

ORIGINAL PAPER

Ecological succession of bryophytes and lichens on mineral-soil habitats originated within windthrows (Kampinos National Park, central Poland)

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ABSTRACT

Windthrows are common, natural disturbances in forest ecosystems. One of the effects of these disturbances is the exposure of mineral soil, which is gradually colonised by plants and other organisms *via* secondary succession. The aim of this research, conducted in the windthrows in the Kampinos National Park (central Poland), was to determine the changes in composition, richness, and abundance of the bryophytes and lichens inhabiting the mineral habitats of uprooted trees and to identify the level of its distinctiveness from the surrounding forest floor. The largest number of species (28) was found in pits; fewer species were found on the lower part of the uproot mounds (21), and in the vicinity of the uprooted trees (16). Many species differed in abundance and in their fidelity to the selected habitat types. Significant changes in the species richness and composition of the habitat types were observed between the first and third year after the disturbance. A large number of species inhabited the pits, and there was a gradual increase in the lower parts of the uproot plates. The communities of the pits and lower parts of the mounds were similar in the first year after the windthrow. After three years the pits became more similar to the undisturbed sites, whereas the opposite tendency was observed in relation to lower parts of the mounds. There were important differences in (a) condition between the studied habitats as estimated using ecological indicator values, and (b) the share of species with different types of growth forms and life strategies.

KEY WORDS

colonist species, ecological indicator values, liverworts, mosses, mound, pit, treefall disturbance

Introduction

Windthrows (*i.e.*, trees uprooted by wind) are one of the most common natural disturbances in forest ecosystems (Schaetzl *et al.*, 1989b; Fischer *et al.*, 2002). Although in close-to-natural forests, the size of windthrow disturbances is usually relatively small, they still cause significant changes in the local habitat composition and diversity (Attiwill, 1994; Fischer *et al.*, 2002). Wind-felled trees become a source of new lying dead wood in the forest ecosystem. There are

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also patches of exposed mineral soil that are associated with fallen trees. They originate within the uproot plates and pits of newly uprooted trees (Pawlik, 2012). The local soil exposures are the initial habitats, which are then gradually colonised by plants and other organisms (Ulanova, 2000; Ouden and Alaback, 2004; Löhmus *et al.*, 2010; Simon *et al.*, 2011; Šebková *et al.*, 2012; Plotkin *et al.*, 2017). They are particularly suitable for colonisation by bryophytes (Bazzaz, 1983; McCarthy, 2001; Kimmerer, 2005; Staniaszek-Kik *et al.*, 2017).

The colonisation of local soil exposures is highly dynamic (Bazzaz, 1983). The initial stages of succession are characterised primarily by the expansion of species, especially bryophytes, specialised in the settlement of sites with less competition such as disturbed, mineral soil (Grime, 1979; Ulanova, 2000). A large share of these are pioneer, light-demanding species, which are not usually found in the forest communities (Brokaw, 1985; Ulanova, 2000). Due to the specific nature of the changes in these habitats over time, the pioneer species gradually disappear from the environment, giving way to the typical forest taxa (Brokaw, 1985).

Bryophytes inhabit the initial terrestrial habitats that are formed as a result of disturbances relatively quickly (Lindholm and Nummelin, 1983; Jonsson and Esseen, 1998). They are favoured by the lack of competition and the regenerative potential of many species that have vegetative reproduction (Newton and Mishler, 1994; During, 1997; Jonsson and Esseen, 1998; Glime, 2017). The life strategies of bryophytes are also often adapted to colonising new habitats (During, 1997; Glime, 2017). Lichens are also able to colonise the pits and mounds of uprooted trees, especially stones, roots, small fragments of wood, soil, and humus (Staniaszek-Kik and Szczepańska, 2011), although this process tends to be rather slow.

Research on disturbances in forest ecosystems has been mainly concerned with changes in the structure of the vegetation and flora of vascular plants, with much less frequent reference to other groups of plants or fungi (Attiwill, 1994). The windthrows in the Kampinos National Park (KNP) made it possible to observe the processes that take place in this type of disturbed habitat. The research aimed to determine the bryophyte and lichen species richness of the two initial epigeic habitats (mineral parts of uproot mounds and uproot pits), to assess the fidelity of individual species for the specific habitat types, to characterize the ecological conditions of habitats based on ecological indicator values of species, and to assess changes in species composition.

Materials and methods

The research was conducted at two windthrow sites in KNP (central Poland), which had originated in 2017 in Różin (forest compartment 258) and Grabina (forest compartment 125). Both sites are under active conservation. However, no activities were carried out within them after the windthrows. The dominant vegetation of the Różin site was acidophilous oak forest *Calamagrostio-Quercetum* Hartm. 1934 Scam. et Pass. 1959 and in case of the Grabina site was wet mixed oak-pine forest *Quercus-Pinetum* (W.Mat. 1981) J.Mat 1988 *molinietosum*. The age of stands was 104 and 84 years, respectively. The distance between sites was ca. 5.5 km. Thirty uprooted trees were chosen where the immediate surroundings were covered to the least extent by other fallen trees (ten on the Grabina site and twenty on the Różin site): ten for sessile oak *Quercus petraea* (Matt.) Liebl., ten for silver birch *Betula pendula* Roth, and ten for Scots pine *Pinus sylvestris* L. The mean \pm SD height of the mineral part of uprooted tree mounds was 130 ± 31 cm, and the mean \pm SD depth of its was 42 ± 13 cm. Fieldwork was conducted during the vegetation seasons of 2018 and 2020 (the first and the third year after disturbance). A set of floristic lists of bryophytes and lichens was prepared for the two uprooted tree habitats each identified by an initial character: uproot

pits (P) and the mineral (lower) parts of the uproot mounds (M). We treated the mineral part of the mound as the part located from the pit site. In both cases, the soil mineral material was derived from deeper parts of the root plate. The average area of sampled uproot pits was 1.4 m²; for uproot mounds 2 m². For the control site, a set of undisturbed (U) plots adjacent to the uproots was established (2 m² each, located within 1 m from the edge of a pit of an uprooted tree), and additional lists of species were prepared. There was no deadwood recorded within undisturbed plots. The Barkman *et al.* scale was used with cover as a recommended measure of species abundance (Barkman *et al.*, 1964; Dengler *et al.*, 2008). This scale is similar to the original Braun-Blanquet, the main advantage being the use of twice narrower ranges for the higher cover classes. Only the first-year (2018) sampling of the control sites could be defined as reflecting an undisturbed habitat (natural surroundings), because the neighbourhood of the sites was frequently disturbed by trampling by scientists carrying out observations (this study was part of a larger project). Most of the species were identified in the field, and small samples of the remaining ones were collected for further morphological and anatomical laboratory analyses. The frequency of species recorded within the variants was defined as the percentage of inhabited sites.

Species richness was calculated using the rarefaction curves method (Colwell *et al.*, 2004). This approach allows comparing the visual alignment of 95% confidence intervals of species richness means. It is especially useful for comparing the species richness of unequally sampled environments. The arithmetical (Tüxen and Ellenberg, 1937) transformation of vegetation data was used, with average cover % values in the classes. Then the average cover of species was calculated. The ecological indicator values (EIV) of the bryophyte species inhabiting the sample plots were used to assess the habitat conditions, according to Ellenberg and Leuschner (2010). The EIV for lichen *Placynthiella dasaea* (Stirton) Tønsberg were obtained from Fabiszewski and Szczepańska (2010), after simple transformation from 1-5 to 1-9 scale, based upon comparable ecological conditions between Poland and Germany. Light (L), humidity (F) and acidity (R) values were used in this study. The commonly recommended arithmetic mean was used to calculate the EIV (Chytrý *et al.*, 2018), which were compared using the non-parametric Kruskal-Wallis, followed by Mann-Whitney (*post hoc*) tests for multiple comparisons ($\alpha=0.05$). False discovery rate correction (FDR) was used for *p*-values adjustment. The fidelity of individual species for the specified habitat types was determined using the phi coefficient. In this case, presence/absence data were used. The significance of phi was determined using Fischer's exact test in accordance with Chytrý *et al.* (2002). Only statistically significant values ($p<0.05$) were included in the results. The diversity of bryophyte and lichen communities was assessed using the NMDS ordination technique. This method enables graphically representing relationships (distribution of similarities) between samples in reduced multidimensional space, allowing for easier interpretation of results. The species frequencies within each of the sample groups were used as the measure of abundance in this analysis. Fifteen groups were identified: three tree species, three habitat types, and two research periods for pits and uproot mounds. The directions of the differentiation of the individual EIV were arrayed on an NMDS plot. Euclidean distance was used in the ordination. The statistical and numerical analyses were performed using JUICE 7 (Tichý, 2002; Tichý and Holt, 2006), PAST 4 (Hammer *et al.*, 2001), and EstimateS 9 (Colwell, 2013) software.

The nomenclature for the liverworts is according to Söderström *et al.* (2016); for the mosses, it follows Hill *et al.* (2006) and for the lichens, it was adopted after Fałtynowicz and Kossowska (2016). Classification of growth forms were taken after Smith (2004), and life strategies after Dierßen (2001).

Results

There were 31 bryophytes (3 liverworts and 28 mosses) and one lichen species recorded in the analysed parts of the uprooted trees and in their vicinity (Table 1). In the vicinity of the uprooted trees, there were 16 species; 28 species were found in the pits, and 21 species occurred on the lower parts of the uproot mounds.

There were significant differences in the species richness of habitat types (Fig. 1). There were fewer species in lower parts of the uproot plates in 2018 than in 2020, and also fewer species than in pits in 2018 and 2020. Undisturbed surroundings did not differ from the other microhabitats in terms of species richness, which was intermediate in these habitats.

Some of the species were characterized by high and significant fidelity to particular habitat types. The species significantly related to the undisturbed habitats were *Hylocomium splendens* (Hedw.) Schimp., *Hypnum cupressiforme* Hedw., *Plagiomnium affine* (Blandow ex Funck) T. Kop., *Pleurozium schreberi* (Willd. ex Brid.) Mitt. and *Sciuro-hypnum oedipodium* (Mitt.) Ignatov & Huttunen (Table 1). With the exception of *H. splendens*, these were also the most common species in the vicinity of a windfall. In terms of abundance, *H. cupressiforme*, *P. affine*, *P. schreberi*, *Pseudoscleropodium purum* (Hedw.) M.Fleisch. and *S. oedipodium* dominated.

The initial habitats within the fallen trees were favoured by *Bryum moravicum* Podp., *Ceratodon purpureus* (Hedw.) Brid., *Dicranella heteromalla* (Hedw.) Schimp., *Dicranoweisia cirrata* (Hedw.) Lindb., *Pellia epiphylla* (L.) Corda, *P. affine*, *Plagiothecium curvifolium* Schlieph. ex Limpr., *P. schreberi*, *Pohlia nutans* (Hedw.) Lindb., *Polytrichastrum formosum* (Hedw.) G.L.Sm., *Polytrichum juniperinum* Hedw., *Polytrichum piliferum* Hedw., *S. oedipodium* and *P. dasaea* (Table 1). The most commonly recorded were *C. purpureus*, *D. heteromalla* and *P. nutans*, and the most abundant were *C. purpureus*, *D. heteromalla*, *P. curvifolium*, *P. schreberi*, *P. nutans*, *P. juniperinum* and *S. oedipodium*.

Differences in habitat conditions between the selected habitat types, estimated by EIV of recorded species, were also visible (Fig. 2). There were significantly higher values of light (L) in the pits and lower parts of mounds compared to the control sites, both one and three years after a disturbance. The difference between disturbed and undisturbed sites increased with time (Fig. 2a). The opposite relationships were found in the case of moisture (F) and acidity (R) (Fig. 2b-c). These differences were also significant.

Differences in the share of species with different types of growth forms and life strategies were observed between the analysed habitat types (Fig. 3). Plagiotropic (pleurocarpous) bryophytes predominated on the undisturbed patches, while the pits and lower parts of mounds were primarily inhabited by orthotropic (acrocarpous) species (fig. 3a). Species with a 'perennial' life strategy definitely dominated in undisturbed habitats and 'colonists' were found more often in disturbed ones (Fig. 3b).

Based on NMDS analysis (Fig. 4), changes in species composition of the bryophytes and lichens in the two types of disturbed habitats were divergent. The communities of the pits and lower parts of the mounds were similar in the first year after the windthrow. However, in the third year after the disturbance the pits became more similar to the undisturbed sites. The opposite tendency was observed in the lower parts of the uproot mounds.

Discussion

Uprooted trees are a permanent element of the early post-windthrow landscape. These objects play an important role in the regeneration of vegetation after a disturbance (Bazzaz, 1983). A whole range of microhabitats, characterised by reduced competition, originates as a result of the exposure

Table 1.

Frequency [%] with statistically significant fidelities (Fisher test $p < 0.05$) and average cover [%] of bryophyte and lichen* species within initial habitats of uprooted trees (P – pit, M – lower part of mound) and the adjacent undisturbed plots (U); sampling periods: 1 – 2018, 2 – 2020

	Frequency [%]					Cover [%]				
	U1	P1	P2	M1	M2	U1	P1	P2	M1	M2
<i>Atrichum undulatum</i> (Hedw.) P.Beauv.	7	23	20	3	23	0.12	0.43	0.63	0.02	0.46
<i>Aulacomnium androgynum</i> (Hedw.) Schwäger.	0	3	10	0	10	–	0.02	0.02	–	<0.01
<i>Brachythecium salebrosum</i> (Hoffm. ex F.Weber & D.Mohr) Schimp.	3	3	3	7	7	0.02	0.02	0.02	0.03	0.02
<i>Bryum argenteum</i> Hedw.	0	0	0	0	3	–	–	–	–	<0.01
<i>Bryum moravicum</i> Podp.	0	3	10 ^{22.8}	0	0	–	0.02	0.29	–	–
<i>Ceratodon purpureus</i> (Hedw.) Brid.	0	17	53 ^{28.2}	7	63 ^{39.3}	–	0.12	3.73	0.03	3.98
<i>Dicranella heteromalla</i> (Hedw.) Schimp.	13	27	47 ^{19.9}	10	47 ^{19.9}	0.15	3.32	4.62	0.66	1.31
<i>Dicranella schreberiana</i> (Hedw.) Dixon	0	3	0	0	0	–	<0.01	–	–	–
<i>Dicranoweisia cirrata</i> (Hedw.) Lindb.	0	0	0	0	10 ^{28.6}	–	–	–	–	<0.01
<i>Dicranum polysetum</i> Sw. ex anon.	7	3	3	0	0	0.20	0.10	0.10	–	–
<i>Dicranum scoparium</i> Hedw.	13	17	23	3	13	0.13	0.13	0.04	0.02	0.03
<i>Funaria hygrometrica</i> Hedw.	0	3	0	0	0	–	<0.01	–	–	–
<i>Herzogiella seligeri</i> (Brid.) Z.Iwats.	0	0	3	0	0	–	–	0.02	–	–
<i>Hylocomium splendens</i> (Hedw.) Schimp.	7 ^{23.2}	0	0	0	0	0.02	–	–	–	–
<i>Hypnum cupressiforme</i> Hedw.	70 ^{28.4}	33	47	23	37	2.65	0.87	0.89	0.07	0.40
<i>Lophocolea heterophylla</i> (Schräd.) Dumort.	0	7	7	0	3	–	0.03	0.03	–	0.02
<i>Marchantia polymorpha</i> L.	0	3	0	0	0	–	0.02	–	–	–
<i>Pellia epiphylla</i> (L.) Corda	0	13 ^{33.1}	0	0	0	–	0.22	–	–	–
<i>Placynthiella dasaea</i> (Stirton) Tønberg* (Blandow ex Funck) T. Kop.	0	0	3	0	40 ^{55.7}	–	–	<0.01	–	<0.01
<i>Plagiomnium affine</i> (Blandow ex Funck) T. Kop.	60 ^{33.7}	17	47 ^{19.0}	7	17	3.45	0.05	0.40	0.02	0.05
<i>Plagiomnium cuspidatum</i> (Hedw.) T.J.Kop.	7	3	3	0	0	0.03	0.02	0.02	–	–
<i>Plagiothecium curvifolium</i> Schlieph. ex Limpr.	3	10	23 ^{28.3}	0	3	0.02	1.25	1.37	–	0.02
<i>Pleurozium schreberi</i> (Willd. ex Brid.) Mitt.	50 ^{32.6}	23	37 ^{16.7}	0	3	5.35	2.84	3.63	–	<0.01
<i>Pohlia annotina</i> (Hedw.) Lindb.	0	0	0	3	7	–	–	–	0.02	0.02
<i>Pohlia nutans</i> (Hedw.) Lindb.	27	73	80 ^{16.0}	57	87 ^{23.0}	0.38	2.82	1.86	0.58	2.89
<i>Polytrichastrum formosum</i> (Hedw.) G.L.Sm.	13	7	23	3	27 ^{17.0}	0.13	0.31	0.08	<0.01	0.17
<i>Polytrichastrum longisetum</i> (Sw. ex Brid.) G.L.Sm.	0	3	10	0	10	–	<0.01	0.02	–	0.03
<i>Polytrichum juniperinum</i> Hedw.	3	3	27	23	47 ^{32.1}	0.02	0.02	0.12	0.18	1.50
<i>Polytrichum piliferum</i> Hedw.	0	0	10	3	23 ^{30.7}	–	–	0.12	<0.01	0.07
<i>Pseudoscleropodium purum</i> (Hedw.) M.Fleisch.	17	10	17	0	0	1.55	0.74	0.25	–	–
<i>Sciuro-hypnum oedipodium</i> (Mitt.) Ignatov & Huttunen	80 ^{34.8}	40	77 ^{31.5}	13	17	5.49	1.16	1.84	0.05	0.15
<i>Tetraphis pellucida</i> Hedw.	0	0	3	0	0	–	–	<0.01	–	–
Σ of species / average Σ cover:	16	24	24	13	21	19.71	14.49	20.10	1.68	11.14

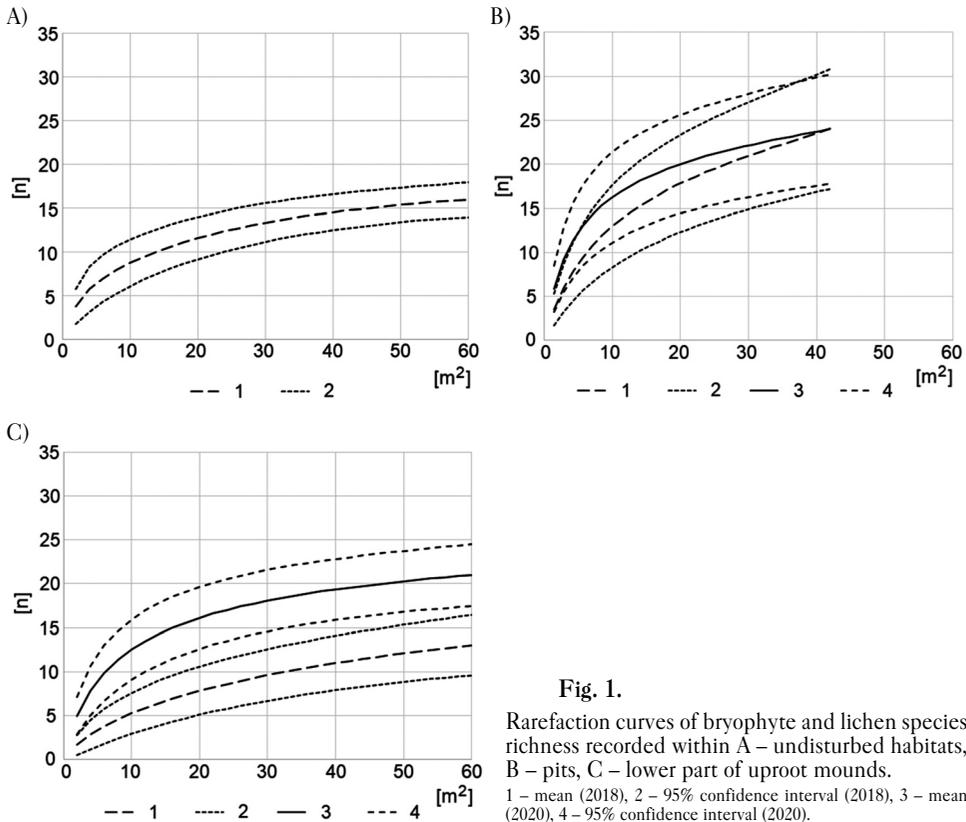


Fig. 1.

Rarefaction curves of bryophyte and lichen species richness recorded within A – undisturbed habitats, B – pits, C – lower part of uproot mounds.

1 – mean (2018), 2 – 95% confidence interval (2018), 3 – mean (2020), 4 – 95% confidence interval (2020).

of mineral soil within the uproot. Varying degrees of humidity and light availability are the most important differentiation factors (Beatty and Stone, 1986; Ulanova, 2000). It has been observed that uprooted trees are colonised relatively quickly, especially by bryophytes (Bazzaz, 1983; Rambo and Muir, 1998), which was also confirmed by this study. Mosses and liverworts were observed in the next growing season, one year after the disturbance. The only lichen species (*P. dasaea*) appeared two years after the disturbance, which is probably the result of the general lack of lichens in the surrounding terrestrial habitats and the much slower colonisation rate of the lichens from other habitats. A similar lack of epigeic lichens was described, for example, by Boch *et al.* (2013) from Germany.

Greater species richness is a common feature of disturbed sites (Lindholm and Nummelin, 1983; Jonsson and Esseen, 1998; Mills and MacDonald, 2004). Our results confirmed an increase in the species richness in the initial habitats of the uprooted trees. Uproot pits were species-rich both in 2018 and 2020. Species richness significantly increased between 2018 and 2020 in the case of mineral parts of uproot mounds.

Among the species that colonise the initial habitats of uprooted trees in the KNP, there is a group that is particularly associated with these habitats. Most of them rapidly colonise mineral soil in disturbed places, especially *C. purpureus*, *D. heteromalla*, *P. nutans* and *P. juniperinum* (Jonsson, 1993; Fenton *et al.*, 2003; Ryömä and Laaka-Lindberg, 2005). On the other hand, of interest here is the appearance of species that usually prefer different substrate types, such as *Aulacomnium androgynum* (Hedw.) Schwägr., *Herzogiella seligeri* (Brid.) Z.Iwats., *Tetraphis pellucida* Hedw. and

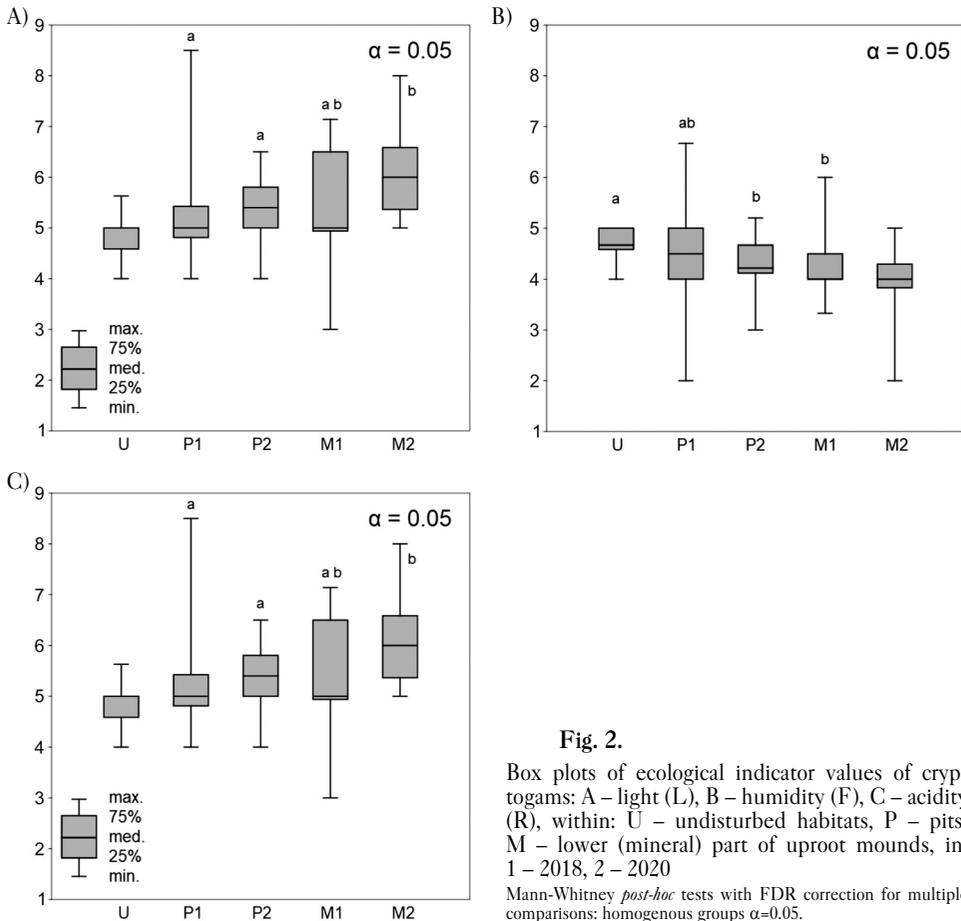


Fig. 2.

Box plots of ecological indicator values of cryptogams: A – light (L), B – humidity (F), C – acidity (R), within: U – undisturbed habitats, P – pits, M – lower (mineral) part of uproot mounds, in: 1 – 2018, 2 – 2020

Mann-Whitney *post-hoc* tests with FDR correction for multiple comparisons: homogenous groups $\alpha=0.05$.

P. dasaea (they usually grow on dead wood) and *D. cirrata* (epiphyte). A similar occurrence of epiphytes and epixyles in disturbed terrestrial habitats was described by von Oheimb *et al.* (2007). Many authors have described the encroachment of typically non-forest species into disturbed habitats in forests that have mineral soil (Ross-Davis and Frego, 2004; Ryömä and Laaka-Lindberg, 2005; Staniaszek-Kik *et al.*, 2016; Zielińska *et al.*, 2017). A similar phenomenon was observed in this study, in this case, they included *Bryum argenteum* Hedw., *D. schreberiana*, *Funaria hygrometrica* Hedw., *Marchantia polymorpha* L., *P. annotina* and *P. piliferum*. Some of these were observed only in the first year after the disturbance.

The uprooted trees are described as dynamic habitats that change over time (Bazzaz, 1983; Šamonil *et al.*, 2010). These changes concern, among others, shape, substrate stability, soil properties (moisture content, organic matter content) or light availability (Beatty and Stone, 1986; Schaeztl *et al.*, 1989a). As a result, their biota also changes over the years, which was observed in this study despite the short period of research. Diverse changes in the species composition and abundance of species both in the pits and lower parts of the uproot plates were observed. Some species such as *D. schreberiana*, *F. hygrometrica*, *M. polymorpha* and *P. epiphylla* disappeared from the pits after the first year of the research. This situation may have been caused by fallen leaves as their accumulation was observed in most of the examined pits. The negative impact

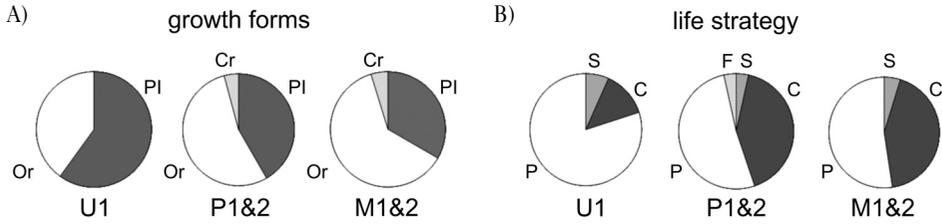


Fig. 3.

A – differentiation of growth forms (Or – orthotropic, PI – plagiotropic, Cr – crustose), and B – life strategies (C – colonist, F – fugitives, P – perennials, S – short-lived shuttle) within: U – undisturbed habitats, P – pits and M – lower part of mounds in: 1 – 2018, 2 – 2020 (percentage share of species).

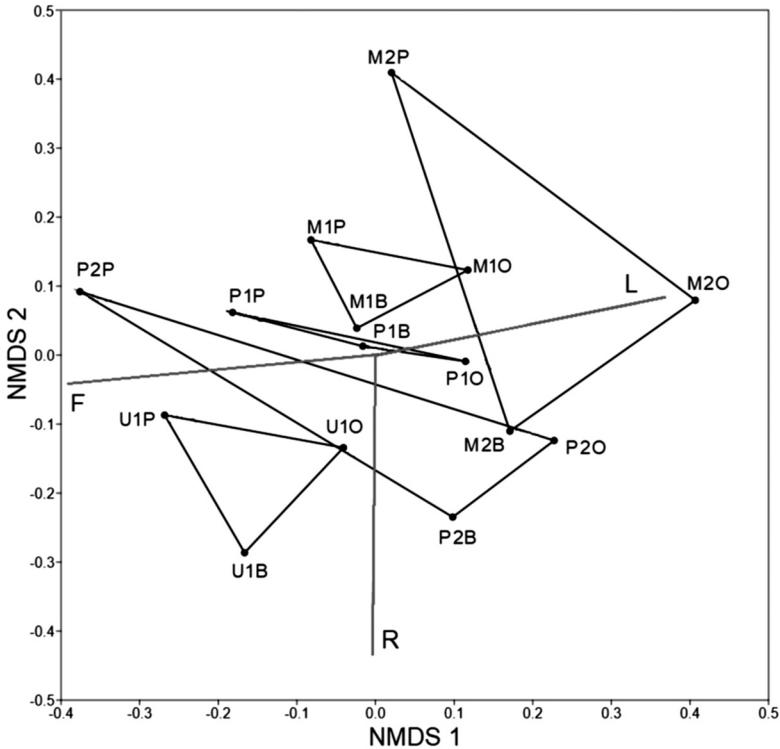


Fig. 4.

Differentiation of bryophyte and lichen communities (based on species frequencies) within initial part of uprooted trees and their surroundings: U – undisturbed plots, P – uproot pits, M – lower part of uproot mounds, years 1 – 2018, 2 – 2020; B – birch, O – oak, P – pine; environmental indicator values plotted as lines: L – light, F – humidity, R – acidity (2d NMDS, stress: 0.1513; R2: NMDS 1=0.40, NMDS 2=0.26).

of litter cover on the occurrence of bryophytes and other plants is a phenomenon that has often been described in the literature (Peterson and Campbell, 1993; Jonsson and Esseen, 1998; von Oheimb *et al.*, 2007; Márialigeti *et al.*, 2009; Simon *et al.*, 2011; Kövendi-Jakó *et al.*, 2016). The organic layer usually inhibits the development of plants by limiting access to light, but it is also a barrier that limits the inflow of spores to the mineral soil and thus their germination. This can have a significant impact on the species richness and dynamics of plant communities (Beatty and Sholes, 1988; Facelli and Pickett, 1991).

Slight changes in the composition and abundance of the bryoflora were also observed in the surroundings of the uprooted trees. However, these results were excluded from the study because they were at least partially of anthropogenic origin. Several years of comprehensive research has been carried out in the area of the windthrows and their surroundings, which has resulted in their being relatively strongly trampled. In 2020, three new, light-demanding species appeared, which are often mentioned as colonisers of disturbed habitats: *Campylopus introflexus* (Hedw.) Brid., *C. purpureus* and *P. juniperinum*. Particularly noteworthy species is *C. introflexus*, a moss of foreign origin that is dynamically spreading in Europe, including Poland (Mikulášková *et al.*, 2012; Żarnowiec *et al.*, 2019). Disturbances, even periodic ones, generally favour not only the diversity of indigenous biota, but also the entry and spread of alien species (Lozon and MacIsaac, 1997; Lonsdale, 1999; Eschtruth and Battles, 2014). *C. introflexus* is found in disturbed habitats with reduced competition relatively often (Hasse, 2007; Jukoniene *et al.*, 2015; Alegro *et al.*, 2018).

The process of encroachment of a species into initial habitats can be conditioned by a decrease in competition connected with disturbance, and also by, *e.g.*, the physical properties of new habitats such as light intensity or substrate humidity and acidity (Beatty and Stone, 1986; Schaetzl *et al.*, 1989a; Peterson *et al.*, 1990). The diversity of species composition that was observed in the pits and lower parts of the mounds largely resulted from differences in the microhabitat conditions. This was indicated by a comparison of the average values of selected EIV of the species growing on the different types of habitats. In the case of light, an increase in the mean value was recorded in both the pits and lower parts of the uproot plates compared to the surroundings. Windthrows are known to significantly improve the local light conditions on the forest floor (Peterson *et al.*, 1990; Ulanova, 2000), which means that light-demanding species, including non-forest ones, can easily settle in the vicinity of the uprooted trees (in this study, particularly *B. argenteum*, *F. hygrometrica* and *P. piliferum*), or non-indigenous species (*C. introflexus*). The importance of increased light availability for shaping the biodiversity of disturbed forest habitats has been emphasised by other authors (*e.g.*, Schaetzl *et al.*, 1989a; Jonsson and Essen, 1990; von Oheimb *et al.*, 2007).

In the case of humidity, a decrease in the average value was recorded in both the pits and lower parts of the uproot plates. This indicates that these habitats (especially the uproot plates) are less humid compared to their surroundings. Exposed mineral soil is more susceptible to drying. This finding confirms the dependencies that have also been described by other authors (Beatty and Stone, 1986; Peterson *et al.*, 1990; Peterson and Campbell, 1993; Samonil *et al.*, 2010). Similarly, in the case of acidity, a decrease in average value was recorded in both the pits and on lower parts of the mounds compared to the undisturbed sites. Greater acidification of mineral soil on disturbed sites was also described by Beatty and Stone (1986) and Šamonil *et al.* (2010). The results obtained using the EIV confirm that the diversity of the communities that formed in the disturbed habitats was a response to the changing quality of the newly emerged habitats (Yamamoto, 1992; Muscolo *et al.*, 2014).

The colonisation of initial habitats, such as the exposure of mineral soil in the new uprooted trees, depends on three sources of diaspores: establishment from the close vicinity of clonally reproducing individuals, germination from the soil bank of diaspores, and the inflow of wind-dispersed propagules from the outside (Rydgren and Hestmark, 1997; Ross-Davis and Frego, 2004). It is also possible that epizoochory may be involved in bringing in plant fragments, thus resulting in the establishment of bryophytes (Heinken *et al.*, 2001; Heinken and Zippel, 2004). The observed emergence of non-forest species such as *F. hygrometrica* or *B. argenteum* in the disturbed habitats of this large forest complex indicates a relatively distant source of some of the diaspores. Numerous authors have reported the possibility of the long-distance transport of the

relatively light, anemochoric propagules (spores or other gemmae) of bryophytes and lichens (Miller and McDaniel, 2004; Hutsemekers *et al.*, 2008; Glime, 2017). These propagules germinate under favourable conditions or enter the soil bank of diaspores (During, 2001; Ross-Davis and Frego, 2004; Kövendi-Jakó *et al.*, 2016). Regeneration from the spore bank seems to be particularly important in the group of species that are typical for the early succession stages such as *P. nutans* or *P. juniperinum* (Jonsson, 1993; Rydgren and Hestmark, 1997).

A disturbance promotes the establishment of species with less competitive ability such as bryophytes and lichens (Grime, 1979; Strazdiņa, 2010). Bryophytes colonise mineral soil relatively quickly (Jonsson and Essen, 1990, 1998), as confirmed by this research. Because of the reduced competition, the diversity of species inhabiting the surveyed initial habitats of uprooted trees, both in terms of form and life strategies, differed in relation to the neighbouring sites. The surroundings were dominated by plagiotropic perennials, while in the disturbed habitat patches, orthotropic forms were predominant and the proportion of colonists was much greater, which was similar to other studies (*e.g.*, During, 1979; Jonsson and Essen, 1990; Mills and MacDonald, 2004).

Despite the relatively short period of the observations of the cryptogam communities of the habitats in the KNP, some dynamic trends could be observed. The similarity between the pits and the adjacent undisturbed environment increased over time, while the distinctiveness of the lower parts of mounds became more visible. This is probably the result of habitat changes and the growing difference between the pits and lower parts of mounds, especially with regard to moisture of the substrate (Peterson *et al.*, 1990; Peterson and Campbell, 1993; Šamonil *et al.*, 2010).

Authors' contributions

B.F. – concept, fieldworks, statistics, literature review, writing; P.Z. – fieldworks, statistics, literature review, writing.

Conflict of interest

No conflict of interest declared.

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STRESZCZENIE

Sukcesja ekologiczna mszaków i porostów w obrębie mineralnych siedlisk inicjalnych na wiatrołomach (Kampinoski Park Narodowy, środkowa Polska)

Wiatrołomy to jedno z najczęściej spotykanych naturalnych zaburzeń występujących w ekosystemach leśnych. W wyniku powalenia drzew powstają odsłonięcia mineralnej gleby związane z wykrotami (w misie wykrotu i na spodzie karpki korzeniowej). Są to siedliska o charakterze inicjalnym, stopniowo kolonizowanym przez wiele grup organizmów, w tym mszaki i porosty.

Celem badań było określenie bogactwa gatunkowego mszaków i porostów dwóch inicjalnych siedlisk naziemnych (mis wykrotowych i mineralnych, spodnich części karp), określenie wierności poszczególnych gatunków względem badanych siedlisk, charakterystyka warunków ekologicznych panujących w tych siedliskach na podstawie ekologicznych liczb wskaźnikowych, a także przesledzenie zmian w ich składzie gatunkowym.

Badania prowadzono na terenie wiatrołomów powstałych w 2017 r. na terenie Kampinoskiego Parku Narodowego (uroczyska Różin i Grabina). Inwentaryzacji poddano 30 wykrotów (po 10 wykrotów brzozy, dębu i sosny) oraz ich najbliższe otoczenie (w promieniu 1 m). Dla mis wykrotowych, mineralnych części karp i ich najbliższego otoczenia sporządzono listy florystyczne mszaków i porostów. Za miarę obfitości przyjęto pokrycie. W pracy wykorzystano dane z pierwszego i trzeciego roku po wystąpieniu wiatrołomu. W przypadku sąsiedztwa wykrotów, ze względu na późniejsze antropogeniczne zaburzenia, wykorzystano dane jedynie z 2018 r. Bogactwo gatunkowe obliczono metodą krzywych rarefakcji. Wierność gatunków względem badanych siedlisk obliczono w oparciu o wskaźnik phi. Warunki siedliskowe scharakteryzowano za pomocą ekologicznych liczb wskaźnikowych. Zmiany w składzie gatunkowym zbiorowisk mszysto-porostowych przesledzono za pomocą ordynacji NMDS.

Odnotowano łącznie 31 gatunków mszaków (3 wątrobowce i 28 mchów) oraz 1 gatunek porostu (tab. 1). Największa liczba gatunków występowała w misach wykrotów (28), na spodach karp rosło 21 gatunków, zaś w otoczeniu wykrotów – 16 gatunków. Wiele gatunków charakteryzowało się istotnym przywiązaniem do analizowanych siedlisk. W trakcie kolejnych sezonów badawczych odnotowano istotne zmiany w bogactwie gatunków na analizowanych siedliskach (ryc. 1). Szczególnie duży istotny wzrost odnotowano w obrębie spodnich części karp. Wartości ekologicznych liczb wskaźnikowych gatunków istotnie różnicowały się pomiędzy misami i na spodach karp w porównaniu z otoczeniem (ryc. 2). Na analizowanych typach siedlisk zaobserwowano różnice w udziale gatunków o różnym typie wzrostu i strategiach życiowych (ryc. 3). Wyniki analizy NMDS (ryc. 4) wskazują na rozbieżne zmiany w obrębie składu gatunkowego mszaków i porostów siedlisk związanych z wykrotami. Zbiorowiska mis wykrotowych i spodniej części karp były do siebie bardziej podobne w pierwszym roku po wystąpieniu wiatrołomu. Natomiast w trzecim roku po wiatrołomie podobieństwo florystyczne mis przesunęło się w kierunku otoczenia wykrotów. Odwrotną tendencję zaobserwowano w stosunku do spodniej części karp.

Przeprowadzone badania potwierdziły, że odsłonięcia mineralnej gleby w wykrotach są stosunkowo szybko kolonizowane przez mszaki. Ponadto w kolejnych latach odnotowano istotne zmiany w składzie gatunkowym i obfitości występowania gatunków zarówno w misach, jak i na spodach karp. Z biegiem czasu wzrastało podobieństwo między misami i otoczeniem, przy jednoczesnym zwiększaniu się odrębności spodu karp. Na podstawie zróżnicowania ekologicznych liczb wskaźnikowych w obrębie badanych siedlisk inicjalnych przyjęto, że czynnikami mogącymi mieć największy wpływ na odmienną kolonizację siedlisk wykrotowych były oświetlenie, wilgotność i kwasowość podłoża. Znaczenie miały najprawdopodobniej również źródło diaspor i potencjał kolonizacyjny gatunków.