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Intermediate disturbance by off-road vehicles promotes endangered pioneer cryptogam species of acid inland dunes

Moderate Störungen durch Geländefahrzeuge fördern gefährdete Pionier-Kryptogamenarten in sauren Binnendünen

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Abstract

Psammophilous grassland communities of inland dunes often occurring together with common juniper scrub are among the most threatened habitat types in Central Europe. Once they were related to disturbance caused by traditional agriculture and forest management (sheep grazing, burning, litter raking and overexploitation of forests). Currently, after the above-mentioned drivers have disappeared, those communities are subjected to secondary succession leading to loss of their typical biodiversity, an important component of which are cryptogams (bryophytes and lichens). In the presented study we ask whether the recently increasing off-road activity, concentrated in dune areas, can maintain such habitats and their biodiversity or instead leads to an even faster deterioration.

To answer this question, we studied the cryptogam diversity in an off-road disturbed inland dune environment of a seldom used military training area located in Central Poland. A set of vegetation samples was collected, together with a range of measured or estimated variables including soil parameters, off-road disturbance intensity and factors related to ecological succession, like common juniper scrub cover.

The obtained results suggest that highest off-road intensity led to a transformation of the habitat into its very initial stage with active dune processes, while within undisturbed patches the succession led to the development of initial pine forest. The highest number of lichen and bryophyte species occurred within not or only slightly disturbed habitats. However, lichens preferred less shrub cover than bryophytes. Nevertheless, pioneer, typical psammophilous grassland species, which also include some threatened lichen species, benefited from small to medium disturbance intensity. Diverse and spatially complex off-road activity increases the number of microhabitats and can thus be a positive factor promoting the coexistence of all ecological groups of cryptogams connected with the acid inland dune environment. In our opinion, off-road activity may to some extent be used as an inexpensive nature conservation tool in order to maintain open, cryptogam-rich dune habitats.

Keywords: bryophytes, disturbance, *Juniperus communis*, lichens, military training site, psammophilous grassland, *Stereocaulon*

Erweiterte deutsche Zusammenfassung am Ende des Artikels

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1. Introduction

Grasslands on acid inland dunes comprise an important habitat for the conservation of biodiversity in Europe and are protected as Natura 2000 habitats (EUROPEAN COMMISSION 2013). In nemoral and boreal vegetation zones, they are principally semi-natural habitat types, created as a result of man-made deforestation and long-lasting intensive human-induced disturbance (including high grazing pressure) (SCHWABE et al. 2013, DENGLER et al. 2020a). Their area significantly decreased in the 20th century, primarily due to the abandonment of traditional land-use practices and subsequent intentional afforestation as well as natural succession (WOLFF et al. 2017, DENGLER et al. 2020b). Habitat patches dominated by cryptogam vegetation (the so-called “lichen steppes”) are of particularly high conservation value as they are the main habitat for many rare and threatened lichens (KETNER-OOSTRA et al. 2012). In Central Europe open inland dunes are also often occupied by common juniper, *Juniperus communis* (BARKMAN 1985). Nowadays this species is also in increasing danger of extinction in Europe, mainly due to habitat loss and low natural regeneration (VERHEYEN et al. 2009, BROOME et al. 2017).

Although military training sites are to be found all over the world, they have still been insufficiently explored. Scientific research on the development of biological diversity under conditions of intensive exploitation by military manoeuvres has been undertaken on a somewhat larger scale since the 1990s, when as a result of political changes those areas became more accessible to civilians. Military training grounds are specific sites where intensive disturbance caused by human activities dramatically changes the environment (MILCHUNAS 2000) and the heterogeneity of the landscape is higher than that of its surroundings (VANDERPOORTEN et al. 2005). Surprisingly, in times of abandonment of traditional agricultural land-use practices, it turned out that many ecosystems and species that were once widespread and related to agricultural landscapes found their only refuge within military training areas (WARREN & BÜTTNER 2008, JENTSCH et al. 2009). This may be due to the diverse and heterogeneous habitat properties of military training areas, where newly created microsites such as exposed soil, blast craters, tyre tracks of heavy vehicles, trenches and burned parts can become valuable habitats, e.g. psammophilous grasslands and heathlands, accommodating a large number of species (IUCN 1996, ROMAHN 1998, MILCHUNAS et al. 2000, WARREN et al. 2007, GUGNACKA-FIEDOR & ADAMSKA 2010, KRAWCZYK et al. 2019 etc.). Good light conditions coupled with suitably intense landscape disturbance processes like those occurring in military areas are particularly important for the conservation of endangered bryophytes and lichens, especially those related to otherwise disappearing pioneer conditions (MOTIEJUNAITE 1996, VANDERPOORTEN et al. 2005, DINGOVÁ 2010, GUGNACKA-FIEDOR & ADAMSKA 2010, ADAMSKA & DEPTUŁA 2015, KRAWCZYK et al. 2019).

The use of off-road vehicles in dune systems is considered a negative factor in many countries (e.g. RICKARD et al. 1994, KUTIEL et al. 2000). In some parts of Central and Eastern Europe, this problem has only recently arisen, and former military training areas are becoming heavily utilised by off-road amateurs. There have only been a few studies on the relationship between off-road impact and cryptogam biology, which focused mainly on the recovery time of cryptobiotic soil crusts after disturbance (BELNAP 1993, LALLEY & VILES 2008). There is little information about the relationship between off-road disturbance and cryptogam richness in changing, dynamic habitats. Some valuable bryophytes are known to be connected with a disturbed environment (VANDERPOORTEN et al. 2005), and there is a high probability that lichens may also benefit from it.

Due to political changes in the world and changes in military doctrine resulting from technological progress, some military facilities were closed, e.g. in Poland after 1989 (IUCN 1996). This poses a threat to valuable disturbance-dependent ecosystems and species (JENTSCH et al. 2009). Off-road activity very often appears in abandoned military training areas as their landscape heterogeneity and often unregulated ownership status attracts both legal and illegal off-road activities. In the presented study we wanted to check whether off-road activities can successfully replace the former military disturbance in an abandoned training area and maintain the threatened cryptogam biodiversity in its acid sandy grasslands. To achieve this, we tried to define the main ecological factors influencing cryptogam communities in the disturbed, changing environment of an open acid inland dune area of a partly abandoned military training area including, among other environmental variables, off-road disturbance intensity.

2. Study area

The research was carried out within a military training area called Grochalskie Piachy (ca. 250 ha), located in Central Poland (52°24’15”N, 20°37’05”E), 22 km northwest of the capital city, Warsaw. The site is nowadays part of the Kampinos National Park. The area lies within the pre-glacial Vistula river valley on deep river sands remodelled by the aeolian process in the early Holocene and is part of one of the largest and best-developed dune belts in Europe (ZGORZELSKI & PAWŁOWSKA 2003). The mean annual temperature of the site is 7.7 °C, the mean annual rainfall 546.9 mm, the mean annual temperature amplitude 24.6 °C, the mean daily amplitude 9.1 °C and the length of the growing period 185 days (ANDRZEJEWSKA 2003). The terrain of the military range is rugged, with many small depressions and hills, but altitude differences are small (77–83 m a.s.l.). Nowadays dune processes are still present in large parts of the site. However, only small dune forms (sand ripples and low hillocks) are observed. The open areas of the military range were created on purpose by deforestation (as foreground of a fortress) in the late nineteenth and early twentieth century, and until the last decade of the 20th century, they were used only for military purposes. The military range is composed of three open sand fields with active dune processes triggered by military activities. The open areas (ca. 100 ha) are predominantly covered with *Corynephorion canescentis* Klika 1931 vegetation (MATUSZKIEWICZ 2015). Nowadays the northern part of the site is still under heavy disturbance caused by regular demolition of old unexploded bombs from World War II. The remnant part, where the study was conducted, is not used for military purposes, and no other forms of management have been applied in recent decades. The whole non-forested area of the military training area is utilised by enthusiasts of off-road vehicles such as four-wheel drive cars, all-terrain vehicles (ATVs), motorcycles and motocross vehicles.

3. Material and methods

3.1 Sampling methods

The fieldwork was carried out in the growing season of 2010. In order to minimise the risk of sampling the same habitat path more than once, the following procedure was applied: The central and southern part of the military range was evenly covered with a 25 m × 25 m grid. Within the squares, only evenly disturbed habitat patches were sampled. No more than one sample per square was taken (Fig. 1). Squares with no suitable habitat patches were omitted. Each sample was a 64 m^2 square plot.

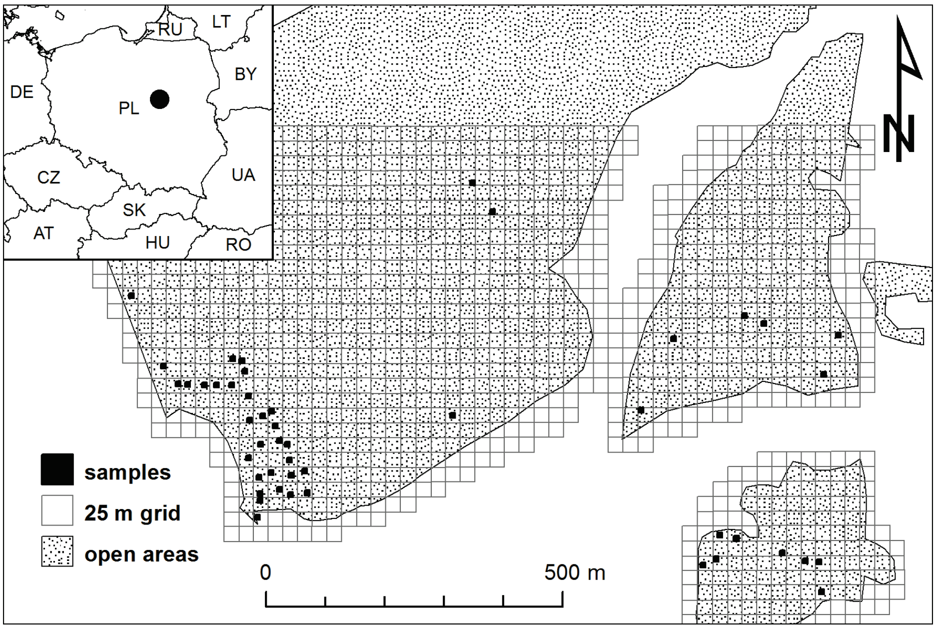

Fig. 1. Location of sampling plots within the Grochalskie Piachy military training area.

Abb. 1. Lage der Untersuchungsflächen auf dem militärischen Übungsgelände Grochalskie Piachy.

The relatively large plot size was chosen in order to obtain averaged results as within these highly dynamic habitats, disturbance intensity and shrub cover vary. The cover of trees and shrubs, of common juniper in the shrub layer and of open substrate and litter were visually estimated with a precision of 5%. Vascular plants in the herb layer, terrestrial bryophytes, liverworts and lichens were sampled using a modified (BARKMAN et al. 1964) BRAUN-BLANQUET (1928) scale (original vegetation data provided in Supplement E1 and environmental variables in Supplement E2). Samples of problematic species were collected for laboratory analyses. To account for natural habitat variability originating from topography, the inclination of each plot was measured with the use of a hand inclinometer. In each sampling plot a set of 25 evenly distributed sampling points (2 m apart from each other) was selected. The visible off-road disturbance and dune processes were noted as present or absent in each of these sampling points. As off-road disturbance we classified any sign indicating that the area had been driven on during the growing season, usually visible as linear tyre tracks. This included situations when the soil crust was compressed or even broken as well as situations when a tyre track appeared within a completely bare patch of sand. Dune processes representing naturally occurring disturbance were identified by visible sand ripples and/or partially buried plants of *Corynephorus canescens*. Hillocks and grooves made by insects were rather rare and not taken into account. No other natural disturbances were recorded within the study plots. From the 9 sampling points in the centre (Fig. 2), mixed soil samples were collected from a depth of 5–10 cm.

3.2 Species determination and laboratory analyses

Cryptogam species were determined using standard morphological and anatomical methods: for bryophytes according to SMITH (2004), for lichens according to SMITH et al. (2009) and for liverworts according to DAMSHOLT (2002). Thin Layer Chromatography (TLC) was also used for the determination of lichen chemical compounds in the *Cladonia chlorophaea* and *C. coccifera* groups according to ORANGE et al. (2001). Sieving analysis of the soil samples was performed with mesh sizes of 1 mm (very coarse sand and gravel), 0.5 mm (coarse sand), 0.25 mm (medium sand) and 0.1 mm (fine sand),

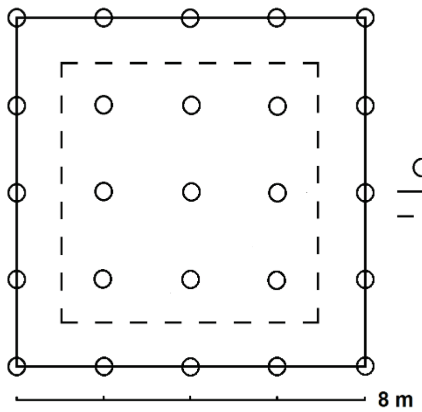

Fig. 2. Method of data collection within a 64-m^2 sampling plot 1) sampling points located 2 m apart from each other, 2) 25 points used for the assessment of disturbance and dune processes intensity, 3) 9 central points used for the soil sample collection.

Abb. 2. Methode der Datenerfassung innerhalb einer 64-m^2-Fläche 1) 2 m voneinander entfernte Untersuchungsflächen; 2) Störungsintensität und Dünenprozesse wurden an allen 25 Punkten beurteilt; 3) an den mittleren 9 Punkten wurden Bodenproben genommen.

the remaining fractions representing very fine sand, silt and clay. For chemical analysis the soil samples were cleaned using a 1-mm sieve. Conductivity and pH were determined with an electronic pH/conductivity meter in a suspension of 1 part of sand and 5 parts of water by volume after standing for 24 hours. The total organic matter content was measured as loss on ignition at 550 °C.

3.3 Cryptogam groups and nomenclature

Valuable cryptogam species were assessed according to Polish national red lists (OCHYRA 1992, CIEŚLIŃSKI et al. 2006) and lists of species protected by national law. Ecological groups of cryptogams were described according to KETNER-OOSTRA et al. (2012) and slightly modified to adapt them to local climatic conditions according to succession models of FALIŃSKI et al. (1993). Recorded lichens were assigned to four groups: pioneer, humicolous, humicolous/aero-hygrophytes and aero-hygrophytes (KETNER-OOSTRA et. al. 2012). The nomenclature of vascular plants follows MIREK et al. (2002), liverworts DAMSHOLT (2002), bryophytes SMITH (2004) and lichens SMITH et al. (2009). We decided to use *Cladonia chlorophaea* s.l. (including recognised *C. chlorophaea*, *C. merochlorophaea* and *C. grayi*), *Cladonia coccifera* s.l. (including recognised *C. diversa* and *C. pleurota*), *Cladonia macilenta* s.l. (including recognised *C. macilenta* and *C. floerkeana*) and *Hypnum cupressiforme* s.l. Abbreviations of cryptogam species names used in the presented figures are explained in Table 1. Species names of vascular plants are abbreviated using the first three letters of the genus name and the first four letters of the species epitheton.

3.4 Statistical analysis

The values obtained for the intensity of off-road disturbance and dune processes (ranging from 0 to 25, cf. section 3.1) were recalculated into percentages and used as continuous variables in the analysis. After that, a pairwise correlation analysis of all independent variables was conducted using Pearson's linear correlation coefficient. In cases where $|r| > 0.7$, one of the strongly correlated variables was removed from further analyses until no such cases were left. Firstly, a very strong correlation ($r = 0.99$) appeared between total shrub cover and cover of common juniper in the shrub layer. Only the first variable was used in further analyses, but it can be assumed that they can be used interchangeably. We also removed from further analyses bare soil cover and intensity of dune processes, which were correlated to disturbance intensity (probably because disturbance creates open sand and triggers dune processes), litter cover, which was correlated to shrub cover, and soil pH, which was negatively correlated to organic matter content. Also, middle soil fractions were removed as they were correlated either with the largest or the smallest soil separates (Table 2). The set of values representing the spatial arrangement of sampling plots (x, y, xy, x^2, y^2, x^3, y^3, x^2y and xy^2) was calculated according to BORCARD et al. (1992) on the basis of their coordinates in the PUWG 1992 metric coordinate system. These were used

Table 1. Cryptogam species recorded within 47 samples with information about their ecological status (KETNER-OOSTRA et al. [2012], slightly modified according to FALIŃSKI et al. [1993]), and their conservation status (CIEŚLIŃSKI et al. 2006). Abbreviations: pio = pioneer, hum = humicolous, aero-hyg = aero-hygrophyte, epi = epigeic epixylite

Tabelle 1. In den 47 Vegetationsaufnahmen vorkommende Kryptogamenarten, mit Informationen über ihr ökologisches Verhalten (KETNER-OOSTRA et al. [2012], leicht modifiziert nach FALIŃSKI et al. [1993]), sowie ihren Rote Liste und Schutzstatus (CIEŚLIŃSKI et al. 2006).

Species name	Abbreviation	Ecological status	Red List / National law protection status	Frequency (%)
Ceratodon purpureus	Cer_pur	pio	-/-	47
Cetraria aculeata	Cet_acu	pio	-/+	79
*Cladonia cervicornis*ssp. *verticillata*	Cl_cerv	pio	-/-	45
Cladonia foliacea	Cl_foli	pio	-/-	2
Cladonia mitis	Cl_miti	pio	-/+	85
Placynthiella uliginosa	Pla_ulig	pio	-/-	36
Polytrichum piliferum	Pol_pili	pio	-/-	85
Racomitrium canescens	Rac_cane	pio	-/-	9
Stereocaulon condensatum	Ste_cond	pio	VU/+	15
Trapeliopsis granulosa	Tra_gran	pio	-/-	40
Baeomyces rufus	Bae_rufu	hum	-/-	2
Brachythecium albicans	Bra_albi	hum	-/-	4
Cephaloziella divaricata	Cep_diva	hum	-/-	9
Cladonia chlorophaea s.lat.	Cl_chlo	hum	-/-	19
Cladonia coccifera s.lat.	Cl_cocc	hum	-/-	36
Cladonia fimbriata	Cl_fimb	hum	-/-	19
Cladonia furcata	Cl_furc	hum	-/-	4
Cladonia glauca	Cl_glau	hum	-/-	21
Cladonia macilenta s.lat.	Cl_maci	hum	-/-	40
Cladonia phyllophora	Cl_phyl	hum	-/-	45
Cladonia subulata	Cl_subu	hum	-/-	57
Placynthiella oligotropha	Pla_olig	hum	-/-	11
Polytrichum juniperinum	Pol_juni	hum	-/-	2
Stereocaulon incrustatum	Ste_incr	hum	EN/+	4
Cetraria islandica	Cet_isla	hum / aero-hyg	VU/+	6
Cladonia cornuta	Cl_corn	hum / aero-hyg	-/-	9
Cladonia deformis	Cl_defo	hum / aero-hyg	-/-	23
Cladonia squamosa	Cl_squa	hum / aero-hyg	-/-	2
Cladonia uncialis	Cl_unci	hum / aero-hyg	-/-	47
Sciuro-hypnum oedipodium	Sci_oedi	hum / aero-hyg	-/-	11
Pohlia nutans	Poh_nuta	hum / aero-hyg	-/-	11
Cladonia arbuscula	Cl_arbu	aero-hyg	-/+	2
Cladonia crispata	Cl_cris	aero-hyg	-/-	2
Cladonia gracilis	Cl_grac	aero-hyg	-/-	19
Dicranum polysetum	Dic_poly	aero-hyg	-/+	23
Dicranum scoparium	Dic_scop	aero-hyg	-/+	17
Hylocomium splendens	Hyl_sple	aero-hyg	-/+	2
Hypnum cupressiforme s.lat.	Hyp_cupr	aero-hyg	-/-	13
Lophocolea heterophylla	Lop_hete	aero-hyg	-/-	2
Pleurozium schreberi	Ple_schr	aero-hyg	-/+	26
Placynthiella dasaea	Pla_dase	epi	-/-	4
Hypogymnia physodes	Hyp_phys	epi	-/-	2

Table 2. Summary of all environmental variables recorded within the study plots. Variables included in the pCCAs are indicated with a "+".

Tabelle 2. Zusammenfassung aller innerhalb der Untersuchungsflächen gemessenen Umweltvariablen. Diejenigen, die nach der Entfernung der stark korrelierten Variablen in die beiden pCCA einbezogen wurden, sind mit "+" gekennzeichnet.

Variable	Abbreviation	Unit	Mean	SD	Median	Min	Max	Predictor
Inclination	INCL	°	2.66	2.70	3	0	11	+
Cover of tree layer	A_COV	%	1	5	0	0	30	+
Cover of shrub layer	B_COV	%	21	25	10	0	100	+
Common juniper cover in shrub layer	JC_B	%	21	25	10	0	100	-
Share of plot area with visible dune processes	DUNE_INT	%	29	41	0	0	100	-
Share of plot area disturbed by off-road vehicles	DIST_INT	%	57	35	64	0	100	+
Cover of visible open substrate	bare_soil	%	51	35	50	0	100	-
Cover of litter	Litter	%	8	12	3	0	45	-
pH of upper soil horizon	pH	-	5.32	0.44	5.40	4.05	6.04	-
Electrical conductivity of upper soil horizon	EC	$\mu S*cm^{-1}$	35.5	26.7	27.9	15.6	142.6	+
Weight loss on ignition of upper soil horizon	ORGANIC	%	0.67	0.61	0.54	0.14	3.13	+
Share of soil fractions > 1 mm	fr_coarse	%	0.50	0.49	0.33	0.02	2.30	+
Share of soil fractions 0.5–1 mm	fr_coarse_sand	%	8.68	6.04	6.34	1.65	29.62	-
Share of soil fractions 0.25–0.5 mm	fr_med_sand	%	55.35	6.83	56.50	20.83	67.20	-
Share of soil fractions 0.1–0.25 mm	fr_fine_sand	%	34.07	9.82	33.61	19.51	76.47	-
Share of soil fractions < 0.1 mm	fr_fine	%	1.40	0.69	1.14	0.42	3.39	+

as covariates in all of the performed multivariate analyses to remove the variance related only to the spatial arrangement of plots. In order to identify the most important ($p < 0.05$) environmental variables (Table 2) influencing the analysed ground vegetation, we performed a partial Canonical Correspondence Analysis (pCCA) with manual forward selection of explanatory variables (1) for both herb and cryptogam layers, which were combined and transformed arithmetically according to TÜXEN & ELLENBERG (1937), and (2) for presence-absence data of cryptogams only. The significance of the species-environment relations was checked with a Monte Carlo test (499 runs). After the selection of the most relevant variables, a set of Generalised Additive Models (GAM) for calculated biodiversity and ecological indices of cryptogams (Table 3) was calculated together with XY(Z) plots according to recommended procedures (ŠMILAUER & LEPŠ 2014). They showed the response of the cryptogam species groups to disturbance intensity and shrub cover. The relevance of these gradients was supported by the results of the partial CCA. All analyses were performed using the software packages R and CANOCO 5 with Canodraw for Windows (ŠMILAUER & LEPŠ 2014, R CORE TEAM 2019).

4. Results

4.1 Cryptogam richness and ecological groups

A total of 29 vascular plant, 12 moss, 2 liverwort and 32 lichen species were recorded in the samples. The cryptogam species represented all ecological groups occurring on dune habitats (KETNER-OOSTRA et al. 2012). In the study 10 pioneer, 14 humicolous, 7 humicolous/aero-hygrophyte and 9 aero-hygrophyte species were found. One species was considered as an epigeic epiphyte and one as an epigeic epixylic species. Ten cryptogam species

Table 3. Summary of dependent variables used in the analysis (protection of species according to Polish law, red-listing according to CIEŚLIŃSKI et al. [2006], lichen ecological groups according to KETNER-OOSTRA et al.]012] with slight modifications based on work by FALIŃSKI [1993]).

Tabelle 3. Zusammenfassung der abhängigen Variablen, die in der Analyse verwendet wurden (Schutzstatus nach polnischem Recht, Rote Liste nach CIEŚLIŃSKI et al. [2006], Flechtenökologische Gruppen nach KETNER-OOSTRA et al. [2012] mit leichten Modifikationen basierend auf Arbeiten von FALIŃSKI [1993]).

Variable	Abbreviation	Mean	SD	Median	Min	Max
No. of valuable (protected, red listed) lichen species	lich_val	1.91	0.86	2	0	3
No. of bryophyte species	n_moss	2.60	2.13	2	0	9
No. of lichen species	n_lichen	6.77	4.34	7	0	15
No. of all cryptogams (bryophytes, lichens)	n_cryptogam_species	9.36	5.70	9	0	20
No. of pioneer species	Pioneer n	4.43	2.14	5	0	8
No. of humicolous species	Hum n	2.74	2.31	3	0	7
No. of humicolous/aero-hygrophytes	Hum-Aero n	1.09	1.08	1	0	4
No. of aero-hygrophytes	Aero n	1.06	1.62	0	0	6

protected by national law and three epigeic lichen species red-listed in Poland were found. Two of them, *Stereocaulon condensatum* and *S. incrustatum,* have the highest conservation status (Table 1). Within the study plots we recorded up to 20 cryptogam species (9.36 on average) and up to 15 species of lichens (6.77 on average) (Table 3).

4.2 Main factors influencing the cryptogam community structure

The partial Canonical Correspondence Analysis performed for the combined herb and cryptogam layers revealed the disturbance intensity, shrub and tree cover, conductivity and gravel content to be relevant ($p < 0.05$) variables influencing the community structure (Fig. 3, Table 4). The influence of soil organic matter content as well as fine soil particles content proved not to be relevant ($p > 0.05$) in the applied model. The second partial Canonical Correspondence Analysis conducted only for presence-absence data in the cryptogam layer also indicated the disturbance intensity and tree and shrub cover as well as the share of the smallest fractions in the soil to be significant factors in the model (Fig. 4). In both cases the tree (first pCCA1: r = -0.6272, second pCCA1: r = 0.6561) and shrub (first pCCA1 r = -0.6865, second pCCA1 r = 0.8101) cover vectors were correlated with the first ordination axis whereas the disturbance intensity turned out to be unrelated to the first but connected with the second most important ordination axis (first pCCA2: r = 0.8690, second pCCA2: r = -0.7022). This indicates that off-road disturbance and shrub density are the most important factors influencing cryptogams within the study area.

4.3 Cryptogam biodiversity and response of ecological groups to disturbance level and shrub cover

The GAM fitting shrub cover and disturbance intensity to biodiversity indices and ecological groups of cryptogams produced significant results ($p < 0.05$) throughout (Table 5). In the case of valuable lichen and pioneer cryptogam species numbers, the responses to disturbance intensity were strongly non-linear (non-linearity test $p < 0.01$) (Table 5). According to XY(Z) plot analyses, the highest numbers of cryptogam species occurred in not or only slightly disturbed patches with medium shrub cover. The lowest numbers of species were

Table 4. Results of the Canonical Correspondence Analysis of the uncorrelated variables.

Tabelle 4. Ergebnisse der kanonischen Korrespondenzanalyse der unabhängigen Variablen.

Variable	Explains (%)	Contribution (%)	*pseudo-F*	*p*
EC	11.6	25.8	5	**0.002**
DIST_INT	11	24.5	5.3	**0.002**
fr_skeleton_sum	6.5	14.4	3.3	**0.002**
INCL	4.1	9.2	2.2	**0.024**
B_COV	3.9	8.6	2.1	**0.02**
A_COV	3.7	8.2	2	0.068
fr_silt_clay	2.2	4.9	1.2	0.282
ORGANIC	2	4.5	1.1	0.29

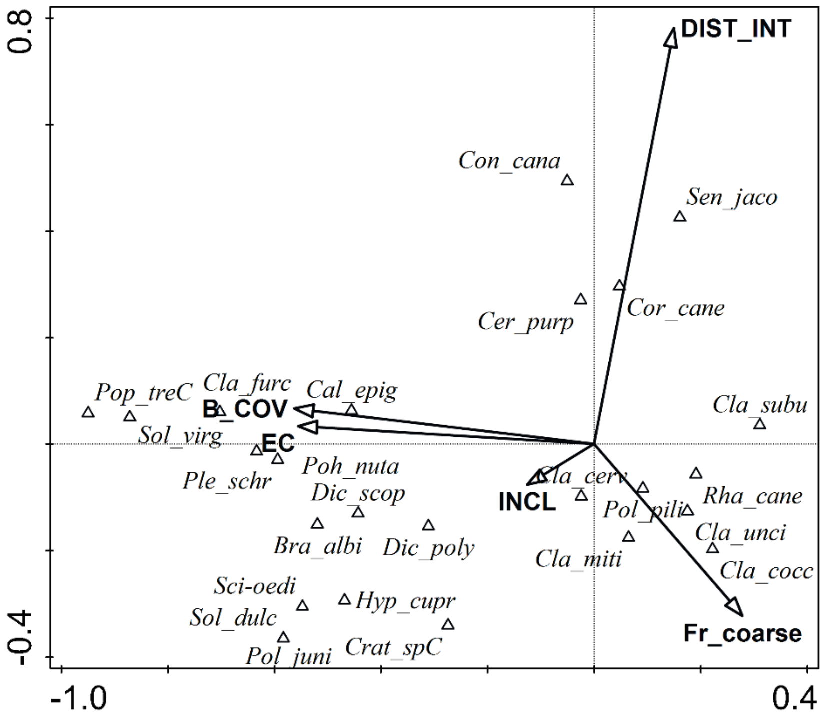

Fig. 3. Result of the partial Canonical Correspondence Analysis for combined herb and cryptogam layers. Only significant ($p < 0.05$) factors influencing the species data are shown (B_COV – Cover of shrub layer, DIST_INT – Share of plot area disturbed by off-road vehicles, EC – Electrical conductivity of upper soil horizon, Fr_coarse – Share of soil fractions larger than 1 mm, INCL – inclination). Abbreviations of cryptogam species names are explained in Table 1. Species names of vascular plants are abbreviated using the first three letters of the genus name and the first four letters of the species epitheton.

Abb. 3. Ergebnis der kanonischen Korrespondenzanalyse (CCA) für Gefäβpflanzen und Kryptogamen. Nur signifikante ($p < 0,05$) Faktoren werden gezeigt. Abkürzungen der Kryptogamenarten sind in Tabelle 1 erläutert. Abkürzungen der Gefäßpflanzenarten bestehen aus den ersten drei Buchstaben des Gattungsnamens und den ersten vier Buchstaben des Artnamens.

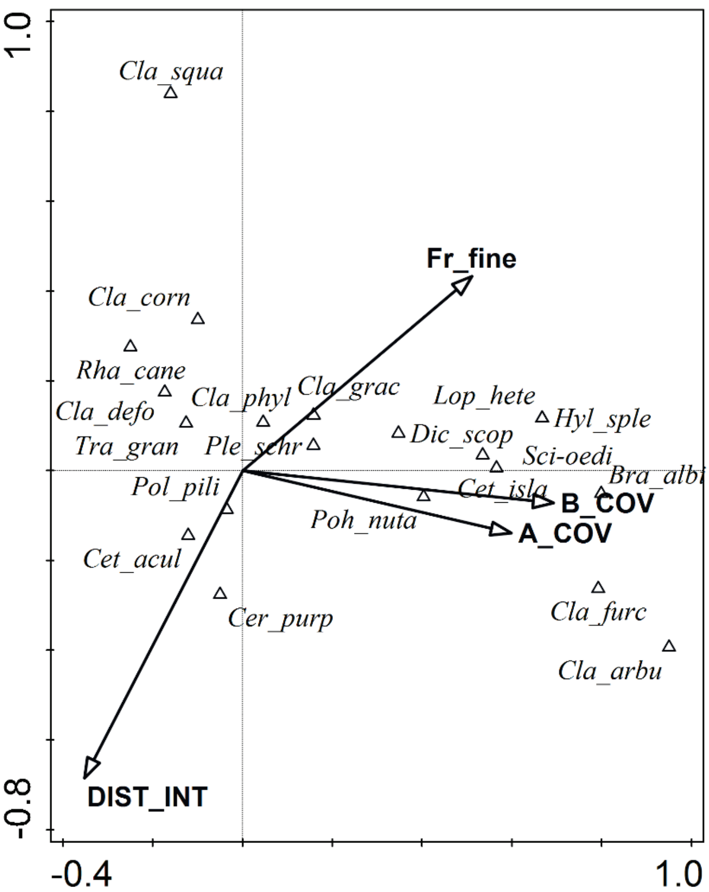

Fig. 4. Result of the partial Canonical Correspondence Analysis for the cryptogam layer using binominal (presence/absence) species data. Only significant ($p < 0.05$) factors influencing the species data are shown (A_COV – Cover of tree layer, B_COV – Cover of shrub layer, DIST_INT – Share of plot area disturbed by off-road vehicles, Fr_fine – Share of soil fractions smaller than 0.1 mm). Abbreviations of cryptogam species names are explained in Table 1.

Abb. 4. Ergebnis der partiellen kanonischen Korrespondenzanalyse (pCCA) für die Kryptogamen mit binominaler Behandlung der Artendaten (Anwesenheit/Abwesenheit). Nur signifikante ($p < 0,05$) Faktoren werden gezeigt. Abkürzungen der Kryptogamenarten sind in Tabelle 1 erläutert.

noted in sites with the highest disturbance levels and no shrub cover (Fig. 5a). Lichen richness was also highest in undisturbed patches, although with lower shrub cover (Fig. 5b). Bryophyte richness, on the other hand, clearly increased with increasing shrub cover, and at the same time showed a slight preference towards somewhat disturbed areas (Fig. 5c). The highest numbers of valuable lichen species occurred when the anthropogenic disturbance levels were medium and the shrub cover was below 40% (Fig. 5d).

The results of both multivariate analyses revealed that very high off-road intensity leads to the development of an initial stage of psammophilous grassland with active dune processes and low species diversity (very few species except for *Corynephorus canescens*) (Fig. 3 and 4). Medium disturbance is related with more species-rich pioneer communities with

Tabelle 5. Ergebnisse des verallgemeinerten Additivmodells, zur Untersuchung des Einflusses der Gehölzdeckung und Störungsintensität auf Biodiversitätsindizes und ökologische Kryptogamengruppen.

Table 5. Results of the Generalised Additive Model (GAM) fitting shrub cover and disturbance intensity to biodiversity indices and ecological groups of cryptogams.

Index	*F*	*p*	Tests of non-linearity of response (p)	
			B_COV	DIST_INT
lich_val	5.7	0.00091	0.27183	**0.00409**
n_moss	32.1	< 0.00001	0.10504	0.06103
n_lichen	18.5	< 0.00001	**0.02309**	0.08864
n_cryptogam_species	27.1	< 0.00001	**0.01658**	**0.03812**
Pioneer n	15.0	< 0.00001	**0.00255**	**0.00013**
Hum n	13.5	< 0.00001	0.11844	0.47264
Hum-Aero n	9.8	0.00001	0.28905	0.29838
Aero n	20.5	< 0.00001	0.47838	0.09156

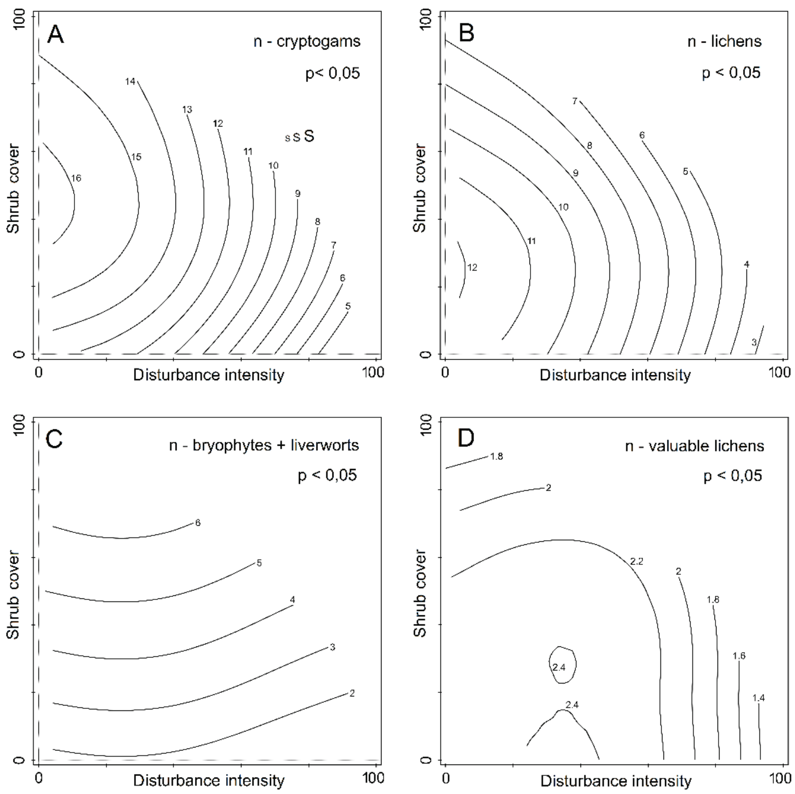

Fig. 5. XY(Z) plots showing the responses of cryptogams to disturbance intensity and shrub cover (GAM). **a)** total number of cryptogam species, **b)** total number of lichen species, **c)** total number of bryophytes, **d)** total number of valuable lichen species (protected and threatened according to CIEŚLIŃSKI et al. 2006).

Abb. 5. XY(Z)-Diagramme zum Einfluss der Störungsintensität und Gehölzdeckung (GAM) auf **a)** Gesamtartenzahl der Kryptogamen, **b)** Gesamtartenzahl der Flechten, **c)** Gesamtartenzahl der Moose, **d)** Gesamtartenzahl der Flechtenarten mit hohem Naturschutzwert.

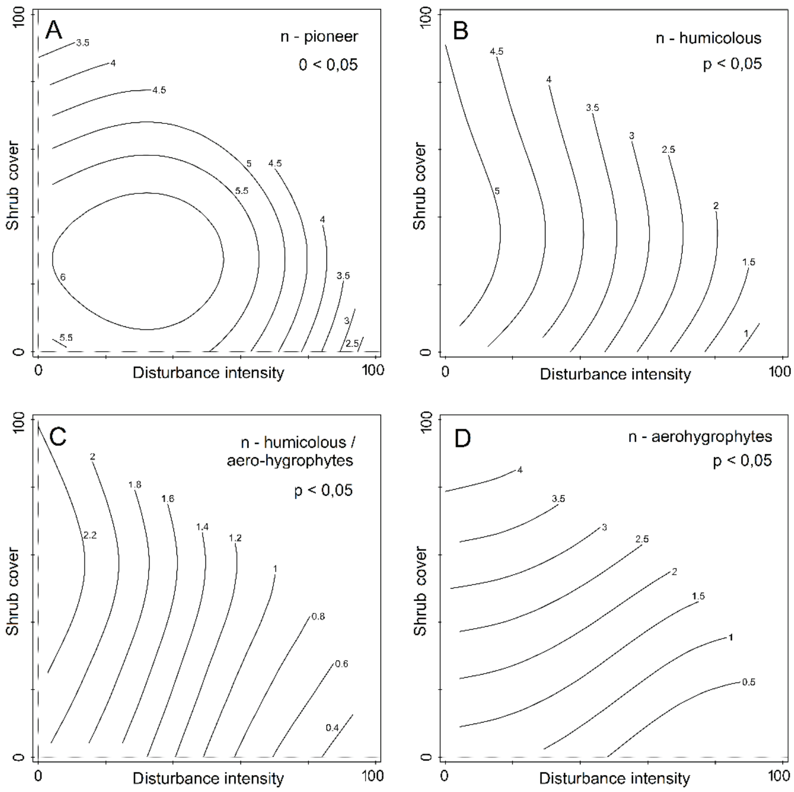

Fig. 6. XY(Z) plots showing the responses of main ecological cryptogam groups (KETNER-OOSTRA et al. 2012, slightly modified according to succession models of FALIŃSKI et al. 1993) to disturbance intensity and shrub cover (GAM). **a)** total number of pioneer species, **b)** total number of humicolous species, **c)** total number of humicolous/aero-hygrophyte species, **d)** total number of aero-hygrophyte species.

Abb. 6. XY(Z)-Diagramme zum Einfluss der Störungsintensität und Gehölzdeckung (GAM) auf **a)** Gesamtzahl der Pionierarten, **b)** Gesamtzahl der humicolen Arten, **c)** Gesamtzahl der humicolen/aerohygrophytischen Arten, **d)** Gesamtzahl der aerohygrophytischen Arten.

C. canescens and *Spergula vernalis*, characterised by the presence of many pioneer cryptogams (Fig. 6a). The maximum pioneer species numbers occurred in patches of low or medium disturbance with low to medium shrub cover (5–45%). A decreasing impact of disturbance led to the gradual encroachment of humicolous species (Fig. 6b). The maximum numbers of cryptogam species belonging to this group were recorded within not or only slightly disturbed patches with medium shrub cover (15–60%). Humicolous/aero-hygrophytes (Fig. 6c) preferred undisturbed patches with high shrub cover (around 60%). The number of aero-hygrophytes increased gradually with a decrease in disturbance intensity and an increase of shrub cover, reaching its maximum where the shrub cover exceeded 70% (Fig. 6d).

5. Discussion

5.1 The interaction of ecological succession and off-road disturbance influences the cryptogam community structure

Military disturbance increases non-forest area (MILCHUNAS et al. 2000), reduces the cover of the herb layer and increases the exposed surface of the soil (SHAW & DIERSING 1990, PROSSER et al. 2000). The intensity of military use is an important factor competing with ecological succession. Excessive use of a training area can lead to a situation where the disturbance processes occur faster than the regeneration processes (HIRST et al. 2000, MILCHUNAS et al. 2000). On the other hand, some military training areas where disturbing human activities have ended suffer from rapid succession and require active management in order to save their valuable habitats (PRACH et al. 2000, JENTSCH et al. 2009). In our study partial Canonical Correspondence Analyses for the ground layer revealed that off-road disturbance and variables connected with ecological succession represented by shrub cover are the main independent factors explaining the structure of the whole dataset (Fig. 3). These are typical factors also described as influencing the vascular vegetation of other military training areas (e.g. HIRST et al. 2000, MILCHUNAS et al. 2000, PRACH et al. 2000). If only the presence of cryptogams was considered, the same factors turned out to be the most important (Fig. 4). This indicates that cryptogams respond to environmental factors similarly to vascular plants. What is more important, vectors representing both factors turned out to be perpendicular, suggesting that they are independent. It implicates that disturbance can influence the community at different successional stages, from an initial *Corynephorus* stand to dense *Juniperus* scrubland. Additionally, the observed high correlation between the presence of dune processes and the disturbance intensity rather than the successional stage suggests that off-road disturbance can trigger natural geomorphological processes typical for active inland dune habitats. In the presented study the increase of conductivity was also found to be a relevant factor following succession. It was probably connected with the rising concentrations of H^+ ions caused by the presence of organic acids in humus-enriched soils (Fig. 3). The presented relationships remain relevant within the whole dataset despite some heterogeneity of soils exhibited by variations in the dust, gravel or organic matter contents.

5.2 Habitat heterogeneity and intermediate disturbance promote cryptogam diversity

Landscape heterogeneity significantly influences the diversity of grassland ecosystems (JANIŠOVÁ et al. 2014, ZULKA et al. 2014). It is already known to positively correlate with the diversity of bryophytes and other organisms on military training sites (VANDERPOORTEN et al. 2005, DENGLER et al. 2020a). The presence of juniper scrub increases the small-scale heterogeneity of grasslands, mainly by providing valuable microhabitats for many terricolous cryptogam species (FALIŃSKI et al. 1993). It enhances their diversity primarily because it creates niches by increasing both shade and soil organic matter, which benefits late successional species in patches dominated by early successional ones (KALAPOS & MÁZSA 2001, BOCH et al. 2016). Army vehicles are already known to create bare ground microhabitats (SHAW & DIERSING 1990, PROSSER et al. 2000). In the presented study the bare ground appeared to be positively correlated with off-road disturbance. It can be assumed that the interaction of these two factors increases the small-scale heterogeneity of the research site. Thirty-two terrestrial lichen species (including rare and endangered ones) recorded only within the sampled plots is a number fully comparable with Western European sites rich in epigeic lichens, e.g. Hulshorsterzand in the Netherlands (KETNER-OOSTRA et al. 2012). This high gamma (landscape level) diversity of the studied area may be related to the landscape heterogeneity created by unevenly distributed juniper scrub and off-road disturbance.

At plot level (i.e. alpha) diversity, the highest richness of valuable lichens and pioneer species was found under moderate levels of disturbance (Fig 5d and 6a). High disturbance intensity increased the bare soil area and decreased the number of cryptogam species (Fig. 5). Cryptogams are rather scarce in habitats directly affected by the dune process, and in such habitats only *Corynephorus canescens* remains relatively vital (KETNER-OOSTRA et al. 2012), an observation that was also made in our study area. On the other hand, it is known that pioneer species can only occur in areas with bare soil patches available for colonisation (COLE 1990, BELNAP 1993, LALLEY & VILES 2008). Ecological succession leads to the gradual disappearance of psammophilous grassland communities and the formation of initial pine forest communities (FALIŃSKI 1993). Within undisturbed habitat patches with high shrub cover, the vanishing of pioneer species and an increase in other ecological groups of cryptogams were registered (Fig. 6). In the presented study the presence of juniper scrub enhanced the species number of all registered groups of cryptogams (Fig. 5). The richness optima of ecological groups (Fig. 6) were connected consecutively with rising shrub cover. The aero-hygrophytes, which are already forest species, were the last to appear when the habitat was no longer open.

The most important factor maintaining high lichen species numbers was variable disturbance intensity connected with high microhabitat diversity representing all of the main successional stages. Within moderately disturbed patches disturbance and regeneration processes were probably somewhat balanced. This ensured the continuation of ecological niches and short-distance colonisation as the most sufficient lichen dispersal occurs within less than a few metres (HEINKEN 1999). One can assume that off-road disturbance additionally helped to move cryptogam fragments and inoculate new niches. Thus, many new habitat patches could be quickly colonised. The observed importance of moderate levels of disturbance for the maintenance of high species richness and conservation of some valuable species agrees well with the "intermediate disturbance hypothesis" (CONELL 1978, WILKINSON 1999).

5.3 Can off-road vehicle use maintain the high terrestrial cryptogam diversity of military training areas?

The conservation of endangered species in operating military training areas can generate many conflicts (JENNI et al. 2012), and it is difficult to balance the necessary military use, not always legal off-road use and conservation of natural values at one location, even within the borders of a National Park. Acid inland dunes are temporary habitats of high conservation value and need management to persist. One recently applied management practice of open acid dune habitats is tree and shrub removal and grazing management to maintain open landscape structures. The restoration of more altered habitats requires expensive topsoil removal (KETNER-OOSTRA et al. 2012). According to the results of the presented study, off-road disturbance may also be used as an inexpensive alternative to these activities. Spatially diverse off-road disturbance of low to medium intensity may be used in habitat management, whereas intensive off-road use may be implemented as a tool for the restoration of the initial stage of the habitat with active dune processes.

6. Conclusions

Increasing shrub cover related to successional processes and off-road activity were the two most important factors influencing cryptogam richness and community composition on acid inland dune habitats in the studied military training area. Pioneer cryptogam species and valuable lichens benefited from low and medium off-road disturbance. At the same time, other species were instead associated with higher successional stages found in undisturbed patches with rising juniper scrub cover. We interpret the growing intensity of disturbance as a factor leading to the redevelopment of the initial stage of the habitat, where dune processes can also occur. Diverse off-road activity locally reversed successional progress and thus was a positive factor promoting the coexistence of all ecological groups of cryptogams connected with the acid inland dune environment. In our opinion, off-road vehicle activity may to some extent be used as an inexpensive nature conservation tool in order to maintain epigeic, open-habitat cryptogam species. However, we are aware of the limitations of our study, in which we were not able to fully disentangle the impact of off-road disturbance from the naturally occurring one, especially as they seem to be closely related. Thus, we think that our results should be verified in a system in which both types of disturbance can be better controlled (e.g. in an experimental study).

Erweiterte deutsche Zusammenfassung

Einleitung – Auf Binnendünen wachsende, psammophile Pflanzengesellschaften mit Wachholder (*Juniperus communis*) gehören zu den am meisten bedrohten Lebensraumtypen in Mitteleuropa. Einst standen sie im Zusammenhang mit Störungen, die durch die traditionelle Land- und Forstwirtschaft verursacht wurden (Schafweiden, Brennen, Streunutzung, Abholzen von Wäldern). Wird die Nutzung aufgegeben, sind diese Vegetationstypen einer sekundären Sukzession unterworfen. Diese führt zum Verlust der charakteristischen Artenkombination und der typischen Biodiversität. Ein wichtiger Bestandteil dieser typischen Vegetation sind Kryptogamen (Moose und Flechten; WOLFF et al. 2017, DENGLER et al. 2020a). In dieser Studie untersuchten wir, ob die in letzter Zeit zunehmende Off-Road-Aktivität mit Geländefahrzeugen in Dünengebieten solche Lebensräume und ihre Biodiversität erhalten kann oder stattdessen zur weiteren Verschlechterung der Habitatqualität führt. Um diese Frage zu beantworten, untersuchten wir die Kryptogamendiversität in einer durch Off-Road-Aktivitäten gestörten Dünenlandschaft eines selten genutzten militärischen Übungsgeländes im Binnenland Zentralpolens.

Untersuchungsgebiet – Die Untersuchung wurde auf einem militärischen Übungsgelände namens Grochalskie Piachy (ca. 250 ha) in Zentralpolen (52°24'15"N 20°37'05"E), 22 km nordwestlich der Hauptstadt Warschau, durchgeführt. Das Gebiet liegt im voreiszeitlichen Weichseltal auf tiefem Flusssand, der durch den äolischen Prozess im frühen Holozän umgestaltet wurde. Es ist Teil eines der größten und am besten entwickelten Dünengürtel in Europa (ZGORZELSKI & PAWŁOWSKA 2003) und entstand durch Abholzung im späten 19. und 20. Jahrhundert. Das Gebiet umfasst drei offene Sandfelder mit aktiven Dünenprozessen, die durch militärische Aktivitäten mobilisiert wurden. Die offenen Flächen (ca. 100 ha) sind überwiegend mit Pflanzengesellschaften des *Corynephorion canescentis* Klika 1931 bedeckt. Der nördliche Teil des Geländes ist noch immer durch die regelmäβige Neutralisierung alter, nicht explodierter Bomben aus dem Zweiten Weltkrieg stark gestört. Der restliche Teil des Gebiets, in dem die Studie durchgeführt wurde, ist heute nicht mehr militärisch genutzt. Das gesamte nicht bewaldete Gebiet des Geländes wird momentan Geländefahrzeugliebhabern genutzt.

Material und Methoden – Wir erstellten 47 Vegetationsaufnahmen und erfassten eine Reihe von gemessenen oder geschätzten Variablen, wie Bodenparameter und Störungsintensität sowie Faktoren die im Zusammenhang mit der Sukzession stehen, wie die Gehölzdeckung. Zur Auswahl der unabhängigen erklärenden Variablen verwendeten wir Pearson-Korrelationen. Mittels partieller Kanonischer

Korrelationen (CCAs) ermittelten wir die wichtigsten Bodenvegetation-beeinflussen Variablen. Anhand von GAM-Modellen untersuchten wir den Einfluss der Störungsintensität und der Gehölzbedeckung auf die Kryptogamendiversität und weitere ökologische Kryptogamen-Indizes.

Ergebnisse – Die Struktur der psammophilen Kryptogamengemeinschaften wurde vor allem durch Störungen von Geländefahrzeugen und der Gehölzbedeckung beeinflusst (Abb. 3, 4). Die höchste Störungsintensität durch Geländefahrzeuge führte zu einer Transformation des Lebensraums zum Initialstadium mit aktiven Dünenprozessen, in ungestörten Bereichen entwickelte sich hingegen ein Kiefernwald im Laufe der Sukzession. Die höchste Anzahl von Flechten- und Moosarten trat innerhalb nicht oder nur leicht gestörter Lebensräume auf. Flechten bevorzugten jedoch eine geringere Gehölzdeckung als Moose (Abb. 5). Dennoch profitierten Pionier- und typische Arten psammophiler Vegetationstypen, zu denen auch einige bedrohte Flechtenarten gehören, von einer geringen bis mittleren Störungsintensität (Abb. 6).

Diskussion – Vielfältige und räumlich komplexe Off-Road-Aktivitäten mit Geländefahrzeugen zusammen mit einer variablen Gehölzdeckung waren positive Faktoren, die die Koexistenz aller ökologischen Kryptogamengruppen der sauren Binnendünen förderten, womöglich aufgrund der erhöhten Lebensraumheterogenität und Anzahl Mikrohabitate. Auf moderat gestörten Flächen waren die Störungs- und Regenerationsprozesse wahrscheinlich eher ausgeglichen, was sich positiv auf den Erhalt wertvoller Flechten- und Pionierartengruppen auswirkte. Die Ergebnisse stützen die "mittlere Störungshypothese" (CONELL 1978, WILKINSON 1999). Unserer Meinung nach können Off-Road-Aktivitäten mit Geländefahrzeugen bis zu einem gewissen Grad als ein kostengünstiges Naturschutzinstrument eingesetzt werden, um offene, Kryptogamen-reiche Dünenlebensräume zu erhalten.

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Author contribution

PZ – fieldwork, laboratory work, literature survey, statistics, writing,
LK – fieldwork, laboratory work, literature survey, statistics, writing,
MW – laboratory work, literature survey, writing

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Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Original vegetation data used in the analyses.

Anhang E1. Ursprüngliche Vegetationsdaten, die in den Analysen verwendet wurden.

Supplement E2. Raw environmental data used in the analyses.

Anhang E2. In den Analysen verwendete Rohdaten der Umweltvariablen.

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Supplement E1.Original vegetation data used in the analyses.

Anhang E1. Ursprüngliche Vegetationsdaten, die in den Analysen verwendet wurden.

NO_PLOT	short name	layer	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
tree layer cover [%]	A_COV		0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	30	0	5	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
shrub layer cover [%]	B_COV		0	0	10	30	5	0	0	0	0	30	5	30	3	70	60	60	30	10	0	80	65	100	20	40	40	5	0	1	3	1	0	0	30	55	40	20	15	10	25	20	15	35	20	5	5	0	0
herb layer cover [%]	C_COV		40	20	2	5	5	10	0	10	1	25	30	5	10	3	2	5	10	5	5	2	10	2	5	5	5	5	1	5	10	10	10	0	30	15	5	30	15	20	10	5	5	15	10	20	20	5	1
moss layer cover [%]	D_COV		60	2	95	2	1	70	0	60	1	20	2	70	70	50	65	80	70	80	1	65	70	80	50	40	40	3	0	1	25	95	40	0	35	20	5	30	10	2	15	5	10	80	70	40	10	1	0
tree layer																																																	
Pinus sylvestris	Pin_sylA	tree																2a				3	r	1								1																	
Betula pendula	Bet_penA	tree			+																																												
shrub layer																																																	
Juniperus communis	Jun_comB	shrub			2a	3	1					3	1	3	1	4	4	4	3	2a		5	4	5	2b	3	3	1		+	1	+			3	4	3	2b	2b	2b	2b	2b	2b	3	2b	1	1		
Pinus sylvestris	Pin_sylB	shrub										+						1					1	+		+															+	+			+	+	r		
Berberis vulgaris	Ber_vulB	shrub														+			+																														
Rosa sp.	Rosa_spB	shrub																				+																											
herb layer																																																	
Crataegus sp.	Crat_spC	herb												r																																			
Sorbus aucuparia	Sor_aucC	herb														r			+																														
Juniperus communis	Jun_comC	herb			r						+			+	+				r						1	+	r										r	+					r				r		
Quercus rubra	Que_rubC	herb																				r									r																		
Quercus robur	Que_robC	herb																+	+																											r			
Pinus sylvestris	Pin_sylC	herb	r														r	+	+			+				+	r		r			+						r					r	r	r	r	r		
Populus tremula	Pop_treC	herb																						r																									
Agrostis vinealis	Agr_vine	herb			+																																							+				1	
Senecio jacobea	Sen_jaco	herb																																				r											
Calluna vulgaris	Cal_vulg	herb																+						+			1																			2a	+		
Calamagrostis epigejos	Cal_epig	herb																				+																											
Convolvulus arvensis	Con_arve	herb																				r																											
Corynephorus canescens	Cor_cane	herb	3	2b	r	1	+	2a	r	2a		2b	3	+	2a	r	+	+	1	1	1	+	1		1	1	1	1	r	1	1	2a	2a	r	3	2b	1	3	2b	2b	2b	1	+	2a	1	1	2b	1	r
Conyza canadensis	Con_cana	herb										+																							+														
Festuca ovina	Fes_ovin	herb			+		+			r		r		+		+	+	+	+			r	r		+											+					+			+					
Festuca rubra	Fes_rubr	herb				+						+					+			r		r															+						+	r					
Hieracium pilosella	Hie_pilo	herb										+						+	+					r			+											r							r				
Hypochoeris radicata	Hyp_radi	herb	r																			r																						+					
Peucedanum oreoselinum	Peu_oreo	herb															r																																
Polygonatum odoratum	Pol_odor	herb																+																															
Solanum dulcamara	Sol_dulc	herb														+																																	
Solidago virgaurea	Sol_virg	herb	r																					+																									
Spergula vernalis	Spe_vern	herb			r		+			1		+		1	+	1	+		+				1		+	1	1			r	1	+	1		+								+	2a	1	1	1		
Taraxacum officinale s.lat.	Tar_offi	herb																				r																											
Thymus serpyllum	Thy_serp	herb	r							+						r		1																															
moss layer																																																	
Brachythecium albicans	Bra_albi	moss														+						+																											
Ceratodon purpureus	Cer_purp	moss	3			+	r	r				2b	+					r	1					r	1	1		r							2b	+	1	1	1	+	1	1	+	r					
Rhacomitrium canescens	Rha_cane	moss								+									+	+			r																										
Polytrichum piliferum	Pol_pili	moss	+		2b	+	r	1		2b	r	+	+	3	2a	+	1	r	2b	4	+	r	2a	r	2a	2b	2b	+			2b	5	1		1	2b	+	2b	1	+	1	+	+	+	1	2b	1		
Polytrichum juniperinum	Pol_juni	moss														1																																	
Dicranum scoparium	Dic_scop	moss														1		1				1	+	+	+																			r	+				
Dicranum polysetum	Dic_poly	moss														1	1	1						+			r														+	r		r	+	1	+		
Pleurozium schreberi	Ple_schr	moss														2b	1	2b	+			3	2a	4	+																+			+	+	1			
Hylocomium splendens	Hyl_sple	moss																+																															
Hypnum cupressiforme s.l.	Hyp_cupr	moss										+				1			+			+	+				+																						
Pohlia nutans	Poh_nuta	moss												r			+	1						1		+																							
Siuro-hypnum oedipodium	Sci-oedi	moss										+				1	+	+				+																											
Cephaloziella divaricata	Cep_diva	moss															+								+	+	+																						
Lophocolea heterophylla	Lop_hete	moss																+																															
Baeomyces rufus	Bae_rufus	moss																								+																							
Cetraria aculeata	Cet_acul	moss	+	+	+	r	r	1		1	r	+	r	2a	2a		+	+	1	1	r					1	r	+		r	1	+	2b		1	1	r	1		+	1	+	+	r	1	+	+	r	
Cetraria islandica	Cet_isla	moss																1				1	1																										
Cladonia arbuscula	Cla_arbu	moss																				1																											
Cladonia mitis	Cla_miti	moss	+	+	3	r	r	3	r	1	r	+	r	3	4	1	2b	2b	1	1		r	3	+	3	1	2a	+		r	1	+	2b		+	+	+	r			+	+	1	2b	3	1	1		
Cladonia cervicornis ssp. verticillata	Cla_cerv	moss						+		+				+	r	+	+		+	+		r			+	+	r	r			r	+						r			r		r	+		+	+		
Cladonia coccifera s.l.	Cla_cocc	moss			+			r		r				r			+	r	+	+		+	+			+	1	r				1												r	r	r			
Cladonia cornuta	Cla_corn	moss			+													+	+								+																						
Cladonia deformis	Cla_defo	moss			+			r									+		r						+		+					+											+	r	r	r			
Cladonia fimbriata	Cla_fimb	moss	+		+		r					r		r					+					r	+																	r							
Cladonia foliacea	Cla_foli	moss															r																																
Cladonia furcata	Cla_furc	moss																				+		+																									
Cladonia glauca	Cla_glau	moss			+		r			+								+	1						+						r	+												r	r				
Cladonia chlorophaea s.l.	Cla_chlo	moss			+										+		+		1			+	+				1																r			+			
Cladonia gracilis	Cla_grac	moss						+							r		+	1					+	+	r	r																		+					
Cladonia macilenta s.l.	Cla_macil	moss			+			r				r		1	+		+		1	+			+	+	r	+		r				+											+	+	r	r	r		
Cladonia phyllophora	Cla_phyl	moss			2b			2b		+						+	2b	1	2b	+		+	1	+	+	+	+	r				+											+	2b	1	1	r		
Cladonia subulata	Cla_subu	moss	+		r		r		r			r		+	r		+	+	1			r	1	+	+	r		r			+							r	r	r	r	r	+	+	+	r	r		
Cladonia uncialis	Cla_unci	moss		+	1			+		+	r				r	+								+	+		r	r				+	+		r	+		r					+	1	+	r	+	r	
Placynthiella dasaea	Pla_das	moss																	+							r																							
Placynthiella oligotropha	Pla_olig	moss												+	+											+											+								+				
Placynthiella uliginosa	Pla_ulig	moss	1					+		2b				1	+								+		+		r	+									+	+			+		+	1	1	+	+		
Stereocaulon condensatum	Ste_cond	moss								2b				1	1																										r			r		+	+		
Stereocaulon incrustatum	Ste_incr	moss	2b	+																																													
Trapeliopsis granulosa	Tra_gran	moss	+		+			+		1				r	+	r			1	1			r		+	1					+	r			r						r		+	2b	r				
Cladonia crispata	Cla_crisp	moss																																										+					
Cladonia squamosa	Cla_squa	moss			+																																												

Supplement E2. Raw environmental data used in the analyses.

Anhang E2. In den Analysen verwendete Rohdaten der Umweltvariablen.

NO_PLOT		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Variable	Abbreviation & unit																								
Inclination	INCL [°]	3	3	0	4	6	4	3	11	11	0	4	3	3	0	1	0	0	1	1	1	1	6	0	3
Cover of tree layer	A_COV [%]	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	30	0	5	0	0
Cover of shrub layer	B_COV [%]	0	0	10	30	5	0	0	0	0	30	5	30	3	70	60	60	30	10	0	80	65	100	20	40
Common juniper cover in shrub layer	JC_B_COV [%]	0	0	10	30	5	0	0	0	0	30	5	30	3	70	60	55	30	10	0	80	60	100	20	40
Share of plot area with visible dune processes	DUNE_INT [%]	0	0	0	14	0	0	25	0	25	21	19	0	0	0	0	0	0	0	25	0	0	0	0	0
Share of plot area disturbed by off-road vehicles	DIST_INT [%]	13	23	2	18	18	8	25	15	25	19	23	5	5	2	6	4	10	3	25	0	1	0	5	19
Cover of visible open substrate	bare soil [%]	15	80	2	85	90	20	99	35	99	35	70	15	20	2	15	5	15	15	95	0	10	0	35	50
Cover of litter	Litter [%]	1	1	2	5	2	1	0	1	0.5	15	0	5	2	40	10	20	15	1	0	45	15	45	10	10
pH of upper soil horizon	pH	5.2	5.7	4.9	5.4	5.7	5.4	5.3	5.7	5.7	5.2	5.8	5.5	5.3	4.8	5.3	4.5	4.7	5.1	5.2	4.2	4.8	4.1	5.4	5.7
Electrical conductivity of upper soil horizon	EC [µS*cm-1]	143	23	35	39	25	24	29	22	31	27	23	28	26	40	50	35	42	21	28	109	25	143	26	20
Weight loss on ignition of upper soil horizon	ORGANIC [%]	0.00	0.00	0.01	0.01	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.00	0.02	0.01	0.03	0.01	0.00
Share of soil fractions larger than 1 mm	fr_coarse [%]	0.80	0.33	0.22	0.20	0.36	0.27	0.55	0.59	0.49	0.03	0.71	0.65	0.29	0.11	0.38	0.14	0.16	0.16	0.39	0.36	0.74	0.09	0.33	0.57
Share of soil fractions between 0.5 and 1 mm	fr_coarse_sand [%]	7.57	7.27	5.65	2.23	4.94	5.46	18.14	7.17	11.78	3.33	9.11	4.87	6.03	4.55	6.34	4.55	6.65	5.47	13.13	10.20	13.58	8.48	5.20	13.18
Share of soil fractions between 0.25 and 0.5 mm	fr_med_sand [%]	61.45	64.52	50.37	50.78	60.29	67.20	60.80	54.26	56.50	47.21	58.41	59.60	60.27	58.94	54.35	49.65	56.98	54.95	58.69	56.48	55.88	59.59	59.40	58.28
Share of soil fractions between 0.1 and 0.25 mm	fr_fine_sand [%]	28.05	26.77	41.31	46.02	33.61	26.02	19.51	36.98	30.26	47.93	31.24	34.08	32.16	34.20	36.86	42.26	34.24	37.33	27.31	30.33	27.87	29.99	33.82	27.01
Share of soil fractions smaller than 0.1 mm	fr_fine [%]	2.13	1.11	2.45	0.77	0.80	1.05	1.00	1.00	0.97	1.50	0.53	0.81	1.25	2.21	2.08	3.39	1.97	2.08	0.48	2.63	1.94	1.85	1.25	0.97
X coordinate PUWG1992	x	610.11	610.14	609.83	609.73	609.73	609.75	609.53	609.59	609.61	609.73	609.73	609.75	609.75	609.77	609.80	610.73	610.70	610.60	610.57	610.39	610.53	610.55	609.70	609.72
Y coordinate PUWG1992	y	505.33	505.28	504.80	504.93	504.86	504.80	505.14	505.02	504.99	505.01	504.97	504.89	504.83	504.84	504.80	505.07	505.00	505.09	505.10	504.94	504.73	504.73	505.03	505.03
X coordinate WGS84	x	20.6190	20.6195	20.6147	20.6133	20.6133	20.6136	20.6105	20.6112	20.6116	20.6133	20.6133	20.6136	20.6136	20.6138	20.6143	20.6280	20.6276	20.6261	20.6257	20.6230	20.6249	20.6253	20.6130	20.6132
Y coordinate WGS84	y	52.4028	52.4023	52.3981	52.3992	52.3987	52.3981	52.4012	52.4001	52.3998	52.4000	52.3996	52.3989	52.3984	52.3984	52.3981	52.4003	52.3997	52.4005	52.4007	52.3993	52.3973	52.3973	52.4002	52.4001

NO_PLOT		25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
Variable	Abbreviation & unit																							
Inclination	INCL [°]	1	6	3	1	0	0	3	7	0	0	0	4	0	3	3	0	7	1	4	3	3	4	3
Cover of tree layer	A_COV [%]	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cover of shrub layer	B_COV [%]	40	5	0	1	3	1	0	0	30	55	40	20	15	10	25	20	15	35	20	5	5	0	0
Common juniper cover in shrub layer	JC_B_COV [%]	40	5	0	1	3	1	0	0	30	55	40	20	15	10	25	20	15	35	20	5	5	0	0
Share of plot area with visible dune processes	DUNE_INT [%]	0	0	22	16	0	0	0	25	20	19	21	13	18	10	0	0	0	0	0	0	0	24	25
Share of plot area disturbed by off-road vehicles	DIST_INT [%]	3	24	25	24	13	1	14	25	20	18	21	20	22	23	14	20	21	4	11	4	16	22	25
Cover of visible open substrate	bare soil [%]	50	95	99	95	70	1	55	99	35	35	70	50	80	75	70	85	85	10	25	50	75	97	100
Cover of litter	Litter [%]	5	1	0	1	2	3	0	0	15	35	25	5	3	2	10	5	3	10	5	2	2	0	0
pH of upper soil horizon	pH	5	5.6	6	5.8	5.9	5.6	5.7	5.2	5.6	5.6	5.7	5.6	5.6	5.4	5.3	5.1	5.4	5.3	5.2	4.5	5.2	5.7	5.8
Electrical conductivity of upper soil horizon	EC [µS*cm-1]	24	17	34	19	38	24	27	22	31	28	45	29	28	29	33	28	30	30	22	44	16	25	37
Weight loss on ignition of upper soil horizon	ORGANIC [%]	0.03	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.01	0.01	0.01	0.01	0.02	0.01	0.00	0.00
Share of soil fractions larger than 1 mm	fr_coarse [%]	1.96	1.31	0.94	0.91	0.74	1.59	0.25	2.30	0.02	0.18	0.13	0.20	0.34	0.31	0.13	0.11	0.31	0.51	0.08	1.26	0.27	0.10	0.66
Share of soil fractions between 0.5 and 1 mm	fr_coarse_sand [%]	21.67	17.75	19.37	19.61	10.89	13.68	5.29	29.62	1.65	4.24	4.07	6.07	3.85	6.72	3.57	2.27	5.39	7.87	3.66	12.93	4.37	2.75	16.02
Share of soil fractions between 0.25 and 0.5 mm	fr_med_sand [%]	53.72	55.73	58.31	57.90	58.25	54.86	51.40	44.63	20.83	54.72	49.30	54.75	57.82	58.40	48.54	51.02	61.53	59.94	57.53	53.78	50.88	54.95	57.62
Share of soil fractions between 0.1 and 0.25 mm	fr_fine_sand [%]	20.75	24.35	20.96	20.69	28.52	28.76	41.41	22.42	76.47	40.04	45.15	37.84	36.98	33.70	46.54	45.65	31.97	29.63	37.04	29.79	41.36	41.74	24.42
Share of soil fractions smaller than 0.1 mm	fr_fine [%]	1.91	0.85	0.42	0.86	1.61	1.11	1.65	1.03	1.02	0.82	1.36	1.14	1.00	0.87	1.23	0.95	0.81	2.06	1.69	2.24	3.12	0.46	1.28
X coordinate PUWG1992	x	610.08	609.77	609.78	609.76	609.78	609.80	609.80	609.80	609.83	609.78	609.75	609.75	609.63	609.66	610.45	610.50	610.52	610.63	610.67	610.69	610.70	609.68	609.70
Y coordinate PUWG1992	y	504.94	504.94	504.92	504.93	504.89	504.89	504.86	504.83	504.84	504.81	504.79	504.76	504.99	504.99	505.06	504.68	504.69	504.70	504.69	504.69	504.64	504.99	504.99
X coordinate WGS84	x	20.6184	20.6139	20.6140	20.6137	20.6141	20.6143	20.6143	20.6144	20.6147	20.6140	20.6136	20.6135	20.6118	20.6122	20.6239	20.6245	20.6248	20.6265	20.6270	20.6274	20.6274	20.6126	20.6129
Y coordinate WGS84	y	52.3992	52.3994	52.3991	52.3993	52.3989	52.3989	52.3986	52.3984	52.3984	52.3982	52.3980	52.3978	52.3998	52.3998	52.4003	52.3969	52.3970	52.3971	52.3969	52.3969	52.3965	52.3998	52.3998