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Temperate forest floors: Ecosystem hub in transition?

Friederike Lang[1], *Jörg Prietzel*[2], *Frank Hagedorn*[3], *Klaus Kaiser*[4], *Stefanie Schulz*[5], *Mathias Mayer*[6, 3], *Lars Vesterdal*[7], *Jürgen Bauhus*[8], *Mai Bergmann*[9], *Sebastian Bibinger*[5], *Martin I. Bidartondo*[10,11], *Jingxuan Olivia Chen*[12], *Philipp de Jong*[3,20], *Trung Hieu Doan*[8], *Simon Haberstroh*[14], *Jonas Hahn*[1], *Peter Hartmann*[15], *Anis Mahmud Khokon*[16], *Martin Kohler*[8], *Laura M. Suz*[11], *Ina C. Meier*[9], *Richard Neumann*[17], *Heinke Paulsen*[18], *Heike Puhlmann*[15], *Helmer Schack-Kirchner*[1], *Stefan Scheu*[12,13], *Lexie Schilling*[1,7], *Patrick Schleppi*[3], *Michael Schloter*[5,19], *Kai Schwärzel*[17], *Kenton P. Stutz*[1], *Gabriela Villalba*[2], *Melissa Wannenmacher*[14], *Markus Weiler*[18], *Nicole Wellbrock*[17], *Christiane Werner*[14], *Jörg Niederberger*[1]

Corresponding authors:

Friederike Lang[1], friederike.lang@bodenkunde.uni-freiburg.de

Jörg Niederberger[1], joerg.niederberger@bodenkunde.uni-freiburg.de

Affiliations

1) Chair of Soil Ecology, Institute of Forest Sciences, University of Freiburg, Freiburg Germany.

2) Chair of Restoration Ecology, TUM School of Life Sciences, Technical University Munich, Freising, Germany.

3) Soil biogeochemistry, Forest and soil ecology, Swiss federal institute for forest, snow and landscape research (WSL), Birmensdorf, Switzerland.

4) Soil Science and Soil Protection, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany.

5) Research Unit Comparative Microbiome Analysis, Helmholtz Center Munich, Neuherberg, Germany.

6) Climate and Biodiversity, Institute of Forest Ecology, Department of Ecosystem Management, BOKU University, Vienna, Austria.

7) Department of Geosciences and Natural Resource Management, University of Copenhagen, Copenhagen, Denmark.

8) Chair of Silviculture, Institute of Forest Sciences, University of Freiburg, Freiburg, Germany.

9) Functional Forest Ecology, Department of Biology, University of Hamburg, Hamburg, Germany.

10) Life Sciences, Imperial College London, United Kingdom.

11) Ecosystem Stewardship, Royal Botanic Gardens, Kew, United Kingdom.

12) Animal Ecology, JFB Institute of Zoology and Anthropology, University of Göttingen, Göttingen, Germany

13) Centre of Biodiversity and Sustainable Land Use, University of Göttingen, Göttingen, Germany.

14) Chair of Ecosystem Physiology, Institute for Earth and Environmental Sciences, University of Freiburg, Freiburg, Germany.

15) Department of Soils and Environment, Forest Research Institute Baden-Wuerttemberg, Freiburg, Germany.

16) Biosciences Division, Oak Ridge National Laboratory, Oak Ridge, TN, USA.

17) Thünen Institute of Forest Ecosystems, Eberswalde, Germany.

18) Chair of Hydrology, Institute for Earth and Environmental Sciences, University of Freiburg, Freiburg, Germany.

19) Chair for Environmental Microbiology, Department for Life Sciences, Technical University of Munich, Freising, Germany.

20) Soil Resources, Department of Environmental Systems Science, ETH Zurich, Zürich, Switzerland,

Definition Forest Floor: In our review, the term Forest Floor comprises the organic horizons that lie on top of the mineral soil in forests. According to a coarse subdivision, it consists of up to three different horizons, which differ in their degree of decomposition.

Abstract

The forest floor (FF) plays a key role in carbon, nutrient, and water cycling. It is the biologically most active compartment of forest soils, highly responsive to environmental conditions. Yet, its response on currently changing forests is understudied. Here we (1) compile existing knowledge on provision of ecosystem services by the FF, (2) evaluate its vulnerability to environmental change, and (3) identify crucial knowledge gaps about future functioning of FFs. Reinforcing interactions between FF biota and abiotic FF components show multifactorial dependencies with environmental conditions and control FF turnover. Vice versa, the turnover of the FF regulates its role in carbon, nutrient, and water cycling. With slow litter decomposition and limited bioturbation, organic matter accumulates, nutrients are tightly cycled within the FF, and water is channelled through preferential flowpaths. In contrast, with rapid litter decomposition and intense bioturbation, FF accumulation is low, the mineral soil is the main nexus for plant nutrient

uptake and organic matter transformation, and water infiltrates more homogeneously into the mineral soil. A characteristic feature of the FF is its interconnectedness with the adjacent ecosystem compartments making it a central hub of forest processes. FF morphology reflects these processes and therefore has untapped potential as an indicator of soil and ecosystem health. Under forest change FFs might lose their functionality with negative impacts on nutrient provision, water storage, and carbon sequestration. Consequences for sustained forest growth might be strong and even catastrophic. Therefore, improved knowledge of FF characteristics and their linkages to mineral soils and aboveground ecosystem compartments is crucial for assessing forest resilience to ongoing environmental changes.

1 Our forest floor knowledge is insufficient to assess its response to forest change

In the forest floor organic matter, nutrients and energy of plant detritus are transformed, transiently stored and/or transferred to other ecosystem compartments. It results from complex interactions between plants, soil organisms, litter, and the underlying mineral soil. The FF provides central ecosystem services by supplying trees with water and nutrients, processing carbon (C), and harboring a wide diversity and abundance of soil biota, with strong feedbacks to the FF properties and the element cycles within the FF. As the FF is the most reactive part of forest soils, with organic matter often turning over at higher rates than in mineral soil, it would be expected to be the most responsive to the ongoing worldwide ‘forest change' (Seidl et al. 2014, Mc Dowell et al. 2020), encompassing climate change, nitrogen eutrophication, as well as shifts in tree species composition and overall forest management intensity (Callesen et al. 2003; Vesterdal et al. 2013; Mayer et al. 2020; Mayer et al. 2023b; Klein-Raufhake et al. 2025). Consequently, FFs will likely change in the near future and there is evidence that FF stocks are already responding to changing environmental conditions. Repeated soil surveys have documented decreasing FF stocks in German forests during the last decade (Wellbrock et al. 2017). This agrees with studies indicating decreasing FF mass with increasing temperature along elevation gradients (Hagedorn et al. 2019). Yet, Merilä et al. (2024) observed the opposite effect along a latitudinal gradient in Fennoscandia. This suggests that mono-factorial approaches are too simplistic to explain FF changes. Uncertainty is particularly high for temperate forests representing transition ecosystems, wherein even minor changes in the controlling factors might induce shifts between organic layer-dominated to mineral soil-dominated forests.

Traditionally, the FF has been considered a key aspect of ecological forest site assessment and survey (Green et al. 1993). However, it has frequently been ignored in forest research. This shortcoming is more prevalent in studies conducted in temperate than in boreal climate zones, where the FF is more often considered in soil related research. In many studies, litter and more decomposed FF layers are removed before soil sampling (see review by Berthrong et al. 2009). Other studies refer to depth-related soil analyses without specifying the depth at which the FF ends and the mineral soil begins, which hampers the discussion of results (Lembrechts et al. 2022). One reason for this neglect of the FF is its temporal and spatial variability as well as methodological and analytical challenges (Vogt et al. 1983, Yanai et al. 2003). Consequently, FFs are poorly incorporated in forest soil biogeochemical models, usually as a simple litter compartment (Peltoniemi et al. 2007) and often neglected in soil water models. Under a changing climate, several FF services have become increasingly critical, yet our knowledge remains limited. The aim of this review is to (1) compile existing knowledge on FFs, their characteristics and contributions to forest ecosystem services, (2) assess the vulnerability of FFs to forest change, and (3) identify the most important gaps in our scientific knowledge of FFs.

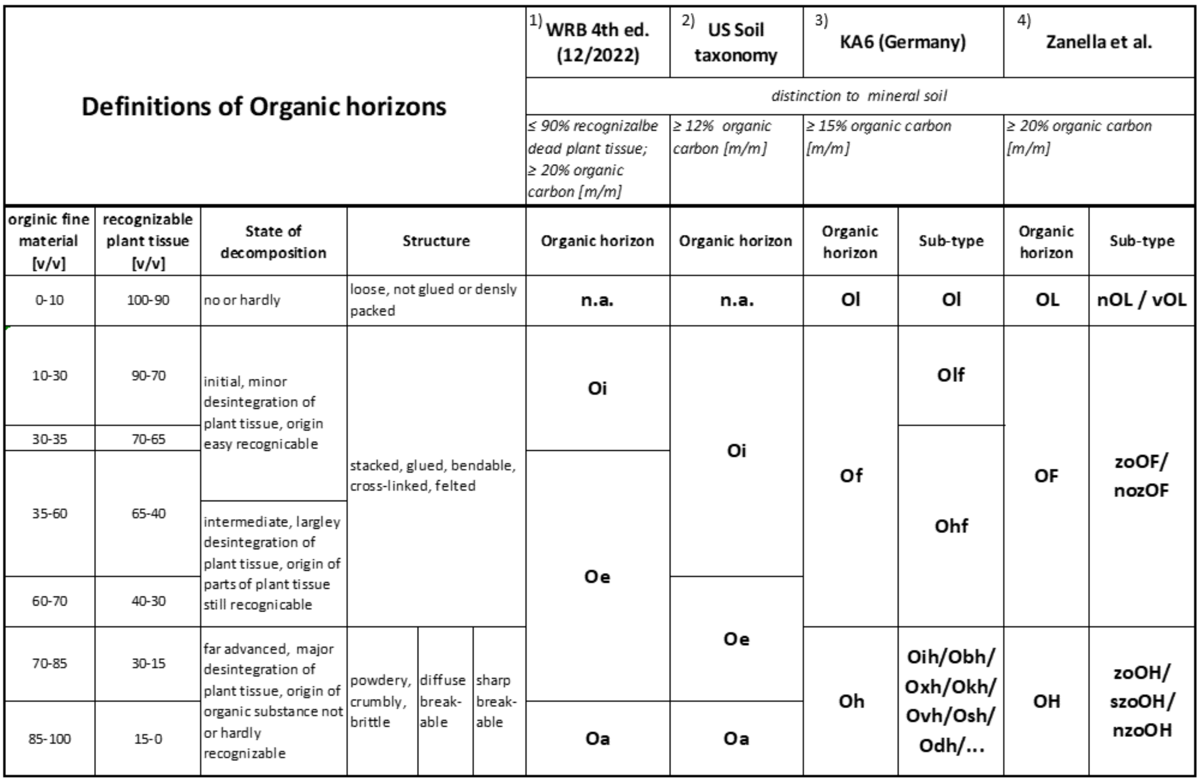
2 Definitions, classifications and the terminology used in this review

We lack an internationally standardized terminology regarding the forest litter in various stages of decomposition sitting on top of the mineral soil or the parent material. There is not even an agreement as to whether this organic material belongs to the soil or represents a separate ecosystem compartment. Common terms such as organic layer, litter layer, humus layer and forest floor are often used inconsistently (see reviews Berthrong et al. 2009, Chertov and Nadporoshskaya, 2018). During the last decades the demand for an international agreement was stated by several authors and although several proposals for a humus form classification system have been made (Brethes et al. 1995; Green et al. 1996; Klinka et al. 1981; Ponge, 2003; Wachendorf et al. 2023; Zampedri et al. 2023; Zanella et al. 2018d), there is still no agreed classification. Different publications use different terms describing the sum of organic layers as an entity. For instance, a Web of Science search of the terms “litter layer” and “forest” (performed Jan. 2025) showed, within the first 50 matches (ranked by decreasing number of citations), that in 30% of the papers the term *litter layer* was used for freshly fallen, undecomposed litter (IUSS Working Group WRB 2022), while the authors of 70% of those papers used *litter layer* as a synonym for the entire FF. Such inaccuracies can easily lead to misinterpretations, especially when comparing different studies. In this review, we use ‘forest floor’ to refer to the surface layers of forest soils mainly consisting of litter in various stages of decomposition or transformation (Prescott and Vesterdal 2021) and overlaying mineral soil horizons or bedrock. The FF is composed of one or several horizons, which must exceed a minimum content of organic C ranging from 12% (w/w) (Soil Survey Staff 2022) up to 20% (w/w) (IUSS working group WRB 2022; Zanella et al. 2018a; see Table 1). Surface organic layers may develop under aerobic as well as under anaerobic conditions, which leads either to terrestrial or aero-hydromorphic or hydromorphic humus forms (Frank et al. 2023; Wachendorf et al. 2023; Zanella et al. 2018a, 2018c), which are also called FF (Jauhiainen et al. 2005; Solondz et al. 2008). Aero-hydromorphic and hydromorphic humus forms are restricted to specific climatic and morphological conditions (Frank et al. 2023; Zanella et al. 2018c). We focus on FFs and humus forms developed for the most part under aerobic conditions.

The horizons of FFs are, like mineral soil horizons, strata with a set of characteristic properties. They are commonly differentiated according to the state of decomposition and share of fine humus material (Table 1). However, soil classification systems differ regarding the exact definition and the acronym of individual organic horizons. A general distinction is usually made between layers or horizons (Table 1) (illustrated by Wachendorf et al. 2023; Zanella et al. 2018b). (1) Litter layer (OL; L) is characterized as being hardly decomposed or at an initial state of decomposition, where the origin of the material can easily be identified. (2) Fermented layer (Oi/Oe; OF), a horizon of intermediate state of decomposition, with a considerable amount of organic fine substance, but still at least partially identifiable plant tissue origin, and (3) Humic layer (Oa; OH), a horizon at an advanced state of decomposition, dominated by organic fine material with macroscopic unidentifiable origin. Due to the high interannual variability, the World Reference Base for Soil Resources (WRB) 4th edition and the US soil taxonomy exclude, in contrast to other classification systems, the fresh fallen or hardly decomposed litter (OL, L) (IUSS Working Group WRB 2022; Soil Survey Staff 2022).

The term *humus form* describes a well-defined sequence of organic layers (supplement Table S2), specific properties of the mineral topsoil horizon, as well as of the transition between the FF and the mineral soil. Six out of the eleven national soil classification systems reviewed define humus forms and organic horizons (supplementary Table S1). However, according to a literature review (first 60 matches) in the Web of Science Database (performed June 2025, keywords: Forest Floor, Litter Layer), only 3% of the publications that have addressed explicitly the terms forest floor or litter layer either in the abstract or key words, described the humus form. At least 44% differentiated between organic horizons or layers. Nevertheless, half of publication addressing forest floor properties did not differentiate between organic horizons, and far less the humus form.

Table 1: Definitions of organic horizons in the forest floor, across soil classification systems.



Definitions of Organic horizons				1) WRB 4th ed. (12/2022)	2) US Soil taxonomy	3) KA6 (Germany)		4) Zanella et al.	
				distinction to mineral soil					
				≤ 90% recognizalbe dead plant tissue; ≥ 20% organic carbon [m/m]	*≥ 12% organic carbon [m/m]*	*≥ 15% organic carbon [m/m]*		*≥ 20% organic carbon [m/m]*	
orginic fine material [v/v]	**recognizable plant tissue [v/v]**	**State of decomposition**	**Structure**	**Organic horizon**	**Organic horizon**	**Organic horizon**	**Sub-type**	**Organic horizon**	**Sub-type**
0-10	100-90	no or hardly	loose, not glued or densly packed	**n.a.**	**n.a.**	**Ol**	**Ol**	**OL**	**nOL / vOL**
10-30	90-70	initial, minor desintegration of plant tissue, origin easy recognicable	stacked, glued, bendable, cross-linked, felted	**Oi**	**Oi**	**Of**	**Olf**	**OF**	**zoOF/ nozOF**
30-35	70-65						**Ohf**		
35-60	65-40	intermediate, largley desintegration of plant tissue, origin of parts of plant tissue still recognicable		**Oe**					
60-70	40-30				**Oe**				
70-85	30-15	far advanced, major desintegration of plant tissue, origin of organic substance not or hardly recognizable	powdery, crumbly, brittle diffuse break-able sharp break-able			**Oh**	**Oih/Obh/ Oxh/Okh/ Ovh/Osh/ Odh/…**	**OH**	**zoOH/ szoOH/ nzoOH**
85-100	15-0			**Oa**	**Oa**				

1) WRB: World Reference Base for Soil Resources. International soil classification system for naming soils and creating legends for soil maps. 4th edition 2022; 2) US Soil Taxonomy - A Basic System of Soil Classification for Making and Interpreting Soil Surveys, 2nd edition 1999; 3) KA6: Bodenkundliche Kartieranleitung KA6, German soil classifiction system 6th edition, 2024; 4) proposed European Humus Form Reference Base Zanella et al. 2018d.

Mull, moder, and mor are the three main humus forms representing a gradient regarding the environmental properties which control the rate of decomposition and bioturbation of litter, and thus FF turnover (see Figure 1; Ponge 2003; Prescott and Vesterdal 2021; Wachendorf et al. 2023; Zampedri et al. 2023, Zanella et al. 2018d). Accordingly, mull occurs at sites with favorable pH, rich in plant nutrients, highly degradable litter, sufficient precipitation and temperate to warm climates. It consists of thin organic layers poor in organic fine material due to strong bioturbation and fast belowground transfer and decomposition of litter. Some classification systems also distinguish between L-mull (OF horizons not present; humus form with maximum turnover) and F-Mull (FFs having OL and OF horizons, Wachendorf et al. 2023). Moder occurs on sites with intermediate site conditions and forms at least one horizon with high share of organic fine material (OH), usually in well aggregated form due to less intense bioturbation of litter with the mineral soil, but still high biological activity. Mor typically occurs on acidic forest sites with cool and moist climate, and low nutrient content of the mineral soil. It consists of thick humus layers that are, in typical form, assumed to be decoupled from the mineral soil and in soils where soil fauna plays a minor role for litter transformation and translocation. In general, the classification of humus forms relies on morphological properties indicating decisive biological processes, rather than on quantitative criteria. The share of organic fine material which is used to differentiate between the different organic layers is an exception. The mass of FF or the mass of different FF horizons is not considered in classification. However, it is widely assumed that from mull over moder to mor the FF mass increases and FF turnover rates decrease (Klein-Raufhake et al. 2025). Accordingly, we considered this assumption in our conceptual figures (see Figures 1 and 3a-f). For these figures, the response of FF characteristics on increasing FF mass is referenced by the characteristic value assumed for L-mull. With regard to FF functioning, it is important to consider that with the different humus forms, the biochemical and physical properties of the FF also change. The presence of organic fine material increases the bulk density of the FF and the connectivity of pores between FF and mineral soil unless growing fine roots and fungal hyphae at the interface between FF and mineral soil disrupt this pore continuity humus form mor; Figure 1).

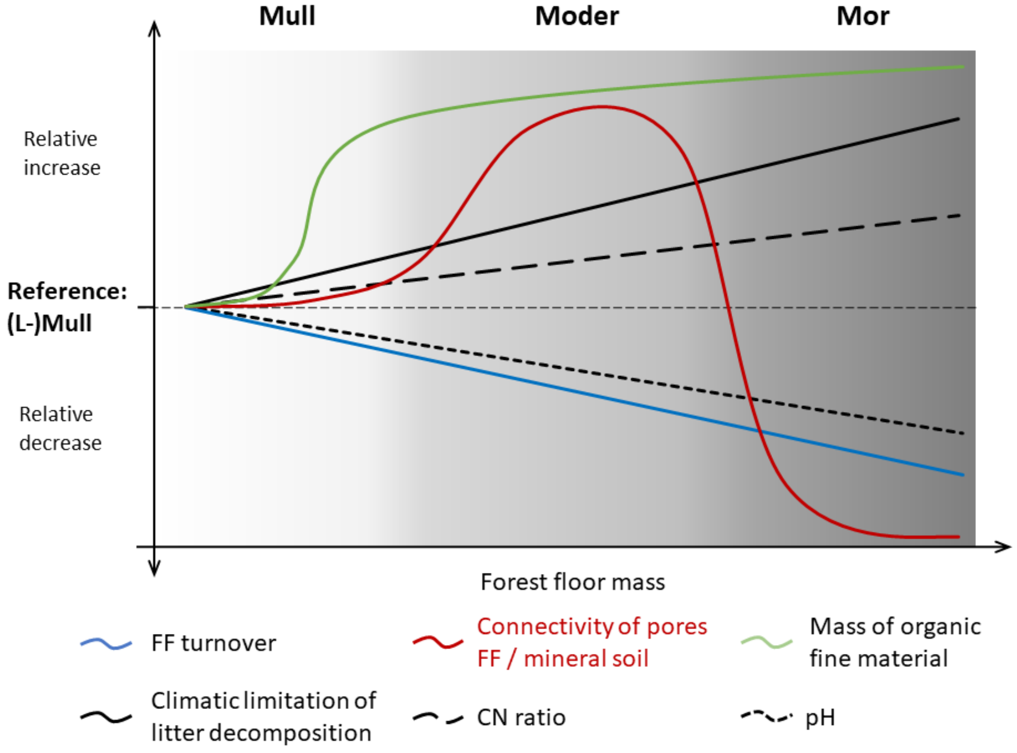


Figure 1: Comparison of the conditions controlling decomposition and bioturbation (in black) and of resulting key properties (colored) as assigned to the main humus forms assuming constant litter fall for all humus forms. Different shades of gray represent different humus forms, which are not clearly differentiated in terms of mass. Proposed changes (specific FF mass minus L-mull value) are referenced to the L-mull value.

3 The relevance of forest floors for ecosystem functioning

Controlling factors of FF dynamics and properties include environmental conditions, the vegetation, soil organisms, and the processes they induce. In general, FF turnover, which is mirrored by its mass, thickness, or humus form, depends on litter and root input, conditions for decomposers, the organisms that contribute to bioturbation (Figure 2), and their interactions with other FF biota. Principally, FF turnover increases with temperature, moisture (if oxygen is not limiting), nutrient availability, and litter decomposability (Grigal and Vance 2000), resulting in decreasing FF thickness. In general, the relevance of the given controls is widely accepted (Grigal and Vance 2000). However, there are many unknowns regarding the quantitative importance of these factors and even more regarding their interactions.

Functioning as a major reservoir of organic matter and nutrients, the FF plays a vital role in regulating ecosystem processes and associated ecosystem services (Gosz et al. 1976, Figure 2). Nutrient, C and water cycling in forests can completely change with changing FF turnover and with changing FF controls. We compiled the results of studies addressing the relevance of FFs for different soil-related ecosystem services and linked published results to FF mass, turnover and humus form in the following sections.

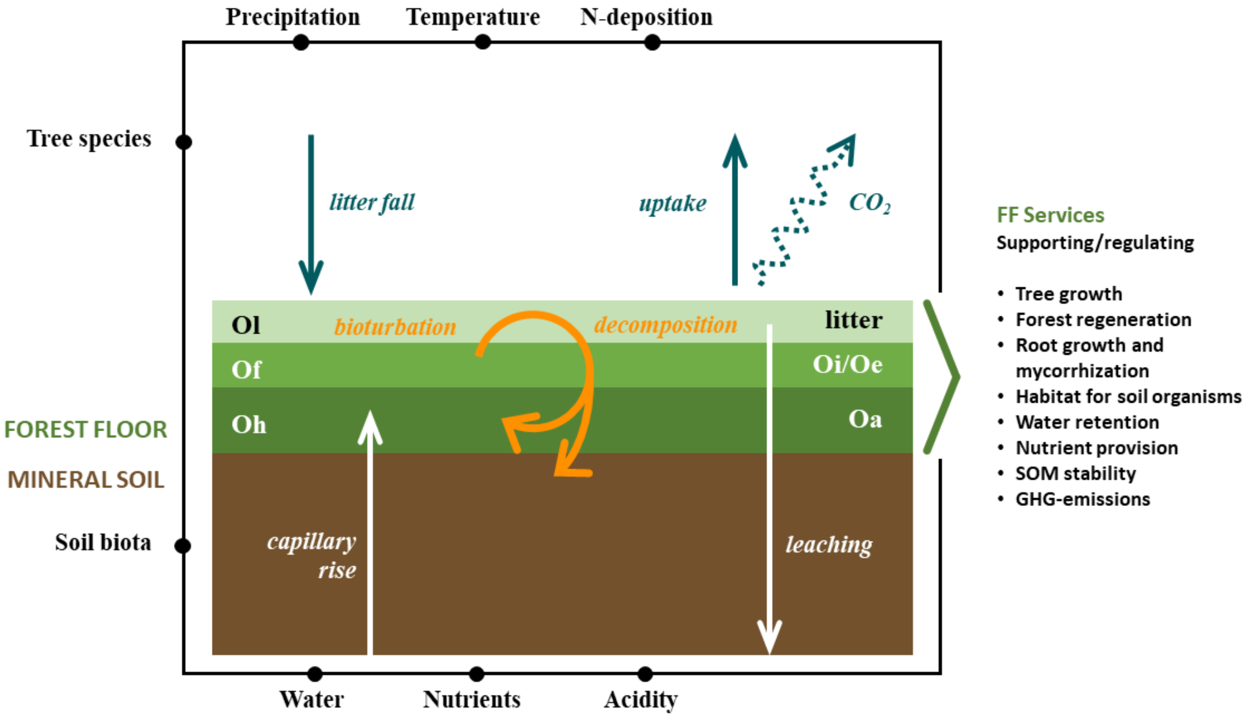


Figure 2: Controlling factors of FF characteristics and related target ecosystem services, Ol, Of, Oh: organic horizons according KA6 (Wachendorf et al. 2023), litter, Oi/Oe, Oa: organic horizons according WRB (IUSS Working Group WRB 2022).

The role of the forest floor for the mineral nutrition of trees within ecosystems

The FF first received attention in ecology because of the observed correlation of the FF thickness with forest productivity (Babel 1971). Thin, mull-type FFs have been assumed to indicate high fertility linked to high litter quality and fast release of nutrients, while thick, mor-type FFs have been assumed to indicate low biological activity and nutrient availability (Müller 1887; Olson 1963; Hartmann 1965; Green et al. 1993; Bardgett et al. 2005). Yet, it must be considered that thick FFs are often the consequence rather than the cause of low fertility. Many publications show that thick FFs are important for forest nutrition at sites with nutrient-poor mineral soil, which is particularly well documented for phosphorus (P; Paré and Bernier 1989; Jonard et al. 2009; Lang et al. 2017; Prietzel et al. 2022). Studies quantifying the contribution of FFs to overall nutrient uptake in forests are scarce. Lang et al. (2017) and Prietzel et al. (2022) presented a rough estimate for beech forests based on the share of overall fine root biomass present in the FF. They found that a minimum of 20% (P-rich site) to 92% (P-poor site) of the total P taken up from down to 1 m mineral soil depth was provided by the FF and the upper 5 cm of the mineral soil, depending on the parent material and P availability at the study sites. Based on isotopic tracing (^{26}Mg), van der Heijden et al. (2015) determined that 43% of the Mg taken up by a beech forest on an acid, nutrient-poor soil was acquired from the FF.

The role of the FF in forest nutrition depends on nutrient stocks, nutrient availability and rooting intensity, which all change with FF mass (Figure 3a, d) and influence the contribution of FFs to overall tree nutrient uptake.

Leaf litter has long been assumed to be the most important source of FF nutrients (Ukonmaanaho et al. 2008), though root and mycorrhizal necromass are increasingly recognised (Phillips et al. 2013). Mineral particles introduced into the FF from underlying soil horizons by bioturbation or formed *in situ* may also contribute to FF nutrient dynamics (Prietzel et al. 2020b, 2023). Furthermore, nutrients can be transported into the FF by capillary rise of the mineral soil solution. At present, quantitative information is missing to assess the relevance of these processes.

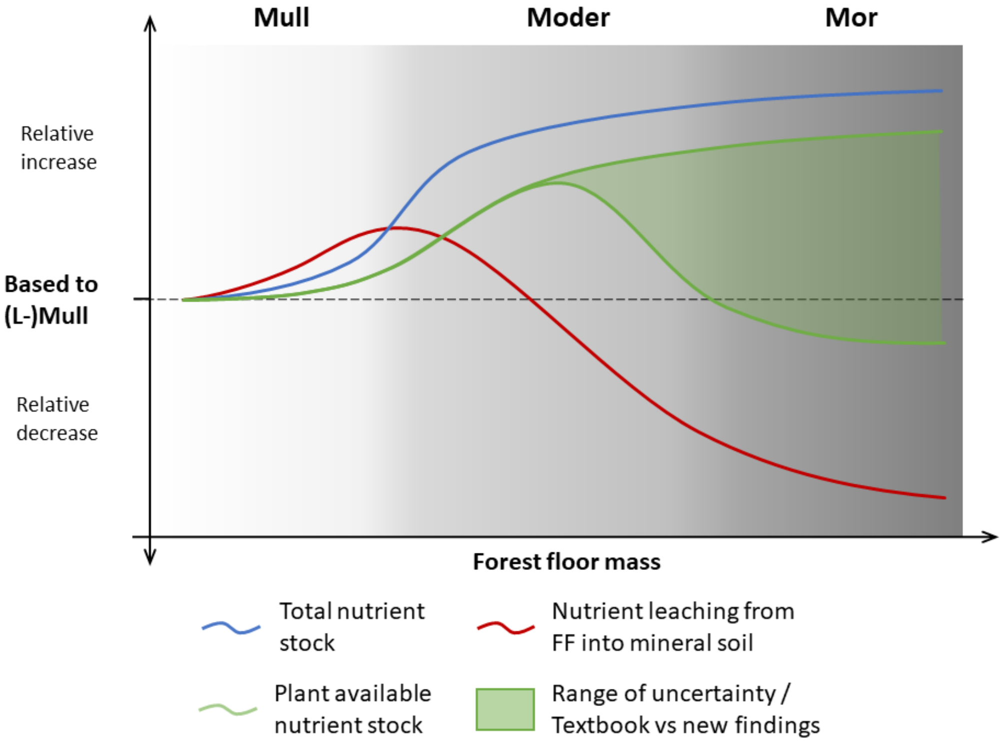


Figure 3a: Total nutrient stocks, plant availability and nutrient leaching from FF into the mineral soil depending on FF mass and humus form – all values are referenced by the L-mull value.

With increasing FF mass, the stock of nutrients tends to increase, but also the proportion of more decomposed material increases. Therefore, the relationship between the mass and nutrient stocks in FFs depends on litter decomposition stoichiometry and on the fate of mineralized nutrients. Nutrients can be mineralized faster, as fast, or slower than C (Berg et al. 2017). Depending on the case, the increase in nutrient stocks can be slower, the same, or faster than the increase in the mass of organic matter. Literature reviews on the release of nutrients during litter decomposition indicate that these relationships are element specific. Synthesizing results of 68 litter decomposition studies mainly of pine and spruce in boreal and temperate forests, Berg et al. (2017) observed that calcium (Ca) and potassium (K) concentrations of decomposing litter decreased with time (after a first concentration increase for Ca). Increasing concentrations of manganese (Mn), nitrogen (N), P, and sulfur (S) have been observed at later decomposition stages (Berg et al. 2015; Gunina and Kuzyakov 2022). These results are confirmed by observations of FFs along a stand chronosequence by Covington (1981) and by FF stoichiometry changes from OL to OF/OH layers as reported by Vesterdal et al. (1995). In view of the low turnover rate of organic matter in thick FFs, decoupling of C and nutrient dynamics can make them a significant factor in forest nutrition. Yet, knowledge on the stoichiometry along litter decomposition in FFs and how it is related to the availability of nutrients to plants and microorganisms is missing (Dincher et al. 2020). Furthermore, the relevance of FFs for the nutrition of trees strongly depends on tree species, their rooting pattern, and associated microorganisms. Ectomycorrhizal fungi particularly support the nutrient uptake by trees based on nutrient mining (see below; Smith et al. 2008; Pena et al. 2010; Khokon et al. 2023).

Though often ignored, the ecological relevance of FF internal nutrient cycling has already been stressed some time ago in a review by Currie et al. (1999). According to this review, high amounts of N can be retained in FFs by microbial immobilization. Högberg et al. (2020) provided evidence that at high C:N ratio, ectomycorrhizal fungi are responsible for the observed immobilization, while at lower C:N ratio bacteria might be more important. For thick FFs with low turnover it has been shown that P mineralization rates are well synchronized with the P uptake by fine roots, thus contributing to close P recycling within FFs in P-poor systems (Hauenstein et al. 2018; Spohn et al. 2018; Brödlin et al. 2019) and decreasing nutrient leaching into the mineral soil (Figure 3a). In agreement, Vogt et al. (1986) observed significantly higher mean residence times for N than for C in FFs of coniferous forests compared to other ecosystems. This could indicate an internal N (re)cycling within the FF, complementing nutrient uptake by plants.

The role of the forest floor in soil carbon dynamics

Carbon stocks in FFs of European forest soils range from 1 Mg C ha^{-1} in thin mull-type FF to around 70 Mg C ha^{-1} in thick mor-type FF. Despite this variability, on average the FF accounts for 20% of the soils' C stocks down to 1 m based on a survey of 4914 plots among 22 European countries (De Vos et al. 2015). A previous survey of European forest soils reported a similar range of C stocks in FFs (Baritz et al. 2010). According to De Vos et al. (2015), the humus form explained most of the variability of FF C stocks (Figure 3b).

The FF consists of a continuum of compounds ranging from minimally decomposed litter to highly transformed organic matter in OH horizons. While litter-derived organic matter dominates throughout the FF (Cools et al. 2014; Berg and McClaugherty 2020), the share of plant-derived tissue (e.g., foliage, wood, bark) and compounds therein (e.g., lignin, cellulose, hemicellulose) decreases with depth relative to microbial metabolites and necromass (Buckeridge et al. 2020; Prescott and Vesterdal 2021). The exception are roots: the OF and OH horizons harbor considerable root biomass and thus experience substantial inputs of root residues (Guidi et al. 2023). The biomass of roots in Norway spruce FFs increased strongly from mull- to mor-type forest floors, driven both by soil fertility and thinning intensity gradients (Vesterdal et al. 1995; see also Figure 3d). In boreal forests, for instance, Fahey and Hughes (1994) and Clemmensen et al. (2013) showed that 50–70% of the FF C stock can be derived from roots and root-associated microorganisms. Accordingly, the contribution of above-ground C input into FF will decrease with increasing FF mass (Figure 3b).

The OF and OH horizons can also contain considerable amounts of mineral-associated organic C, as shown by density fractionation (Villalba-Ayala et al. 2025). The proportion of mineral-associated C increases with the degree of decomposition and depth unless bioturbation is impaired (Figure 3b) and may contribute to C stabilization within the FF (Prietzel et al. 2020b). Exceptions are soils, where the FF directly overlies bedrock material. Associated humus form is Tangel which forms directly over solid or coarse carbonate bedrock (Kolb and Kohlpaintner 2018; Zanella et al. 2019).

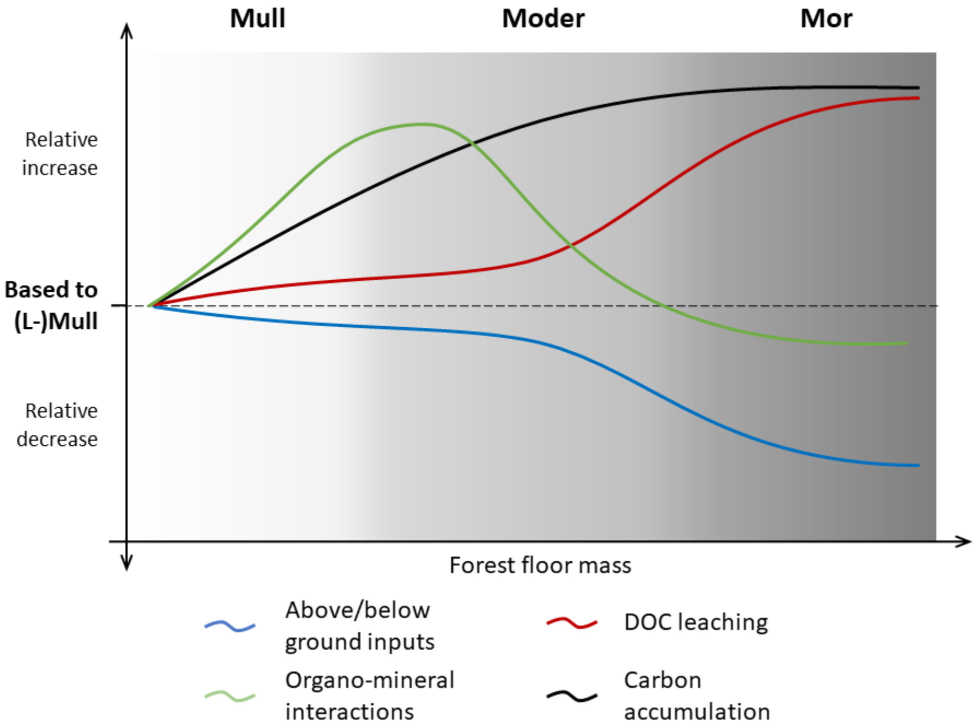


Figure 3b: Share of organic matter present as organo-mineral interactions, ratio between above and below-ground input of organic matter into FFs and transfer of DOC and litter from FF into the mineral soil as depending on FF mass and humus form – all values are referenced by the L-mull value.

The FF is a key reactor for C in forest soils through the processing of a major part of plant detritus produced by net primary production. Carbon inputs into the FF are either mineralized to CO_2, leached as DOC into deeper soils, transferred into the mineral soil by soil fauna, or stabilized by microorganisms against further decomposition (Fahey et al. 2013; Hagedorn et al. 2019; Kohl et al. 2021; Figure 3b, Figure 3d). The relative and quantitative contributions of these FF processes to the C balance of forest soils is still uncertain and highly context-specific (Kammer et al. 2012; Stutz et al. 2019) as they depend on interrelated factors including litter quality, climatic conditions, and the properties of the soil beneath FFs (Berg and McClaugherty 2020; Desie et al. 2020). Large-scale assessments of litter decomposition using litter bags have revealed that climate variables (mean annual temperature and precipitation) and litter quality, particularly lignin content, C/N ratio, and Mn content, are key factors controlling litter mass loss (Berg and McClaugherty 2020). Much less is known about the fate of the C lost during decomposition from such litter bags. A one-year study using ^{13}C-labeled beech litter in a mull-type FF showed that 29–34% of added litter-C had been mineralized, 4–5% leached as DOC, and 23–31% remained in the FF (Kammer et al. 2012). Additionally, 3–4% and 2–7% of the litter-derived C were recovered in particulate and mineral-associated organic C, respectively, in the 2 cm of soil underneath the FF, while approximately 30% were translocated into deeper mineral soil via bioturbation.

In particular, the processes governing the transformation and stabilization of organic matter within the FF itself remain poorly understood, especially at longer time scales and in relation to FF morphology. Radiocarbon-based assessments indicate turnover times of up to 40 years for mor-type organic layers across Scandinavia (Fröberg et al. 2011). Earlier studies suggest only partial transformation of organic matter occurs within the FF (Guggenberger and Zech 1992; Guggenberger et al. 1994; Lindahl et al. 2007), and that transformation products differ from those in the mineral soil due to different composition and activity of microbial communities (Paul 2016), particularly in mor-like FFs with little incorporation of minerals (Heckman et al. 2011). More recently, Prescott and Vesterdal (2021) stress that transformation of litter may cause the accumulation of *de novo* materials that persist within the FF. Nutrients may matter: Under conditions of low nutrient availability, it has been assumed that the necromass of ectomycorrhizal fungi might represent a significant and rather stable C pool in OH horizons (Clemmensen et al. 2013), while additional mechanisms of stabilization might be active at high N availability (Högberg et al. 2020). Thus, the stability of FF organic matter under current and future conditions remains uncertain. Long-term tracer studies across different humus forms and tree species appear as the most powerful approach to increase our understanding of the FF as a hub for soil C dynamics.

Forest floors as habitat for tree roots and seedlings

From the overall compilation of publications dealing with the FF as a habitat for various organisms, it is evident that the FF is the consequence of interactions and self-reinforcing mechanisms. On the one hand, the species composition in the forest and the FF determines its turnover and other properties, while on the other hand, the respective organisms, such as plants, fungi, bacteria or fauna often benefit greatly from FFs with the specific properties that they themselves participate in shaping. For this reason, we will consider both in the following subsections, the relevance of the FF for the biota inside as well as the relevance of the biota for FF properties.

In their global meta-analysis of root depth distribution, Schenk and Jackson (2002) found that in over 90% of the 475 soil profiles that were sampled for fine roots, at least 50% of roots were identified in the upper 30 cm, including the FF. Meier et al. (2018) observed that two thirds of the total fine root biomass to 240 cm soil in a European beech forest resided in the FF and mineral topsoil. Leuschner et al. (2022) found that the total amount of fine root biomass of European beech in the FF increased with elevation and higher FF thickness (Figure 3d), which was not the case in the top 10 cm of the mineral soil (Leuschner et al. 2022).

These examples illustrate that the FF is of great importance for plant roots. In particular, at nutrient-poor sites with thick FFs, it provides extremely suitable conditions for plant roots. While the risk of low oxygen levels is low close to the surface (Schenk and Jackson 2002) and water holding capacity of the FF is high (Schenk and Jackson 2002; Gao et al. 2021), readily available nutrients from litter and organic matter decomposition strongly favor fine root growth (Sayer et al. 2006). Roots in the FF show higher absorptive capacity for nutrients than roots in the mineral soil (Gao et al. 2021), illustrating the nutrient-acquiring purpose of these fine roots in the FF often associated with mycorrhizal fungi (see below). However, organically bound nutrients present in the FF are mostly not plant-available and need further decomposition to be taken up by the plant. Providing readily degradable photosynthates in root exudates to microorganisms, plants can accelerate this decomposition, called priming effect (Rohrbacher and St-Arnaud 2016). Supporting this, Meier et al. (2017) brought forward that nitrogen cycling is accelerated through root exudation. Tückmantel et al. (2017), Rohrbacher and St-Arnaud (2016) and Vives-Peris et al. (2020) found that especially the presence of organic N – as found in the FF – increases the amount of root exudation. In contrast, Leuschner et al. (2022) found a negative relationship between the quantity of root exudation and the N content in the topsoil. However, in this latter study, the exudation sampling was always conducted at the same soil depth, sometimes sampling in the forest floor and sometimes in the mineral soil, depending on the site. Root exudation might differ substantially between the forest floor and the mineral soil, which might explain these opposing findings. It is worth mentioning that the relevance of FFs for root growth strongly varies with FF mass, humus form (Fig. 2d), mineral soil and other site conditions as well as with tree species composition and stand conditions (see above, Vesterdal et al. 1995).

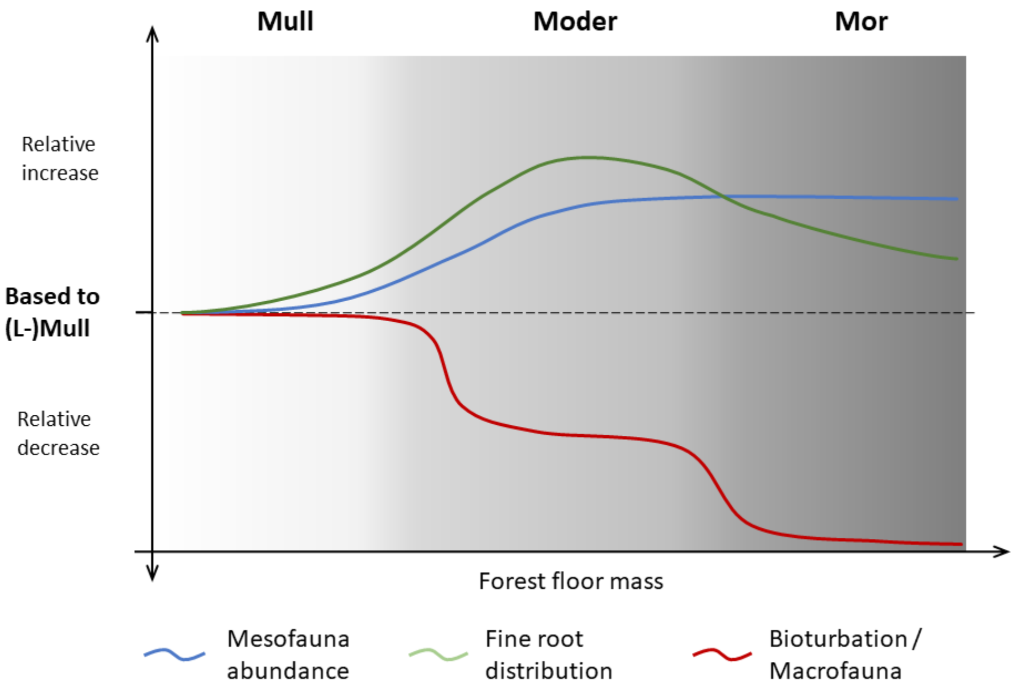


Figure 3d: The relevance of the FF for tree roots and the soil mesofauna as depending on FF mass and humus form – all values are referenced by the L-mull value.

In turn, roots can contribute strongly to the accumulation or loss of organic C in the surrounding soil (Piorier et al. 2018), either by producing recalcitrant litter or by enhancing stabilization of organic matter based on microbial processing (Sokol et al. 2019). However, high allocation of roots to the FF increases the sensitivity to prolonged drought or against windthrow. In agreement, the relative importance of the FF as fine root habitat in nutrient-poor forest stands decreased exponentially with increasing risk of summer drying (Meier and Leuschner 2008).

Another trade-off of thick FFs might involve the regeneration of trees. The early establishment of seedlings consists of different stages of development, in each of which FF plays a different role: serving as a seedbed prior to emergence and as a growing medium for seedlings post-emergence. Information on how FF properties influence seedling establishment, both in direction and magnitude, is often ambiguous and context- and species-specific (Madsen et al. 1995; Major et al. 2013; Sayer 2005). Positive services of FFs for seeds and seedlings consist of its role as a water-retaining medium (Tiebel at al. 2023), a habitat for mycorrhizal fungi and their spore banks (Sayer 2005) and shelter against grainivors such as birds and rodents (Myster and Pickett 1993; Hulme and Borelli 1999). On the other hand, FF also may have inhibitory effects on plant establishment. Thick FFs may act as a mechanical barrier that reduces light transmittance and prevents seedling roots from reaching the mineral soil (Sayer 2005; Baskin and Baskin 2014).

Phytotoxins, present in the litter of certain plant species (e.g., *Picea abies*) can hinder the germination and early seedling growth of some woody and herbaceous species (Koorem et al. 2011; Zeidler 2023). Responses to FF conditions vary with ontogeny, making it difficult to determine favourable conditions for establishment success. In a study of 15 North American tree species, increased emergence was found in the absence of litter, but litter presence prolonged post-emergence survival under drought condition (Fisichelli et al. 2015). Additionally, the habitat function of FF for seeds and young plants may be affected by interactions between FF properties and abiotic (e.g., nutrient availability and precipitation) and biotic factors (e.g., plant competition and fungal pathogens). For example, thick FF under wet spring conditions harbours fungal pathogens (Butin 2011) and molluscs which reduce seed vitality and contributes to regeneration failure in several broadleaved tree species (Ibáñez et al. 2007; Fisichelli et al. 2015; Zimmermann 2008). In a previous study, increased survivorship of moisture-sensitive species in scarified seedbeds compared to undisturbed FF conditions under drought has been observed, which could be attributed to the more stable water holding capacity of mineral soil relative to soil beneath hydrophobic dry litter (Clark and D'Amato 2023). Regarding plant nutrition, in P-poor beech forests, FF may be an important P supply for both mature trees and seedlings (Hauenstein et al. 2018; Lang et al. 2017) and decreasing FF thickness may intensify the competition for P by dominant trees, which are more competitive than seedlings due to their extensive root systems (Coomes and Grubb 1998, 2000).

Given the complex ways in which FF may influence tree regeneration, understanding of how seedling establishment responds to FF conditions is still poor. Further experimental research is essential to clarify these pathways and to deepen the understanding of vegetation shifts under interacting FF properties and climate changes. Reflecting the previously mentioned definitional issue, most research on plant establishment has focused predominantly on the presence or absence of the litter layer, rather than considering the FF in the full range of its forms and properties (Fisichelli et al. 2015; Tiebel et al. 2023; Wang et al. 2022).

Forest floors as habitat for mycorrhizal fungi

Most tree species associate with either arbuscular mycorrhizal fungi (AMF) or ectomycorrhizal fungi (EMF). Trees associated with AMF dominate in warmer environments with thinner FFs and more rapid nutrient mineralization, while trees associated with EMF dominate in cooler or colder environments with thicker FFs and delayed organic matter decomposition (Soudzilovskaia et al. 2015). These differences in FF properties can be attributed to leaf and root chemical traits of the two types of host trees, which influence the palatability and decomposability of tree litter and the accumulation of SOM (Phillips et al. 2013). Compared with trees colonized by AMF, trees forming interactions with EMF have greater hyphal necromass production and lower leaf and root litter quality, which leads to slower litter decomposition and thicker FFs (Vesterdal et al. 2013). Furthermore, EMF have been shown to decelerate litter decomposition at low soil fertility (Mayer et al. 2023a) due to competition with saprotrophic fungi (Figure 3e); a phenomenon that has been described first by Gadgil and Gadgil (1971) and is since then known as the Gadgil effect. However, as Fernandez et al. (2020) clearly pointed out in their review, caution is advised when generalizing this hypothesis, since all the underlying mechanisms are not yet known. For conifer forests, EMF and their hyphae are assumed to contribute to FF accumulation (Högberg et al. 2020). At the same time, they seem to be well adapted to the specific FF properties they are causing. EMF have developed the capacity to secrete extracellular enzymes involved in litter C degradation (Meier et al. 2015; Carteron et al. 2020), which facilitates organic and inorganic nitrogen (N) uptake for their host trees primarily from the fragmented or humified FF horizons (McGuire et al. 2013; Khokon et al. 2021; Khokon et al. 2023). Accordingly, the relevance of FFs for plant nutrition as catalyzed by EMF may increase from the humus form mull over moder to mor (Figure 3e). Since AMF have limited capacity to produce hydrolytic extracellular enzymes, they predominate in the mineral soil and their host trees must rely on nutrient mobilization by saprotrophic microbes (Talbot et al. 2008; Lin et al. 2017) or on nutrient acquisition from mineral resources. In addition to their own environmental preference, the occurrence of mycorrhizal fungi also depends on host root biomass. Since fine root biomass is concentrated to the thicker FF in cold-moist or highly acidic and infertile forest stands (Leuschner et al. 2006; Finér et al. 2007; Meier et al. 2018), mycorrhizal colonization of roots (by EMF) is high in these environments (Lilleskov et al. 2019).

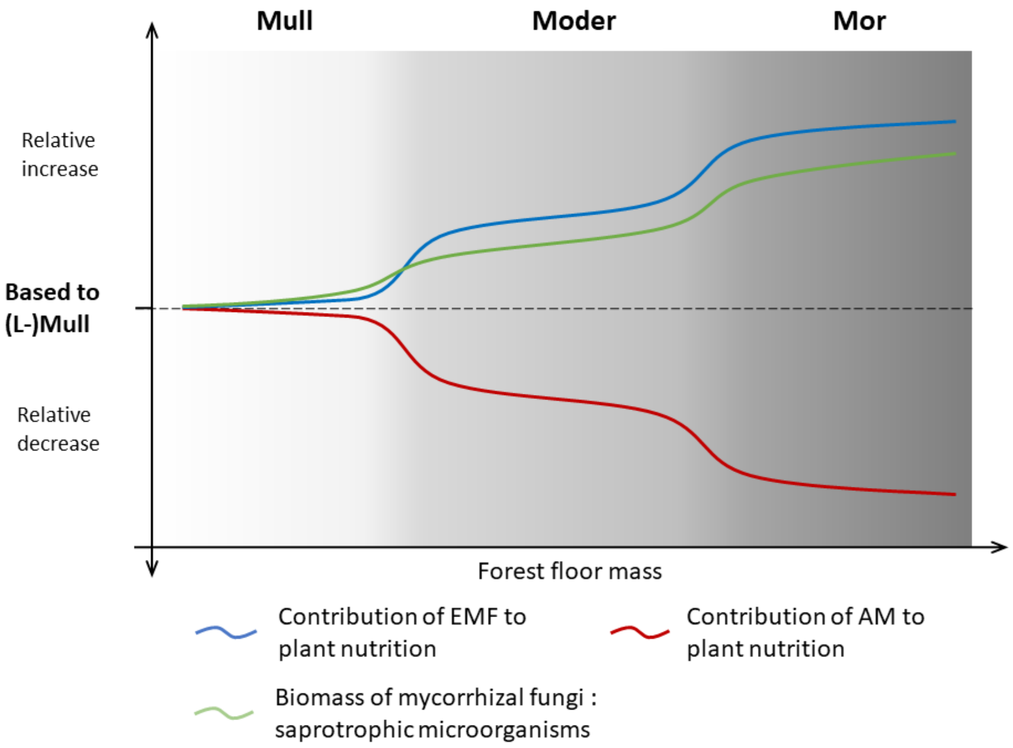


Figure 3e: The relevance of the FF for mycorrhizal fungi as depending on FF mass and humus form – all values are referenced by the L-mull value.

Forest floors as habitat for soil saprotrophic fungi and bacteria

Current literature indicates that at the scale of the soil profile, the FF often represents the zone with the highest microbial activity (Pollierer et al. 2015; Lladó et al. 2017). However, it declines with soil depth as demonstrated for a broad range of potential enzyme activities (Preusser et al. 2019; Baldrian et al. 2013), litter degradation rates (Buresova et al. 2021) as well as based on DNA and RNA profile comparisons (Žifčáková et al. 2016) and from mull over moder to mor humus forms (Figure 3f) (Hellwig et al. 2019). This is further accompanied by changes in microbial community composition either within kingdoms or across, for example from bacteria to fungi or within fungi (Žifčáková et al. 2016; Asplund et al. 2018). If the mineral soil is characterized by low nutrient contents and or low pH, the FF provides a particularly important habitat for soil organisms (Scheu et al. 2003, Salmon et al. 2008; Jonard et al. 2009; Gomez-Brandon et al. 2017b; Khokon et al. 2021).

In addition, the FF is characterized by significant temporal as well as spatial heterogeneity. Peaks in microbial activity of mull FFs may be highly correlated with litter fall periods, which require quick adaptation of the microbiome to changing conditions through community changes and/or versatile metabolic capacities. The large amount of decomposable organic material in the FF (Lang et al. 2017) supports mineralizing bacteria, mycorrhizal and saprotrophic fungi and other microeukaryotes with species distribution, diversity and functionality depending on FF layer and type (Lindahl et al. 2007; Solly et al. 2017; Bonanomi et al. 2019). Consequently, we assume that overall microbial diversity increases with increasing FF thickness (Figure 3f). Lindahl et al. (2007) showed that among the fungal community, saprotrophic organic C degraders dominate the litter layer, and nitrogen mobilizing mycorrhizal fungi the OF and OH layers. Typically, the initial stages of litter decomposition are dominated by saprotrophic fungi like basidiomycete and ascomycete microfungi (Osono 2007; Eichlerová et al. 2015; Khokon et al. 2021), as well as Proteobacteria and Bacteriodetes, making up 60 and 30% of the active community in a *Picea abies* (Norway spruce) dominated temperate forest, respectively (Žifčáková et al. 2016). However, substrate quality changes strongly as litter decomposition progresses, that is with time and along the FF profile, indicating temporal and spatial fluctuation of the microbiome (Žifčáková et al. 2016). In particular, bacteria respond significantly to changes in litter C:N ratio, while fungi are more driven by tree species composition (Urbanova et al. 2015). In general, it has been observed that soil respiration and microbial biomass decrease from OL to OF and OH layers (Figure 3f, Kanerva and Smolander 2007). Despite huge differences in substrate quality (micro- and macronutrients) and in C:N:P ratios of habitats (Takahashi 2021), the concept of microbial homeostasis (Cleveland and Liptzin 2007) is still a valid concept and a driver of bacterial functional community composition as indicated by similar microbial C:N:P ratios in FF and mineral soil (Zederer et al. 2017). This poses the question at which level of organization microbial regulation in FF takes place: at the level of microbial biomass, at the level of microbial communities, or at the level of gene expression of single microorganisms.

In addition to the FF material itself, living fine roots in the FF provide an additional microhabitat and substrate within OF and OH layers (Kanerva and Smolander 2007). The rhizosphere serves as a sink and a source for nutrients at the same time, mainly during the growth period. Trees rely on the nutrients provided by microbial processes in the soil and mycorrhizal transfers, and directly compete for those, especially N and P. On the other hand, trees provide easily available C sources for microbial nutrition, by-passing the need for the degradation of complex C sources provided by the litter. However, nutrient acquisition strategies differ among tree species. For example, spruce is known to release nitrification inhibitors and is thus directly altering microbial N turnover and nutrient stoichiometry (Stempfhuber et al. 2017). In this context, studies of mineral forest soils demonstrated the importance of ammonia-oxidizing archaea in acidic spruce stands to maintain this important ecosystem function (Stempfhuber et al. 2014). However, if this also holds true for the FF is not yet clear. The large amount of fungal biomass in FFs (Högberg and Högberg 2002) makes the hyphosphere another relevant microhabitat, particularly for bacteria, which might serve as nutrient source, but also as a fungal highway to bypass nutrient-poor microsites (Bielcik et al. 2019; Simon et al. 2015; Meier et al. 2015). Bacteria were shown to be invaders as well as degraders of fungal cell walls, where the dynamics of decomposition processes strongly depend on the chitin and melanin contents of the hyphae.

Knowledge on FF layer-specific composition and functionality of the microbial community is still missing as well as knowledge on the influence of those FF microbiota on the microbial community in the mineral soil beneath. Observations at local (Wang et al. 2021) as well as latitudinal scales (Shi et al. 2013) have indicated that effects are likely. The interactions within and between different trophic levels may play an important role in terms of competition for nutrients (bacteria versus EMF), collaborative or competitive decomposition (soil fauna vs. microorganisms, saprotrophic fungi vs. bacteria) or substrate or nutrient transfer between FFs and mineral soils e.g., by soil fauna. These issues are particularly interesting in the FF, as nutrient quality and amount significantly differ along the litter degradation gradient in the FF. Finally, the degree of accumulation of FF biomass may be the result of those trophic interactions. However, quantitative, general knowledge about these interrelationships along the FF layers is missing, and studies comparing FF versus mineral soil indicate different overall interactions across different trophic groups (Mundra et al. 2021).

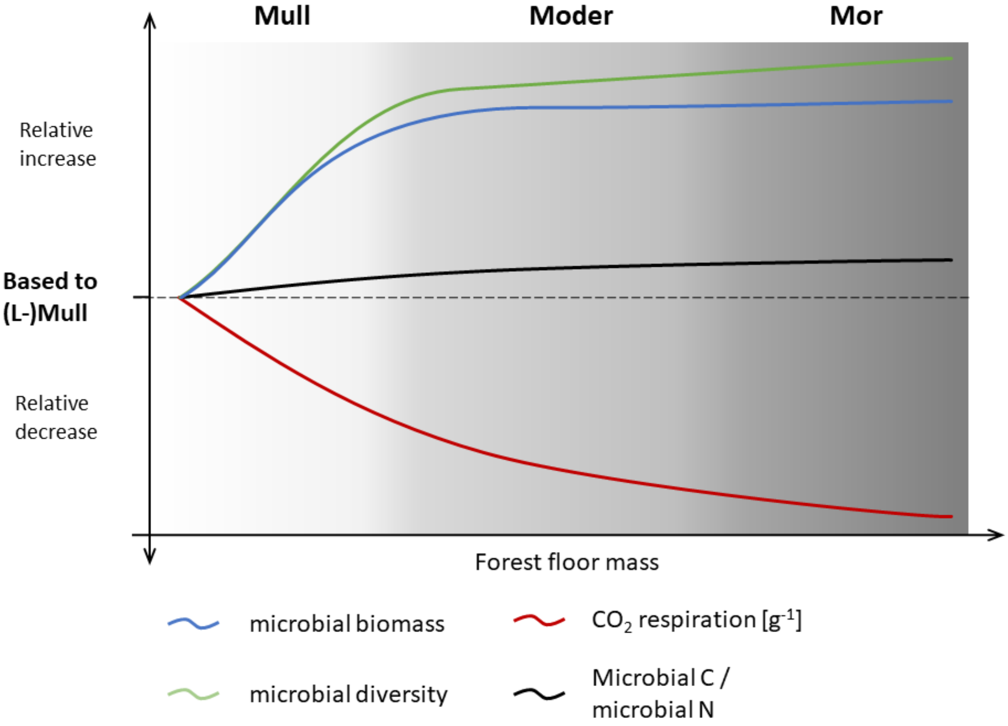


Figure 3f: The relevance of the FF for soil microorganisms as depending on FF mass and humus form – all values are referenced by the L-mull value.

Forest floors as habitat for soil fauna

Animals completing their full life cycle in soil comprise macrofauna (e.g., earthworms, millipedes, isopods) with body size larger than 2 mm, mesofauna (e.g., springtails, oribatid mites, enchytraeids) with body size ranging from 100 µm to 2 mm, and microfauna (e.g., protists, nematodes) with body size below 100 µm (Swift et al. 1979; Nielsen 2019). Additionally, there are "part-time employees," which include various mammals, soil-dwelling insect larvae, and mound-building insects (Wolters 2001). Early observations highlighted the link between the formation of FFs and the actions of soil animals including arthropods and earthworms (Müller 1887). Since then, it has been realized that animal communities in soil are structured vertically, with many species predominantly inhabiting the FF (Scheu and Falca 2000; Decaëns et al. 2006; Berg and Bengtsson 2007). This reflects that aboveground litter provides essential resources for soil animal communities, although it is increasingly recognized that belowground, root-derived resources contribute to fueling soil animal food webs (Zieger et al. 2017; Zhou et al. 2023).

Forest floor layers provide a wide range of food quality for soil fauna with diverse feeding strategies, ranging from primary decomposers feeding on plant litter, to secondary decomposers predominantly feeding on microorganisms, in particular fungi, to predators and scavengers, characterised by many detritivore taxa including oribatid mites (Oribatida) and springtails (Collembola) (Scheu and Falca 2000; Schneider et al. 2004; Chahartaghi et al. 2005, Chen et al. 2025). Microarthropods tend to dominate FFs

(Mitchell 1978; Arribas et al. 2021) and prefer intermediate stages of litter decay (Fuji and Takeda 2017; Marian et al. 2018). Low-quality litter, characterized by a high C/N ratio, deterrents such as phenolics, and recalcitrant compounds, typically is not readily consumable by soil fauna (Bal 1970). Detritivore animals often rely on microbial processing of litter, transforming it into a more digestible form (Maraun and Scheu 1996; Frouz 2018). The OL layer, composed of little decomposed plant residues, provides habitat for macrofauna detritivores but also a wide range of larger microarthropods, all characterized as epedaphic or epigeic species. The OF and OH layers, enriched in nutrients and microorganisms, are heavily colonized by microbial feeders and secondary decomposers characterized as hemiedaphic species (Huhta and Hänninen 2001; Zanella et al. 2018; Figure 3d). The mineral soil with its more limited pore space, by contrast, typically is colonized by blind and small microarthropods including springtails, oribatid mites, and gamasid mites, but also soil dwelling and burrowing macrofauna such as earthworms characterized as euedaphic or endogeic (Nielsen 2019). Additionally, the FF acts as buffer against environmental fluctuations, resulting in a stable microclimate for soil fauna (Walsh and Voigt 1977; Sayer 2005, see paragraph on thermal properties of FFs). The organic layers also offer essential physical structures that serve as shelter and breeding grounds (Bal 1970; van Straalen 2023). Generally, the distribution of animals in the soil profile is closely linked to animal body size (Coleman et al. 2024). Protists and microfauna, such as rotifers, tardigrades and nematodes occupy water films, while mesofauna is confined to the existing soil structure (Erktan et al. 2020). Macrofauna, by contrast, can actively shape their environment by burrowing (Scheu and Setälä 2002; Lavelle and Spain 2002; vanVliet and Hendrix 2007).

The soil fauna of the FF sustains various ecosystem services. Soil animals directly participate in litter decomposition by fragmentation and feeding (Frouz 2018; Nielsen 2019; Potapov et al. 2022). Large detritivores such as earthworms, millipedes, and isopods, but also microarthropods such as springtails and oribatid mites transform litter into fecal pellets comprising small litter fragments (Nielsen 2019; Potapov et al. 2022). Soil animals also indirectly affect litter decomposition processes by regulating the soil environment and interacting with microbial communities (Scheu et al. 2005; Frouz 2018; Potapov et al. 2022). A number of processes are responsible for soil animal-mediated changes in microbial litter decomposition. The transformation of litter into fecal pellets has been shown to accelerate decomposition processes (Coulis et al. 2016; Frouz 2018; Joly et al. 2020). Grazing on saprotrophic fungi by fungivores accelerates litter decomposition presumably due to mobilization of nutrients in fungal hyphae (Seastedt 1984; Scheu et al. 2005; A'Bear et al. 2014). The contribution of soil animals to litter decomposition has been assessed at local and regional scales (Handa et al. 2014; Peng et al. 2023). On average, soil fauna has been found to increase litter decomposition by 27% across ecosystems and climate zones, but the effect varies among biomes and with litter quality (Garcia-Palacios et al. 2013).

Soil animals play a crucial role in nutrient cycling. In addition to mobilizing nutrients bound in microbial and fungal tissue, they alter nutrient cycling by changing the size, composition, and activity of microbial communities (Coleman 1985; Bardgett 2005; Scheu et al. 2005; Shutenko et al. 2022). Excretion of nutrients by soil animals contributes to nutrient availability in soil. Bacterivorous nematodes, for instance, excrete significant amounts of mineral nitrogen thereby facilitating plant growth (Griffiths 1994; Ferris et al. 1998; Laakso et al. 2000). Earthworms, as major soil macro-detritivores, also increase nutrient mineralization and plant growth (Scheu 2003; Van Groenigen et al. 2014). The effects of large soil detritivores on microorganisms and plants are linked to their ability to physically alter the soil environment (Stockdill 1982; Eisenhauer et al. 2007; Craven et al. 2017).

The composition of soil fauna has a significant impact on the humus form. Macrofauna, particularly earthworms, affect the abundance and diversity of mesofauna through various pathways such as modification of the soil habitat, i.e., by bioturbation (Maraun et al. 2001; Eisenhauer et al. 2010). In soils with mull-type FF, macrofauna biomass is high, with anecic and endogeic earthworms most abundant (Jabiol et al. 1995; Parkinson et al. 2004; Edwards and Arancon 2022). The former forage for litter on the soil surface and pull it into their burrows in the soil, but both anecic and endogeic earthworms contribute to bioturbation (Bouché 1977; Ferlian et al. 2020; Edwards and Arancon 2022). Bioturbation by macrofauna is crucial in shaping the soil profile, as their activity redistributes organic matter and enhances nutrient cycling. This process is also decisive for the presence of specific humus forms: In soils of lower pH (typically < 4.5) and with input of litter of low to intermediate quality, a moder-type FF develops. Here, the density and diversity of endogeic and anecic earthworms are notably lower compared to mull FFs, resulting in less bioturbation (Bouché 1975; Frouz 2018; Bardgett 2005 Edwards and Arancon 2022; Figure 3d). Under these conditions, the bioturbation is primarily maintained by litter-feeding macroarthropods, such as millipedes, isopods and dipteran larvae (Schaefer and Schauermann 1990; Frouz 2018). In mor-type FFs, bioturbation by fauna is minimal, as macrofauna activity is greatly reduced (Bardgett 2005; Frouz 2018). Therefore, bioturbation is high in mull soils, declines sharply in moder soils, and is virtually absent in mor-type FFs (Figure 3d). In particular, in mull FFs, mesofauna suffers from bioturbation by earthworms, which may result in massive decline in the abundance and diversity of springtails and oribatid mites (Eisenhauer et al. 2010; Ferlian et al. 2018; Jochum et al. 2021). As forest floor mass increases from mull to moder, mesofauna abundance rises while that of macrofauna declines (Schaefer and Schauermann 1990; Maraun and Scheu 2000; Frouz 2018). The increase in mesofauna abundance, particularly of springtails, is closely correlated with root biomass (Potapov et al. 2017).

Generally, the shift from macrofauna- to mesofauna-dominated ecosystems along the transition from mull to moder FFs is closely linked to soil pH (see also Figure 1 and 2). This reflects the more pronounced pH sensitivity of macrofauna than mesofauna decomposers. In millipedes and isopods this sensitivity is related to reduced availability of Ca, which is needed for hardening their cuticle (Hopkin and Read 1992; Zimmer 2003). Earthworms are also sensitive to low pH, likely because of aluminum (Al) toxicity (Phillips and Bolger 1998; Edwards and Arancon 2022), causing the virtual absence of endogeic and anecic earthworms in acidic soils and the formation of moder-like FF. By contrast, in northern North America, where indigenous earthworm species are lacking, moder occurs also on soils with high pH, and these FFs have been transformed into mull after invasion of European earthworms (Alban and Berry 1994; Parkinson et al. 2004). This invasion allowed for tracking the transformation of moder into mull FFs and the associated changes in faunal species composition, food webs and soil functions (Bohlen et al. 2004; Addison et al. 2009; Ferlian et al. 2018). The results underline the role of macrofauna and mesofauna in the formation of different FFs in forests (Figure 3d).

Overall, the role of macrofauna in litter decomposition and translocation processes has received considerably more attention than that of mesofauna (Jouquet et al. 2006; Joly et al. 2015, 2020; Ganault et al. 2022). Studies investigating the combined role of both macro- and mesofauna in structuring FFs and their microbial communities are scarce, which limits understanding of their combined effects on the formation and dynamics of FFs. Therefore, long-term experiments under natural conditions and covering diverse ranges of soil fauna are required to fill the knowledge gap.

4 Forest changes cause forest floor changes

In the following section we summarize the most important anthropogenic drivers of possible FF changes. They can be primarily attributed to the change in the controlling factors illustrated in Figure 2 (Section 3). Furthermore, we provide a knowledge base regarding the consequences of those changes and we address uncertainties.

Nitrogen and sulphur deposition and acidification. Past input of S and N widely impacted biochemical cycles in natural ecosystems (de Vries et al. 2014). Especially from 1960–1990, both led to pH declines in forest soils, while N input also caused eutrophication of forest ecosystems (Schöpp et al. 2003).

It is reasonable to assume that the deposition dynamics up to the 1990s are still reflected in the properties of FFs. Consequences of acidification include loss of K, magnesium (Mg) and Ca, and increasing release of Al ions (Al^{3+}) as well as heavy metals into the soil solution. Acidification suppresses microbial activity and impairs soil macrofauna, and thereby reduces litter decomposition (Shen et al. 2021; Růžek et al. 2021). Over the last three decades, however, atmospheric S and N emissions have decreased across Europe and several studies indicate that the reduced deposition rates have already changed the soil C cycle (Oulehle et al. 2011). Accordingly, Grüneberg et al. (2019) suggest that the FF mass loss observed in Germany is related to increased decomposition in response to rising pH. This explanation is supported by the controls of dissolved organic matter dynamics as reviewed by Kalbitz et al. (2000).

There still continues to be a high level of N deposition in many temperate forests. Due to the retention of N inputs, they accumulate in soils and can trigger ecological responses even at low doses if sustained over time (Phoenix et al. 2012). Of particular importance if P: Several studies indicate that high N input into forest ecosystems increases the risk of nutritional imbalances between N and P (Peñuelas et al. 2012; Jonard et al. 2015; Krüger et al. 2020). The P supply of trees is closely linked to FF properties and turnover (Vesterdal and Raulund-Rasmussen 1998; Lang et al. 2017). The P concentration of leaf litter also shapes the microbial decomposer community (Bergkemper et al. 2016a), which may contain more than 20% of total P in FFs (Bauhus and Khanna 1999). Furthermore, the availability of base cations (Desie et al. 2020), Al (Leuschner et al. 2006) and Mn (Roth et al. 2022; Spohn and Stendal 2023) under continuous N input and acidification likely will remain crucial factors in controlling FF turnover.

The potential impact of increased N deposition on FF thickness is still controversial. The reported negative correlation between N availability and FF thickness suggests that N deposition might cause decreasing FF thickness (Forstner et al. 2019). In contrast, other studies showed that high N concentrations can impair decomposition by inhibiting lignin degradation (Berg and Matzner 1997; Bonner et al. 2019). Moreover, N-induced P deficiency in forest nutrition may lead to an accumulation of FF mass via depletion of litter P upon intense resorption of P from senescing tissues by trees (Sohrt et al. 2018), rendering litter less decomposable. In their recent review, Kuyper et al. (2023) conclude that decreased decomposition is the dominant impact of N deposition on C cycling.

In summary, the current continuously high N deposition leads to lower turnover and higher mass of FFs even under overall decreasing acid deposition.

Climate change effects are becoming more prominent around the globe, where climatic variations (e.g., high temperatures, drought, extreme weather events) and associated biological disturbances (e.g., shifts in plant, microbial and animal communities) significantly impact the structure and functioning of forest ecosystems (Helm et al. 2017; Seidl et al. 2020; Mayer et al. 2024). The FF is particularly sensitive to climatic disturbances that alter defining processes, such as litter decomposition (Callesen et al. 2003; Krishna and Mohan 2016). Short-term effects of increasing temperatures at sufficient moisture are increased microbial activity and C mineralization rates; long-term effects are increased C losses, particularly in FFs due to absent or only small protection by association with minerals. Several studies already demonstrated the vulnerability of FF to climate warming, reporting decreases in C stocks in FF (Wellbrock et al. 2017; Prietzel et al. 2016, 2020a) and increased losses of DOC due to elevated temperatures (Borken et al. 2011). In support, elevation gradient studies show decreasing FF mass thickness with increasing air temperatures (Hagedorn et al. 2019; Labaz et al. 2014; Oulehle et al. 2011). Furthermore, a recent study provides evidence for the high sensitivity of microarthropods in the FF to climatic changes (Chen et al. 2025). In contrast, longer periods without precipitation might reduce litter decomposition and thus increase FF mass (Bottner et al. 2000; Guidi et al. 2022). Based on a survey across France, Ponge et al. (2011) concluded that climate warming might have opposing effects on FF thickness, depending on water availability: a decrease under sufficient water supply and an increase at dry conditions due to reduced decomposition (Bottner et al. 2000; Guidi et al. 2022). Obviously, mineralization peaks after re-wetting (Brunn et al. 2023) are not able to (over)compensate the decreased decomposition during dry periods. Adding even more complexity, Baldrian et al. (2013) emphasized that consecutive warmer winters may elevate microbial activities during an otherwise dormant season, which has been confirmed by recent observations of increased ecosystem C release in winter (Sanders-DeMott et al. 2020; Liu et al. 2020). In addition, more frequent and increasingly strong drought events during the vegetation period will decrease the vitality of trees and the biomass input into FFs, while strong precipitation events during rewetting will affect processes within FFs.

In summary, climate change-related drivers of FF changes are (1) increasing temperature, which will accelerate microbial activity at sufficient moisture, thereby decreasing FF mass, (2) decreasing soil moisture, which will result in increasing FF mass unless decomposition peaks after re-wetting, and (3) a combination of both with unpredictable consequences. Thus, the resulting changes in FFs are highly uncertain.

Forest management includes a wide variety of measures, which feeds back to various FF drivers such as forest microclimate, as well as litter quality and quantity. Tree species selection, stand structure and density control, and removal of biomass by harvest represent the most relevant management practices. Tree species composition is one major FF control (see also section 3; Prietzel and Bachmann 2012; Vesterdal et al. 2013; Guckland et al. 2009), which may even result in tree species-specific humus forms under similar climatic conditions (Prietzel and Bachmann 2012; Bayranvand et al. 2017). The impact of trees on FF accumulation can be traced back to the quantity and quality of leaf and root litter (Binkley and Giardina 1998), root exudates (Meier et al. 2017), and to the impact on soil microorganisms and soil fauna (Hobbie et al. 2006); even individual trees can locally affect FF and soil processes if they differ enough from their surroundings (Stutz and Lang 2023). Previously, intensive management of temperate forests promoted a high share of conifer over broadleaved species. Generally, conifer litter has a lower decomposition rate, because it has a higher lignin:N ratio than deciduous leaf litter (Prescott et al. 2000**;** Leuschner and Ellenberg 2017). The high contents of tannins and other protein-precipitating polyphenols in conifer litter may further hamper decomposition processes (Stempfhuber et al. 2017). Accordingly, higher FF mass has been observed with increasing contribution of conifers (Wilcke et al. 2024, Moreno-

Duborgel et al, 2025). Mixing broadleaved species into previously conifer-dominated stands in many Central European forests has been shown to accelerate the litter decomposition rate (Achilles et al. 2021), causing shifts of humus forms from moder/mor to mull/moder (Labaz et al. 2014). Also, the spatial variability in FF masses and humus form at stand level was found to be higher in mixed than pure beech stands (Aubert et al. 2006).

Besides the slower decomposition of conifer litter, also the microclimatic conditions in dense, mostly younger and even-aged, pure (conifer) stands may inhibit microbial processes, thus slow down decomposition and, hence, foster the FF accumulation (Albers 2004; Berger and Berger 2012, 2014). The structure and openness of the canopy has a strong influence on moisture availability and temperature at the ground surface, both of which affect rates of decomposition and nutrient mineralization. Uneven-aged and mixed stands, characterized by higher structural complexity, often have lower diurnal temperature ranges and vapor pressure deficits than even-aged and pure stands (Ehbrecht et al. 2017, 2019; Schnabel et al. 2025). For European beech it has been shown that the litter concentrations of nutrients such as N, Mg and K decrease with stand age, causing lower litter decomposition rates (Trap et al. 2013).

Silvicultural measures such as thinning (Vesterdal et al. 1995) or harvesting of mature trees can affect the decomposition of foliar litter and nutrient mineralization. Clear cutting or gap harvesting were reported to cause marked increases in soil nitrate concentration due to reduced microbial assimilation in response to reduced C input (Bauhus 1996; von Wilpert et. al. 2000; Prescott 2002; Prescott et al. 2003) and, perhaps to a greater magnitude, reduced nitrate uptake by trees (Schleppi et al. 2017; Ward and Bradford 2025).

To summarize, existing literature provides evidence for decreasing FF masses with increasing share of broadleaved trees. Recent studies indicate that forest stand properties may affect FF thickness and structure, directly via litter input and indirectly via microclimatic control. How these relationships are modified by climate change remains largely unresolved.

Natural forest disturbances such as wildfires, windthrow, droughts and insect infestations have increased in recent decades, and ongoing climate change is predicted to accelerate this trend (Seidl et al. 2017; Patacca et al. 2023; Haberstroh et al. 2022). Natural disturbances can have strong and long-lasting effects on the FF by reducing litter input and promoting losses through erosion or changes in micro-climatic conditions (Thom et al. 2023). Meta-analyses of the effects of natural disturbances suggest a general decline in FF stocks following stand damage (Zhang et al. 2015; Nave et al. 2022; Mayer et al. 2024). Wildfires can cause rapid losses by direct combustion of FF material. The associated reduction in N availability may cause reduced net primary productivity (Pellegrini et al. 2018; Mack et al. 2021). Wildfires also induce the formation of pyrogenic organic matter characterized by high biogeochemical stability

(Schmidt et al. 2011; Pellegrini et al. 2022). Fire-prone forests may thus have particularly large C stocks in the mineral soil despite concurrent FF losses during single fire events (Eckmeier et al. 2010). Large reductions in FF stocks have also been reported from windthrown mountain forests, possibly due to increased surface erosion and temperature-related acceleration of organic matter decomposition (Gerber et al. 2002; Christophel et al. 2015; Mayer et al. 2024). Soil mixing via uprooting of trees may also result in the burial of FF beneath mineral soil layers. Insect infestations have been shown to have smaller impacts on FFs following stand damage than wildfire and windthrow (Mayer et al. 2024). This may be due to the input of frass debris (e.g., litter, faeces) into the FF, off-setting losses following infestations (Le Mellec and Michalzik 2008; Yang and Gratton 2014). The duration and magnitude of FF losses in response to natural disturbances appear to be most pronounced when FF layers are thick, while thin FF layers appear more resilient to stand damage (Mayer et al. 2024).

In summary, literature indicates a decrease in FF mass through forest disturbance and emphasized that the vulnerability of FFs to environmental changes is context specific and might increase with FF mass.

5 Forest Floors: Ecosystem hubs at risk

Our **synthesis** of the literature prompts us to call for a paradigm shift. Instead of viewing the FF as an ecological anomaly, particularly in the case of intensive accumulation of organic matter, it should be recognised as an integral part of forests, resulting from interactive adaptations to environmental conditions. As an interface between the atmosphere, biosphere and pedosphere, the FF is unique in terms of its position, size, extent, and vulnerability. We emphasise that the FF reflects the ecosystem's response to nutrient status, soil acidity, temperature and precipitation, mediated by biotic interactions that evolved over millions of years (Ponge, 2013). The long-term adaptation of plants and soil organisms to specific combinations of environmental factors determine not only the habitat quality of FFs, but also energy and element fluxes within forests. Depending on FF turnover, crucial processes of the C, nutrient, and water cycles take place in the FF (Figure 3a-f): With slow FF turnover, energy and element cycling within the FF is tight and supports forest nutrition, water retention, and microbial processing of litter. With fast FF turnover, mineralization and fragmentation of aboveground litter occurs in the FF and elements are translocated into the mineral soil, the groundwater, or back into the atmosphere.

The strong interconnectedness of FF processes to the mineral soil and the aboveground ecosystem compartments justify defining the FF as the ‘central ecosystem hub’. As outlined below, tight interconnectedness of processes and multifactorial dependencies (Figure 4) explain the vulnerability of FFs to environmental change and large uncertainties, which call for new avenues for research and management.

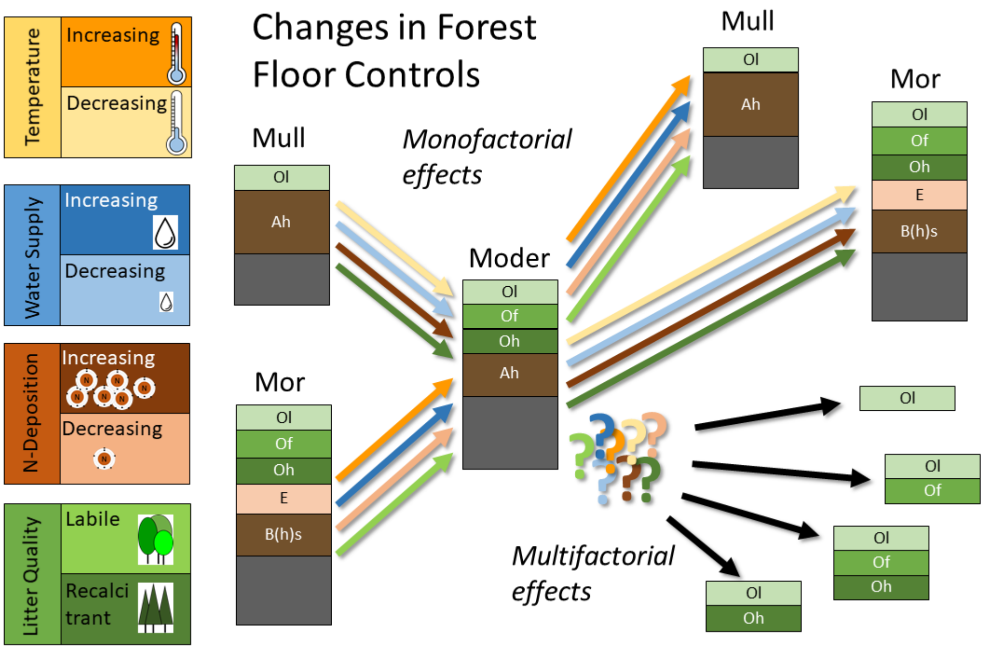


Figure 4: Forest floor controls and proposed impact of changing controls as well as related open questions.

Interconnectedness. The soil biota of the FF translate different human-induced changes into different nutrient, C, and water transformations, thereby changing their availability, uptake, and storage. More so, processes in the FF control the development of the FF through strong feedbacks to organisms, water, nutrient, and C fluxes (e.g., litter input drives microbial release of nutrients that supports plant growth and litter input; Stutz 2023). Exploring the efficiency of the manifold interactions, mechanisms, and organisms as well as how they relate to mineral soil and aboveground ecosystem functioning is challenging. However, since the FF integrates key ecosystem processes, understanding such interconnectedness is crucial for assessing forest change and offers great potential for the development of forest health indicators. A promising approach is a coupling of morphological properties (Section 2) with specific ecosystem processes.

Multifactorial dependencies. The properties and characteristics of the FF are driven by plants and soil organisms, which use it as a source for C and energy, nutrients, water or as habitat. The means by which organisms use these FF services is determined by environmental conditions. Specifically, adaptation to a particular factor is constrained by interactions with other factors. The combination and interplay of various factors rather than any single factors thus would be decisive for FF development and functioning. Trade-offs between ecosystem adaptation to different factors are particularly likely when novel combinations of factors rapidly emerge and create conditions the ecosystem has never experienced before and for which no suitable adaptation strategies have been developed. This happens to be the case for human impacts on global element and energy cycles. We conclude that such novel combinations of controlling factors pose a major threat to the functionality of the FF–mineral soil continuum.

Human-induced N deposition illustrates the ***de-coupling of factors***. Over decades, N deposition has affected the interactions of factors controlling FF properties. In forest ecosystems unaffected by N deposition, nitrate concentrations in soil solution are controlled by nitrification rates. Net nitrification increases with pH and temperature and for this reason, in the past mainly ecosystems with soils showing higher pH and warmer climate feature high soil nitrate concentrations. Due to long-range air pollution, N deposition increased in particular in mountainous regions with higher precipitation. Nitrate concentrations in soils affected by N deposition have become less affected by soil temperature, pH, or other plant nutrients, resulting in fundamental biogeochemical changes (de Vries et al. 2024) and nutrient imbalances (Peñuelas et al. 2020).

Recent changes in temperature and soil acidification provide an impressive example of ***disproportional changes*** causing novel combinations of environmental factors. At global scale, the occurrence of acid soils is linked to high precipitation and low temperatures (Slessarev et al. 2016). This is because high leaching rates support continuous soil base cation depletion and decrease in soil pH. Yet, natural soil acidification in humid regions is a slow process and it is also slowly reversible. Fast temperature increases accompanied with less precipitation as currently observed could cause pronounced disequilibria between modern climatic conditions and soil properties, thereby changing the interplay of factors controlling FFs and ecosystems. Processes, organisms, and forests benefitting from temperature-limited decomposition of litter and the associated accumulation of FF material would be especially impaired by climate warming and result in highly vulnerable FFs.

Assessing FF vulnerability and developing appropriate management strategies require answers to several **research questions**:

- How does the interconnectedness of controlling factors, key organisms and key processes shape the structural and functional characteristics of FFs?
- Which combinations of environmental factor characteristics are hazardous and constrain the provision of which FF ecosystem services?
- How does the high sensitivity of the FF to natural and human factors feedback on the functioning of mineral topsoil horizons and the overall functioning of forest ecosystems?

An essential starting point for addressing these questions is agreement on a unified global terminology for describing FFs. Furthermore, FF research strictly requires interdisciplinary approaches for exploring the interactions among key organisms in relation to FF characteristics. Promising opportunities to target the above mentioned research questions include: (1) observational studies at sites with rare combinations of controlling factors, (2) long-term monitoring including retrospective analyses of archived samples, (3) experiments with different types of labeled litter to trace the fate of C and nutrients and with defined access of soil organism groups to FFs, and (4) experiments with targeted manipulation of FF properties.

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Sup. Table S1: Selection of accessible*) soil classification systems, defining organic horizons and or humus forms

Region or system	**Classification**	**Version**	**Definitions**	
			Organic Horizons	Humus Form
International / Organizational	World Reference Base for Soil Resources (WRB)	2022, 4th edition	Yes	No
	FAO Guidelines for Soil Description	2006, 4th edition	Yes	No
	ICP Forest Manual Part X: Sampling and Analysis of Soil	2020-1	Yes	No
National				
USA	USDA soil taxonomy	2012, Version 3.0	Yes	No
Canada	The Canadian System of Soil Classification	1998, 3rd edition	Yes	No§)
New Zealand	New Zealand Soil Classification	2010 3rd edition	Yes	No
Australia	The Australian Soil Classification %)	3rd edition Online version (14 June 2023	Yes	No
Germany	Bodenkundliche Kartieranleitung	2024, 6. Auflage	Yes	Yes
Austria	Österreichische Bodensystematik	2011	Yes	Yes
France	Référentiel pédologique	2008	Yes	Yes
Suisse	Klassifikation der Böden der Schweiz	2010, 3. Auflage	Yes	Yes
Poland	Roczniki Gleboznawcze	2011	Yes	Yes
Russia	Russian Soil Classification system	2001	Yes $)	Yes $)
Brazil	Brazilian Soil Classifcation System	2018. 5th edition	Yes #)	No
Humus form classification	Bodenkundliche Kartieranleitung	2024, 6. Auflage	Yes	Yes
	Zanella et al.	2018	Yes	Yes
	Green et al.	1996	yes	yes
	Klinka et al.	1981	yes	yes

*) accessible in terms of either an English version available or one of the authors could read the original version.

§) the Canadian Soil classification define organic horizons, and use humus forms to distinguish between soil types, but do not define humus forms.

%) the Australian soil classification us the USDA Soil taxonomy for describing organic horizons

$) the Russian classification describes a various number of different organic horizons and humus forms.

#) the Brazilian System knows an organic horizon with various different possible properties, leading to different organic soils, but no different organic horizons or humus forms.

Sup. Table S2: Humus form and soil systematics or classifications, describing a humus form (Supp. Tab. S1); focusing of the three at all classification system present humus forms Mull, Moder and Mor; with typical horizon sequence and specific requirements that must be met to qualify as the specific humus form.

Classification/ Current version	Focus	Litter included	O horizon, requirements	**Humus form** typical horizon sequence specific requirements		
				Mull	**Moder**	**Mor (Rohumus)**
Germany Bodenkundliche Kartieranleitung 2024, 6. Auflage	Soil	yes	OC ≥ 15 % (w/w)	(Ol)-(Of)-Ah/Ax/Au	Ol-Of-Obh-Ah (Ee)	Ol-Of-Osh/Okh-Ah-Ee/Ee-Ah
				•no Oh, •Ah present	non	Sharp transition O to A or E horizon
Zanella et al., 2018	Humus form	yes	OC ≥ 20 % (w/w)	(OL)-maA	OL-zoOF-zoOH-miA	OL-nozOF-(szoOH)-AE/EA
				•no OH •ma A	•OH •no nozOF •no maA	•no maA, meA •nozOF, •$pH_{H_2O} < 4.5$ •A absent or structure massive/single grain •sharp transition O to A/E horizon
Austria Österreichische Bodensystematik 2011	Soil	yes	OM ≥ 35 % (w/w)	L-(Fzo)-Ah	L-F-H-Ah	L-F-H-Ah/Ae
				non	L < F and H	• L, F and H present • L+F+H>5cm, • Sharp transition O to A horizon
France Référentiel pédologique 2008	Soil	yes	OC ≥ 17-20 % (w/w)	(Ol)-A	OL-OFzo-OHzo-A	OL-OFnoz-(OHnoz)-E/(Eh)
				•maA •Sharp transition O to A horizon	•miA •diffuse transition O to A horizon	•Sharp transition O to A horizon
Poland Roczniki Gleboznawcze 2011	Soil	yes		Ol/A	Ol-Ofh-A	Ol-Of-Oh-A
				non	non	non
Swiss: Klassifikation der Böden der Schweiz 2010, 3. Auflage	Soil	yes	OM > 30% (M/M)	Ol-(Of)-Ah	Ol-Of-(Oh)-Ah/(EAh)	Ol-Of-Oh-(EAh)/AE
				non	non	non