

Soil fungal communities across land use types

Sujan Balami⁽¹⁾,
Martina Vašutová⁽¹⁻²⁾,
Douglas Godbold⁽²⁻³⁾,
Petr Kotas⁽⁴⁾,
Pavel Cudlín⁽²⁾

Land use change is one of the major causes of biodiversity loss, mostly due to habitat change and fragmentation. Belowground fungal diversity is very important in terrestrial ecosystems, however, the effect of land use change on soil fungal community is poorly understood. In this review, a total of 190 studies worldwide were analyzed. To monitor the effect of land use change, different fungal parameters such as richness, diversity, community composition, root colonization by arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) fungi, spore density, ergosterol, and phospholipid fatty acid (PLFA) content and AM fungal glomalin related soil protein (GRSP) were studied. In general, results from analyzed studies often showed a negative response of fungal quantitative parameters after land use change from less-intensive site management to intensive site management. Land use change mostly showed significant shifts in fungal community composition. Considering land use change types, only 18 out of 91 land use change types were included in more than 10 studies, conversion of primary and secondary forest to various, more intensive land use was most often represented. All these 18 types of land use change influenced fungal community composition, however, the effects on quantitative parameters were mostly inconsistent. Current knowledge is not sufficient to conclude general land use impacts on soil fungi as the reviewed studies are fragmented and limited by the local context of land use change. Unification of the methodology, detailed descriptions of environmental factors, more reference sequences in public databases, and especially data on ecology and quantitative parameters of key fungal species would significantly improve the understanding of this issue.

Keywords: Soil Fungi, Land Use Change, Fungal Diversity, Species Composition, Mycorrhizal Fungi

Introduction

Soil fungi represent one of the most diverse assemblages of organisms on the Earth. They inhabit a wide range of ecological niches and play an essential role in ecological and biogeochemical processes (Dix & Webster 2012). Taxonomically, they are grouped mainly within the nine phyla – Opisthosporidia, Chytridiomycota, Neocallimastigomycota, Blastocladiomycota, Zoopagomycota, Mucoromycota, Glomeromycota, Basidiomycota and Ascomycota (Naranjo-Ortiz & Gabaldón 2019) – and catego-

rized into four ecological guilds – endophytes, mycorrhizal fungi, saprotrophs, and pathogens (Zanne et al. 2020). Endophytic fungi inhabit living plants and do not cause disease. Mycorrhizal fungi are symbionts that assist plants in nutrient and water uptake from soil and coping with stress conditions (Smith & Read 2008). Most terrestrial plants live in symbiosis with arbuscular mycorrhizal (AM) fungi, phylogenetically uniform groups within Glomeromycota and characterized by a low host specificity. Ectomycorrhizal (ECM) fungi are

highly host specific symbionts of only 4.5% of terrestrial plants (mainly trees, often dominated in boreal and temperate forests) and evolved several times within Basidiomycota and Ascomycota (Brundrett 2009). For this reason, there is no simple marker that would distinguish them from other trophic groups without identification to the genus. In contrast, pathotrophs cause diseases to plants and other biota (Agrios 2005). The saprotrophs serve as primary degraders of organic matter in the soil (Setälä & McLean 2004). Thus, being a component of soil microbiota, soil fungi are sensitive to any kind of alteration in the soil environment and any associated changes in the aboveground environment, such as human-mediated land use change.

The term “land use” can be defined as human employment of land cover type (biophysical state of the earth’s surface and immediate subsurface, e.g., forest, grassland, cropland, etc.) for certain purpose or function (Briassoulis 2019). It is often difficult to define the types of land use because it varies with land cover and the anthropogenic activities on it. In a broader sense, the changes in land use types from one state (e.g., primary forest, pasture) to other states (e.g., secondary forest, secondary grassland, cropland, etc.) can be defined as land use change. A particular

□ (1) Department of Botany, Faculty of Science, University of South Bohemia, Na Zlaté stoce 1, České Budějovice 37005 (Czech Republic); (2) Department of Carbon Storage in the Landscape, Czech Academy of Sciences, Lipová 1789/9, České Budějovice 37005 (Czech Republic); (3) Institute of Forest Ecology, University of Natural Resources and Life Sciences, Peter-Jordan-Straße 82, Wien 1190, Vienna (Austria); (4) Department of Ecosystem Biology, Faculty of Science, University of South Bohemia, Branišovská 1760, České Budějovice 37005 (Czech Republic)

@ Sujan Balami (balamisujan@gmail.com)

Received: Sep 08, 2019 - Accepted: Sep 17, 2020

Citation: Balami S, Vašutová M, Godbold D, Kotas P, Cudlín P (2020). Soil fungal communities across land use types. *iForest* 13: 548-558. - doi: [10.3832/ifor3231-013](https://doi.org/10.3832/ifor3231-013) [online 2020-11-23]

Communicated by: Alberto Santini

Tab. 1 - Land use type change considered in the reviewed publications. The figure in each cell indicate the number of publications that considered corresponding land use change. If one paper dealt with several land use types, e.g., change of forest to pasture and then to cropland, score one was added to each land use change. Abbreviations of land use types: (PF) Primary forest; (SF) Secondary forest; (PL) Plantation forest; (PS) Primary shrubland; (SS) Secondary shrubland; (PG) Primary grassland; (SG) Secondary grassland; (WL/RL) Woodland or Rangeland; (PA) Pasture; (AL) Abandoned land; (AF) Agroforestry; (PC) Perennial cropland; (CR) Cropland; (Others) Bareland/ Eroded land. Increase in land use intensity follows the order of: PF<SF<PL, PG<SG<CR, SG<PA<PC<CR, SF<AL<CR, etc.

Land use types	PF	SF	PL	PS	SS	PG	SG	WL/RL	PA	AL	AF	PC	CR
SF	24	-	-	-	-	-	-	-	-	-	-	-	-
PL	17	15	-	-	-	-	-	-	-	-	-	-	-
PS	0	1	0	-	-	-	-	-	-	-	-	-	-
SS	5	6	2	1	-	-	-	-	-	-	-	-	-
PG	0	2	2	1	1	-	-	-	-	-	-	-	-
SG	11	20	6	1	7	5	-	-	-	-	-	-	-
WL/RL	0	1	0	0	1	1	4	-	-	-	-	-	-
PA	13	11	8	1	1	1	10	1	-	-	-	-	-
AL	4	8	7	0	2	2	8	1	2	-	-	-	-
AF	2	4	1	0	0	0	1	0	2	1	-	-	-
PC	16	10	5	0	0	0	5	0	4	3	1	-	-
CR	23	27	15	1	6	13	26	5	18	19	3	10	-
Others	2	2	2	0	0	0	0	0	0	0	1	0	4

ters (Oehl et al. 2003, 2010, Peerawat et al. 2018), no review studies were published so far. For soil carbon, two meta-analyses were carried out on the effect of land use change on a global scale (Guo & Gifford 2002) and for tropical areas only (Don et al. 2011). These two studies illustrate that the greatest loss in soil carbon occurs after the conversion of primary sites to cropland but pointed out the occurrence of local constraints that limit the formulation of a broad conclusion. Accordingly, in the case of soil fungi also, published studies differ in several parameters (geographic region, habitat, methods, and target fungal group) such that it can be very difficult to reach a clear conclusion. As land use change is so widespread in a global context, we aimed (i) to summarize the present knowledge on land use change impact on soil fungi, (ii) highlight the limits of the various methodological approaches, and (iii) describe the current knowledge gaps to encourage further research on this topic.

Current studies

A total of 190 published original research articles worldwide were identified (April 2020) using keywords “Land use AND Fungi”, “Land use AND Microorganisms”, “Restoration AND Fungi”, “Restoration AND Microorganisms” “Secondary succession AND Fungi”, “Secondary succession AND Microorganisms”, “Succession AND Fungi”, “Succession AND Microorganisms” through Web of Science®, Google Scholar® and from the references of the selected papers (Tab. S1 in Supplementary material). These studies were selected based on the following criteria: (i) at least two land use types were compared (Tab. 1); (ii) at least one soil fungal parameter was assessed (Tab. 2). Studies dealing with only one land use type with different management (forest clearing, logging, or thinning, fertilization, crop rotation, tillage system, etc.) and

land use type can be either intensive or extensive based on the degree of anthropogenic activities.

In general, land use change is a function of changes in vegetation structure, soil properties, and anthropogenic activities which are known to influence the soil fungal communities (Sepp et al. 2018). Change in aboveground plant diversity, coverage, and community composition can influence soil fungi by regulating microclimatic conditions, nutrient addition to soil or exudation of allelochemicals, presence/absence of

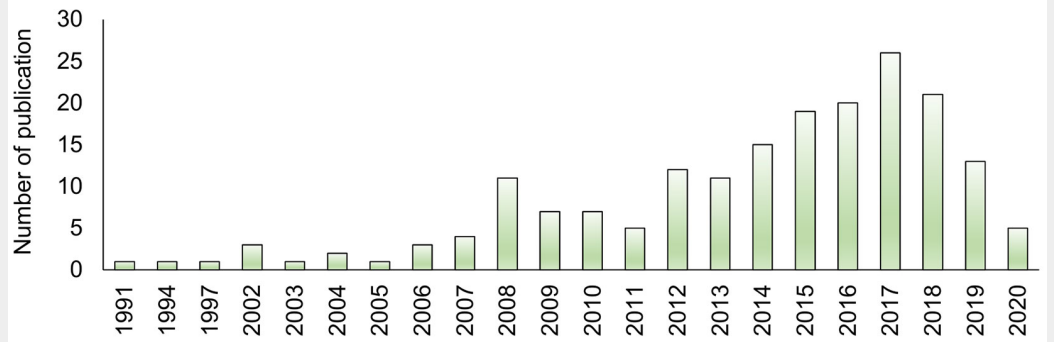
host plants for mycorrhizal fungi, etc. (Sene et al. 2012, Voriskova et al. 2016, Bainard et al. 2017). Moreover, soil factors (soil porosity, soil pH, carbon, nitrogen, phosphorus content, etc.) can significantly shape soil fungal communities (Oliveira et al. 2016, Wang et al. 2017). Likewise, anthropogenic activities like tillage, logging/mowing, fertilization, etc. have pronounced effects on soil fungal communities (Tomao et al. 2020).

Although many studies have shown the land use change impact on fungal param-

Tab. 2 - Effect of land use change (intensification) on different fungal parameters. The figure in each cell indicates the total number of papers dealing with fungal parameter. Publication list is given in Tab. S1 (Supplementary material).

Fungal parameter	Variable	No difference	Decrease	Increase	Varying	Change in community
1. Species richness and diversity	(a) species / OTUs richness	10	28	12	29	-
	(b) diversity	14	23	9	20	-
2. Community structure	(a) Higher taxa/guilds abundance	4	5	-	37	-
	(b) Species/OTUs composition	4	-	-	-	89
3. Root colonization	-	3	14	4	8	-
4. Spore density	-	4	17	10	11	-
5. Fungal biomass	(a) Phospholipid fatty acid content	3	17	4	17	-
	(b) Soil ergosterol content	-	3	-	-	-
	(c) ITS copy number/ Gene copy number	1	8	1	1	-
5. Glomalin related soluble protein	-	1	7	-	4	-
6. Others	(a) % hyphal length	1	3	-	1	-
	(b) Colony forming unit	1	1	1	2	-

Fig. 1 - Number of publications based on years of appearance.



chronosequence in single land use were not included. We focused this study on rural land-use change, thus publications dealing with urban and mining areas were excluded. In such land use types severe disruption of spontaneous soil development, heavy metals, and other chemicals can seriously affect the soil fungal community. For each publication, the land use type, soil fungal parameters, the fungal group (ECM/AM/total fungi) under study, the identification method used, and an overview of results were summarized. Also, the place of study, publication date, soil types, and climate information were tabulated (Tab. S1, Tab. S2, Tab. S3, Tab. S4 in Supplementary material). Most of the studies were carried out after 2008 (Fig. 1).

An increase in the number of studies in the last decade appears to be driven by an increasing concern of the effects of land use change, as well as by the use of next-generation sequencing methods (NGS) of environmental samples that has facilitated soil fungal research. A higher number of studies were carried out in Asia (73 studies) followed by Europe (49), South America (32), North America (17), Africa (12), Oceania (7). European and South American studies were distributed throughout the continent, whereas the Asian studies were mainly concentrated in the temperate region of China.

A higher proportion of studies compared natural and semi-natural habitats (primary/secondary forest, grassland, shrubland, and woodland/rangeland) with croplands, which represent a typical example of extensive land use and intensive land use types, respectively. In addition, extensive land use types resulting from agricultural land abandonment, abandonment of pasture, plantation in disturbed areas, or natural successional changes, are also commonly compared (33 studies). Tab. 1 shows the number of studies analyzed for various types of land use change. The majority of studies (27) compared secondary forest with cropland, 26 studies croplands with secondary grassland, 24 studies primary with secondary forests, and 23 studies primary forest with cropland.

In general, all fungal groups were assessed in studies after the introduction of the NGS methods (ca. 2008). Before this date, most studies were focused on AM

fungi and considerably fewer studies dealt with ECM fungi (9) or saprotrophic fungi (micromycetes) assessed by cultivation methods (6 – Fig. 2). The low numbers of studies on ECM fungi could be due to the absence of ECM trees for comparative evaluation across the land use types. In the earlier studies identification of the fungi was based mostly on morphology.

Land use change impact on soil fungi

Following a land use change, different fungal parameters showed a negative re-

sponse to land use intensification (e.g., primary forest < secondary forest < plantation forest < cropland). However, positive response or varying/no-difference in observed fungal parameters were also found. The clear result was found in the case of fungal community composition. Eighty-nine out of 93 studies focusing on changes in community composition showed a significant change in fungal community composition (Tab. 2). The majority of the studies also showed a decrease in quantitative fungal parameters following land use intensification. In the following subsections,

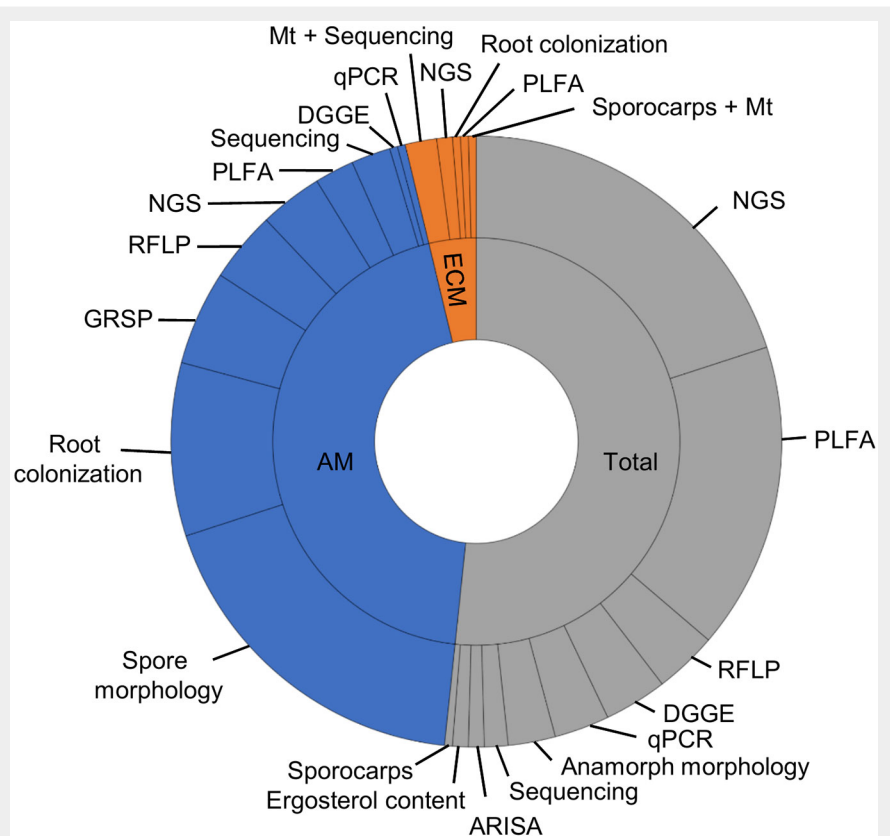


Fig. 2 - Proportion of published papers dealing with monitoring the impact of land use change according to the fungal group studied (AM: arbuscular mycorrhizal fungi; ECM: ectomycorrhizal fungi; and total fungi) and the different methods used to measure fungal parameters. If a particular paper deals with more than one group of fungi (total, AM, or ECM fungi), each group is scored with 1. (PLFA): phospholipid fatty acid analysis; (RFLP): restriction fragment length polymorphism; (DGGE): denaturation gradient gel electrophoresis; (Mt): morphotyping; (ARISA): automated ribosomal intergenic spacer analysis; (GRSP): glomalin related soil protein; (qPCR): quantitative PCR; (Sequencing): Sanger sequencing; (NGS): next generation sequencing.

some representative results have been described briefly.

Species richness and diversity

Studies on the effects of land use change on soil fungal richness and diversity (measured using different indices) used direct analysis of soils, or used soils incubated in a greenhouse with trap plants, such as *Sorghum* sp., *Plantago* sp., *Allium* sp. (Oehl et al. 2003). In early studies, identification of species to quantify species richness and diversity was based on morphological characteristics, such as spore morphology of AM fungi (Bedini et al. 2007), ECM morphotypes, sporulation of anamorphs (saprotrophs – McLean & Huhta 2002), and sporocarp morphology (Tedersoo et al. 2006). Along with these methods, molecular fingerprint methods, such as denaturing gradient gel electrophoresis (DGGE – Dong et al. 2008), restriction fragment length polymorphisms (RFLPs – Kasel et al. 2008), and automated ribosomal intergenic spacer analysis (ARISA – Okubo & Sugiyama 2009) were also used. Later, next-generation sequencing methods (454 pyrosequencing, Illumina sequencing, and Ion Torrent platform) have been introduced (Taylor et al. 2017). For DNA based analysis, the SSU (Moora et al. 2014), LSU (Voriskova et al. 2016) or ITS region (Wakelin et al. 2016) were usually amplified using appropriate primers. The estimates were then expressed in terms of actual species number or operational taxonomic unit (OTUs).

Generally, soil fungal richness decreased with the conversion of primary forest/grassland/shrubland to the more intensive land use sites, like secondary forest, plantation forest, perennial cropland, cropland (monoculture or crop rotation system – Oehl et al. 2003, Sene et al. 2012). For instance, during the conversion of forested areas to cropland, or to perennial cropland and fallow land (Tchabi et al. 2008), a reduction in the AM fungal richness was found. Likewise, when analyzing ECM fungal richness in roots of poplar plants in different land use (former cropland, former grassland, and former spruce stand), lower ECM fungal richness was found in former cropland sites compared to that found in the former spruce forest or former grassland (Gherghel et al. 2014). Although a decrease in species/OTUs richness values were common after increasing land use intensity, some contrasting results were also observed. The richness value either increases with increasing land use intensity (10 studies) or there is no clear direction of change (29 studies – Tab. 2). For example, higher AM fungal species richness was found in the secondary forest compared to the primary forest in the Amazon (Stürmer & Siqueira 2011). Higher observed OTUs richness was found in Jungle Rubber than in the rain forest in Sumatra, Indonesia (Brinkmann et al. 2019). While comparing perennial cropland (vineyard) to the adjacent sclerophyllous forest in the Mediter-

anean, there was no significant difference in total fungal species richness (Castaneda et al. 2015).

Similar to the total species richness estimates, diversity estimates based on the Shannon index of AM fungi (Honnay et al. 2017), ECM fungi and total fungi were found to decrease significantly with land use intensification (Gherghel et al. 2014). The comparison of perennial cropland sites with the secondary forest and fallow land showed a lower value of the Shannon diversity index of AM fungi for cropland (Snoeck et al. 2010). Likewise, higher OTUs diversity of AM fungi was observed by comparing grassland sites with agricultural sites (Manoharan et al. 2017). Lumini et al. (2010) found that the sites with low inputs (pasture and covered vineyard) showed a higher AM fungal diversity than those subjected to human inputs (managed meadow and tilled vineyard). But there were some equivocal results also. For instance, the conversion to intensive land use sites (primary forest to secondary forest) did not necessarily lead to the decrease in species richness, and/or a change in the diversity index of soil fungi (Kerfahi et al. 2016). Comparable diversity was reported while comparing the soybean field with plantation forests in temperate China (Sui et al. 2019). A higher Shannon diversity index of AM fungi was found in cropland sites compared to Atlantic forest sites (Pereira et al. 2014). Conversion of the pristine forest into other land uses (in tropical humid Amazon) did not reduce AM fungal diversity (Stürmer & Siqueira 2011). Similarly, McGuire et al. (2015) did not find significant differences in total fungal diversity between primary forest, regenerating forest, and oil palm plantation.

The maintenance of species richness may be due to the increase in plant diversity, density/coverage, as well as abiotic factors among land uses that promote diversity even in intensive land use systems. A pattern of increased AM fungal richness in cropland, agroforestry, and secondary forest sites compared to mature tropical forest sites has been explained by an increasing number of plant species that harbor different AM fungi growing in these land use types (Stürmer & Siqueira 2011). It has been observed that some mature tropical forests with climax plant communities are associated with the low richness of AM fungi (Siqueira et al. 1998). However, unaltered richness and diversity estimates do not mean that species composition has not changed. Using species richness as a parameter, replacement of species can result in a similar level of diversity and is indistinguishable from no impacts of land use change (Ying et al. 2013).

Community structure

Modification of soil fungal species/OTU composition (estimated by the same methods mentioned in the previous chapter) after land use change is quite common and

most obvious while comparing forest sites with cropland sites. As expected, various native forest types showed different fungal species composition compared to secondary forest (Mueller et al. 2016), plantation forest (Kasel et al. 2008, Moora et al. 2014, Brinkmann et al. 2019), pasture (Wang et al. 2014), grassland (Yurkov et al. 2012), and perennial cropland (Li et al. 2013). After the conversion of rain forest sites to rubber plantation, Kerfahi et al. (2016) observed changes from a Basidiomycota dominated to an Ascomycota dominated community. However, a study from China's Loess Plateau showed increasing abundance of Ascomycota and decreasing abundance of Basidiomycota while comparing cropland to plantation (Yang et al. 2017). During the conversion of primary forest to oil palm monoculture (in lowland evergreen rain forest of peninsular Malaysia dominated by Dipterocarpaceae), representatives of *Archaeorhizomycetales*, *Hypocreales*, and *Saccharomycetales* were found more abundant, whereas *Cantharellales* and *Mortierellales* dominated the primary forest sites. For ECM genera *Amanita* and *Lactarius* were more abundant in the regenerating forest, whereas *Craterellus* and *Russula* were more abundant in the primary forest (McGuire et al. 2015). Replacement of grassland with willow and poplar plantation leads to the enrichment of putative pathogenic and ECM fungi associated with trees (Xue et al. 2016). Significant differences in fungal communities were found in different land use types (bog, rough grazing site, and forest plantation sites) when investigating ericoid mycorrhizal diversity in two different ericaceous plant species, *Vaccinium macrocarpon* and *Calluna vulgaris* (Hazard et al. 2014).

Comparing AM composition of forests, croplands, and grasslands in the southern part of Tibetan Plateau, Glomeraceae were less abundant in forests, Gigasporaceae in grasslands, and Acaulosporaceae in croplands than in other land use types (Xu et al. 2017). In agricultural systems, the occurrence of *Acaulospora denticulata*, *Glomus ambisporum*, and *Claroideoglomus etunicatum* was significantly affected by cropping and non-cropping systems in Taita Hills, Kenya (Jefwa et al. 2012). A study in Terceira Island (Azores, Atlantic Ocean) showed that semi-natural pastures were dominated by species of *Acaulospora* and *Scutellospora*, particularly *S. calospora* and *A. cf. myriocarpa*. Whereas, for intensively farmed pastures, species with glomoid spores, and members of the two genera *Claroideoglomus* and *Paraglomus* were found most frequent and abundant (Melo et al. 2014).

Root colonization by AM and ECM fungi

Mycorrhizas on roots have also been quantified to evaluate the land use change impacts on AM and ECM communities. In ECM fungi, the percentage of root colonization (proportion of mycorrhizal and non-mycorrhizal root tips) and for AM fun-

gi the percentage of arbuscules, vesicles, and hyphae were quantified. For both types of mycorrhizas, the extent of colonization showed variation with land use change and could be explained by alteration of soil properties after land use change (Muthukumar et al. 2003).

The percentage of colonization by ECM fungi of *Salix* sp. was found to be higher in the natural forest compared to short rotation coppice (Hryniewicz et al. 2012). The difference was explained by soil water content, an initial inoculum of ECM fungi, host genotype, and soil pH. In a study of edaphic effects on symbiosis during soil development, mycorrhizal colonization shifted from AM fungi to ECM fungi (the plants had both types of mycorrhizal association) in response to decreasing phosphorus content in the soil. Such a shift in mycorrhizal association enables the acquisition of organic phosphorus via extracellular phosphatase activity (Albornoz et al. 2016).

The effect of increasing intensity of land use on AM fungal colonization is less clear than that for ECM fungi, being this possibly due to lower host specificity of AM fungi (Guadarrama et al. 2008). In the investigation of Islas et al. (2016), no relationship between the degree of land use intensification (pristine soil to agricultural soil) and root colonization of AM fungi was observed. On the other hand, the conversion of natural forested areas to grassland/pasture increased AM fungal colonization (Palta et al. 2016). Analysis of AM colonization in experimental plants established in degraded forest and in planted forest sites, showed lower root colonization in planted forest sites than in degraded forest (Sene et al. 2012). This difference was explained by the increased canopy of the planted forest reducing light and temperature at the forest floor, and thus plant density and hence lower root colonization.

Such increases or decreases in root colonization by ECM and AM fungi after land use intensification can be explained also with soil nutrient availability and perturbation in soil (Palta et al. 2016). Often the increase in soil nutrient availability has a negative impact on mycorrhizal colonization (Treseder 2004). Perturbation of the soil (e.g., soil compaction) reduces the porosity of soil, thereby reducing passages for organic nutrients and decreasing fungal mycelium ramification (Drew et al. 2003). On the other hand, the tillage in agricultural land breaks the extraradical mycelium into smaller units, and thus it increases the infectivity of fungal mycelium (Boddington & Dodd 2000).

Spore density

AM fungi produce thick-walled spores as their propagules, and morphological variations in such spores were traditionally employed for genus identification (Schenck & Perez 1990). Quantifying spore number per volume of soil by direct microscopic counting (Daniels & Skipper 1982) and express-

ing this count as a spore density/abundance, was used to observe land use effects.

Undisturbed areas, like natural grasslands and rangelands, were reported to harbor higher spore density in comparison to fallow land, pasture, plantation sites, and cropland (Jefwa et al. 2012, Li et al. 2013). The effect of land use intensification on spore density was observed also at the species level (Oehl et al. 2010). For instance, in a comparison of natural sites with pasture, the spore density of *Glomus* sp. was higher in natural sites while *Acaulospora* sp. was higher in pasture sites (Oliveira et al. 2016). Alternatively, spore density was also expressed as infective propagule numbers (the number of spores that can infect the test host plant, determined by the Most Probable Number technique). The total number of infective propagules was found to be significantly higher in pasture compared to traditionally managed cropland (Sousa et al. 2013). However, other studies reported comparable spore density of AM fungi in forested sites and fallow sites (Tchabi et al. 2008). They reported that apart from the overall land use impacts, soil organic carbon and pH levels affect the sporulation of AM fungi. While comparing short fallow land with the perennial cropland and secondary forest, significantly higher spore density was observed in short fallow and found to be related with C:N ratio in soil (Snoeck et al. 2010). Also, the impact of vegetation has been highlighted. It is known that grassland species have a more abundant fine-root system than trees in a mature forest, and this correlates positively with AM fungal colonization and sporulation (Muleta et al. 2008).

Fungal biomass

Quantification of fungal biomass using lipid components of fungi, namely soil ergosterol content and phospholipid fatty acids (PLFA), including neutral fatty acids (NLFA), have also been employed to monitor land use impacts on soil fungi. The unsaturated fatty acid 18:2 ω -6,9 was used as a marker of fungal biomass in the community profile (Olsson 1999). For AM fungi, 16:1 ω -5c (Sousa et al. 2013), and for ECM and saprotrophic fungi, 18:2 ω -6,9c and 18:1 ω -9c (Balser et al. 2005) were also applied. Additionally, estimates of ITS copy number (a proxy estimate of fungal biomass) from quantitative PCR were also used to show land use change effects on fungi (Grantina et al. 2011).

In a comparison of farmland and forest sites, soil ergosterol contents were found to follow the order of the intensity of land use, i.e., intensively cropland < pasture < forest soils (Turgay & Nonaka 2002). The plantation in mangrove forest sites with coconut, rubber, etc. was also found to reduce the soil ergosterol content by up to 90% (Dinesh & Chaudhuri 2013).

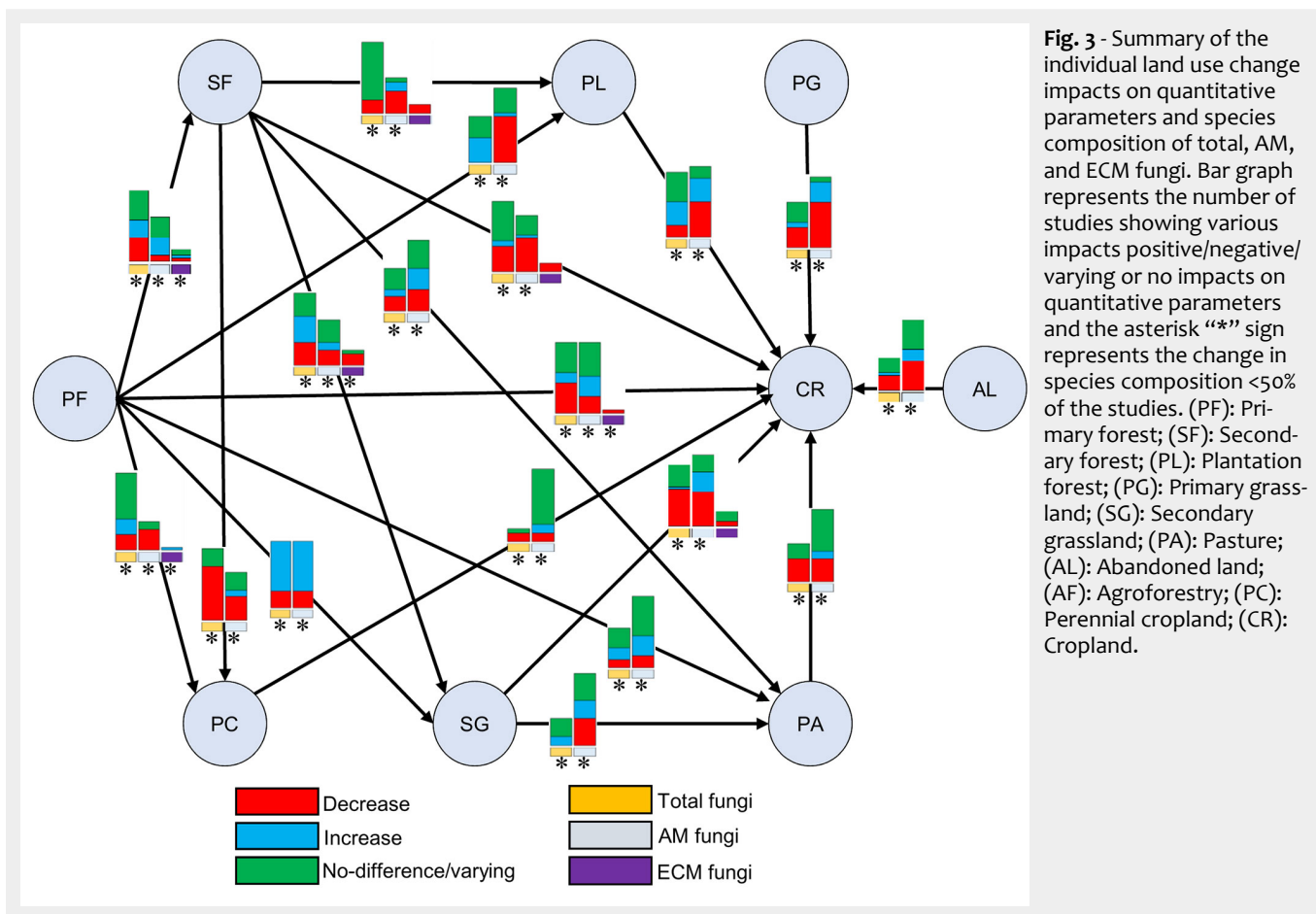
The decreasing value of fungal PLFA

(18:2 ω -6,9) content with increasing land use intensity was reported by Hamer et al. (2008). Similarly, higher fungal PLFA content was found in forest sites compared to perennial cropland (Dong et al. 2008). The content of PLFAs of AM fungi was lower in forest soils compared to abandoned and heathland soils, whereas the PLFAs of saprophytic and ECM fungi were more abundant in ancient forest soils (Olsson 1999). Such trends shown by AM and ECM fungi plus saprophytic fungi have been explained by soil nutrient conditions and differences in host plants. Higher amounts and structural complexity of carbon sources in forests form a bigger niche availability for ECM and saprophytic fungi, whereas higher concentrations of N and P in the former arable site support the AM fungi. However, some contrasting results have also been observed. With some exceptions, higher fungal biomass measured with the PLFA (18:2 ω -6,9) was observed in perennial agricultural soil compared to coastal grassland (Drenovsky et al. 2010). Similarly, PLFA content (18:2 ω -6,9) was found to be increased in the transition from forest to pasture to an abandoned field, due to the availability of nutrients as grass litter decomposed faster compared to the forest (Potthast et al. 2012). However, a study of the conversion of native grassland to pasture showed no significant difference in fungal PLFAs (Wong et al. 2015). It was suggested that no significant differences in soil properties (e.g., available P, soil pH, and vegetation cover) maintained an equal amount of fungal PLFAs in native grassland and pasture. Wang et al. (2017) also found no differences in fungal PLFA content with the conversion of natural forest to rubber plantations, but the AM fungi PLFA marker (16:1 ω -5c) was found to be higher in the natural forest than in the rubber plantation. It has been explained that soil acidification and higher phosphorus content reduced AM fungal biomass in rubber plantation sites.

Using a qPCR approach, no difference in the log number of copies of gene/gm of soil was found in abandoned land compared with plantation forest, but its values were significantly lower than mixed forest (Li et al. 2013). Similarly, no significant change in the log number of copies of gene/gm of soil between secondary grassland, pine plantation, and cropland was found (Ying et al. 2013). A study by Grantina et al. (2011), showed the order of log number of copies/gm of soil as former forest > agriculture > pasture > agricultural land.

Glomalin related soil protein (GRSP) of AM fungi

Glomalin is a proteinaceous substance produced by AM fungi which is released to the soil during hyphal turnover and after the death of the fungus (Driver et al. 2005). Different fractions of this protein, namely immunoreactive soil protein (IRSP) and



easily extractable immunoreactive soil protein (EE-IRSP) were quantified in soil to assess land use change impacts (Rillig 2004).

In the soil of grasslands, total glomalin related soil protein (GRSP) content was higher compared to a plantation site and was even lower in a maize monoculture (Bedini et al. 2007). Similarly, native mixed deciduous forest (*Acer*, *Alnus*, *Juglans*, *Carya*, etc.) contained a higher concentration of GRSP compared to agricultural and afforested sites (Sousa et al. 2013). Total GRSP was lower in cropland and fallow land when compared to forest soils covered by the AM-forming timber species *Combretodendron macrocarpum*, *Piptadeniastrum africanum* and *Disternonanthus benthamianus* (Fokom et al. 2012). Likewise, glomalin concentration was found lower in cropland than the native forest of temperate Himalaya (Nautiyal et al. 2019). Here, it has been explained that an increase in the root network of trees in the forest leads to an increase in AMF colonization which contributed to higher glomalin concentration. Prolonged arable land use of former grassland soils reduced the content of GRSP further (Preger et al. 2007). However, some studies showed no changes in GRSP content after land use change. For example, when poplar plantation was compared with cropland (maize field) no significant change in GRSP content was found (Wang et al. 2015).

Summary of the individual land use change impacts on soil fungal parameters

Generally, conclusions on the impact of land use change on soil fungi are limited by the number of replications. However, 18 types of land use change were considered in ≥ 10 replicated studies (Tab. 1). Thus, to extract generalized information needed for stakeholders, a summary of these replicated studies was made. Fig. 3 shows the overall impacts of these 18 types of land use change on qualitative (species composition) and quantitative fungal parameters (richness, diversity, root colonization, spore density of AM fungi, and fungal biomass – Tab. S5 and Tab. S6 in Supplementary material). If we set $\geq 50\%$ of the results as a boundary of increase/decrease or change, all 18 land use types showed changes in the community composition of all fungal groups (Tab. S5, Tab. S6). When comparing primary forest to secondary forest, secondary grassland, pasture, and cropland, no fungal quantitative parameters were changed. AM fungal quantitative parameters decreased when the primary forest was changed to plantation forest, perennial cropland, or cropland. Surprisingly, total fungal quantitative parameters increased when the primary forest was changed for plantation forests. Brinkmann et al. (2019) explained this pattern based on the intermediate disturbance hypothesis, which proposed that the highest diver-

sities will occur in ecological systems with moderate disturbances.

There are no clear changes in fungal parameters when the secondary forest is compared with secondary grassland and pasture. But converting of secondary forest to plantation forest, or perennial cropland or cropland, showed decreases in AM fungal parameters. There are also negative impacts on total fungal parameters following changes of secondary forest to perennial cropland. Only AM fungal parameters decreased when the plantation forest is changed to cropland.

These results demonstrate that it is very difficult to evaluate the response of soil fungal communities based on quantitative parameters. The fact that AM fungi provide a clearer response is probably due to their similar life strategy and low specificity. In contrast, total fungi contain many groups with so many different life strategies that their responses overlap, and the response is very much context-dependent.

Limitations of methodological approaches

The major limitation in evaluating the effect of the land use change on soil fungal communities is a poor consensus in land use type categorization. For instance, some studies defined land use types through the climatic zone (Thomson et al. 2015), some by plant cover type (Sousa et al. 2013), and some considered parent bed-

rock composition in single land use types (Oehl et al. 2003). In addition, some studies poorly described the vegetation, soil types, and climate of their experimental plots (Makiola et al. 2019). So, the effect of land use change cannot be correctly interpreted, because these factors could surpass land use change impact.

The other difficulty in the interpretation of land use change effects is a sampling design. As the experimental plots are distributed at a landscape level, homogeneous replicate plots selection is often difficult. However, there is also the limitation of selecting all studied land use types at one locality. Consequently, plot replicates in a distant location could influence soil fungi due to changes in environmental conditions. For instance, in fragmented agricultural fields, the management of soil fertility may be different, which affects soil fungi. Similarly, during the abandonment of the agricultural field, less productive fields are abandoned earlier, such that it can be presumed that the soil conditions are already different compared to previous land use. Therefore, as much information as possible should be gathered about land use history by interviewing local people.

Discrepancies in sampling is also another important factor. Some studies sampled soil along a transect with plot size as small as 1 m² (Bainard et al. 2017), whereas others sampled 1 ha plots with replicates of soil cores (Pereira et al. 2014). The preparation of composite soil samples from replicates of soil cores was a common method among studies. A few studies also considered fractions of different soil horizons (Rillig et al. 2003). The preparation of composite soil samples may overlay the vertical differences, *i.e.*, the land use change effect might be only in the topsoil layer, and deeper soil layer remains unaffected. In the case of predictor variables, many studies considered land use types as a typical predictor and soil factors as additional predictors. However, a comprehensive description of vegetation (as a next predictor) was missing in most studies (Zhang et al. 2017, Brinkmann et al. 2019).

In early studies, delimitation of species (evaluation of species richness and diversity) was based on morphological characteristics such as AM fungal spore morphology (Bedini et al. 2007), ECM morphotypes, (McLean & Huhta 2002), and sporocarps morphology (Tedersoo et al. 2006) that relied on expert knowledge and could differ between studies. Molecular fingerprinting methods like denaturing gradient gel electrophoresis (DGGE) can overlook less abundant species. Introduction of NGS methods (454 pyrosequencing, Ion Torrent platform, Illumina sequencing – Taylor et al. 2017) has solved the aforementioned issue. However, it has the limitation that appropriate primers for all fungal groups during PCR amplification must be used (Tedersoo et al. 2015) and several other technical issues (Zinger et al. 2019). The species-level identi-

fication could be also limited due to missing reference sequences in public databases. Moreover, knowledge of the ecological requirements of many taxa remains unknown (Nguyen et al. 2016) that arises difficulties in the interpretation of obtained data (Peay 2014). During root colonization assays, obtaining the identity of fine roots from particular plants could be difficult in a field-based investigation. Although the use of trap plants solves this problem, trap plants may not reflect the exact field conditions. The age of plants and the proportion of fine roots could also affect root colonization by AM and ECM fungi. Further, studying spore density in soil could be limited in the sporulation capacity of a particular taxon. Sporulation of AM fungi could differ between AM species and could be influenced by differences in seasonal dynamics (Oehl et al. 2009). Assessment of fungal and AM biomass was also employed in several land use change studies. PLFA method has its advantages of being rapid and inexpensive, sensitive, and reproducible but the interpretation of PLFAs as indicative of different groups of organisms is not straightforward. The specificity of different fatty acid markers (e.g. 16:1 ω -5c for AM fungi, 18:2 ω -6,9c for ECM fungi and 18:1 ω -9c for saprophytic fungi) has been questioned (Frostegård et al. 2011). In the case of AM fungi, GRSP is reputed to be a protein of AM fungi, but its presence in AM fungi only is unclear (Whiffen et al. 2007). Humic substances present in the soil could also interfere with the measurement of GRSP using colorimetric assays (Moragues-Saitua et al. 2019). Consequently, origin of the soil will influence the results. For instance, GRSP represents a good indicator of land use change effect in herb dominated ecosystems, being more concentrated in permanent than temporal systems. Its content in forests depends probably on mycorrhizal types of dominant trees (AM/ECM). As the amount of GRSP content in soil depends upon hyphal growth and spore production, individual species that remains unaffected by land use change may also have roles in determining the differences in concentrations of GRSP across sites (Rillig et al. 2001). To obtain more robust and reliable data usage of several methods, *i.e.*, NGS method accompanied by any morphological method (sporocarps, morphotypes, spores, root colonization) and biomass measurement (PLFA content, GRSP content), is highly recommended.

Conclusion and future perspectives

We found 190 relevant studies dealing with land use impact on soil fungi. The studies came mostly from Asia and Europe and were based mainly on next-generation sequencing, PFLA analysis, or spore morphology of AM fungi. Around 80% of these studies were published in the last decade. Land use type classification in these studies was mainly dependent on the local con-

text. The most studied land use change was a conversion from primary forest to cropland/secondary forests, cropland to plantation forest/secondary grassland/pasture. From 91 types of land use change, only 18 were included in more than 10 studies.

Most of the results showed that species richness and diversity were negatively impacted by land use change, but the results are not unequivocal. This means land use change does not necessarily lead to the changes in the soil fungal diversity. Generally, land use change has greater impacts on community composition. Root colonization of AM and ECM decreases in intensive land use sites. For AM fungi, several studies showed decreases in spore density with increasing land use intensity. Soil ergosterol, PFLA, and glomalin contents were found to follow the order of the intensity of land use, however, also equivocal results were published.

Our study suggests that current knowledge is not sufficient to reach conclusions on the effect of single land use change on soil fungi. This is due to the low number of replicates, extreme variability of local conditions worldwide, different methodological approaches and their limitations, the high species richness of fungi, and different responses of various fungal guilds, dependent on plant cover and soil conditions.

A proper description of land use history and environmental factors and a sufficient number of replicates is required for good comparisons. During soil sampling, it should be taken into account that larger plots are limited by sufficient replication and smaller plots by the representativeness of samples. Thus, widely accepted soil sampling strategies can be devised to have at least some uniformity of plot size, soil core size, and the number of replications, etc. Controlled long-term experiments can be one possible option on how to disentangle loss of diversity due to disturbance and management from natural changes caused by a change of associated host plants or soil properties (Heinemeyer et al. 2004).

As NGS methods provide a new level of information in soil fungal research, it should be a basic method to assess community composition. However, it is often unclear whether DNA sequences originate from hyphae, spores, or relic DNA (Carini et al. 2017). Thus, non-molecular methods, such as biomass estimation, provide an important cross-check and additional information. This is especially useful in studies of AM fungi because, due to redundancy caused by a high diversity and many life strategies, quantitative parameters of total fungi often do not change.

Although different parts of the world are covered to date, studies in tropical Asia, temperate areas of the Hindukush region, East Asia, Eurasia, and Africa are very few. Forest conversion to agricultural lands is increasing in tropics, Asia, and Africa (FAO 2016). Because these areas are also an im-

portant habitat for biodiversity protection (Yesson et al. 2007), more studies are needed to fill this gap.

Apart from methodological issues, the main problem of the reviewed studies is in the interpretation of data obtained. In the case of quantitative parameters, there are no generally accepted average values for a particular land use type. Due to the above-mentioned variability, such values can be obtained only in a local context, with sufficient replicates.

A promising tool for species data interpretation is a trait approach that has been widely used in vegetation science (Violle et al. 2007). However, data on fungal ecology are limited to main guilds assessment only (Nguyen et al. 2016) without any details about biology and niche requirements of selected species. In a European context, some information could be assessed based on red lists, indicator species lists, or monographies, but in other parts of the world, these sources are mostly not yet available.

Moreover, many fungal species are undescribed for science, and if so, have no reference sequence in public databases (e.g., Dothideomycetes, Leotiomycetes). Data on the properties of higher taxa are very rough and often contrasting life strategies are present within one genus. Therefore, we strongly recommend building the database of key species characteristics to move our knowledge from description and comparison to functionality. It is crucial to obtain more data on the ecology of key species (Peay 2014) to develop ideas on the functional significance of changes in species composition.

This review reveals that soil fungal response to land use change needs further evaluation. Soil fungal community dynamics can be reflected as an indicator of land use change. This understanding will help in combating land change impacts on other biotic communities and assist land-management strategies.

List of abbreviations

(AM): Arbuscular Mycorrhiza; (ARISA): Automated Ribosomal Intergenic Spacer Analysis; (DGGE): Denaturation Gradient Gel Electrophoresis; (ECM): Ectomycorrhiza; (GRSP): Glomalin Related Soil Protein; (ITS): Internal Transcribed Spacer; (LSU): Large Subunit; (NGS): Next Generation Sequencing; (OTU): Operational Taxonomic Unit; (PLFA): Phospholipid Fatty Acid Analysis; (RFLPs): Random Amplified Fragment Length Polymorphism; (SSU): Small Subunit.

Acknowledgement

This work was supported by the Ministry of Education, Youth and Sports of Czech Republic within the CzeCOS program, grant no. LM2018123. We thank all the authors who contributed to the original research articles.

References

- Agrios GN (2005). Plant pathology (5th edn). Academic Press, London, UK, pp. 358-611.
- Albornoz FE, Lambers H, Turner BL, Teste FP, Laliberté E (2016). Shifts in symbiotic associations in plants capable of forming multiple root symbioses across a long-term soil chronosequence. *Ecology and Evolution* 6: 2368-2377. - doi: [10.1002/ece3.2000](https://doi.org/10.1002/ece3.2000)
- Bainard LD, Chagnon PL, Cade-Menun BJ, Lamb EG, LaForge K, Schellenberg M, Hamel C (2017). Plant communities and soil properties mediate agricultural land use impacts on arbuscular mycorrhizal fungi in the Mixed Prairie ecoregion of the North American Great Plains. *Agriculture, Ecosystems and Environment* 249: 187-195. - doi: [10.1016/j.agee.2017.08.010](https://doi.org/10.1016/j.agee.2017.08.010)
- Balsler TC, Treseder KK, Ekenler M (2005). Using lipid analysis and hyphal length to quantify AM and saprotrophic fungal abundance along a soil chronosequence. *Soil Biology and Biochemistry* 37: 601-604. - doi: [10.1016/j.soilbio.2004.08.019](https://doi.org/10.1016/j.soilbio.2004.08.019)
- Bedini S, Avio L, Argese E, Giovannetti M (2007). Effects of long-term land use on arbuscular mycorrhizal fungi and glomalin-related soil protein. *Agriculture, Ecosystems and Environment* 120: 463-466. - doi: [10.1016/j.agee.2006.09.010](https://doi.org/10.1016/j.agee.2006.09.010)
- Boddington CL, Dodd JC (2000). The effect of agricultural practices on the development of indigenous arbuscular mycorrhizal fungi. I. Field studies in an Indonesian ultisol. *Plant and Soil* 218: 137-144. - doi: [10.1023/A:1014966801446](https://doi.org/10.1023/A:1014966801446)
- Briassoulis H (2019). Analysis of land use change: theoretical and modeling approaches. *Web Book of Regional Science 3*, Regional Research Institute, West Virginia University, Morgantown, WV, USA, pp 11-12.
- Brinkmann N, Schneider D, Sahner J, Ballauff J, Edy N, Barus H, Irawan B, Budi SW, Qaim M, Daniel J, Polle A (2019). Intensive tropical land use massively shifts soil fungal communities. *Scientific Reports* 9 (1): 16732. - doi: [10.1038/s41598-019-39829-4](https://doi.org/10.1038/s41598-019-39829-4)
- Brundrett MC (2009). Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. *Plant and Soil* 320: 37-77. - doi: [10.1007/s11104-008-9877-9](https://doi.org/10.1007/s11104-008-9877-9)
- Carini P, Marsden PJ, Leff JW, Morgan EE, Strickland MS, Fierer N (2017). Relic DNA is abundant in soil and obscures estimates of soil microbial diversity. *Nature Microbiology* 2 (3): 37. - doi: [10.1038/nmicrobiol.2016.242](https://doi.org/10.1038/nmicrobiol.2016.242)
- Castaneda LE, Godoy K, Manzano M, Marquet PA, Barbosa O (2015). Comparison of soil microbial communities inhabiting vineyards and native sclerophyllous forests in central Chile. *Ecology and Evolution* 5: 3857-3868. - doi: [10.1002/ece3.1652](https://doi.org/10.1002/ece3.1652)
- Daniels BA, Skipper HD (1982). Methods for the recovery and quantitative estimation of propagules from soil. In: "Methods and Principles of Mycological Research" (Schenck NC). The American Phytopathological Society, St. Paul, MN, USA, pp. 29-35.
- Dinesh R, Chaudhuri SG (2013). Soil biochemical/microbial indices as ecological indicators of land use change in mangrove forests. *Ecological Indicators* 32: 253-258. - doi: [10.1016/j.ecolind.2013.03.035](https://doi.org/10.1016/j.ecolind.2013.03.035)
- Dix NJ, Webster J (2012). Fungal ecology (1st edn). Springer Science and Business Media, London, UK, pp. 1-5. [online] URL: <http://books.google.com/books?id=3XXwCAAQBAJ>
- Don A, Schumacher J, Freibauer A (2011). Impact of tropical land-use change on soil organic carbon stocks-a meta-analysis. *Global Change Biology* 17: 1658-1670. - doi: [10.1111/j.1365-2486.2010.02336.x](https://doi.org/10.1111/j.1365-2486.2010.02336.x)
- Dong X, Huai-Ying Y, De-Yong GE, Huang CY (2008). Soil microbial community structure in diverse land use systems: a comparative study using Biolog, DGGE, and PLFA analyses. *Pedosphere* 18: 653-663. - doi: [10.1016/S1002-0160\(08\)60060-0](https://doi.org/10.1016/S1002-0160(08)60060-0)
- Drenovsky RE, Steenwerth KL, Jackson LE, Scow KM (2010). Land use and climatic factors structure regional patterns in soil microbial communities. *Global Ecology and Biogeography* 19: 27-39. - doi: [10.1111/j.1466-8238.2009.00486.x](https://doi.org/10.1111/j.1466-8238.2009.00486.x)
- Drew EA, Murray RS, Smith SE, Jakobsen I (2003). Beyond the rhizosphere: growth and function of arbuscular mycorrhizal external hyphae in sands of varying pore sizes. *Plant and Soil* 251: 105-114. - doi: [10.1023/A:1022932414788](https://doi.org/10.1023/A:1022932414788)
- Driver JD, Holben WE, Rillig MC (2005). Characterization of glomalin as a hyphal wall component of arbuscular mycorrhizal fungi. *Soil Biology and Biochemistry* 37: 101-106. - doi: [10.1016/j.soilbio.2004.06.011](https://doi.org/10.1016/j.soilbio.2004.06.011)
- Fokom R, Adamou S, Teugwa MC, Boyogueno AB, Nana WL, Ngonkeu MEL, Zollo PA (2012). Glomalin related soil protein, carbon, nitrogen and soil aggregate stability as affected by land use variation in the humid forest zone of south Cameroon. *Soil Tillage Research* 120: 69-75. - doi: [10.1016/j.still.2011.11.004](https://doi.org/10.1016/j.still.2011.11.004)
- FAO (2016). State of the world's forests 2016 - Forests and agriculture: land use challenges and opportunities. *FAO Report, Food and Agriculture Organization of the United Nations*, Rome, Italy, pp. 10-23.
- Frostegård A, Tunlid A, Bååth E (2011). Use and misuse of PLFA measurements in soils. *Soil Biology and Biochemistry* 43: 1621-1625. - doi: [10.1016/j.soilbio.2010.11.021](https://doi.org/10.1016/j.soilbio.2010.11.021)
- Gherghel F, Behringer D, Haubrich S, Schläu M, Fey-Wagner C, Rexer KH, Kost G (2014). Former and host genotype influence the mycorrhizal colonization of poplar roots. *Forests* 5: 2980-2995. - doi: [10.3390/f5122980](https://doi.org/10.3390/f5122980)
- Grantina L, Seile E, Kenigsvalde K, Kasparinskis R, Tabors G, Nikolajeva V, Muiznieks I (2011). The influence of the land use on abundance and diversity of soil fungi: comparison of conventional and molecular methods of analysis. *Environmental and Experimental Biology* 9: 9-21.
- Guadarrama P, Castillo-Argüero S, Ramos-Zapata JA, Camargo-Ricalde SL, Alvarez-Sánchez J (2008). Propagules of arbuscular mycorrhizal fungi in a secondary dry forest of Oaxaca, Mexico. *Revista de Biología Tropical* 56: 269-277. [online] URL: <http://www.scielo.sa.cr/pdf/rbt/v56n1/art19v56n1.pdf>
- Guo LB, Gifford RM (2002). Soil carbon stocks and land use change: a meta-analysis. *Global Change Biology* 8: 345-360. - doi: [10.1046/j.1354-1013.2002.00486.x](https://doi.org/10.1046/j.1354-1013.2002.00486.x)
- Hamer U, Makeschin F, Stadler J, Klotz S (2008).

- Soil organic matter and microbial community structure in set-aside and intensively managed cropland soils in NE-Saxony, Germany. *Applied Soil Ecology* 40: 465-475. - doi: [10.1016/j.apsoil.2008.07.001](https://doi.org/10.1016/j.apsoil.2008.07.001)
- Hazard C, Gosling P, Mitchell DT, Doohan FM, Bending GD (2014). Diversity of fungi associated with hair roots of ericaceous plants is affected by land use. *FEMS Microbiology Ecology* 87: 586-600. - doi: [10.1111/1574-6941.12247](https://doi.org/10.1111/1574-6941.12247)
- Heinemeyer A, Ridgway KP, Edwards EJ, Benham DG, Young JPW, Fitter AH (2004). Impact of soil warming and shading on colonization and community structure of arbuscular mycorrhizal fungi in roots of a native grassland community. *Global Change Biology* 10: 52-64. - doi: [10.1111/j.1365-2486.2003.00713.x](https://doi.org/10.1111/j.1365-2486.2003.00713.x)
- Honnay O, Helsen K, Van Geel M (2017). Plant community reassembly on restored semi-natural grasslands lags behind the assembly of the arbuscular mycorrhizal fungal communities. *Biological Conservation* 212: 196-208. - doi: [10.1016/j.biocon.2017.06.017](https://doi.org/10.1016/j.biocon.2017.06.017)
- Hryniewicz K, Toljander YK, Baum C, Fransson PM, Taylor AF, Weih M (2012). Correspondence of ectomycorrhizal diversity and colonisation of willows (*Salix* spp.) grown in short rotation coppice on cropland sites and adjacent natural stands. *Mycorrhiza* 22: 603-613. - doi: [10.1007/s00572-012-0437-z](https://doi.org/10.1007/s00572-012-0437-z)
- Islas AT, Guijarro KH, Eyherabide M, Rozas HS, Echeverría HE, Covacevich F (2016). Can soil properties and agricultural land use affect arbuscular mycorrhizal fungal communities indigenous from the Argentinean Pampas soils? *Applied Soil Ecology* 101: 47-56. - doi: [10.1016/j.apsoil.2016.01.005](https://doi.org/10.1016/j.apsoil.2016.01.005)
- Jefwa JM, Okoth S, Wachira P, Karanja N, Kahindi J, Njuguni S, Huisin J (2012). Impact of land use types and farming practices on occurrence of arbuscular mycorrhizal fungi (AM fungi) Taita-Taveta district in Kenya. *Agriculture, Ecosystems and Environment* 157: 32-39. - doi: [10.1016/j.agee.2012.04.009](https://doi.org/10.1016/j.agee.2012.04.009)
- Kasel S, Bennett LT, Tibbitts J (2008). Land use influences soil fungal community composition across central Victoria, south-eastern Australia. *Soil Biology and Biochemistry* 40: 1724-1732. - doi: [10.1016/j.soilbio.2008.02.011](https://doi.org/10.1016/j.soilbio.2008.02.011)
- Kerfahi D, Tripathi BM, Dong K, Go R, Adams JM (2016). Rainforest conversion to rubber plantation may not result in lower soil diversity of bacteria, fungi, and nematodes. *Microbial Ecology* 72: 359-371. - doi: [10.1007/s00248-016-0790-0](https://doi.org/10.1007/s00248-016-0790-0)
- Li JJ, Zheng YM, Yan JX, Li HJ, He JZ (2013). Succession of plant and soil microbial communities with restoration of abandoned land in the Loess Plateau, China. *Journal of Soils and Sediments* 13: 760-769. - doi: [10.1007/s11368-013-0652-z](https://doi.org/10.1007/s11368-013-0652-z)
- Lumini E, Orgiazzi A, Borriello R, Bonfante P, Bianciotto V (2010). Disclosing arbuscular mycorrhizal fungal biodiversity in soil through a land-use gradient using a pyrosequencing approach. *Environmental Microbiology* 12: 2165-2179. - doi: [10.1111/j.1462-2920.2009.02099.x](https://doi.org/10.1111/j.1462-2920.2009.02099.x)
- Makiola A, Dickie IA, Holdaway RJ, Wood JR, Orwin KH, Glare TR (2019). Land use is a determinant of plant pathogen alpha - but not beta - diversity. *Molecular Ecology* 16: 3786-3798. - doi: [10.1111/mec.15177](https://doi.org/10.1111/mec.15177)
- Manoharan L, Rosenstock NP, Williams A, Hedlund K (2017). Agricultural management practices influence AM fungi diversity and community composition with cascading effects on plant productivity. *Applied Soil Ecology* 115: 53-59. - doi: [10.1016/j.apsoil.2017.03.012](https://doi.org/10.1016/j.apsoil.2017.03.012)
- McGuire KL, D'Angelo H, Brearley FQ, Gedalovich SM, Babar N, Yang N, Mansor P (2015). Responses of soil fungi to logging and oil palm agriculture in Southeast Asian tropical forests. *Microbial Ecology* 69: 733-747. - doi: [10.1007/s00248-014-0468-4](https://doi.org/10.1007/s00248-014-0468-4)
- McLean M, Huhta V (2002). Microfungal community structure in anthropogenic birch stands in central Finland. *Biology and Fertility of Soils* 35: 1-12. - doi: [10.1007/s00374-001-0431-7](https://doi.org/10.1007/s00374-001-0431-7)
- Melo CD, Walker C, Rodríguez-Echeverría S, Borges PA, Freitas H (2014). Species composition of arbuscular mycorrhizal fungi differ in semi-natural and intensively managed pastures in an isolated oceanic island (Terceira, Azores). *Symbiosis* 64: 73-85. - doi: [10.1007/s13199-014-0303-1](https://doi.org/10.1007/s13199-014-0303-1)
- Moora M, Davison J, Opik M, Metsis M, Saks U, Jairus T, Zobel M (2014). Anthropogenic land use shapes the composition and phylogenetic structure of soil arbuscular mycorrhizal fungal communities. *FEMS Microbiology Ecology* 90: 609-621. - doi: [10.1111/1574-6941.12420](https://doi.org/10.1111/1574-6941.12420)
- Moragues-Saitua L, Merino-Martín L, Stokes A, Staunton S (2019). Towards meaningful quantification of glomalin-related soil protein (GRSP) taking account of interference in the Coomassie Blue (Bradford) assay. *European Journal of Soil Science* 70: 727-735. - doi: [10.1111/ejss.12698](https://doi.org/10.1111/ejss.12698)
- Mueller RC, Rodrigues JL, Nüsslein K, Bohannan BJ (2016). Land use change in the Amazon rain forest favours generalist fungi. *Functional Ecology* 30: 1845-1853. - doi: [10.1111/1365-2435.12651](https://doi.org/10.1111/1365-2435.12651)
- Muleta D, Assefa F, Nemomissa S, Granhall U (2008). Distribution of arbuscular mycorrhizal fungi spores in soils of smallholder agroforestry and monocultural coffee systems in southwestern Ethiopia. *Biology and Fertility of Soils* 44: 653-659. - doi: [10.1007/s00374-007-0261-3](https://doi.org/10.1007/s00374-007-0261-3)
- Muthukumar T, Sha L, Yang X, Cao M, Tang J, Zheng Z (2003). Distribution of roots and arbuscular mycorrhizal associations in tropical forest types of Xishuangbanna, southwest China. *Applied Soil Ecology* 22: 241-253. - doi: [10.1016/S0929-1393\(02\)00156-7](https://doi.org/10.1016/S0929-1393(02)00156-7)
- Nautiyal P, Rajput R, Pandey D, Arunachalam K, Arunachalam A (2019). Role of glomalin in soil carbon storage and its variation across land uses in temperate Himalayan regime. *Biocatalysis and Agricultural Biotechnology* 21: 101311. - doi: [10.1016/j.bcab.2019.101311](https://doi.org/10.1016/j.bcab.2019.101311)
- Nguyen NH, Song Z, Bates ST, Branco S, Teder-soo L, Menke JS, Kennedy PG (2016). FUNGuild: an open annotation tool for parsing fungal community datasets by ecological guild. *Fungal Ecology* 20: 241-248. - doi: [10.1016/j.funeco.2015.06.006](https://doi.org/10.1016/j.funeco.2015.06.006)
- Naranjo-Ortiz MA, Gabaldón T (2019). Fungal evolution: diversity, taxonomy and phylogeny of the Fungi. *Biological Reviews* 94: 2101-2137. - doi: [10.1111/brv.v94.6](https://doi.org/10.1111/brv.v94.6)
- Oehl F, Sieverding E, Ineichen K, Mäder P, Boller T, Wiemken A (2003). Impact of land use intensity on the species diversity of arbuscular mycorrhizal fungi in agroecosystems of Central Europe. *Applied and Environmental Microbiology* 69: 2816-2824. - doi: [10.1128/AEM.69.5.2816-2824.2003](https://doi.org/10.1128/AEM.69.5.2816-2824.2003)
- Oehl F, Sieverding E, Ineichen K, Mäder P, Wiemken A, Boller T (2009). Distinct sporulation dynamics of arbuscular mycorrhizal fungal communities from different agroecosystems in long-term microcosms. *Agriculture, Ecosystems and Environment* 134: 257-268. - doi: [10.1016/j.agee.2009.07.008](https://doi.org/10.1016/j.agee.2009.07.008)
- Oehl F, Laczko E, Bogenrieder A, Stahr K, Bösch R, Van Der Heijden M, Sieverding E (2010). Soil type and land use intensity determine the composition of arbuscular mycorrhizal fungal communities. *Soil Biology and Biochemistry* 42: 724-738. - doi: [10.1016/j.soilbio.2010.01.006](https://doi.org/10.1016/j.soilbio.2010.01.006)
- Okubo A, Sugiyama SI (2009). Comparison of molecular fingerprinting methods for analysis of soil microbial community structure. *Ecological Research* 24 (6): 1399-1405. - doi: [10.1007/s11284-009-0602-9](https://doi.org/10.1007/s11284-009-0602-9)
- Oliveira SP, Cndido MJ, Weber OB, Xavier FAS, Escobar MEO, Oliveira TS (2016). Conversion of forest into irrigated pasture I. Changes in the chemical and biological properties of the soil. *Catena* 137: 508-516. - doi: [10.1016/j.catena.2015.10.017](https://doi.org/10.1016/j.catena.2015.10.017)
- Olsson PA (1999). Signature fatty acids provide tools for determination of the distribution and interactions of mycorrhizal fungi in soil. *FEMS Microbiology Ecology* 29: 303-310. - doi: [10.1111/j.1574-6941.1999.tb00621.x](https://doi.org/10.1111/j.1574-6941.1999.tb00621.x)
- Palta S, Lermi AG, Beki R (2016). The effect of different land uses on arbuscular mycorrhizal fungi in the northwestern Black Sea Region. *Environmental Monitoring and Assessment* 188 (6): 1379. - doi: [10.1007/s10661-016-5350-z](https://doi.org/10.1007/s10661-016-5350-z)
- Peay KG (2014). Back to the future: natural history and the way forward in modern fungal ecology. *Fungal Ecology* 12: 4-9. - doi: [10.1016/j.funeco.2014.06.001](https://doi.org/10.1016/j.funeco.2014.06.001)
- Peerawat M, Blaud A, Trap J, Chevallier T, Alonso P, Gay F, Suvannang N (2018). Rubber plantation ageing controls soil biodiversity after land conversion from cassava. *Agriculture, Ecosystems and Environment* 257: 92-102. - doi: [10.1016/j.agee.2018.01.034](https://doi.org/10.1016/j.agee.2018.01.034)
- Pereira CMR, Da Silva DKA, De Almeida Ferreira AC, Goto BT, Maia LC (2014). Diversity of arbuscular mycorrhizal fungi in Atlantic forest areas under different land uses. *Agriculture, Ecosystems and Environment* 185: 245-252. - doi: [10.1016/j.agee.2014.01.005](https://doi.org/10.1016/j.agee.2014.01.005)
- Potthast K, Hamer U, Makeschin F (2012). Land use change in a tropical mountain rainforest region of southern Ecuador affects soil microorganisms and nutrient cycling. *Biogeochemistry* 111: 151-167. - doi: [10.1007/s10533-011-9626-7](https://doi.org/10.1007/s10533-011-9626-7)
- Preger AC, Rillig MC, Johns AR, Du Preez CC, Lobe I, Amelung W (2007). Losses of glomalin-related soil protein under prolonged arable cropping: a chronosequence study in sandy soils of the South African Highveld. *Soil Biology and Biochemistry* 39: 445-453. - doi: [10.1016/j.soilbio.2006.08.014](https://doi.org/10.1016/j.soilbio.2006.08.014)
- Rillig MC, Wright SF, Nicholas KA, Schmidt WF, Torn MS (2001). Unusually large contribution of arbuscular mycorrhizal fungi to soil organic matter pools in tropical forest soils. *Plant and Soil*

- 233: 167-177. - doi: [10.1023/A:1010364221169](https://doi.org/10.1023/A:1010364221169)
- Rillig MC, Ramsey PW, Morris S, Paul EA (2003). Glomalin, an arbuscular-mycorrhizal fungal soil protein, responds to land use change. *Plant and Soil* 253 (2): 293-299. - doi: [10.1023/A:1024807820579](https://doi.org/10.1023/A:1024807820579)
- Rillig MC (2004). Arbuscular mycorrhizae, glomalin, and soil aggregation. *Canadian Journal of Soil Science* 84 (4): 355-363. - doi: [10.4141/S04-003](https://doi.org/10.4141/S04-003)
- Schenck NC, Perez Y (1990). Manual for the identification of VA mycorrhizal fungi (3rd edn). Synergistic Publications, Gainesville, FL, USA, pp. 286.
- Sene G, Samba-Mbaye R, Thiao M, Khasa D, Kane A, Manga A, Sylla SN (2012). The abundance and diversity of legume-nodulating rhizobia and arbuscular mycorrhizal fungal communities in soil samples from deforested and man-made forest systems in a semiarid Sahel region in Senegal. *European Journal of Soil Biology* 52: 30-40. - doi: [10.1016/j.ejsobi.2012.05.005](https://doi.org/10.1016/j.ejsobi.2012.05.005)
- Sepp SK, Jairus T, Vasar M, Zobel M, Opik M (2018). Effects of on arbuscular mycorrhizal fungal communities in Estonia. *Mycorrhiza* 28: 259-268. - doi: [10.1007/s00572-018-0822-3](https://doi.org/10.1007/s00572-018-0822-3)
- Setälä H, McLean MA (2004). Decomposition rate of organic substrates in relation to the species diversity of soil saprophytic fungi. *Oecologia* 139: 98-107. - doi: [10.1007/s00442-003-1478-y](https://doi.org/10.1007/s00442-003-1478-y)
- Siqueira JO, Carneiro MAC, Curi N, Da Silva Rosado SC, Davide AC (1998). Mycorrhizal colonization and mycotrophic growth of native woody species as related to successional groups in Southeastern Brazil. *Forest Ecology and Management* 107 (1-3): 241-252. - doi: [10.1016/S0378-1127\(97\)00336-8](https://doi.org/10.1016/S0378-1127(97)00336-8)
- Smith SE, Read DJ (2008). *Mycorrhizal symbiosis* (3rd edn). Elsevier - Academic Press, London, UK, pp. 1-9.
- Snoeck D, Abolo D, Jagoret P (2010). Temporal changes in VAM fungi in the cocoa agroforestry systems of central Cameroon. *Agroforestry Systems* 78: 323-328. - doi: [10.1007/s10457-009-9254-6](https://doi.org/10.1007/s10457-009-9254-6)
- Sousa CDS, Menezes RSC, Sampaio EVDSB, Lima FDS, Oehl F, Maia LC (2013). Arbuscular mycorrhizal fungi within agroforestry and traditional land use systems in semi-arid Northeast Brazil. *Acta Scientiarum Agronomy* 35: 307-314. - doi: [10.4025/actasciagron.v35i3.16213](https://doi.org/10.4025/actasciagron.v35i3.16213)
- Stürmer SL, Siqueira JO (2011). Species richness and spore abundance of arbuscular mycorrhizal fungi across distinct land uses in Western Brazilian Amazon. *Mycorrhiza* 21 (4): 255-267. - doi: [10.1007/s00572-010-0330-6](https://doi.org/10.1007/s00572-010-0330-6)
- Sui X, Zhang R, Frey B, Yang L, Li MH, Ni H (2019). Land use change effects on diversity of soil bacterial, Acidobacterial and fungal communities in wetlands of the Sanjiang Plain, northeastern China. *Scientific Reports* 9: 1-14. - doi: [10.1038/s41598-018-37186-2](https://doi.org/10.1038/s41598-018-37186-2)
- Taylor JD, Helgason T, Opik M (2017). Molecular community ecology of arbuscular mycorrhizal fungi. In: "The Fungal Community: its Organization and Role in the Ecosystem" (Dighton J, White JF eds). CRC Press, Boca Raton, FL, USA, pp. 3-23. - doi: [10.1201/9781315119496-2](https://doi.org/10.1201/9781315119496-2)
- Tchabi A, Coyne D, Hountondji F, Lawouin L, Wiemken A, Oehl F (2008). Arbuscular mycorrhizal fungal communities in sub-Saharan Savannas of Benin, West Africa, as affected by agricultural land use intensity and ecological zone. *Mycorrhiza* 18: 181-195. - doi: [10.1007/s00572-008-0171-8](https://doi.org/10.1007/s00572-008-0171-8)
- Tedersoo L, Suvi T, Larsson E, Kõjalg U (2006). Diversity and community structure of ectomycorrhizal fungi in a wooded meadow. *Mycological Research* 110: 734-748. - doi: [10.1016/j.mycres.2006.04.007](https://doi.org/10.1016/j.mycres.2006.04.007)
- Tedersoo L, Anslan S, Bahram M, Põlme S, Riit T, Liiv I (2015). Shotgun metagenomes and multiple primer pair-barcode combinations of amplicons reveal biases in metabarcoding analyses of fungi. *Mycology* 10: 1-43. - doi: [10.3897/mycokeys.10.4852](https://doi.org/10.3897/mycokeys.10.4852)
- Thomson BC, Tisserant E, Plassart P, Uroz S, Griffiths RI, Hannula SE, Martin F (2015). Soil conditions and intensification effects on soil microbial communities across a range of European field sites. *Soil Biology and Biochemistry* 88: 403-413. - doi: [10.1016/j.soilbio.2015.06.012](https://doi.org/10.1016/j.soilbio.2015.06.012)
- Tomao A, Bonet JA, Castaño C, De-Miguel S (2020). How does forest management affect fungal diversity and community composition? Current knowledge and future perspectives for the conservation of forest fungi. *Forest Ecology and Management* 457: 117678. - doi: [10.1016/j.foreco.2019.117678](https://doi.org/10.1016/j.foreco.2019.117678)
- Treseder KK (2004). A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO₂ in field studies. *New Phytologist* 164: 347-355. - doi: [10.1111/j.1469-8137.2004.01159.x](https://doi.org/10.1111/j.1469-8137.2004.01159.x)
- Turgay OC, Nonaka M (2002). Effects of land use and management practices on soil ergosterol content in andosols. *Soil Science and Plant Nutrition* 48: 693-699. - doi: [10.1080/00380768.2002.10409259](https://doi.org/10.1080/00380768.2002.10409259)
- Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007). Let the concept of trait be functional! *Oikos* 116: 882-892. - doi: [10.1111/j.0030-1299.2007.15559.x](https://doi.org/10.1111/j.0030-1299.2007.15559.x)
- Voriskova A, Janoušková M, Slavíková R, Pánková H, Daniel O, Vazačová K, Münzbergová Z (2016). Effect of past agricultural use on the infectivity and composition of a community of arbuscular mycorrhizal fungi. *Agriculture, Ecosystems and Environment* 221: 28-39. - doi: [10.1016/j.agee.2016.01.012](https://doi.org/10.1016/j.agee.2016.01.012)
- Wakelin SA, Gerard E, Van Koten C, Banabas M, O'Callaghan M, Nelson PN (2016). Soil physicochemical properties impact more strongly on bacteria and fungi than conversion of grassland to oil palm. *Pedobiologia* 59: 83-91. - doi: [10.1016/j.pedobi.2016.03.001](https://doi.org/10.1016/j.pedobi.2016.03.001)
- Wang Q, Bao Y, Liu X, Du G (2014). Spatio-temporal dynamics of arbuscular mycorrhizal fungi associated with glomalin-related soil protein and soil enzymes in different managed semiarid steppes. *Mycorrhiza* 24: 525-538. - doi: [10.1007/s00572-014-0572-9](https://doi.org/10.1007/s00572-014-0572-9)
- Wang Q, Wang W, He X, Zhang W, Song K, Han S (2015). Role and variation of the amount and composition of glomalin in soil properties in farmland and adjacent plantations with reference to a primary forest in North-Eastern China. *PloS One* 10: e0139623. - doi: [10.1371/journal.pone.0139623](https://doi.org/10.1371/journal.pone.0139623)
- Wang J, Ren C, Cheng H, Zou Y, Bughio MA, Li Q (2017). Conversion of rainforest into agroforestry and monoculture plantation in China: consequences for soil phosphorus forms and microbial community. *Science of the Total Environment* 595: 769-778. - doi: [10.1016/j.scitotenv.2017.04.012](https://doi.org/10.1016/j.scitotenv.2017.04.012)
- Whiffen LK, Midgley DJ, McGee PA (2007). Polyphenolic compounds interfere with quantification of protein in soil extracts using the Bradford method. *Soil Biology and Biochemistry* 39: 691-694. - doi: [10.1016/j.soilbio.2006.08.012](https://doi.org/10.1016/j.soilbio.2006.08.012)
- Wong MR, Morgan JW, Wong NK, Cavagnaro TR (2015). The incorporation of fungal to bacterial ratios and plant ecosystem effect traits into a state-and-transition model of land use change in semi-arid grasslands. *Agriculture, Ecosystems and Environment* 201: 11-19. - doi: [10.1016/j.agee.2014.10.012](https://doi.org/10.1016/j.agee.2014.10.012)
- Xu M, Li X, Cai X, Li X, Christie P, Zhang J (2017). Land use alters arbuscular mycorrhizal fungal communities and their potential role in carbon sequestration on the Tibetan Plateau. *Scientific Reports* 7 (1): 151. - doi: [10.1038/s41598-017-03248-0](https://doi.org/10.1038/s41598-017-03248-0)
- Xue C, Penton CR, Zhang B, Zhao M, Rothstein DE, Mladenoff DJ, Tiedje JM (2016). Soil fungal and bacterial responses to conversion of open land to short-rotation woody biomass crops. *GCB Bioenergy* 8: 723-736. - doi: [10.1111/gcbb.12303](https://doi.org/10.1111/gcbb.12303)
- Yang Y, Dou Y, Huang Y, An S (2017). Links between soil fungal diversity and plant and soil properties on the Loess Plateau. *Frontiers in Microbiology* 8: 34. - doi: [10.3389/fmicb.2017.02.198](https://doi.org/10.3389/fmicb.2017.02.198)
- Yesson C, Brewer PW, Sutton T, Caithness N, Pahwa JS, Burgess M, Culham A (2007). How global is the global biodiversity information facility? *PLoS One* 2 (11): e1124. - doi: [10.1371/journal.pone.0001124](https://doi.org/10.1371/journal.pone.0001124)
- Ying JY, Zhang LM, Wei WX, He JZ (2013). Effects of land utilization patterns on soil microbial communities in an acid red soil based on DNA and PLFA analyses. *Journal of Soils and Sediments* 13: 1223-1231. - doi: [10.1007/s11368-013-0704-4](https://doi.org/10.1007/s11368-013-0704-4)
- Yurkov AM, Kemler M, Begerow D (2012). Assessment of yeast diversity in soils under different management regimes. *Fungal Ecology* 5: 24-35. - doi: [10.1016/j.funeco.2011.07.004](https://doi.org/10.1016/j.funeco.2011.07.004)
- Zhang C, Liu G, Song Z, Qu D, Fang L, Deng L (2017). Natural succession on abandoned cropland effectively decreases the soil erodibility and improves the fungal diversity. *Ecological Applications* 27: 2142-2154. - doi: [10.1002/eap.1598](https://doi.org/10.1002/eap.1598)
- Zinger L, Bonin A, Alsos IG, Bálint M, Bik H, Boyer F, Chariton AA, Creer S, Cossac E, Deagle BE, Barba MD, Dickie IA, Dumbrell AJ, Ficentola GF, Fierer N, Fumagalli L, Gilbert MTP, Jarman S, Jumpponen A, Kausered H, Orlando L, Pansu J, Pawłowski J, Tedersoo L, Thomsen PF, Willerslev E, Tabriet P (2019). DNA metabarcoding - Need for robust experimental designs to draw sound ecological conclusions. *Molecular Ecology* 28: 1857-1862. - doi: [10.1111/mec.15060](https://doi.org/10.1111/mec.15060)
- Zanne AE, Abarenkov K, Afkhami ME, Aguilar-Trigueros CA, Bates S, Bhatnagar JM, Busby PE, Christian N, Cornwall WK, Crowther TW, Flores-Moreno H, Floudas D, Gazis R, Hibbett D, Kenndey P, Lindner DL, Maynard DS, Milo AM, Nilsson RH, Powell J, Schildhauer M, Schilling J,

Treseder KK (2020). Fungal functional ecology: bringing a trait-based approach to plant-associated fungi. *Biological Reviews* 95: 409-433. - doi: [10.1111/brv.12570](https://doi.org/10.1111/brv.12570)

Supplementary material

Tab. S1 - List of publications reviewed: land use types and sites.

Tab. S2 - List of publications reviewed: fungal guilds, fungal parameters and methods used.

Tab. S3 - List of publications reviewed: parameters analyzed.

Tab. S4 - List of publications reviewed: geographic and environmental variables.

Tab. S5 - Impact of particular land use change on soil fungi.

Tab. S6 - Summary of Tab. S5.

Link: [Balami_3231@suppl001.pdf](#)