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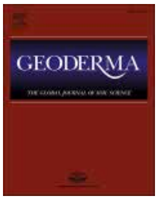

Life history traits in microarthropods: Evidence for a soil animal economics spectrum

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ABSTRACT

Evolution optimizes the performance of living organisms through budgeting of limited resources, leading to life-history trade-offs. Many life-history traits are related to body size with larger species typically exhibiting a slower pace of life and lower fecundity. However, soil-living organisms may exhibit size-independent life-history strategies due to habitat space constraints, but this has never been tested. Here, we synthesize life-history traits in springtails (Insecta: Collembola) and mites (Acari: Oribatida, Astigmata, Mesostigmata), the most abundant microarthropods worldwide, living mainly in litter and the pore space of soil. We related life-history traits to body size and individual metabolic rate, and showed that life-history traits of soil microarthropods display a trade-off between lifespan and reproductive rate, spanning a continuum from fast to slow life-history strategies. Oribatida exhibit remarkably slow life-histories and long lifespans with lower reproductive rates than Collembola, Astigmata and Mesostigmata. Despite fresh body mass of soil microarthropods varying by three orders of magnitude, fast and slow life-history strategies occurred in all size classes suggesting largely size-independent life-history strategies. Overall, these findings indicate a soil animal economics spectrum that bears key implications for understanding local biodiversity and the coexistence of soil animal species, such as how Collembola and Oribatida coexist worldwide.

1. Introduction

Every organism follows a life cycle that includes birth, growth, potential reproduction and eventual death (Stott et al. 2024). The allocation of limited resources to growth and reproduction is captured in life-history traits, which are key for the fitness of living organisms (Stearns 1976, Capdevila et al. 2020). Body size is of fundamental importance for understanding the variation in life-history traits and ecological strategies in living organisms. Many physiological and life-history traits are strongly correlated with body size (Blueweiss et al. 1978, Martin and Palumbi 1993). For example, larger animals tend to be more K-selected, i.e. are slow growing and live longer with lower metabolic rates (Song et al. 2012, Hutchings 2021). Further, body size correlates with generation time in organisms ranging from bacteria to whales, arguing for the generality of the relationship across broad taxonomic scale (Southwood et al. 1974, Bonner et al. 1985, Junker et al. 2023). However, this relationship may not exist within narrower taxonomic scale, and small animals can have long generation time due to slow life history strategy or constraints by limited habitat space (Charnov and Charnov 1993, Sibly and Brown 2007). Indeed, larger species use more space, which can be limited for example in soil (Jetz et al. 2004, Erktan et al. 2020). Facing the constraint of habitable space, species may diversify life-history strategies without changing size, and this likely applies to microarthropods living in the pore space of litter and soil.

Soil microarthropods are cosmopolitan and among the most abundant group of animals worldwide. Global-scale estimations suggest that springtails and mites account for 95 % of soil arthropod numbers on earth (Rosenberg et al. 2023). Soil microarthropods account for about

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20 % of soil arthropod biomass globally (Fierer et al. 2009, Rosenberg et al. 2023), and regulate microbial activities through trophic and non-trophic interactions (Scheu et al. 2005). Soil microarthropods are trophically diverse, with springtails (Insecta: Collembola), oribatid mites (Acari: Oribatida) and astigmatid mites (Acari: Astigmata) being mainly decomposers, and mesostigmatid mites (Acari: Mesostigmata) being predators (Potapov et al. 2022). As members of soil mesofauna, they are mostly small ranging in body length from 200 to 2500 μm, living mainly in topsoil, and therefore soil pore space influences their movement and foraging due to limited habitable space (Erktan et al. 2020). Their high local species richness has sparked research into niche differentiation and species coexistence in soil (Anderson 1975, Maraun et al. 2023). Spatial and trophic niche differentiations have been widely reported within Oribatida, Collembola and Mesostigmata (Schneider et al. 2004, Chahartaghi et al. 2005, Klarner et al. 2013), and increasing evidence suggests that their trophic niches are closely linked to their vertical distribution in litter and soil (Potapov et al. 2016, 2019b). Microscale studies stressed that soils are highly heterogeneous due to vertical stratification and pore space architecture (Nunan et al. 2003). Although understanding of life-history strategies of soil microarthropods improved considerably (Siepel 1994, Lindo 2015, Pfingstl and Schatz 2021), the allometric relationship between life history traits and body size remains understudied. The question remains also how soil animals, such as Collembola and Oribatida, which overlap in size, habitat and feeding niches, coexist. Life-history strategies are likely to provide critical dimensions for understanding the coexistence of soil animal species.

Here, we synthesize data of life-history traits in springtails and mites. We relate life-history traits including longevity, lifespan and reproductive rate with body size and individual metabolism to evaluate life-history strategies in microarthropods. Altogether, these traits reflect the budgeting of time and energy allocated to reproduction, growth and survival in microarthropods. We address the following questions: (1) Does the covariation and possibly trade-off in life-history traits lead to distinct life-history strategies in Collembola, Oribatida, Astigmata and Mesostigmata? (2) How is body size related to other life-history traits in soil microarthropods? We discuss the implications of the results in the context of conservation and understanding the coexistence of soil animal species.

2. Methods

2.1. Trait data

Literature was screened in Google Scholar for life-history related traits of microarthropods. Following the method of Junker et al. (2023), six traits were considered including four life-history traits, i.e. (1) lifespan, (2) egg incubation time, (3) age at maturity, (4) reproductive rate, as well as (5) body size and (6) individual metabolic rate. We chose scoping rather than systematic review because the focus of this study was not to be extensive, but to identify the general patterns in life-history strategies among the most abundant groups of soil microarthropods. To collect traits from literature, we used the following combination of keywords (“life history” OR “life cycle”) AND (“microarthropod” OR “springtail” OR “mite” OR “Collembola” OR “Acari”). Although potentially forming part of Oribatida (Dabert et al. 2010, Pachl et al. 2021), Astigmata were separated from Oribatida because they have been treated separately in most of the literature due to different ecology (Norton 1994, Behan-Pelletier and Lindo 2023). The literature found in Google scholar may be biased towards more recent publications. However, we acknowledge that we did not intend to review life-history characteristics of each of the animal groups as this would require an in-depth coverage of the old literature. Until August 16, 2023, at species level we compiled 17 records on Collembola, 38 on Oribatida, 18 on Astigmata and 20 on Mesostigmata, resulting in a total of 93 species. We followed nomenclature of GBIF database for species and higher taxonomy. Additional searches using the species names and missing traits on life-history or body size were carried out to improve data coverage and completeness of the species included (Appendix S1).

Life-history traits are features related to reproduction and growth that affect the fitness of a species due to natural selection. In detail, lifespan is defined as the number of days from hatching to death of adults. Egg incubation time is the number of days taken from egg to the hatch of juveniles. Age at sexual maturity is defined as the mean time between the day of hatching and the first reproduction. Reproductive rate is the number of eggs or offspring per female every year. Body size was measured as body length, i.e. the distance between the front end of the head to the posterior end of the abdomen in Collembola (Hopkin 1997), or the tip of the rostrum in Oribatida or gnathosoma in Mesostigmata and the posterior edge of the idiosoma (Weigmann 2006, Pourbahram et al. 2022). Body size was converted to adult fresh mass using power equations with group-specific coefficients (Appendix S2). The accuracy of body mass can be improved by including body width and finer group-specific allometric coefficients. However, we did not put effort into this as we aimed at including as many species as possible and covering all six traits as well as possible. Metabolic rate reflects the total use or turnover of chemical energy and was derived from fresh mass (M, mg) using the allometric equation $I = i_0\ M^a\ e^{-E/kT}$, where I is the metabolic rate ($J\ h^{-1}$), i_0 a normalization factor, a the allometric exponent, E the activation energy (eV), k the Boltzmann’s constant (8.26×10^{-5} eV K^{-1}) and T temperature in Kelvin. Group-specific coefficients (i_0, a, E) of Collembola, Oribatida and Mesostigmata followed Ehnes et al. (2011). Because coefficients (i_0, a, E) of Astigmata were not available, we derived them from the literature in this study (Appendix S3, S4).

2.2. Data analyses

Permutational multivariate analysis of variance (PERMANOVA) was conducted on Bray-Curtis dissimilarity to test the difference in life-history traits between taxonomic groups. We retained species that included more than three traits for multivariate analysis. Regarding the missing trait values, we used a random forest algorithm to fill the missing values at each taxonomic group. Data imputation was based on *missForest*, which is a nonparametric imputation method using random forest and performs well on life-history trait dataset (Penone et al. 2014). All life history traits were compared using means with each species considered as replicate. The metabolic rate scales allometrically with body size, reflecting that larger individuals typically have higher metabolic rates. To address this dependency and to focus on the metabolic rate as an independent life-history trait, we standardized the metabolic rate by dividing it by the fresh mass, yielding the specific metabolic rate – a measure of metabolic activity per unit biomass. In this way, we ensure that the specific metabolic rate is independent of body size and reflects the energy expenditure relative to biomass. We then included the specific metabolic rate in the multivariate analysis. Life-history traits were first log-transformed to improve normal distribution and then standardized to the mean of zero and unit standard deviation before multivariate analysis. For visualization, principal component analysis (PCA) was used to present the distribution of life-history traits. Further, multiple linear models were conducted to relate life-history traits to taxonomic group and adult body mass (log-transformed). The reference temperature of life-history trait measurement was chosen at 25 °C, although measurements were conducted at temperatures ranging from 9–30 °C (median 25 °C). It was not possible to avoid variations in temperature as some cold-adapted species may not preproduce at reference temperature and thus extrapolation of life-history trait values to reference temperature was not always realistic. To avoid bias, temperature was included as covariable, and reference temperature was used to calculate metabolic rate which all did not change the overall patterns presented in Figs. 1 and 2, suggesting that temperature is of secondary importance when comparing differences among taxa in this study. Therefore, we analyzed the data without

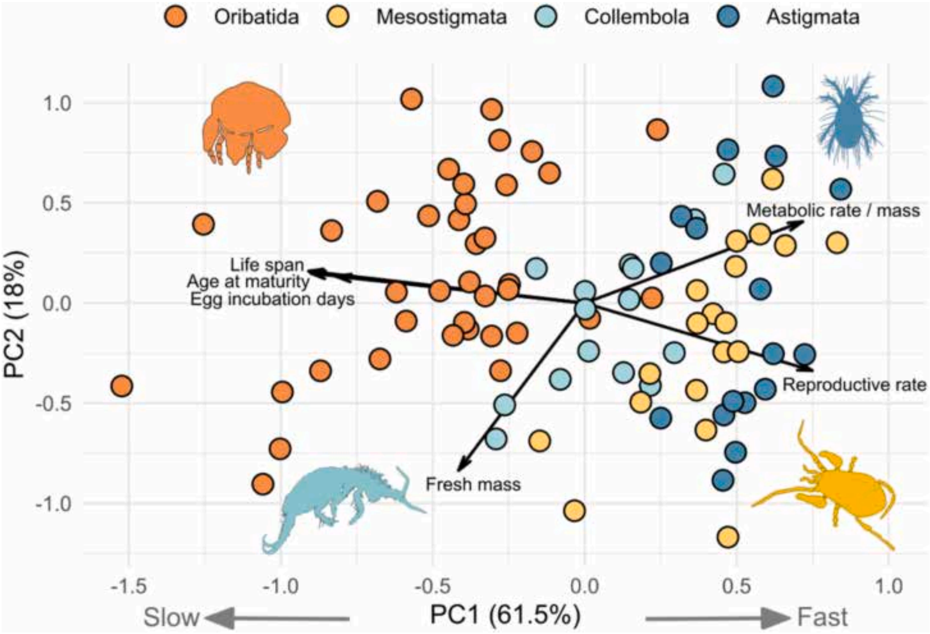

Fig. 1. Principal component analysis of life-history traits in soil microarthropods. Life-history traits include life span, age at maturity, egg incubation days, fresh mass, reproductive rate and individual metabolic rate (normalized by fresh mass). Microarthropods include Oribatida (n = 38), Mesostigmata (n = 20), Collembola (n = 17), Astigmata (n = 18). Each dot represents one species.

extrapolation of life-history trait measures to the reference temperature. All analyses were conducted in R version 4.3.2 (https://www.r-project.org/).

3. Results

Life-history trait combinations significantly differ among the microarthropod groups studied, forming different trait syndromes (PERMANOVA, $F_{3,86} = 29.5$, $P = 0.001$). Oribatida differ from Collembola, Mesostigmata and Astigmata by higher life span, later maturity and longer egg incubation days, and have lower reproductive rate and mass-corrected individual metabolic rate (Fig. 1). Further, Collembola differ from Astigmata by larger fresh mass and lower normalized metabolic rate (Fig. 1) as well as higher life span and lower reproductive rate (Fig. 2). By contrast, Mesostigmata did not differ significantly in fresh mass, mass-corrected metabolic rate and reproductive rate from Collembola (Figs. 1, 2).

Irrespective of body size, both life span and reproductive rate varied among microarthropod groups. On average, life span declined in the order Oribatida > Collembola > Mesostigmata ≥ Astigmata (Fig. 2a), while reproductive rate declined in the order Astigmata ≥ Collembola = Mesostigmata ≥ Oribatida (Fig. 2b). Across microarthropod groups life span but not reproductive rate positively correlated fresh mass (Fig. 2c, d). Although only marginally significant, both the relationship between body mass and life span as well as the relationship between body mass and reproductive rate varied among microarthropod groups (the interaction between body mass and taxonomy for life span reproductive rate, respectively: $F_{3,77} = 2.77$, $P = 0.08$ and $F_{3,57} = 3.10$, $P = 0.06$). Fresh mass positively correlated with life span for Oribatida and Collembola, but not for Mesostigmata and Astigmata, and reproductive rate positively correlated with fresh mass in Astigmata and Collembola but negatively with Oribatida.

The phylogenetic tree indicates that Astigmata are more closely related to Oribatida than to Mesostigmata (Fig. 3). Mites (Astigmata, Oribatida, Mesostigmata) form a paraphyletic group relative to Collembola, and Oribatida is the only group of the studied mites that display a slow life-history strategy compared to Astigmata, Mesostigmata and Collembola. Many microarthropod species reproduce via parthenogenesis, in particular Oribatida. Due to the lack of producing males, they experience a two-fold advantage in reproduction per generation. Based on information on reproduction mode we conducted additional analyses for species this information was available in the literature. The results generally support our conclusions that the two-fold advantage in reproductive rate in parthenogenetic species does not fundamentally change the life history differentiation between the studied microarthropod groups (Fig. S1).

4. Discussion

Animal economics spectrum is an emerging concept that provides a unifying framework in linking life-history and metabolic theory (Junker et al. 2023). Analogous to the well-established plant economics spectrum (Wright et al. 2004, Chave et al. 2009), this framework holds significant promise for advancing animal ecology by using common traits across taxa allowing to identify key axes of variation in ecological strategies (Turnbull et al. 2014, George and Lindo 2015). The application of the economics spectrum concept also to animals is timely (Gibb et al. 2023, Junker et al. 2023, Zhang et al. 2024), given the increasing interest in trait-based ecology for community and ecosystem research (Neyret et al. 2024). In this study, our analysis revealed a microarthropod economics spectrum, with a principal axis of variation reflecting a continuum of life history strategies from slow to fast (Healy et al. 2019). Trade-offs in life-history traits, mainly between longevity and reproductive rate, reflect contrasting life-history strategies that differentiated Oribatida from other groups of microarthropod decomposers (Collembola, Astigmata) and predators (Mesostigmata). Fast life-histories are characterized by maturing young, short lifespan and high reproductive rate in Collembola, Astigmata and Mesostigmata, while slow life-histories in Oribatida are characterized by long lifespan and low reproductive rate suggesting K-attributes in Oribatida (Lebrun et al. 1991, Norton 1994). Reproductive rate positively correlated with biomass-normalized metabolic rate; similarly, longevity, age at first production and egg incubation time are highly intercorrelated, whereas they little correlated with adult fresh mass.

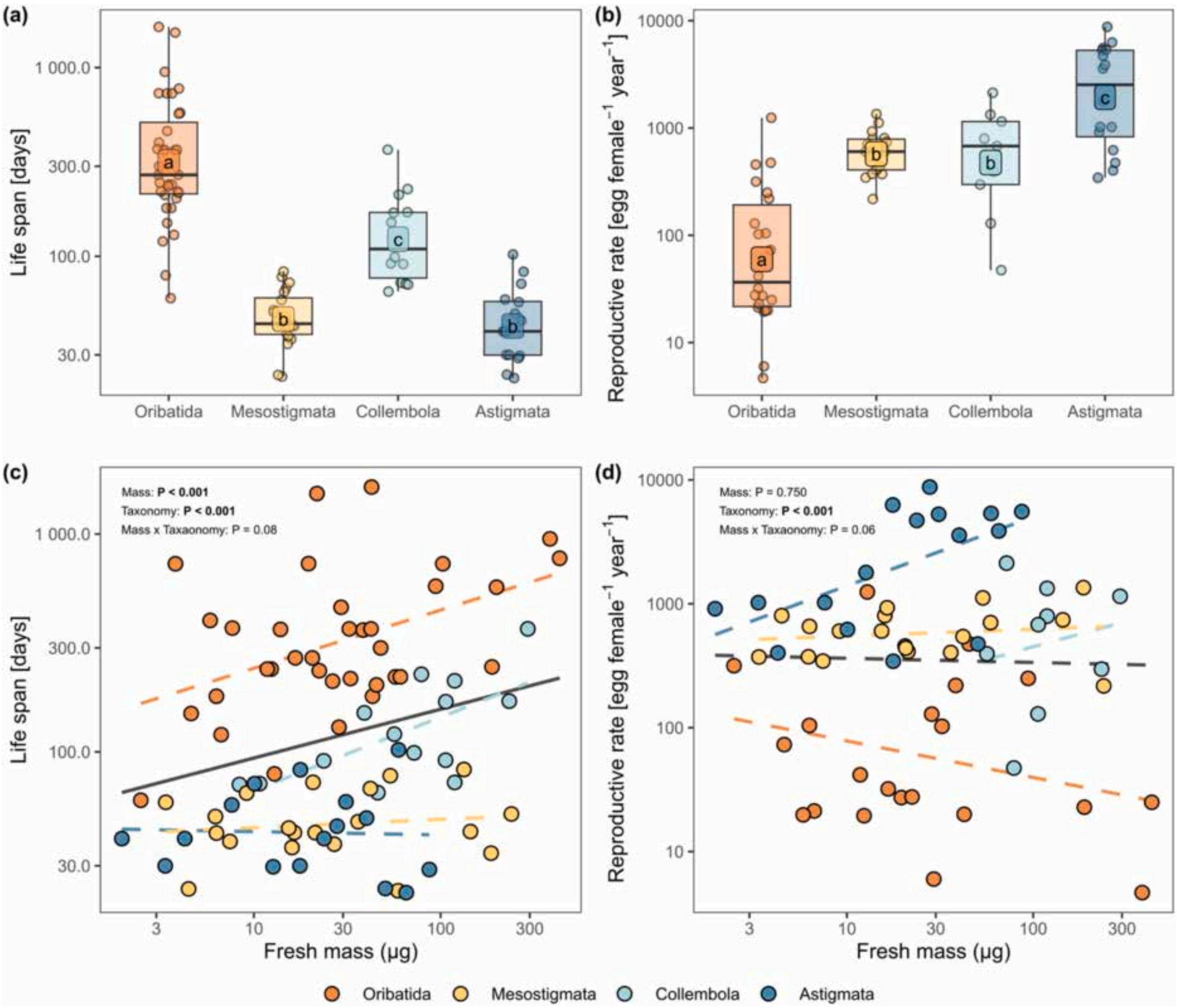

Fig. 2. Boxplots showing the median, interquartile range and overall range of (a) life span and (b) reproductive rate in Oribatida, Mesostigmata, Collembola and Astigmata. Scatter plots with regression lines depicting the relationship between (c) life span (days) and (d) reproductive rate (number of eggs per female and year) with fresh biomass (µg) of Oribatida, Mesostigmata, Collembola and Astigmata. Letters in (a) and (b) indicate results of post-hoc comparisons. Each dot represents one species.

4.1. *Body size-independent animal economics spectrum*

Life-history theory predicts that larger animals live longer and have fewer offspring, typical K-attributes (Stearns 1976, Junker et al. 2023). However, this does not apply to the soil microarthropod taxa studied as shown in trait-space. The independence of body size from the continuum of trait variations within the microarthropod economics spectrum is largely due to the overlap in body size of Oribatida with Mesostigmata, Astigmata and Collembola. Many soil microarthropods live in soil pore spaces, but pore space is limited in soil and only soil macropores (>60 µm) are accessible to at least some microarthropods (Erktan et al. 2022). The studied microarthropod species span 200–2500 µm in body length, and larger species are typically more restricted to the litter and upper soil layers where large pores are generally are more frequent (Brady and Weil 2008). This limited habitable space may pose evolutionary constraints as well as opportunities for body-size diversification in the heterogeneous soil matrix (Erktan et al. 2020). Small body size may allow microarthropods to access soil pores for food as well as protection against desiccation and predation. The evolutionary diversification under the constraint of size is evident by small body width, for example in euedaphic springtails (Potapov et al. 2016) as well as slender mites (Bolton et al. 2014). Natural selection may therefore impose evolutionary constraints on body size diversification, a possible cause for life-history divergence independent of body size, contrasting the general animal economics spectrum (Junker et al. 2023).

Within the microarthropod groups studied, the prediction that larger animals typically display more K-attributes is supported for Oribatida, weakly in Collembola and rejected in Astigmata and Mesostigmata. Further, the assumption that more soil surface-living animals exert more r-attributes (shorter lifespan and higher reproductive rate) due to higher resource availability (van Straalen 2023) does not generally apply to soil microarthropods; in fact according to our results it is only weakly supported in Collembola and not at all in Oribatida. When using body size as a proxy for vertical distribution, since larger animals are typically living close to the soil surface (Rusek 1998), larger Oribatida display more K-attributes. Although this synthesis represents only a small number of all described microarthropod species, our main conclusion for a soil animal economics spectrum is unlikely to be biased. It is worthy highlighting that the diversification of life-history traits within groups is substantial, which is interesting and calls for more detailed data in each of the four microarthropod groups (Pfingstl and Schatz 2021). Further, although K-attributes are generally more pronounced in Oribatida than in Astigmata, there also are Oribatida species with fast life-histories such as *Oppiella nova* (Kaneko 1988). Additionally, many Oribatida species reproduce via parthenogenesis (Heethoff et al. 2009, Pachl et al. 2021) and thereby display higher reproductive rate considering the two-fold

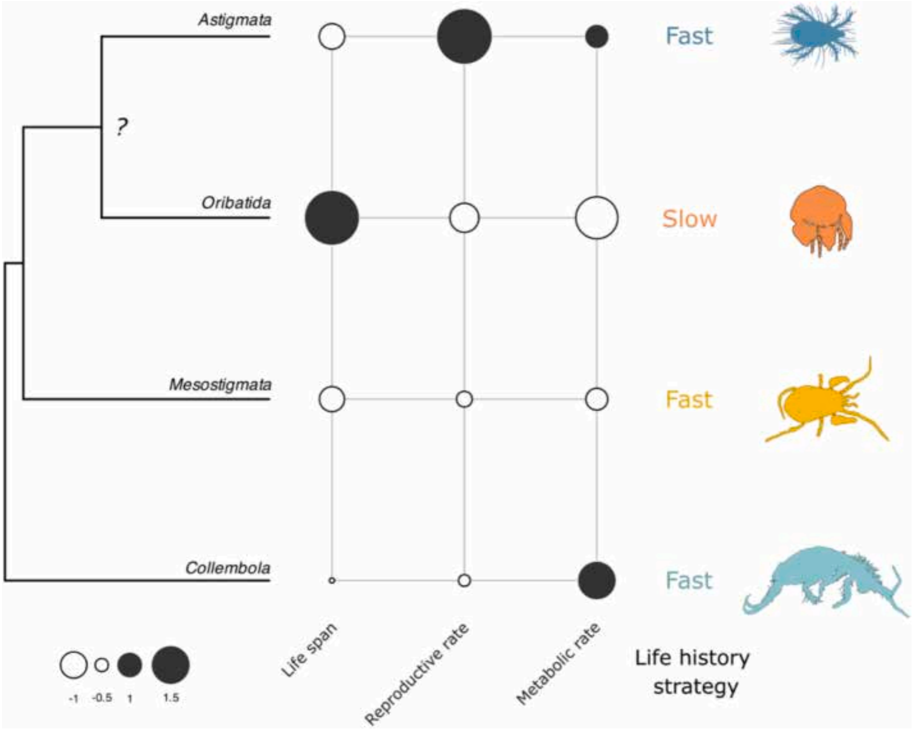

Fig. 3. Phylogeny of Oribatida, Mesostigmata, Collembola and Astigmata, together with life span, reproductive rate and metabolic rate (normalized by fresh mass). Life history traits were standardized ($\mu = 0$, $\sigma = 1$). Slow and fast life history strategies were interpreted from their position in the life history trait space. The phylogeny is based on data from timetree.org using *Adoristes ovatus*, *Ixodes ricinus*, *Acarus siro* and *Tomocerus minor* as representatives.

advantage of not producing males thereby switching to more r-selected attributes, providing a life-history perspective for understanding the ecological success of parthenogenetic species when colonizing new habitats (MacArthur and Wilson 1967, Norton 2007).

4.2. *Slow–fast continuum of life-history strategies*

Life-history traits are remarkably diverse in mites (Norton 1994). Oribatida are unique, characterized by slow-living and old-dying with low reproductive rate. Their slow pace of life has been suggested to be due to low metabolic rate and their consumption of low-quality food, which is reflected in their chelicerate mouthparts that only become efficient in ingesting solid food together with subcapitular rutellae (Norton 1994, Alberti et al. 2011). The slow metabolic rate may lead to long adulthood, which puts selective pressure for evolving iteroparity in reproduction and diverse defense traits, such as hardened cuticle, long setae, chemical defense and camouflage (Norton 1994). Oribatida are also choosy in where they lay their eggs, although simple, maternal care is often developed such as egg-laying in exuviae or crevices to avoid predation and desiccation, which is also reflected in their remarkable ovipositor, sometimes as long as the female's body (Walter and Proctor 2013), all pointing towards K-attributes. These life-history traits in Oribatida are not simply phylogenetically constrained at group level, because Astigmata, presumably a paedomorphic lineage of Oribatida (Norton 1998), display a distinct fast life-history due to the loss of the tritonymph from their ancestral lineage in Oribatida (Norton 1994).

Astigmata are abundant in agroecosystems and have been treated separately from Oribatida due to their contrasting ecology and traditionally different taxonomic expertise. As Oribatida and Astigmata differ in life-history strategies, it is ecologically meaningful to keep Oribatida and Astigmata as separate functional groups. However, morphological and molecular evidence suggest that Astigmata evolved within Oribatida (Norton 1998, Dabert et al. 2010, Li and Xue 2019). In contrast to Astigmata, Oribatida maintain the ancestral developmental traits with egg, two larval stages, three octopod nymphal stages and reproductive adult (Walter and Proctor 2013), and this may well be linked to their long lifespan and elaborated defense traits. From an evolutionary perspective, losing the tritonymph stage with a phoretic deutonymph in Astigmata is likely a key evolutionary shift driving diversification in life-history strategies in Astigmata, gaining advantage towards a faster life-history in exploiting high quality food that is patchily distributed in space and time accompanied with mainly sexual reproduction (Norton 1994, 1998), which in fact also applies to many Prostigmata and Mesostigmata (Walter and Proctor 2013).

Compared to Oribatida, Collembola, Astigmata and Mesostigmata are characterized by relatively fast life-history strategies with high fecundity and metabolic rate, short lifespan and adulthood. However, it is interesting to note that based on the life-history traits included in our study Collembola and Astigmata overlap little in life-history space, mainly due to smaller body size of Astigmata than Collembola. The size differentiation between Collembola and Astigmata may allow coexistence in, for example, agricultural soils (Behan-Pelletier 1999). On the other hand, Mesostigmata overlap with Collembola and Astigmata in life-history traits, which may imply competition, but Mesostigmata are mainly predators and Collembola are mainly detritivores (Klarner et al. 2013), therefore allowing coexistence of both when considering the trophic axis which was not included in our study. The fast life-history strategy and range of body size in Mesostigmata imply that they can quickly respond to changes in food resources, which made them widely commercialized as biological control agents (Beaulieu and Weeks 2007). Although predators are typically larger than their prey, in particular in aquatic food webs (Potapov et al. 2019a), this does not apply to Mesostigmata (Klarner et al. 2013). The wide range of body size in Mesostigmata in fact allows them to forage in the complex soil matrix especially for small prey dwelling in small pores and being physically protected from predators (Erktan et al. 2020). The switch of Mesostigmata from ancestral particle feeding species of Parasitiformes to fluid feeders also may have opened up the potential to feed on larger prey (Walter and Proctor 1998), and indeed Mesostigmata have become one of the dominant predators in the soil-litter system (Koehler 1999).

4.3. Implications for species coexistence and biodiversity conservation

Collembola and Oribatida overlap in body size and trophic niches (Pollierer et al. 2009), yet both coexist in soils worldwide from the tropics to the polar and from forests to deserts (Maraun et al. 2007, Potapov et al. 2023). The coexistence of Collembola and Oribatida arguably represents one of the world most common and numerous association, yet the question on how Collembola and Oribatida, with both typically reaching high density and species number, can coexist in soil has been little addressed. Evidence of bottom-up control argues for competition as an important driving force structuring soil animal communities (Hairston et al. 1960, Scheu and Schaefer 1998). However, the Gaussian exclusion principle (Hardin 1960) seems of little relevance considering the uniform coexistence of Collembola and Oribatida across ecosystems and biomes. The diversity of their life-history strategies provides a new perspective of their niche differentiation and suggests that an economics spectrum of soil-dwelling animals holds key for explaining their ubiquitous local coexistence today but also throughout the history of soils (Whalley and Jarzembowski 1981, Schaefer et al. 2010). Given that both groups are abundant in virtually any soil, life-history divergence indicates that their ecological success results from fundamentally different evolutionary trajectories. The slow pace of life and the ability to consume organic materials of low nutritional value allows Oribatida to occupy a different ecological niche than Collembola (Norton 1994) along the speed of life axis (Lancaster et al. 2017). This suggests that even though their fundamental trophic niches may be similar, as shown in feeding experiments (Hutchinson 1957, Maraun et al. 1998, 2003), their realized niches differ due to different encounter probability with prey (food) and interaction with other species such as fast-living microorganisms over their life time. Slow life-histories in Oribatida suggest that they are poor in exploiting high-quality resources, but are well adapted to cope with periods of harsh environmental conditions associated with low food availability (Mitchell 1977). This is not to say that Oribatida do not also benefit from high-quality food, however, they may not be as good as Collembola and Astigmata in exploiting resource hotspots especially if they vary in time, i.e., at “hot moments” in soil (Kuzyakov and Blagodatskaya 2015). The low population growth rate, low specific metabolic rate and low moving ability in Oribatida limits their competitive ability to consume microbial hotspots that may disappear within hours or days. Further, different pace of life may also contribute to explaining the discrepancy between laboratory feeding experiments, showing similar food preferences among species, and field observations, showing pronounced trophic niche differentiation of oribatid mite species (Maraun et al. 1998, Lu et al. 2022). The different lifespan of Collembola and Oribatida may reflect a phylogenetic constraint, but the split of Astigmata from Oribatida suggests that phylogenetic constraints can be overcome, and this contributes to the diverse life-history strategies in mites (Norton 1994).

Facing the silent loss of soil invertebrates due to global change (Eisenhauer et al. 2019), soil microarthropods as key members of soil biodiversity are likely to be differently affected due to their contrasting life-history traits. Oribatida are more vulnerable to frequent disturbances and only few species occur in typically low abundance as opposed to other microarthropod groups such as Astigmata in agricultural soils, while in more stable environments such as forest soils they reach high abundance together with Collembola and Mesostigmata (Maraun and Scheu 2000). In face of climate change, increasing conversion of natural ecosystems by humans and increasing intensity of land use, the contrasting response of microarthropod groups as indicated by life-history theory lays the foundation for their use as bioindicators of environmental changes (Behan-Pelletier 1999, Koehler 1999, Ashwood et al. 2023). The different life histories of microarthropods argue for the necessity to consider them separately to exploit their potential as indicators of environmental change and ecosystem maturity (Odum 1969). Overall, long-lived organisms are less resilient and more persistent in numbers than short-lived organisms (Pimm 1984), and the diversity in life-history traits of soil animals likely contributes to the stability of soil communities which is an essential component for the provisioning of ecosystem services.

In conclusion, our cross-taxonomic comparisons reveal that fast-slow continuum in life history strategies is the major structuring axis in soil springtails and mites. This continuum is a critical knowledge gap as life-history strategies have been poorly studied in invertebrates other than insects (Stott et al. 2024). For the first time, we show that major life-history traits of soil microarthropods are not closely related to body size, challenging the common assumptions of size-dependent life-history strategies (Hutchings 2021, Junker et al. 2023). The identified size-independent life-history divergence highlights the importance of habitat constraints in body size evolution of soil microarthropods, which may also apply to other animal taxa constraint by habitat space. Microarthropods are highly diverse, with many species and groups not covered in this study due to a lack of comparable data. Reviews on life-history characteristics of a wider range of species and groups is needed for a more comprehensive synthesis allowing to better understand life history strategies of microarthropods. Further, the well-established framework of life-history strategies provides a promising perspective for understanding life-history diversity and ecological strategies across soil animal taxa, allowing to finally resolve the enigma of soil animal diversity and its contribution to the functioning of the belowground communities (Anderson 1975, Junker et al. 2023).

CRediT authorship contribution statement

Jing-Zhong Lu: Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Tobias Pfingstl:** Writing – review & editing, Validation, Supervision, Methodology, Data curation, Conceptualization. **Robert R. Junker:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization. **Mark Maraun:** Writing – review & editing, Validation, Supervision, Resources, Methodology. **Amandine Erktan:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Stefan Scheu:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Stefan Scheu, Amandine Erktan report financial support was provided by Deutsche Forschungsgemeinschaft. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2025.117206.

Data availability

The data supporting the results have been archived in Dryad at https://datadryad.org/stash/share/LdB2jJmDQu6DeGGL6-oigylQajyk3alN79fq0gCzRG4

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