Invasion of central-European habitats by the moss *Campylopus introflexus*

Invaze mechu *Campylopus introflexus* v biotopech střední Evropy

Eva M i k u l á š k o v á[1,2], Zuzana F a j m o n o v á[1,3] & Michal H á j e k[1,3]

[1]*Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, CZ-61137 Brno, Czech Republic, e-mail: evamikul@gmail.com;* [2]*Department of Botany, Faculty of Science, Charles University, Benátská 2, CZ-128 01 Prague, Czech Republic;* [3]*Department of Vegetation Ecology, Institute of Botany, Academy of Sciences of the Czech Republic, Lidická 25/27, CZ-657 20 Brno, Czech Republic*

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Although invasions by vascular plants are frequently studied, little is known about invasive bryophytes. *Campylopus introflexus* is an invasive moss endangering natural vegetation in western Europe and currently extending its secondary area eastwards. Therefore, we studied its ecology in the Czech Republic (central Europe). We updated its distribution, described colonized habitats in term of the composition of the vegetation, investigated substrate and water demands and which habitats in the Czech Republic are potentially at risk of invasion by *C. introflexus*. The first dataset contained 78 vegetation plots with *C. introflexus* from across the whole of the area investigated and included all the habitats colonized. The second dataset contained results of previous studies of the vegetation of pine forests both with and without *C. introflexus* and was used to determine the fine scale features of its habitat preferences within this habitat. Records of the vegetation plots in both datasets were numerically classified. We further calculated the similarity of the species composition of vegetation plots with *C. introflexus* with that of 26,998 vegetation plots without *C. introflexus* that were stored in a large database in order to predict the habitats that were likely to be colonized. Ecological demands were characterized by in situ research (soil samples from 52 vegetation plots) and ecological interpretation of the pine forest dataset. Further, a cultivation experiment was established with populations from 20 of the sites studied in order to test the ability of *C. introflexus* to grow in different soil and moisture conditions, and the data were evaluated by linear mixed effect models. We found that *C. introflexus* invades dry, nutrient poor acidic soils in a range of vegetation types, and is most common in coniferous forest plantations and drained bogs, where it colonizes open patches resulting from anthropogenic disturbance where there is little competition from other plants. The vegetation plots from the database that were similar in species composition to those with *C. introflexus* are mainly forest habitats broadly distributed in the Czech Republic. Cultivation experiments showed that this species does badly when growing in lime-rich or waterlogged soils. We conclude that the species has the potential to be common in central Europe because of the wide range of habitats with favourable vegetation compositions and ecological parameters. However, it presently represents no risk for endangered plant species and communities.

K e y w o r d s: *Campylopus introflexus*, central Europe, cultivation, invasive species, plant communities, threat

Introduction

Plant invasions are seen as a major threat to ecosystem diversity (Simberloff & Rejmánek 2011). Numerous studies report the effect of invasive species on native species and community structure and identify invasion-threatened habitats (e.g. Williamson 1996, Chytrý et al. 2009, Hejda et al. 2009). They indicate that invasive species can dramatically change current species composition or affect the natural succession of plant communities. A plant species may be invasive either because it shares habitats with resident native species and outcompetes them or because it colonizes habitats different from those of native species and thus occupies vacant niches (Sakai et al. 2001). Spread of invasive species after establishment is affected by their ability to colonize new habitats and/or outcompete native species. These factors are thus important when evaluating the threat to the native flora.

Habitat filters are important in plant invasions (Carranza et al. 2011, Pinke et al. 2011). Conditions under which a species invades may differ from those under which it usually occurs in its native area. In an invaded area, the range of occupied habitats increases with time after initial colonization, depending on an invader's ability to establish in new communities (Sakai et al. 2001). This may lead to a higher threat to native habitats from an invader and contribute to its successful naturalization. The broad-scale analyses of functional plant traits, habitat characteristics and vegetation composition can be used as a good predictor of the future spread of an invader (Pyšek & Richardson 2007, Chytrý et al. 2008, Moravcová et al. 2010).

Although there are a large number of studies that explain and predict plant invasions, most of them concern vascular plants. Ecological studies on invasions of non-flowering plants, such as bryophytes, are rather rare. Compared to the percentage of vascular plants that are alien (~ 36% of European flora is classified as alien either in Europe as a whole or at least in some European country; Lambdon et al. 2008, Winter et al. 2011), alien species of bryophytes make up a minor part (~ 2%) of the European bryoflora (DAISIE 2009). Bryophytes have small spores, which are dispersed over great distances even across continents. Consequently, direct classification as "alien species" is sometimes problematic when based only on a disjunct occurrence. Therefore, the classification is often based on indirect evidence as e.g. biogeography, genetics and history of records. There are 45 bryophyte species that are considered to be alien at least in some parts of Europe, including 13 cryptogenic species with an unclear history of occurrence in Europe (Söderström 1992, Essl & Lambdon 2009, Essl et al. 2011). Only five alien and three cryptogenic species have invaded more than five countries. The native range of these species is mainly in the Southern Hemisphere, but a few species (e.g. *Lunularia cruciata*) are native in some region of Europe and invade other European countries. The majority of the alien bryophytes have colonized regions with oceanic climates. Only two neophytes, *Campylopus introflexus* and *Orthodontium lineare*, occur widely throughout Europe.

The native range of *Campylopus introflexus* is in the Southern Hemisphere (South America, southern part of Africa and Australia, New Zealand; Frahm 1984). The first finding in Europe was recorded in 1941 in Great Britain (Richards 1963) and later in 1954 in French Bretagne (Størmer 1958). It is also possible that the moss may have invaded Europe from several points independently (Richards 1963). It was probably introduced either on shoes of travellers or in boxes of articles covered with moss carried by ships sailing from the Southern Hemisphere. Then it spread eastward and currently occurs in 21 countries (Hassel & Söderström 2005, Essl & Lambdon 2009).

Since the 1980s the ecological aspects of the *Campylopus introflexus* invasion of diverse habitats and its competitive potential have been investigated (e.g. Berg 1985). In contrast to most alien bryophytes colonizing predominantly human-disturbed habitats (gardens, roadsides, walls), *C. introflexus* has become naturalized in near natural vegetation, such as coastal dunes, bogs and pine forests (Essl & Lambdon 2009). *Campylopus introflexus* forms dense compact cushions which could negatively affect the germination of spores and seeds of other species (Equihua & Usher 1993). Invaded native communities could change into communities with only a few mosses or lichens, with a strong dominance of *C. introflexus*. This species characteristically forms extremely dense turfs extending over hundreds of square meters in sandy areas of the Netherlands, in which almost no other bryophyte or lichen species can survive (van der Meulen et al. 1987, Biermann & Daniëls 1997, Ketner-Oostra & Sýkora 2000, 2004, Sparrius & Kooijman 2011). The changes in the composition of the vegetation negatively affect other groups of organisms, e.g. carabid beetles and spiders (Schirmel et al. 2011).

Disturbance seems to be an important factor facilitating invasion by *C. introflexus*. However, the present knowledge about this species colonization dynamics is mainly for western-European dry sandy grassland vegetation. Biermann & Daniëls (1997) record rapid increase of *C. introflexus* cover after formation of gaps in the vascular-plant or lichen canopy. *Campylopus introflexus* appears in the initial successional phases (e.g. Hasse & Daniëls 2006). Frequent observations indicate that *C. introflexus* inhibits the colonization of native species (Biermann & Daniëls 1995, 1997).

Campylopus introflexus was reported first from the Czech Republic in 1988 from southern Bohemia (Novotný 1990). In the following years, the number of new localities increased exponentially and currently more than 80 localities are recorded. The rapid increase in localities after 1998 is attributed to both a faster rate of spread after the moss population became fertile and a greater attention given to this species by bryologists (Soldán 1996, 1997, Mikulášková 2006).

Although *C. introflexus* is listed among representative invasive species in Europe (DAISIE 2009) the knowledge of its ecology is sketchy. All research is for those parts of Europe with oceanic climates (e.g. Hasse & Daniëls 2006, Sparrius & Kooijman 2011). Although it is known that *C. introflexus* colonizes wide spectrum of habitats, most studies have been on sandy dunes and grasslands dominated by *Cladonia* lichens and *Corynephorus canescens*. Hasse (2007) indicates that the plant invader concepts for vascular plants are only partially applicable to *C. introflexus*. In central Europe, which was colonized rather recently, there is only information on its geographical distribution. Nevertheless, the mechanisms that influence its spatial pattern could reflect regionally specific environmental conditions, which are different in oceanic and inland parts of Europe. It is therefore worth investigating the possible influence of this species on and threat to native communities in inland Europe. The Czech Republic is a good example of a central-European region recently colonized and where currently there is a sufficient number of populations of *C. introflexus*.

Aims of this study are (i) to update the distribution of *C. introflexus* in the Czech Republic; (ii) to describe habitats colonized by *C. introflexus* in terms of the composition of the vegetation; (iii) to characterize the light, substrate and water demands of *C. introflexus*; (iv) to investigate which habitats in the Czech Republic are potentially at risk of being invaded by *C. introflexus*.

Methods

Sampling of vegetation and environmental data

Distribution of *Campylopus introflexus* in the Czech Republic was updated on the basis of our own records, review of the literature, revisions of herbarium specimens and verbal information from other bryologists. Hence, the occurrence of this species was recorded independently by many specialists, whose total area of interest covers almost the entire area of the country. Each locality was georeferenced. Size (total area covered by all moss cushions in sampled vegetation) and fertility (fertile/sterile, i.e. occurrence of sporo-phytes) of *C. introflexus* populations as well as type of habitat were recorded.

In order to describe the vegetation and environmental conditions of habitats colonized by *C. introflexus*, two datasets were used. **Dataset A** (Appendix 1) consisted of 78 plots of vegetation of 1 m^2 area sampled in different types of vegetation in which *C. introflexus* occurred across the entire area of the Czech Republic. The plots were situated where the major concentrations of cushions of *C. introflexus* occurred at each locality. Selection of localities within the whole study area reflected the actual general knowledge about the dis-tribution of the species. The aim of the sampling was to include all the habitats colonized by *C. introflexus* in this country. In each plot, all species of vascular plants, bryophytes and lichens were recorded and their percentage cover estimated. Population size of *C. intro-flexus* in each type of vegetation sampled and its fertility status were recorded.

Ecological characteristics that were investigated in the plots were those known to deter-mine the occurrence of terrestrial bryophytes. The most important abiotic factors are sub-strate properties (e.g. type of litter, soil characteristics), water and light availability, and temperature. The following variables were recorded in each plot in situ: total percentage cover within vegetation layers, slope inclination, aspect and needle to broadleaf litter ratio. In 52 plots, soil samples were taken from under moss tufts to a depth of 3 cm and the fol-lowing parameters were determined: ratio of organic to mineral components by loss-of-ignition treatment, pH, and concentrations of NH_4, NO_3 and PO_4 ions. The soil samples were mixed and air-dried. For determination of ratio of organic to mineral components, the samples were annealed at 300° C for 2 hours, 400° C for 1 h, 500° C for 3 h and 800° C, cooled and then weighed. Relation between organic and mineral components was calcu-lated from difference in the weight of the soil before and after burning off the organic mat-ter. Measurement of pH(H_2O) was performed in a soil suspension of soil:demineralized water of 1:5. With the help of a mechanical shaker soil suspension was intensively stirred for 5 minutes. After standing for 4 hours the pH was measured using a pH glass electrode. The ions were determined spectrophotometrically using a flow analyzer FIA-Star (Tecator, Sweden). Further, the ability of soil to retain water was determined using metal tubes with a volume of 100 cm^3. The tubes were filled with the soil collected from under cushions of *C. introflexus*, then left to become saturated with distilled water over a period of 5–6 days, dried at 120° C for 6 days and finally at 90° C for 1 day. The tubes were weighed after saturating with water (W) and after drying (D). The ability of soil to retain water (V_{max}) was calculated as a percentage by weight $V_{max} = 100 \cdot (W - D) / D$. Five types of soil were distinguished on the basis of this calculation: < 5% very weakly water retain-ing soil, 5–10% weakly water retaining soil, 10–30% medium water retaining soil, 30–50% strongly water retaining soil, > 50% very strongly water retaining soil.

Dataset B contained results for 68 vegetation plots sampled in pine forests (alliance *Dicrano-Pinion*) in the region of Plzeň (western Bohemia). The sampled forests were 3.5–9.0 km from the city of Plzeň (Pecháčková & Peksa 2010) and included all the different kinds of pine forest in the area. Thirteen of these plots contained *C. introflexus*. The plot size was 15 × 15 m. The cover of all species of vascular plants, bryophytes and lichens was recorded using the nine-grade ordinal Braun-Blanquet scale (Westhoff & van der Maarel 1978).

The habitats in the Czech Republic that are at risk of invasion by *C. introflexus* were investigated using **dataset C,** which includes the results for vegetation plots in the Czech National Phytosociological Database (Chytrý & Rafajová 2003). All plots assigned to syntaxa at least at the level of class and with the ground layer recorded were selected. The geographical distribution of these plots was uneven because some regions as well as some habitats were investigated more intensively than others (Chytrý & Rafajová 2003), which may lead to overestimates of geographical over ecological variation. Geographical stratification of the dataset was therefore performed to obtain a geographically balanced distribution of habitats. Only one plot from each vegetation unit was selected from a grid cell of 1.25' longitude and 0.75' latitude (approximately 1.5 × 1.4 km). Recently recorded plots were preferred over older records. The stratified dataset C contained records for 26,998 vegetation plots.

Besides field studies, a cultivation experiment was established during summer 2005 in order to test the ability of *C. introflexus* to grow in different soil and moisture conditions. A total of 20 populations sampled at different localities were cultivated. Small moss cushions (10 gametophores) from each population were cultivated in standard laboratory conditions (12-h light-dark cycle; constant room temperature 18°C, 60% moisture) for one year in rounded ceramic pots (9 cm in diameter). The number of living gametophores was counted at the end of the experiment.

Different soil conditions were simulated using seven different types of substrate: sand (organic components max 1%), commercial substrate (Peaty-soil substrate for plants, seedlings and others; Jiránek company, Bečice n. Jizerou, reg. no. 0427/2000, organic components min 25%, components above 20 mm in size up to 5%, moisture up to 65%), sandy soil (mixture of sand and commercial substrate 1:1, organic components min 10%), peaty soil (mixture of peat and commercial substrate 1:1, organic components min 50%), peat (Garden peat without additives; Jiránek company, Bečice n. Jizerou, reg. no. 0738/2000, organic components min 70%, components above 10 mm in size up to 5%, moisture 45–65%), spruce litter and commercial substrate enriched with crushed limestone. The effect of different soil moisture levels on growth of *C. introflexus* was tested independently of the experiment with different soil substrates. Plants were cultivated using the commercial substrate and three levels of watering: permanently wet (watered twice a week), medium-wet (watered once a week) and dry (watered once every three weeks).

Data analyses

All vegetation datasets were imported into software JUICE (Tichý 2002). Different species abundance scales were transformed into percentages. Records for plants not determined at the species level were deleted. Seedlings of trees and shrubs in the herbaceous layer were also deleted because they were not recorded in all plots. Multiple records of

species in different layers were combined so that all species appeared in a dataset only once. Records of critical taxa in the sense of determination were combined. This was the case for *Betula* spec. div., *Empetrum nigrum* agg. (*E. nigrum*, *E. hermaphroditum*), *Molinia caerulea* agg. (*M. caerulea*, *M. arundinacea*), *Vaccinium oxycoccos* agg. (*V. oxycoccos*, *V. microcarpum*), *Sphagnum recurvum* agg. (*S. angustifolium, S. fallax, S. flexuosum*), and *Hypnum cupressiforme* s.l. (*H. cupressiforme*, *H. jutlandicum*). Nomenclature of taxa follows Danihelka et al. (2012) for vascular plants, Kučera et al. (2012) for bryophytes and Vězda & Liška (1999) for lichens.

Vegetation plots in datasets A and B were classified separately into plant communities on the basis of species composition. In both cases, the TWINSPAN algorithm (Hill 1979) with modified stopping rules according to cluster heterogeneity (Roleček et al. 2009) was used, with pseudo-species cut levels set at 0, 5, and 25% of species cover and Whittaker's beta diversity as a dissimilarity measure for assessing cluster heterogeneity. *Campylopus introflexus* was deleted from the datasets prior to the analyses. The plant communities were described with the help of diagnostic, constant and dominant species. Diagnostic species were those with a high fidelity to a given community using the phi coefficient as the fidelity measure (Chytrý et al. 2002). For the calculation of the phi coefficient, numbers of plots in the communities were standardized (Tichý & Chytrý 2006). The species with a phi ≥ 0.2 were considered diagnostic. Constant species were defined as those with a frequency of occurrence in a given community ≥ 50% and dominant species as those occurring with a cover ≥ 25% in at least 10% of the plots of a given community.

Variability of the vegetation with *C. introflexus* and its relationships to environmental variables was determined using 52 samples from dataset A with all soil parameters determined by detrended correspondence analysis (DCA), using CANOCO 4.5 package (ter Braak & Šmilauer 2002). The percentage frequency of species was log-transformed and rare species were down weighted.

Pine forest plant communities (dataset B) were ecologically interpreted by means of Ellenberg indicator values (EIV) (Ellenberg et al. 1992). Ellenberg indicator values were determined for species of central-European vascular plants. Based on field observations they reflect ecological behaviour of particular species with respect to light, moisture, nutrients, soil reaction, temperature and continentality. Unweighted averages of EIV were calculated for each vegetation plot in program JUICE.

As different growth abilities and responses to substrate and/or watering level might have been expected for individual moss populations, the cultivation experiment was analysed using linear mixed effects models, following the protocol of Zuur et al. (2009: 90–92), with population included as a random factor to account for various population means, slopes and/or variances. First, several models with the most complex fixed effect part (experiment treatment factor) and different random effects were built: (0) linear model without random effects, (1) model with random intercept (allowing for different means of gametophores per population – localities), (2) model with random intercept and random slope (allowing for different means and response rates per population), (3) model with allowance for different variances within watering/soil groups, (4) model with random intercept and allowance for different variances within watering/soil groups, (5) model with random intercept and random slope and allowance for different variances within watering/soil groups. The parameters of random effects were estimated by REML (restricted maximum likelihood approach) and the combination of random effects resulting

in the lowest model AIC (Akaike's information criterion) was selected. Afterwards, the fixed part of the models was simplified following data exploration: several new models were built with the treatment levels with the most similar growth abilities grouped together, while the random effects were kept the same (those selected in the previous step). The models were fitted using ML (maximum likelihood) during the fixed part simplification, and model AICs were calculated and compared. The most parsimonious model was refitted using REML and considered to be the final model. The R program, version 2.12.0 (R Development Core Team 2010) and the 'nlme' library (Pinheiro et al. 2011) were used for constructing and testing the mixed effects models.

Invasibility of habitats in the Czech Republic by *C. introflexus* was assessed by calculating the similarity in species composition of vegetation plots in all the habitats in the Czech Republic (dataset C) and six groups of plots in which *C. introflexus* was recorded that represent the invaded habitats in the area. From them, four groups were identified based on the classification of plots of dataset A, one group was composed of 13 plots from pine forests in dataset B, and one group of 16 plots from drained peatbog vegetation in which *C. introflexus* occurred (Konvalinková 2010). All records of lichens were deleted for this analysis because they were recorded only in some of the plots in dataset C. The similarity was calculated using the frequency index in the function Matching in program JUICE. The frequency index (FQI) is defined as the sum of frequencies of species i (FQ_i) in plots of a given vegetation unit (group of plots) divided by sum of frequencies over all species in that vegetation unit. Species present in the assessed plot are indicated as i–R and species present in the vegetation unit as i–C (Tichý 2005). Vegetation plots with a similarity ≥ 40% with any of the groups were considered as similar in their species composition to the vegetation where *C. introflexus* occurs and therefore potentially at risk of being invaded. The similar plots were grouped into phytosociological classes based on their original assignment and the groups characterized by species with a frequency of occurrence ≥ 50%. Finally, we created a map of potentially suitable habitats in which we mapped both the locations of the records of vegetation plots that appeared to be similar to those already invaded and the distribution of habitats that correspond to corresponding phytosociological units. The distribution of particular habitats was obtained manually from the Habitat catalogue of the Czech Republic (Chytrý et al. 2010). Nomenclature of the sytaxonomical units follows that of Moravec et al. (1995) and Moravec (1998, 2000, 2002).

Results

Distribution of Campylopus introflexus in the Czech Republic

Campylopus introflexus has been recorded in the entire area of the Czech Republic; more than 100 herbarium specimens and published as well as unpublished records have been collected to date (Fig. 1). The centre of its distribution is in western and southern Bohemia (western part of the Czech Republic), only 12 localities have been recorded in Moravia (eastern part of the Czech Republic). Its distribution is concentrated in area of temperate deciduous forests, ranging from hilly country to montane belt (208–1140 a.s.l.). Most populations in the Czech Republic are sterile, but reports of the occurrence of sporophytes have recently increased (about 30 fertile populations in 2011). Vegetative propagation by deciduous stem apices is common. Size of populations varies from few plants to cushions
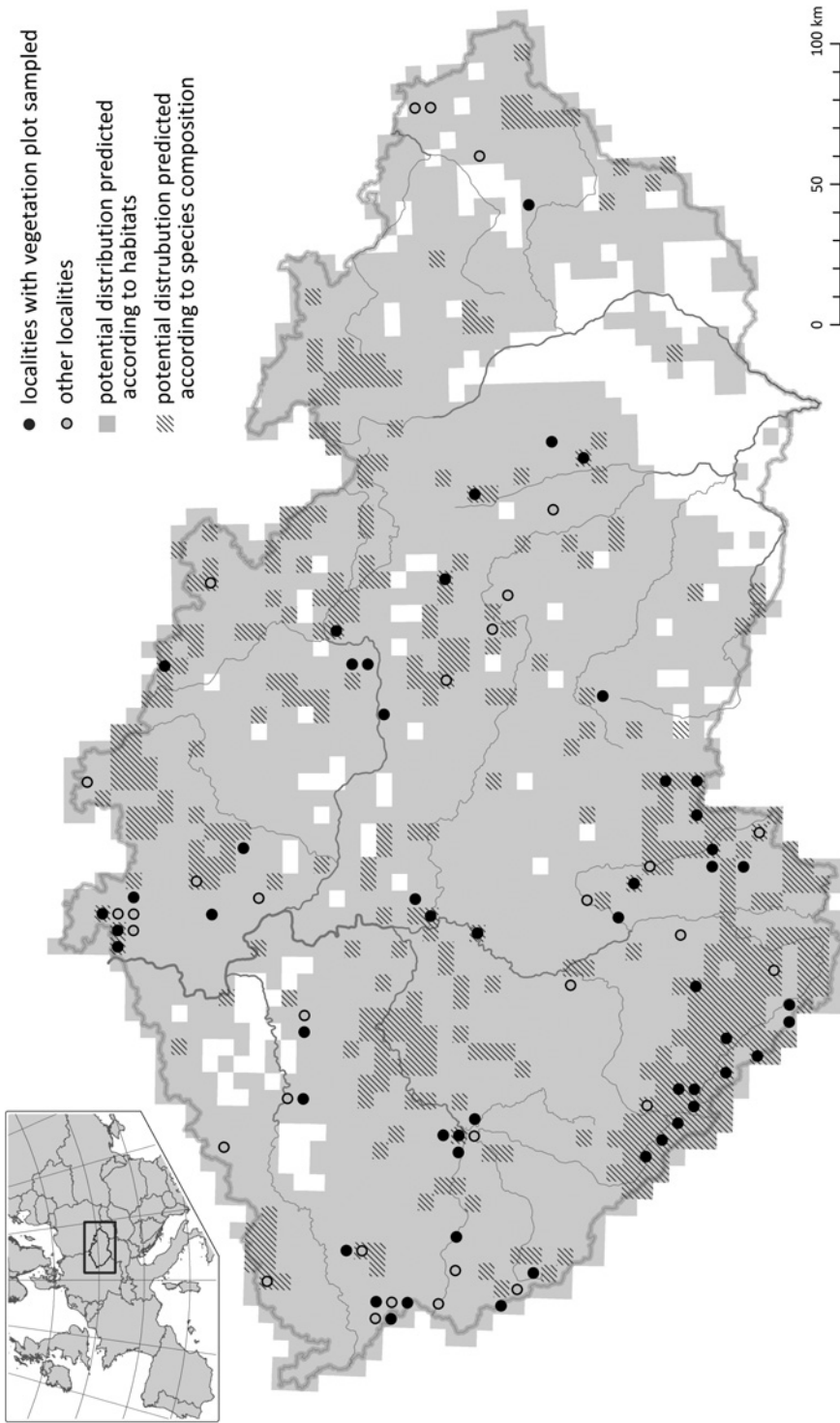
Fig. 1. – Map showing the distribution of habitats that are suitable for *Campylopus introflexus* and this species present distribution in the Czech Republic, the grid cells of which are 3′ longitude and 7′ latitude. Hatched squares show the distribution of vegetation plots included in the Czech National Phytosociological Database, which appear to be similar to those with *C. introflexus*. Grey squares show the complete distribution of the most often invaded habitats and habitats with a similar species composition (see Results for details). Black dot – cell with a sampled vegetation plot (dataset A), empty dot – cell without a sampled vegetation plot, but with recorded occurrence of *C. introflexus*.

Legend:
- localities with vegetation plot sampled
- other localities
- potential distribution predicted according to habitats
- potential distribution predicted according to species composition

0 50 100 km

of more than 100 m^2, but smaller discontinuous tufts up to a few square metres in area are more frequent. The habitats most frequently occupied by *C. introflexus* in the Czech Republic are edges of spruce plantations and pine forests with the young outplanting, forest clearings and bare areas in damaged peat bogs. All these habitats are influenced by human disturbance. *Campylopus introflexus* grows on bare soil or in gaps created by animals or man. Field observations indicate that this moss does badly on permanently waterlogged substrates and is not present in permanently wet or damaged bogs with a restored water regime.

Vegetation composition of habitats

On the basis of the TWINSPAN classification, four plots from dataset A were excluded from the analyses because they differed in their species composition. The classification of the other 74 plots of dataset A distinguished four plant communities with *C. introflexus* (Table 1). **Group 1** includes microhabitats in pine forests and peat bogs, which are characterized by a pine tree layer, *Vaccinium myrtillus* in herbaceous plant layer and several species of the genus *Cladonia* in the ground layer. This group also includes two plots from oak forest and one from a spoil tip. **Group 2** includes plots from very different habitats. They include edges of spruce forests, peat bogs with birch, drained peat bogs, banks of fish ponds, spruce-beech and birch-pine forests. Plots of group 2 usually contain birch in the tree layer, *C. introflexus* and *Pohlia nutans* in the ground layer and a high percentage of broadleaf litter. **Group 3** includes spruce forests, mainly forestry plantations. Compared to other groups, this habitat is the most strongly shaded by trees (*Picea abies*) and the herbaceous plant layer is not well developed. Only a few bryophytes and lichens with low percentage covers occur there and most of the surface of the ground is bare of plants and covered with needle litter. **Group 4** includes vegetation that develops under very open tree canopies of pine, spruce and/or birch and where the competition from other bryophytes and lichens is high. This vegetation is usually recorded at the edges of rather dry spruce-forests and trails, and also along forest trails, in forest rides and clearings and at the edges of bogs.

Species associated with *C. introflexus* in the vegetation plots in dataset A (Table 1) belong to common elements of the European flora that occur in areas with a continental climate. The species are widespread in temperate-boreal forests and have wide realised ecological niches.

Campylopus introflexus was rarely found in other habitats, as indicated by only four outliers. They were sampled in (i) a beech forest, where the species grew close to the edge of a clearing in the forest, (ii) moist clearings in a spruce forest and (iii) bank of a brook, where the species was associated with hygrophilous bryophyte species. In addition, this species was not sampled but once recorded in boulder scree with relict flora and once on a fallen trunk in an advanced stage of decay. Despite the seeming heterogeneity of all these habitats, they have one common feature: the species grew on bare soil where there was little competition from vascular plants.

The vegetation samples from pine forests (dataset B) were classified into five well-distinguished plant communities (Table 2). They are differentiated by the composition of the tree layer, different nutrient availability and soil moisture: (1) nutrient-rich forests with oak, without *Vaccinium myrtillus*, (2) humid forests with oak and *Vaccinium myrtillus*, (3) extremely species-poor dry lichen forests (4) dry lichen forests, (5) pine forests with spruce. The first two types of pine forest do not contain plots with *C. introflexus*, while this species is present in some plots sampled in the other three communities.

Table 1. – Characteristics of habitats with *Campylopus introflexus* (dataset A) classified using a modified TWINSPAN analysis. Threshold value of phi coefficient for diagnostic species was 0.2 (0.5), minimum frequency of occurrence for constant species was 50% (species with 80% are shown in bold), for dominant species 10% with cover of at least 25%. E3 – tree layer, E1 – herbaceous plant layer, E0 – ground layer. All values are averages for a group with (±) standard deviation.

Cluster	No. of popula-tions	Diagnostic species	Constant species	Dominant species	Altitude [m a.s.l.]	Soil characteristics	Needle : leaf litter	Content of burnable components in soil	Cover of vegetation layers
Pine forests and peatbogs	25	**Pinus sylvestris**, *Calamagrostis villosa*, *Cladonia pyxidata*, *Luzula luzuloides*, *Calluna vulgaris*			480±232	PO_4 ions 6.7±2.1 mg·kg^{-1}, NH_4 ions 51.1±21.3 mg.kg^{-1}, soil pH(H_2O) 3.7±0.2	80:20±36	55±35%	E3 8±12%, E1 30±22%, E0 70±22%
Mixed forests with birch	16	**Betula spec. div.**, **Pohlia nutans**	**Pohlia nutans**, *Polytrichum formosum*	*Pohlia nutans*, *Polytrichum formosum*, *Betula* spec. div., *Avenella flexuosa*	670±238	PO_4 ions 7.4±1.7 mg·kg^{-1}, NH_4 ions 56.4±15.7 mg.kg^{-1}, soil pH(H_2O) 3.7±0.4	60:40±40	45±30%	E3 12±21%, E1 35±30%, E0 60±29%
Spruce forests	12	**Picea abies**, *Cladonia fimbriata*	**Picea abies**, **Cladonia fimbriata**, *Avenella flexuosa*	*Picea abies*, *Hypnum cupressiforme* s.l., *Avenella flexuosa*	608±227	PO_4 ions 7.4±1.8 mg·kg^{-1}, NH_4 ions 80.7±46.9 mg.kg^{-1}, soil pH(H_2O) 3.7±0.2	85:15±23	53±26%	E3 30±19%, E1 22±24%, E0 74±23%
Forest edges and paths	21	*Dicranella heteromalla*, *Cladonia fimbriata*, *Avenella flexuosa*	*Cladonia fimbriata*, *Avenella flexuosa*, *Polytrichum formosum*, *Pohlia nutans*	*Avenella flexuosa*, *Polytrichum formosum*, *Cladonia fimbriata*	670±245	PO_4 ions 8.3±2.5 mg·kg^{-1}, NH_4 ions 81.1±58.7 mg.kg^{-1}, soil pH(H_2O) 3.7±0.2	80:20±26	52±30%	E3 2±6%, E1 35±20%, E0 80±26%

Table 2. – Characteristics of pine forests (dataset B) based on diagnostic, constant and dominant species. Threshold value of phi coefficient for diagnostic species was 0.2 (species with 0.5 are shown in bold), minimum frequency of occurrence for constant species was 50% (species with 80% are shown in bold), for dominant species 10% with cover of at least 25%.

Forest type	Diagnostic species	Constant species	Dominant species
Nutrient-rich pine forest	**Poa nemoralis, Brachythecium rutabulum, Plagiomnium affine, Quercus petraea agg., Impatiens parviflora, Arrhenaterum elatius,** Galeopsis speciosa, Sorbus aucuparia, Hieracium laevigatum, Mycelis muralis, Moehringia trinervia, Quercus rubra, Festuca rubra, Calamagrostis epigejos, Quercus robur, Festuca ovina	**Pinus sylvestris, Avenella flexuosa, Plagiomnium affine, Brachythecium rutabulum, Quercus petraea agg., Hypnum cupressiforme s.l.,** Dicranum scoparium, Poa nemoralis, Sorbus aucuparia, Quercus robur, Pleurozium schreberi, Calamagrostis epigejos, Betula spec. div.	Pinus sylvestris, **Avenella flexuosa, Quercus petraea agg., Pleurozium schreberi,** Calamagrostis epigejos, Brachythecium rutabulum
Humid pine forest	Rubus idaeus, Luzula pilosa, Frangula alnus, Plagiothecium succulentum, Molinia caerulea s.l., Dryopteris carthusiana, Lysimachia vulgaris, Eurhynchium angustirete, Calliergon cordifolium, Melampyrum pratense, Vaccinium myrtillus, Carex pilulifera, Plagiomnium affine, Hieracium lachenalii	**Vaccinium myrtillus, Pinus sylvestris, Avenella flexuosa, Pleurozium schreberi, Hypnum cupressiforme s.l.,** Vaccinium vitis-idaea, Rubus idaeus, Plagiomnium affine, Dicranum scoparium, Betula spec. div., Polytrichum formosum, Pohlia nutans, Melampyrum pratense, Frangula alnus, Dryopteris carthusiana	Pinus sylvestris, **Avenella flexuosa, Vaccinium myrtillus, Pleurozium schreberi, Hypnum cupressiforme s.l., Plagiothecium succulentum,** Molinia caerulea s.l., Betula spec. div.
Lichen pine forest, species poor	Aulacomnium androgynum, Cladonia furcata, Ptilidium ciliare, Pilosella officinarum, Festuca ovina agg., Rumex acetosella	**Pinus sylvestris, Hypnum cupressiforme s.l., Dicranum scoparium, Avenella flexuosa, Pleurozium schreberi,** Pohlia nutans, Betula spec. div., Ptilidium ciliare, Cladonia furcata	Pinus sylvestris, Dicranum scoparium, Pleurozium schreberi
Lichen pine forest	**Cladonia arbuscula, Cladonia gracilis, Cetraria islandica,** Cladonia macilenta, Leucobryum glaucum, Dicranum spurium, Cladonia uncialis, Cladonia squamosa, Vaccinium vitis-idaea, Cladonia rangiferina, Calluna vulgaris, Cladonia furcata	**Pinus sylvestris, Dicranum scoparium, Pleurozium schreberi, Vaccinium vitis-idaea, Vaccinium myrtillus, Hypnum cupressiforme s.l.,** Avenella flexuosa, Pohlia nutans, Calluna vulgaris, Leucobryum glaucum, Dicranum polysetum	Pinus sylvestris, Pleurozium schreberi
Spruce pine forest	**Picea abies**, Hylocomium splendens, Cladonia ochrochlora, Pohlia nutans, Melampyrum pratense, Campylopus introflexus, Polytrichum formosum	**Pinus sylvestris, Avenella flexuosa, Pohlia nutans, Pleurozium schreberi, Hypnum cupressiforme s.l., Dicranum scoparium, Picea abies, Vaccinium myrtillus,** Betula spec. div., Vaccinium vitis-idaea, Dicranum polysetum, Calluna vulgaris, Polytrichum formosum	Pinus sylvestris, Pleurozium schreberi, Vaccinium myrtillus, **Avenella flexuosa**

Ecological characteristic of the habitats: field data

The habitats where *C. introflexus* was found (dataset A) have usually low cover of trees. Cover of other layers is similar in all the plant communities in which it occurs. *Campylopus introflexus* grows generally on acid substrates, or on alkaline substrate if at least a small amount of spruce or pine needle litter is present (Table 1). There is no difference in the range of pHs among the plant communities. Needle litter was present at 75% of the localities and the ratio of needle:broadleaf litter is more equal in mixed forests with birch. Mean values of PO_4 and NH_4 ion contents are only slightly different among vegetation types from dataset A (Table 1), but the range of values is high. Amount of NH_4 ions in soil under cushions varies from 20.5 to 248.02 mg/kg, amount of PO_4 ions from 4.4 to 12.7 mg/kg and of NO_3 ions (data not shown) from 0.56–38.7 mg/kg. Percentages of soil organic and mineral components vary in all communities and loss-of-ignition ranges between 2% (pine forests) and 98% (bog communities). *Campylopus introflexus* grows on medium up to strongly water-retaining soils, but it is able to grow on very slightly water-retaining soil with a maximum water content of 10%. Slope inclination is low at all localities, with the one exception of the boulder scree in the Krkonoše Mts, where there were no preferences for a particular slope orientation (data not shown). The mean altitudes for particular types of vegetation derived from dataset A reflects the distribution of respective plant communities in Czech Republic; pine forests and drained peatbogs prevail at lower altitudes (Table 1).

In the ordination space, the vegetation groups are well distinguished along the first two ordination axes (Fig. 2). Distribution of the plots along the first ordination axis correlates with altitude, while distribution along the second ordination axis correlates with concentration of PO_4 and NH_4 ions, pH and character of the litter (needles versus leaves). Percentage cover, population size and fertility of *C. introflexus* decreases along the first axis, which is associated with the vegetation change from lowland pine forests and edges of bogs to high-altitude spruce forests.

Ellenberg indicator values indicate ecological differences among particular types of pine forests (dataset B). The first two groups differ from the others in both having higher soil reactions (Fig. 3A) and nutrients (Fig. 3B). No apparent differences were found for the other EIV parameters (data not shown). *Campylopus introflexus* was not recorded in any plot in the first two groups, therefore it seems that soil reaction and quantity of nutrients in the soil can be limiting environmental factors for *C. introflexus* in pine forests.

Cultivation experiment

The results of the cultivation experiment generally confirmed the results of the field studies. Protonema started to grow two weeks after the start of the experiment on most soil types and levels of watering used. Protonema covered the whole surface of the substrates within the first month. Gametophores started to grow during the first and second month, and covered the whole surface of pots after a few months. On sand, sandy soil and the dry treatment protonema started to grow in the second month, with new gametophores growing adjacent to the initial cushion. On the lime-enriched substrate the growth of protonema was inhibited and the protonema mainly developed on the initial plants. Most gametophores died on lime-enriched soil within six months; when gametophores grew, they were spindly, weak and had only a few small leaves. In the permanently wet treatment, the protonema started to grow in the first month but the young gametophores soon died.
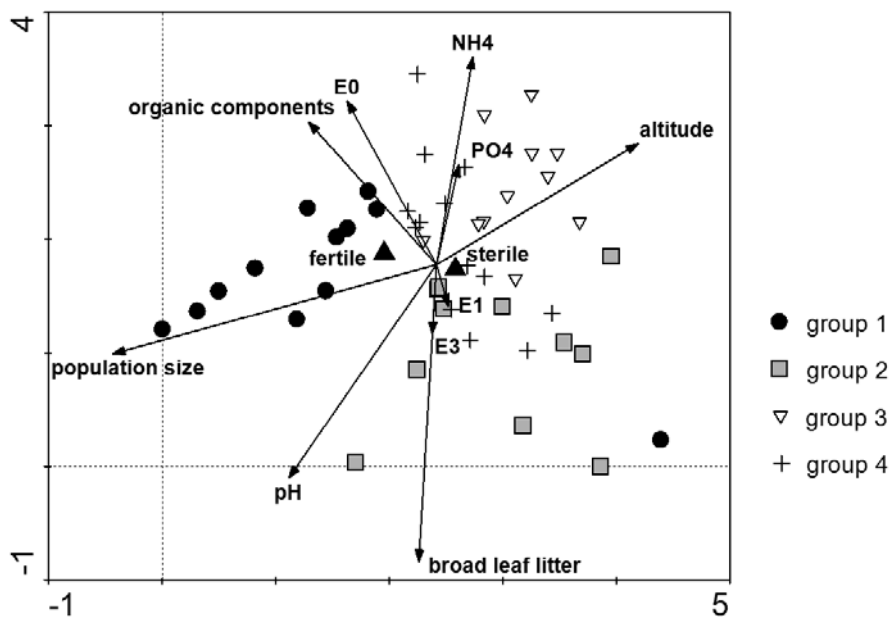
Fig. 2. – DCA ordination diagram of 52 vegetation plots of dataset A and environmental variables passively projected onto the ordination. The first and second ordination axes are displayed. The groups of plots were classified using a modified TWINSPAN analysis. Identification of groups: (1) pine forests and bog edges, (2) mixed forests with birch, (3) spruce forests, (4) spruce forest edges and trails.

Soil type and moisture regime had statistically significant effects on the viability and fitness of *C. introflexus*. For testing the effect of soil type, the random component (4) of the linear mixed effects model was the most parsimonious (Table 3). Similar growth rates were recorded on four of the types of soil used, the commercial substrate for plants, peaty soil, peat and spruce litter, which based on the AIC, could be grouped together into an "organic soil group" without any loss of information. However, any further groupings resulted in a considerably higher model AIC, suggesting that the moss differed in terms of growth in the remaining treatments (the final model $F = 100.54$, $P < 0.0001$, numerator DF = 3, and denominator DF = 99). The mean number of developed gametophores decreased from organic soils, through sandy soil and sand to lime-enriched soil (Table 4, Fig. 4A). Gametophore production was ~5 times lower on the soil mixed with limestone compared to that achieved on organic soils, which indicates that lime enrichment had a considerable harmful effect on *C. introflexus*.

For testing the effect of watering, the random component (2) was chosen (Table 3). All the treatment groupings caused a considerable increase in AIC, suggesting there were significant differences in the ability of the moss to grow in the different treatment groups (the final model $F = 220.87$, $P < 0.0001$, numerator DF = 2, and denominator DF = 38). Fewer gametophores developed on permanently wet soil (~10 and 13 times, respectively) than on medium-wet and dry soils (Table 4, Fig. 4B), indicating that *C. introflexus* does not thrive in very wet conditions. On the other hand, the number of gametophores produced on the medium-wet soil was slightly higher than on dry soil, implying that *C. introflexus* benefited from moderate moisture.
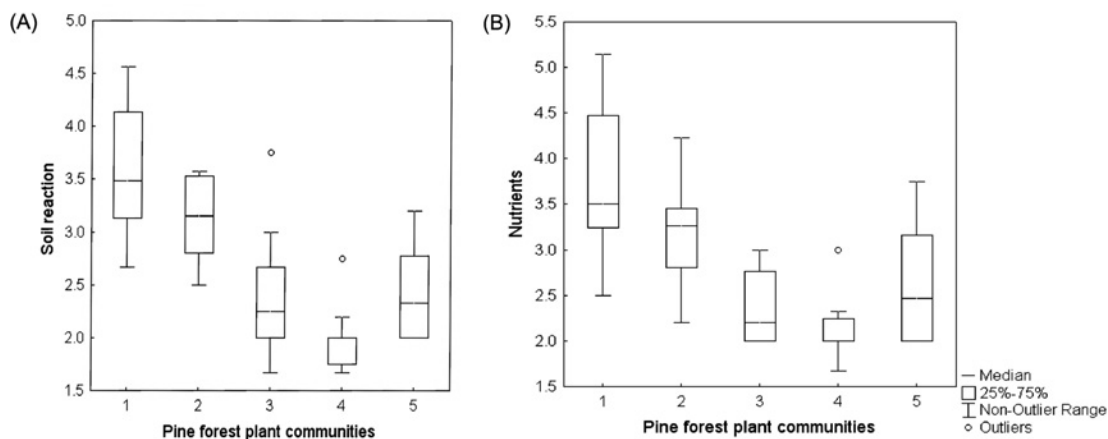
Fig. 3. – Average Ellenberg indicator values for nutrients and soil reaction for pine forest plant communities (dataset B). The higher EIV, the higher the soil reaction (from acidic to basic) and nutrient demands of plant species in a community. For both parameters, the values range from one to nine. Identification of groups: (1) nutrient-rich forests with oak, without *Vaccinium myrtillus*, (2) wet forests with oak and *Vaccinium myrtillus*, (3) dry lichen forests, species-poor (4) dry lichen forests, (5) pine forests with spruce.

Invasibility of vegetation by Campylopus introflexus

From the total number of 26,998 vegetation plots in dataset C, 938 were chosen as floristically similar to the vegetation invaded by *C. introflexus* based on the Frequency Index (Fig. 1). They were originally assigned to nine classes of vegetation (Table 5). Most of the plots belong to *Querco-Fagetea, Vaccinio-Piceetea* and *Quercetea robori-petrae*. These classes also have the highest proportion of chosen plots of all the plots in dataset C. The selected plots were assigned mostly to the alliances *Dicrano-Pinion, Piceion excelsae, Genisto germanicae-Quercion, Luzulo-Fagion* and *Fagion*. The plots assigned to the alliance *Fagion* were mainly those sampled in spruce forestry plantations or mixed forests rather than typical beech forests, classified probably on the basis of the potential vegetation of the stand. Except for forest clearings of the *Epilobietea angustifolii* class, non-forest vegetation is represented rather marginally. No vegetation of drained peatbogs was selected. This habitat may not be well represented in the Czech National Phytosociological Database or the vegetation plots did not meet the requirements for inclusion in dataset C. Some samples of later successional stages of drained peat bogs may also have been assigned to *Dicrano-Pinion*.

Distribution of the selected plots as well as complete distribution of corresponding habitats is shown in Fig. 1. The following habitats were mapped based on data in the Habitat catalogue (Chytrý et al. 2010): L5.4. Acidophilous beech forests; L7 Acidophilous oak forests; L8 Dry pine forests; L9.1. Montane *Calamagrostis* spruce forests; T5 Sand and shallow soil grasslands (except for the unit T5.5. Acidophilous grasslands on shallow soils, which represent widespread, but small-scale open roadside and forest-margin siliceous grassland on ranker soils, but where *Campylopus introflexus* was never observed) and R3.4. Degraded raised bogs.

Table 3. – Akaike information criterion (AIC) values of the linear mixed effects models for the cultivation experiment of *Campylopus introflexus* in different soils and levels of moisture. The AIC values were used to select the most parsimonious random components (in bold), while the fixed part of the model was kept constant. Df – the degrees of freedom used for parameter estimation. For random components' types (0)–(5), see Methods.

Random component type	Water supply		Soil type	
	df	AIC	df	AIC
(0) no random effect	4	348	8	753
(1) random intercept	5	337	9	743
(2) random intercept and slope	10	**323**	36	749
(3) different variances	6	337	14	757
(4) r. intercept + diff. var.	7	333	15	**738**
(5) r. intercept and slope + diff. var.	12	327	42	765

Table 4. – Coefficients of the linear mixed effects models showing the estimated mean, its standard error (SE) and relative variance of the number of gametophores of *Campylopus introflexus* per treatment group. Different variances per treatment group were only allowed in the soil experiment. Organic soil group represents the four soil treatments grouped together during the analysis: commercial substrate for plants, peaty soil, peat and spruce litter.

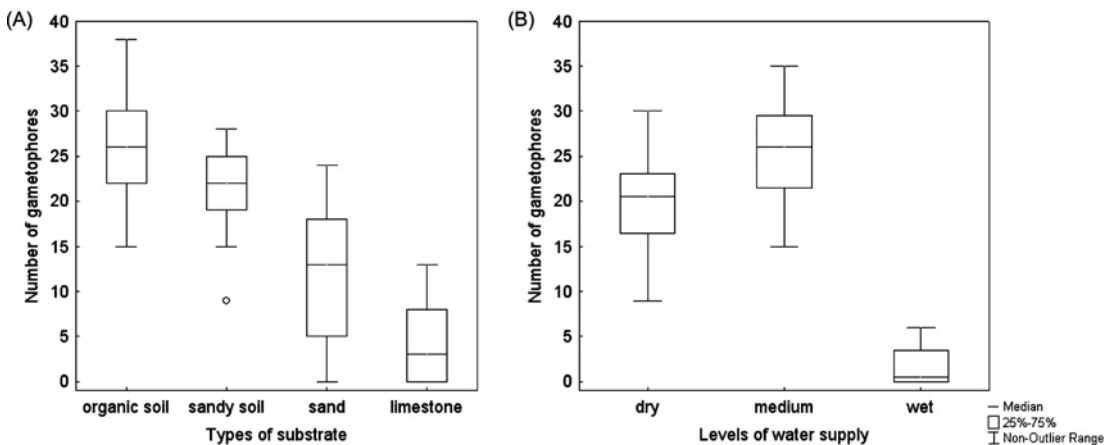| Experiment	Treatment	Estimated mean number of gametophores	SE	Variance estimates
Soil type	organic soil group	26.28	0.94	0.54
	sandy soil	21.64	1.22	0.49
	sand	11.53	2.07	1.00
	lime-enriched soil	4.47	1.46	0.64
Water supply	permanently wet	1.80	0.49	–
	medium-wet	25.45	1.17	–
	dry soil	19.95	1.13	–

Fig. 4. – The effect of soil type and watering on the number of gametophores of *Campylopus introflexus*. Level of water supply – dry, medium-wet, permanently wet. Types of substrate: organic soil group = commercial substrate for plants + peaty soil + peat + spruce litter; sandy soil; sand; lime-enriched soil.

Table 5. – Vegetation types that have similar species composition to vegetation already invaded by *Campylopus introflexus*. The similarity was calculated using the Frequency Index in the Matching function in the program JUICE, using the data in the stratified Czech National Phytosociological Database. Minimum frequency of occurrence for constant species was 50% (species with 80% are shown in bold).

Vegetation class	No. of similar samples	All samples in stratified database	Percentage of similar samples	Habitat	Constant species in similar samples
Vaccinio-Piceetea	348	984	35.4	pine and spruce forests	**Picea abies**, **Avenella flexuosa**, **Vaccinium myrtillus**, Vaccinium vitis-idaea, Dicranum scoparium, Polytrichum formosum
Quercetea robori-petrae	93	355	26.2	acid oak forests	Betula species, Pinus sylvestris, **Quercus petraea** agg., **Avenella flexuosa**, Festuca ovina, Hieracium murorum, Luzula luzuloides, Melampyrum pratense, **Vaccinium myrtillus**, Dicranum scoparium, Hypnum cupressiforme s.l., Pleurozium schreberi, Pohlia nutans, Polytrichum formosum
Querco-Fagetea	428	4157	10.3	beech forests and oak forests	Abies alba, Fagus sylvatica, **Picea abies**, **Avenella flexuosa**, Dryopteris dilatata, Hieracium murorum, Oxalis acetosella, Vaccinium myrtillus, Dicranum scoparium, Hypnum cupressiforme s.l., **Polytrichum formosum**
Epilobietea angustifolii	35	469	7.5	forest clearings	Picea abies, **Avenella flexuosa**, Calamagrostis villosa, Dryopteris dilatata, Epilobium angustifolium, Rubus idaeus, Vaccinium myrtillus, Dicranum scoparium, **Polytrichum formosum**
Erico-Pinetea	2	27	7.4	pine forests on serpentines	Picea abies, **Avenella flexuosa**, Calamagrostis villosa, Dryopteris dilatata, Epilobium angustifolium, Rubus idaeus, Vaccinium myrtillus, Dicranum scoparium, **Polytrichum formosum**
Oxycocco-Sphagnetea	14	354	4.0	high/low raised peat bogs	Picea abies, **Avenella flexuosa**, Eriophorum vaginatum, **Vaccinium myrtillus**, Vaccinium uliginosum, **Vaccinium vitis-idaea**, **Calluna vulgaris**, Dicranum scoparium, Pleurozium schreberi, Pohlia nutans, Polytrichum commune, Sphagnum magellanicum, Sphagnum recurvum agg.
Mulgedio-Aconitetea	8	254	3.2	high mountain herbaceous vegetation	Sorbus aucuparia, **Avenella flexuosa**, Dryopteris dilatata, Dryopteris filix-mas, Geranium robertianum, **Dicranum scoparium**, **Hypnum cupressiforme s.l.**, Plagiothecium laetum, **Pleurozium schreberi**, Pohlia nutans, **Polytrichum formosum**, Ptilidium pulcherrimum
Nardo-Callunetea	9	814	1.1	heaths	Avenella flexuosa, Melampyrum pratense, Nardus stricta, Potentilla erecta, **Vaccinium myrtillus**, Vaccinium vitis-idaea, Calluna vulgaris, Dicranum polysetum, Dicranum scoparium, **Pleurozium schreberi**, Pohlia nutans
Scheuchzerio-Caricetea fuscae	1	1448	0.1	mires	**Pinus mugo**, **Picea abies**, **Avenella flexuosa**, **Calamagrostis villosa**, **Carex nigra**, **Carex rostrata**, **Empetrum nigrum** agg., **Eriophorum angustifolium**, **Eriophorum vaginatum**, **Juncus filiformis**, **Molinia caerulea** agg., **Vaccinium oxycoccos** agg., **Vaccinium myrtillus**, **Vaccinium vitis-idaea**, **Warnstorfia fluitans**, **Pleurozium schreberi**, **Pohlia nutans**, **Polytrichum commune**, **Polytrichum strictum**, **Sphagnum majus**, **Sphagnum recurvum** agg.
Species with the highest percentage frequency of selected samples from the database					*Avenella flexuosa* 90%, *Vaccinium myrtillus* 85%, *Picea abies* 82%, *Polytrichum formosum* 80%, *Dicranum scoparium* 76%, *Oxalis acetosella* 47%, *Pleurozium schreberi* 45%, *Dryopteris dilatata* 42%, *Hypnum cupressiforme* s.l. 40%, *Pohlia nutans* 36%, *Pinus sylvestris* 35%, *Calamagrostis villosa* 34%, *Abies alba* 34%, *Hieracium murorum* 33%, *Rubus idaeus* 33%, *Sorbus aucuparia* 30%, *Luzula luzuloides* 30%, *Fagus sylvatica* 29%, *Maianthemum bifolium* 27%, *Vaccinium vitis-idaea* 27%, *Senecio nemorensis* agg. 27%

Species with the highest frequency of occurrence in the chosen vegetation plots of respective classes (Table 5) characterize vegetation similar to the vegetation invaded by *C. introflexus*. All of these species are widespread and common in central Europe. *Picea abies*, *Avenella flexuosa*, *Vaccinium myrtillus*, *Polytrichum formosum* and *Dicranum scoparium* were recorded in more than 75% of all the plots selected (Table 5).

Discussion

Distribution pattern in the Czech Republic

The number of localities recorded in the Czech Republic increased from three in 1996 (Soldán 1996) to almost 80 in 2006 (Mikulášková 2006) and more than 100 in 2011 (Fig. 1). The increase in the number of localities is apparent mainly in the western part of the country, while in the eastern part records are still rare. Because the distribution of *Campylopus introflexus* was not systematically mapped, it can be assumed that many undetected populations exist in the area and the real distribution of the species in the Czech Republic is denser. Nevertheless, we believe that collecting the field records and all accessible information about new localities resulted in a wide and representative dataset reflecting the actual distribution pattern of this species in the Czech Republic. Most of the records are for coniferous forests (~ 70%) in both the up till 2006 and 2006–2011 periods. The next common habitat for both periods is peaty soil at edges of peat bogs or in drained peat bogs (~ 20%). Rare occurrence of the species in other habitats such as broadleaf forests, spoil tips or sumps is also similar in both periods. The habitat preferences thus seem not to have changed during the invasion.

Rate of colonization by an invasive species is regulated by production, transport and establishment of diaspores. *Campylopus introflexus* reproduces both sexually and asexually in the Czech Republic and in the western part of the country there is a high concentration of populations. The colonization of suitable habitats in the western part is higher than in the eastern part because of higher propagule pressure. The uncolonized area and distances between populations increase eastward even though there are still a high number of potentially suitable habitats in the east (Fig. 1). Taking into account that this species is spreading from western Europe eastwards, the pattern suggests that the long distance spreading by spores is more important for initial colonization. For subsequent spreading, importance of asexual reproduction increases. This pattern of colonization during the initial phase of an invasion is characteristic when colonization of new areas is mainly dispersal-limited and very different from that of widely distributed species that are limited by availability of habitats (Mulligan & Gignac 2001). In contrast, *Orthodontium lineare*, the second most invasive moss species in central Europe, seems to be habitat-limited (Herben 1994) rather than dispersal-limited (Hedenäs et al. 1989a, b). Taking into account the difference in the dispersal ability of different taxonomic groups of organisms, with bryophytes being better dispersers than vascular plants or some animals (Hájek et al. 2011), we can expect that the first phase of the invasion by *C. introflexus* will be rather short and that the distribution of this species will become habitat-limited.

Recently invaded habitats and their ecological characteristics

Currently, little is known about ecology of *C. introflexus*, particularly about its ecological preferences in central Europe. Field observations reveal that this species tolerates a wide spectrum of temperatures, from long freeze periods at high altitudes (e.g. Krkonoše Mts and Šumava Mts in the Czech Republic; Mikulášková 2006) to temperatures at the surface of the moss cover of above 40°C in acidic geothermal fields (Italy; Chiarucci et al. 2008). In the field part of the present study, we investigated substrate characteristics and light conditions of microhabitats with *C. introflexus*. In the field, plant growth is determined also by inter-specific competition. To determine the precise effect of particular environmental factors on the growth of a species it is necessary to supplement field observations with cultivation under standard conditions and in specified treatments. We used such experiments to determine the ability of *C. introflexus* to grow on different substrates and with different levels of water supply.

Using both a large-scale field study and cultivation experiments we demonstrated the great affinity of *C. introflexus* for moderately wet acidic soils, with a high proportion of organic matter (peat, forest humus) and rather low nutrient availability. On the basis of the results of the cultivation experiment we can say that lime-rich soils are not suitable for *C. introflexus.* However, the field observations showed that this species can occur in areas with a calcium-rich bedrock when at least a shallow layer of acidic spruce or pine litter is present (see also Hasse & Daniëls 2006) or a peat horizon has developed (Schlüsslmayr 2005). Due to soil acidification by humic acids the soil pH is sufficiently acidic to allow *C. introflexus* to colonize such areas. That *C. introflexus* in the cultivation experiment grew poorly on sand and sandy soils as well as dry soils contrasts with its frequent occurrence in pine forests and other sandy habitats in the Czech Republic and open sand dunes and sandy grasslands in western and northern Europe (e.g. Biermann & Daniëls 2001, Hasse 2007). Strong invasive character of this moss in these habitats may be due to low competition from vascular plants. Lack of strong competition could compensate for the unfavourable conditions for growth and thus *C. introflexus* forms large cushions in these habitats and poses a risk for the native flora (Equihua & Usher 1993, Klinck 2008). The data from western Europe further suggest it survives well under enhanced ammonium concentrations (Sparrius & Kooijman 2011). Cultivation experiments showed that *C. introflexus* prefers moderately wet soils, but can survive long-term desiccation, as it is recorded in some sandy habitats. High soil moisture seems to limit the growth of *C. introflexus*.

The occurrence in mostly open habitats with a low coverage of shrubs and trees indicates high demands of this species for light. Absence of treeless habitats (e.g. grasslands) that are colonized by this species in the Czech Republic is probably because of factors other than light (e.g. competition from vascular plants), because this moss is commonly found in habitats that lack shrubs and trees in western and northern Europe (e.g. Biermann & Daniëls 1997, Hasse 2007).

Because habitats with all of these ecological parameters are usually overgrown by dense growths of vascular plants or competitively strong bryophytes (such as *Sphagnum* in nitrogen-polluted bogs, Hájková et al. 2011), *C. introflexus* occupies disturbed patches. The success of *C. introflexus* in central Europe thus cannot be explained by a strong competitive ability as in the case of some vascular plant invaders. Instead, disturbance-mediated competition (Schooler et al. 2010) or, purely an ability to colonize quickly bare acidic soil after anthropogenic disturbance, explain the recent spread of this species in central Europe.

At the habitat level, we found that *C. introflexus* occurs frequently in open coniferous forests with an abundance of dwarf shrubs (e.g. *Vaccinium* spec. div., *Calluna vulgaris*), where there is a low cover of herbaceous plants and a poorly developed ground layer. Such coniferous forests are represented predominantly by spruce and pine plantations at low altitudes, but natural pine forests are also invaded. Frequent co-occurrence of *C. introflexus* and pine is possible because of the more open tree layer in pine forests, compared to forests dominated by other conifers or broadleaf trees. Another reason could be the frequent occurrence of pine in the initial stages of succession, which are also preferred by *C. introflexus* (Klinck 2008) or the unfavourable soil conditions in these habitats, which unlike most other species *Pinus* sp. and *C. introflexus* can tolerate. However, we found that some pine forests are not invaded, and they either have a higher soil reaction and nutrient availability, or are waterlogged (e.g. bog woodlands with an undisturbed water regime). These observations are in accordance with the results of our cultivation experiment, as well as the results of Zerbe & Wirth (2006) who found that *C. introflexus* invades predominantly dry, nutrient poor and strongly acid lichen pine forests.

Besides natural pine forests and forestry plantations *C. introflexus* colonizes floristically similar drier edges of peat bogs and abandoned drained peat bogs. Equihua & Usher (1993) found that in drained bogs, *C. introflexus* can inhibit the natural succession of native bryophytes and vascular plants. Nevertheless, this risk is relevant only in drained bogs or drier edges of bogs where there is a transition into a spruce forest or *Nardus* grassland, because in well-hydrated parts with restored water regime, *C. introflexus* is limited by waterlogging.

Invasion potential

The present pattern of the *C. introflexus* invasion indicates that it does not pose a threat to the native flora, which contrasts with the situation in western Europe (Biermann & Daniëls 1997, Hasse & Daniëls 2006, Klinck 2008, Sparrius & Kooijman 2011). This pattern, however, may be only due to the fact that this species in the Czech Republic is still in the initial phase of its invasion. The assessing of this species invasion potential seems to be difficult because *C. introflexus* differs from most other invasive species. The habitats that are invaded by *C. introflexus* in the Czech Republic correspond neither to habitats that are usually invaded by other species in central Europe (Chytrý et al. 2005, 2008, Hejda et al. 2009) nor to the native habitats of the invader (eucalyptus forests, grasslands, savannas, schrub-lands, heathlands; DAISIE 2009, Frahm 2007). Moreover, *C. introflexus* is probably not a strong competitor (Hasse 2007). In central Europe, this species therefore occurs mostly in disturbed stands of low conservation value, where autogenic succession is blocked. However, the high frequency of habitats that can be potentially colonized by *C. introflexus* indicates that this species has the potential to become a common component of the Czech bryoflora. Its invasion intensity seems to be dependent mainly on the frequency of suitable microhabitats and the number of both generative and vegetative diaspores in the diaspore bank.

The present invasion by *C. introflexus* can be compared with that of another invasive moss *Orthodontium lineare,* which is considered to be already established in the Czech Republic (Hassel & Söderström 2005). It is currently a common species in the central-European bryoflora, especially in habitats on sandstone (Soldán & Kučera 2004, Hassel &

Söderström 2005). Both mosses share some invasive characteristics. They have a high spore production (Herben 1994), but only prevail in plant communities where the competition from native species is low (Hedenäs et al. 1989a) and usually do not colonize sites where rare native species occur (Hedenäs et al. 1989a, Herben 1994). Therefore, we can conclude that *C. introflexus* presents no threat to the native flora in central Europe. However, we can expect a faster and wider spread of *C. introflexus* in the future for three reasons (similarly Hassel & Söderström 2005): (i) *C. introflexus* has a wider substrate tolerance than *O. lineare* (Hedenäs et al. 1989a); (ii) *C. introflexus* frequently produces vegetative diaspores; (iii) the predicted suitable habitats for colonization by *C. introflexus* are more widely distributed than those colonized by *O. lineare*, which is probably subject to stronger habitat filters (Hedenäs et al. 1989a, b, Kučera 2004).

Conclusions

Campylopus introflexus has already colonized the whole of the Czech Republic, but is more frequent in the western part (Fig. 1). This is due to both the earlier colonization and higher propagule pressure in the western part of the Czech Republic. This species invades predominantly coniferous forests and plantations and disturbed (drained) peat bogs, where it occupies patches where there is little competition from other plants, which are most often created by anthropogenic disturbances. Cultivation experiments confirmed that the species grows best on organic, moderately wet soils, and has a low fitness on lime-rich and waterlogged soils.

Our results further suggest that even pine plantations, the most frequently invaded habitat, may not be invaded equally. Wet pine forests, nutrient-rich pine forests and oak-pine forests currently appear unlikely to be invaded, except for small dry open patches in these forests. Invasion of lichen-rich pine forests seems to depend on the intensity of competition between *C. introflexus* and the lichens.

Analysis of species composition of already invaded communities and its comparison with a large phytosociological database suggests that there are many suitable habitats for *C. introflexus* in central Europe and therefore this species has the potential of a geographically wider distribution. In spite of this the current threat to the native flora seems to be small, because the plant communities that could be potentially invaded represent widespread communities composed of quite common species, rather than rare communities with a unique species composition in which invasion by *C. introflexus* might cause a conservation problem.

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Souhrn

Ačkoliv jsou rostlinné invaze často studovány, většina prací je zaměřena na cévnaté rostliny. Tato práce je zaměřena na studium ekologických nároků invazního mechu *Campylopus introflexus* v České republice. Studovali jsme ekologické a vegetační nároky druhu a aktualizovali data o jeho současném rozšíření. Ekologické nároky druhu jsme zkoumali jak in situ, tak i pomocí in vitro experimentů. Pro testování schopnosti druhu *C. introflexus* růst za různých půdních a vlhkostních podmínek jsme založili kultivační experimenty, které jsme vyhodnotili pomocí smíšených lineárních modelů. Pomocí klasifikace a ordinace fytocenologických snímků s výskytem druhu jsme popsali diverzitu vegetace, do které druh u nás vstupuje. Na základě floristické podobnosti existujících snímků s výskytem druhu a všech snímků uložených v České národní fytocenologické databázi jsme obecně charakterizovali již invadovaná stanoviště a predikovali, jaké biotopy mohou být v budoucnu v České republice invadovány. Z našich výsledků vyplývá, že *C. introflexus* není extrémně specializován a vyskytuje v různých rostlinných společenstvech. Kultivační experimenty ukázaly, že špatně prosperuje na vápníkem obohacených a zamokřených půdách. Druh v České republice expanduje převážně v jehličnatých monokulturách a na narušených rašeliništích. V těchto biotopech osídluje otevřená místa s nízkou konkurencí cévnatých rostlin, která jsou často vytvořená lidskými zásahy. Došli jsme k závěru, že *C. introflexus* má potenciál stát se běžným druhem bryoflóry střední Evropy. V současné době nepředstavuje vážné riziko pro domácí druhy.

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