Impacts of soil disturbance on plant diversity in a dry grassland

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Abstract

Dry grasslands are among the most species rich habitats in Europe, but they are also among the most threatened. Threats include too high and too low levels of disturbance. The aim of this study is to examine the effect of soil disturbance intensity on species composition and diversity in a dry grassland in Mols Bjerge National Park in Denmark. We recorded vascular plant species inside and just outside patches of bare sand, and in the transition zone between these. We found that the number of species was highest in the dense vegetation, intermediate at the transition and lowest in bare sand areas. However, an analysis of plant traits showed that the number of small annual species was highest in the transition zone. High abundance of small annual species may therefore indicate intermediate disturbance regimes. Based on a literature study we demonstrate that many threatened species are adapted to such habitats. This suggests that dry grasslands should be managed to maintain areas with intermediate disturbances intensities to maintain optimal conditions for many threatened species. To our knowledge, this is the first time it has been documented that small annual species can indicate intermediate disturbance regimes in dry grasslands.

Introduction

Grasslands are among the most species-rich habitats in Europe and hold a considerable part of Europe´s biodiversity (Silva et al. 2008), but they are also one of the most threatened habitats (Janssen et al. 2016). Especially the dry grasslands are threatened with about 60 % characterized as threatened (critically endangered, endangered or vulnerable) and 16 % characterized as near threatened in the European Red List of Habitats (Janssen et al. 2016), which identifies absence of grazing as one of the biggest threats to dry grasslands.

Herbivores generally have a positive effect on species diversity in grasslands (Olff and Ritchie 1998). This is predominantly attributed to their consumption of plants, which reduces the dominance of the most competitive species (Koerner et al. 2018). However, herbivores also affect species richness through other mechanisms, including seed dispersal and soil disturbance by trampling (Olff and Ritchie 1998). Disturbances that lead to the occurrence of bare soil is increasingly recognized as having a positive effect on species diversity in grasslands (Warren et al. 2007; Ödman et al. 2012; Schnoor et al. 2015). This effect is often seen on military training areas that host a disproportionately large number of threatened and endangered species associated with a wide range of disturbance intensities (Warren et al. 2007). This suggests that many endangered species are adapted to disturbances and that they could be threatened by extinction in the absence of disturbances (Ödman et al. 2012).

Soil disturbance is particularly important for species that depend on bare soil for regeneration (Grubb 1976; Klaus et al. 2016), especially if they are short-statured and short-lived and therefore poor competitors (Grubb 1977). Patches with bare soil or sand enable rapid seedling establishment and regeneration, which favours some of the species that are unique to grasslands with sufficient levels of natural disturbance. These disturbance-adapted species, that were labelled ruderal (R) species by Grime (Grime 1974); they are often short-statured, herbaceous and with limited lateral expansion.

In the absence of disturbances, the ruderal species become less abundant, as competitive (C) or stress-tolerant (S) species take over (Grime 1977). The competitive species are those that are able to efficiently capture and utilize light, water, nutrients and space when resources are abundant. They outcompete other plants due to their high growth rates, by being tall, and by being capable of extensive lateral spread. However, this strategy is nutrient dependent, and plants with a competitive strategy are therefore rare in nutrient-poor grasslands. Such areas favour stress-tolerant species that are able to allocate resources to maintenance and defence, which allows them to survive grazing, but not to sustain high growth rates. The relative dominance of species that use either a C, S or R strategy is important for characterizing habitats, and can be used for predicting whether these are suitable for endangered species with particular strategies.

In addition to the species that employ just one strategy, we find a host of species that are adapted to intermediate intensities of competition, stress and disturbance (Grime 1977). Sites with a wide range of disturbance regimes therefore provide suitable habitats for more species than sites with only high or low levels of disturbance (Grime 1973). As a result, the highest species diversity in dry grasslands can be expected at intermediate levels of disturbance, as previously suggested to be the case for tropical rain forests and coral reefs (Connel 1978).

In this study, we examined the effect of soil disturbance on species composition and diversity in a dry *Nardus* grassland in Denmark. This is a priority habitat in the European Union (EU), meaning that it is in danger of disappearing and that it occurs predominately within the EU. The area covered by the habitat type has declined in Europe in the last decades because of intensification of agriculture in some areas, and too low intensity of use in others (Galvánek and Janák 2008). We expected soil disturbance to influence the species composition in three ways: 1) by causing R species to be most frequent in disturbed bare-sand areas, 2) by causing species with an intermediate R and S strategy to be most frequent in the transition between bare sand and dense vegetation, in areas with intermediate disturbance, and 3) by causing species with an S or C strategy, or a mixture of these, be most frequent in areas with low disturbance levels. The study is one of the first quantitative studies of how soil disturbance influences the species composition along natural disturbance gradients in dry northern European grasslands, and it thus improves our ability to manage the grasslands to maintain disturbance regimes that are optimal for the endangered species in these habitats.

Methods

The study was conducted in a 90-ha enclosure in a dry grassland in Mols Bjerge National Park (56°13N 10°33E) in eastern Jutland, Denmark. It is situated in a hilly coastal landscape which was formed during last ice age where material was pushed up by ice forming a sand and gravel moraine. Mean annual precipitation is 675 mm and the mean annual temperature is 8.9 °C (Scharling and Cappelen 2016). The dominant vegetation in the study area is the EU habitat type 'Species-rich *Nardus* grassland' (EU habitat directive 92/43/EEC), which is characterized by plant species such as *Festuca ovina, Galium saxatile*, *Lathyrus montanus, Polygala vulgaris, Potentilla erecta, Veronica officinalis and Viola canina.*

The vegetation at the study site was broken by scattered patches of bare sand that most likely result from trampling by the cattle (Dexter) and horses (Icelandic) that graze the area. On adjacent un-grazed areas, no bare-sand patches were found. In this study we mapped all sand patches with an area >5 m^2 within the study area. These were identified and delimited based on an orthophoto from spring 2017. A total of 24 patches were identified and assigned a unique number.

For each sand patch, three transects were randomly placed on the orthophoto at the transition between sand and dense vegetation, perpendicularly to the edge of the patch (Figure 1). These were placed as far apart as possible, and in all cases ≥1 m apart on the photo. Each transect extended 1m towards the patch centre from the vegetation edge and 2 m away from the edge of the vegetation. If three transects with a minimum spacing of 1 m could not be located, the site was excluded from the study. Patches closer to each other than 4 m were also excluded to reduce statistical autocorrelation. We therefore retained only 16 patches with an area between 11 and 101 m^2 (median: 44 m^2). These were easily located in the field, and transitions between bare sand and dense vegetation were easily recognizable (Figure 2).

Each transect was marked with three bamboo sticks, one at the transition between dense vegetation and sand, and one at either end. The sticks defined the centres of three Raunkiaer circles (Raunkiaer 1909), each with an area of 0,1 m^2. These were labelled 'plot A', 'plot B' and 'plot C', starting from the centres of the sand patches (Figure 1). Within each plot all species of vascular plants were recorded.

We used Grime's triangles to investigate whether soil disturbance influenced species composition as expected in plots A, B and C. To do so, we plotted the Grime values for the species found in each of the three plot types based on values obtained from Grime et al. (1988). We tested 1) if the number of observations of species with an R strategy (0 % C and S) was higher in bare sand areas (A plots) than in either of the other two types of plots; 2) whether the number of observations with intermediate R and S strategies (0 % C) was higher in B plots than in the other two types of plots; and 3) whether C and S strategies (0 % R) were highest in the C plots. This we did visually based on the Grime triangles. However, for six of the 63 registered species no C-S-R value was available, and these were excluded from the analysis. This included the species *Artemisia campestris, Corynephorus canescens, Myosurus minimus, Scleranthus perennis, Aphanes sp.* and *Veronica verna*.

All dry grassland species on the Danish Red List (Moeslund et al. 2019) were plotted in each C-S-R triangle for comparison if their C-S-R values were provided by Grime (1988). Species were classified as dry grassland species if they had Ellenberg indicator values L>5 (i.e. adapted to semi-shade) and F≤5 (adapted to dry habitats), following Hill (1999). Ellenberg values were only available for 78 of the 81 vascular plants on the Danish red list with available C-S-R values, and of these only 27 were classified as dry grassland species.

The analysis based on C-S-R strategies was complemented with an analysis based on plant traits, which was available for all species. Analyses based on plant traits have the advantage that they can also be applied in the field. Since we were interested in finding disturbance regimes that are optimal for endangered species, we analysed the distribution of plants having the same traits as *Veronica verna,* the only red listed species registered in this study. Traits that are particularly important as proxies for plant strategies are plant height and life form (Grime 1977). *Veronica verna* is a small annual species, and in this respect it resembles several other red listed species on sandy grasslands, including *Trifolium micranthum, Medicago minima* and *Spergula morisonii* (Moeslund et al. 2019). We divided the annual species in our study into large and small species based on values from Mossberg and Stenberg (2005). The ones ≤20 cm tall were labelled 'small', whereas the remainder were labelled 'large'.

We tested if the number of small annual species (≤20 cm tall) was higher in A plots than in B plots using a generalized linear mixed model. This was supplemented with an analysis of whether the number of large annual species was higher in A plots than in B plots. The response variable was number of species (Poisson distributed), plot type was included as fixed effect and patch number was included as random variable in all models. Models were fitted using the glmer function in the lme4-package for R (Bates et al. 2015). Models were tested for signs of overdispersion based on the residual deviance.

Results

A total of 63 species of vascular plants were found in the 144 Raunkiaer plots, averaging 5.4 species per plot (range: 0–15). In 9 plots there was only sand and no plants. The number of species was highest in C plots outside the sand patches (average: 7.8), second highest in the B plots on the edge of the patches (average: 5.8) and lowest in A-plots inside the patches (average: 2.7). The total number of species was 55, 39 and 26 in C, B and A plots, respectively. The most frequent species was *Agrostis capillaris*, which was recorded in 93 plots, followed by *Aira praecox* (71 plots), *Teesdalia nudicaulis* (69 plots), *Rumex acetosella* (66 plots) and *Hypochoeris radicata* (51 plots). Sixteen species were only found in one plot.

Most observed species had strategies belonging in the lower part of the C-S-R triangle (Figure 3), which includes species with R and S strategies combined with low competitive abilities. In fact, there were no species with a 100 % C strategy and only 2 species with 75 % C strategy (2 % of all observations). Looking at the C-S-R triangles for each of the three plot types (A, B and C) we found that:

1) The frequency of species with a 100 % R strategy was highest in the C plots, contrary to what we had expected. Species with this strategy were recorded 30 times: 50 % in C plots, 30 % in B plots and 20 % in A plots.

2) Species with intermediate R and S strategies, stress-tolerant ruderals (R-S), were most frequent in the B plots, as expected. The R-S strategy (50 % R) was the most frequent strategy in the study. Most of the

species exhibiting this strategy (13 of 14 species) were annuals, whereas the two red-listed species that had this strategy were biennials (Table 1). The number of annual species ≤20 cm was higher in B plots than in A plots ($P<0.001$, $z = 5.076$, figure 4), and also higher in B plots than in C plots ($P <0.001$, $z = –4.437$). The number of plants >20 cm was higher in B-plots than in A plots ($P<0.001$, $z = 6.145$), but not significantly different in B and C plots ($P= 0.097$, $z = –1.658$).

3) Species with an S or C strategy, or a mixture of these, were most frequent in C plots, as expected. About 70 % of the recordings of species with a 100 % S strategy were in C plots.

Most of the dry grassland red-listed species also exhibited strategies in the lower part of the C-S-R triangle (Figure 3). Only 4 of the 27 red-listed species had a C strategy, and none of them had >50 % C. The remaining 23 red-listed species with Grime values had a combination of R and S strategies (0 % C), and most predominately the S strategy (8 had a 100 % S strategy). The red list species exhibited the S strategy more often, and the R strategy less often, than most of the plants observed in this study. This means that the majority of the red list species are more adapted to stress and less adapted to high levels of disturbance than the average of the plants observed.

Discussion

This study shows that soil disturbance affects the composition of plant species in dry grasslands, leading to a higher abundance of stress tolerant ruderal species at intermediate disturbance levels and stress-tolerant species at low disturbance levels. This highlights the importance of heterogenic disturbance regimes for maintaining plant diversity at landscape scale, which is in line with other recent studies from Sweden and Germany (Ödman et al. 2012; Schnoor et al. 2015; Klaus et al. 2016).

Growth strategies in plots with different disturbance intensities

Species with a ruderal strategy were expected to be most frequent in the highly disturbed patch centres where plants are exposed to high levels of trampling and wind erosion, but we found that they were more abundant in the dense vegetation outside the patches. The level of soil disturbance in the sand patches therefore appears to be too high to allow even the fast-growing ruderal species to establish. In such highly disturbed habitats, species with clonal spreading may be better adapted than ruderals, as they are able to more rapidly establish a robust root system (Fahrig et al. 1994). This likely explains why the rhizomatous, perennial grass *Agrostis capillaris* is the most frequent species in the centres of the patches.

At the transition between bare sand and dense vegetation species with intermediate ruderal and stress-tolerant strategies were most frequent, as expected. Especially stress tolerant ruderals (SR species; with 50% S and 50 % R) that are adapted to lightly disturbed, unproductive habitats, were common in the transition zone. All but one of the SR species were annuals and appeared more frequently in the transition zone than in plots with other disturbance intensities. However, only small annual species (≤20 cm tall) occurred in higher numbers at in these plots, whereas large annual species (>20 cm) were most abundant in the less disturbed vegetation outside the patches. This is probably because the small annual species cannot compete for light in the dense vegetation outside the sand patches.

Nardus grasslands usually consist of closed, perennial vegetation (Galvánek and Janák 2008) which is not favourable for annual species (Grime 1974). The high frequency of large annual species (> 20 cm) outside the sand patches in the Mols Bjerge study site suggests that this grassland is relatively open near the sand patches, even in areas without visual soil disturbances. The reason for this is most likely that the boundaries of the patches are dynamic, as shown in Figure 5, and that the areas close to the patches have been disturbed recently. However, the time since the last disturbance appears to be long enough for the vegetation to become too dense to allow small annual species to persist.

Soil disturbance can help red-listed species and promote overall diversity

The relative abundance of plants with different traits can help us determine if the disturbance regime of a grassland is optimal for threatened species. Conservation of threatened species is important for the maintenance of biodiversity, as they are most at risk of extinction. In the most disturbed plots, we observed the smallest number of species and also the smallest number of species with traits that resembled those of threatened species (Fig. 3A). In general, we expect ruderal species to be associated with disturbed areas, and the absence of species with a pure ruderal strategy among the Danish red-listed dry grassland species for which Grime values were available (Table 1) suggests that highly disturbed areas are not important for rare grassland species. Overall, very few species are adapted to this habitat (Grime 1977; Herben et al. 2018), and the areas with the highest levels soil disturbance therefore appear to be unimportant for maintenance of diversity in dry nutrient-poor grasslands. However, high disturbance can be a prerequisite for the development of highly diverse vegetation including red-listed species found at intermediate disturbance levels.

The plots with intermediate disturbance levels at the transition between sand patches and dense vegetation were characterized by a high abundance of SR species. Two of the dry grassland species in the Danish Red List, *Gentianella amarella* and *Carlina vulgaris*, were SR species, and both regenerate entirely by seeds and depend on gaps in the vegetation for successful seed germination (Grime et al. 1988; Křenová et al. 2019). This is also the case for all species in the genus *Gentianella*, most of which have declined dramatically throughout Europe due to abandonment or intensification of land-use (Křenová et al. 2019). These species are likely to be favoured by intermediate disturbance intensities. This most likely also applies to the only red-listed species in our study, *Veronica verna*, which we, based on its traits, assume to be a SR species. We only found the species in a single plot, and although this was located outside the sand patch the vegetation in the plot resembled the open, low vegetation generally found in plots with intermediate disturbance. Outside the plots *Veronica verna* was found on the transition between bare sand and dense vegetation.

In addition to the stress-tolerant ruderals adapted to moderate levels of disturbance (SR) the Danish Red List includes ten more stress-tolerant dry grassland species adapted to minor disturbances (S/SR). These species include geophytic orchids that survive severe stress by allocating resources to underground storage organs and that have small seeds which causes them to depend on gaps for seedling establishment. In our study, we only recorded one species that employed the S/SR-strategy, namely the biennial herb *Jasione montana*. Although it occurred most frequently at intermediate disturbance levels, there were too few records to make the species valuable as an indicator species.

Our study shows that soil disturbance creates habitats suitable for red-listed species. We found most red-listed species with strategies adapted to intermediate disturbance levels indicating that intermediate disturbances levels are particularly important for red-listed species and therefore plant diversity in dry grasslands.

Plant traits as indicators of growth strategies

One caveat of using Grime values for characterizing growth strategies is that they are not available for all species. Among the 323 vascular species in Denmark only 81 have available C-S-R values. This makes it desirable using more easily observable plant traits as indicators of growth strategies, to make it possible to easily assess whether an area is suitable for endangered species that employ a particular strategy. In our study, small annual species (≤20 cm tall) were significantly more abundant in the transition zone, suggesting that plant height and longevity can be used as indicators of habitats with intermediate disturbance levels, and thus that areas where small annual species are suitable for threatened species like the *Gentianella* species. The prevalence of plants with different traits therefore appears to be a useful indicator of disturbance intensity. This can be useful in the management of dry grasslands where the presence of threatened species cannot be used directly as an indicator of high-value habitats, such as in our study area. Even areas with no threatened species can be managed to favour plants with particular traits, thus facilitating the establishment of threatened species with similar traits at a later point. The impact of management is often assessed based on the occurrence and positive population trends of threatened species (Schnoor et al. 2015), but the absence of threatened species does not necessarily indicate that the disturbance regimes that such species depend on are missing. Many other factors determine the establishment success of plant species, e.g. availability of seed sources, dispersers, mycorrhiza or nutrients. Therefore, plant traits for groups of species are better than presence of individual species as indicators of how suitable an area is for the establishment of threatened species in the future (Kahmen and Poschlod 2008; Schnoor et al. 2015).

Our study shows that soil disturbance plays an important role for the composition and structural diversity of grasslands, and that it can have a positive effect on species diversity. This is in line with the findings of several other studies (Warren et al. 2007; Ödman et al. 2012; Schnoor et al. 2015). We found that the majority of species in our study area were adapted to intermediate or low soil disturbance levels, which is also the case for the Danish red-listed species in dry grasslands. This suggests that the highest plant species diversity occurs in areas with both undisturbed areas and patches with intermediate levels of soil disturbances. While it can be easy to tell when soil disturbance levels are low, it can be very difficult to tell when they are intermediate. Therefore, our finding that small annual species may indicate intermediate disturbance regimes are of great importance to the management of dry grasslands and the conservation of red-listed habitats. To our knowledge, this is the first time it has been documented that small annual species can indicate intermediate disturbance regimes in dry grasslands.

Declarations

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Conflicts of interest/Competing interests: The authors have no conflicting interests.

Ethics approval: Not applicable.

Consent to participate: All authors have agreed to participate in this research project.

Consent for publication: All authors consent to publishing the research in its current form.

Availability of data and material: The authors agree to make data publicly available in an electronic supplement.

Code availability: The code used for analysing the data can be made available upon request.

Authors' contributions: LINN designed the study; JNN performed data analyses; all authors participated in writing the paper.

References

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67: . https://doi.org/10.18637/jss.v067.i01

Connel JH (1978) Diversity in Tropical Rain Forests and Coral Reefs. Science (80-) 199:1302–1310

Fahrig L, Coffin DP, Lauenroth WK, Shugart HH (1994) The advantage of long-distance clonal spreading in highly disturbed habitats. Evol Ecol 8:172–187 . https://doi.org/10.1007/BF01238248

Galvánek D, Janák M (2008) Managment of Natura 2000 habitats. 6230* Species-rich Nardus grasslands

Grime JP (1974) Vegetation classification by reference to strategies. Nature 250:26–31

Grime JP (1977) Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. Am Soc Nat 111:1169–1194

Grime JP (1973) Competitive Exclusion in Herbaceous Vegetation. Nature 242:344–347

Grime JP, Hodgson JG, Hunt R (1988) Comparative plant ecology: a functional approach to common British species. Spinger

Grubb PJ (1976) A theoretical background to the conservation of ecologically distinct groups of annuals and biennials in the chalk grassland ecosystem. Biol Conserv 10:53–76 . https://doi.org/10.1016/0006-3207(76)90025-2

Grubb PJ (1977) The maintenance of species-richness in plant communities: The importance of regeneration niche. Biol Rev 52:107–145 . https://doi.org/10.1111/j.1469-185X.1977.tb01347.x

Herben T, Klimešová J, Chytrý M (2018) Philip Grime's fourth corner: are there plant species adapted to high disturbance and low productivity? Oikos 127:1125–1131 . https://doi.org/10.1111/oik.05090

Hill MO (1999) Ellenberg's indicator values for British plants. ECOFACT Volume 2 Technical Annex

Janssen JAM, Rodwell JS, Garcia Criado M, Gubbay S, Haynes T, Nieto A, Sanders N, Landucci F, Loidi J, Ssymank A, Tahvanainen T, Valderrabano M, Acosta A, Aronsson M, Arts G, Attorre F, Bergmeier E, Bijlsma R-J, Bioret F, Biţă-Nicolae C, Biurrun I, Calix M, Capelo J, Čarni A, Chytrý M, Dengler J, Dimopoulos P, Essl F, Gardfjell H, Gigante D, Galdo GG del, Hájek M, Jansen F, Jansen J, Kapfer J, Mickolajczak A, Molina JA, Molnár Z, Paternoster D, Piernik A, Poulin B, Renaux B, Schaminée JHJ, Šumberová K, Toivonen H, Tonteri T, Tsiripidis I, Tzonev R, Valachovič M (2016) European red list of habitats

Kahmen S, Poschlod P (2008) Effects of grassland management on plant functional trait composition. Agric Ecosyst Environ 128:137–145 . https://doi.org/10.1016/j.agee.2008.05.016

Klaus VH, Schäfer D, Kleinebecker T, Fischer M, Prati D, Hölzel N (2016) Enriching plant diversity in grasslands by large-scale experimental sward disturbance and seed addition along gradients of land-use intensity. J Plant Ecol 10:581–591 . https://doi.org/10.1093/jpe/rtw062

Koerner SE, Smith MD, Burkepile DE, Hanan NP, Avolio ML, Collins SL, Knapp AK, Lemoine NP, Forrestel EJ, Eby S, Thompson DI, Aguado-Santacruz GA, Anderson JP, Anderson TM, Angassa A, Bagchi S, Bakker ES, Bastin G, Baur LE, Beard KH, Beever EA, Bohlen PJ, Boughton EH, Canestro D, Cesa A, Chaneton E, Cheng J, D'Antonio CM, Deleglise C, Dembélé F, Dorrough J, Eldridge DJ, Fernandez-Going B, Fernández-Lugo S, Fraser LH, Freedman B, García-Salgado G, Goheen JR, Guo L, Husheer S, Karembé M, Knops JMH, Kraaij T, Kulmatiski A, Kytöviita MM, Lezama F, Loucougaray G, Loydi A, Milchunas DG, Milton SJ, Morgan JW, Moxham C, Nehring KC, Olff H, Palmer TM, Rebollo S, Riginos C, Risch AC, Rueda M, Sankaran M, Sasaki T, Schoenecker KA, Schultz NL, Schütz M, Schwabe A, Siebert F, Smit C, Stahlheber KA, Storm C, Strong DJ, Su J, Tiruvaimozhi Y V., Tyler C, Val J, Vandegehuchte ML, Veblen KE, Vermeire LT, Ward D, Wu J, Young TP, Yu Q, Zelikova TJ (2018) Change in dominance determines herbivore effects on plant biodiversity. Nat Ecol Evol 2:1925–1932 . https://doi.org/10.1038/s41559-018-0696-y

Křenová Z, Brabec J, Rössler S, Kindlmann P (2019) Can we learn from the ecology of the Bohemian gentian and save another closely related species of Gentianella? PLoS One 14:1–17 . https://doi.org/10.1371/journal.pone.0226487

Moeslund JE, Nygaard B, Ejrnæs R, Bell N, Bruun LD, Bygebjerg R, Carl H, Damgaard J, Dylmer E, Elmeros M, Flensted K, Fog K, Goldberg I, Gønget H, Helsing F, Holmen M, Jørum P, Lissner J, Læssøe T, Madsen HB, Misser J, Møller PR, Nielsen OF, Olsen K, Sterup J, Søchting U, Wiberg-Larsen P, Wind P (2019) The Danish Red List

Mossberg B, Stenberg L (2005) Den Nye Nordiske Flora, 1st edn. Gyldendal

Ödman AM, Schnoor TK, Ripa J, Olsson PA (2012) Soil disturbance as a restoration measure in dry sandy grasslands. Biodivers Conserv 21:1921–1935 . https://doi.org/10.1007/s10531-012-0292-4

Olff H, Ritchie ME (1998) Effects of herbivores on grassland plant diversity. Trends Ecol Evol 13:261–265 . https://doi.org/10.1016/S0169-5347(98)01364-0

Raunkiaer C (1909) Formationsundersøgelse og Formationsstatistik. Bot Tidsskr 30:20–132

Scharling M, Cappelen J (2016) DMI rapport 16-19 ver. 2 (inkl. regneark) Måneds-og årsvaerdier for temperatur, nedbør og solskin Kommunernes generelle vejr og klima. 2:1–210

Schnoor T, Bruun HH, Olsson PA (2015) Soil disturbance as a grassland restoration measure - Effects on plant species composition and plant functional traits. PLoS One 10:1–16 . https://doi.org/10.1371/journal.pone.0123698

Silva JP, Toland J, Jones W, Elridge J, Thorpe E, O’Hara E (2008) LIFE and Europe´s grasslands: Restoring a forgotten habitat

Warren SD, Holbrook SW, Dale DA, Whelan NL, Elyn M, Grimm W, Jentsch A (2007) Biodiversity and the heterogeneous disturbance regime on military training lands. Restor Ecol 15:606–612 . https://doi.org/10.1111/j.1526-100X.2007.00272.x

Table

*Table 1 List of C-S-R-values of plot species with corresponding values of red-listed species of dry grasslands. They are sorted by decreasing disturbance (R-values) and increasing competitive ability (C-strategies). The highest frequencies of a species in a plot type are marked by grey – except species with only one or two occurrences all together. *The species grows in salt-meadows.*

Grime strategy	Species	Life-form	Max. height (cm)	Frequency Total Nr.	Plot A (%)	Plot B (%)	Plot C (%)	Red list category
R	*Bromus hordeaceus*	Annual	90	20	20	15	**65**	
R	*Poa annua*	Annual	30	9	22	**56**	22	
R	*Polygonum aviculare*	Annual	80	1	0	100	0	
R	*Odontites litoralis**	Annual						EN
R/SR	*Viola tricolor ssp. tricolor*	Annual	25	1	0	0	100	
R/SR	*Veronica hederifolia*	Annual	30	1	0	100	0	
R/SR	*Trifolium micranthum*	Annual						EN
R/SR	*Geranium lucidum*	Annual						VU
SR	*Aira praecox*	Annual	12	71	24	**51**	25	
SR	*Teesdalia nudicaulis*	Annual	15	69	22	**54**	25	
SR	*Erophila verna*	Annual	15	3	33	**67**	0	
SR?	*Veronica verna*	Annual	15	1	0	0	100	NT
SR	*Logfia minima*	Annual	20	18	17	**56**	28	
SR	*Scleranthus annuus ssp. annuus*	Annual	20	15	27	**60**	13	
SR	*Myosotis ramosissima*	Annual	20	2	50	50	0	
SR	*Cerastium semidecandrum*	Annual	25	24	13	42	**46**	
SR	*Veronica arvensis*	Annual	25	16	0	13	**88**	
SR	*Spergularia rubra*	Annual	25	3	0	33	**67**	
SR	*Trifolium striatum*	Annual	25	2	0	0	**100**	
SR	*Trifolium arvense*	Annual	30	1	0	100	0	
SR	*Ranunculus bulbosus*	Perennial	35	5	0	20	**80**	
SR	*Erodium cicutarium*	Annual	50	10	10	50	**40**	
SR	*Gentianella amarella*	Biennial						EN
SR	*Carlina vulgaris*	Biennial						NT
S/SR	*Jasione montana*	Biennial	35	6	0	**67**	33	
S/SR	*Coeloglossum viride*	Perennial						RE
S/SR	*Spiranthes spiralis*	Perennial						RE
S/SR	*Neotinea ustulata*	Perennial						CR
S/SR	*Ophrys insectifera*	Perennial						CR
S/SR	*Draba incana*	Biennial						EN
S/SR	*Anacamptis pyramidalis*	Perennial						VU
S/SR	*Ophrys apifera*	Perennial						VU
S/SR	*Anacamptis morio*	Perennial						NT

S/SR	*Inula conyzae*	Perennial						NT
S/SR	*Scabiosa columbaria*	Perennial						NT
S	*Festuca ovina*	Perennial	30	20	5	30	65	
S	*Sedum acre*	Perennial	12	2	0	0	100	
S	*Campanula rotundifolia*	Perennial	50	1	0	0	100	
S	*Stachys officinalis*	Perennial						CR
S	*Helianthemum nummula-rium ssp.nummularium*	Perennial						EN
S	*Lycopodium alpinum*	Perennial						EN
S	*Antennaria dioica*	Perennial						NT
S	*Carex ericetorum*	Perennial						NT
S	*Epipactis atrorubens*	Perennial						NT
S	*Galium sterneri*	Perennial						NT
S	*Helianthemum nummula-rium ssp. obscurum*	Perennial						NT
SR/CSR	*Anthoxanthum odoratum*	Perennial	40	10	10	40	50	
SR/CSR	*Rumex acetosella*	Perennial	40	66	20	0	80	
SR/CSR	*Botrychium lunaria*	Perennial						NT
S/CSR	*Festuca brevipila*	Perennial	70	1	0	0	100	
S/CSR	*Luzula campestris*	Perennial	20	18	0	11	89	
S/CSR	*Pilosella officinarum*	Perennial	10	28	0	18	82	
S/CSR	*Hypericum montanum*	Perennial						NT
SC/CSR	*Carex arenaria*	Perennial	40	32	25	38	38	
SC/CSR	*Galium verum*	Perennial	60	2	0	0	100	
SC/CSR	*Jacobaea erucifolia*	Perennial						EN
SC	*Calluna vulgaris*	Perennial		3	0	0	100	
SC	*Cytisus scoparius*	Perennial	75	6	17	17	67	
SC	*Prunus spinosa*	Perennial	150	1	0	0	100	
SC	*Brachypodium pinnatum*	Perennial	400					NT

Figures

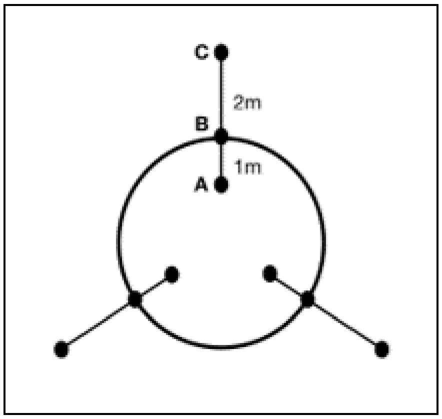

Figure 1

Experimental design for a site. Three transects (lines) were placed at the transition between sand and dense vegetation (circle) as shown in the figure. Raunkiaer circles (dots) were placed along the transects on the transition between dense vegetation and sand (B), on bare sand (A) and in dense vegetation (C).

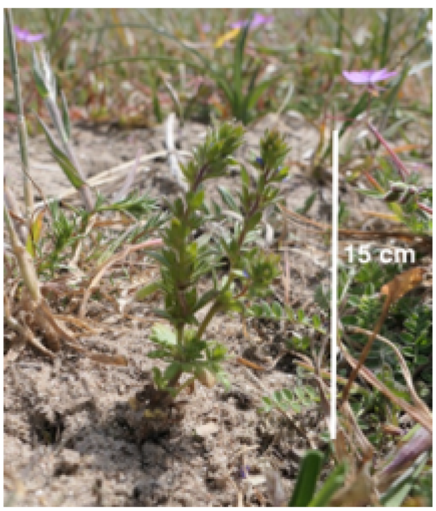

Figure 2

Left: Veronica verna. Right: One of the two sites where Veronica verna was recorded.

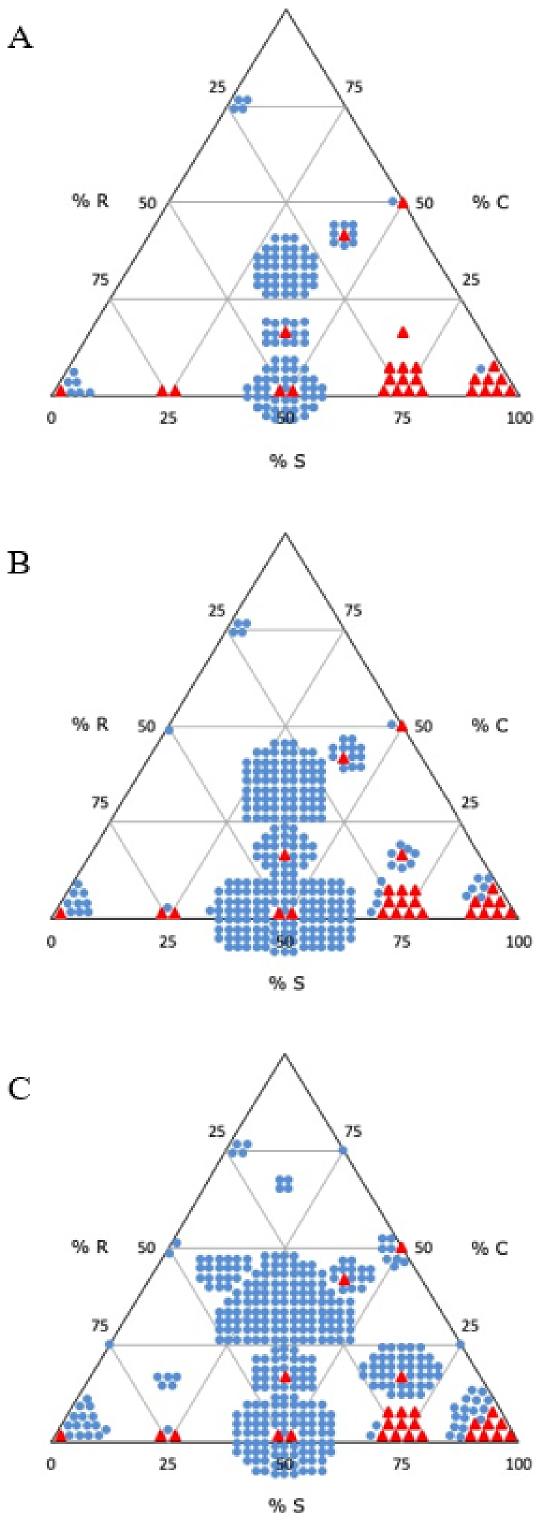

Figure 3

Grime's life strategy triangles for the three plot types: A, B and C. Each registration is represented by a dot at the Grime strategy of the registered species. Red triangles represent numbers of red-listed species with a specific strategy,

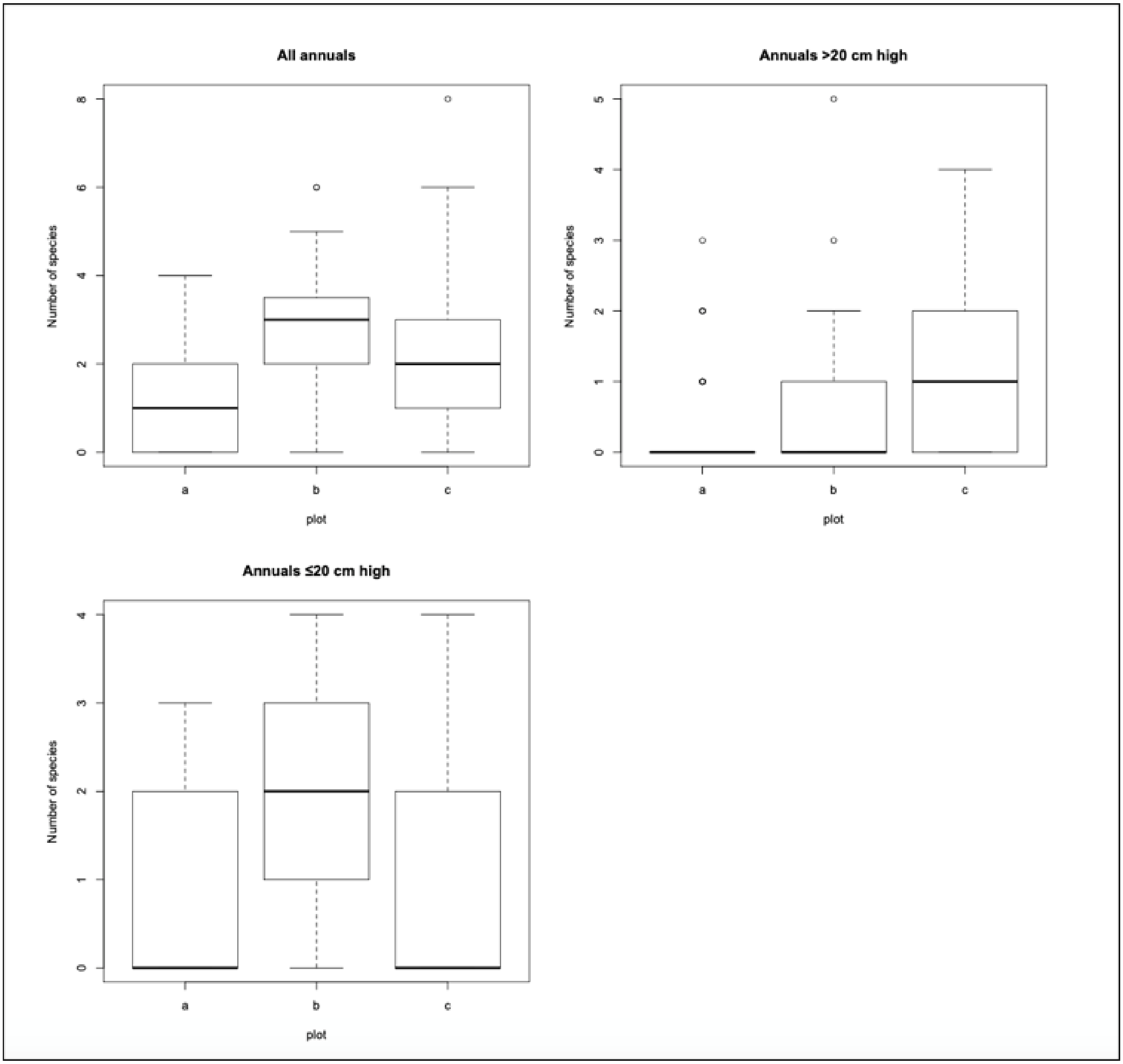

Figure 4

The number of annual species in A, B and C plots respectively. Top left: All annual species. Top right: Annual species higher than 20 cm. Bottom left: Annual species with a maximum height of 20 cm.

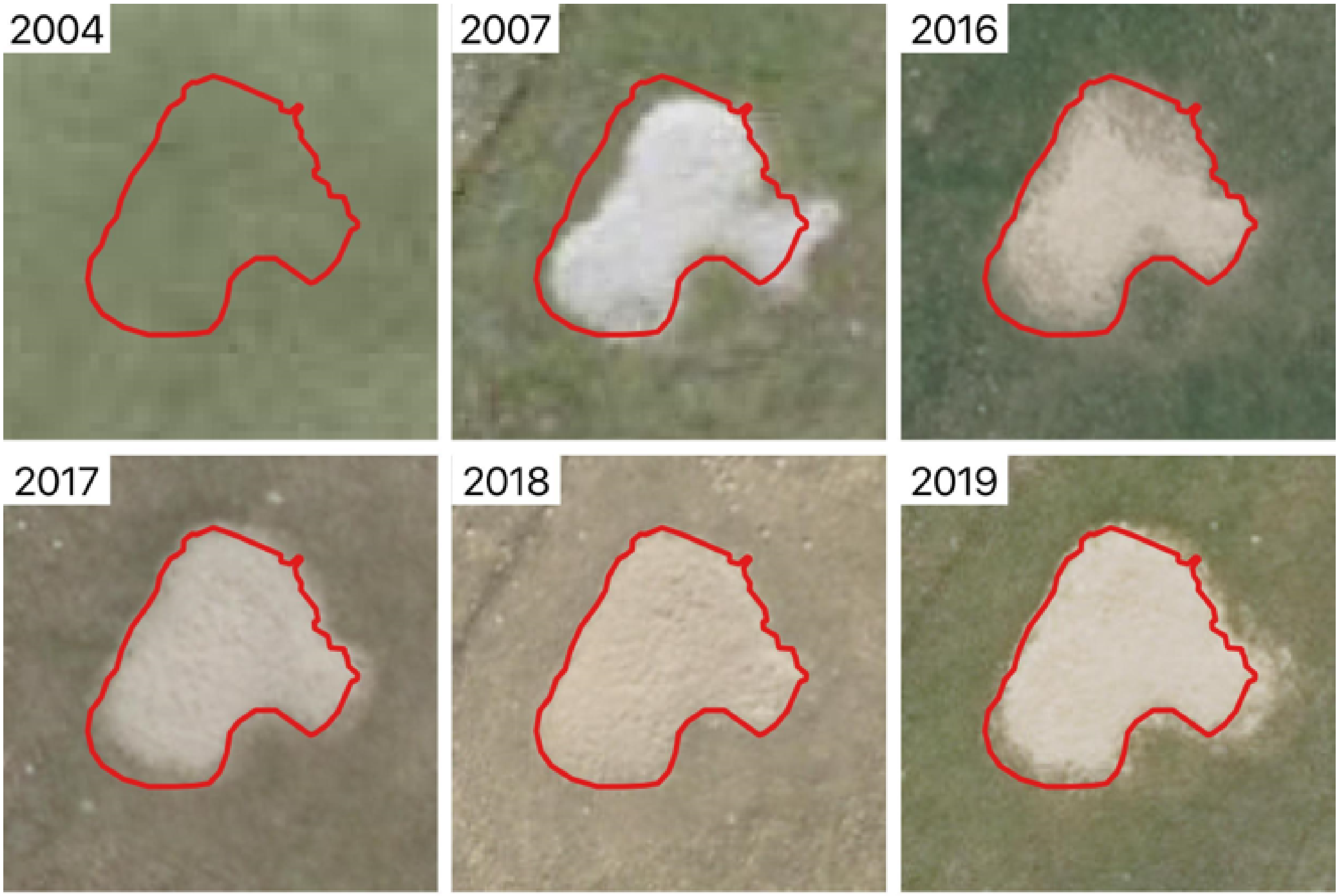

Figure 5

Changes in delimitation of a sand patch from 2004 to 2019. The red line marks the delimitation in 2018 when the field work was conducted. The photos show that it is primarily the boundary zone between bare and dense vegetation that changes. In 2004 the vegetation at the site was continuous with no patches of bare soil, suggesting that the density of large herbivores was low in 2004.