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Vascular flora changes in canopy gaps caused by wind

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Abstract. A study on the importance of wind-induced canopy gaps was conducted in Kampinos National Park (Poland) between 2018 and 2021. Two types of habitats were considered – dry mesotrophic oak forest and wet Scots pine forest (*Molinio-Pinetum*). Canopy gaps were characterized by higher plant species richness than in adjacent areas, and their effect was weaker in oligotrophic coniferous forest than in mesotrophic deciduous oak stand.

Key words: canopy gaps, plants, species richness, vascular flora changes, natural disturbances

1. Introduction

The fundamental condition for the conservation of forest ecosystems is the existence of diverse microhabitats that ensure the continuous presence of many coexisting species. This is of great importance for shaping biodiversity as well as for forest regeneration (Holeksa 1998, 2003; Gutowski *et al.* 2004). In both protected and managed forests, natural disturbances caused by wind are a key process for maintaining and increasing local diversity. This is because the loss of canopy-building trees above the forest floor allows for an increased access to light and precipitation, improves mineralization of organic matter and modifies microclimatic conditions compared to those under the forest stand. Air temperature and humidity also change in gaps (Dobrowolska 2006). This opens up the possibility for full development and closure of life cycles of many plant species which previously could not survive under reduced light conditions. Gaps are an important element of the forest ecosystem structure, they are a fundamental part of forest life and their importance for forest dynamics has been widely documented (Hiura 1995; Townsend & Scarsbrook 1997; Dobrowolska 2010). In addition, many microhabitats are created within wind-induced canopy gaps as a result of soil exposure (windthrow) and influx of woody debris, which is a substrate for mosses, liverworts, vascular plants and many animal taxa (Gutowski *et al.* 2004; Stokland *et al.* 2012; Zacharyasiewicz *et al.* 2021). Previous experience from a small-scale disturbance of the forest floor caused by factors other than wind, e.g. digging animals (Kurek 2019; Kurek & Cykowska-Marzencka 2016) confirms that the much more spatially extensive windthrow effect can be a crucial factor in shaping diversity.

In managed forests similar random phenomena are undesirable and their effects are quickly eliminated (e.g. Kapusta *et al.* 2020) by removing deadwood, preparing the soil for future artificial plantings and simultaneously mechanically removing stumps. Therefore, the lack of interference with natural processes that ensure the formation of canopy gaps and the accompanying important elements of forest structure (woody debris, windsnaps, windthrows) in protected areas creates an opportunity for a further study of this phenomenon and its impact on forest ecosystem diversity. Long-term monitoring of flora changes in canopy gaps enables tracking the persistence of their effects over time. The aim of this study was to assess the impact of small-scale wind-induced disturbances on the formation of vascular plant species richness in stands with different species composition, found under different habitat conditions as well as to

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identify the persistence and direction of the changes in time – differentiation or unification of vascular plant communities.

2. Materials and methods

The research was carried out on three canopy gaps created in 2017, located in Kampinos National Park (Poland). Two ellipsoidal gaps were created in the stand with dimensions of 30×90 m and 30×60 m, characterized by a 90% share of oak *Quercus petraea* aged 104 years and a 10% share of birch *Betula pendula*. The third examined gap, elliptical in shape and measuring 30×70 m, was created in an 84-year-old Scots pine *Pinus sylvestris* stand with a singly found aspen *Populus tremula* and a birch. Within the described gaps the stands were completely damaged with broken and uprooted trees. Therefore the monitoring studies covered the entire surface of the windthrow gaps (hence three study areas in total). Due to the soil and habitat conditions and the prevailing tree species composition, the study plots could be divided into two groups located in: 1) a sessile oak stand showing intermediate features between the acidophilic oak forest *Calamagrostio arundinaceae-Quercetum* and the subcontinental mixed forest *Querco roboris-Pinetum* (hereinafter referred to as oak forest) and 2) in a Scots pine stand on wet habitat *Molinio-Pinetum* (hereinafter referred to as Scots pine forest).

A system of circular research plots (3.14 m^2, r = 1 m) on a 10×10 m grid was created in each of the three studied gaps. 125 circular study plots were established in two habitat types: 80 in the oak forest (38 in gaps and 42 in undisturbed vegetation) and 45 in the Scots pine forest (22 in gaps and 23 in undisturbed vegetation). Due to habitat differences, the gaps were divided into two groups (oak and Scots pine forest). For each group one reference plot (hereinafter referred to as undisturbed vegetation) was established in the same but undisturbed habitat type, located in random direction distant from the gap by at least two stand heights (ca. 50 m). Some study plots located in gaps were excluded from further study because they were shaded by expanding tree crowns over time, and thus the number of plots in gaps and in undisturbed vegetation is not equal. The minimal distance between two monitored gaps among in oak forest was 100 m. The distance between gaps in oak and Scots pine forest was 5500 m. In 2018-2021 floristic censuses were carried out in all study plots. For each circular plot floristic lists were made in June-July when the undergrowth on mesotrophic habitats reached full development. Plants were quantified on a percentage scale with a 5% interval.

Statistical analysis of data was carried out with repeated measures ANOVA with two factors – time (year) and plot type (gap and undisturbed vegetation) using R (R Core Team 2021) with ‘rstatix’ (Kassambara 2021), ‘tidyverse’ (Wickham *et al.* 2019) and ‘ggpubr’ (Kassambara 2020) packages. Data from both gaps in the oak stand were analyzed together. *P*-values were adjusted using the Bonferroni multiple testing correction method. For repeated measures ANOVA, the default of the function: get_anova_table() [‘rstatix’ package] is to apply automatically the Greenhouse-Geisser sphericity correction. To obtain equal sample size and fit analysis assumptions for ANOVA random plots representing undisturbed vegetation were excluded from further computations. To obtain normal or almost normal distribution extreme outliers were removed from the dataset. The similarity of plant communities was analyzed for all plots with Detrended Correspondence Analysis (DCA), taking into account data from the end of the research period for gap and undisturbed vegetation plots from both habitat types with CANOCO 5 (Šmilauer & Lepš 2014).

3. Results

3.1. Number of plant species

As a result of the 2018-2021 research 71 plant species were found within the canopy gaps in the oak forest (Table 1), while 31 species were found in the undisturbed vegetation plots (Table 2). The effect of both year ($F_{1.96,\ 72.49} = 37.88$, $P < 0.001$) and plot type ($F_{1,\ 37} = 171.14$, $P < 0.001$) on the plant species number

Table 1. Plant species from plots (N = 38) in canopy gaps in oak forests with their frequency in first (2018) and last season of the research period (2021)

No.	Species	Frequency 2018		Frequency 2021	
		n	%	n	%
1	*Mycelis muralis*	30	78.9	37	97.4
2	*Quercus petraea*	28	73.7	35	92.1
3	*Festuca ovina*	30	78.9	29	76.3
4	*Luzula pilosa*	24	63.2	26	68.4
5	*Frangula alnus*	22	57.9	23	60.5
6	*Anthoxanthum odoratum*	17	44.7	21	55.3
7	*Melampyrum pratense*	26	68.4	20	52.6

8	*Populus tremula*	7	18.4	18	47.4
9	*Prunus avium*	6	15.8	16	42.1
10	*Impatiens parviflora*	14	36.8	15	39.5
11	*Taraxacum officinale*	10	26.3	15	39.5
12	*Hieracium lachenalii*	15	39.5	14	36.8
13	*Stellaria media*	22	57.9	14	36.8
14	*Solidago virgaurea*	7	18.4	13	34.2
15	*Galeopsis tetrahit*	16	42.1	12	31.6
16	*Pyrus pyraster*	7	18.4	11	28.9
17	*Betula pendula*	0	0.0	9	23.7
18	*Deschampsia flexuosa*	1	2.6	9	23.7
19	*Hieracium pilosella*	3	7.9	9	23.7
20	*Poa pratensis*	14	36.8	8	21.1
21	*Urtica dioica*	4	10.5	8	21.1
22	*Agrostis tenuis*	0	0.0	6	15.8
23	*Prunus serotina*	1	2.6	6	15.8
24	*Sorbus aucuparia*	5	13.2	6	15.8
25	*Moehringia trinervia*	8	21.1	5	13.2
26	*Carex pilulifera*	0	0.0	4	10.5
27	*Carpinus betulus*	0	0.0	4	10.5
28	*Holcus lanatus*	0	0.0	4	10.5
29	*Linaria vulgaris*	2	5.3	4	10.5
30	*Maianthemum bifolium*	2	5.3	4	10.5
31	*Sambucus racemosa*	1	2.6	4	10.5
32	*Acer platanoides*	0	0.0	3	7.9
33	*Chaerophyllum temulum*	2	5.3	3	7.9
34	*Chamaecytisus ratisbonensis*	1	2.6	3	7.9
35	*Conyza canadensis*	2	5.3	3	7.9
36	*Fagus sylvatica*	6	15.8	3	7.9
37	*Hieracium murorum*	0	0.0	3	7.9
38	*Hypochaeris radicata*	1	2.6	3	7.9
39	*Melica nutans*	1	2.6	3	7.9
40	*Pinus sylvestris*	2	5.3	3	7.9
41	*Rubus* sp.	1	2.6	3	7.9
42	*Solidago gigantea*	1	2.6	3	7.9
43	*Viola reichenbachiana*	1	2.6	3	7.9
44	*Achillea millefolium*	2	5.3	2	5.3
45	*Calamagrostis epigejos*	0	0.0	2	5.3
46	*Carex hirta*	2	5.3	2	5.3
47	*Convallaria majalis*	2	5.3	2	5.3
48	*Deschampsia caespitosa*	1	2.6	2	5.3
49	*Festuca gigantea*	1	2.6	2	5.3
50	*Fragaria vesca*	1	2.6	2	5.3
51	*Hieracium umbellatum*	0	0.0	2	5.3
52	*Peucedanum oreoselinum*	4	10.5	2	5.3
53	*Prunus cerasifera*	2	5.3	2	5.3
54	*Vaccinium myrtillus*	2	5.3	2	5.3
55	*Bidens* sp.	1	2.6	1	2.6
56	*Brachypodium sylvaticum*	0	0.0	1	2.6
57	*Campanula rotundifolia*	0	0.0	1	2.6
58	*Erechtites hieracifolia*	0	0.0	1	2.6
59	*Lycopus europaeus*	0	0.0	1	2.6
60	*Milium effusum*	0	0.0	1	2.6
61	*Rumex acetosella*	1	2.6	1	2.6
62	*Tilia cordata*	0	0.0	1	2.6
63	*Veronica officinalis*	1	2.6	1	2.6
64	*Viburnum opulus*	1	2.6	1	2.6
65	*Epilobium parviflorum*	1	2.6	0	0.0
66	*Lactuca serriola*	1	2.6	0	0.0
67	*Rubus saxatilis*	1	2.6	0	0.0
68	*Sedum maximum*	1	2.6	0	0.0
69	*Quercus robur*	1	2.6	0	0.0
70	*Sambucus nigra*	2	5.3	0	0.0
71	*Torilis japonica*	1	2.6	0	0.0

Table 2. Plant species from undisturbed vegetation plots (N = 42) in oak forests with their frequency in first (2018) and last season of the research period (2021)

No.	Species	Frequency 2018		Frequency 2021	
		n	%	n	%
1	*Solidago virgaurea*	3	7.1	35	83.3
2	*Festuca ovina*	27	64.3	33	78.6
3	*Melampyrum pratense*	15	35.7	22	52.4
4	*Luzula pilosa*	9	21.4	14	33.3
5	*Hieracium lachenalii*	7	16.7	9	21.4
6	*Frangula alnus*	5	11.9	5	11.9
7	*Prunus avium*	6	14.3	5	11.9
8	*Pyrus pyraster*	3	7.1	4	9.5
9	*Calamagrostis arundinacea*	3	7.1	3	7.1
10	*Carex pilulifera*	0	0.0	3	7.1
11	*Vaccinium myrtillus*	3	7.1	3	7.1
12	*Hieracium pilosella*	0	0.0	2	4.8
13	*Peucedanum oreoselinum*	2	4.8	2	4.8
14	*Polygonatum odoratum*	2	4.8	2	4.8
15	*Prunus serotina*	0	0.0	2	4.8
16	*Quercus petraea*	11	26.2	2	4.8
17	*Deschampsia caespitosa*	2	4.8	1	2.4
18	*Deschampsia flexuosa*	2	4.8	1	2.4
19	*Holcus lanatus*	0	0.0	1	2.4
20	*Impatiens parviflora*	1	2.4	1	2.4
21	*Juniperus communis*	1	2.4	1	2.4
22	*Hypochaeris radicata*	0	0.0	1	2.4
23	*Moehringia trinervia*	3	7.1	1	2.4
24	*Pinus sylvestris*	0	0.0	1	2.4
25	*Poa pratensis*	0	0.0	1	2.4
26	*Quercus robur*	3	7.1	1	2.4
27	*Stellaria media*	2	4.8	1	2.4
28	*Sorbus aucuparia*	2	4.8	0	0.0
29	*Mycelis muralis*	1	2.4	0	0.0
30	*Poa nemoralis*	1	2.4	0	0.0
31	*Viburnum opulus*	1	2.4	0	0.0

was significant. In the entirety of the study period it increased greatly in the plots located in the gaps, with the highest value observed in the final, fourth season in 2021 (Fig. 1). In contrast to the gap plots, in the undisturbed vegetation plot the growth of plant species number was much smaller (Fig. 1). Throughout the entire study period 31 plant species were found within the canopy gap in the Scots pine forest (Table 3), while 16 species in the undisturbed vegetation plots (Table 4). Contrary to the one of year ($F_{1.69, 35.43} = 3.19$, $P = 0.061$) the effect

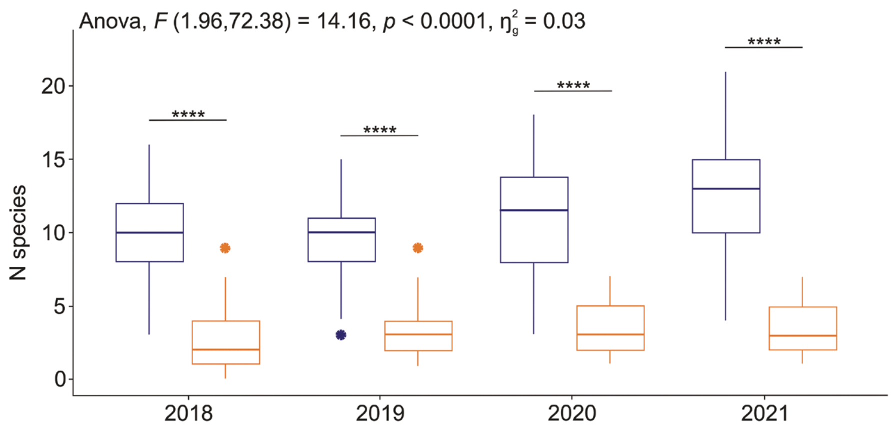

Fig. 1. Number of plant species recorded within the canopy gaps (blue) and within the undisturbed vegetation (orange) in the oak forests with significant plot type × time interaction. Median, Q2, Q3 – box, min-max – whiskers. **** – P < 0.0001

Table 3. Plant species from plots (N = 22) in canopy gap in Scots pine forests with their frequency in first (2018) and last season of the research period (2021)

No.	Species	Frequency 2018		Frequency 2021	
		n	%	n	%
1	*Frangula alnus*	20	90.9	22	100.0
2	*Molinia coerulea*	21	95.5	22	100.0
3	*Vaccinium myrtillus*	19	86.4	19	86.4
4	*Dryopteris carthusiana*	11	50.0	13	59.1
5	*Rubus* sp.	6	27.3	11	50.0
6	*Lysimachia vulgaris*	10	45.5	10	45.5
7	*Impatiens parviflora*	6	27.3	9	40.9
8	*Quercus petraea*	8	36.4	8	36.4
9	*Maianthemum bifolium*	7	31.8	6	27.3
10	*Vaccinium vitis-idaea*	3	13.6	5	22.7
11	*Carex acutiformis*	1	4.5	4	18.2
12	*Luzula pilosa*	4	18.2	4	18.2
13	*Milium effusum*	5	22.7	4	18.2
14	*Populus tremula*	6	27.3	4	18.2
15	*Sorbus aucuparia*	3	13.6	4	18.2
16	*Trientalis europaea*	18	81.8	4	18.2
17	*Betula pubescens*	2	9.1	3	13.6
18	*Betula pendula*	2	9.1	2	9.1
19	*Calamagrostis arundinacea*	1	4.5	2	9.1
20	*Equisetum sylvaticum*	2	9.1	2	9.1
21	*Juncus effusus*	0	0.0	2	9.1
22	*Pteridium aquilinum*	2	9.1	2	9.1
23	*Poa pratensis*	1	4.5	1	4.5
24	*Corylus avellana*	0	0.0	1	4.5
25	*Urtica dioica*	0	0.0	1	4.5
26	*Juncus conglomeratus*	1	4.5	1	4.5
27	*Mycelis muralis*	2	9.1	0	0.0
28	*Convallaria majalis*	1	4.5	0	0.0
29	*Deschampsia caespitosa*	1	4.5	0	0.0
30	*Pinus sylvestris*	1	4.5	0	0.0
31	*Sanguisorba officinalis*	1	4.5	0	0.0

Table 4. Plant species from undisturbed vegetation plots (N = 23) in Scots pine forests with their frequency in first (2018) and last season of the research period (2021)

No.	Species	Frequency 2018		Frequency 2021	
		n	%	n	%
1	*Frangula alnus*	23	100.0	23	100.0
2	*Vaccinium myrtillus*	23	100.0	22	95.7
3	*Molinia coerulea*	21	91.3	21	91.3
4	*Pteridium aquilinum*	18	78.3	18	78.3
5	*Trientalis europaea*	16	69.6	15	65.2
6	*Vaccinium vitis-idaea*	14	60.9	12	52.2
7	*Dryopteris carthusiana*	9	39.1	8	34.8
8	*Sorbus aucuparia*	6	26.1	8	34.8
9	*Betula pubescens*	7	30.4	6	26.1
10	*Quercus petraea*	8	34.8	6	26.1
11	*Rubus sp.*	5	21.7	5	21.7
12	*Luzula pilosa*	5	21.7	4	17.4
13	*Calluna vulgaris*	1	4.3	1	4.3
14	*Carex acutiformis*	0	0.0	1	4.3
15	*Festuca ovina*	1	4.3	1	4.3
16	*Deschampsia caespitosa*	1	4.3	0	0.0

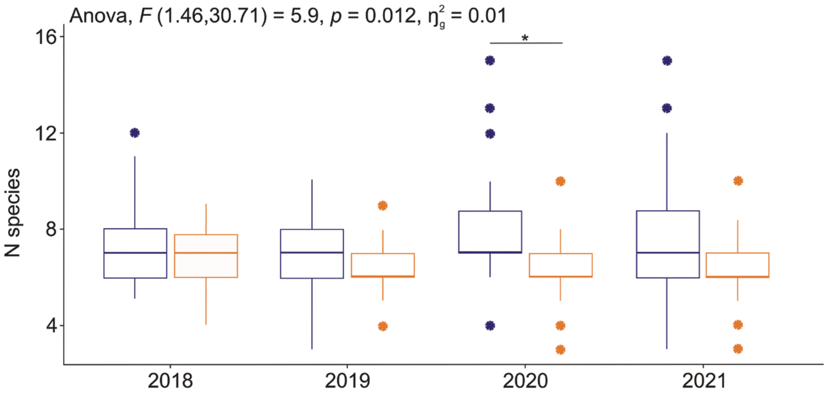

Fig. 2. Number of plant species recorded within the canopy gap (blue) and within the undisturbed vegetation (orange) in the Scots pine forest with significant plot type × time interaction. Median, Q2, Q3 – box, min-max – whiskers. * – P < 0.05

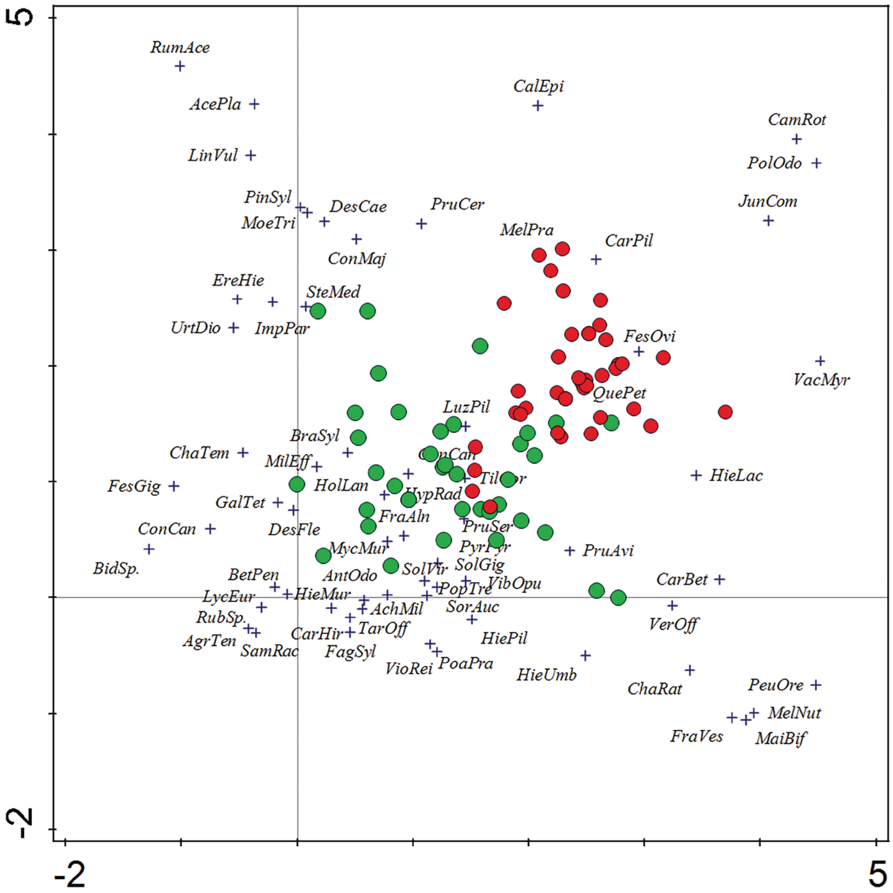

Fig. 3. Detrended Correspondence Analysis (DCA) scatterplot showing the relationships between the examined plant species communities from 38 plots within the gaps (green circles) and 42 within the undisturbed vegetation (red circles) in the oak forest on the first two axes. The first and the second axis explained 13.03% of the variation

Abbreviations of the species (marked with +): AcePla = *Acer platanoides*, AchMil = *Achillea millefolium*, AgrTen = *Agrostis tenuis*, AntOdo = *Anthoxanthum odoratum*, BetPen = *Betula pendula*, BidSp. = *Bidens* sp., BraSyl = *Brachypodium sylvaticum*, CalEpi = *Calamagrostis arundinacea*, CamRot = *Campanula rotundifolia*, CarHir = *Carex hirta*, CarPil = *Carex pilulifera*, CarBet = *Carpinus betulus*, ChaRem = *Chaerophyllum temulum*, ChaRat = *Chamaecytisus ratisbonensis*, ConMaj = *Convallaria majalis*, ConCan = *Conyza canadensis*, DesCae = *Deschampsia caespitosa*, DesFle = *Deschampsia flexuosa*, EreHie = *Erechtites hieracifolia*, FagSyl = *Fagus sylvatica*, FesGig = *Festuca gigantea*, FesOvi = *Festuca ovina*, FraVes = *Fragaria vesca*, FraAln = *Frangula alnus*, GalTet = *Galeopsis tetrahit*, HieLac = *Hieracium lachenalii*, HieMur = *Hieracium murorum*, HiePil = *Hieracium pilosella*, HieUmb = *Hieracium umbellatum*, HolLan = *Holcus lanatus*, HypRad = *Hypochaeris radicata*, ImpPar = *Impatiens parviflora*, JunCom = *Juniperus communis*, LinVul = *Linaria vulgaris*, LuzPil = *Luzula pilosa*, LycEur = *Lycopus europaeus*, MaiBif = *Maianthemum bifolium*, MelPra = *Melampyrum pratense*, MelNut = *Melica nutans*, MilEff = *Milium effusum*, MoeTri = *Moehringia trinervia*, MycMur = *Mycelis muralis*, PeuOre = *Peucedanum oreoselinum*, PinSyl = *Pinus sylvestris*, PoaPra = *Poa pratensis*, PolOdo = *Polygonatum odoratum*, PopTre = *Populus tremula*, PruAvi = *Prunus avium*, PruCer = *Prunus cerasifera*, PruSer = *Prunus serotina*, PyrPyr = *Pyrus pyraster*, QuePet = *Quercus petraea*, RubSp. = *Rubus* sp., RumAce = *Rumex acetosella*, SamRac = *Sambucus racemosa*, SolGig = *Solidago gigantea*, SolVir = *Solidago virgaurea*, SorAuc = *Sorbus aucuparia*, SteMed = *Stellaria media*, TarOff = *Taraxacum officinale*, TilCor = *Tilia cordata*, UrtDio = *Urtica dioica*, VacMyr = *Vaccinium myrtillus*, VerOff = *Veronica officinalis*, VibOpu = *Viburnum opulus*, VioRei = *Viola reichenbachiana*

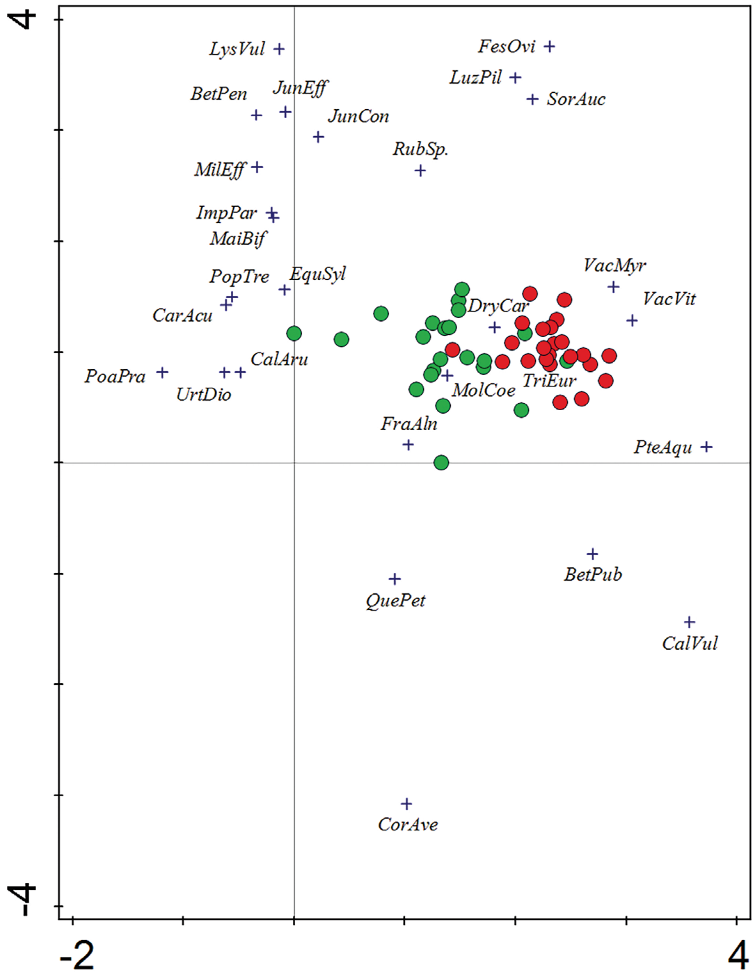

Fig. 4. Detrended Correspondence Analysis (DCA) scatterplot showing the relationships between the examined plant species communities from 22 plots within the gap (green circles) and 23 within the undisturbed vegetation (red circles) in the Scots pine forest on the first two axes. The first and the second axis explained 29.39% of the variation

Abbreviations of the species (marked with +): BetPen = *Betula pendula*, BetPub = *Betula pubescens*, CalAru = *Calamagrostis arundinacea*, CalVul = *Calluna vulgaris*, CarAcu = *Carex acutiformis*, CorAve = *Corylus avellana*, DryCar = *Dryopteris carthusiana*, EquSyl = *Equisetum sylvaticum* , FesOvi = *Festuca ovina*, FraAln = *Frangula alnus*, ImpPar = *Impatiens parviflora*, JunCon = *Juncus conglomeratus*, JunEff = *Juncus effusus*, LuzPil = *Luzula pilosa*, LysVul = *Lysimachia vulgaris*, MaiBif= *Maianthemum bifolium*, MilEff = *Milium effusum*, MolCoe = *Molinia coerulea*, PoaPra = *Poa pratensis*, PopTre = *Populus tremula*, PteAqu = *Pteridium aquilinum*, QuePet = *Quercus petraea*, RubSp. = *Rubus* sp., SorAuc = *Sorbus aucuparia*, TriEur = *Trientalis europaea*, UrtDio = *Urtica dioica*, VacMyr = *Vaccinium myrtillus*, VacVit = *Vaccinium vitis-idaea*

of plot type ($F_{1, 21}$ = 2.74, P = 0.113) on plant species number was not even close to significant (Fig. 2). As a result it increased only slightly and was higher in the gap than in the undisturbed vegetation plots. However, the differences were not as distinct as in the oak stand. Both in the Scots pine and the oak forest the plot type × time (year) interaction was significant (Figs. 1-2).

3.2. Differentiation of flora assemblages

The DCA analysis showed that after four years of research plant species composition from both gap and undisturbed vegetation plots underwent a qualitative differentiation. There are two assemblages of plants clearly distinguishable in the oak forest, with more plant species found in the canopy gaps (Fig. 3). All of those species have similar habitat requirements and the main gradient of variation, decreasing from bottom left to top right in Fig. 3, which relates to the amount of light reaching the forest floor. In the Scots pine forest the qualitative differentiation of the plant assemblage between gap and undisturbed vegetation plots can also be observed (Fig. 4) with a similar light availability gradient, where it runs decreasingly from left to right on the graph.

4. Discussion

The disturbances of the forest floor related to the increased access to light are a major factor in differentiating microhabitats, thus enabling the settlement of new plant species (Piskorz & Klimko 2001; Staniaszek-Kik & Żarnowiec 2013), which under undisturbed conditions would not be able to complete their reproductive cycle and establish a stable population. Such disturbances include small-area gaps in the canopy caused by the death of one or several trees, as well as large-scale disturbances causing a stand loss over a large area, such as fires, wind and insect outbreaks (Muscolo *et al.* 2014). These phenomena result in an increase in the species richness of plants compared to the surrounding areas and the qualitative and spatial differentiation of the forest floor plant assemblages (Holeksa 2003). In the temperate zone forests gaps in the canopy are places of initiation and greater survival of tree regeneration (Yamamoto 2000; Holeksa *et al.* 2021). Free space in the canopy, caused by natural succession and growth of trees and shrubs inside and adjacent to the gap itself, gradually decreases and the gap disappears over time (Muscolo *et al.* 2014). In order to maintain species diversity it is crucial to have a repetitive disturbance pattern that ensures microhabitat diversity, and thus the presence of microhabitats suitable for early successional species (Hiura 1995; Townsend & Scarsbrook 1997).

The canopy gaps, both in the oak forest and in the Scots pine forest, resulted in a diversity of plant communities in terms of quantity (number of species) and quality (similarity of assemblages) in relation to the surrounding undisturbed vegetation plots. In terms of the number of species this effect was less pronounced in the Scots pine stand than in the oak stand. Thus, it seems that in a mesotrophic habitat the effect of a gap on vascular plant species richness is much more distinct than in an oligotrophic habitat (Figs. 1-2). The quantitative differentiation of plant assemblages in the Scots pine forest may be limited by low habitat fertility, as well as by subsequent increase in coverage by local dominants, such as *Pteridium aquilinum*, *Frangula alnus* and *Molinia coerulea*. Given the increased supply of light, these species are vigorous growers and can reach significant sizes in short time, therefore shading other small herbaceous plants, e.g. *Trientalis europaea*, causing them to disappear through competitive displacement. Hence it can be expected that the number of species may decrease over time due to the abundant expansion of the shrub layer, dominated by *Frangula alnus,* or the developing upper layers of herbaceous vegetation, e.g. *Molinia caerulea* and *Pteridium aquilinum*. Limiting the settlement of new species by local dominants can be observed in a gap in the oligotrophic habitat (Fig. 2). The phenomenon of competitive displacement may also be important (Orczewska 2009) in the case of alien and invasive species (Kurek *et al.* 2015). The recurrence of wind blowdowns in time and space in the forest environment is also of particular importance in the context of the species, whose survival is determined by disturbance (Hiura 1995; Townsend & Scarsbrook 1997). This concerns plants associated with open areas, such as: *Sanguisorba officinalis*, *Deschampsia caespitosa*, *Poa pratensis* (Table 3). Their presence confirms the effect of disturbance as the main factor influencing species richness in forests.

After completing four years of the study the similarity between the plant assemblages in gap and undisturbed vegetation plots clearly decreased and they differentiated qualitatively (Figs. 3-4). In the oak stand these differences are much greater than in the Scots pine stand. More fertile habitats (here the oak forest) provide many more opportunities for a large number of species to settle down than the poor oligotrophic habitats dominated by the Scots pine. This also applies to alien and invasive species establishment. This is one of the reasons why the invasive *Impatiens parviflora* can be found in mesotrophic habitats disturbed by windthrow, like the oak forest. However, it reaches a low coverage and frequency (Table 1) and most likely does not currently pose a threat to the native flora. Some authors report that the invasive plant species can significantly modify species composition of the native communities (Chabrerie *et. al.* 2010; Godefroid *et al.* 2005; but see Chabrerie *et al.* 2008; Halarewicz & Żołnierz 2014). And yet Hejda (2012) revealed that *I. parviflora* does not pose a real threat to the plant species richness of the forest floor. This statement complies with our results.

Natural disturbance in a forest, apart from its unquestionable positive influence on the shaping of species richness, also carries the risk of alien elements of the flora, other than *I. parviflora,* to emerge. The early stages of succession are the most prone to invasion, as resources and colonisation opportunities are enhanced after the disturbance (Catford *et al.* 2011). It is therefore quite surprising that light-seeded and anemochorous alien species such as *Solidago gigantea* and *Conyza canadensis* did not find favorable conditions for their populations to develop within the studied gaps, and their frequency and quantity hardly changed during the study period (Table 1-4).

Natural disturbances in the canopy play an important role in regulating ecosystem elements, in particular its biodiversity (Dobrowolska 2010). Our research confirms these relationships. The appearance of gaps, as a result of a natural process without any human intervention, in both types of habitats (oak and Scots pine forest) caused an increase in the number of plant species. The disturbance effect expressed particularly by the diversity of vascular plant species is much more visible in the mesotrophic than in the poor oligotrophic habitat. In both cases, however, wind blowdowns are of considerable importance for the development of vascular plant species diversity in the forest. After each disturbance occurs the number of plant species generally increases, and because of that maintaining continuity of similar natural phenomena in forests is highly desirable.

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