Artenschutz report

Heft 46/2022

Biodiversity and conservation of Basidiomycetes: The importance of urban areas and associated forests for species conservation

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Deutſche Waldlandſchaft mit Baſidien-Pilzen.

Fig. 1 *The picture of a mushroom-rich forest comes from the book of Warburg (1913): Die Pflanzenwelt Vol. 1 with colored plates by H. Eichhorn. The illustration shows a great understanding of the life of fungi. The herb layer indicates a light canopy, and the juniper indicates grazing. The tree species in the foreground are pine and birch, which also play a special role in this study. Beech is in the background. There is no dead wood in the forest except for tree stumps, because lying wood was intensively used as firewood at that time. The following mushroom species (from top left to bottom right) are shown: Birch porling, parasol mushroom, true irritant, chanterelle, tinder fungus, liverwort, broad-leaved henbane, clove swallow, hawk mushroom, boletus, pepper boletus, pine fire fungus, spittlebug, green-leaved sulfur head, bottle sapling, common root fungus, fly agaric, Hallimasch, long-stalked garlic swallow.*

Introduction

Fungi are among the most species-rich organisms in our forests, with approximately 75,000 species in Europe (SENN-IRLET et al. 2007) (MICHAEL et al. 1985, HAWKSWORTH 1991, HAWKSWORTH & LUECKING 2017). They are associated with plants as mycorrhizae (Smith & Read, 1997), they decompose complex organic molecules in deadwood (STOCKLAND et al. 2012) and soil (ZECH & KÖGEL-KNABNER 1994), and they influence vegetation composition as parasites (TANUNCHAI et al. 2022). They are popular for people as edible mushrooms (GMINDER 2009, GERHARDT 2020).

In the following, we restrict ourselves to the wood-associated basidiomycetes, which can be recognized and collected in the forest. These basidiomycetes occur in Germany with about 3,300 species, of which 8% are endangered (Red List 0 to 3 and G, DÄMMRICH et al. 2016). In the study area of Jena, 35% of the wood-associated basidiomycetes and even 14 % of the Red List species of Germany are found (GÜNTHER et al. 2019).

In order to protect macrofungi, more public education about the importance of fungi, leaving dead wood and habitat trees is needed (SENN-IRLET et al.

Fig. 2 View of Jena in the direction to the west. The far-stretched ridge is the high plateau of Cospeda with the Paulsberg as the highest elevation (351 m NN). The city of Jena is located at 150 m NN (photo: E.-D. SCHULZE).

2007). However, the importance of urban environments for the conservation of fungal species diversity and especially for endangered species is still poorly understood. In this context, the Jena area seems to be a suitable study area to understand the distribution of fungi in urban habitats and to develop conservation concepts.

In the following paper, we report on fungal diversity in forests close to the city of Jena. These are intensively and variably used forests where timber is harvested, drinking water is obtained, and where the population seeks recreation.

The study area and methods

Jena, with about 110,000 inhabitants, is located in the middle Saale valley in eastern Thuringia (50° 55' N, 11° 35' E, 140-397 m NN) (Fig. 2).

During the Saale Ice Age, glacial masses advanced as far as Jena. The Saale drained to the west at that time. Only after the melting of the ice shield, the Saale flow northward in the preformed valley and cut canyon-like through the limestone layers of the middle Mesozoic. Thus, steep eastern and western slopes were formed. Free rock is visible on the hard oolite, terebrate and Schaumkalk layers (SCHULZE et al. 2006). Remnants of the terminal moraine with acidic rocks are located in the valley basin and on the Muschelkalk plateau at the southern edge of Jena. Thus, the study area is dominated by Mesozoic limestone on the slopes and alluvial quartz sands and clays from the Thuringian Forest in the valley.

In the post-glacial vegetation development, pine and birch formed the first forests about 10,000 years ago. Hazel followed, shortly after oak, elm and linden. It was not until about 5,000 years ago that the beech migrated, followed somewhat later by the hornbeam. However, already earlier than beech, spruce establish itself in Central Germany (LANG 1994, FIRBAS 1949). Already FIRBAS (1952) defined the border to the postglacial Atlantic climate period for the central German dry area by increasing *Tilia* pollen values and by the beginning of a continuous curve of *Picea abies*. A pollen diagram from the Erlensee near Weimar (SCHMIDT 2011, 10 km distance to Jena) also supports this classification (Fig. 3). Here, values above 6 % of the pollen sum refer to a regional presence of this woody species. Cereal pollen occurs since the band ceramics in the early Atlantic and thus before beech arrived. Pollen diagrams from the Jena area document furthermore that spruce remained an integral part of the vegetation in the Jena area even after the immigration of beech (SIEBERT et al. 2004, TIPOLD 2010). Also, in the oldest flora of Jena by RUPP (1718) spruce was mentioned. Thus, it is a natural element of the Jena flora.

The Jena region is remarkable for a documented dramatic change in land use over the last 150 years (Fig. 4). Ernst Haeckel, known for accurate drawings of organisms, drew a watercolor of the western slopes of the Saale Valley in 1858. This watercolor shows overgrazed slopes. Trees existed only in the softwood floodplain along the Saale. Hedgerows can be seen on the east side of the Saale and at road cuts. Despite this extensive devastation of

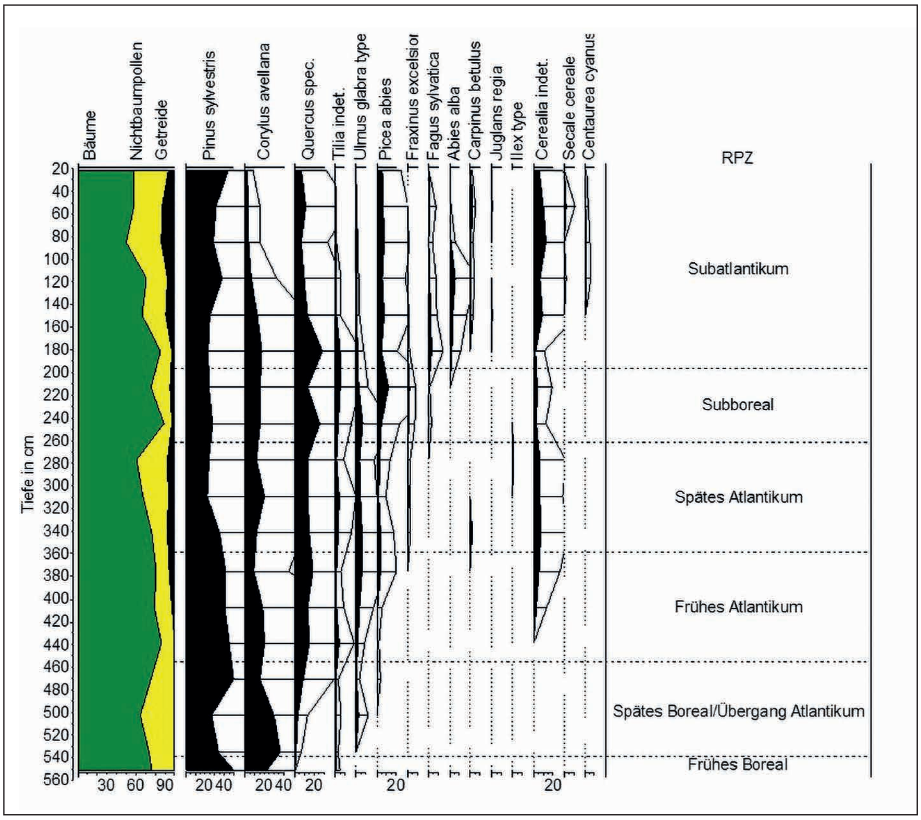

Fig. 3 Strongly simplified pollen diagram from Lake Erlensee (south of Weimar) in percent related to the pollen sum (after Schmidt 2011). The coarsely striped bars are a 5-fold exaggeration of the pollen findings for better marking of low pollen amounts.

Fig. 4 Watercolor by Ernst Haeckel, 1858, showing from right to left the Kernberge (375 m NN), the Ziegenhain valley with the village of Ziegenhain in the background, the Wilhelmshöhe with the Fuchsturm (391 m NN), the Gemden valley, the Jenzig (385 m NN), the Kunitz (385 m NN) and the Tautenburg forest (330 m NN) on the northeastern horizon. The picture was drawn from a site now occupied by the administrative buildings of Schott glass company.

forest vegetation in the Saale valley, there were forest remnants only on the limestone plateau and in deeper valley cuts (SCHÖNHEIT 1850).

The bare slopes of 1858 were afforested since 1850 (LOMMER 1896) and are forested today (see figure in SCHULZE et al. 2006, p. 117). The forest succession has not been completed until today. The first forest generation of pines is still recognizable in today's emerging deciduous forest.

Until now, it has been unclear whether fungal recolonization has occurred. It is a goal of this work to analyze the status of fungi after 150 years of reforestation. Due to historical forest devastation, no old growth forests exist in the Jena area. Even solitary old trees of beech and oak that were used for feeding pigs, lack typical fungal species such as, which are observed on old trees in other regions.

The studied region was divided into 24 subplots based on ordinance maps (Fig. 5), and the fungal findings were assigned to the respective quadrant as the locality. The present tree species composition is determined by the high proportion of private forest and by the management of the large forest owners (state and communal forest). In part, the forest composition is also the result of uniform management of the private forest during the GDR period.

In the study area, deciduous forest has the highest area share of 46 % (Tab. 1) on a total of 2,565 ha in all its forms of forests. Pine, including black pine, covers a larger area than beech. Spruce has an area share of only about 4%. Shrub vegetation and hedges do not belong to the forest area, but cover about 5 % of the open land (pers. comm. M. Rindt, Municipal Forestry Office).

The region around Jena is characterized by a diversity of forest ownership. 11 % is state forest, 33 % is communal forest and 56 % is private forest, with communal forest belonging to different municipalities and in private forest the plots are mostly under 5 ha.

This paper is a summary of published fungal data for 300 years (RUPP 1726, BENEDIX 1947) and the results of a 30-year fungal survey from 1988 to 2018 (GÜNTHER et al. 2019) and an evaluation of these fungal collections (PURAHONG et al. 2022).

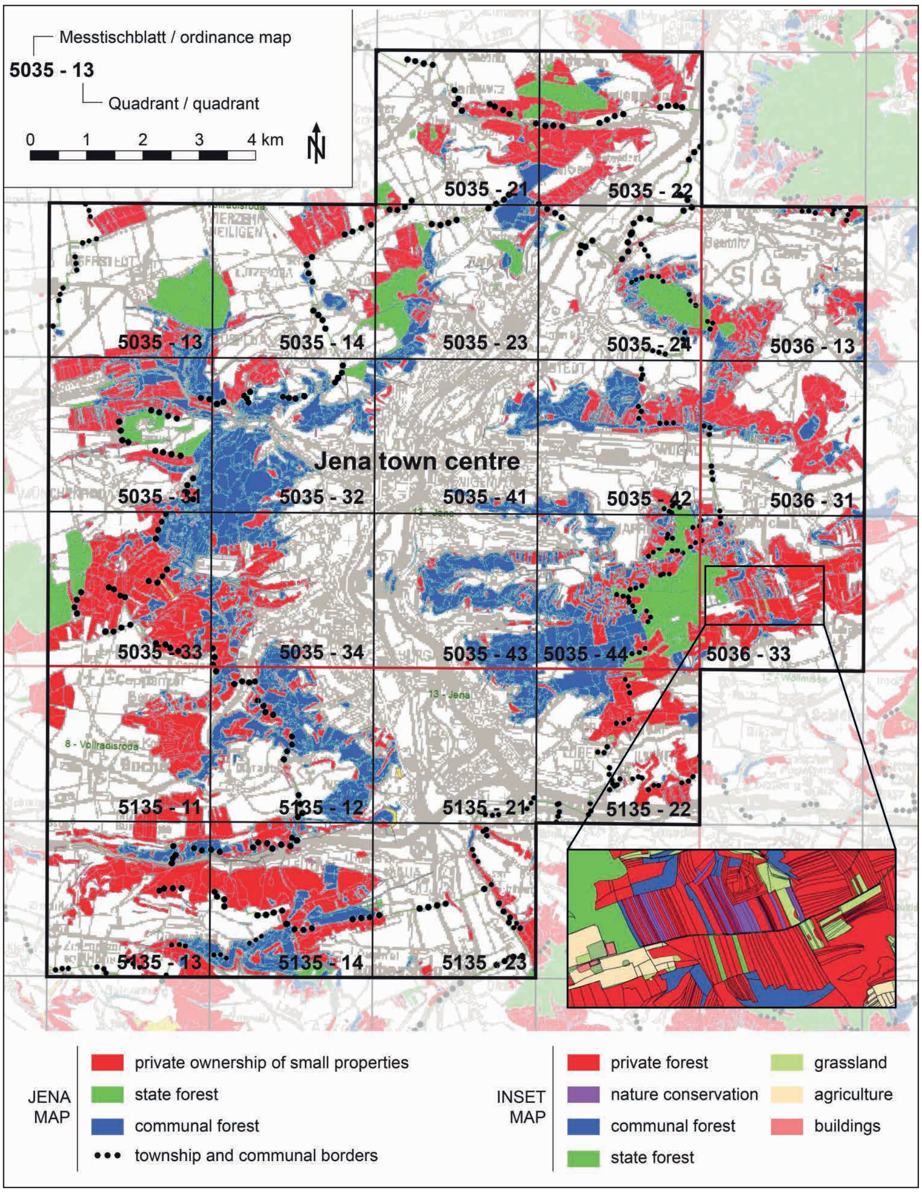

Fig. 5 The study area with the different ownerships in the forest.

Table 1 Area distribution of tree species in the study area (GÖTZE 2018). Hardwoods include the genera maple, ash, hornbeam, elm, walnut. Softwoods considered are the genera birch, alder, poplar, willow, linden.

Tree species	Cover in ha	% of forest area
Pine	1.755	39
Hardwood	990	22
Beech	900	20
Softwood	675	4
Oak	450	10
Spruce	180	4
Sum	**4.500**	**100**
Area of the study region	**12.000**	**37 % forest**
Shrubs and hedges	200	5 % of non-forest area

Basidiomycetes were found on 64 woody or woody plant species in Jena. These **host species** were grouped according to the following definitions (PURAHONG et al. 2022):

- Dominant, silviculturally used tree species: beech, oak, spruce, pine.
- Hardwood: maple, ash, hornbeam, elm, walnut (cherry is assigned to fruit trees)
- Softwood: birch, alder, linden, poplar, willow
- Fruit trees: apple, pear, cherry, peach, plum
- Non-native tree species: Douglas fir, hemlock, arborvitae, black locust
- Shrub and hedge species: barberry, broom, blackberry, box elder, buckthorn, honeysuckle, broom, laburnum, dogwood, hazel, elderberry, currant, buckthorn, privet, peony, rose, buckthorn, blackthorn, snowball, spirea, juniper, hawthorn
- Climbing plants: Ivy, Clematis
- Woody species: bracken, finger shrub, meadowsweet, peony, sage, reed
- Ornamental shrubs: forsythia, jasmine, mulberry, summer lilac, dwarf medlar

In addition to the plant groupings, we distinguish two silviculturally important groupings of tree species:

- Hardwood: maple, birch, beech, rowan, oak, alder, ash, hornbeam, chestnut, linden, poplar, sycamore, elm.
- Softwood: yew, spruce, pine, larch, fir

Classification into functional groups of woody plants is difficult for some species:

Juniper, for example, has been placed with shrubs because this species follows grazing. Walnut is classified as hardwood, although this species is considered more of a cultivated plant because of the fruits. Hazel is a typical hedge species. However, it was also planted in plantations in the Jena area because of its fruits. Willows were assigned to trees as softwood, although there are also shrubby willows.

The following functional groups were distinguished among **fungi**:

- ***Mycorrhizal fungi*** are the species that form a symbiotic relationship with the plant, absorb water and nutrients, and are supplied with carbohydrates from the plant (SMITH & READ 1997). Among the mycorrhizal fungi, there are different forms that are important in this work:
  - The ectomycorrhiza, which invades the root cortex between the root cells but not the cells of the host. The ectomycorrhiza is the typical symbiont of the Gymnosperms and the Fagales, among others. In addition, many saprobionts belong to this group. This group of fungi was studied in the present work.
  - The endomycorrhiza (arbuscular mycorrhiza), which invades the cells of the root cortex of the host and forms tangled structures (vesicles). These are glomeromycota, which were not studied in this work. Arbuscular mycorrhiza occurs on herbs and on shrubby woody plants (hedge species). In addition, it is found on trees whose families have tropical or subtropical distribution (maple, ash, and others).
  - There are other types of mycorrhizae, e.g., ericoid mycorrhiza, but they are not important for the present study.
- ***Saprobionts*** are species that live on dead organic matter.
- ***Parasites*** are plant pests called pathogens.

Among fungi, we distinguish in this work between **generalists**, which live on many host plants, and **specialists**, which occur as hosts on only one or a few woody plant species.

For a comprehensive list of host plants, the findings from Jena were compared with the basidiomycetes of Baden-Württemberg (KRIEGLSTEINER 2000a, b, 2001, 2003, 2010).

Results

1. The numbers of protected and endangered fungal species in the Jena area is comparable to the number of species in the forests around Ulm and in the Hainich National Park.

The Ulm and Jena areas are mycologically well-studied limestone regions (ENDERLE 2004, GÜNTHER et al. 2019). In both regions, the first fungal publications appeared in the early 18th century.

"Die Pilzflora des Ulmer Raumes" of 2004 includes 2,157 fungal species (excluding phytoparasites, slime molds) in a space of 16 ordinance map sheets (16 sheets á 132 km² = 2112 km²). The study area of Jena is smaller with 2 ordinance map sheets (about 185 km²), contains a total of 1966 large fungal species (excluding phytoparasites, slime molds) by 2018. The species number of the Hainich National Park is lower with 1,646 species on 75 km². At the landscape level, species saturation is apparently reached with about 2,000 fungal species in a study area of about 200 km^2.

2. Conifers harbor a surprising diversity of fungal species. The importance of hedgerow species has been underestimated.

The species richness of fungi for individual tree species, if they would develop as a monoculture in the same climate over a large area, is not known. However, it is surprising that spruce is associated with almost as many fungal species (>86%) as beech on one-fifth of the growing area (Table 2). Hedgerows and shrubs, taken as a group of woody species, also contain an unexpectedly high number of fungal species, although this vegetation type has been insufficiently studied.

Mycorrhizal fungi are similarly species-rich as saprobionts in the main tree species beech, spruce, oak, and pine. In contrast, saprobionts outnumber species in hardwoods, softwoods, fruit trees, and shrub species, keeping in mind that some of these woody species are associated with arbuscular mycorrhizae, which were not studied here (Wang and Qiu, 2006, see also Table 3).

Among softwoods, birch was colonized by the highest number of basidiomycetes, followed by linden. Among hardwoods, hornbeam has the highest number of basidiomycetes. The remaining hardwood species are also associated with arbuscular mycorrhiza. Thus, the number of ectomycorrhizal fungi is lower compared to the number of saprobionts (Table 3).

Among the red list species, the main tree species show the highest numbers of species. The high number of category 2, 3, and G species is striking.

For the less well-studied hedgerows and shrubs, Table 2 further highlights the fungi that occur with these woody species. It can be seen that most of the shrubs growing in hedges are associated with arbuscular mycorrhiza. This results in an apparent dominance of saprobionts over mycorrhizal fungi, since arbuscular mycorrhizae were not identified in the present work. Among the hedge species, hazel has the most basidiomycetes, since hazel has no arbuscular mycorrhiza. Elderberry, hawthorn, and roses are also basidiomycete-rich, whereas arbuscu-

Table 2 Total number of species of fungi (basidiomycetes) found and number of species separated by functional groups (myk = mycorrhizal fungus, sap = saprobiont, par = parasite) and Red List status. Occurrence on the dominant tree species, softwoods, hardwoods, fruit trees, and hedgerows of Jena are shown separately. The columns cannot be summed up because the same fungal species can occur on several hosts and thus on different functional groups of woody plants.

Tree species	Species number of fungi	myk	sap	par	sap/ par	myk/ sap	Red List	RL 1	RL 2	RL 3	RL G	RL R
Beech	778	341	349	3	60	28	112	3	20	40	44	5
Spruce	673	312	304	2	28	28	80	4	9	32	27	8
Oak	637	283	276	3	58	19	84	2	16	29	32	5
Softwood	536	166	655	9	169	13	52		5	13	33	1
Hardwood	500	260	684	9	137	72	68		12	18	35	3
Pine	487	206	244	2	19	15	47	1	7	20	18	1
Larch	128	42	72		9	4	1			1		
Orchard-trees	340	8	153	5	164	10	12		1		11	
Hedges	953	112	645	8	169	21	46		5	9	26	6

lar mycorrhiza dominates in the other shrubs and in ornamental shrubs. The low number of parasitic basidiomycetes is particularly striking in hedgerow shrubs (Table 3).

The importance of a single tree species to fungal diversity cannot be determined from the total number of fungal species associated with specific tree species. This is in part due to the different areal proportions of the hosts in the cover in the study area. In addition, most fungal species colonize multiple hosts, the importance of a single tree species to fungal diversity cannot be directly inferred. PURAHONG et al. (2021) therefore used a model experiment to computationally successively remove individual tree species from the study area and determine how fungal diversity would suffer from the loss of a woody species as a host (Table 4).

It can be seen that if beech and oak are lost, the impact on fungal diversity is less than if spruce and pine are lost. The deciduous trees have mainly fungal species that are also found on other woody species. The conifers harbor numerous fungal species that are only tied to them. Thus, the loss of conifers due to drought and bark beetles in recent years has had a greater impact than if beech were affected.

Table 3 Number of Red List species of wood-inhabiting basidiomycetes on the hedge species, their way of life and mycorrhizal type.

Genus	Species number of fungi	Mykorrhiza-Type	myk	sap	par	sap & par	myk & sap
Juniperus	37	AM+ECM	8	24		4	
Berberis	3	AM		2		1	
Buxus	5	AM		3		2	
Cornus	38	AM	1	27		9	1
Corylus	249	ECM	61	146	1	38	3
Crataegus	63	AM+ECM		49	1	9	4
Cytisus	1	AM				1	
Euonymus	16	AM		13		3	
Frangula	22	AM+ECM		15		6	1
Genista	5	AM		5			
Hippophae	3	AM	1			2	
Laburnum	8	AM		3		4	1
Ligustrum	11	AM		8		3	
Lonicera	17	AM		14		3	
Rhamnus	8	AM		8			
Ribes	10	AM		8	1	1	
Rosa	51	AM		45		5	1
Rubus	21	AM+ECM				19	2
Salix	281	AM+ECM	41	184	2	46	8
Sambucus	91	AM+ECM		79	3	12	
Spiraea	2	AM		2			
Viburnum	11	AM		10		1	

AM= arbuskular Mykorrhiza, ECM= Ekto-Mykorrhiza

Table 4 Computational experiment on the effect of losing a tree species (PURAHONG et al. 2022). In one experiment, beech and oak were removed first and the effect on fungal species diversity was considered. In a second experiment, spruce and pine were taken first, and the effect on fungi was considered.

Model experiment	Total loss of fungal species	Loss of common species	Loss of red-list species
Beech and oak as first tree species removed	88	60	28
Spruce and pine as first tree species removed	117	86	31

3. **There is no fungal species growing on or with all occurring woody species. At the same time, there are few fungal specialists.**

Generalists

Among the generalists that colonize more than 30 host species, the bark fungi stand out as having a particularly wide host range (Table 5):

- The elderberry bark fungus (*Lyomyces sambuci*), which belongs to the order of the bristly shibbles (Hymenochaetales), is the fungus with the highest host species spectrum (32) on woody plants (Fig. 6a). Nationwide, *L. sambuci* occurs on more than 50 woody plants.
- The flesh-red cystid bark fungus (*Peniophora incarnata* and the gray-blue cystid bark fungus (*P. lycii*) are representatives of the Russulales and colonize 32 and 31 host species, respectively.
- The leathery wrinkled fungus (*Byssomerulius corium*) is a member of the stem porling family (Polyporales) (30 host species).
- The Removable Stumpfoot (*Crepidotus cesatii*) (Fig. 6b), the Velvet-footed Ruffle (*Flammulina velutipes*) (Fig. 6c), and the Detaching Bark Fungus (*Cylindrobasidium laeve*) are assigned to the order Mushroom-like (Agaricales) (30 host species).
- The butterfly bramble (*Trametes versicolor*) belongs to the Polyporales (cover photo, Table 5) was found on 30 host species).

Despite the wide range of host species of most fungi, only 3 tree species (beech, oak, and willow) are colonized by all generalists despite large differences in wood structure and wood chemistry. Obviously, the generalists belong to very different families. They are phylogenetically very diverse, and a common strategy for colonization requires further investigation.

Specialists

Specialists are those fungal species that occur only on one or a few woody species

Table 5 The saprobionts with the broadest host range. A threshold of 30 host species was set for this work. This threshold may not be universal.

Fungal species	**myk/sap/par**	*Abies*	*Juniperus*	*Larix*	*Picea*	*Pinus*	*Pseudotsuga*	*Taxus*	*Tsuga*	**Conifers**	**Deciduous trees**	**Fungi per tree species**
Lyomyces sambuci	sap	1			1	1		1		4	28	32
Peniophora incarnata	sap	1			1	1				3	29	32
Peniophora lycii	sap	1	1		1	1				4	27	31
Byssomerulius corium	sap	1		1	1	1				4	26	30
Crepidotus cesatii	sap	1		1	1	1				4	26	30
Cylindrobasidium laeve	sap	1		1	1	1				4	26	30
Flammulina velutipes	sap/par	1			1	1				3	27	30
Trametes versicolor	sap/par	1	1		1	1				4	26	30

Fig. 6a
Elderberry bark fungus (Lyomyces sambuci)

Fig. 6b
Removable-leaved stump-foot (Crepidotus cesatii)

Fig. 6c
Velvet-footed turnip (Flammulina velutipes)

(photos: M. THEISS)

of a genus. A distinction is made between the "apparent" specialists, which occur only in the flora of Jena or Baden-Württemberg on one woody species but colonize other woody species in other regions of Germany, and the "actual specialists", which, as far as we know, also occur in Europe only on one woody species.

Among the apparent specialists (specialists s. l.) the highest number of host-specific fungi is found on spruce, followed by beech, whereas among the actual specialists (s. str.) birch and pine have the most species. It is unclear why birch and pine have so many specialized fungal species. One reason could be that these two genera were the first tree species to recolonize Central Europe after the last ice age. As landscape features, they arrived earlier after glaciation and therefore they are at least twice as old as most other tree species in this region. This may have promoted host specificity. The history of colonization after the ice age and the recolonization of the Jena area by forest species could thus be an important factor in understanding the species diversity of fungi.

The specialists (s. str.) are mainly mycorrhizal fungi (Table 6 and Fig. 7). Among the saprobionts, there are only a few specialists in total; oak stands out with 3 species: the mosaic layer fungus (*Xylobolus frustulatus*), the oak Schillerporling (*Inonotus dryophilus*), and the oak leaf-thread helminth (*Mycena polyadelpha*).

Fig. 7 shows two representatives of specialists among mycorrhizal fungi: the

Table 6 The distribution of specialists s. l. and s. str. on different tree species, in total and separately by mycorrhizal fungi and saprobionts.

	Birch	Pine	Larch	Beech	Spruce	Alder	Willow	Oak	Hornbeam	Hazel	Populus
Number of host specific fungi s. l.	13	20	8	21	24	5	4	9	3	1	2
Number of host specific fungi s. str.	11	10	7	7	5	4	4	3	2	1	1
Mykorrhizae	10	9	7	7	4	4	3	1	2	1	1
Saprobionts	1	1	0	0	1	0	1	3	0	0	0

Fig. 7a *Bitter sooty porling (Boletopsis grisea) (photo: J. WIESNER).*

Fig. 7b *Spruce irritant (Lactarius deterrimus) (photo: A. GMINDER).*

Fig. 7c *Mosaic layer fungus (Xylobolus frustulatus) on heartwood of old oaks (near Stadtroda) (photo: A. GÜNTHER).*

Fig. 7d *Pine fire fungus (Porodaedalea pini) (photo: A. GÜNTHER).*

rare *Boletopsis grisea* on Scots pine and the common *Lactarius deterrimus* and in Fig. 7 c+d two representatives of specialists among saprobionts: the mosaic layer fungus (*Xylobolus frustulatus*) on oak and the pine fire fungus (*Porodaedalea pini*) on Scots pine.

The aforementioned division into generalists and specialists are cornerstones of a distribution (Fig. 8) that has a maximum among the specialists. The number of fungal species decreases with the number of host species that can be colonized by a species and reaches very low values for the true generalists. The division between mycorrhizal fungi and saprobionts shows that mainly mycorrhizal species are specialized. There is no mycorrhizal species among the generalists.

Fig. 8 does not indicate the importance of individual plant hosts. Since the number of fungal species colonizing different numbers of hosts is continuously decreasing, a quotient was formed from the number of species of fungi growing on hardwood species and the number of fungi growing on softwood. A high quotient means that more fungal species are found on hardwoods than on softwoods. A low quotient means that coniferous wood determines the diversity of fungi. This quotient is now examined in terms of the number of host plants that a fungal species colonizes, i.e., we examine the dependence of the quotient of fungal species on hardwood to softwood as a function of the number of host species per fungal species. Here, a high value on the x-axis represents the group of generalists and a low value the group of specialists. Similarly, the quotient was also examined for fungi on shrub species in relation to the number of fungi on coniferous wood. As the number of host species per fungal species decreases, the quotient decreases linearly, i.e., the importance of conifers as hosts increases. Generalists are thus found mainly on hardwoods and on shrub species. Specialists, on the other hand, are mainly found on conifers.

Referring to the recolonization of the Jena area after forest devastation in the 18th and 19th centuries, Fig. 9 is an indication that generalists survived the period of deforestation on shrub species and migrated back to hardwoods only after reforestation. In this context, beech was a "neutral" wood that was colonized by a particularly large number of saprobionts. This also explains the finding in Table 4 that beech extinction would have relatively little effect on Jena fungi. The situation is different for fungal specialists that depend on coniferous wood. Coniferous wood must have been present in the Jena area during the period of deforestation.

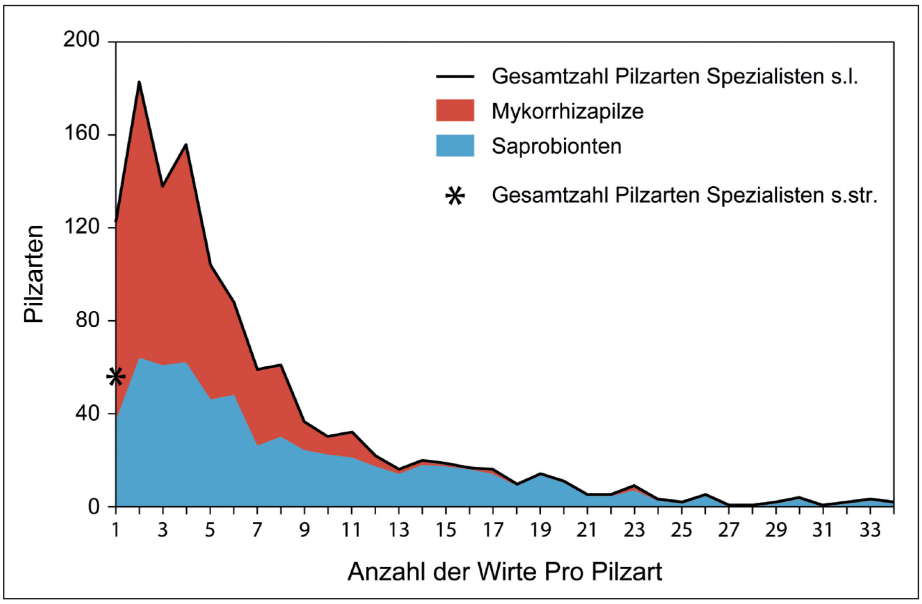

Fig. 8 *The number of fungal species (y-axis) colonizing different numbers of host species (x-axis: number of hosts per fungal species). The figure is based on the findings in the study area and treats the specialists s. l., i.e. fungal species that also have other hosts elsewhere in Europe. Therefore, the number of specialists in the narrower sense (s. str.) was additionally entered as a point.*

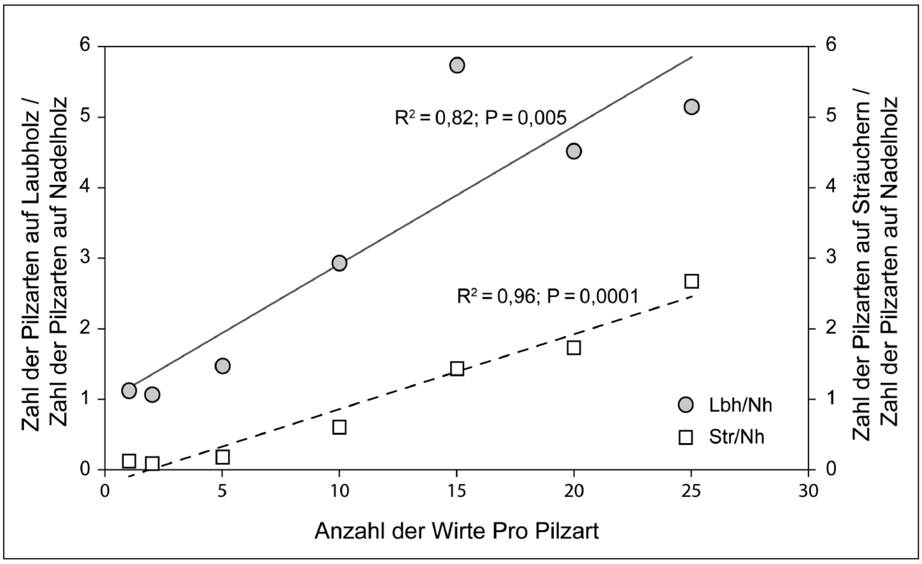

Fig. 9 *Ratio of fungal species on hardwood to softwood (left y-axis) and ratio of fungal species on shrub species to fungal species on softwood (right y-axis) in relation to the number of wood species colonized by a fungal species (x-axis). The dashed line indicates fungal species on shrub species and the closed line indicates fungal species on hardwoods per coniferous wood.*

4. Contribution of exotic trees, lianas, herbs and ornamental plants to the diversity of mycorrhizal and wood-associated basidiomycetes.

Exotic trees, lianas, herbs, and ornamentals harbor only 15% (178 of the total species list) of woody-associated basidiomycetes and thus show low fungal diversity. Douglas fir, *Pseudotsuga menziesii*, and black locust, *Robinia pseudoacacia*, are obvious exceptions. Douglas-fir hosts 86 species (60% saprobionts, 30% ectomycorrhizae) and black locust 80 species (100% saprobionts, 0% ectomycorrhizae, as black locust has only arbuscular mycorrhiza). The species richness of fungi on Douglas-fir and black locust is confirmed by other studies (CIERJACKS et al. 2013; PURAHONG et al. 2019). It could be that *Pseudotsuga* and *Robinia* were more commonly grown and used. Douglas-fir is managed on about 2% of the German forest. For Robinia, a more precise figure on the growing area is not avaiable, since this tree is also part of a ruderal flora outside the forest area and was technically used mainly in landscaping to fortify steep embankments. *Pseudotsuga* and *Robinia* are examples of recent integration of non-native floral elements.

Because the vegetation history of Douglas-fir and *Robinia* is fairly well known, these two species provide opportunities to assess fungal colonization of new habitats. American Douglas-fir was imported to Germany in 1850. However, it has been cultivated on a larger scale for forestry purposes only after 1945 (SCHÜTT et al. 2004). This means that forest fungi have been able to colonize Douglas-fir for about 70 years. In terms of the total number of fungi associated with Douglas-fir, this would be a colonization rate of about 1 fungal species/year. In contrast, *Robinia* has been used in southern Germany since 1700, mainly for stabilization of special sites (railroad embankments) (SCHÜTT et al. 2006). Over 300 years, 80 fungal species colonize black locust, which would be a colonization rate of 1 fungal species/3 years on special sites.

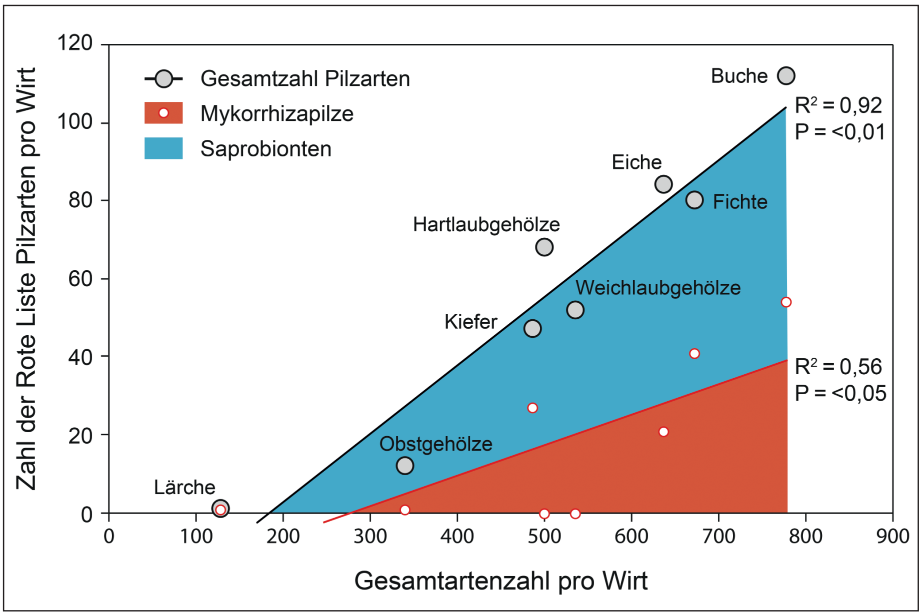

Fig. 10 *The relationship between Red List fungal species and the total number of fungal species found on a woody host.*

5. Red lists and rare species

One would suspect that on sites or tree species with few fungal species, they would be rare or endangered more frequently. Further, one would expect the number of Red List species to reach saturation. However, in the present study, a significant linear correlation was found between the total number of fungi and the number of rare fungal species per host (Fig. 10), intersecting the x-axis. This correlation is surprising and should not actually exist because the total number of species has evolved independently of the number of protected species. The observation that where there is much, there is also relatively much at risk requires further analysis. The relative proportion of Red List species reaches saturation at about 16%. This is due to the change in the total number of fungi per tree species. The increase is not due to differences in classification of mycorrhizal fungi and saprobionts.

The Red List of fungal species contains large uncertainties due to identification difficulties for some genera and because of annual fluctuations in the occurrence of fruiting bodies (DAHLBERG & MUELLER 2011). This leads to a comparatively high number of species classified as D (data situation insufficient).

Since Red List data are based on the occurrence of fruiting bodies, it should be noted that some species may not be as rare or threatened as previously thought, but remain in the soil as mycelia or as spores, waiting for suitable conditions to form fruiting bodies, making correct classification difficult (GLASSMAN et al. 2016). The classification of “rare” and “endangered” appears to be overlapping and difficult because mycorrhizae are dependent on the host. It remains to be discussed whether rare species are endangered. Changing host vitality may affect fruiting body formation, and thus the fungus may apparently become rare (DEL CASTILLO et al. 2022). The failure of spruce with increasing drought has a new quality. The decline of conifers by the bark beetle and by forest conversion could have a serious impact on the fungi.

6. The highest diversity of species is located where the diversity of property is high.

To our knowledge, this is the first time that a relationship between diversity of ownership and species diversity has been established. The study area is characterized by a mix of ownerships (from state forest for timber production to community recreational forest to small private forest for firewood production). Quadrants with the highest fungal diversity have a mix of ownership types (Fig. 11). Apparently, high and diverse land use intensity, which assumes a high diversity of ownership and property types, promotes fungal diversity. Different land types and ownership generate diversity in land use intensity and this promotes plant diversity (VON LÜPKE et al. 2011, MÖLDER et al. 2021) and thus fungal diversity.

The inset in Fig. 5 shows the 325 properties. The narrowest plot was 4 m wide and 500 m long. The average plot size was 0.5 ha/owner. Private forests of small landowners are always richer in tree species than state forests (VON LÜPKE et al. 2011). The intensity of use of this small private forest is extremely heterogeneous, ranging from log-wise use for timber or energy wood to ownerships that neglect any management. Despite wide dispersion, the data suggest that fungal diversity is low where only one ownership type is prevalent. It is a mix of ownership that provides an opportunity for greater diversity of shrubs and trees. There is one point of high fungal diversity even with one ownership. In this case, it is communal forest that was used as coppice in the Middle Ages.

Conclusions

- The present research suggests that an urban area with small-scale variation in properties and associated management is the basis for the observed plant diversity and associated diversity of mycorrhizal and wood-inhabiting basidiomycetes.
- Conifers, along with deciduous trees, are important components for maintaining fungal diversity. Decisions to convert coniferous forest to deciduous forest should consider fungal diversity.
- Shrubs have been undermapped to date. Most fungi associated with shrubs can also colonize deciduous trees. Apparently, only generalists occur on shrubs. This had a significance in the recolonization of the study area after overuse of forests in the 17th and 18th centuries. The fungal species of the shrubs are found on the deciduous trees of the newly established forest.
- Exotic and introduced tree species provide an opportunity to estimate the rate of fungal colonization by new hosts. This ranges from 1 to 0.3 species/year for Douglas-fir and black locust, but can vary depending on year of introduction and frequency.

The observations in this work provide an indication that fungal species diversity in

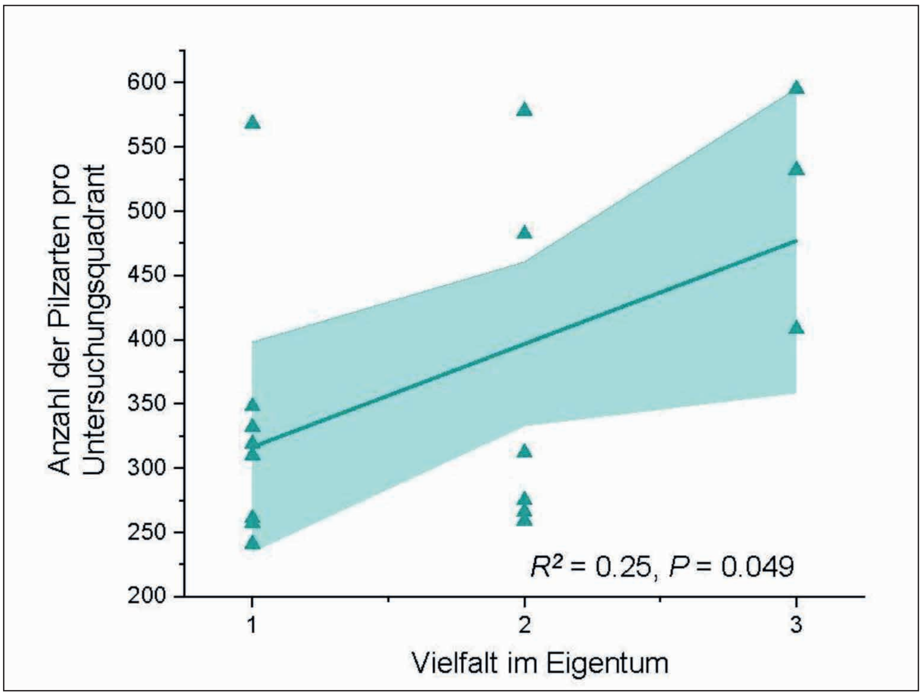

Fig. 11 *The number of fungal species in relation to diversity in property on the survey map quadrant. X-axis: relative measure of mixing of state forest, community forest, and private forest. 1: Only one form of ownership present on survey quadrant, 2: At least two forms of ownership present. 3: Three forms of ownership present in approximately equal proportions. y-axis: fungal species richness.*

urban habitats can be enhanced by maintaining small-scale ownership structure and land use.

Summary

- Site-referenced basidiomycetes were collected in the vicinity of the city of Jena from1988 to 2018 and cross-referenced with older publications. A total of approximately 2,000 fungal species were recorded over an area of 12,000 ha. 74% of these mapped fungi are wood-associated basidiomycetes found on 64 tree and shrub species. The study area contains 2,000 ha of grassland, 4,500 ha of forest, and 5,500 ha of urban land with parks and gardens. 11% of the forest area is state forest, 33% is communal forest, and 56% is private forest with different management. The study area was almost completely deforested 150 years ago and was not reforested until the 19th century.
- The number of basidiomycetes of Jena is comparable to those of the Hainich National Park. The species diversity of the fungi is based on the specific occurrence on deciduous trees, conifers and shrubs. The generalists among the fungi survived the period of deforestation on shrub species and are dominated by the bark fungi. After the reforestation of the study area, the fungi seem to have moved from the shrubs mainly to the deciduous trees. The specialists among the fungi are mainly mycorrhizal species, whereby a distinction must be made between apparent (s. l.) and true specialists (s. str.). Apparent specialists occur in the study area on only one host species, but colonize other hosts elsewhere in Europe. Spruce is the tree species with the highest number of s. l. specialists. Only the true specialists (s. str.) colonize only one host species, and this group is found mainly on pine and birch.
- Exotic and immigrant species host only 15% of the fungal species studied. Among these, Douglas fir with 86 species (60% saprobionts 30% ectomycorrhizae) and black locust with 80 species (100% saprobionts) are relatively rich in species. The colonization rate of Douglas-fir and black locust appears to be 0.3 to 1 fungal species/year.
- A significant linear correlation is observed between the total number of fungi and the number of endangered fungal species per host.
- High diversity of ownership and associated diversity in forest management conditions high fungal species diversity in this urban habitat.

Thanks to

We thank Mr. M. Barfod (Stadtroda Forestry Office), Ms. K. Karnahl (Jena City Council), and Mr. M. Rindt for help in preparing the ownership map, Mr. F. Dämmrich (Limbach-Oberfrohna) for information on fungal red lists and fungal generalists, and Ms. A. Boerner (http://www.dn.com.au/annett-boerner.html) for preparing the map of the study area and graphics. For the information on the trees and shrubs of Jena we thank M. Rindt. We thank Uli Weber for translation with DeepL.

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Cover photo: *The Butterfly Trametes (Trametes versicolor) is found on tree stumps, more rarely on lying wood. The species is mostly found on deciduous trees (birch, beech), more rarely on conifers (spruce, pine) (photo: A. GÜNTHER).*