Continuous Replanting Could Degrade Soil Health in Short-Rotation Plantation Forestry

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Abstract

Purpose of Review Continuous replanting of land with the same or similar plant species can result in the accumulation of harmful soil microbes, which can lead to crop failure. In this review, we explore the influence of constant replanting on the health of short-rotation forestry soil, focusing on the accumulation of deleterious microbes and the decline of beneficial microbes. We also suggest possible practical solutions to address this problem and consider future research that could be conducted to better understand and reduce the build-up of deleterious soil microbes in short-rotation forestry soil.

Recent Findings Compelling evidence that continuous replanting of the same tree species in short-rotation plantation forestry might contribute to the build-up of deleterious soil microbes is still lacking. However, our assessment of existing soil microbiome data from global short-rotation plantation environments suggests a high risk of an accumulation of harmful microbes and a loss of beneficial microbes in plots that were continually replanted with the same tree species. Based on this evidence, and that from agriculture, we propose further research to acquire a better understanding of the build-up of harmful soil microbes in short-rotation plantation forestry, and suggest crop rotation and intercropping strategies to avoid this malady in the future.

Summary The accumulation of microbes detrimental to plantation trees and the decline of microbes beneficial to these trees are realistic risks when plantations are continually replanted with the same tree species. Extensive research is necessary to evaluate the impact of short continuous planting rotations on the biodiversity of soil microbes in plantations and to develop strategies that would alleviate the build-up of detrimental microbes.

Introduction

Plantation forestry is important to the global economy, and it is increasingly realised that intensively managed plantations have a major role to play in the circular economy by providing sustainable material and replacing fossil-based products [1]. Forests cover about four billion hectares of the world's land surface, of which about 291 million hectares are planted forests [2]. The commercial forestry sector is continuously expanding due to an increasing global population and demand for forest-based products. Since 1990, the global primary forest area has been steadily decreasing at a rate that is especially high in low-income countries [3]. To compensate for the loss of natural forest resources, nearly all countries are in some way engaged in commercial

forestry, which also provides important sources of employment and income [2].

It is unlikely that the global demand for forest-based products will decrease in the future, and this is especially due to the development of numerous novel applications, such as microfibers and composite wood products. Plantation forestry using fast-growing tree species that produce high yields, especially in temperate, tropical and subtropical regions is an important source of these products [4,5]. Hence, forestry companies are continuously seeking sources of rapidly growing genotypes of commercially important tree species with the fit for purpose wood and tolerance to biotic and abiotic stresses [6,7]. These genotypes will substantially reduce rotation periods, and consequently, forest land is likely to be replanted more frequently.

Short-rotation plantation forestry (5–20-year rotation) has the potential to substantially meet the global

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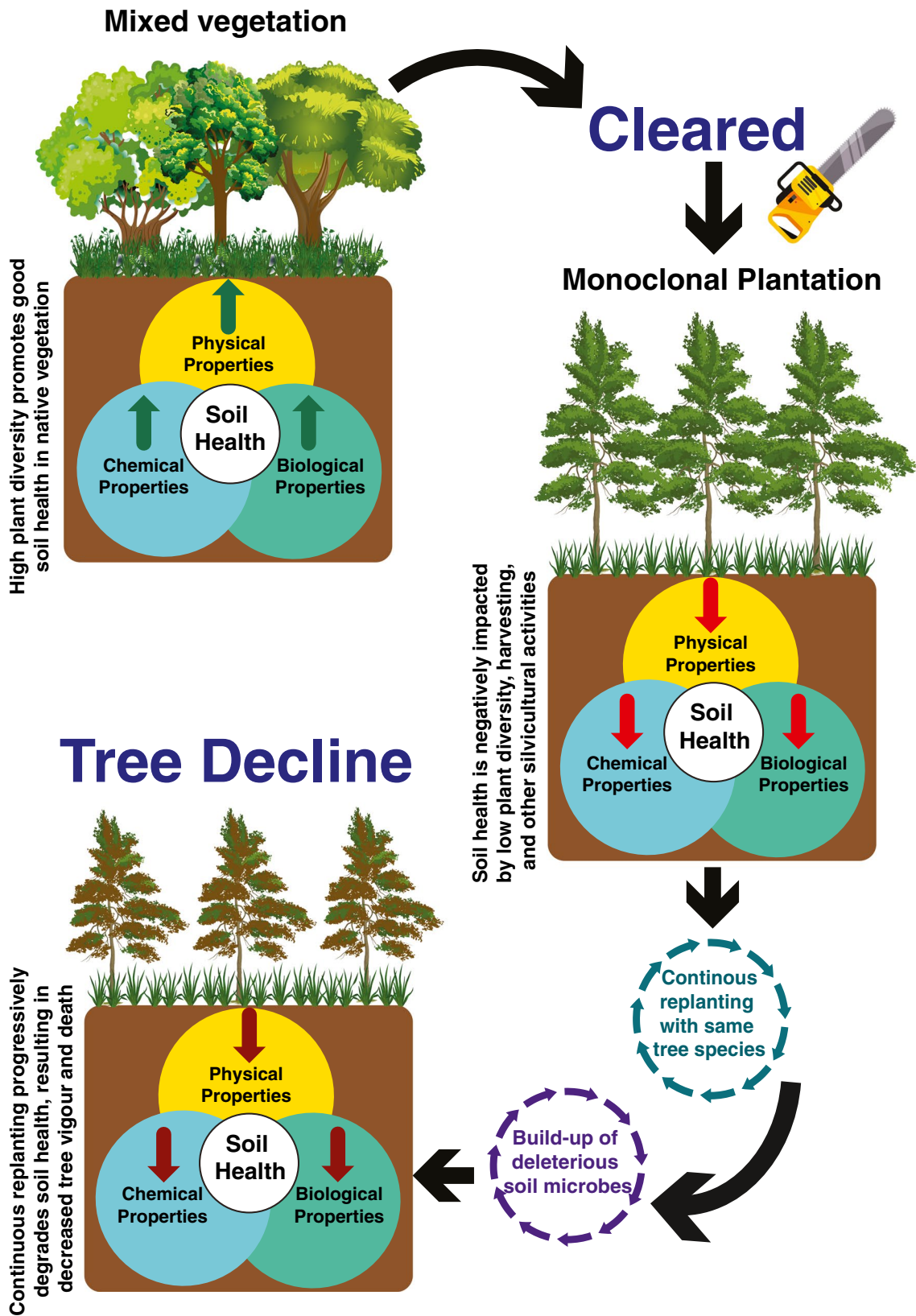Extended author information available on the last page of the article

◀**Fig. 1** Soil health is fostered by the synergistic effect of the physical, chemical and biological properties of the soil. High plant diversity in native vegetation promotes good soil health. However, when vegetation is cleared to set up monoculture plantations, soil health suffers as a result of the low biodiversity of soil microbes triggered by reduced plant diversity, harvesting and other silvicultural activities. This poor soil health in plantations is exacerbated by continuous short rotations of the same or nearly identical tree genera, which deteriorate soil health and promote the build-up of deleterious microbes, causing tree decline

demand for forest-based products because of the faster accrual of biomass by various species of *Eucalyptus*, *Pinus*, *Acacia* and *Populus* [8]. However, continuous short rotations of the same or closely related tree species or genotypes may have unintentional ecological consequences (Fig. 1). Competition for plant-derived nutrients allows a large number of microbes to colonize the rhizosphere [9,10], collectively referred to as the rhizobiome, and successive replanting on the same land can lead to a build-up of detrimental microbes that can negatively affect long-term productivity [11]. In a newly established monoclonal plantation, the levels of soil-borne plant pathogens are typically not problematic. Successive short rotations of the same tree genotypes can, however, result in soils with increased loads of deleterious microbes, which could cause crop failure [12, 13••].

In this review, we evaluate the data from soil microbiome research conducted on short-rotation forest soils to assess the impact of continuous replanting, with an emphasis on detecting evidence for the accumulation of deleterious microbes and the reduction of beneficial ones. Based on this evidence, we recommend directions for further studies required to gain a better understanding of the accumulation of deleterious microbes in short-rotation forestry soils and to minimise the effect of this malady in the future.

Soil Health in Managed Forest Environments

Soil properties, the chemical composition of the plant litter and above-ground vegetation significantly influence the soil microbiome [14•, 15–17]. Monoclonal plantations of exotic trees often have poor litter quality and limited diversity in above-ground vegetation. This, along with changes in land use and management techniques can negatively impacts the biodiversity of soil microbes [18–21]. This is especially concerning because the soil microbiome is responsible for several nutrient cycles and also improves soil fertility [14, 22, 23]. The poor biodiversity of soil microbes can be

further intensified through harvesting and subsequent replanting of stands to the same exotic tree species [24–27] (Fig. 1), ultimately leading to a gradual deterioration of soil health [28, 29]. This, for example, has been documented in a recent study by Guo et al. [30••], in which the authors reported that the transformation of natural broadleaved forests into *Cunninghamia lanceolata* monocultures resulted in the degradation of soil physiological properties as well as lower diversity and richness of soil microbial communities. Other research that compared the microbial diversity, soil nutrients, and structure of short-rotation tree plantations and natural forests found a comparable pattern [31–33].

Soil microbes serve an essential function in forests by recycling nutrients and restoring the physical properties of the soil [9, 11, 34]. Amongst these microbes, fungi act as the primary decomposers and simultaneously improve the physical properties of the soil [9, 35, 36]. In addition, plant symbiotic fungi such as mycorrhizae facilitate nutrient uptake, improve plant resistance to pathogens and enhance stress tolerance [37, 38]. Similarly, soil-inhabiting bacteria such as nitrifying bacteria, mycorrhization helper bacteria [39] and plant growth-promoting rhizobacteria [40] enrich the soil with nutrients, enhance mycorrhizal associations [39] and stimulate plant growth [41].

Soil Health and Multiple Rotations—Lessons from Agriculture and Horticulture

Agricultural and horticultural plantings provide alarming examples of the 'replanting syndrome'. Two well-documented cases are the take-all disease of wheat and apple replant disease (ARD). The soil-borne fungal pathogen *Gaeumannomyces tritici* causes take-all disease, one of the most damaging root diseases of wheat [42]. This disease is widespread in temperate wheat-growing regions of the world, causing significant economic losses [43, 44]. *G. tritici* also infects other cereal crops, including barley, rye and triticale. Usually, this fungus survives saprophytically within plant debris during the intercropping period. Primary infection occurs when the roots of wheat seedlings come into contact with the fungal mycelia. The infection begins with the fungus colonising the root and progresses to the plant's vascular tissue [45, 46]. Infected plants have distinctive white heads caused by premature ripening of the ears, as well as blackened stem bases [47•]. The severity of this disease increases with continuous replanting [48]. A comparable scenario has been documented in horticultural settings in the form of ARD.

ARD has been reported in almost all apple-growing areas in the world [49, 50•, 51]. Symptoms of this

syndrome include stunted tree growth, discoloured roots, reduction of the root mass and necrosis of the root tips. The degree of susceptibility varies greatly among apple genotypes [52]. Nonetheless, symptoms appear soon after planting into continuously replanted soil [50•, 53–55]. Apart from apples, various other rosaceous crops are also known to be affected by this disease [56, 57]. ARD is known to be caused by biotic components since fumigation, and other methods of disease control can suppress this syndrome [57, 58]. Several different soil-borne necrotrophic fungi and oomycete pathogens, such as species of *Fusarium*, *Cylindrocarpon*, *Phytophthora*, *Pythium* and *Rhizoctonia*, have been recovered from symptomatic trees. Therefore, it appears unlikely that it is caused by a single pathogen, but rather by a pathogen complex [49, 50•, 55, 59–63]. In addition, certain edaphic factors can also increase the severity of the disease, such as soil structure, pH and nutrients [55, 57]. Continuous replanting, for example, alters soil microbial interactions and metabolism [64, 65]. Inefficient litter decomposition can result in the build-up of phenolic compounds such as phlorizin, benzoic acid and vanillic aldehyde [66]. The combined effect of these biochemical processes negatively influences essential soil components such as pH, organic matter, moisture levels and the availability of N, K and P [67] and can adversely affect soil microbes, leading to the development of ARD.

In both the above-mentioned examples, chemical control is expensive, usually ineffective and environmentally unsustainable. Various isolates of *G. tritici* are known to be resistant to commonly used fungicides [68], and chemical control for ARD is hazardous to the environment and is not sustainable due to the scale of the affected areas [57]. In this regard, disease-resistant crop varieties are often considered as a solution to the problem. Various resistant apple rootstocks have thus been developed, which are partially resistant to ARD [69], but for take-all disease, no disease-resistant wheat cultivars are currently available [44]. For both of these diseases, however, crop rotation is an effective control strategy [44, 48, 57, 58].

Crop rotation involves cultivating different, unrelated plant species sequentially on the same land [70, 71], a strategy that can significantly reduce the build-up of unfavourable microbes [49, 59, 72]. At the same time, crop rotation increases the nutrient levels and physical properties of the soil [48, 73–77]. Such a rotation of crops is especially effective in reducing plant diseases caused by biotrophic pathogens, because these microbes lack saprotrophic life stages, and cannot survive without a living host [78]. The efficacy of crop rotation is substantially less effective in the case of plant pathogens that have a broad host range or that produce thick-walled structures such as sclerotia, chlamydospores or thick-walled oospores, which can overcome unfavourable conditions [79,80].

The selection of an appropriate rotation programme is important for this strategy to be effective [74, 81, 82]. For example, alternating between wheat and legumes is commonly practised to control the take-all disease caused by *G. tritici* [48]. The legumes restore soil nitrogen and minimize the build-up of pathogen propagules resulting in higher grain yield, while the grains improve the physical structure of the soil providing niches for the survival of beneficial microbes [74, 81, 83, 84]. Similarly, rice is usually rotated with maize and various leguminous crops to improve soil nutrients and structure [85–87]. Likewise, potato, an important cash crop, is often rotated with buckwheat, oats, ryegrass or clover to reduce the inoculum of *Rhizoctonia solani* in the soil [88–91] (Table 1). These are examples where crop rotation is an effective and sustainable method for improving the health of agricultural soils and, as a result, it is extensively used when growing annual crops. However, for fruit tree orchards, the situation is more complex due to the long lifespans of the plants and the specialized nature of the cropping system.

Evidence for Accumulation of Detrimental Soil Microbes in Plantation soils

Short-rotation plantation forestry plots are often established by clearing land that was previously covered by other vegetation types (Fig. 1). After clearing the previous, in some cases native vegetation, a suitable tree species is selected based on performance under the prevailing conditions in the region, including climate, soil and other factors. These plantations are often continuously replanted to the same genera, every 10–15 years. Recent investigations comparing the community of soil microbes in monoclonal planted forests and neighbouring mixed natural forest areas have revealed that plantation soils harbour higher levels of microbes that are pathogenic to the plantation tree species [92••, 93••, 94••]. In all of these studies, the community composition of microbes associated with plantation soils differed significantly from that of adjacent native forests.

Jimu et al. [92••] compared the community composition of soil fungi associated with exotic *Eucalyptus grandis* and adjacent woodlands in Zimbabwe. In that study, the soil mycobiota of the *E. grandis* plantation included fungal taxa

Table 1 List of studies revealing the accumulation of detrimental microbes and reduction of beneficial microbes in short-rotation forestry, together with the common examples of the similar occurrence in agriculture

Host plants	Country	Microbial groups		Soil properties	Comments	References
		Accumulation of detrimental microbes	Decline in beneficial microbes			
Short-rotation forestry						
Eucalyptus grandis	Zimbabwe	Yes	Unknown	Unknown	The soil of *E. grandis* plantations had higher amount of *Eucalyptus* pathogens from the families Davidiellaceae, Mycosphaerellaceae and Teratosphaeriaceae	[92••]
Pinus radiata, Agathis australis	New Zealand	Yes	Unknown	Poor in *P. radiata* plantation hence the higher abundance of ectomycorrhizal fungi	A high number of saprophytes in native *A. australis* forest. The pine forest soil was a pathogen reservoir that could in future jeopardise the sustainability of the *A. australis* forest.	[93••]
Eucalyptus grandis, Acacia mearnsii, natural mixed forest	South Africa	Yes	Unknown	Unknown	The species richness of *Phytophthora* was higher in the adjacent natural mixed forest soils. The plantation soils of exotic trees included *Phytophthora* species that are pathogenic to those trees.	[94••, 98]
Cunninghamia lanceolata	China	Yes	Unknown	Unknown	Upsurge in *Fusarium* and *Penicillium* species. The authors could not distinguish between plant pathogenic and non-pathogenic species of *Fusarium*. However, they concluded that the deterioration of the soil microbial community was likely caused by the continual replanting of the plots	[12]
Pinus radiata, Eucalyptus globulus	Bolivia	Unknown	Unknown	Unknown	Root exudates of the non-native trees affected the diversity of understory vegetation and soil microbes.	[207]

Table 1 (continued)

Host plants	Country	Microbial groups		Soil properties	Comments	References
		Accumulation of detrimental microbes	Decline in beneficial microbes			
Casuarina equisetifolia	China	Unknown	Unknown	Unknown	Litter exudates of *C. equisetifolia* altered the diversity of leaf litter decomposers.	[208]
Eucalyptus, Manglietia glauca	China	Unknown	Unknown	Decline	Compared to monoclonal *Eucalyptus* plots, inter-planting *Eucalyptus* with *M. glauca* enhanced soil fertility and increased the number and richness of beneficial fungi and bacteria.	[106•]
Eucalyptus species	China	High	Yes	Yes	Continuous replanting of *Eucalyptus* reduced the community diversity of saprophytes and pathogenic soil fungi, increased mycorrhizae, and also negatively impacted the physiochemical properties of the soil.	[105•]
Cunninghamia lanceolata	China	Unknown	Yes	Unknown	Monoclonal plantation of *C. lanceolata* had reduced microbial activity required for decomposing leaf litter.	[209]
Cunninghamia lanceolata	China	Unknown	Yes	Decline	The conversion of natural forests to monoclonal *C. lanceolata* decreased the gene copies of ammonia-oxidizing archaea, bacteria, and nitrogen fixation but increased denitrification gene copies.	[30••]
Pinus massoniana, Pinus rigida, Pinus elliottii	China	Unknown	Yes	Unknown	Catabolic diversity and function of soil microbial community were low in the monoclonal forest compared to mixed forest.	[33]
Castanea henryi	China	Unknown	Yes	Decline	Low abundance of beneficial Proteobacteria and Actinobacteria in plantation soil.	[31]

Table 1 (continued)

Host plants	Country	Microbial groups		Soil properties	Comments	References
		Accumulation of detrimental microbes	Decline in beneficial microbes			
Araucaria cunninghamii	Australia	Unknown	Yes	Unknown	Soil fungal communities, especially saprophytes, were lower in the second rotation plantation of *A. cunninghamii*.	[32]
Eucalyptus species	China	Unknown	Yes	Unknown	Low levels of inoculum of both ectomycorrhizae and endomycorrhizae in *Eucalyptus* plantations.	[107•]
Acacia mearnsii	Brazil	Unknown	Yes	Unknown	Low genetic diversity of rhizobial species in continuously replanted *A. mearnsii* plantation.	[112••]
Agricultural crops						
Wheat, barley, rye, triticale	Temperate regions of the world	Yes	Unknown	Unknown	Accumulation of *Gaeumannomyces tritici* in the soil causes the take-all disease.	[47•]
Barley, oats, wheat and rye	Worldwide	Yes	Unknown	Unknown	Accumulation of *Heterodera avenae*, an obligate parasite of cereal crops. Infected plants are highly susceptible to various fungal diseases.	[210,211]
Wheat, barley	Australia, USA	Yes	Unknown	Unknown	Accumulation of *Rhizoctonia solani* anastomosis group 8 (AG-8).	[212,213]
Apple and various rosaceous crops	Worldwide	Yes	Unknown	The decline of edaphic variables and accumulation of phenolic compounds intensify the disease	Continuous cropping leads to apple replant disease. Various fungal pathogens have been isolated from symptomatic trees, including species of *Fusarium, Cylindrocarpon, Phytophthora, Pythium* and *Rhizoctonia*.	[50•, 55, 57]
Peach, almond, apricot, cherry, plum, grapes	Worldwide	Yes	Unknown	Unknown	Accumulation of *Mesocriconema xenoplax* causing Peach Tree Short Life disease. Similar symptoms are seen in other hosts.	[214]

Table 1 (continued)

Host plants	Country	Microbial groups		Soil properties	Comments	References
		Accumulation of detrimental microbes	Decline in beneficial microbes			
Potato	Worldwide	Yes	Unknown	Unknown	Accumulation of *Streptomyces scabies* in soil. Ideally, potatoes are rotated with leguminous crops to reduce the impact of the disease.	[215,216]
Potato, tomato	Worldwide	Yes	Unknown	Unknown	Accumulation of *Phytophthora infestans*. Rotating potatoes with various crops from the Brassicaceae family can reduce the impact of this pathogen and also the early blight caused by *Alternaria solani*.	[217,218]
Tomato	Worldwide	Yes	Unknown	Unknown	Accumulation of *Ralstonia solanacearum*.	[219]
Tobacco	Worldwide	Yes	Unknown	Unknown	Accumulation of *Meloidogyne* spp.	[220,221]
Wide range of crops such as tobacco, carrot and cotton	Worldwide	Yes	Unknown	Unknown	Accumulation of *Thielaviopsis basicola*.	[222]
Tomato and various plants from families Solanaeae, Cucurbitaceae, Cruciferae, Leguminosae, Umbelliferae, Liliaceae, Chenopodiaceae	Worldwide	Yes	Unknown	Unknown	Accumulation of *Fusarium oxysporum* f.sp. *radicis-lycopersici* in soil.	[223]
Radish	Worldwide	Yes	Unknown	Unknown	Accumulation of *Rhizoctonia solani*.	[224]
Cabbage	Worldwide	Yes	Unknown	Unknown	Accumulation of *Plasmodiophora brassicae*	[225]
Melons	Worldwide	Yes	Unknown	Unknown	Accumulation of *Fusarium oxysporum* f. sp. *melonis*.	[226]
Various leguminous crops	USA, Europe, Australia, New Zealand and Japan.	Yes	Unknown	Unknown	Accumulation of *Aphanomyces euteiches* in soil.	[227]
Strawberry	Worldwide	Yes	Unknown	Unknown	Accumulation of *Fusarium oxysporum* f. sp. *fragariae*.	[228]
Sugar beets, cabbage, broccoli and radish	Worldwide	Yes	Unknown	Unknown	Accumulation of *Heterodera schachtii*.	[229,230]

Table 1 (continued)

| Host plants | Country | Microbial groups | | Soil properties | Comments | References |
		Accumulation of detrimental microbes	Decline in beneficial microbes			
Rice	South-east Asia	Unknown	Yes	Reduction of soil properties nitrogen and carbon	Continuous rotation of rice negatively impacted the soil nutrients and microbial diversity leading to a reduction in production.	[85,231]

from families such as the Davidiellaceae, Mycosphaerellaceae and Teratosphaeriaceae, which include species that are known as *Eucalyptus* pathogens. Similarly, continuous replanting of many other tree species over several generations has been shown to have deleterious effects on tree health due to disturbance of soil microbial diversity [13, 95••].

Cunninghamia lanceolata is native to China. This tree is planted due to its rapid growth, high yields and the fact that it adapts to a wide range of climatic conditions. There have been reports of replanting problems with the monocultures of this tree. Continuous replanting with *C. lanceolata* reduces soil fertility and negatively affects the soil microbial community [13••, 30••, 95••]. Xia et al. [12] demonstrated that soil microbial community compositions differ between the first and second rotations of *C. lanceolata* plantings. For example, an upsurge in *Fusarium* and *Penicillium* species was observed during the second rotation. However, the authors could not distinguish between pathogenic and non-pathogenic species of *Fusarium*. The authors hypothesised that the deterioration of the soil microbial community was likely caused by the continual replanting of the plots (Table 1). To alleviate this problem, *C. lanceolata* is now often rotated with *P. massoniana* [96].

Various *Phytophthora* species, such as *P. alticola*, *P. cinnamomi* and *P. frigida*, are important soil-borne pathogens of plantation trees. Studies in which the community of *Phytophthora* species were compared between plantations, and natural mixed forests indicated an accumulation of specific *Phytophthora* species that are pathogenic to the plantation tree species [94••, 97, 98]. They also showed that the species composition of *Phytophthora* was different from the adjacent mixed natural forests [94••, 98]. The species richness of non-pathogenic *Phytophthora* species was substantially lower in the plantation soil and roots of non-native plantations trees, *E. grandis* and *Acacia mearnsii*, but included those that are known pathogens of these trees [94••, 98] (Table 1).

There is currently very little compelling experimental evidence that continuous planting of the same or nearly similar tree species in short-rotation forestry results in the accumulation of detrimental microbes that cause tree decline. This is due to the lack of long-term research monitoring the accumulation of soil microbes in short-rotation plantation forest plots. However, the research cited above provides evidence that some pathogenic microbes can become more prevalent in short-rotation forest soils. Thus, it cannot be excluded that continuous replanting of the same tree species in a plot already loaded with detrimental microbes, as practised in short-rotation forestry, could allow these pathogens to become more abundant over time, resulting in tree decline (Fig. 1; Table 1).

Evidence for the Reduction of Beneficial Soil Microbes in Plantation Soils

Reduced presence of beneficial microbes, such as saprophytes, mycorrhizae and rhizobia, in plantation soil can also have an adverse impact on plant health. As a result, in short-rotation plantations, the synergistic impact of pathogen accumulation and the decline of beneficial microbes can lead to a deterioration of soil and tree health. Beneficial microbes are fundamentally important in the regulation of soil biogeochemical processes because they are the primary drivers of nutrient cycling and soil quality improvement [99, 100]. Saprophytes, mycorrhizal fungi and rhizobia, for example, play critical roles in decomposing plant biopolymers, as well as promoting nutrient uptake, boosting plant metabolism and increasing disease resistance [9, 101, 102].

Saprotrophic fungi are essential components of the nutrient cycle in terrestrial environments. They are the primary decomposers of plant litter, and their hyphal networks, which spread along the soil-litter interface, represent active routes through which these nutrients are efficiently distributed [103, 104]. Xu et al. [105••] reported that continuous replanting of *Eucalyptus* can reduce the relative abundance of dominating microbial groups. The authors reported that switching from *P. massoniana* (coniferous) to *Eucalyptus* (broadleaf) improved soil fungal colonisation in the early phases (first and second generations). However, subsequent generations negatively impacted the physiochemical properties of the soil and the community diversity of soil microbes. Soil bacterial communities changed from carbon-utilizing to nitrogen-utilizing, whereas the fungal communities shifted from saprophytic and pathogenic to symbiotic. Earlier, Xu et al. [106•] compared the effect of continuous monoculture of *Eucalyptus* plantations on nutrient levels and microbial biomass (fungi and bacteria) to that of inter-planting *Eucalyptus* with *Manglietia glauca*. When compared to monoclonal *Eucalyptus* plots, inter-planting *Eucalyptus* with *M. glauca* enhanced soil fertility and increased the number and richness of beneficial fungi and bacteria (Table 1).

Mycorrhizal fungi mobilise nutrients, such as N and P, to the host plant and boost the host's tolerance to abiotic (drought, salt, heavy metals) and biotic (root pathogens) stress. *Eucalyptus* species form associations with both ecto and endomycorrhizae. Chen et al. [107•] reported low levels of inoculum of both ectomycorrhizae and endomycorrhizae in plantation soil when documenting the mycorrhizal biodiversity associated with short-rotation *Eucalyptus* plantations in China over a 2-year period. In contrast, Xu et al. [105••] showed that the relative abundance of mycorrhizal fungi was initially low during the early rotational phase (first and second generation). Later on, when soil fertility declined (third and fourth generation), the abundance of mycorrhizal fungi increased. This trend was similar in a number of other studies conducted on *E. grandis* [108] and *E. saligna* [109] (Table 1). However, during the early stages of replanting, when mycorrhizal abundance is minimal in the soil, pathogen abundance can be higher [105•]. As a result, the presence of soil-borne pathogens may have an adverse effect on the future colonisation of *Eucalyptus* roots by mycorrhizal fungi. For example, as demonstrated with *Eucalyptus gomphocephala*, the presence of *Phytophthora multivora* in the soil lowers fine root biomass, resulting in reduced ectomycorrhizal fungal colonisation [110, 111] (Table 1).

Acacia species are important plantation trees in the tropical regions of the world. As leguminous trees, they form symbiotic associations with rhizobia that fix atmospheric nitrogen. de São José et al. [112••] investigated the rhizobial diversity associated with *A. mearnsii* at multiple sampling sites located in Brazil. The authors reported that the genetic diversity of rhizobial species was higher at sampling sites that were planted for the first time with *A. mearnsii*, whereas sites that were continuously replanted with *A. mearnsii* had lower genetic diversity of rhizobial species (Table 1). Thus, continuous replanting of *A. mearnsii* in the same plot can intensify the selection of specific groups of rhizobia, consequently reducing diversity. A similar trend has been recorded for certain key leguminous cash crops, such as soybeans [113], cowpeas [114] and peanuts [115, 116], where the loss of rhizobial diversity led to a decline in plant vigour.

Why Is Crop Rotation Rarely Implemented in Plantation Forestry?

Even though crop rotation is beneficial to plant health, this is not a practice commonly implemented in short-rotation plantation forestry. There are multiple reasons for this. These include the fact that tree rotations are considerably longer (roughly 5 to 20 years for *Eucalyptus* and *Pinus* species under moderate climatic conditions) compared to the typical annual cycles of agronomic crops. Furthermore, compared to agriculture, fewer plant species are exploited in commercial forestry. The demand for specialised wood products and the availability of land that can be used for plantations are major challenges that discourage corporate and small forestry enterprises from implementing rotation programmes for plantation trees. Thus, populations of unfavourable microbes can be expected to become more abundant over successive rotations. This is strongly supported by data from recent soil microbiome studies involving commercially managed forests, which provide convincing evidence of an increase in pathogenic microbes in soils of continuously

replanted forests [92••, 93••, 107•, 117]. Hence, despite the considerable challenges faced by commercial forestry, it is worth considering strategies to reduce or at least minimize the build-up of unfavourable microbes in planted forest environments.

Alternative Options to Mitigate the Negative Effect of Successive Replanting in Short-Rotation Forestry

In commercial forestry environments, two commonly used post-harvest residue management regimes are burning and mulching [118–120]. Burning is an economical and effective way to remove surplus residue, reduce fire hazards and manage pests and weeds [121–123]. It does, however, have a number of drawbacks, including the loss of soil nutrients, organic carbon and plant residues that reduce soil erosion [123, 124]. In contrast, retaining post-harvest residue and mulching with these residues can significantly enhance soil nutrient content, which is lost through continual replanting [125–127]. Retaining post-harvest residue also allows the restoration of soil microbes in continually replanted short-rotation plantations [126, 128, 129••]. Consequently, these microbes decompose the residues, allowing soil nutrients to be recycled as well as improve the physical and water retention properties of the soil [25, 122, 130].

A majority of studies assessing the efficacy of post-harvest residue management have focussed on quantifying the soil nutrients but rarely catalogue the community composition of microbes. However, Bose et al. [129••] recently evaluated the effects of three post-harvest residue management regimes, where residue was retained, removed, and removed and fertilized, on soil-associated fungal diversity in South Africa. This study showed that *Eucalyptus* plots where post-harvest residues were retained had a higher diversity of saprotrophs and symbiotrophs and fewer pathotrophs, compared to the other two regimes. In contrast, retention of tree stumps in plantations in the Northern Hemisphere increases the prevalence of Heterobasidion root rot among conifers. However, the removal of these stumps does not affect the biodiversity of beneficial microbes, such as mycorrhizae and saprotrophs [131, 132]. While these scenarios in *Eucalyptus* plantations and conifer forests are very different in nature, it highlights the potential that retained post-harvest residue could harbour certain pathogens. Therefore, further research is needed to verify the efficacy of various post-harvest residue management regimes in improving soil health and associated microbial biodiversity in relevant local scenarios.

Biochar is a carbon-rich, stable organic product made from the pyrolysis of organic biomasses such as leaves, sawdust, animal dung and wood [133]. During carbonization, biochar releases phosphate into the soil along with other mineral nutrients, improving its fertility [133,134]. Biochar also improves the physical properties [133] and microbial biodiversity of the soil, which could further increase soil nutrient availability and carbon storage [135–137]. However, the positive impact of biochar on soil is often contested [138,139]. In comparison to agriculture [140,141], our understanding of the impacts of biochar application on plantation forest soils is limited [133, 142•]. Some recent studies from commercial forestry settings have shown that biochar improved soil nutrients and microbes and reshapes the microbial community [142•, 143–145]. Early evidence is thus that biochar has considerable potential to enhance soil properties, nutrients and microbes in continuously replanted forests. Further research, however, is needed to acquire a better knowledge of its impacts on plantation soil health.

The use of beneficial microorganisms to improve plant health and sustainability is common in agriculture, but not in forestry [146–148]. This is due to the difficulty, low efficacy and cost of applying a microbial supplement to trees over large areas in forest environments. These treatments, however, can be potentially performed in nurseries at the seedling stage [149–151]. Mycorrhizal associations, for example, play an important role in a tree's long-term survival in forests [9, 11]. However, the diversity and abundance of mycorrhizae and nitrogen-fixing bacteria are significantly lower in continually replanted forests [107•, 112••]. Treating the seedlings of commercial tree species in nurseries with mycorrhizae, nitrogen-fixing bacteria and endosymbiont mixtures could be explored as an option to promote planting success in commercial forests [149–152]. Diverse communities of these beneficial microbes could also allow planted seedlings to survive more readily in continuously replanted forest soil having a low nutrient content and a high concentration of harmful microbes [11, 153–157].

Adequate silviculture practices, such as crop rotation and intercropping, can alleviate the possible negative consequences of continuous replanting in short-rotation plantation forestry. Rotating between two distantly related tree species, such as *Eucalyptus*, *Acacia mearnsii* and conifers, can prevent the accumulation of harmful soil microbes detrimental to these trees (Fig. 2). For example, in South Africa, *Eucalyptus* and *A. mearnsii* are not infected by the same *Phytophthora* species. *Eucalyptus* species are susceptible to *P. alticola*, *P. frigida* and *P. cinnamomi*, whereas *P. nicotianae* infects *A. mearnsii* [158]. Thus, cycling between two non-host tree genera would likely reduce the population of either group of *Phytophthora* species to a level that will not cause a decline of either of the

tree genera planted. Furthermore, rotating nitrogen-fixing leguminous tree species such as *Acacia* with mycorrhizal tree species like *Eucalyptus* or pines has the potential to further promote both soil and tree health (Fig. 2). Alternating between these trees could increase the availability of nitrogen in the soil through fixation [159] and improve the quality of plant litter [160], thereby enhancing the diversity of saprotrophic soil fungi [161], as well as improving mycorrhizal colonization [162]. Similarly, mycorrhizal fungi would also help to decompose leaf litter and mobilise essential nutrients in the soil, such as phosphorus [163, 164], and promote the sequestration of carbon [165].

Future Research Needs and Opportunities

Most evidence for the build-up of soil-borne pathogens in planted forests emerges from short-term studies using short-read sequencing platforms. The diversity data from these studies provide some clues on the build-up of deleterious soil microbes due to continuous short to medium rotations of the same or nearly the same tree genotypes, yet they do not provide conclusive evidence [92••, 97, 98]. Even though short-read sequencing platforms are widely used to catalogue microbial diversity from various environments, they have several drawbacks, including limitations in taxonomic
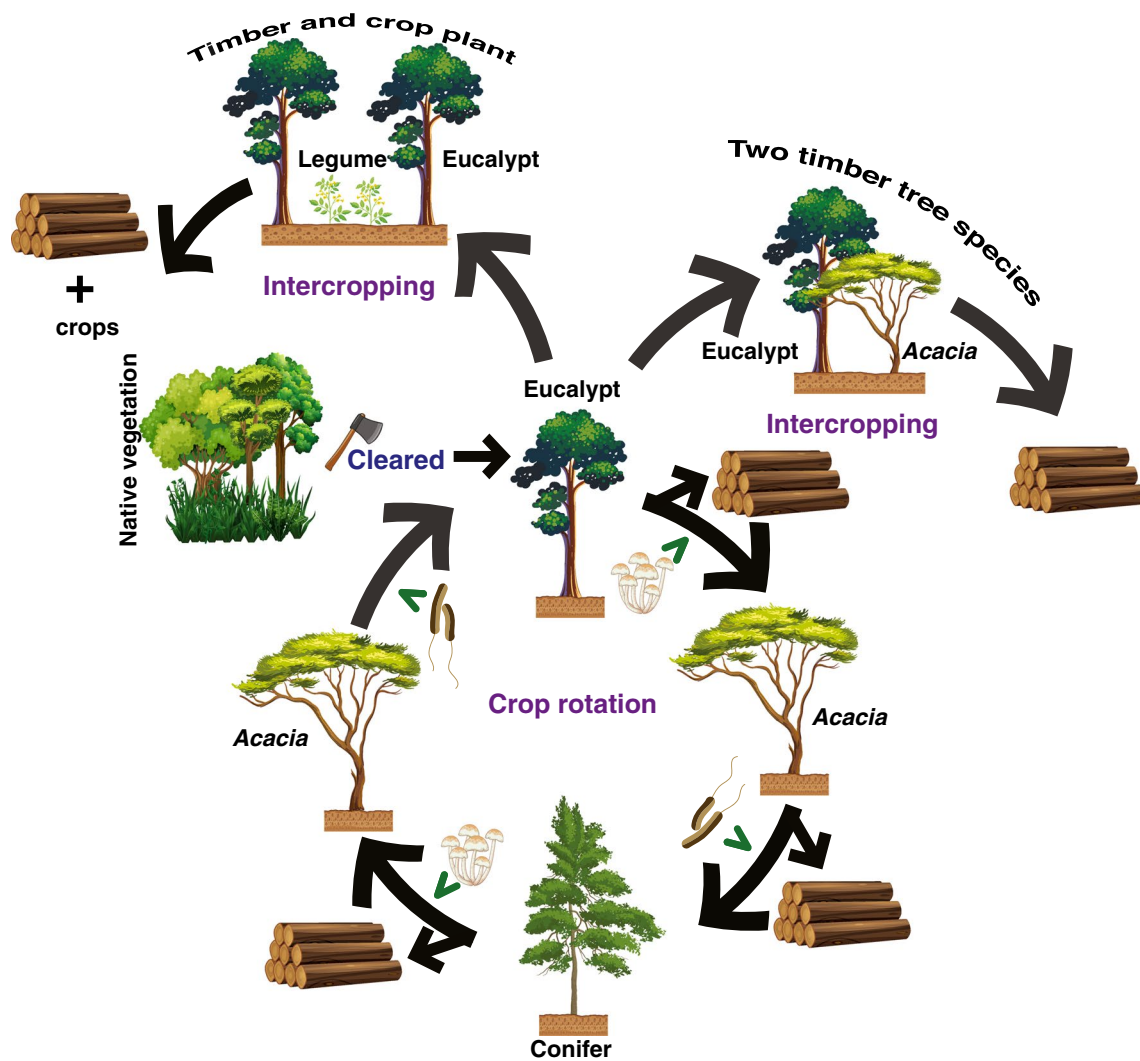

Fig. 2 Three potential schemes for minimizing the accumulation of detrimental microbes in monoculture plantations induced by the continuous replanting of the land with the same tree genus. Crop rotation involves alternating between mycorrhizal and rhizobial tree species such as *Eucalyptus*, *Acacia* and conifers. The other two systems involve intercropping with either two timber-producing trees or one each of timber and a crop plant such as legumes and tuber crops. When selecting the two timber schemes, intercropping a mycorrhizal and a rhizobial tree would be ideal. Intercropping of plantation trees and agricultural crops can allow agriculture and plantation to share land resources while also increasing soil carbon content and land productivity.

identification, taxonomic bias and amplification of dead microbes that are not a part of the immediate biodiversity, among others [94••, 166, 167]. Long-term monitoring programmes using third-generation (long-read) DNA sequencing platforms that improve taxonomic resolution and significantly reduce the possibility of amplifying dead organisms are required to address this shortfall in knowledge [168–172].

Long-term monitoring programs allow the sampling of soils from continuously replanted experimental plots at regular intervals. Microbiome data emerging from such experimental plots could be used to track the build-up of unfavourable microbes resulting from continuous replanting. Understanding the origin and perpetuation of disease-conducive soils in forestry environments will allow for the development and improvement of strategies to mitigate this problem. Simultaneously, species-level identification of these disease-conducive microbes is equally important for implementing mitigating strategies.

Although crop rotation is one of the most important strategies used in agriculture to mitigate the build-up of deleterious microbes, the efficacy of this approach has not been thoroughly tested in forestry environments, nor would it be practical for all forestry companies. An ideal approach to experimentally test the value of crop rotation would be to use relatively short rotations of *Eucalyptus* and *Acacia* as a model system (Fig. 2). This is because rotation and intercropping of these two tree species have been shown to improve the soil's microbial diversity, nutrients and structure [162, 173, 174••, 175, 176]. Species of *Pinus* and other gymnosperms could also be included in these experimental rotations (Fig. 2).

In agroforestry, intercropping of timber-producing trees with agricultural crops such as legumes, tuber crops and a few others has also resulted in promising research outcomes [177–180] (Fig. 2). This approach allows sharing of land resources between agriculture and plantation forestry, while also enhancing soil carbon content and land productivity. Other advantages of this system include reduced soil erosion, weed management, improved biodiversity of soil microbes, improved soil quality, improved yield and yield stability and suppression of pests and pathogens [181,182]. Consequently, further research is needed to examine the feasibility of this system as a standard operational procedure. Soil microbiome data emerging from such studies at regular intervals would increase our understanding of the benefits of crop rotation and intercropping in managed forest environments. This could also result in environmentally and economically resilient plantations.

Advances in technologies are substantially influencing our understanding of the plant microbiome [183,184]. There is a clear shift in focus from issues relating to diversity towards a deeper understanding of changes in the functions of the microbial community in response to various environmental factors and their impact on tree health [185–187]. New techniques allow synthetic microbial communities (SynCom) to be designed with a defined set of microbes with known functions, such as improving plant immunity, nutrient acquisition and stress tolerance [188,189]. Such synthetic microbiomes make it possible to understand the effect of these communities on plant health in response to various environmental stresses, including plant pathogens [171, 183, 189–191]. For example, in maize, removing a single strain of *Enterobacter cloacae* disrupted a microbial community that was capable of lowering the severity of *Fusarium verticillioides* ear rot [192]. Similarly, in *Arabidopsis thaliana*, a synthetic microbiome has been utilised to predict plant phenotype [193]. However, the majority of these studies have focussed on microbes associated with crop plants or with model plants. Evaluating the influence of SynCom on the health of commercially important tree species, such as *Eucalyptus*, would be valuable.

In forest nurseries, fortifying plants with mycorrhizae and nitrifying bacteria can be explored to increase their establishment on constantly replanted land that is often low in biodiversity of beneficial microbes [149–151]. Nonetheless, the use of non-native but beneficial microbes could have unknown negative impacts, e.g. non-native strains aggressively competing with the native microbial population, which can impede the stability of the ecosystem [194–200]. Beneficial microbes should ideally be locally sourced strains that may be found in adjacent native forest patches and plantations because invasive plants frequently exploit them to colonise these environments [201–206]. Consequently, research is needed to identify these native beneficial microbes, such as ectomycorrhizae, develop strategies for their long-term establishment in plantations and assess their impact on the health and vigour of exotic plantation trees in non-native habitats.

Conclusions

Continuous replanting practised in short-rotation plantation forests is likely to be accompanied by a high risk of 'replanting syndrome' in plantations. While long-term monitoring programs to document the changes in soil microbiomes are still lacking and should be urgently initiated, the available evidence suggests that short-rotation forest plantation enterprises could be restrictive when successively establishing new plots with the same or nearly the same genotypes. Furthermore, it is necessary to assess the efficacy of crop

rotation, inter-cropping, post-harvest residue management regimens and the inoculation of seedlings with beneficial microbes in treating this malady in short-rotation forestry environments.

Compliance with Ethical Standards

Human and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any of the authors.

Conflict of Interest The authors declare no competing interests.

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