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Impacts of soil disturbance on plant diversity in a dry grassland

Louise I. Nabe-Nielsen · Jens Reddersen · Jacob Nabe-Nielsen

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Abstract Dry grasslands are not only amongst the most species-rich habitats in Europe but also amongst the most threatened. Threats include habitat destruction as well as modification to the historic disturbance regime under which native plants have evolved (e.g. too high or too low levels of disturbance). The aim of this study is to examine the effects 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 at the transition between bare sand and dense vegetation outside the patches. We found that species richness was highest in the dense vegetation, intermediate in the transition zone 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. Moreover, literature indicates that many threatened species are adapted to such habitats, which suggests that dry grasslands should be managed to maintain areas with intermediate disturbance intensities to improve conditions for many threatened species. High abundance of small annual species thus indicates that favourable management has been achieved.

Keywords Dry grassland · Effects of trampling · Grime's plant strategies · Management · Plant diversity · Plant traits · Soil disturbance · Wallowing

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L. I. Nabe-Nielsen
Center for Macroecology, Evolution and Climate, University of Copenhagen, Copenhagen, Denmark
e-mail: louise.nabe-nielsen@sund.ku.dk

J. Reddersen
Mols Bjerge National Park, Rønde, Denmark
e-mail: jered@danmarksnationalparker.dk

J. Nabe-Nielsen (✉)
Department of Bioscience, Aarhus University, Frederiksborgvej 399, 4000 Roskilde, Denmark
e-mail: jnn@bioscience.au.dk

Introduction

Grasslands are amongst 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 (European Commission 2016). In fact, 60% of European dry grasslands are classified as 'critically endangered, endangered or vulnerable', with an additional 16% identified as threatened in the European Red List of Habitats (European Commission 2016), where absence of grazing is identified as one of the biggest threats to dry grasslands. It is therefore critical to obtain a better understanding of the mechanisms that contribute to maintenance of grassland diversity to improve management.

Grassland species composition is largely shaped by herbivores (McNaughton 1985; Milchunas et al. 1988; Olff and Ritchie 1998; Hanke et al. 2014). This is predominantly attributed to the herbivores' consumption of plants, which reduces the dominance of the most competitive species and increases dominance of species adapted to grazing (Grime 1973, 1979; Huston 1979; Milchunas et al. 1988; Koerner et al. 2018). However, herbivores also affect species composition through other mechanisms, including seed dispersal, dung-borne nutrient input and by increasing soil disturbance through trampling and wallowing (Olff and Ritchie 1998; Martin et al. 2005; Lezama and Paruelo 2016; Reinecke et al. 2021). Disturbances that promote bare soil are increasingly recognized as having a positive effect on species diversity in dry grasslands (Warren et al. 2007; Ödman et al. 2012; Schnoor et al. 2015). The herbivores' consumption of plants generally has a positive effect on diversity in productive areas and a negative effect under harsh conditions (Bakker et al. 2006; Huston 2014; Herrero-Jáuregui and Oesterheld 2018), but herbivores may have a positive effect on overall diversity even in relatively unproductive grasslands when they maintain microhabitats with soil disturbance levels that would not be present otherwise (Eskelinen and Virtanen 2005; Brunbjerg et al. 2014). The degree to which a plant community consists of species adapted to more or less productive conditions or to particular levels of disturbance is reflected in the life forms present in the community (Grime 1974, 1977).

Soil disturbance is particularly important for species that depend on bare soil for regeneration (Grubb 1976; Renne et al. 2006; Renne and Tracy 2013; 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 favour some of the species that are unique to grasslands with soil disturbance. These disturbance-adapted species, that are often short-statured, herbaceous and with limited lateral expansion, were labelled ruderal (R) species by Grime (Grime 1974). In the absence of disturbance, ruderal species become less abundant whilst the dominance of competitive (C) and stress-tolerant (S) species increases (Grime 1977). 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 (Bakker et al. 2006; Huston 2014). 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 growth strategies.

In addition to the species that employ just one strategy, plant communities include numerous 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; Roxburgh et al. 2004; Hanke et al. 2014; Klaus et al. 2016). Whether this means that the highest species diversity can be expected at intermediate levels of disturbance in dry grasslands, as previously suggested for tropical rain forests and coral reefs (Connel 1978), is likely to depend on the productivity of the grasslands (Worm et al. 2002) and on whether intermediate disturbance levels result in creation of microhabitats with different levels of soil disturbance. The relative importance of different aspects of grazing and disturbance in shaping grassland community composition has only been addressed in few studies in northern Europe.

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 highly disturbed areas, (2) by causing species with an intermediate R and S strategy to be most frequent at 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 favourable for 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°13 N 10°33 E) 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 and wallowing 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.

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 (Fig. 1). These were placed as far apart as possible, and in all cases ≥ 1 m apart. Each transect extended 1 m 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

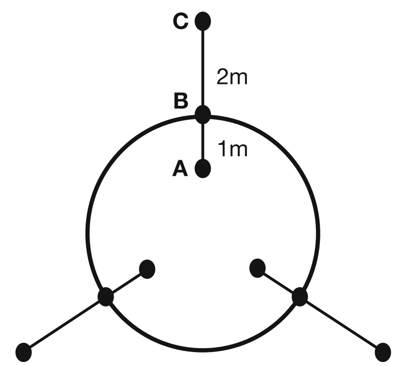


Fig. 1 Distribution of plots around a sand patch. Three transects (lines) were placed perpendicularly to the transition between sand and dense vegetation. The transition zone is shown with a black circle. Plots were placed along the transects on the transition between dense vegetation and sand (**B**), on bare sand (**A**) and in dense vegetation (**C**)

autocorrelation. We therefore retained only 16 of the 24 patches originally identified. These had 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 (Fig. 2). Throughout this manuscript we use the phrase 'transition zone' for the narrow ecotone where the vegetation changes from dense to bare sand.

Three plots were placed along each transect, one at the transition between dense vegetation and sand and one at either end. The extent of each plot was defined using Raunkiaer circles (Raunkiaer 1909) with an area of 0.1 m^2. The three types of plots were labelled A (bare sand), B (transition) and C (dense vegetation; Fig. 1). Within each plot all species of vascular plants were recorded.

We used Grime's triangle to investigate whether plant growth strategies were related to soil disturbance. To do so, we plotted Grime values for species found in each of the three plot types based on values obtained from Grime et al. (1988). We tested (1) if species using an R strategy (0% C and S) occurred more frequently in A plots than in the other two types of plots; (2) whether species using intermediate R and S strategies (0% C) occurred more frequently in B plots than in the other two types of plots and (3) whether species with a combination of C and S strategies (0% R) were most frequent in C plots. This we did visually based on the Grime triangle. For six of the 63 registered species no C–S–R value was available, and these were excluded from the analysis.

Fig. 2 Left: *Veronica verna*, the only red-listed species recorded in this study. Right: one of the two sand patches where *Veronica verna* was recorded

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 $F \leq 5$ (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.

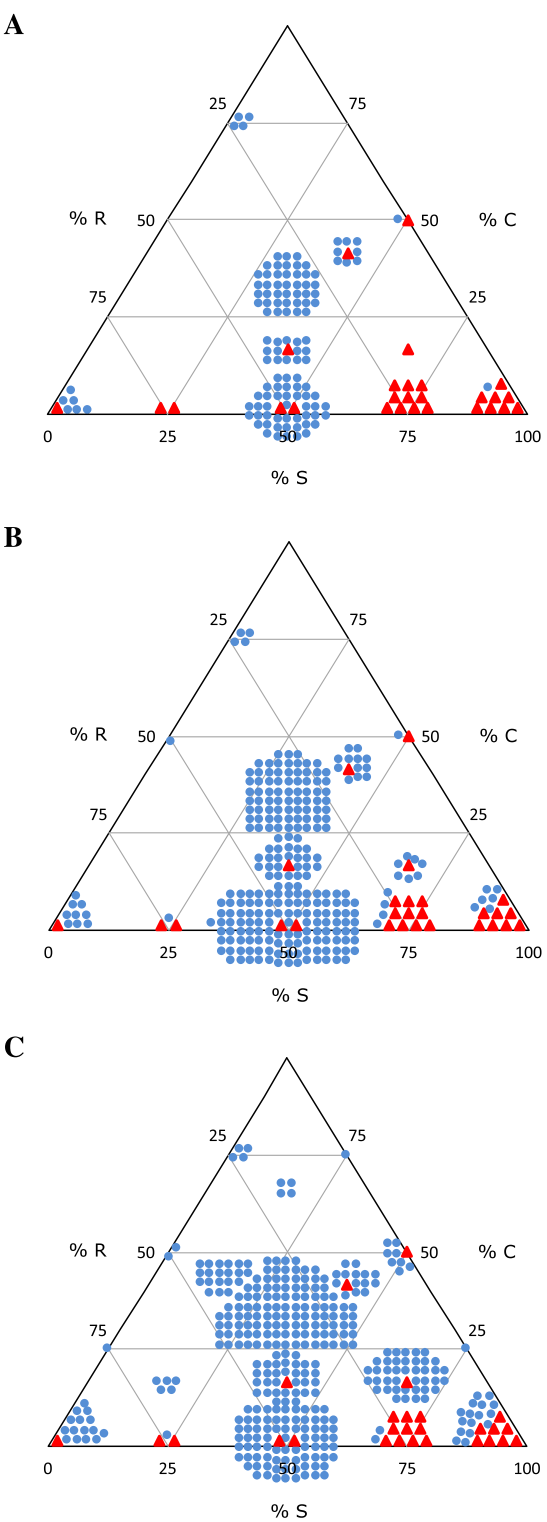
The analysis based on C–S–R strategies was complemented with an analysis based on plant traits, which was available for all species. Analyses based on plant traits have the advantage that they can also be applied in the field. Since we were interested in finding disturbance regimes that facilitate endangered species growth, 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 $\leq$ 20 cm tall were labelled ‘small’, whereas the remainder were labelled ‘large’.

We tested if the number of small annual species ($\leq$ 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 5.6 species per plot (SD = 3.4; range 0–15). In 9 plots there was only sand and no plants. The species richness was highest in C plots outside the sand patches (8.3 $\pm$ 3.0; mean $\pm$ SD), second highest in the B plots on the edge of the patches (5.9 $\pm$ 2.4) and lowest in A plots inside the patches (2.7 $\pm$ 2.3). 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 (Fig. 3), which includes species with R and S strategies combined with low competitive abilities. In fact, there were no



◀**Fig. 3** Grime's life strategy triangle for **A** bare sand plots, **B** transition and **C** dense vegetation plots. Each registration is represented by a blue dot. Red triangles represent Danish red-listed species associated with dry grassland habitats

species with a 100% C strategy and only 2 species with 75% C strategy (2% of all observations). The C–S–R triangles for each of the three plot types (A, B and C) revealed 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 in 30 plots: 50% in C plots, 30% in B plots and 20% in A plots.
2. Species with intermediate R and S strategies, i.e. 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 Danish red-listed species with this strategy were biennials (Table 1). The number of small annual species was higher in B plots than in A plots ($P < 0.001$, $z = 5.076$, Fig. 4) and also higher in B plots than in C plots ($P < 0.001$, $z = -4.437$). The number of large annual plants 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 27 dry grassland red-listed species where Grime values were available were found in the lower part of the C–S–R triangle (Fig. 3). Only four had a C strategy, but in no case > 50% so. The remaining 23 had a combination of R and S strategies (0% C), including eight that had a pure S strategy. Amongst the red list species the S strategy is more common and the R strategy less common, than for the majority of the plants observed on our study site in Mols Bjerge. This means that the majority of the red list species are more adapted to stress and less adapted to high levels of disturbance than most plants in our study.

Table 1 List of C–S–R values for plot species and Danish red-listed species occurring in dry grasslands

Grime strategy	Species	Life-form	Max. height (cm)	Frequency				Red list category
				Total Nr	Plot A (%)	Plot B (%)	Plot C (%)	
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 nummularium ssp.nummularium*	Perennial						EN
S	*Lycopodium alpinum*	Perennial						EN
S	*Antennaria dioica*	Perennial						NT

Table 1 continued

Grime strategy	Species	Life-form	Max. height (cm)	Frequency				Red list category
				Total Nr	Plot A (%)	Plot B (%)	Plot C (%)	
S	*Carex ericetorum*	Perennial						NT
S	*Epipactis atrorubens*	Perennial						NT
S	*Galium sterneri*	Perennial						NT
S	*Helianthemum nummularium 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

Sorted by Grime strategy (R: decreasing and C: increasing). Italic values indicate plot types where species are most frequent, omitting species observed in less than three plots. Red list categories are *EN* endangered, *VU* vulnerable, *NT* near threatened, *RE* regionally extinct and *CR* critically endangered

Discussion

This study shows that soil disturbance affects the composition of plant species in dry grasslands, and that it can lead to increased abundance of stress-tolerant ruderal species at intermediate disturbance levels and of stress-tolerant competitive species in less disturbed areas. This highlights the importance of spatial variability in disturbance intensity for maintaining plant diversity at the 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 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. Stress-tolerant ruderals (SR species; with 50% S and 50% R) that are adapted to lightly disturbed, unproductive habitats, were especially 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

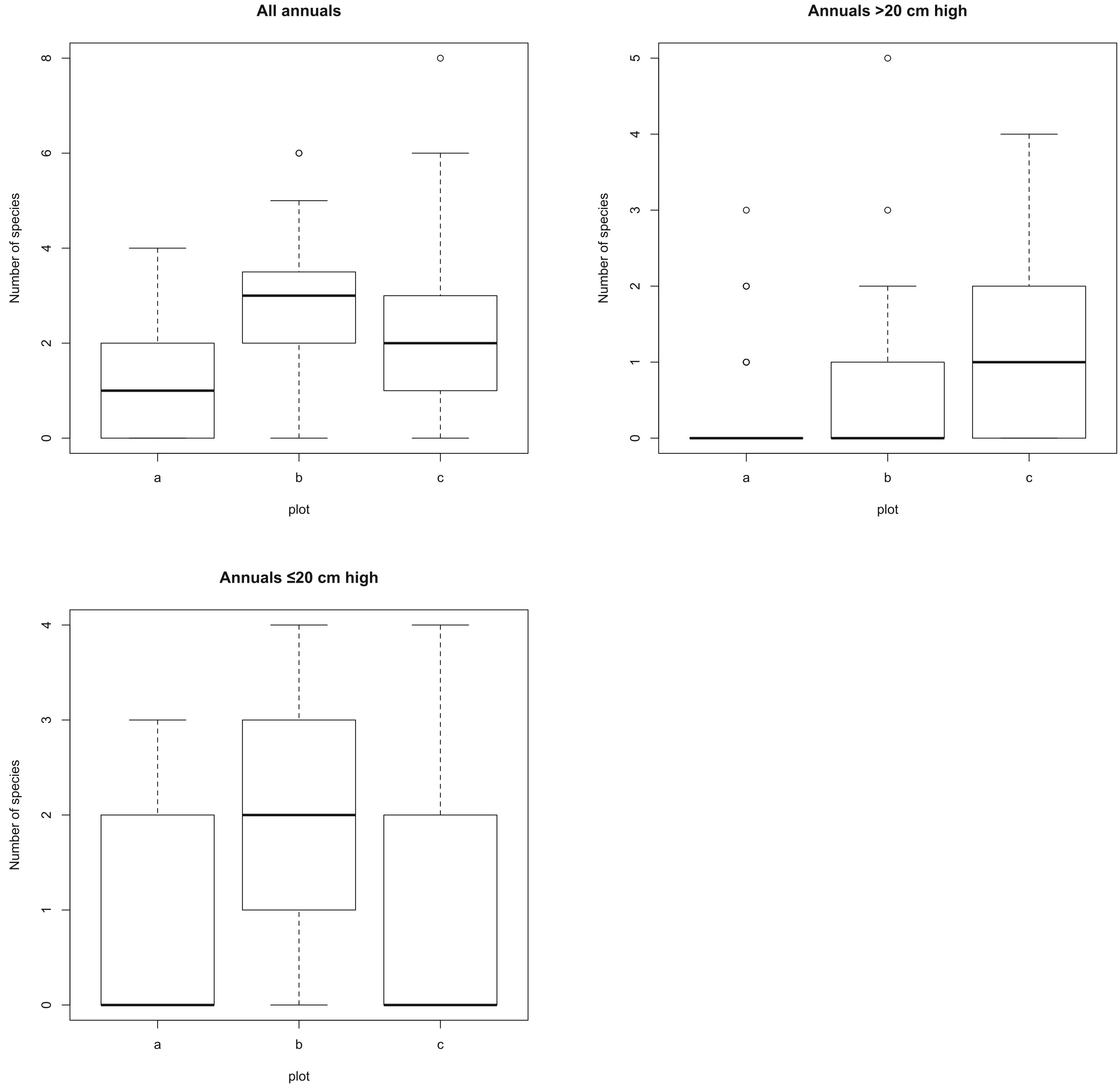


Fig. 4 The number of annual species in **A**, **B** and **C** plots, respectively. Top left: All annual species. Top right: Annual species higher than 20 cm. Bottom left: Annual species with a maximum height of 20 cm

intensities. However, only small annual species (≤ 20 cm tall) occurred in higher numbers in these plots, whereas large annual species (> 20 cm) were equally abundant in the transition zone and in the dense vegetation outside the patches. The difference between small and large annual species is presumably that small plants are unable to compete for light in the dense vegetation outside the sand patches and transition zone.

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 competition for space is reduced 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 Fig. 5, and that some areas close to the existing sand patches have been disturbed

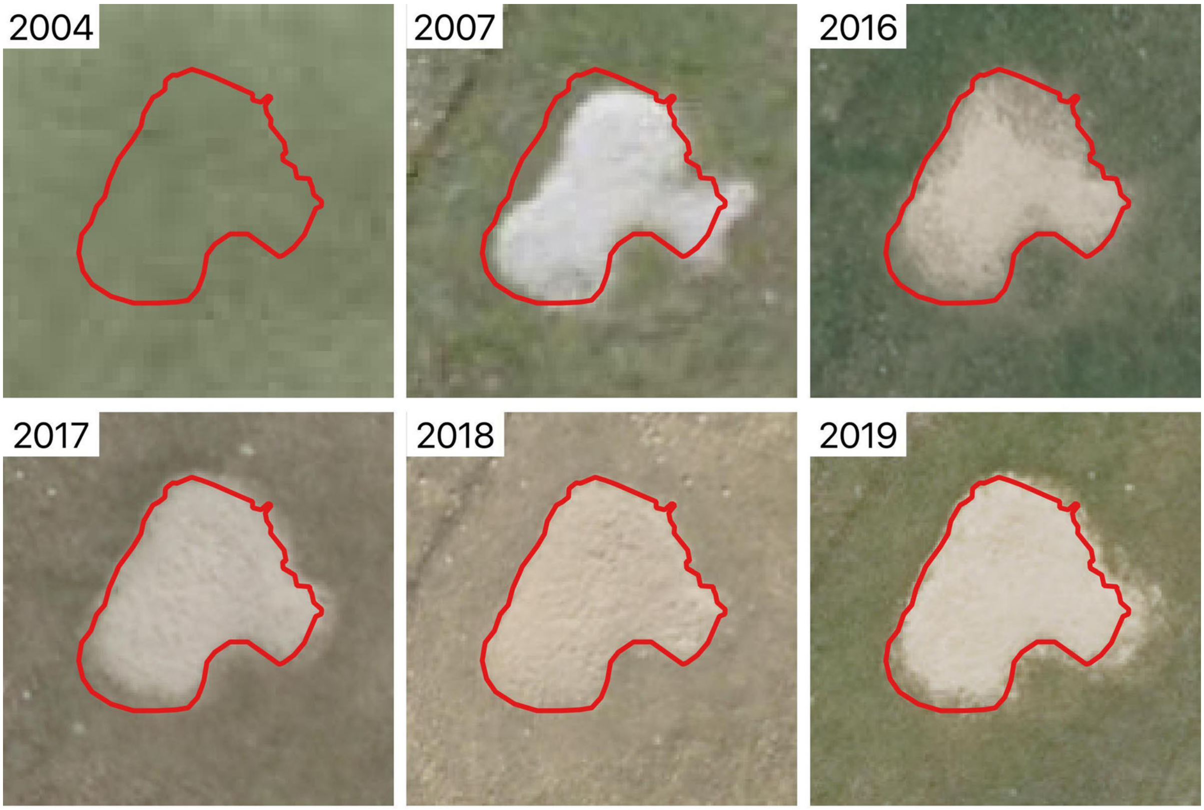


Fig. 5 Changes in delimitation of a sand patch from 2004 to 2019. The red line marks the delimitation in 2018 when the field work was conducted. The photos show that it is primarily the boundary zone between bare and dense vegetation that changes. In 2004 the vegetation at the site was continuous with no patches of bare soil, suggesting that the density of large herbivores was low in 2004

recently. However, the disturbances are apparently not so recent that small annual species can survive in the competition with larger species.

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 well suited 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 in our study the species richness was low, and few species had 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 amongst 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 areas with very high levels of soil disturbance therefore appear to be unimportant for maintenance of diversity in dry nutrient-poor grasslands. However, highly disturbed areas can be a prerequisite for the development of species-rich vegetation found at intermediate disturbance levels and thus for the persistence of many red-listed species.

The plots with intermediate disturbance levels at the transition between bare sand areas 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*, are 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 an 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. From orthophoto it can be seen that the vegetation in and around the plot has been disturbed recently (eastern part of sand patch in Fig. 5). Outside the plots *Veronica verna* was found on the transition between bare sand and dense vegetation.

In addition to the stress-tolerant ruderals (SR species) adapted to moderate levels of disturbance, the Danish Red List includes ten dry grassland species adapted to more stress and lower levels of disturbance (S/SR species). 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. Most red-listed dry grassland species are adapted to intermediate disturbance levels, indicating that soil disturbance is important for the persistence of red-listed species in dry grasslands and therefore also for the maintenance of diversity.

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. C–S–R values are only available for 81 of the 324 red-listed vascular species in Denmark. It is therefore desirable using easily observable plant traits as indicators of growth strategies. In our study, small annual species were significantly more abundant in the transition zone, which was also the place where stress-tolerant ruderals were particularly abundant. This suggests that presence of small annual plants can be used as an indicator of the intermediate disturbance intensities that appear to favour many rare species. The presence of plants with particular traits can therefore be used to guide management. Currently, the impact of management is often assessed based on the occurrence and positive population trends of threatened species (Schnoor et al. 2015). But in areas where no threatened species occur, perhaps for historical reasons, the prevalence of plants with particular traits can be used to indicate whether areas are managed in a way that favours the establishment of threatened species in the future (Kahmen and Poschlod 2008; Schnoor et al. 2015).

Importance of productivity and heterogeneity

Species richness is related to disturbance intensity in the Mols Bjerge grassland, but the effects of disturbances are likely to depend on productivity (Worm et al. 2002; Huston 2004; Renne et al. 2006). Grime described how species richness is expected to decrease when environmental conditions are favourable, biomass is high and competition is intense (Grime 1973, 1979). Under such conditions, niche partitioning can play an important role in maintaining diversity (Von Felten et al. 2009; Barry et al. 2019; Michalet et al. 2021). Under less favourable conditions fewer species are competitively excluded and species richness is maintained through facilitation. Several studies have demonstrated how this can lead to higher diversity in environments of intermediate productivity (Mulder et al. 2001; Michalet et al. 2006; Brooker et al. 2008; Nabe-Nielsen et al. 2017). In our study, the overall productivity is low, as evidenced by the abundance of stress-tolerant species even in the relatively dense vegetation outside the sand patches. In these patches the vegetation is apparently so open that competition plays a minor role for most species. In other, more productive grasslands, species richness would likely be more affected by competition in undisturbed patches with dense vegetation (e.g. Huston 2004). In such grasslands the highest diversity would likely be found in habitats exposed to disturbance, where plants would face lower levels of competition, and perhaps to a larger extent benefit from facilitation, than in the dense vegetation. The relationship between disturbance intensity and species richness is therefore likely to be tightly associated with the overall productivity.

Another factor that may play a role for species richness is the heterogeneity introduced by trampling, which increases overall diversity by introducing more different habitat types, allowing species with different growth forms to persist (Adler et al. 2001; Klaus et al. 2016). Although grazing, trampling and other disturbances can have negative effects on small-scale diversity, they generally favour higher diversity at larger spatial scales (Warren et al. 2007; Hanke et al. 2014; Tonn et al. 2019), which conforms with the intermediate disturbance hypothesis as originally formulated (Roxburgh et al. 2004). One obvious factor to consider when assessing the potential impacts of trampling and grazing on overall plant diversity is therefore to what extent animals aggregate in particular parts of the landscape, and the extent to which they tend to stay in the same areas for extended periods of time, as appears to be the case in Mols Bjerge (Fig. 5). The positive effect of soil disturbance which is often reported from grasslands (Warren et al. 2007; Ödman et al. 2012; Schnoor et al. 2015) suggests that the positive effects of increased habitat heterogeneity often outweigh negative fine-scale effects on diversity.

Conclusion

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 landscape scale diversity occurs in areas with both undisturbed areas and patches with intermediate levels of soil disturbances. Whilst 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 can be used as indicators of intermediate disturbance is 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.

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

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Data availability 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.

Declarations

Conflict of interest The authors have no conflicting interests.

Informed consent All authors have agreed to participate in this research project.

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