Continental data on cave-dwelling spider communities across Europe (Arachnida: Araneae)

Stefano Mammola†,‡, Pedro Cardoso§, Dorottya Angyal¶, Gergely Balázš#, Theo Blick², Hervé Brustel³, Julian Carter⁴, Srečko Ćurčič⁵, Samuel Danflous⁶, László Dányi⁷, Sylvain Déjean⁸, Christo Deltchev⁹, Mert Elverici¹, Jon Fernández¶, Fulvio Gasparo¹, Marjan Komnenov², Christian Komposch⁶, L’ubomír Kováč⁸, Kadir Boğac Kurt⁹, Andrej Mock¹, Oana Moldovan⁷, Maria Naumova⁹, Martina Pavlek¹⁰, Carlos E. Prieto¹, Carles Ribera⁸, Robert Rozwalska¹, Vlastimil Růžička¹¹, Robert S. Vargovitsh¹², Stefan Zaenker¹, Marco Isaia†

† Department of Life Sciences and Systems Biology, University of Turin, Turin, Italy
‡ Laboratory for Integrative Biodiversity Research (LIBRe), Finnish Museum of Natural History, University of Helsinki, Helsinki, Finland
§ Department of Zoology, Hungarian Natural History Museum, Budapest, Hungary
¶ UMDI, Faculty of Sciences, UNAM National Autonomous University of Mexico, Sisal, Mexico
# Department of Systematic Zoology and Ecology, Eötvös Loránd University, Budapest, Hungary
≠ Independent Researcher, Hummeltal, Germany
« Ecole d’Ingénieur de Purpan, Toulouse, France
» Amgueddfa Cymru National Museum Wales, Cardiff, United Kingdom
‘ Faculty of Biology, Institute of Zoology, University of Belgrade, Belgrade, Serbia
‘’ Conservatoire d’Espaces Naturels de Midi-Pyrénées, Toulouse, France
‘‘ Conservatoire d’Espaces Naturels de Midi-Pyrénées, Toulouse, France
‘’ National Museum of Natural History, Bulgarian Academy of Sciences, Sofia, Bulgaria
‘’’ Department of Biology, Faculty of Science and Arts, Erzincan Binali Yildirim University, Erzincan, Turkey
¢ Independent researcher, Basque Country, Spain
€ Comissionene Grotte “E. Boegan”, Società Alpina delle Giuile, C.A.I., Trieste, Italy
£ Independent Researcher, Blwdr Kuzman Josifovski Pitu, Skopje, Macedonia
P OEKOTEAM - Institute for Animal Ecology and Landscape Planning, Graz, Austria
A Institute of Biology and Ecology, Faculty of Science, Pavol Jozef Safarik University, Košice, Slovakia
Œ Zoological Collection of Cyprus Wildlife Research Institute, Kyrenia, Cyprus
F Department of Biology, Faculty of Science, Eskişehir Technical University, Eskişehir, Turkey
Ț Emil Racovița Institute of Speleology, Cluj-Napoca, Romania
N Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Sofia, Bulgaria
K Rudr Bašković Institute, Zagreb, Croatia
₵ Croatian Biospeleological Society, Zagreb, Croatia
† Department of Evolutionary Biology, Ecology and Environmental Sciences & Biodiversity Research Institute, University of Barcelona, Barcelona, Spain
‡ Department of Zoology & Animal Cell Biology, Faculty of Science and Technology, University of the Basque Country, Bilbao, Spain
³ Faculty of Biology and Environmental Sciences, Cardinal Stefan Wyszyński University, Warsaw, Poland
‡‡ Biology Centre, Institute of Entomology, České Budějovice, Czech Republic
§§ Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, Kiev, Ukraine
|| Verband der deutschen Höhlen- und Kunstforscher e.V., Fulda, Germany

© Mammola S et al. This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.
Abstract

Background

Spiders (Arachnida: Araneae) are widespread in subterranean ecosystems worldwide and represent an important component of subterranean trophic webs. Yet, global-scale diversity patterns of subterranean spiders are still mostly unknown. In the frame of the CAWEB project, a European joint network of cave arachnologists, we collected data on cave-dwelling spider communities across Europe in order to explore their continental diversity patterns. Two main datasets were compiled: one listing all subterranean spider species recorded in numerous subterranean localities across Europe and another with high-resolution data about the subterranean habitat in which they were collected. From these two datasets, we further generated a third dataset with individual geo-referenced occurrence records for all these species.

New information

Data from 475 geo-referenced subterranean localities (caves, mines and other artificial subterranean sites, interstitial habitats) are herein made available. For each subterranean locality, information about the composition of the spider community is provided, along with local geomorphological and habitat features. Altogether, these communities account for >300 unique taxonomic entities and 2,091 unique geo-referenced occurrence records, that are made available via the Global Biodiversity Information Facility (GBIF) (Mammola and Cardoso 2019). This dataset is unique in that it covers both a large geographic extent (from 35° south to 67° north) and contains high-resolution local data on geomorphological and habitat features. Given that this kind of high-resolution data are rarely associated with broad-scale datasets used in macroecology, this dataset has high potential for helping researchers in tackling a range of biogeographical and macroecological questions, not necessarily uniquely related to arachnology or subterranean biology.
Keywords

Araneae; cave; Europe; spiders; subterranean biology; troglophile; troglobiont

Introduction

Spiders (Arachnida: Araneae) are widespread in caves and other subterranean ecosystems worldwide, representing an important component of subterranean trophic webs (Deharveng and Bedos 2019). They are distinctive for their key ecological role as predators and for the variety of functional adaptations, representing therefore ideal model organisms for exploring a variety of ecological and evolutionary topics (Mammola and Isaia 2017). For example, different spider species have been used for studying silk's mechanical and structural properties (Lepore et al. 2012, Piorkowski et al. 2017), for exploring a range of morphological, metabolic and behavioural adaptations (Cardoso and Scharff 2009, Doran et al. 2001, Doran et al. 2017, Hadley et al. 1981, Lipovšek et al. 2018, Lipovšek et al. 2017, Miller 2005, Yancey et al. 2018, Chiavazzo et al. 2015, Michalik et al. 2014, Hesselberg et al. 2019), for shedding light on the mechanisms of speciation and the processes underpinning biological radiations (Arnedo et al. 2007, Hedin 2015, Růžička et al. 2013, Yao et al. 2016, Zhang and Li 2013), as well as for testing ecological hypotheses (Cardoso 2012, Mammola et al. 2016, Mammola et al. 2019, Novak et al. 2010, Lunghi 2018).

Yet, the accessible information about the ecology of most subterranean spiders is still limited, especially when considering broad-scale spatial and temporal patterns of subterranean communities (that is, a macroecological perspective). Indeed, due to the general paucity of information on most subterranean spiders (e.g. Huber 2018, Mammola et al. 2018, Cardoso 2012) and the lack of broad-scale databases about their distribution (Culver et al. 2013, Mammola 2019), global-scale diversity patterns of subterranean spiders remain virtually undescribed (Mammola et al. 2018a, Mammola and Isaia 2017). In an attempt to overcome this impediment, we created an international network of araneologists and cavers (that we called the "CAWEB" network; Mammola et al. 2017) to compile the first continental-scale geo-referenced dataset of cave-dwelling and other subterranean spider communities (Mammola et al. 2019b). In this data paper, we describe these datasets and make them freely available online for future use. We aim to provide an accessible tool for exploring continental patterns of subterranean species distribution, as well as to further expand the CAWEB network and thus the geographical coverage of these datasets.

Geographic coverage

Description: Europe.

Coordinates: 35.0 and 67.0 Latitude; –9.0 and 37.0 Longitude.
**Taxonomic coverage**

**Taxa included:**

| Rank      | Scientific Name | Common Name |
|-----------|-----------------|-------------|
| order     | Araneae         | Spiders     |

**Usage rights**

**Use license:** Creative Commons Public Domain Waiver (CC-Zero)

**Data resources**

**Data package title:** Cave_dwelling_spiders_Europe

**Number of data sets:** 3

- **Data set name:** GBIF_occurrence_cave_spiders
- **Download URL:** https://doi.org/10.15468/ygocko
- **Data format:** Tab delimited file (.csv).

**Description:** A dataset with all the referenced distribution points of the species considered in the subterranean localities included in the CAWEB project. This biodiversity dataset is constructed following the Darwin Core standard.

| Column label         | Column description                                                                                                                                 |
|----------------------|---------------------------------------------------------------------------------------------------------------------------------------------------|
| id                   | An alphanumeric identifier (“Ara” followed by a progressive number; e.g. Ara0001) for the Occurrence (as opposed to a particular digital record of the occurrence). |
| basisOfRecord        | The specific nature of the data record. Categorical variable. Either "PreservedSpecimens" (data record based on specimens stored in a museum or private collection), "Literature" (data record based on literature information) or HumanObservation (data record based on personal observations by the author of each records). See "notes" and "referencesSpecies" columns in the "Cave description.csv" dataset for full bibliographic details. |
| collectionCode       | For "PreservedSpecimens", the name identifying the collection or dataset from which the record was derived. Note that, in spelling institutions and collection names, we have omitted accents (e.g. â, é, ô) and special characters (e.g. à, ç, ê) in order to avoid formatting problems. |
| informationWithheld  | Additional information relative to each record, indicating the person to contact for information about the record. Note that, in spelling contact names, we have omitted accents (e.g. â, è, õ) and special characters (e.g. à, ç, ê) in order to avoid formatting problems. |
| datasetName          | The name of the dataset from which the record was derived. |
|----------------------|----------------------------------------------------------|
| bibliographicCitation| The bibliographic reference for the resource, indicating how individual records should be cited (attributed) when used. |
| country              | The name of the country or major administrative unit in which the verbatimLocality is situated. |
| locationID           | An identifier for the set of location information. Same as the column ID in the "Cave_description" dataset. |
| verbatimLocality     | The original textual description of the locality. |
| decimalLatitude      | The geographic latitude (in decimal degrees, using the spatial reference system given in geodeticDatum) of the geographic centre of a location. |
| decimalLongitude     | The geographic longitude (in decimal degrees, using the spatial reference system given in geodeticDatum) of the geographic centre of a location. |
| geodeticDatum        | The ellipsoid, geodetic datum or spatial reference system (SRS) upon which the geographic coordinates, given in decimalLatitude and decimalLongitude, are based. |
| georeferenceProtocol | A description or reference to the methods used to determine the spatial footprint, coordinates and uncertainties. |
| phylum               | The full scientific name of the phylum or division in which the taxon is classified. |
| class                | The full scientific name of the class in which the taxon is classified. |
| order                | The full scientific name of the order in which the taxon is classified. |
| family               | The full scientific name of the family in which the taxon is classified. |
| genus                | The full scientific name of the genus in which the taxon is classified. |
| specificEpithet      | Specific epithet of the taxonomic record. |
| specificName         | The full scientific name, with authorship and date information if known. |
| scientificNameAuthorship | The authorship information for the scientific name formatted according to the conventions of the applicable nomenclatural code. |
| taxonRank            | The highest taxonomic rank in the specificName – either a genus or a species. |

**Data set name:** Cave_description

**Download URL:** 10.6084/m9.figshare.8224025

**Data format:** Tab delimited file (.csv)

**Description:** A dataset with all the information about the subterranean localities included in the CAWEB project. The R notation 'NA' is used for missing values.
| Column label     | Column description                                                                                                                                                                                                 |
|-----------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| ID              | An alphanumeric identifier ("CAVE_" followed by a progressive number; e.g. CAVE_001) for the subterranean locality. Note that the exact same "ID" is used in the "Community_composition" dataset, in order to unambiguously link each subterranean locality with its spider community's composition. |
| locality        | Name of the cave/subterranean locality. Not translated in English.                                                                                                                                                  |
| country         | The name of the country or major administrative unit in which the subterranean locality is situated.                                                                                                               |
| decimalLongitude| The geographic longitude of the entrance of the subterranean locality.                                                                                                                                              |
| decimalLatitude | The geographic latitude of the entrance of the subterranean locality.                                                                                                                                              |
| geodeticDatum   | The ellipsoid, geodetic datum or spatial reference system (SRS) upon which the geographic coordinates given in decimalLatitude and decimalLongitude are based.                                                          |
| elevation       | Altitude a.s.l. of the subterranean locality's main entrance in metres (m).                                                                                                                                           |
| aspect          | The direction that the main entrance of the cave/subterranean locality faces. Categorical variables. N = North; S = South; E = East; W = West; flat = entrance in a plane terrain.                                                   |
| entranceNumber  | Number of known subterranean localities' entrances (if any).                                                                                                                                                         |
| entranceType    | The general morphology of the subterranean locality's main entrance. Categorical variables. ascendent = ascending; descendent = descending entrance; horizontal = horizontal entrance; pit = vertical entrance.       |
| entranceSize    | Size (base x height) of the subterranean locality's main entrance in square metres (m²).                                                                                                                             |
| entranceHabitat | Prevalent habitat in which the subterranean locality opens. Categorical variables. Either "agricultural", "forest", "grass", "rocky", "shrubs" or "urbanized".                                                             |
| entranceHabitatVerbatim | A verbatim description of the habitat in which the subterranean locality opens.                                                                                                                                       |
| development     | The subterranean locality total planimetric development in metres (m).                                                                                                                                              |
| positiveDrop    | Total ascent of the subterranean locality in metres (m).                                                                                                                                                           |
| negativeDrop    | Total descent of the subterranean locality in metres (m).                                                                                                                                                           |
| caveType        | The type of subterranean locality. Categorical variable. Either "artificial" (e.g. mine, mineshafts, military bunkers, railways, subterranean blockhouses, cellars etc.), "ialine" (ialine caves), "ice" (ice caves), "karst" (karst caves, dolines etc.), "other" (other types; e.g. interstitial habitats), "tectonic" (talus caves, cracks, faults etc.), "volcanic" (volcanic caves, lava tubes etc.). |
| caveMorphology  | The general morphology of the subterranean locality (i.e. prevalent morphology along the locality). Categorical variables. ascendent = prevalently an ascending morphology; descendent = prevalently a descending morphology; horizontal = prevalently a horizontal morphology; pit = primarily a vertical pit/abyss. |
caveActive | Binary variable. If the subterranean locality is active (1) or not (0). An active cave is a cave which has a stream flowing in it.
caveTouristic | Binary variable. If the subterranean locality is open to general tourists (1) or not (0).
notes | Additional notes about the subterranean locality.
referencesLocality | References with additional information about the subterranean locality (if any).
referencesSpecies | References with additional information about the spider species reported for the subterranean locality (if any).
contributorName | Name(s) of the person(s) who contributed information about the subterranean locality. Note that, in spelling contributors names, we have omitted accents (e.g. á, è, ò) and special characters (e.g. ä, č, ê) in order to avoid formatting problems.
contributorEmail | E-mail address(es) of the person(s) who contributed information about the subterranean locality.

**Data set name:** Community_composition

**Download URL:** [10.6084/m9.figshare.8224025](10.6084/m9.figshare.8224025)

**Data format:** Tab delimited file (.csv).

**Description:** A dataset with the spider community composition (species presence/absence data) of each subterranean locality included in the CAWEB project.

| Column label       | Column description                                                                                                                                 |
|--------------------|---------------------------------------------------------------------------------------------------------------------------------------------------|
| Family             | The full scientific name of the family in which the taxon is classified.                                                                           |
| Genus              | The full scientific name of the genus in which the taxon is classified.                                                                             |
| Species            | Species epithet of the scientificName.                                                                                                             |
| Author             | The authorship information for the scientificName formatted according to the conventions of the applicable nomenclaturalCode.              |
| specificName       | Genus and species combined together.                                                                                                               |
| taxonRank          | The highest taxonomic rank available (either genus or species).                                                                                   |
| Adaptation         | Habitat preference of the species. Note that accidental species are not included in the dataset – full details in Mammola et al. (2018a). Binary variable. Either troglobiont (1) or troglophile (0). |
| species_lsid       | Unique Life Science Identifier (LSID) for the taxon, based on the World Spider Catalog (doi: 10.24436/2). The LSID allows a user to keep track of taxonomical changes in the status of species or link together datasets regardless of taxonomical changes. |
Alphanumeric codes (CAVE_number) in progressive order

Each column after the first eight columns is labelled with an alphanumeric identifier ("CAVE_", followed by a progressive number; e.g. CAVE_001), referring to the subterranean locality as in the column "ID" of the "Community_composition" dataset. For each Genus_species in the dataset, the presence (1) or absence (0) within the subterranean locality is indicated.

Additional information

The CAWEB dataset comprises data for 475 subterranean localities (Fig. 1) in 27 European countries (Fig. 2). Spider communities refer to different types of caves (karst, talus, volcanic and ialine caves), artifical subterranean sites (mines, blockhouses, cellars etc.), as well as interstitial habitats. However, it is worth noting that the majority of records are from karst caves (Fig. 3), a typical bias in subterranean datasets (Mammola and Leroy 2018, Zagmajster et al. 2010, Niemiller and Zigler 2013, Christman and Culver 2002). These localities open in different types of habitats, with a prevalence of forests and shrublands (Fig. 5).

Figure 1. doi
Distribution of the subterranean localities in Europe included in the CAWEB dataset. Shades of grey represent altitude. Light blue patches are karst rocks, based on the World Map of Carbonate Rock Outcrops (version 3.0).
Figure 2. Number of subterranean localities included in the CAWEB dataset for each European country.

Figure 3. Number of records included in the dataset for each typology of subterranean locality.
Subterranean localities included in the dataset account for over 300 spider species, that is more than half of the subterranean spider diversity in Europe (Mammola et al. 2018a). The number of spider species per cave ranges from 0 to 15 (mean= 4.3, s.d.= 2.35; Fig. 4).

Figure 4. Spider species richness in subterranean localities of the CAWEB dataset. Species richness is expressed as the number of species + morphospecies.

Figure 5. Number of records included in the CAWEB dataset for each typology of habitat at the entrance.
Altogether, these species account for 2,091 unique geo-referenced occurrence records across Europe. While most of the species in the dataset are recorded from one or a few caves, some troglophile species are more widely represented in the dataset (Fig. 6).

Figure 6.
The distribution of the four most abundant species in the CAWEB dataset. Shades of grey represent altitude.

a: Distribution of the troglophile spider *Metellina merianae* (Scopoli, 1763) (Araneae: Tetragnathidae) in Europe, based on 238 occurrences. *Metellina merianae* is a common inhabitant of the twilight zone of caves, although it possesses rather poor adaptations to the subterranean conditions (Hesselberg and Simonsen 2019).

b: Distribution of the troglophile spider *Meta menardi* (Latreille, 1804) (Araneae: Tetragnathidae) in Europe, based on 211 occurrences. *Meta menardi* is probably the most well-known species in the twilight zone of European caves (Hesselberg et al. 2019, Mammola and Isaia 2014), where it often coexists with *Metellina merianae* (Novak et al. 2010).

c: Distribution of the troglophile spider *Tegenaria silvestris* L. Koch, 1872 (Araneae: Agelenidae) in Europe, based on 92 occurrences. This species is a frequent inhabitant of shallow cave sectors (Mammola et al. 2018a).

d: Distribution of the troglophile spider *Porrhomma convexum* (Westring, 1851) (Araneae: Linyphiidae), based on 86 occurrences. This species inhabits caves, mines and other mesic habitats up to the alpine level. It is widely distributed in Europe (Nentwig et al. 2019).

The over-arching goal of the CAWEB project was to assemble a continental dataset with information about the spider community composition of subterranean localities across the European latitudinal range. This dataset also contains local data on geomorphological and habitat features of these localities. Similar high-resolution data are rarely associated with broad-scale datasets used for macroecological analyses. Therefore, the CAWEB dataset can be used to explore a range of biogeographical and macroecological questions, potentially extending beyond arachnology and subterranean biology (see Mammola et al. 2019b for an example).
Acknowledgements

One of the experts who provided data for this data paper, Boyan Petrov (1973–2018), sadly disappeared during the ascension of Mount Shishapangma (8,027 m a.s.l.) in the Himalaya. We are thankful to Jeremy Miller for his wise editorial guidance and to Gustavo Hormiga, Stano Pekar, Darrell Ubick and Cor Vink for useful suggestions for improvements.

Author contributions

SM wrote the first draft of the paper. PC supervised data submission. MI coordinated the network of experts who provided data to compile the dataset. AM and LK provided data from Slovakia. CD, MN, and SC provided data from Albania, Bulgaria, Greece and Serbia. CK provided data from Austria. TB and SZ provided data from Germany. DA, LD and GB provided data from Hungary. CEP, CR and JF provided data from Spain. FG provided data from Slovenia. KBK and ME provided data from Turkey. MK and MP provided data from North Macedonia and Montenegro. MI and SM provided data from Italy. MP provided data from Croatia and Bosnia and Herzegovina. OTM provided data from Romania. PC provided data from Finland and Portugal. RR provided data from Poland. RSV provided data from Ukraine. VR provided data from the Czech Republic.

References

• Arnedo M, Oromí P, Múrria C, Macías-Hernández N, Ribera C (2007) The dark side of an island radiation: systematics and evolution of troglobitic spiders of the genus Dysdera Latreille (Araneae: Dysderidae) in the Canary Islands. Invertebrate Systematics 21 (6): 623-660. https://doi.org/10.1071/is07015
• Cardoso P, Scharff N (2009) First record of the spider family Symphytognathidae in Europe and description of Anapistula ataecina sp. n. (Araneae). Zootaxa 2246: 45-45.
• Cardoso P (2012) Diversity and community assembly patterns of epigean vs. troglobiont spiders in the Iberian Peninsula. International Journal of Speleology 41 (1): 83-94. https://doi.org/10.5038/1827-806x.41.1.9
• Chiavazzo E, Isaia M, Mammola S, Lepore E, Ventola L, Asinari P, Pugno NM (2015) Cave spiders choose optimal environmental factors with respect to the generated entropy when laying their cocoon. Scientific Reports 5 (1): 7611. https://doi.org/10.1038/srep07611
• Christman M, Culver D (2002) The relationship between cave biodiversity and available habitat. Journal of Biogeography 28 (3): 367-380. https://doi.org/10.1046/j.1365-2699.2001.00549.x
• Culver DC, Trontelj P, Zagmajster M, Pipan T (2013) Paving the way for standardized and comparable subterranean biodiversity studies. Subterranean Biology 10: 43-50. https://doi.org/10.3897/subtbiol.10.4759
• Deharveng L, Bedos A (2019) Diversity of terrestrial invertebrates in subterranean habitats. Cave Ecology 107-172. https://doi.org/10.1007/978-3-319-98852-8_7
- Doran NE, Richardson AMM, Swain R (2001) The reproductive behaviour of the Tasmanian cave spider *Hickmania troglodytes* (Araneae: Austrochilidae). Journal of Zoology 253 (3): 405-418. [https://doi.org/10.1017/s0952836901000371](https://doi.org/10.1017/s0952836901000371)
- Doran NE, Richardson AMM, Swain R (2017) The biology of *Hickmania troglodytes*, the Tasmanian cave spider. The Other 99%: The Conservation and Biodiversity of Invertebrates 330-332. [https://doi.org/10.7882/rzsnsw.1999.062](https://doi.org/10.7882/rzsnsw.1999.062)
- Hadley NF, Ahearn GA, Howarth FG (1981) Water and metabolic relations of cave-adapted and epigean lycosid spiders in Hawaii. Journal of Arachnology 9: 215-222.
- Hedin M (2015) High-stakes species delimitation in eyeless cave spiders (*Cicurina*, Dictynidae, Araneae) from central Texas. Molecular Ecology 24 (2): 346-361. [https://doi.org/10.1111/mec.13036](https://doi.org/10.1111/mec.13036)
- Hesselberg T, Simonsen D (2019) A comparison of morphology and web geometry between hypogean and epigean species of *Metellina* orb spiders (family Tetragnathidae). Subterranean Biology 31: 53-65. [https://doi.org/10.3897/subtbiol.31.36222](https://doi.org/10.3897/subtbiol.31.36222)
- Hesselberg T, Simonsen D, Juan C (2019) Do cave orb spiders show unique behavioural adaptations to subterranean life? A review of the evidence. Behaviour 156 (10): 969-996. [https://doi.org/10.1163/1568539x-00003564](https://doi.org/10.1163/1568539x-00003564)
- Huber B (2018) Cave-dwelling pholcid spiders (Araneae, Pholcidae): a review. Subterranean Biology 26: 1-18. [https://doi.org/10.3897/subtbiol.26.26430](https://doi.org/10.3897/subtbiol.26.26430)
- Lepore E, Marchioro A, Isaia M, Buehler M, Pugno N (2012) Evidence of the most stretchable egg sac silk stalk, of the European Spider of the Year *Meta menardi*. PLoS One 7 (2): e30500. [https://doi.org/10.1371/journal.pone.0030500](https://doi.org/10.1371/journal.pone.0030500)
- Lipovšek S, Leitinger G, Novak T, Janžekovič F, Gorgoš S, Kamińska K, Rost-Roszkowska M (2017) Changes in the midgut cells in the European cave spider, *Meta menardi*, during starvation in spring and autumn. Histochemistry and Cell Biology 149 (3): 245-260. [https://doi.org/10.1007/s00418-017-1623-z](https://doi.org/10.1007/s00418-017-1623-z)
- Lipovšek S, Novak T, Janžekovič F, Brdelak N, Leitinger G (2018) Changes in the midgut diverticula epithelial cells of the European cave spider, *Meta menardi*, under controlled winter starvation. Scientific Reports 8 (1): 13645. [https://doi.org/10.1038/s41598-018-31907-3](https://doi.org/10.1038/s41598-018-31907-3)
- Lunghi E (2018) Ecology and life history of *Meta bourneti* (Araneae: Tetragnathidae) from Monte Albo (Sardinia, Italy). PeerJ 6: e6049. [https://doi.org/10.7717/peerj.6049](https://doi.org/10.7717/peerj.6049)
- Mammola S, Isaia M (2014) Niche differentiation in *Meta bourneti* and *M. menardi* (Araneae, Tetragnathidae) with notes on the life history. International Journal of Speleology 43 (3): 343-353. [https://doi.org/10.5038/1827-806x.43.3.11](https://doi.org/10.5038/1827-806x.43.3.11)
- Mammola S, Piano E, Isaia M (2016) Step back! Niche dynamics in cave-dwelling predators. Acta Oecologica 75: 35-42. [https://doi.org/10.1016/j.actao.2016.06.011](https://doi.org/10.1016/j.actao.2016.06.011)
- Mammola S, Isaia M (2017) Spiders in caves. Proceedings of the Royal Society B: Biological Sciences 284 (1853): 20170193. [https://doi.org/10.1098/rspb.2017.0193](https://doi.org/10.1098/rspb.2017.0193)
- Mammola S, Gasparo F, Komnenov M, Růžička V, Déjean S, Danflous S, Brustel H, Vargovitsch RS, Rozwalka R, Moldovan OT, Pavlek M, Deltshav C, Petrov B, Naumova M, Ćurčić S, Mock A, Kováč L, Cardoso P, Dányi L, Angyal D, Balázs G, Ribera C, Prieto CE, Fernández J, Komposch C, Carter J, Isaia M (2017) Spiders in caves: the CAWEB project. In: Goodacre SL (Ed.) Abstract book of the 30th European Congress of Arachnology. 30th European Congress of Arachnology, ECA 2017, University of Nottingham – UK, 20–25 August 2017. Nottingham, 163 pp.
Mammola S, Leroy B (2018) Applying species distribution models to caves and other subterranean habitats. Ecography 41 (7): 1194-1208. https://doi.org/10.1111/ecog.03464

Mammola S, Cardoso P, Ribera C, Pavlek M, Isaia M (2018) A synthesis on cave-dwelling spiders in Europe. Journal of Zoological Systematics and Evolutionary Research 56 (3): 301-316. https://doi.org/10.1111/jzs.12201

Mammola S (2019) Finding answers in the dark: caves as models in ecology fifty years after Poulsón and White. Ecography 42 (7): 1331-1351. https://doi.org/10.1111/ecog.03464

Mammola S, Cardoso P (2019) cave_dwelling_spiders_europe. Biodiversity Data Journal. Occurrence dataset accessed via GBIF.org on 2019-10-08. https://doi.org/10.15468/ygocko

Mammola S, Piano E, Malard F, Vernon P, Isaia M (2019a) Extending Janzen's hypothesis to temperate regions: a test using subterranean ecosystems. Functional Ecology 33 (9): 1638-1650. https://doi.org/10.1111/1365-2435.13382

Mammola S, Cardoso P, Angyal D, Balázs G, Blick T, Brustel H, Carter J, Ćurčić S, Danflous S, Dányi L, Déjean S, Deltshev C, Elverici M, Fernández J, Gasparo F, Komnenov M, Komposch C, Kovčič L, Kunt KB, Mock A, Moldovan O, Naumova M, Pavlek M, Prieto CE, Ribera C, Rozwalka R, Růžička V, Vargovitsh RS, Zaenker S, Isaia M (2019b) Local versus broad scale environmental drivers of continental beta diversity patterns in subterranean spider communities across Europe. Proceeding of the Royal Society B: Biological Sciences In press.

Michalík P, Ramírez M, Wirkner C, Lipke E (2014) Morphological evidence for limited sperm production in the enigmatic Tasmanian cave spider Hickmania troglodytes (Austrochilidae, Araneae). Invertebrate Biology 133 (2): 180-187. https://doi.org/10.1111/ivb.12046

Miller J (2005) Cave adaptation in the spider genus Anthrobia (Araneae, Linyphiidae, Erigoninae). Zoologica Scripta 34 (6): 565-592. https://doi.org/10.1111/j.1463-6409.2005.00206.x

Nentwig W, Blick T, Gloor D, Hänggi A, Kropf C (2019) Araneae Version 09.2019. https://www.araneae.nmbe.ch. Accessed on: 2019-7-02.

Niemiller M, Zigler K (2013) Patterns of cave biodiversity and endemism in the Appalachians and interior plateau of Tennessee, USA. PLoS One 8 (5): e64177. https://doi.org/10.1371/journal.pone.0064177

Novak T, Tkavc T, Kuntner M, Arnett A, Delakorda SL, Perc M, Janžekovič F (2010) Niche partitioning in orbweaving spiders Meta menardi and Metellina meriana (Tetragnathidae). Acta Oecologica 36 (6): 522-529. https://doi.org/10.1016/j.actao.2010.07.005

Piorkowski D, Blamires SJ, Doran NE, Liao CP, Wu CL, Tso IM (2017) Ontogenetic shift toward stronger, tougher silk of a web-building, cave-dwelling spider. Journal of Zoology 304 (2): 81-89. https://doi.org/10.1111/jzo.12507

Růžička V, Šmilauer P, Mlejnek R (2013) Colonization of subterranean habitats by spiders in Central Europe. International Journal of Speleology 42 (2): 133-140. https://doi.org/10.5038/1827-806x.42.2.5

Yancey ME, Mann N, Milne M, Zigler K (2018) Egg sacs of Liocranoides Keyserling, 1881 (Araneae: Zoropsidae) cave spiders. Journal of Arachnology 46 (3): 553-555. https://doi.org/10.1636/joa-s-17-074.1

Yao Z, Dong T, Zheng G, Fu J, Li S (2016) High endemism at cave entrances: a case study of spiders of the genus Uthina. Scientific Reports 6 (1): 35757. https://doi.org/10.1038/srep35757
• Zagmajster M, Culver DC, Christman MC, Sket B (2010) Evaluating the sampling bias in pattern of subterranean species richness: combining approaches. Biodiversity and Conservation 19: 3035-3048. https://doi.org/10.1007/s10531-010-9873-2

• Zhang Y, Li S (2013) Ancient lineage, young troglobites: recent colonization of caves by *Nesticella* spiders. BMC Evolutionary Biology 13 (1): 183. https://doi.org/10.1186/1471-2148-13-183