

Environmental conditions of new sites of *Morchella steppicola* Zerova (Ascomycetes, Morchellaceae) in Slovakia (Central Europe)

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Abstract

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The steppe morel (*Morchella steppicola*) was the subject of a study in Slovakia, a country that represents the northern limit of its distribution in this part of Central Europe. A total of 30 sites were selected for the collection of environmental data and information on current landscape management practices. The soils at the studied sites are predominantly neutral to slightly alkaline in nature, exhibiting a pH range of 6.6–7.75 with an average value of 7.25. These soils are primarily derived from loess or sandstones. The sites represent thermophilic habitats, predominantly in the form of pastures or dry steppic grasslands, situated at altitudes ranging from 97 to 326 metres above sea level. Among 30 studied sites, eight are characterised by the presence of man-made landscape features. The threats to habitats of *M. steppicola* in Slovakia are discussed, with reference to the cessation of grazing at some sites and the potential overgrowing by shrubs and trees, resulting in forests.

Keywords

fungi, loess, management, morel, pastures, soil pH, steppe

Introduction

The genus *Morchella* Dill. ex Pers.: Fr. is increasingly well-known and popular, from several points of view. The fruiting bodies of this genus are among the world's most prized for their culinary properties and they have been cultivated a considerable period of time. The genus is predominantly distributed in the temperate regions of the Northern Hemisphere, notably in deciduous forests and a comparatively less so in coniferous forests. Grasslands are a rare habitat for the genus (DU et al., 2015). Despite the existing body of literature on the subject, scientists continue to focus on the ecology (LOIZIDES, 2017), taxonomy (CLOWEZ and MOREAU, 2021; LOIZIDES et al., 2022), phylogeny (YATSIUK et al., 2016; PETRŽELOVÁ and SOCHOR, 2019) and trophic status (KIRÁLY and CZÖVEK, 2007; DU et al., 2015). However, more recently, studies have also examined the medicinal effects (KANIBOLOTSKAYA et al., 2008; TIETEL and MASAPHY, 2018; SARIKURKCU

et al., 2022; GAFFOROV et al., 2023). A significant proportion of discussions also focus on the molecular analysis of *Morchella* spp., given the well-documented high degree of morphological plasticity of macroscopic characters within species of the genus (see, for example, DU et al., 2012; RICHARD et al., 2015; LOIZIDES et al., 2022).

As demonstrated in the study by LOIZIDES et al. (2022), over 80 species-level lineages of *Morchella* were delimited using molecular phylogenetic analysis. *M. steppicola* (Fig. 1) is one of the few species whose fruiting bodies can easily be identified and recognised in the field. It is distinguished by its distinctive cerebriform pileus and stout stipe and is clearly defined (ZEROVA 1941; CLOWEZ and MOREAU, 2021; LOIZIDES et al., 2022). One specific character is the presence of internal chambers, which are observable in the stipe when the ascocarp is sectioned longitudinally. This species belongs to one of the earliest diverging lineages of the Esculenta clade (LOIZIDES et al., 2021).

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Fig. 1. Young fruiting body of *Morchella steppicola* (10 April 2015, Bakov). Photo by Vladimír Kunca.

Like many other morel species, *M. steppicola* is characterised by its specificity to particular regions and continents. It was originally described by ZERVA (1941) from a steppe meadow situated within the territory of Ukraine. It has also been documented in Central Europe and Central Asia, in Europe including countries such as Croatia, Germany, Hungary, Moldova, Russia, Serbia, North Macedonia, Slovakia, and Ukraine (HELUTA, 2017; KAREDELEV et al., 2019; BOZOK et al., 2020; LOIZIDES et al., 2022) and is considered endemic to Eurasia (LOIZIDES et al., 2021).

The steppe morel is an organism that has adapted to its specific habitat, which HÄFFNER and LUKÁCS (1995/1996) and RICHARD et al. (2015) define as dry continental meadows. The species has been found in various environments, including the virgin steppe and disturbed plant communities in Ukraine. These environments include burnt land, areas used for off-road motor vehicles, heavily trampled pastures, areas near railroad tracks, post-fire areas in forest plantations and neglected land (SUKHOMLYN et al., 2007), as well as other man-made or man-disturbed habitats (CLOWEZ and MOREAU, 2021). Additionally, forest-steppe habitats are considered the species' typical habitats of in the eastern part of its distribution area (DUNAEV et al., 2020).

Morels are generally considered to be saprotrophs (see KANIBOLOTSKAYA et al., 2008; DUNAEV et al., 2020). However, there is some indication that they could form ectomycorrhiza (see DU et al., 2015; LOIZIDES, 2017; ORI et al., 2017; BADALYAN et al., 2023), form complex interactions with plant roots (see DU et al., 2015; LOIZIDES, 2017) or form endophytic associations with plants (see ORI et al.,

2017). Consequently, CLOWEZ and MOREAU (2021) concluded that the trophic behaviour of *M. steppicola* meant this species could not be exclusively saprotrophic.

In the field of mycology, there is an ongoing initiative to address the critical requirements for *Morchella* species collections for research purposes in Europe (DU et al., 2012). This paper presents new sites and data on *Morchella steppicola* in Slovakia, paying particular attention to several abiotic parameters. Additionally, it provides a thorough overview of the management of all known species sites.

Materials and methods

The experiment was designed to summarise knowledge of *M. steppicola* sites in Slovakia, including efforts to find the new ones. At all known sites, we evaluated various environmental factors, such as the type of parent rock, soil pH, mean annual air temperature zone, current site management and the origin of the habitat within the landscape.

Database and sampling of fruiting bodies

An extensive database encompassing of *Morchella steppicola* specimens was compiled for Slovakia. The data covers all sites within the country for which there is verifiable evidence. Thirty sites with *M. steppicola* were discovered or registered between 2014 and 2025 (see Electronic Supplement). We present the names of these sites alongside the names of nearby villages and settlements. The precise geographical coordinates of the locations are not provided in order to protect the sites from unauthorised mushroom harvesting. Voucher specimens have been deposited in the private fungarium of V. Kunca (PVKU) and in public herbaria (BRA). These specimens are representative samples of the fungus (fruiting body) that are preserved for scientific study, documentation, and verification of its identity and location. The collector cut the fresh fungal fruiting body lengthwise into 3–4 mm thick slices, dried them and stored them in a resealable bag.

Geological, soil and climatic conditions

Data on the parent rock were obtained from online maps of the Slovak Republic (geological map: <http://apl.geology.sk/gm50js/>) and verified visually at the localities. Soil pH (H₂O) was measured in soil samples taken at a depth of around 5–20 cm from the fruiting bodies, in approximately 100 cm³. Not all values or evaluations were obtained for all parameters presented (soil pH for 26 sites and geological substrate for 28 evaluations). The distribution map of *M. steppicola* used several zones of different mean annual air temperature from the map layers of the Slovak Republic for 1960–1990 (ŠŤASTNÝ et al., 2002) as a background map.

Management method and man-made objects at studied sites

We evaluated the effectiveness of various current manage-



Fig. 2. *Morchella steppicola* habitat – intensive pasture (29 March 2024, Ladmovce). Photo by Vladimír Kunca.

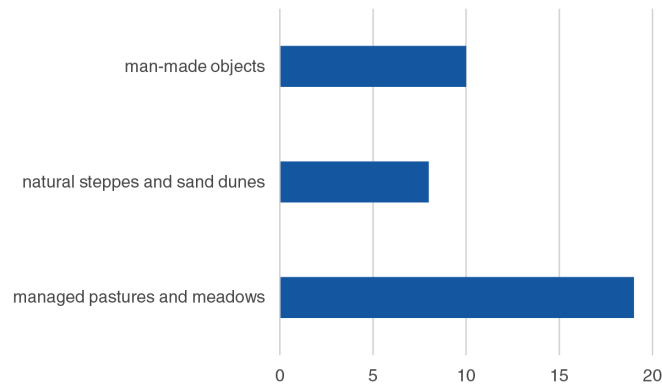


Fig. 3. Proportion of sites per habitat and management type at the 37 studied habitats for *Morchella steppicola* in Slovakia

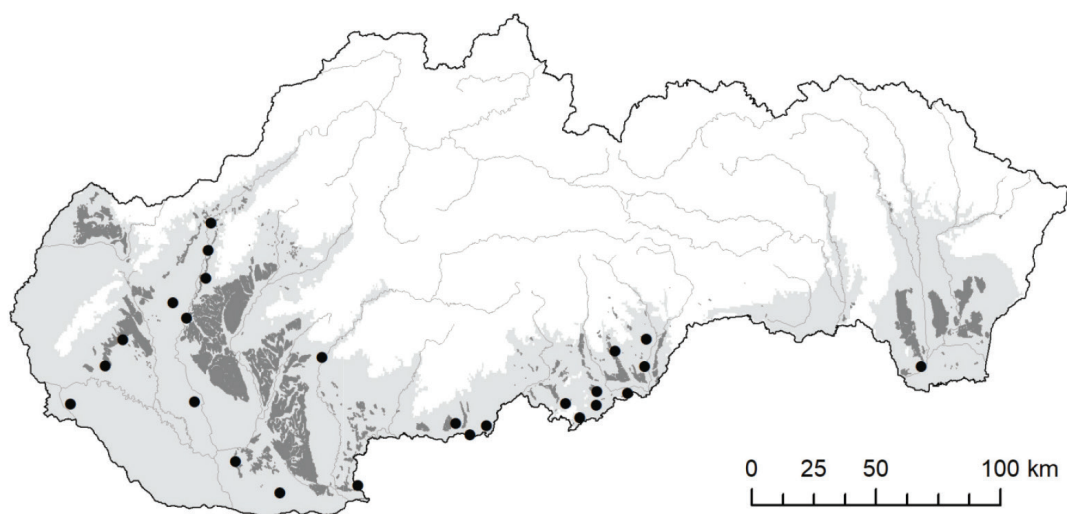
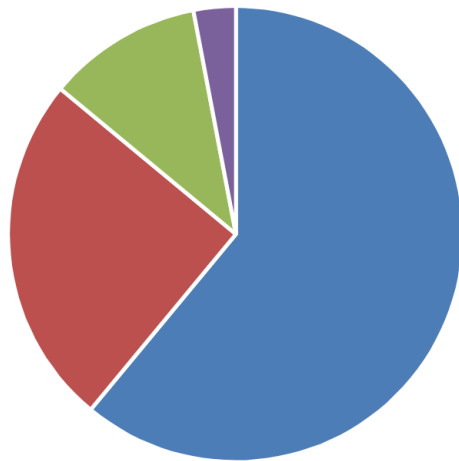


Fig. 4. The distribution of *Morchella steppicola* in Slovakia based on data listed in the Electronic Supplement (30 sites). One dot may represent two nearby sites. The light-shaded area represents the territory with a mean annual air temperature above 8.5 °C. Dark grey patches indicate the presence of loess in the soil.



■ loess overlap ■ sandstone ■ sand ■ loess loam

Fig. 5. Geological substrates at the 28 sites studied for *Morchella steppicola* in Slovakia.

ment methods and visible human influences on the landscape in the study areas. For this study, we assessed two of the possible management methods: mowing and grazing. We also judged the current state of the sites in relation to management across three categories:

- Natural – not managed constant steppe or meadow (occasionally partly overgrown by woody plants); sand dune; or forest steppe.
- Managed – managed by grazing (either intensive or extensive pasture; see Fig. 2) or mowing (either manual or mechanical), including areas with felled trees from the former meadow.
- Man-made objects – front gardens, mowed lawns, railway embankments, river embankments, agricultural fields, or roads.

We also used combinations of terms such as ‘overgrown pasture’, ‘forest and meadow edge’ or ‘field, and meadow edge’ for a more detailed description. We evaluated the data using descriptive statistics, specifically the arithmetic mean.

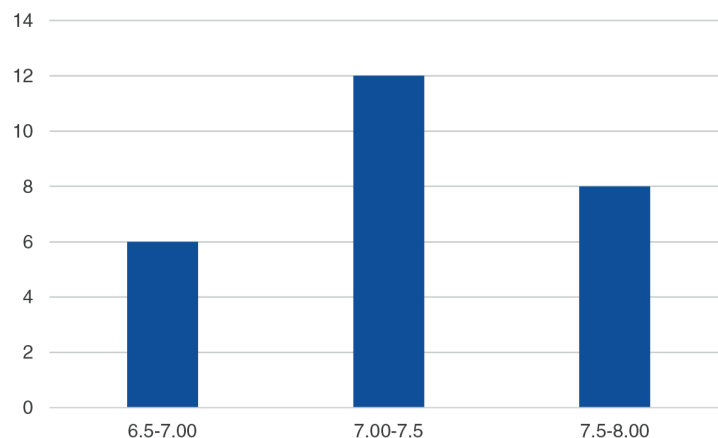


Fig. 6. Soil pH values of *Morchella steppicola* sites in Slovakia.

Results

Through our research, we have increased the number of known *M. steppicola* sites in Slovakia to 30. This species is found in various grassy habitats, primarily pastures and meadows (19 sites), in lowland areas with occasional hills (see Fig. 3). The lowest known sampled site is located at 97 m above sea level in Ladmovce, while the highest is at 326 m above sea level in Beckov.

All of these sites are situated in Slovakia’s warmer, southern regions of particularly in areas where the mean annual temperature exceeds 8.5 °C (see Fig. 4). This area is a transitional zone between the montane regions of the Western Carpathians and the Pannonian Basin.

The geological substrates at these sites are primarily loess overlays and sandstones (see Fig. 5). The soil was found to be neutral or alkaline, with a pH ranging from 6.6 to 7.75 (see Fig. 6), and an overall mean value of 7.25, which is generally indicative of neutral soils. Our data on current management, which incorporates 37 evaluations, shows that multiple habitats can occur within a single locality. The most prevalent sites are those managed by grazing, primarily as intensive pastures, accounting for 19 of the totals. Eight sites are natural areas with no visible management, while man-made landscape features support species at ten sites (Fig. 3).

Discussion

Climate and land use are major drivers of species diversity, including fungi (ENGLMEIER et al., 2023). Morels often grow in areas of the landscape that have been altered by human activity (PILZ et al., 2007; SUKHOMLYN et al., 2007; LOIZIDES, 2017). In Slovakia, for example, centuries of agricultural activity in various habitats have created a structured mosaic of landscapes (HREŠKO et al., 2010). A certain degree of environmental heterogeneity is also a common feature in *M. steppicola* habitats (HELUTA, 2017).

M. steppicola is commonly found in steppe meadows and dry grasslands in the central part of Europe and the

Balkans (LOIZIDES et al., 2016). However, our records also indicate its presence in other unusual locations, such as fallow areas, pastures, and areas affected by human activity, as referenced in the work of GAFFOROV et al. (2023). One record from Slovakia (LUTHER, 2013) is also presented from an old vineyard. However, this cannot be confirmed as it has not been proven by a voucher specimen. Furthermore, despite visiting areas of Slovakia that are occasionally managed by burning, we could not find any fruiting bodies of the species. This may be due to a lack of regular burning, as suggested by YATSIUK et al. (2016) for this species.

Abiotic factors significantly influence macrofungal diversity, also in the Pannonian biogeographic region (GEML et al., 2022, AMBROSIO et al., 2024). YATSIUK et al. (2016) linked *M. steppicola* to calcareous and clay soils, CLOWEZ and MOREAU (2021) also noted that the species is typically found in calcareous soils. However, our results differ in that clay soils are incompatible with our findings. Sand and loess/silt (Fig. 5) belong to in different geological and soil categories to clay. Soil structural properties are also related to soil pH, which is a crucial factor for the habitat preferences of fungi (GEML et al., 2022; JANOWSKI and LESKI, 2022) and morel fruiting (PILZ et al., 2007). Soil analysis by HUSSAIN and SHER (2021) showed that five morel species appeared most frequently in soils with a pH ranging from slightly acidic to neutral (mean = 6.4). Our results, which also include several values related to slightly acidic soils, are very similar. Nevertheless, the diversity of fungi may depend crucially on the species of host plant (SUGIYAMA et al., 2021), and as previously mentioned, the unclear trophic status of *M. steppicola* may alter our perception of its ecology.

Based on the occurrence of fruiting bodies of the species in the rugged landscapes of Slovakia (Fig. 4), we agree with GAFFOROV et al. (2023) in classifying *M. steppicola* as a thermophilic fungus. Clearly, the species is adapted to arid habitats with herbaceous plants (CZÖVEK and KIRÁLY, 2005), and it can also be characterised as a xerothermic species (HELUTA, 2017). It is well documented that climatic conditions also influence the phenology of the fruiting bodies. In Ukraine, for example, the fruiting bodies appear between April and May, as they do in Uzbekistan (SUKHOMLYN et al., 2007; GAFFOROV et al., 2023). PERIĆ and RADIĆ (2014) published records from March and April. This is consistent with our own records (see Electronic Supplement).

Further research is needed to identify new sites and perhaps to study the co-occurrence of non-woody plants. SUKHOMLYN et al. (2007) and PERIĆ and RADIĆ (2014) presented several plant species from the vicinity of the fruiting bodies. We observed *Eryngium campestre* at almost all sites, but *M. steppicola* was not present where this species was found. YATSIUK et al. (2016) also mention this plant species in relation to the occurrence of *M. steppicola*.

M. steppicola is an excellent edible mushroom species (YATSIUK et al., 2016; CLOWEZ and MOREAU, 2021). We have only occasionally observed mushroom hunters collecting the fruiting bodies of this species. No large-

scale harvesting of the fruiting bodies was observed in Slovakia. However, in some other countries, harvesting can pose a threat to the survival of *M. steppicola* (DUNAIEV et al., 2020). We suppose that the number of known sites of the species may be underestimated, primarily due to its short fructification season.

The main threat to sites with *M. steppicola* in Slovakia is the current absence of grazing, which could lead to overgrowth and tree succession. This phenomenon has been observed frequently in Slovakia, particularly in specific habitats where the species is also present (WIEZIK et al., 2018). Taking this threat into account, the new Red List of Fungi in Slovakia (PEIGER et al., NNNN) has classified *M. steppicola* as an endangered species (EN).

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Supplementary material

The Supplementary material for this article can be found online at: <https://goo.su/D8Ozp>.

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