



Pogonoloma macrorrhizum (Basidiomycota, Agaricales) in Slovak landscape: a distinct fungus of *Quercus cerris* stands transitional in space and time

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Abstract

The lack of precise data on the environmental requirements of the conspicuous fungus with a northern distribution limit in Slovakia, *Pogonoloma macrorrhizum*, initiated our study. Its identity was verified by sequencing of ITS and 28 S nrDNA regions. The analysis of trophic status by stable-isotope ratio of carbon and nitrogen suggested that the species is probably ectomycorrhizal. For the seventeen sampling sites, environmental data were obtained and information on landscape development and management were retrieved from historical maps and aerial orthophotographs. All these parameters were analysed by multivariate ordination methods. In Slovakia, *P. macrorrhizum* is found in thermophilous to mesophilous stands on acidic soils with a pH ranging from 4.1 to 6.2. These habitats are dominated by *Quercus cerris*, with non-frequent tree taxa of *Carpinus betulus* and *Quercus petraea* agg. The key environmental drivers shaping the habitat of *P. macrorrhizum* were identified as time since deforestation, with the presence of old *Q. cerris* individuals (former solitary trees of pastures) and soil characteristics. The fungus appears to be a species of transitional habitats historically affected by grazing. These transitions occur between thermophilic and mesophilic sites, including oak forest communities, dry steppic grasslands and forest edges, as well as spontaneously overgrown pastures and forests with a closed canopy. It is regrettable that the *Q. cerris* stands in Slovakia are under threat, particularly because of felling and the lack of grazing in forests. Furthermore, recent silvicultural practices have resulted in the replacement of oaks (*Quercus* spp.) by hornbeam (*Carpinus betulus*) and the formation of closed stands.

Keywords Grazing · Landscape ecology · *Pogonoloma macrocephalum* · Thermophilous species · Vegetation · Wood pastures

Introduction

The trophic status, environmental requirements, and responses to human impacts of numerous fungal species remain largely unknown (Tomao et al. 2020). This even applies to large, conspicuous agarics such as *Pogonoloma macrorrhizum* (Quél.) Dima & P.-A. Moreau. This rare species is distinguished by the production of exceptionally large and fleshy fruiting bodies with fasciculate stems (Ludwig 2000: 42.11.) and possesses a very specific smell. Over the past two decades, the phylogenetic placement and nomenclature of this species have undergone significant changes (Tkáčec and Mešić 2002; Vizzini et al. 2012; Sánchez-García et al. 2014; Alvarado et al. 2018). It belongs to a well-supported lineage, along with *Pogonoloma spinulosum* (Kühner and Romagn.) Sánchez-García. The genus *Pogonoloma* is only

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distantly related to the genera *Porpoloma* or *Leucopaxillus*, where *P. macrorrhizum* was formerly placed. The following synonyms have been applied for *P. macrorrhizum*: *Leucopaxillus macrorrhizus* (Quél.) Sacconi and Lazzari, *L. macrocephalus* Huijsman ex Bohus, *Pogonoloma macrocephalum* (Bon) Sánchez-García, *Porpoloma macrorrhizum* (Quél.) Bon or *Porpoloma macrocephalum* Bon (for a comprehensive synonymy see Alvarado et al. 2018).

Pogonoloma macrorrhizum is considered rare in both central and southern Europe (Siller et al. 2006; Alvarado et al. 2018), with fruiting occurring between May and November. The species is distributed in France (Alvarado et al. 2018), Italy (Sánchez-García et al. 2014), Switzerland (Marchand 1986; Senn-Irlet et al. 2007), Germany (Ludwig 2021; DGFM 2019), Austria (AMS 2015), Slovenia (Jurc et al. 2005), Croatia (GDK 2011), Slovakia (Dermek 1985), Hungary (e.g. Bohus 1966; Siller et al. 2006), Serbia (Uzelac 2009) and Greece (GMS 2017). Additionally, the species has been reported from Turkey (Marchand 1986) and Iran (GenBank: MH595847). It is absent in northern Europe (Knudsen and Vesterholt 2012). It is rare throughout Europe, but more frequent in regions with suitable environmental conditions. For example, more than 20 localities are known in the warmer eastern part of Austria (AMS 2015) and more than 30 in Slovenia (Jurc et al. 2005).

The published records and environmental requirements of *P. macrorrhizum* are scarce. It is anticipated that it is a species of thermophilous temperate and Mediterranean oak and oak-hornbeam forests (e.g., Dermek 1985; Ludwig 2001; Siller et al. 2006; Dämon and Krisai-Greilhuber 2017; Alvarado et al. 2018). Our data from Slovakia indicated that *P. macrorrhizum* occurs in thermophilous forests with Turkey oak (*Quercus cerris*) influenced by grazing. *Quercus cerris* is a southeastern European species, with the northern border of its natural distribution to be found in Slovakia (Blanár 2017). It typically forms stands in which the canopy is not completely closed. Semi-open *Quercus* woodlands represent important hotspots of fungal diversity (Berg et al. 2002; Paltto et al. 2006; Ranius et al. 2008). However, the mycobiota of *Q. cerris* forests remains relatively understudied (Laganà et al. 1999; Salerni et al. 2000, 2001; Ambrosio and Zotti 2015; Angelini et al. 2015; Ambrosio et al. 2018a, b). Furthermore, the current climatic and land use changes have a significant impact on the species composition and functional diversity of the plant and fungal communities (Andrew et al. 2016).

In order to comprehend the environmental requirements and distribution of any organism in space and time, occurrence data must be gathered at spatial and temporal scales (Andrew et al. 2017). It is also important to consider that the landscape itself undergoing change as a result of habitat succession and human impacts. To date, there has been

a lack of research investigating the influence of landscape development and management history on forest macrofungi (e.g., Horak et al. 2014; Kutszegi et al. 2015; Tervonen et al. 2019). Hilmers et al. (2018) emphasised the strong effects of succession on forest biodiversity at both early and late successional stages. These stages of succession frequently drive notable species diversity, particularly among fungi. Berg et al. (2002) revealed high species richness for both forest areas that formerly were pastures and wood pastures. These patchy habitats represent one of the most important biodiversity hotspots in Europe. The occurrence of fungi is driven by edge effects, with resources and microclimatic conditions varying along a gradient from the forest edge to closed stands (Ruete et al. 2017). Moreover, the fungal community of semi-open forest habitats is poorly documented in most regions (Horák et al. 2018; Kunttu et al. 2019; Tervonen et al. 2019, 2022).

The lack of accurate data on the environmental requirements of *P. macrorrhizum* initiated our study in Slovakia. Using preliminary occurrence data collected by the first author since 2015, we hypothesised that the Slovak population of *P. macrorrhizum* prefers thermophilous forests affected by grazing and the fungus has a trophic association with *Quercus cerris*. We analysed these assumptions with aim (1) to reveal the environmental requirements of the species in Slovakia, especially parent rock and soil pH, climatic conditions, type of vegetation, history of land use and management, (2) to check the taxonomic status of the Slovak population of *P. macrorrhizum* using sequencing, (3) to estimate the possible trophic interaction of *P. macrorrhizum* with *Quercus cerris* and (4) to evaluate local vulnerability and demand of protection of *P. macrorrhizum* and its habitats.

Materials and methods

Sampling of *P. macrorrhizum* and co-occurring fungi

Fifteen localities with 17 sampling sites (corresponding probably to a fungal individual) have been discovered or registered by the first author (Electronic Supplement 1, Fig. 1). Some records were provided by local amateur mycologists and verified by the first author. The aim was to search for the species evenly over the entire territory of Slovakia in the warmer part of the country with the presence of oaks (*Quercus* spp.). The data obtained cover all Slovak localities between 2015 and 2020. Collections were identified according to Alvarado et al. (2018). The coordinates of exact sampling sites are not listed to protect the localities which are co-inhabited by rare fungal species, mostly thermophilic boletes from undesirable

Fig. 1 *Pogonoloma macrorrhizum*, example of habitats and fruiting bodies. a, b – Bečov, PRM 961,153; c, d – Kráľová; e, f – Sása, PRM 953,771 (JH39/2019). For details on localities, vouchers, and days of photographing/vegetation sampling please refer to Electronic Supplement 1



mushroom picking, which is unfortunately a significant issue in Slovakia. Nevertheless, the coordinates can be obtained from the first author upon request. The voucher specimens have been deposited in the fungarium of the Mycological Department of the National Museum, Prague (PRM) and in the private fungarium of V. Kunca (PVKU).

A list of selected, easily identifiable fungi co-occurring at localities of *P. macrorrhizum* (mostly species generally considered as thermophilic, see e.g. Fellner 1984) was compiled by the first author using his records and records of collaborating amateur mycologists (Electronic Supplement 3, Acknowledgements). Their occurrence was observed in a radius of approximately 100 m surrounding each sampling site of *P. macrorrhizum*. Some of these records are documented by vouchers in the PVKU. Potential records of *Cantharellus pallens* were included under *C. cibarius*.

Molecular identification

DNA was extracted from two herbarium specimens (Sása: PRM 953,771, see Fig. 1f; Hostie: PRM 953,772) using of pileus trama. The DNA isolation, PCR, sequencing of nuclear rDNA regions (ITS and 28 S), sequence editing and aligning were performed according to Holec and Zehnálek (2020). The newly generated sequences were deposited in GenBank. The obtained sequences were combined with 17 sequences of the ITS region and 12 of the 28 S region of *Pseudoclitocybaceae* species deposited in GenBank (Electronic Supplement 12), which were selected with respect to the phylogeny published by Alvarado et al. (2018). The final concatenated alignment comprised 19 sequences and 1158 characters with *Infundibulicybe geotropa* serving as the out-group. The most suitable evolutionary model, TPM2uf+I, was selected and employed in the software jModelTest (version 2.1.5.) (Darriba et al. 2012). A phylogenetic analysis

Table 1 The parent rock, soil type and soil pH values at localities where *Pogonoloma macrorrhizum* was studied. Further details on localities and sampling sites can be found in the electronic supplement 1

Locality	Parent rock	Soil type	pH value
Kalinovo	quartz sandstones	Cambisols	5.98
Poltár A	fluvial sediments	Gleysols or Stagnic Glossisols	4.63
Suché Brezovo	volcanic sandstones	Cambisols	6.20
Bečov	volcanic sandstones	Cambisols	6.01
Očová	volcanic breccias	Cambisols	4.19
Budča	volcanic breccias	Cambisols	4.71
Kráľová	andesite pyroclastic flows	Leptosols	5.12
Sása A	andesite lava flows	Cambisols	6.20
Breziny	volcanic breccias	Cambisols	4.12
Hostie A	slates with inserts of sandstones	Cambisols	4.84
Šahy	tuffs of andesite	Cambisols	5.02
Dobrá Niva	deluvial sediments	Cambisols	4.86
Jabloňovce A, B	andesite lava flows	Cambisols	5.61/5.13

was conducted using the Bayesian inference with MrBayes 3.2.6 (Ronquist et al. 2012). Two independent runs were performed with 20 million generations sampled every 1000th generation.

Trophic status

The method proposed by (Hobbie 1999) was employed. The stable isotopic composition of nitrogen and carbon was determined by Thermo Flash 2000 elemental analyser connected to a Thermo Delta V Advantage isotope ratio mass spectrometer in a Continuous Flow IV system (Thermo Fischer Scientific, USA) using the standard protocol provide by the manufacturer. The biomass of dried fruiting bodies without obvious damage and alien particles obtained from seven herbarium specimens (Table 1) was ground in a coffee grinder to gain a volume of homogeneous material roughly equivalent to one 1.5 ml Eppendorf tube for each sample. The isotope ratios were reported as delta (δ) values and compared with the standards mentioned by Hobbie et al. (1999). The analyses were conducted at the Research Centre for Radiogenic and Stable Isotopes of the Institute of Geochemistry, Mineralogy and Mineral Resources, Faculty of Science, Charles University in Prague.

Geological, soil and climatic conditions

The data on the parent rock and soil type were obtained from online maps of the Slovak Republic. The geological map can be accessed via the following link: <http://apl.geology.sk/gm50js/>. The bonited soil-ecological units can be found at the following website: www.podnemapy.sk,

Table 2 The mean values for isotope ratios and nitrogen (N) and carbon (C) contents (%) in fruiting bodies of *Pogonoloma macrorrhizum* from Slovakia. The values represent the means of two measurements for each specimen. For further details on the sampled specimens please refer to the electronic supplement 1

Specimen	$^{15}\text{N}/^{14}\text{N}$ (st. dev.)	$^{13}\text{C}/^{12}\text{C}$ (st. dev.)	N (%)	C (%)
PRM 961,153	1.131 (0.03)	-24.393 (0.07)	3.38	39.95
PRM 961,151	0.359 (0.06)	-26.217 (0.19)	2.20	39.30
PRM 961,154	1.418 (0.14)	-25.723 (0.12)	2.96	38.75
PRM 961,156	0.900 (0.05)	-25.613 (0.03)	1.77	37.81
PRM 961,155	1.493 (0.01)	-26.731 (0.01)	3.43	39.40
PRM 953,771	3.005 (0.18)	-25.997 (0.00)	3.08	38.96
PRM 953,772	2.210 (0.02)	-23.911 (0.02)	2.86	38.86

section BPEJ. The pH (H_2O) of the soil was measured in soil samples of 100 cm^3 obtained from a depth of approximately 5 cm and approximately 20 cm from fruiting bodies at all the localities studied (Table 2). The distribution map of *P. macrorrhizum* was created using several zones of different mean air annual temperature from map layers of the Slovak Republic for 1960–1990 (Štrastný et al. 2002).

Landscape structure and management history (Electronic Supplement 2)

The data were obtained using historical maps and aerial orthophotographs (Fig. 2). The historical maps provided information on the landscape structure in the late 18th century (First Military Survey, ca. 1782), the middle of the 19th century (Second Military Survey, ca. 1846) and the end of the 19th century (Third Military Survey and its reambulations around 1900). The land use in the 20th century was derived from panchromatic aerial orthophotographs from 1949 (Historical orthoimagery © GEODIS SLOVAKIA s.r.o., and Historical LMS © Topographical Institute of Banská Bystrica, available at <http://mapy.tuzvo.sk>) in combination with historical military maps dating from 1952 to 1956. The current land use was derived from coloured aerial orthophotographs from 2019 (© EUROSENSE, s.r.o., and GEODIS SLOVAKIA, s.r.o., available as a web map service at: <https://www.geoportal.sk/sk/služby/mapove-služby/wms/wms-zbgis.html>). All historical maps are available as web map service provided by the Slovak Environment Agency (<https://arc.sazp.sk/arcgis/rest/services/ng/rastre/MapServer>). The landscape structure, in particular the presence of forests and pastures, was interpreted visually by colours or by cartographic signs in the historical maps or by structural characteristics of the land cover in the aerial orthophotographs (Fig. 2) in accordance with the methodology proposed by Olah (2009). In order to facilitate comparisons between landscape management practices across different periods, the proportions of land cover types (forests, permanently open patches and cutting areas, permanent

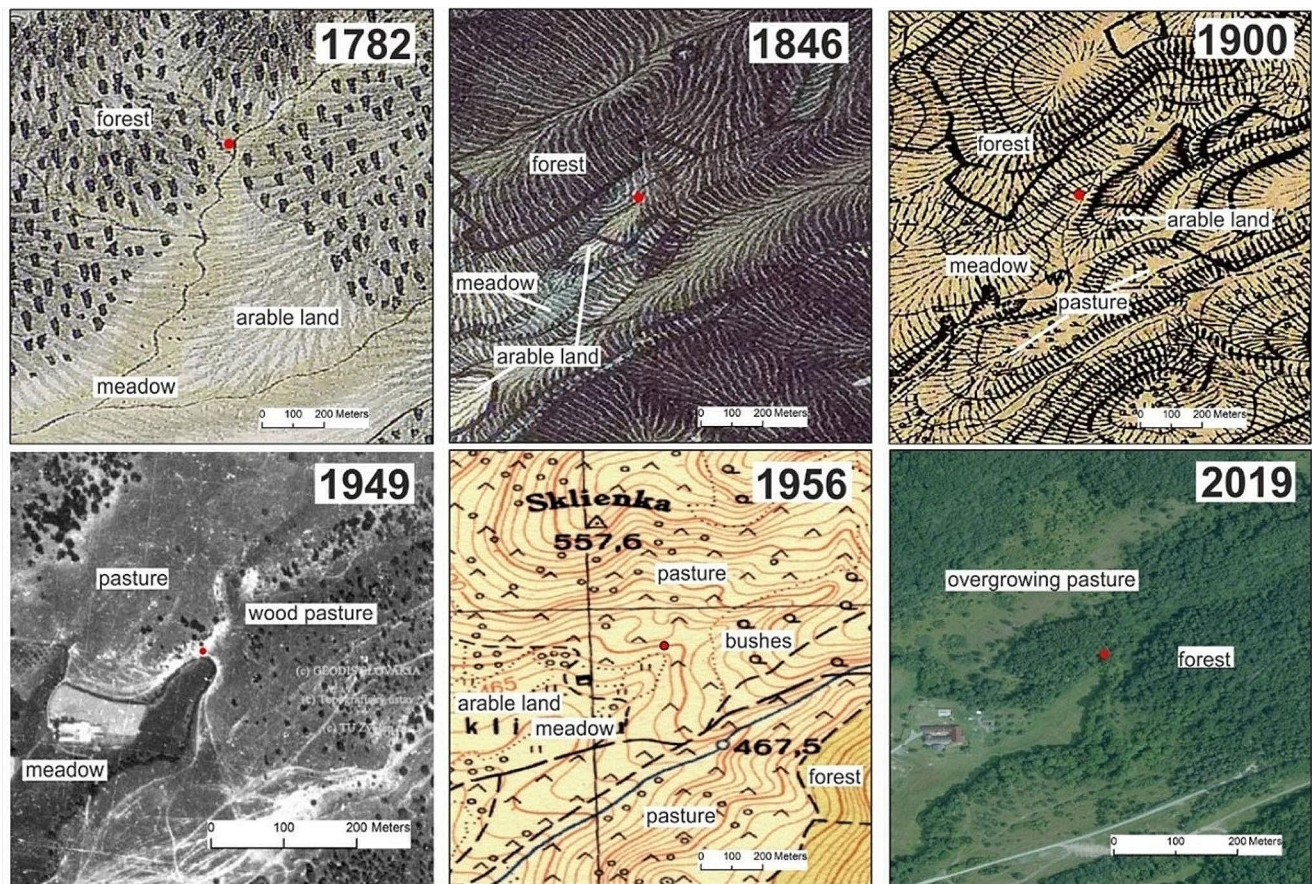


Fig. 2 *Pogonoloma macrorhizum*, locality Sása (red dot): example of landscape development documented by historical maps and orthophotographs

grasslands, or arable lands) were evaluated within a 100-meter radius of each sampling site of *P. macrorhizum*.

Vegetation data

Vegetation samples (phytosociological relevés) were collected by the fifth author in an area of approximately 225 m² surrounding the sampling sites of *P. macrorhizum*. The tree (E_3), shrub (E_2) and herb (E_1) layers were sampled separately using the Braun-Blanquet phytosociological approach (Kent 2012). The ten-degree ordinal scale was employed to transform the cover values into abundance values (see explanations in Electronic Supplement 4). The plant names follow Euro+Med (2006), while the names of the syntaxa were sourced from Jarolímek et al. (2008). To facilitate comparison with the synthesis of deciduous forests in Slovakia, a frequency table of higher units was compiled (for further details, please refer to the Electronic Supplement 4). The diagnostic and constant values were taken from Jarolímek and Šibík (2008). Additionally, the concept of ancient forest species, which indicates the degree of forest naturalness (AFS), as proposed by Hermy and Verheyen (2007), was applied. The trunk diameter of *Q. cerris*

individuals was measured using a calliper at breast height. Values were averaged from 10 trees surrounding fruiting bodies of *P. macrorhizum*.

Statistical analyses

As a preliminary step, we computed the principal component analysis (PCA) in Canoco 5.12 software (ter Braak and Šmilauer 2012) to eliminate collinearity between inter-related habitat parameters (see Electronic Supplements 6–9). Subsequently, three substitute variables representing three orthogonal PCA1–3 axes were utilised instead of the original parameters (see Electronic Supplement 8). These ordinations do not represent results but a simplification of environmental data. To achieve the same objective, an unconstrained gradient analysis (Detrended Correspondence Analysis, DCA) was conducted to determine the plant species pattern using data from vegetation samples of *P. macrorhizum* collection sites (Electronic Supplement 5). The largest DCA gradient was 3.48, therefore detrending by segments was employed to avoid the arch effect, and the linear methods were selected for further analyses due to the relatively homogeneous vegetation cover. The three main

DCA axes, which represent the main vegetation gradients, were therefore used for further analyses instead of the plant species pattern (Electronic Supplements 6, 7).

The significance of environmental parameters over the vegetation pattern of *P. macrorhizum* sampling sites was tested using the direct gradient analysis (a redundancy analysis, RDA), which was carried out by the constrained ordination framework with linear response. The explanatory effects of particular environmental parameters (Electronic Supplement 6) were evaluated by Monte Carlo permutation test (MCPT, number of permutations 4999) with a stepwise forward selection procedure which selected independent parameters with the best fit to species data. All these analyses were applied using Canoco 5.12 software (ter Braak and Šmilauer 2012).

Results

Pogonoloma macrorhizum: identity and distribution in Slovakia

The ITS and 28 S nrDNA sequences were successfully obtained from both specimens under study (PRM 953,771, PRM 953,772). Phylogenetic analysis demonstrated with high bootstrap support that the Slovak collections are conspecific with other sequenced materials of *P. macrorhizum* (Fig. 3).

In the period between 2015 and 2020, we identified 15 localities of *P. macrorhizum* with 17 sampling sites that we ourselves had studied. All these localities were in the southern parts of Slovakia, with the highest frequency in

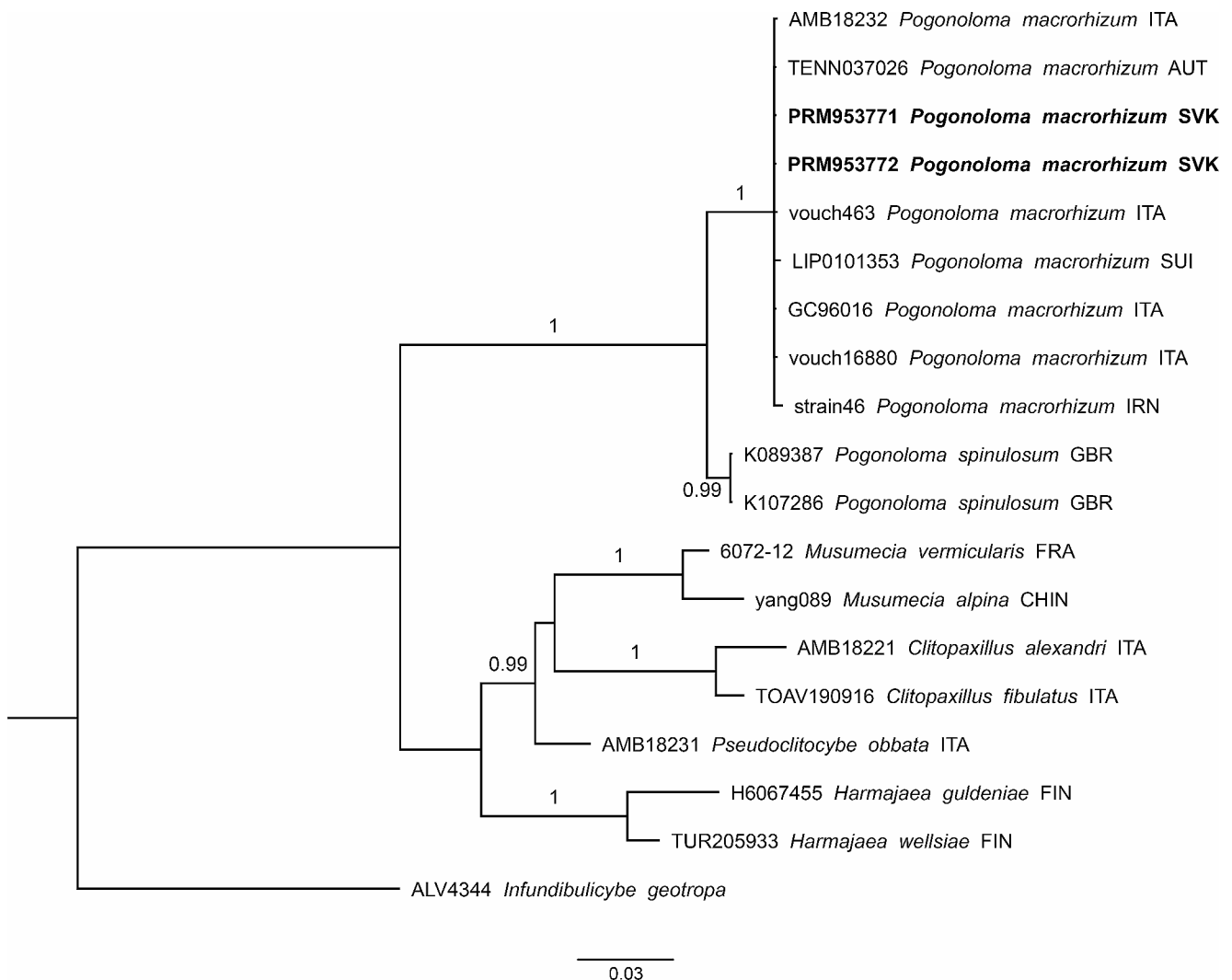


Fig. 3 The phylogenetic tree of *Pogonoloma macrorhizum* and related taxa based on ITS and 28 S markers, derived from Bayesian inference. The branches of the tree are provided by values of Bayesian posterior probabilities ≥ 0.95 . The sequences are labelled by their voucher/strain

number, fungal name, and country of origin. Scale bar expresses number of substitutions per branch length. Those sequences printed in bold were obtained during this study. For GenBank codes, please refer to Electronic Supplement 12

its central region (Fig. 4). No records from other regions of Slovakia have been found.

Trophic status

Analyses of stable isotopes of nitrogen and carbon were conducted on seven specimens from different sampling sites (Table 1). The measured values ranged between 0.359 and 3.005 as the ratio of $^{15}\text{N}/^{14}\text{N}$ isotopes and between -26.731 and -23.911 as the ratio for $^{13}\text{C}/^{12}\text{C}$ (Table 1).

Co-occurring fungi

Two species were identified at all localities: the thermophilous *Boletus aereus* and the ubiquitous *Cantharellus cibarius*, which fruited together with *P. macrorrhizum* (Electronic Supplement 3). *Butyriboletus regius* was present at most localities. Other frequently encountered species included *Amanita caesarea*, *Butyriboletus appendiculatus*, *Butyriboletus fuscroseus*, *Leccinellum crocipodium* and *Omphalotus olearius*, all of which exhibit thermophilic characteristics.

Vegetation ecology

In Slovakia, fruiting bodies of *P. macrorrhizum* is distributed in thermophilous to mesophilous broadleaved forests (Electronic Supplement 4). These stands are dominated by

Quercus cerris, with *Carpinus betulus* and *Quercus petraea* agg. as admixed trees. In some sites, other species typical for thermophilous Pannonian oak forests (*Acer campestre*, *Cornus mas* and *Sorbus torminalis*) were present (Jarolínek et al. 2008; Valachovič et al. 2021). *Fagus sylvatica* was occasionally present in lower abundances. Planted *Picea abies* was rarely observed at sites of higher elevations (510 and 670 m a.s.l.). The presence of *Betula pendula*, *Pinus sylvestris*, *Populus tremula* and *Prunus avium* was observed at low coverages.

The sampling sites exhibited variability in the shrub and herb layers. The species composition of these layers was not specific for characterising vegetation associations, but often contained species that are specific for thermophilous Pannonian, subcontinental, and acidophilous oak and/or mesophilous oak-hornbeam forest habitats. For further details on phytosociological units, please refer to Electronic Supplement 4. For information on transitional positions of sites, please see Electronic Supplement 5 b, d. The presence of plant species favouring open habitats characteristic of dry steppic grasslands and/or forest edges was particularly pronounced.

The unconstrained detrended correspondence analysis (DCA) revealed the existence of three main vegetation gradients. The first gradient (DCA axis 1) represents a continuous transition from closed forest stands to open steppe/fringe communities (Electronic Supplement 5 a, b). This gradient depicts the light conditions of *P. macrorrhizum*

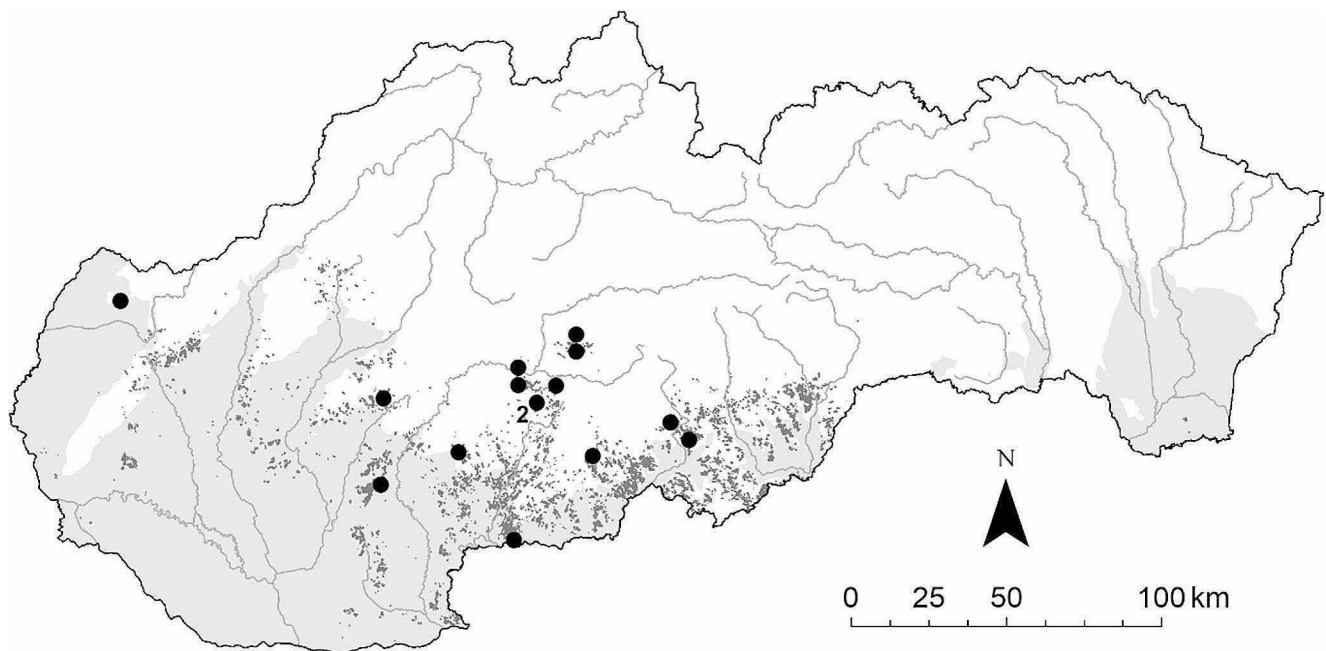


Fig. 4 The distribution of *Pogonoloma macrorrhizum* in Slovakia based on data listed in the Electronic Supplement 1 (15 localities). The dot marked with number 2 represents two close localities. The light shaded area represents the area with a mean annual air temperature

above 9°C . The dark grey patches represent the occurrences of Turkey oak (*Quercus cerris*) with at least 50% abundance in forest stands, as derived from internal database of the National Forest Centre, Zvolen, Slovakia

habitats. Along the second axis (DCA2), the acidophilous plant species exhibited high scores. This gradient represents a gradient of soil pH. The third gradient (DCA3, Electronic Supplement 5 c, d) illustrates an elevation gradient, with plant species exhibiting a preference for lower altitudes that ascend in the diagram.

Environmental drivers, history of land use and management

The localities of *P. macrorrhizum* were observed in the warmer southern parts of Slovakia (Fig. 4), in lowland areas, warm basins and hilly landscape. The lowest known sampling site is located at 170 m a.s.l. (Čifáre), while the highest one is at 670 m a.s.l. (Kráľová). Most sites were situated in areas with a mean annual temperature exceeding 9 °C (Fig. 4). This area represents a transitional zone between the montane areas of the Western Carpathians and the Pannonian basin.

The parent rock varied among localities. It was represented by sandstones, different volcanic sediments, lava flows, and fluvial or deluvial sediments. The soil reaction was more or less acidic, with a pH range between 4.1 and 6.2 (Table 2), with an average value of 5.2.

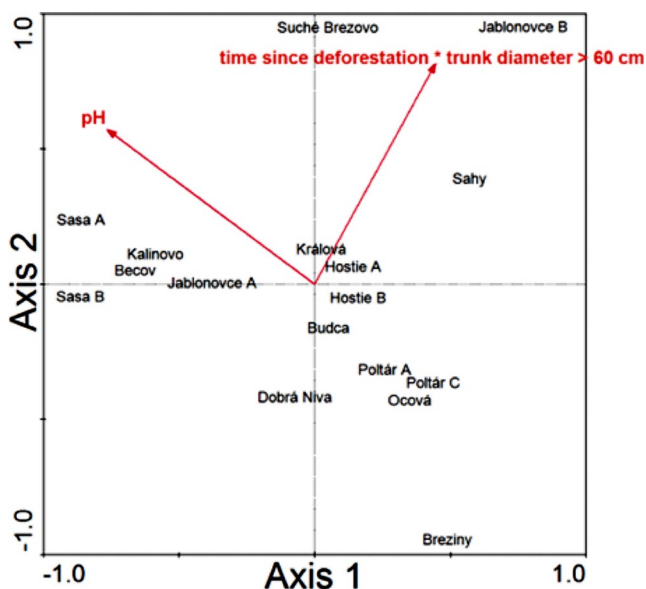


Fig. 5 Redundancy analysis (RDA) of plant species composition surrounding the sampling sites (numbers) of *Pogonoloma macrorrhizum* and representing the most significant environmental drivers as arrows (see Electronic Supplement 1 for site names) (pH: $p=0.04$; deforest*tr60+: $p=0.05$). Statistical details are given in Electronic Supplements 2 and 6. For further insight, please refer to Electronic Supplement 10, which contains analogous biplots visualising the plant species pattern. Abbreviations: time since deforestation – duration of forest openness, pH – soil reaction (Table 1), trunk diameter > 60 cm – presence of old *Quercus cerris* individuals having trunk diameter at breast height more than 60 cm, * – variables in interaction.

Prior to the year 1800, the majority of localities where *P. macrorrhizum* was studied were forested (Electronic Supplement 2), with the exception of agricultural terraces (Suché Brezovo) and deforested areas (Jablonovce). By 1900, the situation remained similar, although some sites had been converted to pastures with shrubs (Sása, Šahy, Dobrá Niva). During the first half of the 20th century, most localities were transformed into (semi-)open landscapes, characterised by pastures, grasslands, forest edges and areas with solitary trees, as a result of intensified grazing practices. In the subsequent period, up to the present, these localities have undergone a gradual regrowth in tree cover. The frequency of pastures was less common before 1950 but after this period they were present at most localities, although they subsequently disappeared again by the beginning of the 21st century (Electronic Supplement 2). The most notable changes are observed at the Sása site (Fig. 2).

In the analysis of the colinearity of environmental parameters at the collection sites of *Pogonoloma macrorrhizum* (Electronic Supplement 9a), the first (horizontal) PCA1 axis represents the following parameters: the time since deforestation, which is correlated with historical grazing. Prior to 1950, Pearson's correlation coefficient r was 0.75, with a p value of less than 0.001. Similarly, soil reaction (pH) demonstrated a correlation coefficient of $r=0.55$, with a p value of 0.024 (Table 2). These parameters, along the first axis, are negatively correlated with forest cover prior to 1990 ($r=-0.93$, $p<0.001$). The second (vertical) PCA2 axis (Electronic Supplement 9a) represents older forests with thicker trunks and a parameter that correlates positively with forest cover before 1950 ($r=0.51$, $p=0.046$) but negatively with old forests present in 1782 ($r=-0.51$, $p=0.042$). The opposite side of the graph represents modern history, namely, open stands that have not been grazed in the 21st century ($r=-0.73$, $p=0.001$). The third PCA3 axis (Electronic Supplement 9 b: vertical axis) reflects altitudinal zonation.

Following the removal of the variance attributed to vegetation (DCA1–DCA3 were filtered out as covariates), the significant parameters influencing the vegetation pattern surrounding the sampling sites of *P. macrorrhizum* (Fig. 5, Electronic Supplement 10) were identified. These were soil pH (explained variance 13.5%, F-ratio=1.7, p -value=0.04), while the presence of old *Q. cerris* individuals combined with time since deforestation explained 10.5% of the variance (F-ratio=1.67, p -value=0.05). The ancient forest species (AFS), defined as plants indicative of a longer forest history (Hermy and Verheyen 2007), exhibited high scores along DCA1 (see Electronic Supplement 11). This characterises older forests, with notable examples including *Athyrium filix-femina*, *Carex pallescens*, *C. sylvatica*, *Circaea lutetiana*, *Impatiens noli-tangere*, *Melica uniflora*, etc. Some plant taxa, typical of spring aspect, such as *Galium*

odoratum, *G. sylvaticum*, *Lathyrus vernus*, *Pulmonaria officinalis* agg., *Sanicula europaea*, had low scores along DCA1 and followed deforested habitats. The deforestation is significantly negatively correlated with ancient forests. These findings can be found in the Electronic Supplement 7.

Discussion

Phylogeny and spatial distribution of *Pogonoloma macrorrhizum* in Slovakia

Our DNA sequences are the first to confirm the presence of *P. macrorrhizum* in Slovakia based on molecular data. The high support is consistent with the findings of Alvarado et al. (2018) and our Bayesian phylogenetic analysis has confirmed the position of *P. macrorrhizum* within the family Pseudoclitocybaceae, with sister species *P. spinulosum* (Fig. 3). The similarity of sequences within the *P. macrorrhizum* clade was greater than 99%.

Based on vouchers from the most important Slovak herbarium (Slovak National Museum, BRA), only two localities of *P. macrorrhizum* were documented in Slovakia up to 2014: Bratislava-Lamač (1973, BRACR31306) and in vicinity of Lukavica village in the Zvolen district (1978, 5 vouchers in BRA, locality cited in Dermek 1985; see also Electronic Supplement 1).

In the period between 2015 and 2020, data was collected on 15 localities (17 sampling sites). Of these, 13 were analysed in detail in this study (Electronic Supplement 2). The expansion of knowledge about *P. macrorrhizum* within the Slovak mycological community has contributed to the increase of the number of localities. This is evidenced by the enhanced use of internet media such as www.nahuby.sk. Furthermore, the global climate change, as evidenced by studies such as Kausarud et al. (2012) and Yu et al. (2023), appears to facilitate the spread of thermophilic species, a phenomenon that also been observed in Slovakia (Gera et al. 2019). For instance, increase in the number of Slovak localities where *Amanita caesarea*, a thermophilous fungus, has been observed, is currently being documented (based on a comparison of 36 localities given in Škubla 2003 with 51 new localities since 2004 registered by the BRA herbarium, www.nahuby.sk, and the first author). However, the absence of data on the occurrence of *P. macrorrhizum* at specific localities over of several decades (compare Holec et al. 2016 for the case of *Gymnopilus suberis*, where these data were available) made impossible to test the “spread hypothesis”. Furthermore, the impact of climate change is difficult to separate from other factors, such as the succession of vegetation (Hilmers et al. 2018) at localities of *P. macrorrhizum* (see subsequent sections).

Trophic status

The trophic status of *P. macrorrhizum* has not yet been tested. Siller et al. (2005) classified the species as “saprobiontic”, while Sánchez-García et al. (2014) considered is to be “presumably saprotrophic”. The species belongs to the Pseudoclitocybaceae, a group that has traditionally been regarded as saprotrophic. Conversely, Ambrosio and Zotti (2015) consider *P. macrorrhizum* to be ectomycorrhizal, while Alvarado et al. (2018) suggest it may be “doubtfully saprobic (possibly ectomycorrhizal?)”. Stable isotope ratios can reveal the origin of these elements in the fungal biomass, as they differ depending on whether they originate from decomposition or are directly provided by the plant. The discovered ratios of carbon stable isotopes (ranging from -26.731 to -23.911) correspond to values previously reported for ectomycorrhizal fungi (Taylor et al. 2003; Trudell et al. 2004). In the case of nitrogen (0.359 – 3.005), the result is similar, but the minimum limit slightly overlaps with the range typical for saprotrophic fungi (Taylor et al. 2003; Trudell et al. 2004). These results demonstrate that *P. macrorrhizum* takes carbon and nitrogen from a tree host, which supports the hypothesis that it is a mycorrhizal fungus. This interpretation is supported by our field data, which demonstrate that *P. macrorrhizum* fruiting bodies were found in close proximity to *Quercus cerris* individuals at all sampling sites (Electronic Supplement 1). However, other tree species were also present. The accurate trophic status of *P. macrorrhizum* cannot be revealed using this indirect method. The most compelling evidence would necessitate the reestablishment of mycorrhiza in dual culture, followed by subsequent testing under controlled conditions or with a molecular check to ascertain the ectomycorrhiza on fine roots belong to *P. macrorrhizum*. Notably, Harder et al. (2023) demonstrated that plant-fungal relationships can be challenging to disentangle, as various *Mycena* species (typically considered saprotrophic) are capable of invading living roots of several tree species.

Associated trees and co-occurring fungi

Our data from Slovakia indicates that *P. macrorrhizum* is associated with *Q. cerris*. Dermek (1985) also mentions *Q. robur* agg. In Austria, seven of the nine records with potential host trees indicated were close to *Quercus* sp., while two were under *Q. cerris* (AMS 2015). An older work from Italy (Gallinari et al. 1983) mentioned mainly *Quercus* sp., but also *Castanea sativa*. Alvarado et al. (2018) published records under *Castanea sativa* and *Quercus pubescens* agg. from Italy.

The funga of thermophilous oak forests is composed, except for some ubiquists, of numerous specific fungi, with the majority belonging to the ectomycorrhizal genera

Amanita, *Boletus* s.l., *Cortinarius*, *Inocybe*, *Lactarius*, *Russula* and *Tricholoma* (e.g., Fellner 1984; Laganà et al. 1999). All evaluated localities of *P. macrorrhizum* are characterised by the occurrence of several thermophilous fungi (Electronic Supplement 3). This fungal community has been formally described as *Boleto (aerei)-Russuletum luteotactae* Šmarda (1972) and subsequently amended by Fellner (1988). One of its distinctive species is *Boletus aereus*, which was present at all localities of *P. macrorrhizum*. Furthermore, other thermophilous species including *Butyriboletus appendiculatus*, *B. regius*, *Leccinellum crocipodium* and *Omphalotus olearius*, were observed in the area. A list of other species frequently co-occurring with *P. macrorrhizum* can be found in Electronic Supplement 3. Some of these species were also documented in Italian localities of *P. macrorrhizum* (Ambrosio and Zotti 2015; Ambrosio et al. 2018b). Further research was conducted by Salerni et al. (2000) in *Q. cerris* forests on acidic soils (pH 4.5–4.7). A comparison of the list of species revealed that *Aureoboletus gentilis*, *Boletus aereus*, *Cantharellus cibarius*, and *O. olearius* were present in both datasets. Other species recorded at our localities (*Amanita caesarea*, *B. appendiculatus*, *Hemileccinum impolitum*, *L. crocipodium*, *Suillellus queletii*) were found by Salerni et al. (2000) in oak forests but not under *Q. cerris*. These data demonstrate that the fungus is at least partially similar in different European localities of *P. macrorrhizum*.

Vegetation ecology

The three main gradients revealed for the vegetation of *P. macrorrhizum* sampling sites (DCA1–3: Electronic Supplements 5, 9) are in agreement with the general vegetation ecology of oak forests in Slovakia (Roleček 2005, 2007; Hegedúšová et al. 2021). The sampling focused on occurrences of *P. macrorrhizum* and restricted the assignment of the relevés only to the vegetation units of the alliance level, not to associations (Electronic Supplements 4, 5). The leading vegetation gradient was represented by canopy openness of *P. macrorrhizum* sampling sites (Electronic Supplement 5 a, b: the horizontal axis). The flora and vegetation of open habitats in dry thermophilous oak forests are well documented (Škodová et al. 2014; Valachovič and Hegedúšová Vantarová 2014; Hegedúšová Vantarová et al. 2021). Many of these plants indicate both open-forest and non-forest communities (Electronic Supplement 4: grey columns showing their presence in higher units). Furthermore, our vegetation samples contained a diverse array of herbaceous species that are characteristic of dry grasslands and wood margins (*Agrimonia eupatorium*, *Carex caryophyllaea*, *Centaurea jacea*, *Festuca stricta* subsp. *sulcata*, *Galium verum*, *Pimpinella saxifraga*, *Securigera varia*, *Trifolium medium*). This indicates a past opening of the landscape by

agriculture and pasturing, a fact subsequently confirmed by the retrieved historical data (Electronic Supplement 2). Furthermore, seedlings and young individuals of *Prunus avium* and *Pyrus communis* were found in the shrub layer (Electronic Supplement 4), usually together with *Juniperus communis*, a species indicating former pasturing. Finally, our data demonstrate that *P. macrorrhizum*, a presumed ectomycorrhizal partner of *Q. cerris* (see Trophic status), follows its host to sites grown by various vegetation units. However, it exhibits a preference for open sites that have been affected by past grazing.

The ancient forest species of plants (Hermy and Verheyen 2007) did not demonstrate a clear link to older forests (Electronic Supplement 11), as some of them also exhibited the inverse gradient (deforestation). In fact, these species flower during the spring aspect of unfoliated trees.

Environmental parameters, history of land use and management

The data on the environmental requirements of *P. macrorrhizum* is difficult to compare with other publications due to the lack of similar studies. However, some parameters highlighted by us (soil pH, openness of *P. macrorrhizum* habitats, presence of old *Q. cerris* individuals and thermophilous plant species) are at least mentioned in other works. According to Siller et al. (2006), *P. macrorrhizum* appears to prefer warm and slightly open forests with a dominance or presence of oaks. In Italy, the species has been reported from a managed forest with a dominance of *Q. cerris* with mean annual temperature of 12 °C (Ambrosio et al. 2018b). In Austria, *P. macrorrhizum* is found in warm regions with a mean annual temperature ranging from 7 °C to 10 °C (AMS 2015), which corresponds to our findings. Our data indicate that *P. macrorrhizum* is also present in Slovakia outside the warmest regions, like its host *Q. cerris* (Fig. 4). However, these occurrences are mostly represented by south-facing slopes of warmer microclimate (Electronic Supplement 1).

Soil pH represents one of the principal filters in ecology (Glassman et al. 2017; Bahnmann et al. 2018; Tervonen et al. 2019, 2022). Our results document the occurrence of *P. macrorrhizum* on more or less acidic soils having pH values between 4.1 and 6.2 (Table 2). At Italian localities of *P. macrorrhizum*, Ambrosio and Zotti (2015) report average soil pH at a depth of 20 cm as 4.27, which is close to the lowest values detected by us. No data on the occurrence of *P. macrorrhizum* on alkaline soils have been published to date.

We hypothesised that *P. macrorrhizum* is a distinctive species of Slovak pasture forests. The influence of the history of land use on fungi has not been sufficiently studied until now. However, Andrew et al. (2019) found that land use is strongly correlated with fungal richness at large spatial

scales. Kutszegi et al. (2015) demonstrated that only the ectomycorrhizal fungi were influenced by landscape structure compared to other functional groups. Given that we assume that *P. macrorrhizum* is ectomycorrhizal, the evaluation of the history of land use, which strongly affects its potential host *Q. cerris*, is of great relevance.

From approximately the 13th to the 19th century, a significant portion of the Slovak landscape underwent a rotation cycle of land use. Small areas of forests, meadows, and arable lands were alternately occupied (Olah et al. 2009; Špulerová et al. 2017). Grazing of livestock was the primary disturbance regime responsible for maintaining the open structure of wood pastures until the first half of the 20th century (Wiezik et al. 2018). Furthermore, the grazing of pigs was a common practice in oak forests, with acorns being a particularly favoured food source (Hudáček 2014; Wiezik et al. 2018). The traditional management techniques, which were widely employed across the European countryside (selective cutting, leaf harvesting, forest grazing), have resulted in the formation of semi-open forest habitats. Such sites often exhibit high biodiversity, including high fungal species richness. This is likely due to the microclimatic differences among microsites of different openness (Berg et al. 2002; Horak et al. 2014; Holec et al. 2016), as well as the influence of a specific disturbance regime (cattle grazing). Forest pastures are often characterised by the presence of veteran trees, with oaks being a particularly common species (e.g., Paltto et al. 2006; Ranius et al. 2008; Bergmeier and Roellig 2015; Horák et al. 2018). Although such giant tree individuals were not present at our sites (such giant trees are more typical for *Quercus robur* agg. than *Q. cerris*), we did observe the presence of older and thicker trees with low crowns at some of them (Breziny, Kráľová, Sása, Suché Brezovo). This suggests that these trees may have originated from formerly opened wood pastures. This assumption was subsequently confirmed by the analysis of historical maps (e.g., Fig. 2). One of the localities under study (Suché Brezovo) exhibited the presence of man-made terraces, which could be linked to pastoral activities (Slámová et al. 2017).

In general, the communities of ectomycorrhizal fungi in wood pastures are not determined by grazing, but rather by the tree species composition and soil properties (Ter-vonen et al. 2019). However, both past and present grazing increases the amount of light at ground level and soil temperature (Olff and Ritchie 1998), which improves the growing conditions for some mycorrhizal fungi (Andrew et al. 2019). Furthermore, mycorrhizal fungi may also benefit from grazing (Murray et al. 2010; Ba et al. 2012), provided that it is not too intense, as this can result in reduction in litter on the soil surface (Arnolds 1991).

In summary, *P. macrorrhizum* is most prevalent at sites that have been demonstrably affected by historical grazing, which is a key factor influencing its distribution.

Conservation prospects

Wood pastures – the main Slovak habitat of *P. macrorrhizum* – are currently threatened, although their fragments are still numerous, especially in central Slovakia (Wiezik et al. 2018). Many of these sites are changing due to the recent absence of grazing and the subsequent succession leading to reforestation (Horak et al. 2014). Thus, parts of the central Slovak landscape are gradually regrown by forest. On the other hand, many fields and meadows have been abandoned (Gallay and Gallayová 2011), resulting in “new vegetation edges” due to the tree overgrowth. In such places, ectomycorrhizal fungi often find suitable conditions (Crockatt 2012; Pešková et al. 2015; Grove et al. 2019). This seems to be the case for *P. macrorrhizum*. However, some of the current sites are likely to disappear due to ongoing natural succession.

Another threat is the homogenisation of the landscape and loss of habitat due to forest management and silvicultural practices, which alter microclimatic and soil conditions (Tomao et al. 2020). Most of the forests studied in our paper are currently managed for timber production. Moreover, forest stands with *Q. cerris* dominance in Slovakia are currently threatened by the gradation and outbreaks of the *Q. cerris* pest *Lymantria dispar*, the “gypsy moth” (Zúbrik et al. 2016). This is similar to the situation in neighbouring Hungary, where *Q. cerris* was also considered relatively common but later appeared to be declining (Siller et al. 2006). Unfortunately, salvage logging is usually used as a consequence measure. After felling or coppicing, the tree species composition is often unintentionally (successional) or intentionally (silvicultural) changed towards stands dominated by *Carpinus betulus*. In addition, many sites in Slovakia are not registered and managed by foresters but have become a part of agricultural land. Unfortunately, such stands can be harvested at any time without restrictions.

Appropriate conservation measures, mainly grazing and mowing at appropriate intensities and the use of selective cutting, would be required to conserve the sites of *P. macrorrhizum*. Some red-listed or protected fungi that co-occur with *P. macrorrhizum* (Electronic Supplement 3) can be used to emphasise the need for site protection, e.g. *A. caesarea*, *Aureoboletus moravicus*, *Butyriboletus fuscroseus* or *Imperator rhodopurpureus*.

Finally, *P. macrorrhizum* is certainly a candidate for both the Slovak and the European Red lists.

Limitations of data and methodology applied

We investigated the requirements of the species only at the northern limit of its distribution in this part of Europe. This may somewhat reduce the comparability of our data to regions in the middle of the species' range. Although the fungal species are known to be closely associated with plant dominants in specific communities, their most important drivers may not be identical. If there is a limited amount of data available, this may provide some guidance in the determination of the environmental drivers to characterize the requirements of *P. macrorrhizum*.

Conclusions

Pogonoloma macrorrhizum in Slovakia is a species occurring in association (probably ectomycorrhizal) with *Quercus cerris* and mostly inhabiting transitional ecosystems. The transitions are represented by gradients between (1) thermophilic and mesophilic sites, (2) Pannonian and subcontinental thermophilous oak forests versus dry steppe grasslands and forest margins and (3) spontaneously overgrown pastures and closed forest stands, both with the presence of *Q. cerris*. Some parameters were shown to significantly influence the environmental pattern of the species sampling sites, namely insolation, acidic soil pH, the presence of past deforestation and historical grazing, and the presence of thicker *Q. cerris* individuals. These thicker trees either occur in older closed forest stands or represent former solitary trees of pastures, surrounded by shrubs.

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Data availability The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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