Czech Mycology 77(2): 193–211, December 22, 2025 (online version, ISSN 1805-1421)

Distribution and ecology of genus *Sarcoscypha* in Ukraine: what can we learn from citizen science, morphology, barcoding, and eDNA?

Yuliia Leshchenko[1]*, Oleh Prylutskyi[2,3], Iryna Yatsiuk[4,5]

[1] Department of Botany, Faculty of Science, Charles University, Benátská 433/2, CZ-12800, Prague, Czech Republic
[2] Falz-Fein Biosphere Reserve "Askania Nova" of the National Academy of Agrarian Sciences of Ukraine, Metrolohichna St. 12, UA-03143, Kyiv, Ukraine
[3] V.N. Karazin Kharkiv National University, Svobody sq. 4, UA-61022, Kharkiv, Ukraine
[4] Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi 52, EE-51006, Tartu, Estonia
[5] Institute of Evolutionary Biology, Faculty of Biology, Biological and Chemical Research Centre, University of Warsaw, Zwirki i Wigury 101, PL-02-089, Warsaw, Poland
*corresponding authorr: leshchey@natur.cuni.cz

Leshchenko Y., Prylutskyi O., Yatsiuk I. (2025): Distribution and ecology of genus *Sarcoscypha* in Ukraine: what can we learn from citizen science, morphology, barcoding, and eDNA? – Czech Mycol. 77(2): 193–211.

In this study, we combined classical taxonomy, DNA barcoding, environmental metabarcoding, and citizen science to assess the diversity and distribution of the genus *Sarcoscypha* in Ukraine. A targeted citizen science campaign yielded 53 specimens, enabling detailed morphological and molecular characterisation. Only two species, *S. austriaca* and *S. coccinea*, were confirmed. Morphological identification was best achieved based on the shape of the excipular hairs and spore size, although some overlap was observed.

The ascoma survey revealed that *S. austriaca* is the most common and widely distributed species in Ukraine, whereas *S. coccinea* is rare and geographically restricted. However, environmental DNA detected in soil samples revealed a broader range for *S. coccinea* than indicated by fruitbody records, suggesting that climatic or microhabitat constraints may limit the formation of apothecia.

Modelling the probability of presence of the genus *Sarcoscypha* based on 298 fruitbody records and 13 environmental variables showed that the proportion of deciduous tree species was the strongest predictor of presence, with limited explanatory power of climatic variables. Our results demonstrate the power of integrating citizen science and molecular tools to assess fungal diversity, while also revealing the limitations of presence-only models in capturing ecological nuances in ephemeral fungi.

Key words: *Pezizales*, microscopy, metabarcoding, species distribution modelling.

Article history: received 12 November 2025, revised 15 December 2025, accepted 16 December 2025, published online 22 December 2025 (including Electronic Supplements).

DOI: https://doi.org/10.33585/cmy.77206

Leshchenko Y., Prylutskyi O., Yatsiuk I. (2025): Rozšíření a ekologie rodu *Sarcoscypha* na Ukrajině: co nám říká občanská věda, morfologie, barcoding a eDNA? – Czech Mycol. 77(2): 193–211.

V této studii jsme zkombinovali klasickou taxonomii, DNA barcoding, environmentální metabarcoding a občanskou vědu s cílem zhodnotit diverzitu a rozšíření rodu *Sarcoscypha* na území Ukrajiny. Cílená kampaň v rámci občanské vědy přinesla 53 vzorků, které umožnily podrobnou morfologickou a molekulární charakterizaci. Potvrzeny byly pouze dva druhy – *S. austriaca* a *S. coccinea*. Morfologická identifikace byla nejspolehlivější na základě tvaru excipulárních chloupků a velikosti spor, i když byl zaznamenán určitý překryv znaků.

Záznamy nálezů plodnic ukázaly, že *S. austriaca* je na Ukrajině nejběžnějším a nejrozšířenějším druhem, zatímco *S. coccinea* je vzácný druh s geograficky omezeným výskytem. Analýza environmentální DNA však odhalila širší rozšíření *S. coccinea* v půdních vzorcích, než naznačují záznamy o plodnicích, což naznačuje, že tvorbu apothecií mohou omezovat klimatické nebo mikrostanovištní faktory.

Modelování rozšíření na úrovni rodu, založené na 298 záznamech plodnic a 13 environmentálních proměnných, ukázalo, že nejvýznamnějším prediktorem výskytu byl podíl listnatého porostu, zatímco klimatické proměnné měly jen omezenou vysvětlující sílu. Naše výsledky ukazují sílu integrace občanské vědy a molekulárních nástrojů při hodnocení diverzity hub a zároveň odhalují omezení modelů založených pouze na údajích o výskytu při zachycování ekologických nuancí u efemérních hub.

INTRODUCTION

Sarcoscypha (Fr.) Boud. is a genus of *Ascomycota* inhabiting fine wood debris. The genus comprises over 30 accepted species, distributed worldwide (Index Fungorum, www.indexfungorum.org). In Europe, species of *Sarcoscypha* are widely appreciated for their large, bright red apothecia, which typically appear in the spring. The most common European species are *S. austriaca* (Beck ex Sacc.) Boud., and *S. coccinea* (Jacq.) Lambotte. Another species, *S. jurana* (Boud.) Baral, is less often reported, and has few annotated sequences in public repositories (Baral 2004, GBIF on-line).

Although species of *Sarcoscypha* are generally thought to be morphologically separable, the apothecia of the European species mentioned above are very similar *in oculo nudo*. For this reason, these species have long been known collectively as *S. coccinea* sensu lato, until H.-O. Baral delimited them based on the following microscopic characters: shape of excipular hairs, ascospore shape, and ascospore contents (Baral 1984). However, these characters often represent overlapping intraspecific variation, which causes misidentification (Harrington 1990, Öpik et al. 2000). Moreover, morphological identification requires examination of living specimens (*in statu vivo)*, limiting the time for identification.

The ecological niches of European *Sarcoscypha* species also overlap considerably, both in substrate preference and phenology. All three taxa fructify from late autumn to early spring. Even though *S. jurana* is markedly restricted to

wood of *Tilia* spp., the other two species inhabit many deciduous tree species, thus showing little substrate specificity (Öpik et al. 2000, Baral 2004). The geographical ranges of *S. jurana*, *S. coccinea*, and *S. austriaca* also overlap, although *S. jurana* is limited to southern and central Europe, while *S. austriaca* becomes progressively dominant toward northern latitudes (Butterfill & Spooner 1995, Harrington & Potter 1997, Pidlich-Aigner 1999, Öpik et al. 2000, Baral 2004, Matočec & Kušan 2008, Jeppson 2018). This all makes distinguishing these taxa in the field generally impossible without microscopic or molecular confirmation.

In Ukraine, the first records of genus *Sarcoscypha* date back to the second half of the 20th century. In the identification guide to the fungi of Ukraine, two species, *S. coccinea* sensu lato and *S. protracta* (Fr.) Sacc., were described (Morochkovskyi et al. 1969). While the latter belongs to genus *Microstoma* (Kanouse 1948), the description of the first species corresponds rather to *S. austriaca* than *S. coccinea* sensu stricto. Subsequently, records of *S. coccinea* were also made at several localities in the northern and western parts of Ukraine (Zykova 2011, 2015), the Forest-Steppe zone (Smitska 1975, Smytska 1980, Karpenko 2011), the Ukrainian Carpathians (Bublyk 2017, Heluta et al. 2019), and the Crimean Mountains (Kuzub 2003, Sarkina 2013). Reports of *S. austriaca*, primarily from the forests of eastern Ukraine, appeared in later publications (Morozova 2015, Prylutskyi et al. 2017, Yatsiuk 2017).

Numerous environmental factors potentially influence the distribution of genus *Saroscypha* in Ukraine. In particular fungi, including spring-fruiting saprotrophs, are known to be sensitive to climatic conditions, especially temperature (Gange et al. 2007, Kauserud et al. 2010, Andrew et al. 2016, 2018, Bässler et al. 2022). Given that Ukraine spans three climatic subbiomes – temperate deciduous forests, forest-steppe, and grass-steppe (Loidi et al. 2022) – we were interested in identifying climatic and habitat factors influencing the distribution of *Sarcoscypha* species under the ongoing climate change.

In this study, we aimed to (1) identify the species composition, and (2) study distribution patterns of the genus *Sarcoscypha* in Ukraine and environmental drivers behind them. To this end, we revised collected specimens using microscopy and DNA barcoding, and also mined recent environmental DNA survey data and data gathered by means of citizen science. We used species distribution modelling to reveal key environmental drivers of occurrence of the genus.

MATERIAL AND METHODS

Morphological studies. Most of the specimens of *Sarcoscypha* spp. used in this study were obtained through a citizen science campaign announced in the Fungi of Ukraine Facebook group (Rudenko on-line). As fresh apothecia of *Pezizales* decay quickly during transportation, losing

their characteristics, volunteers dried fruitbodies at a temperature not exceeding 50 °C. Along with the specimens, volunteers submitted geographic coordinates of the collection, date of collection, a description of the locality and habitat, and photographs of the locality.

A total of 53 specimens of *Sarcoscypha* spp. were studied, comprising 24 *in statu vivo* and 29 *in statu mortuo*. One specimen of *S. coccinea* was collected in Adjara (Georgia), one specimen of *S. austriaca* was collected in Borjomi (Georgia), and the remaining 51 were collected in Ukraine. Voucher specimens were deposited in the herbarium of the Department of Mycology and Plant Resistance CWU (MYC) of V.N. Karazin National University, Kharkiv, and in the Mycological Herbarium of the National Herbarium of Ukraine (KW-M), M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, Kyiv. Duplicates of nine specimens have been deposited in the herbarium of the Department of Botany (PRC) of Charles University, Prague (Czech Republic). Primary data for the specimens are summarised in Supplementary Table S1 (see Electronic Supplements), also available through the GitHub repository (https://github.com/olehprylutskyi/Sarcoscypha).

Morphological identification was carried out by examining microstructures using light microscopy. Microscope slides were mounted in tap water and examined with a Granum R 60 Premium Trino microscope (Granum, China). We examined the following microscopic characters: shape of hairs on the ectal excipulum, shape of paraphyses, ascospore size, shape and guttulation patterns, and the presence/absence of conidiogenesis on ascospores (Baral 1984, 2004, Harrington 1990).

Barcoding. We sequenced the ITS region for 25 specimens of *Sarcoscypha* spp. with the Sanger method (Schoch et al. 2012).

DNA from dry fruitbodies was extracted using a NeoPrep100 DNA plant kit (Neogene Therapeutics Inc., Ukraine) according to the manufacturer's instructions. PCR was performed with primer pair (5'–3') ITS1 (TCCGTAGGTGAACCTGCGG) / ITS4 (TCCTCCGCTTATTGATATGC). PCR load was performed with 5x HOT FIREPol Blend Master Mix Ready to Load (with 10 mM $MgCl_2$; Solis BioDyne, Tartu, Estonia) with 0.25 µM of each primer and 0.5 µl of 0.1x diluted DNA extract. The PCR cycle included pre-denaturation at 96 °C for 10 min; 30 cycles 95 °C/1 min – 56 °C/1 min – 72 °C/1 min each; and final elongation at 72 °C for 10 min. Sequencing was performed by Macrogen Europe (Amsterdam, The Netherlands). Nine DNA samples for which sequencing failed were amplified again and sequenced using the same primers in the sequencing laboratory of the Faculty of Science, Charles University, Prague (Czech Republic).

Obtained sequences were uploaded to GenBank or UNITE; their accession numbers along with the sequences downloaded from GenBank used in this study are summarised in Supplementary Table S1.

To verify specimen identification, a phylogenetic tree was constructed using the maximum likelihood method with the IQ-TREE web server (Trifinopoulos et al. 2016). Branch support was estimated with 1000 ultrafast bootstrap replications. Two sequences of *Sarcoscypha tatakensis* Yei Z. Wang & C.L. Huang (Wang et al. 2016) were used as an outgroup.

Environmental DNA. As an additional data source, we mined soil eDNA sequences obtained through Illumina sequencing of the ITS2 region of 224 soil samples collected across Ukraine in 2023, following the SPUN soil sampling protocol (https://www.spun.earth/expeditions/sampling-protocol). Fungal OTUs were clustered using VSEARCH within the LotuS2 software (Özkurt et al. 2022) with a 97% similarity level, with subsequent exclusion of very low read counts and chimeric sequences. Putative taxonomy was assigned using BLASTN search against UNITE version 8.3 (Abarenkov et al. 2010), with default parameters. As a result, we included 12 sampling points where *S. coccinea* or *S. austriaca* were identified (two points including both species), in the analysis as confirmed species occurrences.

Ecological modelling. To explore environmental drivers of the distribution of *Sarcoscypha* in Ukraine, we used species distribution (habitat suitability) modelling. Since morphological identification to the species level in the field is dubious, and both species are known to follow a similar distributional pattern, we built a model at the genus level.

We mined *Sarcoscypha* occurrence data from the Fungi of Ukraine Facebook group (Rudenko on-line; 29 observations), iNaturalist (https://www.inaturalist.org/; 618 observations), GBIF (GBIF on-line; 738 observations), UkrBIN (UkrBIN on-line; 27 observations), and PlutoF (Nilsson et al. 2010; 64 observations). An additional 24 observations were obtained through personal communication. Only records with positional certainty up to 200 m were selected. After the removal of spatial duplicates, 298 occurrences remained for analysis.

As an initial set of covariates for the *Sarcoscypha* distribution model, we used 37 environmental variables, reflecting climate and vegetation. For climate data, we used CHELSA climatological variables (Karger et al. 2017), at a spatial resolution of 30 arcsec (~1 km). We selected 19 bioclimatic variables for current conditions (bio1–bio19, means of 1981–2010), as well as additional climatological covariates, incl. annual range (cmi_range) and mean monthly (cmi_mean) climate moisture index, annual range (hurs_range) and mean monthly (hurs_mean) near-surface relative humidity, frost change frequency (fcf), annual number of days with snow cover (scd), and growing season length (gsl).

We also incorporated land cover data from the Global Plant Functional Types (PFT) dataset, v2.0.8, of the European Space Agency (Harper et al. 2023). The dataset encompasses 14 PFTs at a spatial resolution of 300 m, describing annual circle (deciduous, evergreen), leaf type (broad-leaved, needle-leaved), life form (tree, shrub, herb), naturalness (natural, managed), in different combinations. Since all *Sarcoscypa* species are strictly bound to woodland, we picked two datasets describing the fraction (0–100%) of a plant functional type for two categories, broad-leaved deciduous trees and needle-leaved evergreen trees.

To reflect vegetation dynamics, we incorporated Earth observation data as three season-constrained vegetation indices – Normalized Difference Vegetation Index (NDVI), Normalized Difference Water Index (NDWI), and Enhanced Vegetation Index (EVI) for the summer (May–September) and winter (November–March) seasons, i.e. six indices in total. The data source consisted of two MODIS-derived datasets, the MOD13A1.061 Terra Vegetation Indices 16-Day Global 500m and MODIS Combined 16-Day NDWI datasets, accessed through the Google Earth Engine Data Catalogue (Gorelick et al. 2017). All indices were calculated using the Google Earth Engine by applying the 'median' function for the temporal subset of all available images between 2010 and 2022, for respective months.

Since both MODIS-derived and plant functional type data have a finer spatial resolution than CHELSA data, we upscaled rasters of vegetation indices to the same spatial extent and resolution as CHELSA, using the *terra* R package v. 1.8 (Hijmans et al. 2025). The final resolution of the covariate set had a horizontal resolution of 30 arcsec, which corresponds to approximately 600×900 metre pixels for Ukraine.

After collinearity control, we selected 13 covariates, i.e. mean diurnal air temperature range (bio02), precipitation seasonality (bio15), mean monthly precipitation amount of the coldest quarter (bio19), frost change frequency (fcf), growing season length (gsl), mean (hurs_mean) and annual range (hurs_range) of monthly near-surface relative humidity, snow cover days (scd), Enhanced Vegetation Index for both the summer and winter seasons (EVIs, EVIw), Normalized Difference Water Index for the winter season (NDWIw), broad-leaved deciduous tree proportion (TREES_DB), and needle-leaved evergreen tree proportion (TREES_NE).

We used the MaxEnt method (Phillips et al. 2006) as a modelling technique, based on presence-background data. For this purpose, we randomly generated 100 times more background points than presence points we had within the Ukraine administrative boundary spatial polygon, covering the variation of environmental conditions in the area of modelling, using the *spsample()* function of the "sp" R package, v. 1.6 (Pebesma & Bivand 2005). After removing duplicates, 20,916 background points remained. Upon these data, we fitted 100 models with a random seed and independent splitting of the data into training and testing sets through k-fold cross-validation. The models were evaluated using the Area Under the Receiver Operating Characteristic Curve (AUC) metric. We derived prediction uncertainty as the standard deviation of predictions among 100 fitted models.

We used the R programming language (R Core Team 2024) and the following packages: *dismo* v. 1.3 (Hijmans et al. 2024), *sp* v. 1.6 (Pebesma & Bivand 2005), *spThin* v. 0.2 (Aiello-Lammens et al. 2015), *usdm* v. 2.1 (Naimi et al. 2014), *terra* v. 1.8 (Hijmans et al. 2025), *raster* v. 3.6 (Hijmans 2025), and *ggplot2* v. 3.5 (Wickham 2016). For more details on the data preparation, variable selection, and modelling procedure, see the Species Distribution Modelling section of the GitHub repository (https://github.com/olehprylutskyi/Sarcoscypha?tab=readme-ov-file#species-distribution-modelling).

RESULTS

Species diversity

We documented the presence of two *Sarcoscypha* species in Ukraine, *S. austriaca* and *S. coccinea*, based on morphological identification and DNA barcoding. Despite extensive sampling and broad geographic coverage, *S. jurana* was not detected in Ukraine.

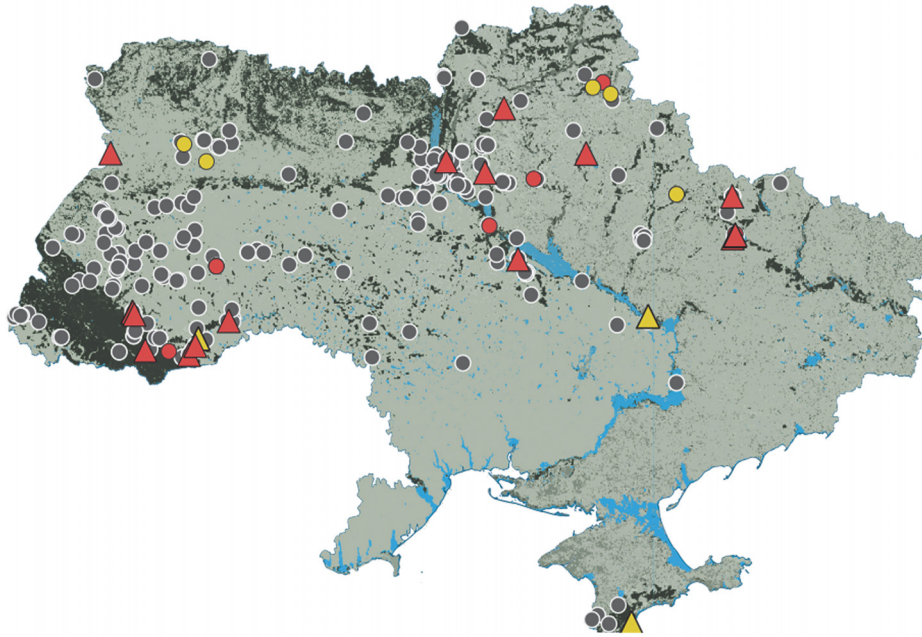
The phylogenetic tree confirmed a clear grouping of all barcoded specimens within two species (Fig. 1). All environmental sequences of *Sarcoscypha* spp. detected in soil samples also matched either of the two species.

A survey based on fruitbodies indicated that *S. austriaca* is more common than *S. coccinea* in Ukraine, with 41 and 3 barcoded specimens, respectively. However, preliminary results from soil metabarcoding did not support this pattern. Among 12 sampling sites where *Sarcoscypha* spp. were detected, *S. austriaca* was found at five sites, *S. coccinea* at five, and both species co-occurred at two sites (Fig. 1, Supplementary Table S2).

Morphology

We did not observe any consistent macroscopic features which would help differentiate between *S. austriaca* and *S. coccinea* in the field (Figs 2A–B). Among the microscopic characters, the hairs on the outer layer of the excipulum proved to be the most reliable morphological feature for identification. In *S. coccinea*, the excipular hairs were straight, whereas in *S. austriaca*, they ranged from undulate to distinctly curved (Figs 2C–D). Specimens with slightly undulate hairs, initially considered ambiguous, were confirmed by DNA barcoding to be *S. austriaca*.

Fig. 1. Top: distribution map of *Sarcoscypha* in Ukraine based on barcoded specimens, soil sequences, and citizen science observations. Bottom: ML phylogenetic tree based on the ITS region, showing sequences of *Sarcoscypha* from Ukraine grouping in two species, *S. austriaca* and *S. coccinea*. The numbers above the branches represent maximum likelihood bootstrap values. ►



Barcoded specimens

Sarcoscypha austriaca

Sarcoscypha coccinea

Soil sequences

Sarcoscypha austriaca

Sarcoscypha coccinea

***Sarcoscypha* spp., citizen science observations**

coccinea

99/99

100/100

ON651244 Sarcoscypha coccinea Dnipro UA
MZ227236 Sarcoscypha coccinea Chernivtsi UA
ON645203 Sarcoscypha coccinea Crimea UA
UDB0754117 Sarcoscypha coccinea Ajaria GE
MT366726 Sarcoscypha coccinea CL
U66015 Sarcoscypha coccinea Oregon US
U66014 Sarcoscypha coccinea Washington US
U66013 Sarcoscypha coccinea California US

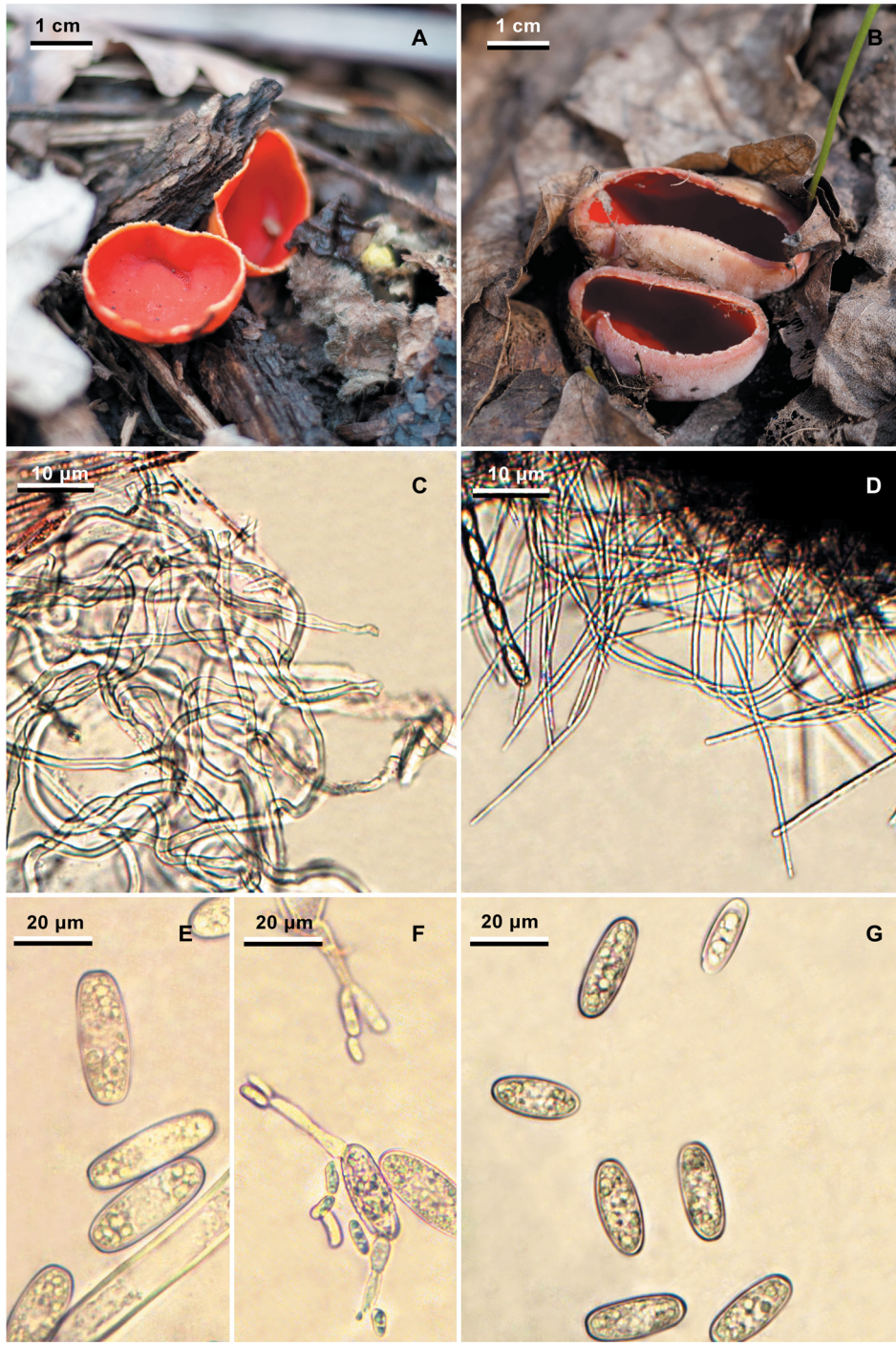
98/100

austriaca

MZ227235 Sarcoscypha austriaca Kyiv UA
MZ227237 Sarcoscypha austriaca Chernivtsi UA
MZ227231 Sarcoscypha austriaca Chernihiv UA
MZ227233 Sarcoscypha austriaca Lviv UA
U66012 Sarcoscypha austriaca SK
U66011 Sarcoscypha austriaca US
UDB0754114 Sarcoscypha austriaca Kharkiv UA
UDB0754115 Sarcoscypha austriaca Kharkiv UA
UDB0754109 Sarcoscypha austriaca Kharkiv UA
UDB0754113 Sarcoscypha austriaca Kharkiv UA
ON651241 Sarcoscypha austriaca Ivano-Frankivsk UA
MZ227232 Sarcoscypha austriaca Kyiv UA
ON892119 Sarcoscypha austriaca Bakuriani GE
MZ227234 Sarcoscypha austriaca Ivano-Frankivsk UA
UDB0754108 Sarcoscypha austriaca Kharkiv UA
UDB0754110 Sarcoscypha austriaca Kharkiv UA
UDB0754116 Sarcoscypha austriaca Kharkiv UA
MT374024 Sarcoscypha austriaca Iowa US
U66010 Sarcoscypha austriaca NO
ON651239 Sarcoscypha austriaca Sumy UA
UDB0754111 Sarcoscypha austriaca Kharkiv UA
ON651243 Sarcoscypha austriaca Ivano-Frankivsk UA
ON651240 Sarcoscypha austriaca Chernivtsi UA
ON651245 Sarcoscypha austriaca Ivano-Frankivsk UA
ON651246 Sarcoscypha austriaca Chernivtsi UA
UDB0754112 Sarcoscypha austriaca Sumy UA
ON651242 Sarcoscypha austriaca Cherkasy UA
MT374025 Sarcoscypha austriaca Iowa US

KT716836 Sarcoscypha tatakensis Taiwan
NR 156601 Sarcoscypha tatakensis Taiwan

Tree scale: 0.01


1 cm
A
1 cm
B
10 µm
C
10 µm
D
20 µm
E
20 µm
F
20 µm
G

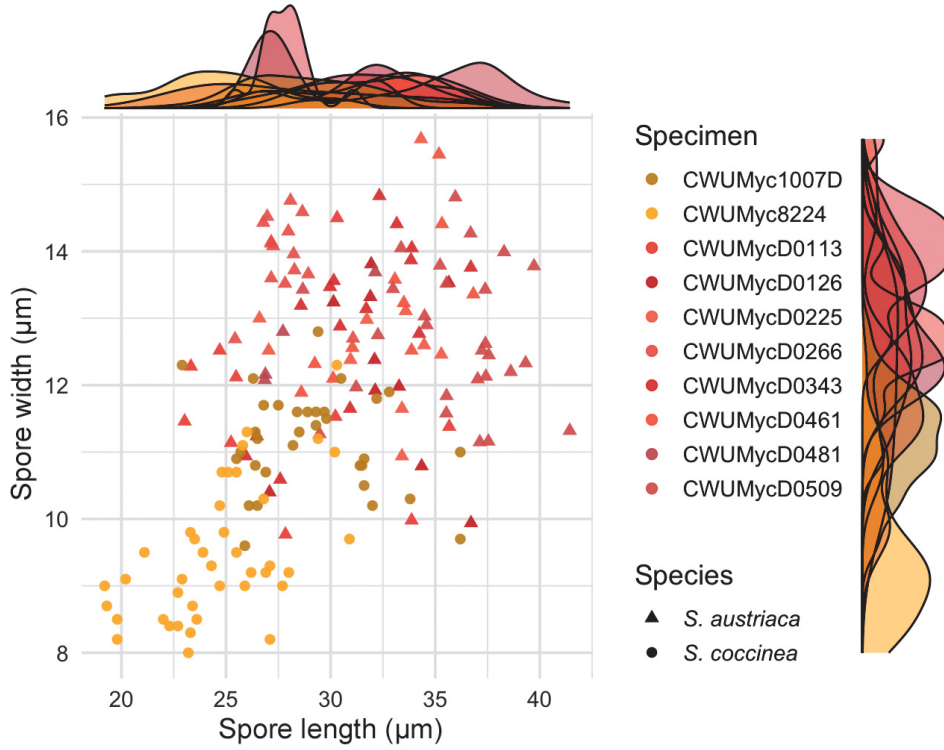


Fig. 3. Density plot of ascospore sizes based on measurements of collected material. Measurements are based on two available specimens of *Sarcoscypha coccinea* (measured *in statu mortuo*) and eight specimens of *S. austriaca* (measured *in statu vivo*).

◄ **Fig. 2.** Morphological traits of *Sarcoscypha austriaca* (left) and *S. coccinea* (right). **A–B** – ascomata; **C–D** – hairs of the ectal excipulum; **E–G** – ascospores. Conidiogenesis was frequently observed on the ascospores of *S. austriaca* (**F**). Scale bars = 1 cm (A–B), 10 µm (C–D), 20 µm (E–G). Photos by anonymous contributor (A), Iryna Yatsiuk (B, C, E–G), Yuliia Leshchenko (D).

Germination of ascospores within the apothecia, resulting in conidiogenesis, was frequently observed in overmature specimens of *S. austriaca*, but not in *S. coccinea* (Figs 2E–G). Spore size also differed significantly between the two species: specimens of *S. austriaca* generally had longer and wider ascospores (Fig. 3). Two-way ANOVA revealed a significant effect of species on ascospore length [$F(1, 164) = 125.8$, $p < 0.001$] as well as a substantial effect of specimen identity [$F(8, 164) = 16.85$, $p < 0.001$]. This suggests that, in addition to species-level differences, variability among individual specimens also plays a notable role in ascospore morphology.

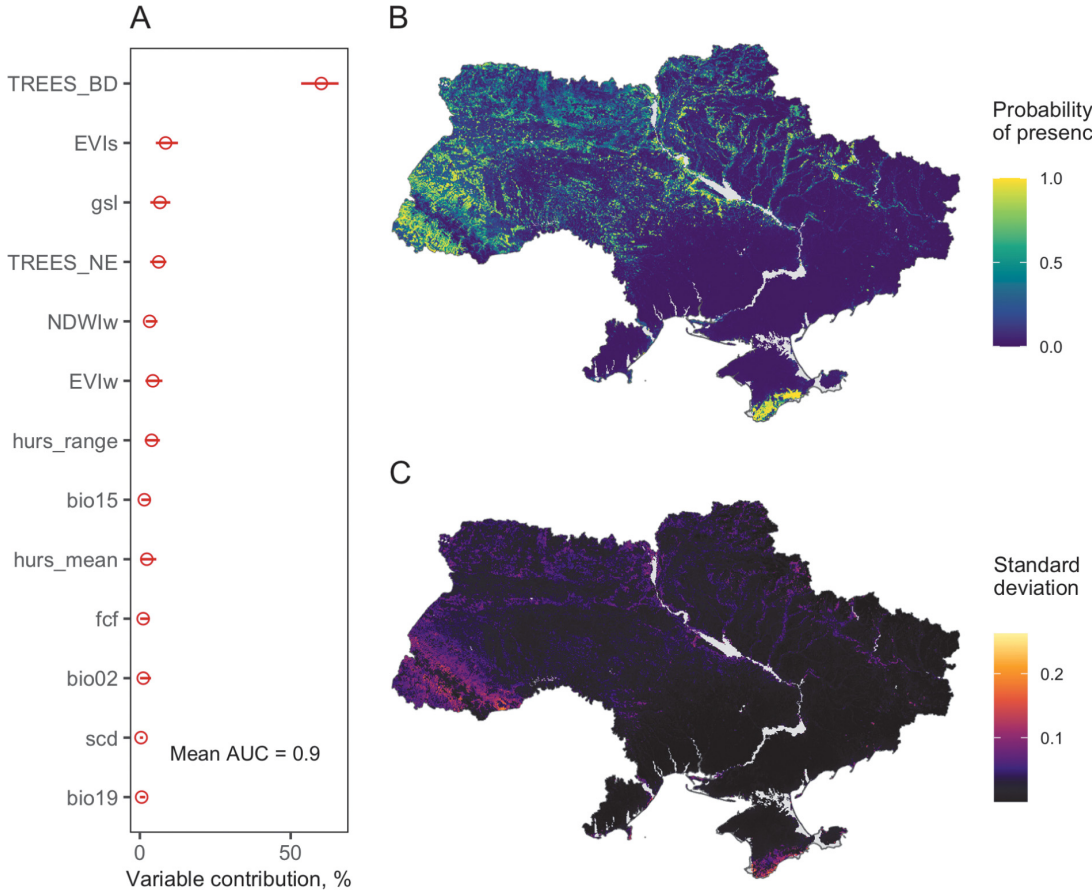


Fig. 4. Results of habitat suitability modelling for both species of the *Sarcoscypha* genus in Ukraine, based on an ensemble of 100 MaxEnt models with random seeds and independent splitting into training and testing points. **A** – variable contribution: dots indicate mean values, lines indicate ranges between the minimum and maximum values for 100 models. TREES_BD – deciduous tree proportion, TREES_NE – coniferous tree proportion, EVIs – Enhanced Vegetation Index (summer months), EVIw – Enhanced Vegetation Index (winter months), NDWIw – Normalized Difference Water Index (winter months), bio02 – mean diurnal air temperature range, bio15 – precipitation seasonality, bio19 – mean monthly precipitation amount of the coldest quarter, fcf – frost change frequency, gsl – growing season length, hurs_mean – mean monthly near-surface relative humidity, hurs_range – annual range of monthly near-surface relative humidity, scd – snow cover days. **B** – predicted probability of presence, as the mean value of 100 predictions for each pixel. **C** – prediction uncertainty is the standard deviation of 100 values of each pixel's predicted probability of presence. Predictive performance was estimated as the mean and range of the Area Under the Receiver Operating Characteristic Curve (AUC) for 100 models.

However, these results should be interpreted with caution, as measurements for *S. coccinea* were based on three available specimens only, one of which was excluded due to immaturity. Additionally, the spores of *S. austriaca* were obtained from fresh specimens and measured *in statu vivo*, whereas the fruitbodies of *S. coccinea* were obtained through a citizen science campaign in a dry state, and spores were therefore measured *in statu mortuo*. Despite these limitations, the observed differences in spore size are consistent with the collections by Baral (1984).

Species distribution modelling

An average predictive power (AUC) of 90% was reached and varied from 86% to 94% across all fitted models, indicating high predictive performance.

Among the 13 covariates, the most influential predictor was habitat-related, with deciduous tree proportion contributing an average of 60.2% across 100 model runs. This was followed by the summer Enhanced Vegetation Index (8.5%), growing season length (6.7%), and coniferous tree proportion (6.3%). Most climatic variables contributed less than 5% each (Fig. 4A).

The probability of *Sarcoscypha* species presence was the highest in the temperate regions of Ukraine, specifically in the forest and forest-steppe zones, as well as the Crimean Mountains (Fig. 4B). In contrast, the arid steppe zone contained almost no areas with a high probability of presence. The highest prediction uncertainty (Fig. 4C) was observed in areas of the Carpathian and Crimean Mountains, as well as in some parts of the deltas of the Danube and Dnipro rivers, where riparian forests are present.

DISCUSSION

Sarcoscypha species in Ukraine

Observations of the genus *Sarcoscypha* are frequently reported on citizen science platforms such as iNaturalist.org and social media. However, species-level identification of these fungi based on images taken in the field only has appeared to be impossible. The most consistent morphological character distinguishing *S. austriaca* from *S. coccinea* is the structure of the hairs on the ectal excipulum, a trait which requires examination under a basic light microscope (Fig. 5). Ascospore shape and content can be a secondary criterion for identifying species *in statu vivo*.

Despite this limitation, *Sarcoscypha* proved to be a particularly engaging subject for a targeted citizen science campaign. In response to a single announcement posted in the Fungi of Ukraine Facebook group in spring 2020, a total of 36

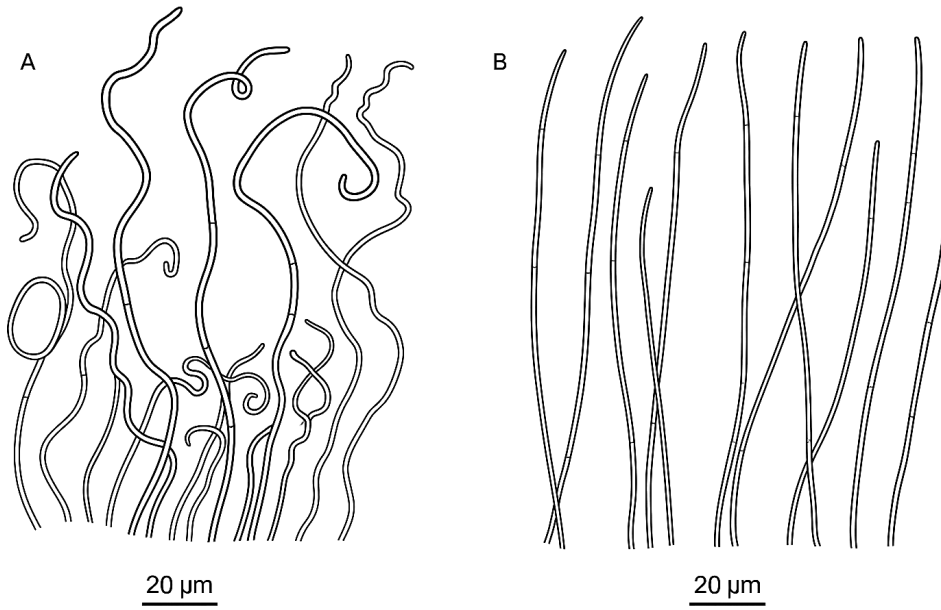


Fig. 5. Hairs of the outer layer of the excipulum: **A** – *Sarcoscypha austriaca*, **B** – *S. coccinea*. Scale bars = 20 µm. Drawing © Yuliia Leshchenko.

dried specimens of *Sarcoscypha* were sent from different regions across Ukraine. This allowed for microscopic examination and molecular verification (barcoding), enabling accurate species identification.

The results of the ascoma survey showed that *S. austriaca* is the most common and widely distributed species in Ukraine. In contrast, *S. coccinea* is rare and geographically restricted. No records of *S. jurana* were found, which may be explained by its known substrate association with *Tilia platyphyllos*, a tree species not native to Ukraine and rarely present in natural forests (Baral 2004, Caudullo et al. 2017). *Sarcoscypha jurana* can be characterised most consistently as a lignicolous species of wet, decaying lime twigs/branches, with a clear ecological emphasis on *Tilia platyphyllos* (Kotlaba & Pouzar 2007), which naturally reconciles broader wording (*Tilia* spp.) with a more specific focus on *T. platyphyllos*. At the same time, a biogeographical hypothesis can be added for Ukraine: in the chorological concept of the atlas of Central European flora (Meusel & Jäger 1992), the distribution range of *T. platyphyllos* is delimited eastwards by the Carpathians, whereas *T. cordata* extends much further to the east. If *S. jurana* is tightly linked to humid ravine-forest microhabitats where continuously wet lime deadwood occurs, then a restricted overlap between (i) such ravine conditions and (ii) the presence of *T. platyphyllos* may contribute to the apparent absence

(or strong rarity/under-detection) of *S. jurana* in Ukraine, which is worth regarding explicitly as a plausible ecological-chorological filter.

Distribution patterns based on fruitbody and eDNA survey

The confirmed records of *S. coccinea* were limited to the southern and western parts of Ukraine, namely the Carpathian montane forests, the Crimean submediterranean forest, and the border between the Pontic steppe and the East European forest steppe ecoregions. This indicates that *S. coccinea* in Ukraine occurs at the northern border of its distribution range, in agreement with H.-O. Baral's observations (Baral 2004).

Interestingly, soil metabarcoding data showed the presence of *S. coccinea* also in northern regions of Ukraine, where no ascomata were recorded.

Mycologists have been arguing the extent to which molecular surveys can correspond to ascoma inventories. In particular, Ovaskainen et al. (2013) detected 198 fungal species via high-throughput ITS sequencing in Norway spruce logs as compared to 137 species identified from collected specimens, with 69% overlap for species revealed by both approaches. Frøslev et al. (2019) found that fruitbody data identified fewer species in total and per site, and had larger variance in site richness. Blaschke et al. (2023) showed that metabarcoding detected significantly more species than the traditional fruitbody inventory. Species of several orders forming inconspicuous or hypogeous fruitbodies were detected by metabarcoding only, while several wood decomposers were recorded in the fruitbody inventory only. Baptista et al. (2015) reported that soil DNA pyrosequencing and fruitbody surveys reveal contrasting diversity for various fungal ecological guilds in chestnut orchards. Alternatively, Saine et al. (2020) reported that data collected by fruitbody- and DNA-based survey methods yield consistent species-to-species association networks in wood-inhabiting fungal communities.

The main reasons for discrepancies between fruitbody and eDNA data are usually considered to be a fungal feature, such as sporadic fructification, different sexual-asexual mating behaviour, species with inconspicuous sporocarps, cryptic species (Tóth & Barta 2010), and high fungal substrate specificity limits (Vašutová et al. 2021). For wood-inhabiting fungi, it was reported that most molecularly detected species formed fruitbodies at short distances, reflecting the high spatial variability of fungal mycelia (Runnel et al. 2015). Most research, however, emphasises that the most comprehensive insight into a fungal community can be obtained by combining both fruitbody and eDNA survey methods (Saine et al. 2020), especially monitoring rare and threatened species (Frøslev et al. 2019, Rieker et al. 2024).

Predictors of species occurrence

We are inclined to explain the discrepancy between eDNA detection and fruitbody occurrence to be reflected by climatic constraints on spring cup fungus fructification. Schreiber et al. (2024) showed that soft-fleshed fungi were more likely to fruit in closed-canopy (humid) plots than in open-canopy (dry) plots, indicating that microclimate plays a critical role in fruitbody formation. We hypothesise that the mycelium of *Sarcoscypha* can colonise buried deadwood relatively easily, but that (micro)climatic conditions limit fruitbody formation. Further metabarcoding studies involving sampling deadwood buried in the soil are needed to test this hypothesis.

At the genus level, the outputs of habitat suitability modelling align well with the occurrence patterns of *Sarcoscypha* spp. in Ukraine (Fig. 1, Fig. 4B). Observations confirm that the genus is occasional to common in temperate forests and extends into the semi-arid forest-steppe through patches of deciduous forests ('bayrak forests'), often along river valleys. Further southeast, *Sarcoscypha* species completely vanish to reappear in the forested Crimean Mountains, where moderately humid Mediterranean-type conditions prevail, after a ~350 km disjunction across the arid lowlands of the Northern Black Sea.

The MaxEnt model predicted the presence of *Sarcoscypha* in the southernmost continental floodplain forest ecosystems of Ukraine, located in the deltas of the Dnipro and Danube rivers. Mycologists from Kherson and Odesa have examined these forests for decades, yet records of *Sarcoscypha* as well as citizen science observations remain absent. This discrepancy suggests the action of additional, as yet undisclosed, constraints on *Sarcoscypha* distribution in arid parts of Ukraine, potentially of a climatic nature.

As spring-fruiting fungi with fleshy, moisture-dependent apothecia, *Sarcoscypha* species were expected to respond strongly to climatic factors, especially winter severity, temperature, and humidity (Kauserud et al. 2010). However, our modelling showed a weak climatic signal. The most influential predictors were habitat-related, with deciduous tree proportion dominating, followed by Enhanced Vegetation Index (which can be treated as a proxy for primary productivity) and growing season length. The latter was the only climatic variable among the top predictors, supporting the idea that resource accumulation during the previous season is important (Andrew et al. 2018).

A strong association with forests is evident. These fungi grow exclusively on decaying twigs and branches buried in the litter and upper soil layers. Therefore, forests provide the essential microhabitat and substrate for their growth. Yet, the presence of deciduous forests alone did not explain the distribution. For example, the model predicted high suitability in the riparian forests of the Danube and Dnipro deltas, but *Sarcoscypha* remains unrecorded there. This suggests that

unmeasured factors, such as microhabitat specificity, climatic thresholds, or dispersal limitations, constrain its distribution.

CONCLUSIONS

In Ukraine, the genus *Sarcoscypha* is represented by two species, *S. austriaca* and *S. coccinea*. Despite considerable effort and a combination of citizen science, barcoding, and eDNA approaches, we have not detected any other species of this genus in the studied area.

In the survey of ascomata (morphological and barcoding), *S. austriaca* was found to be much more common and widely distributed than *S. coccinea*, the latter being limited to the southern and southwestern parts of Ukraine. In contrast, preliminary results from soil metabarcoding showed the presence of *S. coccinea* also in the northern areas, where no fruitbodies were recorded. This discrepancy between eDNA detection and fruitbody occurrence may reflect climatic constraints on fructification at the species level.

The distribution of *Sarcoscypha* spp. at the genus level depends primarily on the availability of deciduous forests. Climatic conditions play a role at the species level only. The absence of records from seemingly suitable yet unoccupied areas highlights the complexity of fungal ecology and limitations of correlative models. Further surveys, including the collection of microclimatic data and sampling deadwood buried in the soil, are needed to verify this.

Data and code availability

All data snapshots and codes used in this research are available through the GitHub repository (https://github.com/olehprylutskyi/Sarcoscypha) under the GNU General Public License, version 3.0.

ACKNOWLEDGEMENTS

The authors express their gratitude to the members of the Fungi of Ukraine Facebook community for collecting and sending us *Sarcoscypha* specimens: A. Anikulayesi, A. Atamanchuk, O. Babiychuk, O. Bohoslavets, T. Danchuk, K. Federova, T. Gorelova, Y. Hetman, V. Hukov, E. Kanibolotskyi, I. Kantor, L. Kulievich, A. Lukava, O. Miskova, S. Ovsianyk, A. Sadogurska, O. Sckorochod, S. Stepanyuk, Zh. Storozhenko, N. Sudakova, V. Yanush, M. Yosymenko, and O. Zlenko. The authors also express their sincere gratitude to M. Zykova for organising the transfer of the specimen from Crimea. We are further grateful to all amateur mycologists who provided data of ascoma occurrences. The authors wish to acknowledge Dr Olexandr Zinenko, who significantly helped with the DNA barcoding.

Funding: Soil eDNA sequences were obtained under a project named Tracking Trade across Symbiotic Networks, funded by the Human Frontier Science Program, Scientist4Scientist Initiative in 2022/2023 (awarded to Oleh Prylutskyi, grant no. R/010525). The research was supported by a microgrant to Yuliia Leshchenko from a Ukrainian science popularisation community named Dovkolabotanika.

References

Abarenkov K., Nilsson R.H., Larsson K.-H., Alexander I.J., Eberhardt U., Erland S., Høiland K., Kjøller R., Larsson E., Pennanen T., Sen R., Taylor A.F.S., Tedersoo L., Ursing B.M., Vrålstad T., Liimatainen K., Peintner U., Kõljalg U. (2010): The UNITE database for molecular identification of fungi – recent updates and future perspectives. – New Phytologist 186: 281–285. DOI: https://doi.org/10.1111/j.1469-8137.2009.03160.x

Aiello-Lammens M.E., Boria R.A., Radosavljevic A., Vilela B., Anderson R.P. (2015): spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. – Ecography 38: 541–545. DOI: https://doi.org/10.1111/ecog.01132

Andrew C., Heegaard E., Halvorsen R., Martinez-Peña F., Egli S., Kirk P.M., Bässler C., Büntgen U., Aldea J., Høiland K., Boddy L., Kauserud H. (2016): Climate impacts on fungal community and trait dynamics. – Fungal Ecology 22: 17–25. DOI: https://doi.org/10.1016/j.funeco.2016.03.005

Andrew C., Heegaard E., Høiland K., Senn-Irlet B., Kuyper T.W., Krisai-Greilhuber I., Kirk P.M., Heilmann-Clausen J., Gange A.C., Egli S., Bässler C., Büntgen U., Boddy L., Kauserud H. (2018): Explaining European fungal fruiting phenology with climate variability. – Ecology 99: 1306–1315. DOI: https://doi.org/10.1002/ecy.2237

Baptista P., Reis F., Pereira E., Tavares R.M., Santos P.M., Richard F., Selosse M., Lino-Neto T. (2015): Soil DNA pyrosequencing and fruitbody surveys reveal contrasting diversity for various fungal ecological guilds in chestnut orchards. – Environmental Microbiology Reports 7: 946–954. DOI: https://doi.org/10.1111/1758-2229.12336

Baral H.-O. (1984): Taxonomische und ökologische Studien über *Sarcoscypha coccinea* agg., Zinnoberrote Kelchbecherlinge. – Zeitschrift für Mykologie 50: 117–145.

Baral H.-O. (2004): The European and North-American species of *Sarcoscypha*. – http://www.gbif-mycology.de/HostedSites/Baral/Sarcoscypha.htm [accessed 11 December 2025]

Baral H.-O. (on-line): Host preference (*Sarcoscypha*). – http://www.gbif-mycology.de/HostedSites/Baral/Sarcoscypha_hosts.htm [accessed 16 December 2025]

Bässler C., Heilmann-Clausen J., Andrew C., Boddy L., Büntgen U., Diez J., Heegaard E., Egli S., Gange A.C., Halvorsen R., Kauserud H., Kirk P.M., Krisai-Greilhuber I., Kuyper T.W., Nordén J., Senn-Irlet B., Krah F.-S. (2022): European mushroom assemblages are phylogenetically structured by temperature. – Ecography: e06206. DOI: https://doi.org/10.1111/ecog.06206

Blaschke M., Siemonsmeier A., Harjes J., Okach D.O., Rambold G. (2023): Comparison of survey methods for fungi using metabarcoding and fruit body inventories in an altitudinal gradient. – Archives of Microbiology 205: 269. DOI: https://doi.org/10.1007/s00203-023-03606-9

Bublyk Ya.Yu. (2017): Ekolohichni hrupy rann'ovesnianykh askomikotiv (*Ascomycota*) NPP "Skolivs'ki Beskydy" [Ecological groups of early-spring ascomycetes (*Ascomycota*) in the Skolivski Beskydy National Nature Park]. – Naukovi zapysky Derzhavnoho pryrodoznavchoho muzeiu [Scientific Notes of the State Museum of Natural History] 33: 153–164. DOI: https://doi.org/10.36885/nzdpm.2017.33.153-164 [in Ukrainian]

Butterfill G.B., Spooner B.M. (1995): *Sarcoscypha* (*Pezizales*) in Britain. – Mycologist 9: 20–26. DOI: https://doi.org/10.1016/S0269-915X(09)80243-7

Caudullo G., Welk E., San-Miguel-Ayanz J. (2017): Chorological maps for the main European woody species. – Data in Brief 12: 662–666. DOI: https://doi.org/10.1016/j.dib.2017.05.007

Frøslev T.G., Kjøller R., Bruun H.H., Ejrnæs R., Hansen A.J., Læssøe T., Heilmann-Clausen J. (2019): Man against machine: Do fungal fruitbodies and eDNA give similar biodiversity assessments across broad environmental gradients? – Biological Conservation 233: 201–212. DOI: https://doi.org/10.1016/j.biocon.2019.02.038

Gange A.C., Gange E.G., Sparks T.H., Boddy L. (2007): Rapid and recent changes in fungal fruiting patterns. – Science 316: 71. DOI: https://doi.org/10.1126/science.1137489

GBIF (on-line): Genus *Sarcoscypha* – GBIF occurrence download. – DOI: https://doi.org/10.15468/dl.j3qx6j [accessed 16 December 2025]

GORELICK N., HANCHER M., DIXON M., ILYUSHCHENKO S., THAU D., MOORE R. (2017): Google Earth Engine: Planetary-scale geospatial analysis for everyone. – Remote Sensing of Environment 202: 18–27. DOI: https://doi.org/10.1016/j.rse.2017.06.031

HARPER K.L., LAMARCHE C., HARTLEY A., PEYLIN P., OTTLÉ C., BASTRIKOV V., SAN MARTÍN R., BOHNENSTENGEL S.I., KIRCHES G., BOETTCHER M., SHEVCHUK R., BROCKMANN C., DEFOURNY P. (2023): A 29-year time series of annual 300 m resolution plant-functional-type maps for climate models. – Earth System Science Data 15: 1465–1499. DOI: https://doi.org/10.5194/essd-15-1465-2023

HARRINGTON F.A. (1990): *Sarcoscypha* in North America (*Pezizales*, *Sarcoscyphaceae*). – Mycotaxon 38: 417–458.

HARRINGTON F.A., POTTER D. (1997): Phylogenetic relationships within *Sarcoscypha* based upon nucleotide sequences of the internal transcribed spacer of nuclear ribosomal DNA. – Mycologia 89: 258–267. DOI: https://doi.org/10.1080/00275514.1997.12026779

HELUTA V.P., DUDKA I.O., PRYDIUK M.P., TYKHONENKO YU.YA., AKULOV O.YU., HAYOVA V.P., ZYKOVA M.O., ANDRIANOVA T.V., DZHAHAN V.V., SCHERBAKOVA YU.V. (2019): Gryby zapovidnykiv i natsional'nykh pryrodnykh parkiv Ukrains'kykh Karpat [Fungi of reserves and national nature parks of the Ukrainian Carpathians]. – Naukova dumka, Kyiv. [in Ukrainian]

HIJMANS R.J. (2025): raster: Geographic Data Analysis and Modeling. R package. – https://CRAN.R-project.org/package=raster [accessed 16 December 2025]

HIJMANS R.J., BIVAND R., PEBESMA E., SUMNER M.D. (2025): terra: Spatial Data Analysis. R package. – https://CRAN.R-project.org/package=terra [accessed 16 December 2025]

HIJMANS R.J., PHILLIPS S., LEATHWICK J., ELITH J. (2024): dismo: Species Distribution Modeling. R package. – https://CRAN.R-project.org/package=dismo [accessed 16 December 2025]

JEPPSON M. (2018): Projekt Sarcoscypha 2018 – en preliminär rapport [Sarcoscypha project 2018 – a preliminary report]. – Svensk Mykologisk Tidskrift 39: 28–38. [in Swedish]

KANOUSE B.B. (1948): The genus *Plectania* and its segregates in North America. – Mycologia 40: 482–497. DOI: https://doi.org/10.1080/00275514.1944.12017726

KARGER D.N., CONRAD O., BÖHNER J., KAWOHL T., KREFT H., SORIA-AUZA R.W., ZIMMERMANN N.E., LINDER H.P., KESSLER M. (2017): Climatologies at high resolution for the earth's land surface areas. – Scientific Data 4: 170122. DOI: https://doi.org/10.1038/sdata.2017.122

KARPENKO K.K. (2011): Makrohriby zapovidnykh terytorii Sumskoi oblasti [Macrofungi of the protected areas of the Sumy region]. 2nd revised and expanded ed. – Vinnychenko M.D. Publishing, Sumy. [in Ukrainian]

KAUSERUD H., HEEGAARD E., SEMENOV M.A., BODDY L., HALVORSEN R., STIGE L.C., SPARKS T.H., GANGE A.C., STENSETH N.C. (2010): Climate change and spring-fruiting fungi. – Proceedings of the Royal Society B: Biological Sciences 277: 1169–1177.

KOTLABA F., POUZAR Z. (2007): Ohnivec jurský – *Sarcoscypha jurana* (*Ascomycota*) v České republice [*Sarcoscypha jurana* (*Ascomycota*) in the Czech Republic]. – Mykologické listy 99: 10–12. [in Czech]

KUZUB V.V. (2003): Fitotrofni mikromitsety Yaltynskoho hirsko-lisovoho pryrodnoho zapovidnyka [Phytotrophic micromycetes of the Yalta Mountain-Forest Nature Reserve]. Avtoreferat dysertatsii na zdobuttia naukovoho stupenia kandydata biolohichnykh nauk [PhD thesis abstract]. – M.G. Kholodny Institute of Botany, NAS of Ukraine, Kyiv. [in Ukrainian]

LOIDI J., NAVARRO-SÁNCHEZ G., VYNOKUROV D. (2022): Climatic definitions of the world's terrestrial biomes. – Vegetation Classification and Survey 3: 231–271. DOI: https://doi.org/10.3897/VCS.86102

MATOČEC N., KUŠAN I. (2008): The genus *Sarcoscypha* in Croatia: ecological and distribution patterns. – Mycologia Montenegrina 10: 95–118.

MEUSEL H., JÄGER E.J., eds (1992): Vergleichende Chorologie der zentraleuropäischen Flora. Band III. – Gustav Fischer, Jena, Stuttgart, New York.

MOROCHKOVSKYI S.F., ZEROVA M.YA., LAVITSKA Z.G., SMITSKA M.F. (1969): Vyznachnyk hrybiv Ukrainy. Tom 2. Askomitsety [Handbook of the fungi of Ukraine. Vol. 2. Ascomycetes]. – Naukova dumka, Kyiv. [in Ukrainian]

MOROZOVA I.I. (2015): Poperezhni dani pro dyskomitsety Mokhnatskoho lisovoho masyvu (Kharkivskyi lisostep) [Preliminary data on discomycetes of the Mokhnach Forest Massif (Kharkiv Forest-Steppe)]. – Ukrainian Botanical Journal 72: 29–38. [in Ukrainian]

NAIMI B., HAMM N.A.S., GROEN T.A., SKIDMORE A.K., TOXOPEUS A.G. (2014): Where is positional uncertainty a problem for species distribution modelling? – Ecography 37: 191–203. DOI: https://doi.org/10.1111/j.1600-0587.2013.00205.x

NILSSON R.H., TEDERSOO L., ABARENKOV K., RYBERG M., KRISTIANSSON E., HARTMANN M., UNTERSEHER M., PORTER T.M., BENGTSSON-PALME J., WALKER D.M., DE SOUSA F., GAMPER H.A., LARSSON E., LARSSON K.-H., KÕLJALG U., EDGAR R.C. (2010): Taxonomic reliability of DNA sequences in public sequence databases: a fungal perspective. – PLoS ONE 5: e11950. DOI: https://doi.org/10.1371/journal.pone.0000059

ÖPIK M., KULLMAN B., KOLLOM A. (2000): *Sarcoscypha austriaca* (*Pezizales*) in Estonia. – Folia Cryptogamica Estonica 36: 107–112.

OVASKAINEN O., ABREGO N., HALME P., DUNSON D. (2013): Using latent variable models to identify large networks of species-to-species associations at different spatial scales. – Methods in Ecology and Evolution 4: 549–555. DOI: https://doi.org/10.1111/2041-210X.12501

ÖZKURT E., FRITSCHER J., SORANZO N., NG D.Y.K., DAVEY R.P., BAHRAM M., HILDEBRAND F. (2022): LotuS2: an ultrafast and highly accurate tool for amplicon sequencing analysis. – Microbiome 10: 1–14. DOI: https://doi.org/10.1186/s40168-022-01365-1

PEBESMA E.J., BIVAND R.S. (2005): Classes and methods for spatial data in R. – R News 5(2): 9–13.

PHILLIPS S.J., ANDERSON R.P., SCHAPIRE R.E. (2006): Maximum entropy modeling of species geographic distributions. – Ecological Modelling 190: 231–259. DOI: https://doi.org/10.1016/j.ecolmodel.2005.03.026

PIDLICH-AIGNER H. (1999): *Sarcoscypha austriaca* und *S. coccinea* in der Steiermark. – Joannea Botanik 1: 5–26.

PRYLUTSKYI O.V., AKULOV O.Y., LEONTYEV D.V., ORDYNETS A.V., YATSIUK I.I., USICHENKO A.S., SAVCHENKO A.O. (2017): Fungi and fungus-like organisms of Homilsha Forests National Park, Ukraine. – Mycotaxon 132(3): 705. DOI: https://doi.org/10.5248/132.705

R CORE TEAM (2024): R: A language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna. https://www.R-project.org/ [accessed 16 December 2025]

RIEKER D., RUNNEL K., BALDRIAN P., BRABCOVÁ V., HOPPE B., KELLNER H., MOLL J., TLÁSKAL V., BÄSSLER C. (2024): How to best detect threatened deadwood fungi – comparing metabarcoding and fruit body surveys. – Biological Conservation 296: 110696. DOI: https://doi.org/10.1016/j.biocon.2024.110696

RUDENKO Y. (on-line): Fungi of Ukraine [Facebook group]. – https://www.facebook.com/groups/Hryby.Ukrayiny [accessed 16 December 2025]

RUMIANTSEV M., LUK'YANETS V., KOBETS O., OBOLONYK I., TARNOPILSKA O., POZNIAKOVA S., MUSIENKO S., TUPCHII O. (2021): Distribution and natural regeneration of *Tilia cordata* Mill. in Ukrainian plain forests in a changing climate. – Folia Forestalia Polonica 63: 125–137. DOI: https://doi.org/10.2478/ffp-2021-0014

RUNNEL K., TAMM H., LÕHMUS A. (2015): Surveying wood-inhabiting fungi: most molecularly detected polypore species form fruit-bodies within short distances. – Fungal Ecology 18: 93–99. DOI: https://doi.org/10.1016/j.funeco.2015.08.008

SAINE S., OVASKAINEN O., SOMERVUO P., ABREGO N. (2020): Data collected by fruit body- and DNA-based survey methods yield consistent species-to-species association networks in wood-inhabiting fungal communities. – Oikos: oik.07502. DOI: https://doi.org/10.1111/oik.07502

SARKINA I.S. (2013): Taksonomicheskii, tsenoticheskii, ekologicheskii i sozologicheskii sostav makromitsetov PZ "Mys Martyan" [Taxonomic, cenotic, ecological and conservation composition of

macrofungi of the Mys Martyan Nature Reserve]. – Nauchnye zapiski prirodnogo zapovednika "Mys Martyan" [Scientific Notes of the Mys Martyan Nature Reserve] 4: 47–55. [in Russian]

SCHOCH C.L. ET AL. (2012): Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for Fungi. – Proceedings of the National Academy of Sciences of the USA 109: 6241–6246. DOI: https://doi.org/10.1073/pnas.1117018109

SCHREIBER J., BALDRIAN P., BRABCOVÁ V., BRANDL R., KELLNER H., MÜLLER J., ROY F., BÄSSLER C., KRAH F.-S. (2024): Effects of experimental canopy openness on wood-inhabiting fungal fruiting diversity across succession. – Scientific Reports 14: 16135. DOI: https://doi.org/10.1038/s41598-024-67216-1

SMITSKA M.F. (1975): Pezizoidni hryby Ukrainy [Pezizoid fungi of Ukraine]. – Naukova dumka, Kyiv. [in Ukrainian]

SMITSKA M.F. (1980): Flora gribov Ukrainy. Operkulyatnye diskomitsety [Fungi of Ukraine. Operculate discomycetes]. – Naukova dumka, Kyiv. [in Russian]

TÓTH B.B., BARTA Z. (2010): Ecological studies of ectomycorrhizal fungi: an analysis of survey methods. – Fungal Diversity 45: 3–19. DOI: https://doi.org/10.1007/s13225-010-0052-2

TRIFINOPOULOS J., NGUYEN L.-T., VON HAESELER A., MINH B.Q. (2016): W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. – Nucleic Acids Research 44: W232–W235. DOI: https://doi.org/10.1093/nar/gkw256

UKRBIN (on-line): Ukrainian Biodiversity Information Network [public project & web application]. – http://ukrbin.com/ [accessed 16 December 2025]

VAŠUTOVÁ M., JIROUŠEK M., HÁJEK M. (2021): High fungal substrate specificity limits the utility of environmental DNA to detect fungal diversity in bogs. – Ecological Indicators 121: 107009. DOI: https://doi.org/10.1016/j.ecolind.2020.107009

WANG Y.-Z., HUANG C.-L., WEI J.-L. (2016): Two new species of *Sarcoscypha* (*Sarcosyphaceae*, *Pezizales*) from Taiwan. – Phytotaxa 245: 169–177. DOI: https://doi.org/10.11646/phytotaxa.245.2.8

WICKHAM H. (2016): ggplot2: Elegant Graphics for Data Analysis. 2nd ed. – Springer, Cham. DOI: https://doi.org/10.1007/978-3-319-24277-4

YATSIUK I. (2017): Dyskomitsety Kharkivskoho lisostepu (Ukraina): anotovanyi spysok [Discomycetes of Kharkiv Forest-Steppe (Ukraine): an annotated checklist]. – Chornomors'kyi Botanical Journal 13: 333–344. DOI: https://doi.org/10.14255/2308-9628/17.133/8 [in Ukrainian]

ZYKOVA M.O. (2011): Rann'ovesniani dyskomitsety Natsionalnoho pryrodnoho parku "Prypiat'-Stokhid" [Early-spring discomycetes of Prypiat'-Stokhid National Nature Park]. – In: Zuzuk F.V., ed., Pryroda Zakhidnoho Polissia ta prylehlykh terytorii: zbirnyk naukovykh prats [Nature of Western Polissya and adjacent territories: collection of scientific papers], pp. 108–112. Lutsk. [in Ukrainian]

ZYKOVA M.O. (2015): Dyskomitsety Zakhidnoho Polissia Ukrainy [Discomycetes of Western Polissya of Ukraine]. – Dysertatsiia na zdobuttia naukovoho stupenia kandydata biolohichnykh nauk [PhD thesis]. M.G. Kholodny Institute of Botany, NAS of Ukraine, Kyiv. [in Ukrainian]