SOIL ORGANISMS **92** (3) · December 2020 pp. 161–188

Towards a global synthesis of Collembola knowledge – challenges and potential solutions

Anton Potapov[1,2]*, Bruno C. Bellini[3], Steven L. Chown[4], Louis Deharveng[5], Frans Janssens[6], Ľubomír Kováč[7], Natalia Kuznetsova[8], Jean-François Ponge[9], Mikhail Potapov[8], Pascal Querner[10], David Russell[11], Xin Sun[12], Feng Zhang[13], Matty P. Berg[14,15]

[1] A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninsky prospekt 33, 119071 Moscow, Russia
[2] J.F. Blumenbach Institute of Zoology and Anthropology, University of Göttingen, Untere Karspuele 2, 37073 Göttingen, Germany
[3] Department of Botany and Zoology, Biosciences Center, Federal University of Rio Grande do Norte, Natal, Brazil
[4] Securing Antarctica's Environmental Future, School of Biological Sciences, Monash University, Victoria 3800, Australia
[5] Institut de Systématique, Évolution, Biodiversité (ISYEB), UMR7205, CNRS, Muséum national d'Histoire naturelle, Sorbonne Université, EPHE, 45 rue Buffon, 75005 Paris, France
[6] Department of Biology, University of Antwerp, Prinsstraat 13, 2000 Antwerpen, Belgium
[7] Institute of Biology and Ecology, Faculty of Science, P.J. Šafárik University, Šrobárova 2, 041 54 Košice, Slovakia
[8] Moscow State Pedagogical University, Institute of Biology and Chemistry, Kibalchicha str. 6k3 129164 Moscow, Russia
[9] Muséum National d'Histoire Naturelle, CNRS UMR 7179, 4 avenue du Petit-Château, 91800 Brunoy, France
[10] University of Natural Resources and Life Sciences, Department of Integrated Biology and Biodiversity Research, Institute of Zoology, Gregor-Mendel-Straße 33, A-1180 Vienna, Austria
[11] Senckenberg Museum of Natural History, Soil Zoology Division, Postfach 300 154, 02806 Görlitz, Germany
[12] Key Laboratory of Urban Environment and Health, Institute of Urban Environment, Chinese Academy of Sciences, Xiamen 361021, China.
[13] Department of Entomology, College of Plant Protection, Nanjing Agricultural University, Nanjing 210095 China
[14] Vrije Universiteit Amsterdam, Department of Ecological Science, De Boelelaan 1085, 1081 HV, Amsterdam, The Netherlands
[15] Groningen University, Conservation and Community Ecology Group, Nijenborgh 7, 9747 AG, Groningen, The Netherlands
* Corresponding author: potapov.msu@gmail.com

Received 15 October 2020 | **Accepted** 22 November 2020
Published online at www.soil-organisms.de 1 December 2020 | **Printed version** 15 December 2020
DOI 10.25674/so92iss3pp161

Abstract

Collembola are among the most abundant and diverse soil microarthropods, which are found in almost all (semi)terrestrial environments and often serve as model organisms in empirical studies. Diverse data collected on the biology and ecology of Collembola over the last century are waiting for synthesis studies, while developing technologies may facilitate generation of new knowledge. Collembola research in 2020 is entering the stage of global synthesis and in this opinion paper we address the main challenges that the community of collembologists is facing on this avenue. We first discuss the present status and social context of Collembola taxonomy and the potential use of novel technologies to describe new species. We then focus on aspects of community ecology, reviewing the processes of dispersal, environmental and biotic filtering, from the spatial scale of microhabitat to the globe. We also discuss the involvement of Collembola in ecosystem processes and which proxies, such as functional traits, can be used to predict the functional roles of species. Finally, we provide recommendations on how we can improve community data collection by using standard methods and better data handling practices. We call for (1) integrating morphological descriptions with high-resolution photographs and genetic barcodes for species descriptions and developing of user friendly software and machine learning approaches to facilitate deposition of structured taxonomic knowledge on web platforms; (2) multiscale studies on biodiversity distribution and community processes, especially including dispersal mechanisms; (3) recording and sharing functional, not only morphological, trait data in controlled experiments and field surveys; (4) knowledge

ISSN 1864-6417 (print) · **ISSN** 2509-9523 (online)

synthesis and meta-analysis studies on the topics of ecosystem roles of Collembola, conservation of its diversity, feeding behaviour, protection mechanisms and dispersal of different Collembola species, and effects of land use and climate change on collembolan communities; (5) joint efforts in covering the gaps in Collembola knowledge, especially in underexplored regions (predominantly tropics and subtropics) using standard methodologies; (6) data sharing and its integration in open structured databases. We believe that Collembola studies could make use of new technologies and ongoing changes in society. To facilitate the progress across these research topics by 2040, we have established #GlobalCollembola, a distributed-effort community-driven initiative that aims to provide open and global data on Collembola taxonomic and genetic diversity, abundance, traits and literature and to coordinate global efforts in covering the key knowledge gaps.

Keywords springtails | taxonomy | macroecology | functional traits | #GlobalCollembola

1. General introduction

Collembola, or springtails, are among the most abundant and diverse soil microarthropods. With a true global distribution, these animals are found from the high Arctic to Antarctica, on mountain tops over 5000 m high and in caves as deep as 1760 m. They typically live in soils of forests, meadows, arable fields, (salt) marshes, tundra and deserts, but also in tree canopies, on buildings in cities and some even on the surface of standing water. Springtails graze on litter, fungi, pollen, algae, leaves and roots; they produce faeces that are important in soil formation; they disperse propagules of microorganisms and plants; they interact with other soil fauna, and are food for many soil predators (Hopkin 1997, Rusek 1998). As such they play a central role in soils and soil food webs.

Collembola are an ancient group of animals. The first records date back to over 400 MY (Whalley & Jarzembowski 1981). The history of Collembola research is much younger and goes back to Christian Frommann, who in 1684 published an observation of a group of jumping ‘insects’ on snow, and to Carl de Geer, when he described the first four species of ‘Podurae’ in 1740 (http://www.collembola.org/publicat/unavaila.htm).

Since then nearly 9000 species of Collembola have been described to date (Bellinger et al. 1996-2020), which likely represents not more than 20 % of the expected existing species (see discussion below). With the current rate of taxonomic descriptions, documenting most of the diversity of Collembola seems hardly feasible within the next decades. On the other hand, technological advances and developing social interactions (e.g. social media, citizen science) may allow us to streamline the taxonomic work across the globe and more closely link it to ecological and evolutionary studies, if applied correctly.

Many species have yet to be described, but even more remains to be learned about their biology and ecology. Environmental factors alone have only limited explanatory power when predicting Collembola abundance and community composition (Saraeva et al. 2015, Widenfalk et al. 2016), while biotic interactions and dispersal are difficult to study in the opaque soil environment. Moreover, these factors interact on different spatial and temporal scales (Berg 2012, Heiniger et al. 2014). The small size of most species further complicates ecological studies. Recent experiments and proliferation of genetic and other molecular approaches allowed us to open this black box and advance our understanding of the assembly and functioning of Collembola communities (Auclerc et al. 2009, Chauvat et al. 2014, Chen et al. 2017, Potapov et al. 2016, Zhang et al. 2019). Functional trait approaches, rapidly developing in invertebrate ecology, offer much promise to provide a mechanistic understanding of species occurrences and their ecosystem roles (Krab et al. 2010, Vandewalle et al. 2010, Makkonen et al. 2011, Bokhorst et al. 2012, Salmon & Ponge 2012, Dooremalen et al. 2012, Joimel et al. 2017), but the question remains – which key traits should we measure to understand assembly and functioning of Collembola diversity from a microhabitat to a global scale?

Most of the Collembola expertise, both taxonomically as well as ecologically is concentrated in Europe, and the Palaearctic is by far the most well studied biogeographic realm globally for this group of soil fauna. The gap in our knowledge on other zoogeographic regions is likely to bias our perception of the macroecology and evolution of Collembola. Moreover, data on community composition that have already been collected varies greatly according to collection methods, identification quality and are often not available in a structured format. It is clear that we need to agree on better practices of data collection and sharing in the future (White et al. 2020) if we wish to understand the distribution of Collembola on Earth and its fate under global change.

Here we reflect on how we can improve our science using past experience, new methods and knowledge we have at our disposal, as well as on where we would like to see Collembola research in 2040. This opinion paper brings together perspectives from classical taxonomists, molecular biologists, community and ecosystem ecologists, and addresses some of the key challenges that Collembola research faces. We build our reflection around four general problems: (1) To obtain a full understanding of springtail diversity, how can we enhance the rate of species descriptions? (2) Which key processes determine Collembola diversity across a hierarchy of spatial scales? (3) How significant is the contribution of Collembola to ecosystem functioning? (4) How to improve data collection and data sharing to efficiently cover the major gaps in the global knowledge on Collembola? These questions are put in context and addressed in the following sections.

2. Integrative taxonomy to facilitate species description

The central objective of taxonomy is to name, describe and order taxa, providing base data essential for ecology, biogeography, evolutionary biology, conservation biology and other biological disciplines. About two centuries of taxonomic work have resulted in the documentation of nearly 9000 species of springtails (Fig. 1A). The most complete global checklist of springtails is available now at http://collembola.org (Bellinger et al. 1996-2020), while a comprehensive checklist of European springtail species was compiled in the framework of Fauna Europaea (de Jong et al. 2014).

The approximately 9000 described species to date are believed to be a small fraction of the total number of springtail species on earth. A rough total of at least 50,000 existing species was expected by Hopkin (1998). This number is remarkably close to the extrapolation of the number of molecular 'species' (as compared to morphological species) from Canada to global scale, which resulted in the estimation of ca. 65,000 species (Porco et al. 2014, Turnbull & Stebaeva 2019). However, these are very rough calculations based on limited evidence. After exploring genetic diversity of *Lepidocyrtus*-species in Panama, Cicconardi et al. (2013) advanced the number of 500,000 species of Collembola on Earth. However, in the absence of any ecological or biological character differentiating molecular lineages, assigning them to species is at best premature. This discussion reflects that we still need to understand a lot about the factors driving genetic variability and speciation in Collembola (Porco et al. 2014).

Our knowledge on springtail diversity is unevenly distributed across the world, which also affects the estimation of global species numbers. Traditionally, a high number of Collembola studies has been conducted in Europe, and to a lesser extent in North America and Asia. This may explain the high number of described species in these zoogeographic regions. The documentation of the Palaearctic fauna, consequently, is much more complete than that of other regions (Fig. 1B), with a number of synopses on taxonomic groups of springtails published (Bretfeld 1999, Dunger & Schlitt 2011, Jordana 2012, Potapov 2001, Thibaud et al. 2004) or in preparation. The taxonomic impediment is especially evident in tropical regions, where only few taxonomical studies take place, but where most of the undescribed species are probably to be found. For instance, about 50 % or more of unknown species is commonly observed in the fauna surveys coming from Africa (Thibaud 2013), southeast Asia (Shveenkova 2011) and Latin America (Culik & Filho 2003, Ferreira et al. 2018). It is primarily understudied taxa and understudied regions that control the speed of species description. Description rate remained stable over the last 70 years (about 100-120 new species described annually; Fig. 1C) and has relied on a limited number of productive taxonomists (Fig. 1D), only few of which are still active. Thus, Collembola taxonomists would need at least another 400-500 years to cover the estimated unknown global diversity of this group. It can be anticipated that in this time frame many species will go extinct due to environmental change before being described. The question arises – how can we facilitate the description of the remaining majority of unknown Collembola, especially in the regions where our knowledge is poor?

2.1 Integration of the novel tools in traditional taxonomy

Traditional taxonomic methods have been the main approach to delimit taxa and describe species based on specific morphological characters. This is a very time-consuming task that requires well-skilled experts. The development of Collembola taxonomy in the foreseeable future has to be considered in a global scientific context, which is marked on the one hand by the dissemination of molecular approaches and high-resolution imaging in taxonomic work, developing of machine learning, and on the other hand by the fast development of associated scientific activities (conservation, citizen science, ecosystem management), which rely largely on more simplified taxonomic approaches. This poses methodological challenges, since most of Collembola are minute and fragile animals. with complex morphological features, yielding little DNA, and requiring expensive devices to be imaged.

The main morphological feature used for precise delineation of collembolan species is chaetotaxy, which is the comparative study of the number, shape and arrangement of body chaetae. Many complex systems aim at labelling and comparing the body and appendages chaetae of different groups of Collembola (e.g. Betsch & Waller 1994, Cassagnau 1974, Deharveng 1983, Fjellberg 1999, Jordana & Baquero-Martin 2005, Potapov 2001, Szeptycki 1979, Yosii 1960) It is possible to track the homologies of such structures among different instars, species, genera, families and to some extent even orders. However, understanding of chaetotaxic patterns and application of chaetotaxy to describe species requires years of training. The challenge here is not only to attract and train students in this field, but also to provide them job perspectives and academic recognition, with proper funding and commitment to biological collections (de Carvalho et al. 2005, Ebach et al. 2011). Even so, the boundary between species is sometimes difficult to define by morphological features, for instance when available morphological characters are limited or vary within species (Sun et al. 2017). Especially in such cases, molecular tools come at hand.

In recent years combining evidence from morphology and DNA sequencing has been promoted as a more integrative approach to resolve species delineation (DeSalle et al. 2005, Schlick-Steiner et al. 2010, Sun et al. 2017). The replacement of traditional taxonomy by DNA ‘barcoding’, of the mitochondrial gene cytochrome c oxidase I (COI) gene or another genetic markers, has often been presented as an ineluctable evolution. Indeed, a 658-base fragment of COI has proven to be effective in species boundary determination and is used to calculate inter- or intra-specific genetic distances (Hebert et al. 2003). Many COI sequences are openly available from the Barcode of Life (BOLD) platform that provides

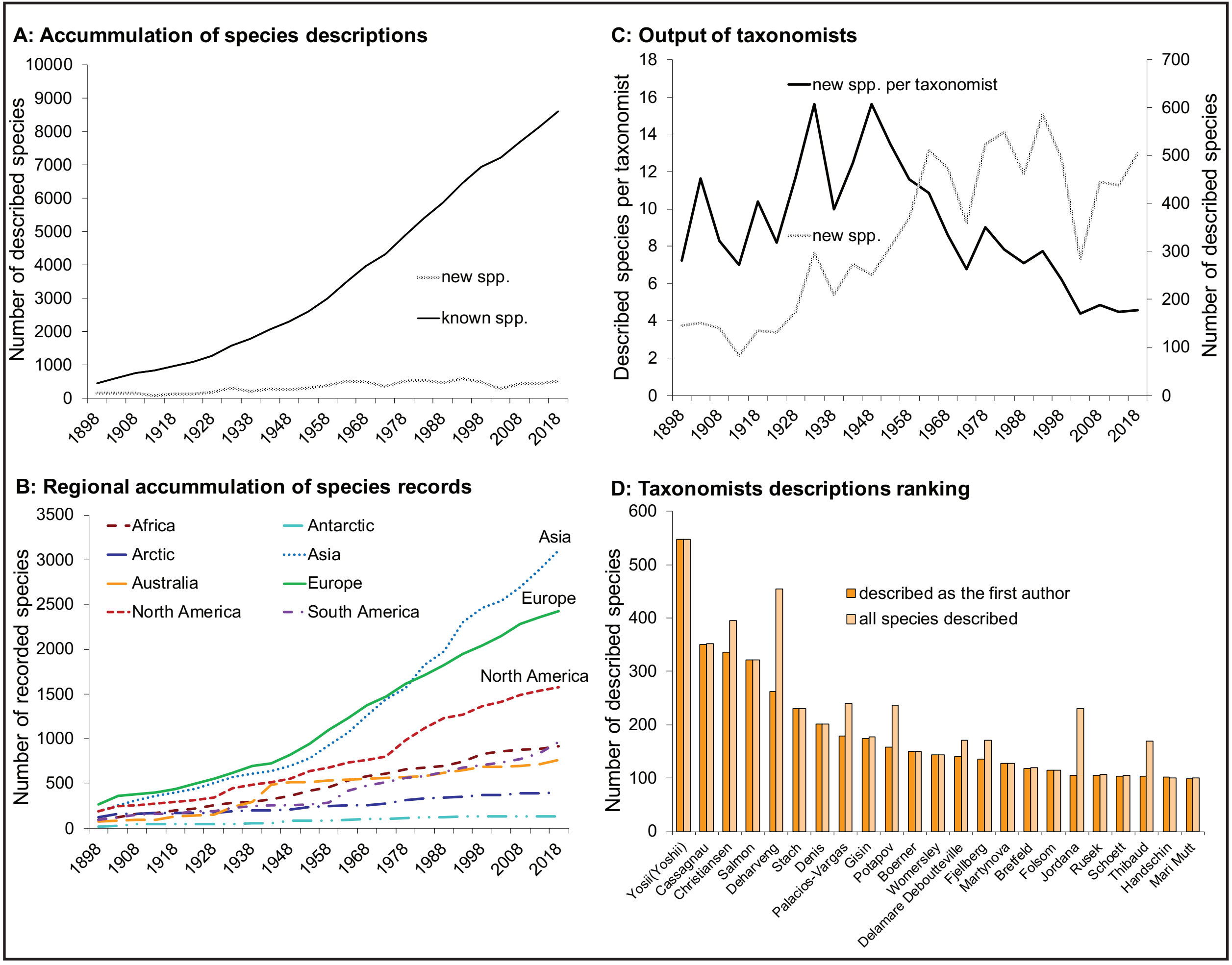

Figure 1. Trends in Collembola taxonomy. New species description accumulated up till the 1960’s but stays linear afterwards (**A**); Most of species were recorded from Asia, Europe and North America (**B**); While the rate of species description stays unchanged for the last 70 years, the number of described taxa per taxonomist (first authorship) declines (**C**); The number of species described is driven by a low number of productive taxonomists, with the first 23 highly productive taxonomists (5.6% of all first authors of species descriptions) being responsible for ca. 50% of total known Collembola species (**D**). All estimations for the panels A, B and C were calculated in 5-year intervals. For the panel D only persons listed in the authorship of the species were included in the analysis. The figure is produced based on the data from September, 2020 available from http://collembola.org (Bellinger et al. 1996-2020).

education, hosting, identification and analysis services for COI data (https://www.boldsystems.org/). At present, COI is the most recorded fragment of the Collembola genome with over 150,000 sequences representing ca. 6000 BINs (molecular taxonomic units) publicly available on the BOLD data portal. Among other sequences, the most data are available for 28S rRNA (ca. 3500 sequences of 660 taxonomic units) and 18S rRNA (ca. 1000 springtails of 450 taxonomic units), with 16 whole genomes reported on the NCBI (https://www.ncbi.nlm.nih.gov/nucleotide/). DNA barcoding, in association with morphology, has been applied to delimit species in a number of Collembola genera, including among others *Deutonura* (Porco et al. 2010), *Entomobrya* (Katz et al. 2015), *Heteromurus* (Lukić et al. 2015), *Homidia* (Pan 2015), *Lepidocyrtus* (Soto-Adames 2002), *Protaphorura* (Sun et al. 2017), and *Dicranocentrus* (Zhang et al. 2018). However, in many cases, COI has also confirmed the power of morphological characters. For example, Yoshii's colour pattern species concept was validated in the study of 17 species of the genera *Lepidocyrtus* and *Pseudosinella* in Puerto Rico (Soto-Adames 2002). Parapseudocelli, a long-neglected structure in Onychiuridae, is proven to be of great taxonomic value in species discrimination based on results from 17 populations of the genus *Protaphorura* in northeast China (Sun et al. 2017). The use of COI to describe new species is not without problems as well. Reported values of divergence in COI sequences between congeneric species of Collembola commonly range between 16 and 25 %, but striking exceptions exist (Sun et al. 2018). Due to a high geographical variation observed in COI in Collembola, 28S rRNA and 18S rRNA, or gene combinations are more commonly used to reconstruct Collembola phylogeny (Schneider et al. 2011, Xiong et al. 2008, Zhang et al. 2014). Considering that the data on these fragments are much more limited than that on COI, one of the important missions in the next decades is to expand 28S rRNA, 18S rRNA and other reference libraries.

The strength of molecular taxonomy as a single method to describe species is, however, cast into doubt, due to numerous cases of high genetic variation among populations of the same morphological species of Collembola (Porco et al. 2012, Zhang et al. 2018). Matches between species and barcodes need to be drawn from large reference libraries that would include morphologically-described species and their corresponding barcodes. Such libraries do not exist for Collembola, except for some regions. Barcodes will also not provide information on morphological, anatomical, physiological and biological traits, leaving large room for traditional approaches and image analysis to solve ecological problems. Therefore, morphological approaches cannot be replaced by molecular methods, and vice versa, but both are the ingredients of integrative taxonomy. Molecular approaches can help to discover new valuable morphological characters and look for evidence of integrated taxonomy from more aspects (such as geography, biology, physiology, etc.), resulting in increased accuracy of species classification and deeper understanding of biological diversity and its evolution. High quality reference libraries, linking DNA and morphology are also the necessary basis for metabarcoding biodiversity assessments (Liu et al. 2019, Oliverio et al. 2018).

Given that an image says more than a thousand words, 'pictorial descriptions' are one of the promising directions to describe Collembola species. Imagery techniques are developing at a fast pace, with a positive impact on taxonomic work, which is likely to increase in the future. More high-quality photos are becoming available and published on websites. Relying on reference libraries, image analysis technology can be applied for trait extraction and Collembola specimen recognition, orienting on the progress achieved in other groups of organisms (e.g. self-learning applications https://www.inaturalist.org/ or 'Obsidenitify'). The technology is particularly suitable for epigaeic Collembola with patterned coloration, making it possible to identify living specimens of Collembola in the near future. This will promote qualitative field research, including that based on citizen science. However, the approach can also facilitate quantitative ecological studies, if a large reference library of ethanol-based Collembola pictures is compiled. The approach is not new (e.g. Janssens & Dazzo 2004), but has much more potential with new technological advances in photography and machine learning. For instance, image analysis of community photographs could serve as a tool for rapid assessment of community-level, or individual, morphological diversity. There is an important role for classical skilled Collembola taxonomists to make sure the pictorial libraries are of high quality. Developing of these approaches can build bridges between taxonomy and ecology, two disciplines were developing partly independent over last decades.

The technological development of genetic, imaging and machine learning tools is fast and now within reach of many laboratories and this trend will magnify in the future (Riedel et al. 2013, Ströbel et al. 2018). Integrative taxonomy needs to make use of these developing technologies. Traditional textual descriptions need to be supplemented with machine-readable information such as high-resolution pictures and genetic sequences (e.g. COI; Fig. 2). Progress in usage of taxonomic knowledge in ecology and related disciplines will be possible only if communication of taxonomic knowledge in the form of peer-reviewed publications is complemented with openly accessible online resources, where pictures, taxonomic descriptions, morphological characters, drawings and sequences can be searched for across studies (Fig. 2).

It would be misleading to advertise the use of new technologies as a tool that can help immediately facilitate the speed of species descriptions, since establishing and using such technologies require time, money and skills. And this mission should not be suggested only for taxonomists to pursue, but rather considered as a community challenge. To make this realistic and really improve the description rate, efficient digital tools need to be developed to communicate taxonomic descriptions in a structured format without creating additional work for taxonomists, but rather saving their time. Those could include user-friendly writing assistants for taxonomic descriptions that will make them machine-readable (some basic prototypes exist, e.g https://www.morphdbase.de/; Meid et al. 2017); naming assistants which will test new names; structured databases which will allow search and summarisation of taxonomic diagnoses and traits across taxa (http://plazi.org/, https://portail.betsi.cnrs.fr/, http://ecotaxonomy.org); publishing tools which will automatically deliver pictures, traits and diagnoses to such databases; machine learning tools that will create differential diagnoses and identification keys and other. All tools should be made openly available for any researcher, especially those in developing countries. Something can be done already by each taxonomist – we encourage to send all new species descriptions to Frans Janssens, who is voluntarily supporting the global checklist https://www.collembola.org. The checklist will be included in the next release of the Catalogue of Life (https://www.catalogueoflife.org) and will serve as a basis for global resources such as https://gbif.org. Long-term maintenance of a global checklist can only be done jointly and will be beneficial for researchers both within and outside the collembologist community.

2.2 The public face of taxonomy

The development of taxonomy as a discipline depends largely on funding and recruitment. Traditional Collembola taxonomists will still exist in 2040, a situation not so different from that described 16 years ago by Deharveng (2004). Zoological museums must maintain expertise in traditional morphological taxonomy and develop further modern approaches, but they have limited recruitment capabilities. 'Pure' taxonomy is often not recognized by authorities as a legitimate research field, resulting in under-funding. Thus, for future 'taxonomists' a 'double formation' in taxonomy in combination with another research field (e.g. ecology, evolution, conservation biology) might be necessary. It may provide better job perspectives and this has to be considered while training young specialists.

A promising socio-economic aspect of taxonomy development could be the building of taxonomic expertise

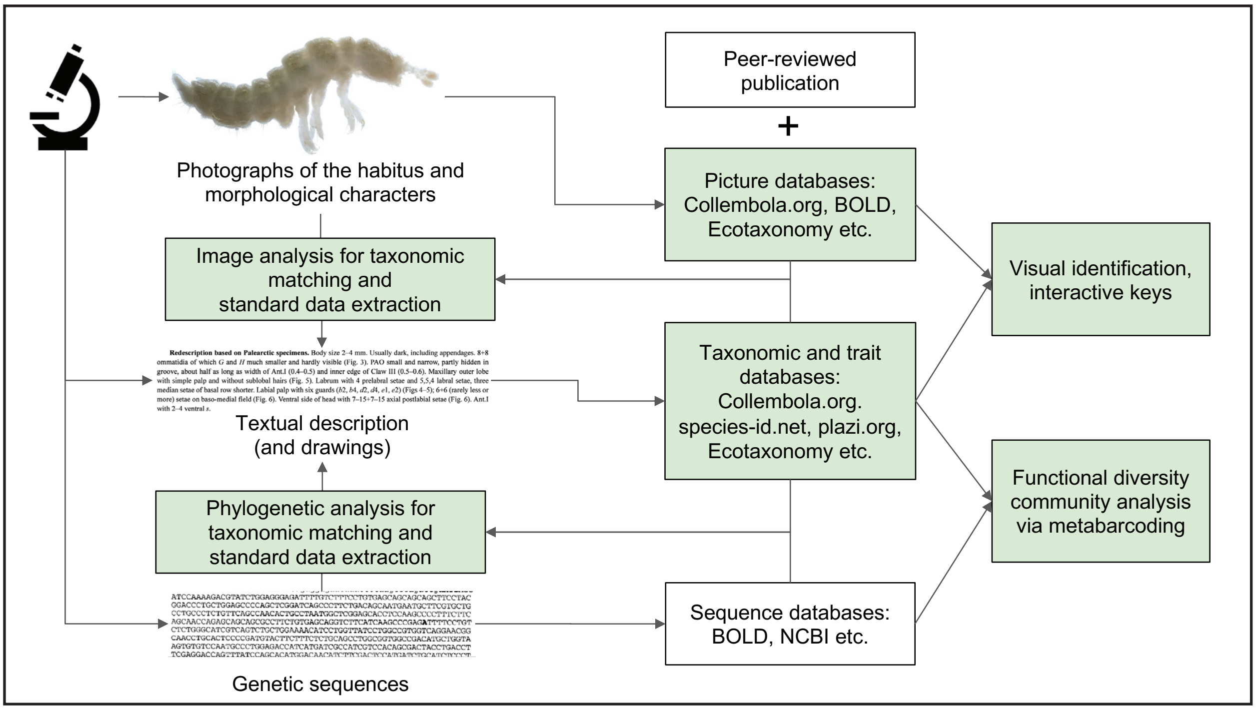

Figure 2. Communication of taxonomic knowledge on Collembola should include open online databases. Large image and genetic collections will allow semi-automated processes of species description and identification to be established. Green shaded boxes list components that need to be included in future common practices.

in developing tropical countries, where the majority of undescribed biodiversity is present. Considering the existing inequality in incomes between the developing and developed countries, well-organised allocation of funding on an international basis (several international programs exist already and could be expanded) and systematic taxonomic training have the potential to considerably increase the number of taxonomists in regions with poorly described fauna. Such taxonomists need to be supported with open knowledge, checklists, literature, and digital tools.

Published species descriptions and revisions are scattered across a huge number of rather low impact, small journals. Reorganizing taxonomic publications in journals with a wider audience is on course and has been relatively successful now for two decades. This has taken place largely outside the large publishing companies, contrary to journals of most other scientific fields, making it a praiseworthy achievement (e.g. Zootaxa https://www.mapress.com/j/zt/, ZooKeys https://zookeys.pensoft.net, Zoosystema http://sciencepress.mnhn.fr/en/periodiques/zoosystema). Development of taxonomic press in the coming years will depend on the number of active taxonomists, hence on recruitment and funding. Recruitment and funding, in turn, will depend on recognition of taxonomy as the base of other biological disciplines which can be facilitated by developing e.g. appropriate impact metrics for taxonomic literature (Zeppelini et al. 2020).

Some large international programmes on biodiversity during the last two decades were for a large part designed around taxonomic expertise and approaches: Fauna Europaea https://fauna-eu.org/, EDIT (https://cordis.europa.eu/project/id/18340/fr), AFBA (https://antarcticbiogeography.org/the-afba-project/) among others. Such opportunities are likely to emerge again, bringing substantial funding. However, most of the funds allocated to large biodiversity programmes go to molecular and ecological oriented laboratories. Developing technologies and demand for ecological monitoring and conservation allow a branch of efficient commercial ‘taxonomic services’ to be further developed. Such services could be integrated in routine ecological surveys, conservation surveys (especially in the realm of government-run monitoring or biodiversity survey programmes) and molecular-oriented projects, providing services of species description and/or identification and thus concentrating the power of molecular methodologies and expert taxonomists. These services must naturally be paid for by the projects or programmes across various biological and conservation disciplines, in part providing funds for basic taxonomic tasks usually not financed directly via institutional scientific research funding programmes.

One of the main problems is doublespeak. Even if taxonomy is the driving force, it is usually hidden behind more fancy topics, such as climatic changes, ecological or evolutionary themes for reasons of fundability and high-impact publications. However, while the prestige of pure taxonomy is often low at academic and political levels, it is paradoxically high at public level. A number of initiatives, organizations and foundations are emerging during the last two decades on the web, which also involve Collembola. They represent the ‘bottom-up’ citizen science. Initiatives such as Taxon Expeditions https://taxonexpeditions.com/) are emblematic in this respect and may attract public attention to the role of traditional taxonomy in understanding the richness and complexity of nature. In the future, the taxonomy community needs to learn how to direct such initiatives, expand and efficiently integrate them in the biodiversity description workflow. Once achieved, it would allow not only to directly facilitate the taxonomic progress, but also to recruit future generations of taxonomists and to increase the public, and thus political recognition of the field. Overall, potential for development of a new generation of taxonomists is higher than ever. However, its realisation heavily depends on the evolution of politico-socio-economic situation at the national and international levels, which is difficult to predict.

3. Collembola diversity, from individual to global scale

Collembola form multispecies communities in various biomes, widely ranging in species composition, total diversity and abundance. In a given regional context, the local biodiversity of Collembola is often far from its full potential not only because of environmental filtering and human pressure, but also due to dispersal limitation (Heiniger et al. 2014) and species saturation (Winkler & Kampichler 2000). A large part of variation in species composition always remains unexplained (Ingimarsdóttir et al. 2012, Salmon et al. 2014). The low explanatory power in local statistical analyses often are driven by (1) only one process of community assembly considered (dispersal limitation, environmental filtering or biotic interactions); and/or (2) only one spatial scale is considered (Martins da Silva et al. 2012). At the local community scale, species interactions may prevail over environmental selection (Widenfalk et al. 2016), while the explanatory power of environmental drivers increases to a large extent at medium scales (Ponge & Salmon 2013) and dispersal limitation plays a major role at regional (metacommunity) and global scales (Collins et al. 2019, Martins da Silva et al. 2012). All processes and patterns in ecological communities are scale-dependent and abiotic, biotic and spatial controls act at each of the scales, varying in their relative importance. Thus, a comprehensive understanding of biodiversity drivers can be derived only from multiscale analysis (Table 1; Berg 2012, Ettema & Wardle 2002). So how do we describe interrelationships among the main processes in Collembola community assembly across different scales?

3.1 Microscale – movement, adaptations and reproduction

A single individual and its home range defines the microscale. To increase its fitness, an individual should effectively feed, avoid environmental hazards and predators via movement or other morphological or physiological adaptations (Ponge 2020). The actual movement and spatial scale where an individual operates is largely unknown, especially for euedaphic species. It was shown that olfaction helps Collembola find the right food may direct their movement at a distance of 1-40 centimetres (Erktan et al. 2020a; Salmon et al. 2019, Salmon & Ponge 2001). Other studies have shown that during certain periods of the year some species, especially in the family Hypogastruridae can migrate over larger distances, up to several hundred meters (Hagvar 2000). The average home range of species will probably range between these minimum and maximum values, but currently we do not know average home ranges nor the factors that determine them.

Food selection and feeding generalism impact survival, which varies among different populations and species. Reproduction and development also depend on their diet (Scheu & Folger 2004). Feeding interactions in soil often cannot be observed directly but can be disentangled with gut content, stable isotope, fatty acid and gut DNA analyses (King et al. 2008, Pollierer et al. 2019, Ponge 2000, Potapov et al. 2019, Ruess and Chamberlain 2010). Most Collembola have a wide spectrum of digestive enzymes and thus are likely to be able to feed on various food items (Berg et al. 2004). Despite that, the feeding preference optima of Collembola species differ substantially (Potapov et al. 2016) also in correlation with mouthpart structure (Malcicka et al. 2017, Raymond-Léonard et al. 2019). Despite the availability of several methods to explore feeding generalism (Potapov et al. 2020), comprehensive species-specific data are still lacking, and systematic reviews or experiments on this topic have not been made.

Adaptation to environmental extremes favours survival of certain individuals and differs between species (Chown et al. 2007, Holmstrup 2018, Phillips et al. 2020), or populations (Bahrndorff et al. 2006, van Straalen et al. 1987), which can be explained or even predicted by species tolerance traits (Bokhorst et al. 2012, Makkonen et al. 2011).

Table 1. Processes in Collembola communities at different spatial and temporal scales. At each scale some processes predominate but all processes act across scales.

Scale \ Process	Genetic changes	Movement and dispersal	Environmental filtering	Biotic interactions
Fine/micro Individual Microsite (centimeters) Daily variations	Epigenetic changes	Active movement, vertical migration	Adaptation / tolerance to fine scale physical and chemical habitat characteristics	Feeding preferences, protection against predation, other biotic interactions
Small/meso Community Site (meters) Weeks, seasons	Epigenetic changes	Active movement, horizontal migration	Adaptation/ tolerance to local environment, land-use effects	Reproduction efficiency, interspecific competition, top-down control, other biotic interactions
Large/meta Metacommunity Landscape, region (kilometers) Decades	Local genetic changes	Passive dispersal	Regional climatic conditions, landscape configuration	Regional diversity (species pool)
Global/macro Biome, climatic zone, continent (countries) Hundreds of years and longer	Speciation, extinction	Passive dispersal	Global climate, geological zone and land-use gradients	Global diversity distribution

Finally, survival of an individual largely depends on its ability to avoid predation. The presence of characters, such as furca and protective metabolites suggests that top-down control drove some adaptations during Collembola evolution. Several metabolites were shown as an alarm or protective mechanism in a number of Collembola species from various families (Salmon et al. 2019). However, systematic research on the effectiveness of different protective mechanisms is clearly needed to understand the effect of top-down control on Collembola communities.

Collembola lifespan in the laboratory ranges from a few months to several years (Hopkin 1997), but nothing is assuredly known under field conditions, given the high rate of predation on eggs and individuals, in particular juveniles. Many Collembola are parthenogenetic, in particular those living belowground where movement and perception of pheromones are limited. Individual traits such as reproduction mode, growth rate and clutch size vary greatly among species (Chahartaghi et al. 2006, Malmström 2012) and even within species (Tully & Ferrière 2008) depending on the environmental stressors (Posthuma et al. 1993, Witteveen & Joosse 1987), but the data on these traits are limited and scattered across different publications.

Movement speed, olfaction, feeding flexibility and efficiency, reproduction efficiency, environmental tolerance and protection against predation jointly define the survival of individuals and populations of Collembola at microscale. To measure, predict and analyse these characteristics, functional trait approaches have been suggested (Pey et al. 2014, Violle et al. 2007). Functional traits are morphological, physiological, phenological or behavioural features which are associated with the performance of an individual. Many functional traits need to be measured on living individuals and are available for only a limited number of species (e.g. tolerance to frost, drought, clutch size, growth rate, life duration). Morphological features such as furcular development, number of ocelli, presence of pigmentation may act as proxies for ecophysiological functional traits. At present, the most comprehensive collection of morphological trait definitions and trait values for Collembola could be requested from the BETSI database (https://t-sita.betsi.cnrs.fr/ and https://portail.betsi.cnrs.fr/). A number of morphological traits are traditionally summarised as ‘life form’ that is linked to above or below ground way of life (Ellers et al. 2018, Gisin 1943, Rusek 2007). Noteworthy, the real vertical distribution of Collembola may considerably deviate from the one predicted from life form composition (Berg, *unpublished data*). Moreover, some morphological traits such as leg length and furca development, are not necessarily related to a higher dispersal ability of individuals and species (Auclerc et al. 2009). This poses a challenge for measuring and summarising the ‘real’ functional traits in laboratory experiments on living specimens, in order to test the usability of morphological proxies for predicting functional responses of Collembola.

3.2 Mesoscale – environmental filtering, biotic interactions and spatial structures

The mesoscale is the scale of communities, composed of populations of species that co-occur and interact locally. Community assembly processes are usually envisioned as species from a regional species pool that have to ‘pass’ a set of assembly filters that allows them to live in a local community (HilleRisLambers et al. 2012). These filters are often defined as a dispersal, environmental and biotic (e.g. limiting similarity) filter. A large body of literature is dedicated to the effects of environmental factors on community composition of Collembola, such as e.g. moisture (Kuznetsova 2003, Ponge 1993), pH (Ponge 1993, Salmon et al. 2014), litter layer thickness (Takeda & Abe 2001), root biomass (Fujii et al. 2013, Potapov et al. 2017). Environmental factors define available food, risk of desiccation and other environmental extremes for Collembola and thus were naturally in research focus for many years. However, evidence is accumulating that on mesoscale, in the absence of strong environmental gradients, environmental drivers have a limited explanatory power on Collembola distribution in space (Gao et al. 2018, Liu et al. 2019, Saraeva et al. 2015, Widenfalk et al. 2016).

Biotic filter of community assembly is often attributed to competitive interactions. Inferring the importance of competition can be made by analysing trait clustering in a community. Trait over-dispersion (or co-occurring species diverging in trait values) is a sign of strong competition, while trait under-dispersion (co-occurring species converging in trait values) suggest a strong environmental assembly filter. If Collembola that have similar niche requirements co-occur in samples more often than is expected by chance, strong environmental filtering is likely to drive local community assembly, such as e.g. in salt marshes (Widenfalk et al. 2015). By contrast, if similar Collembola species co-occur in samples more rarely than expected by chance, competition can play an important role, such as e.g. in pine forests (Widenfalk et al. 2016). Species ‘similarity’ in this case could be defined by a set of functional traits (morphology, feeding habits, environmental tolerance) or associated proxies, e.g. phylogenetic relatedness. Exploring the mechanisms of niche differentiation and/or partitioning and the degree of flexibility, (e.g. trophic generalism) in different species could potentially explain much of the community composition and its variation in space and time.

Collembola are also well recognised as a prey for a range of soil, litter and surface-dwelling predators (Eitzinger et al. 2019, McNabb et al. 2001, Zuev et al. 2020). There is experimental evidence that top-down control affects density and community composition of Collembola (Schneider & Maraun 2009). Predation may represent another biotic filter, but generalisations about this mechanism are waiting for more detailed data on protective mechanisms of different Collembola species and their effectiveness versus different groups of predators.

Collembola communities often exhibit spatial structures and aggregate, not only because of environmental gradients, but also due to intrinsic population processes, e.g. reproduction and random drift (Vellend 2010). Collembola aggregations result from local reproduction, hotspots of food and/or structures that protect them against environmental hazards (Joosse 1969, Saraeva et al. 2015, Verhoef & Nagelkerke 1977). Aggregative behaviour is conditioned by pheromones (Salmon et al. 2019) and the patterns of spatial distribution are shown to be species-, or life form-specific and repeatable in time and space (Saraeva et al. 2015, Widenfalk et al. 2015). However, we still do not know whether multi-species aggregations exist, as claimed by Shaw and Usher (1996) since correlations among different species are rarely repeatable across samples from different sites.

Spatial population structures should be considered together with dispersal ability of species, their biotic interactions and small-scale environmental filtering processes if we want to understand Collembola diversity in communities. For instance, it has been shown in habitats with fluctuating environmental conditions, such as riparian forests, that adaptations to environmental conditions combined with small-scale (tens of meters) active and passive dispersal drive dynamic of the local community composition (Russell 2008). Disentangling biotic, abiotic and spatial factors driving community composition can be done with e.g. partial redundancy analysis, which suggests that within one habitat stochastic and spatial processes in Collembola communities are often more important than the distribution of environmental factors, although all factors can never be measured (Martins da Silva et al. 2015, Gao et al. 2018, Liu et al. 2019). The main challenge remains to reveal what drives the relative contribution of environmental, biotic and intrinsic spatial processes in community assembly of Collembola at mesoscale across different ecosystem types.

3.3 Metascale – dispersal

Local communities are connected with each other via dispersal of species, resulting in a stable meta-community while local communities can differ substantially in viability over time. The spatial scale of these interactions between local communities defines the meta-scale. Several studies show that the landscape configuration has an effect on Collembola found in a specific site, which is likely related to the landscape history and passive dispersal (Chust et al. 2003, Martins da Silva et al. 2012, Ponge et al. 2006, Querner et al. 2013, Russell & Gergócs 2019). At such large spatial scales (dozens of kilometres and more), movement by passive transport via wind, birds, water or human activities is probably the dominant method of exchange between communities. There are some studies suggesting that passive dispersal of Collembola and other microarthropods by wind is common (Dunger et al. 2002, Hawes & Greenslade 2013, Lehmitz et al. 2011). Collembola have been trapped behind airplanes (Gressitt et al. 1960) and found on green roofs (Joimel et al. 2018). Often it seems to involve epedaphic species that are resistant to drought as they are easily picked-up by wind or birds and can survive better the transportation. However, currently we lack experimental evidence of the movement distances of species and in case of wind dispersal the rate of survival of different Collembola life forms - whether it is adults or eggs attached to soil particles, and in which conditions they can establish a new population.

The same holds for rafting via water surfaces. A number of Collembola species are hydrophobic and thus may raft on the water. It is assumed that Collembola that live in the intertidal zone are able to survive on the surface of seawater, which potentially could mean trans-oceanic dispersal, aided by sea and wind currents (Coulson et al. 2002, Lindo 2020). For instance, it was shown that similarity in species composition between sites across maritime and coastal continental Antarctica is not related to distance between these sites (Baird et al. 2019), suggesting a very efficient way of long-distance wind, water, bird and/or human dispersal in this region. The importance of dispersal processes in the regional distribution of Collembola diversity can also be illustrated with a positive relationship between species diversity and the age of post-glacial landscapes (Hågvar 2010, Zaitsev et al. 2013). Insight in the mechanisms of passive dispersal, actual distances covered, and drivers controlling the population establishment is key in our understanding of metascale community dynamics.

3.4 Macroscale – climate, regional history and soil biotic homogenisation

The macroscale is the scale of large countries, continents and the whole globe, where exchange between different regions can occur, or not, and where global changes in the biosphere should be considered. Naturally, Collembola communities at the global scale are driven by climate gradients and regional history. Human activities further induce global environmental changes, typically involving landscape modification, spread of invasive alien species, climate change, pollution, overexploitation, and interactions between them (Chown & Gaston 2008, IPBES 2019). These changes modify distribution of Collembola diversity across the globe and the rate of this process is likely higher than ever.

Regional history such as landscape age is often overlooked when the diversity assessments are made. However, it may be very important on an evolutionary time scale. For example, Eurasia experienced several glaciation events during the Pleistocene (Grosswald & Hughes 2002). Extensive biodiversity surveys showed that the number of collembolan species at a local scale is about two times lower in forests of the post-glacial Eastern European Plain than in forests of the Caucasus region, where refugia persisted during the last glaciation, and is about 3-4 times lower than in forests of the Primorsky Krai of Russia, where no glaciers occurred during the Pleistocene (Fig. 3). Thus, rarely considered evolutionary-geological factors together with mechanisms of species dispersal may be the key for explaining differences in regional species richness patterns, at least in the regions with succession dynamics.

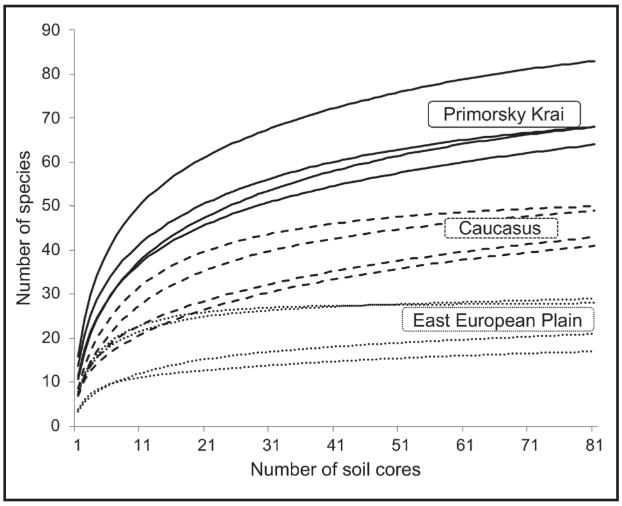

Figure 3. Local species richness depends on landscape age? Data from three forested regions in Russia with similar vegetation but different glaciation history: Primorsky Krai (no glaciation in the Pleistocene, solid lines), Caucasus (partial glaciation, dashed lines) and East European Plain (post-glacial landscape, dotted lines). Each line represents a distinct sampling locality with 81 cores of 8 cm^2 collected from an area of 100 m^2. Data from (Kuznetsova et al. 2019a, 2019b).

Climate is expected to play a large role in the global distribution of Collembola since the majority of species exhibit preferences for moist habitats and inhabit soils with developed organic horizons (see above), that formed under specific climatic conditions (Hengl et al. 2017). However, global, e.g. latitudinal distribution of Collembola was not assessed. Preliminary data show pronounced effects of different climate parameters on Collembola communities with the highest density of Collembola observed in the Arctic but no clear latitudinal trends in diversity (#GlobalCollembola *unpublished data*).

In keeping with expectations for the soil fauna and more generally small ectotherms (Chown et al. 2011, Coyle et al. 2017, Dillon et al. 2010), climate change is supposed to have a significant impact on Collembola, both through changes in temperature and water availability (especially drought). What form these impacts will take is not straightforward to predict, however; they may be relatively direct and in the direction expected from Collembola physiological sensitivity (Kardol et al. 2011, Makkonen et al. 2011, Raschmanová et al. 2018). Yet they are also likely to be influenced by differential effects of habitat, resource availability, and predation, and by trait variation associated with vertical stratification and dispersal ability (see sections above). Responses may also be indirect as a consequence of other ecosystem responses to changing climates, such as vegetation dynamics (Krab et al. 2019) or plant physiological responses (Sticht et al. 2008). Complex changes are also induced by the globally ongoing land-use change, now especially intensive in the tropics (Newbold et al. 2015). Agricultural landscapes alter environmental conditions and are usually characterised by strong changes in community composition of Collembola (Chauvat et al. 2007, Sousa et al. 2006, Yin et al. 2019).

Collembola are both influenced by invasive alien species and constitute such species themselves. Diversity, abundance and/or community composition of Collembola may be impacted by plant invasions, depending on circumstances (Liu et al. 2012, Rusterholz et al. 2014, Sterzyńska et al. 2017). Human activities, in particular, are causing appearance of alien species of Collembola in local faunas across the globe. With increased human activities, alien species have been recorded from many different remote environments, including polar regions (Baird et al. 2019, Coulson et al. 2013, Greenslade 2018, Janion-Scheepers et al. 2016, Porco et al. 2014). Alien Collembola may make up a significant proportion in local fauna, especially on islands, and many of these species are so widespread and abundant that they are rightly considered invasive (Cicconardi et al. 2017, Greenslade

2018, Terauds et al. 2011). For example, a study has found that about 30% of soil-dwelling Collembola species are genetically very similar across several remote oceanic islands around the globe (Cicconardi et al. 2017).

Biotic homogenisation and environmental changes are likely changing global distribution of Collembola at a high rate. However, even a rough assessment of the current global distribution of Collembola is lacking. As is the case with so many features of impacts on the soil fauna (Coyle et al. 2017), studies on land-use change are not distributed globally, with much remaining unknown especially in subtropical and tropical environments. To be able to predict the future of Collembola diversity and related changes in ecosystem functioning, a global assessment of abundance and diversity distribution is also urgently needed (see below the 'integrative data' section).

3.5 Multiscale diversity

Diversity of Collembola at each scale, from micro to macro is driven by processes that operate across scales. Although competition and predation are the main structuring factors at the meso scale (Berg 2012, Ettema & Wardle 2002), they do play a role at the micro and meta scale as well. The same holds for passive movement, which dominates meta-community processes but also plays at smaller and larger scales. For instance, global climate change (especially warming, but also drought) may benefit invasive over indigenous Collembola because of greater tolerance or phenotypic plasticity of invasive species at the individual level (Chown et al. 2007, Janion-Scheepers et al. 2018, Phillips et al. 2020). Also, the estimated difference in diversity between two communities or regions is likely to be scale-dependent (Chase & Knight 2013).

The research question determines the scale of interest, and to avoid misleading conclusions the scale of interest should be clearly defined for each study, preferably accompanied by how observations scale up or down and effects that propagate from other scales. Various community assembly processes, should be considered in the design, or discussed. For a comprehensive comparison of biodiversity at meso- and metascale, sampling designs including several spatial scales could be considered (Ponge & Salmon 2013, Saraeva et al. 2015). Multiscale diversity can be described in detail by statistical analyses of data aggregated at multiple scales, using e.g. extrapolation of species richness with rarefaction methods (see Chao & Jost 2012) and Hill's numbers (Hill 1973). Synthesis of the existing knowledge is needed as a basis for establishing multiscale relationships between diversity of Collembola and environmental, biotic and spatial factors. Further studies exploring changes in such relationships due to land use or climate change would give a more comprehensive picture of diversity variations in Collembola communities with further consequences for ecosystem processes beyond local scales.

4. Role of Collembola in ecosystem processes

Many activities of Collembola in soil may potentially have repercussions for ecosystem processes. Collembola ecosystem function is somewhere in between those of microfauna, such as Nematoda, ensuring nutrient cycling and microbial control, and of macrofauna, such as earthworms having a strong engineering role in the soil (Coleman et al. 2017, Swift et al. 1979). Although Collembola can potentially be involved in a number of ecosystem processes, the real contribution of this group to rates of ecosystem processes is not often quantified and may vary considerably across biomes and experimental settings. It is often stated that Collembola are key organisms for ecosystem processes rates, but high-quality data to prove this are scarce. A critical evaluation on how important Collembola actually are, relatively to other groups (e.g. mites, nematodes, oligochaetes) for decomposition, C-storage and nutrient cycling across ecosystems is needed. With high morphological and ecological diversity, different groups of Collembola may play very different ecosystem roles (Potapov et al. 2016). The main challenge is to quantify the role of Collembola and soil processes and how we can predict contribution of different communities to ecosystem functioning with only a basic knowledge about ecology of species.

4.1 Functions that are potentially affected by Collembola

The ecosystem processes that Collembola are associated with may be classified in four (non-exhaustive) classes (Fig. 4):

Supporting nutrient cycling in rhizosphere and bulk soil and decomposition of litter, such as leaves, roots and dead wood. By grazing on microorganisms and consumption of litter, Collembola release nutrients in the environment and which support plant growth (Gange 2000, Hassall et al. 2006). The presence of Collembola affects nutrition and metabolism of plants primarily due to their feeding activities in the rhizosphere (Endlweber & Scheu 2007, Graf et al. 2019, Johnson et al. 2005). Feeding on roots and root-associated microorganisms is suggested to be specifically common among lower litter- and soil-dwelling species, while upper litter- and surface-dwelling species are feeding primarily on fungi, algae and lichens (Ponge 2000, Potapov et al. 2018, 2016). The presence of microarthropods, including Collembola, normally enhances decomposition in litter bag experiments, but their effect may also be neutral or negative, depending on the climate and experimental setting (Kampichler & Bruckner 2009, Wall et al. 2008). Collembola usually contribute less than 10 % to the total soil animal community metabolism, but in some coniferous woodlands and pastures this value can increase to about 14 to 37 % (Petersen & Luxton 1982). Van Straalen (1989) calculated that the consumption of Collembola can reach about 6 % of the total annual litter fall in a temperate forest, but systematic analyses of Collembola feeding activity in different biomes across the globe are yet to be done.

Although the direct contribution of Collembola to decomposition and nutrient cycling is significantly less than that of microorganisms, they are believed to be one of the main regulating agents of the microbial compartment (Crowther et al. 2011, Thakur & Geisen 2019). By feeding on fungi and bacteria they contribute to maintain the microbial biomass in an active state (Kaneda & Kaneko 2008) and decrease competition among microbial strains by feeding preferentially on those growing faster (Newell 1984). Although still in need of research, it can be expected that selective grazing of microbial colonies (Crowther et al. 2011) increases soil microbial biodiversity locally (A'Bear et al. 2012), analogous to what has been repetitively shown to occur within grassland plant communities under moderate herbivore grazing (reviewed in Metera et al. 2010). An experimental study showed that life form composition of Collembola communities considerably changes microbial communities and their functioning (Coulibaly et al. 2019). Stable isotope analysis further provided evidence that Collembola prefer saprotrophic over mycorrhizal fungi in temperate forest soils (Potapov & Tiunov 2016), which may have large consequences for carbon cycling in these ecosystems (Averill et al. 2014). However, quantification of microbial grazing is needed to estimate the potential effect of Collembola on ecosystem functioning.

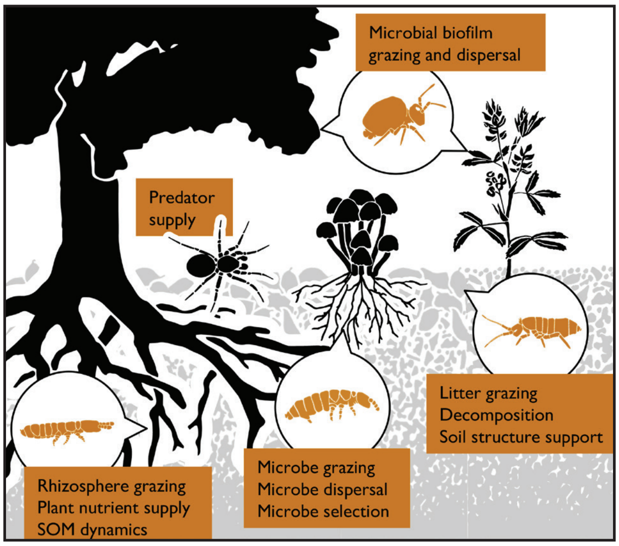

Figure 4. Ecosystem processes that can be affected by different functional groups of Collembola. Soil-dwelling Collembola such as Onychiuridae are associated with roots and involved in rhizosphere processes. Many litter-dwelling Isotomidae and Tomoceridae are associated with decomposition processes by grazing and transformation of litter. Most of Hypogastruridae and Neanuridae and litter-dwelling Entomobryidae are largely microbivores and impact directly microbial communities in the litter. Surface-dwelling Symphypleona, Entomobryidae and Paronellidae affect microbial biofilms aboveground. Collembola, especially large surface-dwelling species, support various groups of terrestrial invertebrate predators. Summarised from Potapov et al. (2020, 2016) and Rusek (1998).

Supporting soil structure via plant detritus shredding and production of faecal pellets. In this way Collembola are indirectly linked to soil formation, which may impact soil processes such as water infiltration, soil erosion and nutrient leaching. Collembola can be involved in soil aggregation, both via direct organic matter production (eggs, pellets, moults), soil organic matter feeding, and via interactions with microbial communities (Maaß et al. 2015). Experimental studies in this direction are scarce. Although it has been shown that microbial soil aggregation is modulated by Collembola (Erktan et al. 2020b; Siddiky et al. 2012), it has to be seen if their effect surpasses that of other microbivores (nematodes and mites) or soil engineers such as enchytraeids and earthworms (Coleman et al. 2017).

Dispersing microbial and plant propagules attached to the body and/or inside the digestive system while foraging and moving. Abundant and diverse fungal and bacterial propagules are found in the guts of Collembola (Anslan et al. 2018, Ponge 1991, Tebbe et al. 2006) and thus these animals are thought to contribute to the dispersal of microflora in addition to purely trophic relationships. This dual aspect of faunal-microbial relationships is fundamental for understanding soil microbial dynamics and co-evolution of these two groups, similarly to the relationships between pollinators and plants. This promising field of research is rarely considered so far (Hassall et al. 2006). Interestingly, Collembola are involved in plant dispersal as well, since living soil algae are readily found in faecal pellets (Buse et al. 2014) and Collembola specifically 'pollinate' mosses (Rosenstiel et al. 2012). Through their effects on assembly processes in microbial communities, Collembola may exert an indirect effect on ecosystem functioning, however it is not easy to quantify their effect. A better understanding of these interactions would be possible with more data on how Collembola move and select their food (see above).

Supporting biodiversity of predatory arthropods. There are many soil arthropods that feed on Collembola, some of them even specialized, such as some carabid beetles (*Notiophilus*, *Elaphrus*), pseudoscorpions, spiders (Linyphiidae). Being less protected than many soil mites, Collembola are the most abundant prey type in their size class in many ecosystems. Since predator-prey interactions are commonly size structured (Cohen et al. 1993, Potapov et al. 2019), Collembola as prey may support the majority of terrestrial invertebrate predators of ca. 0.5 to 20 mm long. Thus, supporting Collembola diversity may have a bottom-up cascading positive effect on terrestrial invertebrate diversity in general. From the applied point of view, this ecosystem function has an ability to improve e.g. pest control by invertebrate predators in agricultural fields.

Overall, springtails make versatile direct and indirect contributions to ecosystem functioning, sometimes with prominent effects. The direction and magnitude of these effects vary in different ecosystems and the outcome is often hard to quantify, let alone predict due to the complexity of interactions and context dependency due to environmental conditions. Quantitative measurements and establishment of effect size in experiment where diversity, abundance and composition of Collembola is manipulated in presence of the whole food web are very rare. Experiments directly linking Collembola effects with that of microbial communities and other mesofauna are needed (Coulibaly et al. 2019). Experimental approaches are further hampered by the limited number of species that are culturable in the laboratory. This underlines the unrealistic conditions of laboratory settings, where *Folsomia candida* (Fountain & Hopkin 2005) dominates, while this species is uncommon in most natural ecosystems. These issues potentially could be addressed with well-designed field experiments, in combination with stable isotope labelling. Synthesizing laboratory and field experiments with observed patterns of Collembola distribution in nature could contribute to understanding the mosaic of ecosystem processes in the soil.

4.2 Functional traits as proxies

Many effects of Collembola on soil processes are probably taxon-specific, hence we need to be able to predict the ecosystem roles of species. Trait based-approaches have been been suggested as a tool that could address this question (McGill et al. 2006, Pey et al. 2014, Violle et al. 2007). Traits that inform about the effect of an organism on ecosystem processes are termed ‘effect’ traits (Lavorel & Garnier 2002, Violle et al. 2007). A common set of morphological traits, starting with body size and life form as a proxy of vertical distribution in the soil, might be used to infer relationships of species with litter decomposition, microbial dispersal and other processes (Coulibaly et al. 2019, Eisenhauer et al. 2011). However, easily measurable and commonly used morphological traits are often indirectly linked to Collembola effects in a given setting. Since most of the ecosystem effects of Collembola are related to their feeding activities, ‘trophic traits’, i.e. estimators of the diet, may provide a more realistic indication of the ecosystem roles of different individuals, populations and species. Fine mouthpart morphology could potentially be informative, but only few ecological studies have considered this trait complex (Raymond-Léonard et al. 2019). Even though morphological traits could be measured on local populations, morphological responses are very limited due to phylogenetic body architecture constraints. Biochemical traits were put in the framework of the trait approach in Collembola by Chen et al. (2017), who showed that fatty acids can inform on both phylogenetic constraints and the local microbial food resources of populations. Multiple biochemical traits are at the disposal of ecologists and some of them, like stable isotope composition, are relatively easy to measure (Potapov et al. 2020). These traits could be used in combination with morphological traits and phylogeny to develop a model for predicting the ecosystem roles of Collembola species. A comprehensive data on such traits and a robust phylogeny are needed to progress in this research topic.

5. Towards integrative data on Collembola abundance and diversity

The historical skewed distribution of Collembola studies, with a concentration of expertise in Europe has resulted in a very uneven distribution of data on Collembolan communities around the globe. This became especially evident after the launch of the #GlobalCollembola initiative in July 2019 at the 10th International Seminar on Apterygota in Paris. The overall aim of the initiative is to provide open data on Collembola abundance, diversity, community composition, regional fauna lists, traits and literature for the scientific community and beyond, to coordinate global efforts in covering key existing knowledge gaps and to popularize Collembola. The data collected during the first year of the initiative emphasized major knowledge gaps in certain parts of the world, especially in tropical and subtropical regions (Fig. 5). More than 50 % of global data on Collembola communities comes

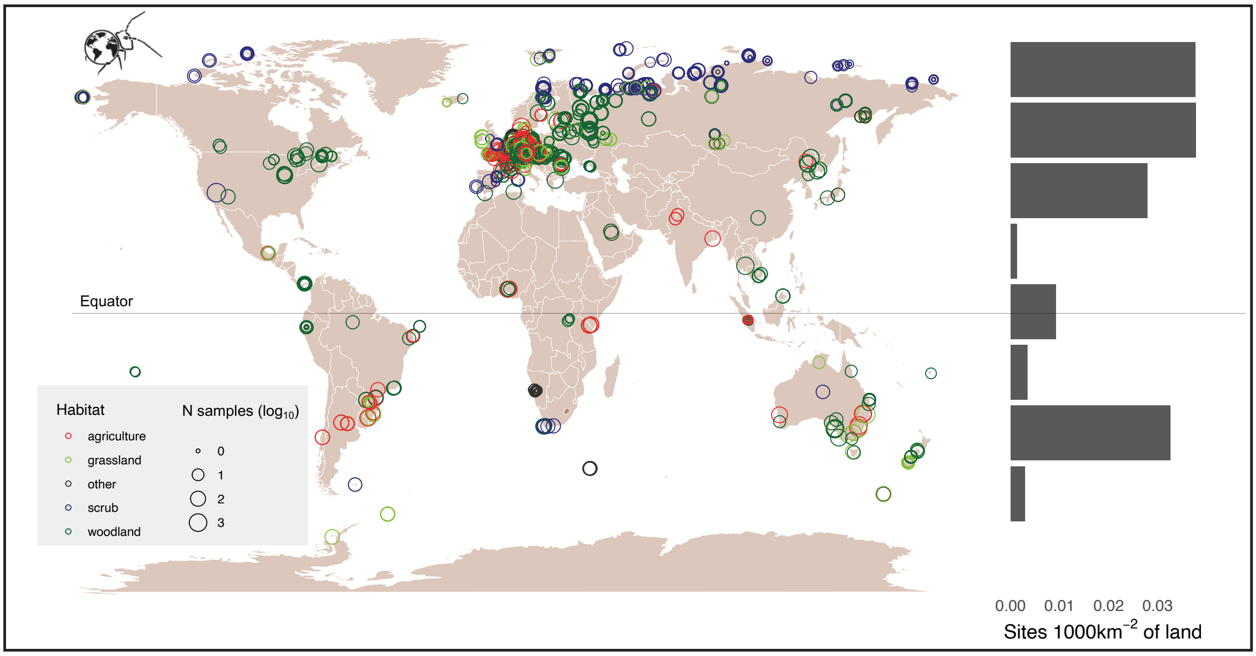

Figure 5. Distribution of sampling sites in the #GlobalCollembola across the world map (in July, 2020). Circles represent locations with recorded estimations of Collembola area-based density and/or species richness. Circle colour indicates from which habitat type data are retrieved; circle size indicates the sampling effort (number of samples taken) for each site. Histogram shows the number of sites in each 20-grad latitudinal belt, relative to the total land area in this belt.

from Europe. As relationships between Collembola and the biotic and abiotic factors described are often context dependent, and because these factors are qualitatively and quantitatively different across biomes, filling these gaps is one of the major challenges of Collembola research in upcoming decades. It will increase not only our understanding of the global distribution of abundance and diversity of this soil invertebrate group, but also will give further inside in how communities are assembled, structured and maintained. The accumulation of large amounts of data will also allow for reassessment of recurring ecological topics, such as modelling population dynamics, on a new level.

While working to cover these geographic gaps, we need to learn some lessons from the past. #GlobalCollembola data collected so far, coming from ca. 2500 sampling sites by over a hundred researchers, is often poorly comparable due to the different collection and extraction methods used, variation in sampling efforts, and the identification quality, among others. It took over a year to standardize and clean the data, with the joint efforts of data contributors, coordinator and technical assistants to be able to perform global scale analyses. It is evident that, to reveal macro-ecological patterns we should standardize our collection methods and extraction methods, and apply better practices of data handling and publishing than has been performed to date.

5.1 Standardizing sampling methods

Collembola live in various microhabitats, such as soil pores, litter layer and on vegetation, each with its own challenges when it comes to quantitative sampling. Therefore, no single sampling method collects all species appropriately and a comprehensive assessment of a community is possible only with a combination of methods (Geisen et al. 2019, White et al. 2020). Numerous methods are available, including Berlese-Tullgren and Macfadyen extraction by heat, light and drought, pitfall traps, aspirator and hand collection, flotation, air suction, malaise traps, stem eclectors, fogging, vegetation beating, sweep-netting, bark brushing. These methods target different groups of Collembola, with some methods providing only qualitative data, while others give quantitative data. Their specifics are reviewed elsewhere (e.g. Hopkin 1997). The eu- and hemiedaphic species are normally extracted from soil and litter samples, often using Berlese-Tullgren funnels or high-gradient Macfadyen/Kempson extractors (Macfadyen 1961, Straalen & Rijninks 1982). Macfadyen extractors are better standardized, but more laborious to build (for mesofauna extraction with Macfadyen see ISO23611-2, https://www.iso.org/standard/37027.html). Despite high-gradient extractors reported to have a lower extraction bias (Macfadyen 1961, Marshall 1972), Berlese-Tullgren extractors are more widely used, since they are easily self-built. Since extraction conditions depend on the climate and sample conditions, e.g. soil type, moisture content etc. (Macfadyen 1953, Semenina et al. 2015), a common extraction protocol is difficult to give and ecosystem-specific extraction settings may be more important for the extraction efficiency, than the device itself. Nevertheless, there are four basic rules one should follow when using Berlese-Tullgren extraction to avoid widespread mistakes: (1) do not overheat samples during sampling and transportation; (2) finish extraction only after the substrate is completely dry, this may take some time; (3) a gentle, hence long, extraction is preferred since it yields more animals than a short and intense extraction; (4) limit the amount of substrate put on the funnel, leave empty space to allow animals to move down.

Next to the methods of extraction also the number of samples determines species richness and abundance estimates, as well as where the samples are taken. The number and size of samples depend on the aim of the sampling and soil specifics (Marsh & Ewers 2013, Potapov et al. 2017). Usually between 5 and 20 soil cores of 3 to 10 cm in diameter for litter and 5 to 10 cm of underlying soil are collected per site, each extracted individually. To estimate diversity, Bruckner et al. (2000) proposed to collect a large number of soil samples and identify aliquots after pooling all extracted animals. However, this approach does not allow species co-occurring in the same soil core and local beta diversity to be analysed. Most studies employ some sort of random sampling designs to account for local variation in Collembola distribution. However, spatially-explicit sampling designs are highly valuable as they allow analyses of community structure and aggregation sizes. If coordinates of each soil core are known, the spatial structure of communities can be analysed and potentially related to environmental and biotic gradients (see ‘mesoscale’ section above) (see Rossi et al. 1992, Widenfalk et al. 2015). This further opens perspectives for multiscale diversity analyses and more comprehensive diversity descriptions if several sampling distances are considered within a sampling site (Kuznetsova & Saraeva 2017, Marsh & Ewers 2013, Fig. 6).

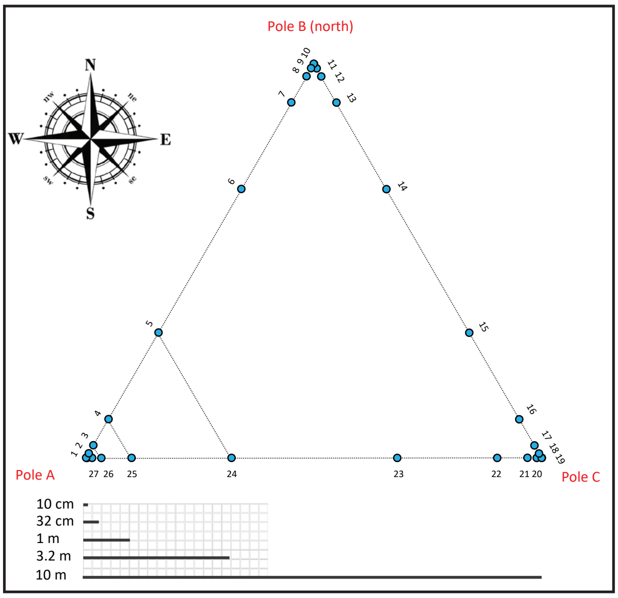

Figure 6. Example of a spatially-explicit soil sampling design, based on five nested triangles. Dots with numbers represent soil core samples, distributed between thee base poles (A, B, C). Distances between the samples follow a decimal logarithmic scale. The largest triangle edge length is 10 meters. Note that some samples are directly next to each other. A more extensive design based on triangles or rectangles can be found in Saraeva et al. (2015) or Widenfalk et al. (2015), respectively.

Density, richness and abundances are expressed by sample surface area (individuals m^{-2}), which is independent of sampling depth, or to volume/mass when litter thickness is very heterogeneous. Since springtails also live in the subsoil, area-based sampling of only the surface layer introduce biases for some ecosystems in meta analyses, because it overlooks Collembola in the subsoil (Andre et al. 2002, Potapov et al. 2017). Therefore, it is advisable to sample deeper in soils with a developed organic horizon to provide a more realistic estimation of the total richness and density and avoid errors due to variation in the humus form. Separate extraction of litter and soil, or even the subsequent organic horizons of the litter layer can make the data on specific layers more comparable across soils and especially give more mechanistic understanding of the dynamics in species composition if the litter thickness is recorded (e.g. Berg et al. 1998).

Surface-active species often escape from soil cores and are best collected in pitfall traps or with an aspirator. Up to ten pitfall traps are usually placed per site and exposed for a few days to a few months. Querner and Bruckner (2010) found a low species overlap between Berlese-Tullgren extraction and pitfall trapping and showed that most epedaphic species were confined to pitfall traps and euedaphic species to soil cores. Despite being well complementary for faunal surveys, data produced by pitfall traps and Berlese-Tullgren extraction cannot be compared in terms of density or species richness per area since pitfall catches cannot be extrapolated to a specific area if pitfall is not placed inside a fenced area. To obtain area-based estimates of density for surface-dwelling species, sampling could be done with an air sucking machine on a given area (Wallace 1972). The method is not often applied in studies of Collembola, but it likely provides a more comparable and complete density estimation than aspirator-based surveys, which are highly affected by the collector experience. Irrespective of the methods, sample completeness has to be taken in account using e.g.

rarefaction analyses (see above 'multiscale diversity').

We see a strong need to standardize sampling methods for Collembola to compare results across sites, ecoregions, years and institutions. Currently, a single recommendation is hard to give since a systematic review of the different sampling practices, for instance when applied to sample the same community is rare but needed. Whenever it is possible, we recommend to (1) use a spatially-explicit sampling design; (2) define which microhabitats and which scales are targeted for the study; (3) combine Berlese-Tullgren or high-gradient extraction with other methods to obtain a comprehensive species list (if such is needed); (4) take samples deeper in the soils with deeper organic horizons; (5) report both surface area, depth and volume for the samples.

5.2 Standard and open data

Not only collection methods, but also data management practices need to be standardized and improved. Any macroecological question, or meta-analysis of experimental studies demands large amounts of data in a standard, structured format (Wieczorek et al. 2012). The common practice of data sharing still remains a report of summary statistics for density and diversity in a tabular format in a journal article, which often is delegated to supplementary material. The raw data is then kept in a private archive, being inevitably lost with time ('file drawer' phenomenon). This loss of raw data, which has a high added value compared to summary statistics, cannot be accepted as a good sustainable practice for scientific knowledge accumulation.

In recent years, this problem has been repeatedly emphasized in the framework of the open science concept (https://www.go-fair.org/fair-principles/). It has been proposed that we should aim to make scientific data FAIR, i.e. findable, accessible, interoperable and reusable (Wilkinson et al. 2016). A number of biodiversity-related platforms following these principles have been established, e.g. Global Biodiversity Information Facility (GBIF, https://gbif.org). Sharing the raw data with the publication is not only a community service that allow for meta-analyses, but also has individual benefits of establishing new collaborations, increasing visibility, findability and credibility of the research (Popkin 2019).

Providing raw data (spreadsheets) in an open public repository (e.g. https://figshare.com/, https://datadryad.org/) should be a minimum requirement for a scientific publication. This practice is already accepted in a number of international peer-reviewed journals and even if not required, we encourage our community to follow it. However, these repositories do not integrate data from different studies, nor do they often capture environmental metadata, so that their use in overarching macroecological analyses still requires intensive manual compilation. Therefore, a next step would be the deposition of data in a standard form to a structured database (which preferably follows the TRUST principles; Lin et al. 2020), allowing for the structured data search and analysis across studies. Apart from general biodiversity data aggregators, such as GBIF, specific databases for soil animal biodiversity have been developed, such as Edaphobase (https://portal.edaphobase.org; https://www.eudaphobase.eu). At present, Edaphobase hosts over 380,000 records of soil fauna from over 27,000 sites throughout the world (albeit with a current focus on Europe), from which over 105,000 records pertain to Collembola. Edaphobase employs quality-control procedures during data upload and also hosts metadata on species identification. Such quality-controlled platforms would allow reliable cross-studies data integration and analysis at different spatial and temporal scales. Moreover, general data repositories and structured databases normally provide digital object identifiers (d.o.i.) for the datasets, which can then be cited, providing incentives for data upload. One of our priorities is now to include data collected within the #GlobalCollembola initiative in an open-access structured database and maintain the initiative open for further data submissions.

The key issue hampering the employment of the 'good' data handling and sharing practices is infancy of the tools that will automate the biodiversity data standardization and quality check process. Only few researchers are ready to spend additional time specifically to standardize and share their data due to hard time pressure in academic research nowadays. One of the suggested solutions are online databases with 'virtual research environments' where the data collection process already includes standardization and data publication, which can thus be achieved with a few clicks. These represent a set of custom forms for data input and replaces initial data typing in offline spreadsheets within the scientific data cycle. Existing platforms, e.g. http://ecotaxonomy.org, https://plutof.ut.ee, https://earthcape.com, http://taxonworks.org are rapidly developing and are likely to suggest efficient solutions in the nearest years.

Numerous developing and emerging database initiatives bring some confusion to the field – which to use? One important step for the future of biodiversity data information would be to create 'metasystems' that can link individual databases and provide search tools across them e.g. by the means of ontologies (Gallagher et al. 2020). In this light, any long-term supported and open database that follows common data standards can be viewed as an appropriate data repository.

6. The bright 2040s

In the near future, we hope that the approach of integrated taxonomy will develop fast, enabling the reproducible description of unknown Collembola species on Earth, or at least establishing an efficient way to do it by 2060. We should describe multiscale relationships between diversity of Collembola and environmental, biotic and spatial factors. We would like to establish mechanistic links between biochemical and ecophysiological traits and morphological traits of Collembola to be able to understand Collembola diversity, community assembly and dynamics on the one hand and their effect on ecosystem processes on the other hand. We would like to have a reliable estimation of the alpha- beta- and gamma diversity components of all major ecoregions. Finally, we need to be able to provide open and easy access to taxonomic expertise, literature, digital tools and data produced across different facets of Collembola research. Below we summarize calls that could help achieving this, or at least move in the right direction:

- Move towards integrative taxonomy: combine morphological descriptions with high-resolution imagery and genetic barcodes, deposit taxonomic information in structured databases. The major step forward in reproducibility of taxonomic work could be achieved with development of digital tools, molecular approaches and international cooperation efforts that will facilitate taxonomic workflow. As a community of Collembola researchers we see high value in the website https://collembola.org, which gives an up-to-date overview on the species of Collembola described so far on earth. We highly recommend taxonomists that describe new species to deposit a pdf of their papers to the website, or at least inform the webmaster that new species have been described.
- Think multiscale: Local communities do not operate in isolation and factors that shape the distribution of Collembola are scale-dependent, in space as well as in time. To really understand biodiversity distribution patterns and community processes, including factors such as dispersal, environmental niche and biotic interactions different temporal and spatial scales should be used in our studies. A major step forward in understanding community dynamics and underlying mechanisms would be the availability of quantitative measurements of Collembola movement, home range and dispersal distances, both active and passive.
- Be truly functional: Trait-based approaches have been shown to be of high value in understanding Collembola community responses to environmental gradients, such as drought, habitat fragmentation or the relative importance of the environmental versus limiting similarity filters in assembly. However, to improve our mechanistic understanding we have to measure more insightful but laborious traits, such as ecophysiological traits (i.e. drought tolerance, heat tolerance), performance traits (growth, survival and reproduction) or at least test if the morphological proxies we use, such as life form, are truly affecting species performance and fitness. Too often we infer these links but do not test them. Also, we should put more emphasize on traits Collembola exhibit with which they effect ecosystem processes, such as biochemical traits.
- Synthesize knowledge: a large body of Collembola research has not been reviewed and synthesized, e.g. ecosystem functioning aspects, feeding, movement and dispersal, land-use effects, collection methods, species protection mechanisms and other. Meta-analyses and syntheses of this knowledge would be a crucial step in the progress of community and ecosystem ecology of Collembola.
- Collaborate: Join efforts in covering the major geographical gaps in Collembola knowledge, predominantly on tropical and subtropical ecosystems (Fig. 5). With common methodological approaches and improved communication, the task can be approached in the next years.
- Share the data: provide not only summaries, but also raw community matrices and other information alongside with the publications. Send the published data to include it in the #GlobalCollembola database, or publish it to Edaphobase (https://portal.edaphobase.org) or gbif (https://gbif.org). Efficient digital tools facilitating these processes and establishing connections among different databases are urgently needed.
- Be open: make use of new technologies and social changes. If applied correctly, citizen science can provide a major support to Collembola research and it is necessary to learn how to use this source. Sharing the research with students, and the younger generation in general, using attractive imagery, digital tools and social networks will build capacity in the field for the next decades.

As a community of Collembola researchers we should try to jointly address and target these tasks. The first global synthesis of Collembola diversity and abundance has been nearly completed, within one year, thanks to the joint community efforts and will be published soon. We wish to encourage future community initiatives that could include collecting data on pictures, traits, taxonomic descriptions, genetic data and potentially joint experimentation. Open community calls are welcome and can be spread through the network of specialists with the help of paper authors, if needed. In establishing the #GlobalCollembola initiative, we believe it will be possible to make coordinated progress and more efficiently cover the gaps mentioned above, to obtain and share comprehensive knowledge about Collembola.

7. Acknowledgements

The article is an outcome of the #GlobalCollembola community initiative that has no explicit funding. AP contribution to coordination and data collection was supported by the Russian Science Foundation (project No 19-74-00154). We are grateful to Svenja Meyer who drew images of Collembola and other ecosystem components for the Figure 4. We thank all researchers who provided their data for the global assessment of Collembola abundance and diversity.

8. References

A'Bear, A.D., L. Boddy & T. Hefin Jones (2012): Impacts of elevated temperature on the growth and functioning of decomposer fungi are influenced by grazing Collembola. – Global Change Biology **18**: 1823–1832 [https://doi.org/10.1111/j.1365-2486.2012.02637.x].

Andre, H.M., X. Ducarme & P. Lebrun (2002): Soil biodiversity: myth, reality or conning? – Oikos **96**: 3–24.

Anslan, S., M. Bahram & L. Tedersoo (2018): Seasonal and annual variation in fungal communities associated with epigeic springtails (Collembola spp.) in boreal forests. – Soil Biology and Biochemistry **116**: 245–252 [https://doi.org/10.1016/j.soilbio.2017.10.021].

Auclerc, A., J.-F. Ponge, S. Barot & F. Dubs (2009): Experimental assessment of habitat preference and dispersal ability of soil springtails. – Soil Biology and Biochemistry **41**: 1596–1604 [https://doi.org/10.1016/j.soilbio.2009.04.017].

Averill, C., B. L. Turner & A. C. Finzi (2014): Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. – Nature **505**: 543–545 [https://doi.org/10.1038/nature12901].

Bahrndorff, S., M. Holmstrup, H. Petersen & V. Loeschcke (2006): Geographic variation for climatic stress resistance traits in the springtail *Orchesella cincta*. – Journal of Insect Physiology **52**: 951–959 [https://doi.org/10.1016/j.jinsphys.2006.06.005].

Baird, H. P., C. Janion-Scheepers, M. I. Stevens, R. I. Leihy & S. L. Chown (2019): The ecological biogeography of indigenous and introduced Antarctic springtails. – Journal of Biogeography **46**: 1959–1973 [https://doi.org/10.1111/jbi.13639].

Bellinger, P. F., K. A. Christiansen & F. Janssens (1996-2020): Checklist of the Collembola of the World [WWW Document]. URL http://www.collembola.org/ (accessed 5.29.20).

Berg, M. P. (2012): Patterns of Biodiversity at Fine and Small Spatial Scales. – In: Wall, D. H., R. D. Bardgett, V. Behan-Pelletier, , J. E. Herrick, T. H. Jones, K. Ritz, J. Six. D. R. Strong & W. H. van der Putten (eds): Soil Ecology and Ecosystem Services. – Oxford University Press: 136–152 [https://doi.org/10.1093/acprof:oso/9780199575923.003.0014].

Berg, M. P., J. P. Kniese, J. J. M. Bedaux & H. A. Verhoef (1998): Dynamics and stratification of functional groups of micro-and mesoarthropods in the organic layer of a Scots pine forest. – Biology and Fertility of Soils **26**: 268–284.

Berg, M. P., M. Stoffer & H. H. van den Heuvel (2004): Feeding guilds in Collembola based on digestive enzymes. – Pedobiologia **48**: 589–601 [https://doi.org/10.1016/j.pedobi.2004.07.006].

Betsch, J. & A. Waller (1994): Chaetotaxic nomenclature of the head, thorax and abdomen in Symphypleona (Insecta, Collembola). – Acta Zoologica Fennica **195**: 5–12.

Bokhorst, S., G. K. Phoenix, J. W. Bjerke, T. V. Callaghan, F. Huyer-Brugman & M. P. Berg (2012): Extreme winter warming events more negatively impact small rather than large soil fauna: shift in community composition explained by traits not taxa. – Global Change Biology **18**: 1152–1162.

Bretfeld, G., (1999): Synopses on Palaearctic Collembola: Symphypleona. – Stattliches Museum für Naturkunde Görlitz, Görlitz.

Buse, T., L. Ruess & J. Filser (2014): Collembola gut passage shapes microbial communities in faecal pellets but not viability of dietary algal cells. – Chemoecology **24**: 79–84 [https://doi.org/10.1007/s00049-013-0145-y].

Cassagnau, M. P. (1974): Chaetotaxie et phylogénie chez les Collemboles Poduromorphes. – Pedobiologia **14**: 300–312.

Chahartaghi, M., S. Scheu & L. Ruess (2006): Sex ratio and mode of reproduction in Collembola of an oak-beech forest. – Pedobiologia **50**: 331–340.

Chao, A. & L. Jost (2012): Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. – Ecology **93**: 2533–2547 [https://doi.org/10.1890/11-1952.1].

Chase, J. M. & T. M. Knight (2013): Scale-dependent effect sizes of ecological drivers on biodiversity: why standardised sampling is not enough. – Ecology Letters **16**: 17–26 [https://doi.org/10.1111/ele.12112].

Chauvat, M., G. Perez & J.-F. Ponge (2014): Foraging patterns of soil springtails are impacted by food resources. – Applied Soil Ecology **82**: 72–77 [https://doi.org/10.1016/j.apsoil.2014.05.012].

Chauvat, M., V. Wolters & J. Dauber (2007): Response of collembolan communities to land-use change and grassland succession. – Ecography **30**: 183–192 [https://doi.org/10.1111/j.0906-7590.2007.04888.x].

Chen, T.-W., P. Sandmann, I. Schaefer & S. Scheu (2017): Neutral lipid fatty acid composition as trait and constraint in Collembola evolution. – Ecology and Evolution **7**: 9624–9638 [https://doi.org/10.1002/ece3.3472].

Chown, S. L. & K. J. Gaston (2008): Macrophysiology for a changing world. – Proceedings of the Royal Society B: Biological Sciences **275**: 1469–1478 [https://doi.org/10.1098/rspb.2008.0137].

Chown, S.L., S. Slabber, M. A. McGeoch, C. Janion & H. P. Leinaas (2007): Phenotypic plasticity mediates climate change responses among invasive and indigenous arthropods. – Proceedings of the Royal Society B: Biological Sciences **274**: 2531–2537 [https://doi.org/10.1098/rspb.2007.0772].

Chown, S. L., J. G. Sørensen & J. S. Terblanche(2011): Water loss in insects: An environmental change perspective. – Journal of Insect Physiology, “Cold and Desiccation Tolerance” honoring Karl Erik Zachariassen **57**: 1070–1084 [https://doi.org/10.1016/j.jinsphys.2011.05.004].

Chust, G., J. L. Pretus, D. Ducrot, A. Bedòs & L.Deharveng (2003): Identification of landscape units from an insect perspective. – Ecography **26**: 257–268 [https://doi.org/10.1034/j.1600-0587.2003.03325.x].

Cicconardi, F., P. A. V. Borges, D. Strasberg, P. Oromí, H. López, A. J. Pérez-Delgado, J. Casquet, J. Caujapé-Castells, J. M. Fernández-Palacios, C. Thébaud & B. C.Emerson (2017): MtDNA metagenomics reveals large-scale invasion of belowground arthropod communities by introduced species. – Molecular Ecology **26**: 3104–3115 [https://doi.org/10.1111/mec.14037].

Cicconardi, F., P. P. Fanciulli& B. C. Emerson (2013): Collembola, the biological species concept and the underestimation of global species richness. – Molecular Ecology **22**: 5382–5396 [https://doi.org/10.1111/mec.12472].

Cohen, J. E., S. L. Pimm, P. Yodzis & J. Saldaña (1993): Body sizes of animal predators and animal prey in food webs. – Journal of Animal Ecology **62**: 67–78 [https://doi.org/10.2307/5483].

Coleman, D.C., M. A. Callaham & D. Crossley Jr (2017): Fundamentals of soil ecology, 3d (ed). – Academic press.

Collins, G. E., I. D. Hogg, P. Convey, A. D. Barnes & I. R. McDonald (2019): Spatial and temporal scales matter when assessing the species and genetic diversity of springtails (Collembola) in Antarctica. – Frontiers in Ecology and Evolution **7**: 76 [https://doi.org/10.3389/fevo.2019.00076].

Coulibaly, S. F. M., B. R. Winck, M. Akpa-Vinceslas, L. Mignot, M. Legras, E. Forey & M. Chauvat (2019): Functional assemblages of Collembola determine soil microbial communities and associated functions. – Frontiers in Environmental Science **7**: 52 [https://doi.org/10.3389/fenvs.2019.00052].

Coulson, S. J., A. Fjellberg, , D. J. Gwiazdowicz, N. V. Lebedeva, E. N. Melekhina, , T. Solhøy, , C. Erséus, K. Maraldo, L. Miko, H. Schatz, R. M.Schmelz, G. Søli & E. Stur (2013): Introduction of invertebrates into the High Arctic via imported soils: the case of Barentsburg in the Svalbard. – Biological Invasions **15**: 1–5 [https://doi.org/10.1007/s10530-012-0277-y].

Coulson, S. J., I. D.Hodkinson, N. R. Webb & J.A. Harrison (2002): Survival of terrestrial soil-dwelling arthropods on and in seawater: implications for trans-oceanic dispersal. – Functional Ecology **16**: 353–356 [https://doi.org/10.1046/j.1365-2435.2002.00636.x].

Coyle, D. R., U. J. Nagendra, M. K. Taylor, J. H. Campbell, C. E. Cunard, A. H. Joslin, A. Mundepi, C.A. Phillips & M. A. Callaham (2017): Soil fauna responses to natural disturbances, invasive species, and global climate change: Current state of the science and a call to action. – Soil Biology and Biochemistry **110**: 116–133 [https://doi.org/10.1016/j.soilbio.2017.03.008].

Crowther, T. W., L. Boddy & T. H. Jones (2011): Outcomes of fungal interactions are determined by soil invertebrate grazers: Grazers alter fungal community. – Ecology Letters **14**: 1134–1142 [https://doi.org/10.1111/j.1461-0248.2011.01682.x].

Culik, M. P. & D. Z. Filho Zeppelini (2003): Diversity and distribution of Collembola (Arthropoda: Hexapoda) of Brazil. – Biodiversity & Conservation **12**: 1119–1143 [https://doi.org/10.1023/A:1023069912619].

de Carvalho, M. de, F. Bockmann, D. Amorim, M. de Vivo, M. Toledo-Piza, N. Menezes, J. Figueiredo, R. Macedo Corrêa e Castro, A. Gill, J. McEachran, L. Compagno, R. Schelly, R. Britz, J. Lundberg, R. Vari& G. Nelson (2005): Revisiting the taxonomic impediment. Letters to the editor. – Science **307**: 353.

de Jong, Y., M. Verbeek, V. Michelsen, P. de P. Bjørn, W. Los, F. Steeman, N. Bailly, C. Basire, P. Chylarecki, E. Stloukal, G. Hagedorn, F. T. Wetzel, F. Glöckler, A. Kroupa, G. Korb, A. Hoffmann, C. Häuser, A. Kohlbecker, A. Müller, A. Güntsch, P. Stoev & L. Penev (2014): Fauna Europaea – all European animal species on the web. – Biodiversity Data Journal **2**: e4034 [https://doi.org/10.3897/BDJ.2.e4034].

Deharveng, L. (1983): Morphologie évolutive des Collemboles Neanurinae en particulier de la lignée Neanurienne. – Travaux du Laboratoire d’Ecobiologie des Arthropodes Edaphiques, Toulouse **4**: 1–63.

Deharveng, L. (2004): Recent advances in Collembola systematics. – Pedobiologia **48**: 415–433 [https://doi.org/10.1016/j.pedobi.2004.08.001].

DeSalle, R., M. G. Egan & M. Siddall (2005): The unholy trinity: taxonomy, species delimitation and DNA barcoding. – Philosophical Transactions of the Royal Society B: Biological Sciences **360**: 1905–1916 [https://doi.org/10.1098/rstb.2005.1722].

Dillon, M. E., G. Wang & R. B. Huey (2010): Global metabolic impacts of recent climate warming. – Nature **467**: 704–706 [https://doi.org/10.1038/nature09407].

Dunger, W. & B. Schlitt (2011): Synopses on Palaearctic Collembola: Tullbergiidae. – Soil Organisms **83**.

Dunger, W., H.-J. Schulz & B. Zimdars (2002): Colonization behaviour of Collembola under different conditions of dispersal: Proceedings of the Xth international Colloquium on Apterygota, České Budějovice 2000: Apterygota at the Beginning of the Third Millennium. – Pedobiologia **46**: 316–327 [https://doi.org/10.1078/0031-4056-00139].

Ebach, M. C, A. G. Valdecasas & Q. D. Wheeler (2011): Impediments to taxonomy and users of taxonomy: accessibility and impact evaluation. – Cladistics **27**: 550–557.

Eisenhauer, N., A. C. W.Sabais & S. Scheu (2011): Collembola species composition and diversity effects on ecosystem functioning vary with plant functional group identity. – Soil Biology and Biochemistry **43**: 1697–1704 [https://doi.org/10.1016/j.soilbio.2011.04.015].

Eitzinger, B., N. Abrego., D. Gravel, T. Huotari, E. J. Vesterinen & T. Roslin (2019): Assessing changes in arthropod predator–prey interactions through DNA-based gut content analysis—variable environment, stable diet. – Molecular Ecology **28**: 266–280.

Ellers, J., M. P. Berg, A. T. C. Dias, S. Fontana, A. Ooms & M. Moretti (2018): Diversity in form and function: Vertical distribution of soil fauna mediates multidimensional trait variation. – Journal of Animal Ecology **87**: 933–944 [https://doi.org/10.1111/1365-2656.12838].

Endlweber, K. & S. Scheu (2007): Interactions between mycorrhizal fungi and Collembola: effects on root structure of competing plant species. – Biology and Fertility of Soils **43**: 741–749 [https://doi.org/10.1007/s00374-006-0157-7].

Erktan, A., D. Or & S. Scheu (2020a): The physical structure of soil: determinant and consequence of trophic interactions. – Soil Biology & Biochemistry [https://doi.org/10.1016/j.soilbio.2020.107876].

Erktan, A., M. C. Rillig, A. Carminati, A. Jousset & S. Scheu (2020b): Bacterial and fungal predator – prey interactions modulate soil aggregation (preprint): Biogeophysics: Physical - Biological Coupling [https://doi.org/10.5194/bg-2020-48].

Ettema, C.H. & D. A. Wardle (2002): Spatial soil ecology. – Trends in Ecology & Evolution 17: 177–183.

Ferreira, A. S., I. M. Rocha, S. Dos, B. C. Bellini & A. Vasconcellos (2018): Effects of habitat heterogeneity on epiedaphic Collembola (Arthropoda: Hexapoda) in a semiarid ecosystem in Northeast Brazil. – Zoologia (Curitiba) **35** [https://doi.org/10.3897/zoologia.35.e13653].

Fjellberg, A. (1999): The labial palp in Collembola. – Zoologischer Anzeiger **237**: 309–330.

Fountain, M. T. & S. P. Hopkin (2005): *Folsomia candida* (Collembola): a "Standard" Soil Arthropod*. – Annual Review of Entomology **50**: 201–222 [https://doi.org/10.1146/annurev.ento.50.071803.130331].

Fujii, S., A. Yamada, K. Fukushima, S. Saitoh, K. Kitayama & H. Takeda (2013): Relationships among distribution of fine roots, soil DOC concentration and Collembola. – Plant Root **7**: 21–27.

Gallagher, R. V., D. S. Falster, B. S. Maitner, R. Salguero-Gómez, V. Vandvik, W. D. Pearse, F. D. Schneider, J. Kattge, J. H. Poelen, J. S. Madin, M. J. Ankenbrand, C. Penone, X. Feng, V. M. Adams, J. Alroy, S. C. Andrew, M. A. Balk, L. M. Bland, B. L. Boyle, C. H. Bravo-Avila, I. Brennan, A. J. R. Carthey, R. Catullo, B. R. Cavazos, D. A. Conde, S. L. Chown, B. Fadrique, H. Gibb, A. H. Halbritter, J. Hammock, J. A. Hogan, H. Holewa, M. Hope, C. M. Iversen, M. Jochum, M. Kearney, A. Keller, P. Mabee, P. Manning, L. McCormack, S. T. Michaletz, D. S. Park, T. M. Perez, S. Pineda-Munoz, C. A. Ray, M. Rossetto, H. Sauquet, B. Sparrow, M. J. Spasojevic, R. J. Telford, J. A. Tobias, C. Violle, R. Walls, K. C. B. Weiss, M. Westoby,I. J. Wright & B. J. Enquist (2020): Open Science principles for accelerating trait-based science across the Tree of Life. – Nature Ecology & Evolution **4**: 294-303 [https://doi.org/10.1038/s41559-020-1109-6].

Gange, A. (2000): Arbuscular mycorrhizal fungi, Collembola and plant growth. – Tree **15**: 369–372.

Gao, M., X. Sun, Z. Qiao, H. Hou, T. Lu, D.Wu & G. Jin (2018): Distinct patterns suggest that assembly processes differ for dominant arthropods in above-ground and below-ground ecosystems. – Pedobiologia **69**: 17–28 [https://doi.org/10.1016/j.pedobi.2018.06.003].

Geisen, S., M. J. I. Briones, H. Gan, V. M. Behan-Pelletier, V.-P. Friman, G. Arjen de Groot, S. E. Hannula, Z. Lindo, L. Philippot, A. V. Tiunov & D. H. Wall (2019): A methodological framework to embrace soil biodiversity. – Soil Biology and Biochemistry **136**: 107536 [https://doi.org/10.1016/j.soilbio.2019.107536].

Gisin, H. (1943): Ökologie und Lebensgemeinschaften der Collembolen im schweizerischen Exkursionsgebiet Basels. – A. Kundig, Geneve.

Graf, M., M. Bonn, L. Feldhahn, F: Kurth, T. E. E. Grams, S. Herrmann, M. Tarkka, F. Buscot & S. Scheu (2019): Collembola interact with mycorrhizal fungi in modifying oak morphology, C and N incorporation and transcriptomics. – Royal Society Open Science **6**: 181869 [http://dx.doi.org/10.1098/rsos.181869].

Greenslade, P. (2018): Why are there so many exotic springtails in Australia? A review. – Soil Organisms **90**: 141–156.

Gressitt, J. L., R. E. Leech & C. W. O'Brien(1960): Trapping of air-borne insects in the Antarctic area. – Pacific Insects **2**: 245–250.

Grosswald, M. G. & T. J. Hughes (2002): The Russian component of an Arctic Ice Sheet during the Last Glacial Maximum. – Quaternary Science Reviews, EPILOG **21**: 121–146 [https://doi.org/10.1016/S0277-3791(01)00078-6].

Hågvar, S. (2010): primary succession of springtails (Collembola) in a Norwegian glacier foreland. – Arctic, Antarctic, and Alpine Research **42**: 422–429 [https://doi.org/10.1657/1938-4246-42.4.422].

Hagvar, S. (2000): Navigation and behaviour of four Collembola species migrating on the snow surface. – Pedobiologia **44**: 221–233.

Hassall, M., S. Adl, M. Berg, B. Griffiths & S. Scheu (2006): Soil fauna–microbe interactions: towards a conceptual framework for research. – European Journal of Soil Biology, ICSZ Soil Animals and Ecosystems Services Proceedings of the XIVth International Colloquium on Soil Biology **42**: 54–60 [https://doi.org/10.1016/j.ejsobi.2006.07.007].

Hawes, T. C. & P. Greenslade (2013): The aerial invertebrate fauna of subantarctic Macquarie Island. – Journal of Biogeography **40**: 1501–1511 [https://doi.org/10.1111/jbi.12090].

Hebert, P. D. N., A. Cywinska, S. L. Ball & J. R. deWaard (2003): Biological identifications through DNA barcodes. – Proceedings. Biological Sciences **270**: 313–321 [https://doi.org/10.1098/rspb.2002.2218].

Heiniger, C., S. Barot, J.-F. Ponge, S. Salmon, L. Botton-Divet, D. Carmignac & F. Dubs (2014): Effect of habitat spatiotemporal structure on collembolan diversity. – Pedobiologia **57**: 103–117 [https://doi.org/10.1016/j.pedobi.2014.01.006].

Hengl, T., J. M. Jesus, G. B. M. de, Heuvelink, M. R. Gonzalez, M. Kilibarda, A. Blagotić, W. Shangguan, M. N. Wright, X. Geng, B. Bauer-Marschallinger, M. A. Guevara, R. Vargas, R. A. MacMillan, N. H. Batjes, J. G. B. Leenaars, E. Ribeiro, I. Wheeler, S. Mantel & B. Kempen (2017): SoilGrids250m: Global gridded soil information based on machine learning. – PLOS ONE **12**: e0169748 [https://doi.org/10.1371/journal.pone.0169748].

Hill, M. O. (1973): Diversity and evenness: A unifying notation and its consequences. – Ecology **54**: 427–432 [https://doi.org/10.2307/1934352].

HilleRisLambers, J., P. B. Adler, W. S. Harpole, L. M. Levine & M. M. Mayfield (2012): Rethinking community assembly through the lens of coexistence theory. – Annual Review of Ecology, Evolution, and Systematics **43**: 227–248 [https://doi.org/10.1146/annurev-ecolsys-110411-160411].

Holmstrup, M. (2018): Screening of cold tolerance in fifteen springtail species. – Journal of Thermal Biology **77**: 1–6 [https://doi.org/10.1016/j.jtherbio.2018.07.017].

Hopkin, S. (1998): Collembola; the most abundant insects on Earth. – Antenna **22**: 117–121.

Hopkin, S. P. (1997): Biology of springtails: (Insecta: Collembola). – Oxford Science Publications, Oxford.

Ingimarsdóttir, M., T. Caruso, J. Ripa, Ó. B. Magnúsdóttir, M. Migliorini & K. Hedlund (2012): Primary assembly of soil communities: disentangling the effect of dispersal and local environment. – Oecologia **170**: 745–754 [https://doi.org/10.1007/s00442-012-2334-8].

IPBES (2019): Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. – Paris.

Janion-Scheepers, C., J. Measey, B. Braschler, S. L. Chown, L. Coetzee, J. F. Colville, J. Dames, A. B. Davies, S. J. Davies, A. L. V. Davis, A. S. Dippenaar-Schoeman, G. A. Duffy, D. Fourie, C. Griffiths, C. R. Haddad, M. Hamer, D. G. Herbert, E. A. Hugo-Coetzee, A. Jacobs, K. Jacobs, C. J. Rensburg, S. van Lamani, L. N. Lotz, S. vdM. Louw, R. Lyle, A. P. Malan, M. Marais, J.-A. Neethling, T. C. Nxele, D. J. Plisko, L. Prendini, A. N. Rink, A. Swart, P. Theron, M. Truter, E. Ueckermann, V. M. Uys, M. H. Villet, S. Willows-Munro & J. R. U. Wilson (2016): Soil biota in a megadiverse country: Current knowledge and future research directions in South Africa. – Pedobiologia **59**: 129–174 [https://doi.org/10.1016/j.pedobi.2016.03.004].

Janion-Scheepers, C., L. Phillips, C. M. Sgrò, G. A. Duffy, R. Hallas & S. L. Chown (2018): Basal resistance enhances warming tolerance of alien over indigenous species across latitude. – Proceedings of the National Academy of Sciences **115**: 145–150 [https://doi.org/10.1073/pnas.1715598115].

Janssens, F. & F. B. Dazzo (2004): Image analysis, morphometry and classification of scanned Collembola samples applied to specimen identification. – Checklist of the Collembola of the World.

Johnson, D., M. Krsek, E. M. Wellington, A. W. Stott, L. Cole, R. D. Bardgett, D. J. Read & J. R. Leake (2005): Soil invertebrates disrupt carbon flow through fungal networks. – Science **309**: 1047–1047.

Joimel, S., B. Grard, A. Auclerc, M. Hedde, N. Le Doaré, S. Salmon & C. Chenu (2018): Are Collembola “flying” onto green roofs? – Ecological Engineering **111**: 117–124 [https://doi.org/10.1016/j.ecoleng.2017.12.002].

Joimel, S., C. Schwartz, M. Hedde, S. Kiyota, P. H. Krogh, J. Nahmani, G. Pérès, A. Vergnes & J. Cortet (2017): Urban and industrial land uses have a higher soil biological quality than expected from physicochemical quality. – Science of The Total Environment **584–585**: 614–621 [https://doi.org/10.1016/j.scitotenv.2017.01.086].

Joosse, E. N. (1969): The formation and biological significance of aggregations in the distribution of Collembola. – Netherlands Journal of Zoology **20**: 299–314.

Jordana, R. (2012): Synopses of Palaearctic Collembola: Capbryinae & Entomobryini. – Senkenberg Museum of Natural History Görlitz, Görlitz.

Jordana, R. & E. Baquero-Martin (2005): A proposal of characters for taxonomic identification of *Entomobrya* species (Collembola, Entomobryomorpha), with description of a new species. – Abhandlungen Und Berichte Des Naturkundemuseums Görlitz **76**: 117–134.

Kampichler, C. & A. Bruckner (2009): The role of microarthropods in terrestrial decomposition: a meta-analysis of 40 years of litterbag studies. – Biological Reviews **84**: 375–389 [https://doi.org/10.1111/j.1469-185X.2009.00078.x].

Kaneda, S. & N. Kaneko (2008): Collembolans feeding on soil affect carbon and nitrogen mineralization by their influence on microbial and nematode activities. – Biology and Fertility of Soils **44**: 435–442 [https://doi.org/10.1007/s00374-007-0222-x].

Kardol, P., W. N. Reynolds, R. J. Norby & A. T. Classen (2011): Climate change effects on soil microarthropod abundance and community structure. – Applied Soil Ecology **47**: 37–44 [https://doi.org/10.1016/j.apsoil.2010.11.001].

Katz, A. D., R. Giordano & F. N. Soto-Adames (2015): Operational criteria for cryptic species delimitation when evidence is limited, as exemplified by North American *Entomobrya* (Collembola: Entomobryidae). – Zoological Journal of the Linnean Society **173**: 818–840 [https://doi.org/10.1111/zoj.12220].

King, R. A., D. S. Read, M. Traugott & W. O. C. Symondson (2008): Molecular analysis of predation: a review of best practice for DNA-based approaches. – Molecular Ecology **17**: 947–963 [https://doi.org/10.1111/j.1365-294X.2007.03613.x].

Krab, E. J., S. Monteux, J. T. Weedon & E. Dorrepaal (2019): Plant expansion drives bacteria and collembola communities under winter climate change in frost-affected tundra. – Soil Biology and Biochemistry **138**: 107569 [https://doi.org/10.1016/j.soilbio.2019.107569].

Kuznetsova, N. A. (2003): Humidity and distribution of springtails. – Entomological Review **83**: 9.

Kuznetsova, N. A., A. I. Bokova, A. K. Saraeva & Yu. B. Shveenkova (2019a): Communities of Collembola in the forests of Southern Primorye as a benchmark of high diversity and organization complexity. – Biology Bulletin **46**: 483–491 [https://doi.org/10.1134/S1062359019050066].

Kuznetsova, N. A., A. I. Bokova, A. K. Saraeva & Yu. B. Shveenkova (2019b): Structure of the species diversity of soil springtails (Hexapoda, Collembola) in pine forests of the Caucasus and the Russian plain: a multi-scale approach. – Entomological Review **99**: 143–157 [https://doi.org/10.1134/S0013873819020027].

Lavorel, S. & E. Garnier (2002): Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. – Functional Ecology **16**: 545–556.

Lehmitz, R., D. Russell, K. Hohberg, A. Christian & W. E. Xylander (2011): Wind dispersal of oribatid mites as a mode of migration. – Pedobiologia **54**: 201–207.

Lin, D., J. Crabtree, I. Dillo, R. R. Downs, R. Edmunds, D. Giaretta, M. De Giusti, H. L'Hours, W. Hugo, R. Jenkyns, V. Khodiyar, M. E. Martone, M. Mokrane, V. Navale, J. Petters, B. Sierman, D. V. Sokolova, M. Stockhause & J. Westbrook (2020): The TRUST Principles for digital repositories. – Scientific Data **7**: 144 [https://doi.org/10.1038/s41597-020-0486-7].

Lindo, Z. (2020): Transoceanic dispersal of terrestrial species by debris rafting. – Ecography ecog. 05155 [https://doi.org/10.1111/ecog.05155].

Liu, J., M. Gao, Y. Ma, X. Sun, X. Zhu, S. Adl & D. Wu (2019): Spatial and environmental factors are minor structuring forces in a soil Collembola metacommunity in a maize agroecosystem. – Pedobiologia **76**: 150572 [https://doi.org/10.1016/j.pedobi.2019.150572].

Liu, M., L. J. Clarke, S. C. Baker, G. J. Jordan & C. P. Burridge (2019): A practical guide to DNA metabarcoding for entomological ecologists. – Ecological Entomology **45**: 373–385 [https://doi.org/10.1111/een.12831].

Liu, W. P. A., C. Janion & S. L. Chown (2012): Collembola diversity in the critically endangered Cape Flats Sand Fynbos and adjacent pine plantations. – Pedobiologia **55**: 203–209 [https://doi.org/10.1016/j.pedobi.2012.03.002].

Lukić, M., D. Porco, A. Bedos & L. Deharveng (2015): The puzzling distribution of *Heteromurus* (*Verhoeffiella*) *absoloni* Kseneman, 1938 (Collembola: Entomobryidae: Heteromurinae) resolved: detailed redescription of the nominal species and description of a new species from Catalonia (Spain). – Zootaxa **4039**: 249–275 [https://doi.org/10.11646/zootaxa.4039.2.3].

Maaß, S., T. Caruso & M. C. Rillig (2015): Functional role of microarthropods in soil aggregation. – Pedobiologia **58**: 59–63 [https://doi.org/10.1016/j.pedobi.2015.03.001].

Macfadyen, A. (1953): Notes on methods for the extraction of small soil arthropods. – The Journal of Animal Ecology **22**: 65 [https://doi.org/10.2307/1691].

Macfadyen, A. (1961): Improved funnel-type extractors for soil arthropods. – The Journal of Animal Ecology 171–184.

Makkonen, M., M. P. Berg, J. R. van Hal, T. V. Callaghan, M. C. Press & R. Aerts (2011): Traits explain the responses of a sub-arctic Collembola community to climate manipulation. – Soil Biology and Biochemistry **43**: 377–384 [https://doi.org/10.1016/j.soilbio.2010.11.004].

Malcicka, M., M. P. Berg & J. Ellers (2017): Ecomorphological adaptations in Collembola in relation to feeding strategies and microhabitat. – European Journal of Soil Biology **78**: 82–91 [https://doi.org/10.1016/j.ejsobi.2016.12.004].

Malmström, A. (2012): Life-history traits predict recovery patterns in Collembola species after fire: A 10 year study. – Applied Soil Ecology **56**: 35–42 [https://doi.org/10.1016/j.apsoil.2012.02.007].

Marsh, C. J. & R. M. Ewers (2013): A fractal-based sampling design for ecological surveys quantifying β-diversity. – Methods in Ecology and Evolution **4**: 63–72 [https://doi.org/10.1111/j.2041-210x.2012.00256.x].

Marshall, V. G. (1972): Comparison of two methods of estimating efficiency of funnel extractors for soil microarthropods. – Soil Biology and Biochemistry **4**: 417–426 [https://doi.org/10.1016/0038-0717(72)90056-9].

Martins da Silva, P., M. P. Berg, A. R. M. Serrano, F. Dubs & J. P. Sousa (2012): Environmental factors at different spatial scales governing soil fauna community patterns in fragmented forests. – Landscape Ecology **27**: 1337–1349 [https://doi.org/10.1007/s10980-012-9788-2].

Martins da Silva, P.M., M. P. Berg, A. A. da Silva, S. Dias, P. J. Leitão, D. Chamberlain, J. Niemelä, A. R. M. Serrano & J. P. Sousa (2015): Soil fauna through the landscape window: factors shaping surface-and soil-dwelling communities across spatial scales in cork-oak mosaics. – Landscape Ecology **30**: 1511–1526 [https://doi.org/10.1007/s10980-015-0206-4].

McGill, B. J., B. J. Enquist, E. Weiher & M. Westoby (2006): Rebuilding community ecology from functional traits. – Trends in Ecology & Evolution **21**: 178–185 [https://doi.org/10.1016/j.tree.2006.02.002].

McNabb, D.M., J. Halaj & D. H. Wise (2001): Inferring trophic positions of generalist predators and their linkage to the detrital food web in agroecosystems: a stable isotope analysis. – Pedobiologia **45**: 289–297 [https://doi.org/10.1078/0031-4056-00087].

Meid, S., R. Baum, P. Bhatty, P. Grobe, C. Köhler, B. Quast & L. Vogt (2017): Developing a module for generating formalized semantic morphological descriptions for morph·D·Base. – Biodiversity Information Science and Standarts **1**: e15141 [https://doi.org/10.3897/tdwgproceedings.1.15141].

Metera, E., T. Sakowski, K. Słoniewski & B. Romanowicz (2010): Grazing as a tool to maintain biodiversity of grassland-a review. – Animal Science Papers and Reports **28**: 315–334.

Newbold, T., L. N. Hudson, S. L. Hill, S. Contu, I. Lysenko,R.A. Senior, L. Börger, D. J. Bennett, A. Choimes, B. Collen & Purvis A. (2015): Global effects of land use on local terrestrial biodiversity. – Nature **520**: 45–50.

Newell, K. (1984): Interaction between two decomposer basidiomycetes and a collembolan under Sitka spruce: distribution, abundance and selective grazing. – Soil Biology and Biochemistry **16**: 227–233.

Oliverio, A. M., H. Gan, K. Wickings & N. Fierer (2018): A DNA metabarcoding approach to characterize soil arthropod communities. – Soil Biology and Biochemistry **125**: 37–43 [https://doi.org/10.1016/j.soilbio.2018.06.026].

Pan, Z.-X. (2015): Two closely related *Homidia* species (Entomobryidae, Collembola) revealed by morphological and molecular evidence. – Zootaxa **3918**: 285–294 [https://doi.org/10.11646/zootaxa.3918.2.9].

Petersen, H. & M. Luxton (1982): A comparative analysis of soil fauna populations and their role in decomposition processes. – Oikos **39**: 288–388 [https://doi.org/10.2307/3544689].

Pey, B., J. Nahmani, A. Auclerc, Y. Capowiez, D. Cluzeau, J. Cortet, T. Decaëns, L. Deharveng, F. Dubs, S. Joimel, C. Briard, F. Grumiaux, M.-A. Laporte, A. Pasquet, C. Pelosi, C. Pernin, J.-F. Ponge, S. Salmon, L. Santorufo & M. Hedde (2014): Current use of and future needs for soil invertebrate functional traits in community ecology. – Basic and Applied Ecology **15**: 194–206 [https://doi.org/10.1016/j.baae.2014.03.007].

Phillips, L. M., I. Aitkenhead, C. Janion-Scheepers, C. K. King, m. A. McGeoch, U. N. Nielsen, A. Terauds, W. P. A. Liu & S. L. Chown (2020): Basal tolerance but not plasticity gives invasive springtails the advantage in an assemblage setting. – Conservation Physiology 8 [https://doi.org/10.1093/conphys/coaa049].

Pollierer, M. M., T. Larsen, A. Potapov, A. Brückner, M. Heethoff, J. Dyckmans & S. Scheu (2019): Compound-specific isotope analysis of amino acids as a new tool to uncover trophic chains in soil food webs. – Ecological Monographs **89**: e01384 [https://doi.org/10.1002/ecm.1384].

Ponge, J.-F. (1991): Food resources and diets of soil animals in a small area of Scots pine litter. – Geoderma **49**: 33–62 [https://doi.org/10.1016/0016-7061(91)90090-G].

Ponge, J.-F. (1993): Biocenoses of Collembola in atlantic temperate grass-woodland ecosystems. – Pedobiologia **37**: 223–244.

Ponge, J.-F. (2000): Vertical distribution of Collembola (Hexapoda) and their food resources in organic horizons of beech forests. – Biology and Fertility of Soils **32**: 508–522.

Ponge, J.-F. (2020): Move or change, an eco-evolutionary dilemma: The case of Collembola. – Pedobiologia **79**: 150625 [https://doi.org/10.1016/j.pedobi.2020.150625].

Ponge, J.-F. & S. Salmon (2013): Spatial and taxonomic correlates of species and species trait assemblages in soil invertebrate communities. – Pedobiologia **56**: 129–136 [https://doi.org/10.1016/j.pedobi.2013.02.001].

Ponge, J.-F., F. Dubs, S. Gillet, J. Sousa & P. Lavelle (2006): Decreased biodiversity in soil springtail communities: the importance of dispersal and landuse history in heterogeneous landscapes. – Soil Biology and Biochemistry **38**: 1158–1161 [https://doi.org/10.1016/j.soilbio.2005.09.004].

Popkin, G. (2019): Data sharing and how it can benefit your scientific career. – Nature 569: 445–447 [https://doi.org/10.1038/d41586-019-01506-x].

Porco, D., A. Bedos & L. Deharveng (2010): Description and DNA barcoding assessment of the new species *Deutonura gibbosa* (Collembola: Neanuridae: Neanurinae), a common springtail of Alps and Jura. – Zootaxa **2639**: 59–68 [https://doi.org/10.11646/zootaxa.2639.1.6].

Porco, D., D. Skarżyński, T. Decaëns, P. D. N. Hebert & L. Deharveng (2014): Barcoding the Collembola of Churchill: a molecular taxonomic reassessment of species diversity in a sub-Arctic area. – Molecular Ecology Resources **14**: 249–261 [https://doi.org/10.1111/1755-0998.12172].

Porco, D., A. Bedos, P. Greenslade, C. Janion, D. Skarżyński, M. I. Stevens, B. J. van Vuuren & L. Deharveng (2012): Challenging species delimitation in Collembola: cryptic diversity among common springtails unveiled by DNA barcoding. – Invertebrate Systematics **26**: 470–477 [https://doi.org/10.1071/IS12026].

Posthuma, L., R.A. Verweij, B. Widianarko & C. Zonneveld (1993): Life-history patterns in metal-adapted Collembola. – Oikos **67**: 235–249 [https://doi.org/10.2307/3545468].

Potapov, A., U. Brose, S. Scheu & A. Tiunov (2019): Trophic position of consumers and size structure of food webs across aquatic and terrestrial ecosystems. – The American Naturalist **194**: 823–839 [https://doi.org/10.1086/705811].

Potapov, A. M., A. A. Goncharov, E. E. Semenina, A. Y. Korotkevich, S. M. Tsurikov, O. L. Rozanova, A. E. Anichkin, A. G. Zuev, E. S. Samoylova, I. I. Semenyuk, I. V. Yevdokimov & A. V. Tiunov (2017): Arthropods in the subsoil: Abundance and vertical distribution as related to soil organic matter, microbial biomass and plant roots. – European Journal of Soil Biology **82**: 88–97 [https://doi.org/10.1016/j.ejsobi.2017.09.001].

Potapov, A. M., A. Yu. Korotkevich & A. V. Tiunov (2018): Non-vascular plants as a food source for litter-dwelling Collembola: Field evidence. – Pedobiologia **66**: 11–17 [https://doi.org/10.1016/j.pedobi.2017.12.005].

Potapov, A. M., M. M. Pollierer, S. Salmon, V. Sustr & T.-W. Chen (2020): Multidimensional trophic niche approach: gut content, digestive enzymes, fatty acids and stable isotopes in Collembola. – BioRxiv.

Potapov, A. M., E. E. Semenina, A.Yu. Korotkevich, N. A. Kuznetsova & A. V. Tiunov (2016): Connecting taxonomy and ecology: Trophic niches of collembolans as related to taxonomic identity and life forms. – Soil Biology and Biochemistry **101**: 20–31 [https://doi.org/10.1016/j.soilbio.2016.07.002].

Potapov, A. M. & A. V. Tiunov (2016): Stable isotope composition of mycophagous collembolans versus mycotrophic plants: Do soil invertebrates feed on mycorrhizal fungi? – Soil Biology and Biochemistry **93**: 115–118 [https://doi.org/10.1016/j.soilbio.2015.11.001].

Potapov, A. M., A. V. Tiunov & S. Scheu (2019): Uncovering trophic positions and food resources of soil animals using bulk natural stable isotope composition. – Biological Reviews **94**: 37–59 [https://doi.org/10.1111/brv.12434].

Potapov, M. (2001): Synopses on palaearctic Collembola: Isotomidae. Sttatlisches Museum für Natürkunde Görlitz, Görlitz.

Querner, P. & A. Bruckner (2010): Combining pitfall traps and soil samples to collect Collembola for site scale biodiversity assessments. – Applied Soil Ecology **45**: 293–297 [https://doi.org/10.1016/j.apsoil.2010.05.005].

Querner, P., A. Bruckner, T. Drapela, D. Moser, J. G. Zaller & T. Frank (2013): Landscape and site effects on Collembola diversity and abundance in winter oilseed rape fields in eastern Austria. – Agriculture, Ecosystems & Environment **164**: 145–154 [https://doi.org/10.1016/j.agee.2012.09.016].

Raschmanová, N., V. Šustr, Ľ. Kováč, A. Parimuchová & M. Devetter (2018): Testing the climatic variability hypothesis in edaphic and subterranean Collembola (Hexapoda). – Journal of Thermal Biology **78**: 391–400 [https://doi.org/10.1016/j.jtherbio.2018.11.004].

Raymond-Léonard, L. J., D. Gravel & I. T. Handa (2019): A novel set of traits to describe Collembola mouthparts: taking a bite out of the broad chewing mandible classification. – Soil Biology and Biochemistry **138**: 107608 [https://doi.org/10.1016/j.soilbio.2019.107608].

Riedel, A., K. Sagata, Y. R. Suhardjono, R. Tänzler & M. Balke (2013): Integrative taxonomy on the fast track - towards more sustainability in biodiversity research. – Frontiers in Zoology **10**: 15 [https://doi.org/10.1186/1742-9994-10-15].

Rosenstiel, T. N., E. E. Shortlidge, A. N. Melnychenko, J. F. Pankow & S. M. Eppley (2012): Sex-specific volatile compounds influence microarthropod-mediated fertilization of moss. – Nature **489**: 431–433.

Rossi, R. E., D. J. Mulla, A. G. Journel & E. H. Franz (1992): Geostatistical tools for modeling and interpreting ecological spatial dependence. – Ecological Monographs **62**: 277–314 [https://doi.org/10.2307/2937096].

Ruess, L. & P. M. Chamberlain (2010): The fat that matters: Soil food web analysis using fatty acids and their carbon stable isotope signature. – Soil Biology and Biochemistry **42**: 1898–1910 [https://doi.org/10.1016/j.soilbio.2010.07.020].

Rusek, J. (1998): Biodiversity of Collembola and their functional role in the ecosystem. – Biodiversity and Conservation **7**: 1207–1219 [https://doi.org/10.1023/A:1008887817883].

Rusek, J. (2007): A new classification of Collembola and Protura life forms. – In: Tajovský, K., J. Schlaghamerský & V. Pižl (eds): Contributions To Soil Zoology in Central Europe. – ISB BC AS CR: 109–115.

Russell, D. J. (2008): Metacommunity responses of soil Collembola to inundation intensity in the Upper Rhine Valley. – Peckiana **5**: 127–143.

Russell, D. J. & V. Gergócs (2019): Forest-management types similarly influence soil collembolan communities throughout regions in Germany – A data bank analysis. – Forest Ecology and Management **434**: 49–62 [https://doi.org/10.1016/j.foreco.2018.11.050].

Rusterholz, H.-P., J.-A. Salamon, R. Ruckli & B. Baur (2014): Effects of the annual invasive plant *Impatiens glandulifera* on the Collembola and Acari communities in a deciduous forest. – Pedobiologia **57**: 285–291 [https://doi.org/10.1016/j.pedobi.2014.07.001].

Salmon, S. & J.-F. Ponge (2001): Earthworm excreta attract soil springtails: laboratory experiments on *Heteromurus Nitidus* (Collembola: Entomobryidae). – Soil Biology and Biochemistry **33**: 1959–1969 [https://doi.org/10.1016/S0038-0717(01)00129-8].

Salmon, S. & J.-F. Ponge (2012): Species traits and habitats in springtail communities: A regional scale study. – Pedobiologia **55**: 295–301 [https://doi.org/10.1016/j.pedobi.2012.05.003].

Salmon, S., J.-F. Ponge, S. Gachet, L. Deharveng, N. Lefebvre & F. Delabrosse (2014): Linking species, traits and habitat characteristics of Collembola at European scale. – Soil Biology and Biochemistry **75**: 73–85 [https://doi.org/10.1016/j.soilbio.2014.04.002].

Salmon, S., S. Rebuffat, S. Prado, M. Sablier, C. D'Haese, J.-S. Sun & J.-F. Ponge (2019): Chemical communication in springtails: a review of facts and perspectives. – Biology and Fertility of Soils **55**: 425–438 [https://doi.org/10.1007/s00374-019-01365-8].

Saraeva, A.K., M. B. Potapov & N. A. Kuznetsova (2015): Different-scale distribution of collembola in homogenous ground vegetation: Stability of parameters in space and time. – Entomological Review **95**: 699–714 [https://doi.org/10.1134/S0013873815060032].

Scheu, S. & M. Folger (2004): Single and mixed diets in Collembola: effects on reproduction and stable isotope fractionation. – Functional Ecology **18**: 94–102 [https://doi.org/10.1046/j.0269-8463.2004.00807.x].

Schlick-Steiner, B. C., F. M. Steiner, B. Seifert, C. Stauffer, E. Christian & R. H. Crozier (2010): Integrative taxonomy: a multisource approach to exploring biodiversity. – Annual Review of Entomology **55**: 421–438 [https://doi.org/10.1146/annurev-ento-112408-085432].

Schneider, K. & M. Maraun (2009): Top-down control of soil microarthropods – Evidence from a laboratory experiment. – Soil Biology and Biochemistry **41**: 170–175 [https://doi.org/10.1016/j.soilbio.2008.10.013].

Schneider, C., C. Cruaud & C. A. D'Haese (2011): Unexpected diversity in Neelipleona revealed by molecular phylogeny approach (Hexapoda, Collembola). – Soil Organisms **83**: 383–398.

Semenina, E. E., A. E. Anichkin, O. L. Shilenkova, S. G. Ermilov & A. V. Tiunov (2015): Rapid extraction of invertebrates from tropical forest litter using modified Winkler apparatus. – Journal of Tropical Ecology **31**: 191–194.

Shaw, P. & M. Usher (1996): Edaphic Collembola of lodgepole pine *Pinus contorta* plantations in Cumbria, UK. – European Journal of Soil Biology **32**: 89–98.

Shveenkova, Y. (2011): Springtail communities (Collembola, Hexapoda). – In: Tiunov A.V. (ed): Structure and Functions of Soil Communities of a Monsoon Tropical Forest (Cat Tien National Park, Southern Vietnam). – KMK Scientific Press, Moscow: 131–147.

Siddiky, M. R. K., J. Kohler, M. Cosme & M. C. Rillig (2012): Soil biota effects on soil structure: Interactions between arbuscular mycorrhizal fungal mycelium and collembola. – Soil Biology and Biochemistry **50**: 33–39 [https://doi.org/10.1016/j.soilbio.2012.03.001].

Soto-Adames, F. N. (2002): Molecular phylogeny of the Puerto Rican *Lepidocyrtus* and *Pseudosinella* (Hexapoda: Collembola), a validation of Yoshii's "color pattern species." – Molecular Phylogenetics and Evolution **25**: 27–42 [https://doi.org/10.1016/S1055-7903(02)00250-6].

Sousa, J. P., T. Bolger, M. M. da Gama, T. Lukkari, J.-F. Ponge, C. Simón, G. Traser, A. J. Vanbergen, A. Brennan, F. Dubs, E. Ivitis, A. Keating, S. Stofer & A. D. Watt (2006): Changes in Collembola richness and diversity along a gradient of land-use intensity: A pan European study. – Pedobiologia **50**: 147–156 [https://doi.org/10.1016/j.pedobi.2005.10.005].

Sterzyńska, M., J. Shrubovych & P. Nicia, (2017): Impact of plant invasion (*Solidago gigantea* L.) on soil mesofauna in a riparian wet meadows. – Pedobiologia **64**: 1–7 [https://doi.org/10.1016/j.pedobi.2017.07.004].

Sticht, C., S. Schrader, A. Giesemann & H.-J. Weigel (2008): Atmospheric CO2 enrichment induces life strategy- and species-specific responses of collembolans in the rhizosphere of sugar beet and winter wheat. – Soil Biology and Biochemistry, Special Section: Functional Microbial Ecology: Molecular Approaches to Microbial Ecology and Microbial Habitats **40**: 1432–1445 [https://doi.org/10.1016/j.soilbio.2007.12.022].

Straalen, N. M. van & P. C. Rijninks (1982): Efficiency of Tullgren apparatus with respect to interpreting seasonal changes in age structure of soil arthropod populations. – Pedobiologia **24**: 197–209.

Ströbel, B., S. Schmelzle,, N. Blüthgen & M. Heethoff (2018): An automated device for the digitization and 3D modelling of insects, combining extended-depth-of-field and all-side multi-view imaging. – ZooKeys **759**: 1–27 [https://doi.org/10.3897/zookeys.759.24584].

Sun, X., A. Bedos & L. Deharveng (2018): Unusually low genetic divergence at COI barcode locus between two species of intertidal *Thalassaphorura* (Collembola: Onychiuridae). – PeerJ **6** [https://doi.org/10.7717/peerj.5021].

Sun, X., F. Zhang, Y. Ding, T. W. Davies, Y. Li & D. Wu (2017): Delimiting species of *Protaphorura* (Collembola: Onychiuridae): integrative evidence based on morphology, DNA sequences and geography. – Scientific Reports **7**: 8261 [https://doi.org/10.1038/s41598-017-08381-4].

Swift, M. J., O. W. Heal & J. M. Anderson (1979): Decomposition in terrestrial ecosystems. University of California Press, Berkeley.

Szeptycki, A. (1979): Chaetotaxy of the Entomobryidae and its Phylogenetical Significance. Morpho-systematic Studies on Collembola. IV.,(Polska Akademia Nauk, Zak\lad Zoologii Systematycznej i Doswiadczalnej, Panstwowe Wydawnictwo Naukowe: Warszawa-Kraków, Poland.). – Doswiadczalnej. Krakow **218**.

Takeda, H. & T. Abe (2001): Templates of food–habitat resources for the organization of soil animals in temperate and tropical forests. – Ecological Research **16**: 961–973 [https://doi.org/10.1046/j.1440-1703.2001.00450.x].

Tebbe, C. C., A. B. Czarnetzki & T. Thimm (2006): Collembola as a habitat for microorganisms. – In: König, H. & A. Varma (eds): Intestinal Microorganisms of Termites and Other Invertebrates. – Springer: 133–153.

Terauds, A., S. L. Chown & D. M. Bergstrom (2011): Spatial scale and species identity influence the indigenous–alien diversity relationship in springtails. – Ecology **92**: 1436–1447 [https://doi.org/10.1890/10-2216.1].

Thakur, M. P. & S. Geisen(2019): Trophic regulations of the soil microbiome. – Trends in Microbiology S0966842X19301027 [https://doi.org/10.1016/j.tim.2019.04.008].

Thibaud, J. (2013): Essay on the state of knowledge of collembolan diversity in the African-Malgasy Region. – Russian Entomological Journal **22**: 233–248.

Thibaud, J.-M., H.-J. Schulz & M. M. da Gama Assalina (2004): Synopses on Palaearctic Collembola: Hypogastruridae. Sttatlisches Museum für Natürkunde Görlitz, Görlitz.

Tully, T. & R. Ferrière (2008): Reproductive flexibility: Genetic variation, genetic costs and long-term evolution in a Collembola. – PLOS ONE **3**: e3207 [https://doi.org/10.1371/journal.pone.0003207].

Turnbull, M. S. & S. Stebaeva (2019): Collembola of Canada. – ZooKeys **819**: 187–195 [https://doi.org/10.3897/zookeys.819.23653].

van Straalen, N. M. (1989): Production and biomass turnover in two populations of forest floor Collembola. – Netherlands Journal of Zoology **39**: 156–168.

van Straalen, N. M., T.B.A. Burghouts, M. J. Doornhof, G. M. Groot, M. P. M. Janssen, E. N. G. van Joosse, J. H. Meerendonk, J. P. J. J. Theeuwen, H. A. Verhoef & H. r. Zoomer (1987): Efficiency of lead and cadmium excretion in populations of *orchesella cincta* (Collembola) from various contaminated forest soils. – Journal of Applied Ecology **24**: 953–968 [https://doi.org/10.2307/2403992].

Vandewalle, M., F. de Bello, M. P. Berg, T. Bolger, S. Dolédec, F. Dubs, C. K. Feld, R. Harrington, P. A. Harrison, S. Lavorel, P. M. Silva, M. da, Moretti, J. Niemelä, P. Santos, T. Sattler, J. P. Sousa, M. T. Sykes, A. J. Vanbergen & B. A. Woodcock (2010): Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. – Biodiversity and Conservation **19**: 2921–2947 [https://doi.org/10.1007/s10531-010-9798-9].

Vellend, M. (2010): Conceptual synthesis in community ecology. – The Quarterly Review of Biology 85: 183–206 [https://doi.org/10.1086/652373].

Verhoef, H. A. & C. J. Nagelkerke (1977): Formation and ecological significance of aggregations in Collembola: An experimental study. – Oecologia **31**: 215–226 [https://doi.org/10.1007/BF00346922].

Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel & E. Garnier (2007): Let the concept of trait be functional! – Oikos **116**: 882–892 [https://doi.org/10.1111/j.0030-1299.2007.15559.x].

Wall, D.H., M. A. Bradford, M. G. St. John, J. A. Trofymow, V. Behan-Pelletier, V., Bignell, D.E., Dangerfield, J.M., Parton, W.J., Rusek, W. Voigt, V. Wolters, H. Z. Gardel, F. O. Ayuke, R. Bashford, O. I. Beljakova, P. J. Bohlen, A. Brauman, S. Flemming, J. R. Henschel, D. L. Johnson, T. H. Jones, M. Kovarova, J. M. Kranabetter, L. Kutny, K.-C. Lin, M. Maryati, D. Masse, A. Pokarzhevskii, H. Rahman, M. G. Sabará, J.-A. Salamon, M. J. Swift, A. Varela, H. L. Vasconcelos, D. White & X. Zou (2008): Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. – Global Change Biology **14**: 2661–2677 [https://doi.org/10.1111/j.1365-2486.2008.01672.x].

Wallace, M. M. H. (1972): A portable power-operated apparatus for collecting epigaeic Collembola and Acari. – Australian Journal of Entomology **11**: 261–263 [https://doi.org/10.1111/j.1440-6055.1972.tb01629.x].

Whalley, P. & E. A. Jarzembowski (1981): A new assessment of *Rhyniella*, the earliest known insect, from the Devonian of Rhynie, Scotland. – Nature **291**: 317-317.

White, H. J., L. León-Sánchez,V. J. Burton, E. K. Cameron, T. Caruso, L. Cunha, T. Dirilgen, S. D. Jurburg, R. Kelly, D. Kumaresan, R. Ochoa-Hueso, A. Ordonez, H. R. P. Phillips, I. Prieto, O. Schmidt & P. Caplat (2020): Methods and approaches to advance soil macroecology. – Global Ecology and Biogeography **29**: 13156 [https://doi.org/10.1111/geb.13156].

Widenfalk, L. A., J. Bengtsson, Å. Berggren, K. Zwiggelaar, E. Spijkman, F. Huyer-Brugman & M. P. Berg (2015): Spatially structured environmental filtering of collembolan traits in late successional salt marsh vegetation. – Oecologia **179**: 537–549 [https://doi.org/10.1007/s00442-015-3345-z].

Widenfalk, L. A., A. Malmström, M. P. Berg & J. Bengtsson (2016): Small-scale Collembola community composition in a pine forest soil – Overdispersion in functional traits indicates the importance of species interactions. – Soil Biology and Biochemistry **103**: 52–62 [https://doi.org/10.1016/j.soilbio.2016.08.006].

Wieczorek, J., D. Bloom, R. Guralnick, S. Blum, M. Döring, R. Giovanni, T. Robertson & D. Vieglais (2012): Darwin core: An evolving community-developed biodiversity data standard. – PLOS ONE **7**: e29715 [https://doi.org/10.1371/journal.pone.0029715].

Wilkinson, M. D., M. Dumontier, M., J. Aalbersberg, G. Appleton, M. Axton, A. Baak, N. Blomberg, J.-W. Boiten, L. B. da Silva Santos, P. E. Bourne, J. Bouwman, A. J. Brookes, T. Clark, M. Crosas, I. Dillo, O. Dumon, S. Edmunds, C. T. Evelo, R. Finkers, A. Gonzalez-Beltran, A. J. G. Gray, P. Groth, C. Goble, J. S. Grethe, J. Heringa, P.A.C.'t Hoen, R. Hooft, T. Kuhn, R. Kok, J., Kok, S. J. Lusher, M. E. Martone, A. Mons, A. L. Packer, B. Persson, P. Rocca-Serra, M. Roos, R. van Schaik, S.-A. Sansone, E. Schultes, T. Sengstag, T. Slater, G. Strawn, M. A. Swertz, M. Thompson, J. van der Lei, E. van Mulligen, J. A. Velterop, P. Waagmeester, K. Wittenburg, J. Wolstencroft, J. Zhao & B. Mons (2016): The FAIR Guiding Principles for scientific data management and stewardship. – Scientific Data **3**: 160018 [https://doi.org/10.1038/sdata.2016.18].

Winkler, H. & C. Kampichler (2000): Local and regional species richness in communities of surface-dwelling grassland Collembola: indication of species saturation. – Ecography **23**: 385–392 [https://doi.org/10.1111/j.1600-0587.2000.tb00295.x].

Witteveen, J. & E. N. G. Joosse (1987): Growth, reproduction and mortality in marine littoral Collembola at different salinities. – Ecological Entomology **12**: 459–469 [https://doi.org/10.1111/j.1365-2311.1987.tb01027.x].

Xiong, Y., Y. Gao, W. Yin & Y. Luan, Y. (2008): Molecular phylogeny of Collembola inferred from ribosomal RNA genes. – Molecular Phylogenetics and Evolution **49**: 728–735 [https://doi.org/10.1016/j.ympev.2008.09.007].

Yin, R., I. Gruss, N. Eisenhauer, P. Kardol, M. P. Thakur, A. Schmidt, Z. Xu, J. Siebert, C. Zhang, G.-L.Wu & M. Schädler (2019): Land use modulates the effects of climate change on density but not community composition of Collembola. – Soil Biology and Biochemistry **138**: 107598 [https://doi.org/10.1016/j.soilbio.2019.107598].

Yosii, R. (1960): Studies on the Collembolan genus *Hypogastrura*. – The American Midland Naturalist **64**: 257–281 [https://doi.org/10.2307/2422661].

Zaitsev, A. S., N. M. van Straalen & M. P. Berg (2013): Landscape geological age explains large scale spatial trends in oribatid mite diversity. – Landscape Ecology **28**: 285–296 [https://doi.org/10.1007/s10980-012-9834-0].

Zeppelini, D., A. Dal Molin, C. J. E. Lamas, C. Sarmiento, C. A. Rheims, D. R. R. Fernandes, E. F. B. Lima, E. N. Silva, F. Carvalho-Filho, Ľ. Kováč, J. Montoya-Lerma, O. T. Moldovan, P. G. B. Souza-Dias, P. R. Demite, R. M. Feitosa, S. L. Boyer, W. M. Weiner & W. C. Rodrigues (2020): The dilemma of self-citation in taxonomy. – Nature Ecology & Evolution [https://doi.org/10.1038/s41559-020-01359-y].

Zhang, B., T.-W. Chen, E. Mateos, S. Scheu & I. Schaefer (2018): Cryptic species in *Lepidocyrtus lanuginosus* (Collembola: Entomobryidae) are sorted by habitat type. – Pedobiologia **68**: 12–19 [https://doi.org/10.1016/j.pedobi.2018.03.001].

Zhang, F., Z. Chen, R.-R. Dong, L. Deharveng, M. I. Stevens, Y.-H. Huang & C.-D. Zhu (2014): Molecular phylogeny reveals independent origins of body scales in Entomobryidae (Hexapoda: Collembola). – Molecular Phylogenetics and Evolution **70**: 231–239 [https://doi.org/10.1016/j.ympev.2013.09.024].

Zhang, F., Y. Ding, C. Zhu, X. Zhou, M. C. Orr, S. Scheu & Y.-X. Luan (2019): Phylogenomics from low-coverage whole-genome sequencing. – Methods in Ecology and Evolution **10**: 507–517 [https://doi.org/10.1111/2041-210X.13145].

Zuev, A., K. Heidemann, V. Leonov, I. Schaefer, S. Scheu, A. Tanasevitch, A. Tiunov, S. Tsurikov & A. Potapov (2020): Different groups of ground-dwelling spiders share similar trophic niches in temperate forests. – Ecological Entomology: een.12918 [https://doi.org/10.1111/een.12918].