Microplastics and forest fungi: A review and call for comprehensive research

Toktam Farzaneh[1], Christian Laforsch[2], Claus Bässler[1]

*correspondence: Toktam1.Farzaneh@uni-bayreuth.de

Affiliations

1. Chair Ecology of Fungi, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Universitätsstraße 30, 95440 Bayreuth, Germany

2. Chair Animal Ecology of Fungi, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Universitätsstraße 30, 95440 Bayreuth, Germany

Abstract

Fungi are the main drivers of the global carbon and nutrient cycle and act as ecosystem engineers in forest ecosystems by regulating primary production and decomposition. Moreover, fungi are among the most diverse organisms in forest ecosystems and affect almost all forest microhabitats, from the canopy to the soil. In contrast to aquatic and agricultural ecosystems, forest ecosystems have received less attention in assessing the effects of microplastic pollution on biodiversity and ecosystem functioning. However, recent studies have demonstrated that significant amounts of microplastics might reach even remote forests. Thus, we summarize our current understanding of how microplastics enter forests and move within ecosystems to assess potential risks to diverse fungal habitats. Next, we summarize the state of the art concerning how microplastics affect fungal individuals, fungal diversity, and related ecosystem processes. Our review revealed that forest management and recreational activities are the most important direct pathways, whereas atmospheric deposition is recognized as the main indirect pathway by which microplastics enter forest ecosystems. The movement and dynamics of microplastics within forest ecosystems result from complex abiotic and biotic mechanisms; however, these mechanisms remain poorly understood. On the basis of our current understanding of the different exposure pathways, we suggest that microplastic contamination is biologically relevant across all fungal habitats. Nonetheless, evidence is scarce regarding how microplastic loads affect forest fungal diversity across functional lifestyles and related ecosystem processes. Direct evidence is limited, but soil studies from agricultural areas and laboratory experiments suggest that important forest processes, such as primary production and decomposition, are affected via changes in fungal diversity caused by microplastic contamination. We argue that current microplastic research fundamentally underestimates plastic loads and the related consequences for fungal diversity and ecosystem functioning in forest ecosystems. To address this challenge, we propose a conceptual framework based on ecological theory and provide testable hypotheses. Our framework could act as a blueprint for other forest taxa and thus improve predictions about the consequences of microplastics on the many functions and services that forests provide.

Keywords: Microplastic pollution, Forest ecosystems, Fungal communities, Nutrient cycling, Soil health.

Introduction

Microplastics (plastic particles smaller than 5 mm) are increasingly recognized as major environmental contaminants affecting ecosystems during the Anthropocene [1–3]. Recent research suggests that global plastic pollution may already exceed the safe production limits proposed in the planetary boundary framework [3,4]. Forecasts demonstrate that global plastic production could nearly double, rising from approximately 464 Mt in 2020 to approximately 884 Mt by 2050 [5,6]. Numerous studies have demonstrated that microplastic contamination may threaten biodiversity and related ecosystem functions and thus challenge the integrity of ecosystems [7–10]. However, most studies have been conducted in marine environments and agricultural soils [4,11], while our knowledge related to terrestrial forest ecosystems is still limited [8,11,12].

Forests cover approximately one-third of Earth globally and play important roles in human welfare because of the provisioning of essential resources such as timber [13]. Forests provide valuable ecosystem services such as climate regulation, biodiversity maintenance, nutrient cycling, water distribution and regulation, soil stabilization, and Earth cooling [14,15]. Forest ecosystems also function as major carbon sinks, storing substantial amounts of atmospheric carbon in biomass and soils. [15,16]. The benefits of forests extend beyond their borders and, in general, help maintain suitable conditions for life on Earth [17]. However, the health and integrity of forests are threatened by various stressors, such as global warming, increasing atmospheric CO_2 concentrations, forest management, and, as more recent studies emphasize, environmental pollution, including microplastic contamination [17–19].

Recently, it has been emphasized that microplastics can occur in forest environments; however, only a limited number of studies have directly quantified microplastic loads [11,20]. One study indicated that microplastics can accumulate in forest soils at concentrations comparable to those in other terrestrial systems, such as cities and agricultural fields [20]. The few existing studies are unevenly distributed across forest ecosystem types, with a clear emphasis on mangrove or coastal forests and a focus on topsoil layers as a habitat [11,21]. Thus, comprehensive knowledge about microplastic loads, habitat contamination, and the subsequent effects on species diversity and related ecosystem processes is necessary to develop evidence-based mitigation concepts.

Fungi are among the most diverse organisms in forest ecosystems, and their diversity is linked to a wide range of biological functions and ecological processes [22,23]. More specifically, fungal diversity is linked to the carbon and nutrient cycles in forest ecosystems via the evolution of basic functional lifestyles (i.e., mutualists, saprotrophs, and parasites; see Chapter 1) [24]. Owing to their functional specialization, fungi occupy a broad range of forest habitats [14,25], making this taxonomic group particularly relevant for understanding the ecological consequences of microplastic pollution in forests. However, despite their vital role, a comprehensive synthesis of how microplastics interact with fungal habitats, functional groups, diversity, and ecosystem processes in forest ecosystems is lacking.

This review synthesizes current knowledge on the pathways through which microplastics enter forest ecosystems and examines how these inputs may affect forest fungal habitats and their diversity, with consequences for ecosystem functioning (Fig. 1). On the basis of this review, we develop a conceptual framework and fungi-centered perspectives to integrate key knowledge gaps and guide interdisciplinary research aimed at mitigating microplastic impacts in forests (Fig. 2).

1. Importance of fungi in terrestrial forest ecosystems

1.1 Fungal functional lifestyles

Three basic fungal functional lifestyles have evolved: Mutualistic fungi of plants and animals contribute to the build-up of organic matter (i.e., plant primary production and increased fitness in animals, helping to maintain populations). Saprotrophic fungi contribute to the decomposition of all kinds of organic matter (i.e., necromass), and parasitic fungi contribute to the ability of ecosystems to mediate various effects on ecosystem productivity and diversity [26–28].

Among mutualistic fungi, those characterized by mycorrhizal associations with host plants are particularly important for primary production [29,30]. Mutualistic fungi provide water and nutrients such as phosphorus and nitrogen to the host and, in return, receive carbohydrates [28,31–33]. While mycorrhizal fungi are widely recognized for their ability to increase plant nutrient acquisition, their contribution to primary production is context dependent and varies with ecosystem type, nutrient availability, and host specificity. A comprehensive study suggested that mutualistic fungi can contribute substantially to primary production [34]. Moreover, mycorrhizal fungi increase plant diversity, reduce drought stress, and protect their

hosts from plant pathogens [34]. Similarly, relevant in this context is the mutualistic relationship between fungi and algae (mainly from the lineages Trebouxia and Trentophila) or cyanobacteria, which results in the formation of lichens (i.e., lichenized fungi) [35,36]. Among fungal mutualists, some have coevolved with animals. Mutualistic interactions between fungi and animals are exemplified by leaf-cutter ants and wood-boring beetles [37]. Leaf-cutter ants cultivate symbiotic fungi that degrade otherwise indigestible plant material and provide essential nutrients, while fungi benefit from protection and a continuous supply of substrate [38,39]. Similarly, many wood-boring beetles possess mycetangia to transport fungal symbionts that enable wood degradation and habitat colonization [40]. Empirical and theoretical studies indicate that such mutualisms increase partner fitness, expand ecological niche breadth at the population level, and contribute to the maintenance of animal biomass [41].

Saprotrophic fungi decompose all kinds of organic material (i.e., necromass), including plant material (leaf litter and wood), animal material (dung and carcasses), and microbial material (bacterial, archaeal, and fungal biomass) [23,42–45]. Fungi are among the most important decomposers and are even capable of degrading strongly recalcitrant plant-produced lignin [46].

Fungal parasites exploit living resources in various ways, thereby influencing the diversity and structure of other trophic levels and thus determining ecosystem structure and dynamics [47,48]. Specifically, fungal pathogens play a central role in structuring forest plant communities by regulating host abundance, seedling recruitment, and species coexistence through density-dependent effects [49–54]. Thus, fungi can be considered the backbone of forest ecosystems in terms of productivity, diversity, and resilience [55–57] and are among the most important drivers of the global carbon cycle [55,58].

1.2 Fungal habitats in forest ecosystems

The manifold relationships between fungi and other taxa (plants, animals, and microbes) in forest ecosystems make fungi ubiquitous across a broad range of forest habitats: (i) Canopy leaves host diverse endophytic fungal communities [59,60]. These communities are linked to plant fitness by supporting photosynthesis; however, leaves can also host diverse fungal pathogens [61]. (ii) The canopy is further characterized by dead wood (branches), which hosts distinct saprotrophic communities [59,60,62]. (iii) The canopy is also a habitat for a broad range of lichenized fungi, which live as epiphytes on leaves and branches [63]. These fungi are primary producers and are thus crucial for complex food webs within the canopy [64]. For

example, in specific Mediterranean oak forests, lichens constitute up to 30% of the primary production of the entire forest canopy [60]. (iv) Diverse endophytic fungal communities can be found in the trunks of trees [65,66]. However, their ecological role is not always clear; they might suppress pathogens or potential saprotrophs after tree death. (v) Bark is an important habitat for fungi, particularly those with a lichenized lifestyle [64]. Furthermore, these organisms provide important habitats for bark-dwelling organisms (e.g., insects) [67] and contribute to the bark food web as primary producers [68]. (vi) Forest ecosystems are characterized by complex deadwood structures [69]. In addition to variation in dimension (coarse woody debris and fine woody debris), tree identity and type (stump, snag, log) and decay stage are associated with highly diverse and distinct fungal communities [70]. In natural forests, deadwood can constitute approximately 40% of the total living plant biomass (e.g., 140–250 m^3/ha in temperate forests) [71]. Deadwood can be considered a temporarily stable resource, with decomposition processes lasting for decades [72]. (vii) In contrast to dead plant material such as wood and litter, organic material from animals such as dung and carcasses is characterized by high spatiotemporal dynamics [73]. Furthermore, fungi decompose microbial biomass, although studies on this topic are scarce [23,74]. (viii) Soil (mineral and organic layers) hosts diverse fungal communities representing different functional groups. Plant litter is one of the most important carbon sources for soil saprotrophic fungi in forest ecosystems [59,75]. For example, in summer-green broad-leaved trees (e.g., European beech), yearly litterfall can reach approximately 5 t/ha/year [76]. The mycorrhizal mycelium within the soil is associated with plants across forest strata, from cryptogams (e.g., bryophytes) through the herb and shrub layers to potentially several tree layers [59]. Finally, the soil hosts diverse fungal pathogens associated with plants, animals, and microbes [77]

2. How microplastics reach fungal habitats in forests

2.1 Entry pathways

2.1.1 Atmospheric deposition (indirect pathway)

Atmospheric circulation can carry microplastics across large distances, even depositing them in remote forests far from local sources [11,78,79]. Microplastics can be released into the atmosphere through urban and industrial activities, traffic and tire wear abrasion, construction dust, and plastic waste burning. Particles can be carried by wind over short to very long distances and deposited onto terrestrial surfaces through dry or wet deposition [80,81]. Field studies have confirmed that even remote mountain regions receive atmospheric microplastics. For example, Allen et al. [78] reported deposition rates of 300 microplastic particles (fibers,

fragments, and films) per m^2 per day deposited at a remote Pyrenean mountain site (particles traveled approximately 95 km). Furthermore, the detection of microplastics in Arctic and alpine snow indicates long-range atmospheric transport [82,83]. The dispersal range of microplastics strongly depends on their particle size and physical properties. Smaller particles, including $PM_{2.5}$ (fine particulate matter $\leqslant$2.5 μm), are a major component of air pollution [84]. Small plastics can remain airborne for days to weeks and travel hundreds to thousands of kilometers, whereas larger particles settle more quickly [85,86]. Allen et al. [78] detected microplastic particles smaller than ~50 μm at high altitudes, suggesting that small plastic particles can enter the free troposphere and undergo intercontinental transport.

Particles directly settle on forest canopies via dry or wet deposition [82,87]. For example, rain and snow efficiently wash microplastics from the atmosphere to the canopy, especially in wet climates, supplementing the constant background of dry deposition [82,83,87–89]. In forests, studies suggest that most microplastics are input via air transport. The tree canopy can effectively adsorb airborne plastics, which are then transported to the soil by rain (throughfall) and falling leaves (litterfall) (see Chapter 2.2). Generally, forest canopies enhance microplastic capture because their complex structure increases surface roughness and the available adsorption area. Specifically, canopy architecture (e.g., needle vs. broadleaf architecture) can affect dry deposition [20,90,91]. For example, one study reported that pine (conifer) forests experienced roughly constant microplastic deposition, whereas leaf-off deciduous stands presented much lower deposition in the leafless season [20]. In addition, leaf and needle surface micromorphology, including trichomes, grooves, waxy cuticles, and surface roughness, significantly influences particle capture efficiency across multiple tree species [90–92]. Earlier studies also revealed that tree canopies act as biological filters for different types of airborne particles [11,91,93,94].

Weber & Bigalke [20] measured microplastics at different heights in forests (canopy, litter, and soil) via a standardized method to measure microplastics >20 μm. These authors reported high microplastic levels in forest soils, in some cases comparable to or higher than values reported in cities or farmlands. In fact, their model calculations revealed that just a few decades of steady atmospheric deposition could account for the observed soil loads. Moreover, in this study, model estimates suggest that current forest soil loads can be explained by decades of atmospheric input alone. These findings indicate that atmospheric deposition is likely a

dominant pathway through which microplastics reach a wide range of fungal habitats in forest ecosystems.

2.1.2 Runoff from agricultural and urban systems (indirect pathways)

Runoff from agricultural and urban systems is a potentially important indirect pathway for microplastics to reach surrounding environments, including forest ecosystems. Agricultural soils act as major sinks for microplastics because of many plastic-based inputs (e.g., plastic mulch films, greenhouse coverings, irrigation pipes, sewage sludge, and polymer-coated fertilizers) [95–101]. Over time, plastic debris in the field weathers and produces microplastic fragments that accumulate in the soil [102,103]. Several soil and watershed studies have shown that rainfall and erosion can mobilize microplastics from soils, carrying them by overland runoff and subsurface flow into nearby environments such as streams and wetlands [96,98,104–106].

Similarly, some studies have shown that urban stormwater is a major vector for microplastics. For example, one meta-analysis reported concentrations in stormwater runoff ranging from approximately 0.009 to 3,862 particles per liter [107]. In particular, microplastics from road abrasion (including tire and brake wear), synthetic textiles, and construction materials can be washed out into waterways [107–109]. Although direct measurements in forest environments remain limited, hydrological connectivity between agricultural fields, urban landscapes, riparian zones, and downslope forest areas suggests that runoff transport could be an important pathway for microplastic inputs into forests. However, on the basis of current evidence, atmospheric deposition is likely the main source of microplastics in forest soils, and runoff may contribute additional microplastics in certain locations; however, overall, its contribution depends on the local context [20,110].

2.1.3 Tourism (direct pathways)

Although data from forests are scarce, several studies have shown that tourism contributes significantly to plastic waste in outdoor areas. Different studies have shown that tourists play a major role in generating plastic litter in natural settings [111–113]. Field observations revealed that visitor activity is strongly associated with elevated plastic litter loads, often originating from food and beverage packaging, smoking, disposable items, and synthetic clothing worn by visitors such as hikers, mountain bikers, and campers [112,114–117]. The level of contamination can vary with visitor intensity, land-use pressure, and the effectiveness of regulations. For example, areas with high levels of foot traffic have relatively high microplastic

loads [114,118,119]. Contamination is further amplified by improper disposal and insufficient waste management, especially during periods of high visitor pressure [120–123].

Macroplastic deposited from these sources can fragment into microplastics through ultraviolet radiation, mechanical abrasion, and microbial activity [115,124]. In addition to visible litter at the macroscale, microplastics can be released directly through gear and clothing abrasion: synthetic garments shed large quantities of polyester, nylon, and acrylic microfibers during movement, which can settle in forest soils and litter layers [121,125]. The European Environment Agency noted that synthetic textiles release microfibers during both laundering and normal wear [126]. These fibers can become airborne and eventually settle into soils. For example, De Falco et al. [127] reported that wearing garments emits microfibers into the air, which then deposit onto terrestrial surfaces and accumulate in soils [126,127]. Further studies have shown that trail running and other high-intensity activities produce measurable microplastics from shoe outsole abrasion and textile fiber shedding, even in conservation and wilderness areas [128]. Overall, tourism and recreation represent direct and locally significant pathways for both macro- and microplastic inputs and thus may affect soil-related fungal communities.

2.1.4 Forest management (direct pathways)

However, quantitative evidence linking forest management with plastic inputs remains scarce. The most clearly documented plastic input in forest ecosystems is the use of plastic tree shelters and guards, which are typically made of plastics such as polypropylene, in afforestation and regeneration projects [129,130]. This is particularly relevant when such materials are not removed after use, increasing the likelihood of environmental persistence and secondary microplastic generation [131].

Forest management can further increase plastic inputs through roads, vehicles, and machinery. Forest roads and management infrastructure may act as localized hotspots for microplastic accumulation and subsequent redistribution into surrounding forest soils. As tire and traffic-related wear particles are documented near roads and their concentrations decline with distance [132], increased vehicle access for harvesting and transport likely enhances local deposition and runoff-driven transfer of tire-derived particles into forest soils and waters, although empirical evidence remains scarce [132,133].

Finally, plastic deposited in forest ecosystems via forest management can subsequently be taken up again by the atmosphere and transported to other areas, as has been shown in other terrestrial systems (see Chapter 2.1.1) [20,85]. Together, even though data are limited, circumstantial evidence suggests that forest management might be an important pathway and consequently affect fungal communities, probably in soil environments.

2.2 Within-forest transfer and internal redistribution of microplastics

2.2.1 Abiotic redistribution pathways

After microplastics enter forest ecosystems, they can be redistributed vertically and horizontally within the forest due to various processes and thereby potentially reach different fungal habitats. Abiotic redistribution of microplastics in forests results from interactions among atmospheric, hydrological, and physical transport processes.

After reaching forests (e.g., through atmospheric transport, see Chapter 2.1.1) [94,134], downward movement occurs through key hydrological pathways such as throughfall, where rain washes particles off foliage directly to the forest floor and via stemflow [135]. Throughfall (drip and gap flow) and stemflow (trunk-routed flow) can act as major vertical redistribution routes for canopy-adsorbed microplastics [136]. Although stemflow might account for only a small fraction of the total rainfall in many tree species, it concentrates water and associated pollutants at the base of the tree, creating hotspots near the roots [135–137]. Together, these processes establish a vertical transport continuum linking atmospheric inputs to soil-associated fungal habitats through other habitats in between them (e.g., stem area).

In addition to water-driven transport, microplastics can be redistributed within forests by wind through local resuspension and redeposition, although this process remains poorly quantified in forest ecosystems [11,138,139]. Another major pathway is litterfall, through which particles attached to leaves and small branches are transferred to the soil surface [20,140]. After microplastics reach the ground through hydrological or litterfall processes, they accumulate first in organic soil horizons and are then redistributed into mineral layers through litter turnover, leaching, and physical mixing [20,141,142]. Smaller particles can also be transported downward in the soil with infiltrating water via percolation and preferential flow paths through soil macropores [143].

Forest disturbances can increase these movements; for example, logging operations often increase erosion rates [144], thereby increasing microplastic transport via runoff and splash erosion [106]. Erosion, splash processes, and surface flow can drive lateral redistribution across forest floors, as has been shown for other terrestrial ecosystems [106]. Taken together, these redistribution mechanisms create different exposure pathways affecting forest microhabitats. As a result, different fungal groups, such as mycorrhizal, saprotrophic, and pathogenic communities, may encounter plastic particles in distinct ecological niches within the forest system.

2.2.2 Biotic redistribution pathways

Potential biotic redistribution of microplastics via organisms includes movements via external adhesion, ingestion and excretion, burrowing and soil mixing, and trophic transfer, potentially connecting different habitats [142,145–147]. There is evidence that soil organisms can act as plastic transporters via random attachment or ingestion from contaminated food, plant surfaces, or soil particles, followed by redistribution of the material through movement, excretion, or nesting behavior [146,148–152]. Specifically, the vertical transfer of microplastics into deeper soil layers has been shown for burrowing soil organisms [141,151,153–155]. These organisms can relocate microplastics through movement and fecal deposition [140]. For example, studies have shown that soil invertebrates (e.g., springtails, mites, earthworms) can transport micro- and nanoplastics downward through bioturbation and via processes such as ingestion and subsequent movement through soil channels [141,146,149–151]. More recent experimental work has shown that complex soil food webs (e.g., combinations of earthworm functional groups and Collembola) can enhance the downward transport and leaching of microplastics [140,156].

Moreover, scavenging insects, decomposers, birds, and mammals can redistribute microplastics by transporting contaminated material to feeding or nesting sites [157–159]. Large animals (e.g., migratory birds and wild mammals) can carry microplastics over long distances and then deposit them in feces. For example, microplastics are found in high concentrations in wild boar feces, implying that these animals ingest plastics and redistribute them as they move across landscapes [160]. Migratory animals can thus transfer microplastics between distant ecosystems (e.g., urban, farmland, and forest) along their routes, depending on their biology [161,162]. Furthermore, birds incorporate mostly larger plastic debris into their nests; however, this debris can act as long-term sources for microplastics in or near the nest area [163]. Additionally,

pairing predators and prey in laboratory experiments increased microplastic dispersal by approximately 40% compared with that in single-species setups, indicating that the food-web structure can increase transport efficiency [164].

Finally, plants contribute indirectly to microplastic redistribution, e.g., via litterfall, as described above [165]. Moreover, laboratory studies have shown that nanoplastics can enter plant roots and can be further translocated to shoots [166] and other plant organs [167,168]. This internal redistribution pathway may connect soil contamination with the phyllosphere [168–170]. However, this pathway appears to be context-dependent and has not been investigated enough in forests. On the basis of these redistribution pathways, we suggest that most fungal habitats may be secondarily reached after microplastics enter the forest ecosystem, either directly or indirectly.

3. Microplastic types in forest ecosystems

The types, origins, chemical compositions, sizes, and shapes of microplastics that reach forest ecosystems are complex. They can be classified as primary (intentionally manufactured at microscopic size, e.g., in cosmetics and industrial abrasives) or secondary (formed by the degradation of larger plastics such as packaging, agricultural films, and textiles through physical, chemical, and biological weathering) [12,142,171].

Microplastics enter forest ecosystems primarily through atmospheric deposition and accumulate in the canopy and different soil layers, as described above [20,90]. These particles consist of a diverse range of polymers whose compositions in soil and forest throughfall are very similar, indicating their predominant atmospheric origin [20,90]. Common polymers in these environments usually include widely used plastics such as polyethylene (PE), polypropylene (PP), polyamide (PA) and polyethylene terephthalate (PET), which enter the atmosphere from sources such as urban particulate matter, tire wear and textile fibers and are then transported to forests [20,90]. Field studies have shown that forest topsoil can contain thousands of particles per kilogram, with polyethylene (PE), polypropylene (PP), and polyethylene terephthalate (PET) as the dominant polymer types [172].

Microplastics in forests are characterized by different physical forms, mainly fibers, fragments, and films [20,90,173]. Fibers and fragments are most frequently reported in forest soils, whereas films and foams are often ignored because of methodological limitations, and the main focus is on particles smaller than 5 mm [174].

382

383 The persistence and environmental behavior of microplastics differ depending on their polymer
384 chemistry. For example, polyethylene (PE) and polypropylene (PP) are highly persistent
385 because of their stable carbon–carbon backbones and hydrophobic surfaces [175,176]. Other
386 materials, such as polylactic acid (PLA), poly(butylene adipate-co-terephthalate) (PBAT), and
387 polyvinyl chloride (PVC), can degrade more easily; however, they can release additives (e.g.,
388 plasticizers) and metals during aging, which in turn increases ecotoxicological risk [177–180].
389

390 Particle size is another key factor determining environmental behavior and ecological impact.
391 Smaller particles have higher surface-to-volume ratios, which increases their capacity to adsorb
392 heavy metals and organic pollutants [141,178,181–184]. Smaller microplastics can adsorb
393 different organic pollutants [183] or metals such as copper more efficiently and can influence
394 contaminant bioavailability [185]. Particles smaller than 1 mm also show greater horizontal and
395 vertical mobility in agricultural soils, increasing the possibility of biological exposure in forest
396 ecosystems [186].
397

398 Importantly, methodological differences limit comparability among forest microplastic studies.
399 For example, the detection limits differ widely, often ranging from tens to hundreds of
400 micrometers in size, and some studies exclude organic litter layers. Additional challenges
401 include contamination from airborne fibers, the underestimation of fibers due to lower recovery
402 rates, and the potential exclusion of high-density polymers such as PET during density
403 separation procedures [20,187].
404

405 **4. Impact of microplastics on fungal- and fungal-mediated ecosystem processes**

406 **4.1 Effects of microplastics on fungal individuals**

407 Particles in the micro- and nanoplastic size ranges (<5 mm and <1 μm, respectively) interact
408 with fungal cells physically and chemically, leading to disruptions in cellular physiology,
409 metabolic activity, and growth performance [188–192]. At the cellular scale, exposure to
410 polymer particles, such as low-density polyethylene (LDPE), stimulates the production of
411 reactive oxygen species (ROS), increases lipid peroxidation, and alters membrane permeability
412 in filamentous fungi [189]. Oxidative stress responses may occur even when the total fungal
413 biomass remains stable or increases, suggesting that conventional growth measurements may
414 underestimate underlying physiological stress [189]. Changes in membrane integrity and

phospholipid composition can also disrupt transport processes associated with membranes [189].

Owing to their small size and surface reactivity, nanoplastics adhere to fungal cell walls and hyphal surfaces, forming dense coatings that interfere with nutrient transport and trigger cell death [193–195]. Under certain physicochemical conditions (depending on particle size, surface charge, cell wall features and medium ionic strength), nanoplastics may even penetrate fungal cells, inducing intracellular damage [193–195].

Studies have shown that nanoplastic exposure can change fungal gene expression and enzyme activity patterns. These molecular changes could alter metabolic pathway regulation and affect an organism's capacity for nutrient acquisition and ecological performance [191,196]. Furthermore, chemical effects also induce stress: additives and leachates such as bisphenol A (BPA) can cause oxidative damage and reduce fungal cell viability through receptor-independent redox activity, as shown in *Saccharomyces cerevisiae* [197]. These findings emphasize that toxicity is not limited to the polymer matrix itself but also includes associated chemicals.

At the organismal performance level, microplastics have been linked to altered sporulation and germination dynamics. For example, reduced spore germination rates, decreased radial mycelial growth, and modified sporulation patterns have been observed in response to polymer microspheres [188]. Furthermore, the latter study revealed that microplastic exposure changed the balance between beneficial fungi and pathogenic fungi and increased the pathogenicity of *Fusarium solani* in tomato plants. Collectively, the current evidence supports the conclusion that microplastics, particularly nanoplastics, function as active physiological stressors for fungal individuals.

4.2 Effects of microplastics on fungal diversity and phylogenetic and functional type shifts

Microplastics are increasingly recognized as drivers of changes in fungal communities across experimental, field, and synthesis studies. There is evidence that microplastics can reshape fungal diversity patterns and functional organization in soils and organic amendments and that fungal communities are more sensitive to microplastics than are bacterial communities [198,199]. Specifically, microplastics affect fungal community composition (beta diversity), and the relative abundances of co-occurring species shift markedly, even when alpha diversity

remains unchanged or shows only small changes [198–200]. For example, polyethylene (PE) microplastics altered fungal community composition within 30 days without significantly affecting alpha diversity [199]. In this study, co-occurrence networks also changed and showed enrichment of saprotrophic and plastic-associated taxa, ultimately shifting both phylogenetic and functional group structures [199]. Over longer exposure times, however, species richness and Shannon diversity declined, whereas dissimilarity between samples (beta diversity) increased further [200].

The restructuring of communities has also been shown at the phylum level. Across multiple polymer types and experimental designs, the relative abundance of Ascomycota often increases, whereas that of Basidiomycota tends to decrease [198,201–203]. This shift has been attributed to the prevalence of more disturbance-tolerant and saprotrophic taxa at the expense of more sensitive groups. Genera associated with stress tolerance or potential polymer degradation (Mortierella, Nectriaceae, Pleosporaceae, Didymellaceae) and well-known saprotrophic or opportunistic taxa such as Aspergillus, Fusarium, Penicillium, and Pyronemataceae are frequently enriched, especially under relatively high microplastic loads [141,202–205]. These findings suggest that microplastics may act as ecological filters for fungi capable of tolerating chemical stress, exploiting novel carbon substrates, or forming biofilms.

The response of diversity depends strongly on polymer chemistry, particle shape and size, concentration, and environmental context (i.e., soil properties) [204]. For example, microplastic fibers reduce fungal richness under moist conditions, likely due to the leaching of toxic substances into the soil [206]. In contrast, richness increased under drought conditions, probably due to positive effects of microplastics on soil properties such as water-holding capacity or porosity [206]. In composting systems, the presence of polyethylene (PE), polyvinyl chloride (PVC) and polyhydroxyalkanoate (PHA) decreased fungal richness during the thermophilic phase, simplified and destabilized fungal networks, and thereby reduced humification [207]. Similarly, the effects of polylactic acid (PLA) on fungal diversity in compost depend on temperature and concentration: a minimal impact was observed at 25 °C, whereas significant community shifts occurred under thermophilic conditions (50 °C) [208]. Persistent changes at very high PLA loads are accompanied by compost acidification and the dominance of specific species, such as Thermomyces, which are capable of degrading polymers under thermophilic conditions [208].

Mechanistically, microplastics influence fungal communities through multiple pathways. In addition to acting as direct ecological filters or via the modification of environmental conditions (e.g., soil structure), indirect trophic effects also contribute to changes in community composition. For example, high-density polyethylene (HDPE) microplastics reduce soil faunal activity, limiting their regulatory influence on litter-decomposer fungal communities and potentially altering decomposition, carbon turnover, and nutrient cycling [201].

Plastic particles also create a distinct habitat known as the plastisphere [209]. Fungal assemblages colonize plastic surfaces differently from those in surrounding soil or organic matter and often exhibit more stochastic assembly processes, with selective accumulation of potential degraders and opportunistic fungi such as Penicillium and Alternaria [209]. Studies have shown that polybutylene adipate terephthalate (PBAT) and polylactic acid (PLA) plastispheres often exhibit lower alpha diversity but distinct community patterns, enrichment of specific fungal families of polymer-degrading fungi, and higher relative abundances of plants and taxa associated with potential pathogenicity [205,210,211]. A study by Nonthijun et al. [212] further demonstrated that biodegradable butylene succinate-coadipate (PBSA) was strongly colonized by fungal plant pathogens in both broadleaved and coniferous forests, with pathogen abundance exceeding that found in natural leaf litter. This indicates potential risks for tree health and forest ecosystem stability.

Although much of the current evidence comes from agricultural soils and compost systems, synthesis studies suggest that fungal communities across terrestrial ecosystems are broadly sensitive to microplastic inputs in a context-dependent way [198,213,214]. Collectively, the literature has shown that microplastics do not simply reduce fungal diversity but rather restructure fungal communities by selecting disturbance-tolerant, saprotrophic, and potentially pathogenic taxa and altering network stability and trophic interactions. These compositional and functional shifts may have cascading consequences for decomposition, nutrient and carbon cycling, and overall ecosystem functioning.

4.3 Effects of microplastics on mutualistic fungi and host fitness

Among mutualistic systems, mycorrhizal fungi are the best studied group in the context of microplastic exposure. Mycorrhizal fungi are crucial organisms in forest ecosystems, as they regulate tree nutrition, water uptake, and belowground carbon allocation and thereby strongly influence forest productivity and carbon sequestration (see Chapter 1). An increasing number

of studies have shown that microplastics can affect mycorrhizal fungal diversity, plant fitness, and ecosystem productivity. However, most studies have focused on agricultural soils, which are dominated by arbuscular mycorrhizal fungi (AMF), whereas forest ecosystems in which ectomycorrhizal fungi (ECMs) are prevalent can be considered understudied [190,215,216].

Numerous studies have shown that microplastics significantly affect AMF colonization, diversity, and community composition but that the strength and direction strongly depend on polymer type and concentration [204,217–220]. For example, in one study, Gamage et al. [217] examined the effects of two polyethylene types, different sizes, and shapes (PE1 and PE2), on *Zea mays* through AMF-associated fungi. The results of the present study revealed a 77.8% reduction in AMF colonization in response to 0.5% w/w polyethylene (PE1) and a 65.6% reduction in response to PE2 relative to that of the controls, indicating that microplastics can disrupt plant–fungus symbiosis under certain conditions. Similarly, in two agricultural soils, He et al. [221] reported that microplastics, especially at high concentrations of 1% and small sizes, reduced Shannon and Simpson diversity. This study revealed that a reduction in AMF activity and disruption of plant–fungus symbiosis lead to a decrease in plant growth and yield via changes in soil chemical properties (pH and nutrients). A recent study revealed that AMF colonization increases at low microplastic concentrations (<1% w/w) but is suppressed at higher doses and that biodegradable microplastics tend to alter AMF communities more strongly than nonbiodegradable microplastics do [218]. Lammel et al. [204] tested different microplastic types and reported shifts in the AMF community structure, which favored stress-tolerant genera across different soil types. These results suggest that microplastics may act as environmental filters in mycorrhizal systems, selecting fungal taxa adapted to altered physicochemical soil conditions.

Recent research from a mixed temperate forest ecosystem suggested that the addition of microplastics might change rhizosphere soil properties and fine-root traits differently when ectomycorrhizal (ECM) versus arbuscular mycorrhizal (AM) tree species are considered [216]. Here, polystyrene (PS) addition increased soil nitrogen and nitrate reductase activity under ECM trees while decreasing phosphor and phosphatase activity; AM tree sites presented the opposite pattern. Similarly, ECM-root systems have fewer branches but more fungal colonization, whereas AM-associated roots present greater specific root length and tip density with thinner tissues, resulting in a shift toward increased exploration of resources for resource

absorption [216]. These contrasting responses suggest that the effects of microplastics on different nutrient exploration strategies depend on the type of mycorrhizal symbiosis.

Microplastics also exert indirect effects on mycorrhizal fungi by altering soil physical and chemical properties, including bulk density, pore structure, aggregation, and water retention, as well as through modified plant traits (e.g., root traits), which ultimately affect photosynthesis and plant growth [141,216,218]. Such changes might have cascading effects on plant–fungi interactions and nutrient acquisition strategies.

Inconsistencies among studies, including contrasting and context-dependent effects of mycorrhizal fungi on nutrient cycling, highlight the need for a stronger mechanistic understanding under realistic environmental conditions. A major knowledge gap is related to ectomycorrhizal fungi in forest ecosystems, despite their dominance and central role in nitrogen and carbon cycling in temperate and boreal regions [222,223]. Understanding microplastic impacts in these systems is critical for predicting long-term consequences for forest productivity and global carbon dynamics. However, there is evidence that microplastics can influence mycorrhizal fungi both directly and indirectly (e.g., via environmental modification), with consequences for plant fitness and primary production, even though the responses strongly depend on the polymer characteristics, concentration, and environmental (soil) context.

Another group of mutualistic fungal organisms is lichenized fungi, which form symbioses with algae or cyanobacteria and can thus be considered primary producers. Lichens inhabit the canopy (leaves and branches), trunks, deadwood, rocks, and soils of forest ecosystems [224–227]. Lichens rely on atmospheric inputs for water and nutrients, which makes them effective reservoirs of airborne particles and has led to their use as biomonitors for a wide range of atmospheric pollutants, including microplastics [228]. Recent studies have shown that epiphytic lichens (those growing on bark) act as bioindicators of environmental pollution and climate change and suggest that whatever is present in the air can accumulate in lichens [228,229]. Importantly, recent studies have demonstrated that lichens can retain microplastics such as synthetic fibers in their thalli, highlighting their value for microplastic exposure monitoring [228,230]. However, evidence on how microplastics affect lichen performance, diversity, and related ecosystem processes (e.g., lichen primary production) is lacking.

4.4 Effects of microplastics on saprotrophic fungi and decomposition processes

Saprotrophic fungi can be considered the key decomposers in forest ecosystems, regulating carbon and nutrient cycling (see Chapter 1). Direct evidence for microplastic effects on forest saprotrophic diversity and decomposition processes is scarce. Most studies have been conducted in agricultural soils, grasslands, and freshwater systems, where litter is used as organic material. However, these studies offer empirical insights that are most likely also relevant for understanding microplastic effects in forest litter decomposition systems [201,231–233].

Several studies have shown that microplastics can influence decomposition processes by changing fungal community composition and the abundance of key decomposer taxa [196,199,201]. The previously described shift toward an increased relative abundance of Ascomycota compared with Basidiomycota under microplastic exposure [198,201] is particularly relevant in this context, as white-rot fungi in the class Agaricomycetes (Basidiomycota) are uniquely capable of degrading lignin [46]. A reduction in lignin-degrading species may, therefore, limit litter and deadwood degradation, with consequences for carbon turnover [234,235]. This finding is supported by a forest litter mesocosm experiment, which demonstrated that microplastics can disrupt decomposition dynamics not only through direct microbial effects but also by changing interactions between soil fauna and fungal decomposers [201].

Evidence from stream litter systems, which are functionally analogous to forest litter decomposition, further supports these findings. Microplastics reduce fungal-mediated leaf litter decomposition, and the effect intensifies when microplastics are combined with additional stressors [233,236]. Specifically, He et al. [236] reported that microplastics together with cadmium reduce litter decay more than either alone does, suppressing fungal biomass. Similarly, Trabulo et al. [233] reported that mixing microplastics with silver caused greater declines in fungus-mediated leaf decomposition than either contaminant alone did [233]. The proposed mechanisms include the ability of microplastics to inhibit soil extracellular enzymes by adsorbing them and altering soil substrates and properties [237].

More generally, microplastics may also act through physical modifications of litter structure directly or by affecting soil fauna, which in turn influences fungal decomposers. According to mineral soil studies, microplastics reduce aggregate stability, alter aggregate size classes, and modify pore connectivity [141,238,190,239,240]. Structural changes in decomposing organic

material may similarly affect hyphal access to substrates and modify moisture and oxygen dynamics, which are key determinants of fungal activity [190,239,240]; however, evidence in forest systems remains limited.

Finally, microplastics provide novel colonization surfaces (plastispheres, see above), particularly for decomposer assemblages [205,209]. Moreover, microplastics may adsorb dissolved organic matter and associated pollutants such as fungicides, thereby reducing substrate availability for fungal enzymes [141,237,241]. Overall, studies have shown that microplastics can directly and indirectly alter saprotrophic fungal communities and decomposition processes. Although forest-specific studies remain limited, consistent results from soil and stream systems suggest that microplastic contamination in forests may alter fungal community-mediated organic matter turnover, nutrient cycling, and long-term carbon storage [141,201].

5. Key knowledge gaps

Despite increasing recognition that microplastics occur in forest environments, our understanding of how microplastic contamination translates into biological and functional consequences in forests remains incomplete (Fig. 1). Our knowledge of the amount and characteristics of microplastics that accumulate in multiple fungal habitats, originate from direct and indirect sources and are redistributed within forest ecosystems, is largely unexplored. In addition, our understanding of how microplastic loads across different habitats affect fungal diversity, functional group composition, and related ecosystem processes is limited. This knowledge gap is especially critical because fungi are key drivers of carbon and nutrient cycling and plant productivity in forest ecosystems.

Another important limitation is the strong methodological bias toward soil as a study habitat, whereas other fungal habitats, such as the canopy (leaves and branches), understory plant strata, trunk areas, and various forms of necromass (deadwood, dung, carcasses, microbial biomass), have been largely neglected. Even within forest soils, how microplastic exposure affects functional group composition, such as shifts within and among ectomycorrhizal, saprotrophic, and pathogenic fungi, remains unclear. Our mechanistic understanding of direct and indirect (environment-mediated) effects is limited.

Finally, the direct links between microplastic-induced changes in fungal communities and forest ecosystem processes remain largely unexplored. Integrated studies that simultaneously assess microplastic loads, fungal community responses, and ecosystem processes, such as necromass decomposition, enzyme activities, nutrient cycling, and mycorrhiza-mediated plant performance, are rare. Moreover, the potential interactions between microplastic pollution and other forest stressors, such as climate change, land-use change, and additional pollutants, remain poorly understood. Together, these gaps suggest that current approaches are likely to underestimate forest vulnerability to microplastic pollution.

6. Way forward — conceptual framework and predictions

To address these knowledge gaps, we propose a conceptual framework enabling the study of microplastic deposition effects in forest ecosystems, with a focus on fungal communities and related ecosystem processes under real-world conditions. We recommend considering different biomes and landscapes with varying microplastic loads (Fig. 2 A-C). Within biomes, at the landscape scale, microplastic loads should be quantified for different fungal habitats, alongside assessments of fungal community responses and ecosystem processes at appropriate spatiotemporal scales.

On the basis of such a framework, the following predictions could be tested (Fig. 2D). We expect that different fungal habitats will be unequally loaded with microplastics. Direct pathways (e.g., from forest management) may particularly affect soil habitats. Indirect pathways such as atmospheric deposition and subsequent wash-out processes may further amplify soil contamination. However, continuous atmospheric input may also affect canopy habitats, especially in areas with high contamination levels (e.g., urban forest landscapes). Furthermore, we expect that large deadwood structures (coarse woody debris) exposed for decades will accumulate microplastics at levels comparable to those in soils. Contamination may increase nonlinearly over time, as advanced (soft) decay stages may retain more microplastics. Owing to their ephemeral presence and rapid decay, animal and microbial components (such as fungal fruiting bodies and mycelia, which are characterized by high C/N ratios) may accumulate relatively little. In contrast, long-lived organisms such as large mammals may accumulate microplastics throughout their lifespan.

Ecological predictions

If microplastic contamination acts as a habitat filter, we expect species diversity to decline, removing species unable to cope with stressful conditions. Thus, species richness should decrease with increasing contamination, and beta diversity is expected to change through nestedness-driven patterns.

If diversity is positively related to ecosystem functioning, as proposed in biodiversity–ecosystem functioning (BEF) theory [242,243], we expect that reduced fungal diversity will impair ecosystem processes (Fig. 2D). Specifically, the decomposition rates of organic matter may decline, inhibiting nutrient and carbon cycling [244]. This could have cascading effects on energy flow across trophic levels within forest ecosystems [245]. If similar mechanisms operate in plant–fungus mutualisms, reduced fungal diversity and altered community composition may decrease primary production [246]. The described mechanisms may also affect wood decay, dung and carcass decomposition, microbial biomass turnover, lichen primary production, and leaf-endophyte-supported photosynthesis, although to a lesser extent than soil-dominated processes, given the expected microplastic loading patterns.

If the overall fitness of organisms across kingdoms (plants, animals, microbes) declines with increasing contamination, fungal pathogens may generally increase (Fig. 2D). Indeed, microplastics have been shown to directly increase the prevalence of fungal pathogens (see Chapter 4.2). From this, we would expect a decline in ecosystem productivity across kingdoms. On the other hand, ecological theory suggests that increased pathogenicity may regulate ecosystems through density-dependent processes, promoting species coexistence by reducing the probability of dominance by a few abundant species [247,248].

Declarations

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Ethics declaration

Ethics declaration: not applicable.

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1465 **Figures**

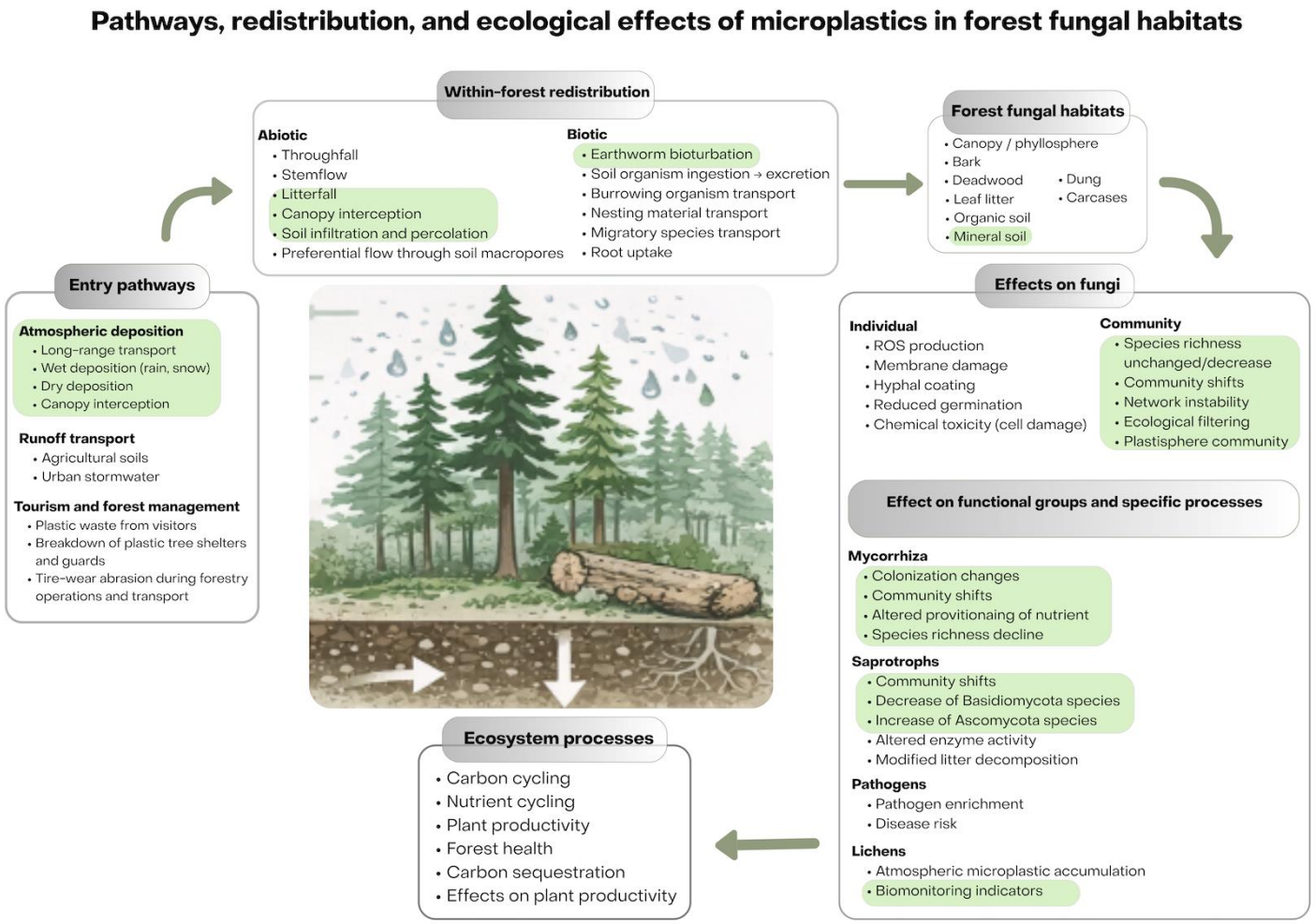

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Fig. 1. Results from the qualitative review of microplastic effects in relation to entry pathways, within-forest distribution, fungal habitats, and fungal diversity components and associated ecosystem functions. The green shaded areas indicate empirical support and relevancy in forest ecosystems; for the other points, we found either weak empirical support or that these topics have not yet been addressed.

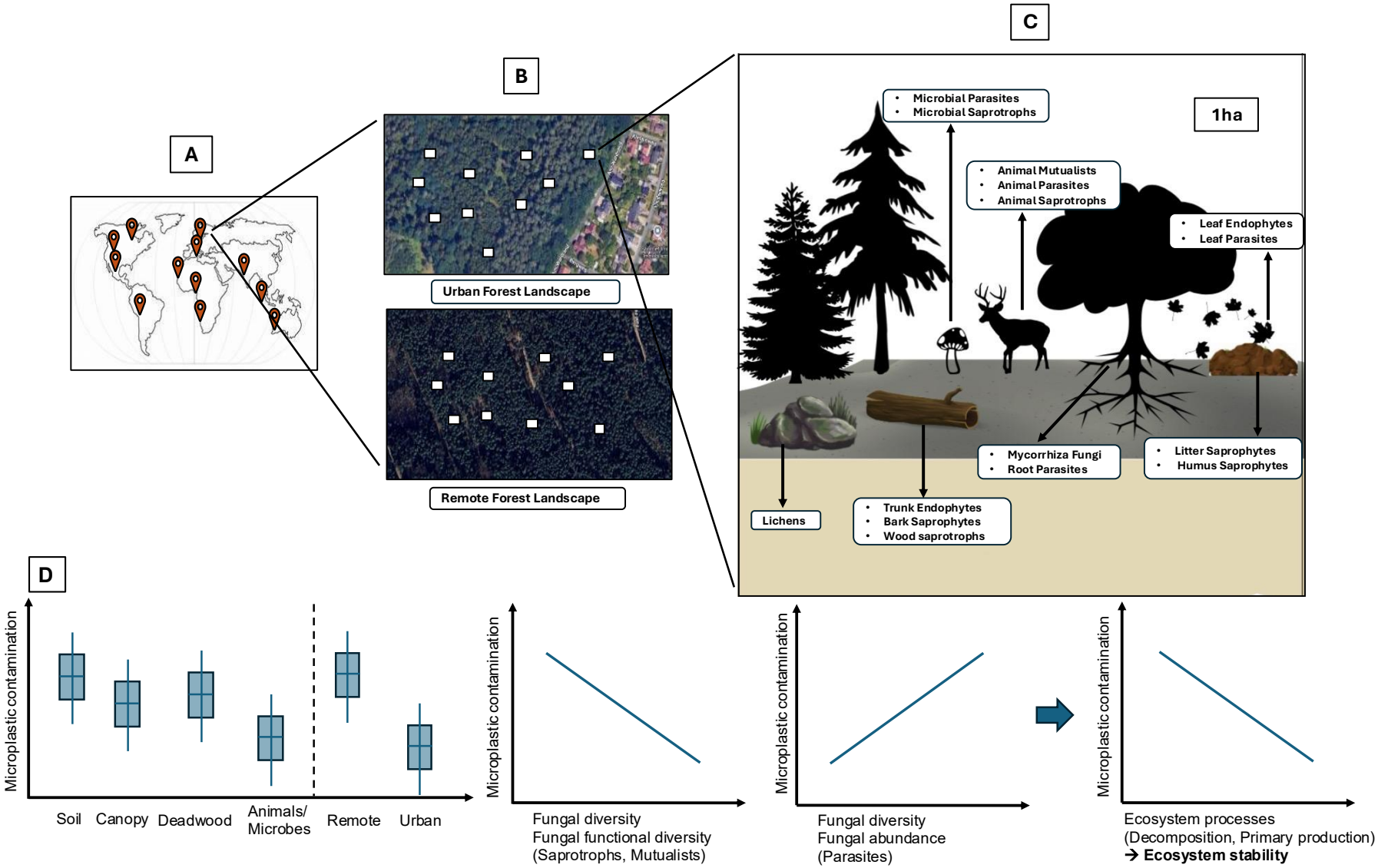
A
B
C
D
Urban Forest Landscape
Remote Forest Landscape
1ha
Microbial Parasites
Microbial Saprotrophs
Animal Mutualists
Animal Parasites
Animal Saprotrophs
Leaf Endophytes
Leaf Parasites
Mycorrhiza Fungi
Root Parasites
Litter Saprophytes
Humus Saprophytes
Lichens
Trunk Endophytes
Bark Saprophytes
Wood saprotrophs
Microplastic contamination
Soil
Canopy
Deadwood
Animals/ Microbes
Remote
Urban
Fungal diversity
Fungal functional diversity
(Saprotrophs, Mutualists)
Fungal diversity
Fungal abundance
(Parasites)
Ecosystem processes
(Decomposition, Primary production)
→ Ecosystem stability

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Fig 2. Suggested coordinated real-world study setting to investigate the effects of microplastic contamination on forest ecosystems, with a focus on fungal diversity and related processes across habitats. We recommend considering different biomes (A) and landscapes with differences in microplastic loadings (B) within each biome. Landscapes should be replicated within biomes, and plots should be randomized and replicated within landscapes. In each plot, the microplastic loading should be quantified together with the sampling of fungi and related ecosystem processes in each of the different habitats (C). Predictions on the basis of the empirical evidence summarized in the review and on an ecological basis (D).