City life of mycorrhizal and wood-inhabiting macrofungi: Importance of urban areas for maintaining fungal biodiversity

Witoon Purahong [a,*], Angela Günther [b], Andreas Gminder [c], Benjawan Tanunchai [a], Martin M. Gossner [d,e], François Buscot [a,f], Ernst-Detlef Schulze [b]

[a] *UFZ-Helmholtz Centre for Environmental Research, Department of Soil Ecology, Theodor-Lieser-Str. 4, D-06120 Halle (Saale), Germany*
[b] *Max Planck Institute for Biogeochemistry, Hans-Knöll-Str. 10, D-07745 Jena, Germany*
[c] *German Mycological Society, Claustorwall 24, 38640 Goslar, Germany*
[d] *Forest Entomology, Swiss Federal Research Institute WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland*
[e] *ETH Zurich, Department of Environmental Systems Science, Institute of Terrestrial Ecosystems, 8092 Zurich, Switzerland*
[f] *German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, D-04103 Leipzig, Germany*

HIGHLIGHTS

- Urban areas maintain a high fungal diversity, even of Red-List species.
- Fagaceae and Pinaceae hosted 90% of total and red-list species detected in this study.
- Conifers contributed 66% and 51% to total and red-list fungal diversity.
- Broad-leaved trees contributed 80% and 74% to total and red-list fungal diversity.
- Red-list species occurred mainly on common forest trees and shrubs, especially in native ones.

ARTICLE INFO

ABSTRACT

The biodiversity of mycorrhizal and wood-inhabiting macrofungi (basidiomycetes) is declining, and many species are threatened in forests. Based on data from a 30-year fruiting body survey from 1988 to 2017 in the region of the city of Jena (100,000 inhabitants, 4500 ha forest), Germany, we evaluated the role of the urban environment with a variation of ownership, property size, associated management, and high diversity of woody species for the presence of non-red list and red-list fungal species. We found that (i) the urban area hosted 1172 mycorrhizal and wood-inhabiting basidiomycete macrofungi, identified on 64 woody host genera, representing 23% of the total German basidiomycetes on 0.4‰ of the German forest area. Among these species, 194 species (16%) are threatened according to the German Red List; (ii) a few common forest tree genera (Fagaceae and Pinaceae) hosted 90% of the total and red-list fungal species detected in this study; (iii) plant identity and host functional groups rather than plant phylogeny shaped the community composition and richness of mycorrhizal and wood-inhabiting macrofungi; (iv) conifers contributed 68% and 51% and broad-leaved trees 81% and 74% to total and red-list fungal diversity, respectively; (v) red-list species occurred mainly on common forest trees and shrubs from Fagaceae, Pinaceae, Betulaceae, Salicaceae, and Oleaceae, especially on native ones; and (vi) a few exotic trees (*Robinia pseudoacacia* and *Pseudotsuga menziesii*) supported a diverse native fungal flora. We conclude that urban areas can serve as an important zone for maintaining mycorrhizal and wood-inhabiting macrofungi by promoting a high heterogeneity of land use, ownership, and a high diversity of woody species.

1. Introduction

Mycorrhizal and wood-inhabiting macrofungi from the phylum

Basidiomycota include saprotrophic, mycorrhizal, and parasitic fungi that play essential roles in nutrient turnover, plant performance, and fertility of forest soils (Bani et al., 2018; Fukasawa & Matsukura, 2021;

Herrmann & Bauhus, 2018; Hodge & Peterken, 1998; Rajala et al., 2012). However, it has been shown that their biodiversity is declining in forests, and many species are highly threatened (Dahlberg et al., 2010; Nordén et al., 2013; Purahong et al., 2014). Given the various ecosystem functions and services macrofungi provide, it is important to understand the conditions under which fungal diversity can be maintained or even promoted. Land-use intensity has been identified as a major cause of diversity losses, but this has not been generally documented for fungal species in forests (Lonsdale et al., 2008; Tomao et al., 2020). Forest structural components, such as horizontal heterogeneity and deadwood diversity, which are affected by forest management (Burrascano et al., 2013), have been shown to promote wood-inhabiting fungi (Penone et al., 2019).

To better understand the role of land use on fungal diversity, we chose to investigate an urban region with generally very high land-use intensity but also very diverse land-use practices. Forests in the surroundings of a city generally experience a high diversity of forest land uses, ranging from areas for wood production, water supply and recreation. At the same time, these forests maintain a high diversity of ownership and management regimes, ranging from state forests for wood production, communal forests for recreation towards small holders, who use their forests mainly for their personal firewood supply, or leave them unmanaged. Historically, these small properties also maintain the highest diversity of woody species (Von Lüpke et al., 2011). This high diversity of land-use intensities and ownership provides a unique background for studying land-use effects on fungal diversity.

The high and diverse land-use intensities in urban areas and their surroundings may not always be harmful to biodiversity. Some studies have already demonstrated that urban areas may serve as hotspots for plant, insect, and microbial biodiversity, even for native species (Barrico et al., 2018; Theodorou et al., 2020). Availability of diverse tree host species covering many plant functional groups in urban forests (Barrico et al., 2018) give macrofungi the chance to select between many more different host plants in urban areas than temperate forests in Europe, which have a limited number of plant species (Schulze et al., 2016). At the same time, many forest tree species have been introduced to urban areas and their surroundings which contribute to the nutrient sources of mycorrhizal and wood-inhabiting macrofungi and other organisms. Despite the high potential of urban areas for the conservation of mycorrhizal and wood-inhabiting macrofungi, no study to date has addressed this ecosystem. There are many important questions remaining, including: (i) how many wood-associated fungi, including red list (endangered) and non-red list fungi, can be maintained in a city and its surrounding, (ii) which and how many plant taxa (genera or species) are needed for maintaining fungal biodiversity in a city and (iii) what are the effects of plant identity, phylogenetic and functional groups on richness and community composition of wood-associated and mycorrhizal fungi. Reliable information on which plant taxa provide habitat to many or distinct fungi is important and could be incorporated into urban greenspace planning with emphasis on native species.

In this study, we used the opportunity of a unique assessment of macrofungi around the city of Jena, Germany, where mycorrhizal and wood-inhabiting basidiomycetes were collected and documented systematically over the last 30 years (data during 1988 to 2017) on 4500 ha of forest land surrounding the city and its city parks (Günther et al., 2019). This city is situated in a canyon-like valley, where the slopes were formerly used mainly for grazing sheep and goats. In fact, the forests in this region were almost totally devastated 150 years ago, surviving only in steep side valleys and in shallow soils (Schulze et al., 2016). At present, these slopes are afforested, providing the basis for wood and water supply, and for recreation of city inhabitants. The native forest vegetation would be dominated by broadleaf species. According to Ellenberg (1978), *P. abies* is not a natural component. State forests in this area are generally managed as high forests. In contrast, private forests are managed by selective logging. Communal forests of Jena contain both, high forests and selectively logged stands, as well as successional stages

from non-forest areas. Dörfelt & Kirsche (1988) discussed the possibility that dry slope may have been a natural habitat for *Pinus sylvestris*. The distribution of pine has been altered by humans. In 1752, large afforestation stations of pine and spruce were recorded. In 1850, approximately 100,000 *P. sylvestris* saplings were planted, and the first trials of *Pinus nigra* were installed. Thus, *Picea* and *Pinus* species are regarded as anthropogenic components of the present state and communal forest vegetation. This contrasts with private forests, which harbor a variety of broadleaf tree species, including *Quercus*.

In the first step, we investigated (i) the general role of host plants (plant identity, plant functional groups, and plant phylogeny) in shaping total and red-list mycorrhizal and wood-inhabiting macrofungal richness and community composition, (ii) the role of exotic species, and (iii) native conifers, which were planted in this region, in the presence of total and red-list fungal species. This is particularly relevant because natural conservation tends to exclude conifers and exotic species from forests that would naturally consist of broad-leaved trees only (e.g., Natura-2000 management plans). In the second step, we investigated (iv) how diversity in land ownership and land-use diversity affect the diversity of basidiomycetes. We hypothesized that (i) fungal richness generally benefits from increasing diversity of plants, but not all plant species may be equal in providing suitable habitats, (ii) the city and its surrounding areas would be dominated by common fungi with a small contribution of red-list fungi, (iii) a variation in ownership, property size, and land use would promote fungal diversity in an urban area, provided that the operations are of small scale, and (iv) differences of fungal communities between native and exotic plants might be related to time and exposure to the diversity of native fungal communities. Following common knowledge on phylogeny, we also test the role of evolution of plant species for shaping fungal communities.

2. Material and methods

2.1. Study site

The study area is located in Eastern Thuringia, Germany, in the middle part of the Saale River (50° 55′ N, 11° 35′ E, 140–397 m above sea level, Jena: approximately 100,000 inhabitants) (Fig. 1). The city of Jena is placed at a point that was reached by the Saale-glaciation. At Jena, the Saale River cuts through limestone layers of the middle mesozoicum in a "Canyon-like" fashion, forming steep east- and west-facing slopes with bare rock. Regional geomorphology is an undulating plateau formed by layers of the upper mesozoicum. The valley floor was composed of silt and loam. Thus, the geological history results locally in alluvial acid deposits in a region dominated by Mesozoic limestone. With an annual temperature of 9 °C, Jena is one of the warmest regions in central Germany (weather data available since 1824). The average annual rainfall was 564 mm. Geology, together with the post-Pleistocene geomorphology, is the basis for a high diversity of exposure, soil acidity, and soil depth. The forest cover consists of various kinds of broad-leaved forests (*Fagus*-dominated forest, *Quercus*-forest, *Carpinus*-forest, *and Fraxinus-Acer* forest) whenever soils are deep. On steep slopes, limestone *Pinus* forests dominate. *Populus-Salix* forests line the Saale River. The total area under study is 12,000 ha, which is covered by forest land (4500 ha), grassland (2000 ha), and urban housing, city parks, and gardens (5500 ha). The forest area belongs to different groups of owners. Approximately 1500 ha is a communal forest, of which about 500 ha is under natural conservation, 500 ha is state-owned forest, and about 2500 ha consists of small private forest properties (on average, 0.5 ha; Fig. 1 insert). In this study, the total area was divided into 24 quadrants with different forest covers and ownerships (Fig. 1).

2.2. Datasets

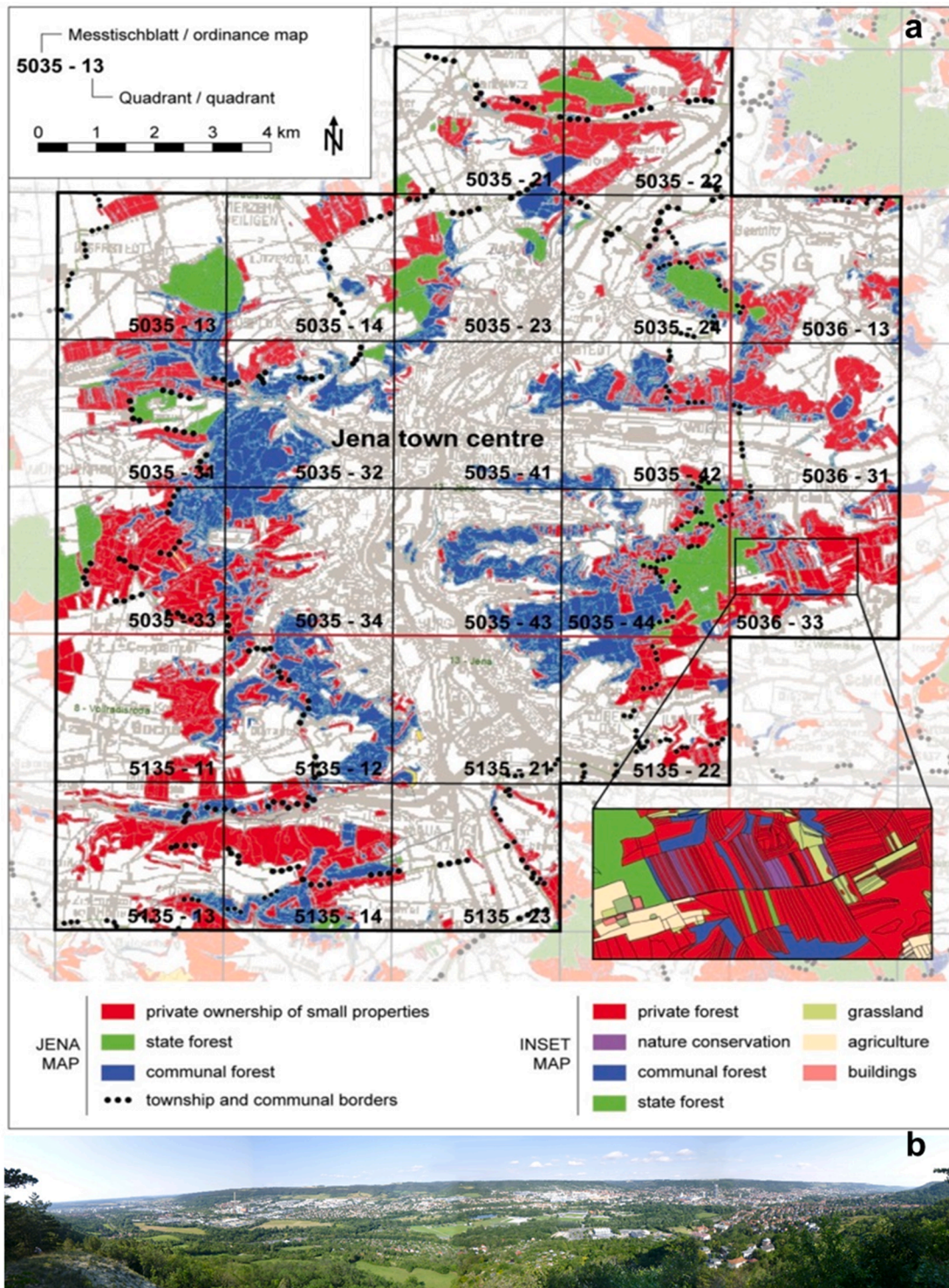Fungal specimens were collected mainly in the forest surrounding

Fig. 1. Study area: (a) Map of study area (Jena city and its surrounding). The total area of study is 12,000 ha, divided into blocks of 1/16th of an ordination map. 4500 ha are forest land. Color signature indicates different ownerships: red: private land, blue: communal land, green: state forest. Insert: the ownerships are not uniform. This is especially true for private land. The insert shows 223 ha, with 160 ha private land of 350 owners, average size of properties 0.5 ha, smallest property was 4 m with and 500 m long. (b) Panorama view of Jena city showing the west-bank of the Saale River. The view shows a total distance from North to South of about 25 km.

the city of Jena, but also in city parks and solitary road trees. Private home gardens have been investigated to a lesser extent. There is a long history of the collection and description of fungi in Jena. The first documentation of the fungi of Jena was published by Rupp (1718), followed by floral assessments by Batsch (1783, 1786, 1789); Jaap (1914); Remischberger (1919); Benedix (1944, 1949) were compiled

from literature and were used for comparison only. In 1988, G. Hirsch (Günther et al., 2019) started a dBase-database with documentation of the observations. All data are public under http://www.pilze-deutsch land.de/. The list of observations backed by physical specimens is very long (850 samples), as documented by Günther et al. (2019). Most of the samples (exsiccates) are stored in the Herbarium Haussknecht in Jena

(JE), some species in the Herbarium in Halle (HAL), Herbarium Senckenbergianum Görlitz (GLM), Herbarium Dresdense (DR), and in private collections.

This study is based on a citizen science project carried out during the past 30 years in which non-professional mycologists collected and recorded fungal observations based on common support for identification (Pilzgruppe Jena, see Günther et al., 2019). There was no major change in land-use, except of a general extension of housing, which took place mainly on agricultural land, or on land that was formerly used as weekend-housing. Land-use intensity changed mainly on agricultural land but remained fairly constant in forest land. All fungal species of this study were found and geo-referenced along a 2.75 km × 3.0 km grid (a 16th of a survey map). All samples were taken in the study area of Jena. No fungal specimens were derived from elsewhere. All plant specimens originated from our study area and identifications are correct. However, due to a certain possible bias in sampling, namely that the sampling teams tended to walk their trail, we decided to use the Flora of Baden Württemberg (Krieglsteiner, 2000a, 2000b, 2001, 2003; Krieglsteiner & Gminder, 2010) as an additional source to widen the spectrum of potential host species of the species found in Jena area, and thus avoided sampling bias. Baden Württemberg has a flora very similar to that of Jena, except that *Abies* is more common in Baden-Württemberg. Thus, the observed fungi of Jena were associated with "potential host species" based on the Flora of Baden Württemberg, which contains a very detailed analysis of fungal host species. Plant genera and species have been identified according to the flora of Germany (Rothmaler, 2017). The classification of trees and shrubs following Rothmaler (2017) is mainly based on plant height (trees are taller than 5 m). In addition, shrubs regenerate from basal buds. Taxonomic and abundance information of all 64 plant genera used in this study is presented in Table S1. In this study, we grouped the plant hosts into six functional groups based on their growth, habit, functions, and nativeness: (i) coniferous trees, (ii) broadleaf trees, (iii) exotic trees, (iv) native shrubs of this region, (v) ornamental plants (Rothmaler, 2008), and (vi) herbaceous, grasses, and liana plants. Herbaceous, grasses, and liana plants have no persistent woody stems, but their stems can also host wood-inhabiting macrofungi (Table S2). Thus, we included herbaceous, grass, and liana plants as functional groups in our analyses. Thirty species of wood-inhabiting basidiomycete macrofungi were identified in this group. It should be noted that two of these 30 species (*Aphanobasidium filicinum*, associated with *Pteridium*, and *Marasmius epiphylloides*, associated with *Hedera*) were not associated with other woody plants in this study. *Prunus* and *Salix* include both tree and shrub species. The red-list status for each fungal species was classified according to the official German Red List of Fungi (Dämmrich et al., 2016). The red-list species include extremely rare species (R), endangered species of unknown extent (G), endangered species (3), highly endangered species (2), and threatened with extinction species (1). Although the inclusion of category R in the Red List as well as the exclusion of category V (vulnerable fungi) is debatable, we followed the German Red List of Fungi (Dämmrich et al., 2016).

2.3. Statistical analysis

Forest cover, property diversity, ownership diversity, and fungal richness data were extracted from each quadrant (Fig. 1a). Each quadrant was used as a replicate (co-ordinates of the middle points of all quadrants are provided in supplementary Table S3). Low-intensity sampling quadrants (containing<30% of the sampling objects) were removed. In total, data from 17 out of the 24 studied quadrants were used for the analyses. Correlations between forest cover, property diversity, and total richness of mycorrhizal and wood-inhabiting basidiomycete macrofungi were analyzed using a partial correlation analysis associated with a Jarque-Bera test for normality, taking into account the spatial location of individual replicates (quadrant). We performed a forward selection method with multiple regression analyses in SPSS (IBM SPSS Statistics 22, New York, NY, United States) to find the

combination of variables that explained the differences in fungal richness best. The effect of the mixture of ownerships on the richness of mycorrhizal and wood-inhabiting macrofungi was analyzed using a *t*-test incorporated with the *F* test for equality of variances and the JB test for normality.

In this study, we also defined fungal richness as "number of basidiomycete species detected in different tree genera, families, and functional groups in Jena city and its surroundings during the past 30 years". Fungal community composition is an assemblage of co-occurring and potentially interacting basidiomycete species, present in wood of different tree genera, families, and functional groups. Plant phylogenetic relationships were visualized using an online tool "phyloT" which generates phylogenetic trees based on the NCBI taxonomy. Comparisons of fungal richness (both total and red-list fungi) in different taxonomic (families) and functional groups of host plants were analyzed using a Kruskal-Wallis (KW) test followed by a Mann-Whitney *U* Test for pairwise comparisons, as their variances were not sufficiently homogenous for one-way ANOVA according to Levene's test. We also corrected the fungal richness for different sampling efforts among different major tree genera by using their associated cover areas. Comparisons of fungal richness (both total and red-list fungi) in native and exotic plants were analyzed using a Mann-Whitney *U* test. In this study, fungal species richness was used as a measure of fungal diversity. The effects of plant identity, phylogeny, and plant functional groups on the community composition of mycorrhizal and wood-inhabiting macrofungi (both total and red-list fungi) were analyzed and visualized using permutational multivariate analysis of variance (PERMANOVA), variance partitioning, and cluster analysis based on presence/absence data. The significance *P* value from the PERMANOVA was based on 999 permutations. The data were analyzed using PAST software version 2.17c (Hammer et al., 2001). The effects of phylogeny on species richness and community composition of mycorrhizal and wood-inhabiting macrofungi (both total and red-list fungi) were analyzed using Spearman's rank correlation and goodness-of-fit statistics obtained by non-metric multidimensional scaling (NMDS) ordination based on Jaccard distances with the envfit function of the vegan package in R version 3.6.1. Correlations between richness of non-red list and red-list fungal species detected across different tree genera were analyzed based on (i) all species and (ii) species with host preference (detected in no more than three plant species) using non-parametric Spearman's rank correlation. Plant genus addition and removal approaches were carried out by adding or removing one by one plant species with the highest richness (α diversity) and calculating the increase or decrease in fungal species richness in the system. As some plant genera contain a high number of common fungi, this approach was also conducted by adding plant genera with the highest richness one by one: (i) total richness, (ii) total specialists (fungi colonize only one host plant species) and (iii) host preference (fungi colonize by one to three host plant species) fungi. Plant genus removal approach was performed to simulate how richness values of total, non-red list and red-list fungi in this ecosystem are impacted by the loss of important plant genera.

3. Results

3.1. General overview of the taxonomic diversity of the mycorrhizal and wood-inhabiting basidiomycete macrofungi in the Jena region

The 4500 ha study area contained a total of 1585 basidiomycetes. Of these, 1172 (74%) species, belonging to 296 genera, were associated with wood as mycorrhizal fungi (45.8% of the species), saprotrophs (43.4% of the species), plant pathogens (0.5%), or a combination of these groups (10.2%) (Table 1 and Table S2). In this study, we focused on the mycorrhizal and wood-inhabiting basidiomycete macrofungi that were associated with 64 plant genera. With 29% of the total number of basidiomycete species, *Cortinarius*, *Russula*, *Inocybe*, *Lactarius*, and *Mycena* were the most species-rich fungal genera (Table 1).

Table 1

Frequently detected fungal genera (containing at least 14 species) associated with 64 plant taxa analyzed in this study and their ecological functions. The most frequently detected genera for plant pathogens, saprotroph/plant pathogens, and saprotroph/mycorrhizal/plant pathogens are also included. Please note that mycorrhizal fungi could potentially be saprotrophs (Lindahl & Tunlid, 2015).

Fungal genus	Number of detected fungi (species)	Number of detected red-list fungi (species)	Functions
Cortinarius	133	32	Mycorrhizal
Russula	77	18	Mycorrhizal
Inocybe	56	6	Mycorrhizal
Lactarius	41	12	Mycorrhizal
Tricholoma	29	6	Mycorrhizal
Hygrophorus	25	7	Mycorrhizal
Amanita	21	3	Mycorrhizal
Boletus s.l.	18	8	Mycorrhizal
Hebeloma	14	2	Mycorrhizal
Tremella	2	0	Plant pathogen
Pluteus	21	0	Saprotroph
Clitocybe s.l.	15	2	Saprotroph
Gymnopus	14	0	Saprotroph
Pholiota	14	1	Saprotroph
Mycena	37	2	Saprotroph
Entoloma	13	2	Saprotroph/Mycorrhizal
Ramaria	12	6	Saprotroph/Mycorrhizal
Amylostereum	3	1	Saprotroph/Mycorrhizal/Plant pathogen
Polyporus	8	0	Saprotroph/Plant pathogen
Other genera (277 genera)	619	86	**Mycorrhizal (123 species); Saprotroph (408 species); Plant pathogen (4 species); Saprotroph/Mycorrhizal (14 species); Saprotroph/Plant pathogen (70 species)**
Sum	**1172**	**194**	**Mycorrhizal (537 species); Saprotroph (509 species); Plant pathogen (6 species); Saprotroph/Mycorrhizal (39 species); Saprotroph/Plant pathogen (78 species); Saprotroph/Mycorrhizal/Plant pathogen (3 species)**

We observed 978 non-red list and 194 red-list species. The non-red list species were ubiquitous fungi (*: 708 species), fungi with deficient data (D: 156 species), fungi not established in Germany (U: 35 species), vulnerable fungi (V: 73 species), and fungal-like species treated by other red lists (◆: 6 species) (Table S2). Red-list species contained 69 genera dominated by *Cortinarius*, *Russula*, and *Lactarius* (Table 1: 32% of the red-list species detected here). These species comprised 18 extremely rare species (R), 79 species that are endangered to an unknown extent (G), 64 endangered species (3), 26 highly endangered species (2), and 7 species threatened with extinction (1) (Table S2). The majority of red-list fungi were mycorrhizal species (130 species), followed by saprotrophs (40 species). Further information on the frequently detected fungal genera (total and red-list fungi) and their ecological functions are presented in Table 1.

3.2. The role of taxonomic and functional group and phylogenetic relationship for fungal richness

Total and red-list fungal richness varied significantly among different plant families (total: $H = 16.54$, $P = 0.011$; red-list: $H = 18.91$, $P = 0.003$) and functional groups (total: $H = 38.37$, $P < 0.001$; red-list:

$H = 36.64$, $P < 0.001$) (Fig. 2, Fig. S1a,-d). Phylogenetic placement of the host plants correlated with neither the total ($\rho = 0.13$, $P = 0.310$) nor the red list ($\rho = 0.05$, $P = 0.673$) fungal richness (Fig. S1e). We detected two peaks of fungal richness, one peak of fungal richness within the Gymnosperms (Pinaceae), and another within the Rosids (Fagaceae and Betulaceae) (Fig. 2). These three plant families had significantly higher total and red-list fungal richness ($P < 0.05$) than the other plant families (Fig. S1c and d). Different plant genera were mixed independently of their phylogeny, carrying vastly different numbers of fungal species (Fig. 2). Some plant genera, especially those from Fagaceae (*Fagus*: 112 and 666 red-list and non-red list species, *Quercus*: 84 and 553 red-list and non-red list species), Pinaceae (*Picea*: 80 and 593 red-list and non-red list species, *Pinus*: 50 and 437 red-list and non-red list species, and *Abies*: 27 and 362 red-list and non-red list species), Betulaceae (*Betula*, *Carpinus*, *Alnus*, and *Corylus*), Salicaceae (*Salix* and *Populus*), and Oleaceae (*Fraxinus*) harbored more than 240 mycorrhizal and wood-inhabiting basidiomycete fungal species, including 9 to 112 red-list species (Figs. 2 and 3a1). Most of these plant genera are deciduous broadleaved and coniferous trees, except *Salix*, which contains both tree and shrub species.

Fagus, *Picea*, *Quercus* and *Pinus* harbored the highest number of red-list and non-red list species among all fungi, mycorrhizal fungi, as well as host preference fungi (Fig. 3a1, 3b1, and Fig. S2a1). These four plant genera also showed the highest number of non-red list saprotrophic fungi, but *Fraxinus*, *Abies*, and *Acer* were more important than *Pinus* (Fig. S2b1). *Fagus* and *Quercus* also harbored the highest number of red- and non-red-list plant pathogens (including saprotrophs and plant pathogens), followed by *Fraxinus*, *Betula*, *Populus*, and *Salix* (non-red list fungi), followed by *Aesculus* and *Castanea* (red-list fungi) (Fig. S2c1).

We consistently observed a negative exponential decrease in non-red list fungal richness (including fungi with host preference that are detected in no more than three plant genera, mycorrhizal, saprotrophic, and potential plant pathogenic fungi) with less common hosts and woodiness (Fig. 3a1 and 3b1 and Fig. S2a1, S2b1, and S2c1). However, saprotrophs and potential plant pathogens were more ubiquitous, as indicated by a "hump" in the exponential decrease curve. Negative exponential decreases were also observed for red-list fungal richness, host preference, and mycorrhizal fungi (Fig. 3a1 and 3b1 and Fig. S2a1).

Strong correlations ($\rho = 0.70$–0.87, $P < 0.001$) between the richness of non-red list fungal species and red-list fungal species were detected across different tree genera in this study, when considering all fungal species, host preference fungi, mycorrhizal fungi, and saprotrophs (Fig. 3a2 and 3b2 and Fig. S2a2 and S2b2). Only a moderate correlation ($\rho = 0.50$, $P < 0.001$) was detected between the richness of non-red list species and red-list species for fungal plant pathogens (Fig. S2c2). Correction of the total and red-list fungal richness in each tree genus by its associated cover area in the total study area showed that *Picea* had the highest richness of mycorrhizal and wood-inhabiting macrofungi (both red-list and non-red list species), followed by *Quercus*, *Fagus*, and *Pinus* (Table 2).

Among the plant functional groups, deciduous broadleaf trees harbored the highest number of total and red-listed mycorrhizal and wood-inhabiting macrofungi (total: 945 species, red list: 144), followed by coniferous trees (769/97), shrubs (336/28), exotic trees (153/5), herbs, grasses and lianas (30/1), and ornamental plants (23/0) (Fig. S1a and S1b). The mean values of all plant functional groups also confirmed that deciduous broadleaf and coniferous trees had significantly higher total and red-list fungal richness than most of the remaining plant functional groups (Fig. S1a, S1b). Native hosts harbored significantly higher total and red-listed fungal species than exotic hosts (Fig. S1f), except if the exotic species were integrated into the native vegetation. The native species which contained the highest fungal diversity were *Fagus* and *Picea*, while the exotic plant species were *Pseudotsuga* and *Robinia*.
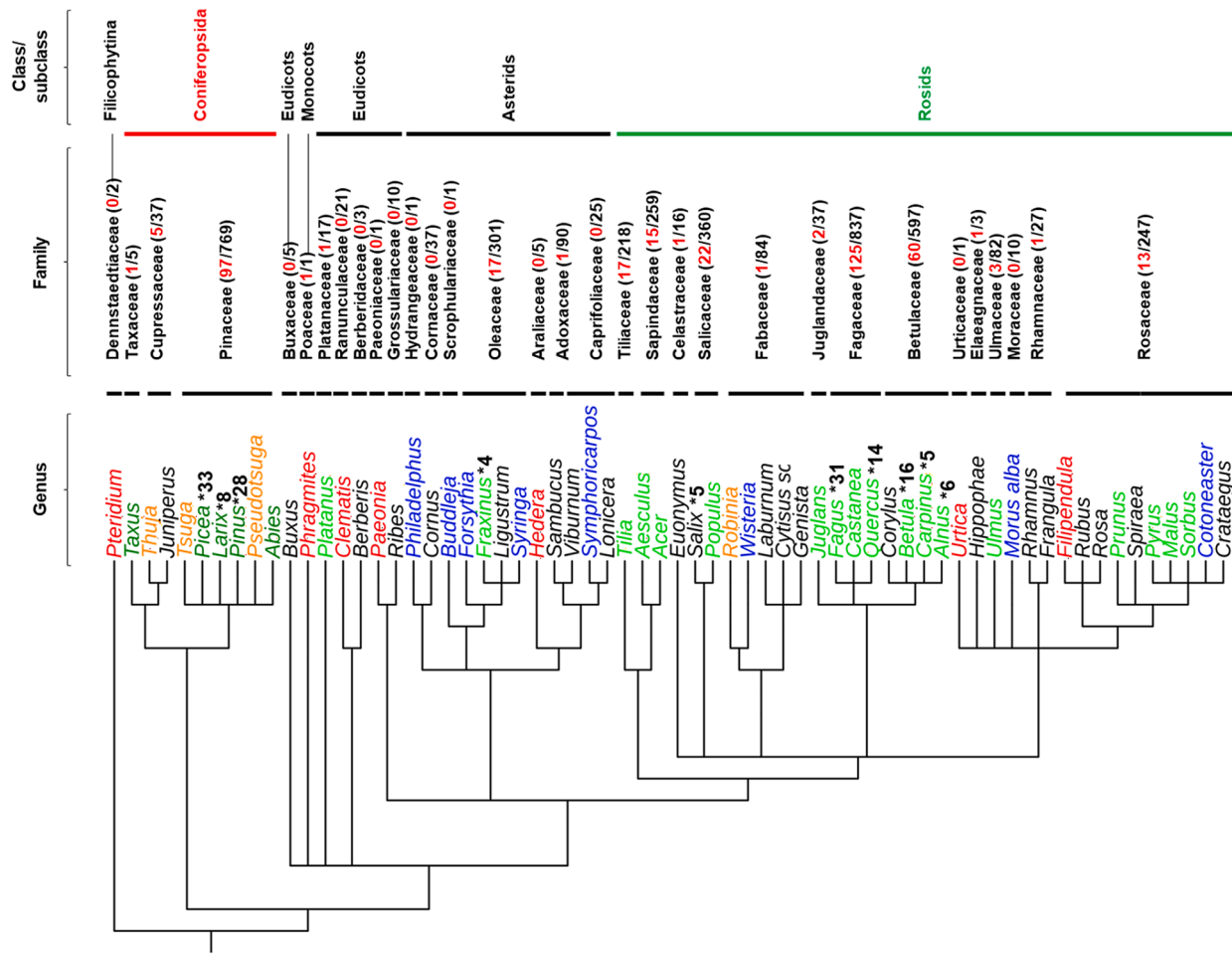
Fig. 2. Dendrogram shows phylogenetic relationships of 64 plant genera based on "phyloT" and richness of mycorrhizal and wood-inhabiting basidiomycete macrofungi associated with different plant families (number of red-list and non-red list species are given in parenthesis after name of each plant family). The star (*) indicates the top-ten plant genera that harbor the highest number of specific fungal species (the number is shown in parenthesis). Plant genera: Dark green – coniferous trees; Bright green – deciduous trees; Black – shrubs; Red – herbs, grass, liana; Brown – exotic plants; Blue – ornamental. Class or subclass of plant species are indicated on the top (green: Rosids, red: Coniferopsida, black: Asterids, Eudicots, Monocots, and Filicophytina).

3.3. Effect of plant identity, phylogeny, and plant functional groups on community composition of mycorrhizal and wood-inhabiting macrofungi

Deciduous and coniferous tree species harbored different total and red-list fungal community compositions compared to other plant functional groups ($F = 1.44$–3.75, $P = 0.001$–0.024), except for fungal communities on exotic trees which were similar to those of conifers ($F = 1.13$–1.47, $P = 0.098$–0.367) (Fig. 4a and 4b). The total ($F = 2.67$, $P = 0.002$) and red-list ($F = 1.97$, $P = 0.002$) fungal community compositions were also significantly different between deciduous broadleaved and coniferous tree species (Fig. 4a and 4b). Shrubs showed a total fungal community composition significantly different from those of broadleaved trees, conifers, ornamental plants ($F = 1.30$–3.75, $P = 0.001$–0.016), and herbs, grasses, and lianas ($F = 1.38$, $P = 0.012$) (Fig. 4a and 4b). Shrubs, exotic, ornamental, herb, grass, and liana plants did not significantly differ in the community composition of red-list species ($F = 0.82$–1.02, $P = 0.112$–1.000) (Fig. 4a and 4b).

Consistent with fungal richness, plant identity and plant functional groups significantly shape the total (plant identity at family level: $F = 1.61$, $P = 0.001$; plant functional group: $F = 2.10$, $P = 0.001$) and red-list fungal community composition (plant identity at family level: $F = 1.32$, $P = 0.002$; plant functional group: $F = 1.41$, $P = 0.001$ Fig. 4a and 4b and Fig. S3). Phylogeny did not significantly shape the total ($r^2 = 0.06$, $P = 0.151$) or red-list ($r^2 = 0.12$, $P = 0.113$) fungal community compositions (Fig. 4c). Regarding the variation partitioning analysis (Fig. S4a), the

combination of plant identity and functional group explained the largest variation (15%) in total fungal community composition, followed by the data on plant functional group (6%), the interaction of plant identity, plant functional group, and plant phylogeny (2%), and plant phylogeny in combination with plant identity (1%). Plant identity and phylogeny alone did not explain any of these variations (Fig. S4a).

Only about 14% (166 species) of the total fungi (dominated by mycorrhizal fungi) were found on 1 plant species (Fig. S4b). The host genus-specific fungi were almost exclusively mycorrhizal fungi (89% of total actual host genus-specific fungi (54 species) Table S4), with *Betula* and *Pinus* having twice as many host-specific mycorrhizal fungi than the other tree species (Table S4). Forty-five percent of all fungi were found in up to three plant genera. There was a clear decrease in fungal species that colonized more than three plant genera. Only 16% of fungi live in more than 10 plant genera. No fungus occupied all the investigated plant genera. *Lyomyces sambuci*, a fungus mainly living on the shrub *Sambucus*, was the most ubiquitous fungus found in 32 plant genera. *Peniophora incarnata*, *Byssomerulius corium*, and *Trametes versicolor* colonized the highest number of native plant genera (25).

Different plant genera were associated with different mycorrhizal and wood-inhabiting macrofungi. The similarity of fungal communities between different plant genera was below 30% (Fig. 4). There was no relationship between the community composition of mycorrhizal and wood-inhabiting macrofungi and the phylogeny of plants. The fungal community composition differed greatly even at the class/subclass
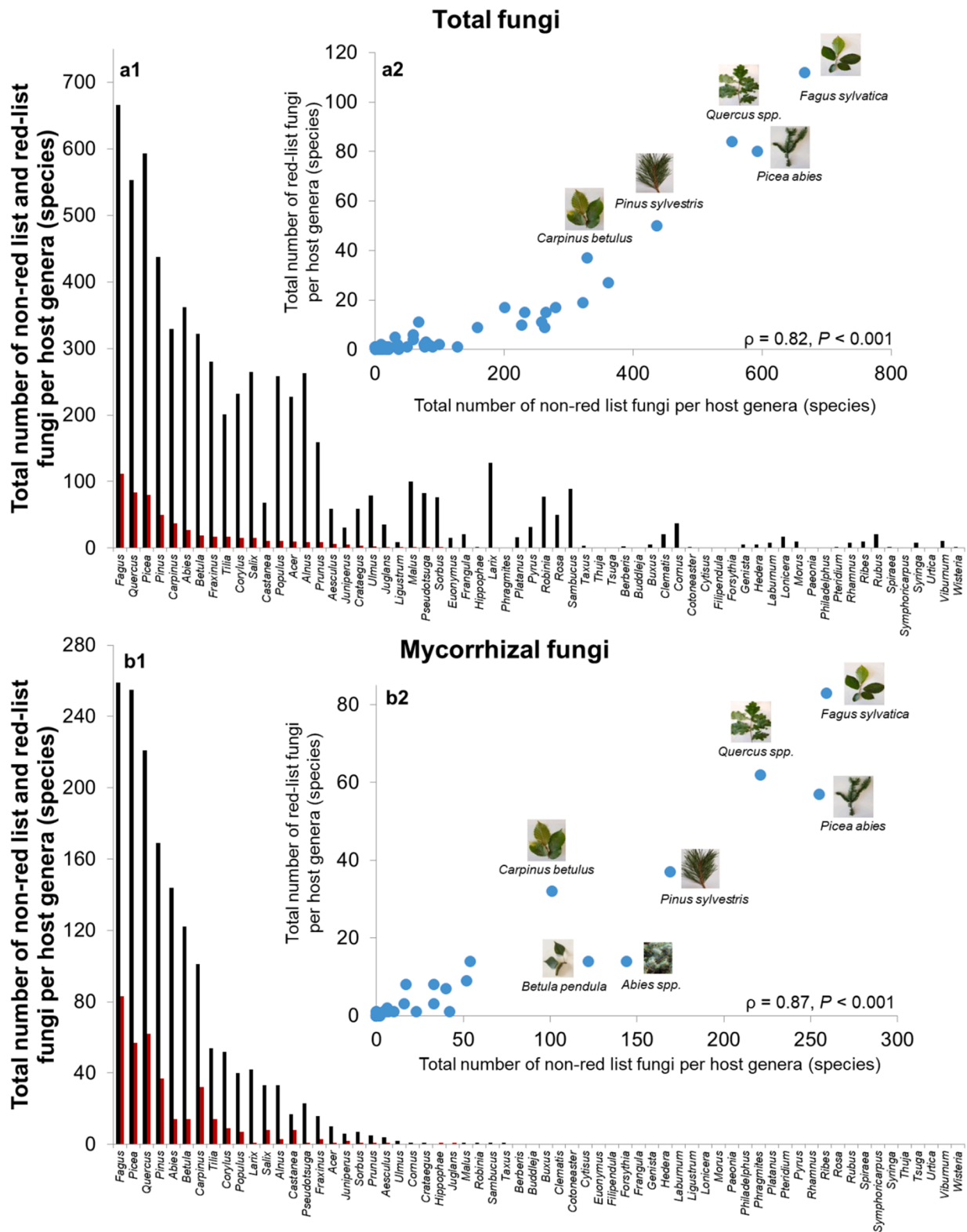
Fig. 3. Number of total (a1) and mycorrhizal (b1) wood-inhabiting macrofungi detected in different plant genera (**first bar** = non-red list species and **second bar** = red-list species). Correlation between detected red-list and non-red list is shown in another graph that integrates to the bar chart (a2 and b2).

levels (Fig. 4). Gymnosperms from Coniferopsida comprised nine genera, but only three species of Pinaceae (*Abies, Picea, Pinus*) formed a distinct group. Nevertheless, there were groups of woody plants that had a large number of fungal species, which formed distinct clusters with similarities higher than 30%. These included Fagaceae (*Fagus* and *Quercus*), Betulaceae (*Betula, Carpinus, Alnus,* and *Corylus*), Salicaceae (*Salix* and *Populus*), Oleaceae (*Fraxinus*), and Tiliaceae (*Tilia*).

Table 2

Red-list and non-red list mycorrhizal and wood-inhabiting basidiomycete macrofungal species richness detected in dominant tree species (with and without correction by its associated cover area).

Plant	% area	Area/tree species (ha)	Red-list fungal species	Total fungal species	Fractional area of *Picea* compared to study species (linear)	Fungi on area of *Picea* (linear)	Red-list fungi on area of *Picea* (linear)	Fractional area of *Picea* compared to study species (non-linear)	Total number of species/area corrected (non-linear)	Red-list species area corrected (non-linear)
Fagus	20	900	112	778	0.20	156	22	0.44	342	49
Picea	4	180	80	673	1.00	673	80	1.00	673	80
Pinus	29	1305	50	487	0.14	67	7	0.38	185	19
Quercus	10	450	84	637	0.40	255	34	0.59	376	50
Other hardwood (*Acer, Carpinus, Fraxinus, Juglans, Ulmus*)	22	990	55	500	0.18	91	10	0.42	210	23
Other softwood (*Alnus, Betula, Populus, Salix*)	15	675	35	536	0.27	143	9	0.50	268	18

3.4. Effects of tree addition and removal

The two simulations, tree species addition and tree species removal, yielded similar results. Four tree genera with the highest fungal richness (*Fagus*, *Picea*, *Quercus*, and *Pinus*) were the most important for maintaining high fungal richness, as shown by the removal approach (Fig. 5). The tree addition approach indicated that adding these four tree genera, having the highest richness of mycorrhizal and wood-inhabiting macrofungi, can maintain a total of 1070 fungal species (91 ± 0.52% (mean ± SD of CI) of total detected fungal species). These fungi included 901 non-red list (92 ± 0.52% of the total detected non-red list species) and 169 red-list (87 ± 1.77% of total detected red-list species) fungal species.

The tree removal approach demonstrated that loss of host that harbored the highest fungal species (*Fagus*) did not significantly affect the overall fungal richness because fungi observed on *Fagus* were also found on other hosts (Fig. 5d). However, loss of the four major tree genera caused significant loss to the system (273 species, 23 ± 1.25% (mean ± SD of CI) of the total detected fungal species). These included the loss of 195 non-red list (20 ± 1.24% of total detected non-red list species) and 78 red-list fungal species (40 ± 4.18% of total detected red-list species). Losing three more tree species (*Abies, Carpinus,* and *Betula*) can be considered as the critical point, as we observed a sharp reduction in both non-red list and red-list mycorrhizal and wood-inhabiting macrofungal richness in the system to 36 ± 1.1% (354 species) and 60.5 ± 3.6% (117 species), respectively. If all 9 genera were removed, this would also cause significant loss to the system (204 and 41 species accounting for 17.5 ± 0.85 and 21 ± 2.65% of detected total and red-list fungal species). Losing *Fagus* in addition to the removal of all conifers caused great losses to the system as the losses of detected total and red-list fungal species reached 26 ± 1.04% and 35 ± 2.81%, respectively. Red-list fungal species were more negatively affected by the removal of tree species than the non-red list species. While 13 tree genera with the highest fungal richness could be removed to maintain approximately 50% of the wood-inhabiting macrofungi in this system, removal of only five of these tree genera (*Fagus, Quercus, Picea, Pinus,* and *Abies*) already reduced species richness of red-list wood-inhabiting basidiomycete macrofungi by almost 50%.

3.5. Does land-use affect fungal diversity?

At the quadrant level, we found that fungal richness was significantly correlated with both forest cover and property diversity (Fig. 6). There was an additional effect, namely, a mixture of ownerships. It emerged that if a quadrant was shared by three owners in a mixed assembly, the fungal diversity was significantly higher than if this quadrant was dominated by just one owner ($t = 3.24$, $P = 0.005$, Fig. S5), independent of whether this owner was the state, the commune, or private. Forest cover and the mixture of ownerships were found to be the predictors that explained high proportion of variances in fungal richness in this ecosystem (Adjusted $R^2 = 0.64$, $F = 15.06$, $P < 0.001$, Table S5).

4. Discussion

4.1. Importance of an urban area for maintaining biodiversity of mycorrhizal and wood-inhabiting basidiomycete macrofungi

Our results clearly show that an urban area and its surroundings serve as an important zone for high taxonomic and functional diversity of mycorrhizal and wood-inhabiting basidiomycete macrofungi. The 64 plant genera of woody species growing in Jena and its surrounding hosts a large number of basidiomycete species (1172 species), accounting for 33.8% and 23% of all basidiomycete fungal species known for the state of Thüringen (3464 species) and Germany (5006 species), respectively (Table S6) on 8‰ of the forest area of Thuringia and on 0.4‰ of the forest area of Germany. The majority of these basidiomycete fungi are mycorrhizal and saprotrophs with a small number of plant pathogens. Plant pathogens in wood are usually underestimated by fruiting body surveys, as most of them reside as mycelia and can only be properly evaluated using molecular approaches (Baber et al., 2016; Purahong, Wubet, Krüger, et al., 2018). The recorded fungi also comprised highly diverse endangered species according to the Red List of Germany (Dämmrich et al., 2016). We found that 27% of the German endangered wood-inhabiting basidiomycetes (representing 16% of the total basidiomycetes on the Red List of Germany) growing in the vicinity of the city of Jena (Table S6). We detected 40% of the German endangered wood-inhabiting basidiomycete macofungi in categories 0 to 3, and even 45% of category G, but only 6% of category R (Table S6).

4.2. Effects of host identity and functional group on mycorrhizal and basidiomycete macrofungi fungal community

The observed significant effect of host identity on mycorrhizal and wood-inhabiting macrofungi is in line with other studies in temperate regions using both fruiting body surveys (Baber et al., 2016; Blaser et al., 2013; Heilmann-Clausen et al., 2005, 2016; Lang et al., 2011; van der Linde et al., 2018) and molecular techniques (Leonhardt et al., 2019; Purahong, Wubet, Krüger, et al., 2018). A low proportion of host-specific fungi were detected in this study. The loss of host specificity may have been enhanced by land-use history. The surrounding area of Jena was an overgrazed grassland with some shrub species until approximately 140 years ago (Schulze & Reichstein, 2019). We expect that some proportion of mycorrhizal and wood-inhabiting basidiomycete macrofungi in old
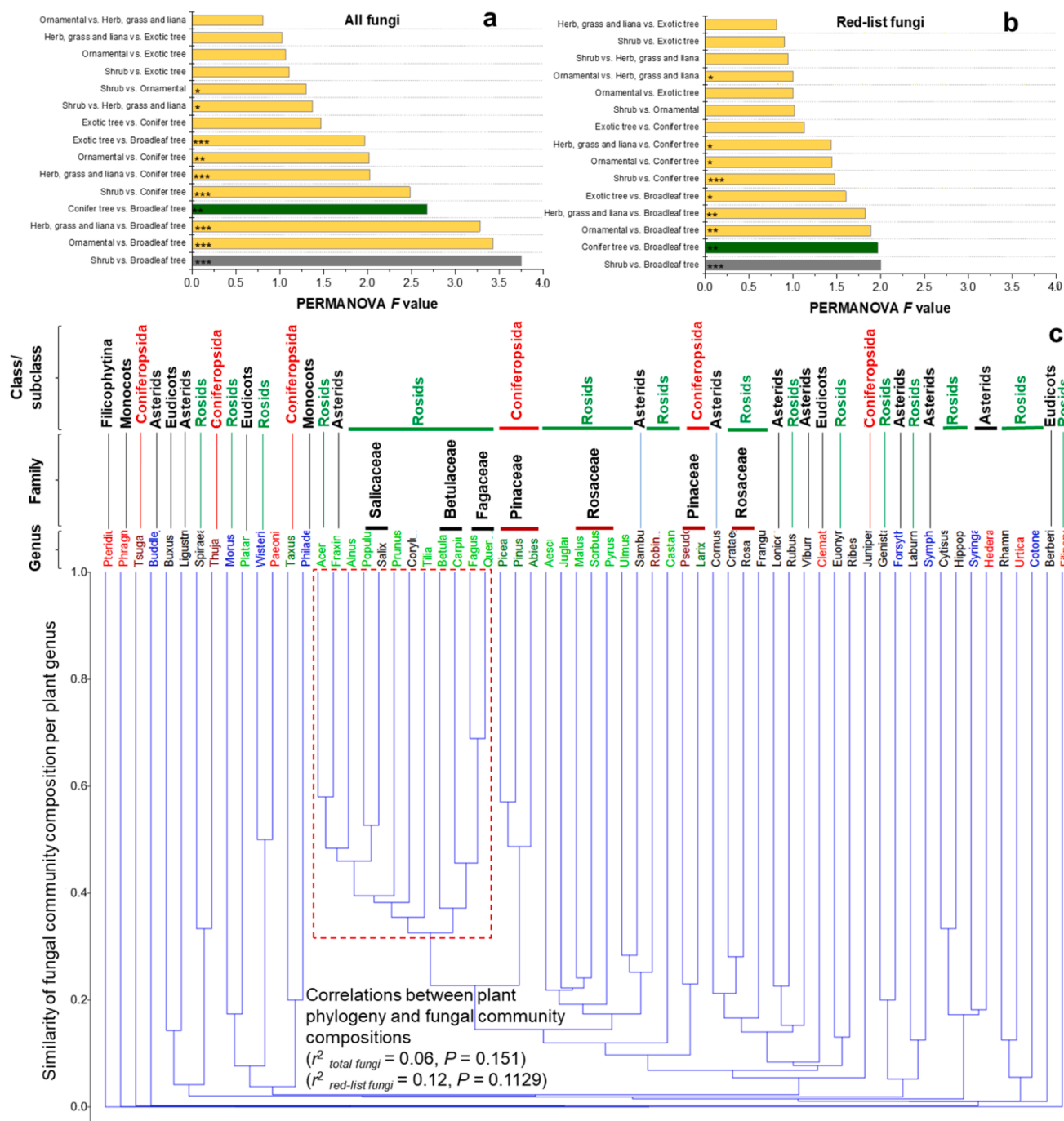
Fig. 4. Effects of plant functional groups on total (a) and red-list (b) basidiomycete macrofungal community composition. (c) Cluster analysis shows effects of plant identity, functional groups, and phylogeny on total fungal community composition. Significant *P* values for PERMANOVA test (a, b) are indicate with asterisk (* $P <$ 0.05, ** $P < 0.01$, and *** $P < 0.001$). Dash-line (c) shows a distinct cluster of trees and shrubs formed with similarity higher than 30%. Plant genera: Dark green – coniferous trees; Bright green – deciduous trees; Black – shrubs; Red – herbs, grass, liana; Brown – exotic plants; Blue – ornamental. Class or subclass of plant species are indicated on the top (green: Rosids, red: Coniferopsida, black: Asterids, Eudicots, Monocots, and Filicophytina).

forests may have remained in the Jena-region living on shrubs after most forest trees had been removed in the Middle Ages. Since 1880, diverse tree and shrub flora have developed together. Thus, the wood-inhabiting basidiomycete macrofungi developed relationships with both tree and shrub species in this study area, which can result in a low proportion of host-specific fungi observed. Almost all basidiomycete species in shrubs detected in this study (414/433 species, 96%) were able to colonize broadleaved trees. The ranking of the tree species harboring the highest richness of total and actual host-specific fungi differed greatly. It remains unclear why *Betula* and *Pinus* host the largest number of host-

specific fungi. One reason, among many others, could be that *Betula* and *Pinus* are the earliest tree species recolonizing Central Europe after the last glaciation (Lang, 1994). They are at least twice as old as most other tree species in the landscape, which may have promoted host specificity. This is in line with a study on phytophagous insects and mites, which showed that time since recolonization is the main driver of fungal species richness in different tree species (Brändle & Brandl, 2001). A longer time for integration into the ecosystem means that host plants can increase the chances of developing relationships with a wide range of macrofungi, including both specialists and generalists. In this
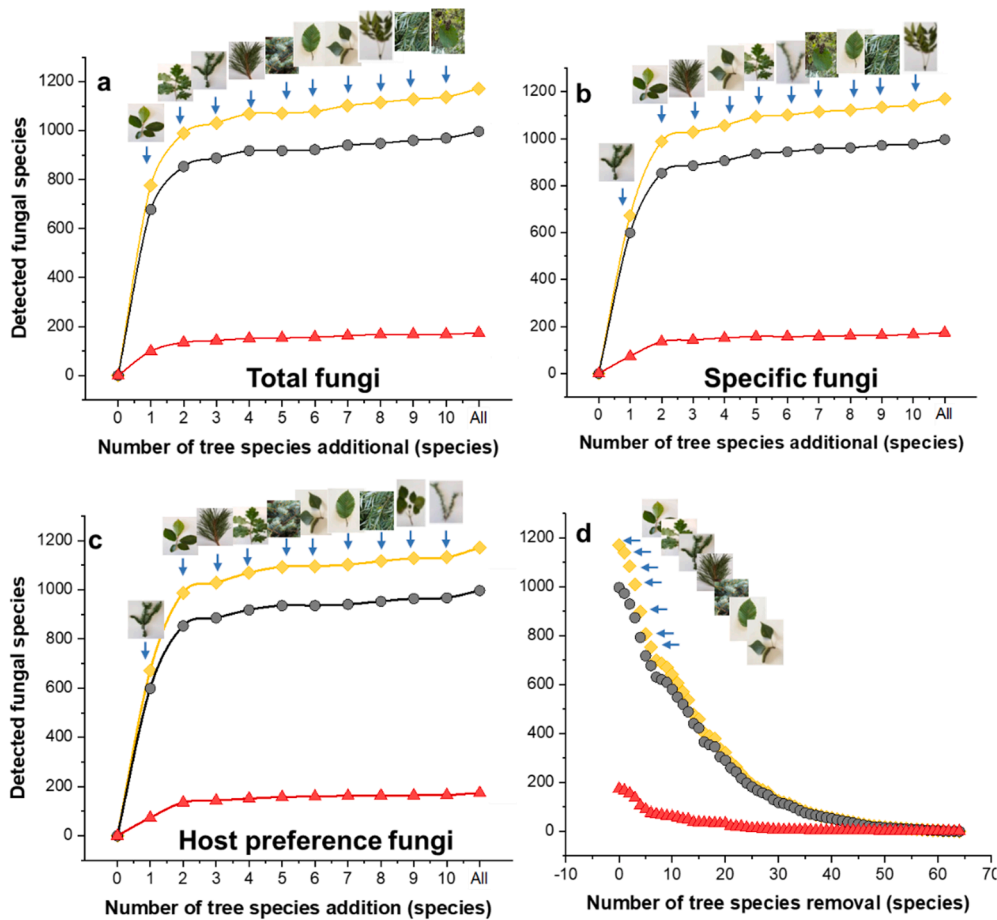
Fig. 5. Number of fungal species detected as the function of tree species addition (a (total fungi), b (specific fungi), c (host preference fungi), and d (removal)). Orders or priorities of tree species addition or removal (a and d) are based on the overall rank of total fungal richness in each tree species (higher richness were added or removed first). Orders of tree species addition in b and c were based on the rank of specific (detected in one tree species) and host preference (detected in 3 tree species) fungal richness in each tree species (higher richness will be added first). Symbol: triangle = red-list fungi, circle = non-red list fungi, and square = total fungi.
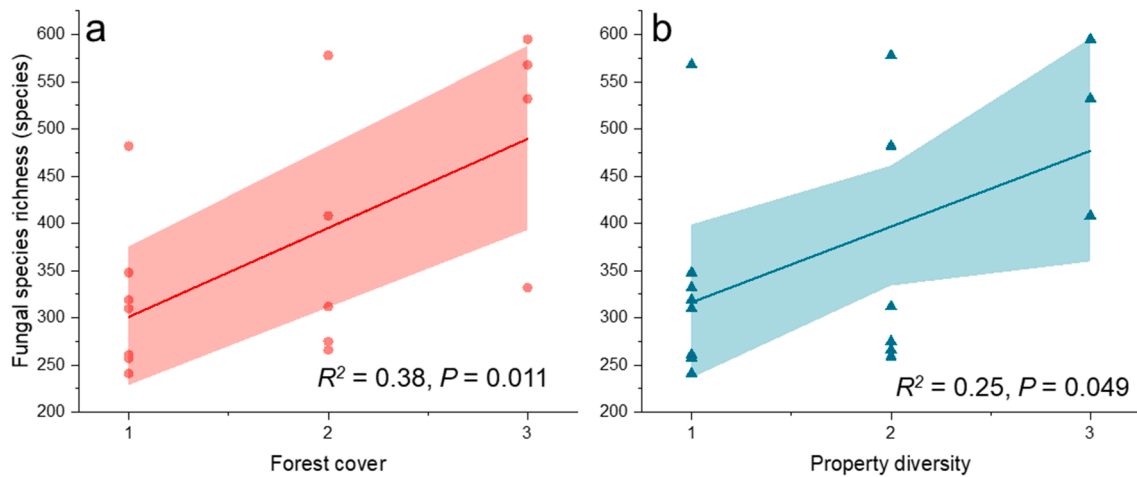

Fig. 6. Pearson correlations (fitted line in linear regression with 95% confidence band) between forest cover, property diversity and fungal richness. The correlation is based on 17 out of a total of 24 quadrats (see Fig. 1). Forest cover: 1 = <30%, 2 = 30–60%, and 3 = more than 60%. Property diversity = proportion of state forest: communal forest: private forest, 1 = (70:10:10), 2 = (50:20:20), and 3 = (30:30:30).

study, we found evidence for host change in mycorrhizal and wood decay fungi during past decades, especially those associated with non-native species, such as *Pseudotsuga* or *Robinia*. Host shifts in fungi may have different origins, for examples climate changes, changes in resource availability, changes in plant species composition (including herbaceous species) (Boddy et al., 2014; Gange et al., 2011; Kauserud et al., 2012; Lee et al., 2015; Mapook et al., 2020). It is very interesting to see that nitrogen fixing *Robinia* assemble more fungal species than

other exotic and even some native plant species. It suggests that new non-native species provide additional resources for mycorrhizal and wood-inhabiting fungal communities, thus their role as a refuge in anthropogenic areas seems to be important.

In this study, we did not detect any fungus that colonized all tree species (true generalists), even though the majority of the plant genera used in this study were common (see Table S1). The fungus *L. sambuci*, associated with the shrub *Sambucus*, is the most ubiquitous fungus,

found in 32 plant genera. This fungus may have persisted in this system for a long time since *Sambucus* is one of the shrub species that remained in this area after the conversion of forest to agriculture and grassland approximately 1000 years ago.

Plant functional groups played an important role in structuring the mycorrhizal and wood-inhabiting macrofungal communities in this study. The differences between the fungal communities associated with conifer and broadleaved trees and shrubs can be explained by the distinct physicochemical properties and anatomy of conifers (Hoppe et al., 2016; Purahong, Wubet, Lentendu, et al., 2018). Although we showed that most fungi associated with shrubs are able to colonize broadleaved trees, we detected significant differences between these two plant functional groups. This is because broadleaved trees host an additional large pool of all mycorrhizal and wood-inhabiting basidiomycete macrofungal species (more then 500 species) that have not been detected in shrubs. Plant architecture (especially size), abundance, taxonomic isolation, and time since recolonization are linked to the host species and contribute to the differences in fungal community assemblages between host species (Heilmann-Clausen et al., 2016; Juutilainen et al., 2011).

4.3. Importance of both deciduous and conifer trees in maintaining fungal diversity

A few common forest trees (*Fagus sylvatica*, *P. abies*, *Quercus* spp., and *Pinus* spp.) hosted the majority of total and red-list fungal species detected in this study, which was consistent after correcting fungal species richness by the area covered by these tree genera (Table 2). Thus, our results may indicate that tree species diversity is less important than host identity and functional groups. The high richness of mycorrhizal and wood-inhabiting basidiomycete macrofungal species in *Fagus*, *Picea*, *Quercus*, and *Pinus* may be explained, at least partly, by their specific wood physicochemical properties and high abundance in the surrounding forest areas. Wood physical (length, diameter, volume, size) and chemical (especially nitrogen, moisture and pH) properties are important factors that influence richness and community composition of wood associated saprotrophic basidiomycete fungi (Purahong, Wubet, Lentendu, et al., 2018). Deadwood of these tree genera provides large habitat patches that can persist for many years with a broad spectrum of substrates and microhabitats for different wood-associated fungi. According to the resources-diversity theory, large trees or volumes of life and dead wood enable fungi to become enriched in these tree species (Purahong, Wubet, Kahl, et al., 2018; Waldrop et al., 2006). Furthermore, the high abundance of *Fagus*, *Picea*, *Quercus*, and *Pinus* in the surrounding forest areas can explain the high richness of both saprotrophic and mycorrhizal basidiomycetes in these tree species (greater than 60% of the total forest cover; Table 2) (Hessenmöller et al., 2011). However, high wood volume and area cover may not always be associated with high fungal richness. For example, *Picea* only covered a small area in the city and surrounding area (180 ha, 4%), but it harbors the highest standardized fungal species richness compared with other plant genera.

The current climate change situation affects conifer and broadleaf trees. However, dieback by drought, together with bark beetles, mainly causes a significant decline in *Picea* and *Pinus*. Thus, future collections may show a strong decline in fungal richness in the study area. Furthermore, nature conservation foresees the eradication of conifers in broad-leaved areas (Ssymank et al., 2019). These situations may lead to significant losses in fungal diversity. In the studied urban system, coniferous tree species harbored 794 basidiomycete fungal species (739 species were hosted by *Picea* and *Pinus* and 204 species were exclusively detected in conifers) as compared to 945 species detected in all broad leaf tree species. Losing *Picea* and *Pinus* from this system would negatively impact fungal diversity. Our results demonstrate that maintaining both broad-leaved and coniferous trees (at least with a certain proportion of coniferous trees) in an urban area and in the vicinity is an important strategy for maintaining fungal diversity.

4.4. What are the values of red-list and rare species and where we can find them?

Plant genera with high fungal richness also have a higher chance of hosting red-list species. The top five tree genera that harbored the highest red-list fungi were *Fagus*, *Picea*, *Quercus*, *Pinus*, and *Carpinus*. We detected a significant correlation between the total number of fungi and the number of rare fungal species per host. In Pinaceae, *Larix* and all other exotic tree species host a very low number of red-list fungal species (0–2 species). Newly introduced species may serve as a "new habitat" for wood-associated fungi, and it seems that colonization of new habitats is more often a chance for generalist species than for those needing small niches (Bässler et al., 2016; Vogel et al., 2017).

The Red List of fungal species contains great uncertainties due to identification difficulties for some genera in the field, and variations in fruiting body occurrence over time (Dahlberg & Mueller, 2011). This results in a comparatively high number of species classified as D (data deficiency). In addition, it remains questionable whether rare species should be incorporated into the assembly of red-list species. As red-list data are based on the occurrence of fruiting bodies, it should be noted that some red-list species may not be as rare or threatened as once thought, but rather they remain as mycelium or in spores, waiting for proper fruiting conditions, making proper identification difficult (Glassman et al., 2016). The inability to produce fruitbodies for long periods may be interpreted as a decline in vitality due to environmental conditions and, therefore, a threat to a species. The large number of fungal species declared as "G = endangered by unknown extent" illustrates the fact that there are no hard data that allow for the calculation of exact percentages of decline over a certain period, as is true for other field such as ornithology. In addition, extremely rare species (R) are debatable, as some species are rare naturally, but some species may, in some cases, be under-recorded due to difficulties in identification or because fruiting bodies have a short life span and the species are thus better classified as D (data deficiency). There is a low proportion of host-specific red-list species per total host-specific species (44/166) and actual host-specific species (12/54). Host-specific fungal species are also prone to extinction if the host trees are removed or disappear from the ecosystem (Purahong, Wubet, et al., 2019).

It is surprising to see a correlation between red-list and non-red-list species, which may hint at a bias in classifying red-list species. To identify the actual status of red-list or endangered fungi at the country scale, molecular approaches such as the application of long-read next-generation sequencing with multigene phylogeny can be helpful in validating the results of fruiting body surveys (Frøslev et al., 2019; Purahong, Mapook, et al., 2019; Purahong, Wubet, et al., 2019; Tedersoo et al., 2018; van der Linde et al., 2018).

4.5. Contribution of exotic trees, liana, herbs, and ornamental plants to mycorrhizal and wood-inhabiting basidiomycete macrofungi diversity

It is noteworthy that exotic trees, liana, herbs, and ornamental plants all together harbored only 15% (178 out of the total species list) of wood-inhabiting basidiomycete macrofungi in the studied urban system. These plants generally do not support fungal diversity. However, there are some exceptions. Among these non-native plants, the exotic tree *Pseudotsuga menziesii* and *Robinia pseudacacia* had the highest richness of wood-inhabiting basidiomycete macrofungi (each tree species harbors 78–85 species). This is consistent with other studies investigating wood-inhabiting basidiomycete macrofungi fungi in European forests (Cierjacks et al., 2013; Purahong, Wubet, Krüger, et al., 2018). This may be explained by the fact that *Pseudotsuga* and *Robinia* are more common in forests (Table S1), especially *Pseudotsuga*, which covers about 2% of the German forest. Thus, *Pseudotsuga* and *Robinia* may serve as examples of the successful modern integration of non-native floral elements. After

all, the so-called native tree species migrated into central Europe after the Pleistocene. *Fagus* arrived about 5000 years ago, became dominant, and had more time for integration than *Psedotsuga* and *Robinia*. With a longer time as a resident of Germany, *F. sylvatica* may have co-evolved with diverse fungi, including ectomycorrhizal fungi from other tree species, without temporal gaps.

4.6. Does high and diverse land-use intensity harm fungal diversity?

Our results demonstrate that very high diversity of land-use intensities in forests in Jena (ranging from state forests for wood production and communal forests for recreation to small private forests for firewood production) do not harm the fungal diversity. In contrast, high and diverse land-use intensity, which is represented by a high diversity of property types and ownership, can even promote fungal diversity. Quadrants with the highest fungal diversity had a mixture of ownership types. Different property types and ownerships can create a gradient of land-use intensity by different forest management practices and promote plant diversity (Von Lüpke et al., 2011; Mölder et al., 2021) which can eventually provide more niches (especially, nutrient sources from different plant species and functional groups) for microbes (Barrico et al., 2018). Thus, small-scale variations in ownership, property size, and associated management can maintain and promote high fungal diversity. The forests of Jena have approximately the same number of fungal species as the National Park Hainich (Gminder, unpublished), which was established on former private land, with a similar property structure as in the forests of Jena. The basis of fungal diversity appears to be the small-scale variation in properties and land use. The inset of Fig. 1 shows the 325 properties. The narrowest land was 4 m wide and 500 m long. The average property size was 0.5 ha/owner. Private forests owned by small landholders are always richer in tree species than state forest land (Von Lüpke et al., 2011). We also observed that fungal diversity was low in all quadrats where one type of ownership was dominant. It is a mixture of ownerships that provides a chance of higher diversity of shrubs and trees. If this land is bought by conservation agencies (as has already begun, see Fig. 1 insert) or absorbed by state or communal forests with uniform management over large areas, this diversity might disappear as creating large-scale sanctuaries results in homogenous land use. Thus, one strategy for maintaining fungal diversity would be to maintain the existing small-scale property structure and land use (Fig. 6 and Fig. S5). At least, the dominant broadleaved deciduous and coniferous trees, which harbor high richness of mycorrhizal and wood-inhabiting basidiomycete macrofungi, should be maintained in urban areas.

4.7. Conclusion and recommendation for maintaining diversity

- Our results suggest that an urban area with small-scale variation in properties and associated management may be the basis for the observed plant diversity and the associated diversity of mycorrhizal and wood-inhabiting basidiomycete macrofungi.
- Conifers, in addition to broad-leaved trees, are important components in maintaining fungal diversity. Decisions, for example, to eradicate conifers in deciduous forests, can strongly negatively impact the biodiversity of mycorrhizal and wood-inhabiting basidiomycete macrofungi, as coniferous tree species harbor substantial diversity of both red-list and host-specific basidiomycete fungi.
- Exotic and introduced tree species are integrated into the system over time and may play an important role in maintaining fungal diversity in urban areas in the future. We recommend preservation of the diversity of properties and management to ensure the diversity of tree species, which consequently maintains fungal diversity.
- Forests which surround cities may be an area that has been insufficiently studied. These areas must be included in future studies to establish and maintain fungal diversity.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.landurbplan.2022.104360.

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