Carex pulicaris abundance is positively associated with soil acidity, rainfall and floristic diversity in the eastern distribution range

Zofia Sotek1, Małgorzata Stasińska1, Ryszard Malinowski2, Renata Gamrat2, Małgorzata Gałczyńska3, Thea Kull4, Sergej Mochnacky5, Grzegorz Grzejszczak6, Dariusz Paprota2 & Vladislav Kolarčik7*

Carex pulicaris is considered an endangered species, and further losses are forecast under the influence of even moderate climate change. Local studies indicate that temporal declines in C. pulicaris abundance are positively correlated to decreases in precipitation and increases in air temperature. Determining ecological properties on larger scales than local ones can help develop effective protection programs for the species. We hypothesize that the local relationships observed between C. pulicaris abundance and precipitation, air temperature and soil properties will be confirmed in a spatially-oriented large-scale study performed in situ. Therefore, the present study takes a novel, large-scale integrated approach to (1) precisely characterize the ecological requirements of C. pulicaris within its eastern distribution range, and (2) determine the influence of its community type, soil properties and climatic conditions on its abundance. It was found that C. pulicaris is not a dominant or codominant species in the studied phytocoenoses in the eastern distribution range. Five natural vegetation groups including C. pulicaris, with significantly diverse species compositions, were resolved: well supported Estonian, Polish, Slovak and Radecz groups, and a weakly-supported Ambiguous group. The abundance of C. pulicaris was found to be positively correlated with the composition of the geographically-diversified plant communities and atmospheric precipitation, and to be also negatively associated with latitude and soil pH. Although the species is adapted to a relatively wide range of soil types, such adaptation requires appropriate substrate moisture level and light conditions. The species prefers moist organic and mineral soils and grows on both acid and neutral medium, characterized by a narrow C:N ratio, with various amounts of digestible total P, Mg and N, and low levels of digestible K. Climate change, manifested by reduced rainfall, may be one of the most important predictors negatively affecting the occurrence of C. pulicaris.

All conservation initiatives are subject to the influence of climate change, which will undoubtedly have a dramatic impact on many ecosystems1–4. Such changes will be reflected in species distribution and phenology, as well as in interspecies interactions, among others, and they are expected to become the main threat to biodiversity. Of these species, the most vulnerable will be the rare and endangered ones, as they are usually characterized by a narrower niche width5. Therefore, one of the core goals of conservation biology is to understand the distribution,
abundance and ecological requirements of rare species. Such studies are urgently needed for species whose natural habitat is fragmented and vulnerable under anthropogenic pressure. Some regional differences related to climate, geology and the history of land use may occur within the species range. It is also important to note that conservation efforts should focus not only on populations from the centers of their distribution, but even more on those located at the edges, where the risk of extinction is highest.

Global climate change has increased the risk of summer droughts, which makes fen habitats one of the most sensitive habitats in Europe. In many cases, this damage is exacerbated by anthropogenic land transformations of varying intensity, such as extensive landscape degradation and drainage. Unfortunately, habitat restoration programmes may fail to recover the biodiversity of degraded peatlands. As a result, many fen species are believed to be at risk of extinction, and species conservation has become a priority in wetland ecosystems.

Wetland ecosystems, and peatlands in particular, are a refuge for many rare plant species associated with specific habitat conditions and which significantly enrich the biodiversity of a given region. Many of these are stenotopic organisms, with a very narrow ecological niche. As a result of the transformation and disappearance of peatland habitats, the population of these plants decreases, which, in turn, may lead to the disappearance of their localities and their withdrawal from previously-occupied areas. Such losses may cause disjunctions within their species range and, in drastic cases, even a shrinkage of the range itself.

Carex pulicaris (flea sedge) is a typical fen species, occurring in western and northern Europe, ranging from Spain and Ireland in the west to Scandinavia in the north, with its eastern distribution limits in Baltic countries (Estonia, Lithuania, Latvia and Poland), Belarus and central Europe (Slovakia); the species does not reach the Mediterranean region. The occurrence of Carex pulicaris has a fragmented, island-like character at the eastern edge of its distribution range, with a disjunction in Poland east of the Bay of Puck between Atlantic and Eastern Baltic sites. Several studies have already documented a loss of Carex pulicaris localities in recent decades, e.g. in southern Germany, in Slovakia, northwest Poland and Estonia. Indeed, the species is classified in various threat categories in many European countries, being considered endangered in Central Europe or vulnerable in Fennoscandia.

In Estonia, according to the last Red Data Book assessment, the species is near threatened. Populations of Carex pulicaris are mainly associated with wet and periodically wet habitats, and occasionally strongly transformed ones. They occur in low and transitional bogs, lags of raised bogs, peaty meadows and wet forest habitats, and less often on impermeable loam and clay slopes. The species is found on both acidic and neutral soils, preferring peat soils. It is less common on soil-glial soils. Carex pulicaris does not usually contribute much to the construction of plant communities. It is considered a species typical for the Caricetalia davallianae order and the Caricion davallianae alliance. It is a frequent element of plant communities classified into the new, recently-distinguished Sphagno warstorfianyi—Tomenthypion alliance, belonging to the Caricetalia davallianae order. It is also a part of the Caricion nigrae and Caricion lasiocarpae alliance of the Scheuchzerio-Caricetea nigrae class, and encroaches into the Calthion and Molinion alliance of the Molino-Arrenathereteta class.

Carex pulicaris is a highly vulnerable species. Distribution models suggest that it will be lost from many regions along its eastern distributional limits in response to moderate climate change. Further studies also suggest that assisted migration may be a beneficial management strategy for the species, with reintroduction being another potential management strategy. As the species is a weak competitor, low nutrient availability and low competition for light may favour its long-term survival. A case study performed at the regional scale found that negative changes in hydrological regimes occurring since 1950, influenced mainly by lower summer precipitation and higher mean annual temperature, both driven by climate change, are significantly associated with predicted extinctions of Carex pulicaris populations occurring at lower altitude limits. However, all these results were obtained from modelling based on climate-only data or regional studies. There is a lack of detailed studies of habitat conditions across a larger area of occurrence; such research is extremely important, especially at the edges of the distribution range, where the species is less likely to find favorable conditions for development, and its sites are more vulnerable to disappearance.

Hence, there is a pressing need to identify the factors determining the abundance of Carex pulicaris with more comprehensive studies of the habitat parameters and floristic diversity of plant communities over a larger area, including the climate conditions. Such data can be used to identify appropriate protective measures to prevent the emergence of disjunctions and the projected shrinkage of the eastern range as a result of projected climate change. We expect that in the eastern range of Carex pulicaris, its abundance is significantly influenced by temperature and rainfall, vegetation type and substrate properties (soil type, organic matter content, nutrient abundance and soil acidity). We also hypothesise that both the abundance of Carex pulicaris and the diversity of plant communities in which it occurs may be related to the region of its occurrence.

The present study addresses the following questions:

1. Do the plant communities in which Carex pulicaris occurs vary regionally, and is species abundance related to community diversity?
2. How can climatic factors affect the communities of Carex pulicaris and its abundance at the eastern end of its range, with regard to different latitudes and climatic conditions?
3. What are the properties of the soil in the eastern range of Carex pulicaris, and do they affect its abundance?

Materials and methods

Phytosociological data. Field tests of the conditions favouring the occurrence of Carex pulicaris were performed at 17 different locations: three in Denmark (Bornholm), six in Poland and six in Estonia, and two in Slovakia (Fig. 1, Table 1).

Phytosociological relevés were performed in patches of Carex pulicaris communities, using the classic Braun-Blanquet method based on a seven-degree quantitative scale. Statistical analyses were performed on newly-gathered...
phytosociological data (17 relevés), other phytosociological relevés of Poland (13 relevés), which are recorded in the Polish Vegetation Database32, as well as previously published data from Slovakia (13 relevés)29. In total, our analyses were based on 43 phytosociological relevés recorded from 27 localities (1–3 per locality). The syn-taxonomic approach to communities was adopted after Matuszkiewicz (2006)25.

The habitat conditions were assessed based on Ellenberg indicator values (EIVs)33: ecological (L—light value, T—temperature value, K—continental value, F—humidity value, R—acidification value, N—nitrogen value, S—salinity value), sociological (Gr—group of vegetation classes, K.1—class, o—order, v—alliance, u—suballiance) frequency and risk (m—frequency of appearance, D—domination, A—the trend of change, G—threats). In the case of 17 of the examined locations, the soil data were also analysed.

Climatic data. Climatic conditions were evaluated for all the analysed locations based on the rasters collected in the https://worldgrids.org library, developed for the needs of the “Soilgrids” project, organized by the International Soil Reference and Information Centre (ISRIC, https://www.isric.org/explore/soilgrids). The data are currently available in the archive at https://web.archive.org/web/20170619054443/http://www.worldgrids.org/doku.php/start.

The analyses included latitude, longitude, daily minimal temperatures, daily mean temperatures, daily mean temperatures in December/January, and annual mean monthly precipitation (Table 1). The raster resolution for temperature data was 1 km, and 5.6 km for rainfall data.

Chemical composition of soil samples. Composite samples were collected from the surface layer of the rhizosphere (0–20 cm) for each of the natural sites34 (Table 1). In the soil material, the following analyses were performed: loss on ignition (organic matter) by burning soil samples in a muffle furnace at the 550º C; total C, N and S content by elementary analysis (Costech Elementary Analyzer ECS 4010, Italy); pH in H₂O and pH in 1 mol dm⁻³ KCl was determined potentiometrically; salinity by conductometry.

In addition, the content of Mg, K, Ca, Na, Cd, Co, Cu, Ni, Pb, Mn, Fe and Zn soluble in 0.5 mol dm⁻³ HCl (the so-called available forms)35,36 and soluble in concentrated HNO₃ and HClO₄, at the ratio 1:1 (the so-called total forms) was determined using an ICE series 3000 spectrometer with flame atomization (FAAS)37. The content of Na, Ca and K was determined by flame atomic emission spectrometry, while that of the other elements was determined using flame atomic absorption spectrometry. The limits of detection were (mg kg⁻¹): Ca—0.004; Mg—0.002; K—0.001; Na—0.004; Fe—0.004; Cd—0.003; Co—0.010; Cu—0.005; Ni—0.008; Pb—0.013;
Zn—0.003 and Mn—0.002. The content of available and total P was determined with spectrophotometric molybdenum blue method (690 nm wave length) using a Marcel MEDIA™ spectrophotometer. The accuracy and precision of the analytical methods and procedures used were confirmed using certified reference material: CRM036-050 Loamy Sand 4 (CRM 036-050 produced by Resource Technology Corporation, USA and UK). The effectiveness of the process was validated with 90–95% efficiency. The results shown are the mean values of three measurements, with working standards made from Merck standards at a concentration of 1000 mg dm⁻³.

The soil type classification follows the international and regional standards.

Statistical analyses. The abundance of Carex pulicaris was compared with the phytosociological composition of sites and three sets of environmental variables: mean Ellenberg indicator values (EIVs), climate variables (CLIM) and soil variables (SOIL).

The species composition and soil types of the sites were compared by multivariate analyses using the vegan package in R environment: non-metric multidimensional scaling (NMDS) of the species composition data matrix (43 sites × 310 species), and principal component analysis (PCA) of the soil data matrix (17 sites × 34 soil

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| Country     | Locality          | Latitude (N) | Longitude (E) | Mean annual precipitation [mm] | Min. day temp. *°C | Mean day temp. *°C | Mean day temp. Dec/Jan °C |
|-------------|-------------------|--------------|---------------|--------------------------------|--------------------|--------------------|--------------------------|
| Estonia     | Mahtra (EE_Mah)²  | 59° 05.31²   | 25° 00.12²    | 471                            | − 19               | 9                  | − 8                     |
|             | Pühatu (EE_Puh)²  | 58° 56.37²   | 24° 30.54²    | 453                            | − 19               | 9                  | − 8                     |
|             | Üldruma (EE_Urd)² | 58° 47.29²   | 24° 03.06²    | 408                            | − 18               | 9                  | − 8                     |
|             | Lauka (EE_Lau1,   | 58° 55.95²   | 24° 11.37²    | 423                            | − 18               | 10                 | − 6                     |
|             | EE_Lau2)²         |              |               |                                 |                    |                    |                          |
|             | Mulavere (EE_Mul)² | 58° 37.17²   | 26° 34.41²    | 402.5                          | − 18               | 9                  | − 10                    |

**Table 1.** Localities and selected climatic factors. *Minimum value of the 8-day MODIS day-time LST time series data. **Mean value the 8-day MODIS day-time LST time series data. *Mean value of the 8-day MODIS day-time LST time series data for Dec/Jan. *Localties where the authors made phytosociological relevés and took soil samples.
The raw species composition data matrix and Bray dissimilarity index were subjected to NMDS, to superimpose soil variables over NMDS ordination of species composition data (n = 16 sites in total). All groups, followed by ANOVA with Tukey’s post hoc test. The significance was set at p < 0.05 in all analyses. Statistical analysis of the obtained results was performed using the vegan package to test for differences between means of particular parameters of different vegetation groups. Prior to analysis, assumptions of ANOVA, data normality and homogeneity of variance, were tested applying the envfit function was used to test for differences between means of particular parameters of different vegetation groups. Prior to analysis, assumptions of ANOVA, data normality and homogeneity of variance, were tested applying the Shapiro–Wilk test and Levene’s test, respectively. Slight deviations from data normality were tolerated. The level of significance was set at p < 0.05 in all analyses. Statistical analysis of the obtained results was performed using R or in Past 3.10.

Regarding the tested chemical properties of the soil, the statistical significance of the differences between means was determined by testing the normality of distribution in each group and homogeneity of variance in all groups, followed by ANOVA with Tukey’s post hoc test. The significance was set at p < 0.05. These analyses were performed using Statistica 12.5 PL software (StatSoft Inc., Tulsa, OK, USA).

Results

Vegetation types with the occurrence of C. pulicaris. In total, 310 moss and vascular plant species were recorded (59 mosses, 251 vascular plants). Carex pulicaris locations were found to demonstrate a range of species compositions. Our cluster analysis of the similarity in species composition between sites (Fig. 2) revealed five natural vegetation groups, as presented throughout the manuscript. These groups roughly correspond to the region of origin: Estonian sites (Estonian group), Polish sites including Danish sites (Polish group), Slovakian sites (Slovak group), relevés from Radecz in Poland, which appear as a separate group (Radecz group) and a final group composed of sites of different regions (Ambiguous group); not surprisingly, the final group has low statistical support (Fig. 2).

Most of the recorded species are very rare in the dataset, with 69.03% being present in fewer than five plots, i.e. approximately 10% of all of investigated plots. In contrast, only ten species are present in more than half of all plots with C. pulicaris. These are Potentilla erecta (83.37% of all analysed plots), Carex panicea (83.72%), Briza media (79.07%), Succisa pratensis (65.12%), Molinia caerulea (62.79%), Galium uliginosum (55.81%), Cirsium palustre (53.49%), Calliergonella cuspidata (51.16%), and Holcus lanatus (51.16%).

Other species were found to accompany C. pulicaris in particular vegetation types. Carex davalliana dominates in the Estonian and Slovak groups (83.33% and 100% of sites, respectively), Anthoxanthum odoratum is common in the Polish and Ambiguous groups (92.31% and 75%, respectively), and Lotus uliginosus is also common in the Polish group (76.92%). The Slovak group is floristically very rich (results presented below), with Campylium stelatum (92.31%), Fissidens adianthoides (92.31%), Bryum pseudotriquetrum (76.92%), Eriophorum angustifolium (76.92%), Carex echinata (69.23%), Carex flava (69.23%), Parnassia palustris (69.23%) and Plagiomnium palustre (69.23%) commonly found together with C. pulicaris. Many species are commonly observed with C. pulicaris in the Radecz group, but these data were obtained from only three related relevés.

Statistically significant differences in diversity between natural vegetation groups were found for species richness, Shannon’s H diversity index, as well as for evenness index. The Estonian group differs from all other groups in species richness and Shannon’s H diversity index (Fig. 3). Our data showed that the phytocoenoses with C. pulicaris are moderately rich, with the number of species per relevé varying between 13 and 59. Comparatively high species richness was also observed in the Polish (35.38 ± 6.62), Ambiguous (35.00 ± 5.53), Slovak (42.92 ± 9.31) and Radecz groups (41.67 ± 1.53), but lower in the Estonian group (18.00 ± 3.95) (Fig. 3). Shannon’s H diversity index, reflecting species richness, ranged from 2.40 to 3.97 between groups, being high in the Polish (3.32 ± 0.11), Ambiguous (3.39 ± 0.20), Slovak (3.53 ± 0.23) and Radecz groups (3.52 ± 0.03), but lower in the Estonian group (2.61 ± 0.20). The evenness index varies from 0.88 to 0.98, and is always higher than 0.90 within a particular group (Fig. 3), suggesting that species composition has quite an even distribution between sites.

Mosses are prevalent in the Radecz (11–15 species per site, mean 12.3) and Slovak groups (7–18 species per site, mean 11.3); however, they are rare or even absent in the rest, where number of moss species per site ranged from 0 to 8.
Environmental data assessment of sites with *C. pulicaris* with regard to their vegetation composition and the abundance of *C. pulicaris*. The NMDS grouping of the whole dataset corresponds to the cluster analysis. Four groups, viz. the Estonian, Slovak, Polish and Radecz groups, are compact and well resolved on the NMDS ordination biplot (Fig. 4A); however, the members of the Ambiguous group, weakly supported in cluster analysis, are scattered across the NMDS ordination biplot. The abundance of *Carex pulicaris* is significantly correlated with the NMDS ordination of plant communities. CCA performed on mean EIV scores with a forward selection procedure revealed 11 statistically-significant variables (p < 0.05) out of a total of 16 (Fig. 4B). Reducing the set of EIV variables in the CCA explains 37.86% (constrained) of the total variance.

Most of the relevés are located in the upper half of the CCA plot (Fig. 4B). Two groups dominate: the Polish group on the left side of the CCA plot and the Slovak group on the right. The relevés from Radecz are nested...
within the Slovak group, those of the Ambiguous group are scattered across ordination, while those of the Estonian group are found on the left and lower part of the plot. The EIV indicators suggest that the left–right separation of relevés derives mostly from the presence of species with higher values for Light, sociological class and Humidity (all positively associated with CCA1), as well as Continentality, sociological group of vegetation classes, trend of change and Nitrogen (negatively associated with CCA1). The relevés are separated across the second CCA2 axis by soil reaction and frequency of appearance. The abundance of *C. pulicaris* is also significantly correlated with the CCA-constrained ordination of plant communities. In general, NMDS and CCA correspond to each other and the abundance of *C. pulicaris* is significantly associated with vegetation type, whose differentiation seems to be driven by factors acting on large geographic scales.

The NMDS analyses of the species composition data of the reduced dataset (27 localities, Fig. 5A) found the overall groupings identified in the NMDS results of the whole dataset to be preserved. Latitude, Longitude, Mean precipitation and Minimal daily temperature, as well as *C. pulicaris* abundance, were found to significantly correlate with NMDS ordination.

Figure 4. Ordination biplot of non-metric multidimensional scaling (NMDS) and canonical correspondence analysis (CCA). (A) NMDS of species composition data showing grouping of localities with maximal variance explained along NMDS1 and NMDS2. Ellenberg indicator values (EIVs, p < 0.05) fitted to ordination biplot; (B) Canonical correspondence analysis (CCA) performed on matrices of species composition data and mean EIVs. Only significant variables (p < 0.05) explaining constrained variation, identified based on forward selection, were used in parsimonic CCA. Locality abbreviations follow Table 1. Colouring corresponds to clustering pattern, symbol size reflects *Carex pulicaris* abundance. *Carex pulicaris* abundance vector is fitted to NMDS and CCA models (p < 0.05). Colouring of symbols: black—Estonian group, blue—Slovakian group, orange—Radecz group, purple—Ambiguous group, red—Polish group.
The CCA analyses performed on the independently-gathered database of climate data described above (Fig. 5B) found that while the reduced CCA model was statistically significant (p = 0.001), only the first two axes were statistically significant (p < 0.05). The forward selection procedure suggests that only Latitude and Mean precipitation are statistically significant variables (p < 0.01). However, this CCA model explains only 11.24% (constrained) of the total variance. The resulting general grouping pattern of vegetation relevés appears slightly changed, with the Estonian group and Polish relevés being found in the right and upper parts of the plot, and the Slovakian group in the lower left part (Fig. 5B). The abundance of \( C. \) pulicaris was found to fit significantly to the groupings observed in the reduced CCA model; it also correlated negatively with Latitude, which is reflected on CCA ordination (Fig. 5B).

**Soil properties at sites with \( C. \) pulicaris.** The studies on soils associated with \( C. \) pulicaris in Estonia, Poland, Denmark and Slovakia indicate that the species prefers moist habitats: peat bogs with various degrees of decay (Murshic Histosols) and humus mineral soils (Umbric Gleysols).
In Poland and Estonia, some sites were located in fens with a weakly moorsh forming process. At the surface level (rhizosphere), they were characterized by low ash content (< 20%) and acidic or slightly acidic pH. In Slovakia, *C. pulicaris* also grew in fen, but strongly decayed bogs with high ash content (> 40%) and slightly acidic or neutral pH. The rhizospheres of the bogs differed significantly with regard to total nitrogen content (Table 2). The soils from Estonia contained on average about 80% more total nitrogen than those in Poland and Slovakia. No significant differences were found in mean total sulfur content, C/N ratio or salinity. The soils on which *C. pulicaris* occurred were characterized by a varying content of available phosphorus (from small to medium amounts) and magnesium (from small to very large amounts) and a very low content of available potassium. The Estonian, Polish and Slovak bogs did not differ significantly in their available K or Na content. The peatlands from Poland contained significantly more available P than those from Slovakia, which were richer in available Ca and Mg (Table 2).

### Table 2. Basic soil properties and macronutrient contents.

| The localizations of *Carex pulicaris* | Organic matter | Total | pH | Salinity | Available macroelements (soluble in 0.5 mol dm⁻³ HCl) |
|--------------------------------------|----------------|-------|----|----------|---------------------------------------------------|
|                                      |                |       |    |          | P      | Na   | K   | Ca   | Mg     |
|                                      |                | C    | N  | S       | C/N   | H₂O | KCl | µS cm⁻¹ | mg kg⁻¹ |
| Estonia                              |                |      |    |         |       |     |     |        |         |
| Organic soils (Murshic Histosols)−Eo |                |      |    |         |       |     |     |        |         |
| Laukna 1                            | 80.28          | 40.37| 2.96| 0.34    | 13.77 | 6.49| 6.02| 353.33  | 191.37  |
| Müllavere                           | 72.30          | 36.66| 2.63| 0.36    | 14.17 | 6.91| 6.53| 140.00  | 204.36  |
| Piibatu                              | 87.76          | 42.87| 2.69| 0.28    | 16.01 | 6.43| 5.70| 176.67  | 183.6   |
| x                                    | 80.11c         | 39.97| 2.76| 0.33a   | 14.65a| 6.61| 6.08bcd| 223.33a | 170.36a |
| Mineral soils (Umbric Gleysols)−Em   |                |      |    |         |       |     |     |        |         |
| Laukna 2                            | 12.23          | 5.48 | 0.34 | 0.04    | 15.95 | 6.83| 6.24| 135.00  | 217.35  |
| Mahtra                              | 18.29          | 7.83 | 0.73 | 0.16    | 11.84 | 7.00| 6.29| 380.00  | 247.8   |
| Údrauma                              | 17.61          | 8.96 | 0.69 | 0.10    | 12.38 | 7.01| 6.21| 130.00  | 150.37  |
| x                                    | 16.04a         | 7.72 | 0.59 | 0.10a   | 13.99a| 6.95| 6.25cd| 215.00a | 205.17ab|
| Denmark (Bornholm)                   |                |      |    |         |       |     |     |        |         |
| Organic soils (Murshic Histosols)−Po |                |      |    |         |       |     |     |        |         |
| Domysłów                            | 84.38          | 46.42| 1.22 | 0.22    | 38.05 | 5.91| 5.03| 150.00  | 284.6   |
| Rozwarowskie Marshi                  | 98.18          | 48.52| 0.8  | 0.07    | 60.65 | 5.78| 5.16| 423.00  | 310.3   |
| Beka                                | 72.17          | 35.22| 1.55 | 0.6    | 13.85 | 6.3 | 5.83| 678.00  | 417.2   |
| x                                    | 84.91c         | 43.42c| 1.52 | 0.30a   | 38a   | 5.99a| 5.34ab| 471a    | 337.37b |
| Mineral soils (Umbric Gleysols)−Pm   |                |      |    |         |       |     |     |        |         |
| Nosalin                              | 12.66          | 6.00 | 0.38 | 0.02    | 15.79 | 6.04| 5.65| 116.00  | 631.0   |
| Piaśnickie Łąki                      | 7.65           | 5.07 | 0.37 | 0.09    | 13.70 | 5.68| 5.14| 104.00  | 567.3   |
| Polana Białego Potoku               | 12.27          | 5.38 | 0.43 | 0.14    | 12.51 | 5.47| 4.7 | 1114.00 | 381.7   |
| x                                    | 10.86a         | 5.48a| 0.39 | 0.08a   | 14.00a| 5.73a| 5.16a| 444.67a | 526.67c |
| Slovakia                            |                |      |    |         |       |     |     |        |         |
| Organic soils (Murshic Histosols)−So |                |      |    |         |       |     |     |        |         |
| NP Polominy NPR 1                    | 50.36          | 20.24| 1.22 | 0.26    | 19.17 | 6.04| 5.83| 824.00  | 124.3   |
| NP Polominy NPR 2                    | 51.86          | 22.82| 1.52 | 0.32    | 18.31 | 6.07| 5.87| 820.50  | 114.4   |
| NP Polominy NPR 3                    | 52.21          | 23.71| 1.62 | 0.33    | 14.78 | 6.13| 5.86| 867.00  | 103.4   |
| x                                    | 51.48b         | 22.25b| 1.45abc| 0.30a | 17.42a| 6.08abc| 837.17a | 114.03a |
| Organic calcareous soils (Calcic Murshic Histosols)−Sac |                |      |    |         |       |     |     |        |         |
| Ružomberok-Podsucha 1                | 35.54          | 25.38| 2.04 | 0.59    | 12.53 | 7.03| 6.80| 676.00  | 172.7   |
| Ružomberok-Podsucha 2                | 37.93          | 27.41| 1.94 | 0.42    | 14.66 | 7.07| 6.88| 669.00  | 154.0   |
| Ružomberok-Podsucha 3                | 34.38          | 21.74| 1.11 | 0.19    | 21.06 | 7.11| 6.91| 673.50  | 148.5   |
| x                                    | 35.95b         | 24.84b| 1.69 | cd 0.40a | 16.08a| 7.07b| 6.86d| 672.83a | 158.40a |

In Poland and Estonia, some sites were located in fens with a weakly moorsh forming process. At the surface level (rhizosphere), they were characterized by low ash content (< 20%) and acidic or slightly acidic pH. In Slovakia, *C. pulicaris* also grew in fen, but strongly decayed bogs with high ash content (> 40%) and slightly acidic or neutral pH. The rhizospheres of the bogs differed significantly with regard to total nitrogen content (Table 2). The soils from Estonia contained on average about 80% more total nitrogen than those in Poland and Slovakia. No significant differences were found in mean total sulfur content, C/N ratio or salinity. The soils on which *C. pulicaris* occurred were characterized by a varying content of available phosphorus (from small to medium amounts) and magnesium (from small to very large amounts) and a very low content of available potassium. The Estonian, Polish and Slovak bogs did not differ significantly in their available K or Na content. The peatlands from Poland contained significantly more available P than those from Slovakia, which were richer in available Ca and Mg (Table 2).
Carex pulicaris was also found on moist mineral soils (Umbric Gleysols) with a mean organic matter content of 10 to 16% and a C/N ratio ranging from 13 to 14. Despite their similar systematic affiliation, the surface soil layers (rhizospheres) differed in their chemical composition between Estonia, Denmark and Poland (Table 2). The soils in Estonia were slightly acidic, with a low content of assimilable phosphorus and potassium but with an abundance of Mg. On the other hand, soils from Denmark and Poland were acidic and poor in assimilable K and Mg; however, the soils from Estonia and Denmark demonstrated significantly lower assimilable P and considerably lower exchangeable Na content than those from Poland. Moreover, all three groups of soils were characterized by a low salt concentration and a similar content of exchangeable Ca. All analyzed soils contained small amounts of bioavailable and total forms of heavy metals (Cd, Co, Cu, Pb, Mn and Fe; Tables 3 and 4).

The PCA analysis of the soil dataset (17 sites × 34 soil variables) found that the site groupings reflect generally geographic locations and soil types; in addition, this patterning appears to be irrespective of plant community type, and of the abundance of Carex pulicaris (Fig. 6A,B). In contrast, the results of the NMDS analysis of plant communities with regard to soil subset (16 sites × 194 species, plant community data are missing for single locality from Slovakia—SK_PodR) are roughly in line with the relevé grouping in the whole dataset (43 sites × 310 species). NMDS analysis separated the Estonian and Polish vegetation groups, on the right of the plot, from the Ambiguous group and one Slovakian relevé, on the left of the plot (Fig. 6C). The only soil variables significantly fitted to this NMDS grouping were pH and total Pb. Most importantly, Carex pulicaris abundance fits significantly to the NMDS groupings (p < 0.01) (Fig. 6C).

| The localizations of Carex pulicaris | Available heavy metals (soluble in 0.5 mol dm⁻³ HCl) | Cd | Co | Cu | Ni | Pb | Mn | Fe | Zn |
|--------------------------------------|-----------------------------------------------|----|----|----|----|----|----|----|----|
| **Estonia**                          |                                               |    |    |    |    |    |    |    |    |
| Organic soils (Murshic Histosols)    |                                               |    |    |    |    |    |    |    |    |
| Laukna 1                             | 0.46                                         | 0.5 | 2.8 | 2.37 | 8.53 | 20.56 | 1901.33 | 7.32 |
| Mullavere                            | 0.13                                         | 0.32 | 0.63 | 0.36 | 3.37 | 30.72 | 1299.9 | 6.61 |
| Põlhu                                | 0.29                                         | 0.38 | 0.75 | 0.36 | 9.63 | 21.34 | 3376   | 10.94 |
| x                                    | 0.29ac | 0.40ab | 1.39ab | 1.03a | 7.18a | 24.21ab | 2192.41ab | 8.29a |
| Mineral soils (Umbric Gleysols)—Em   |                                               |    |    |    |    |    |    |    |    |
| Laukna 2                             | 0.06                                         | 0.53 | 1.57 | 0.45 | 7.61 | 10.1  | 1163   | 5.27 |
| Mähtna                               | 0.14                                         | 0.68 | 2.7  | 1.31 | 5.79 | 20.87 | 1438   | 9.15 |
| Üdruma                                | 0.17                                         | 1.39 | 1.55 | 0.71 | 8.59 | 41.07 | 2337.67 | 15.02 |
| x                                    | 0.12c | 0.87ab | 1.94ab | 0.82a | 7.33a | 24.01ab | 1646.22ab | 9.81a |
| **Denmark (Bornholm)**               |                                               |    |    |    |    |    |    |    |    |
| Mineral soils (Umbric Gleysols)—Dm   |                                               |    |    |    |    |    |    |    |    |
| Sandvig                              | 0.37                                         | 0.51 | 1.05 | 0.16 | 8.93 | 77.74 | 893    | 2.89 |
| Rønnekaer Lake                      | 0.79                                         | 1.1  | 6.67 | 1.6  | 18.38 | 159.4 | 1158   | 14.37 |
| Bastemose                            | 0.41                                         | 1.05 | 7.55 | 1.54 | 14.2 | 44.06 | 1000   | 7.01 |
| x                                    | 0.52ab | 0.89ab | 5.09b | 1.10a | 13.84a | 93.73b | 1017.00ab | 8.09a |
| **Poland**                           |                                               |    |    |    |    |    |    |    |    |
| Organic soils (Murshic Histosols)—Po |                                               |    |    |    |    |    |    |    |    |
| Domysłów                             | 0.16                                         | 0.01 | 0.88 | 0.54 | 6.82 | 42.45 | 2617   | 23.47 |
| Rozwarowickie Marsh                  | 0.47                                         | 0.21 | 2.56 | 0.13 | 35.6 | 14.46 | 1309   | 36.57 |
| Beka                                 | 0.27                                         | 0.01 | 1.27 | 0.79 | 4.87 | 3.57  | 178.9  | 5.28 |
| x                                    | 0.30abc | 0.08a | 1.57ab | 0.49a | 15.76a | 20.16a | 1368.30ab | 21.77ab |
| Mineral soils (Umbric Gleysols)—Pm   |                                               |    |    |    |    |    |    |    |    |
| Nosaln                               | 0.21                                         | 0.02 | 2.16 | 0.56 | 13.49 | 662.2 | 23.93  | 23.93 |
| Piasnicksie Łęki                     | 0.37                                         | 0.1  | 2.23 | 1.31 | 6.57 | 6.33  | 996.4  | 11.18 |
| Polana Bialogo Potoku                | 0.52                                         | 0.97 | 2.76 | 1.66 | 14.29 | 27.75 | 1565   | 28.26 |
| x                                    | 0.37abc | 0.36ab | 2.33ab | 1.44a | 15.86a | 1074.53ab | 21.12ab |    |
| **Slovakia**                         |                                               |    |    |    |    |    |    |    |    |
| Organic soils (Murshic Histosols)—So |                                               |    |    |    |    |    |    |    |    |
| NP Poloniny NPR 1                    | 0.7                                          | 1.08 | 11.03 | 9.74 | 24.31 | 67.48 | 2664.55 | 16.66 |
| NP Poloniny NPR 2                    | 0.67                                         | 1.04 | 10.59 | 9.12 | 23.07 | 61.7  | 2387.3 | 15.62 |
| NP Poloniny NPR 3                    | 0.68                                         | 1.03 | 10.39 | 9.03 | 22.73 | 62.72 | 2285.05 | 16.72 |
| x                                    | 0.68ab | 1.05b | 10.67c | 9.30b | 23.37a | 63.97ab | 2445.63b | 16.33a |
| Organic calcareous soils (Calcic Murshic Histosols)—SoC |   |    |    |    |    |    |    |    |    |
| Ružomberok-Podsucha 1                | 0.57                                         | 0.4  | 0.4  | 0.71 | 0.23 | 234.76 | 228.31 | 41.6  |
| Ružomberok-Podsucha 2                | 0.59                                         | 0.49 | 0.8  | 0.84 | 8.29 | 254.18 | 447.19 | 39.24 |
| Ružomberok-Podsucha 3                | 0.58                                         | 0.34 | 0.36 | 0.73 | 4.27 | 253.74 | 213.99 | 40.82 |
| x                                    | 0.58ab | 0.41ab | 0.52a | 0.76a | 4.26a | 247.56c | 296.30a | 40.55b |

Table 3. Content of available heavy metals in soils.
| The localizations of Carex pulicaris | Total macro and heavy metals |
|----------------------------------|-----------------------------|
|                                  | P   | Na  | K    | Ca   | Mg  | Cd  | Co  | Cu  | Ni  | Pb  | Mn  | Zn  |
|                                  | mg  | kg  | kg   | kg   | kg  | kg  | kg  | kg  | kg  | kg  | kg  | kg  |
| **Estonia**                      |     |     |      |      |     |     |     |     |     |     |     |     |
| Organic soils (Murthic Histosols)—Eo |     |     |      |      |     |     |     |     |     |     |     |     |
| Laha 1                          | 808.5 |    | 1176.4 |      |     |     |     |     |     |     |     |     |
| Mällivere                      | 960.67 |    | 803.83 |    | 2062.67 | 39,478.33 |     |     |     |     |     |     |
| Põhatsa                        | 1598.67 |    | 661.73 |      | 1849.83 | 26,120 |      | 1646.67 | 0.53 | 5.17 | 5.97 | 0.69 |
| **Śweden**                      | 1122.61ab |    | 880.65a |    | 1768.04a | 35,378.33a | 2523.56a | 0.83a | 8.45a | 6.85ab | 2.64a | 13.08a |
| Mineral soils (Umbric Gleysols)—Em |     |     |      |      |     |     |     |     |     |     |     |     |
| Laha 2                          | 1287 |    | 674.6 |      | 1608.75 | 3568 |     | 1603.50 | 0.16 | 10.04 | 2.69 | 2.84 |
| Mahtna                         | 850.67 |    | 1590.97 |    | 3039.17 | 9032.5 |      | 1089.75 | 0.54 | 6.68 | 7.54 | 1.66 |
| Ühtama                         | 1094.5 |    | 1032.6 |      | 2270.13 | 11,386.7 |      | 1445.67 | 0.26 | 9.86 | 4.64 | 1.68 |
| **Śweden**                      | 1077.39abc |    | 1099.39a |    | 2306.02a | 8762.39a | 1379.64a | 0.32a | 8.86a | 4.96ab | 2.06a | 14.30a |
| **Denmark (Bornholm)**         |     |     |      |      |     |     |     |     |     |     |     |     |
| Organic soils (Murthic Histosols)—Po |     |     |      |      |     |     |     |     |     |     |     |     |
| Dømålsøen                      | 924 |    | 2331 |      | 321 | 22,500 | 749.5 | 0.55 | 2.64 | 7.56 | 3.59 | 23.71 |
| Rozewarstowske Marsh            | 1716 |    | 3604 |      | 5005 | 8404 |      | 1002.5 | 0.55 | 4.83 | 3.08 | 2.27 |
| Bekä                           | 1716 |    | 1024.8 |    | 2895 | 18,276.7 | 3378.6 | 0.4 | 8.4 | 5.49 | 1.92 | 41.6 |
| **Śweden**                      | 1452.01abc |    | 2319.93a |    | 2740.33a | 16,393.57a | 1710.20a | 0.50a | 5.29a | 5.38ab | 2.59a | 37.26a |
| Mineral soils (Umbric Gleysols)—Pm |     |     |      |      |     |     |     |     |     |     |     |     |
| Nosaline                       | 1924 |    | 2012 |      | 1872.5 | 8990 |      | 1410 | 0.45 | 6.06 | 3.35 | 3.79 |
| Pisnieckie Łęki                 | 1342 |    | 2200 |      | 1401 | 10,970 | 1379 | 0.75 | 6.79 | 2.28 | 2.64 | 21.5 |
| Polana Białego Potoku          | 1430 |    | 1906 |      | 2879.5 | 5571 |      | 768 | 1.44 | 10.34 | 3.96 | 4.24 |
| **Śweden**                      | 1598.67c |    | 2039.33a |    | 2051.00a | 8510.33a | 1185.67a | 0.75a | 6.79a | 2.28a | 2.64a | 21.5 |
| **Poland**                      |     |     |      |      |     |     |     |     |     |     |     |     |
| Organic soils (Murthic Histosols)—So |     |     |      |      |     |     |     |     |     |     |     |     |
| NP Poloniny Np 1                | 369.05 |    | 434.26 |      | 715.35 | 15,250 |      | 2673.15 | 0.98 | 6.94 | 25.27 | 22.48 |
| NP Poloniny Np 2                | 378.4 |    | 458.75 |      | 529.45 | 14,710 |      | 2530.5 | 0.88 | 7.48 | 24.12 | 21.23 |
| NP Poloniny Np 3                | 371.8 |    | 620.29 |      | 576.55 | 14,695 |      | 2477 | 0.95 | 8.44 | 25.36 | 23.52 |
| **Śweden**                      | 373.08a |    | 504.43a |    | 607.12a | 14,885.00a | 2562.26a | 0.94a | 7.62a | 24.92c | 21.23a | 31.11ab |
| Organic calcareous soils (Calcic Murthic Histosols)—Soc |     |     |      |      |     |     |     |     |     |     |     |     |
| Ružomberok-Podolschuka 1        | 343.75 |    | 225.69 |      | 1330.25 | 135,750 |      | 3190.53 | 1.42 | 10.68 | 9.26 | 4.09 |
| Ružomberok-Podolschuka 2        | 333.85 |    | 229.74 |      | 1040.55 | 362,418 |      | 2881.83 | 1.07 | 6.06 | 7.88 | 3.43 |
| Ružomberok-Podolschuka 3        | 312.95 |    | 496.23 |      | 1099.75 | 173,071.5 |      | 3062.01 | 1.27 | 7.67 | 9.12 | 4.33 |
| **Śweden**                      | 330.18a |    | 317.22a |    | 1156.85a | 223,746.50b | 3044.79a | 1.25a | 8.14a | 8.75a | 3.95b | 35.29b |

Table 4. Total content of macroelements and heavy metals in the soil.

Discussion

The Estonian, Slovak and Radecz groups, which were most closely related to a particular region within the range of *C. pulicaris*, were characterized by a homogeneous type of vegetation. The Estonian group was represented by communities of the Molinion caeruleae alliance, sometimes with a significant share of *Carex davalliana* and the other two by communities of the Caricetalia davallianae order. In Slovakia, *C. pulicaris* is associated with non-forest communities of minerotrophic fens, particularly with the Sphagno warnstorfiani-Tomentypinion alliance. In turn, the Polish and Ambiguous groups showed greater diversity: their composition included communities from both of the above-mentioned syntaxonomic units, with the Polish group including some from the Caricetalia nigrae order, with some tendency towards the Narido-Callunetalia class.

Throughout its entire range, *C. pulicaris* is commonly derived from the communities of the Molinion alliance, and this can be seen in Slovenia, the Netherlands and Sweden. In France, it was recorded in acidic fen grasslands (Carex nigrae communities), and in Great Britain, in communities such as calcicolous grassland community Sesleria albicans—*Galium sterneri* in the *Carex pulicaris*—*Carex panicea* subcommunity, mire community Carex dioica—*Pinguicula vulgaris* and Molinia caerulea—*Cirsium dissectum* fen-meadow (according to
Figure 6. Ordination biplot of principal component analysis (PCA) of soil dataset. (A) including Slovak sites SK_Pod1 and SK_PodR and (B) excluding them (lower panel). Grouping circles according to classically recognised soil types; (C) non-metric multidimensional scaling (NMDS) of species composition data showing grouping of localities, with maximal variance explained along NMDS1 and NMDS2. Soil variables significant at p < 0.05 fitted to ordination biplot. Locality abbreviations follow Table 1. Colouring corresponds to clustering pattern, symbol size reflects Carex pulicaris abundance. Carex pulicaris abundance is not related to PCA grouping patterns (p > 0.05) but significant to plant community grouping (p < 0.05). Colouring of symbols: black—Estonian group, blue—Slovakian group, orange—Radecz group, purple—Ambiguous group, red—Polish group, white—locality in Slovakia with the occurrence of C. pulicaris, but lacks species composition data. Note: Averages from three subsamples were inputs for localities SK_Pod1 and SK_PodR.
The last of these communities is the British equivalent of Cirsi-Molinietum Sissingh & de Vries 1942, described from the Netherlands, Belgium, Germany and Ireland.

The groups of plant communities separated as a result of the analyses were generally characterized by considerable plant species diversity, with the only exception being the Estonian group (Fig. 3); the lower diversity indices in this group was undoubtedly influenced by the high share of Molinia caerulea in the studied phytocoenoses. This is a highly competitive grass, and its presence in large clumps not only limited the number of safe places for the germination of other plant species diaspores, but also hindered their development. This was especially true for annual plants, and to a lesser extent, the perennials, which show vegetative reproduction. Moreover, most of the plant patches were partially shaded by the crowns of trees growing in the immediate vicinity. Under these conditions, Carex pulicaris often grew in the Molinia clumps. We observed this phenomenon not only in the locations in Estonia, but also in the Rozwarowskie Marshes in Poland (PL_BagR).

Regardless of the research area, Carex pulicaris was often accompanied by species associated with grassland communities, particularly meso- and eutrophic hay meadows and riverside herbaceous plant communities; these are permanently, or at least periodically, moist (order Molinietalia caeruleae). The significant share of these species in some of the examined patches of Carex pulicaris communities from the Caricetalia davallianae order (e.g. in Slovakia) may indicate the presence of fluctuations in the water regime and/or a slightly increased availability of nutrients for plants. Such coexistence of species may take place over a longer period of time, and in the case of a permanent change in habitat conditions, it may lead to another stage of succession towards meadow communities from the Molinion caeruleae alliance. Hence, it is sometimes difficult to unequivocally define the syntaxonomic affiliation of plant communities from Carex pulicaris.

The share of Carex pulicaris in the analyzed groups was diversified, and it was neither a dominant nor a codominant species in any of the phytocoenoses. In contrast to the eastern end of its range, Carex pulicaris can be found abundantly in the remainder of its distribution area; it has been reported as the dominant or codominant species in some phytocoenoses, for instance in Great Britain and Ireland. As Carex pulicaris is a poorly-germinating, light-requiring species that is weak in competition, its abundance is favored by extensive land use, which limits the development of tall, expansive perennials. Our findings indicate that the mowing of meadows in areas where Carex pulicaris occurs (Domysłów and Rozwarowskie Marshes) favors its survival, even under conditions of high competition from Molinia caerulea, and in the vicinity of Phragmites australis plantations. It is classified as a species dependent on mowing in the area of the fenoscanadian limestone forest meadows, and was only found in mowed areas in the costal grasslands in the Stockholm archipelago. Also in the Netherlands, this type of land use is necessary to maintain the structure and species composition of meadows belonging to the Molinion caeruleae alliance, where Carex pulicaris is present. This prevents the succession towards scrub and forest, especially when the habitat is fragmented.

Our findings also indicate that a higher abundance of Carex pulicaris is correlated with greater precipitation, albeit to a small extent (Fig. 5). This relationship is demonstrated by the fact that the species was most abundant at the Polana Bialy Potok (Tatry Mts) site (PL_PolB), which had the highest mean annual precipitation (915 mm) of the examined sites. Carex pulicaris is a sub-Atlantic ranging type, indicating that it favors areas with a significant amount of rainfall. It is a common species in Great Britain, being sometimes codominant in plant communities, and is often observed in densely-tufted patches with Sesleria albicans; in this country, it has been found in areas with an annual rainfall of 1239 mm.

An important factor limiting the range of Carex pulicaris, as well as other sub-Atlantic species, may be the occurrence of winter frost. Comparing the isotherms of the mean month temperatures of the coldest month (°C) calculated for sea level with the species distribution data, a clear relationship can be seen between the limit of its range and the -4 °C isotherm. The results of local studies from mountain areas in southern Germany highlight the significant role played by both temperature and precipitation on the occurrence of Carex pulicaris. In contrast, while our present findings do not show any clear relationship between species abundance and air temperature, the CCA analysis (Fig. 5B) suggests that rainfall is of greater importance.

Our results suggest that in the eastern edge of the Carex pulicaris distribution range, its abundance may be latitude dependent, with a lower abundance observed in plant communities in more northerly locations. In addition, it grew sparingly in the north-eastern part of our research area, including almost all the Estonian sites, but had a fairly significant share in the community patches in the south-east, including most Slovak sites. However, no such relationship was observed in the north-western extremities of its range, where in some plant communities, it is very common and is the dominant species; it should be noted though that, being a sub-Atlantic species, the conditions for development in these areas are very favorable.

Carex pulicaris is found on various types of bogs, including fen, transitional and lag of raised bogs, as well as wet heathlands, Nardus grasslands and wet meadows. In addition to organic soils, it also often inhabits humus and moist mineral soils, while it is less common in other habitats, such as clay or sandy peat soils. In the sites in the present study, Carex pulicaris grew in humid but diversified habitats: from bogs, where the Murshic Histosols soils developed, to humus mineral Umbric Gleysols soils, regardless of whether it was at the edge or the center of the distribution range. Carex pulicaris occurs on a variety of soil types with organic matter content ranging from 1.6 to nearly 100%.

Certain chemical and physical properties of soils have a strong influence on the occurrence of plants. Our research showed that the surface layers (rhizospheres) of the soils in the tested areas demonstrated great variation in their physical and chemical compositions. Murshic Histosols were acidic to slightly acidic, while Umbric Gleysols were acidic to neutral.

The areas across Europe where Carex pulicaris occurs demonstrate similar variations in soil pH. However, Carex pulicaris generally preferred slightly acidic soils, and did not favour strongly acidic and alkaline soils. Our study showed that soil pH was significantly correlated with the grouping of plant communities with Carex pulicaris participation. Soil acidity affects such features as the trophic nature of the habitat, the quantity and quality of...
humus, and the abundance of assimilable macro- and microelements. The wide range of soil pH values tolerated by *Carex pulicaris* may indicate a well-developed adaptability to various environmental conditions; however, this contrasts with previous observations, i.e., that the species occurs in bags of a narrow ecological amplitude.

Nitrogen, K and P levels are particularly important for plant community stability. In wet habitats, an increase of P, K and N levels in soil can lead to a decline in the diversity and abundance of plant species. The results of our analyses showed that both organic and mineral soils were generally low in available P and K, which may support the growth of *Carex pulicaris*. These habitats have previously been found to have low nitrogen content and data from areas within the *Carex pulicaris* range suggest that its communities require low N, P and K concentrations. However, our present results do not indicate any significant relationship between the abundance of *Carex pulicaris* itself and the P, N and K content of the soil. The plant communities of *Carex pulicaris* are sensitive to excess N–NH₄ levels and N–NO₃ deficiency; this relationship is related to long-term stagnation of water on the soil surface, resulting in the development of anaerobic conditions.

Our own studies indicate that *Carex pulicaris* abundance is not significantly affected by soil Ca, Mg and salt content. The species was recorded in soils with various Mg, Ca and salinity levels, and its associated plant communities have been observed in habitats relatively rich in nutrients. It has also been found to grow in soils containing low levels of heavy metals.

*Carex pulicaris* appears quite resistant to anthropogenic influences known to increase habitat trophy, as indicated by our finding that macro- and micronutrient content appears to have no clear effect on its abundance in plant communities. On the other hand, distinct changes in soil moisture and the cessation of pratotechnical practices may limit its abundance.

*Carex pulicaris* responds well to surface floods in the autumn–summer period as well as to strong falls in groundwater level in summer. Short periodic floods cause a reduction in the mineralization of organic matter; they also drive the release of nutrients, which are beneficial for the habitat, and stimulate the formation of Fe, Ca and P complexes, which are normally inaccessible to plants. However, if maintained for too long, excessive soil moisture levels result in changes in the oxidoreductive and chemical properties of the soil that are unfavorable for the growth of *Carex pulicaris*. In contrast, a rise in the level of groundwater may favor paludification processes, which in turn will lead to the disappearance of *Carex pulicaris* as a result of the reconstruction of plant communities with more competitive members. In addition, excessive dehydration and oxygenation of the habitat causes rapid mineralization of organic matter and the release of large quantities of mineral nutrients; this is also unfavorable for *Carex pulicaris*, and favors the entry of expansive perennials, trees and shrubs.

Finally, most of the Estonian sites were characterized by large shares of trees in the vegetation patches; this can increase shading and thus may be the reason for the low abundance of *Carex pulicaris*. The specific humidity requirements described above explain the sensitivity of this species to changes in humidity in the habitat.

**Conclusions**

Within the eastern end of its range, *Carex pulicaris* is present in five natural phytocoenological groups: four closely correspond to geographic regions, viz. Estonia, Poland, Slovakia and Radecz (Poland), and a fifth Ambiguous group scattered throughout the study region. In general, the groups show a significant diversity of species composition. The Estonian group was represented by communities from the Molinion caeruleae alliance, the Slovak and Radecz groups by communities from the Caricetalia davallianae order, while the other two showed greater diversity with regard to their syntaxonomic units. However, *Carex pulicaris* was not dominant or codominant in any of the groups with regard to the studied phytocoenoses.

Our findings indicate that the abundance of *Carex pulicaris* is positively correlated with the composition of its geographically-diversified plant communities and atmospheric precipitation. In the eastern part of its range, *Carex pulicaris* grows on organic (Murshic Histosols) and mineral (Umbric Gleysols) soils associated with high groundwater conditions. These soils are characterized by an acidic to neutral reaction, narrow C:N ratio, low salinity, mostly low levels of available P and K and micronutrients, and varying levels of available Mg, Ca and Na. *Carex pulicaris* appeared to grow most abundantly in plant communities which prefer slightly acid soils.

**Data availability**

All data matrices that support the findings of this study are available from the corresponding author upon request.

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**References**

1. Lawler, J.J. Climate change adaptation strategies for resource management and conservation planning. The year in ecology and conservation biology. *Ann. N.Y. Acad. Sci.* 1162, 79–98. https://doi.org/10.1111/j.1749-6632.2009.04147.x (2009).
2. Dawson, T. P., Jackson, S. T., House, J. I., Prentice, I. C. & Mace, G. M. Beyond predictions: biodiversity conservation in a changing climate. *Science* 332(6023), 53–58. https://doi.org/10.1126/science.1200303 (2011).
3. Walworth, T. E. et al. Management for network diversity speeds evolutionary adaptation to climate change. *Nat. Clim. Change* 9(8), 632–636. https://doi.org/10.1038/s41558-019-0518-5 (2019).
4. Morelli, T. L. et al. Climate-change refugia: Biodiversity in the slow lane. *Front. Ecol. Environ.* 18(5), 228–234. https://doi.org/10.1002/fee.2189 (2020).
5. Vincent, H., Bornand, C. N., Kempel, A. & Fischer, M. Rare species perform worse than widespread species under changed climate. *Biol. Conserv.* 246, 108586. https://doi.org/10.1016/j.biocon.2020.108586 (2020).
6. Corlett, R. T. & Westcott, D. A. Will plant movements keep up with climate change? *Trends Ecol. Evol.* 28(8), 482–488. https://doi.org/10.1016/j.tree.2013.04.003 (2013).
7. Janssen, J. & Bijlsma, R.J. Molinia meadows on calcareous, peaty or clayey-silt-laden soils (*Molinion caeruleae*) (6410) in the Netherlands, in: Bijlsma, R.J. et al. Defining and applying the concept of favourable reference values for species habitats under the EU
46. Muller, S. Diversity of management practices required to ensure conservation of rare and locally threatened plant species in grasslands: A case study at a regional scale (Lorraine, France). Biodiv. Conserv. 11(7), 1173–1184. https://doi.org/10.1007/s10535-001-9021-8 (2002).

47. Rodwell, J. S. (ed.) British plant communities. Grasslands and montane communities. Vol. 3 (Cambridge University Press. 1992).

48. Rodwell, J.S., Morgan, V., Jefferson, R.G. & Moss, D. The European context of British Lowland Grasslands. INCC Report No. 394, INCC, Peterborough, UK (2007).

49. Carter, S.P., Proctor, J. & Slingsby, P. R. Soil and vegetation of the Kent of Hamar serpentine. Søndefjord. J. Ecol. 75(1), 21–42. https://doi.org/10.2307/2260534 (1987).

50. de Vere, N. Biological flora of the British Isles: Cirsium dissectum (L.) Hill (Cirsium tuberosum (L.) All. subsp. anglicum (Lam.)Bonjour; Cnicus pratensis (Huds.) Willd., non Lam.; Cirsium anglicum (Lam. DC.). J. Ecol. 85, 876–894. https://doi.org/10.1111/j.1365-2745.2007.01265.x (2007).

51. Fernández-Pascual, E. Comparative seed germination traits in Fennoscandian wooded meadows. Plant Ecol. 215(9), 953–962. https://doi.org/10.1007/s11284-014-0347-4 (2014).

52. Meusel, H., Jäger, E. & Weinert, E. Comparative chorology of the Central European flora. VEB Gustav Fischer Verlag, Jena, Germany (1965).

53. Hill, M.O., Preston, C.D. & Roy, D.B. PLANTATT. Attributes of British and Irish Plants: Status, Size, Life History, Geography and Habits. Centre for Ecology and Hydrology, Huntingdon, UK (2004).

54. Dahl, E. The phytogeography of Northern Europe (British Isles, Fennoscandia and adjacent areas). Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9780511565182 (1998).

55. Bartoszek, W., Kuczur, A., Mirek, Z. & Oklejewicz, K. Flea sedge Carex pulicaris L., in: Mirek, Z. & Piątkowska-Mirkowa, H. (Eds.), Red data book of the Polish Carpathians. Vascular plants. Polish Academy of Sciences Institute of Botany W. Szafer, Cracow, pp. 523–525, (in Polish) (2008).

56. Hereźniak, J. Carex pulicaris L. – flea sedge, in: Olaczek R. (Ed.), Red Book of Plants of the Lodzkie Voivodship. Botanical Garden in Łódź, University of Łódź, Łódź, pp. 50–51, (in Polish) (2012).

57. Wolejko, L., Pawlaczyk, P. & Stankowiak, R. (Eds.). Alkaline fens in Poland—diversity, resources, conservation. Naturalists’ Club, Świebodzin, Poland (2019).

58. Koopman, J., Timmerman, A., Hosper, U. & Wielow, H. Distribution, ecology and morphology of three Ceratocystis hybrids in the Province of Fryslân, the Netherlands (Carex, Cyperaceae). Gorteria 41(1), 14–20 (2019).

59. Laughlin, D. C. & Bebb, S. R. Abiotic and biotic factors explain independent gradients of plant community composition in ponderosa pine forests. Ecol. Modell. 205(1–2), 231–240. https://doi.org/10.1016/j.ecolmodel.2007.02.018 (2007).

60. Austrheim, G., Gunilla, E., Olsson, A. & Grøntvedt, E. Land-use impact on plant communities in semi-natural sub-alpine grasslands of Budalen, central Norway. Biol. Conserv. 87(3), 369–379. https://doi.org/10.1016/S0006-3207(98)00071-8 (1999).

61. Dahl, E. The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. J. Ecol. 86(5), 717–738 (1998).

62. McCrea, A. R., Trueman, I. C., Fullen, M. A., Atkinson, M. D. & Besenyei, L. Relationships between soil characteristics and species richness in two botanically heterogeneous created meadows in the urban English West Midlands. Biol. Conserv. 97(2), 171–180 (2001).

63. Wamelink, W., van Dobben, H.E., Goedhart, P.W. & Jones-Walters, L.M. The role of abiotic soil parameters as a factor in the success of invasive plant species. Emerg. Sci. J. 2(6), 308–365. https://doi.org/10.28991/esj-2018-01155 (2018).

64. Iansens, F. et al. Relationship between soil chemical factors and grassland diversity. Plant Soil 202(1), 69–78. https://doi.org/10.1023/A:1004399614865 (1998).

65. Tallonin, J. R. B. & Smith, R. E. N. Restoration of a Cirsio-Molinietum fen meadow on an agriculturally improved pasture. Restor. Ecol. 9(2), 167–178. https://doi.org/10.1111/j.1526-100x.2001.0092167.x (2001).

66. Venterink, H. O., van der Vliet, R. E. & Wassen, M. J. Nutrient limitation along a productivity gradient in wet meadows. Plant Soil 234(2), 171–179. https://doi.org/10.1023/A:1017922157903 (2001).

67. Linderoth, E. Management of nature reserves—with Valön nature reserve in focus. Bachelor of Science with specialization in Environmental Science, pp 1–26, (in Swedish) (2018).

68. Iansens, A. M. & Roelofs, J. G. Restoration of Cirsio-Molinietum wet meadows by sod cutting. Aquat. Bot. 215(9), 279–298. https://doi.org/10.1016/j.aquabot.2016.01.001 (2016).

69. Jurzyk, S. & Wrobel, M. Co-occurrence of two species Molinia caerulea L. and “red-list” species Carex pulicaris L. in western Pomerania (Poland). Pol. J. Ecol. 71(3), 363–367 (2003).

70. Boyer, M. L. H. & Wheeler, B. D. Vegetation patterns in spring-fed calcareous fens: Calcite precipitation and constraints on fertility. J. Ecol. 111(7), 597–609. https://doi.org/10.1111/j.1365-2745.2001.00187.x (2001).

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Author contributions

Z.S., M.S., R.M., R.G., and T.K. designed the study and obtained financial support for the study; Z.S., M.S., G.G., T.K., R.G., M.G. and S.M. determined composition and ecological preference of phytocoenoses; R.M. and D.P. performed chemical composition of soil samples; M.G. gathered climatic data; Z.S., R.M. and V.K. analysed the data; Z.S., M.S., R.M. and V.K. wrote the manuscript; all authors contributed to the draft manuscript and gave final approval for publication.

Competing interests

The authors declare no competing interests.

Additional information

Correspondence and requests for materials should be addressed to V.K.
