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Disturbed peatlands as a habitat of an invasive moss *Campylopus introflexus* in Lithuania

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Distribution of *Campylopus introflexus* in disturbed peatlands was investigated throughout Lithuania in 2010–2011. Frequency and abundance of the invasive moss species were evaluated according to the parameters of peat (pH, total nitrogen, phosphorus, potassium and organic matter), prevailing herb-layer species, percentage of cover of herb and tree layers, amount of litter, and time since the abandonment of the area. *Campylopus introflexus* was recorded in 68.7% of the investigated disturbed peatlands, of these, 63.8% had recently been managed. The cover of the invasive moss did not correlate with most parameters of peat, but it differed significantly among the plots (1) with different prevailing herb-layer species, (2) abandoned for different lengths of time, (3) with developed and undeveloped tree layer, and (4) with different pH.

Introduction

Campylopus introflexus is an immigrant bryophyte species that appeared in Europe in the 20th century. Due to its biological features — numerous small spores and abundant vegetative propagation — it is considered an aggressive invader (Söderström 1992). The species causes a problem in many grasslands and heathlands, because it can reach high densities, built dense carpets, modify habitat conditions and inhibit regeneration of the original vegetation (Equihua and Usher 1993, Biermann and Daniels 1997). It was first recorded in Great Britain in 1941. Nowadays it is widespread in central and western Europe, and shows tendency to expand towards the east (Hassel and Söderström 2005). The species is reported to be rare in most countries at the northeastern part of its present range, i.e. Latvia (Abolina and Reriha 2004), Estonia (Vellak *et al*. 2009), European part of Russia (Razgulyaeva *et al*. 2001), and Lithuania (Jukonienė 2003). Studies of the distribution of *C. introflexus* in Europe show that the species is adapted to acidic and nutrient-poor habitats with sparse vegetation cover (van der Meulen *et al*. 1987, Stieperaere and Jacques 1995, Biermann and Daniels 1997, Biermann 1999, Ketner-Oostra and Sýkora 2000, 2004, Chiarucci *et al*. 2008). Depending on the region, *C. introflexus* is distributed in various habitats: coastal sandy dunes, sandy edges of forest roads, young pine and spruce plantations, forest cuttings on sandy soils, exposed peat, etc. (Fudali *et al*. 2009). In Lithuania, three of the four records were from cutover peatlands (Jukonienė 2003), which may indicate that this

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is the most probable habitat for the invasive species in the country.

Peat industry in Lithuania was extensive in the mid-20th century with the peak in 1970s (Janukonis 1995). In 1980–1990, the peat extraction gradually decreased; however, new peat fields were prepared (deep drainage and removal of the vegetation layer) for future mining activities. Since the 1990s, due to social and economic conditions, many of such peatlands were abandoned. Nowadays peat quarries comprise about 3.5% of the area of all peatlands in Lithuania, and 21% of the quarries are abandoned (Povilaitis *et al*. 2011). Most of the disturbed and abandoned peatlands have recently been covered by secondary vegetation. In some areas, especially in managed peatlands, spontaneous vegetation was disturbed by peat companies to prevent overgrowing. Therefore, large areas of disturbed peatlands at different stages of various recovering vegetation occur in the country. Many pioneer or short-lived species take part in spontaneous regeneration of vegetation (van Tooren *et al*. 1990). Having assessed the potential suitability of peatland habitats for expansion of a non-native colonizer *C. introflexus* throughout Lithuania, in 2010 we started to study the distribution of the species. Our main task was to reveal the extent of distribution of *C. introflexus* in disturbed peatlands of Lithuania and ascertain the main factors affecting its distribution and abundance. We sought the answers to the following questions: (1) what are the main environmental characteristics of the habitats of *C. introflexus* in peatlands of Lithuania (pH, total nitrogen, potassium, phosphorus and organic matter) and are they different from those of other habitats?; (2) how does *C. introflexus* abundance change over time after disturbance of natural vegetation?; (3) what is the relationship between the cover of vascular plants (herb and tree layers) and the cover of *C. introflexus*?; (4) what are the differences in abundance of *C. introflexus* in the areas with different prevailing vascular plant species?; (5) what native bryophyte species can compete with the invasive species in cutover peatlands?

Material and methods

Distribution of *Campylopus introflexus* was checked in potential habitats, which were determined after a pilot study in 2009. Study sites with such habitats (drained peatlands with areas of open vegetation) were selected using ArcGIS maps. Field work was carried out in August–September 2010 and 2011. Thirty two peatlands were checked during the study. Half of the peatlands had recently been managed, while another half had been abandoned (Fig. 1). Detailed studies on the abundance of *C. introflexus* and its dependence on various ecological factors were performed in 15 peatlands, which ensured sufficient number of study plots at various stages and types of recovering vegetation (Table 1).

Ecology of *C. introflexus* was studied in 80 circular plots (10 m in diam.). The vegetation within those plots was classified into tree (trees > 2 m), shrub (trees < 2 m and shrubs > 0.5 m), herb (trees and shrubs < 0.5 m, dwarf shrubs and herbs) and bryophyte (including lichens) layers. Cover (%) of each layer was evaluated (cover of moss and lichens were evaluated separately) and all vascular plant and bryophyte species in the study plots were recorded. The abundance (percentage of cover) of all moss and vascular plant species as well as total bryophyte, vascular plant and lichen cover were estimated in 20 neighbouring subplots of 0.25 m^2, arranged in one randomly selected strip across the centre of the study plot. Neighbouring subplots covered scattered and patched vegetation in the study plot. A total of 1600 subplots were described.

For each study plot, we estimated a series of environmental variables: time since abandonment; prevailing herb species; total tree, shrub and herb cover; and peat parameters (pH, amounts of total nitrogen (N), potassium (K), phosphorus (P) and organic matter). Peat samples were taken from the surface layer of each habitat (up to five cm depth) at ten randomly selected sites, and a pooled sample (approx 500 g of peat) was prepared. The analyses of peat parameters were carried out at the Labtarna chemical laboratory, Vilnius. Peat pH was determined using a glass electrode in a 1:5 (volume fraction) suspension of soil in potassium chloride solution (LST ISO 10390:2005). Total nitrogen was determined using the modified Kjeldahl method (LST EN 13654-1:2002), total phosphorus with the spectrophotometric method after mineraliza-

Fig. 1. Map of Lithuania showing checked peatlands.

tion (standard operating procedure No. 5.4-145), potassium content was determined by the atomic absorption spectrometry method after dissolution (ISO 14869-2:2002), and organic matter content (OMC) by the high temperature combustion gravimetric method (LST EN 13039:2003).

Following Dierβen (2001), we separated the plots into three groups according to peat acidity: (1) extremely acidic (pH < 3.3), (2) highly acidic (pH 3.3–4) and (3) considerably acidic (pH > 4).

According to the time since the last disturbance of vegetation, all study plots were divided

Table 1. Characteristics of the peatlands, in which studies on abundance and frequency of *Campylopus introflexus* were performed.

Peatland	Lat. N	Long. E	Management of peatland	Number of study plots	Time since abandonment of plots
Aukštumalė	55°22´	21°24´	peat extraction	3	10–20
Degesynė	56°07´	25°29´	peat extraction	5	0–5, 10–20, > 20
Ežerėlis	54°52´	23°37´	peat extraction	2	0–5, > 20
Galai	55°25´	26°11´	peat extraction	3	0–5, 5–10
Laukagalis	55°22´	24°16´	abandoned	8	5–10, 10–20, > 20
Laukėsa	55°09´	22°32´	peat extraction	9	0–5, 5–10, 10–20
Lebeliai	56°16´	22°47´	peat extraction	8	0–5, 5–10, 10–20, > 20
Mūšos Tyrelis	56°11´	23°18´	peat extraction	6	> 20
Palios	54°34´	23°40´	peat extraction	8	10–20, > 20
Paraisčiai	55°32´	24°55´	peat extraction	5	5–10, 10–20
Raudonplynis	54°49´	23°29´	abandoned	2	> 20
Rėkyva	55°50´	23°16´	peat extraction	5	10–20
Sulinkiai	55°43´	23°24´	peat extraction	5	0–5, 5–10, 10–20, > 20
Šepeta	55°47´	25°02´	peat extraction	7	10–20
Tyruliai	55°50´	23°16´	abandoned	3	0–5, > 20

into four groups: (1) < 5 years, (2) 5–10 years, (3) 10–20 years, and (4) > 20 years. Time since abandonment or since the last disturbance of the vegetation was obtained by interviewing peatland owners and users.

The plots and subplots were also divided into six groups according to prevailing herb-layer species: *Calamagrostis epigeios*, *Calluna vulgaris*, *Equisetum arvense*, *Eriophorum angustifolium*, *Phragmites australis* and *Vaccinium vitis-idaea*. The plots with prevailing *Carex viridula*, *Conyza canadensis*, *Eriophorum vaginatum*, *Festuca ovina* and *Juncus effusus* were excluded from the statistical analyses due to an insufficient number of plots. The seventh group comprised subplots with sparse herb cover (< 10%) that were treated as subplots with undeveloped herb layer. Thus, in total seven groups were distinguished.

Frequency of *C. introflexus* in a study plot was a percentage of subplots in which the species was recorded.

We used the Kolmogorov-Smirnov one-sample test to assess the distribution of moss abundance and site variables. As most site parameters and *C. introflexus* cover were non-normally distributed, we used Spearman's rank-order correlation analysis to study the relationships between *C. introflexus* and site properties. To assess the effects of soil acidity, time for colonization and vascular plants on the performance of invasive moss, we compared frequencies and abundances of *C. introflexus* among the plots grouped according to their pH, time since abandonment and dominant vascular plant species using an analysis of variance (one-way ANOVA). To meet the assumptions of ANOVA, *C. introflexus* cover data were square-root transformed for the analysis to reduce their skewness and to approximate normal distribution (Underwood 1997). The sample sizes used for ANOVA exceed 1400. Multiple comparisons of *C. introflexus* cover were performed using Tukey's HSD test.

Differences in frequency of *C. introflexus* were tested with the Kruskal-Wallis one-way analysis of variance. If significant differences were found, the Mann-Whitney *U*-test was performed to determine which groups differed significantly from the others. A non-parametric procedure was used because of non-normal data distribution before and after transformations.

To evaluate whether the plots with developed and undeveloped tree layers differ in *C. introflexus* abundance (square-root-transformed) we used an independent-sample *t*-test. To assess the relationship between covers of *C. introflexus* and litter we used linear regression analysis. For the linear regression, *C. introflexus* and litter-cover data were square-root transformed. The data were analysed using the statistical software package SPSS ver. 16.0 (SPSS Inc., Chicago, IL). Differences were considered significant at $p < 0.05$.

Results

Distribution of *Campylopus introflexus* and peatland management

Campylopus introflexus was recorded in 21 peatlands (68.7% of all checked peatlands throughout the territory). It was found growing in managed (still used for peat extraction) peatlands (63.8 %) and peatlands abandoned for a long time (27.2%) (Fig. 1). Peatlands (80%) where *C. introflexus* was not recorded were abandoned for a long time.

One-way ANOVA revealed significant differences in cover and frequency of *C. introflexus* among the plots differing by time since abandonment ($F_{3,1576} = 10.579$, $p < 0.001$ and $F_{3,75} = 3.811$, $p = 0.013$, respectively). The abundance the species was the highest in the plots abandoned 5–10 years ago. The cover of *C. introflexus* in the plots that were abandoned for 5–10 years differed significantly from its cover in the plots at initial stages of colonization during the first five years since abandonment, and in the plots abandoned more than 10 years ago (Fig. 2). The frequency of the species showed, similar tendencies but significant differences were found only between the plots that had been abandoned for 5–10 years and more than 20 years (Mann-Whitney *U*-test, $p = 0.007$) (Fig. 3).

Characteristics of peat parameters

The habitats of *C. introflexus* varied from extremely acidic to considerably acidic (pH 2.5–4.9) (Table 2). The soils of most habitats were rich in organic matter and total nitrogen, while

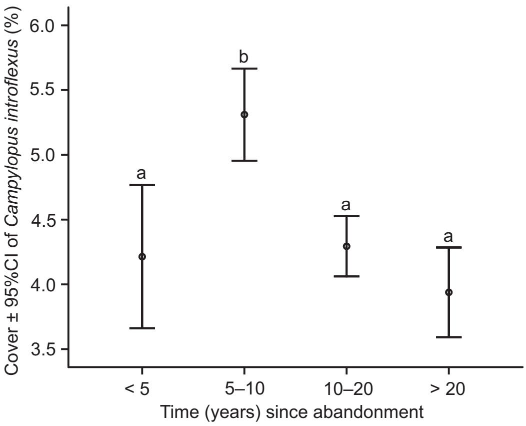

Fig. 2. Cover of *Campylopus introflexus* in the plots differing by time since abandonment. Data on cover of *C. introflexus* are square root transformed. Different letters indicate significant differences (one-way ANOVA, Tukey's HSD test).

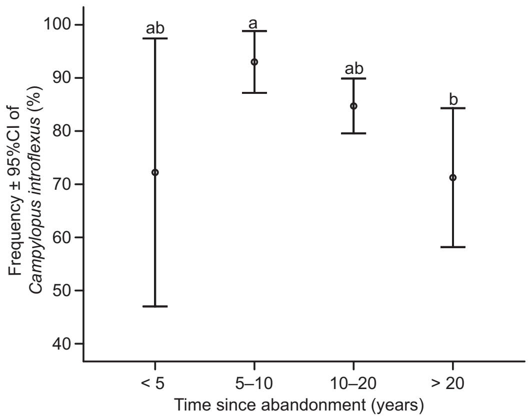

Fig. 3. Frequency of *Campylopus introflexus* in the plots differing by time since abandonment. Different letters indicate significant differences (Mann-Whitney *U*-test).

poor in phosphorus and potassium (Table 2). The organic matter content varied little: the peat in 15.2%, 54.4%, 23.8% and 6% of the study plots contained 95%–98%, 90%–95%, 80%–90%, and < 80% of organic matter, respectively. The *C. introflexus* cover did not correlate (Spearman's correlation, r_S) with the amounts of organic matter, total nitrogen and phosphorus. The correlation between the species cover and total potassium was negative but due to its extreme weakness ($r_S = -0.163$, $n = 80$, $p < 0.001$) the relation may be considered inconsequential.

The cover of *C. introflexus* was the highest in highly acidic habitats and differed significantly from that in extremely acidic and considerably acidic habitats (Fig. 4).

Campylopus introflexus and vegetation of disturbed peatlands

In the habitats of *C. introflexus*, 155 vascular plant species and 9 bryophyte species were recorded. The total number of vascular plant species ranged from 4 to 32 (mean ± SD = 13.9 ± 5.78) per plot, and from 0 to 9 (mean ± SD = 1.84 ± 1.538) per subplot. Bryophytes were less diverse: from 1 to 9 (mean ± SD = 4.03 ± 1.40) per plot, and from 0 to 4 (mean ± SD = 1.35 ± 0.749) per subplot. None of vascular plant or bryophyte species was as frequent as *C. introflexus* (Fig. 5).

The most frequent vascular plants in the habitats were *Calamagrostis epigeios Calluna vulgaris*, *Equisetum arvense* and *Betula pendula* (70%–98% present in studied peatlands). Only in some peatlands *Eriophorum angustifolium*, *E. vaginatum*, *Phragmites australis*, *Molinia caerulea*, *Festuca ovina* and *Vaccinium vitis-idaea* were quite frequent.

Only about 10 species were dominant in the herb layer. The cover of *C. introflexus* was significantly different in the plots with different prevailing herb-layer species (one-way ANOVA, $F_{6,1429} = 36.752$, $p < 0.001$) (Fig. 6). It was the

Table 2. Characteristics of peat in the studied habitats; DOM = dry organic matter.

Parameters	*n*	Min	Max	Mean	SD
N (mg kg^{-1})	80	5593.00	27035.00	15682.78	4435.58
P (mg kg^{-1})	80	50.00	945.09	351.20	196.52
K (mg kg)	80	75.00	1146.00	271.90	203.20
DOM (%)	80	44.49	98.23	90.08	8.543
pH	80	2.50	4.90	3.61	0.56

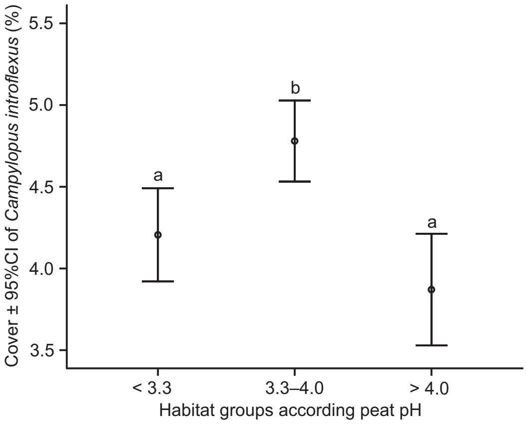

Fig. 4. Cover of *Campylopus introflexus* in the habitats of different peat acidity: extremely acidic (pH < 3.3), highly acidic (pH 3.3–4.0) and considerably acidic (pH > 4.0) (grouped after Dierβen 2001). Different letters indicate significant differences (one-way ANOVA: $F_{2,1577} = 9.813$, $p < 0.001$ and Tukey's HSD test; *C. introflexus* cover square-root transformed).

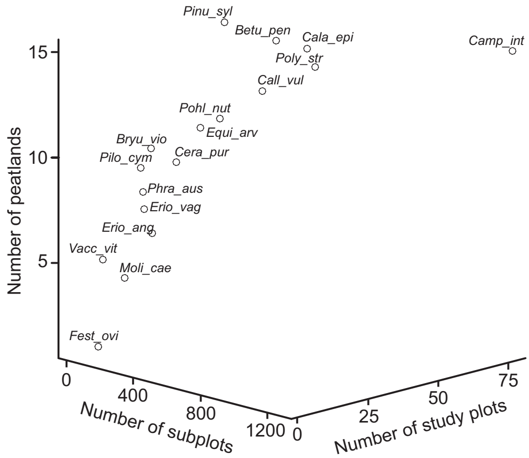

Fig. 5. Distribution of the most frequent plant species in the studied plots. Abbreviations of species names are underlined: *Campylopus introflexus*, *Calamagrostis epigejos*, *Polytrichum strictum*, *Equisetum arvense*, *Betula pendula*, *Calluna vulgaris*, *Pinus sylvestris*, *Pohlia nutans*, *Pilosella cymosa*, *Bryum violaceum*, *Rumex acetosella*, *Phragmites australis*, *Eriophorum vaginatum*, *Eriophorum angustifolium*, *Festuca ovina*, *Vaccinium vitis-idaea*.

highest in the *Phragmites australis* stands, high in the plots dominated by *Calamagrostis epigeios*, and the lowest in the plots dominated by *Calluna vulgaris* and *Vaccinium vitis-idaea*.

Frequency of *C. introflexus* was significantly different in the plots with different prevailing herb-layer species as well (Kruskal-Wallis test, ($\chi^2 = 17.307$, df = 6, $p = 0.008$) (Fig. 7). It was the lowest in *Calluna vulgaris* and *Vaccinium vitis-idaea* stands and it differed significantly from frequencies of the species in the study plots where *Phragmites australis* and *Calamagrostis epigeios* dominated (Mann-Whitney *U*-test: $p < 0.05$).

In 34% of all subplots, the only bryophyte species was *C. introflexus*. *Polytrichum strictum* was recorded in 87% of all peatlands, in 77% of all study plots and 25% of subplots, and *Pohlia nutans* in 73%, 48% and 14%, respectively. Lichens were recorded in 40% of all subplots. Even though the correlations between the cover of *C. introflexus* and the covers of *Polytrichum strictum* and lichens existed, due to their extreme weakness (($r_S = -0.115$, $p < 0.001$, and $r_S = -0.146$, $p < 0.001$, respectively) they were of no consequence.

About 30% of all plots were without developed tree layer. The cover of *C. introflexus* was significantly lower in the plots with the developed tree layer as compared with that in the plots without trees (*t*-test: $t = 3.425$, df = 1580, $p = 0.001$). Linear regression revealed that only about 25% of the variation in the cover of *C. introflexus* could be explained by litter cover (*see* Fig. 8).

Discussion

Increased distribution of *Campylopus introflexus* and peatland management

Our study shows that disturbed peatlands providing suitable habitats for *C. introflexus*. As compared with the data gathered ten years ago (Jukonienė 2003), the number of records nowadays is six times higher (4 and 23 localities, respectively). Similar tendency is observed in other countries of Europe, e.g. in Great Britain the number of records has doubled between the years 1991 and 2008 (Hill *et al*. 2009). In Poland, the first specimens of *C. introflexus* were collected in 1986, recently the species has been reported from 67 localities (Fudali *et al*. 2009). It is uncertain, whether such increase in the number of localities in Lithuania is due to a rapid spread

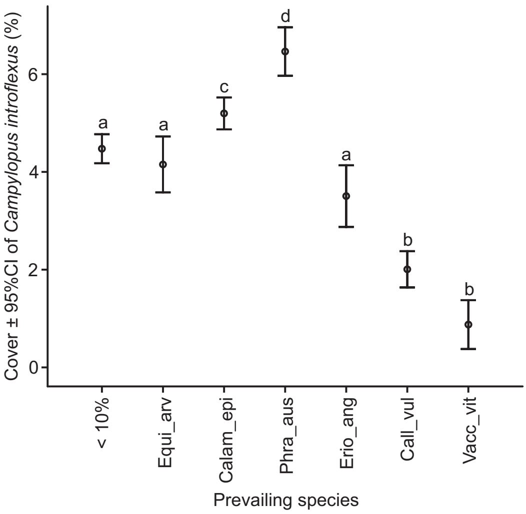

Fig. 6. Cover of *Campylopus introflexus* in the plots with different prevailing plant species. Data on cover of *C. introflexus* are square-root transformed. Different letters indicate significant differences (one-way ANOVA, Tukey's HSD test).

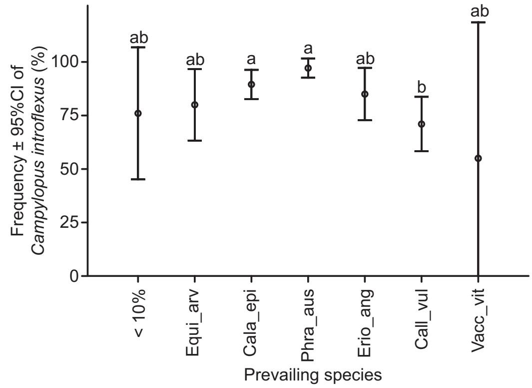

Fig. 7. Frequency of *Campylopus introflexus* in the plots with different prevailing plant species. Different letters indicate significant differences (Mann-Whitney *U*-test).

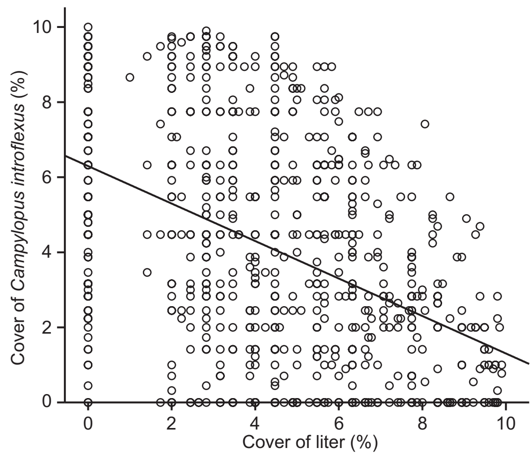

Fig. 8. Linear regression ($y = -0.499x + 6.296$, $r^2 = 0.242$, $n = 660$, $p < 0.001$) between cover of litter and cover of *Campylopus introflexus* (both data are square-root transformed).

of the species after a lag phase or due to the lack of information on its earlier distribution. An increase in suitable habitats is one of the factors determining lag time (Crooks and Soulé 1999, Lockwood *et al*. 2007). About 90% of recent records of the species are in cutover peatlands. It is obvious that large-scale peatland abandonment during 1990–2000 created suitable habitats for *C. introflexus*. This moss can colonize drier places in natural bogs (Hallingbäck *et al*. 1985, Fudali *et al*. 2009), meanwhile cutover peatlands provide larger areas for the establishment of the species. Certain population size is necessary for a rapid spread of an invasive species (Hobbs and Humphries 1995).

The fact that most of the peatlands, in which we observed *C. introflexus*, had recently been managed and that the species was most abundant and frequent in the plots that were abandoned 5–10 years ago, supports the hypothesis that disturbances are necessary for population renewal. Abandoned fields within managed peatlands are often at the stage of preparation for the future use. Tree cutting or removal of the vegetation from managed peatlands promotes vegetative fragmentation of the species and its further dispersal and expansion. Simultaneously, the disturbance of the natural vegetation creates open gaps suitable for establishment of the species. As it was found by several authors (Pakeman *et al*. 1997, Piessens *et al*. 2008), activities that result in creating open gaps within existing vegetation, e.g. increased grazing, also increased cover of *C. introflexus* in heathland and moorlands as well as on coastal dunes.

Impact of peat parameters on distribution of *Campylopus introflexus*

Besides large-scale disturbances, cutover peatlands provide suitable habitat conditions for *C. introflexus* — acid and nutrient-poor soils. Relatively acidic soils (pH 4–6) are indicated as optimal environment for the species in Europe (Ketner-Oostra and Sýkora 2000, Dierβen 2001, Farrell and Doyle 2003, Sparrius and Kooijman 2011). We found the species to be most abundant in cutover peatlands in Lithuania on peat with acidity $3 < \text{pH} < 4$. Similar pH range was found in the habitats of *C. introflexus* on coastal dunes by Isermann (2005). On peat with $\text{pH} > 4$, the cover of *C. introflexus* was lower as compared with that in highly acidic habitats. Our results regarding the species tolerating extremely acidic condition ($\text{pH} < 3$) agrees with the findings of Chiarucci *et al.* (2008) who recorded the species in geothermal fields of Italy. Considering that the species also grows on fen peat with pH 6.5–7.0 (Equihua and Usher 1993), it seems likely that being adapted to wide range of pH, the species finds optimal conditions in many habitats.

In most of the studied plots, the amounts of soil organic matter were generally high. Differences that were found probably result from the level of peat degradation and the depth of peat excavation. Investigations in dune sands show that increased organic matter content leads to a more favourable growth conditions for the species (Sparrius and Kooijman 2011). Anyway, the lowest amounts of organic matter in habitats studied by us were significantly higher than those in sands (van der Meulen *et al.* 1987, Isermann 2005, Hasse 2007) and recorded variation — from 40% to 98% — had no effect on *C. introflexus* abundance.

Variation in total nitrogen content in the habitats of *C. introflexus* was quite wide: from low amounts that are characteristic of dried ombrotrophic bogs (0.5%) to quite high amounts (2.7%). As in case of organic matter, it might be a result of peat degradation process and uneven depth of peat excavation (Vaičys 2001). Despite the investigations carried out by many authors (Helsper *et al.* 1983, Ketner-Oostra and van der Loo 1998, Rochefort *et al.* 2003, Pilkington *et al.* 2007, Sparrius and Kooijman 2011), which show increased cover of mosses in response to nitrogen addition, we did not find any differences in abundance of the species within recorded amounts of nitrogen.

Harvested peatlands are often phosphate-limited (Rochefort *et al.* 2003). We found low amounts of total phosphorus in the habitats of *C. introflexus* as well: maximum values not exceeding 0.09% (mean 0.03%). It is not surprising that such low amounts had no effect on the abundance of the invasive moss species, though Pilkington *et al.* (2007) indicated increasing cover of *C. introflexus* with additional supply of phosphorus. Contrary to other elements, the amounts of total potassium in the studied habitats of *C. introflexus* were relatively high (maximum 0.1%) for a bog peat (Vaičys 2001). Although we found a significant relationship between potassium content and abundance of *C. introflexus*, it was so weak that practically this element had no effect on the species abundance. Based on the results that indicate the moss to be frequent in peatlands disturbed by fire (Richards 1963, Richards and Smith 1975), we expected to find positive correlation between abundance of *C. introflexus* and the amount of potassium; however, there was none.

The characteristics of peat in the habitats of *C. introflexus* repeatedly indicate preference of the species for very poor peat (Renou-Wilson *et al.* 2008). Low pH and high amounts of organic matter are usually characteristic of top surfaces of the bogs. Most of our study plots were not deeply excavated, only with the removed surface layer. Variations in peat parameters within the limits recorded in the studied habitats had practically no effect on *C. introflexus* abundance.

Campylopus introflexus and vegetation of disturbed peatlands

Cutover peatlands are essentially changed habitats, in which re-establishment of typical peatland vegetation on deeply-drained sites never occurs as a dry peat surface may be a hostile environment to vegetation and thus hamper succession (Tuittila *et al.* 2000, Poulin *et al.* 2005, Herbichowa *et al.* 2009, Orru and Ramst 2009). We recorded more than 150 vascular plant species in the habitats of *C. introflexus*, however the vegetation in most study plots and subplots was quite sparse and consisted only of a few species. Many studies found easily-dispersed, ruderal species reaching this harsh environment, but they do not become dominant and disappear within a few years (Grime *et al*. 1988, Kucerová *et al*. 2008, Bastl *et al*. 2009). Dominant in the habitats of *C. introflexus* were either wetland plants (*Eriophorum angustifolium*, *E. vaginatum*, *Phragmites australis*) or species favouring dry habitats with low amounts of nutrients (*Calamagrostis epigejos*, *Calluna vulgaris*, *Equisetum arvense*, *Festuca ovina* and *Vaccinium vitis-idaea*). *Campylopus introflexus* usually is an initial colonizer of bare peat especially created by multiple cuttings (Cooper *et al*. 2001). As investigations of sand-dune habitats show, carpets of the invasive moss can hinder germination of other plants and cryptogams (Biermann and Daniels 2001), wide carpets of the species limit space for settlement of some native plant species (Ketner-Oostra and Sýkora 2004, 2009, Hasse 2005, 2007).

We found that abundance of *C. introflexus* is differently affected by prevailing herb species. It is obvious that invasive moss species (both by its abundance and frequency) benefit from open ground and tall vegetation, e.g. *Phragmites australis*, *Calamagrostis epigeios*, *Equisetum arvense*. Usually a negative effect of *C. introflexus* carpets on regeneration of *Calluna vulgaris* has been indicated (Equihua and Usher 1993). We found *C. introflexus* to be significantly less abundant and less frequent in the stands of *Calluna*. Low, compact cover of *Calluna vulgaris* and *Vaccinium* spp. may hinder the establishment of *C. introflexus* directly due to shortage of space or by creating insufficient light conditions. *Campylopus introflexus* is characterized as photophytic species growing in full light (Dierβen 2001). We found that in the plots dominated by other low-growing, but summer-green species, *Eriophorum angustifolium*, abundance of *C. introflexus* species was significantly higher, although no differences in frequency were found.

We ascertained that abundance of *C. introflexus* was lower in afforested plots than in those without trees. This could be related to changes in light conditions or to increased cover of litter, the main part of which was made up of birch leaves. In our study however, the increase in litter cover explained only 25% of the decrease of the cover of *C. introflexus*.

Our study shows that *C. introflexus* being the dominant species in the moss layer was also competing with other bryophyte species. The most frequent bryophyte species was *Polytrichum strictum* that usually occurs in mire habitats, the others were typical colonists occurring in ruderal habitats. Most of other bryophyte species were not abundant but all species were quite frequent. Only *Polytrichum strictum* — most frequent, quite abundant, of similar size to *C. introflexus*, and whose cover in some areas reached over 50% — was most probably competing with *C. introflexus*. Unlike *C. introflexus* whose early vegetative reproduction allows for rapid colonization, *Polytrichum strictum* due to slow, but constant vegetative reproduction and long-lived individuals establishes itself slowly (Li and Vitt 1995). So, both species can occupy large areas by forming monotonous vegetation. Distribution of *C. introflexus* in the areas, which overlap with *Polytrichum strictum*, is restricted due to shortage of open areas. A moss of the same genus, *Polytrichum piliferum*, is the main competitor of *C. introflexus* in sand communities (Hasse 2007). As in sand communities, in cutover peatlands *C. introflexus* competes with lichens. According to Grime (1979), lichens are intolerant of frequent disturbances, but they can occupy primarily disturbed habitats not leaving space for *C. introflexus*. When *C. introflexus* lost vitality, it was frequently used as a substrate by lichens as was also observed in sand communities (Ketner-Oostra and Sýkora 2004) and in case of *Polytrichum strictum*.

The expansion of *C. introflexus* in disturbed peatlands appears to be affected by various vegetation types. Already during establishment, the moss competes for space with lichen and native bryophyte (especially *Polytrichum strictum*) species. However, with the increasing cover of herb layer, the cover of *C. introflexus* has a tendency to decrease, its abundance is differently affected by prevailing vascular plant species. Usually the studied moss forms wider carpets in tall vegetation stands as compared with that at sites where low-growing plants prevail.

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