Unravelling the Enigma of Soil Animal Diversity: An Integrated Perspective from Functional Traits to Evolutionary History

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Abstract

Why does a single square meter of forest soil harbour thousands of animal species? Fifty years after Jonathan M. Anderson raised this question, soil ecology still struggles with a fragmented view on the coexistence of species. Researchers often study taxonomy, functional traits, and phylogeny in isolation. Each approach adds insight but leaves gaps in the picture of soil biodiversity.

In this paper, I propose a Community-Trait-Phylogenetic Ecology framework which links evolutionary and ecological views, and explains how soil animal communities form and persist. The framework combines three research fields:

- Biogeography – describes species composition across local, regional, and global scales.
- Functional traits – divided into α-niche traits (resource use) and β-niche traits (environmental tolerance), showing whether resource partitioning or filtering by environment drives community assembly.
- Phylogeny – shapes trait expression and defines the pool of species.

Evidence from springtails (Collembola, Hexapoda) and oribatid mites (Oribatida, Acari) shows the value of this framework. Global data synthesis reveals a mismatch between density and diversity, which challenges traditional biogeographic predictions. Trait analyses show that environmental filtering occurs at global scales. At regional and local scales, cryptic species that diverged millions of years ago coexist with distinct habitat preferences. In addition, ancient and recent lineages coexist across elevations. Morphological and physiological traits usually follow phylogenetic constraints. In contrast, trophic traits show high flexibility, which allows closely related species to coexist.

This integrative view shifts soil animal ecology from describing patterns to understanding the mechanisms responsible for them. It also supports predictions of community responses to climate change and land-use change. Finally, it guides conservation strategies that protect trait, functional, and evolutionary diversity along with species richness.

Keywords: coexistence mechanisms; community assembly; environmental filtering; evolution; ecology; functional traits; niche; phylogenetic comparative methods; resource partitioning; soil arthropods; soil biodiversity; soil macroecology; species pool

Fifty years ago, British ecologist Jonathan M. Anderson posed a deceptively simple yet profoundly difficult question: *Why can a single square meter of forest soil harbour thousands of animal species comprising millions of individuals* (Anderson, 1975)? This question challenges our understanding of biodiversity and species coexistence mechanisms, revealing the complex and delicate balance of natural forces.

The Astonishing Complexity of Soil Life

In a temperate deciduous forest just one square meter of litter and soil contains 10,000 to 200,000 tiny animals. These animals represent 60-200 "mesofauna" species (Petersen and Luxton, 1982). They measure about 0.2mm to 2mm in width and are often overlooked by the naked eye. Nevertheless, these animals are crucial for maintaining the proper functioning of terrestrial ecosystems (Bardgett and van der Putten, 2014). Among mesofauna taxa, springtails (Collembola, Hexapoda) and oribatid mites (Oribatida, Acari) stand out for their remarkable abundance and ecological importance. These two taxa comprise approximately 95% of global soil arthropod abundance (Rosenberg et al., 2023) and are among the most diverse soil animal taxa with >9000 and >11,000 described species, respectively (Potapov et al., 2020; Subías, 2022). Despite sharing the same habitat and feeding on similar resources, hundreds of these species coexist without apparent conflict. This is a phenomenon that traditional soil ecology cannot fully explain. How is it possible? The answer requires understanding of soil biodiversity from three complementary perspectives.

Limitations and Breakthroughs of Traditional Approaches

Community ecology and biogeography take species as the units. They focus on how environmental factors, such as temperature, moisture, and soil pH, correlate with species occurrence, and how species interactions and dispersal limitations shape local community composition (Potapov et al., 2023). Although precise, this taxonomy-based approach is labour-intensive and time-consuming. Species determination requires considerable training. It is also defective because, though it indicates which species adapt to which environments (i.e. habitat niches), it struggles to explain how they adapt to the environment and how species achieve coexistence. Thus, the traditional species-centred perspective describes the patterns of coexistence but not the mechanisms responsible for coexistence.

Functional trait ecology brought a breakthrough. Rather than treating each species as an independent entity, it identifies niche dimensions based on specific attributes of the organisms (i.e. traits) (Winemiller et al., 2015). Different species differ in multiple traits, such as morphology (body size, colouration), life history (reproductive strategy, development rate), and resource utilization (diet). These traits are assumed to be functional and to affect their fitness (but see Gould and Lewontin, 1979). Through analysing functional traits, it is possible to predict which species are able to coexist and how communities change along environmental gradients (Brousseau et al., 2018). However, even this integrative perspective has shortcomings. In particular, it typically overlooks the profound influence of evolutionary history on traits. Traits do not appear from nowhere but are the result of millions of years of evolution (van Straalen, 2021).

Phylogenetic and comparative methods reveal the deep shared evolutionary history of species. The evolutionary past of species influences which traits they possess and how ecological roles are constrained. Related species tend to resemble each other, and such a pattern is called "phylogenetic signal” (Silvertown et al., 2005). However, until today evolutionary perspectives are little considered by soil ecologists as it requires specific conceptual and practical skills. As a consequence, soil animal research typically treats ecology and evolution as separate domains (but see Ponge, 2020 and van Straalen, 2021).

An Integrative Perspective: The Community-Trait-Phylogenetic Ecology Framework

To overcome the limitations of the three traditional approaches and to better understand soil animal communities, I propose a "Community-Trait-Phylogenetic Ecology" (CTPE) framework (**Figure 1**). This framework attempts a more holistic understanding of the complex mechanisms driving the composition of soil animal communities.

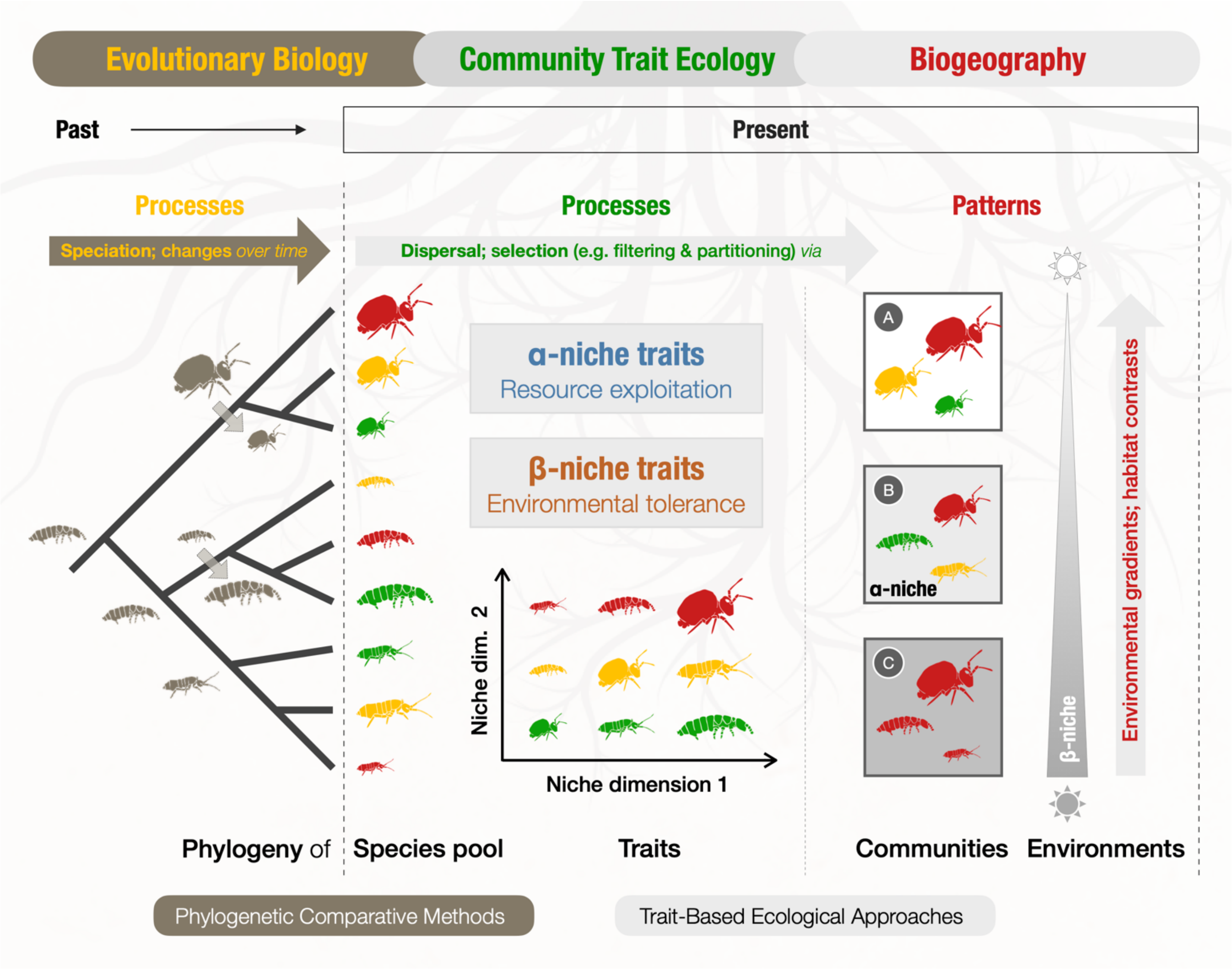

Figure 1. The "Community-Trait-Phylogenetic Ecology" (CTPE) Framework for Studying Soil Animal Diversity. The CTPE framework integrates ecological and evolutionary processes to understand mechanisms driving soil biodiversity across spatial scales. The spatial distribution of soil communities is the central focus of biogeography (right, red panel). Even when species richness remains constant, species composition often changes along environmental gradients, leading to local communities that differ in their trait composition (for

example, body size, colour and shape). Functional traits reflect multidimensional ecological niches and help explain species occurrence in particular habitats. For examples, community A occurs at high elevation where solar radiation is strong, while community C is located at low-elevation forest cover with dense canopy cover. By examining functional traits, defined as α-niche traits (associated with resource use and partitioning) and β-niche traits (related to environmental tolerance), this framework can infer the processes shaping community patterns and predict community responses to environmental changes (middle, green panel). In community A, springtail species share a similar body shape but differ in body size and colour, whereas in community C, species are similar in colour but differ in the other two traits. Patterns in trait distributions, when compared to null expectations, reveal the underlying deterministic processes of community assembly. With phylogenetic comparative methods, the CTPE framework also infers the evolutionary processes that have generated present-day trait variation among species, offering a historical context for contemporary ecological patterns (left, yellow panel). Over evolutionary time, species have diversified from common ancestors by shifting traits (for example, from large to small body size, or *vice versa*). Speciation and trait evolution have thus shaped the regional species pool from which local communities assemble under the combined influence of environmental filtering and niche partitioning.

This framework comprises three elements.

The first element is the **species level - multiscale variation in community composition**. Variations in soil animal community is reflected not only in differences in species richness but also in species composition and their distribution across space and time (biogeographic patterns; e.g. Gao et al., 2014; Potapov et al., 2023; Junggebauer et al., 2024). To understand changes in soil animal diversity, it is necessary to ask what patterns characterize communities at local, regional, and global scales.

The second element is the **functional level - two niche processes reflected by traits**. Functional traits of species may be divided into two categories, α- and β-niche traits (Ackerly and Cornwell, 2007). Each category refers to different yet complementary community assembly processes (Chen et al., 2017; Noske et al., 2024). The β-niche traits reflect species environmental tolerances, such as body surface pigmentation (affecting thermoregulation and UV resistance; Xie et al., 2022) and temperature-moisture tolerance (Janion-Scheepers et al., 2018). Coexisting species typically resemble each other in these traits, indicating that they tolerate similar environmental conditions. By contrast, the α-niche traits reflect resource utilization strategies of species. Despite sharing the same habitat in soil, springtails and oribatid mites may exploit different food resources, including plant roots and exudates, organic matter, bacteria, fungi, lichens, mosses, algae, and even other soil animals (Potapov et al., 2022). Differences in the use of these resources are likely to reduce competition, thereby allowing to coexist locally. Therefore, the distinction between β- and α-niche traits helps predict which species are able to coexist and how communities change along environmental gradients.

Third is the **phylogenetic level – evolutionary constraints and possibilities**. Evolutionary history not only provides context for trait variation but also constrains ecological possibilities. Combining molecular techniques (such as mitochondrial genome sequencing; Xie et al., 2022) with comparative methods (such as phylogenetic signal testing; Revell, 2024), makes it possible to determine the nature of traits. It allows to identify which traits are of ancient evolutionary origin and which evolved recently in response to contemporary selection processes, or which traits are novel or have changed their original functions so that species exploit novel niches. Morphological and physiological traits typically show strong phylogenetic signal; conversely, trophic traits (resource utilization) often lack phylogenetic signal (Chen et al., 2017; Gong et al., 2018; Xie et al., 2022; Noske et al. 2024). This suggests that environmental tolerance is evolutionarily constrained and that resource utilization strategies have evolved independently multiple times. In combination, these allow closely related species to partition resources and coexist.

Evidence from Springtails and Oribatid Mites: from Global to Local

The international collaboration, the Global Collembola Initiative (#GlobalCollembola; Potapov et al., 2020), compiled nearly 3000 community composition records. These records cover eight biogeographic regions and 10 biomes from the tropics to the poles (Potapov et al., 2024). This unprecedented dataset reveals a striking mismatch between density and diversity. Polar regions show high density but only moderate species richness, temperate forests are characterized by moderate density yet highest richness, tropical regions show lowest density but highest richness, and arid systems show both low density and low richness (Potapov et al., 2023). This "density-diversity mismatch" challenges traditional perspectives.

Recent compilation of data by the Global Collembola Initiative on 10 different traits from over 7000 springtail species and the ongoing global-scale trait distribution analyses, provide evidence for the effect of environment on traits. The compilation indicates that springtail body pigmentation, colour patterns, ommatidia number, furca development, and body size are differentially influenced by habitat type, latitude, biome, and local density (Chen, T.-W. et al., unpubl. data). This suggests that environmental filtering operates at global scales, selecting particular trait combinations.

At the regional level, recent biogeographic research on soil animals of Changbai Mountain in Northeast Asia tracked variation in isotomid springtail communities across 1400m of elevation (Xie et al., 2022). This study found that soil nitrogen content, changing with elevation, acts as a key environmental filter selecting particular pigmentation patterns and trait combinations. This mountain study also raises an evolutionary puzzle: are mountains "cradles" of speciation? Or are they "museums" preserving ancient lineages? Linking phylogeny with geological events reveals that both scenarios apply to isotomid springtails. Ancient lineages persist while new species have emerged alongside mountain uplift. These patterns provide the basis for inferring historical speciation and diversification processes that shaped the current species pools from which local communities are assembled (Vasconcelos et al., 2022).

At local scales, ongoing research on the winter springtail communities in the wetlands, secondary forests, farmlands, and plantations of northeastern China, revealed different dominant community assembly processes across habitats (Chen, T.-W., unpubl. data). Even within a single community, species are simultaneously influenced by both filtering and partitioning processes, depending on the traits considered. For example, compared to forests, farmland springtails show similarity in furca and eye traits presumably due to environmental filtering, while body size, pigmentation, and colour patterns reveal niche partitioning among coexisting species. This suggests how trait-based perspectives on two niche processes can operate simultaneously within the same community.

The Multidimensional View of Trophic Ecology: Soil Animal Diets are Complex

Even though morphological traits can reflect partitioning processes, traits more directly related to the use of food resources (α-niche) are usually derived from food-web methods that characterize soil animal diet or food resources (i.e. trophic niches; Potapov et al., 2021). Gut contents, digestive enzymes, neutral lipid fatty acids, and stable isotopes (^{15}N and ^{13}C), each provide complementary information on the diet of consumers. Most pairwise correlations of trophic niche parameters deduced from these methods are weak, indicating that each method captures different dimensions of the trophic niche (Potapov et al., 2021). Stable isotope values and gut microbiota of winter-active springtails show that they actually feed on resources on snow cover (such as cyanobacteria) rather than from litter (Hao et al., 2020). These results indicate that by combining multiple methods can we truly understand soil animal diets and reveal their realized trophic niches.

Furthermore, microbiota associated with soil animals can be viewed as a special type of trait (Gong et al., 2018, 2022; Hao et al., 2025). The study on bacteria and fungi associated with oribatid mites reveal subtle differences in how evolutionary history and trophic ecology of oribatid mites influence their microbial communities (Gong et al., 2018). Variations in fungal communities are better explained by stable isotope differences than by phylogenetic distance between mite species, suggesting fungi as food resources. Bacterial communities, in contrast, are more strongly related to host phylogeny than to trophic niche differences, indicating that closely related mites harbour similar bacteria, presumably shaped by host physiology. This suggests that mite-bacteria associations evolved interdependently. The ancient coevolution between animal hosts and gut symbionts results in a phylogenetic signal of bacterial communities across soil oribatid mite species.

Neutral lipid fatty acids also reveal the distinction between trait evolutionary dependence and resource flexibility (Chen et al., 2017). In this study we measured neutral lipid fatty acid composition in springtails and found closely related species to share similar fatty acid profiles. Long-chain polyunsaturated fatty acids, which are related to physiological function (β-niche), show a strong phylogenetic signal, while fatty acid biomarkers representing food resources (bacteria, fungi, and plants; α-niche) show almost no signal. This means that β-niche physiological functions are evolutionarily constrained, whereas α-niche resource utilization is highly flexible, indicating closely related species evolve different feeding strategies.

From Deep Time to Present: Multiscale Coupling of Evolution and Ecology

The CTPE framework reveals how evolution and ecology interact across different temporal scales. Springtails and oribatid mites have persisted since the Paleozoic (Schaefer et al., 2010; Yu et al., 2024). At hundred-million-year scales, they diversified alongside plant evolution and geological events (such as continental drift and mountain building), forming regional species pools (Schaefer and Caruso, 2019; Xie et al., 2022). At million-year scales, even cryptic species indistinguishable morphologically have long diverged at the genetic level (Heethoff et al., 2007; Zhang et al., 2018). For example, three lineages of the springtail *Lepidocyrtus lanuginosus* diverged about 15.9 to 9.7 million years ago (Miocene), yet still coexist in the same region today, each preferring different habitats (forest, grassland, or farmland; Zhang et al., 2018), demonstrating that both persistence of old lineages and environmental filtering are at work. At contemporary ecological timescales, in addition to long evolutionary paths, present community composition remains highly determined by current environmental conditions and resource availability. Evolution provides the "toolbox" (traits), while contemporary ecological conditions determine which "tools are selected" (species coexistence). This suggests tight evolutionary-ecological coupling in soil animals: species diverged in deep time yet achieve contemporary coexistence. Trait evolution enables environmental (β-niche) differentiation at large spatial and long evolutionary time scales but resource (α-niche) partitioning at both small spatial and temporal scales.

Insights and Significance of the CTPE Framework

This integrative framework brings several novel insights to soil ecology. First, traits reveal processes. Measuring functional traits is not merely for describing patterns. Combinations of traits can reveal which ecological processes dominate in communities. Environmental filtering is usually revealed by similar β-niche traits, while partitioning processes can be shown in different resources (α-niche) used by coexisting species. Second, evolutionary history reveals constraints and opportunities. Physiological functions are usually evolutionarily constrained and exhibit a phylogenetic signal. In contrast, resource utilization strategies are less constrained evolutionarily, with more convergent evolution being reveal. Instead, they display flexibility between (e.g. convergent evolution; Schaefer and Caruso, 2019) and even within species (e.g. trophic plasticity, 2019; Krause et al., 2019; Yang et al., 2025). Contemporary ecological processes then reshape communities under these conditions. Third, coexistence arises from multiple overlapping mechanisms. Evolution adds trait diversity, the environment selects particular traits, and resource differentiation enables local diversity. Finally, soil animals are far more complex than previously recognized, as they are no longer merely microscopic "detritivores" but ecosystem multitaskers (Bonfanti et al., 2025). They occupy diverse soil niches, utilize various sources, and display remarkable adaptability. They are mediators, ensuring ecosystem functioning through redundancy and complementarity.

Future Applications: from Understanding to Prediction and Conservation

By integrating species distribution and community patterns, multiple trait measurements, and phylogenetic analyses, we are making progress toward understanding the enigma Jonathan M. Anderson posed fifty years ago (Anderson, 1975). This understanding is essential for predicting consequences of global change: Climate change alters temperature and moisture regimes, thereby changing directions and strengths of environmental filtering and selecting different trait combinations (Ferrín et al., 2023). Land-use change may fragment communities and limit connectivity (Susanti et al., 2021). Invasive species may disrupt the existing functional and phylogenetic structures of communities (Janion-Scheepers et al., 2018). Understanding which traits confer ecosystem resistance and resilience (Bonfanti et al., 2022), and which are shaped by evolution (Noske et al., 2024), enables the prediction of structural and functional changes of soil animal communities under these scenarios, and allows to identify key species and vulnerable taxa, thereby providing the basis for optimizing conservation strategies that maintain multidimensional diversity. The CTPE framework, thus, also emphasizes that protecting soil functioning is not just a matter of species numbers. It requires maintaining multiple levels of diversity including trait diversity, functional diversity, and evolutionary diversity across scales

(Véron et al., 2019). Insights gained from the CTPE framework are useful for global soil conservation policy.

Why This Matters

Soil animals differ in their sensitivity to environmental stress, making them valuable bioindicators of ecosystem health (Shimano, 2011; Yin et al., 2020). They contribute to essential ecosystem functions by regulating nutrient cycling, supporting plant production, and mediating carbon sequestration (Bonfanti et al., 2025). How can we integrate ecological processes, functional traits, and evolutionary history to better understand and predict biodiversity? Although this question resonates across taxa and ecosystems (Junker et al., 2022; Luza et al., 2023), the “enigma of soil animal diversity” goes beyond academic curiosity. Fifty years after Anderson’s original formulation, researchers now have new tools, new theories, and new frameworks to solve this enigma. Advances in high-throughput sequencing, stable isotope analysis, fatty acid and amino acid profiling, and computational methods now enable unprecedented data integration and synthesis. The coming decade of soil biodiversity research will elucidate the mechanisms that generate and maintain soil biodiversity and help predict how it responds to climate change, land-use alteration, and other global pressures. Soil will no longer be a black box but a kaleidoscope revealing the hidden wealth of life beneath our feet (Andrén and Balandreau, 1999; van Straalen, 2023).

Concluding Remarks

- The integrated "community-trait-phylogenetic" framework depicts soil biodiversity as a multidimensional pattern shaped by ancient evolutionary processes and maintained by contemporary ecological processes. Community coexistence depends on multiple mechanisms operating in parallel: environmental filtering, resource differentiation, and evolutionary constraints and novelty.
- Past environmental conditions shaped ancient lineages with specific traits and their descendants now display unique preferences in contemporary habitats.

- β-niche traits (such as morphological and physiological traits which reflect environmental tolerance) often show a strong phylogenetic signal, indicating evolutionary constraints. Coexisting species in communities typically are characterized by trait similarity, reflecting contemporary environmental filtering.

- α-niche traits (such as multidimensional trophic niche parameters which reflect resource utilization) can be revealed through complementary diet methods. These traits typically show no, or a weak, phylogenetic signal, highlighting ecological opportunity.

- Microbiota associated with soil animals can be viewed as functional traits. Bacteria (especially symbionts) are closely tied to host evolutionary history, while fungi serve primarily as food resources, reflecting the trophic niches of the animals.

- Integrating knowledge of community ecology, functional traits, and evolutionary history helps predict soil biodiversity responses to global change and their effects on ecosystem functioning.

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