e-ISSN 1734-9168
http://www.isez.pan.krakow.pl/en/folia-biologica.html

Folia Biologica (Kraków), vol. 73 (2025), No 3
https://doi.org/xx.xxxxxxxxxx

Rediscovery of *Stomaphis radicicola* Hille Ris Lambers, 1947 (Hemiptera, Aphididae, Lachninae) in Europe – potential past and future distribution of a large but cryptic, arbicolous aphid species

Thomas Sobczyk, Bernhard Seifert, Agnieszka Bugaj-Nawrocka, and Łukasz Depa

Accepted July 23, 2025 *Published online August 28, 2025* *Issue online*

Original article

Sobczyk T., Seifert B., Bugaj-Nawrocka A., Depa Ł. 2025. Rediscovery of S*tomaphis radicicola* Hille Ris Lambers, 1947 (Hemiptera, Aphididae, Lachninae) in Europe – potential past and future distribution of a large but cryptic, arbicolous aphid species. Folia Biologica (Kraków) **73**: 104-117.

Aphids of the genus *Stomaphis* are among the largest aphids, living on tree trunks in the Palaearctic, always with an obligate mutualistic relationship with ants. Some species are very common and abundant, but a few of them are very rare and known only from single sites. *Stomaphis radicicola* was described in 1947 and since its description, it has been found only three times prior to 2024, when an abundant population was discovered in Germany, close to the UNESCO biosphere reserve Upper Lusatia Heath and Pond Landscape. Detailed studies on the species' biology and modelling of its potential past, current and future distribution indicate its relatively narrow habitat specialisation towards riparian forests, with *Alnus glutinosa* as a predominant host plant. With such a level of specialisation, its distribution during the Last Glacial Maximum was very limited, and the current rarity across Europe may result from a bottleneck effect. The species' future range may shift eastwards under climate change, but it will depend on finding riparian habitats and host ant species.

Key words: habitat loss, bottleneck effect, glacial refugium, climate change.

Thomas Sobczyk, Diesterwegstraße 28, D-02977 Hoyerswerda, Germany.
E-mail: thomassobczyk@aol.com
Bernhard Seifert, Department of Entomology, Senckenberg Museum für Naturkunde, Goerlitz, Germany.
E-mail: bernhard.seifert@senckenberg.de
Agnieszka Bugaj-Nawrocka, Institute of Biology, Biotechnology and Environmental Protection, Faculty of Natural Sciences, University of Silesia in Katowice, Poland.
E-mail: agnieszka.bugaj-nawrocka@us.edu.pl
Łukasz Depa✉, Institute of Biology, Biotechnology and Environmental Protection, Faculty of Natural Sciences, University of Silesia in Katowice, Poland.
E-mail: lukasz.depa@us.edu.pl

Giant stem aphids of the genus *Stomaphis* Walker, 1870 are distributed within the Palaearctic. The genus is comprised of more than 30 species, with approximately 10 species occurring in Europe. They are relatively rare and are usually only found through targeted searches due to their hidden way of life, with some species are known only from single sites (Depa *et al*. 2013, 2014, 2015). In Europe, they are mainly monophagous or oligophagous species, living in small colonies under the bark, or in cracks in the bark of older deciduous trees, with some also found on coniferous trees, and are necessarily cared for and protected by ants of the genus *Lasius* (mutualism) (Depa *et al*. 2017). The adult females are relatively large (4.5-7 mm) and have an extremely elongated proboscis (rostrum) that is significantly longer than the body, which is carried under the body, pointing backwards when moving. The species are polymorphic – there are winged and apterous females as well as apterous, dwarfish males, which do not feed. Parthenogenetic females form the summer generations.

Thieme & Eggers-Schumacher (2003) list only two species from Germany: *Stomaphis quercus* Linnaeus, 1758, and *S. longirostris* Fabricius, 1787. Surprisingly, a targeted search for other species led to the discovery of *S. radicicola* Hille Ris Lambers in 1947, in Upper Lusatia (Saxony). This species is considered to be extremely rare and, so far, despite long-term studies of this genus by the senior author, it has been reported only from three sites: in Leersum (Netherlands), where its *locus typicus* is found (Hille Ris Lambers 1947); in St. Medare (which is Saint-Médard-en-Jalles in Gironde), coll. 13.XI.1956 by Remaudière (Depa *et al.* 2015); and in 2011 in Svätý Jur (Slovakia) (Depa *et al.* 2013). On 8th July 2024, the first author found an alate female of *Stomaphis* at the Istrichteich near Deutschbaselitz. Such alate (winged) specimens are rarely found and, in the case of this species, it was the first recorded finding of this morph and the first record of *S. radicicola* in Germany.

Rare species are usually very specialised and vulnerable to environmental changes. Among the current threats, climate change seems to be one of the leading factors affecting these species, while predicting how rare and endangered ones will react to climate change is a major current challenge in the field of ecology (Vincent *et al.* 2020). The rarity of the species has been linked to endemic climatic conditions, with remnants of the former, usually glacial climate (Ohlemūller *et al.* 2008), often confining such species to small ranges limited by particular climatic situations. Obviously, such climatic glacial refugia provided conditions triggering speciation events in higher latitudes, thus promoting increased diversity (Willis & Whittaker 2000). In the case of *Stomaphis* aphids, such a hypothesis has already been presented by Depa & Mróz (2013) in the case of *S. graffii*, which is a quite an abundant species across Europe. *Stomaphis radicicola* is one of the most rarely found species in this genus. However, the reasons for its rarity seem to be insufficiently recognised. One of the causes may be its very cryptic life mode, which in the case of another species of this genus – *S. wojciechowskii* led it to remain undiscovered up to 2012 (Depa *et al.* 2012), raising questions about the rarity of these aphids, e.g. in Great Britain (Hodgson *et al.* 2019). Other factors, such as climatic conditions and ecological niche requirements, may also be involved in the rarity of some species. One of the suggested modes of diversification in *Stomaphis* is also a host shift (Yamamoto *et al.* 2020b; Maatsuura *et al.* 2023). It can be assumed that climate change may cause a host shift in this genus through altered host plant availability under different climatic conditions. Still, none of these factors have been unambiguously proven in the case of giant *Stomaphis* aphids, due to the overlapping of these factors. A novel rediscovery of quite an abundant but very local population of *S. radicicola* in Germany allowed us to analyse its ecological niche and life mode, and to model its potential current, past and future distribution.

Materials and Methods

Study site

The *S. radicicola* were found in the heath and pond landscape in the middle part of Upper Lusatia (51°24´N 14°12´E). This area is located on the southernmost edge of the North German lowlands and is part of the Upper Lusatian heath and pond area. It was shaped by the ice sheet during the last glacial period and is touched by the Lusatian glacial valley of the Saale glaciation. Sands from the Weichselian glaciation overlie the ground and terminal moraines. The valley sands and low terraces stemming from the Weichselian glaciation, with some high groundwater levels, determine the geological picture. The climate is classified as a subcontinental inland climate. However, pseudo-Atlantic climate effects also occur in some areas due to the numerous ponds, lowlands and open-cast mining lakes. The heathlands to the north are more continental in character. The fluctuations in annual and daily temperatures are higher than the Central European average. The average annual precipitation is between 600 and 700 mm, depending on the location, although in recent years they have been rather dry. The altitude of the sites ranges between 105 and 155 m above sea level.

Many swamps originally crossed this area. The river systems of the Black Elster, Spree, White and Black Schöps, and the Neisse run through the region from south to north. From the Middle Ages onwards, these areas were largely reclaimed, with numerous pond areas being created. In recent decades, brown coal mining has led to a large-scale depletion of groundwater, and large lakes have been created since the mining ceased (Fig. 1ab).

In 2024, the first author specifically examined the trunks of deciduous trees for the presence of *Stomaphis* species. Potential host trees were examined in the lower trunk area, from the ground to a height of about two metres (Fig. 1c). The search focused on black alder (*Alnus glutinosa*) and silver birch (*Betula pendula*) trees. The search for other *Stomaphis* species was carried out on oaks (*Quercus* spp.), linden (*Tilia* spp.), maple (*Acer* spp.) and walnut (*Juglans regia*) Trees.

Aphids were also searched for on ashes (*Fraxinus* spp.) and elms (*Ulmus* spp.).

Special attention was paid to the presence of the *Lasius* species of ants. If these were present, whether the ants migrated into the treetops in trails and returned 'loaded' was checked. This was a sign that they were using aphid colonies living in the treetops. If clusters of several ants were found in cracks in the bark in the lower parts of the trunk, and several ants were observed walking in no particular direction, the search method was changed. Particular attention was paid to protective shelters made of dead plant materials, mainly constructed by *Lasius brunneus*. Larger colonies of black ants on birch trees usually turned out to be *Lasius fuliginosus*, which regularly uses *Stomaphis quercus*. Colonies of *Lasius brunneus* on alder trunks, on the other hand, were signs of *S. wojciechowskii* Depa, 2012. The discovery of a female of *S. radicicola* on an alder trunk (Fig. 2a) led to an intensification of the searches on this tree species. Since the searches on the trunks initially did not yield any further evidence of *S. radicicola*, the search was expanded to include the *Lasius* species that live in the soil. Their presence is usually not visible from the outside during the day. Therefore, a few centimetres of the soil litter, vegetation or the humus layer were removed from the base of the trunk using a garden rake, and a search was done for the ants, which gathered in the exposed areas after a short time. The bases of the trunks were further exposed at these locations (Fig. 1c).

The collected specimens of aphids and ants were preserved in 70% ethanol. The first author made microscopic preparations of individual specimens of aphids. Bernhard Seifert carried out the determination of the ants. The senior author identified the *Stomaphis* species (mainly apterous females and larvae), according to Depa *et al.* (2015). Details on the collection sites of the studied samples of *Stomaphis* are presented in the supplementary file SM.01.

Modelling of the distribution

1. Occurrence data

The occurrence data was obtained from specimens examined in museum collections, the scientific literature and from private contributors. In total, 20 unique occurrence localities were compiled for the representatives of *S. radicicola* in Europe (supplementary file SM.01 – Table and Figure S1). The Geographic Distance Matrix Generator 1.2.3 was used to calculate the geographic distance between each pair of localities (Boria *et al.* 2014; Ersts 2016). To reduce the inherent geographic biases (effects of spatial autocorrelation) associated with the collecting methods, points within less than 10 km of each other were excluded from the modelling. Detailed occurrences and localities used in the model are available in the supplementary file SM.02. All the localities were georeferenced using Google Earth 10.73.0.1 (Google Inc. 2025; http://www.google.com/earth/index.html), with the coordinates collected in decimal degrees (datum: WGS84). The natural range boundary for the major host plant, *Alnus glutinosa*, was sourced from https://data.mendeley.com/datasets/hr5h2hcgg4/18 (DOI: 10.17632/hr5h2hcgg4.18; Caudullo *et al.* 2017) via https://www.euforgen.org/.

2. Environmental and climate predictors

Nineteen current bioclimatic variables were obtained from the WorldClim 2.1 dataset (Fick & Hijmans 2017; http://www.worldclim.org), as well as downscaled paleoclimate data for the Last Interglacial (LIG; ~120,000−140,000 years ago), the Last Glacial Maximum (LGM; between 26,500 and 19,000−20,000 years ago) and the Mid-Holocene (about 6,000 years ago) from the WorldClim 1.4 dataset (Hijmans *et al.* 2005). The potential distribution of *S. radicicola* under the conditions of global climate change was estimated for four periods (2021-2040, 2041-2060, 2061-2080 and 2081-2100), while four future representative shared socioeconomic pathways (SSPs) (SSP1-2.6, SSP2-4.5, SSP3-7.0 and SSP5-8.5). The average results for three future climate scenarios were based on data from the Coupled Model Intercomparison Project Phase 6 (CMIP6): ACCESS-ESM1-5, CNRM-ESM2-1 and MIROC-ES2L. A spatial resolution of 30 arc seconds (~1 km^2) for the continental models was selected (downloaded from WorldClim 2.1; 30 arc-second spatial resolution grids). All the maps were prepared in QGIS 3.34.14 (QGIS Development Team, 2025; http://www.qgis.org) using the WGS84 datum and EPSG: 4326 or 3857 (Web Mercator).

SAGA GIS 9.5.1 (Conrad *et al.* 2015; SAGA Development Team 2025) was used to extract raw environmental data from all raster layers of the species occurrence records. A Spearman rank correlation test was conducted using the Excel (ver. 2207) add-in program Analysis ToolPak (Microsoft Corporation 2025), in order to reduce the number of variables by discarding those that were highly correlated ($r \geq 0.75$). Variables that did not significantly contribute to the model were eliminated. Finally, six variables that demonstrated a reasonable impact on the habitat preferences of the studied aphid, without showing a high correlation, were selected for the analysis. These variables included Bio06, Bio10, Bio14, Bio15, Bio18 and the digital elevation model (refer to the Results section for expanded abbreviations and a further discussion of these variables).

3. Ecological niche modelling

We used MaxEnt software (version 3.4.1; http://www.cs.princeton.edu/~schapire/maxent) to model the potential niches and distribution of *S. radicicola*. MaxEnt, a machine learning tool based on maximum entropy, was configured with various feature types (auto or linear, quadratic and product features combined (LQP)) and regularisation multiplier values (0.5 to 1.75) to optimise the predictions, as the default settings may not have been ideal (Phillips *et al*. 2006; Merow *et al*. 2014; Kumar *et al*. 2014; Bugaj-Nawrocka *et al*. 2021) (supplementary file SM.02).

Models that produced biologically nonsensical curves (e.g. very jagged or multimodal) were either removed or assigned a low score. Distinguishing the environmentally unsuitable areas from undersampled areas was challenging. To address this, a method was employed that gave weight to records with few neighbours in the geographic space, while acknowledging that some areas had sparser records and the sampling efforts varied. In MaxEnt modelling, a bias file is used to weigh the selection of background points, accounting for the sampling intensity and potential sampling bias. All of the distribution records of *S. radicicola* were weighted by a Gaussian kernel with a standard deviation (SD) of 50 km (using kernel density estimation) in SAGA GIS, to create a bias grid file. A range of 50 km was chosen based on the assumption that aphids such as *S. radicicola* could spread over several kilometres per year, sometimes with irregular short-term dispersals, due to their sedentary life history, long rostrum and obligate ant mutualism. The resulting grid was scaled to have values ranging from 1 to 20 (using grid normalisation) (Elith *et al*. 2010; Syfert *et al*. 2013).

A ten-fold cross-validation was conducted, utilising all the data for the validation and optimising small datasets (Phillips *et al*. 2006; Phillips & Dudík 2008). The logistic output of MaxEnt was chosen, with the prediction values ranging from 0 (unsuitable habitat) to 1 (optimal habitat). A model evaluation was performed using the sample size corrected Akaike's information criterion (AICc and ΔAICc), which measures the relative quality of models for a given dataset, which was calculated with ENMTools (Warren *et al*. 2010). Additionally, the area under the receiver operating characteristic (ROC) curve (AUC), which assesses the model performance by considering omission and commission errors, and the partial area under the ROC curve (pAUC), calculated with Niche Analyst 3.0 (Qiao *et al*. 2015), were also used for the model evaluation (supplementary file SM.02).

Initially, consideration was given to including the distribution of the host plant and associated ant species in the modelling. However, the distribution of *Alnus glutinosa* is very wide across Europe. This is shown by the collection of individual data in GBIF (https://www.gbif.org/species/2876213) or more general maps defining the overall range (Claessens *et al*., 2010; https://forest.jrc.ec.europa.eu/en/european-atlas/qr-trees/black-alder/). We also considered the presence-absence approach. Unfortunately, only GBIF offers this, and even in this case there are too few of them for the modelling to make sense, because almost 60,000 records come from Sweden, 1461 from Portugal, then only a dozen or so from Norway, Belgium, the Russian Federation, France, Finland, Poland and the United Kingdom. This is too few records and too focused on Scandinavia to give rational results.

The situation with the ant species related to *S. radicicola* also complicates the implementation of this approach. This is because we are dealing with not one but several species: *Lasius umbratus*, *L. brunneus*, *L. emarginatus*, *L. fuliginosus*, *L. niger*, *L. platythorax* and *Myrmica rubra*. We did not know on what basis to decide which of these species could be dominant, because our current data does not provide a clear answer. Modelling each of them implies the use of a huge amount of data. Therefore, we decided not to include such layers due to the bias in the available records on the platforms.

Results

Description of *Stomaphis radicicola* alate female (Fig. 1)

Body in life: abdomen greyish-white, slightly wax dusted, thorax and head dark, greyish-brown (Fig. 2), wings dark pigmented. Mounted specimen: body length – 5.20 mm; head sclerotised, 0.97 mm wide, dark and smooth, without frontal tubercles, with a median suture clearly visible; covered sparsely with short, pointed setae. Compound eyes are well-developed, with triommatidium. Antennae 6-segmented, 2.11/2.12 mm long, 0.41 of the body length, dark brown over the entire length. Length of antenno-

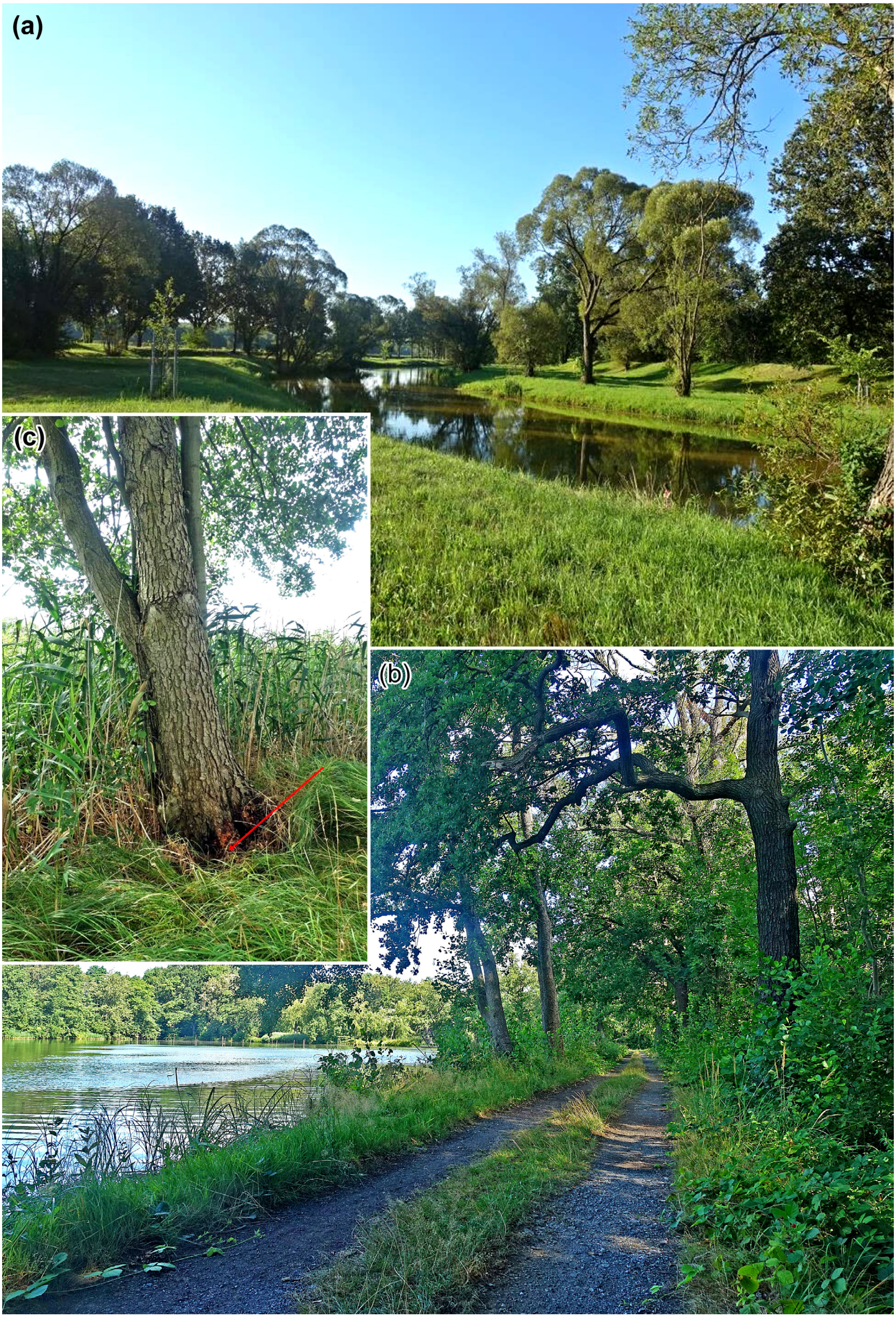

Fig. 1. Study site of *S. radicicola*: a, b – habitat of the studied species; c – location of feeding on a tree.

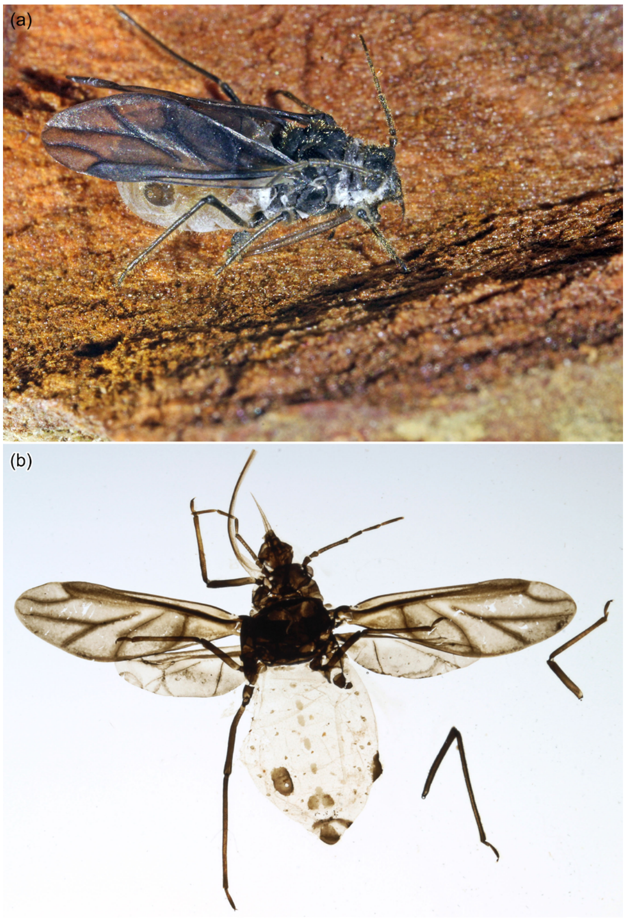

Fig. 2. Alate female of *S. radicicola*: a – live specimen; b – mounted specimen.

meres: I – 0.200/0.215, II – 0.138, III – 0.600/0.615, IV – 0.308, V – 0.385/0.369, VI – 0.476/0.477; antennomeres III with 10/12 and IV with four secondary rhinaria, often unequal in their diameter, placed in a row along the entire length of the segments; processus terminalis with a round apex, 0.16 of the base of antennomere VI. Clypeus massive, comparable in volume to the head, covered with many short setae, labrum covered with ca. 40 fine setae. Rostrum not totally preserved, segment II covered with short setae which arise from small scleroites.

Thorax heavily sclerotised. Forewing 4.462 mm long, with very dark pigmentation of the veins and their borders, especially on the proximal cubital vein. Media of the forewing with one fork. Pterostigma and radial sector elongated. Hindwings 2.72 mm long, small, with reduced venation and weaker pigmentation. Legs are dark, with distal parts of the tibiae slightly brighter, covered with many long and thin setae, some of them as long as 1.75 of the diameter of the tibia. Hind femur 1.35/1.37, hind tibia 2.08/2.11 mm long. The second segment of the hind tarsus is 0.38/0.39 mm long and is 1.33/1.39 times the length of the second segment of the middle tarsus, which is 0.28 mm long.

Abdomen membranous, wholly covered with short, pointed setae. On abdominal sternites II-VII, single darker, elongated oval sclerotic plates along the middle axis of the body, the first one of a crescent shape, and the last one merged with the genital plate. The genital plate is relatively small, trapezoid, with a broader edge distally, sclerotic, merged anteriorly in the middle with the last ventral plate, covered with pointed setae ca. 80-100 µm long and slightly weaker sclerotisation along its middle, 0.49 mm wide and 0.28 mm long. Dorsal sclerotisation is absent, except for intersegmental muscle sclerites and sclerotised abdominal tergite VIII. Reniform spiracles are placed at the posterior end of small sclerites. Siphunculi in the form of round pores ca. 0.085 mm in diameter, on the apex of flat, distinctly elongated and conical sclerotic plates with irregular margins, 0.36 mm wide and 0.58/0.64 mm long, covered with fine setae 100-130 µm long. Cauda short, 0.15 mm long, semicircular, covered with many longer, pointed setae ca. 100-130 µm long, similar to those occurring on the anal plate and abdominal tergite VIII. Perianal tubercles are a little sclerotised and are weakly visible.

Life mode of *Stomaphis radicicola*

After a few failures, the intensive search on alder trunks was successfully extended to possible underground occurrences, in accordance with the initial description. The colonies of the few aphids were located just below the surface of the soil, especially in the transition zones between living and dead wood, in hollows, etc. The feeding sites were partially built over with dead organic material (Fig. 3).

All the *S. radicicola* finds were made in locations influenced by groundwater or surface water in the immediate vicinity. The distance from the water was usually only one to two metres. In one case alone, it was ten metres. This included flowing and standing water (ponds and water-bearing ditches). The soils at the sites were rather acidic. The lowest part of the trunk was populated (base of the trunk and the beginnings of the roots) (Fig. 1c). These were usually covered with a layer of organic material (leaves, detritus, moss, humus, etc.) and extended from the actual ground level somewhat higher on the trees. In most cases, there was no evidence of aphids or ants above the ground. The aphids sat on the trunk or very close to the trunk, under the ground, or on the bark. Only occasionally have they been found at a distance

Fig. 3. Placement of a colony of *S. radicicola*: a – on an exposed root, under removed soil cover; b – position of the aphids during feeding.

Fig. 4. Reproduction of *S. radicicola*: a – apterous, dwarfish male; b, c – oviparous females during copulation within the colony; d – oviparous female with eggs.

of more than 20 cm from the trunk on the roots. The name (*radicicola* = 'root-dwelling') is somewhat misleading in this respect, as they were rarely found deeper than 10 cm below ground level. The colonies were regularly built over by the ants and kept clean by them. Chambers with aphids were connected to each other and to the actual ant nest. If there were several females and the colony size exceeded the space available for suitable feeding points (from around 5-10 specimens), the aphids were transported to new locations and cared for there. If disturbed, the aphids were defended and sometimes frantically dragged away. The oviparous females, after copulation with dwarfish arostate (having no mouthparts) males (Fig. 4a-c), laid a few yellow eggs, ca. 2.2-2.3 mm long and ca. 1.2-1.3 mm in diameter (n = 18) (Fig. 4d), which darkened after a few days.

The black alder (*Alnus glutinosa*) was the preferred host plant. A small colony of *S. radicicola* was found on a single occasion on a silver birch (*Betula pendula*). At this site, there were several alders with significantly larger colonies situated nearby. Three females and one male on *Acer platanoides* next to a colony of *S. graffii* Cholodkovsky, 1894 may be considered an exception.

A winged female of *S. radicicola* was found on 8 July 2024, 1.2 m high on an alder trunk. It was accompanied by two larvae and was tended by *Lasius brunneus*. The spot was overbuilt by the ants. Another winged adult female, on a different tree, was found in an underground colony three weeks later. This female may have founded the colony. The wax layer was barely present and one forewing was missing, and there were two other wingless females and five juveniles in the colony.

The higher-up finds on tree trunks (> 1 m) with winged females (along with individual juvenile specimens) may represent early colonisation episodes. The specimens may be transported to the underground nests at a later time. This would also explain the discovery of a winged female in such a nest and the underground presence of the Braconidae (*Protaphidius wissmannii*).

The following other *Stomaphis* species were found in the investigation area: *Stomaphis quercus* (with *Lasius fuliginosus*) was found several times on the trunks of older birch trees. Only once was this species found in a colony close to the ground on roots, near the village of Oßling. Colonies of *S. wojciechowskii* were found twice (Commerau and Mönau) in the root area of *Betula pendula*, which were not visible from the outside. The host ant in each case was *L. brunneus*. *Betula pendula* was not previously known as a host plant for *S. wojciechowskii*. The latter was found at the base of alder trees with approximately the same frequency as *S. radicicola*. This species was not previously known to live underground.

Mutualism with ants

The description of *S. radicicola* was based on specimens from Leersum (Netherlands) found on *Betula* roots in October and November 1938, which were cared for by *Lasius umbratus* (Nylander, 1846). Our first finding in Upper Lusatia was also made on an alder trunk (at a height of about 1.2 m), where a winged female and two juvenile specimens were being cared for by *L. brunneus*.

Further records led to a surprisingly broad spectrum of associated ant species. In addition to *L. umbratus* and *Myrmica rubra*, which are already mentioned in the literature, there were five other species: *L. brunneus* (four colonies of *S. radicicola*), *L. emarginatus* (4), *L. fuliginosus* (3), *L. niger* (5) and *L. platythorax* (3).

At one site (Spreewitz-Siedlung), *S. wojciechowskii* was found on an alder tree in addition to numerous *S. radicicola*. This tree, located in the floodplain of the Spree, was eye-catching from a distance owing to a thick layer of brown, gnawed plant material at the base of the trunk, resulting from a very large ant colony of *L. fuliginosus*. The bark cracks in the lower part of the trunk were heavily frequented by ants, while under the bark, at the edge of damaged areas, *Stomaphis* colonies of (sometimes) more than 30 specimens were found. In total, several hundred specimens of *S. radicicola* were found underground on this tree. Above ground, *S. radicicola* was found up to a height of 0.6 m. Two small colonies of *S. wojciechowskii* were also found separately in this range of 0.4-0.6 m. The site itself was rich in species. On a stretch of about 250 m along the Spree, there were colonies of *S. quercus* (on *Quercus robur* and *Salix alba*), *S. longirostris* (on *Salix alba*), *S. radicicola* (separately on *Alnus glutinosa*) and *S. wojciechowskii* (on *Alnus glutinosa*, together with *S. radicicola*).

At another location (Bröthen, north of the Großer Ziegelteich), three females and one male were found at the base of an *Acer platanoides* trunk. They were being cared for by *L. brunneus*. About 20 centimetres away, the same ant colony was caring for *S. graffii*. So far, there have been no known cases of several *Stomaphis* species being cared for within one ant colony.

Parasites

Only once a female aphid of *S. radicicola* (found as a mummy) was observed to be parasitised by *Protaphidius wissmannii* (Ratzeburg, 1848) (Fig. 5). Thus, our observation of *S. radicicola* represents a new host of this Braconidae known from the *Stomaphis* species. When a cocoon was found in the underground burrow, a question regarding how the parasitisation occurred was raised. The underground lifestyle should provide greater protection compared to the lifestyle in bark crevices. It is however possible that the Braconidae laid their eggs in the aphid at a different location (e.g. during feeding above the area where it was found, unprotected on the trunk).

Fig. 5. A parasitic wasp, *Protaphidius wissmannii*, recorded in the colony of *S. radicicola*: a – mummy of an aphid containing a pupa; b – adult parasitic wasp.

Distribution and climatic requirements

1. Evaluation of the models and importance of environmental predictors

In this study, we analysed results from three prediction periods: past (Last Interglacial (LIG) (Fig. 6d), Last Glacial Maximum (LGM) (Fig. 6c) and Mid-Holocene (Fig. 6b)); present (Fig. 6a); and future (four time periods and four SSPs: SSP1-2.6,

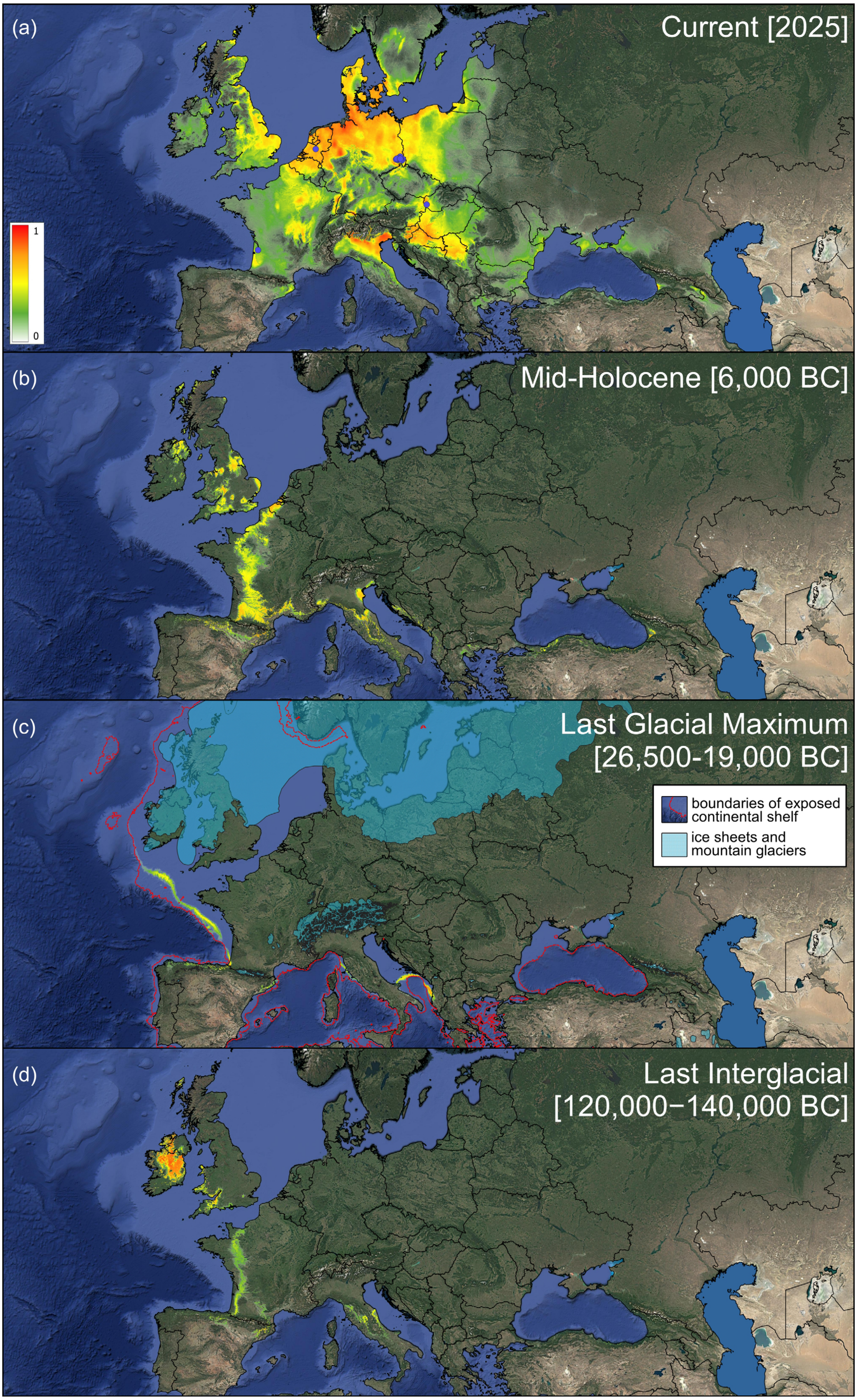

Fig. 6. Modelled distribution of *S. radicicola* in various geological periods.

SSP2-4.5, SSP3-7.0 and SSP5-8.5; Fig. 7). The training and test AUC values showed differences from random for all models. The setting selection for the model was primarily based on the results of pAUC, AICc and ΔAICc. Higher pAUC, AICc and ΔAICc values were observed when auto features were used. Regularisation multiplier settings were also analysed, and a default value of 1 was found to be effective. For the maximum number of iterations, the optimal results were achieved with a setting of 750 (supplementary file SM.02).

A jackknife test (refer to supplementary file SM.03 for more details and MaxEnt outputs) indicated that the minimum temperature of the coldest month (Bio06) was the most informative environmental variable independently, and it contained a significant amount of unique information not found in other variables (Fig. S3.1). The coldest month in Europe typically encompasses January, while occasionally extending into February. In regions with hot summers, humid continental climates and humid subtropical climates, the average temperature falls below 0°C or −3°C during the coldest month. The mean temperature in areas where *S. radicicola* has been identified is −2.3°C. The mean precipitation seasonality (Bio15), which quantifies the variations in monthly precipitation amounts throughout the year, averages at approximately 23%. The precipitation of the driest month (Bio14) was also notable, with the average rainfall for the studied areas in April (or May) measuring 39 mm. The average precipitation of the warmest quarter (Bio18) in Europe, which includes the months from June to September, is213 mm of rainfall. Meanwhile, the average temperature in the warmest quarter (Bio10) fluctuated around 17.8°C. The analysis also included an altitude model (Elevation). This allowed us to limit the prediction to lowland areas, because the study of the previously reported locations shows that the discussed aphid occurs in areas ranging in altitude from 22 to 159 m above sea level.

2. Potential distribution

All resulting maps show the median of the output grid of ten model replicates. For the present model in Europe (Fig. 6a) – the native range of *S. radicicola* – the results suggest that the most suitable areas for this species are located mainly in Belgium, the Netherlands, northern Germany, Denmark and north-western Poland, as well as in Slovakia (areas where it has already been recorded), eastern Hungary and the bordering regions of Slovenia, Croatia and Serbia. In addition, the model indicated areas in northern Italy in the Po Valley. The current climatic conditions in France suggest that the region from which one of the specimens was recorded in 1956 may no longer be suitable. However, it is recommended that these locations be revisited to verify their suitability. The central and north-eastern regions of France are considered to be more appropriate due to their favourable climatic conditions.

The results obtained for the last interglacial period (~120,000-140,000 years ago) (Fig. 6d) indicate that Ireland, the western part of present-day France and the central part of Italy were potentially the most suitable areas for the development of aphids, based on the current favourable conditions. However, given the current distribution of this aphid, it seems more likely that its range at this time was centred on the Atlantic coast of present-day France. The analysis of the results for the period of the last glacial maximum (26,500 to 19,000-20,000 years ago) (Fig. 6c) suggests that significant climatic changes likely pushed this aphid to the edge of the continent that existed at that time, including areas in present-day France and along the Adriatic Sea, from the border of the western Balkan Peninsula. In turn, the conditions during the mid-Holocene favoured the further spread of *S. radicicola* (Fig. 6b) in western France and further north, toward areas of Belgium and the Netherlands. The situation was similar in Italy, where the species could have later migrated north, thereby reaching its present distribution in Slovakia.

The results for potential future climate changes indicate that until the year 2100, *S. radicicola* may find suitable niches further northeast of its current ranges (Fig. 7). Climate changes may primarily affect the occurrence of *S. radicicola* in central and eastern Europe. In the scenarios for higher CO2 concentrations (SSP3-7.0 and SSP5-8.5, Fig. 7cd), the maps show the clear shift of a suitable niche to the territories of Poland, Ukraine, Belarus, Lithuania, Latvia, Estonia, the south of Finland and Sweden. In turn, the areas of France, Belgium and the Netherlands may become very unfavourable. A complete overview of the results for all four periods and the future representative shared socioeconomic pathways is available in the supplementary file SM.04.

Due to the small number of points and their high concentration in Germany, despite all attempts to eliminate a sampling bias, it should be remembered that the obtained results could change if a larger number of samples is obtained.

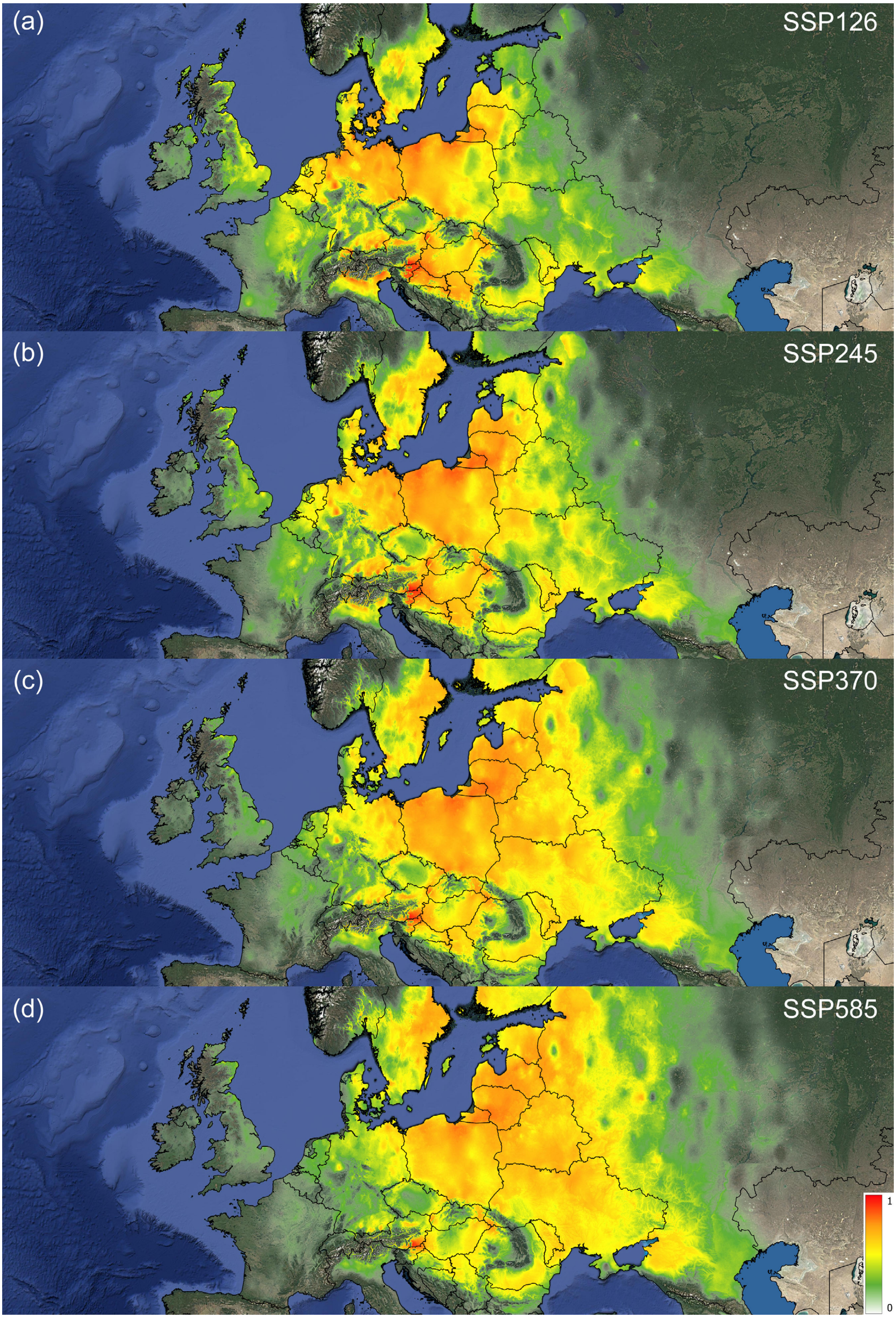

Fig. 7. Modelled future distribution (years 2080-2100) under various predicted concentrations of atmospheric CO_2.

Discussion

To date, although *S. radicicola* has been extremely rare to find, the newly recorded site of this species consists of quite a high number of recorded colonies. This species obviously has a very strict ecological requirement concerning its habitat, which possibly impacts its geographical range and may be classified as western Palearctic under an Atlantic influence. It seems that the species prefers lowland areas with relatively mild winters and significant rainfall, although apparently, the soil moisture is important, as its occurrence remains very close to the waters in wet riparian but not marshy areas. The latter results from restrictions on the attending *Lasius* ants, which rarely nest in regularly flooded or continuously wet areas. Although *S. radicicola* has a quite strict connection to a host plant, as it predominantly feeds on *Alnus glutinosa*, it also utilises *Betula* sp. and may feed on *Acer platanoides*, within the habitat in which the main host plant is present. While currently, *A. glutinosa* is relatively widely distributed across Europe, its range seems to have been significantly limited during the last glacial maximum. Paleological data shows it had a limited range across southern Europe, as far east as the Balkans and the northern coast of the Black Sea during the last glaciation (Havrdová *et al*. 2015). The climatic conditions deduced for *S. radicicola* from currently-known finding sites indicate a very limited distribution during glaciation. The models showed only two possible refugia of this aphid species – one across the western edge of Europe, directly exposed to the influence of the Atlantic Ocean; and a second one on the west coast of the Italian Peninsula and on the southern coast of the Adriatic and Balkan peninsula (Fig. 5b). In both cases, the area of the available habitat was extremely narrow, presumably much more narrow than the general range of the host plants at that time. *Alnus glutinosa* is relatively resistant to cold, and its range spreads further north and eastwards than the actual and modelled range of *S. radicicola* (Cleassens *et al*. 2010). We can therefore suppose that the glacial range of *S. radicicola* was significantly narrower than that of its host plant, and its modelled range during glaciation covered the known glacial range of *A. glutinosa* and temperate trees in general (Tzedakis *et al*. 2013).

It is difficult to estimate the possible migration route of the species after the glacial period. The mid-Holocene distribution pattern suggests the possibility of a migration route from the Balkan peninsula across the Po Plain and subsequently through the Basin of the Sava River to the Pannonian Plain. This route, however, leads through the uplands between the Alps and Dinaric Mountains and does not fully follow the migration pattern of *A. glutinosa*, which had a direct migration route from the south-eastern Balkans directly to the Pannonian Basin via the Carpathian Mountains. As is evident from the model, *S. radicicola* strictly avoids montane habitats, which makes this route less probable.

The second possibility is a migration route directly from the west, through the Great European Plain, following the migration route of *A. glutinosa* from its western refugium (Havrodová *et. al*. 2015). The locations of the known records of *S. radicicola* support this route, as most of them lie on the European Plain. The presence of *S. radicicola* at the western edge of the Carpathians in Slovakia may have resulted from its migration eastwards through the Elbe valley between the Ore Mountains and the West Sudeten Mountains.

The supposed current rarity may be the result of a very limited range during glaciation, which affected the species with the bottleneck effect. In the previous interglacial and during the last glacial maximum, *S. radicicola* was affected by limited habitat availability, as is shown by the distribution modelling. In such conditions, it also avoided any specialisation with its host ant species, with a broad spectrum of ants involved in mutualistic relations. The presence of paraaitoids that can infect *Stomaphis* through ant shelters may also be involved (Yamamoto *et al*. 2020a). Although the input data for this modelling was very small, all the current sites of *S. radicicola* nonetheless have relatively uniform climatic conditions. There is no reason to dismiss such climatic requirements in the past. If so, the current rarity of *S. radicicola* may have resulted from a bottleneck effect, with a radical decrease of the abundance of this species during the last few glacial periods of the Pleistocene. The high abundance in Upper Lusatia may also have resulted from its unique habitat, comprising wetlands under the influence of the Atlantic climate, being a remnant of glacial meltwaters and in the direct vicinity of the UNESCO biosphere reserve Upper Lusatia Heath and Pond Landscape (Culmsee & Wesche, 2017). Such an abundant population of this species strongly proves that the studied habitat matches the requirements of this species. Its rarity in other places may also have resulted from habitat loss and fragmentation, taking place in recent centuries under the enormous amount of human activity (Orczewska *et al*. 2024). Progressing irrigation and the drop in water levels, followed by broadening agricultural landscapes, could have substantially diminished the availability of proper habitats.

Regarding the ecological niche of this species, in part due to its climatic conditions, a question arises regarding whether ongoing climate change may alter its future distribution. Aphids of the genus *Stomaphis* seem to be fairly slowly dispersing aphids, due to their high body mass and long rostrum, in addition to the requirements of finding proper host plants and host ant species. The performed modelling of the distribution of *S. radicicola* under ongoing climate warming showed a significant increase in the area available for its settlement and also indicated a shift of the species distribution eastwards. It must be highlighted, however, that the modelling only shows areas which will conform to the climatic requirements and not the actual habitat that will occur, as many other factors will affect the species occurrence. One of the dangers is a lack of forest stands near waters consisting of *A. glutinosa*, with the latter also being affected by the drawdown of water. It is also disputable whether the species can migrate eastwards and find proper conditions for settlement before its western habitat disappears. In any case, the presented scenario shows that the conditions in Upper Lusatia should not change dramatically, and there is a high probability that the species will remain in this area until 2100.

Author Contributions

Research concept and design: T.S., Ł.D.; Collection and/or assembly of data: T.S., B.S.; Data analysis and interpretation: B.S., A.B.-N., Ł.D.; Writing the article: T.S., A.B.-N., Ł.D.; Critical revision of the article: T.S., B.S., A.B.-N., Ł.D.; Final approval of article: T.S., B.S., A.B.-N., Ł.D.

Conflict of Interest

The authors declare no conflict of interest.

Supplementary Materials

Supplementary Materials to this article can be found online at:

http://www.isez.pan.krakow.pl/en/folia-biologica.html

Supplementary files:

SM.01. Detailed occurrences and localities used in the model with biological observations.

SM.02. The results of the evaluation methods for the different MaxEnt settings.

SM.03. MaxEnt model outputs.

SM.04. Results of models predicting possible ecological niches under the pressure of potential climate change.

References

Boria R.A., Olson L.E., Goodman S.M., Anderson R.P. 2014. Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. Ecol. Model. **275**: 73-77. https://doi.org/10.1016/j.ecolmodel.2013.12.012

Bugaj-Nawrocka A., Taszakowski A., Gierlasiński G. 2021. From Asia to Europe? Where Could the Geographical Place of Origin of *Polymerus* (*Pachycentrum*) *carpathicus* (Horváth, 1882) (Hemiptera: Miridae) Be? Zool. Stud. **60**: 1-13. https://doi.org/10.6620/ZS.2021.60-42

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

Cleassens H., Oosterbaan A., Savill P., Rondeux J. 2010. A review of the characteristics of black alder (*Alnus glutinosa* (L.) Gaertn.) and their implications for silvicultural practices. Forestry **83**: 163-175 https://doi.org/10.1093/forestry/cpp038

Conrad O., Bechtel B., Bock M., Dietrich H., Fischer E., Gerlitz L., Wehberg J., Wichmann V., Böhner J. 2015. System for Automated Geoscientific Analyses (SAGA) version 7.3.0. Geosci. Model Dev. **8**: 1991-2007.

Culmsee H., Wesche K. 2017. Das Biosphärenreservat Oberlausitzer Heide- und Teichlandschaft: Vielfalt in Biodiversität und Landnutzung. Tuxenia, Beiheft **10**: 25-47.

Depa Ł., Kanturski M., Junkiert Ł., Wieczorek K. 2015. Giant females vs dwarfish males of the genus *Stomaphis* Walker (Hemiptera: Aphididae) – an aphid example of the ongoing course to permanent parthenogenesis? Arthropod Syst. Phylo. **73**(1): 19-40.

Depa Ł., Kanturski M., Taszakowski A., Wieczorek K. 2014. Atypical, ventro-ventral copulation position in aphids of the genus *Stomaphis* Walker (Insecta, Hemiptera). Contributions to Zoology **83**: 177-183.

Depa Ł., Mróz E. 2013. Central European Acer- and Salicaceae-feeding aphids of the genus *Stomaphis* (Insecta: Aphidoidea: Lachnidae) – separate species or populations? Zool. Sci. **30**: 509-518. https://doi.org/10.2108/zsj.30.509

Depa Ł., Mróz E., Brożek J. 2013. Description of oviparous female and new data on the biology of extremely rare aphid *Stomaphis radicicola* Hille Ris Lambers 1947 (Hemiptera, Aphidoidea). Entomol. Fennica **24**: 100-106.

Depa Ł., Mróz E., Bugaj-Nawrocka A., Orczewska A. 2017. Do ants drive speciation in aphids? A possible case of ant-driven speciation in the aphid genus *Stomaphis* Walker (Aphidoidea, Lachninae). Zoological Journal of the Linnean Society **179**: 41-61. https://doi.org/10.1111/zoj.12437

Depa Ł., Mróz E., Szawaryn K. 2012. Molecular identity of *S. quercus* and description of a new species. Eur. J. Entomol. **109**: 435-444.

Elith J., Kearney M., Phillips S. 2010. The art of modelling range-shifting species. Methods Ecol. Evol. **1**: 330-342. https://doi.org/10.1111/j.2041-210X.2010.00036.x

Ersts P.J. 2016. Geographic Distance Matrix Generator, version 1.2.3. American Museum of Natural History. Center for Biodiversity and Conservation. https://biodiversityinformatics.amnh.org/open_source/gdmg. (Accessed 17 December 2024).

Fick S.E., Hijmans R.J. 2017. Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. **37**: 4302-4315. https://doi.org/10.1002/joc.5086

Google Inc. 2025. Google Earth, version 10.73.0.1. Mountain View, CA, USA. http://www.google.com/earth/index.html (Accessed 21 January 2025)

Havrdová A., Douda J., Krak K., Vít P., Hadincová V., Zákravský P., Mandák B. 2015. Higher genetic diversity in recolonized areas than in refugia of *Alnus glutinosa* triggered by continent-wide lineage admixture. Mol. Ecol. **24**: 4759-4777. https://doi.org/10.1111/mec.13348

Hijmans R.J., Cameron S.E., Parra J.L., Jones P.G., Jarvis A. 2005. Very high-resolution interpolated climate surfaces for global land areas. Int. J. Climatol. **25**: 1965-1978. https://doi.org/10.1002/joc.1276

Hodgson J., Kaszyca-Taszakowska N., Masłowski A., Depa Ł. 2019. The alate morph of *Stomaphis wojciechowskii* – first description and implications for species ecology. Bull. Insectology **72**: 233-240.

Kumar S., Neven L.G., Yee W.L. 2014. Evaluating correlative and mechanistic niche models for assessing the risk of pest establishment. Ecosphere **5**: 1-23. https://doi.org/10.1890/ES14-00050.1

Matsuura T., Yamamoto T., Matsumoto Y., Itino T. 2023. Evolutionary host shifts across plant orders despite high host specificity in tree stem surface-living *Stomaphis* aphids inferred from molecular phylogeny. J. Asia-Pac. Entomol. **26**: 102138. https://doi.org/10.1016/j.aspen.2023.102138

Merow C., Smith M.J., Edwards T.C., Guisan A., McMahon S.M., Normand S., Thuiller W., Wüest R.O., Zimmermann N.E., Elith J. 2014. What do we gain from simplicity versus complexity in species distribution models? Ecography **37**: 1267-1281. https://doi.org/10.1111/ecog.00845

Ohlemüller R., Anderson B.J., Araújo M.B., Butchart S.H.M., Kudrna O., Ridgely R.S., Thomas C.D. 2008. The coincidence of climatic and species rarity: high risk to small-change species from climate change. Biology Lett. **4**: 568-572. https://doi.org/10.1098/rsbl.2008.0097

Orczewska A., Dulik A., Długosz P., Depa Ł. 2024. Intensive agriculture vs. Invertebrate biodiversity: a case study of woodland islets in a matrix of arable land. Agriculture **14**: 1400. https://doi.org/10.3390/agriculture14081400

Phillips S.J., Anderson R.P., Schapire R.E. 2006. Maximum entropy modelling of species geographic distributions. Ecol. Model. **190**: 231-259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Phillips S.J., Dudík M. 2008. Modelling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography **31**: 161-175. https://doi.org/10.1111/j.0906-7590.2008.5203.x

QGIS Development Team, 2025. QGIS Geographic Information System. Open-Source Geospatial Foundation Project. http://qgis.osgeo.org. (Accessed 21 January 2025).

Qiao H., Escobar L.E., Peterson A.T., Ji L., Soberón J., Campbell L.P. 2015. NicheA: Creating Virtual Species and Ecological Niches in Multivariate Environmental Scenarios. Ecography **39**: 805-813. https://doi.org/10.1111/ecog.01961

SAGA Development Team, 2025. System for Automated Geoscientific Analyses (SAGA) version 9.5.1. Institute of Geography at the University of Hamburg, Germany. http://www.saga-gis.org. (Accessed 21 January 2025).

Syfert M.M., Smith M.J., Coomes D.A. 2013. The effects of sampling bias and model complexity on the predictive performance of MaxEnt species distribution models. PlosOne **8**: e55158. https://doi.org/10.1371/journal.pone.0055158

Thieme T., Eggers-Schumacher H.A. 2003. Verzeichnis der Blattläuse (Aphidina) Deutschlands. Entomofauna Germanica **6**: 167-193.

Tzedakis P.C., Emerson B.C., Hewitt G.M. 2013. Cryptic or mystic? Glacial tree refugia in northern Europe. Trends Ecol. Evol. **28**: 696-704. https://doi.org/10.1016/j.tree.2013.09.001

Vincent H., Bornand C.N., Kempel A., Fischer M. 2020. Rare species perform worse than widespread species under changed climate. Biol. Conserv. **246**: 108586. https://doi.org/10.1016/j.biocon.2020.108586

Warren D.L, Glor R.E., Turelli M. 2010. ENMTools: a toolbox for comparative studies of environmental niche models. Ecography **33**: 607-611. https://doi.org/10.1111/j.1600-0587.2009.06142.x

Willis K.J., Whittaker R.J. 2000. The refugial debate. Science **287**: 1406-1407.

Yamamoto T., Hasegawa H., Nakase Y., Komatsu T., Itino T. 2020a. Cryptic diversity in the aphid-parasitizing wasp Protaphidius nawaii (Hymenoptera: Braconidae): discovery of two attendant-ant-specific mtDNA lineages. Zool. Sci. **37**: 117-121. https://doi.org/10.2108/zs190093

Yamamoto T., Hattori M., Matsumoto Y., Ueda S., Itino T. 2020b. Evolutionary diversification of Japanese *Stomaphis* aphids (Aphididae, Lachninae) in relation to their host plant use and ant association. Sci. Nat. **107**: 14. https://doi.org/10.1007/s00114-020-1671-4