

Forest microbiome and global change

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Abstract

Forests influence climate and mitigate global change through the storage of carbon in soils. In turn, these complex ecosystems face important challenges, including increases in carbon dioxide, warming, drought and fire, pest outbreaks and nitrogen deposition. The response of forests to these changes is largely mediated by microorganisms, especially fungi and bacteria. The effects of global change differ among boreal, temperate and tropical forests. The future of forests depends mostly on the performance and balance of fungal symbiotic guilds, saprotrophic fungi and bacteria, and fungal plant pathogens. Drought severely weakens forest resilience, as it triggers adverse processes such as pathogen outbreaks and fires that impact the microbial and forest performance for carbon storage and nutrient turnover. Nitrogen deposition also substantially affects forest microbial processes, with a pronounced effect in the temperate zone. Considering plant–microorganism interactions would help predict the future of forests and identify management strategies to increase ecosystem stability and alleviate climate change effects. In this Review, we describe the impact of global change on the forest ecosystem and its microbiome across different climatic zones. We propose potential approaches to control the adverse effects of global change on forest stability, and present future research directions to understand the changes ahead.

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Introduction

Forest ecosystems cover approximately 30% of Earth's land surface – 42 million km² – and store 45% of the carbon found in terrestrial ecosystems (Fig. 1), being responsible for 50% of terrestrial net primary production¹. They also act as an important carbon sink that captures 7.6 Gt of carbon dioxide (CO₂) per year². Trees are the dominant primary producers in forests, and provide a multitude of habitats for microorganisms and other biota, such as the rhizosphere (soil surrounding plant roots) and phyllosphere (surface and interior of leaves). Trees also substantially influence the remaining parts of the ecosystem, mainly because they supply the bulk of the carbon that enters the forests. Some of this carbon is deposited in the soil by trees through roots or through the mycelia of root-symbiotic fungi in the form of simple organic molecules, whereas another fraction, represented by the dead biomass of wood, litter or roots, provides a pool of recalcitrant biopolymers³.

Structured by trees, forest ecosystems are complex and consist of multiple habitats of specific features and specific microbiomes⁴. The activity of these microbiomes, which comprise fungi, bacteria, archaea, protists and viruses, will determine the functioning of the forest. The role of microorganisms is especially important in the topsoil (composed of a litter layer, soil and roots of trees), where they mediate the cycling of nutrients. The litter layer, dominated by fungal activity, is a hot spot of recycling nutrients from plant biomass. Soil consists of more recalcitrant organic matter and the microbiomes are rich in bacteria and mycorrhizal fungi that transport carbon from roots to soil and nutrients from soil to trees⁵. Roots and rhizospheres are enriched on these plant-symbiotic fungi. Microbiomes of deadwood consist of microorganisms adapted to efficient decomposition and nitrogen limitation, that is decomposer fungi and nitrogen-fixing bacteria⁶. Specific, yet less abundant, are the microbiomes of tree phyllospheres and rock surfaces⁴. Fungi are the most studied forest microbes due to their important ecosystem functions. Mycorrhizal fungi are key to the mobilization and sequestration of nitrogen and phosphorus in forest soils, and in the transport of carbon from tree roots into soil. There are two major types of mycorrhizal symbioses: ectomycorrhizal, which can decompose organic matter and access organic nitrogen⁷ and are more efficient under nutrient limitation, and arbuscular mycorrhizal, which cannot decompose soil organic matter and are restricted to the use of mineral forms of nitrogen and phosphorus. Saprotrophic fungi are important decomposers in forest litter and soils due to their wide range of extracellular enzymes that break down recalcitrant biopolymers, whereas plant pathogenic fungi may substantially affect ecosystem productivity through predation and reductions in host fitness and growth⁴. Bacteria represent another integral part of forest ecosystems, although they are less explored. In addition to their contribution to the decomposition of plant and microbial biomass⁸, bacteria substantially contribute to multiple nitrogen cycling processes, including the fixation of atmospheric N₂, nitrification and denitrification^{6,9}. Both bacteria and fungi contribute to nutrient mobilization by mineral weathering⁴. Protists, on the other hand, often act as predators on fungal or bacterial cells¹⁰. The role of archaea in forests is typically constrained to specific microhabitats, and their importance varies, contributing to, among other processes, methane (CH₄) and nitrogen cycling¹¹. Although viruses are common in forest soils¹², the extent of their contribution to ecosystem processes remains unclear. The functions of the microbiome components should not be seen as separate. Decomposition and cross-feeding on decomposition products, mycorrhizal establishment, and predation on and decomposition of microbial biomass can be viewed as examples of processes integrating

multiple microbiome components, as is also the case for the cycling of nitrogen, phosphorus and other nutrients (Fig. 2).

In this Review, we explore the varied effects of global change on forest microbiomes, including changes in microbial abundance and microbiome composition, as well as the impact on the performance of root-symbiotic fungi and microbial pathogens in soils and other habitats that are tightly linked to the forest ecosystem properties and processes (decomposition, nutrient cycling, carbon storage or greenhouse gas emissions). By combining observations of past development, experimental approaches simulating global change factors and observations on the realized niches of microorganisms and biogeochemistry, we discuss the ongoing and future changes in forest ecosystems across climatic zones. Finally, we provide an example of forest management strategies to mitigate adverse effects of global change on forest microbiomes and ecosystem performance and stability, and suggest forthcoming research directions needed to understand the future of global forests.

Forests under global change

Human activity has transformed the surface of the planet over millennia, having a major impact on land use and land cover worldwide. The deforestation and land-cover change associated with agriculture together with industrial activities induced a global change, which encompasses several phenomena and processes and has been intensified in the last centuries. Fossil fuel burning has locally increased the deposition of nitrogen and increased the concentrations of CO₂ in the atmosphere, a heat-trapping gas responsible for climate change through the warming of the atmosphere, ocean and land (global warming)¹³. The increase in temperature on the planet involves altered atmospheric circulation patterns and changes in precipitation regimes across the globe, causing heatwaves and drought events that are more intense and recurrent. Reduced precipitation and warmer weather increase the frequency and intensity of fires and induce the outbreaks of many pests¹⁴.

Similar to other biomes, forests both contribute to and are affected by these global change processes^{15–17} (Fig. 3). Because of their complex nature, the response of forest ecosystems to global change is both complex and context-dependent, but the decreased rates of global forest carbon storage appear to be one of the consequences of global change¹⁸. The carbon sink saturation and the increase in carbon losses in forests are the linked result of CO₂ fertilization, rising air temperatures or drought impact and tree mortality. The understanding of forests under future environmental conditions, their functioning and the functioning of their microbiomes is still insufficient, but of critical importance for modelling, management and conservation purposes.

Elevated CO₂ concentration (eCO₂), warming and changes in precipitation and nitrogen deposition are the most important global change factors affecting forests, independent of land management decisions such as deforestation or transformation of natural forests into plantation forests (Fig. 3). Each factor has specific consequences, but they also act in combination. Among other consequences, climate-driven risks may compromise the capacity of forests to act as carbon sinks across large spatial scales¹⁴.

Increasing CO₂ concentrations were predicted to boost the net primary production of forests, but free-air CO₂ enrichment experiments show that the net primary production increase diminishes over time¹⁹. The higher belowground carbon input under eCO₂ is compensated by faster carbon turnover due to accelerated microbial growth, metabolism and respiration, higher enzymatic activities and priming of soil carbon, nitrogen and phosphorus pools under warming²⁰. Warming

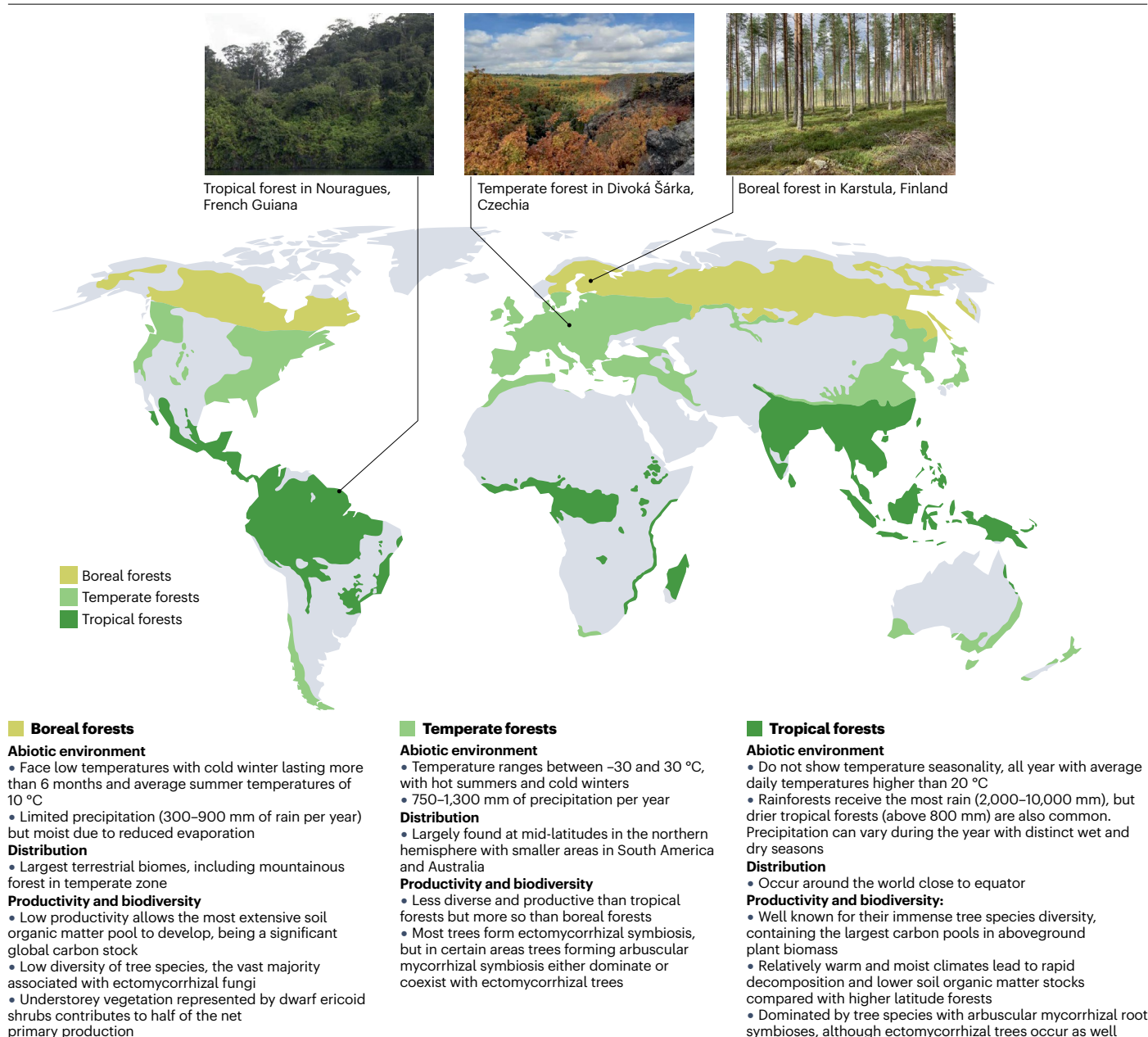


Fig. 1 | Global distribution and features of forest ecosystems. Natural areas and properties of boreal, temperate and tropical forests are constrained by climatic factors: temperature, precipitation and length of the growing season.

The diversity of tree vegetation at the plot scale increases from boreal to tropical forests. The temperate forest zone is the one most affected by forest management.

was the main driver of the global soil microbial biomass decrease of 3.4% observed between 1992 and 2013, especially at high latitudes with high soil microbial carbon stocks²¹. Although precipitation may both increase and decrease with changing climate, the latter phenomenon, leading to temporary or permanent drought, has a much stronger effect on ecosystems than the former. The combination of warming and drought may lead to the extinction of tree species²² and, ultimately, the replacement of tree cover by shrubs or grasses²³. Drought affects a wide range of ecosystem properties, leading to the reduction in

net primary production, soil carbon and microbial biomass, among other effects²⁴.

Unlike other global change factors, atmospheric nitrogen deposition is spatially associated with human activity and, thus, is highly spatially variable²⁵. As available nitrogen is often limiting in forests, nitrogen deposition may positively affect net primary production in such environments²⁶, but it also increases phosphorus limitation in phosphorus-limited soils that are globally more common²⁷. Nutrient limitation affects carbon storage as nutrient-rich forests show

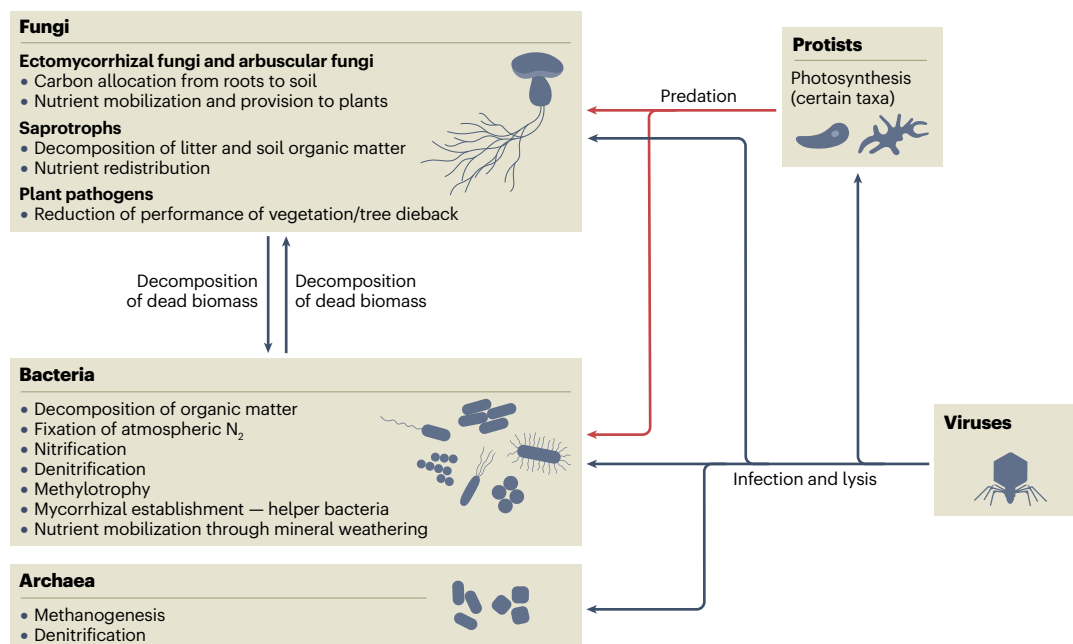


Fig. 2 | Roles of the members of forest microbiomes. Fungi, bacteria, archaea, protists and viruses compose the forest microbiome. Although the roles of fungi and bacteria are widely studied and known, there is much less information about the other microbiome members. The abundance of archaea in forest soils appears rather limited and may be associated with specific habitats, such

as forested peatlands. Protists and viruses are ubiquitous in forests and are known to affect the other members of the microbiome through predation and cell lysis, yet the extent of their importance is unclear. The biomass of dead microorganisms — fungi and bacteria — is largely recycled by the same two groups, with bacteria probably being more important in the process.

higher carbon use efficiency and, thus, sequester more carbon than nutrient-limited forests²⁸. Similar to the change of CO_2 concentrations, it is expected that atmospheric nitrogen deposition will increase in upcoming decades²⁵.

The negative effects of global change, such as the combination of drought induced by warming and precipitation reduction, weaken forests. Dieback of suffering trees, triggered by dry and hot climatic conditions, has been documented on all continents^{29–31}. Climate change led to an increased incidence of biotic pests in weakened trees but also in healthy trees, as the winter survival of insect pathogens is higher in warmer climates¹⁴. In positive feedback, forests weakened by insect or fungal pathogens are more sensitive to adverse climatic conditions and more prone to dieback²⁹. Increased tree mortality combined with warmer and drier climatic conditions results in the observed increase in forest fire frequency, exposing larger areas of forest to fire risk across longer fire weather seasons³². Altogether, pest and fire incidence are significantly correlated with tree mortality and stress³³. Climate models thus predict that tree mortality and connected disturbances, including forest fires, will further increase in the future^{33,34}.

The future challenges to forest ecosystems may be partly offset by their ability to adapt. Tree mortality is taxonomically biased and changes species composition³¹, where trees and their mycorrhizal symbionts may, in the long term, adapt by migration through seedling establishment in places with more favourable conditions²². The change in vegetation is already visible in most global change experiments, especially when multiple factors are combined³⁵. The potential of forest adaptation is, however, limited by the fact that forest resilience has already declined in the past decade due to a multitude of global change factors, in which water limitation and climate variability played

major roles. More than 20% of intact undisturbed forests have already supposedly reached a critical threshold of resilience beyond which they experience further degradation³⁶ and adaptation is less likely.

Boreal, temperate and tropical forests under global change

Although some aspects of global change appear to have universal consequences, their effects are largely modulated by the specific features of boreal, temperate and tropical forests and their microbiomes. This is because climatic and edaphic factors make these forests distinct in multiple aspects: the climate selects local tree species pools, and the diversity of dominant trees determines the turnover rate of organic matter and affects the composition of tree–fungal symbioses involved in nutrient cycling (Fig. 1). Globally, the gross primary production of forests benefits from higher temperatures and precipitation, whereas net primary production saturates above a threshold of either 10 °C mean annual temperature or 1,500 mm precipitation³⁷. In the past 20 years, boreal forests showed, on average, an increasing trend in resilience, probably benefiting from warming and fertilization through eCO_2 , which might have outweighed the adverse effects of climate change on tropical and temperate forests. With temperatures above the limit, temperate and tropical forests experienced a significant decline in resilience, probably related to increased water limitations and climate variability³⁶. The future of forests and their microbiomes should thus be explored separately by forest type (Fig. 1).

Boreal forests

Because of slow decomposition limited by low temperatures and low nutrient contents, boreal forests (and analogous mountainous forests

at higher altitudes in the temperate zone) represent a large stock of carbon in their upland and peatland soils, including soils with permafrost³⁸. They also represent an important carbon sink driven by the production of roots and mycelia of root-associated fungi forming ectomycorrhizal and ericoid mycorrhizal fungi symbioses³⁹.

The productivity of boreal forests has been on the rise due to rapidly increasing temperatures and longer growing seasons¹⁶; the warming, predicted to be faster than that in other forest biomes in the future⁴⁰, may also tend to support this trend. However, the decomposition potential of fungal communities in boreal forest soil has also increased due to warming⁴¹, and could increase further due to the

temperature sensitivity of respiration⁴². Thus, carbon storage rates are likely to decline in the future.

Although there is a large gradient in water availability in the boreal zone, drought-induced mortality has been reported in several regions and is predicted to increase further, amplifying the extent, frequency and severity of biotic and abiotic disturbances, including fires¹⁶. Forest fires represent an important phenomenon in the boreal zone, with 1% of boreal forest areas burnt annually. The frequency of intense fires that burn much of the organic matter will likely increase because of climate change removing high amounts of carbon, decreasing carbon and nitrogen availability and retarding ecosystem development⁴³.

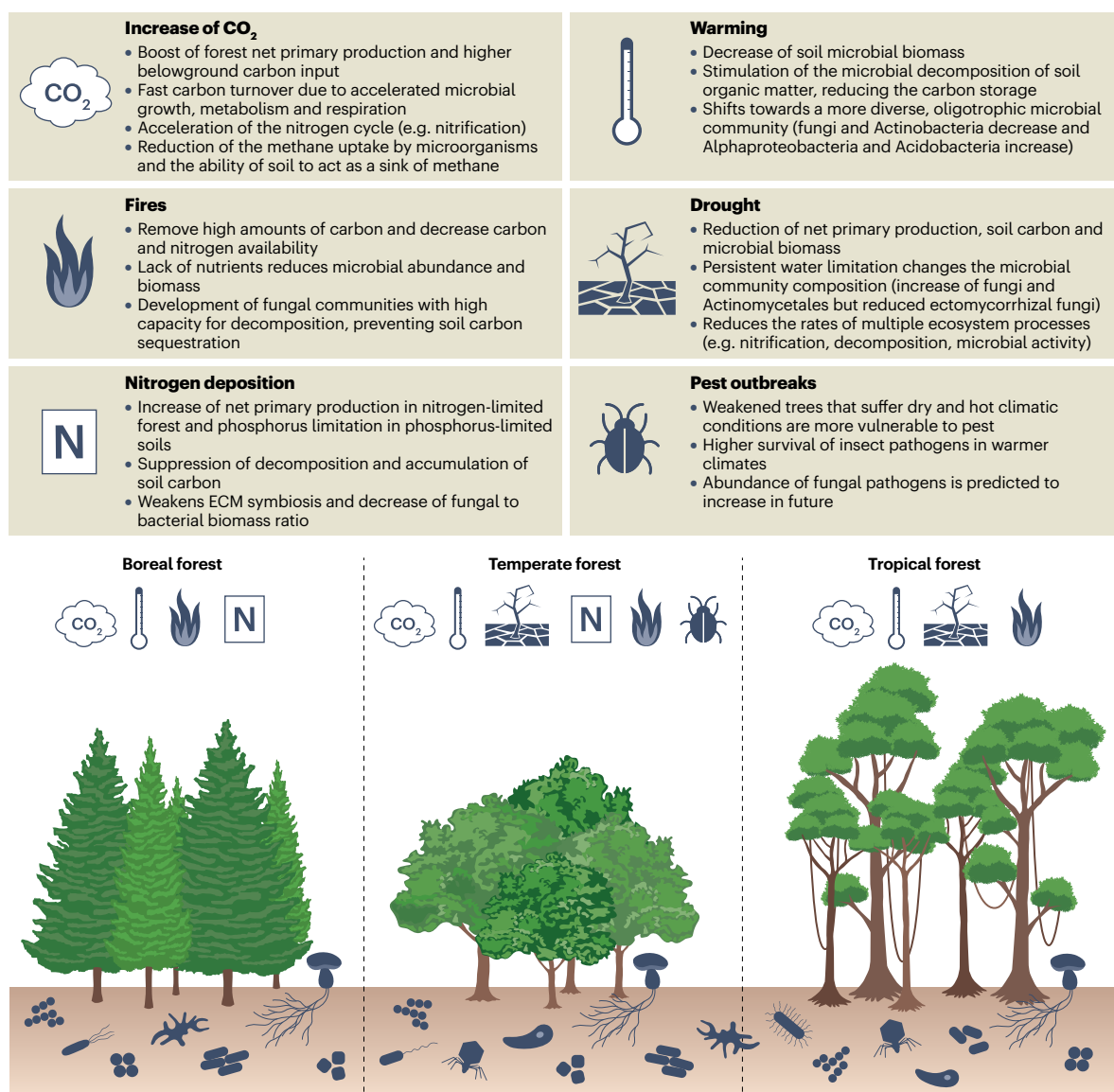


Fig. 3 | Global change factors affecting forest ecosystems and their microbiomes. The most important processes that affect forest ecosystems independently from management decisions (such as conversion of forests to croplands) comprise globally occurring ones, such as elevated carbon dioxide concentration (eCO₂) and warming, and those that vary in intensity across space, such as reduced precipitation and drought resulting from climatic

factors, and nitrogen deposition derived from local anthropogenic pressure (industrial activity and transportation). Forest fires and pest outbreaks are local factors largely triggered by other global change processes that can make forest ecosystems susceptible to these disturbances. Although locally one of the global change factors may dominate in importance, forest ecosystems are always affected by their combination.

Furthermore, in areas with permafrost, fire exposes frozen organic matter to microbial decomposition, causing positive feedback to global warming⁴⁴. Fire has multiple effects on the soil microbiome. The lack of nutrients decreases microbial abundance⁴⁵, including fungal biomass and, consequently, enzyme activity⁴⁶. The overall diversity of fungi and ectomycorrhizal tree symbionts decreases⁴⁷, resulting in an increased ericoid mycorrhizal to ectomycorrhizal fungal ratio and the development of soil fungal communities with a high capacity for organic matter decomposition, which may prevent soil carbon sequestration^{39,48}. Compared with fungi, bacterial communities are less affected by forest fires in boreal ecosystems⁴⁹. Although, for a certain time, specific post-fire microbial communities can develop^{49,50}, the recovery to pre-fire conditions often takes up to several decades⁴⁴.

Boreal forests are typically nitrogen-limited⁵¹, and atmospheric nitrogen deposition can thus offset the limitations of plant productivity⁵² and carbon storage⁵³. Nitrogen addition to boreal soils increases the share of bacteria, and available ammonia promotes nitrification, leading to leaching of nitrate and losses of nitrogen oxides through denitrification. High nitrogen content also weakens ectomycorrhizal symbiosis and decreases the share of ectomycorrhizal fungi that liberate nitrogen from soil organic matter^{51,54}. However, the future development of nitrogen deposition in boreal zones is uncertain as even across all the highly populated regions of Sweden, the deposition of nitrogen has decreased in the last decade⁵⁵. Nitrogen deposition in less populated boreal areas is, nevertheless, of very low intensity⁵⁶.

The permafrost thaw in boreal forests substantially changes local hydrology⁵⁷ and increases the area of inundated land⁵⁸. As waterlogged soils developing after thaw are an important source of CH₄, it is projected that CH₄ emissions will increase substantially, although the extent of such an increase is unclear⁵⁸. In areas where permafrost thawed, the relative abundance of mycorrhizal fungal taxa as well as mycorrhizal plant productivity decreased whereas the relative abundance of putative fungal pathogens increased⁵⁷, but it is uncertain whether this is a common trend.

Along with permafrost thaw, warming shifts climatic zones on the forest ecotone, which is the border zone between the forest and non-forest ecosystems. Although treeline shift develops through the establishment of seedlings and their root symbionts, the speed of forest advance is one order of magnitude slower than the speed of warming¹⁶. Additionally, in high mountains, the treeline shift to higher elevations lags behind climate warming⁵⁹, and ectomycorrhizal fungal advance is delayed even further, likely due to dispersal limitation⁶⁰, setting limits to climate-driven tree expansion. As a consequence, potential forest expansion into so far unforested areas of tundra lags behind warming, which limits the extent of carbon storage that forest expansion may potentially bring.

Temperate forests

Temperate forests, especially those in North America and Europe, are the subject of intensive research comprising experiments with CO₂ enrichment, simulated warming and nitrogen addition that run sufficiently long and allow to understand the effect of global change in these ecosystems at a deeper and more detailed level than in other forest biomes.

Temperate forest microbiomes under climate change. Free-air CO₂ enrichment experiments in temperate forests indicate that eCO₂ increases the production of fine roots and litter but has a limited effect on carbon storage due to their rapid turnover^{61,62}. Indeed, accelerated

microbial turnover of root-derived carbon under elevated CO₂ is sufficient in magnitude to offset increased belowground inputs⁶³. Carbon losses are associated with accelerated nitrogen cycling, including nitrification, suggesting that trees exposed to elevated CO₂ not only enhance nitrogen availability by stimulating microbial decomposition of soil organic matter via priming but also increase the rate at which nitrogen cycles through microbial pools^{63,64}. Despite accelerated carbon and nitrogen cycling, microbial abundance is not substantially affected by elevated CO₂ (ref. ⁶⁵). CH₄ uptake by soil microorganisms is substantially decreased under elevated CO₂ (ref. ⁶⁶). The globally important sink of CH₄ in temperate forest soils resulting from the activity of methylophilic bacteria⁶⁷ may thus decrease in the future.

The longest forest warming manipulation has been run in the Harvard Forest for almost 30 years⁶⁸. The experiment indicated that ecosystem responses changed over time. Rapid carbon loss through respiration was followed by increased degradation of more recalcitrant carbon compounds⁶⁸. The microbial community underwent reorganization with a shift towards a more diverse, oligotrophic community with decreased abundance of fungi and Actinobacteria, increased abundance of Alphaproteobacteria and Acidobacteria⁶⁹, and potentially higher involvement of bacteria in decomposition⁷⁰. Long-term warming ultimately results in the depletion of soil organic carbon with corresponding reductions in microbial biomass⁶⁸. Because temperate forests show weather seasonality, it is expected that warming should increase decomposition in winter months when soils are not drought-limited⁷¹.

This is important as rising global temperatures with limited precipitation increase drought frequency and severity in temperate forests¹⁴. Although short droughts have limited effects, persistent water limitation changes the microbial community composition⁷², increasing the proportion of fungi and filamentous bacteria of the Actinomycetales⁷³ and reducing the abundance and diversity of ectomycorrhizal fungi⁷⁴. Furthermore, as many specialized bacteria, including ammonia oxidizers, sulfur oxidizers and CH₄ oxidizers, are drought-sensitive⁷⁵, drought reduces the rates of multiple ecosystem processes. For example, the persistent decline in ammonia-oxidizing bacteria as a consequence of drought led to massive reductions in gross nitrification rates and nitrate availability in a mountainous forest, ultimately resulting in reduced nitrogen uptake by *Fagus sylvatica* seedlings⁷⁶. Drought can reduce microbial abundance and enzyme activity in litter and soil^{72,77} and alter fungal community composition in deadwood⁷⁸, thus decreasing their decomposition. Enhanced carbon storage due to a decrease in decomposition can, however, hardly compensate for the loss of tree net primary production under drought. At a long timescale, sustained pressure of drought and warming promotes the shift of tree species composition, as occurred in the 'Mediterranization' of forests in South Europe⁷⁹, and may lead to changes in their associated microbiomes.

As in boreal forests, drought combined with warming will increase the frequency and severity of wildfires in temperate forests^{50,80}. Although decomposition may be slowed down shortly after fire, temperate forests recover to pre-fire states much more rapidly than boreal forests⁸¹, reflecting the development of vegetation^{82,83}. Moreover, wildfires leave behind biological legacies, such as fire-adapted fungi, which may promote ecosystem recovery after subsequent fires^{80,81}. Fire frequency increases the relative abundance of ectomycorrhizal trees, which are better able to cope with nutrient limitation following fire losses because symbiosis with ectomycorrhizal fungi is more efficient in nitrogen acquisition⁸⁴. Drought was also a direct or indirect trigger of past outbreaks of insects and pathogens that resulted in millions of

hectares of forest defoliation, canopy dieback, declines in forest growth and forest mortality in North America and Europe in recent decades. Not surprisingly, there is positive feedback on fire frequency and severity^{17,85}.

Nitrogen deposition effects in temperate forests. Due to the intensity of human activity, nitrogen deposition is particularly pronounced in the temperate zone. In the absence of disturbance, nitrogen deposition enhances the growth of most of the dominant tree species in the United States, potentially leading to increased tree carbon storage⁸⁶. Across several experiments, simulated nitrogen deposition resulted in soil acidification, accumulation of soil organic matter and changes in its composition, including higher lignin accumulation. Soil carbon accumulation in response to long-term nitrogen enrichment was largely due to the suppression of organic matter decomposition rather than enhanced carbon inputs to soil via litter fall and root production⁸⁷.

The response of the bacterial community to simulated nitrogen deposition is moderate compared with that of fungi⁸⁸. A decrease in the fungal to bacterial biomass ratio was frequently observed^{187,89,90}, but this response was context-dependent. Although fungal biomass and richness increased with simulated nitrogen deposition at sites with low ambient deposition, they were reduced at sites where ambient nitrogen deposition was high^{91,92}. The fungal community undergoes profound restructuring that particularly affects ectomycorrhizal fungi supplying their tree hosts with nitrogen⁹³. A large survey of ectomycorrhizal fungi associated with forest trees in Europe shows that, as those ectomycorrhizal fungi that decompose organic matter to obtain nitrogen are associated with low nitrogen deposition, nitrophilic fungi that use inorganic nitrogen are associated with high nitrogen deposition⁹⁴. Whereas nitrophilic fungi increase under simulated nitrogen deposition^{92,95}, the diversity and mycelial production of ectomycorrhizal fungi both decline as their activity is less important for their tree hosts^{95,96}.

Decomposition is generally suppressed by nitrogen addition^{89,97} through the reduction in the activity of extracellular enzymes mediating plant cell wall decay^{89,98}. Not surprisingly, nitrogen addition also shifts the bacterial and archaeal potential for nitrogen fixation, ammonification, denitrification and nitrate reduction as a reflection of increased availability of inorganic nitrogen⁹⁹. When deposition results in nitrogen saturation of soils, bacterial and archaeal nitrification and denitrification increase and may result in the efflux of nitrogen compounds (nitrate, N₂ or nitrous oxide gas) from the ecosystem^{97,100,101}.

Temperate forest adaptation to global change. Climatic factors are already changing the composition of temperate forests. Northwards tree species migration is observed in the United States, although the speed is species-specific¹⁰². Because the survival of tree seedlings under modest warming and drought differs widely among tree species¹⁰³, it is apparent that future forests will be different from the present ones, possibly with higher tree diversity¹⁰⁴.

The present distribution of trees forming arbuscular mycorrhizal and ectomycorrhizal symbioses is primarily driven by climate and anthropogenic influences, for example nitrogen deposition¹⁰⁵. The latter, in concert with warming, have already increased arbuscular mycorrhizal tree dominance during the past three decades in the eastern United States¹⁰⁶. Because trees associated with arbuscular mycorrhizal fungi (AM) promote soil microbial communities with higher nitrogen cycling potential and activity relative to those in soils under trees with ectomycorrhizal fungi¹⁰⁷, the ongoing shift of ectomycorrhizal to arbuscular mycorrhizal forests will have important functional consequences. The future arbuscular mycorrhiza-dominated forests in the eastern

United States will likely show accelerated nutrient turnover with critical consequences for forest productivity, ecosystem carbon and nutrient retention, and feedback to climate change¹⁰⁶. Indeed, gene expression studies reveal a 3.5 times greater transcription of nitrogen-cycle genes in arbuscular mycorrhiza-dominated soils than in ectomycorrhiza-dominated soils and a linear increase in volatile reactive nitrogen gases with an increasing share of arbuscular mycorrhizal trees¹⁰⁸. Therefore, shifts from ectomycorrhizal to arbuscular mycorrhizal tree species associated with global change have predictable consequences for nitrogen cycling, which include a faster nitrogen turnover in the future and an increase in losses in the volatile form¹⁰⁸.

Tropical forests

Despite threats of deforestation, degradation and disturbance¹⁰⁹ that call for attention, tropical forests are heavily understudied with respect to their response to global change¹¹⁰. The structural complexity, tree species diversity and inaccessibility of tropical forests make experimentation and predictions difficult. Experimental 2-year warming of a soil profile in a Panama rainforest increased CO₂ emissions by 55% compared with soil at ambient temperature, which was considerably higher than model predictions. The additional CO₂ originated from heterotrophic sources, indicating faster decomposition¹¹¹. However, considering the complex response of temperate forests to warming, it is unclear what would happen at longer timescales in tropical forests. Because nutrient limitation is widespread in tropical forests¹¹², the potential positive effects of elevated CO₂ fertilization are probably limited.

Drought is probably the major factor affecting tropical forests. Water availability has a strong positive effect on biomass stocks and tree growth, and a predicted increase in drought intensity might, potentially, reduce carbon storage¹¹³. The increase in atmospheric water stress driven by climate warming was probably also the main factor responsible for the doubling of tree mortality risk in tropical forests of Australia over the past 35 years¹¹⁴. Prolonged, severe droughts can have profound effects on global carbon storage: it has been speculated that the Amazon drought caused the exceptional increase in atmospheric CO₂ concentrations in 2005 (ref. ¹¹⁵). The impact of drought on the microbiome of tropical forests is unclear. It was assumed that tropical soils have a low adaptive capacity to perturbations due to lower seasonality, yet the first experiments indicate that the diversity and composition of soil microbial communities in tropical forests are sensitive to small changes in soil water content¹¹⁶. Modest changes in water potential also altered the functional potential and activity of the microbiome. Drought resulted in an increase in hydrolytic enzyme activity and oxidation of complex carbon compounds, such as cellulose, chitin, lignin and pectin¹¹⁶.

Because of the high tree species diversity, natural tropical forests weakened by drought are likely less vulnerable to insect pests and plant pathogen effects than temperate and boreal forests. Drought waves, however, induce severe fires with multiple consequences³⁰. Current climatic scenarios predict that fire intensity, recurrence and burned area size will all increase in several areas of Brazil. An increase in fire impact is predicted for 97% of the Amazon area¹¹⁷. Moreover, frequent recurrence of fires can create positive feedback as areas that burn repeatedly are more susceptible to new fires. The vegetation in these locations does not recover fully after fires and is not able to restore productivity¹¹⁷, which has consequences for the plant-dependent microbiome.

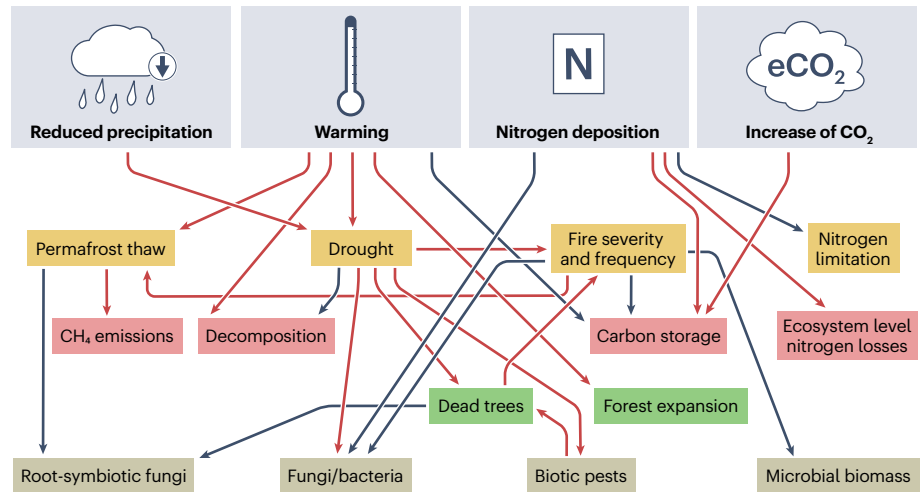
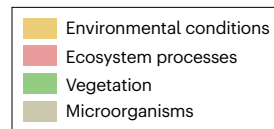
The extent of nitrogen deposition is likely of limited importance in most tropical systems⁵⁶. Although it might locally increase productivity in nitrogen-limited soils, nitrogen deposition would increase

Review article

Boreal forest



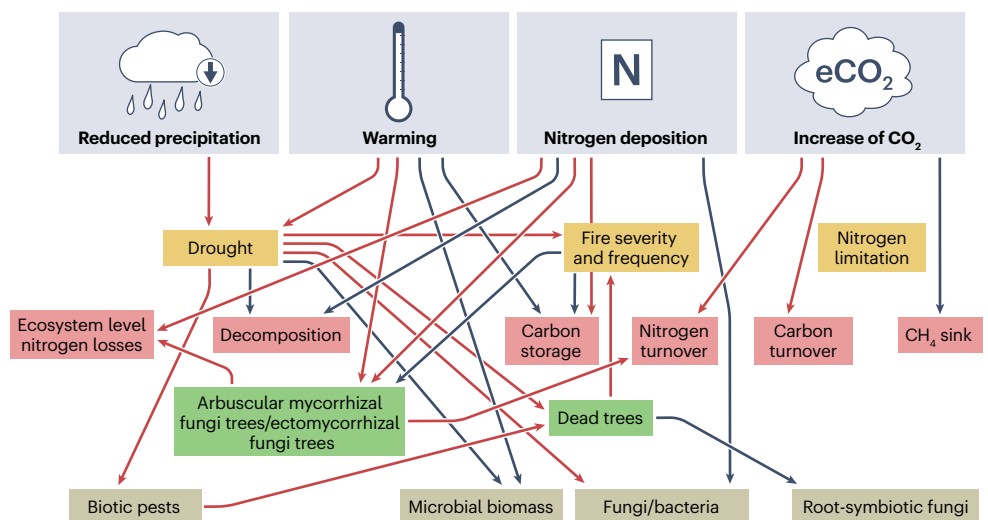
Ectomycorrhizal fungi



Temperate forest



Ectomycorrhizal fungi AM



Tropical forest



Ectomycorrhizal fungi AM

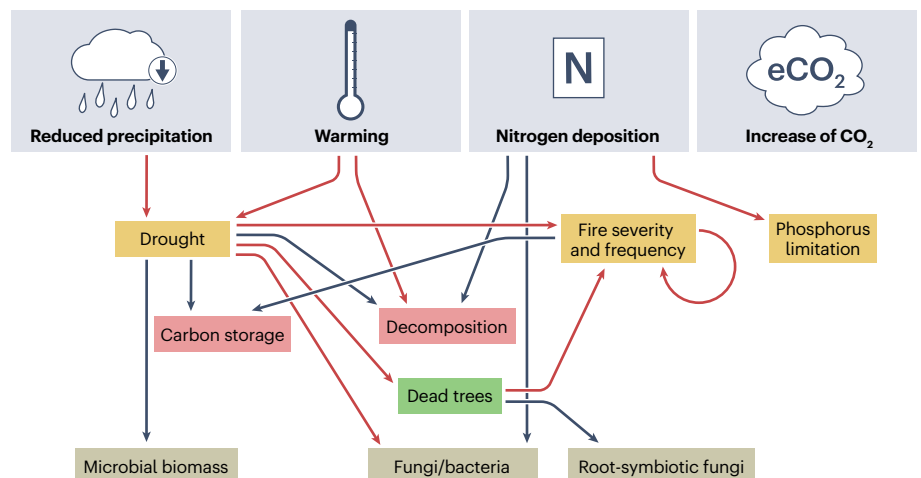


Fig. 4 | Effects of global change in boreal, temperate and tropical forest ecosystems. Climatic factors (reduced precipitation, warming, nitrogen deposition and increase of CO₂) have complex direct and indirect effects on environmental conditions, ecosystem processes, vegetation and the microbiome of forests. Whereas certain effects of global change are universal, such as the combination of warming and reduced precipitation inducing drought that itself brings a multitude of consequences. The importance of global change factors varies among forest biomes because climate, tree species diversity (low in boreal forests, high in tropics) and dominant mycorrhizal symbioses differ, the proportion of trees forming arbuscular mycorrhiza increasing from high latitudes to the tropics. Arrows indicate positive effects (red) and negative effects

(blue). Although boreal forests may benefit from higher productivity under a warmer climate and higher CO₂ concentrations, they will be under danger of drought, fire and pathogens. Temperate forests are expected to mostly suffer from drought-increased mortality and its consequences, and the microbiome will reflect changes in the relative share of ectomycorrhizal and arbuscular mycorrhizal trees. For tropical forests, the largest challenge will likely be the consequences of droughts. Nitrogen deposition may relieve nitrogen limitation in boreal forests whereas it may induce phosphorus limitation in tropical forests; in the temperate forests, nitrogen deposition may lead to saturation and induce ecosystem-level nutrient losses. AM, arbuscular mycorrhizal fungi; CH₄, methane; eCO₂, elevated carbon dioxide concentration.

phosphorus deficiency in soils where this element is limited, which are more common across the tropics¹¹². Nitrogen additions in the tropics had similar consequences to those in temperate forests, decreasing ectomycorrhizal fungi colonization, changing community composition and reducing the activity of several enzymes¹¹⁸.

Microbiome response to global change

General trends

Although the responses of forests to global change partly reflect specific conditions, some responses of the forest microbiome are general and can act across biomes. One example is the limited effect of eCO₂ on microbial communities. Elevated CO₂ is likely to have a limited effect because soil CO₂ concentrations are normally higher than those in the atmosphere⁶⁵. Any community changes that occur under elevated CO₂, such as the increase in copiotrophic microorganisms and the decrease in oligotrophic microorganisms such as Acidobacteria, reflect elevated rhizodeposition (trafficking of carbon by tree roots into soil)⁸. Soil respiration generally increases with temperature to a maximum at approximately 25 °C and decreases at higher temperatures. As no alteration of this pattern due to warming was observed¹¹⁹, ecosystem responses will depend on actual climatic conditions, that is, an increase in cold biomes and a decrease in the tropics.

The effects of drought are also similar across biomes. Based on a meta-analysis, net primary production, aboveground net primary production, belowground net primary production, total biomass, aboveground biomass, root biomass, gross ecosystem productivity and net ecosystem productivity are all decreased by drought, and the responses are more pronounced with drought intensity and duration. These effects, along with decreased soil moisture and increased soil pH, result in a consistent decrease in soil microbial biomass and an increase in fungal to bacterial biomass ratios²⁴. Fungi are better adapted to drought than bacteria due to their filamentous growth, which gives them the possibility to redistribute water to the actively growing parts of the mycelia⁷⁵. Additionally, among bacteria, filamentous taxa increase in dry conditions, whereas unicellular, flagellate bacteria are more abundant in wetter conditions and decrease with increasing water deficit⁷³. Drought effects on the bacterial community are consistent: whereas the share of Actinobacteria (including filamentous taxa) and Firmicutes increases, that of Proteobacteria, Verrucomicrobia and Bacteroidetes decreases⁸.

Not surprisingly, global change-driven disturbances of forests tend to reduce microbial abundance in soils due to reduced tree activity, more in the case of abiotic (fire, windthrow) than biotic (insects or pathogenic fungi) disturbances¹²⁰. Due to the dependence of mycorrhizal fungi on tree roots, disturbances decrease the share of mycorrhizal taxa, overall fungal biomass and the fungal to bacterial biomass ratio in soils¹²¹. Although microbial responses to nitrogen deposition reflect soil nitrogen

availability, acidification by nitrogen deposition generally increases the share of acidotolerant bacterial phyla such as Acidobacteria and Alphaproteobacteria at the expense of Bacteroidetes and Actinobacteria⁸. As in the case of drought, shifts in bacterial community due to nitrogen deposition suggest a change in soil bacterial lifestyle from copiotrophy to oligotrophy, which may affect carbon cycling processes involving bacteria, such as the decomposition of soil organic matter, impacting the forest functioning⁸.

Species-level responses to global change

Microbial communities are composed of individual taxa, and the ecosystem response can be seen as the sum of species-specific responses. Species are constrained to their realized niches that define the conditions under which they can survive and reproduce in the presence of biotic interactions. The realized niche can be derived from the observed species distribution and abundance across habitat properties, including climatic factors¹²², offering the possibility to predict the suitability of the present and future conditions for individual microbial taxa.

According to a global meta-analysis, climate is the main driver of the distribution of individual fungal taxa and the composition of fungal communities¹²³. Climatic niches – ranges of mean annual precipitation and mean annual temperature – of fungal species differ among fungal guilds. There is considerably less information on the climatic niche space in bacteria, although temperature and moisture content both contribute to shaping bacterial communities^{124,125}. Considering the sensitivity of bacteria to the nitrogen content and pH in soils¹²⁴, nitrogen deposition is expected to have a profound effect on bacterial community composition. In a laboratory experiment, fungi and bacteria exhibited a wide range of respiration responses to water potential¹²⁶. Water potential preferences had coarse taxonomic-level signals, suggesting that the moisture niche of soil microorganisms is highly conserved. In particular, strains that were capable of producing biofilms had drier moisture optima and wider niche breadths¹²⁶.

As vegetation composition is expected to change in response to global change, its future development will influence microbial communities' composition. The impact is expected to be larger in fungi than in bacteria because of their closer association with plants as hosts or dead plant biomass as a nutrition source¹²⁷. Although plant host shifts in fungi appear to be a consequence of ongoing global change¹²⁸, it is unlikely that such shifts will be frequent and rapid.

If global change factors cause the disappearance of certain microbial taxa, these losses are unlikely to be rapidly compensated by the colonization of adapted microbes⁶⁰. However, the microbiomes of forest habitats are complex, with a high level of species diversity¹²⁹ and functional redundancy, where several functions are performed by hundreds of microbial species⁵. We may speculate that the negative effects of global change on certain taxa may be functionally compensated

Glossary

Arbuscular mycorrhizal fungi

(AM). Fungi that form a mycorrhizal symbiosis with a plant host. This is typical for certain trees and most non-woody plants and is characterized by fungal hyphae that penetrate plant cell walls, where they form highly branched structures known as arbuscules. AM belong to a single monophyletic lineage of Glomeromycota. They are not able to decompose biopolymers.

Biopolymers

Polymeric molecules consisting of organic building blocks, typically forming cell walls of plant biomass (for example, cellulose, hemicelluloses, lignin, pectin), bacterial biomass (for example, peptidoglycan) or fungal biomass (for example, chitin).

Copiotrophic microorganisms

Microorganisms found in environments or microhabitats rich in nutrients, particularly carbon.

Ectomycorrhizal fungi

Fungi engaged in a mycorrhizal symbiosis that is characterized anatomically by fungal hyphae that wholly enclose the fine roots of the tree host. Ectomycorrhizal fungi include diverse species from the Basidiomycota and Ascomycota

phyla. Some ectomycorrhizal fungi are involved in organic matter decomposition.

Ericoid mycorrhizal fungi

Fungi in a mycorrhizal symbiosis with certain members of the plant family Ericaceae that are characterized by the penetration of hair root cells and the formation of hyphal coils. Ericoid mycorrhizal fungi include diverse species from the Basidiomycota and Ascomycota phyla, and can efficiently decompose biopolymers.

Free-air CO₂ enrichment

An experimental approach that raises the concentration of carbon dioxide (CO₂) in a specified experimental system, such as a forest stand, and allows the response of the ecosystem to be analysed.

Oligotrophic microorganisms

Microorganisms found in environments or microhabitats poor in nutrients, particularly carbon, or those habitats where carbon is contained in complex macromolecules that are difficult to utilize.

Resilience

The capacity of an ecosystem to recover from perturbations.

by the activity of other unaffected community members. Even when global change factors may not cause a clear compositional shift in the active microbial community, they might affect transcription of genes involved in key biochemical processes in these ecosystems¹³⁰. For example, anthropogenic nitrogen deposition downregulates the expression of fungal genes involved in organic matter decomposition and increases the abundance of bacterial ones, thus altering the interactions between soil and bacteria in charge of degrading organic matter in forest soil¹³¹.

Global change affects not only species distribution and gene expression but also physiology. One example is the increased length of the fruiting season of saprotrophic and ectomycorrhizal fungi in Europe paralleling the extension of the vegetation season, as a consequence of warming. The ectomycorrhizal fruiting season is more constrained, probably due to the necessary cues from the host¹³². The ecological implications may be diverse, but their effect on ecosystem processes remains yet unclear.

The future of microbial tree root symbionts and pathogens

Microbial symbionts – especially tree root-symbiotic ectomycorrhizal fungi and AM – are essential for forest functioning due to the provision

of nutrients to trees as well as the transfer of recently photosynthetically fixed carbon into soil. The global distribution of each of these groups of trees is climatically constrained: ectomycorrhizal symbiosis dominates in forests where seasonally cold and dry climates inhibit decomposition and is predominant at high latitudes and elevations. In contrast, arbuscular mycorrhizal trees dominate in unseasonal, warm tropical forests and occur with ectomycorrhizal trees in temperate biomes in which seasonally warm and wet climates enhance decomposition¹³³. As stated above, global warming and nitrogen deposition shift the dominance in favour of arbuscular mycorrhizal trees with consequences for fungal symbioses. Changes in the relative share of ectomycorrhizal fungi and AM then affect bacterial communities. This is because the mycorrhizosphere and mycosphere of ectomycorrhizal fungi have large absorptive areas where fungal hyphae exude labile compounds. This gives these soil compartments distinct features that select for specific bacterial communities¹³⁴. The lower mycelial stock of AM does not strongly affect bacterial communities⁸. With the ectomycorrhizal to arbuscular mycorrhizal tree shift, we can thus expect a decrease in the spatial diversity of soil bacterial communities with unclear consequences for ecosystem functioning. From a functional viewpoint, arbuscular mycorrhizal symbiosis will lead to faster nitrogen cycling and potential nitrogen losses¹⁰⁸ but may also alleviate phosphorus limitation at higher nitrogen levels due to the specialization of AM in phosphorus acquisition¹³⁵.

Global change also affects the species composition within ectomycorrhizal and arbuscular mycorrhizal guilds. Importantly, ectomycorrhizal fungal species inhabit narrow ranges of mean annual temperature and mean annual precipitation with generally lower temperature optima¹²³. With the projection of future warming and reduced precipitation, the ecological constraints of the distribution of these fungi may lead to their relative reduction. Future climate models indeed locally predict a decrease in ectomycorrhizal fungal diversity¹³⁶. This is in line with the observed decrease in their diversity with increasing mean annual temperature across Japan¹³⁷. In AM, temperature and pH are the main determinants of niche space¹²². Acidification, as a result of nitrogen deposition and warming, can thus potentially change arbuscular mycorrhizal communities. Because the carbon to nitrogen ratio and pH are also important drivers of community composition on non-AM^{123,138}, atmospheric nitrogen deposition likely adds further constraints to the stress on fungi under the influence of warming or changed precipitation.

The realized niche of ectomycorrhizal fungi is significantly narrower than that of fungal plant pathogens, with optima at lower temperatures and intermediate levels of precipitation¹²³. Global warming and droughts may thus disproportionately affect ectomycorrhizal fungi and open a window of opportunity for fungal pathogens. A recent global model of the future distribution of plant pathogens predicts increases in pathogen abundance, with increasing mean annual temperature being its major driver^{139,140}. Forest ecosystem stability might be at risk if trees struggle in recruiting ectomycorrhizal symbionts and are simultaneously challenged by an increase in pathogen abundance. Such an increase in the share of plant pathogens as a response to experimental warming was occasionally observed¹⁴¹, as was the potential effect of climate on fungal pathogen that likely contributed to a decline of a specific tree species¹⁴².

Conclusions and outlook

Global change will undoubtedly affect the functioning of forest ecosystems, including their microbiomes, in a profound and complex way. Although boreal forests may benefit from higher productivity, they

will be threatened by drought, fire and pathogens. Temperate forests are expected to mostly suffer from drought-increased mortality and reflect changes in nitrogen saturation. For tropical forests, the largest challenge will likely be the consequences of droughts (Fig. 4). Forest management will have decisive effects on the health of forest ecosystems and their ability to store carbon. Although natural shifts in tree species composition are a lengthy process, planting tree species suitable for future climate or assisted migration¹⁴³ may be a rapid alternative applicable in managed forests. As forest trees are long-lived organisms, forest management needs to consider future climatic conditions when establishing future forests. Shifts from monocultures to mixed stands should increase resilience, as observed when comparing monocultures and mixed stands in Central Europe¹⁴⁴. The increased resilience may be due to a multitude of factors including the limited response to outbreaks of tree species-specific insects or pathogens, or due to better resource sharing in mixed stands¹⁴⁵. There are a wide range of silvicultural measures that come into consideration to mitigate the effects of global change and to promote carbon storage in forest soils (Box 1).

The applicability and efficiency of each management type is largely context-dependent, and the evaluation of management outcomes is essential for the development of smart forestry approaches.

The present level of understanding of the future development of forest ecosystems clearly has its limitations. One of the constraints is geographical. There is far less information from tropical ecosystems and their microbiomes. The same is true for forests on permafrost and in other remote areas^{110,146,147}. These gaps in knowledge should be filled by targeted exploration of microbiomes of undersampled locations¹⁴⁸.

Clearly, experimental manipulations such as free-air CO₂ enrichment, warming or simulated nitrogen deposition are important sources of information on the potential future trajectories of ecosystem development. Their establishment in underexplored areas is thus an urgent need. Furthermore, the changes in the ecosystem response to manipulation over time make it clear that the running experiments should be maintained across sufficiently long time intervals to cover the whole duration of ecosystem transition. Because global change is an ongoing process, the establishment of a time series of forest microbiome

Box 1

Forest management strategies to mitigate the effects of global change

Promotion of carbon storage through tree species selection

The carbon storage potential of forest soils is tree species-dependent¹⁶⁰, and tree species selection is thus one of the possibilities affecting the rate of carbon storage at any certain condition.

Continuous-cover silviculture

The maintenance of forest canopy cover, for example through successive harvesting campaigns as the opposite of clearcutting of whole forest stands, helps conserve carbon stocks and biodiversity and retain the connectivity of ectomycorrhizal networks across the forest life cycle. Because of the latter, seedling establishment is promoted due to availability of root-symbiotic fungi¹⁶.

Nitrogen fertilization

In nitrogen-limited boreal forests, nitrogen fertilization was demonstrated to increase soil carbon stocks due to increased input of carbon in the form of root-associated mycelium⁵⁴. The effect of fertilization may, however, be undesirable from a biodiversity perspective.

Deadwood retention

It is not fully clear how deadwood decomposition contributes to carbon storage¹⁶¹, yet considering the size of the global deadwood pool, this contribution may be significant. Deadwood retention appears to increase both the carbon storage and diversity of the microbiome as well as the diversity of insect communities¹⁵⁴.

Increase in stress resistance

Controlling stand density at intermediate levels may increase forest resistance to drought by alleviating competition among individuals¹⁶². The stress resistance of forest stands may be

further increased by selecting tree species tolerant to dieback under stress.

Planting of forests on peatlands

Especially in the boreal zone, peatlands are an important source of methane (CH₄) emissions produced by soil anaerobes. CH₄ emissions are lowered if forests are planted on peat soils¹⁶³ as the transpiration of trees lowers the water table level in the peatland and increases the thickness of the soil oxic zone where CH₄ is oxidized by methylotrophic microorganisms¹⁶⁴.

Prescribed burning

To mitigate mega-fires, prescribed burning helps reduce wildfire intensity and, thus, the amount of nutrients that are lost during fires of high intensity, helping conserve the desired functionality of forest ecosystems¹⁶⁵.

Restoration of converted lands

Restoration of forests converted to other land use could offset the negative effects of global change. It was recently estimated that restoring 15% of converted lands in priority areas could avoid 60% of expected extinctions while sequestering 299 Gt of carbon dioxide (CO₂) (ref. ¹⁶⁶).

Biodiversity conservation

A recent meta-analysis indicated that biodiversity increased ecosystem functioning in both ambient conditions and under simulated climate change. Positive effects were larger in stressful environments induced by global change drivers, indicating that high-diversity communities were more resistant to environmental change¹⁶⁷.

observations is important as trend changes need to be separated from random variation in microbiome composition¹⁴⁹.

Future improvements in understanding tree physiology and in dynamic monitoring are needed to improve the clarity of future predictions of changes in forest composition²². This is tightly linked to the exploration of links between ectomycorrhizal community composition and host tree performance, which allows to assess the effects of reduced diversity or shift to nitrophilic ectomycorrhizal species on forest productivity. Considering ecosystem processes, studies should focus on cycles of nutrients other than carbon – most obviously nitrogen and phosphorus – given their potential role as limiting factors of ecosystem productivity. In addition, big data technology will bring new opportunities in analysing the expected increasing volume and complexity of data in climatic research¹⁵⁰. The development and application of new technologies such as sensors, satellites and drones and the resolution of remote sensing observation data will allow to detect changes in forest vegetation, to monitor forestry parameters and forest growth, and to improve fire prevention and disease detection^{151–153}.

Although vegetation and microorganisms make up most of the forest ecosystem biomass, there are other groups of organisms that can significantly affect forest ecosystem functioning, such as invertebrates. The decomposition rates of wood across global forests are significantly affected by insects and their interaction with decomposer fungi¹⁵⁴. Interactions with soil animals also affect the performance of fungi¹⁵⁵. Research in tropical forests has shown that termites, decomposers that have mutualistic relationships with microbes, can mitigate the effects of drought and accelerate litter decomposition during dry periods¹⁵⁶. On the other hand, an experiment in boreal forests found that the activity of invertebrate detritivores decreased when warming and drought were combined, what may also directly affect the decomposition of organic matter by microbial communities due to lower fragmentation of litter¹⁵⁷. Incorporation of additional groups of organisms into the models of forest response to global change is thus highly desirable.

As is apparent throughout this Review, soil is the most critical component of forest ecosystems in terms of microbial processes, and upper layers of soils are the most targeted components of microbiome analyses. Nevertheless, microbiomes of deep soil, which contribute to mineral weathering and carbon immobilization in organo-mineral complexes, as well as microbial communities of other less explored habitats in forest ecosystems should also be assessed. In this sense, as leaf microbiome diversity is positively linked to ecosystem productivity and may mediate drought response in trees, studying how these microbiomes interact with global change will be essential to optimize or maintain primary production in forests^{8,158,159}.

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