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Research review

Ectomycorrhizas and tipping points in forest ecosystems

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Summary

The resilience of forests is compromised by human-induced environmental influences pushing them towards tipping points and resulting in major shifts in ecosystem state that might be difficult to reverse, are difficult to predict and manage, and can have vast ecological, economic and social consequences. The literature on tipping points has grown rapidly, but almost exclusively based on aquatic and aboveground systems. So far little effort has been made to make links to soil systems, where change is not as drastically apparent, timescales may differ and recovery may be slower. Predicting belowground ecosystem state transitions and recovery, and their impacts on aboveground systems, remains a major scientific, practical and policy challenge. Recently observed major changes in aboveground tree condition across European forests are probably causally linked to ectomycorrhizal (EM) fungal changes belowground. Based on recent breakthroughs in data collection and analysis, we apply tipping point theory to forests, including their belowground component, focusing on EM fungi; link environmental thresholds for EM fungi with nutrient imbalances in forest trees; explore the role of phenotypic plasticity in EM fungal adaptation to, and recovery from, environmental change; and propose major positive feedback mechanisms to understand, address and predict forest ecosystem tipping points.

Ecosystem tipping points

There is a growing focus by governments and businesses on planting trees and increasing forest area to increase carbon (C) sequestration and thus mitigate global climate change. However, the resilience of forests is compromised by human-induced environmental changes, with increasing impacts on the ecosystem processes, functions and services that forests provide (Reyer *et al.*, 2015). Environmental changes and anthropogenic perturbations can affect ecosystems until a threshold is reached, at which point abrupt shifts in ecosystem states occur that can be difficult to reverse. Such abrupt shifts between ecosystem states after small environmental changes have been conceptualized as tipping points (Scheffer *et al.*, 2001). A tipping point is defined as a rapid and unexpected major change in a system state driven by positive feedback mechanisms often linked to changes in an external driver. Tipping points result in major shifts that are difficult to predict and manage. The abruptness of the shift depends on the inherent characteristics of the system, and hinges on the relative strength of negative and positive feedbacks among species and the environment, as these determine the response and resilience of the system to environmental change (Lever *et al.*, 2020). Understanding, detecting and addressing forest ecosystem tipping points (Box 1) in response to environmental change is therefore timelier than ever (Duke *et al.*, 2020; Krüger *et al.*, 2020).

In the past 15 yr there has been an ‘exploding’ body of literature on tipping points almost exclusively based on aquatic (e.g. lakes and coral reefs) and aboveground systems (e.g. savannah vegetation and drylands) with clear predicted response and effect traits (Dakos *et al.*, 2019; Lever *et al.*, 2020). By contrast, little is known about belowground systems, where change is not as visible, the timescale may differ and recovery may be slower. Monitoring and understanding the soil system, where an enormous range of organisms interact, has long lagged behind those of water and air. To date, the concept of tipping points has been applied only a few times to fungal-dominated belowground ecosystems. For instance, Lindahl & Clemmensen (2016) suggested a potential tipping point in boreal conifer forests when the costs to a tree of maintaining mutualistic ectomycorrhizal (EM) symbiosis are no longer met by symbiotic nutritional benefits, but forests would be unlikely to pass beyond that tipping point under natural conditions. With atmospheric nitrogen (N) deposition, these forests could be brought past the tipping point. Under low N deposition, however, Clemmensen *et al.* (2021) also suggested a tipping point in belowground C sequestration from tundra to subalpine forests mediated by changed functionality of EM communities, but the existence of thresholds and positive feedbacks that generate such drastic changes was not discussed. Furthermore, Jassey *et al.* (2018) showed how drought generated aerobic conditions that, by favouring saprotrophic fungi over bacteria and enhancing decomposition and nutrient mineralization, transformed a moss and ericoid-dominated bog into a graminoid-dominated ecosystem; and Forstner *et al.* (2019) described how long-term N addition caused changes in saprotrophic fungal C, N and phosphorus (P) use efficiencies, and suggested that microbial P limitation could ultimately lead to a tipping point.

Tipping points involve a nonlinear response of a measurable component of an ecosystem (e.g. species composition) to natural or anthropogenic forces that directly or indirectly cause ecosystem changes (Brook *et al.*, 2013). This nonlinear response involves 'hysteresis', whereby the critical transition (tipping point) from ecosystem state A to B occurs at a different condition than the reversal from B to A. Therefore, technically, the tipping point is not a specific point, but a domain with different points for the transition regardless of whether the system moves from A to B or from B to A. A major consequence of hysteresis is that it takes much more effort to revert from the alternative state to the original state (Fig. 1), and hence restoration efforts can easily result in disappointing results, if we fail to understand alternative states in management.

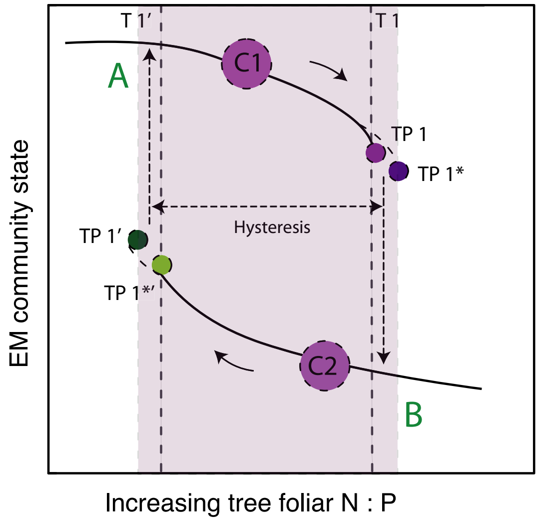

Fig. 1 Ecological hysteresis. The forest is in stable equilibrium (state A) until it crosses threshold 1 (T1) at increasing foliar nitrogen (N) : phosphorus (P) ratios (N : P), the upper stable equilibrium disappears (tipping point, TP1), and the ecosystem state drops abruptly to the lower (alternative) stable state (B). The alleviation of P limitation leads to restoration of stable state A at the crossing of threshold 1′ (TP1′). The difference between forward (TP1) and backward (TP1′) tipping points marks the hysteresis, where the system can only be restored by pushing back significantly further the threshold causing tipping (T1′). When phenotypic plasticity occurs in ectomycorrhizal (EM) fungal communities (C1 and C2), lagged responses delaying the forest tipping point are indicated with an asterisk. The purple area depicts the tipping point domain. Based on Dakos *et al*. (2019).

To gain a mechanistic understanding of species losses and gains, it is necessary to identify biological traits that predispose species to thrive or be replaced under environmental pressure, and how these traits are linked to traits that influence ecosystem functioning (Brook *et al.*, 2013). Organismal traits can act as effect traits when they influence ecosystem functions, or as response traits when they influence the response of the organism to the environment (Lavorel & Garnier, 2002). However, certain traits of EM fungi, such as a preference for N source (e.g. inorganic vs organic) or exploration strategy, can act both as effect and response traits (Koide *et al.*, 2014). Metrics that neglect nonlinear responses of communities are not ideal for biomonitoring because they may overlook communities reaching critical thresholds, and lack of substantial changes in community structure might not indicate ecosystem stability (King & Baker, 2010).

Changing forests

Since the industrial revolution, air pollution has risen dramatically due to human activity, transforming the biosphere. In temperate terrestrial ecosystems, N primarily limits productivity (Elser *et al.*, 2007), so anthropogenic N deposition often initially results in enhanced tree productivity. Alleviation of N limitation increases demand for other essential nutrients, including P; therefore, N deposition can eventually generate P limitation (Gress *et al.*, 2007). When soil nutrient supply is insufficient to meet the demands of faster growing trees, tree mineral nutrition deteriorates, as reflected in the combination of increased leaf N : P ratios and decreased P concentrations, and 'alarming' nutrient imbalances become evident in forests (Jonard *et al.*, 2015; Krüger *et al.*, 2020). Although average N deposition has declined in the last three decades in some areas of Europe, further forest recovery may be limited because the accumulation of N in soil could have a large impact in these ecosystems (Schmitz *et al.*, 2019). These trends compromise the sustainability of the fundamental environmental and economic roles of forests, leading to a decrease in wood supply, C sequestration, and forest resilience to pests and drought (Krüger *et al.*, 2020).

Nutrient uptake in most temperate and boreal trees is dominated by ectomycorrhizas, where tree fine roots are sheathed by fungal tissue forming diverse and widespread plant–fungal symbioses that mediate tree nutrient uptake and C storage in soil. Although EM plants make up only 2% of plant species, EM trees comprise *c.* 60% of tree stems on Earth (Steidinger *et al.*, 2019) and store *c.* 100 GT of C aboveground (Soudzilovskaia *et al.*, 2019). Temperate EM forests store far more C per unit of N than temperate arbuscular mycorrhizal (AM) forests (Averill *et al.*, 2014), and EM plants profit more from the CO_2 fertilization effect than AM trees, probably due to the ability of EM plants to mobilize N from soil organic matter (Terrer *et al.*, 2021). However, whether EM trees will continue to benefit from CO_2 fertilization at high N deposition when leaf and needle P concentrations decline has not been addressed so far.

Responses are probably mediated through fungal community composition changes, as different EM fungi vary in their functional traits, involving different soil exploration abilities and enzymatic capabilities that determine their relative contributions to ecosystem processes such as N and P acquisition and C sequestration (Lilleskov *et al.*, 2011; Kuyper, 2017).

The challenge of understanding belowground change

Temporal changes in community composition through gains and losses of species, and their altered relative abundances and dominance are central in ecology. So far it has been impossible to study temporal change in fungi and the soil environment at large scales, observationally or experimentally, due to the cryptic lifestyle of soil fungi and the lack of a standardized baseline. This problem fuelled an alternative approach, namely analysis of phenological change in fruitbodies over the last few decades, which showed, particularly for Northern Europe, that EM fungal reproduction had changed markedly, with the reproductive period becoming longer (Boddy *et al.*, 2014). However, whether changes in reproductive phenology reflect changes in diversity, activity, abundance, biomass and/or distribution of fungi and whether changes over time in belowground communities can be inferred from changes along spatial environmental gradients (van der Linde *et al.*, 2018) remains unknown. Lack of direct evidence of large-scale EM temporal change in fungal community structure or function over time, long available for far more apparent organisms such as animals and plants (Pecl *et al.*, 2017), represents a fundamental knowledge gap, leading to the roles of a keystone functional guild being largely intractable, a ‘black box’. Crucially, this situation seems to have prevented the application of tipping point theory to mycorrhizal symbioses. For example, major aboveground tree condition changes driven by increasing N deposition leading to P limitation in trees have been suggested to be causally linked to soil acidification, changes in fine root biomass and EM fungal changes belowground, with worrying trends in foliar nutrition (Jonard *et al.*, 2015; Krüger *et al.*, 2020), defoliation and discoloration in EM conifers and broadleaves as N deposition increases (Veresoglou *et al.*, 2014). Given that the EM sheath largely impedes direct contact between roots and the soil solution, these studies invoke EM fungal changes as explanatory mechanisms.

Mycorrhizal tipping points

Concept and mechanisms

In a strongly N-limited conifer forest (reflected in low needle N concentration and N : P ratio), the biomass of EM fungi is very high. Nitrogen immobilization in EM mycelium, described as the ‘nitrogen trap’ by Franklin *et al.* (2014), can be so high that tree growth becomes negatively related to tree C supply to EM fungi (Henriksson *et al.*, 2021). If N deposition increases, there will be an initial positive effect for both tree and fungus (Lindahl & Clemmensen, 2016). Many EM fungi favouring soils under severe N-limitation form abundant hyphae and rhizomorphs (medium-distance exploration type; Agerer, 2001) to acquire nutrients. These hyphae and rhizomorphs contain large amounts of N and retain a large proportion of acquired N (nitrogen trap). With further N enrichment these EM fungi decline, because of the interaction between reduced C allocation from tree to fungus and direct soil effects, as these fungi, specialized for acquisition of N through mining of soil organic matter, may be negatively impacted by high mineral N levels, especially ammonium (Lilleskov *et al.*, 2019). Simultaneously, enhanced concentrations of mineral N stimulate nitrotolerant or nitrophilic EM fungi that generally produce limited extramatrical mycelium (short or contact soil exploration types) and whose ability to immobilize N in mycelium is restricted. Increased N therefore switches system feedbacks from negative (keeping the forest N-trapped) to positive (decline of nitrophobic EM fungi reduces N immobilization in mycelium and hence increases N availability that benefits nitrotolerant and nitrophilic EM fungi), resulting in increasing amounts of mineral N that further reduce nitrophobic EM fungi (Fig. 2). This positive feedback will ultimately result in ecosystem N-saturation and leaching of nitrate and cations such as Mg, Ca and K (Midgley & Phillips, 2014). The strong feedback will result in a situation where finally small changes in N inputs have large effects, most nitrophobes disappear, EM fungal biomass declines, and while trees have access to sufficient N, they increasingly run the risk of P-limitation and P-deficiency (Fig. 2). This level of N deposition, where small changes result in major effects, is the critical load determined by this tipping point. Disentangling the major players in each response is critical.

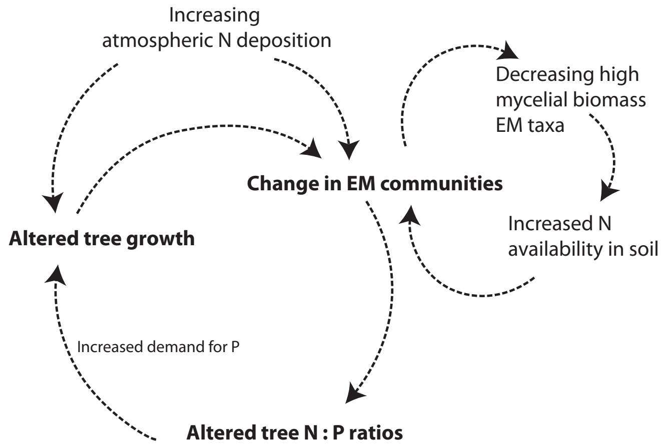

Fig. 2 Feedbacks in forests. Increasing atmospheric nitrogen (N) deposition is the external driver of a feedback between tree growth, ectomycorrhizal (EM) fungal communities and tree foliar N : phosphorus (P), potentially leading to a forest tipping point. Internal feedback leads to changes in EM fungal communities.

While the above mechanism provides a positive feedback, as demanded by tipping point theory, tipping points are more likely to occur in ecosystems dominated by a small number of species, with limited functional and response diversity (Scheffer, 2009). However, whereas tree species diversity is low in boreal and temperate EM forests, species richness of EM fungi can be high. One may therefore wonder whether, with individualistic species responses, the conditions for tipping points exist. We suggest phylogenetic conservatism plays a major role in this respect. Species or lineages tend to retain ancestral traits over time and closely related species tend to occupy similar ecological niches (Crisp & Cook, 2012). Although functional redundancy within genera varies (e.g. within *Cortinarius* in Lindahl *et al.*, 2021), many congeneric EM fungal species have similar morphologies (Agerer, 2001) and physiologies (Lilleskov *et al.*, 2011) and hence sensitivity to N, so there could be concerted species turnover along an N-deposition gradient.

Empirical evidence

We recently analysed *c.* 40 000 mycorrhizas of oak, spruce, pine and beech across 137 long-term forest intensively monitored plots in 20 European countries (van der Linde *et al.*, 2018). Based on threshold indicator taxon analysis (TITAN2, Baker & King, 2010) at the community level, we observed sharp thresholds for change in EM fungal species composition with changes in environmental and tree conditions. At the species level, we detected indicator taxa decreasing (z−) and increasing (z+) with increasing influential variables. Moreover, some fungi appeared to show phenotypic plasticity (Box 1), that is producing more or fewer hyphae and/or rhizomorphs (within the same exploration type), depending on environmental conditions. Phenotypic plasticity reflects how these fungi adapt to, and might recover from, change.

The observed large-scale environmental thresholds in EM fungal communities linked to N deposition and tree foliar N : P ratios indicate a tipping point in forest ecosystems (Fig. 3). Ectomycorrhizal fungal richness and evenness decline sharply across large spatial gradients of increasing atmospheric N deposition, with major shifts in dominant fungi showing different functional traits (exploration types) linked to changes in foliar N : P. These changes in EM fungal species composition correlate with differential preference for organic and inorganic N sources, and sensitivity to N deposition (Hobbie & Agerer, 2010; Lilleskov *et al.*, 2011, 2019; Suz *et al.*, 2014). The good match between our conceptual model and the data (Fig. 4) calls for refinement of critical loads for N deposition as assessment tools in these ecosystems and their alignment with EM tipping points, where fungal communities shift drastically in abundance, diversity, activity or species composition. The exact tipping point will differ for different tree species and their characteristic EM fungal communities (e.g. the critical load for conifer-specific EM fungi is probably lower than for broadleaf-

Box 1 Defining forest tipping point and potential response and effect traits.

Ecosystem tipping point: Shift to nutritionally deficient forest trees and soil eutrophication.
Organisms: EM fungi and EM trees.
Environmental drivers: Nitrogen deposition, increased CO_2, phosphorus limitation.
Response and effect traits: Hyphae, rhizomorphs, exoenzyme release, species turnover or extinction, N-mobilizing traits, P-mobilizing traits in EM fungal communities.
Ecosystem effects of trait change: Tree nutritional deficiencies (tree foliar N : P), soil eutrophication.
Forest stable states: Healthy trees and soils vs nutritionally imbalanced trees and eutrophic soils.
EM fungal phenotypic plasticity: Intraspecific variation in the production of hyphae and rhizomorphs within the same soil exploration type.

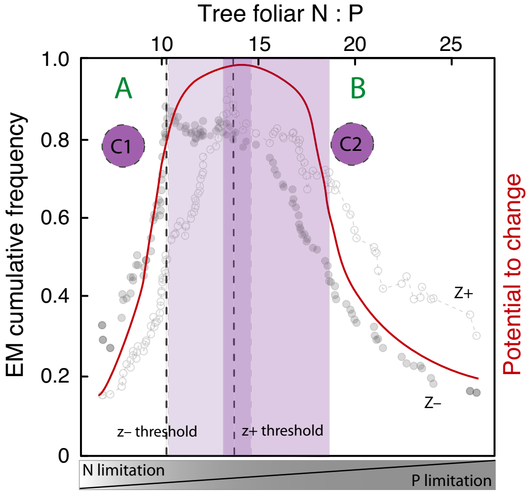

Fig. 3 Tipping point in forests linked to changes in ectomycorrhizas and tree foliar nutrition. Small circles show the proportions (ectomycorrhizal (EM) fungal cumulative frequency) at each of 137 forest monitoring plots (ICP Forests) of EM fungi showing significantly contrasting relationships – dark grey (z−), mostly decreasing vs light grey (z+), mostly increasing – with tree foliar nitrogen (N) : phosphorus (P) ratios. Ectomycorrhizal community composition shifts for z− and z+ taxa at increasing foliar N : P ratios at two thresholds. The potential of change leading to a tipping point is indicated by the curve and the purple area (tipping point domain). When phenotypic plasticity occurs in EM fungal communities, lagged responses delaying the forest tipping point are indicated with a darker shade of purple. Changes in EM fungal communities (C1 to C2) lead to a tipping point in the forest ecosystem that shift to an alternative ecosystem state (nutritionally imbalanced trees, from state A to state B). Based on van der Linde *et al*. (2018).

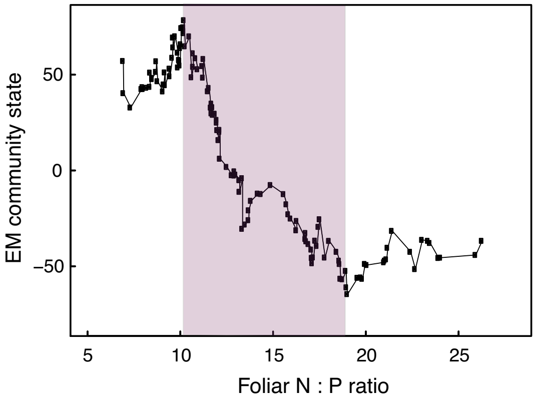

Fig. 4 Empirical data supporting the concept of a tipping point in forests linked to changes in ectomycorrhizas and tree foliar nutrition. Each data point results from the difference between the cumulative response of taxa decreasing and the cumulative response of taxa increasing, calculated by subtracting cumulative z+ (increasing taxa) from z− (decreasing taxa) values of the ectomycorrhizal (EM) communities at each of 137 forest monitoring plots (van der Linde *et al*., 2018). The tipping point domain is in purple.

specific fungi) and will probably also vary to a smaller extent depending on climate (e.g. temperature and rainfall are factors that determine decomposition of organic matter and N mineralization) and soil properties (e.g. how much P is mineral-associated). Studies over large spatial scales in Europe confirm that EM forests show transitions among different EM fungal communities regarding number of species and composition in relation to atmospheric N deposition (Cox *et al.*, 2010; Suz *et al.*, 2014; de Witte *et al.*, 2017; van der Linde *et al.*, 2018), indicating that this EM tipping point is a general phenomenon. Belowground transitions should impact forest capacity to access inorganic, and especially organic, N and P (Lilleskov *et al.*, 2019) with direct consequences for tree nutrition. Understanding the interplay of ectomycorrhizas and forest conditions and functions and the mechanisms of forest ecosystem tipping points has untapped potential to inform fundamental understanding of terrestrial ecosystems, forest management, environmental policy, restoration and conservation practices (Suz *et al.*, 2015).

The role of phenotypic plasticity

The EM extramatrical mycelium is directly involved in N and P mobilization, uptake beyond root depletion zones and transfer to trees, and also the colonization of new roots and reproduction. Linking taxonomic with functional-trait data helps underpin the proposed tipping point mechanism, but we have recently shown that across Europe there are EM fungal taxa that display phenotypic variation in their functional traits and that such variation is linked to environmental conditions (van der Linde *et al.*, 2018). Trait change as a consequence of morphological or physiological plasticity is known to affect tipping points, by delaying them, for instance in ecosystems moved closer to the tipping point by stress gradients, or leading to an earlier tipping point and increasing the risk of ecosystem collapse (Dakos *et al.*, 2019). Ectomycorrhizal fungi show different functional traits that confer different abilities to mobilize inorganic and/or organic P. For instance, EM fungi with medium- and long-distance soil exploration are considered more efficient in P mobilization than short-distance or contact soil explorers, due to their extended colonization of soil and exoenzymatic capabilities (Lilleskov *et al.*, 2011), though empirical confirmation is largely lacking (Plassard *et al.*, 2011, 2019). The more plastic organisms are, the less likely we are to detect tipping points. Understanding how EM fungal functional traits affect ecosystem properties is a key issue to resolve (Zhu *et al.*, 2018), and it is uncertain how individual EM fungal species and communities recover from eutrophication and nutritional deficiencies, or how resilient and plastic EM fungal communities are to change.

The ability to show phenotypic variation has been typically assumed to be fixed within EM fungal species (Agerer, 2001), which would hamper the potential of communities to adapt to change and therefore require community turnover (e.g. overcoming priority effects) for forest resilience to change. Alternatively, we propose traits (e.g. production of hyphae and rhizomorphs) may be plastic within the same exploration type and species, thus making taxa resilient to change until a point where a critical threshold is crossed beyond which community turnover predominates over phenotypic plasticity; that is, we expect phenotypic plasticity will precede community composition changes, modulating the impact of environmental change on ecosystem resilience, recovery and functioning (Fig. 1). We also expect plasticity will predominate over species turnover in EM fungal community recovery to environmental change.

Additional mechanisms

The mechanism of an EM tipping point as proposed here shows similarity with the tipping point that determines the critical transitions of heathland dominated by heathers to one dominated by grasses under N deposition (Berendse & Aerts, 1984). That tipping point is determined by differential litter production, litter nutrient concentration and decomposability of plants of both guilds. It can therefore be relevant to consider whether saprotrophic fungi (fungi nourished by dead organic matter) also play an additional role in the existence of an EM tipping point. Nitrogen deposition reduces the biomass of ligninolytic saprotrophs, increasing C storage (Entwistle *et al.*, 2018). Forstner *et al.* (2019) additionally observed that increasing N loads shift saprotrophic communities towards P-limitation and impacted fungal C and nutrient (N and P) efficiency, while Lucas & Casper (2008) noted that reduced ligninolytic activity due to N deposition correlates with enhanced N mineralization. Lower saprotrophic fungal biomass could further reduce fungal N immobilization and increase N availability (Kemmers *et al.*, 2012). It is therefore likely that additional mechanisms contribute to the EM tipping point.

Implications and concerns

At the continental scale, tree growth in forests is mostly influenced by stand density and age but shows a tipping point at high N deposition levels (Etzold *et al.*, 2020). While we have knowledge of N deposition effects on EM fungal communities, there is still remarkably limited consensus on how N deposition-induced P limitation and deficiency interact with changes in ectomycorrhizas, tree nutrition and soil C fluxes (Lilleskov *et al.*, 2019). At local scales, recent studies detected significant changes in EM fungal communities, tree growth and foliar N : P in response to substantial N and P fertilization in pine and spruce forests (Bahr *et al.*, 2013; Almeida *et al.*, 2019). In fact, there have been numerous recent modelling, observational and experimental studies at local scales of EM fungi and emerging P limitation in European forests (Braun *et al.*, 2010; Bortier *et al.*, 2018; Zavišić *et al.*, 2018; Almeida *et al.*, 2019; Clausing *et al.*, 2021). However, these were conducted on forests well above the N deposition thresholds for drastic changes in EM fungal communities (van der Linde *et al.*, 2018), so they studied already severely negatively impacted EM fungal communities. In particular, it is unclear if there are consistently dominant, potentially nitrophilic P specialist EM fungi, and how their traits would respond to shifts in both N and P limitation (Almeida *et al.*, 2019; Lilleskov *et al.*, 2019; Maaroufi *et al.*, 2019; Ruess *et al.*, 2019).

After a decrease in N addition to the system, there are three different scenarios for EM fungi, as proposed for grassland plants (Payne *et al.*, 2017): instant species richness recovery (no hysteresis); lagged responses at the species/community level, influenced by phenotypic plasticity (ecological hysteresis, Fig. 1); and irreversible changes in communities (e.g. due to limited dispersal abilities and propagule depletion – fundamental regime shift). The dynamics of EM trait changes can affect not only tipping points but also recovery to a previous ecosystem state because the system cannot be restored by retracing the same path (Duke *et al.*, 2020; Lever *et al.*, 2020). Changes in EM functional traits between environmental thresholds can therefore have different consequences for the ecosystem, from delaying or advancing tipping points (acting as effect traits) to leading to functional collapse if species turnover does not occur (acting as response traits).

These findings are of concern because the crossing of environmental and nutrient thresholds leading to alternative stable states in forest ecosystems cannot easily be reversed (Fig. 1; Box 1). Evidence for the negative implications of hysteresis come from observations on fruitbodies of EM fungi in the Netherlands (Van Strien *et al.*, 2018) where partial recovery was stronger if there was a smaller legacy of past N deposition, that is in areas less affected by anthropogenic N deposition. Partial EM recovery below ground (around 50%) occurred in experimental plots 6–15 yr after complete cessation of long-term N additions compared to plots where N application continued, indicating that recovery needs drastic reduction in N, which can be easily achieved in experiments, but is unlikely to occur with N deposition (Högberg *et al.*, 2011).

What is the future of forests if N deposition is not abated, and these forests remain in a state of persistent P-limitation? One possibility is that forests reach a second tipping point, where trees that form EM symbioses are outcompeted by trees that form AM symbioses. Data from the USA (Averill *et al.*, 2018; Jo *et al.*, 2019) indicate that N deposition is causing a shift from EM forests towards AM forests. Again, positive feedbacks could induce critical transitions. Because AM trees produce higher quality litter, rates of C and N cycling would be higher under AM than under EM trees (Keller & Phillips, 2019), which could allow AM trees to retain dominance. In addition to N being a driver, Jo *et al.* (2019) point out additional effects of climate change: under higher temperatures, N mineralization increases and P limitation becomes exacerbated; and elevated CO_2 mitigates the effects of N deposition. Previous studies show that at elevated CO_2 EM fungi forming abundant extraradical mycelium (typically more nitrophobic species) benefitted more than EM fungi with limited mycelium, and elevated CO_2 could therefore contribute to the capacity of EM forests to immobilize N in mycelium and keep N dynamics low (Godbold *et al.*, 1997).

Conclusions

Changes in ectomycorrhizas influence the nutritional balance of trees and risk leading to a tipping point in EM forests that may affect several ecosystem processes directly linked to human wellbeing. Injecting reality into environment models requires soil mechanistic information, large-scale spatial and temporal turnover information, and physiological ecology experiments on dominant and ecologically relevant taxa to challenge ecological thresholds and upscale meaningfully (Kreyling *et al.*, 2014). This information will lead to appropriate monitoring methods for detecting EM fungal communities near environmental stressor thresholds and the assessment of whether and when the ecosystem is recovering, how resilient it can be, if changes are irreversible, or if it will collapse – all major challenges (Groffman *et al.*, 2006). For instance, individual taxon thresholds for decline that occur before or after community thresholds could be used as early warning indicators or indicators of additional ecosystem degradation.

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Author contributions

TWK, LMS and MIB developed concepts. LMS, SvdL and MIB produced the empirical data supporting tipping point concepts. LMS and SvdL generated the figures. LMS and MIB drafted the manuscript and TWK and SvdL provided chief contributions. All authors wrote and reviewed the manuscript.

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