REINTRODUCED MOWING CAN COUNTERACT BIODIVERSITY LOSS IN ABANDONED MEADOWS

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With 4 figures, 1 table, 3 photos, 2 appendices and 1 supplement
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Summary: Habitat loss is one of the primary environmental causes of biodiversity decline across scales; locally to globally. Ecological restoration is acknowledged as an important tool to counteract this negative trend. The semi-natural calcareous sand dune meadows in south-western Norway are known for their high species diversity, much like similar habitats of high conservation value across Europe today. The recent cessation of grazing has caused a decline in several endangered species associated with these habitats due to the advancement of secondary succession. We conducted a long-term restoration experiment in semi-natural dune meadows over 16 years to examine if current trends in biodiversity loss could be reversed and at what time-scale restoration measures take effect. Three treatments were applied; mowing annually, mowing bi-annually, and a control (no mowing). In fields mown annually species richness increased significantly over time. However, the response was slow and significant effects were first seen after year 10. Fields mown bi-annually also showed a similar trend but the response was more variable. Several characteristic meadow species were favoured by annual mowing while they declined in the control fields. Principal component analysis (PCA) revealed a compositional shift, indicating the re-arrangement/-establishment of typical meadow vegetation in the mown sites, contrasting the further successional development in the control. Our results demonstrate the importance of long-term data in supporting good evidence-based management. Annual mowing is effectively restoring this unique habitat, but restoration efforts need to be sustained over many years to show positive effects.

Zusammenfassung: Der Verlust von Habitaten stellt eine der Hauptursachen für den Rückgang der Biodiversität, sowohl auf lokaler als auch auf globaler Ebene dar. Eine ökologische Wiederherstellung kann als wichtiges Instrument angesehen werden, diesem negativen Trend entgegenzuwirken. Die semi-natürlichen Kalk-Sanddünenwiesen im Südwesten Norwegens sind für ihre hohe Artenvielfalt bekannt, ähnlich wie entsprechende Lebensräume mit hohem Erhaltungswert anderswo in Europa. Die Aufgabe der Beweidung hat in der jüngsten Vergangenheit, im Zuge einer fortschreitenden sekundären Sukzession, zu einem Rückgang mehrerer gefährdeter, mit diesen Lebensräumen verbundener, Arten geführt. Über einen Zeitraum von 16 Jahren wurde ein Restaurationsexperiment in den semi-natürlichen Dünenwiesen durchgeführt, um zu prüfen, ob die Trends des Biodiversitätsverlustes rückgängig gemacht werden können und welcher zeitliche Maßstab anzusetzen ist. Es wurden drei unterschiedliche Maßnahmen verglichen; jährliches Mähen, zweijähriges Mähen sowie eine nicht gemähte Kontrollfläche. Auf den jährlich gemähten Flächen stieg die Artenzahl im Laufe der Zeit deutlich an. Allerdings war die Reaktion langsam und signifikante Effekte wurden erstmals nach 10 Jahren festgestellt. Das zweijährige Mähmanagement zeigte einen ähnlichen Trend, allerdings war die Reaktion insgesamt variabler. Mehrere charakteristische Wiesenarten wurden durch das jährliche Mähen begünstigt, während sie in den Kontrollfeldern zurückgingen. Eine Hauptkomponentenanalyse (PCA) zeigte eine kompositorische Verschiebung, welche auf eine Reorganisation / Etablierung der typischen Wiesenvegetation in den gemähten Standorten hindeutet; in deutlichem Kontrast zu der Entwicklung auf den nicht gemähten Kontrollflächen. Die Ergebnisse belegen die Bedeutung von Langzeitdaten für die Beurteilung von Restaurationsmaßnahmen. Jährliches Mähen wirkt effektiv auf diesen einzigartigen Lebensraum, aber um positive Effekte sicherzustellen, müssen die Wiederherstellungsbemühungen über viele Jahre hinweg aufrechterhalten werden.

Keywords: cessation of grazing, coastal sand dune meadows, long-term experiment, plant species richness, ecological restoration, semi-natural grasslands

1 Introduction

Habitat loss and land-use change are the primary environmental causes of biodiversity loss at local, regional and global scales (Wilcove et al. 2000; Balmford et al. 2005; Newbold et al. 2015). Ecological restoration can mitigate some of these adverse effects by increasing biodiversity resilience and ecosystem service delivery (Wortley et al. 2013). The semi-natural grasslands of northern Europe have a long management history, where management represented a type of disturbance pro-

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moting species diversity by increasing accessibility of light and heat and creating a heterogeneous habitat (Eriksson et al. 2002, 2015; Lindborg and Eriksson 2004; Brunbjerg et al. 2015). Changes in agricultural land-use practices during the second half of the last century have led to the abandonment of many European grasslands, including outfield areas in coastal Norway. Recent abandonment typically results in tree and bush encroachment and the loss of species diversity (Eriksson et al. 2002).

These adverse effects of land-use change call for restoration measures in particularly valuable habitats (Moog et al. 2002; Roze and Lemauviel 2004; Måren et al. 2008; Måren and Vandvik 2009). Recently, the Norwegian government prioritized five endangered nature types as 'selected nature types', including traditional meadows (Directorate for Nature Management 2011). At these high latitudes, meadows were important sources of winter fodder. The extensive use of the land produced unique semi-natural open habitats with high species diversity (Austrheim et al. 1999; Jantunen and Saarinen 2002; Vandvik and Goldberg 2006; Johansson et al. 2008; Emanuelsson and Petersson 2009; Brunbjerg et al. 2012, 2015). The modernization of agriculture has caused major changes in land-use, with transitions from traditionally managed meadows to fully cultivated, deep-ploughed, and heavily fertilized high-yielding fields, or contrastingly, to discontinued management and subsequent succession. Such transformations have had an immense negative effect on biodiversity, and in effect the remaining semi-natural grasslands hold a high number of Red-Listed species. In Norway, 105 of the 246 Red-Listed vascular plant species (ca. 43%) are found primarily in semi-natural habitats (Henriksen and Hilmo 2015).

Traditionally, hay meadows were not treated with fertilizers and the productivity levels were typically low to intermediate, but could support a high number of species (Lundberg and Handegård 1996; Fischer and Stöcklin 1997; Franzén and Eriksson 2001; Pywell et al. 2002; Walker et al. 2003), and these meadows have declined drastically across Europe (Johansson 2008; Rydgren et al. 2010). Abandonment is typically accompanied by an increase in species less tolerant to grazing and/or mowing, and over time, a few species tend to dominate. Mowing as a restoration measure, has shown good results as a means of reducing nutrient availability and increasing light levels, in species-rich grasslands across Europe, as the suppression and removal of tall dominant species enables the re-establishment of traditional grassland species, if an adequate source of propagules is still available (von Blankenhagen et al. 2005; Eriksson et al. 2015; Rydgren et al. 2010). The restoration of traditional semi-natural grasslands has become a conservation priority (management target). However, more research is needed to facilitate best practice and promote evidence-based management for such restoration projects in different regions. Here, evidence-based practice is described as the process of systematically finding, appraising, and using evidence of the effectiveness of interventions for informed decision making (Sutherland et al. 2004).

The aims of this study were to investigate (1) if mowing can reverse plant species decline in abandoned coastal dune meadows, (2) whether mowing can reduce tall species growing in dense tufts, and (3) if characteristic and/or endangered species return with restoration efforts over time, and if this is the case, at what time scale. Mowing was experimentally reintroduced in 1999 with three treatment intensities; cut annually, cut bi-annually, and a control without cutting, and species richness and composition were recorded annually in permanent plots under these treatments over a period of 16 years from 1999 to 2014.

2 Materials and methods

2.1 Study area

The mowing experiment was carried out at the island of Karmøy in south-western Norway (59°15' N, 5°10' E, Fig. 1 and Photo 1). The study area covers *ca.*15 ha, situated on the western side of the island, in the sand dune area known as Åkrasanden. Mean annual precipitation is 1270 mm (1961–1990, eklima.no). May is the driest month of the year, with an average precipitation of 69 mm; while October is the wettest with an average of 154 mm. Mean annual temperature is 7.7 °C, which is rather mild for this latitude due to the North Atlantic Drift. August has the highest monthly average temperature of 14.3 °C and February the lowest of 1.7 °C. The growing season (daily mean temperatures > 6 °C) is 210 days (Lundberg 1998; eklima.no). The soils are composed of fine-grained marine sand, rich in minerals and nutrients. The dunes are well drained, and water stress is counterbalanced by the water-storage capacities of the soil's humus layer and the permanent plant cover. The humus layer increases

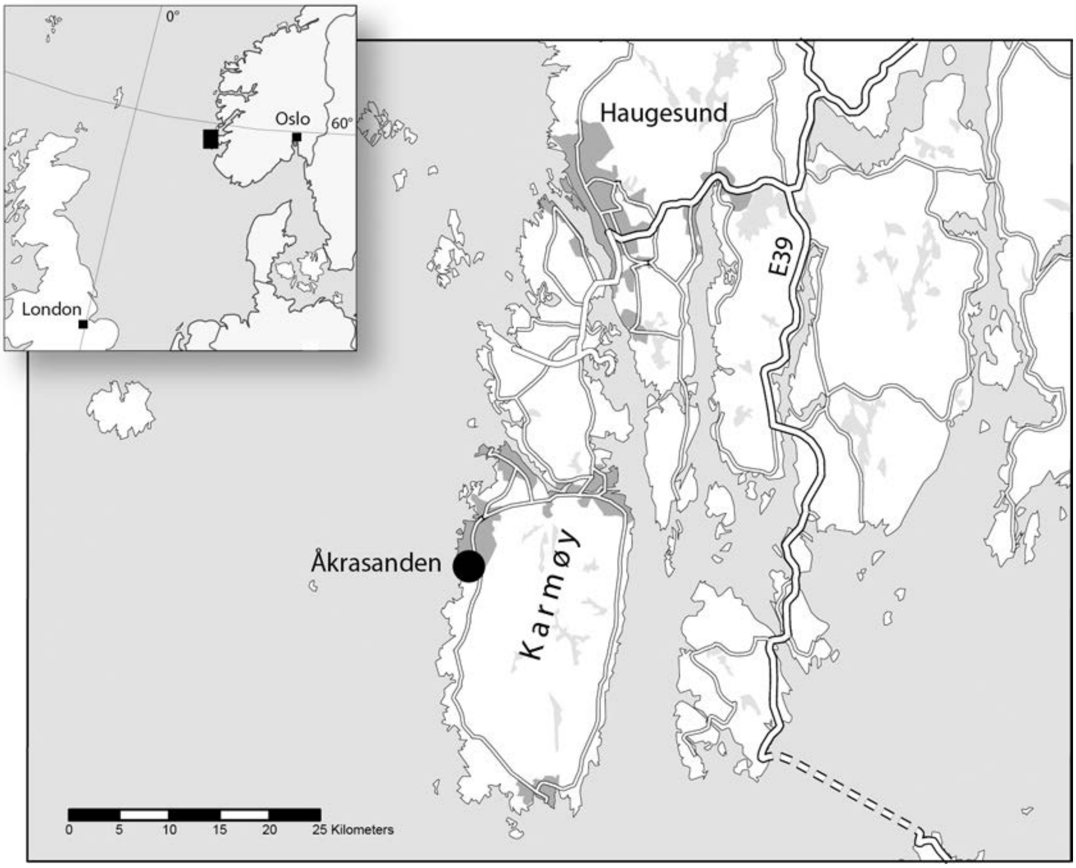

Fig. 1: Map showing the study area of Åkrasanden at the island of Karmøy on the West coast of Norway

the soil's exchange capacity; it is three times higher in dune meadows (10.8-33.1 milliequivalents/100g dry soil) than in the less-developed syrosems of the foreshore (Lundberg 1987, 1993). The soils are rich in calcium (206–601 mg/100g dry soil) and pH is in the range of 7.5-8.5 (Lundberg 1987).

The coastal dune meadows are part of the old farm 'Åkra', dating back to the Middle Ages (Lillehammer 1980), and they have probably been used for pasture and hay-fields for hundreds of years, maybe even longer. Until the 1960s dune meadows were mown in late June or early July, approximately six weeks later than modern meadows. The farms were small on a European scale, often <10 ha, and each farm typically had 6–7 cows, 2–3 calves and 20–25 sheep. In early spring and late summer, after the last mowing, the meadows were grazed by cattle. The fields of each farm were spread across the area and cattle grazed fields successively, often one week at a time. Grazing pressure was low and the late mowing allowed the seeds of grass- and flowering plants sufficient time to ripen. Over time this led to the development of species-rich dune meadows (Tüxen 1967; Lundberg 1987, 1993, 1998). After the 1960s the traditional management of mowing and moderate livestock grazing was discontinued in the study area, mirroring the development of much of coastal Western Norway, which has seen an abrupt discontinuation of management after WW2 (Vandvik et al. 2005, 2014). Typical meadow species, e.g. *Arenaria serpyllifolia* ssp. *lloydii*, *Botrychium lunaria*, *Erigeron acer*, *Gentianella amarella* ssp. *septentrionalis*, *G. campestris*, *Draba incana*, *Erophila verna*, *Gymnadenia conopsea, Saxifraga tridactylites*, *Trifolium arvense* and *T. campestre* are decreasing in both frequency and abundance on a regional scale, while more widespread species seem to be increasing. Some species, e.g. *Arnica montana*, *Coeloglossum viride* ssp. *islandica*, *Isolepis setacea*, and *Pseudorchis albida,* have even disappeared from the dune meadows (Lundberg 1998). Our site was in a state of late secondary succession before the onset of our mowing experiment in 1999 with *Arrhenatherum elatius, Festuca rubra, Galium verum, Geranium sanguineum,* and *Sanguisorba officinalis* as dominant species, however, none of these species had more than 50% cover.

Photo 1: Dune meadow, taken from the south towards the studied area on Karmøy, Western Norway. Photo: Anders Lundberg

2.2 Experimental design

The long-term experiment consisted of three management treatments; i) mown annually, ii) mown bi-annually (every other year), and iii) a control that was not mown. Within the study site at Åkrasanden we chose an area parallel with the ocean front, and approximately 50 m up-shore, for our experiment. We chose this area because it had relatively uniform meadow vegetation in 1999 with no prominent disturbance features (paths, exposed rocks, etc.) and a relatively uniform buffer zone bordering either the upper beach periphery or the more disturbed sections further up-shore (the area is a popular recreational site). Within this area we placed three large plots (40 m x 20 m), and one of the three management treatments were assigned randomly to each of these. Mowing was carried out using a motorized grass mower, and vegetation was cut about 5 cm above the ground surface. The cut vegetation was not removed but quickly air dried and blew away by the persistent coastal winds (pers. obs.). Within each plot we placed and marked 1 m x 1 m permanent quadrats; a total of 18 quadrats were established across the three large treatment plots, i.e. during the 16 years of the experiment a total of 288 vegetation recordings has been sampled. The first vegetation recording of all quadrats took place in Mid-August of 1999 (baseline), prior to the experimental mowing which also started in 1999, and was repeated annually at approximately the same time, including August of 2014, totalling 288 resampling points over the 16-year long experiment. Within each quadrat the abundance of each bryophyte and vascular plant species was measured using the Hult-Sernander cover-abundance scale (1 = < 6.25% cover, 2 = 6.25–12.5%, 3 = 12.5–25%, 4 = 25–50%, and 5 = 50–100%) (van der Maarel and Franklin 2013). Nomenclature of plant species follows Lid and Lid (2005). The mowing treatments were carried out later the same day as the vegetation recording.

2.3 Data analyses

To test for significant changes in species richness we used Dunnett's multiple comparison test considering the year before any treatment application (i.e., year 1999) as the baseline year for comparison. This indicates the time needed to restore species diversity under the different mowing regimes.

Detrended correspondence analysis (DCA; Hill and Gauch 1980) revealed that linear-based ordination methods were appropriate. To reveal the effects of different treatment and time on species composition a principal component analysis (PCA; ter Braak 1994; Jongman et al. 1995) was used. The environmental variables and their interaction (treatment x time) were fitted onto the ordination (R-function 'envfit') for interpretation of the patterns in species composition. Species abundances (in percentage, using the arithmetic means of the Hult-Sernander five-grade abundance scale, i.e. 1=3.125%, 2=9.375%, 3=18.75%, 4=37.5%, 5=75%) were down-weighted and log-transformed ($y' = \log_{10}(y + 1)$) before the analysis. Linear regressions were used to test the responses of individual species to the three treatments. We used linear regressions in order to identify species that are clearly increasing or decreasing over our treatment period. Particularly, we focused on two groups of species: (1) *target species*; species typical for well-managed meadows (based on Lundberg 1987, 1993, 1998) and (2) *undesirable species*; species not found in well-managed dune meadows in the region or species that have increased in abundance since meadows were abandoned and now suppress traditional dune meadow species. All statistical analyses were run in R, version 3.1.0 (R core team 2015) using the packages 'vegan' (Oksanen et al. 2013) for the ordination analysis and 'multicomp' (Hothorn et al. 2008) for the Dunnett's test.

3 Results

3.1 Plant species richness

We recorded altogether 46 taxa of plants over the 16 years of restoration (Appendix 1). Species richness was found to differ significantly between the three treatments ($P_{time:treatment} < 0.001$). Annual mowing was found to have a positive effect on species richness (increase) over time, whereas the opposite effect (decrease in species richness) was found for the control vegetation (Table 1, Fig. 2). We also saw a weak positive trend of bi-annual mowing but this was not statistically significant (Fig. 2b).

At the onset of the restoration experiment the median species richness was 14 (mown annually and mown bi-annually) and 16 (control) species, but after 16 years this changed to 19 (mown annually), 18 (mown bi-annually) and 10 (control) species, respectively. The increase in species richness under annual mowing was, however, gradual; only after 10 years we saw a significant increase (Fig. 2a, Table 1). Bi-annual mowing was found to increase species richness, too (Fig. 2), but the increase compared to the year before treatment was not statistically significant for any time period (Fig. 2c, Table 1). The analysis further revealed the within year variance in species richness for bi-annually mown and control quadrats to be greater than for quadrats mown annually where the number of species varied much less within years over the 16 years of restoration (Fig. 2).

Species richness over time was also tested as an average for quadrats (Appendix 2). The test revealed significant trends for all three treatments. Quadrats mown annually and bi-annually both increased in species richness, with $R^2 = 0.842$ and 0.570, respectively. In the control (never mown), a strong decline in species richness over time was found ($R^2 = 0.850$).

3.2 Plant species composition

The PCA revealed significantly different compositional trajectories of the vegetation under the different treatments over time (Fig. 3). Plant species composition was relatively similar at the onset of the study in 1999, featuring vegetation typical for dune meadows. In the Norwegian Red-List for nature types it is named southern dune meadow, and listed as endangered EN (Lindgard and Henriksen 2011). The ecology of the vegetation in the three large plots were similar, regarding soil properties, microclimate and time since abandonment, and the only major difference was the type of applied treatment in this experiment. However, we see movement away from the initial composition under all three treatments, where the control moves in a different direction (Fig. 3a), showing that the treatments had major impacts. Under the mowing treatments species composition developed in a similar direction (positive direction along PCA axis 1) over time, whereas the composition in the control developed in the opposite direction (negative direction along PCA axis 1). PCA axis 1 was mostly correlated with treatment type 'control' (r=-0.990, p=0.001), while axis 2 was mostly correlated with the bi-annual mowing treatment (r=-0.952, p=0.001). The species composition in the annually mown fields remained virtually unchanged from 2009 and onwards, whereas in the bi-annually mown fields, compositional change was still going on after 2009 (Fig. 3a). At the end of the study period, the species composition under the mowing treatments was characterized by typical dune meadow species such as the target species *Achillea millefolium, Briza media, Pimpinella saxifraga*, and *Thalictrum minus*, and the mosses *Brachythecium albicans* and *Plagiomnium undulatum* (Fig. 3b).

3.3 Individual species' responses to restoration treatments

The five most frequently occurring species over the 16 years of recording were *Festuca rubra* (286), *Geranium sanguineum* (285), *Vicia cracca* (275), *Galium*

Tab. 1: Results from the Dunnett's multiple comparison test. Year 1999 is used as baseline for all comparisons. Lwr/upr = lower/upper limit of the confidence interval for the difference (diff) between the mean of the treatment and the control group (year 1999); p adj = adjusted *P*-value. Only year pairs showing significant difference in species richness are shown. Treatment with bi-annual mowing did not result in any significant changes.

Annual mowing					No mowing				
1999-	diff	lwr	upr	p adj	1999-	diff	lwr	upr	p adj
2009	3.50	0.57	6.43	<0.001					
2010	4.12	1.19	7.06	<0.001					
2011	3.87	0.94	6.81	<0.001					
2012	5.00	2.07	7.93	<0.001	2012	-6.50	-12.64	-0.36	0.004
2013	4.62	1.69	7.56	<0.001	2013	-6.67	-12.80	-0.53	0.003
2014	3.87	0.94	6.81	<0.001	2014	-6.00	-12.14	0.14	0.010

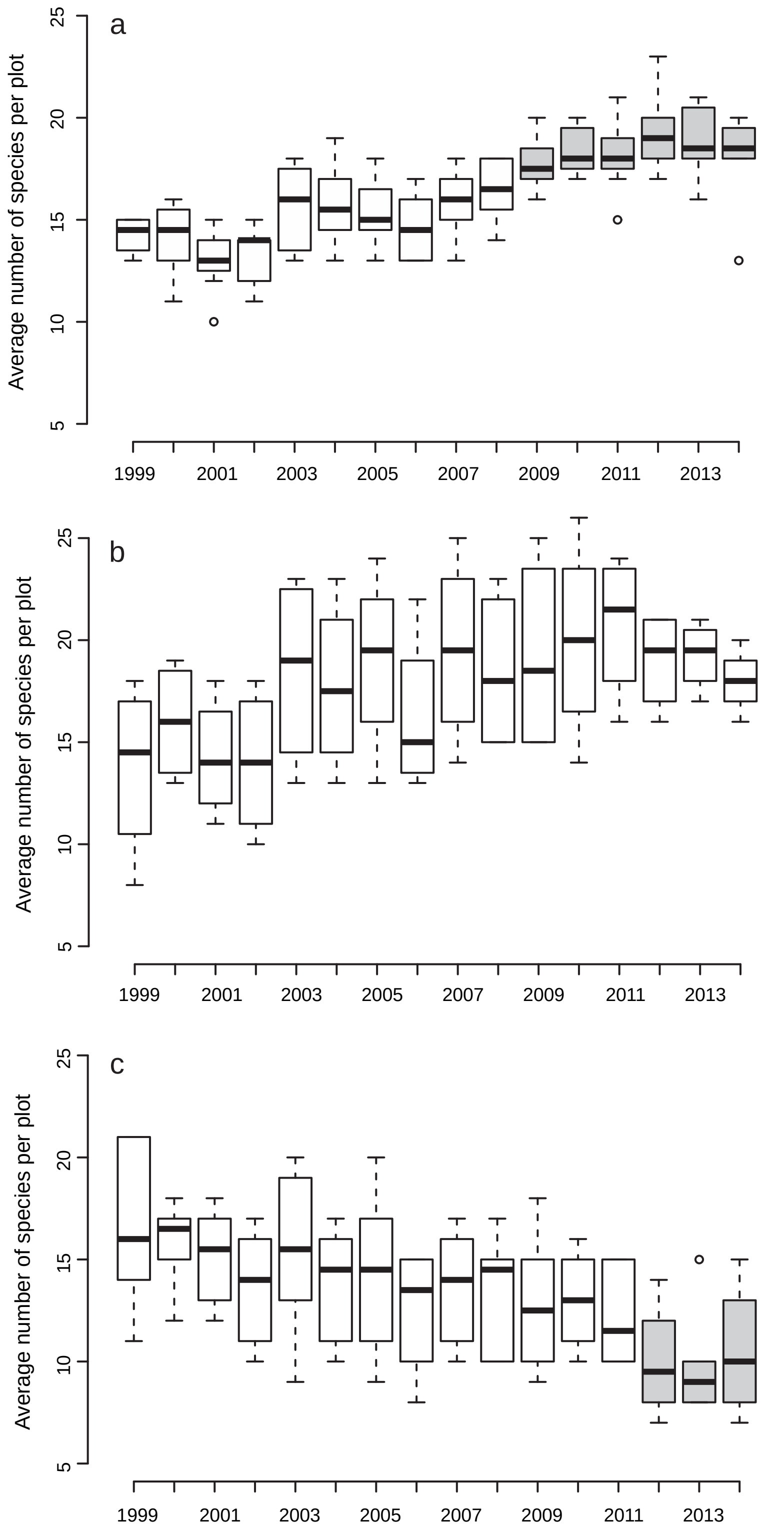

Fig. 2: Average species richness in plots under the three management treatments; (a) annual mowing, (b) bi-annual mowing (every other year), and (c) control (no mowing) over the 16 years of restoration experiment from 1999 to 2014. Box–Whisker plots with median (thick line), 25 and 75%-quantiles (upper/lower box line) and outliers. Years with significantly different species richness compared with baseline year 1999 (based on Dunnett's multiple comparison test) are indicated with grey boxes (see Appendix I for details).

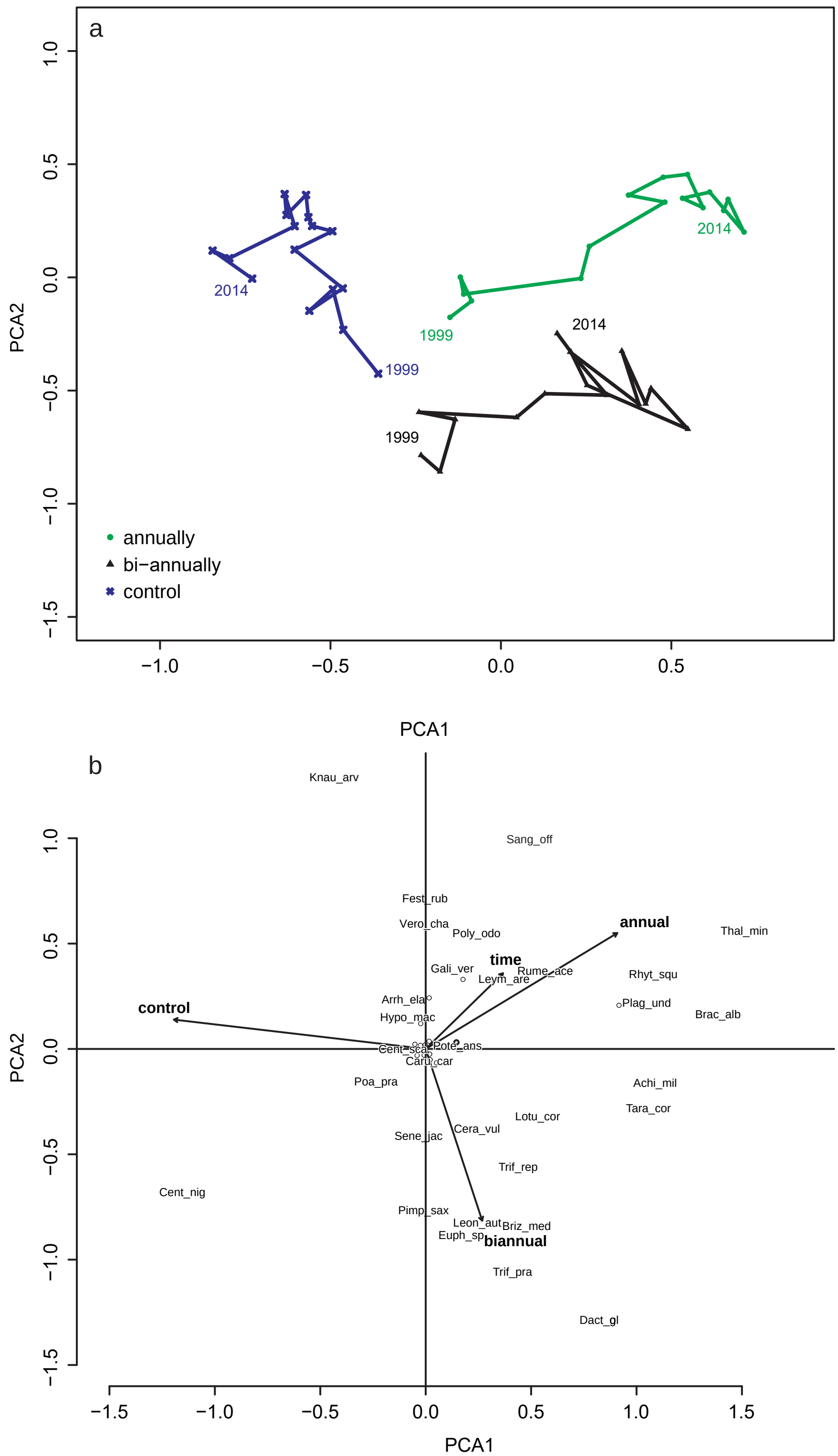

Fig. 3: PCA ordination plot of (a) the change in species composition over time for each of the three mowing treatments (species composition of all plots per year and treatment are depicted using centroids, first and last year shown), and (b) species responses to time and treatment, in the dune meadows of Karmøy, Western Norway, from 1999 to 2014 (see Appendix 1 for 4+3 letter species abbreviations and for details on target/undesirable species).

verum (270), and *Arrhenatherum elatius* (270), the numbers in parenthesis indicating the occurrence in a total of 288 records (Appendix 1). All of these were present and abundant in all three treatments in 1999. The five least commonly occurring species were *Carex arenaria* (2), *Silene uniflora* (2) *Linum catharticum* (3) *Campanula rotundifolia* (3) and *Viola tricolor* (3). Species characteristic for traditional dune meadows, including *Achillea millefolium*, *Galium verum*, *Geranium sanguineum*, *Knautia arvensis*, and *Thalictrum minus,* increased in abundance in fields mown annually, and some new species appeared, such as *Rumex acetosa*, and the mosses *Brachythecium albicans* and *Plagiomnium undulatum* (Appendix 1, Supplement I). In fields mown bi-annually we see the same picture but with less pronounced trends (Fig. 4). Here, the undesirable species *Dactylus glomerata* and *Senecio jacobea* decreased significantly over time and the target species *Galium verum*, *Geranium sanguineum*, *Euphrasia* sp. and *Knautia arvensis* increased. In the control treatment traditional meadow species like *Leontodon autumnalis*, *Lotus corniculatus*, *Pimpinella saxifraga*, *Poa irrigata*, and *Trifolium pratense* disappeared over time and several others decreased in abundance, especially *Geranium sanguineum*. This decrease was paralleled by an increase in the abundance of *Arrhenatherum elatius* and *Centaurea nigra*.

Species showed different responses over time within the different treatments. Under the annual mowing treatment four of the traditional dune meadow target species, *Galium verum*, *Geranium sanguineum*, *Knautia arvensis*, and *Thalictrum minus,* increased over time (Photo 2, Fig. 4, Appendix 1, Supplement I). Another target species, *Pimpinella saxifraga*, showed a significant decrease across all treatments (Fig. 4). The undesirable species *Taraxacum cordatum* and *Heracleum sphondylium* showed an increase, while the most problematic one, *Arrhenatherum elatius* (Photo 3), showed a clear decrease with the annual mowing treatment, contrary to in the bi-annual mowing treatment and in the control where it showed an increase (Fig. 4). Another target species, *Euphrasia* sp., showed an increase under bi-annual mowing, while the undesirable species *Dactylus glomerata* showed a clear decrease under the same treatment (Fig. 4).

Another tall species, *Leymus arenarius,* sometimes occurring in dense clusters did not show any linear trend over time in any of the treatments; its frequency and abundance were continuously low, indicating that this is not a worrisome species in these dune meadows. Without any mowing treatment the target species *Geranium sanguineum* really suffered a substantial decrease in abundance (Fig. 4).

4. Discussion

4.1 Changes in plant species richness and composition over time

We found significant changes in both species richness and composition alongside the restoration treatments over 16 years in the abandoned dune meadows monitored. Increased species richness may not be considered as good per se, as adding more weeds or undesirable species also would increase species richness. However, for the annually mown quadrats, species richness was found to increase significantly due to an increase in target species. Mowing releases space for these light-demanding and less competitive species. In bi-annually mown quadrats some target species increased but less so than in quadrats mown annually and some target species also declined. Bi-annual mowing also caused some

Photo 2: Field mown annually dominated by *Geranium sanguineum,* photo taken in 2009, ten years after the mowing started. Photo: Anders Lundberg

Photo 3: Field mown annually dominated by *Arrhenatherum elatius*, photo taken in 2000, one year after the mowing started. Photo: Anders Lundberg

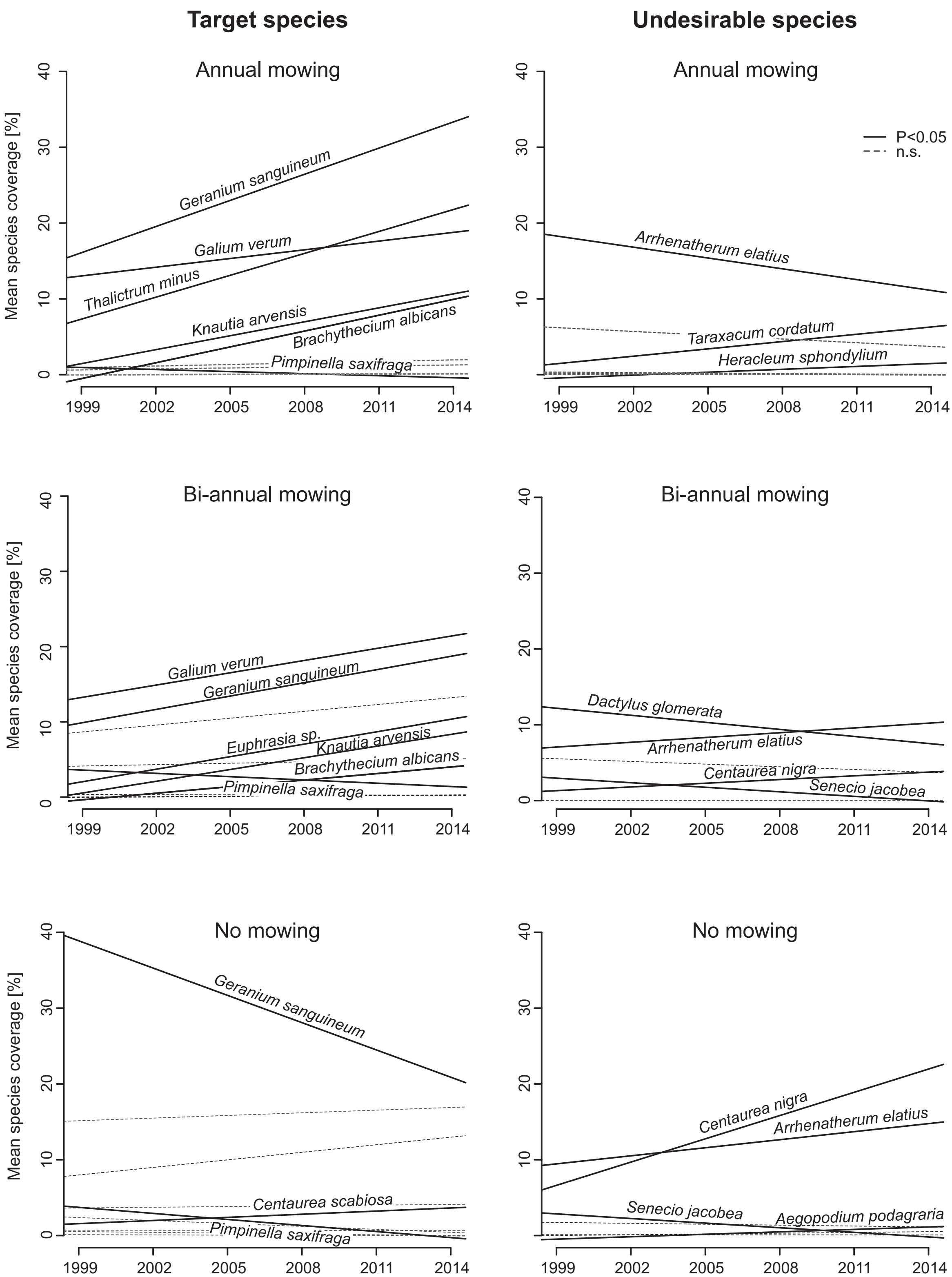

Fig. 4: Linear regressions showing trends in species' mean coverage over time (1999–2014) for 14 target species (left) and 8 undesirable species (right) under the three treatments annual mowing, bi-annual mowing, and control (no mowing). Only species showing a significant positive or negative linear response over time are depicted by name and a solid line.

undesirable species to increase. The lack of mowing in the control treatment caused tall turf-forming species to establish and spread, and with time, we saw a gradual decline in species richness. This picture mirrors development elsewhere; over the past century semi-natural open habitats have suffered dramatic declines in extent all over Europe due to land-use change and fragmentation (Wilcove et al. 2000; Balmford et al. 2005). However, many grassland species with relatively large populations, slow intrinsic dynamics and long life cycles, appear to occur as remnant populations and communities in modern landscapes (Eriksson 2000; Helm et al. 2006), giving hope to successful restoration outcomes in such settings. Consequently, in restoration projects the influx of propagules versus the local availability of propagules is of importance. Stampfli and Zeiter (1999) found that spontaneous long-distance immigration (< 25 m) of native meadow species was insignificant in a restoration study involving mowing of species-rich abandoned meadows in the Alps. They concluded that the traditional species composition of these meadows could not easily be restored after abandonment by mowing alone because many of the meadow species did not have persistent seed banks and were absent from the extant vegetation. In our dune meadows at Karmøy, most traditional dune meadow species are still present, although some in all likelihood with significantly lower abundances than under active land-use. However, seeds are available and do spread in the meadows, as can be seen by the increase in the abundance of traditional dune meadow species under the mowing treatments. This makes a strong argument for scaling up restoration at this and similar sites where characteristic meadow species are still present, although in very low numbers. It is very important to utilize this window of opportunity before the system's extinction debt has been paid and these species disappear. The slow response of semi-natural populations and metapopulations to abandonment and fragmentation has important implications for conservation (Helm et al. 2006) because the transient time in species' responses provides an opportunity for conservation, involving strategic habitat restoration through evidence-based management. The increase in the abundance of some of these traditional dune meadow species may also be explained by increased vegetative dispersal as the abundance of tall, suppressing species decreased with time in the mowing treatments.

One or a few tall grass species often become dominant, overtopping many subordinate species, many of which may disappear or become less abundant as a result of the competition for light (Mitchley and Williems 1995; Losvik 2006). A dense field layer of tall grasses may also cause an increasing litter layer to be formed, inhibiting spore/seed germination and growth (McCain et al. 2010; Loydi et al. 2013). We found no or just a few mosses in the control quadrats, as opposed to the more developed moss layer with time in the annually mown vegetation. After removing 100% of two dominant grass species constraining plant diversity in prairie communities, McCain et al. (2010) found that light availability increased significantly, as well as forb productivity, forb cover, species richness, species evenness, and species diversity, as the removal of the most dominant grass species' provided an opportunity for seeded forb species to increase in abundance. This method is rather time-consuming and challenging for practical management over extensive areas. Encouraging the succession of the parasitic species *Rhinanthus minor* has been suggested as an alternative to targeted removal of tall grasses (Westbury 2004). For example, Davis et al. (1997) found a distinct decline in the proportion of grasses in species-rich grasslands when *Rhinanthus* was present, and a concomitant increase in the proportion of dicotyledones. Mowing is, on the other hand, a well-known and extensively used method to harvest biomass from dominant grass species, consequently altering the micro-site conditions for other, less competitive species. In our study, the dominant grasses received the same mowing treatment as the rest of the plant community, as is commonly practiced in restoration projects across Europe (Austrheim et al. 1999; Cousins and Eriksson 2008; Cousins et al. 2009; Moog et al. 2002). Additionally, mowing is time-efficient and allows the management of extensive areas in relatively short time, e.g. in this instance; one day a year.

In order to allow the detection of ecological change in the direction of the restoration target, it has been suggested that as much as 10 years of treatment might be required (Field et al. 2004; Koch et al. 2011; Joyce 2014), while others suggest a much shorter time (von Blanckenhagen and Poschlod 2005; Schrautzer et al. 2009; Joyce 2014), depending on the ecological and biophysical conditions of the system under restoration. Our study is more in line with the former, most likely explained by the northern location of our study area and the corresponding adverse climate conditions causing a relatively slow recovery. Consequently, we do raise caution against drawing firm conclusions from a typical research project spanning three to four years with regards to the degree of restoration success, regardless of system studied. Short investigation time may miss to pick up on a trend 'in the making', resulting in premature conclusions concerning the degree of restoration success. In an age of short funding schemes and high expectations of concrete policy- and management recommendations, it is utmost important to stress the role of time in ecological processes, and hence the value of long-term experiments.

4.2 Species specific responses to restoration treatments

Our analysis revealed that the responses to mowing treatments were mixed and species specific, as in the case of the two species *Leymus arenarius* and *Arrhenatherum elatius*. Although both species grow in dense tussocks, the tussocks of *L. arenarius* are more open and dispersed in the dune meadows than those of *A. elatius*. The former has its ecological optimum in the primary dunes, whereas in dune meadows it is usually sterile, more scattered, and less abundant (Lundberg 1993; Maun 2009). *Arrhenatherum elatius* is more common and appears with higher abundance in dune meadows than in other parts of the dune system. The occurrence and abundance of *A. elatius* was higher and increased over time, particularly in unmown areas. Here, *A. elatius* increased systematically in all quadrats, from 2 to 3 on the Hult-Sernander scale, corresponding to more or less a doubling in abundance, and this poses a serious threat to the less competitive characteristic meadow species which the restoration was aiming to promote (Appendix 1). Only three species of moss were recorded over the course of the study. The mosses *Brachythecium albicans* and *Plagiomnium undulatum* increased in abundance under the two mowing regimes in contrast to in the unmown control where they most likely got outcompeted by taller plants. In our study the control treatment corresponds to abandoned grasslands. The lack of mowing resulted in vegetation becoming denser over time, and some lower-statured species decreased in abundance, such as *Campanula rotundifolia*, *Euphrasia* sp. and *Viola tricolor*. Our results from Karmøy are consistent with Willems' (2001) findings that mowing as a restoration measure in abandoned limestone grasslands resulted in a marked increase in a number of short-lived species, such as *Arenaria serpyllifolia*, *Centaureum littorale* and *Linum catharticum*.

In a Swedish semi-natural grassland restoration Lindborg and Eriksson (2004) found that abundance of trees/shrubs and time since abandonment were positively associated with species richness at restored sites, while restored area size and time between abandonment of grazing and restoration did not. Our study shows that the species response curves indicate that a number of characteristic dune meadow species are positively affected by time since the practice of mowing was resumed. Lindborg and Eriksson (2004) underline that restoration of abandoned semi-natural grasslands is not a fast process, and should be continued over many years, as also our results indicate.

In summary, this analysis suggests that annual mowing has a positive effect on many of the characteristic dune meadow species, while a lack of mowing causes a further decrease in these and an increase of tall grasses repressing the forbs. Bi-annual mowing also has a positive effect on some dune meadow species but less so than in fields mown annually. Consequently, we suggest that the management practice constituting annual mowing should be scaled up to cover similar areas where the cessation of grazing and mowing has caused similar species declines in recent time. Additionally, management should be carried out with a long-term perspective in mind, and particularly for northern sites like ours. This research should be followed up by further investigations, including socioeconomic outcomes, particularly looking at local people's perceptions of restoration efforts and potential enhancement of ecosystem services, as suggested by Wortley et al. (2013). Depending on outcome, this could potentially anchor management more in local support.

5 Conclusions

Reintroduction of mowing in coastal dune meadows can reverse plant species declines in areas where seed-producing species are still present. Annual mowing in dune meadows results in increasing numbers and abundance of species present, and in particular of characteristic dune meadow species. Bi-annual mowing also increases the number and abundance of species, but to a more stochastic degree and at a slower speed than in fields mown annually. Abandonment (no mowing) over time causes a continued decrease in the number of species present, in particular characteristic dune meadow species, and an increase in undesirable species like in this case *Arrhenatherum elatius* and *Centaurea nigra*. Target species, e.g. *Geranium sanguineum*, show a strong increase in annually mown plots, a slight increase in plots mown bi-annually, and a strong decrease in the control.

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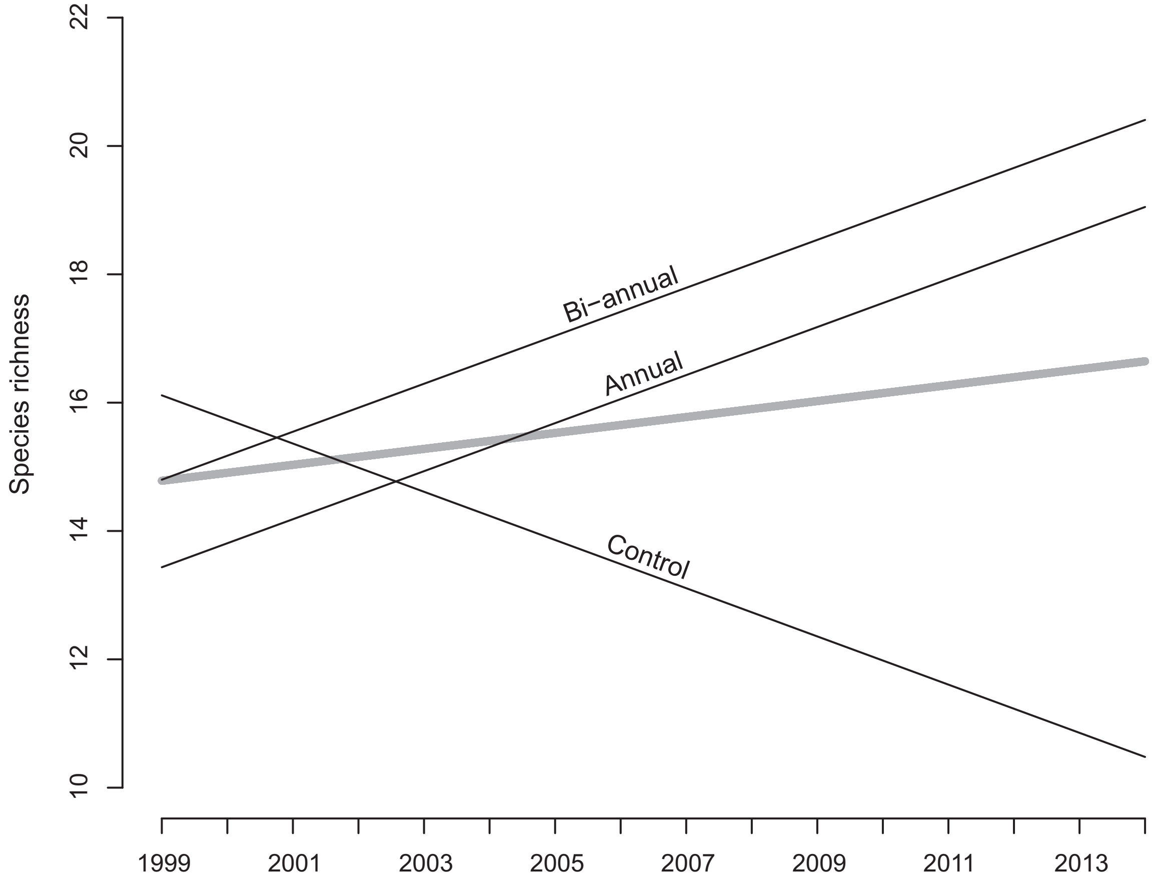
Appendix

Appendix 1: All recorded bryophyte and vascular plant species over the 16 years (1999–2014) of the restoration experiment in the dune meadows at Åkrasanden on the island of Karmøy, West coast of Norway, and results of linear regressions of the yearly mean species coverages with time for the three treatments. Species abbreviations of 4+3 letters used for the ordination diagram (Fig. 3b). C=chamaephyte, G=geophyte, H=hemicryptophyte, T=therophyte

Species	Acronym	Life form	Annually mown			Bi-annually mown			Control (never mown)		
			Intercept	Slope	P-value	Intercept	Slope	P-value	Intercept	Slope	P-value
*Brachythecium albicans**	Brac alb	Moss	-1397.01	0.70	0.000	-530.61	0.27	0.000	3.14	0.00	0.880
Plagiomnium undulatum	Plag und	Moss	-952.68	0.48	0.000	-137.83	0.07	0.000	0.00	0.00	NA
Rhytidiadelphus squarrosus	Rhyt squ	Moss	-863.85	0.43	0.001	-217.88	0.11	0.001	23.15	-0.01	0.330
Achillea millefolium	Achi mil	H, C	-901.99	0.45	0.016	-1303.43	0.65	0.001	469.86	-0.23	0.035
Aegopodium podagraria§	Aego pod	G, H	31.19	-0.02	0.346	0.00	0.00	NA	-214.83	0.11	0.014
Agrostis sp.	Agro sp.	H	-16.04	0.01	0.641	0.00	0.00	NA	21.58	-0.01	0.281
*Ammophila arenaria**	Amm are	G	-17.27	0.01	0.105	0.00	0.00	NA	70.96	-0.04	0.426
Arrhenatherum elatius§	Arrh ela	H	967.90	-0.48	0.000	-413.22	0.21	0.031	-697.91	0.35	0.005
*Briza media**	Briz med	H	-85.50	0.04	0.317	-119.89	0.06	0.609	0.00	0.00	NA
Campanula rotundifolia	Camp rot	H	8.09	0.00	0.467	0.00	0.00	NA	46.17	-0.02	0.105
*Carex arenaria**	Care are	G, H	0.00	0.00	NA	-41.40	0.02	0.160	0.00	0.00	NA
Carum carvi	Caru car	H	0.00	0.00	NA	-138.02	0.07	0.115	14.13	-0.01	0.887
Centaurea nigra§	Cent nig	H	0.00	0.00	NA	-324.81	0.16	0.004	-2037.39	1.02	0.000
*Centaurea scabiosa**	Cent sca	H	0.00	0.00	NA	0.00	0.00	NA	-274.03	0.14	0.007
Cerastium fontanum ssp. *vulgare*	Cera vul	C	-41.35	0.02	0.358	-267.52	0.13	0.269	0.20	0.00	1.000
Cirsium arvense§	Cirs arv	G	40.51	-0.02	0.375	-2.26	0.00	0.918	4.71	0.00	0.848
Dactylis glomerata§	Dact glo	H	335.76	-0.17	0.052	632.28	-0.31	0.000	-67.36	0.03	0.262
Equisetum arvense[A]	Equi arv	G	-57.49	0.03	0.129	-230.14	0.12	0.004	0.00	0.00	NA
Euphrasia sp.*[A]	Euph sp.	T	-133.42	0.07	0.513	-1107.24	0.56	0.010	261.13	-0.13	0.241
Festuca rubra	Fest rub	H	-407.72	0.22	0.013	-2366.20	1.19	0.000	-1289.70	0.66	0.056
*Galium verum**	Gali ver	H	-752.91	0.38	0.000	-1073.06	0.54	0.001	-217.58	0.12	0.460
*Geranium sanguineum**	Gera san	H	-2282.86	1.15	0.000	-1168.29	0.59	0.000	2436.58	-1.20	0.000
Heracleum sphondylium§	Hera sph	H	-254.22	0.13	0.000	0.00	0.00	NA	0.00	0.00	NA
*Hypochoeris maculata**	Hypo mac	H	0.00	0.00	NA	0.00	0.00	NA	-8.57	0.01	0.905
*Knautia arvensis**	Knau arv	H	-1224.96	0.61	0.000	-1039.84	0.52	0.004	-656.51	0.33	0.110
Leontodon autumnalis	Leon aut	H	17.31	-0.01	0.105	124.07	-0.06	0.631	187.89	-0.09	0.011
Leymus arenarius	Leym are	G	1000.80	-0.50	0.000	959.65	-0.48	0.000	199.13	-0.10	0.018
*Linum catharticum**[A]	Linu cat	T	-24.13	0.01	0.467	-34.43	0.02	0.605	0.00	0.00	NA
Lotus corniculatus	Lotu cor	H	202.45	-0.10	0.178	-625.77	0.31	0.000	1142.35	-0.57	0.000
*Pimpinella saxifraga**	Pimp sax	H	181.23	-0.09	0.024	295.26	-0.15	0.046	535.01	-0.27	0.000
Plantago lanceolata	Plant lan	H	-445.40	0.23	0.012	-641.22	0.33	0.144	869.86	-0.43	0.018
Poa pratensis	Poa pra	H, G	-145.88	0.07	0.458	174.01	-0.09	0.469	201.28	-0.10	0.380
Polygonatum odoratum	Poly odo	G	-936.59	0.47	0.000	0.00	0.00	NA	0.00	0.00	NA
Potentilla anserina	Pote ans	H	-174.86	0.09	0.000	0.00	0.00	NA	0.00	0.00	NA
Ranunculus acris	Ranu acr	H	-730.89	0.37	0.009	-936.46	0.47	0.010	-105.37	0.05	0.465
Rumex acetosa	Rume ace	H	-190.13	0.10	0.112	-344.73	0.17	0.069	7.58	0.00	0.931
Sanguisorba officinalis	Sang off	H	471.11	-0.22	0.377	-315.59	0.16	0.025	287.46	-0.14	0.065
Senecio jacobea§	Sene jac	H	5.79	0.00	0.605	402.58	-0.20	0.012	408.60	-0.20	0.000
Silene uniflora	Sile uni	H, C	51.94	-0.03	0.105	0.00	0.00	NA	0.00	0.00	NA
Taraxacum cordatum§	Tara cor	H	-640.44	0.32	0.000	242.08	-0.12	0.134	81.35	-0.04	0.454
*Thalictrum minus**	Thal min	H	-1919.56	0.96	0.000	-597.65	0.30	0.128	-59.14	0.03	0.682
Trifolium pratense	Trif pra	H	540.14	-0.27	0.253	141.14	-0.07	0.669	1478.88	-0.74	0.000
Trifolium repens	Trif rep	C, H	-19.03	0.01	0.817	-925.26	0.46	0.000	41.72	-0.02	0.387
Veronica chamaedrys	Vero cha	C	-2.70	0.00	0.945	194.72	-0.10	0.094	77.30	-0.04	0.056
Vicia cracca	Vici cra	H	-883.96	0.45	0.002	-2198.98	1.10	0.000	-1760.50	0.89	0.000
Viola tricolor ssp. *curtisii**	Viol tri	H	0.00	0.00	NA	14.13	-0.01	0.880	23.09	-0.01	0.105

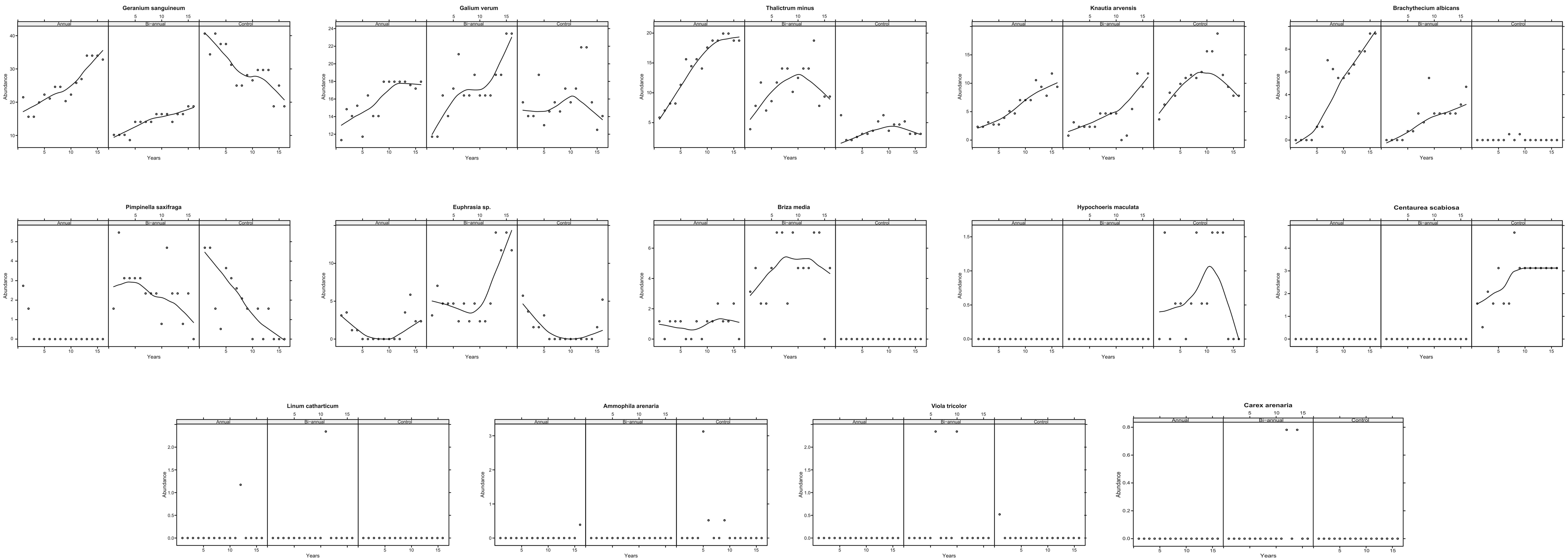
*=target species, §=undesirable species, A=annual (all others perennial)

Appendix 2: Changes in species richness (averages for quadrats) over the 16 years of different mowing treatments. Annual = mown annually (R^2=0.842, P<0.001); Bi-annual = mown bi-annually (R^2=0.570, P<0.001); Control = never mown (R^2=0.850, P<0.001). Slopes and intercepts of the linear mixed effects (LME; R-package nlme) model with years and treatments as fixed and random effects are significant (p<0.001). Thick line represents richness trend for all treatments considered together.



Response curves showing species' coverage over time (1999–2014) for 14 target species and 8 undesirable species under three treatments (annual mowing, bi-annual mowing, and no mowing) on a dune meadow on Karmøy, Western Norway.

Target species



Undesirable species