Symbiosis (2021) 84:337–351
https://doi.org/10.1007/s13199-021-00792-2

Ectomycorrhizal fungi and trees: brothers in arms in the face of anthropogenic activities and their consequences

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Received: 3 February 2021 / Accepted: 28 June 2021 / Published online: 5 July 2021

Abstract

The association between ectomycorrhizal (ECM) fungi and trees is at the heart of forest ecosystems. Nowadays, this association is increasingly facing pressures resulting from anthropogenic activities, impacting the structure, biodiversity and functions of ECM fungal communities and their hosts. Here, we review some of the most common anthropogenic activities (i.e. enrichment of atmospheric carbon dioxide, increase of global temperature, atmospheric pollution, nitrogen deposition, use of pesticides, land use management, introduction of invasive species and biodiversity loss) affecting ECM fungi (i.e. species richness, abundance, taxonomy, production of spores and carpophores, and enzymatic activities) and their tree hosts. The review was conducted at different scales, from species to populations and ecosystems and whenever possible, example including boreal, temperate and tropical forests were reported. To conclude, we discussed about the present challenges hindering a better holistic understanding of our future forest ecosystems hosting ECM fungi. Overall, climate change is expected to affect ECM fungi through an alteration of plant metabolism and spatial distribution of trees. Although industrial pollutants and pesticides effects remains less clear at large scale, N-deposition and/or fertilization could induce ECM shifts and alter nutrient cycling. Regarding other anthropogenic parameters (e.g. land use, invasive species), they may affect ECM fungal communities by impacting their diversity, abundance and richness.

Keywords Climate change · Ectomycorrhizal fungi · Industrial pollutants · Forest ecosystems · Human activities · Community shift

1 Introduction

The first evidence of plant-fungi interactions dates back 400 Ma ago with structures resembling those of the actual arbuscular mycorrhizal (AM) fungi found inside Rhynie cherts (Trewin and Rice 2004; Strullu-Derrien et al. 2018). Based on fossil evidences, ectomycorrhizal (ECM) fungi emerged later, during the Lower Eocene ~50 Ma ago (Beimforde et al. 2011; Strullu-Derrien et al. 2018). Today, the vast majority of Angiosperms establish mutualistic symbioses with mycorrhizal fungi (Smith and Read 2008; Brundrett 2009; Gupta et al. 2019), being vital for the survival and growth of numerous plant families (e.g. *Monotropaceae*, *Pinaceae*, *Orchidaceae*) and beneficial to many others (Smith and Smith 2011). The extraradical mycelium of mycorrhizal fungi (either AM or ECM) can be considered as an extension of the plant roots, increasing the uptake of minerals (e.g. phosphorus, nitrogen), meeting plant nutritional needs (Finlay and Read 1986), in exchange of organic compounds issued from plant photosynthesis (Kiers et al. 2011). Noticeably, between 4 and 20% for AM fungi (Douds et al. 2000) and up to 30% for ECM fungi (Nehls and Hampp 2000) of the total photoassimilate production can be transferred from plant to fungus. Arbuscular mycorrhizal fungi (Glomeromycota phylum) are dominant in grasslands, while ECM fungi (Ascomycota and Basidiomycota phyla) are key players in forests dominated by *Pinaceae*, *Fagaceae*, *Betulaceae*, *Dipterocarpaceae*, *Nothofagaceae* families and many others (Smith and Read 2008; Tedersoo et al. 2010). Both types of fungi are involved in several ecosystem services such as nutrient cycling (e.g. carbon and nitrogen), soil formation, provision of food, etc. (Courty et al. 2010).

In recent decades, human activities have increasingly influenced the Earth system and humans have become the primary driver of changes to the ecosystems (Rockström et al. 2009).

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These gradual changes have decreased the resilience of ecosystems, leading to smooth or abrupt shifts (Scheffer et al. 2001). One symbolic indicator emphasizing human activities is that man-made mass has recently exceeded all of the living biomass (Elhacham et al. 2020). In order to assess the anthropogenic impacts on Earth-system processes, a consortium of scientists has defined nine crucial "planetary boundaries" essential for human survival: climate change, biodiversity loss, excess of nitrogen (N) and phosphorus (P) production, stratospheric ozone depletion, ocean acidification, global consumption of freshwater, change in land use for agriculture, air pollution, and chemical pollution (Rockström et al. 2009). Several of these planetary boundaries (namely climate crisis, biodiversity loss, excess of N and P, change in land use, atmospheric and chemical pollution) are factors that may impact ECM fungal communities directly or even indirectly by affecting the trees. This was already suggested by Arnolds (1991) in the early 1990s, with a decline of ECM fungi in European forests attributed to indirect/direct effects of human activities (air pollution, N deposition, changes in forest management, etc.). About three decades later, the link between anthropocene and mycorrhizas is still a hot topic worth investigating (Jansa and Kohout 2019), and scientific findings about the impact of anthropogenic pressures on ECM fungi are increasing over time (Table 1). In the present review, we investigated the impact of anthropogenic pressures on ECM fungi and their tree associates and the consequences on forest ecosystems.

2 Climate change

2.1 Carbon dioxide enrichment (Fig. 1a)

Since the industrial revolution, the atmospheric CO_2 concentration has increased by 48%, from 277 μmol.mol^{-1} in 1760 to 411 μmol.mol^{-1} in 2019 (Friedlingstein et al. 2019). By the end of the twenty-first century, atmospheric CO_2 concentration is predicted to escalate and reach 550 μmol.mol^{-1} by 2050 and 750 μmol.mol^{-1} by 2100 (Solomon et al. 2007). Such an increase in CO_2 disrupts the balance between carbon sinks and sources, affecting global climate (Le Quéré et al. 2009).

Boreal, temperate and tropical forests act as major carbon sinks (Soepadmo 1993; Martin et al. 2001; Bradshaw and Warkentin 2015) and laboratory and field observations have predicted that an increase in CO_2 would boost the growth of trees, thus increasing forest carbon sinks (Ainsworth and Long 2005). In parallel, the increase in atmospheric CO_2 has been shown to alter biomass production, exudation and respiration of fungi, soil carbon fluxes, and other soil microbes in forest ecosystems (Fransson 2012). For instance, Högberg et al. (2002) estimated that 25% of the C allocated to roots is used for plant growth, while 75% is respired by mycorrhizas. This was further supported by a meta-analysis conducted by Alberton et al. (2005), reporting an increase in mycorrhizal heterotrophic respiration in forest ecosystems. In this analysis, the authors investigated 15 and 19 variables related to ECM fungal and plants' responses to elevated CO_2, respectively and concluded that both ECM fungi and plants responded positively to an increase of CO_2.

In ECM symbiosis, host plants allocate a part of their carbohydrates produced by photosynthesis to the fungal partner, inducing the expression of sugar transporter genes, such as *AmMst1* (Nehls et al. 2001). ECM fungi and root systems of ECM plants can receive up to half of these carbohydrates (Nehls et al. 2010). However, fungal parasitism could be a problem for host plants, so they developed mechanisms to restrict and control the carbohydrate flux (Nehls et al. 2010). In a context of increasing CO_2, current models predict an increase of photosynthesis and a different allocation of C between plants and ECM fungi, correlated with a downregulation of plant C-transporters and an upregulation of fungal C-transporters (Nehls et al. 2001). The consequences of such

Table 1 Numbers of scientific papers published between the early sixties and 2020 on the effects of anthropogenic pressures on ECM fungi. The research was conducted with Scopus® by combining different words in titles, abstracts and keywords. The Table is subdivided according to four period of time (1960–1990, 1990–2000, 2000–2010, and 2010–2020) and anthropogenic pressures: climate change (upper part), industrial pollutants (middle part), and other anthropogenic pressures (lower part)

Anthropogenic pressure	1960–1990	1990–2000	2000–2010	2010–2020
Climate change	0	6	26	137
CO_2 increase	1	17	36	69
Increase of temperature	0	0	2	25
Pollution	5	38	72	100
Pesticides	3	13	20	21
N-fertilization and deposition	3	15	33	36
Forest management	1	7	19	58
Land use	0	0	12	35
Introduction of invasive species	0	0	9	35
Loss of biodiversity	0	2	3	16

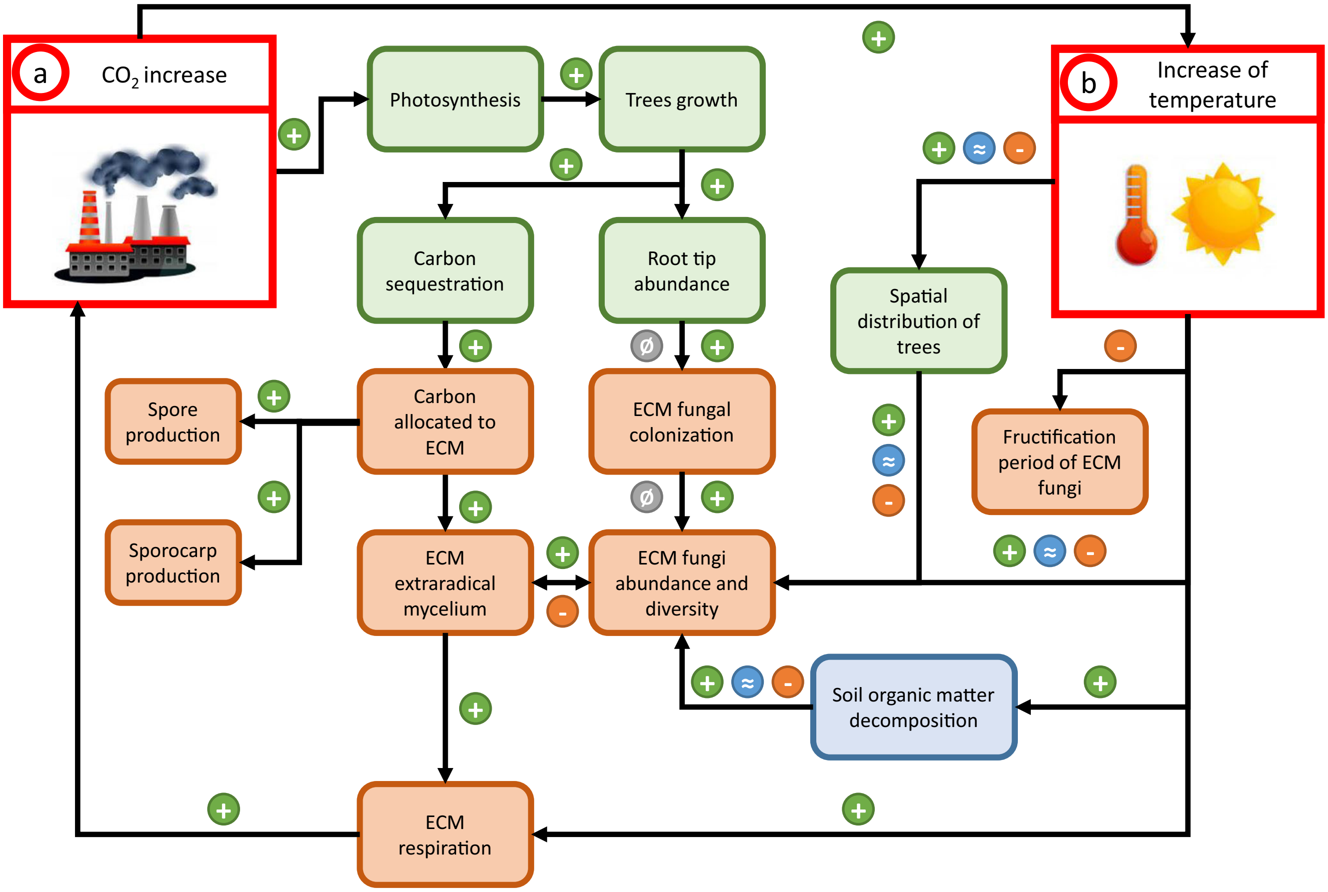

Fig. 1 Overview of the principal effects of climate change on ECM fungal-tree associations based on the scientific literature (see Table 1). Climate change related anthropogenic pressures, namely CO_2 enrichment (Fig. 1a) and increase in temperature (Fig. 1b), are in the red boxes. Plant and fungal related parameters are in the green and brown-reddish boxes, respectively, and the other parameters in the blue box. The relationships between the parameters can be positive (+), neutral (≈), or detrimental (−). Scarce and lacking data are also indicated (Ø). If a relationship includes multiple effects, several symbols are used

changes affect both the plants and their ECM fungal symbionts. Regarding the benefits to plants, an increase in CO_2 will enhance their growth and increase their need for N and P, while for ECM fungi, more C derived from photosynthesis will be available, thus increasing fungal biomass and fitness (Alberton et al. 2005). The proportion of extraradical mycelium (ERM) of ECM fungi in the soil is already high and represents about one-third of the microbial biomass (Högberg and Högberg 2002). If the fungal biomass is going to increase further in the context of elevated CO_2, we can expect a stronger competition between organisms for nutrients, such as P and N (Alberton et al. 2005).

A study by Andrew and Lilleskov (2009), in three areas of American temperate forests, including different ratios of *Populus tremuloides* Michx., *Acer saccharum* Marshall var. *saccharum*, and *Betula papyrifera* Marshall, further reported an increase in sporocarp biomass under high CO_2 concentrations, affecting spore production, dispersal, community composition and fungivory. In another study, the sporocarp production of *Paxillus involutus* was enhanced by 4.8 times under elevated CO_2 concentration (Godbold et al. 2015). In the same study, three dominant ECM species, i.e. *Amphinema byssoides* (Pers.) J. Erikss., *Piloderma* sp. 1 and *Trichophaea hybrida* (Sowerby) T. Schumach., were not affected by the concentration of CO_2 (Godbold et al. 2015). However, some differences of species occurrence were also highlighted, where *Hydnotrya cerebriformis* (Tul. & C. Tul.) Harkn. was common under ambient CO_2 conditions, but not under elevated CO_2. On the contrary, *Trichophaea* sp.1 was common under elevated CO_2, but not under ambient conditions. These authors also emphasized that an increase of CO_2 resulted in a shift of ECM fungal community from short-distance and smooth medium-distance exploration types to contact exploration types.

Regarding ECM fungal diversity, Parrent et al. (2006) reported that the relative abundance of ECM fungi was altered, but the overall diversity remained similar in response to CO_2 enrichment. In another study, under elevated CO_2 (700 ppm), the ECM colonization of *B. papyrifera* and *Pinus strobus* L. increased, but not in *Tsuga canadensis* L. Carr (Godbold et al. 1997). In the same study, although the morphotypes observed under ambient or elevated CO_2 concentrations were similar, these authors noticed that the distribution and frequency of these morphotypes differed between CO_2 conditions. Another study demonstrated that an elevation of CO_2 induced a shift of ECM fungal community, affecting the composition of ECM fungi according to their exploration type (see for details Agerer 2001), where the percentage of root tips with contact exploration types increased from 12% in the ambient treatment to 35% in the elevated CO_2 treatment (Godbold et al. 2015). In this study, the authors argued that this shift was due to increased availability of C and an increase in the frequency of more C-demanding ECM fungal species. A meta-analysis revealed a significant positive effect of elevated CO_2 on both trees and ECM fungal parameters, such as an increase of root tips abundance and fungal colonization, respectively (Cudlin et al. 2007). However, Cudlin et al. (2007) emphasized that these results are not always observed in individual studies, and could be species-specific. Indeed, under high CO_2 concentrations, the root transcriptome of *Eucalyptus grandis* W.Hill ex Maiden is altered, resulting in a decrease of root colonization by *Pisolithus* sp. isolates (Plett et al. 2015).

In brief, an elevation of CO_2 concentration in the atmosphere may increase C sequestration in trees, ultimately resulting in shifts of ECM fungi at different levels: (i) physiological shifts with an increase of mycelial biomass, respiration and sporocarps production; (ii) communities shifts with modifications of the relative abundances of some species. However, the surplus of C non-sequestered by trees may be respired by ECM fungi, resulting in a positive feedback on the rate of atmospheric CO_2 increase (Heath et al. 2005).

2.2 Mean global temperature increase (Fig. 1b)

In addition to an enrichment of atmospheric CO_2, climate change is synonymous with an increase in the mean global temperature. Compared to the beginning of the twentieth century, boreal forests have faced an increase of 1.5 °C, and will presumably be exposed to a drastic warming of 4–6 °C in the next century (Moritz et al. 2002; IPCC 2014).

An increase in the global temperature may affect ECM symbiosis indirectly via the spatial distribution of their host plants. Tree species within forest ecosystems can evolve towards i) migration to more adequate niches, ii) persistence via adaptation to the current conditions and/or iii) extirpation or local extinction (Aitken et al. 2008). As a result, the spatial distribution of trees (altitude and latitude) will be altered under global warming and is expected to be species-specific, modifying species composition in forest communities (Kirschbaum 2000). For instance, the distribution of two dominant ECM tree hosts in southern Santa Rosa mountains (California, USA), namely *Abies concolor* (Gordon) Lindley ex Hildebrand (white fir) and *Pinus jeffreyi* Balf. (Jeffrey pine) moved 96 and 28 m upwards, respectively, in response to climate change between 1977 and 2007 (Kelly and Goulden 2008). Regarding the upward migration of trees and their ECM symbionts, the study of Álvarez-Garrido et al. (2019) conducted in a fir forest-high elevation shrubland ecotone reported a decrease of ECM fungal abundance and richness toward higher elevation. Although the trees migrated upwards, the authors highlighted a time lag shift of ECM fungal species. This time asynchrony in species interactions has already been documented by Peñuelas et al. (2002) and for ECM fungal species more specifically, it may be linked to their dispersal limitation (Álvarez-Garrido et al. 2019).

An increase in global Earth temperature is also correlated to a higher frequency of extreme weather events, affecting moisture patterns (IPCC 2014). It is expected that climate change and its consequences will first impact populations of tree species growing close to their climatic limits, such as *Pseudotsuga menziesii var. glauca* (Douglas-fir) (Griesbauer and Scott Green 2010). Knowing that an increase in global temperature, combined with more severe and frequent extreme events, will trigger aboveground effects altering the distribution of ECM tree species, it is expected that ECM community will shift accordingly. Indeed, the phylogenetic community composition of fungi is mainly driven by the host plant family (Tedersoo et al. 2012).

The increase in air temperature might slightly impact soil temperatures and thus C cycling, mainly driven by the rate of decomposition of soil organic matter (SOM), root turnover and soil microbial processes. Some studies (e.g. Litton and Giardina 2008) have reported that the overall rate decomposition of SOM should increase under elevated temperatures, varying between different soil layers and fractions. In return, this may affect ECM fungal communities. Indeed, Rosling et al. (2003) demonstrated a relationship between the community composition of ECM fungal species and the soil horizons, in natural conditions. *Tomentella submollis* (Svrček) Hjortstam, three *Pilodermas* sp. and *Dermocybe* spp. were found in the upper organic horizons, while *Suillus luteus* (L.) Roussel, *Lactarius utilis* (Weinmann) Fries and three undescribed *Piloderma* species were deeper, in the mineral horizon. If an increase in temperature boosts the rate of decomposition of SOM, and if ECM fungi are heterogeneously distributed in the soil (between organic and mineral horizons), the first ECM fungi affected by global warming would be the ones present in the upper organic soil horizons.

The impacts of long-term warming on ECM fungal communities are not conclusive. Indeed, Clemmensen et al. (2006) reported that after long-term warming, ECM fungal abundance associated with *Betula nana* (arctic birch) increased, whereas Allison and Treseder (2008) noticed an overall decrease in soil respiration in boreal forest soils (hosting *Picea mariana*), correlated with a shift in the community composition of ECM fungi characterized by a decrease of the dominant ECM fungus (*Thelephorales* spp.) after warming, while other saprophytic fungal taxa (Ascomycota and Zygomycota) increased. Long-term warming was also reported to alter richness and composition of taxonomic and functional groups of arctic fungi (Geml et al. 2015). More specifically, ECM fungi richness declined in response to climate warming, while saprophytic fungi, plant and animal fungal pathogens tended to proliferate. These authors also emphasized the importance of species-specific response to climate warming. In North American Pinaceae forests, another study predicted that the warming of boreal-temperate forests will result in a decline or loss of ECM fungal species up to 21%, whereas an opposite effect may occur in eastern temperate forests (Steidinger et al. 2020). Apart from ECM fungi richness and abundance, climate warming also drives functional shifts of ECM fungi. For example, Deslippe et al. (2011) demonstrated that climate warming significantly increased ECM fungi with proteolytic capacities (e.g. *Cortinarius* spp.), while those with high affinities for labile N (e.g. *Russula* spp.) were decreasing. Warming was also reported to significantly reduce the fructification period of ECM fungi (Gange et al. 2007; Kauserud et al. 2008). Another study by Andrew et al. (2018) conducted in central and northern Europe demonstrated that the fruiting behavior of ECM fungi is shifting (spring delay and autumnal acceleration) and strongly linked to temperature, and that climate change is very likely to affect the fungal phenology pattern at a large scale.

Regarding mycorrhizal respiration, one would expect an increase under elevated temperatures. However, Malcolm et al. (2008) demonstrated that ECM fungal acclimation and sensitivity to temperature is species-specific. These authors also suggested that ECM fungal species more resilient to high temperature also require less C from their hosts as compared to sensitive species (Malcolm et al. 2008). From a phytocentric view, we can hypothesize that if host plants want to avoid unnecessary energy costs, they will favor associations with ECM species tolerant to climate warming.

To summarize, climate warming may impact community composition of ECM fungi via i) alteration of the spatial distribution of trees, ii) modification of the soil C cycling via SOM decomposition and fungal respiration, iii) changes in ECM species richness and abundance, iv) favoring fungi with specific enzymatic activities (proteolytic versus labile N-uptake activities), and v) affecting ECM phenology and fruiting body production. However, the ECM response to global warming may be weak and species-specific, because ECM fungi include generalists species, such as *Cenococcum geophilum* Fr. (Jany et al. 2002).

3 Atmospheric and chemical pollution

3.1 Atmospheric pollutants (Fig. 2a)

Human activities (e.g. combustion of fossil fuels in power generation, industry, transport, agriculture and deforestation) are known to generate gaseous pollutants (Shafer and Schoeneberger 1991) such as CO_2, carbon monoxide (CO), methane (CH_4), chlorofluorocarbons (CFC), nitrogen oxides (NO_x), sulfur dioxides (SO_2) and tropospheric ozone (O_3). Impacts of elevated CO_2 on ECM fungi has already been described above (see section 2.1). Increasing atmospheric pollutants generate/accelerate several processes able to affect both above and below-ground organisms: soil acidification, an increase of ultraviolet-B (UV-B) radiation and high atmospheric content of O_3.

Soil acidification accelerates weathering, resulting in an alteration of soil chemistry balance, such as losses of base cations, release of aluminum ions, nitrate leaching, increase of trace elements such as heavy metals and radionuclides (Magill et al. 1997; Brunner 2001). The release of CFC in the atmosphere lead to an increase in UV-B. When plant are exposed to UV-B, their proteins and nucleic acids absorb the radiations, thus generating singlet oxygen and suppressing C assimilation and growth (Shafer and Schoeneberger 1991). If UV-B negatively affects the host plant development, we can hypothesize that ECM fungi will also suffer negative repercussions. However, very few studies have investigated the direct impact of UV-B on ECM fungi and root colonization, and as far as we know, no significant effects have been reported (Newsham et al. 1999; Rosa et al. 2003).

Up to now, the studies conducted on the effects of high levels of O_3 on ECM fungi were not conclusive. Indeed, Wang et al. (2015) noticed that exposure to O_3 decreased the ECM fungi colonization and species richness. Conversely, Kasurinen et al. (2005) demonstrated that the impact of elevated O_3 on ECM fungi is morphotype-dependent, with detrimental or beneficial effects. Another study reported that O_3 exposure might have some negative effect on conifer needles, without significant impacts on C allocation to the roots and on shoot growth and ECM formation (Kainulainen et al. 2000). To complicate the story, plants are also more or less sensitive to O_3 (Rai and Agrawal 2012) that may thus indirectly affect ECM fungi.

Regarding the effects of SO_2 on ECM fungi, the data available so far are scarce and similarly not conclusive. In presence of SO_2, Garrett et al. (2011) noticed a decrease of ECM fungal respiration of three *Pisolithus tinctorius* (Persoon) Coker & Couch isolates. and one *Telephora terrestris* Ehrhart strain. Díaz et al. (1996) further demonstrated that an increase of SO_2 slightly decreased the ECM colonization and a change of mycorrhizal fungi species occurrence, with ectendomycorrhizal fungi replacing ECM fungi. Interestingly, the combination of SO_2 and O_3 on *Pinus halepensis* Miller was significantly more harmful to the host plants than SO_2 alone, with a decrease of photosynthesis, thus reducing the C supply to ECM symbionts (Díaz et al. 1996). However, other studies reported that elevated SO_2 might have no impact on ECM fungi (Adams and O'Neill 1991; Shaw et al. 1992).

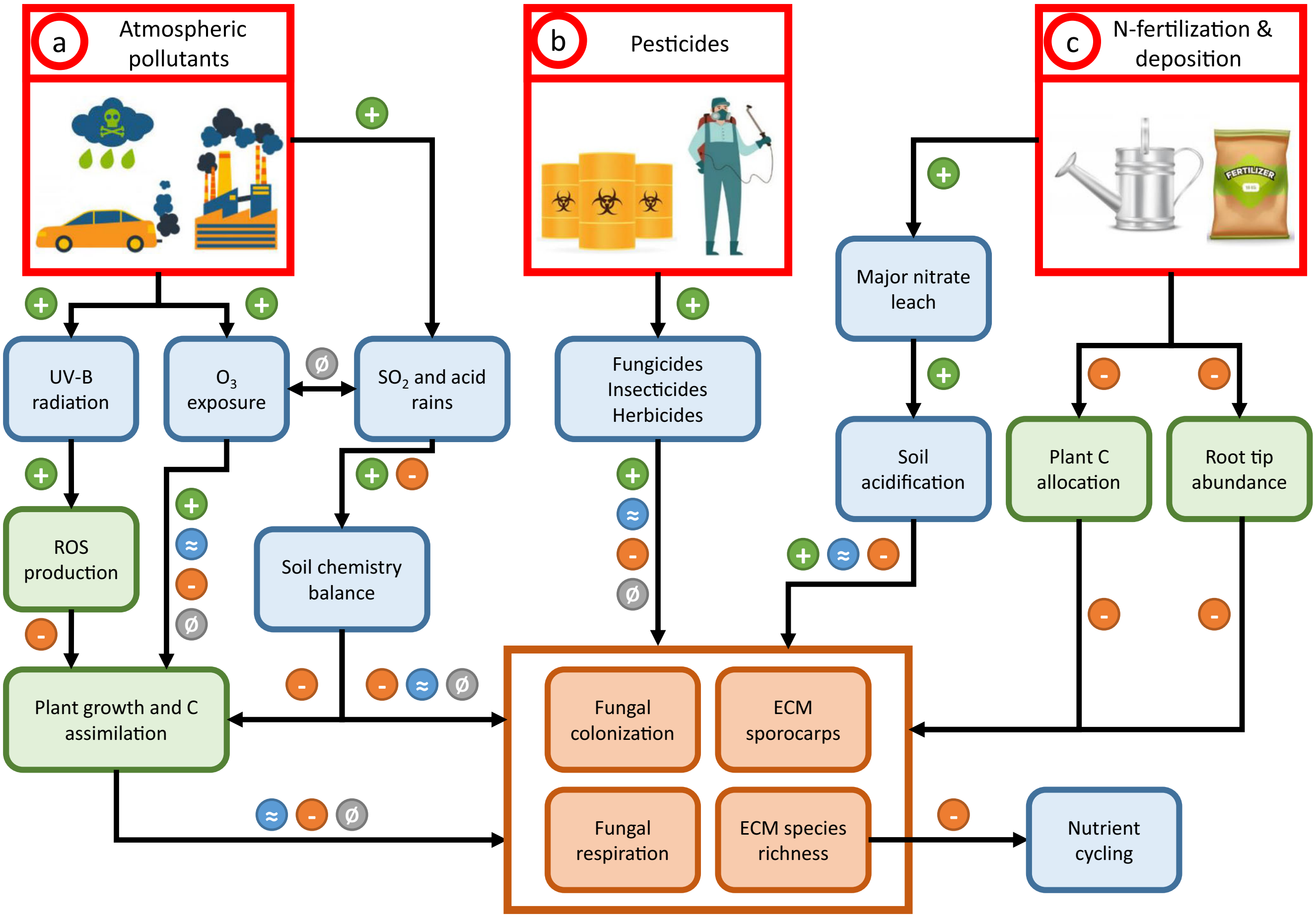

Fig. 2 Overview of the principal effects of industrial pollutants on ECM fungal-tree associations based on the scientific literature (see Table 1). Industrial pollutants related anthropogenic pressures, namely atmospheric pollution (Fig. 2a), chemical pollution and pesticides (Fig. 2b), and nitrogen deposition/fertilization (Fig. 2c) are in the red boxes. Plant and fungal related parameters are in the green and brown-reddish boxes, respectively, and the other parameters are in the blue boxes. The relationships between the parameters can be positive (+), neutral (≈), or detrimental (−). Scarce and lacking data are also indicated (Ø). If a relationship includes multiple effects, several symbols are used

To summarize, phytotoxic air pollutants may affect ECM symbioses, but several points need to be taken into account: i) apart from CO_2, data on other atmospheric pollutants (e.g. SO_2 and O_3) are scarce and not conclusive, ii) the response of ECM fungi and plants to air pollutants seems to be species-specific and/or context-dependent, and iii) we must take into account the potential relationships between O_3, CO_2 (Wang et al. 2016), and SO_2.

3.2 Chemical pollution – pesticides (Fig. 2b)

Pesticides are commonly used for the control of pests and diseases in agricultural systems but also in forests. However, the repeated and long-term use of these compounds, combined with their often high persistence in soils (for months or even years for some) may raise serious concerns about their side effects on non-target macro and micro-fauna and flora (Smith et al. 2000). One of the first review addressing the impact of pesticides on forest ecosystems has been conducted by Trappe et al. (1984) and was long time later updated by Marin (2011). Together, they surveyed over 34 years of scientific studies on pesticide effects on ECM fungal growth, mycorrhizae and spore formation. They emphasized that deciphering the impact of pesticides on the composition of ECM fungal communities is a tricky topic because fungal species and plant hosts respond differently to each class of fungicide/herbicide/insecticide.

Regarding fungicides, compounds such as captan, chlorothalonil, etridiazol and fenaminosulf, had beneficial, neutral or detrimental effects on ECM establishment (as referenced from 14 different studies, Trappe et al. 1984), while seven other studies (listed in Trappe et al. 1984) reported that folpet, maneb, thiram, triadimefon and ziram, were only detrimental to ECM formation. In addition, compounds such as cyclohexamide, ethylmercuric chloride, ferbam, phytoactin, propamocarb hydrochloride, thiophanate methyl and triphenyltin acetate showed no impact on ECM formation (results reported from seven studies in Trappe et al. 1984). Other pesticides, namely herbicides and insecticides, displayed a similar variability of effects, beneficial, neutral or detrimental to ECM formation (Trappe et al. 1984; Marin 2011). Although herbicides reduced the seedling growth in a greenhouse study, the ECM formation remained very high, regardless of application rates (Busse et al. 2004). These application rates correspond to the recommended application field rates and twice these rates, with sulformeturon applied at 0.14 and 0.28 kg active ingredient ha^{-1}; triclopyr applied at 4.5 and 9.0 kg active ingredient ha^{-1}; and imazapyr applied at 1.1 and 2.1 kg active ingredient ha^{-1} (Busse et al. 2004). Fungicides were also used in truffle productions in order to limit competing effect with others ECM fungi (Zambonelli and Iotti 2001). For instance, the application of oxycarbin inhibited the growth of a fungal competitor (*Hebeloma sinapizans* (Paulet) Gillet) and only slightly decreased truffle growth (*Tuber borschii* Vittad.), while four other fungicides (carbendazim, mancozeb, propiconazole and tolclofos-methyl) inhibited either *T. borschii* only or both fungi (Zambonelli and Iotti 2001).

With the elements mentioned above, we can hypothesize that the application of pesticides will affect directly and/or indirectly both the tree hosts (with the use of herbicides and insecticides) and ECM fungi (with the application of fungicides), thus inducing shifts of ECM fungal communities. However, predicting the potential forest outcomes after an application of pesticides remains unclear, mainly because i) plants and fungi might respond differently to one given pesticide (with beneficial, neutral or detrimental effects), ii) there is a wide range of pesticides and novel molecules are regularly developed, and iii) the effect of the pesticide depends on the dosage of application.

3.3 Nitrogen deposition/fertilization (Fig. 2c)

Sylvicultural practices relies on N fertilization. However, when applied in excess, N may have serious consequences on the environment (e.g. eutrophication) (Vitousek et al. 1997) and ECM fungi by altering their morphology or community composition (Leake et al. 2004). In addition, forest soils may also be enriched in N through the deposition of atmospheric NOx produced by anthropogenic activities via acid rains, then transformed into nitrates (Lamarque et al. 2005). By the end of the century, the atmospheric N deposition is expected to increase by a 2.5 factor (Lamarque et al. 2005). Considering an increase of both N deposition and fertilization, Lilleskov et al. (2002) have shown that the proportion of ECM fungi with proteolytic abilities decreased and major leaches of nitrate occurred (Schulze et al. 2000), often resulting in soil acidification (Brunner 2001). For example, in a native oak savanna, Avis et al. (2003) revealed that N-fertilization reduced by more than 50% the total production of ECM sporocarps. Curiously, in their study, they also noticed that some ECM fungal species (i.e. *Russula* spp.) produced five times more sporocarps in highly fertilized soils (17 g of N per m^{-2} yr^{-1}) as compared to treatments with no N or 5.4 g of N per m^{-2} yr^{-1}. They concluded that N-fertilization induced shifts in ECM fungal diversity and community composition, by i) decreasing global ECM diversity and ii) favoring some species inside N-rich environment (e.g. *Russula* species). This was further supported by the study of Jones et al. (2012) in central British Colombia, who noticed that long-term N fertilization decreased ECM fungal species richness and abundance, but did not reduce their ability to degrade SOM in temperate forests. Another study reported that a N-deposition gradient (from 27 to 43 kg of N ha^{-1}.yr^{-1}) in a temperate forest resulted in a dramatic change of ECM community (species richness decreased), root tip abundance (5 times less) and mycelial production (10 times less) (Kjøller et al. 2012).

Similarly to temperate ecosystems, the long-term application of N-fertilization in tropical forests, has been shown to alter ECM fungal communities, reduce ECM root colonization, and to be species-dependent: the relative abundance of *Lactarius* and *Laccaria* species decreased, counterbalanced by an increase in *Cortinarius* species (Corrales et al. 2017). Interestingly, the activity of several enzymes involved in nutrient cycling, such as phosphatase, N-acetyl-glucosaminidase, and β-xylanase were negatively correlated to N-fertilization (Corrales et al. 2017). The authors hypothesize that this decrease of soil enzymatic activity may be due to the reduction of ECM taxa specialized in P and N uptake, resulting in a negative feedback effect on soil nutrient cycling (Corrales et al. 2017).

In a boreal pine forest, Vallack et al. (2012) demonstrated that N-fertilization reduced the allocation of C by plants, resulting in a negative impact on ECM hyphal respiration. According to Lilleskov et al. (2001), it is highly likely that N deposition/fertilization favors “nitrophilic” ECM fungi (e.g. *Lactarius theiogalus*, *Laccaria*, *Paxillus involutus*, and *Hygrophorus olivaceoalbus*), over “nitrophobic” ECM fungi (e.g. *Cortinarius*, *Russula*, *Tricholoma*, *Lactarius rufus*, *Hebeloma*). Boreal field studies demonstrated that increasing N deposition/fertilization decreased dramatically ECM fungal species richness and altered the community structure (Lilleskov et al. 2002). In the latter study, the authors also discussed two consecutive shifts of ECM fungi community: firstly, taxa specialized in N uptake in low-N conditions (e.g. *Cortinarius* and *Piloderma*) were replaced by taxa of high overall nutrient ability (e.G. *tomentella sublilacina* (Ellis & Holw.) Wakef., *Thelephora terrestris*). Secondly, these ECM fungal taxa were replaced later with ECM fungi specialized for P uptake under high-N, low-P, and acidified conditions (e.g. *Paxillus involutus* and *Lactarius theiogalus*). Another study found that addition of N and P to a Norway spruce forest resulted in a decrease of ECM fungi biomass and altered ECM fungi composition (Almeida et al. 2019). Moreover, the study of Almeida et al. (2019) found that the species *Tylospora asterophora* (Bonord.) Donk (known as a short exploration type) responded positively to N increase, and concluded that ECM fungi response to N addition might be species-specific.

In conclusion, nitrogen deposition/fertilization affects significantly both host plants and ECM fungi. Indeed, N deposition/fertilization may i) decrease the global ECM diversity, ii) weaken host plants, and iii) alter the ECM fungal community composition, with species-specific responses, such as detrimental effects on sensitive ECM fungal species (e.g. nitrophobic taxa) and beneficial effects to tolerant ECM fungal species (e. g. nitrophilic taxa). Because N often limits living-organism productivity, N deposition/fertilization has the potential to affect not only ECM fungi, but the entire ecosystems, notably by altering nutrient cycling (Clark et al. 2013).

4 Forest management, land-use change and biodiversity loss

4.1 Forest management and land-use change (Fig. 3a)

Human activities such as the clearance or fragmentation of forests for habitation, transport, agriculture, mining, aesthetics, arboretum, recreational purpose and sylvicultural activities impact forest ecosystems (Matson et al. 1997; Matthews et al. 2000; FAO 2010), as well as their ECM fungal inhabitants (Folke et al. 2004). For instance, practices such as monocultures with homogenous spacing and tree ages, reduce ecosystem diversity and resilience, resulting in a decrease of habitat for other plant species, and thus belowground symbionts (Fall et al. 2011). In addition, land-use changes, like deforestation and vegetation removal have been shown to modify plant biomass and litter input, severely impacting the composition, biodiversity, productivity and functionality of soil microbiota, including ECM fungi (Bååth et al. 1995; Spurgeon et al. 2013). For example, in Canadian boreal forests, the root fungal communities of pine seedlings exposed to anthropogenic disturbances (logging and salvaged logging) differed from their paired controls, while soils from natural disturbances (fire and beetle outbreak) did not (Beck et al. 2020). Another study conducted by Marín et al. (2017) in a Chilean temperate rainforest compared fungal communities in a pristine forest (i.e. a natural old-grown forest) with managed-removal or clear-cut managed forests. They noticed that samples from clear-cut conditions had the highest fungal richness, mainly composed of fungal pathogens, with few saprophytic and ECM fungal species, while the opposite was found in pristine and managed-removal forests, where species richness and abundance of ECM fungi were higher (Marín et al. 2017). Inside temperate forests, the total number of identified ECM fungi and sporocarp production of mushrooms and truffles exposed to green-tree retention (a variant of clear cutting) significantly decreased (Luoma et al. 2004). Regarding tropical forests, the abundance of Agaricales (including many ectomycorrhizal species) declined inside rubber and oil palm plantations, compared to rainforests and rubber jungle (Brinkmann et al. 2019). Logging treatments (open-, partial- or closed-canopy) altered the composition of ECM fungal communities associated to *Shorea parvifolia* Dyer seedlings inside an Indonesian rainforest (Ingleby et al. 1998). Indeed, the authors differentiated two ECM fungal communities: an early- or late-stage ECM community. For example, ECM pioneers such as *Geastrum*, *Suillus* and *Scleroderma* were found in both open and partially closed canopies (Ingleby et al. 1998). On the contrary, close canopy environments were dominated by *C. geophilum, Leccinum* sp., *Russula* spp. and *Suillus* sp. (Ingleby et al. 1998). Many of the mycorrhizal types present on seedlings in open or partially open canopy were not found on seedlings growing under closed canopy. The reasons for their absence are highly speculative. Indeed, successions of mycorrhizal fungi is correlated to the age of the forest communities, these sequences being driven to some extent, by the nature of available photosynthates, root exudates and soil conditions (Mason et al. 1983). Dispersal strategies, are also thought to differ between these fungal groups with `early stage' or pioneering fungi able to colonize new roots via germinating spores or fragmented mycelium, while `late stage' fungi are only able to do so via mycelia connected to mycorrhizas of the mature trees. The authors speculated that such ECM fungal shifts may be linked to ECM fungi community's age, dispersal strategies and/or edaphic conditions.

To conclude about sylvicultural practices, the review of Tomao et al. (2020) demonstrated a negative correlation between the management intensity and ECM fungal diversity. Forest management affecting host trees is crucial to ECM fungal communities and should be used with moderation, by avoiding excessive deforestation and intensive clear-cutting. In order to mitigate their impact on above- and below-ground organisms, and to maintain the complexity of forest ecosystems, sylvicultural practices are evolving and new guidelines and policies are developed and recommended, such as: i) the reduction of ecosystem vulnerability to disturbances, ii) plantation of more diverse species in a wide range of habitats, iii) the reduction of habitat fragmentation and improvement of forest connectivity, iv) low impact logging operations, and v) to enhance structural complexity and late-successional forest characteristics (Campbell et al. 2009; Tomao et al. 2020). Regarding land use, the review of Balami et al. (2020) investigated the relationship between the intensity of land use and ECM fungal parameters. Globally, with an increasing land-use intensity, these authors noticed i) a decrease of ECM fungal richness and diversity indexes (even though some contrasting results were mentioned), ii) a community shift (i.e.

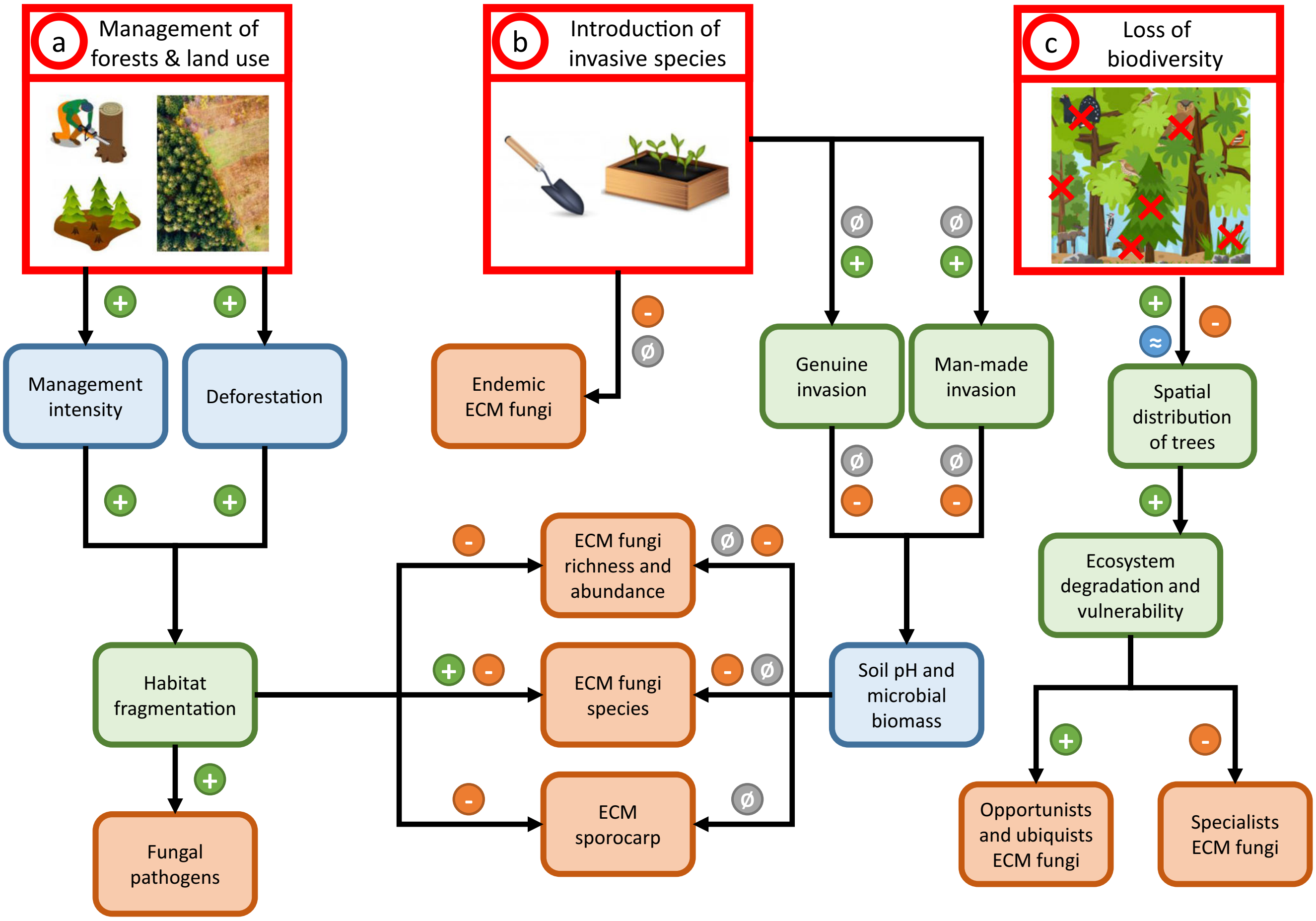

Fig. 3 Overview of the principal effects of other anthropogenic pressures on ECM fungal-tree associations based on the scientific literature (see Table 1). Forest management and land use (Fig. 3a), introduction of invasive species (Fig .3b), and loss of biodiversity (Fig. 3c) are in the red boxes. Plant and fungal related parameters are in the green and brownreddish boxes, respectively, and the other parameters are in the blue boxes. The relationships between the parameters can be positive (+), neutral (≈), or detrimental (−). Scarce and lacking data are also indicated (Ø). If a relationship includes multiple effects, several symbols are used

from Basidiomycota to Ascomycota), iii) a decrease of root colonization (related to soil properties), and iv) a decrease in ECM fungal biomass in the order intensive cropland < pasture < forest soils.

4.2 Introduction of invasive species (Fig. 3b)

Sylvicultural practices may sometimes lead to the introduction of invasive tree species. An invasive plant is defined as a species spreading extensively in its novel habitat, having repercussions on the local and native community, impacting rare and threatened species, or influencing ecosystem properties (Gurevitch and Padilla 2004; Raizada et al. 2008). However, invasive trees may introduce their associated mycorrhizal symbionts too, potentially competing with the endemic ECM fungal species, shifting the overall soil microbial community structure and biomass. For example, the study of Iovieno et al. (2010) in Mediterranean areas including volcanic and calcareous soils reported that the introduction of stone pines (*Pinus pinea* L.) decreased the soil pH and microbial biomass, with an alteration of the microbial community structure, compared to holm oak forests soils. Two other studies demonstrated that pines and eucalyptus species escaped from plantation forests, and became invasive in Africa, Australia and New Zealand thanks to their mycorrhizal symbionts (Richardson et al. 2000; Schwartz et al. 2006). However, the fungal dimension of biological invasion (apart from pathogens) is relatively recent, and lacks sufficient scientific knowledge, making it also difficult to distinguish genuine invasions due to environmental changes from man-made introductions (Desprez-Loustau et al. 2007).

In a context where silvicultural practices relied increasingly on ECM fungal inoculation, we can expect more man-made introductions of ECM fungal species to natural habitats, potentially modifying the composition of local and native ECM fungal communities. In order to understand how invasive species may alter ECM fungal communities, the review of Pringle et al. (2009) identified seven key aspects related to the introduction of an invasive plant and its mycorrhizal symbionts: i) the mycorrhizal status of the plant, ii) the growth response of the invading plant, iii) the plant ability to form mycorrhizas, iv) the plant-fungal feedback dynamics, v) the fungal biogeography, vi) the introductions of mycorrhizal fungi by humans, and vii) the ecosystem and community consequences.

4.3 Loss of biodiversity (Fig. 3c)

The first pillar of an ecosystem is biodiversity. Without species to drive ecosystem processes, no ecosystems are functional (Loreau et al. 2002). Although, the relationship between biodiversity and ecosystem functions is still under investigation, it is widely accepted that the maintenance of biodiversity is a benefit to ecosystems, thus requiring protection (Hooper et al. 2005). We know that ECM fungal symbionts are strongly linked to their tree hosts (Peay et al. 2010). As a result, if the plant community changes due to human activities, ECM fungi may shift too.

Because the loss of biodiversity results from multiple anthropogenic activities, it may be difficult to study its direct link with ECM fungal communities. To achieve this, we need to consider each anthropogenic pressure as a cause, and the biodiversity loss as a consequence. For example, climate change (increase of CO_2, global temperature and frequency of extreme weather events) is expected to alter the spatial distribution of trees and trigger natural selection mechanisms, where the more versatile species will survive at first. This hypothesis may also apply to ECM fungal communities, where highly mobile, opportunistic and/or ubiquitous ECM fungal species with a wide ecological niche (e.g. *C. geophilum*) are expected to survive more easily to forest shifts than other fungi (Dickie 2007). Indeed, *C. geophilum* is known for its wide host and habitat range, coupled with a high degree of genetic diversity (Jany et al. 2002). Moreover, these fungi is also considered by Dickie (2007) as a jack-of-all trade in forest ecosystems, where the same species has been found across soil profiles (Dickie et al. 2002), at all stages of stand development (Gebhardt et al. 2007), at every distance from forest edges (Dickie and Reich 2005), and at every season of the year (Koide et al. 2007). Considering the characteristics of *C. geophilum*, we can hypothesize that this ECM fungal species will still prevail in future forest ecosystems facing anthropogenic pressures.

To summarize, anthropogenic changes in land use (e.g. deforestation, inadequate sylvicultural practices and plant invasion) may accelerate the loss of biodiversity. As a result, the resilience of forests may weaken and have trouble to deal with the expected environmental changes, thus impacting both the future of ECM fungal species and their tree hosts.

5 Conclusion

Today, there is an accumulation of scientific evidence showing that anthropogenic activities impact forest ecosystems and their inhabitants such as ECM fungi. Assessing the current impact of such activities via metadata analysis is important to predict and model future scenarios helping decision-making bodies to draw policies favoring sustainable development with a minimal or controlled impact on ecosystems and ECM fungi. This is a complex issue, mainly because several parameters must be taken into account. To begin with, different scales related to ECM fungi must be considered: from the molecular level (enzymatic activities, genetic responses), to the individual modification (production of spores and carpophores) and the alteration of the community level (mycorrhizal network, diversity, abundance). Because of a time lag between species interactions, shifts of communities can also be more difficult to highlight. Moreover, ECM fungi should not be considered as one homogenous individual, because extraradical hyphae exploring the soil are different structures compared to the ectomycorrhiza organs associated to plant roots. Another crucial point is that ECM fungi are strongly linked to their plant hosts. If human activities affect negatively the host plants, ECM fungal symbionts may be negatively affected too. Moreover, plants are heterogeneous organisms, harboring distinct tissues with different functions (leaves for photosynthesis, stems for transport of saps and roots for assimilation of nutrients). First, ECM fungi interact mainly with the roots to establish the symbiosis, but later, the whole plant is involved in this interaction (by providing ECM fungi with C issued from photosynthesis). Thus, studying anthropogenic impacts on ECM fungi must take into account both the fungi (extraradical hyphae and mycorrhizas) and their hosts (shoots and roots). Further complications arise from anthropogenic activities and their consequences take many different forms, with climate change (increase of global temperature and CO_2), industrialization (inducing air pollution, enrichment of soils with heavy metals), sylvicultural practices (using pesticides and fertilizers), land use management (introduction of exotic species, clear-cutting), and probably much more. Each of these human activities affect ECM fungi in different ways, and most of the studies carried out on this topic are based on a reductionist approach. However, the future environment of our planet will combine all these anthropogenic consequences at the same time. It is possible that the consequences of human activities observed independently will be different on ecosystems when brought all together. For example, Pleijel et al. (2000) and McKee et al. (2000) argued that the harmful effects of O_3 may be compensated by the increase of CO_2.

One of the many priorities is to alleviate the detrimental effects of climate change on forests. However, the study of ECM symbiosis has often been considered as a relation between two individuals. Today, the concept and interest for mycorrhizal networks in forest ecosystems is increasing, opening new research paths (Simard et al. 2012). For example, a EU research project named MixforChange (http://www.mixforchange.eu/en/about-the-project/) aims to investigate the potential of mixed tree plantations (combined with ECM symbioses) on ecosystems resilience. In addition, the study of the real impacts of anthropogenic pressures on ECM fungi could be improved by conducting large-scale studies spread over numerous study sites with contrasting edapho-climatic conditions (Soudzilovskaia et al. 2019). Although large-scale experimental designs are difficult to implement, some platforms are developed, such as TreeDivNet (https://treedivnet.ugent.be/), where 28 experiments are spread across the globe, with more than 1.2 M planted trees.

To put it into a nutshell, deciphering how ECM fungal symbioses will respond to anthropogenic impacts is complex, mainly because of publication and research bias, the variability of species (plants and fungi), location, and the type of stress involved. Reductionist's approaches are important, but they need to be brought in relation with each other if we aim to have a more holistic understanding of our future ecosystems (Fang and Casadevall 2011). The review of Jansa and Kohout (2019) reached the same conclusion and highlighted that current knowledge on the impacts of anthropogenic activities on ECM fungi remains fragmentary, making it difficult to generalize them especially if numerous anthropogenic activities are involved.

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