BENEMÉRITA UNIVERSIDAD AUTÓNOMA DE PUEBLA

FACULTAD DE CIENCIAS BIOLÓGICAS

“Diversity and species composition in macrofungal communities across an urban ecosystem in the Puebla - Tlaxcala valley of Mexico”

Tesis para obtener el grado de:

Maestro en Ciencias Biológicas

Presenta:

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H. Puebla de Z. a 22 de enero de 2026

Asunto: Voto Aprobatorio

Comité Académico del Posgrado
PRESENTE

Por medio de la presente se hace constar que se revisó y aprobó la tesis titulada:

"Diversity and species composition in macrofungal communities across an urban ecosystem in the Puebla-Tlaxcala valley of Mexico"

Que presenta el estudiante Luis Eder Dorantes Marin con número de matrícula 223470511, aspirante al grado de **Maestro en Ciencias Biológicas,** de la Línea de Generación y Aplicación del Conocimiento: "**Sistemática**", notificamos que la tesis reúne los requisitos y se aprueba para su réplica oral en el examen de grado.

Por lo tanto, emitimos los **VOTOS APROBATORIOS** como miembros del **Comité de Jurado de Examen de Grado** como a continuación se indica:

Tutor Interno: Dr. José Antonio González Oreja

Tutor Externo: Dr. Marcos Vinicius Caiafa Sepúlveda

Revisor: Dra. Virginia Ramírez Cruz

Agradecemos de antemano la atención que se sirva prestar a la presente.

DECLARATORIA

Yo, Luis Eder Dorantes Marin, declaro que el trabajo de investigación presentado en este documento titulado "**Diversity and species composition in macrofungal communities across an urban ecosystem in the Puebla - Tlaxcala valley of Mexico"** es resultado de un esfuerzo propio, de ninguna manera ha sido copiado o modificado de otras investigaciones, proyectos o similares, tampoco se usaron ideas ni ilustraciones de otras fuentes que no estén citados de manera correcta.

Esta investigación no ha sido presentada anteriormente para obtener algún título o grado académico, ni ha sido publicada, por lo que me hago plenamente responsable ante la universidad de cualquier irregularidad que pudiera presentarse por el incumplimiento de lo aquí declarado.

Heroica Puebla de Zaragoza 30 de enero del 2026

Dedicatoria

A Gigi

Mi compañía más fiel

Estuvo en cada madrugada silenciosa y en el cansancio.

Fue hogar, calma y sostén sin palabras.

Gracias por acompañarme, de otra forma, hasta el final.

Agradecimientos

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Abstract

Macrofungi are of great relevance to the functioning of terrestrial ecosystems, but habitat transformation can significantly alter the structure of macrofungal communities. Urbanization is regarded as a major threat to biological diversity; however, knowledge of its impact on macrofungi remains scarce. The present study aimed to assess diversity and distribution patterns of macrofungal species across an urban ecosystem in the Puebla–Tlaxcala Valley of Mexico and determine the effect of urbanization on macrofungal communities. Four oak forests were selected along an urbanization gradient, and sampling areas of 0.1 ha were established at each site. Macrofungi were sampled from June to October 2024, with a total of 296 species recorded. Diversity decreased with increasing urbanization. Species composition shifted across the gradient, with the most urbanized sites showing higher turnover. Urbanization, microclimatic, and vegetation structure variables were associated with the observed patterns in diversity and distribution. The findings highlight the importance of native vegetation, microclimatic buffering, and habitat continuity for sustaining macrofungal communities within urban areas. Integrating fungi into urban biodiversity planning is essential to ensure the maintenance of the key functions they provide.

Introduction

Urban growth poses significant challenges for biodiversity conservation, as it has dramatically transformed landscapes and is regarded as a major threat to biological diversity (Antrop, 2004; Hansen et al., 2005; Kowarik, 2011). Urban areas are recognized as ecosystems composed of human-built environments and natural areas hosting significant proportions of non-native animal and plant species (Cousins et al., 2003; McDonnell & Pickett, 1990). Currently, approximately 4.2 billion people live in urban environments worldwide, and projections suggest that this trend will persist, reaching 6 billion urban inhabitants by 2045, representing nearly 70 % of the world's population (McPhearson et al., 2016; UN DESA, 2018; UN-Habitat, 2022). In Latin America, 82 % of the population lives in urban areas, including megacities (over 10 million residents). Mexico reflects this trend, with approximately 88 % of its ca. 132 million people residing in urban areas (Worldometers.info, 2025). Global research on urbanization indicates a decline in species numbers, with human impact on biodiversity decreasing from city centers to wild areas. This may result in differences between urban and surrounding non-urban areas regarding the structure of community groups such as birds, plants, insects, and fungi (Avis et al., 2016; MacGregor-Fors et al., 2015).

Macrofungi, or macromycetes (fungi that produce sporomes visible to the naked eye), are a highly relevant group due to their roles in the functioning of terrestrial ecosystems as organic matter decomposers, mutualists, and pathogens (Bahram & Netherway, 2022; Caiafa et al., 2017; Niego et al., 2023). Decomposer fungi contribute to the nutrient cycle and soil formation; mycorrhizal fungi establish symbiosis associations with plants and contribute to the recruitment of seedlings and the growth of trees; and pathogenic fungi play an important role in regulating populations of plants, animals, and fungi (Bever et al. 2015; Lonsdale et al., 2008; Tedersoo et al., 2010). The diversity of fungal species is estimated at ca. 6.2 million globally (Baldrian et al., 2022), and between 53,000 and 111,000 represent macrofungi (Mueller et al., 2007). For Mexico, estimates suggest more than 250,000 species of fungi (Guzmán, 1998), and approximately 9,000 to 11,000 species of macromycetes (Aguirre-Acosta et al., 2014).

Given the relevance of these organisms to ecosystem functioning, understanding how microclimatic, environmental, and vegetation factors relate to the diversity and distribution of macromycete species is a growing interest in ecological research (Pérez-Rosas et al., 2022).

Studies on the diversity and composition patterns of macrofungi in temperate and tropical forests suggest that species richness and sporome production are mainly related to topographic and microclimatic factors (Brown et al., 2006; Gómez-Hernández & Williams-Linera, 2011; Pérez Rosas et al., 2022; Toledo et al., 2014). Also, vegetation structure and tree species composition can affect macrofungal communities by influencing the amount and quality of resources provided by plants (Brown et al., 2006; Zhang et al., 2010).

Fungal communities are extremely vulnerable to habitat loss caused by urbanization and other anthropogenic activities. This often leads to a decline in species richness and alters species composition in various habitat conditions, mainly influenced by microclimate, and factors related to substrate availability and vegetation structure (Avis et al., 2016; Gómez-Hernández et al., 2019; MacGregor-Fors et al., 2015; Newbound et al., 2010). The impervious surfaces in urban areas can reduce soil's water absorption and impact microclimate (Newbound, McCarthy & Lebel, 2010), and the urban surface capacity to absorb solar radiation and the heterogeneous distribution of vegetation can significantly increase temperature owing to the heat island effect (Arnfield, 2003; Boone & Fragkias, 2012), causing a decrease in macromycete richness and sporome production (Ferris et al., 2000; Rubino & McCarthy, 2003). However, most ecological studies about macrofungi focus on conserved forests, and little is known about the ecology of macrofungal communities in urban areas (Newbound et al., 2010). In Mexico, there is only one study that analyzes the diversity and distribution of species along an urban gradient. This study found that functional diversity and species richness decline with increasing urbanization, and there is high turnover in species composition across the study area, which is linked to microclimatic and urbanization factors. Additionally, their results indicated that some of the available resources in the niche space within the most urbanized sites are not being utilized (Gómez-Hernández et al., 2019).

The Puebla-Tlaxcala Metropolitan Zone (PTMZ), located in the Puebla-Tlaxcala Valley, is the 4th most populous metropolitan zone in Mexico, with ca. 3.2 million inhabitants. About 87 % of the population resides in the State of Puebla, and 13 % resides in the State of Tlaxcala, with 95 % of the total population in the MZPT located in urban areas (INEGI, 2020). However, no studies have been conducted to evaluate the variation of species diversity and composition among macrofungal communities in relation to environmental or urban variables in the States of Puebla and Tlaxcala.

Most mycological studies in Puebla address the use of wild mushrooms within rural communities, the commercialization of sporomes in local markets (Contreras-Cortés et al., 2018; Lemin et al., 2010; Pérez-López et al., 2015), and some studies focus on developing species inventories (Sánchez-Flores et al., 2021; Vázquez et al., 2016). Similarly, in Tlaxcala, most studies focus on ethnomycological topics, with some exploring the taxonomic diversity (Ramírez-Terrazo et al., 2021; Reyes-López et al., 2020).

In this context, the present study aimed to evaluate variation in the diversity and composition of species in macrofungal communities along an urban ecosystem in the Puebla-Tlaxcala Valley of Mexico, and identify how microclimatic, environmental, urbanization, and vegetation structure factors relate to the observed variation. The hypotheses related to the aim of the study were: 1) macrofungal diversity declines as the urbanization increases, showing higher diversity in less urbanized areas, 2) microclimate and vegetation structure are the main drivers of diversity variation along the study area, and are also related to the variation of species composition, and 3) the turnover of species composition is lower between the least urbanized sites and higher between the most urbanized areas.

Materials and methods

Study area

The study was carried out in the Puebla-Tlaxcala Valley of Mexico. Four areas with predominant oak vegetation were selected in localities surrounding the city of Puebla: Flor del Bosque State Park (Site 1) at 2,264 m asl, El Aguacate municipality (Site 2) at 1,922 m asl, Tenancingo municipality (Site 3) at 2,237 m asl, and San Nicolas de los Ranchos municipality (Site 4) at 2,616 m asl. At each site, 10 permanent plots of 10 × 10 m were established, with a distance of approximately 10 m between plots (Williams-Linera et al., 1998). (Figure 1)

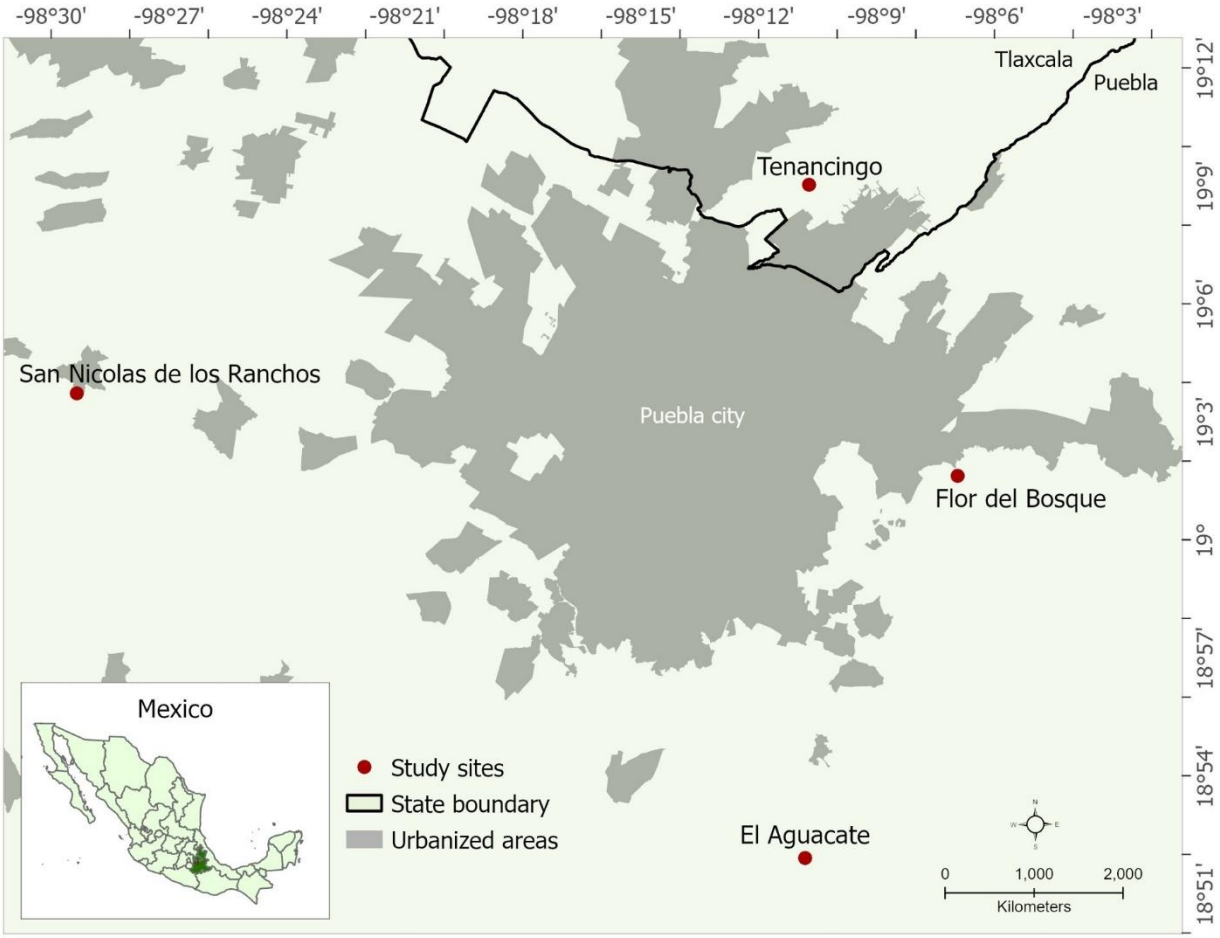

Figure 1 Location of the study sites in the Puebla-Tlaxcala Valley of Mexico.

Macromycete sampling

Sampling was carried out twice a month in every plot at each study site from June to October 2024, which corresponds to the rainy season in the region. Sporomes of the same species within a 50 cm radius, caespitose growth, fairy rings, and growing on the same trunk or branch were recorded as a single collection unit, and abundance was estimated as the number of collection units for each species (adapted from Schmit et al., 1999). All specimens were separated at the species level based on their macromorphological and micromorphological characteristics. Unidentified taxa were classified as morphospecies using a higher taxonomic level. Voucher specimens are deposited in the mycological collection of the Laboratory of Fungal and Plant Diversity and Evolution, BUAP.

Explanatory variables

Within each plot at each study site, microclimatic, environmental, and vegetation structure variables were measured. On each sampling day, air humidity (%), air temperature (°C), soil

humidity (%), and soil temperature (°C) were recorded at the center of each plot. Slope (°) and percentage of soil cover were measured once in each plot. Litter depth was recorded in each plot at the beginning, middle, and end of the sampling season. Woody plants were counted, and their diameter and height were measured. The vegetation structure was characterized as density (individuals ha^{-1}), basal area (m^2 ha^{-1}), and mean, minimum, and maximum tree height (m).

To describe the urbanization gradient in the study area, explanatory variables were measured within a circular buffer zone with a 5-km radius from the center of each study site. The 5-km radius was selected to allow for a considerable distance between buffer boundaries. The urbanization variables included in this study were the extent of built-up areas (km^2), extent of crop areas (km^2), extent of areas with introduced vegetation (km^2), and length of streets and roads (km) (McDonnell & Hahs, 2008). All variables were derived from land-use data layers and census data from the National Institute of Statistics and Geography, and total variable values were calculated by buffer area using zonal statistics in ArcGIS 10.4 (Esri, 2015).

Data analysis

The diversity of macromycetes was measured with the species richness (calculated for each site as the number of recorded species) and the first-order (^1D) True Diversity index (Jost, 2006, 2007), calculated with the "entropart" package in R. The species richness estimator Chao 2 was used to determine the completeness of species inventories at each study site, calculated using the "fossil" package in R. Spearman's rho correlation coefficient was used to determine the relationship between macromycete species richness and microclimatic, environmental and vegetation structure variables, using the "psych" package in R. Linear regression analyses were performed to determine the relationship between the number of macromycete species and urbanization variables along the study area.

The turnover in species composition between study sites was assessed using the Chao-Jaccard similarity index (Chao et al., 2005) with the "fossil" package in R. A Non-metric Multidimensional Scaling (NMDS) analysis was performed to represent on a geometric plane the distance between study sites in relation to the composition of species, using the "vegan" package in R. The relationship between species distribution and a set of microclimatic, environmental, vegetation structure, and urbanization variables was determined by performing a Canonical Correspondence

Analysis (CCA) with the "vegan" package in R. All the analyses mentioned were performed in R v. 3.2.3. (R Core Team, 2017).

A conceptual model was created to clearly visualize how urbanization, microclimate, and vegetation structure interact to influence macrofungal diversity and species composition in the study area. The model was performed in Python using the NetworkX library for network structure and Matplotlib for visualization (Python Software Foundation, 2023).

Results

A total of 879 macromycete individuals were recorded, belonging to 296 species, 60 genera, and 42 families. Of the species recorded, 22 belong to the phylum Ascomycota and 165 to the phylum Basidiomycota (Appendix 1). The least urbanized site was Tenancingo (Site 3: 3157.48), followed by San Nicolas de los Ranchos (Site 4: 5742.49), Flor del Bosque (Site 1: 8026.33), and El Aguacate (Site 2: 11822.23). Flor del Bosque recorded the highest species richness (119 species), followed by Tenancingo (109 species), San Nicolas de los Ranchos (103 species), and El Aguacate (65 species). Correspondingly, the True Diversity index showed that Flor del Bosque had the highest diversity (87), followed by Tenancingo (85), San Nicolas de los Ranchos (76), and El

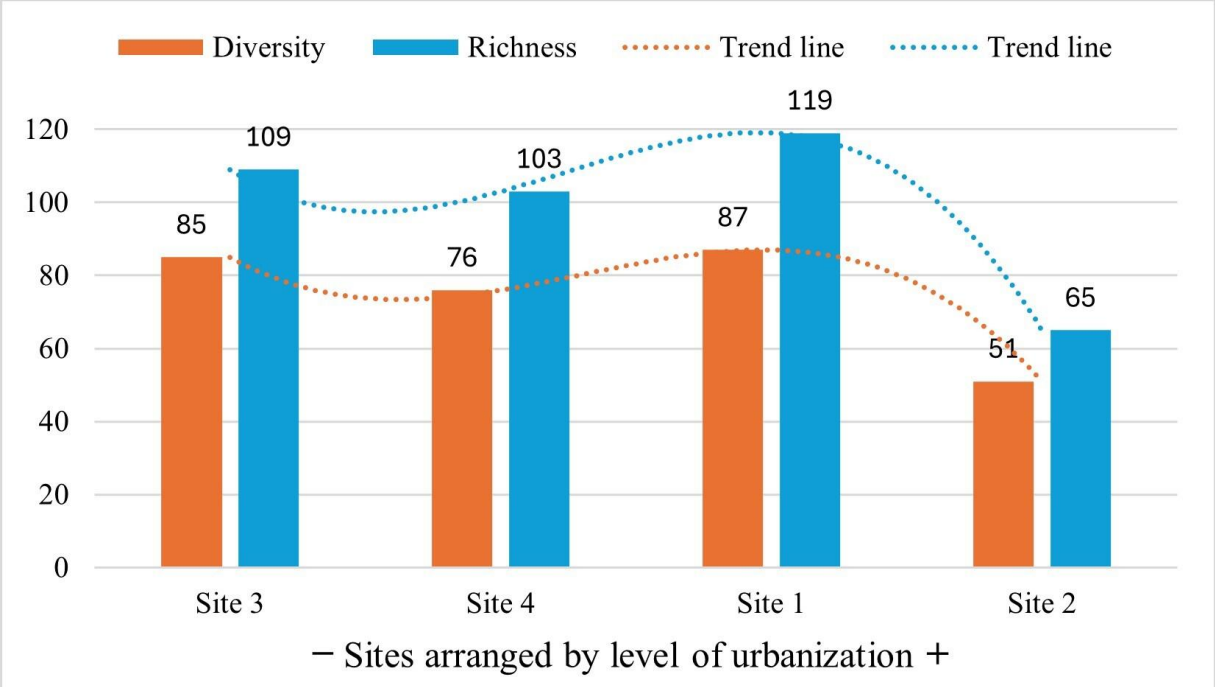

Figure 2 True Diversity index and species richness values in the study sites. Sites are arranged from the least urbanized (Site 3) to the most urbanized (Site 2). Dotted lines indicate the trend of diversity and species richness along the urbanization gradient.

Aguacate (51). Both the diversity index and species richness showed a similar trend of decreasing with increasing urbanization, with a peak at Site 1 (Figure 2). The species richness estimator Chao 2 indicated that the completeness of the macromycete species inventory for Site 1 was 32.74%, 47.05% for Site 2, 34.65% for Site 3, and 31.83% for Site 4.

Spearman's rho correlations indicated a significant negative correlation between macrofungal species richness in the studied area and both air and soil temperature (rho = -0.5277, p = 0.0004; rho = -0.3419, p = 0.0307, respectively). Soil humidity, along with the mean and maximum height of trees, showed a positive correlation with species richness. (rho = 0.5180, p = 0.0006; rho = 0.4141, p = 0.0078; rho = 0.3152, p = 0.0475, respectively) (Table 1).

Table 1. Spearman's correlation coefficients (ρ). Correlation between macromycete species richness in the study area and explanatory variables.

Variable	ρ	***p*-value**
Soil temperature*	-0.3419	0.0307
Air temperature***	-0.5277	0.0004
Air humidity	0.2501	0.1195
Soil humidity***	0.5180	0.0006
Litter depth	-0.0184	0.9098
Canopy openness	-0.0607	0.7097
Slope	-0.0809	0.6196
Basal area	0.1625	0.3162
Minimum height of trees	0.3080	0.0531
Maximum height of trees*	0.3152	0.0475
Mean height of trees**	0.4141	0.0078
Tree density	0.2494	0.1205

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$

The linear regression analyses indicated a positive relationship between species richness, and the extent of built-up areas and length of streets/roads in the study area ($r^2 = 0.18$, F = 8.28, p = 0.006; $r^2 = 0.15$, F = 6.5, p = 0.014, respectively; Figures 3a, 3b).

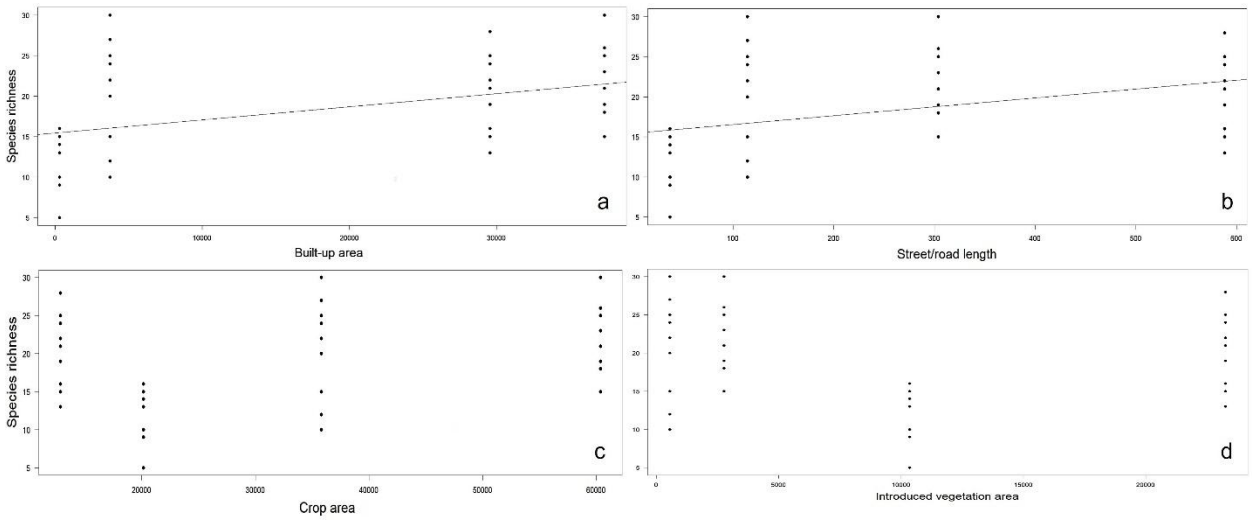

Figure 3 Linear regression analysis between species richness and extent of built-up area, street/road length, crop area, and introduced vegetation area along the urbanization gradient.

The extent of crop areas and the extent of areas with introduced vegetation were not significantly related to the urbanization variables ($P > 0.05$; Figure 3c, 3d). The Chao-Jaccard similarity index indicated that the percentage of similarity in species composition was higher for Sites 3 and 4 (51 %) (Tenancingo-San Nicolas de los Ranchos), which are the less urbanized sites, followed by Sites 1 and 4 (45 %) (Flor del Bosque-San Nicolas de los Ranchos), Sites 2 and 4 (43 %) (El Aguacate-San Nicolas de los Ranchos), Sites 1 and 3 (42 %) (Flor del Bosque-Tenancingo), Sites 2 and 3 (34 %) (El Aguacate-Tenancingo), and the least similar were Sites 1 and 2 (19 %) (Flor del Bosque-El Aguacate), which are the most urbanized sites. Correspondingly, the NMDS showed that Sites 3 and 4 (Tenancingo-San Nicolas de los Ranchos) are the closest in terms of similarity in species composition, whereas Sites 1 and 2 (Flor del Bosque-El Aguacate) are the most distant regarding species composition (Figure 4).

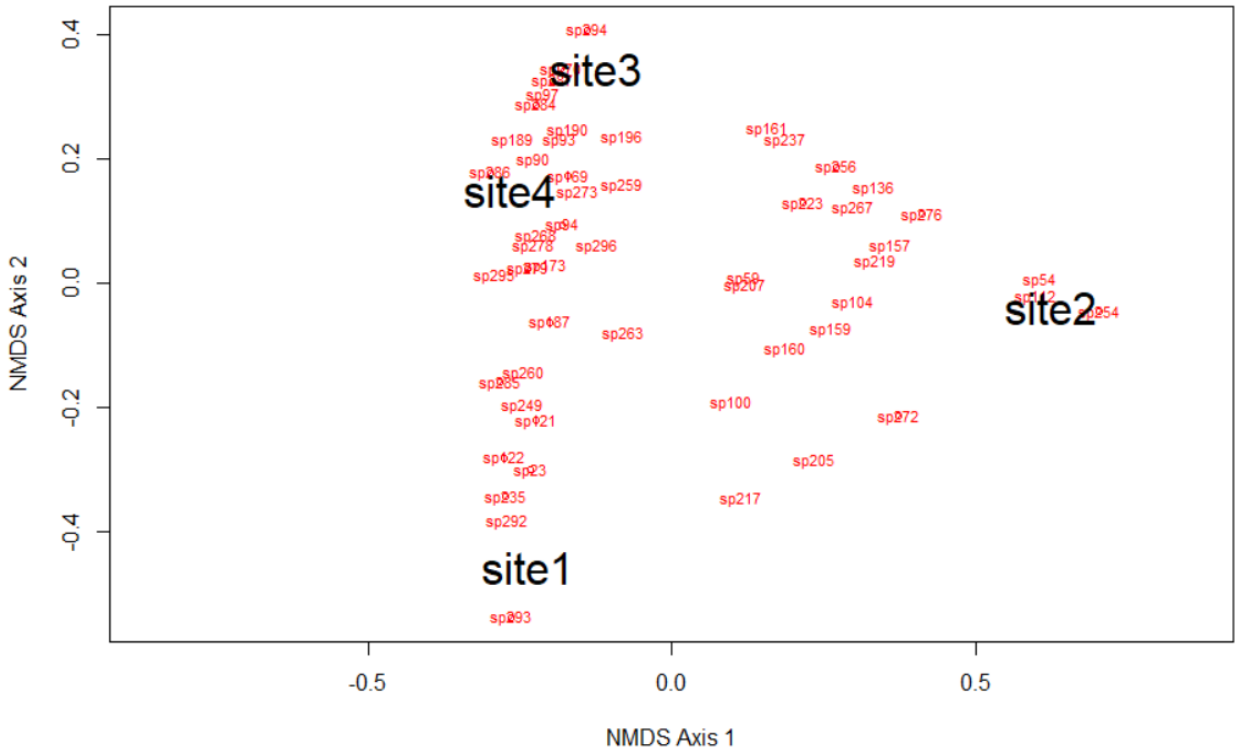

Figure 4 Non-metric Multidimensional Scaling analysis for macrofungal species composition among the four study sites. "sp1, sp2, sp3, sp4…" represents the species recorded in the study area.

The CCA for microclimatic, environmental, and vegetation structure variables included air and soil humidity, air and soil temperature, slope, litter depth, canopy openness, tree density, basal area, and minimum, mean, and maximum tree height, and it was performed for the 296 macromycete species recorded in the study area. Axis 1 (eigenvalue = 0.69) and Axis 2 (eigenvalue = 0.60) accounted for 12 % and 11 % of the explained variance in the relationship between macrofungal species and explanatory variables, respectively. CCA indicated that Site 2 clearly separates from Sites 1, 3, and 4 along axis 1, with higher air temperature in Site 2 as the main related variable, and humidity and vegetation structure as the main variables explaining the species distribution in Sites 1, 3, and 4. The analysis showed a distinct separation of Site 1 from Sites 3 and 4 along axis 2, mainly due to the relationship of the species in Site 1 with higher litter depth and canopy openness, and lower soil temperature in Sites 3 and 4 (Figure 5).

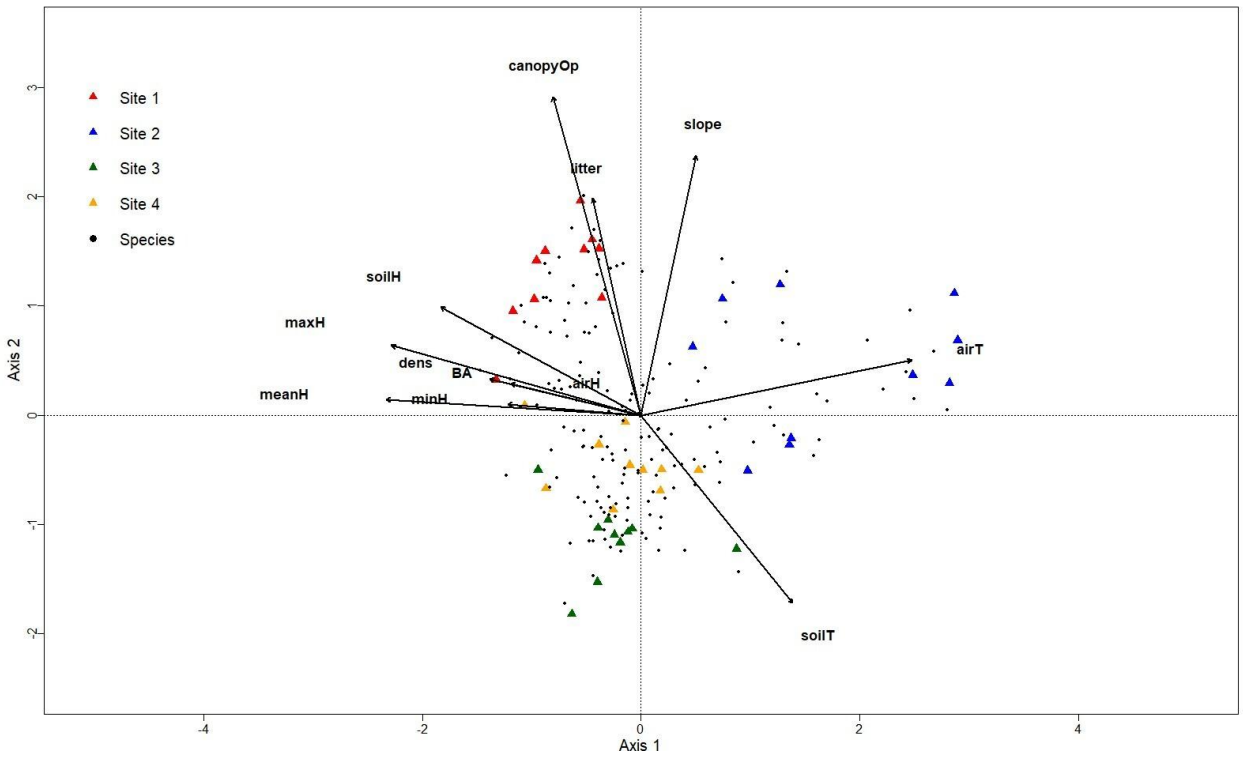

Figure 5 CCA for the macromycete species recorded in the four study sites. Vectors are microclimatic, environmental, and vegetation structure variables: air humidity (airH), soil humidity (soilH), air temperature (airT), soil temperature (soilT), slope, litter depth (litter), canopy opopenness (canopyOp), mean tree height (meanH), minimum tree height (minH), maximum tree height (maxH), tree density (dens), and basal area (BA).

The CCA for urbanization variables included the extent of crop and built-up areas, extent of introduced vegetation areas, and length of streets and roads, and it was performed for the 296 macromycete species, however, the model retained only three variables. Axis 1 (eigenvalue = 0.62) and Axis 2 (eigenvalue = 0.59) accounted for 36 % and 34 % of the explained relationship between species distribution and explanatory variables, respectively. There is a clear separation of Site 1 from Sites 2, 3, and 4 along axis 2, with the species distribution in Site 1 being explained mainly by built-up areas and areas of introduced vegetation, whereas crop areas was the variable more closely associated with Sites 3 and 4. Sites 1, 3, and 4 were clearly separated from Site 2 along axis 1, with crop areas and built-up areas being the main related variables (Figure 6).

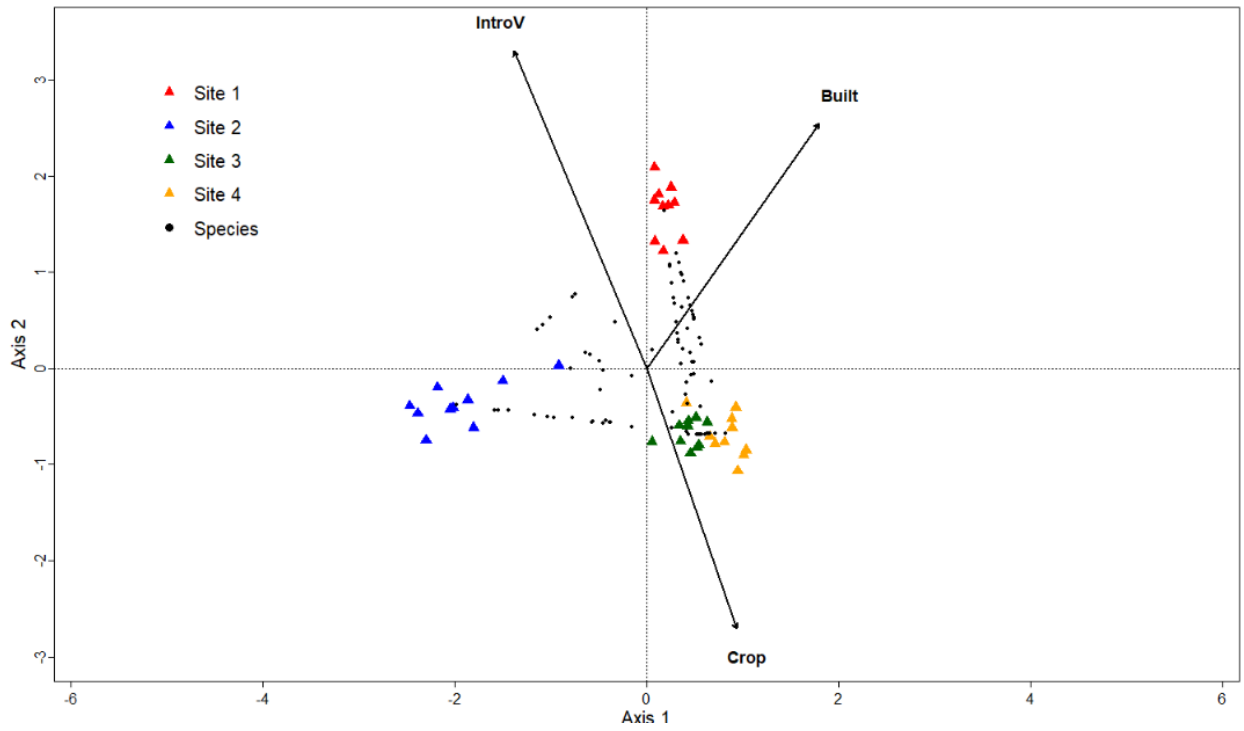

Figure 6 CCA for the macromycete species recorded in the four study sites. Vectors are urbanization variables: extent of built-up areas (Built), extent of cultivated areas (Crop), and extent of areas with introduced vegetation (IntroV).

Discussion

Mexico ranks third worldwide regarding the variety of ecosystems found within its territory (CONABIO, 2008), however, it is considered to be a highly urbanized country, with ca. 82 % of the national population concentrated in urban areas (UN-Habitat, 2025). Despite the importance of macromycetes in terrestrial ecosystems, research in urban areas remains limited (Gómez-Hernández et al., 2021; Pérez Silva, 2018), being more represented studies conducted with birds (Evans et al., 2009; Marzluff, 2016), insects (Lagucki et al., 2017), and plants (Falfán & MacGregor-Fors, 2016; Jara-Toto et al., 2023). The findings obtained in the present study indicate that urbanization affects macrofungal diversity and species distribution in the Puebla-Tlaxcala Valley. The impact of urbanization has led to a decline in diversity and conspicuous variation in species composition across the study area, as well as the likely presence of disturbance-tolerant species at one of the most urbanized sites, associated with variations in vegetation structure and microclimate (Figure 7).

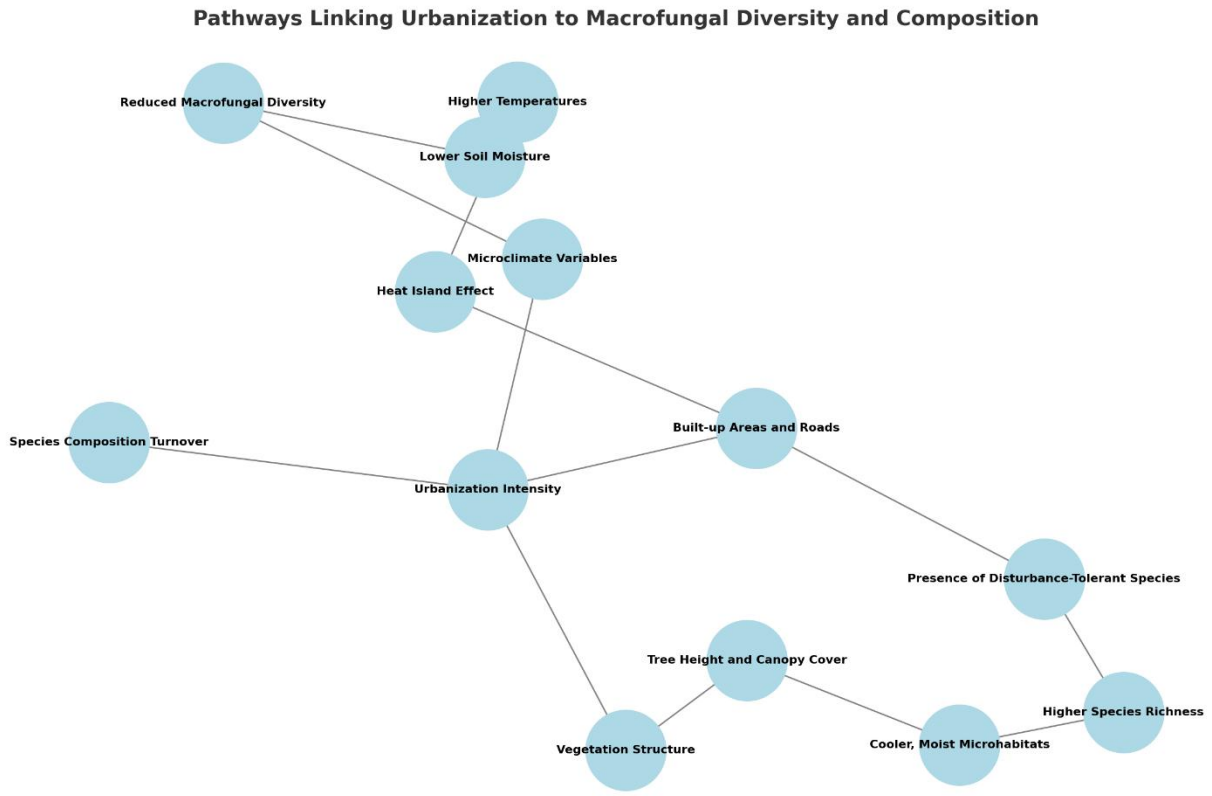

Figure 7 Conceptual model showing how macrofungal diversity and species composition are influenced by the effect of urbanization on microclimate and vegetation structure in the study area. This conceptual model illustrates hypothesized causal pathways; node (circle) proximity and link length do not represent effect strength or statistical magnitude.

Microclimatic factors were found to be strong predictors of species richness. Negative correlations with air and soil temperature, along with positive correlations with soil humidity and tree height, indicate that cooler and wetter habitats favor the proliferation of sporomes, thus underscoring the sensitivity of macrofungi to habitat disturbance and microclimatic changes associated with the likely influence of urban heat islands and the expansion of impervious surfaces (Arnfield, 2003; Boone & Fragkias, 2012; Brown et al., 2006; Ferris et al., 2000; Zhang et al., 2010). The buffering role of canopy cover and tall trees is particularly relevant, as they help regulate temperature, retain soil humidity, and provide abundant woody substrates for xylophagous fungi (Ferrer and Gilbert, 2003; Pérez-Rosas et al., 2022; Vázquez et al., 2016). In contrast, variables such as slope or canopy openness did not show a significant effect, suggesting that in fragmented and urbanized landscapes, vegetation structure and microclimate prevail over topographic factors (Gómez-Hernández et al., 2019; Toledo et al., 2014).

Interestingly, the results revealed a positive relationship between macromycete species richness and the extent of built-up areas and length of streets/roads along the study area, contrasting with the expected negative relationship. Several studies have documented cases in which urbanized areas host higher species diversity than nearby non-urbanized or rural landscapes, which can be partly explained by cities' capacity to create heterogeneous environments that support both native and non-native species (Shochat et al., 2006). The observed relationship between macromycetes and urbanization is likely to be caused by the effect of the Flor del Bosque data in the analysis, since it was the second-most urbanized site and had the highest species richness (119 species). Flor del Bosque is a protected natural area located within the city of Puebla, surrounded by buildings and streets. Its high species richness highlights the role of habitat protection, continuous tree cover, native vegetation, and heterogeneous microhabitats in maintaining diversity (Ferris et al., 2000; Kowarik, 2011; Rubino & McCarthy, 2003). Nevertheless, higher species richness in urban settings does not necessarily equate to higher ecological value (Aronson et al., 2014). It has been observed that disturbance-tolerant macrofungi that exploit novel substrates can be present in urban environments, contributing to the local diversity while simultaneously reducing regional diversity (Avis et al., 2016).

Species distribution analyses also revealed the effects of urbanization. The least urbanized sites (Tenancingo and San Nicolás de los Ranchos) showed the highest macromycete species similarity, whereas the most urbanized sites (Flor del Bosque and El Aguacate) exhibited the lowest similarity. This pattern reflects an increasing species turnover along the urbanization gradient and is consistent with other studies on macrofungi, birds, and plants (Gómez-Hernández et al., 2019; McDonnell & Hahs, 2008; Ortega-Álvarez et al., 2011), where environmental filters have been observed to favor generalist or disturbance-tolerant species, including non-native ones (Cousins et al., 2003; MacGregor-Fors et al., 2015). The results suggest that the effects of soil humidity and tree height on macromycete species distribution are associated with less disturbed sites, while the effects of temperature, canopy openness, built-up areas, and introduced vegetation are linked to more urbanized sites. Studies in forests of temperate affinity indicate that the distribution of macromycete species at the local scale can be driven by the variation of vegetation structure as well as other factors affecting temperature, humidity, and the quality and quantity of available resources (Ferris et al., 2000; Gómez-Hernández et al., 2019; Pérez-Rosas et al., 2022).

The findings of this study highlight the necessity of urban biodiversity management strategies that prioritize microclimatic buffering, habitat continuity, and the conservation of tree cover. These measures can help mitigate the negative effects of urban heat and drought while ensuring that macrofungal communities continue to perform essential ecological functions, such as nutrient cycling, population control of animals, plants, and fungi, and nutrient exchange with vascular plants (Bahram & Netherway, 2022; Niego et al., 2023). For future studies, it would be valuable to include a broader range of vegetation types and examine how urbanization impacts macromycete functional groups. To gain a better understanding of how urbanization affects the structure and ecological functions of macrofungal communities, research should be conducted across different urban ecosystems, incorporating both phylogenetic and functional trait data to assess macromycete diversity and distribution.

Conclusions

This study shows that macrofungal communities in the Puebla–Tlaxcala Valley respond clearly to urbanization, with detectable shifts in diversity and species composition along the urban gradient. The interaction between microclimatic conditions, vegetation structure, and land-use intensity is a key driver of these patterns, underscoring the sensitivity of macrofungi to environmental alterations associated with urban development.

The findings highlight the ecological value of protected and semi-natural habitats embedded within urban ecosystems, as these areas can maintain substantial macrofungal diversity despite surrounding disturbance. At the same time, the prevalence of disturbance-tolerant species in more urbanized sites indicates that urban environments can reshape community assembly processes, with potential implications for ecosystem functioning.

Functional groups relevant to ecosystem functioning must be defined in urban gradients to assess how variations in biotic and abiotic factors affect them, and specific management and conservation strategies should be developed based on the distinct requirements of macrofungal groups and on existing strategies for plants and animals.

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Appendix 1. Macrofungal species and abundances recorded in the four study sites in the Puebla-Tlaxcala Valley of Mexico.

ID number	Morphospecies	Site 1	Site 2	Site 3	Site 4
sp1	Agarical sp.1	0	0	0	1
sp2	Agarical sp.2	1	0	0	0
sp3	Agarical sp.3	0	0	1	0
sp4	Agarical sp.4	0	0	0	1
sp5	Agarical sp.5	0	0	0	2
sp6	Agarical sp.6	1	0	0	0
sp7	Agarical sp.7	1	0	0	0
sp8	Agarical sp.8	1	0	0	0
sp9	Agarical sp.9	3	0	1	0
sp10	Agarical sp.10	1	0	0	0
sp11	Agarical sp.11	0	0	3	1
sp12	Agarical sp.12	0	1	0	0
sp13	Agarical sp.13	0	1	0	0
sp14	Agarical sp.14	2	0	4	0
sp15	Agarical sp.15	1	0	0	1
sp16	Agarical sp.16	0	0	1	0
sp17	Agarical sp.17	0	0	1	0
sp18	Agarical sp.18	0	1	0	0
sp19	Agarical sp.19	0	0	1	0
sp20	Agarical sp.20	0	0	1	0
sp21	Agarical sp.21	0	0	0	1
sp22	Agarical sp.22	0	0	0	1
sp23	Agarical sp.23	3	0	1	0
sp24	Agarical sp.24	1	0	0	0

sp25	Agarical sp.25	0	0	0	1
sp26	Agarical sp.26	0	0	1	0
sp27	Agarical sp.27	0	0	2	0
sp28	Agarical sp.28	2	0	1	0
sp29	Agarical sp.29	0	0	1	0
sp30	Agarical sp.30	0	1	0	0
sp31	Agarical sp.31	2	0	0	0
sp32	Agarical sp.32	1	0	0	0
sp33	Agarical sp.33	0	0	1	0
sp34	Agarical sp.34	0	0	0	1
sp35	Agarical sp.35	0	1	0	0
sp36	Agarical sp.36	0	1	0	0
sp37	Agarical sp.37	0	0	0	1
sp38	Agarical sp.38	0	1	0	0
sp39	Agarical sp.39	0	2	0	0
sp40	Agarical sp.40	0	0	1	0
sp41	Agarical sp.41	1	0	0	0
sp42	Agarical sp.42	1	0	0	0
sp43	Agarical sp.43	0	0	1	0
sp44	Agarical sp.44	1	0	0	0
sp45	Agarical sp.45	0	1	0	0
sp46	Agarical sp.46	1	0	0	0
sp47	Agarical sp.47	0	0	1	0
sp48	Agarical sp.48	1	0	0	0
sp49	Agarical sp.49	0	0	1	0
sp50	Agarical sp.50	0	0	1	0
sp51	Agarical sp.51	0	1	0	0
sp52	Agarical sp.52	0	0	1	0

sp53	Agarical sp.53	1	0	0	0
sp54	Agarical sp.54	0	4	1	0
sp55	Agarical sp.55	1	0	0	0
sp56	Agarical sp.56	0	0	2	0
sp57	Agarical sp.57	0	1	0	0
sp58	Agarical sp.58	0	0	0	1
sp59	Agarical sp.59	1	2	0	4
sp60	Agarical sp.60	0	0	1	0
sp61	Agarical sp.61	1	0	0	0
sp62	Agarical sp.62	0	0	1	0
sp63	Agarical sp.63	0	0	0	1
sp64	Agarical sp.64	0	0	1	0
sp65	Agarical sp.65	2	0	0	1
sp66	Agarical sp.66	1	0	0	0
sp67	Agarical sp.67	2	0	0	0
sp68	Agarical sp.68	0	0	0	1
sp69	Agarical sp.69	0	0	1	0
sp70	Agarical sp.70	1	0	0	0
sp71	Agarical sp.71	1	0	0	0
sp72	Agarical sp.72	1	0	0	0
sp73	Agarical sp.73	0	0	1	0
sp74	Agarical sp.74	1	0	0	0
sp75	Agarical sp.75	0	2	0	0
sp76	Agarical sp.76	0	1	0	0
sp77	Agarical sp.77	0	0	1	0
sp78	Agarical sp.78	1	0	0	0
sp79	Agarical sp.79	1	0	0	0
sp80	Agarical sp.80	0	0	0	2

sp81	Agarical sp.81	0	0	0	1
sp82	Agarical sp.82	0	0	1	0
sp83	Agarical sp.83	1	0	0	0
sp84	Agarical sp.84	0	0	3	0
sp85	Agarical sp.85	7	0	0	0
sp86	*Agaricus campestris*	4	0	0	0
sp87	*Agrocybe*	0	0	0	3
sp88	*Amanita* sp.1	0	0	1	0
sp89	*Amanita* sp.2	0	0	0	1
sp90	*Amanita* sp.3	1	0	4	4
sp91	*Amanita* sp.4	1	0	0	0
sp92	*Amanita bisporigera*	0	0	8	0
sp93	*Amanita* sp.5	3	0	14	3
sp94	*Amanita* sp.6	1	0	2	0
sp95	*Amanita* sp.7	0	0	2	0
sp96	*Amanita* sp.8	0	0	2	0
sp97	*Amanita flavoconia*	0	0	4	3
sp98	*Amanita gemmata*	0	0	0	1
sp99	*Amanita laurae*	1	0	0	0
sp100	*Amanita novinupta*	2	1	0	1
sp101	*Amanita rubescens*	2	0	0	1
sp102	*Amanita* sp.9	0	0	3	0
sp103	*Amanita* tuza	0	0	0	1
sp104	*Astraeus* sp.1	4	8	3	4

sp105	*Astraeus hygrometricus*	0	0	1	0
sp106	*Boletus* sp.1	1	0	0	0
sp107	*Boletus* sp.2	0	0	1	1
sp108	*Boletus* sp.3	0	3	0	0
sp109	*Boletus* sp.4	0	1	0	0
sp110	*Boletus* sp.5	0	1	0	0
sp111	*Boletus* sp.6	0	4	0	0
sp112	*Boletus* sp.7	0	5	0	1
sp113	*Boletus* sp.8	0	5	0	0
sp114	*Boletus* sp.9	0	2	0	0
sp115	*Boletus* sp.10	0	1	0	0
sp116	*Calvatia* sp.1	0	0	3	0
sp117	*Cantharellus cibarius*	0	0	1	0
sp118	*Coltricia* sp.1	0	0	0	7
sp119	*Coltricia* sp.2	0	0	0	1
sp120	*Coprinus* sp.1	0	0	0	1
sp121	*Coprinus* sp.2	2	0	1	0
sp122	*Coprinus* sp.3	4	0	0	2
sp123	*Coprinus* sp.4	1	0	0	1
sp124	*Coprinus* sp.5	1	0	0	0
sp125	*Coprinus* sp.6	1	0	0	0
sp126	*Coprinus* sp.7	1	0	0	0
sp127	*Coprinus* sp.8	0	0	0	1
sp128	*Coprinus* sp.9	1	0	3	0
sp129	*Coprinus* sp.10	0	0	1	0
sp130	*Coprinus* sp.11	0	1	0	0
sp131	*Coprinus* sp.12	0	0	0	1

sp132	*Coprinus* sp.13	0	0	2	0
sp133	*Cortinarius* sp.1	1	0	0	1
sp134	*Cortinarius* sp.2	0	1	0	0
sp135	*Cortinarius* sp.3	0	0	3	0
sp136	*Cortinarius* sp.4	0	2	3	0
sp137	*Cortinarius* sp.5	0	0	1	0
sp138	*Cortinarius* sp.6	0	0	0	1
sp139	*Cortinarius* sp.7	1	0	0	0
sp140	*Cortinarius* sp.8	0	0	2	0
sp141	*Cortinarius* sp.9	0	0	1	0
sp142	*Craterellus* sp.1	0	0	0	1
sp143	*Crepidotus* sp.1	1	0	0	0
sp144	*Crepidotus* sp.2	0	0	0	4
sp145	*Crepidotus* sp.3	1	0	0	0
sp146	*Crepidotus* sp.4	3	0	0	1
sp147	*Crepidotus* sp.5	2	0	0	0
sp148	*Crepidotus* sp.6	1	0	0	0
sp149	*Crepidotus* sp.7	0	0	1	0
sp150	*Dacrymyces* sp.1	0	0	1	0
sp151	*Daldinia* sp.1	3	0	0	1
sp152	*Deconica coprophila*	0	0	0	2
sp153	*Entoloma* sp.1	1	0	1	0
sp154	*Entoloma* sp.2	1	0	0	0
sp155	*Entoloma* sp.3	0	1	0	0
sp156	*Ganoderma* sp.1	0	0	0	2
sp157	*Geastrum* sp.1	0	3	1	2
sp158	*Gymnopus* sp.1	0	0	0	1

sp159	*Gymnopus* sp.2	5	6	3	2
sp160	*Gymnopus* sp.3	1	1	0	1
sp161	*Gymnopus* sp.4	0	2	7	0
sp162	*Gymnopus* sp.5	0	0	0	1
sp163	*Hebeloma* sp.1	1	0	1	0
sp164	*Helvella* sp.1	0	0	2	2
sp165	*Helvella crispa*	0	0	2	0
sp166	*Hydnellum* sp.1	0	0	1	0
sp167	*Hydnum* sp.1	2	0	0	0
sp168	*Hygrocybe* sp.1	1	0	0	0
sp169	*Hygrocybe conica*	1	0	3	0
sp170	*Hygrophorus* sp.1	0	0	3	0
sp171	*Hygrophorus Russula*	0	0	3	0
sp172	*Hymenochaete* sp.1	0	1	2	0
sp173	*Hymenochaete* sp.2	3	0	4	1
sp174	*Hymenochaete* sp.3	0	1	0	0
sp175	*Hymenochaete* sp.4	0	0	2	1
sp176	*Hymenochaete* sp.5	0	0	0	1
sp177	*Hymenochaete* sp.6	0	1	0	0
sp178	*Hymenochaete* sp.7	0	0	1	0
sp179	*Hymenochaete* sp.8	0	0	1	0

sp180	*Hymenochaete* sp.9	0	0	0	4
sp181	*Hymenochaete* sp.10	0	0	0	1
sp182	*Hymenochaete* sp.11	0	0	1	0
sp183	*Hymenochaete* sp.12	0	0	0	1
sp184	*Hypholoma* sp.1	0	0	0	1
sp185	*Hypomyces* sp.1	1	0	0	0
sp186	*Hypomyces lactifluorum*	1	0	0	0
sp187	*Inocybe* sp.1	1	0	1	0
sp188	*Inocybe* sp.2	0	0	1	0
sp189	*Laccaria amethystina*	0	0	1	3
sp190	*Laccaria bicolor*	0	1	10	14
sp191	*Laccaria escamosa*	0	0	0	1
sp192	*Laccaria laccala*	0	0	1	0
sp193	*Laccaria* sp.1	0	1	0	0
sp194	*Lactarius* sp.1	1	0	0	0
sp195	*Lactarius* sp.2	0	1	0	0
sp196	*Lactarius Chrysorreus*	0	1	5	5
sp197	*Lactarius* sp.3	0	1	0	0
sp198	*Lentinus* sp.1	0	1	1	1
sp199	*Lentinus* sp.2	1	0	0	0
sp200	*Lepiota* sp.1	0	0	3	3
sp201	*Lepiota* sp.2	1	1	0	0

sp202	*Lepiota clypeolaria*	5	0	0	0
sp203	*Lepista* sp.1	0	0	0	1
sp204	*Lepista* sp.2	0	1	1	0
sp205	*Lepista nuda*	9	5	0	0
sp206	*Leucoagaricus* sp.1	0	0	2	0
sp207	*Lycoperdon* sp.1	1	1	1	1
sp208	*Lycoperdon* sp.2	1	0	1	1
sp209	*Lycoperdon* sp.3	1	0	0	0
sp210	*Lycoperdon perlatum*	0	0	1	1
sp211	*Lyophyllum* sp.1	0	0	4	0
sp212	*Marasmius* sp.1	0	0	1	1
sp213	*Marasmius* sp.2	0	1	0	0
sp214	*Marasmius* sp.3	6	0	0	0
sp215	*Marasmius* sp.4	1	0	0	0
sp216	*Marasmius* sp.5	0	0	0	1
sp217	*Marasmius* sp.6	3	1	0	0
sp218	*Marasmius* sp.7	5	0	0	0
sp219	*Marasmius* sp.8	0	1	0	1
sp220	*Marasmius* sp.9	0	0	1	1
sp221	*Marasmius* sp.10	1	0	0	0
sp222	*Marasmius* sp.11	0	6	0	0
sp223	*Marasmius* sp.12	0	1	1	1
sp224	*Mycena* sp.1	1	0	0	1
sp225	*Mycena* sp.2	0	0	0	2
sp226	*Mycena* sp.3	0	0	0	4
sp227	*Mycena* sp.4	0	0	2	2

sp228	*Mycena* sp.5	0	0	0	2
sp229	*Mycena* sp.6	1	0	0	0
sp230	*Mycena* sp.7	0	0	0	1
sp231	*Panus* sp.1	0	0	0	1
sp232	*Panus* sp.2	0	0	0	1
sp233	*Panus* sp.3	0	0	1	0
sp234	*Panus conchatus*	1	0	0	0
sp235	*Peziza* sp.1	3	0	0	1
sp236	*Peziza* sp.2	0	1	0	0
sp237	*Peziza* sp.3	0	1	3	0
sp238	*Peziza* sp.4	0	0	0	1
sp239	*Phelinus* sp.1	1	0	0	1
sp240	*Phelinus gilvus*	2	0	0	2
sp241	*Phelodon niger*	3	0	0	0
sp242	*Pisolithus* sp.1	0	2	0	0
sp243	*Pluteus* sp.1	1	0	1	1
sp244	*Pluteus* sp.2	0	0	1	0
sp245	*Polyporus* sp.1	0	0	0	1
sp246	*Polyporus* sp.2	0	0	0	1
sp247	*Polyporus* sp.3	0	0	0	1
sp248	*Polyporus* sp.4	0	1	0	0
sp249	*Psatyrella* sp.1	3	0	1	1
sp250	*Ramaria* sp.1	0	0	0	1
sp251	*Ramaria* sp.2	0	2	0	0
sp252	*Ramaria* sp.3	2	0	0	0
sp253	*Ramaria* sp.4	0	2	0	0
sp254	*Rubro boletus* sp.1	0	1	0	0

sp255	*Russula* sp.1	0	0	1	0
sp256	*Russula* sp.2	0	1	2	0
sp257	*Russula* sp.3	0	0	0	2
sp258	*Russula* sp.4	1	0	0	0
sp259	*Russula* sp.5	0	1	1	6
sp260	*Russula* sp.6	7	0	3	3
sp261	*Russula* sp.7	1	0	0	0
sp262	*Russula* sp.8	0	0	0	1
sp263	*Russula* sp.9	12	3	6	8
sp264	*Russula* sp.10	5	0	0	0
sp265	*Russula* sp.11	1	0	0	0
sp266	*Russula* sp.12	0	0	0	1
sp267	*Russula brevipes*	0	2	2	1
sp268	*Russula foetens*	2	0	3	2
sp269	*Russula pectinata*	0	0	2	0
sp270	*Russula pectinatoides*	0	0	6	2
sp271	*Russula vesicatoria*	0	0	1	0
sp272	*Russula xeromphalina*	4	4	0	0
sp273	*Scleroderma* sp.1	3	1	8	9
sp274	*Sebacina* sp.1	4	0	0	0
sp275	*Sparasis* sp.1	1	0	0	0
sp276	*Stereum ostrae*	0	1	1	0
sp277	*Stereum* sp.1	0	0	2	0
sp278	*Strobilomyces strobilaceus*	3	0	4	3
sp279	*Strobylomyces* sp.1	1	0	1	1

sp280	*Suillus* sp.1	0	0	1	0
sp281	*Trametes* sp.1	1	0	0	0
sp282	*Trametes* sp.2	0	0	0	1
sp283	*Tremella cafe*	1	0	0	0
sp284	*Tremella foliacea*	0	0	1	1
sp285	*Tremella fuciformis*	1	0	0	1
sp286	*Tremella mesenterica*	0	0	0	1
sp287	*Tricholoma* sp.1	0	0	2	1
sp288	*Tricholoma equestre*	3	0	0	0
sp289	*Tricholoma* sp.2	0	0	1	0
sp290	*Tylopillus* sp.1	4	0	0	0
sp291	*Tylopillus* sp.2	1	0	0	0
sp292	*Xerocomus* sp.1	4	0	0	1
sp293	*Xerocomus* sp.2	1	0	0	0
sp294	*Xerocomus* sp.3	0	0	1	0
sp295	*Xeromphalina* sp.1	1	0	0	3
sp296	*Xylaria* sp.1	3	2	1	14