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Current distribution of *Pilularia globulifera* L. in Poland – changes of geographical range and habitat preferences

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Abstract

Pilularia globulifera is a subatlantic European fern threatened with extinction. In Poland, it reaches the eastern border of its continuous range. Up to the end of the 20th century, it was observed here in 21 stands; only 2 of them existed by the second half of the century, so the species was categorized as critically endangered. Five new locations have been found in western and northwestern Poland during the last 10 years. Abundant and permanent populations grow in 3 locations, while 2 stands were ephemeral. All the current stands are situated in anthropogenic habitats with spontaneous vegetation, in oligotrophic to eutrophic waters. One of the new localities is about 280 km distant from the eastern range of the limit known previously. *Pilularia* forms its own plant community *Pilularietum globuliferae*, enters plots of *Ranunculo-Juncetum bulbosi* and occurs in mesotrophic to eutrophic rushes of *Eleocharis palustris*, *Phragmites australis*, *Typha angustifolia* and *Equisetum fluviatile*. Specimens are vigorous and regularly produce sporocarps.

Keywords: water ferns, *Pilularia globulifera*, apophyte, climate warming, Poland

Introduction

The genus *Pilularia* (Marsiliaceae) is represented by 5 to 6 species distributed in North and South America, Europe, the Pacific Islands, New Zealand, Australia and Africa [1–3]. In Europe, two species occur: *Pilularia minuta* Dureu ex A. Braun, limited to the western Mediterranean region, and a widely distributed *Pilularia globulifera* L. [4]. *Pilularia globulifera* is a subatlantic species, originally recorded throughout much of Western Europe's lowlands, from southern Scandinavia to the Iberian Peninsula [5]. In Central Europe, it reaches the eastern boundary of its continuous range and has been reported in Germany [6], the southern part of Czech Republic [7] and western Poland [8]. Some isolated and easternmost stands were recorded on the bank of Kugurluj Lake in the Danube River valley near its delta, as probably accidentally introduced [9], and in the Karelian Isthmus [10]. Generally, in Europe, *P. globulifera* is classified as near threatened (NT) due to lack of information sufficient to assign it to a given threat class – it most likely should be assigned as a vulnerable species [11]. In Central Europe this taxon is classified as endangered (EN) [12]. It is critically endangered in Switzerland [13], Czech Republic [7] and Poland [8], endangered in Germany [14] and Norway [15], vulnerable in Finland [16] and Sweden [17] and very rare in the Netherlands [18].

Pillwort *P. globulifera* is a heterosporous coastal and submerged aquatic fern with numerous cylindrical leaves, propagating by spores or by fragmentation of rhizomes. Usually, it occupies bare gravel or silt at the banks of lakes, ponds, temporary pools and slow flowing rivers, but also survives periods of complete immersion. It is strongly associated with places of fluctuating water levels, which suppress competition from higher plants. The fern prefers neutral to acidic substrates, and permanently damp habitats in summer, warmed rapidly by the sunshine. The chromosome number for the species is $2n = 26$ [4,11,19–22].

In Poland, the species was recorded in the western and northwestern regions, where it occurred in peat bogs, natural and anthropogenic ponds, as well as wet meadows. Up to 1940,

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it was observed in ca. 20 locations [23–30]. The number of locations suddenly declined and at the end of the 20th century, with only two stands existing in Janiszowickie Lake near Lubsko and in a fishpond near the village of Niwica, both in western Poland. In Janiszowickie Lake, *P. globulifera* was recorded in 1982 and 1983, later it disappeared, probably due to increased water level [8]. During regular controls, it has not been confirmed until now. The current high eutrophication of the lake promotes the growth of rushes; even if pillwort survived a period of deep immersion, it might have been overgrown and eliminated by more competitive species. The second population thrived in the years 1988–2001 [8,31]; however, since 2007, it has not been confirmed. The fishpond in Niwica is intensively exploited; the level of eutrophicated water is permanently high.

Pilularia globulifera is classified as a critically endangered species in the "Polish red book" [8,32] and the "Red list of vascular plants" [33,34]. In the first decade of the 21st century we found 5 new locations of this extraordinary fern, and the discovery motivated us to undertake detailed research on the current distribution and ecology of the pillwort in Poland.

Material and methods

The distribution of *P. globulifera* was studied in 2007–2011. Historical information about stands of this species in Poland was verified in field research. In addition, potential locations indicated during a detailed analysis of orthophotomaps on Google Maps and Geoportal (http://maps.geoportal.gov.pl/webclient/), were also examined.

To compare current thermal conditions of stands located between the historic range and the new eastern location, analyses of mean annual and coldest monthly (January) air temperature for the decade 1996–2005 were undertaken. Moreover, the same analyses were made for the decade 1951–1960, to determinate changes of temperature factor caused by climate warming. Maps of mean annual and January air temperature for the decade 1996–2005 were prepared based on data from 250 meteorological stations from Poland and the immediate vicinity abroad. Air temperature averages were obtained from Institute of Meteorology and Water Management and from the freely available databases of the National Climatic Data Center: GHCN-M [35] and GSOD [36]. Data from Germany were obtained from the Deutscher Wetterdienst website [37]. Spatial interpolation was performed using geographically weighted regression-kriging (GWRK), the method which is a two-part modelling procedure consisting of deterministic (local regression) and stochastic (ordinary kriging) components [38]. Deterministic models for annual and January means were specified using step-wise regression and a set of auxiliary environmental variables such as: altitude, longitude, latitude and distance from the sea among others. Regression residuals were spatialized by ordinary kriging technique [39]. Because the access to climatological data from the decade 1951–1960 was limited to only less than 60 stations [35], air temperature fields for that period were estimated using simple linear regression formulas with air temperatures from 1996–2005 as the independent variables. Correlation coefficients between datasets from two decades for annual and January means reached 0.98 and 0.80 respectively. The potential range of the species due to thermal conditions was estimated for each decade separately by combining (logical conjunction) annual and January raster layers, under the assumption that the spatial range is limited by annual mean temperature of less than 8.0°C and a January mean temperature of less than 2.5°C. We estimated values of temperatures determining stability of *P. globulifera* populations in Poland according to temperatures noted in eastern boundary of continuous range of the fern. Statistical and spatial analyses were performed using Statistica 9.1 and ArcGIS 9.3 (with Spatial Analyst and Geostatistical Analyst extensions) software.

Detailed research of existing populations was done on the production of sporocarps, viability of spores, chromosome number and relationship to plant communities. The viability of spores was tested at a stand by, controlling for spontaneous presence of the young fern, and in a laboratory, in water, at room temperature. The number of produced sporocarps was observed in three permanent populations, in Krzyżowa and Brożek in November 2009 and in Poręba Wielka in October 2011, on five 50 × 50 cm plots for each stand.

To count the chromosome number in plants originating from the three permanent stands, root tips were collected from fast growing rhizomes. They were pretreated with 0.004 M oxychinoline for 4 hours at room temperature in the dark and then fixed for 24 hours in a mixture of absolute ethanol and glacial acetic acid (3:1, v/v) at a temperature 5.0°C. The meristems were stained using Feulgen method [40] and then squashed and mounted in a drop of 45% acetic acid.

Relevés were recorded using the Braun-Blanquet scale [41] and stored in a TURBOVEG database [42]. A numerical classification of the plots was made by TWINSPAN software package integrated with JUICE programme [43]. The analysis was based on presence/absence of information on the species. Ordination analysis was done with a CANOCO software [44], data was elaborated using a detrended correspondence analysis (DCA) and canonical correlation analysis (CCA). Plant communities and the diagnostic value of vascular plants were identified according to Matuszkiewicz [45], the diagnostic value of mosses according to Dierßen [46]. The nomenclature of vascular plants is given according to Mirek et al. [47].

A distribution map was generated using GNOMON software in 10 × 10 km squares of the ATPOL grid [48].

Results

Localities

Pilularia globulifera was observed in Poland on 25–27 locations in the 22 ATPOL squares (Fig. 1). The majority of stands (73%) were recorded before 1945 and not confirmed later; the abbreviation l.n.c. denotes a locality checked by the authors and not confirmed after 2001.

AD 55: the eastern bank of Janiszowickie Lake [29], observed only in 1982/ 83 [49], later not confirmed [8,31,32,50], M. Pawlus 1982.09.07 (KRA), l.n.c.; **65:** Lubsko, not confirmed [8,32,50], leg. Struve 1877.06.16 (POZ), l.n.c.; NE of Lubsko, a new water reservoir, Rosadziński 2009, not confirmed since 2010; **68:** Pierzwin near Kożuchów [27], not confirmed [8,32,50], l.n.c.; **73:** two abandoned gravel pits in Brożek near Zasieki, Rosadziński, Szczęśniak and Śliwiński 2007–2011; **83:** a valley stream near spruce, pine and fir trees between Gniewoszyce, Chwaliszczewice and Żarki Wielkie [30], not confirmed [8,32,50], l.n.c.; **84:** Niwica near Mużaków/Muskau [23,27,30], not confirmed [50]; a fishpond near a road to Łęknica [31], confirmed [8,32,51] (the same stand?), J. Chmiel 1990.09.08 (POZ), not confirmed since 2007; **86:** Żary, Struve 1872 (POZ), l.n.c.

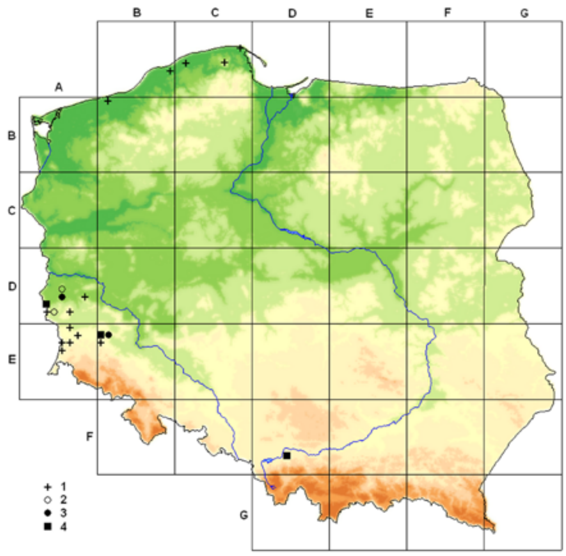

Fig. 1 Distribution of *Pilularia globulifera* L. in Poland. 1 – stands recorded before 1945; 2 – stands recorded in 1945–2001; 3 – stands recorded after 2001, ephemeral; 4 – stands recorded after 2005, currently exist.

AE 06: Syczków pond near Ruszów [hand-made note in a copy of Kryptogamenflora von Schlesien by Ferdinand Cohn (1876) deposited in the library of the University of Opole], l.n.c.; **17:** a heath near Osiecznica [23,27], not confirmed [8,32,50], l.n.c.; **25:** a peat bog near Dłużyna [27], not confirmed [8,32,50], l.n.c.; **26:** a peat bog near Węgliniec [23,27], not confirmed [8,32,50], l.n.c.; **35:** between Jędrzychowice and Żarki Średnie [23,27], not confirmed [8,32,50], l.n.c.; near Zgorzelec, leg. Struve 1852 (POZ), l.n.c.

BA 69: a heath in Bydlino near Słupsk [24–26], not confirmed [8,32,50], l.n.c.; near Słupsk (the same stand?), N.N., 1869 (POZ), l.n.c.

BB 60: a ditch in a peat bog in Stramnica near Kołobrzeg [25,26,52], not confirmed [8,32,50], l.n.c.

BE 10: two fishponds in Krzyżowa near Bolesławiec [53], Szczęśniak, Śliwiński 2007–2011; **11:** a fishpond in Rokitki [54], not confirmed since 2009; **20:** between Osła and Wilczy Las [23,27], not confirmed [8,32,50], l.n.c.; **29:** dry ponds S of Krzywa near Chojnów [23,27], not confirmed [8,32,50], l.n.c.

CA 38: Bielawskie Błoto, S of Ostrowo [28], not confirmed [8,32,50], l.n.c.; **51:** Siecie near Słupsk [25,26], not confirmed [8,32,50], l.n.c.; **56:** Salińskie (Salino) Lake near Lębork [24–26,28], not confirmed [8,32,50], l.n.c.

DF 74: a fishpond in Poręba Wielka near Oświęcim [55], Kruk, Szczęśniak and Śliwiński 2009–2011.

Characteristics of the stands

Pilularia globulifera has been found in five locations within the last five years. All current stands are associated with the spontaneous vegetation of anthropogenic habitats; three occur in fishponds, one in a new recreational pond and one in abandoned gravel pits, partially swamped and immersed. The species was not observed in natural habitats and should be classified as an apophyte in the present Polish flora. Four stands are located within the previous geographical range of *P. globulifera* in Europe; one is ca. 280 km beyond its eastern boundary (Fig. 1). Habitat characteristics of those five locations are presented below.

(***i***) Brożek near Zasieki: two adjacent shallow water reservoirs in old gravel pits situated in the flooding area of the Nysa Łużycka River. The gravel pits were probably abandoned at the end of the 1990s. The succession of forest communities is limited here by the changing level of water and flooding during springtime. *Pilularia* occurs on sandy and oligotrophic initial soils and occupies an area of 60 to 300 m², depending on the water level. The fern develops submersed and emerged forms at the stand in its own community and also occurs in the rushes of *Phragmites australis*.

(***ii***) Lubsko: ephemeral occurrence on an open sandy bank of a new water reservoir. *Pilularia* was observed on an area of ca. 2 m². The reservoir is used by the local community as a recreational pond, thus the pillwort habitats are under extreme human pressure. The species was observed in 2009 and not confirmed later. Possibly, the fern did not survive the winter and was too young or emerged too late to produce sporocarps.

(***iii***) Krzyżowa: two anthropogenic fishponds in a forest, which have been dug in the wet valley of a small stream and are supplied by the stream as well as by oligotrophic water coming from a drainage system. A detailed description of the stand was given by Szczęśniak and Szlachetka [53]. *Pilularia* occurs on open sandy banks and a flat bed and shallow water covering an area of 1 (in 2011) to 1500 m² (in 2007) in the northern pond and 0.5–2 m² in the southern pond; the area depends on the time of clearing of the ponds. The fern developed submersed and emerged shoots forming its own community and entering into *Phragmitetum australis* rushes.

(***iv***) Rokitki: probably ephemeral occurrence in an anthropogenic pond in the western complex of the fishponds. In summer 2008, a few juvenile plants were observed on the sandy bottom of a transiently drying pond [54]. Before they grew enough to produce sporocarps, the pond was filled again and *Pilularia* remained under water. The extinction or survival of the pillwort has not been determined.

(***v***) Poręba Wielka near Oświęcim: an abandoned anthropogenic fishpond, temporarily dried out and partially covered by rushes; part of the large complex of fishponds between Oświęcim and Zator. A detailed description of the stand was given by Kruk and Szymańska [55]. Population developed in clay; it is the most eutrophic habitat of *Pilularia* in Poland. The fern forms dense plots covering over 2000 to 3000 m² at the bottom in the southern part and some small plots dispersed in the northern part. The population is vigorous. *Pilularia* forms its own community; moreover, it occurs in rushes of *Typha angustifolia*, *Eleocharis palustris* and *Equisetum fluviatile*. The locality is controlled every year and over the years 2009–2011, the population area and condition did not change significantly.

Analyses of mean annual and January air temperatures revealed a high similarity of thermal conditions noted in the decade 1951–1960 within the Polish part of *P. globulifera* continuous geographical range with the temperatures noted in the decade 1996–2005 in the surroundings of the new eastern stand. The means for Poręba Wielka in the decades 1951–1960 were 7.9°C and −4.0°C; they increased significantly in the decade 1996–2005 to 8.3°C and −2.2°C, respectively.

Biology and ecology

PROPAGATION. The species is able to propagate vegetatively by fragmentation of branching rhizomes and generatively by formation of sporocarps and the sexual process. Sporulation was observed in Brożek, Krzywa and Poręba Wielka.

Sporocarps occurred on 10 to 30% of the entire population area and matured from August to November. On five plots tested in every stabile population, we noted 50 sporocarps on average in the oligotrophic habitat developed in the flat pond bottom in Krzyżowa, whereas in Brożek, where the habitat is also oligotrophic, but the bottom relief is more diversified, 70 sporocarps occurred on average. The highest number of sporocarps, 112 on average, was observed in Poręba Wielka in the eutrophic habitat with irregular surface of the fishpond bed, where ferns mature earlier.

VIABILITY OF SPORES. The majority of spores were viable, gametophyte development started in about 70% of macrospores. The green parts of the female prothalli protruding from spores were discoid; some of them developed short structures that may be identified as rudimentary rhizoids. Male prothalli were hidden inside spores; male gametes were released faster in warm water.

CHROMOSOME NUMBER. In all populations it was found to be $2n = 26$.

MORPHOLOGY. Depending on water depth, *Pilularia* develops two morphological forms: terrestrial and aquatic. Plants growing on an emerged substratum form short and dense tufts, with erect and succulent leaves up to 10(–12) cm long. The smallest mature specimen of terrestrial form was noted in Poręba Wielka and reached 1.2 cm. Ferns growing in water have delicate and slender leaves, up to 50 cm long. Newly immersed areas are colonized by long rhizomes with internodes up to 14 cm long; secondary branches are short with internodes up to 5 cm, often only a few millimeters long. Long colonizing rhizomes develop in water, ferns growing on emerged stands form mainly shoots with short internodes.

OCCURRENCE IN PLANT COMMUNITIES. The species occurs in two types of plant communities: in pioneer vegetation of the class *Litorelletea uniflorae* Br.-Bl. Et R. Tx. 1943 developed on newly emerged banks and bottoms, and in two-level vegetation consisting of rushes and small herbs associated with areas of low water level or prolonged emersion.

Pioneer vegetation with *P. globulifera* belonged to two plant communities. The fern was observed in the association *Ranunculo-Juncetum bulbosi* (Nordh. 1921) Oberd. 1957 of the alliance *Lobelion* (van den Bergen 1944) R. Tx. et Dierss. ap Dierss. 1972 developed on the wet or immersed banks of ponds in Rokitki and Krzyżowa, under water up to 10 cm deep. Phytocoenoses were moderately rich and consisted of 10–15 taxa. Participation of *P. globulifera* was rather small, it covered about 10% of the relevé area, other species of the *Litorelletea uiflorae* class, i.e. *Juncus bulbosus* or *Hydrocotyle vulgaris* were dominated (Tab. 1, relevés 1–3).

Under optimal habitat conditions, the species formed the subatlantic plant community *Pilularietum globuliferae* R. Tx. 1955 ex Müll. et Görs 1960 of the alliance *Hydrocotylo-Baldenion* R. Tx. Et. Deirss. ap. Dierss. 1972. Plant cover of the richest plots comprised of 14–22 plant species. These areas emerged in late summer and development of emersed phytocoenoses lasted about 3 months. *Pilularia* formed mats covering 50–80% of the area. Permanent elements of the patches were character species of the classes *Litorelletea uniflorae* (e.g., *Ranunculus flammula*, *Juncus bulbosus*), *Isoëto-Nanojuncetea* Br.-Bl. et R. Tx. 1943 (e.g., *Elatine hexandra*, *Peplis portula*, *Gnaphalium uliginosum*), *Scheuchcerio-Caricetea nigrae* (Nordh. 1937) R. Tx. 1937 (e.g., *Juncus articulatus*), *Bidentetea tripartiti* R. Tx., Lohm et Prsg 1950 (e.g., *Bidens frondosa*, *B. radiata*, *Polygonum hydropiper*) and *Phragmitetea* R. Tx. et Prsg 1942 (e.g., *Alisma plantago-aquatica*, *Eleocharis palustris*, *Phragmites australis*), but their contribution was rather small (Tab. 1, relevés 4–12). Moreover, species of the *Phragmitetea* class were almost always undersized

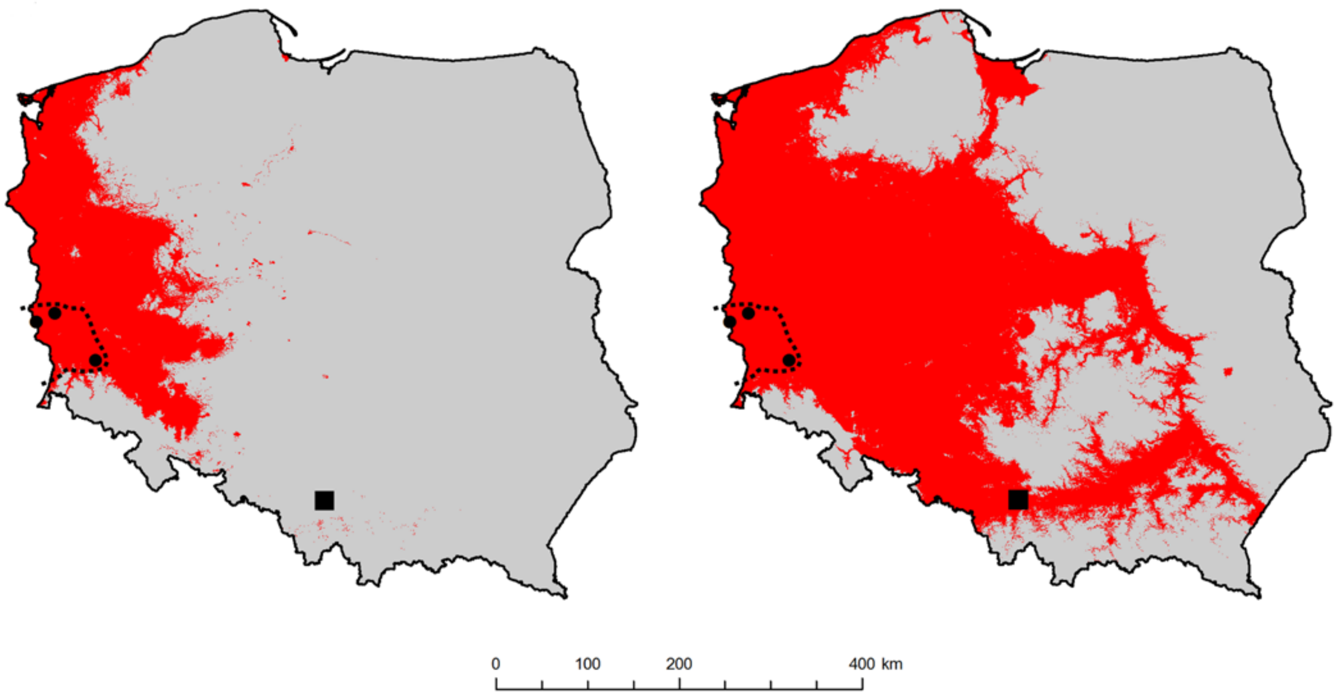

Fig. 2 The area of temperatures sufficient for *Pilularia globulifera* to perform complete vegetation cycle in decades 1951–1960 (left) and 1996–2005 (right). Black circle – stand noted in last 10 years within continuous geographical range; black square – stand noted within last 10 years beyond continuous geographical range; dotted line – border of continuous geographical range.

Tab. 1 Pioneer plant communities of the class *Litorelletea uniflorae* with *Pilularia globulifera*.

No. of relevé	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	Constancy
Month	06	08	08	09	09	09	07	11	08	08	08	11	10	08	09	09	07	10	10	08	10	
Year	08	08	09	10	82	10	09	09	10	10	10	09	11	10	82	10	08	11	11	08	11	
Area in m^2	50	6	6	6	10	10	2	0,5	20	20	15	1	18	12	30	8	9	20	10	10	25	
Cover of herb layer (%)	70	80	70	95	95	100	90	70	95	80	80	70	90	90	90	80	90	95	95	80	30	
Cover of moss layer (%)	.	.	.	+	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	
Location	R	K	K	B	J	B	B	L	P	P	P	L	P	P	J	B	B	P	P	K	P	
No. of species	10	15	14	19	22	17	16	14	18	14	16	14	12	11	11	8	9	5	3	4	6	
Cl. *Litorelletea uniflorae*																						
Pilularia globulifera	1	1	1	5	4	4	4	4	5	4	3	3	5	5	5	5	5	5	5	5	2	V
Ranunculus flammula	1	1	+	+	2	+	.	.	+	+	+	.	+	+	+	.	.	.	.	.	+	III
Juncus bulbosus	.	2	2	+	2	2	1	.	.	.	.	.	.	.	+	r	.	.	.	.	.	II
Hydrocotyle vulgaris	3	3	3	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	II
Carex viridula	2	+	r	+	1	.	.	+	.	.	.	3	.	.	.	.	.	.	.	.	.	II
Eleocharis acicularis	2	.	.	.	.	.	.	+	.	.	.	.	1	.	.	.	.	.	.	.	+	I
Veronica scutellata	1	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I
Eleocharis mamillata	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I
Cl. *Isoeto-Nanojuncetea*																						
Peplis portula	+	.	.	1	.	1	.	.	+	1	+	.	.	.	.	.	+	.	.	.	.	II
Elatine hexandra	.	.	.	2	.	.	.	.	1	1	+	.	+	+	.	.	.	.	.	.	2	II
Gnaphalium uliginosum	1	r	r	.	.	.	.	.	.	.	.	r	+	.	.	.	.	.	.	r	.	II
Plantago intermedia	1	r	+	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	I
Bryum pallens d	.	.	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I
Juncus bufonius	.	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	I
Sporadic: *Fossombronia incurva* d 7(+); *Juncus capitatus* 17(r); *Trichodon cylindricus* d 6(+), 7(+).																						
Cl. *Scheuchcerio-Caricetea nigrae*																						
Juncus articulatus	.	.	+	.	.	2	3	1	+	.	+	2	.	.	.	.	+	.	.	.	+	III
Carex lasiocarpa	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	I
Sporadic: *Agrostis canina* 5(+), 9(r); *Drosera intermedia* 16(+); *Lycopodiella inundata* 16(+); *Riccardia chamedryfolia* d 4(+).																						
Cl. *Phragmitetea*																						
Alisma plantago-aquatica	.	+	+	.	+	r	+	.	+	+	+	.	r	+	.	r	.	1	1	r	+	IV
Eleocharis palustris	.	.	+	+	+	+	.	.	+	+	+	.	+	1	+	.	.	.	1	.	.	III
Phragmites australis	.	.	.	+	.	1	.	.	.	r	.	.	.	.	+	.	+	.	.	.	.	II
Phalaris arundinacea	.	.	.	.	.	+	.	.	.	.	.	.	r	+	.	.	+	.	.	.	.	I
Typha angustifolia	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.		.	2	.	.	.	I
Glyceria fluitans	.	.	.	+	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	I
Sporadic: *Carex elata* 4(+); *C. pseudocyperus* 4(r), 5(1); *Cicuta virosa* 5(+), 15(+); *Galium palustre* 5(+), 15(+); *Glyceria maxima* 9(+), 11(r); *Rorippa amphibia* 15(+).																						
Cl. *Bidentetea tripartiti*																						
Bidens frondosa	.	.	.	.	.	.	r	.	+	1	+	.	.	+	.	.	+	1	.	.	.	II
Bidens radiata	.	+	r	.	.	.	.	.	+	+	r	.	.	.	.	+	.	.	.	r	.	II
Polygonum hydropiper	.	r	.	.	.	.	.	.	+	r	+	.	+	+	.	.	.	.	.	.	.	II
Rorippa palustris	.	+	.	.	+	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	I
Alopecurus aequalis	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	I
Sporadic: *Bidens cernua* 5(+); *Polygonum lapatifolium* 5(+); *P. mite* 14(+); *Ranunculus sceleratus* 8(r), 12(r).																						
Cl. *Molinio-Arrhenatheretea*																						
Lysimachia vulgaris	.	+	+	.	.	.	.	.	+	+	+	.	.	.	.	.	.	+	.	.	.	II
Epilobium palustre	+	r	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.	II
Juncus effusus	.	.	.	+	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	I
Myosotis palustris	.	r	.	.	.	.	.	+	.	.	.	.	r	.	.	.	.	.	.	.	.	I
Juncus conglomeratus	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I
Sporadic: *Agrostis stolonifera* 7(+), 15(+); *Leontodon autumnalis* 5(+); *Lythrum salicaria* 8(r).																						
Accompanying species																						
Lycopus europaeus	.	.	.	1	+	+	r	.	+	r	+	.	+	+	.	r	.	.	.	.	.	III

Tab. 1 *(continued)*

No. of relevé	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	Con.
Myosotis caespitosa	.	.	.	1	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.		.	I

Sporadic: *Calamagrostis epigeios* 16(r); *Carex leporina* 6(r), 7(r); *Ceratodon purpureus* d 4(+), 7(+); *Cirsium arvense* 8(r); *Conyza canadensis* 7(r); *Drepanocladus polycarpos* d 12(+); *Holcus lanatus* 12(r); *Hypochoeris radicata* 12(+); *Juncus acutiflorus* 6(+), 7(+); *Juncus alpinus* 3(r), 5(1); *Mentha aqatica* 5(+); *Nasturtium officinale* 8(r); *Oenanthe aquatica* 6(+), 7(+); *Poa annua* 8(+), 12(+); *Potamogeton gramineus* f. *terrestre* 5(2); *P. amphibium* f. *terrestre* 15(+); *Polygonum persicaria* 5(+); *Salix alba* 4(+), 6(+); *S. aurita* 6(+), 17(+); *S. cinerea* 8(r), 12(r); *S. fragilis* 6(r); *Salix* × *rubens* 6(r), 17(r); *Salix* sp. 2(r), 3(r), 9(+); *Schoenoplectus mucronatus* 9(+), 11(+); *Sonchus asper* 5(+); *Sphagnum denticulatum* d 7(+).

Location: B – Brożek; J – Janiszowice [49]; K – Krzyżowa; L – Lubsko; P – Poręba Wielka; R – Rokitki [54].

and sterile. The poorest plots consisting of 3–12 species emerged in late autumn and development of emersed vegetation lasted about one month. *Pilularia globulifera* covered 80 to 100% of all patches, sometimes forming almost one species aggregation. The other recorded plant species, including therophytes of the classes *Litorelletea uniflorae*, *Isoëto-Nanojuncetea* and *Bidentetea tripartiti*, as well as single plants of perennial rushes of the *Phragmitetea* class, were nearly always juvenile or sterile.

In the second type of vegetation, the pillwort occurred in two-level communities formed by small species of the classes *Litorelletea uniflorae* (e.g., *Juncus bulbosus*, *Ranunculus flammula*) and *Isoëto-Nanojuncetea* (e.g., *Elatine hexandra*, *Peplis portula*, *Gnaphalium uliginosum*), and well-developed mature and flowering perennial plants of the *Phragmitetea* class (e.g., *Alisma plantago-aquatica*, *Eleocharis palustris*, *Phragmites australis*, *Typha angustifolia*; Tab. 2). *Pilularia* can enter the rushes after an increase in water level as in Krzyżowa, where the ponds are still used as fishponds, or rushes enter the habitats of *Pilularietum globuliferae*, when the area is abandoned and devoid of regular periods of emersion and immersion. In such habitats, pillwort was recorded in the communities: *Phragmitetum australis* (Gams 1927) Schmale 1939, *Typhetum angustifoliae* (Allorge 1922) Soó 1927, *Eleocharitetum palustris* Šennikov 1919 and *Equisetetum fluviatilis* Steffen 1931, where it occurred among the rushes and formed the second level of the community structure. It covered 5 to 90% of the plot with regard to the phase of rush succession.

The two main groups of relevés distinguished by TWINSPAN were the plots of *Typhetum angustifoliae* and patches of all other communities developed in all locations of *P. globulifera*. This division was accorded to species richness coincident with surrounding vegetation and the time of succession in area of water reservoirs, not to richness of habitat nor to the form of management. In the results of DCA and CCA analyses, the most important was also the gradient of species richness, the importance of other vectors was similar and small.

Discussion

Pilularia globulifera is a narrowly specialized coastal fern, adapted to changing habitat conditions; it can survive periods of complete immersion, is able to occur in water up to about a meter in depth, and after disappearance during years of exceptional drought, sporocarps may remain dormant for many years and start to grow under favorable conditions [21]; however, the long period of dormancy is contentious [56]. Throughout the entire range the fern is threatened with extinction. The main threats to the species are the stabilization of water levels and the drainage of temporary wetlands [11].

Natural ecological amplitude of *P. globulifera* is rather narrow and the species is associated with oligo- and mesotrophic habitats; occasionally, it was observed in eutrophic stands. A significant factor limiting the presence of the fern is the influence of modern agriculture, particularly acidification and eutrophication as a consequence of ammonium deposition and accumulation [57]. According to Landsdown [11], even a low-level eutrophication may pose a threat as it enables colonization of an otherwise unsuitable habitat by more competitive plants. In contrast, anthropogenic habitats colonized by *Pilularia* are more fertile, up to slightly eutrophic [58]. Opposite points of its ecological scale are the oligotrophic postglacial lakes in Finland, where *Pilularia* occurred with *Isoëtes echinospora*, *I. lacustris*, *Lobelia dortmanna* [59], and an eutrophic habitat observed in Germany, where the species entered flooded fields with *Zea mays* and grew together with *Echinochloa crus-galli* and *Plantago major* [60]. Generally, the pillwort is a weak competitor and grows mainly in habitats that are largely competition free. When competitors are eliminated, the pillwort occurs in habitats of all type of fertility.

Pilularia globulifera is a subatlantic species, which penetrates the central part of Europe and reaches there its eastern boundary of continuous geographical range. Along the eastern periphery, its populations are rare, number of stands and their quantity fluctuate irregularly and distribution of marginal populations depends mainly on winter temperatures. Nowadays, a process of rebuilding of peripheral populations seems to be observed. In Czech Republic, the species has been considered as extinct since the 1930s, but a new locality was discovered in 2007 [7]. In Poland, the number of sites recorded in last ten years is the highest since 1945.

It is difficult to predict how narrowly specialized plant species will respond to climate change. Global warming in connection with human activity results in ground water decrease, which in turn causes the demise of peat bog and wet meadow habitats of *Pilularia* in the western lowlands of Poland [53]. The same factors increase the number of possible locations in anthropogenic ponds. Banks of abandoned anthropogenic ponds are flooded by freshwater in springtime and dry out during summer and autumn. Immersion stops the development of competitive species and pillwort can continually pioneer new bare sites. In ponds still used, banks and beds are permanently immersed and only periodically the entire area emerges due to the fish-breeding cycle. However, water deficit related to summer droughts resulted in a new function of selected ponds in fish-breeding complexes: they became water reservoirs emptying in summer.

Tab. 2 Two-level plant communities of *Pilularia globulifera* and rushes.

No. of relevé	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Constancy
Month	09	09	09	09	09	09	09	08	10	08	10	08	08	10	10	08	08	10	10	10	
Year	82	10	82	10	82	09	09	08	11	10	11	10	10	11	11	10	10	11	11	11	
Area in m^2	20	15	8	15	8	8	10	6	20	30	20	20	15	20	20	15	20	20	20	15	
Cover of herb layer (%)	100	100	95	95	100	90	50	40	70	100	70	100	90	100	50	50	70	80	100	60	
Cover of moss layer (%)	.	.	.	.	+	.	.	.	15	10	.	+	.	.	.	.	.	.	.		
Location	J	B	J	B	J	K	K	K	P	P	P	P	P	P	P	P	P	P	P	P	
No. of species	15	15	9	16	17	14	12	11	25	23	8	15	14	17	17	16	15	15	8	9	
Cl. *Litorelletea uniflorae*																					
Pilularia globulifera	5	5	5	4	3	2	2	+	2	1	2	3	5	4	2	+	2	+	1	1	V
Juncus bulbosus	+	1	+	1	2	3	+	+	.	.	.	.	.	.	.	+	.	.	.	.	III
Ranunculus flammula	1	.	.	.	.	.	.	.	+	+	.	+	+	.	1	+	+	.	.	.	II
Hydrocotyle vulgaris	1	.	.	.	3	2	+	.	.	.	.	.	.	.	.	.	.	.	.	.	I
Eleocharis acicularis	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	1	.	2	I
Sporadic: *Carex viridula* 6(+), 7(r); *Eleocharis mamillata* 11(+).																					
Cl. *Isoeto-Nanojuncetea*																					
Elatine hexandra	.	.	.	.	.	.			+	.	2	.	.	1	2	.	.	+	.	.	II
Peplis portula	.	+	.	1	.	.			.	.	.	.	.	.	1	.	.	.	+	+	II
Gnaphalium uliginosum	.	.	.	+	.	1	.	+	+	.	.	.	.	.	.	.	.	+	.	.	II
Sporadic: *Limosella aquatica* 14(+), 19(+); *Plantago intermedia* 9(+).																					
Cl. *Scheuchcerio-Caricetea nigrae*																					
Juncus articulatus	.	.	.	1	+	.	.	.	.	.	.	.	+	.	.	r	.	.	.	.	I
Agrostis canina	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	r	.	.	.	.	I
Sporadic: *Bryum pseudotriquetrum* d 5(+); *Carex canescens* 4(+).																					
Cl. *Phragmitetea*																					
Phragmites australis	3	4	2	3	2	2	3	2	.	+	.	.	.	.	.	.	r	.	.	.	III
Typha angustifolia	.	.	.	.	.	.			4	4	4	3	+	1	+	+	1	+	+	.	III
Eleocharis palustris	.	1	.	+	.	+	r	+	+	1	.	1	2	3	3	3	3	5	5	.	IV
Equisetum fluviatile	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	+	.	.	3	I
Alisma plantago-aquatica	.	+	.	+	+	+	+	+	1	+	2	+	+	1	1	+	+	+	1	+	V
Cicuta virosa	.	.	+	.	+	.	.	.	+	.	.	+	.	.	+	.	r	+	.	.	II
Galium palustre	+	+	.	.	+	.	+	.	.	.	.	.	.	.	.	.	r	.	.	.	II
Peucedanum palustre	.	.	.	.	.	.	.	.	+	.	.	.	.	+	+	r	.	+	.	.	II
Glyceria fluitans	.	+	.	.	.	.	.	.	.	.	.	.	+	+	1	.	.	.	.	.	I
Sporadic: *Alisma gramineum* 14(r), 18(+); *Carex pseudocyperus* 1(+), 5(+); *Lysimachia thyrsiflora* 5(+); *Mentha aqatica* 5(+); *Phalaris arundinacea* 10(+), 16(r); *Rorippa amphibia* 14(r); *Schoenoplectus lacustris* 2(+); *Scutelaria galericulata* 9(+), 10(+); *Sium latifolium* 1(+), 5(+); *Typha latifolia* 10(+).																					
Cl. *Bidentetea tripartiti*																					
Bidens frondosa	.	r	.	+	.	.	.	.	2	1	.	.	+	+	1	.	+	+	.	.	III
Bidens radiata	.	.	.	.	.	r	+	r	+	+	.	.	.	+	+	r	.	.	.	.	II
Polygonum hydropiper	.	.	.	.	.	.	.	.	1	.	1	+	+	.	.	.	.	.	.	+	II
Bidens cernua	+	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I
Rorippa palustris	.	.	+	.	.	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	I
Polygonum mite	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	r	.	.	.	.	I
Alopecurus aequalis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	I
Cl. *Molinio-Arrhenatheretea*																					
Juncus effusus	.	.	.	+	.	1	+	1	.	3	.	1	.	.	.	.	+	.	.	.	II
Lysimachia vulgaris	.	.	.	.	.	+	+	+	1	+	.	.	.	.	+	.	+	.	.	.	II
Lythrum salicaria	.	r	.	.	.	.	.	.	.	1	.	+	.	.	.	.	+	.	.	.	II
Myosotis palustris	.	.	.	.	.	.	.	.	.	+	.	.	.	+	+	.	.	+	.	.	I
Agrostis stolonifera	+	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I
Epilobium palustre	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.	I
Sporadic: *Cirsium palustre* 9(+); *Galium uliginosum* 9(+); *Juncus conglomeratus* 10(1), 12(+); *Lotus uliginosus* 9(+); *Potentilla anserina* 3(+).																					
Accompanying species																					
Lycopus europaeus	+	+	.	+	+	.	.	.	1	+	+	+	+	.	1	+	+	1	.	+	IV

Tab. 2 *(continued)*

No. of relevé	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Con.
Myosotis caespitosa	.	2	.	1	.	.	.	.	.	.	.	+	+	.	.	+	.	.	.	.	II
Alnus glutinosa juv.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	+	.	.	+	.	.	I
Cirsium arvense	+	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I
Taraxacum sp.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	r	.	.	I
Batrachium sp. juv.														.					.	2	I

Sporadic: *Calamagrostis epigeios* 14(+); *Drepanocladus polycarpos* d 9(1), 12(+); *Galinsoga parviflora* 1(+); *Lemna minor* 19(+); *Philonotis arnelli* d 9(+), 10(+); *Pohlia nutans* d 9(+), 10(+); *Polygonum persicaria* 3(+), 10(r); *Ricciocarpos natans* d 19(+); *Salix alba* 2(+), 4(+); *Salix* sp. 6(+), 7(r), 8(+), 13(+); *Salvinia natans* 16(+); *Tanacetum vulgare* 14(+).

Location: B – Brożek; J – Janiszowice [49]; K – Krzyżowa; P – Poręba Wielka.

This management regime is regulated by humans and does not depend directly on natural factors limiting a water level being favorable for the fern to develop. Nowadays, anthropogenic habitats seem to be one of the most important for the survival of *P. globulifera*. According to correlation of temperature and pillwort continuous range in Central Europe, we define mean annual and January air temperature sufficient for the species to conduct a complete vegetation cycle regularly, as 8.0°C and −3.0°C respectively. These isotherms seem to determine the boundary of hypothetical range of the species in Poland; the increase of this area is significant (Fig. 2). Anthropogenic water reservoirs located in this area seem to become potential habitats of *P. globulifera*.

The location in Poręba Wielka is an example of this kind of stand. It is located about 280 km beyond the eastern boundary of the previous range of *P. globulifera* in Poland. The species was not observed there in the 1990s during a research on *Schoenoplectus mucronatus* population occurring in the same pond [61]. This new location suggests that the species is able to expand and form stabile populations beyond its historical continuous range. The coincidence of the extending range of thermophilous water ferns with climate warming is confirmed by the expansion of *Azolla filiculoides*, which was ephemeral in Poland up to the 1980s and began regular wintering at the end of the first decade of the 21st century [62].

As long as sources of spores are present, the spread of this native species to man-made habitats will be a natural process. The main transporting factors of *P. globulifera* propagules are birds [6]. Adhesive gelatinous mass (mucilage) appearing during the release of spores and surrounding hydrated spores can facilitate transportation. Moreover, we observed swans (*Cygnus olor*) feeding on rhizomes and leaves of *Pilularia* and *Juncus bulbosus* and carrying fragments of both species on their necks and feathers [53].

In Poland, *P. globulifera* is protected by law. Specimens are vigorous and not directly destroyed due to their low attractiveness; the main threats are the disappearance of natural habitats and intensive management of potential habitats in anthropogenic fishponds. Pillwort has possibly occurred in more than five known stands during the most recent ten years, but this is difficult to observe due to the ephemeral presence of habitats and the species. This fern requires active protection, mostly in the form of regulation of emersion and immersion periods of fishponds during the year. It is one of species, which exemplifies the important role of man-made habitats for the survival of endangered plants. The high viability of spores, gametophytes and young sporophytes suggests that the species is vigorous, and if conditions are favorable, that further spread will be possible.

Pilularia globulifera sporocarps and living plants were collected in 2008, from a population in Krzyżowa, and the species is currently cultivated in the Botanical Garden of the University of Wrocław. Plants in cultivation are vigorous and regularly produce sporocarps.

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Authors' contributions

The following declarations about authors' contributions to the research have been made: wrote the paper: ES; field research: ES, SR, KS, JK, MŚ; phytosociological documentation and analyses: ES, SR; climate analyses and map preparation: MS; preparation of distribution map: MŚ; cariological analysis: AK; cultivation and ex-situ research: RK.

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