rate
Year (2)	0.90 n.s.
Successional stage (2)	16.44 *
Block (2)	0.05 n.s.
Year x Successional stage (4)	7.28 **
Year x block (4)	3.03*
Successional stage x block (4)	2.33 n.s.
Year x successional stage x block (8)	2.47 n.s.

**Table 4: F-values obtained in nested ANOVAs for the effects of year, successional stage and treatment (disturbance) in the second and third year.** Block was treated as nested within stage, pair as nested within block.\*\*\*  $p < 0,001$ , \*  $p < 0,05$ , n.s.: not significant.

Effect (df)	Emergence rate
Year (1)	138.32 ***
Successional stage (2)	32.27 ***
Treatment (1)	22.78 ***
Block (6)	2.31 n.s.
Pair (27)	0.83 n.s.
Successional stage x Year (2)	12.17 ***
Treat x Year (1)	84.62 ***
Treat x Successional stage (2)	0.02 n.s.
Year x Successional stage x treat (2)	4.76 *
Year x block (6)	1.24 n.s.
Year x pair (27)	1 n.s.

### Survival rates

Survival rates, i.e. the percentage of the germinated seeds that survived until the next spring are shown in Fig. 3. Pairwise comparisons indicated that survival rates in undisturbed plots differed significantly between the first and the second year in the pioneer forest site ( $t = 7.76$ ,  $p < 0.001$ ), but not in the ruderal site ( $t = 1.93$ ,  $t = 0.080$ ). In the *Corynephorus* site, the difference was not significant after using Bonferroni adjustment ( $t = 2.76$ ,  $p = 0.018$ ).

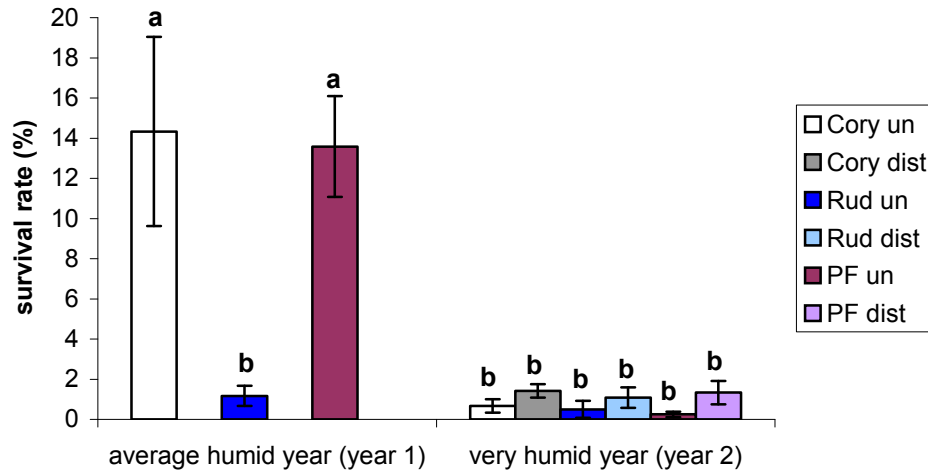


**Fig. 3: Mean survival rates (+ SE) of *Corynephorus canescens* based on germinated seeds in 2 years in 3 successional stages under 2 disturbance regimes.** Cory: *Corynephorus*-site, Rud: ruderal site, PF: Pioneer forest-site, un: without disturbance, dist: with disturbance (vegetation removal). Different letters indicate significant differences in survival rates between successional stages within each year (post hoc test with Bonferroni correction,  $p < 0.01$ ). Note that there was no disturbance treatment in the first year.

**Table 5: F-values obtained in nested ANOVA for the effects of successional stage and year on survival rates in undisturbed plots.** Block was treated as nested within stage. \*\*\*  $p < 0,001$ , \*\*  $p < 0,01$ , \*  $p < 0,05$ , n.s.: not significant.

Effect (df)	Survival rate
Year (1)	31.29*
Successional stage (2)	20.30**
Block (2)	1.71 n.s.
Year x Successional stage (2)	14.97*
Year x block (2)	1.44 n.s.
Successional stage x block (4)	0.61 n.s.
Year x successional stage x block (4)	0.59 n.s.

Successional stage and year had a highly significant impact on survival rates in undisturbed plots and the successional stage x year interaction was statistically significant (Table 5). This indicates that between-habitat variation in survival rates was year-dependent: In the average humid first year, survival rates in the pioneer forest were significantly higher than in the other habitats. In the humid second year, there were no significant differences between successional stages, and survival rates were below 6% in all sites under both treatments (Fig. 3).



**Fig. 4: Mean survival rates (+/- SE) of *Corynephorus canescens* based on originally 100 sown diaspores in 2 years in 3 successional stages under 2 disturbance regimes.** Cory: *Corynephorus*-site, Rud: ruderal site, PF: Pioneer forest-site, un: without disturbance, dist: with disturbance (vegetation removal). Different letters indicate significant differences in survival rates between successional stages within each year (post hoc test with Bonferroni correction,  $p < 0.01$ ). Note that there was no disturbance treatment in the first year.

Treatment had no influence on survival rates in all three successional stages ( $F = 2.53$ ,  $p = 0.12$ ). Using the originally sown 100 diaspores as the reference value, establishment rates in the first year in the *Corynephorus* site and the pioneer forest site were almost equal, and were significantly higher than those in the ruderal site (Fig. 4). This was due to the high emergence rates but low survival rates in the *Corynephorus* site and vice versa in the pioneer forest sites.

In the second year, establishment rates did not differ between successional stages.

## 5. Discussion

Our overall results highlight the crucial importance of small-scale disturbances for the emergence of a key species of open grasslands, *C. canescens*. However, the importance differed considerably between successional stages and changed corresponding to year-to-year variation, indicating complex interactions of environmental factors for the establishment of *C. canescens*.

### **Timing of small-scale disturbances and establishment probabilities of *C. canescens***

Our data indicated that disturbance promoted emergence in the rather humid year, while the opposite was found for the very dry year. Since emergence rates in the climate chambers did not differ between both years, it seems likely that environmental variation rather than seed quality was responsible for the differences in emergence rates in the field. Apparently, when soil moisture was sufficient, the main factor limiting *C. canescens* establishment was competition. However, low emergence rates in the dry year indicated that water became the overriding factor limiting establishment probabilities. Since the disturbances creates patches, which are more exposed to light and high temperatures, they imposed negative effects in the dry year. This is concordant with results from Ryser (1990) who found that under very dry conditions, mortality in gaps might be higher than in closed vegetation. The finding also supports the conclusion made by Pickett and White (1985) that disturbance may interact with stress, resulting in different physical effects of a disturbance at a given site. Further, it demonstrates that establishment processes are largely controlled by environmental variability (Olsvig-Whittaker 1988, Wilson 1990, Jentsch et al 2002). This finding is crucial for habitat management of dry habitats, since it highlights the importance of the correct timing of the disturbance for promoting early successional species. Namely, disturbances, when applied in dry years, may have unwanted detrimental effects on the species' establishment.

In addition to between-year timing of disturbance, within year timing has to be taken into consideration, too. Namely, our findings suggest that survival rates were not affected by disturbance, while emergence rates showed a very strong response. This highlights that the optimal strategy for promoting *C. canescens* is to apply disturbances just before seed dispersal and not during dry years.

### **Refuge function of late successional stages**

Our overall findings are furthermore intriguing in that they suggest an important role of late successional stages for the early establishment of *C. canescens* and persistence of this species in the landscape. Namely, in years water was not limiting, *C. canescens* emerged in higher numbers in open successional stages. However, in the dry year, higher success in the late stages suggests facilitation of *Corynephorus* by late successional species. Thus, as predicted by the stress gradient hypothesis (Bertness and



Callaway 1994, Callaway and Walker 1997), the outcome of biotic interactions shifted from competition during wet years to facilitation during dry years.

Our most intriguing result was the fact that in the extremely dry year, emergence rates did not differ between *Corynephorus*- and pioneer forest site in both disturbed and undisturbed plots. This was probably due to the extremely dry September, which led to low emergence rates in all successional stages. In this very dry year, emergence rates were considerably lower in the *Corynephorus* site than in the first two years, whereas in the pioneer forest sites emergence rates did not differ between years. Thus the “safeness” of a microsite clearly varied from one year to the next (Fowler 1988).

Our data furthermore indicate that safe sites for emergence are characterised not only by open soil, but also by vegetation cover in the shrub-layer and humidity. However, the specific characteristics necessary for successful establishment vary from year to year. Namely, the results demonstrate that survival rates of *C. canescens* were highly variable between years. This is in accordance with Symonides (1977) who reported significant differences in the mortality of seedlings of *C. canescens* from year to year. Symonides (1977) suggested that the main reason for the yearly changes in survival was water availability.

Establishment rates, i.e. the composite measure of regenerative success were equally high in the *Corynephorus*- and the pioneer forest sites in the first and second year. This is interesting since apparently, the *Corynephorus*-site, which was suitable for seedling emergence was not as suitable for seedling establishment, whereas the pioneer forest sites favoured seedling establishment to a much larger extent than emergence. Evidently, emergence and establishment requirements were quite different, highlighting the importance of the regeneration niche (Grubb 1997). Similar findings have been obtained in previous studies (e.g. Schupp 1995, Isselstein et al. 2002, Elmarsdottir et al. 2003). This suggests a within-individual conflict (Schupp 1995), occurring when conditions are advantageous for one developmental stage and disadvantageous for another. Interestingly, facilitation apparently dominated recruitment probabilities at the seedling establishment phase, while no interaction or competition dominated earlier (i.e. during germination). This contradicts results from Callaway and Walker (1997) who suggested that facilitation is more important at early life stages than at late stages.

Pioneer forests were not only advantageous for emergence, but also for survival of seedlings: In the pioneer forests, survival rates reached nearly 80 % in the first year in undisturbed plots, probably due to an improved moisture and temperature regime beneath the pine trees. The importance of protection against water loss and desiccation for successful emergence and establishment has been emphasized by many authors (Harper et al. 1965, Sheldon 1974, Hamrick and Lee 1987). Litter, which may have had a negative influence on emergence, is supposed to have a lower effect on seedling establishment (Xiong and Nilsson 1999).

In summary, late successional stages are not necessarily detrimental for the persistence of open habitats, but play an important role for sustaining early successional stages and thereby for maintaining species richness on a regional scale. Namely, given sufficient seed-availability, the pioneer-forest may be considered a refuge habitat for *C. canescens*. This indicates that facilitation may be an important mechanism for the persistence of protected species in metacommunities (Bruno et al. 2003). Thus successful management of open habitats may require a landscape scale-approach and include active management of adjacent late successional habitats such as pioneer forests.

In contrast to the pioneer forests, the ruderal sites indeed were detrimental for pioneer species, being inappropriate for emergence as well as for seedling survival. This was probably due to the tight matting of the roots of the *Tanacetum vulgare* dominated sites and to different soil properties, which inhibit emergence. Jumpponen et al. (1999) suggested that smooth and compacted surfaces provide few possibilities for successful penetration of the surface by the emerging radicle. Rychnovská-Soudková (1961) suggests that *C. canescens* with its high rate of root transpiration may be limited in later successional stages by decreased aeration due to accumulation of humus.

## **6. Conclusions**

The overall results of this study demonstrate that late successional stages may be of great importance for the persistence of pioneer species during stressful years. Thus, management measures should not only focus on grasslands dominated by *C. canescens*, but should include adjacent pioneer forests with *C. canescens* in the ground layer. However, the beneficial effects of late successional stages for pioneers is traded off against detrimental effects such as being sources for propagules of woody species, which may encroach adjacent open grasslands.

Given our findings and those of previous studies (Jentsch 2001), we suggest that more thought should be given to developing management strategies, which explicitly consider small-scale disturbances. However, if artificial disturbance is adopted as a measure for restoration of *Corynephorus*-grasslands, extremely dry years should be avoided or pioneer forests should be subjected to disturbances, where applicable followed by artificial seeding.

### **7. Acknowledgements**

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