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Variation in macrofungal diversity and species composition across different vegetation types in Oaxaca, Mexico

Variación en diversidad y composición de especies macrofúngicas a través de diferentes tipos de vegetación en Oaxaca, México

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Abstract

Background: Macromycetes play relevant roles in ecosystem functioning as pathogens, mutualists, and organic matter decomposers. Their diversity and distribution are strongly related to environmental conditions and vegetation types, however, there is a lack of ecological studies assessing which biotic and abiotic factors affect macrofungal communities.

Questions: Which vegetation type harbors the highest macromycete diversity? Do macromycete diversity and species composition change among forest types? Which are the main environmental factors related to diversity and distribution patterns along the study area?

Data description: Macromycete species richness and abundance, and environmental variables recorded in temperate forests.

Study site and dates: Ayoquezco de Aldama, Oaxaca. June-November 2019.

Methods: Macromycetes were collected twice a month in oak, oak-pine, pine-oak and pine forests, and environmental variables were recorded at each site. Species diversity and composition turnover were calculated using diversity and similarity indexes. The relation between diversity and species composition with environmental variables was determined with statistical analyses.

Results: A total of 186 species were collected. Oak-dominated forests showed the highest similarity in macromycete diversity and species composition. The observed patterns of diversity and distribution were related mainly to air and soil humidity and temperature, topographic factors, and vegetation structure.

Conclusions: Macromycete diversity and species composition can conspicuously change in short distances owing to the heterogeneity of habitats and resources provided by woody plants, and the topographic characteristic of the landscape. Vegetation type affects both macromycete diversity and distribution due to its influence on local temperature and humidity.

Keywords: macromycetes, oak forest, pine forest, species richness.

Resumen

Antecedentes: Los macromicetos juegan papeles relevantes en el funcionamiento ecosistémico como mutualistas, patógenos y degradadores de materia orgánica. Su diversidad y distribución están relacionadas a condiciones ambientales y tipo de vegetación, pero existe escasez de estudios que evalúen factores bióticos y abióticos afectando comunidades macrofúngicas.

Preguntas: ¿Cuál tipo de vegetación alberga mayor diversidad de macromicetos? ¿La diversidad y composición de especies cambia entre vegetaciones? ¿Cuáles son los factores ambientales relacionados a los patrones de diversidad y distribución en el área estudiada?

Descripción de datos: Riqueza y abundancia de macromicetos, variables ambientales registradas en bosques templados.

Sitio y años de estudio: Ayoquezco de Aldama, Oaxaca. Junio-noviembre 2019.

Métodos: Los macromicetos se recolectaron bimensualmente en bosques de encino, encino-pino, pino-encino y pino, y se registraron variables ambientales. La diversidad y recambio de especie se calcularon con índices de diversidad y similitud. La relación entre diversidad y composición de especies y variables ambientales se determinó con análisis estadísticos (ver Materials and Methods para detalles).

Resultados: Se recolectaron 186 especies. Los bosques de encino tuvieron mayor diversidad y similitud de especies macrofúngicas. Los patrones de diversidad y distribución están relacionados principalmente a la temperatura y humedad, factores topográficos y estructura de la vegetación.

Conclusiones: La diversidad y composición de macromicetos puede cambiar conspicuamente en distancias cortas debido a la heterogeneidad de hábitats y recursos que provén los árboles, así como características topográficas del paisaje. El tipo de vegetación afecta la diversidad y distribución de macromicetos por su influencia en el microclima.

Palabras clave: bosque de encino, bosque de pino, macromicetos, riqueza de especies.

Estimates suggest that 5.1 million fungal species exist worldwide (Blackwell 2011), and that about 53,000-111,000 of them are macromycetes (characterized by the production of fruit bodies visible to the naked eye) (Mueller *et al.* 2007). Geographic variation in species richness and composition of macromycete communities has been related mainly to microclimatic conditions, which can be driven by plant distribution ranges, vegetation structure, and topographic factors (*e.g*., slope and aspect) (Mueller *et al.* 2007, Zhang *et al.* 2010, Singha *et al*. 2017, Gómez-Hernández *et al.* 2019).

Understanding how environmental factors relate to the diversity and distribution of macromycete species is a growing interest in ecological studies due to the roles these organisms play in most terrestrial ecosystems worldwide. Macromycetes interact with other groups as pathogens, where they can be detrimental to plant growth and fitness or regulate plant and animal populations (Termorshuizen 2014). As mutualists, macromycetes can help plants improve nutrient absorption, drought tolerance, and provide pathogen resistance (Barrico *et al.* 2012). Also, macrofungi are the most important decomposers of organic matter in terrestrial ecosystems and play major roles in the carbon and nitrogen cycles (Harley 1971, Dighton 2016).

Knowledge on the factors influencing macrofungal diversity and distribution may be helpful to ascertain which areas support higher diversity, evaluate how macromycete functional groups respond to environmental changes and their effect on ecosystem functioning, and detect processes structuring macrofungal communities in both natural and urbanized environments (Packham *et al.* 2002, Gómez-Hernández *et al.* 2012, Caiafa *et al*. 2017). Several studies have shown that variation in vegetation structure and tree species composition along vegetation types, affects macrofungal communities and the presence of species associated to woody plants, due to differences in the quality and quantity of the resources provided (Ferrer & Gilbert 2003, Richard *et al.* 2004, Brown *et al.* 2006, Zhang *et al.* 2010). In temperate communities, a greater canopy cover has been related to shade provision and increased soil moisture and water-holding capacity, all which influence macrofungal species richness (Ferris *et al*. 2000, Gabel & Gabel 2007). Also, some studies indicate that precipitation (Lange 1978, Salerni *et al*. 2002) or both humidity and temperature (Durall *et al*. 2006) are the main factors related to macromycete diversity (Brown *et al.* 2006). However, most macromycete studies address topics on taxonomy and systematics, and there is a lack of studies relating patterns of diversity and distribution to vegetation, microclimate, and topographic factors (Brown *et al*. 2006, Schmit & Mueller 2007, Braga-Neto *et al.* 2008, Gómez-Hernández *et al*. 2012, Gómez-Hernández *et al*. 2019).

In Mexico, estimates suggest the presence of more than 250,000 species of fungi (Guzmán 1998), and approximately 9,000-11,000 species of macromycetes (Aguirre-Acosta *et al.* 2014). Oaxaca is one of the most biodiverse regions in the world, and one of the most biologically diverse regions in Mexico (Flores-Villela & Gerez 1994, Villaseñor 2016), but mycological studies are scarce in this area (Garibay-Orijel *et al.* 2009) and there are only five studies assessing patterns of diversity and distribution within and across macrofungal communities. Caiafa *et al.* (2017) carried out a study along an elevation gradient in the Costa region and found that the functional diversity of macromycetes varies with elevation, is related more to microclimatic variables than to vegetation structure, and that heterogeneity of trait abundance and niche complementarity increased with elevation. Avendaño (2019) conducted a survey in the Valles Centrales region of Oaxaca, and the results showed that the functional diversity of macromycetes decreased from disturbed to conserved areas, and species composition differed largely between disturbed and conserved sites. The study by Gómez-Hernández *et al*. (2019) in the Sierra Norte region showed markedly different macrofungal communities in forest patches with different development stages of *Pinus patula* Schiede ex Schl. *et* Cham, where substrate availability and vegetation structure were the main factors related to the observed patterns of diversity and distribution. Ruiz-Almenara *et al*. (2019), carried out a study in the Mixteca region and their results indicated that intensive harvesting of wild edible mushrooms did not affect the diversity and distribution of macromycete species, showing that this can be an innocuous activity as long as the general environment and the macromycete habitat are not disturbed. The findings by Gómez-Hernández *et al*. (2021) indicated that some of the available resources in the niche space within the most urbanized sites are not being used, and that urbanization also causes a high degree of niche differentiation among macromycete species within communities in urbanized areas. The aim of this study was to evaluate patterns of macromycete diversity and composition along different vegetation types in

forests of temperate affinity, and identify microclimatic, environmental, and vegetation structure factors related to the observed patterns.

Materials and methods

Study area. This study was carried out in Ayoquezco de Aldama in the political district of Zimátlan de Álvarez, Oaxaca, Mexico. Ayoquezo is located at 16° 36'-16° 44' N and 96° 50'- 96° 57' W, approximately at 1,598 m asl, and is characterized by a rainy season from May to October. The climate is Semi-warm *A(C)* (García 2004). Mean annual temperature is > 18 °C, and annual precipitation ranges from 600 to 800 mm (Unidad de Microrregiones 2005).

In the highlands of Ayoquezco de Aldama, where this study was carried out, the vegetation is represented primarily by oak-pine and coniferous forests, which include woody species like "cuatle" (*Eysenhardtia polystachya* (Ortega) Sarg.), "cuachepil" (*Senna septemtrionali* (Viv.) H.S. Irwin & Barneby), "tepehuaje" (*Lysiloma acapulcensis* (Kunth) Benth.), "cazahuate" (*Ipomoea murucoides* Roem. & Schult.), "enebro" (*Juniperus flaccida* Schlechtendal.), "sabino" (*Taxodium mucronatum* Ten.) and "cedro" (*Cedrela odorata* L.) (INAFED 2016).

Study sites. Four sites were selected to carry out the samplings, and the vegetation type in each one was defined based on the dominant genus of trees: oak forest (Site 1, dominated by *Quercus*), oak-pine forest (Site 2, presence of *Pinus*, dominated by *Quercus*), pine-oak forest (Site 3, presence of *Quercus*, dominated by *Pinus*), and pine forest (Site 4, dominated by *Pinus*). At each site, 10 permanent plots of 10 ×10 m were set up, with a distance of about 10 m between plots and 30 m from the forest edge, to avoid "edge effects" (Williams-Linera *et al.* 1998).

Macromycete sampling. From June to November 2019, macromycete fruiting bodies were collected twice a month in every plot of the four study sites. Sporomes of the same species growing within a 50 cm radius, caespitose growth, fairy rings, and fruit bodies of the same species growing on the same log or branch were all recorded as a single collection unit, and abundance was estimated as the number of collection units (adapted from Schmit *et al.* 1999). Hereafter, for practical purposes, collection units will be referred to as individuals. The collected specimens were identified based on their macro and micro morphological characters aided by identification keys and reference literature (*i.e*., Guzmán 1977, Largent 1986, Læssøe & Petersen 2019). Species that could not be identified were classified as a morphospecies.

Environmental variables. Air temperature and humidity, and soil temperature and humidity were recorded every sampling day at a permanent point in each plot. Slope and aspect (slope orientation) were measured once at each plot. The diameter, height, and number of woody plants with diameters > 10 cm at breast height (1.3 m above the ground) were also recorded. Vegetation structure was characterized as density of trees, mean and maximum height of trees, canopy openness and basal area (Supplementary Material, Table S1).

Diversity and species composition. The diversity of macromycetes was measured by species richness (number of species) and by the True Diversity index of first order (^{1}D), which is a suitable metric to use for macromycete data because it weighs all species by their frequency, without favoring either common or rare species (Jost 2006). This index was calculated with the entropart package in R v. 3.2.3 (R Core Team 2017). The none-parametric species richness estimator Chao 2 was used to determine how complete were the species inventories recorded in every study site. The turnover of species composition between study sites was calculated with the abundance-based Chao-Jaccard similarity index using EstimateS (Colwell 2013). This index is neither sensitive to sample size nor to numerous rare species in a community, as in the case of macromycete communities (Chao *et al.* 2005).

Data analyses. Prior to statistical analyses, the assumption of normality was assessed performing Shapiro-Wilk tests. The Spearman correlation coefficient (ρ) was used to determine the relation between macromycete species richness

and microclimatic, topographic and vegetation variables. A regression tree analysis was carried out to assess how the explanatory variables affect the variation of macromycete species richness in the study area. The relationship between the geographic distance between sites and changes in species composition was calculated using linear regression analyses. A Non-metric multidimensional scaling (NMDS) analysis was used to visualize the distance between each study site according to species composition. The relationship between the distribution of species and the explanatory variables in each community was determined with a Canonical Correspondence Analysis (CCA).

All data analyses mentioned in this section were performed in R v. 3.2.3.

Results

A total of 617 macromycete individuals were registered, belonging to 186 species, 60 genera, and 42 families. Of the species collected, 22 belong to ascomycetes and 165 to basidiomycetes (Supplementary Material, Table S2). The highest species richness was found in Site 3 (75 species) (pine-oak forest), followed by Site 1 (67) (oak forest), Site 2 (60) (oak-pine forest), and Site 4 (49) (pine forest) (Supplementary Material, Table S3). The True Diversity index showed that Site 1 had the highest diversity (49.83), followed by Site 3 (40.86), Site 2 (36.57), and Site 4 (31.17). The species richness estimator Chao 2 indicated that the completeness of the macromycete species inventory in Site 1 was 51.56 %, whereas in Site 2 was 50.21 %, Site 3 was 53.10 %, and Site 4 was 48.42 %.

Spearman correlations indicated a significant negative correlation between macromycete species richness and aspect (ρ = - 0.4307, P = 0.0055) as well as canopy openness (ρ = -0.4321, P = 0.0053). The regression tree analysis (residual mean deviance = 40.05) indicated that from a total of 40 plots in the study area, the variation of species richness in 42.5 % of them occurred when air humidity was under 48.85 %. From this 42.5 % of all plots, species richness in 52.99 % of them was influenced by canopy openness under 27.56 %. Additionally, from the 40 plots, the number of species in 57.5 % of them was affected by air humidity over 48.85 %, and species in 73.91 % of the mentioned 57.5 %, were affected by air temperatures higher than 20.98 °C. Species richness in 52.94 % of the 73.91 % mentioned before, varied when soil humidity was less than 35.41 % (Figure 1).

The Chao-Jaccard similarity index indicated that the similarity of species composition was higher for sites 1 and 2 (0.36) (oak, oak-pine), followed by sites 3 and 4 (0.26) (pine-oak, pine), sites 2 and 3 (0.22) (oak-pine, pine-oak), sites 2 and 4 (0.17) (oak-pine, pine), sites 1 and 4 (0.14) (oak, pine), and lastly site 1 and 3 (0.09) (oak, pine-oak).

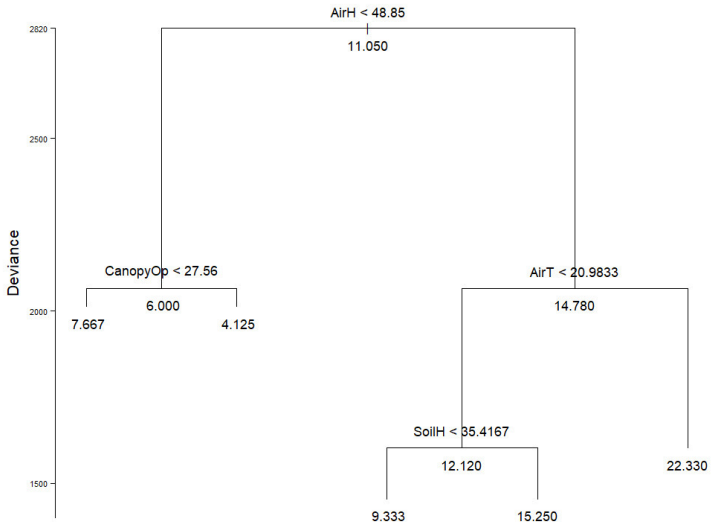

Figure 1. Regression tree for macromycete diversity. Partitions show the environmental variables and the threshold at which the partition was made. The average value of variable effect is indicated at the tips and nodes. Variables are: air humidity (AirH), canopy openness (CanopyOp), air temperature (AirT), and soil humidity (SoilH).

NDMS showed that sites 1 and 2 are the closest in terms of their species composition while sites 2 and 4 are the farthest apart (Figure 2). The CCA for microclimatic, topographic and vegetation variables included 187 macromycete species. The model showed that sites 1 and 2 are clearly separated from sites 3 and 4 along Axis 1 (eigenvalue = 0.7151) and site 3 is separated from site 4 along Axis 2 (eigenvalue = 0.6393). Axis 1 (14.85 %) and Axis 2 (12.83 %) together explained 27.68 % of the total variance (Figure 3).

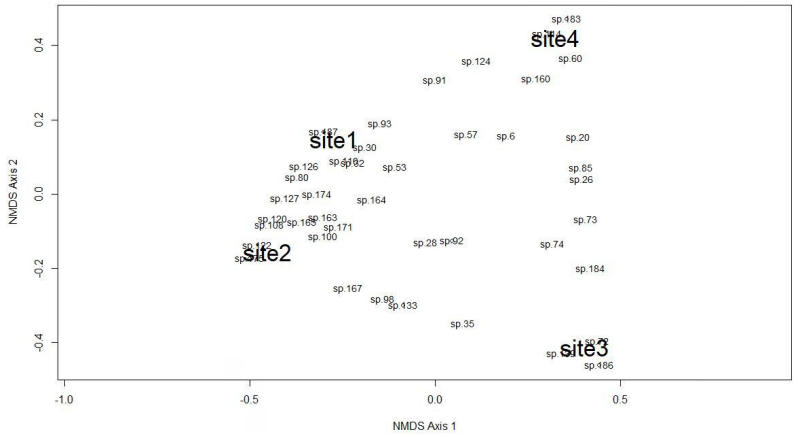

Figure 2. Non-metric Multidimensional Scaling analysis for macrofungal species complementarity among the study sites; Site 1 (oak forest), Site 2 (oak-pine forest), Site 3 (pine-oak forest), and Site 4 (pine forest). "sp1, sp2, sp3, sp4…" represents the species recorded in the study area, and the numbers of the species correspond to the numbers (#) in Supplementary Material, Table S2.

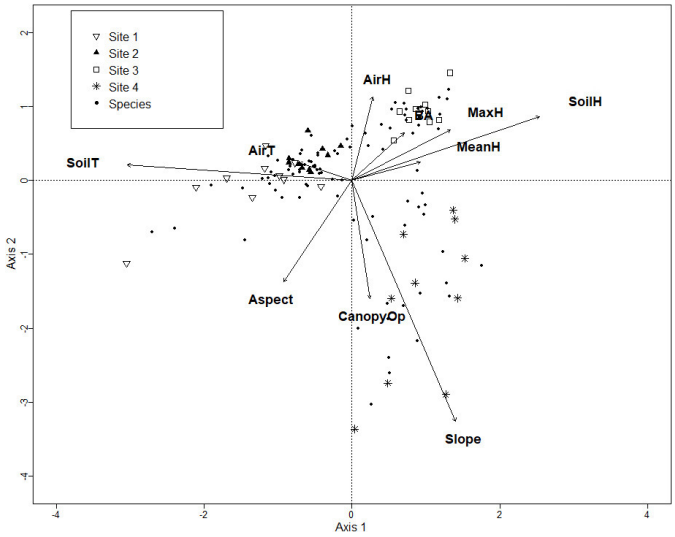

Figure 3. CCA for all the macromycete species recorded in the study; Site 1 (oak forest), Site 2 (oak-pine forest), Site 3 (pine-oak forest), and Site 4 (pine forest). Vectors represent environmental explanatory variables: AirH (air humidity), BA (basal area), MaxH (maximum height of trees), MeanH (average height of trees), SoilH (soil humidity), Slope, CanopyOP (canopy openness), Aspect, SoilT (soil temperature), AirT (air temperature).

Discussion

Our results show significant variation in macromycete diversity between vegetation types. In correspondence with our findings, several studies assessing local patterns of macromycete diversity in both temperate and tropical forests, suggest that the number of macrofungal species and fruitbody production are related to topographic and microclimat-

ic factors, mainly air and soil humidity and temperature (O'Dell *et al*. 2000, Brown *et al*. 2006, Gómez-Hernández & Williams-Linera 2011, Caiafa *et al*. 2017).

In the present study, the regression tree analysis indicated that the number of macrofungal species in the study area is influenced mostly by changes in air humidity, air temperature and soil humidity. The analysis suggests that species richness in most of the sampled area is favored when air humidity is above 48.8 %, however, it has been reported that air humidity can be more advantageous for macromycete productivity when it is around 80 % (Shuhada *et al*. 2020). Comparable to studies showing that macromycete species richness decreases when temperature is over 27 °C (Jang & Hur 2014, Ghate & Sridhar 2016), our results indicated that macromycetes benefit with air temperatures below 20.9 °C. Similarly, it is broadly known that excessive soil water content can inhibit macromycete production and hence, species richness (O'Dell *et al*. 1996, Lodge *et al*. 2004), which corresponds with our finding suggesting that macromycetes benefit with soil humidity under 35.4 %. However, fruitbody production and occurrence of the different macromycete species along the rainy season depend on specific humidity and temperature ranges (Wilkins & Harris 1946, Thoen 1976).

Changes in temperature and humidity affecting macromycete communities along environmental gradients are a function of the varying vegetation structure and factors like slope or aspect (Cavender-Bares *et al*. 2009, Zhang *et al*. 2010, Gómez-Hernández *et al.* 2019). Consistent with our results, studies have found that an open canopy exposes the surrounding soil to sunlight, which can cause high soil temperatures and loss of humidity, both unfavorable for macrofungal growth (Ferris *et al*. 2000, Egli *et al*. 2010, Ford *et al*. 2018). Our results also showed that the aspect of the terrain is negatively related to macrofungal diversity, because landscape topography influences water drainage and evaporation rate, thereby affecting fruit body production and species richness (Rubino & McCarthy 2003, Gómez-Hernández *et al*. 2012).

The turnover of macromycete species composition was high between the four studied sites, with the oak-dominated forests being the most similar. Although geographic distance has been related to species turnover between macromycete communities, there was no correlation between species turnover and geographic distance in our studied area, but the distribution of macromycete species can be explained by variables related to changes in the structure and composition of tree communities (Brown *et al*. 2006, Gómez-Hernández *et al*. 2019). Each of our study sites had their own characteristics, but results indicated that soil temperature, canopy openness, and maximum tree height were the main factors driving macromycete distribution. Studies in forests of temperate affinity have found that macromycete distribution can be influenced by the composition of woody plant species, vegetation structure (*e.g*., basal area, canopy openness, height of trees) and factors buffering temperature rise and humidity loss (Gabel & Gabel 2007, Gómez-Hernández *et al*. 2019). Variation in the composition of tree species and vegetation structure involve changes in microclimatic conditions and in the quality and quantity of available resources, which can highly influence macromycete communities (Lodge 1997, Ferris *et al*. 2000, Gómez-Hernández *et al.* 2019).

Patterns of diversity and composition of macromycete functional guilds along the different vegetation types were not analyzed in this study. However, information on this issue should be of interest and relevance for future studies since changes in vegetation type can alter macrofungal communities due to their trophic strategies make them require biological interactions such as mycorrhizal plant hosts or plant debris as substrates (Gabel & Gabel 2007, Newbound *et al*. 2010). The relationship between vegetation type and macrofungal communities is reflected in host trees affecting macromycete specialization and providing unique habitat availability and different resource quality (Villeneuve *et al*. 1989, Richard *et al.* 2004, Brown *et al.* 2006, Zhang *et al.* 2010). In pine and oak forests, both ectomycorrhizal and saprotrophic richness and composition of species have been observed to change meaningfully as the number of forest layers vary, suggesting that macrofungal communities are mainly shaped by host plants, forest structure, physicochemical attributes of the soil, and quality of the substrata (Dighton & Mason 1985, Villeneuve *et al*. 1989, Fernández-Toirán *et al.* 2006).

This study contributes with ecological knowledge on macromycete communities associated to temperate forests in Oaxaca. Results can be used to assess ecosystem quality and determine changes in ecological dynamics (Rojas *et al*. 2017). Also, the information generated can be useful for conservation decisions and management recommenda-

tions given that forests with high macromycete diversity were identified, and factors limiting species distribution and growth were detected (Gabel & Gabel 2007, Dejene *et al*. 2017).

Our findings showed that macromycete diversity and composition can change conspicuously along relatively small areas due to differences in the local environment regarding the heterogeneity of habitats and resources provided by woody plant species. It should be of interest for future studies to assess how this variation affects the different functional groups along vegetation types. Furthermore, assessing variables related to soil characteristics could be useful to better understand the observed patterns of diversity and distribution. To complement ecological studies on macrofungi and better understand how macromycete diversity and distribution are influenced by biotic and abiotic factors, it is necessary to carry out surveys in different ecosystems and include metrics based on functional and phylogenetic information to make inferences about the evolutionary and ecological processes structuring macrofungal communities.

Supplementary material

Supplemental data for this article can be accessed here: https://doi.org/10.17129/botsci.3012

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Literature cited

Aguirre-Acosta E, Ulloa M, Aguilar S, Cifuentes J, Valenzuela R. 2014. Biodiversidad de hongos en México. *Revista Mexicana de Biodiversidad* **85**: S76-S81. DOI: https://doi.org/10.7550/rmb.33649

Avendaño ME. 2019. *Diversidad funcional y recambio de especies macrofúngicas en un ecosistema urbano del centro de Oaxaca, México*. MSc. Thesis. Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional Unidad Oaxaca.

Barrico L, Azul AM, Morais MC, Pereira-Coutinho A, Freitas H, Castro P. 2012. Biodiversity in urban ecosystems: Plants and macromycetes as indicators for conservation planning in the city of Coimbra (Portugal). *Landscape and Urban Planning* **106**: 88-102. DOI: https://doi.org/10.1016/j.landurbplan.2012.02.011

Blackwell M. 2011. The Fungi: 1, 2, 3… 5.1 million species? *American Journal of Botany* **98**: 426-438. DOI: https://doi.org/10.3732/ajb.1000298

Braga-Neto R, Luizão RCC, Magnusson WE, Zuquim G, de Castilho CV. 2008. Leaf litter fungi in a Central Amazonian forest: the influence of rainfall, soil and topography on the distribution of fruiting bodies. *Biodiversity and Conservation* **17**: 2701-2712. DOI: https://doi.org/10.1007/s10531-007-9247-6

Brown N, Bhagwat S, Watkinson S. 2006. Macrofungal diversity in fragmented and disturbed forests of the Western Ghats of India. *Journal of Applied Ecology* **43**: 11-17. DOI: https://doi.org/10.1111/j.1365-2664.2005.01107.x

Caiafa MV, Gómez-Hernández M, Williams-Linera G, Ramírez-Cruz V. 2017. Functional diversity of macromycete communities along an environmental gradient in a Mexican seasonally dry tropical forest. *Fungal Ecology* **28**: 66-75. DOI: https://doi.org/10.1016/j.funeco.2017.04.005

Cavender-Bares J, Izzo A, Robinson R, Lovelock CE. 2009. Changes in ectomycorrhizal community structure on two containerized oak hosts across an experimental hydrologic gradient. *Mycorrhiza* **19**: 133-142. DOI: https://doi.org/10.1007/s00572-008-0220-3

Chao A, Chazdon RL, Colwell RK, Shen TJ. 2005. A new statistical approach for assessing compositional simi-

larity based on incidence and abundance data. *Ecology Letters* **8**:148-159. DOI: https://doi.org/10.1111/j.1461-0248.2004.00707.x

Colwell RK. 2013. *EstimateS, Version 9.1: statistical estimation of species richness and shared species from samples*. Colorado, United States of Americahttp://viceroy.eeb.uconn.edu/estimates/ (accessed December 2021).

Dejene T, Oria-de-Rueda JA, Martín-Pinto P. 2017. Fungal diversity and succession following stand development in Pinus patula Schiede ex Schltdl. & Cham. Plantations in Ethiopia. *Forest Ecology and Management* **395**: 9-18. DOI: https://doi.org/10.1016/j.foreco.2017.03.032

Dighton J. 2016. *Fungi in ecosystem processes*. New York: Marcel Dekker. DOI: https://doi.org/10.1201/9781315371528

Dighton J, Mason PA. 1985. Mycorrhizal dynamics during forest tree development. *In*: Moore D, Casselton L, Wood DA, Frankland JC, eds. *Developmental Biology of Higher Fungi*. London: Cambridge University Press, pp. 117-139. ISBN: 9780521106276

Durall DM, Gamiet S, Simard SW, Kudrna L, Sakakibara SM. 2006. Effects of clearcut logging and tree species composition on the diversity and community composition of epigeous fruit bodies formed by ectomycorrhizal fungi. *Canadian Journal of Botany* **84**: 966-980. DOI: https://doi.org/10.1139/b06-045

Egli S, Ayer F, Peter M, Eilmann B, Rigling A. 2010. Is forest mushroom productivity driven by tree growth? Results from a thinning experiment. *Annals of Forest Science* **67**: 509-509. DOI: https://doi.org/10.1051/forest/2010011

Fernández-Toirán LM, Ágreda T, Olano JM. 2006. Stand age and sampling year effect on the fungal fruit body community in Pinus pinaster forests in central Spain. *Canadian Journal of Botany* **84:**1249-1258 DOI: https://doi.org/10.1139/B06-087

Ferrer A, Gilbert GS. 2003. Effect of tree host species on fungal community composition in a tropical rain forest in Panama. *Diversity and Distributions* **9**: 455-468 DOI: https://doi.org/10.1046/j.1472-4642.2003.00039.x.

Ferris R, Peace AJ, Newton AC. 2000. Macrofungal communities of lowland Scots pine (Pinus sylvestris L.) and Norway spruce (Picea abies (L.) Karsten.) plantations in England: relationships with site factors and stand structure. *Forest Ecology and Management* **131**: 255-267. DOI: https://doi.org/10.1016/S0378-1127(99)00218-2

Flores-Villela O, Gerez P. 1994. *Biodiversidad y conservación en México: vertebrados, vegetación y uso del suelo*. Ciudad de México, México: Universidad Nacional Autónoma de México. ISBN: 9789683639929

Ford SA, Kleinman JS, Hart JL. 2018. Effects of wind disturbance and salvage harvesting on macrofungal communities in a Pinus woodland. *Forest Ecology and Management* **407**: 31-46. DOI: https://doi.org/10.1016/j.foreco.2017.10.010

Gabel AC, Gabel ML. 2007. Comparison of diversity of macrofungi and vascular plants at seven sites in the Black Hills of South Dakota. *The American Midland Naturalist* **157**: 258-296. DOI: https://www.doi.org/10.1674/0003-0031(2007)157[258:CODOMA]2.0.CO;2

Garibay-Orijel R, Martinez-Ramos M, Cifuentes J. 2009. Disponibilidad de esporomas de hongos comestibles en los bosques de pino-encino de Ixtlán de Juárez, Oaxaca. *Revista Mexicana de Biodiversidad* **80**: 521-534. DOI: http://dx.doi.org/10.22201/ib.20078706e.2009.002.615

Ghate SD, Sridhar KR. 2016. Contribution to the knowledge on macrofungi in mangroves of the Southwest India. *Plant Biosystems* **150**: 977-986. DOI: https://doi.org/10.1080/11263504.2014.994578

Gómez-Hernández M, Avendaño-Villegas E, Toledo-Garibaldi M, Gándara E. 2021. Impact of urbanization on functional diversity in macromycete communities along an urban ecosystem in Southwest Mexico. *PeerJ* **9**: e12191 DOI: https://doi.org/10.7717/peerj.12191

Gómez-Hernández M, Ramírez-Antonio KG, Gándara E. 2019. Ectomycorrhizal and wood-decay macromycete communities along development stages of managed *Pinus patula* stands in Southwest Mexico. *Fungal Ecology* **39**: 109-116. DOI: https://doi.org/10.1016/j.funeco.2018.12.007

Gómez-Hernández M, Williams-Linera G, Guevara R, Lodge DJ. 2012. Patterns of macromycete community assemblage along an elevation gradient: options for fungal gradient and metacommunity analyse. *Biodiversity and Conservation* **21**: 2247-2268. DOI: https://doi.org/10.1007/s10531-011-0180-3

Gómez-Hernández M, Williams-Linera G. 2011. Diversity of macromycetes determined by tree species, vegetation

structure, and microenvironment in tropical cloud forests in Veracruz, Mexico. *Botany* **89**: 203-216. DOI: https://doi.org/10.1139/B11-007

Guzmán G. 1977. *Identificación de los hongos: comestibles, venenosos, alucinantes y destructores de la madera*. Ciudad de México, México: Editorial Limusa. ISBN: 968-18-0123-7

Guzmán G. 1998. Análisis cualitativo y cuantitativo de la diversidad de los hongos en México. *In*: Halffter G, ed. *La Diversidad Biológica de Iberoamérica II.* Xalapa, México: Acta Zoológica Méxicana. pp. 111-175. ISBN 968-7863-33-1

Harley JL. 1971. Fungi in ecosystems. *Journal of Ecology* **8:** 653-668. DOI: https://doi.org/10.2307/2402673

INAFED. [Instituto Nacional para el Federalismo y el Desarrollo Municipal]. 2016. Enciclopedia de los municipios y delegaciones de México. Estado de Oaxaca. http://www.inafed.gob.mx/work/enciclopedia/EMM20oaxaca/municipios/20398a.html (accessed January 2021)

Jang SK, Hur TC. 2014. Relationship between climatic factors and the distribution of higher fungi in Byeonsanbando National Park, Korea. *Mycobiology* **42**: 27-33. DOI: https://doi.org/10.5941/MYCO.2014.42.1.27

Jost L. 2006. Entropy and diversity. *Oikos* **113**: 363-375. DOI: https://doi.org/10.1111/j.2006.0030-1299.14714.x

Læssøe T, Petersen J. 2019. *Fungi of temperate Europe 1-2*. New Jersey, USA: Princeton University Press. ISBN: 9780691180373

Lange M. 1978. Fungus flora in August. Ten years observations in a Danish beech wood district. *Botanisk Tidsskrift* **73**: 21-54.

Largent DL. 1986. *How to Identify Mushrooms to Genus I: Macroscopic Features*. Eureka, USA: Eureka Printing Company. ISBN: 9780916422011

Lodge DJ. 1997. Factors related to diversity of decomposer fungi in tropical forests. *Biodiversity and Conservation* **6**: 681-688. DOI: http://doi.org/10.1023/A:1018314219111

Lodge DJ, Ammirati JF, O'Dell TE, Mueller GM, Huhndorf SM, Wang CJ, Stokland J, Schmit JP, Ryvarden L, Leacock P, Mata M, Umaña L, Wud Q, Czederpiltz, DL. 2004. Terrestrial and lignicolous macrofungi. *In*: Mueller GM, Bills GF, Foster MS, eds. *Biodiversity of Fungi, Inventory and Monitoring Methods*. California, USA: Elsevier Academic Press, pp.127-158. DOI: https://doi.org/10.1016/B978-012509551-8/50011-8

Mueller GM, Schmit JP, Leacock PR, Buyck B, Cifuentes J, Desjardin DE, Halling RE, Hjortstam K, Iturriaga T, Larsson KH, Lodge DJ, May TW, Minter D, Rajchenberg M, Redhead SA, Ryvarden L, Trappe JM, Watling R, Wu Q. 2007. Global diversity and distribution of macrofungi. *Biodiversity and Conservation* **16**: 37-48. DOI: https://doi.org/10.1007/s10531-006-9108-8

Newbound M, Mccarthy MA, Lebel T. 2010. Fungi and the urban environment: A review. *Landscape and Urban Planning* **96**: 138-145. DOI : https://doi.org/10.1016/j.landurbplan.2010.04.005

O'Dell TE, Ammirati JF, Schreiner EG. 2000. Species richness and abundance of ectomycorrhizal basidiomycete sporocarps on a moisture gradient in the Tsuga heterophylla zone. *Canadian Journal of Botany* **77**: 1699-1711. DOI: https://doi.org/10.1139/b99-144

O'Dell T, Smith J, Castellano M, Luoma D. 1996. Diversity and conservation of forest fungi. *In*: Pilz, D, Molina R, eds. *Managing Forest Ecosystems to Conserve Fungus Diversity and Sustain Wild mushroom Harvests*. Oregon, USA: United States Department of Agriculture Forest Service, General Technical Report PNW, pp. 5-18. DOI: https://doi.org/10.2737/PNW-GTR-371

Packham JM, May TW, Brown MJ, Wardlaw TJ, Mills AK. 2002. Macrofungal diversity and community ecology in mature and regrowth wet eucalypt forest in Tasmania: a multivariate study. *Austral Ecology* **27:** 149-161. DOI: https://doi.org/10.1046/j.1442-9993.2002.01167.x

R Core Team. 2017. R: a Language and Environment for Statistical Computing, 3.4.2. Vienna: The R Foundation for Statistical Computing. https://www.R-project.org/

Richard F, Moreau PA, Selosse MA, Gardes M. 2004. Diversity and fruiting patterns of ectomycorrhizal and saprobic fungi in an old-growth Mediterranean forest dominated by Quercus ilex L. *Canadian Journal of Botany* **82**: 1711-1729 DOI: https://doi.org/10.1139/b04-128

Rojas C, Valverde R, Morales R. 2017. Functional variability of macrofungal populations in four different forest types of Costa Rica. *Mycosphere* **8**: 1288-1296. DOI: https://doi.org/10.5943/mycosphere/8/9/3

Rubino DL, McCarthy BC. 2003. Evaluation of coarse woody debris and forest vegetation across topographic gradients in a southern Ohio forest. *Forest Ecology and Management* **183**: 1-3. DOI: https://doi.org/10.1016/S0378-1127(03)00108-7

Ruiz-Almenara C, Gándara E, Gómez-Hernández M. 2019. Comparison of diversity and composition of macrofungal species between intensive mushroom harvesting and non-harvesting areas in Oaxaca, Mexico. *PeerJ* 7(S1): e8325 DOI: https://doi.org/10.7717/peerj.8325

Salerni E, Laganá A, Perini C, Loppi S, de Dominicis V. 2002. Effects of temperature and rainfall on fruiting of macrofungi in oak forests of the Mediterranean area. *Israel Journal of Plant Sciences* **50**: 189-198. DOI: https://doi.org/10.1560/GV8J-VPKL-UV98-WVU1

Schmit JS, Murphy JF, Mueller GM. 1999. Macrofungal diversity of a temperate oak forest: a test of species richness estimators. *Canadian Journal of Botany* **77**: 1014-1027 DOI: https://doi.org/10.1139/b99-055

Schmit JP, Mueller GM. 2007. An estimate of the lower limit of global fungal diversity. *Biodiversity and Conservation* **16**: 99-111. DOI: https://doi.org/10.1007/s10531-006-9129-3

Singha K, Banerjee A, Pati BR, Das Mohapatra PK. 2017. Eco-diversity, productivity and distribution frequency of mushrooms in Gurguripal Eco-forest, Paschim Medinipur, West Bengal, India. *Current Research in Environmental & Applied Mycology* **7**: 8-18.

Shuhada SN, Salim S, Nobilly F, Lechner AM, Azhar B. 2020. Conversion of peat swamp forest to oil palm cultivation reduces the diversity and abundance of macrofungi. *Global Ecology and Conservation* **23**: e01122. DOI: https://doi.org/10.1016/j.gecco.2020.e01122

Termorshuizen AJ. 2014. Root pathogens. *In*: Dighton J, Krumins A, eds. *Interactions in Soil: Promoting Plant Growth*.Dordrecht, Netherlands: Springer Nature, pp. 119-137. DOI: https://doi.org/10.1007/978-94-017-8890-8

Thoen D. 1976. Facteurs physiques et frutification des champignons supérieurs dans quelques pressières d'Ardenne méridionale (Belgique). *Bulletin de la Société linnéenne de Lyon* **45**: 269-284. DOI: https://doi.org/10.3406/linly.1976.10272

Villaseñor JL. 2016. Checklist of the native vascular plants of Mexico. *Revista Mexicana de Biodiversidad* **87**: 559-902 DOI: https://doi.org/10.1016/j.rmb.2016.06.017

Unidad de Microrregiones 2005. http://www.microrregiones.gob.mx/cedulas/localidadesDin/ubicacion/relieve.asp?micro=AYOQUEZCO&clave=203980001&nomloc=AYOQUEZCO%20DE%20ALDAMA (accessed November 2019)

Villeneuve N, Grandtner MM, Fortin JA. 1989. Frequency and diversity of ectomycorrhizal and saprophytic macrofungi in the Laurentide Mountains of Quebec. *Canadian Journal of Botany* **67:** 2616-2629 DOI: https://doi.org/10.1139/b89-338

Wilkins WH, Harris GCM. 1946. The ecology of the larger fungi; an investigation into the influence of rainfall and temperature on the seasonal production of fungi in a beechwood and a pinewood. *Annals of Applied Biology* **33**: 179-188. DOI: https://doi.org/10.1111/j.1744-7348.1946.tb06295.x

Williams-Linera G, Domínguez-Gastelú V, García-Zurita ME. 1998. Microenvironment and Floristics of Different Edges in a Fragmented Tropical Rainforest. *Conservation Biology* **12**: 1091-1102.

Zhang Y, Zhou DQ, Zhao Q, Zhou TX, Hyde KD. 2010. Diversity and ecological distribution of macrofungi in the Laojun Mountain region, southwestern China. *Biodiversity and Conservation* **19**: 3545-3563. DOI: https://doi.org/10.1007/s10531-010-9915-9

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