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Opinion

Living Litter: Dynamic Trait Spectra Predict Fauna Composition

Saori Fujii,^{1,2,*} Matty P. Berg,^{1,3} and Johannes H.C. Cornelissen¹

Understanding what drives soil fauna species composition through space and time is crucial because we should preserve soil fauna biodiversity and its key role in ecosystem functioning in this era of fast environmental change. As plant leaf litter provides both food and habitat for soil fauna, a focus on litter traits that relate to these two functions will help in understanding soil invertebrate community structure and dynamics comprehensively. To advance this agenda, we propose a conceptual framework to explicitly link the invertebrate community composition to the temporal dynamics of the litter trait space defined by two axes: a food-quality axis related to plant resource economics and chemistry and a habitat-quality axis related to litter particle size and shape.

How to Reveal the Hidden Soil Animal Diversity

Soils provide essential ecosystem services to people. These services include soil formation and fertility, carbon storage for climate control, and erosion prevention [1]. Most of these services are directly or indirectly related to litter (dead plant matter) and its decomposition, a process driven by **soil organisms** (see [Glossary](#)) [2,3]. Soil communities are diverse and complex, with many co-occurring species ranging from small microorganisms and microfauna to larger mesofauna and macrofauna. However, our understanding of what drives the composition and dynamics of this hidden biodiversity is limited [4,5]. For example, we still cannot define unified rules for how soil biodiversity is distributed across climatic regions, soil types, and vegetation types at local to global scales [6–8]. The species richness of soil organisms (e.g., microorganisms, nematodes, springtails, oribatid mites, earthworms) does not show concordance with latitudinal gradients of vegetation diversity [9–15], while aboveground species numbers gradually decline from the tropics towards the poles [16,17]. Moreover, the coexistence of soil-dwelling species is rarely explained by resource partitioning, which often explains aboveground and aquatic species diversity [18–20]; for invertebrates, this phenomenon has long been dubbed ‘the enigma of soil animal species diversity’ [21]. In this era of fast environmental changes, which affect belowground organisms and the soil processes they regulate in many ways [22], we need to understand what drives soil biotic community dynamics and diversity and, thereby, belowground ecosystem functioning.

Plants exert a strong effect on soil organisms by providing organic carbon that they produce, leading to strong interactions between plants and soil [23–25]. Variation in **plant traits** might therefore explain how plants affect soil communities [26]. Understanding and prediction of community dynamics from species traits, rather than taxonomic identity, has been a ‘Holy Grail’ in ecology in recent decades, as traits may provide general principles applicable to wide-ranging ecosystems [27–29]. Plant traits can be used to predict not only how plants respond to changing environmental factors, but also how shifts in plant species composition affect other trophic levels and ecosystem properties [30]. Plants supply soil organisms with their main resource in the form of litter [23]. Growing evidence suggests that plant traits determine litter decomposition rates locally

Highlights

Disentangling of what drives the composition and dynamics of belowground diversity is needed to predict ecosystem-level consequences of environmental change.

Incorporating the notion that soil fauna live in ‘a house made of food’ could bridge the gap between soil fauna diversity and plant community solely based on litter traits as a food source.

To assess the dynamic habitat for soil fauna, partly through their own feeding activities, we add temporal aspects into the trait space defined by food- and habitat-related trait axes.

Integration of temporal dynamics in trait-based ecology is critical to assess almost all ecological processes accompanied by temporal change in traits of targeted organisms.

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[31] and even globally as strongly as macroclimate does [32,33]. However, whereas plant traits could explain microbial community composition with some success at both local [34] and landscape (regional) [24] scales, the effects of plant traits on animal community composition and distribution generally remain obscure [7,35,36]. This uncertainty may partly result from our failure to define the key determinants of soil fauna fitness [37]. Here, we focus on the notion that soil animals live in ‘a house made of food’; that is, a habitat composed of litter that varies temporally and spatially in resource quality partly by their own feeding activities. Although many researchers have recognized the habitat function of litter to soil fauna [18,37,38], we still can neither qualify the dynamics of the soil habitat nor separate the food and habitat functions of litter resources. Here, we propose a new conceptual framework to assess the impact of the dynamic nature of the soil organic layer (i.e., the total habitat for soil fauna) by adding the temporal dimension to the space occupied by litter trait variation as defined by two axes. The food-quality axis is related to plant resource economics and chemistry and the habitat-quality axis to litter particle size and shape (see Figure I in Box 1).

Current Research Gaps to Bridge from Plant Traits to Soil Fauna

Litter traits [e.g., nitrogen, phosphorus, and lignin content, specific leaf area (SLA), leaf dry matter content (LDMC)], have been used to link vegetation composition to decomposer communities [2,24,39,40], because these traits predict litter decomposition rates and the decomposers’ contribution to them [31,41]. They are the legacy of important plant functional traits, associated with trade-offs between resource acquisition and resource conservation [42]. This trait axis was first defined as the ‘leaf economics spectrum’ [43] and later extended to the ‘**Plant Economics Spectrum**’ (PES) comprising leaf, stem, and root traits [43,44]. The key PES traits generally specify food quality for soil fauna [41] but may not define habitat quality (i.e., microscale gradients in physical environmental characteristics), which should strongly affect soil animal distribution [45].

Habitat structure and complexity are important for biodiversity in aquatic ecosystems [46] and for fauna diversity in soil [8,37,47]. Gill showed similar abundances and compositions of soil microarthropods between leaf litter and artificial polyester ‘litter’, indicating that physical environmental factors are important [48]. Litter removal and addition experiments showed that litter generally affects soil meso- and macrofauna through microclimate [49,50] and suggest that litter is not a limiting food source (reviewed in [45]). Recent papers have again emphasized the importance of habitat quality for soil communities [51–55]. However, we still lack a proper means to disentangle litter habitat quality from food quality under natural conditions. The single focus on litter as a food source has hampered our understanding of how litter trait composition controls soil animal community structure and dynamics.

Southwood stressed that habitat for animals must be considered in terms of its heterogeneity in time and space [56]. Soil fauna respond strongly to seasonal fluctuations of soil habitat space, which is maintained dynamically through the balance between habitat gain by litter fall and loss by litter decomposition [38]. Hence strong temporal variability in habitat size or quality is a paramount characteristic of the organic soil habitat [57]. While litter soluble components and soft tissues are immediately consumed by decomposers, the recalcitrant part steadily accumulates as humus and forms soil layers. As a result, habitat for soil animals generally comprises various qualities of plant residues at different decomposition stages (from freshly fallen litter to humus), which together build the soil organic layer (see Figure II in Box 1). Most studies using a trait-based approach have used traits of freshly fallen, undecomposed litter (or sometimes green leaves) to infer litter quality for the soil community [34,40,41]. However, for any given species, litter quality in terms of food as well as habitat changes as decomposition progresses. Thus, we have to consider the temporal variability of litter characteristics to assess

Glossary

Plant Economics Spectrum (PES): a multivariate axis of plant functional trait variation representing a gradient of resource-use strategies associated with resource conservation and slow growth and with rapid resource acquisition and fast growth [44].

Plant traits: morphological, physiological, biochemical, and phenological characteristics that represent ecological strategies and determine how an individual plant respond to environmental factors, affect other trophic levels, and/or influence ecosystem properties [69].

Size and Shape Spectrum (SSS): a multivariate axis of plant functional trait variation related to plant (organ) or litter particle size and shape ranging from small and relatively simply shaped to large with more complex shape [62,63].

Soil organisms: organisms inhabiting the soil, ranging from small microorganisms such as bacteria and fungi to microfauna (e.g., protozoans, nematodes), mesofauna (e.g., collembolans, mites), and large macrofauna (e.g., earthworms, millipedes, spiders).

the quality of the total soil organic layer to understand its overall role for most soil fauna [26,57]. A conventionally used index (i.e., ‘humus form’) has also been important in characterizing the type of soil organic layer and linking plant and soil communities [54,58,59]. However, this index has only enabled the subjective, qualitative visual categorization of the soil organic

Box 1. Basic Concept to Link Plant Community and Soil Animal Community through Plant Litter Traits in Terms of a Food–Habitat Template

As plant litter provides ‘a house made of food’ for soil animals, consideration of both the habitat and the food functions of litter is necessary to explain the mechanisms of soil community dynamics from plant litter traits. Food quality relates to litter traits associated with the PES while habitat quality relates to traits associated with the SSS [62]. The effects of litter PES and SSS traits on soil fauna will differ among taxa, ranging from small microfauna to mesofauna and larger macrofauna (Figure I). These differences in the role of litter traits are partly due to animal traits themselves, such as their body size, mobility, and terrestrial/semiaquatic attributes. While microfauna living in the free soil water move over short spatial scales, mesofauna moving through the pore network of the soil organic layer can be more controlled by litter size and shape, and macrofauna that dig through the litter and soil can choose their foods and habitats [2]. Thus, we hypothesize that the relative importance of habitat versus food differs among soil taxa: the effect of litter traits associated with food can be stronger for microfauna and macrofauna than for mesofauna. However, we should also consider trophic interactions; taxa can affect each other by bottom-up or top-down regulation. Also, ecosystem engineers like earthworms, which create habitat for other soil organisms, are a special case in need of in-depth consideration with respect to the food and habitat functions of plant litter.

Soil habitat is maintained dynamically through the balance between habitat gain by litter fall and habitat loss by litter decomposition. These processes, through the action of soil organisms, form the soil organic horizon comprising plant residues at different decomposition stages: OL (litter layer), OF (fragmented litter layer), and OH (humus layer). In Figure II, temporal litter trait variability is described by two dimensions in association with spatial trait variability along the soil vertical profile. With litter fall and decomposition, single litter trait values change continuously with a downward movement of organic residues in the soil vertical profile (blue arrows), while litter traits within a certain layer exhibit repeated fluctuations with new input of organic matter and its loss (orange arrows); this fluctuation within each soil layer will decline from upper to deeper soil layers. Effects of temporal change in litter traits associated with PES and SSS on soil fauna can differ among soil taxa (i.e., positive, +; negative, -; Figure II).

Figure I. Taxon-Specific Effects of Litter Traits Associated with Food and Habitat Functions. (A) Plant Economics Spectrum (PES)-related traits may have different effects on micro/mesofauna consuming microbes versus meso/macrofauna feeding on litter [2], although all soil fauna depend directly or indirectly on plant litter as their food source. (B) With regard to Size and Shape Spectrum (SSS)-related traits, larger-bodied mesofauna and macrofauna are probably more filtered by litter volume or pore size, while microfauna inhabiting the water film around litter particles are more influenced by litter particle size distribution (i.e., litter surface area).

Figure II. Dynamics of 'a House Made Out of Food' for Soil Fauna. Blue arrows show the change of single litter trait values with a downward movement of organic residues in the soil vertical profile, while orange arrows show the fluctuation of litter trait values with new input of organic matter and its loss in each layer. (A) In terms of Plant Economics Spectrum (PES)-related traits, a decrease in litter nutrients (e.g., nitrogen, phosphorus) with decomposition will negatively affect most soil taxa including microbivores, because of associated changes in microbial community composition and activities [24,34]. A decrease in lignin content may positively influence mesofauna or macrofauna chewing litter itself by their molar plates [2]. (B) In terms of Size and Shape Spectrum (SSS)-related traits, a decrease in pore size or litter volume due to decomposition can negatively affect mesofauna and macrofauna, while an increase in litter surface area can positively influence microfauna [70].

layer into three or more types (e.g., Mull, Moder, Mor, Amphi, Tangel) [60]. If we describe the quality of the total soil organic layer with strong short-scale vertical gradients in microclimate, resource quality and particle size, by continuous trait values, we can link plant and soil communities in a more flexible and quantitative way.

Temporal variability of litter traits affects soil fauna at various timescales. On a short scale (e.g., within 1 year in the temperate climate zone), decomposition decreases the quality and quantity of the litter layer [i.e., especially the upper litter layer (OL)]. However, every year fresh litter falls onto the soil, resetting this upper layer to a high quality and quantity (orange arrows in OL, see Figure II in Box 1). This annual fluctuation of litter traits affects habitat availability as well as food supply for litter dwellers and strongly affects community dynamics leading to seasonal patterns in animal activity and abundances [23,38]. Over longer timescales, litter trait variability relates to the time needed to form the soil organic layer through decomposition under a given plant community. Down the soil profile, from freshly fallen to fragmented litter and humus, the amount of nutrients in plant residues decrease, while their particles become smaller in size and more uniform in shape (blue arrows, see Figure II in Box 1). In addition to these changes in single leaf litter, each soil layer shows temporal trait variability (i.e., fresh and fragmented litter layers and humus layer; orange arrows, see Figure II in Box 1). Importantly, this annual trait variability within each layer strongly declines down the soil profile (i.e., slower trait change with decomposition in recalcitrant humus layer than in upper layers). During soil organic layer formation, stable unpalatable plant

residues will accumulate due to low decomposability, promoting litter habitat quality to soil fauna rather than food quality. Litter traits at a given place also vary over a longer timescale that comprises plant species turnover (e.g., vegetation succession). These different timescales for soil habitat formation and change interactively affect soil fauna composition, as the magnitude of temporal litter trait variability with decomposition depends on the changing traits of fresh litter from the above-ground plant communities along plant species replacement. Thus, we should assess soil organic layers in terms of habitat for soil organisms comprehensively by considering these different timescales that determine the temporal variabilities of litter traits, which interactively affect soil community dynamics.

A Trait-Based Framework Targeting the Dynamics of the Food and Habitat Functions of Plant Litter

Here we propose a trait-based approach to understand the dynamics of litter traits and their effects on soil animal communities (Box 1). The resource economy traits constituting the PES (see earlier) [43,61], through strong ‘afterlife’ effects, determine the litter tissue traits [42]. We combine this trait spectrum with the recently proposed ‘Size and Shape Spectrum’ (SSS), which focuses on a trait-based axis related to plant organ – and thereby litter – size and shape [62,63], to assess the respective food and habitat functions of litter. The quality of litter as a food source for soil animals can be explained by traits associated with the PES, while the suitability of the soil organic layer as habitat is likely to be associated more with the SSS [62]. Litter particle size and shape ultimately determine the compaction and cohesion of the soil organic layer and hence its accessibility to soil fauna, with small and relatively simply shaped particles building more compact organic horizons than large and intricately shaped particles [62,64]. The compaction and cohesion of the subsequent soil organic horizons affect pore size from top to bottom, which in turn influences humidity [65]; both factors are strong drivers of soil fauna composition [2,53]. Here we suggest adding a temporal dimension to the trait-based framework based on continuous trait space defined by PES–SSS, in which litter characteristics can be described quantitatively in a temporally and spatially dynamic manner. This framework will enable us to assess the dynamic soil organic layer in terms of habitat as well as food for soil fauna comprehensively (Figures 1 and 2).

The potentially available trait space is defined by axes related to the PES and SSS (Figure 1). All coexisting litter species belong to any of four quadrants in this PES–SSS trait space. For example, some evergreen conifers (e.g., *Taxus baccata*) are categorized in the LL compartment because of their generally nutrient-poor and small-sized litter. Alternatively, some broad-leaved deciduous species (e.g., *Populus tremula*) occupy the HH compartment, as their litter is nutrient-rich, larger, and morphologically more complex. Temporal variability of traits in the fresh litter layer due to annual litter fall is shown by the size of error bars, which varies among compartments. Temporal variability in PES values represents changes in food as well as habitat quality for soil fauna, while temporal variability of SSS values principally equals habitat change and may hardly affect food quality. Figure 1 shows this interaction between the PES and SSS axes through larger error bars on the SSS axis in species with higher PES values (i.e., greater temporal variability of SSS values due to faster decomposition and fragmentation). This indicates that habitat availability/stability for soil organisms is affected by their own feeding activities. Furthermore, the proposed framework allows us to address aspects of temporal variability in litter traits at longer timescales of soil organic layer formation (with long-term decomposition) and plant species turnover. Figure 2 shows how temporal litter trait variability along soil organic layer formation changes with plant species turnover from deciduous broad-leaved to evergreen broad-leaved trees and conifers, as a case of vegetation succession often observed in temperate zones [66]. Here conifers (blue species) have smaller trait variability (i.e., the change in position of the points over quadrants)

Figure 1. Litter Trait Space Defined by the Plant Economics Spectrum (PES) and the Size and Shape Spectrum (SSS) Illustrated with Short-Term Litter Trait Variability. All species are categorized into any of four quadrants in the trait space (LL, low PES and SSS; LH, low PES and high SSS; HL, high PES and low SSS; HH, high PES and SSS). Colors show species and error bars show short-term (e.g., annual) variability of litter traits in the litter layer (i.e., OL). Values of both PES and SSS will decrease as litter decomposition proceeds, but the values return to their original state when new litter falls onto the ground (cf. orange species in HH). The lengths of error bars differ according to the compartment that the species belongs to; here, for convenience, all species in a compartment have the same error bars, although the trait space has continuous trait axes and the lengths of error bars are variable even in the same compartment. We hypothesize that species with high PES values exhibit greater annual variability in PES-related traits than species with low PES values (compare the lengths of the PES-related error bars for HL vs LL or HH vs LH). On the other hand, species with high SSS values should exhibit larger annual variability in SSS-related traits than species with low SSS values (compare LH vs LL or HH vs HL). While the temporal variability of PES should not be affected by the value of SSS (compare LH vs LL or HH vs HL), the temporal variability of SSS is larger in species with higher PES values (compare HL vs LL or HH vs LH).

along the soil vertical profile with smaller variability (i.e., error bar) within each soil organic layer, compared with deciduous broad-leaved trees (orange species).

This approach with continuous trait values for the PES and SSS enables a mechanistic explanation of the difference in soil fauna communities under different plant species classified into the same conventionally used plant functional type or humus type. For example, among yellow and orange species (i.e., similar in PES values but different in SSS values) in the HH quadrant of Figure 1, the trophic chain length within the soil food web may be longer under yellow species with a higher SSS value as the larger pores will allow predators with larger body size access to prey. Furthermore, this approach of combining various timescales using the same trait space defined by the PES and SSS enables the comprehensive capture of key characteristics of the total organic habitat for soil fauna under different vegetation compositions. In this way, we explicitly link plant species traits and vertical stratification of soil animal communities. As biotic communities are

Figure 2. Change of Litter Traits in the Total Soil Organic Layer as Illustrated for Plant Species Turnover by the Use of the Multiple Trait Spaces Defined by the Plant Economics Spectrum (PES) and the Size and Shape Spectrum (SSS). Colors show species and error bars show the short-term (e.g., annual) litter trait variability within soil organic layers. Soil profiles with organic layers under different vegetation are shown by the three cubes. The points with error bars move beyond categories of the trait space with decomposition (A) or plant species turnover (B) (i.e., long-term temporal trait variabilities). As decomposition proceeds, the point of each litter species moves to the compartment of lower PES and lower SSS along the soil vertical organic profile: OL (litter layer), OF (fragmented litter layer), and OH (humus layer). The level of annual fluctuation in litter traits within each soil layer differs depending on the stage of litter decay and strongly decreases from the freshly fallen litter to humus, with the point movement towards the bottom left corner. The pattern of temporal litter trait variability at the timescale of soil organic layer formation depends on which plant species is present according to the turnover in vegetation composition. As plant species are replaced from deciduous broad-leaved tree species to evergreen broad-leaved tree species and coniferous tree species, the points in the OL move from one compartment to other compartments nonlinearly, accompanied by the change in litter trait variability along the soil vertical profile.

strongly affected by dynamic states (e.g., quantity, quality, stability) of resources [67,68], this framework will help to unravel the mechanisms behind soil fauna community dynamics. For example, under plant species with a small annual variability in litter traits (e.g., blue species; Figure 2), the soil animal community may be controlled deterministically by stable habitat structure, such as the reduction in pore size down the soil organic layers. However, under plant species whose annual litter trait variabilities largely differ between soil organic layers (e.g., orange species; Figure 2), community assembly rules can differ among soil organic layers. While stochastic processes may predominate especially in upper litter layers with large annual trait variabilities, in the humus layer with small annual trait variabilities, animal community composition can be controlled deterministically by stable habitat structure. These vertical characteristics of the soil organic profile and soil fauna community dynamics can be explained by plant species using the new framework, although other factors (e.g., climate; Box 2) are also important. Assessment of litter trait changes with succession in 2D trait space defined by the PES and SSS will inform better on the role of litter for soil fauna than 1D changes along the PES axis alone, which has failed to show consistent patterns [35]. In addition, this framework with continuous trait values enables

Box 2. Other Drivers That May Determine Habitat and Food Functions of the Soil Organic Layer

Effects of Climate

Although this paper focuses on litter traits as the determinant of soil community structure and dynamics, we have to incorporate climatic and weather differences, which may modify the effect of litter traits on soil communities, into the framework eventually. For instance, the length of dry spells or heat waves can strongly affect soil community dynamics through litter traits, because litter water content impacts soil organisms [2]. Litter size and shape, which could be strongly related to the water-holding capacity of a litter pack, can interact with weather conditions to determine soil moisture retention and evapotranspiration, while litter shape parameters (e.g., curliness) themselves may also change with soil moisture. In addition, relative effects between SSS-related traits and PES-related traits can differ among climate zones: the effects of SSS-related litter traits on soil community composition may decrease in warmer and wetter climate conditions like in tropical areas, in which activities of soil organisms increase and can be controlled metabolically by the quantity of litter as a food resource [71].

Effects of Carbon Inputs from Non-leaf Sources

We need to investigate if the patterns illustrated for leaf litter in this paper are kept when other plant organs, such as branches, twigs, flowers, and roots, are incorporated. For distal plant organs, such as twigs and fine roots, their chemical traits and decomposability are often correlated with those of leaves [42,72], as PES is defined as a whole-plant economic perspective on the leaf economic spectrum [43,44]. However, with regard to SSS-related traits, we still do not know whether and how they are coordinated between different organs [62], although leaf size and twig size seem positively related [73]. We need to assess the effects of differences in the timing of carbon supply among organs on formation of the soil organic layer. In deeper soil organic layer (Figure I), we should particularly consider the effect of both living and dead fine roots, which constitute important resources in soil systems [74]. In addition, fecal pellets from soil animals may serve a substantial function, especially related to SSS traits [58].

Effects of Plant Diversity

To apply this framework, illustrated for single plant species, to multispecies vegetation, we depict what we need to take into account in Figure II. Moreover, plant diversity often affects decomposition rate and decomposer community in a non-additive way [75]. Thus, we still need to disentangle which PES- or SSS-related trait dissimilarity is important by producing nonadditive effects on different soil taxa.

Figure I. Effects of Plant Roots and Animal Feces. Both plant roots (red) and animal fecal pellets (purple) could reflect the Plant Economics Spectrum (PES)-related trait values of leaf litter (gray) under each vegetation [43,76]. However, roots, which exist in the soil during all stages of plant life, senescence, and decomposition, could exhibit larger trait variabilities (error bars) than leaf litter. Especially in the deeper OH (humus layer), roots can provide more consumable organic compounds to soil fauna than decomposed leaf litter. Variations in Size and Shape Spectrum (SSS)-related trait values of roots and fecal pellets may both be decoupled from leaf litter among species. Although it remains unclear how SSS traits are coordinated between leaves and roots, we propose that the mean values and variabilities of SSS-related traits are likely to be lower among species for roots than for leaves. The sizes and shapes of fecal pellets are generally small and simple irrespective of vegetation or soil organic layer. The rate of production of feces is related to animal feeding activity (i.e., decomposition itself), so the effects of feces as habitat should be affected by litter PES values. As a consequence, the decrease in organic matter particle size by increasing fecal pellets with soil vertical profile could be larger under the plant species with high PES values.

Outstanding Questions

Which ‘Size and Shape Spectrum’ (SSS)-related traits are important to determine habitat quality for soil fauna?

Can we extract a SSS axis that strongly explains soil community structure and composition based on multivariate analyses such as principal components analysis?

Can the four quadrants with differing ‘Plant Economics Spectrum’ (PES) and SSS values for litter predict soil animal community composition?

Can we observe the hypothesized relationships between temporal variability in litter traits and the responses of soil animal community composition in the real world?

Can we link litter traits to (the legacy of) green leaf traits, some of which are already stored in global trait databases, to enable the use of available green leaf traits to explain soil fauna community dynamics?

Should litter particle size and shape become new additions to these databases, as they may often be poorly represented by leaf size and shape and because shape is lacking from these databases in the first place?

us to calculate the additive effects of multiple plant species. We still should consider some practical matters (Box 2) to apply this framework to multispecies vegetation as well as to include other sources of real-world complexity. However, this framework will practically help us choose which plant species combinations should be protected or planted in vegetation management or restoration efforts from the perspective of soil biotic health and diversity.

Concluding Remarks

We propose a PES and SSS trait-based conceptual framework that allows the assessment of how alterations in soil resource quality affect soil fauna more appropriately and comprehensively by integrating temporal variability in litter traits. To ensure the practical applicability of this framework, we need to define the SSS axis by collecting physical litter trait data in addition to a renowned suite of PES-related traits and to test how soil animal community composition responds to temporal variability in these litter traits (see Outstanding Questions). In addition, while this framework assumes that the soil fauna community is predominantly regulated bottom up by their resource [23], we should assess the extent of possible top-down influences of animals themselves. Furthermore, we should assess the interaction with other factors that could affect the habitat and food functions of litter, and we should apply this framework, illustrated here for a single plant species for clarity, to vegetation including multiple species (Box 2). However, the new concept proposed here marks a critical step in producing a promising tool to predict spatiotemporal changes in soil community structure from plant community composition via plant trait afterlife effects.

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References

- Wall, D.H., ed (2012) *Soil Ecology and Ecosystem Services*, Oxford University Press
- Coleman, D.C. *et al.* (2004) *Fundamentals of Soil Ecology*, Elsevier
- Crowther, T.W. *et al.* (2019) The global soil community and its influence on biogeochemistry. *Science* 365, eaav0550
- Bardgett, R.D. and van der Putten, W.H. (2014) Belowground biodiversity and ecosystem functioning. *Nature* 515, 505–511
- Thakur, M.P. *et al.* (2019) Towards an integrative understanding of soil biodiversity. *Biol. Rev. Camb. Philos. Soc.* 95, 350–364
- Wardle, D.A. (2004) Ecological linkages between aboveground and belowground biota. *Science* 304, 1629–1633
- Korbolevsky, N. *et al.* (2016) How tree diversity affects soil fauna diversity: a review. *Soil Biol. Biochem.* 94, 94–106
- Decaens, T. (2010) Macroecological patterns in soil communities. *Glob. Ecol. Biogeogr.* 19, 287–302
- Nielsen, U.N. *et al.* (2014) Global-scale patterns of assemblage structure of soil nematodes in relation to climate and ecosystem properties. *Glob. Ecol. Biogeogr.* 23, 968–978
- Maraun, M. *et al.* (2007) Awesome or ordinary? Global diversity patterns of oribatid mites. *Ecography* 30, 209–216
- Wu, T. *et al.* (2011) Molecular study of worldwide distribution and diversity of soil animals. *Proc. Natl. Acad. Sci. U. S. A.* 108, 17720–17725
- Fierer, N. and Jackson, R.B. (2006) The diversity and biogeography of soil bacterial communities. *Proc. Natl. Acad. Sci. U. S. A.* 103, 626–631
- Fiera, C. and Ulrich, W. (2012) Spatial patterns in the distribution of European springtails (Hexapoda: Collembola). *Biol. J. Linn. Soc.* 105, 498–506
- Van Den Hoogen, J. *et al.* (2019) Soil nematode abundance and functional group composition at a global scale. *Nature* 572, 194–198
- Phillips, H.R. *et al.* (2019) Global distribution of earthworm diversity. *Science* 366, 480–485
- Gaston, K.J. (2000) Global patterns in biodiversity. *Nature* 405, 220–227
- Hillebrand, H. (2004) On the generality of the latitudinal diversity gradient. *Am. Nat.* 163, 192–211
- Petersen, H. (2002) General aspects of collembolan ecology at the turn of the millennium. *Pedobiologia (Jena)* 46, 246–260
- Maaß, S. *et al.* (2015) Environmental filtering vs. resource-based niche partitioning in diverse soil animal assemblages. *Soil Biol. Biochem.* 85, 145–152
- Magilton, M. *et al.* (2019) Oribatid mites reveal that competition for resources and trophic structure combine to regulate the assembly of diverse soil animal communities. *Ecol. Evol.* 9, 8320–8330
- Anderson, J.M. (1975) The enigma of soil animal species diversity. In *Progress in Soil Biology. Proceedings of the 5th International Colloquium on Soil Zoology*, Prague 1973 (Vanék, J., Ed.), pp. 51–58, Academia
- Eisenhauer, N. *et al.* (2019) Recognizing the quiet extinction of invertebrates. *Nat. Commun.* 10, 50
- Wardle, D.A. (2002) *Communities and Ecosystems: Linking the Aboveground and Belowground Components*, Princeton University Press
- de Vries, F.T. *et al.* (2012) Abiotic drivers and plant traits explain landscape-scale patterns in soil microbial communities. *Ecol. Lett.* 15, 1230–1239
- Wubs, E.J. *et al.* (2019) Single introductions of soil biota and plants generate long-term legacies in soil and plant community assembly. *Ecol. Lett.* 22, 1145–1151
- Eisenhauer, N. and Powell, J.R. (2017) Plant trait effects on soil organisms and functions. *Pedobiologia (Jena)* 65, 1–4
- Funk, J.L. *et al.* (2017) Revisiting the Holy Grail: using plant functional traits to understand ecological processes. *Biol. Rev. Camb. Philos. Soc.* 92, 1156–1173
- Violle, C. *et al.* (2007) Let the concept of trait be functional! *Oikos* 116, 882–892
- McGill, B.J. *et al.* (2006) Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* 21, 178–185
- Pérez-Harguindeguy, N. *et al.* (2013) New handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot.* 61, 167–234
- Cornelissen, J.H.C. (1996) An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. *J. Ecol.* 84, 573–582
- Cornwell, W.K. *et al.* (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecol. Lett.* 11, 1065–1071
- Makkonen, M. *et al.* (2012) Highly consistent effects of plant litter identity and functional traits on decomposition across a latitudinal gradient. *Ecol. Lett.* 15, 1033–1041
- Orwin, K.H. *et al.* (2010) Linkages of plant traits to soil properties and the functioning of temperate grassland. *J. Ecol.* 98, 1074–1083
- Maharning, A.R. *et al.* (2009) Soil community changes during secondary succession to naturalized grasslands. *Appl. Soil Ecol.* 41, 137–147
- Leff, J.W. *et al.* (2018) Predicting the structure of soil communities from plant community taxonomy, phylogeny, and traits. *ISME J.* 12, 1794–1805
- Anderson, J.M. (1977) The organization of soil animal communities. *Ecol. Bull.* 25, 15–23
- Takeda, H. (1987) Dynamics and maintenance of collembolan community structure in a forest soil ecosystem. *Res. Popul. Ecol.* 29, 291–346
- Wardle, D.A. (2004) Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science* 305, 509–513
- Raymond-Léonard, L.J. *et al.* (2018) Springtail community structure is influenced by functional traits but not biogeographic origin of leaf litter in soils of novel forest ecosystems. *Proc. Biol. Sci.* 285, 20180647
- Fujii, S. *et al.* (2018) Tree leaf and root traits mediate soil faunal contribution to litter decomposition across an elevational gradient. *Funct. Ecol.* 32, 840–852
- Freschet, G.T. *et al.* (2012) A plant economics spectrum of litter decomposability. *Funct. Ecol.* 26, 56–65
- Freschet, G.T. *et al.* (2010) Evidence of the ‘plant economics spectrum’ in a subarctic flora. *J. Ecol.* 98, 362–373
- Reich, P.B. (2014) The world-wide ‘fast-slow’ plant economics spectrum: a traits manifesto. *J. Ecol.* 102, 275–301
- Sayer, E. *et al.* (2006) Effects of litter manipulation on early-stage decomposition and meso-arthropod abundance in a tropical moist forest. *For. Ecol. Manag.* 229, 285–293
- Kovalenko, K.E. *et al.* (2011) Habitat complexity: approaches and future directions. *Hydrobiologia* 685, 1–17
- Anderson, J. (1978) Inter- and intra-habitat relationships between woodland Cryptostigmata species diversity and the diversity of soil and litter microhabitats. *Oecologia* 32, 341–348
- Gill, R.W. (1969) Soil microarthropod abundance following old-field litter manipulation. *Ecology* 50, 805–816
- Uetz, G.W. (1979) The influence of variation in litter habitats on spider communities. *Oecologia* 40, 29–42
- David, J.-F. *et al.* (1991) Reactions of the macrofauna of a forest mulch to experimental perturbations of litter supply. *Oikos* 61, 316–326
- Mori, A.S. *et al.* (2015) Biotic homogenization and differentiation of soil faunal communities in the production forest landscape: taxonomic and functional perspectives. *Oecologia* 177, 533–544
- Saitoh, S. *et al.* (2014) Effect of habitat structural complexity on collembolan communities. *Ecol. Res.* 29, 81–90
- Nielsen, U.N. *et al.* (2008) Soil pore volume and the abundance of soil mites in two contrasting habitats. *Soil Biol. Biochem.* 40, 1538–1541
- Cassagne, N. *et al.* (2003) Relationships between Collembola, soil chemistry and humus types in forest stands (France). *Biol. Fertil. Soils* 37, 355–361
- Hansen, R.A. (2000) Effects of habitat complexity and composition on a diverse litter microarthropod assemblage. *Ecology* 81, 1120–1132
- Southwood, T.R. (1977) Habitat, the templet for ecological strategies? *J. Anim. Ecol.* 46, 337–365
- Berg, M.P. (2010) Spatio-temporal structure in soil communities and ecosystem processes. In *Community Ecology: Processes, Models, and Applications* (Verhoef, H.A. and Morin, P.J., eds), pp. 69–80, Oxford University Press

58. Ponge, J.F. (2003) Humus forms in terrestrial ecosystems: a framework to biodiversity. *Soil Biol. Biochem.* 35, 935–945
59. Salmon, S. *et al.* (2008) Relationships between soil fauna communities and humus forms: response to forest dynamics and solar radiation. *Soil Biol. Biochem.* 40, 1707–1715
60. Zanello, A. *et al.* (2011) A European morpho-functional classification of humus forms. *Geoderma* 164, 138–145
61. Diaz, S. *et al.* (2016) The global spectrum of plant form and function. *Nature* 529, 167–171
62. Dias, A.T.C. *et al.* (2017) Litter for life: assessing the multifunctional legacy of plant traits. *J. Ecol.* 105, 1163–1168
63. Cornelissen, J.H.C. *et al.* (2017) Are litter decomposition and fire linked through plant species traits? *New Phytol.* 216, 653–669
64. Grootemaat, S. *et al.* (2017) Scaling up flammability from individual leaves to fuel beds. *Oikos* 126, 1428–1438
65. Swift, M.J. *et al.* (1979) *Decomposition in Terrestrial Ecosystems*, Blackwell Scientific
66. Chapin III, F.S. *et al.* (2011) *Principles of Terrestrial Ecosystem Ecology*, Springer
67. Chase, J.M. (2003) Community assembly: when should history matter? *Oecologia* 136, 489–498
68. Tilman, D. (2004) Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proc. Natl. Acad. Sci. U. S. A.* 101, 10854–10861
69. Pérez-Harguindeguy, N. *et al.* (2013) Corrigendum to: New handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot.* 64, 715
70. Vestergaard, P. *et al.* (2001) Reduced particle size of plant material does not stimulate decomposition, but affects the microbivorous microfauna. *Soil Biol. Biochem.* 33, 1805–1810
71. Lavelle, P. *et al.* (1993) A hierarchical model for decomposition in terrestrial ecosystems - application to soils of the humid tropics. *Biotropica* 25, 130–150
72. Tjoelker, M.G. *et al.* (2005) Linking leaf and root trait syndromes among 39 grassland and savannah species. *New Phytol.* 167, 493–508
73. Westoby, M. and Wright, I.J. (2003) The leaf size–twig size spectrum and its relationship to other important spectra of variation among species. *Oecologia* 135, 621–628
74. Pollierer, M.M. *et al.* (2007) The underestimated importance of belowground carbon input for forest soil animal food webs. *Ecol. Lett.* 10, 729–736
75. Hättenschwiler, S. *et al.* (2005) Biodiversity and litter decomposition in terrestrial ecosystems. *Annu. Rev. Ecol. Syst.* 36, 191–218
76. Raubenheimer, D. and Simpson, S.J. (2004) Organismal stoichiometry: quantifying non-independence among food components. *Ecology* 85, 1203–1216