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ORIGINAL RESEARCH PAPER

Distribution and habitat properties of *Carex pulicaris* and *Pedicularis sylvatica* at their range margin in NW Poland

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Abstract
This paper presents the distribution dynamics, soil and phytocoenotical conditions of the occurrence of *Carex pulicaris* and *Pedicularis sylvatica* at the margin of their range in NW Poland. Dynamic cartograms of these species were made on the basis of our field studies and available contemporary and historical records. The studies showed that the plants grow on organic hemic-muck soils, mucky soils and typical muckous soils. The occurrence of these two species on different types of soils proves that they are able to adapt easily to varying habitat conditions of post-bog areas. Populations of *C. pulicaris* and *P. sylvatica* were most frequently not numerous and occurred in small community patches. Analyzed phytocoenoses with *C. pulicaris* have been classified as the community of the alliance *Caricion davallianae* or the alliance *Molinion*. Phytocoenoses with *P. sylvatica* are represented by the association *Nardo-Juncetum squarrosi* and the community of the class *Molinio-Arrhenatheretea*. The distribution dynamics of these species shows that they are disappearing from some parts of this region, which proves the recessive trends. This process is more intensive for *P. sylvatica*, which should be included in the red list of Polish plants like *C. pulicaris*. The disappearance of the populations of both species has been caused by worsening habitat conditions (insufficient moisture, eutrophication), expansion of competitive plant species and land abandonment.

Keywords
endangered species; change in distribution; *Nardo-Juncetum squarrosi*; *Caricion davallianae*; *Molinion*; soil characteristics; Pomerania

Introduction

Carex pulicaris (flea sedge) and *Pedicularis sylvatica* (common lousewort) have a similar range in Europe. *Carex pulicaris* belongs to the European temperate (western) subelement, extending to the Atlantic region of Europe [1]. Apart from its occurrence in the continental part, single stands were recorded in Iceland, the Faroe Islands and the Shetland Islands. *P. sylvatica*, in turns, represents the European temperate subelement, the group of European temperate lowland, of sub-Atlantic range type [1]. It is also known from single stands in North America, on the island of Newfoundland, where it is probably not a native species. Both taxa occur in Western, Northern, and Central Europe; from Spain and Great Britain in the west to Poland in the east (*C. pulicaris* somewhat further to the east extending to Estonia), reaching western and southern Scandinavia in the north. Their occurrence does not extend to the Mediterranean region. The eastern range border of these species runs through Poland [2–4].

In many European countries these taxa are of varied threat categories. *Carex pulicaris* is classified as "endangered" in: the Czech Republic [5], Belgium [6], and Slovakia [7]. It is included into the categories: "vulnerable" on the red lists in Finland [8] and Sweden [9], "near threatened" – in Switzerland [10]. In Germany it is also on the red list of threatened species but of varied threat categories in its different federal states [11]. In turn, *P. sylvatica* has the status of "vulnerable" in Slovakia [7] and Switzerland [10]. In Sweden it has been categorized as "near threatened" [9], and in Germany classified as threatened of varied threat categories in its different federal states [11]. In Poland, *C. pulicaris* has been recognized as an endangered species not only on a regional scale but also countrywide. In the "Red list of the vascular plants in Poland" [12] it is listed among "declining" taxa – "critically endangered", and in the Polish red book of plants [13] – placed into the category "endangered". *Pedicularis sylvatica* is threatened regionally [14,15].

Due to the large scale of threats to these species, it is important to find out their present distribution, especially dynamic trends on the edges of their range. However, the maps showing changes in species distribution over time are extremely scarce. In the atlases of plant distribution for West [16] and East Germany [17] the temporal changes are limited to two periods, whereas the latest atlas for the whole area of Germany [18] comprises three periods. For Great Britain and Ireland, the website of the Botanical Society of Britain and Ireland presents updated retrospective hectad maps of the species for six periods so as to facilitate the determination of species dynamic trends on a given area [19]. In NW Poland, the dynamic distribution of *C. pulicaris* [20] was confined to three periods. Recently, however, new localities have been discovered, what largely contributes to our better understanding of the species dynamics on the limit of its range.

The range of plant species depends on their tolerance to environmental stress [21]. In general, marginal populations (on the range boundary) are more frequently exposed to stress conditions [22,23], besides they are more sensitive to habitat changes [24]. In the case of *C. pulicaris* and *P. sylvatica*, a specific water-soil environment is a vital factor determining their occurrence. Wetlands, their natural habitat, were largely drained and used for agriculture in the twentieth century. Currently, despite various protection programmes, their negative transformations are being observed. Even slight variations in moisture conditions cause irreversible changes in the morphological, physical, and chemical properties of organic soils resulting in plant response [25,26].

The aims of the study were: (***i***) to analyze changes in distribution of *P. sylvatica* and updated distribution of *C. pulicaris* on the range limit of both species in NW Poland, (***ii***) to assess habitat conditions, and (***iii***) to determine the phytocoenotical spectrum.

Material and methods

Study species

Carex pulicaris is a perennial, reaching the height of (5)10–30(35) cm, with stubbly, grooved leaves, shorter than the whole stem and forming loose clusters. Flowers are arranged in a single apical, monoecious, few-flowered spike. Ripe utricles are flexed downwards and remain fairly long on the spike axis. A nut is its fruit. The plant is a hemicryptophyte, with its diaspores dispersed epizoochorically. The species is associated with eutrophic communities of the *Caricetalia davallianae* order. It also occurs on wet heaths, *Molinion caeruleae* meadows, in plant associations of the alliance *Nardion* and in the sallow thickets (*Myrico-Salicetum auritae*) [27–29].

Pedicularis sylvatica is a biennial or perennial parasite reaching 5–20 cm. Creeping runners grow out at the base of its upright stem. They are not branched and their leaves are pinnatisect or pinnate. Dorsiventral flowers form a loose inflorescence cluster. A capsule constitutes its fruit. This plant belongs to hemicryptophytes and is dispersed by myrmecochory and anemochory. Most frequently it grows on wet swards with *Nardus stricta*, of the class *Nardo-Callunetea*, very closely related to

Nardo-Juncetum squarrosi. Quite frequently the species may be encountered on fens and transitional bogs of the class *Scheuchzerio-Caricetea nigrae*, on wet heaths of the order *Sphagno-Ericetalia*, rarely in communities of tall sedges, the alliance *Magnocaricion* and *Molinion caeruleae*, as well as on ruderal sites, i.e., disturbed and trampled areas [27–30].

Study area

The study on the distribution of *C. pulicaris* and *P. sylvatica* was conducted in NW Poland, within Pomerania (ca. 52 000 km^2; 14°07′27″–18°56′51″ E and 52°34′51″–54°50′09″ N). The habitat and phytocoenotical conditions of *C. pulicaris* were assessed in five localities: near Domysłów, on Bagna Rozwarowskie, near Nosalin, on the "Piaśnickie Łąki" and the "Beka" reserves, while in the case of *P. sylvatica* in two localities: near Nosalin and near Debrzno (Tab. 1). Near Nosalin, due to habitat heterogeneity, two plots (objects) with *C. pulicaris*, were designated for study. The first one (Nosalin 1) was situated in a land depression, close to a drainage ditch, whereas the second one (Nosalin 2) was on a small, less moist elevation.

Distribution and dataset

The presentation of the distribution dynamics of *C. pulicaris* and *P. sylvatica* is based on (***i***) floristic data collected between the second half of the nineteenth century and the present, (***ii***) our field studies (1998–2015), (***iii***) available published and unpublished materials, and (***iv***) specimens from Polish herbaria. The database of the *Atlas rozmieszczenia roślin naczyniowych w Polsce* [Atlas of vascular plants distribution in Poland] – ATPOL [31] was used in the supplementary material. Distribution maps

Tab. 1 Characteristics of localities under soil and phytosociological studies.

No.	Locality	Geographical coordinates	Description	Protection programme
Carex pulicaris				
1.	Near Domysłów	53°55.976′ N, 14°37.321′ E	Wet meadow on peatland, mowed once a year (August), separated by two drainage ditches filled with water from the other area.	Natura 2000 – PLH320019 Wolin and Uznam
2.	Bagna Rozwarowskie	53°52.376′ N, 14°45.075′ E	Bogmoor complexes; partially flooded in early spring and autumn and overdrying in the middle of summer; reed plantation; patches with rare species regularly mowed.	Natura 2000 – PLB320001 Bagna Rozwarowskie
3.	Near Nosalin	54°25.198′ N, 16°47.798′ E	Wet meadow in land depression, surrounded by trees, abandoned for ca. 30 years.	-
4.	Piaśnickie Łąki	54°49.388′ N, 18°3.844′ E	Periodically wet abandoned meadow; ca. 40 m from the Piaśnica River.	Reserve; Natura 2000 – PLH220021 Piaśnickie Łąki
5.	Beka	54°39.379′ N, 18°27.699′ E	Wet meadow on peatland, periodically mowed, cut by drainage ditches.	Reserve; Natura 2000 – PLH220032 Zatoka Pucka and Półwysep Helski
Pedicularis sylvatica				
1.	Near Nosalin	54°25.191′ N, 16°47.764′ E	Wet meadow adjoining afforestation, abandoned for ca. 30 years.	-
2.	Near Debrzno	53°32.898′ N, 17°17.183′ E	Wet meadow on peatland in local land depression near the Żuczek Lake, formerly used.	-

were created by applying the technique of cartogram, which is consistent with methodological assumptions for ATPOL [32]. The basic unit of cartogram was a 5 × 5 km square, labeled 00, 01, 10, 11 (cf. Tab. S1). Filling in one unit of cartogram denotes the presence of species on a given area and is treated as a single stand, irrespective of the number of sites within the marked square. In order to illustrate the dynamics of the species we presented the localities before 1900, 1900–1950, 1951–1990, and after 1990. The lists of all localities are included in Tab. S1 and Tab. S2.

In the years 2004–2005, 2012 and 2014–2015, in selected localities with the examined species, phytosociological relevés were made by the method of Braun-Blanquet, and arranged in a phytosociological table (Tab. S3). The relevé area was 10–50 m^2. Syntaxonomic nomenclature was adopted after Matuszkiewicz [28] and Kącki et al. [33]. The names of vascular plants follow Mirek et al. [34], the names of mosses follow Ochyra et al. [35].

Analysis of soil samples

Soil was examined in six sites within the area with *C. pulicaris* (Nosalin 1, Nosalin 2, Bagna Rozwarowskie, the "Beka" and "Piaśnickie Łąki" reserves, and Domysłów). The conditions of the occurrence of *P. sylvatica* were assessed in two localities: near Nosalin (Nosalin 3) and Debrzno (Tab. 1). In the years 2012 and 2015 *P. sylvatica* was not found in Nosalin 3, nevertheless this locality was included in our study because of prior identification of this species there. Examination of the soil and, indirectly, the water regime in this object could allow to identify the habitat threats affecting the occurrence of *P. sylvatica*.

Within each object, three composite samples were collected from the surface layer of rhizosphere (0–25 cm). Altogether, 24 samples were taken for laboratory analyses. Assessment of available macroelements in the soils was based on the Polish limit values processed by IUNG [36] while soil types were identified according to the *Systematyka gleb Polski* [Polish soil classification] [37].

The loss-on-ignition (organic matter) in the soil material was determined by burning soil samples in a muffle furnace at 550°C; content of total forms of: C, N, S by means of elementary analyzer (CHNS-O, Costech, Italy); pH in 1 mol dm^{-3} KCl – potentiometrically; salinity – conductometrically; content of Mg, K, P, and Ca soluble in 0.5 mol dm^{-3} HCl (the so-called available forms) – by using an atomic absorption spectrophotometer Unicam Solaar 929 (Unicam, Great Britain), and phosphorus – colorimetrically.

Statistical analysis

We compared soil properties between the study sites (areas with *C. pulicaris* and *P. sylvatica*). Three samples treated as replications were collected from each plot. The obtained results were analyzed using one-way ANOVA. The requirements for this kind of analysis of variance were met (normal distribution of variables was checked by the Shapiro–Wilk test and homogeneity of variances by the Brown–Forsythe test). The significance of differences between mean values was calculated by the Tukey test.

To determine the relationship between some of examined chemical properties of soils within the areas of occurrence of *C. pulicaris* and *P. sylvatica*, Pearson correlation coefficients were calculated. The software package Statistica 10.0PL (Statsoft Polska) was used for statistical analysis.

Results

Carex pulicaris

In the Pomerania, *C. pulicaris* is connected mainly with the northern areas and does not occur in the south of the region (Fig. 1). Four recently discovered localities

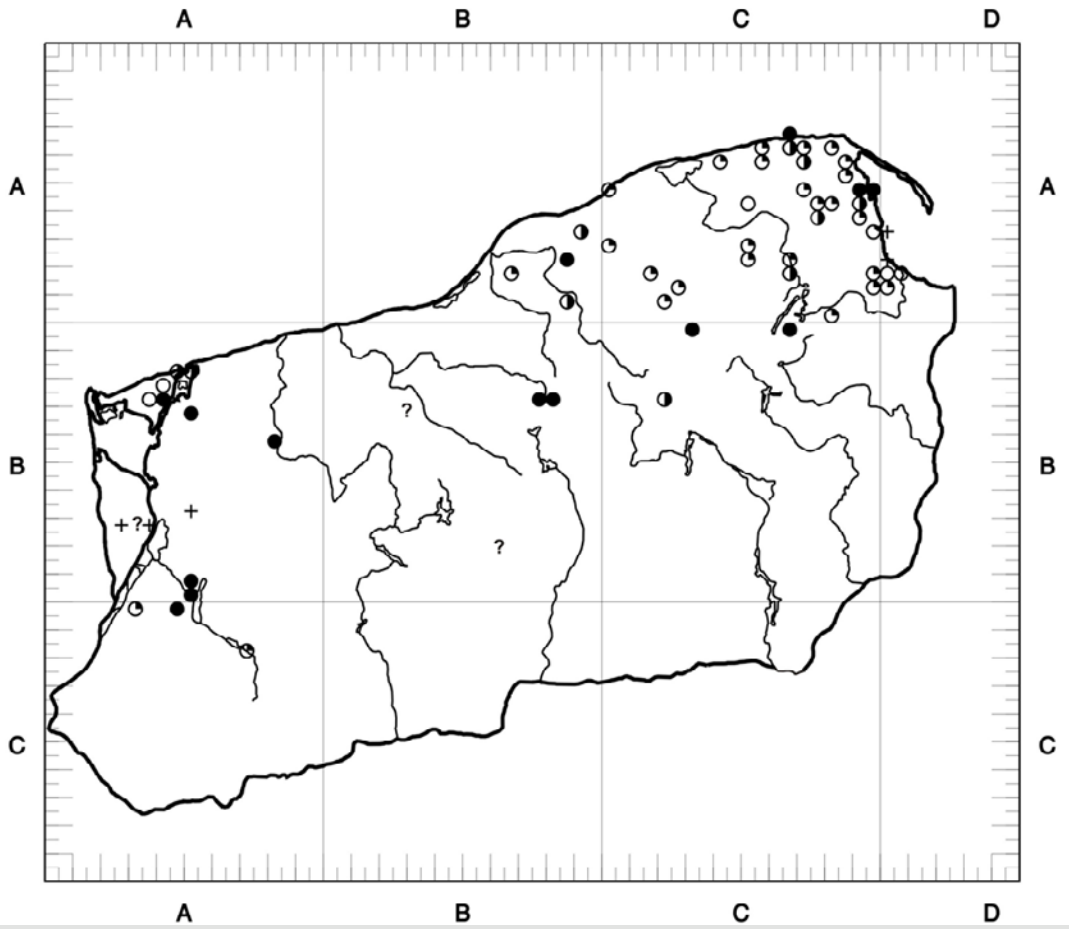

Fig. 1 Distribution of *Carex pulicaris* in NW Poland. White circle – recorded before 1900; 3/4 white circle – recorded in 1900–1950; half white circle – recorded in 1951–1990; black circle – recorded after 1990; "+" – extinct locality; "?" – unconfirmed in 2015.

(Domysłów, Kołbacz, Żelewko, and Czarnowskie lakes) in the Western Pomerania enlarged the number of recorded localities to 78 (Tab. S1). The oldest locality, documented by Klinsmann, was from 1852 in Gdańsk Brętowo. Before 1900, the species was known in 27 localities, two of which were situated in the vicinity of the Gulf of Puck, which still exist. In the first half of the twentieth century, *C. pulicaris* was observed in 51 localities, and in the years 1951–1990 in 22, but in the majority of them for the first time. After 1990, the species was reported from scarce (14), scattered sites. In 2015, it was not found in three (Goślice, Głodzino, near Nadarzyce) out of seven visited localities (Tab. S1).

Large populations of *C. pulicaris* were observed near Domysłów, Nosalin, and the "Beka" reserve. Single plants were scattered over an area of ca. 600 m^2 near Domysłów, whereas in the vicinity of Nosalin this sedge covered an area of ca. 150 m^2. In the period 2004–2005, it formed small patches; in 2012, it grew most often in small, only sporadically larger, clumps. In the "Beka" reserve, the population of *C. pulicaris* occupied about 180 m^2; its individuals generally formed vast clumps, rarely single scattered tufts. In Bagna Rozwarowskie, there were tufts and sparse small patches strongly dispersed over an area of ca. 3 ha. A few small populations, occurring in small areas, were found in the "Piaśnickie Łąki" and "Wrzosowisko Sowno" reserves. The sedge population of "Piaśnickie Łąki" consisted of ca. 20 tufts in a patch of 25 m^2, while only a few tufts were recorded in the "Wrzosowisko Sowno", within an area of ca. 30 m^2.

Plant communities with *C. pulicaris* recorded near Domysłów and the "Beka" reserve were classified to the alliance *Caricion davallianae* (Tab. S3, Nos. 1, 2). *Carex pulicaris* was found on intermittently wet meadows of the alliance *Molinion caeruleae* in Bagna Rozwarowskie, near Nosalin, and the "Piaśnickie Łąki" reserve (Tab. S3, Nos. 3–8). In Nosalin 2, there was a marked share of the species from the alliance *Nardo strictae-Juncion squarrosi*. This locality was characterized by higher diversity

Tab. 2 Some properties of the investigated soils.

Specification			Objects (the localizations of sampling sites)								LSD$_{0.05}$
			Nosalin 1	Nosalin 2	Bagno Rozwarowskie	"Beka" reserve	"Piaśnickie Łąki" reserve	Domysłów	Nosalin 3	Debrzno	
pH$_{KCl}$			5.83*^{c}	5.65^{bc}	5.16^{ab}	5.83^{c}	5.14^{ab}	5.23^{bc}	4.57^{a}	5.08^{ab}	0.63
Salinity		µS cm^{-1}	114^{a}	116^{a}	355^{c}	678^{d}	104^{a}	223^{b}	111^{a}	616^{d}	104
Matter organic		g kg^{-1}	101.4^{a}	126.6^{a}	981.3^{e}	721.7^{c}	76.5^{a}	821.4^{d}	69.1^{a}	652.0^{b}	60.2
Total	C		49.1^{a}	60.0^{a}	485.2^{d}	353.2^{b}	50.7^{a}	434.6^{c}	36.9^{a}	335.6^{b}	34.6
	N		3.23^{a}	3.80^{a}	8.00^{b}	25.51^{d}	3.72^{a}	21.42^{c}	2.17^{a}	27.45^{d}	2.53
	S		0.23^{a}	0.35^{a}	0.70^{a}	6.00^{c}	0.96^{a}	6.39^{c}	0.27^{a}	4.71^{b}	1.27
C:N			15^{a}	16^{a}	63^{b}	14^{a}	14^{a}	20^{a}	17^{a}	12^{a}	15
Available	Mg	mg kg^{-1}	96.7^{ab}	135.8^{ab}	133.0^{ab}	3378.6^{e}	165.2^{b}	468.8^{c}	76.00^{a}	640.7^{d}	121.7
	K		48.6^{a}	53.3^{a}	147.0^{abc}	260.2^{c}	30.7^{a}	101.9^{ab}	112.7^{ab}	205.2^{bc}	79.2
	P		594.0^{b}	631.0^{b}	310.3^{a}	417.2^{a}	567.3^{b}	412.0^{a}	601.0^{b}	416.1^{a}	100.0
	Ca		1376.3^{a}	2085.3^{a}	710.3^{a}	18276.7^{b}	1422.3^{a}	22840.0^{c}	155.6^{a}	22603.3^{c}	2202.2

* Homogeneous groups (groups of insignificant mean values). LSD – least significant difference Tukey's.

in comparison with Nosalin 1. In 2004–2005, flea sedge had a high cover, but was clearly reduced 7 years later. This was followed by an expansion of *Molinia caerulea* or other species of the class *Molinio-Arrhenatheretea*.

Plant communities with *C. pulicaris* occurred on organic hemic-muck soils developed from peat (Bagna Rozwarowskie, the "Beka" reserve, and Domysłów), mucky soils (Nosalin 1 and Nosalin 2), and typical muckous soils (the "Piaśnickie Łąki" reserve).

Organic hemic-muck soils within Bagna Rozwarowskie, the "Beka" reserve, and Domysłów varied significantly in organic matter content (from 721.7 to 981.3 g kg^{-1}). They had acid to slightly acid reaction and a slight concentration of salt (223–678 µS cm^{-1}). Besides, they differed in the content of total nitrogen (8.00–25.51 g kg^{-1}), total sulphur (0.70–6.39 g kg^{-1}), and C:N ratio (14–63). These soils were characterized by a very low to very high content of available magnesium, low to very low content of available potassium, and medium to high content of available phosphorus (Tab. 2). Despite the fact that the soils from the particular study objects belonged to a similar taxonomy group, there were significant differences in some of their chemical parameters (Tab. 2).

Mucky soils and typical muckous soils were significantly poorer in organic matter than the organic hemic-muck soils. The organic matter content ranged from 76.5 g kg^{-1} in the typical muckous soils of the "Piaśnickie Łąki" reserve to 126.6 g kg^{-1} in the mucky soils of Nosalin 2. Soil reaction varied from acid to slightly acid. These soils were characterized by a slight concentration of salt (from 104 to 116 µS cm^{-1}), narrow spectrum of C:N ratio – 14–16, very low content of available magnesium and potassium, and very high content of available phosphorus (Tab. 2). Statistical analysis showed that there were no significant differences in their chemical properties (Tab. 3).

Pedicularis sylvatica

In the Pomerania, *P. sylvatica* occurred in three centers, the largest in the south-eastern part of the region (Fig. 2). Until now, the species has been recorded at

Tab. 3 Pearson correlation coefficients for some chemical properties of the soil.

Specification		Total			C:N	Salinity	pH_{KCl}	Available			
		C	N	S				Mg	K	P	Ca
Organic matter		1.00*	0.70*	0.64*	0.56*	0.67*	0.02	0.38	0.61*	−0.91*	0.60*
Total	C		0.71*	0.66*	0.53*	0.66*	0.00	0.36	0.60*	−0.91*	0.62*
	N			0.93*	−0.17	0.86*	0.12	0.65*	0.75*	− 0.61*	0.96*
	S				−0.22	0.68*	0.15	0.65*	0.59*	−0.51*	0.96*
C:N						0.01	−0.15	−0.21	−0.01	−0.57*	−0.28
Salinity							0.17	0.75*	0.90*	−0.64*	0.68*
pH_{KCl}								0.41*	−0.01	−0.02	0.09
Available	Mg								0.70*	−0.32	0.52*
	K									−0.50*	0.57*
	P										−0.49*

* Correlation coefficients significant at $p < 0.05$. $N = 24$.

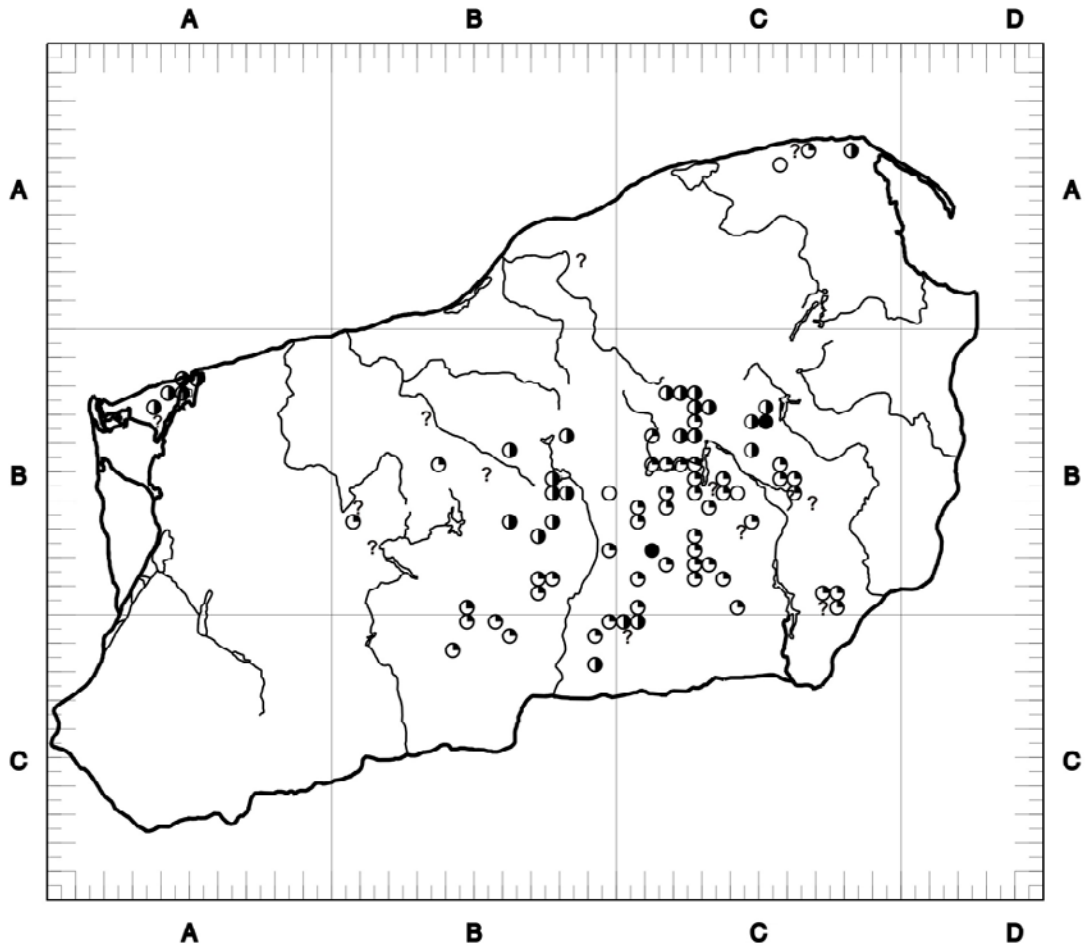

Fig. 2 Distribution of *Pedicularis sylvatica* in NW Poland. White circle – recorded before 1900; 3/4 white circle – recorded in 1900–1950; half white circle – recorded in 1951–1990; black circle – recorded after 1990; "?" – unconfirmed in 2015.

115 sites (Tab. S2). The oldest records come from Wolin Island (Jagienki, Ładzin, and Rabiąż) from 1860 [38]. Before 1900, it was known from 59 localities, nine of them were not confirmed later. Between the years 1900–1950, it was reported from 71 localities, and in the period 1951–1990 from only 34. After 1990, only seven localities were found. In the vicinity of Nosalin, its presence was not confirmed in 2012 and 2015. In 2015, despite precise localization, the species was no longer found near Biała Góra, in the "Diabelskie Pustacie" reserve, and Przybkowo. Efforts to find the plant in Dziwnów-Międzywodzie, Ładzin, Rabiąż, Jagienki, the "Białogóra" reserve, Wolność, and near Łobez, Łowinek, Okoniny, Obrowo, Chojnice, and Krajenka also failed.

In the years 2004–2005, the population of *P. sylvatica* near Nosalin, consisted of nearly 30 individuals and covered ca. 70 m^2, and in 2010 there were only single specimens in the Diabelskie Pustacie reserve. The populations close to Biała Góra and in Przybkowo were much richer, each of them composed of 50–60 specimens. In 2014, the population of Przybkowo drastically decreased to a few individuals – for several years it has been situated in immediate proximity to a housing estate in Barwice. In 2015, the locality close to Debrzno was small – occupied ca. 2 m^2 – but several specimens were found there.

Pedicularis sylvatica recorded near Nosalin was found on species-poor vegetation classified to the association *Nardo-Juncetum squarrosi* (Tab. S3, No. 10). Common lousewort formed small clumps, whose dominant species was *Calluna vulgaris*. In the locality near Debrzno this species occurred on a wet meadow of the community of the class *Molinio-Arrhenatheretea*, in which *Alopecurus pratensis* had the largest share (Tab. S3, No. 9).

Plant communities with a share of *P. sylvatica* occurred, similarly to *C. pulicaris*, on organic hemic-muck soils (Debrzno) and typical muckous soils (Nosalin 3). These soils had similar chemical properties to the soils under the communities with *C. pulicaris* (Tab. 2). However, the organic hemic-muck soils from Debrzno were significantly richer in organic matter, total nitrogen, total sulphur, available magnesium and potassium, and salt concentration, than the sandy typical muckous soils from Nosalin 3 (Tab. 2). No significant differences were found in soil pH and C:N ratio (Tab. 2).

Statistical analysis of collected soil samples from the sites with *C. pulicaris* and *P. sylvatica* showed significant differences between organic hemic-muck soils, mucky soils, and typical muckous soils. The differences resulted mainly from organic matter content with which correlated: total content of nitrogen and sulphur, available potassium, phosphorus and calcium, salt concentration, and soil pH (Tab. 3).

Discussion

For over 160 years the number of known localities of *C. pulicaris* and *P. sylvatica* in the Pomerania has decreased dramatically. The majority of localities were documented before World War II because of the widespread explorations of swamp habitats conducted by former botanists. Currently, these species are sporadically noted in NW Poland, where some of the species localities are found for the first time. It is difficult to state if they have withdrawn to new places or have been overlooked during floristic studies. Such incidents were reported with regard to *C. pulicaris* [20,39], small sedge with inconspicuous leaves. It is not easy to notice the plant, even during flowering and fruiting since it produces a small, single, few-flowered spike. The majority of localities, especially those reported before 1950, were not confirmed later, either because of their disappearance, overlooking, or the lack of further explorations.

However, taking into consideration the substantial, mainly anthropogenic transformations of wet habitats (peatland ecosystems, in particular), it is reasonable to assume that the previously reported localities are only of historical importance. The fact that they were not confirmed within the last 60 years supports our assumption. The authors' attempts to find some of the earlier reported localities have failed in most cases, especially with respect to *P. sylvatica*. Frequently, the localizations of the sites were inaccurate, particularly those given by pre-war German researchers (e.g., [40,41]), which made the search difficult. On the other hand, a single lack of confirmation of a formerly reported locality, if the habitat has not been destroyed or

radically transformed, does not permit us to state that the species has disappeared. Recent years, 2015 in particular, considerably differed from previous years in terms of climatic conditions (a few months' droughts and high air temperature). Therefore, the locality that was once unconfirmed in this period has not been considered as non-existent.

Carex pulicaris often occurs in the plant communities difficult to identify (e.g., [42–44] and a similar problem occurred with the studied phytocoenoses. Hence, it was possible to distinguish vegetation units only to the level of alliance (Tab. S3). These phytocoenoses were characterized by a great diversity in species composition. Flea sedge in the "Beka" reserve and near Domysłów was growing among calciphytes, in the communities of the alliance *Caricion davallianae* on slightly acid, but calcium-rich soil. The same was reported for similar communities of *Caricion davallianae* in other regions of Poland [39] and in Slovakia [42,44]. In the other study areas of the presented research, *C. pulicaris* was a component of the *Molinion* alliance communities, occupying habitats varying in moisture, even within one locality, e.g., near Nosalin. Phytocoenosis in Nosalin 2, compared to that in Nosalin 1, was composed of more numerous species of the class *Calluno-Ulicetea*, which indicates a less moist soil. Flea sedge was recorded in the association *Caricetum davallianae* [44], *Hieracio-Nardetum* [45], *Myrico-Salicetum auritae* [46,47], *Nardo-Juncetum* [48], *Sphagno warnstorfiani-Caricetum davallianae* [42], and *Valeriano-Caricetum flavae* [39]. Most frequently, phytocoenoses with *C. pulicaris* form small patches (e.g., [44,49–53]), occasionally scattered over a large area, which was observed in Bagna Rozwarowskie and the Świętokrzyskie Mts [52]. Irrespective of the type of community, the flea sedge did not have a high cover, except the phytocoenoses near Nosalin in 2004–2005 (cf. Tab. S3). In other regions of Poland as well as Slovakia, this species had a relatively low share in a community composition [42–44,50]. In Poland, *C. pulicaris* occurs in wet and periodically wet habitats, occasionally strongly transformed [48], predominantly on postbog soils, strongly decomposed or humified, with a slight acid reaction, seldom on ground-gley soils [39].

The conducted studies showed that plant communities with *C. pulicaris* occur on hydrotechnically-altered wetlands with a differentiated soil cover. After drainage, bog soils undergo an intensive humification process, leading to mineralization and physical and chemical transformations of organic matter, and thereby to changes in habitat fertility [25,26,54–58]. In turn, rising groundwater level results in secondary bogginess which leads to the transformation of plant communities [59]. In these types of soils, moisture is the main factor determining their properties and affecting the development of plant communities.

Our studies indicate that in northern Poland (Bagna Rozwarowskie, the "Beka" reserve, and Domysłów), *C. pulicaris* prefers organic hemic-muck soils of varying content of organic matter, acid and slightly acid reaction, and a generally narrow spectrum of C:N ratio. Similar soil conditions suitable for this sedge are found in Puścizna Rękowiańska [39]. The narrow spectrum of C:N ratio recorded in the soils where *C. pulicaris* occurs points to intensive microbiological processes facilitating humidification. A wide spectrum of C:N ratio (63) was obtained only in the organic hemic-muck soils of Bagna Rozwarowskie, which reflects the small microbiological activity of soil caused by its high moisture content. Jurzyk and Wróbel [47] draw attention to specific moisture conditions in which *C. pulicaris* grows in Bagna Rozwarowskie (long-term surface inundations in the autumn–spring period, lower groundwater table below the surface only in summer). Apart from peatlands, *C. pulicaris* occurs also on wet mucky soils and typical muckous soils with acid and slightly acid reaction. On the slopes of Magura Małostowska similar occurrences of this species were reported from ground-gley soils, but with a strongly acid reaction [39].

In Poland, *P. sylvatica* is most frequently encountered in wet swards with *Nardus stricta*, in the association *Nardo-Juncetum squarrosi* [60–64]. It was found in this association in a small number in the locality near Nosalin, with *Calluna vulgaris* as a dominant species. A large share of *C. vulgaris* exhibited habitat overdrying, which might be the cause of the disappearance of *P. sylvatica*. The absence of common lousewort in the *Nardo-Juncetum squarrosi* at numerous occurrences of heather was observed in the upper Wisła Valley [65], the Świętokrzyskie Mts [61], and the Częstochowa Upland [62]. In the locality near Debrzno, *P. sylvatica* was growing in the community of the

class *Molinio-Arrhenatheretea*, in a wetter habitat than in Nosalin. It was also detected in a wet meadow in the Sudetes, in the community of the alliance *Calthion* [66]. In the examined localities, like in the Orawa Basin [64] and the Widawka valley [60], the patches of communities with a common lousewort covered small areas and thus were more exposed to transformations as a result of unfavorable habitat changes.

Pedicularis sylvatica in northern Poland grows on organic hemic-muck soils (Debrzno) and typical muckous soils (Nosalin 3). In southern Poland this species was recorded on anthropogenically transformed, shallow peat-muck soils [62], mineral-gley [61], and also wet, acidic sandy soils [60,65]. The communities with *P. sylvatica* prefer sandy, drained *Mollinia* grassland or non-flooded locations situated higher in a valley, or the edges of wetlands with reed vegetation. The soil conditions of both northern and southern Poland where *P. sylvatica* occurs are similar. The soils differ in organic matter, reaction from strongly to slightly acid, and a narrow spectrum of C:N ratio. It is worth mentioning that the present absence of *P. sylvatica* on Nosalin 3 should be attributed to the susceptibility of typical sandy muckous soils to overdrying and subsequent permanent changes in their physical and chemical properties [25,67], followed by the expansion of competitive, less hygrophilous species [61,62,65]. In northern Poland, *C. pulicaris* and *P. sylvatica* occur in similar habitats. Each of them can grow on various kinds of soils varying in chemical properties, which indicates their adaptability.

The range of *C. pulicaris* in Poland comprises mainly southwestern and northwestern parts of the country, bounded by the Wisła River [31], further to the east there is a disjunction extending to the eastern Baltic states. In turn, the Polish range of *P. sylvatica* clearly bypasses northeastern areas [31]. According to Dahl [68], the distribution of *C. pulicaris* and *P. sylvatica* in Northern Europe is correlated with a climatic parameter, namely, the mean temperature of the coldest month. For both species it is −4°C. The comparison of the isotherms of the coldest month's mean temperature (°C) calculated for sea level [68] with the distribution of *C. pulicaris* in Pomerania and other regions of Poland [31] indicates a relationship between the species range boundary and the isotherm −2°C, while in the case of *P. sylvatica* with the isotherm −4°C.

Some plant species at the limit of their range are prone to local extinctions [29,69]. Peripheral populations are frequently smaller than the populations at the center of the species range [70,71], and therefore they are more vulnerable to extinction, especially if they are isolated [20,29,72]. Pomeranian populations of *C. pulicaris* and *P. sylvatica* are generally small, as in other regions of Poland [39,73,74]. In addition, some of them are encountered in isolated and small areas where unfavorable habitat conditions can occur more easily and more frequently [13] and they are predominantly threatened with extinction. This has been confirmed in the case of the small isolated population of *P. sylvatica* near Nosalin, and also by the population of this species in the "Diabelskie Pustacie" reserve.

In the case of *P. sylvatica* near Nosalin and Przybkowo, growing on wet meadows, previously used for agricultural purposes, their disappearance is caused by habitat changes and land abandonment. Traditional use of meadows for extensive grazing or mowing has a beneficial impact on seedlings [30]. Cessation or intensification (especially mechanical) of grassland use had been stated before as the reason for the extinction of many populations [75]. The locality in Przybkowo, due to the adjacent housing estate, is additionally exposed to habitat changes caused by eutrophication. In 2015, no single specimen was found here for the first time. Unfavorable habitat conditions, manifested by insufficient soil moisture (e.g., Wolność, "Diabelskie Pustacie" and "Białogóra" reserves), encroachment of trees and bushes (e.g., Łobez, "Białogóra" reserve), and common reed expansion (e.g., Dziwnów-Międzywodzie, Rabiąż) may have contributed to the lack of confirmation of *P. palustris* in some of the earlier reported localities. The worsening moisture conditions and habitat eutrophication caused a partial loss of localities in the Lower Silesia [73].

Extensive land use has a positive impact on the population of *C. pulicaris*, a heliophilous, non-competitive species, since it restricts the development of tall expansive perennials such as *Phragmites australis*. Mowing meadows in Bagna Rozwarowskie, where flea sedge occurs, allows for further preservation of this population despite the existence of a reed plantation there.

Some localities have ceased to exist not only because of habitat transformation but due to its complete destruction as a result of urban development, e.g., the localities of *C. pulicaris* [24]. They were situated in the vicinity of: the Gulf of Gdańsk, within the area of Sopot and Gdynia, and within Pilichowo and Glinki – the present suburban districts of Szczecin, and Goleniów.

At present, in the Pomerania there are several occurrences of the two species, much fewer in the case of *P. sylvatica*. This plant belongs to the flora elements of special concern in other regions of Poland and is included in regional red lists of plants, red books, frequently in the category: E (declining), Ex (extinct), e.g., in the Pomerania [14,15], central Poland [76,77], and Lower Silesia [78,79]. The problem of *C. pulicaris*' disappearance, not only in the Pomerania but across the entire country, has been emphasized by changing its threat category from vulnerable to endangered in the latest edition of the Polish red book of plants [80,81]. In the Pomerania, most localities are within the area of Natura 2000, only three of *C. pulicaris* and four of *P. sylvatica* in the areas under reserve protection.

Conclusions

Analysis of the present distribution of *C. pulicaris* and *P. sylvatica* in NW Poland, on the eastern limit of their range, shows that they have withdrawn from certain parts of that region, reflecting the recessive trends. This process is more intensive in the case of *P. sylvatica*, which was in the past observed in more localities in comparison with *C. pulicaris*, whereas now it is present only in a few stands. Despite the disappearance of stands with these species, single new localities are reported, although this does not compensate for the extinction or the lack of confirmation of former populations. Therefore, *P. sylvatica*, classified into different threat categories in other parts of the country, should be included in the Polish red list of plants like *C. pulicaris*.

The occurrence of *C. pulicaris* and *P. sylvatica* on the soils with extremely diverse chemical properties indicates that they possess a potential of adapting to varying habitat conditions on postbog areas. On the other hand, they may disappear from presently occupied areas as a result of soil degradation or worsening moisture conditions (e.g., *P. sylvatica* from Nosalin 3).

Due to the fact that populations of *C. pulicaris* and *P. sylvatica* are generally small and occur in community patches covering rather small areas, their preservation depends on the maintenance of suitable habitats and limitation of the natural succession of expansive plant species. Thus, the most appropriate form of their protection is an active reserve protection or non-extensive use of their habitats.

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Supplementary material

The following supplementary material for this article is available at http://pbsociety.org.pl/journals/index.php/asbp/rt/suppFiles/asbp.3507/0:

Tab. S1 List of *Carex pulicaris* localities in NW Poland.

Tab. S2 List of *Pedicularis sylvatica* localities in NW Poland.

Tab. S3 Plant communities with *Carex pulicaris* and *Pedicularis sylvatica* in NW Poland.

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