Microbiology and Nature
Volume 2, Issue 1 pages 200-212
ISSN 2664-388X
https://doi.org/10.26167/f6f4-0q76

Microbiol. Nat.

Société Ivoirienne de Microbiologie

MICROBIOLOGY AND NATURE
Journal homepage: www.microbiologyandnature.com

Forest soil mycobiome composition within Sudanian and Sudano-Guinean ecoregions of Benin

Kassim Issifou Tchan[1]*, Gbètondji Basile Hounwanou[1], Nourou Soulemane Yorou[1]

[1]Research Unit in Tropical Mycology and Plant-Soil Fungi Interactions, LEB, University of Parakou, BP 123, Parakou, Benin

Received, September 14th 2022, Revised, October 12th 2022, Accepted November 20th 2022, Published online Dec. 5th 2022

Abstract

The soil mycobiome is a major biological component involved in environmental and host functioning. Despite fungi fundamental role in ecosystem processes there is a lack of data on their distribution and biogeography in Subsaharian Africa. This study investigated the soil mycobiome composition within two ecoregion of Benin using the ITS region and 18S-V9 sequences extracted from the Global Soil Mycobiome Consortium (GSMc) open database (https://doi.org/10.15156/BIO/2263453). A beta diversity analysis followed by NMDS was applied to determine the similarities and differences between the climatic zones in terms of soil mycobiome composition. The multipatt function followed by a redundancy analysis (RDA) was applied to identify the species confined to each climatic zone and the drivers that govern the composition of the soil mycobiome. A total of 18 phyla were identified at the sampled sites with a dominance of Ascomycota in the Sudanian zone (53.34%) and Basidiomycota in the Sudano-Guinean zone (57.98%). The functional guilds were dominated by saprotrophs (21.52%) followed by ectomycorrhizae (10. 51%), arbuscular mycorrhizal fungi (10.16%) and plant pathogens (6.49%). The diversity indices and similarity analysis indicate a difference with some overlap (R = 0.3854), but not significant (p = 0.0566) in terms of soil mycobiome composition between the two areas. However, Aspergillus niger is confined (p = 0.0302) to the Sudan zone, while *Fuscoporia senex* (p = 0.0302) and *Conocybe dunensis* (p = 0.0302) are indicative of the Sudan-Guinea zone. This specificity of mycobiome composition is influenced by climate (temperature; p = 0.008). This study is among the pioneer works on soil mycobiomes according to climatic zones and environmental factors responsible for their distribution in Benin and also highlights the need for future research.

Keywords : Soil mycobiomes; environmental factors; Benin; climatic zone; indicator species; diversity.

Résumé

Le mycobiome du sol est un composant biologique majeur impliqué dans le fonctionnement de l'environnement et de l'hôte. Malgré le rôle fondamental des champignons dans les processus écosystémiques, il existe un manque de données sur leur distribution et leur biogéographie en Afrique subsaharienne. Cette étude a examiné la composition du mycobiome du sol dans deux écorégions du Bénin en utilisant les séquences de la région ITS et 18S-V9 extraites de la base de données ouverte du Global Soil Mycobiome Consortium (GSMc) (https://doi.org/10.15156/BIO/2263453). Une analyse de la diversité bêta suivie par NMDS a été appliquée pour déterminer les différences entre les zones climatiques en termes de composition du mycobiome du sol. Une analyse de redondance (RDA) a été appliquée pour identifier les espèces confinées à chaque zone climatique et les drivers qui gouvernent la composition du mycobiome. Au total, 18 phyla ont été identifiés sur les sites échantillonnés avec une dominance d'Ascomycota en zone soudanienne (53,34%) et de Basidiomycota en zone soudano-guinéenne (57,98%). Les guildes fonctionnelles sont dominées par les saprotrophes (21,52 %) suivis des ectomycorrhizes (10,51 %), des champignons mycorrhiziens à arbuscules (10,16 %) et des phytopathogènes (6,49 %). Les résultats des indices de diversité et de l'analyse de similarité indiquent une différence avec quelques chevauchement (R = 0,3854), mais non significative (p = 0,0566) en terme de composition du mycobiome entre les zones. Cependant, Aspergillus niger est confiné (p = 0,0302) à la zone soudanienne, tandis que Fuscoporia senex (p = 0,0302) et Conocybe dunensis (p = 0,0302) sont des espèces indicatrices de la zone soudano-guinéenne. Cette spécificité de la composition du mycobiome est influencée par le climat (température ; p = 0,008). Cette étude, faisant partie des travaux pionniers sur les mycobiomes du sol met en évidence les possibilités de recherches futures.

Mots clés : Mycobiome du sol, facteur environnemental, Bénin, zone climatique, espèces indicatrices, diversité.

Corresponding author E-mail address: …Kassim I. Tchan kassimtchan@gmail.com

Introduction

Soil fungi play a central role in the functioning of terrestrial ecosystems through decomposition and carbon recycling (Bahram et al. 2018; Bach et al. 2020), and interact with plants and animals by mutualistic, pathogenic and commensal relationships (Delgado-Baquerizo et al. 2017). As such, the composition of soil fungal communities is intimately linked with their ecological functions and thus their ability to intervene in key life support processes. Until recently, studies on soil fungi were very limited in tropical Africa due to lack of technology and specialists. However, with the next generation sequencing and the global mycobiome data initiative (Tedersoo et al. 2021; Davison et al. 2021; Rincon et al. 2021; Touré et al. 2021), West Africa now has important sequences datasets on soil fungal diversity, opening up new opportunities to test interesting hypotheses and deepen our knowledge of the ecology of this globally poorly understood group of organisms.

Whether at a global or regional scale, abiotic factors such as climate (precipitation and temperature) and soil physicochemical properties are identified among the main predictors of soil mycobiome diversity and composition (Tedersoo et al. 2014; Bahram et al. 2018; Cowan et al. 2022). In this respect, several studies have highlighted the pivotal role of pH in structuring fungal communities by determining the availability of other nutrients such as phosphorus, nitrogen and potassium (Zhang et al. 2016; Tedersoo et al. 2020). In alpine and temperate regions, nitrogen, the main nutrient deficiency, has a significant influence on soil fungal assemblage (Li et al. 2019).

However, in the tropics and particularly in West Africa it is rather phosphorus that is the primary limiting nutrient (Verde et al. 2014), suggesting that it could be a key driver in fungal community assembly through modulation of vegetation and promotion of certain ecological groups (Schappe et al. 2017). However, we lack small-scale evidence to support this claim.

Benin is located in West Africa. It is covered by three ecoregions (Sudanian, Sudano-Guinean, and Guinean), each with homogeneous climatic conditions (Withe 1983). Soil types and vegetation vary between the ecoregions, with specific plant species in each (Adomou et al. 2006). Consequently, the area is a valuable study system for understanding the influence of abiotic variables in the structuring of soil fungal communities.

In this study, we extracted DNA sequences for two climatic zones from the global mycobiome database of which Benin contributed to study the soil mycobiome and its relationship with environmental and edaphic variables in Benin. We tested the following hypotheses: (1) with the difference of precipitation and temperature between the Sudano-Guinean ecoregion and sudanian zone, there is a significant difference within the mycobiome composition of both climatic zones; (2) in line with the biological market theory (Konvalinkoý et al. 2017), the amount of available phosphorus is the factor that best predicts the diversity and composition of soil fungal communities; (3) the specificities of the ecoregions led to the existence of typical species, confined to each of them.

Materials and Methods

Molecular data and metadata acquisition

For this study, DNA sequences were extracted from the Global Soil Mycobiome Consortium (GSMc) open dataset (Tedersoo et al. 2021). For more details on the global dataset, please consult the following link https://doi.org/10.15156/BIO/2263453 . Data on DNA sequences from Benin sampling (OTU; total_reads; best_match_accession; sequence_similarity; metadata…) extracted from the global database.

Using geographic coordinates taken at the different sampling sites (Figue 1), data on the original vegetation description (fire history) were assigned to biomes (Olson et al. 2001) and land cover types.

We obtained climate data (Table 1) specifically for variables such as precipitation, minimum and maximum temperature, and humidity, using the AFRICLIM spatial database (Platts et al. 2015 a; b).

Statistical analysis

We computed OTUs richness, Shannon diversity, and Phylogenetic diversity (PD) to measure the fungal community within the climatic zones. To determine whether or not

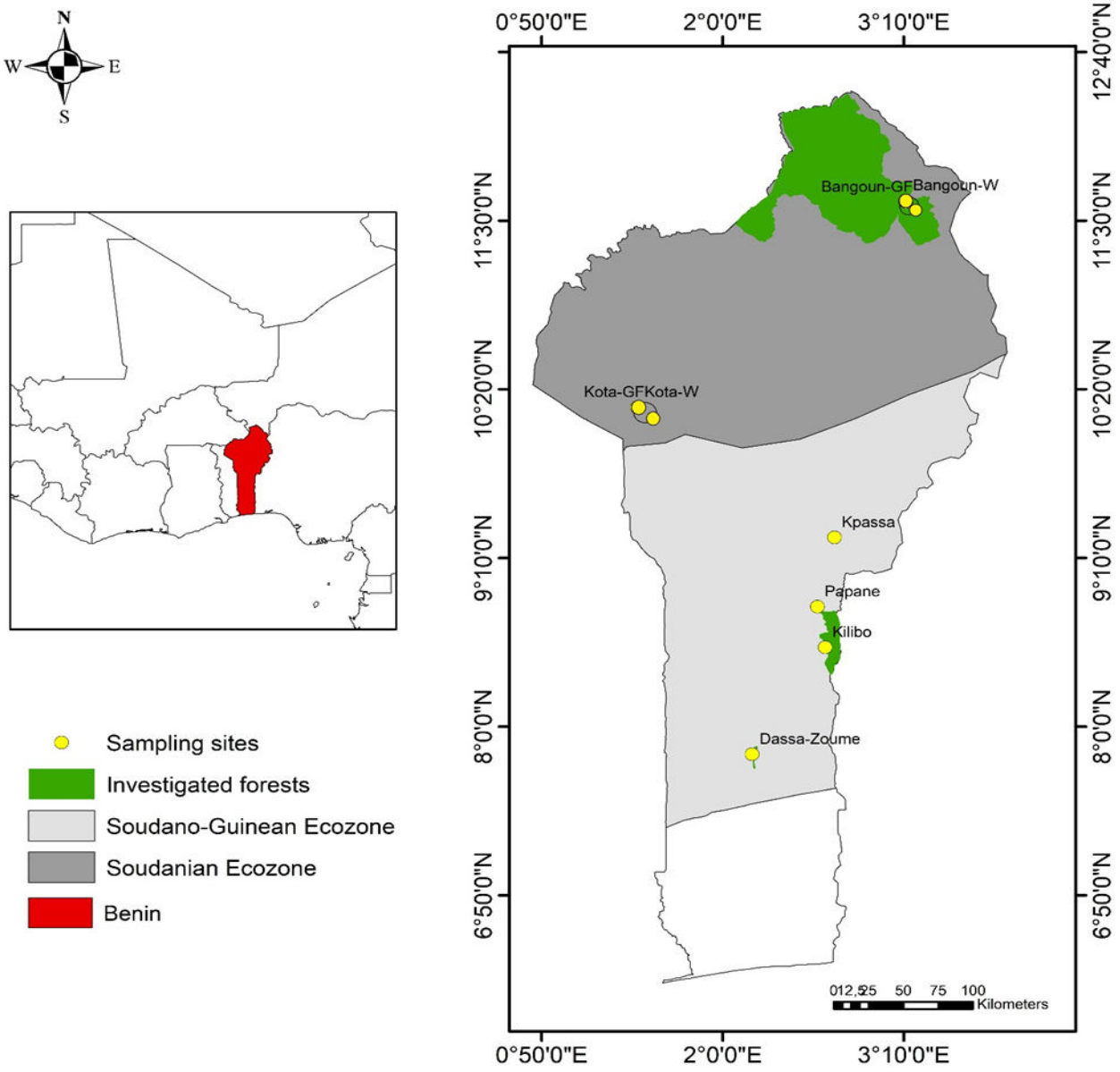

Figure 1: Study area and the sampling site

there is a difference in the soil mycobiome communities, the phylogenetic distance ("Phyloseq" package in R) between sets of taxa was estimated using the unifrac method. A non-metric multidimensional scaling (NMDS) ordination was then performed to examine the variation between the fungal communities based on the phylogenetic distance and the ANOSIM similarity analysis ("Vegan" package in R) was run to test the significance.

To assess the influence of environmental factors (maximum and minimum monthly temperature, precipitation, air moisture) on the diversity and composition of the soil mycobiome, we first downloaded high resolution global climate projections ("raster" and "sp" package in R). A redundancy analysis ("Vegan" package in R) was conducted to extract and summarize the variation in species abundance that can be explained by climatic variables and soil nutrients (delta15N, and the amount of nitrogen, and phosphorus). The absolute values of pairwise correlations were considered. When two drivers have a high correlation, the one with the highest mean absolute correlation was deleted.

Finally, a species indicator analysis ("indicspecies" package in R) was conducted to examine the species confined to each climatic zone.

Table1: Characteristics of sampling sites

Climate zone	Site	Biome	delta15N	N_conc_g_kg	P_conc_mg_kg
Sudanian zone	Bangoun 1	forest: tropical broadleaf forest biome	4,1104024838022	0,88924829	11,08128079
	Bangoun 2	woodland: tropical woodland biome	3,5339153237581	1,87149424	9,58566871
	Kota 1	woodland: tropical woodland biome	1,74277760008724	0,944842484	5,761483146
	Kota 2	forest: tropical broadleaf forest biome	1,95985461022555	2,797122267	1,19459364
	Kpassa	woodland: tropical woodland biome	2,83954434447662	1,6418806660056	3,678797106966
Sudano-guinean Zone	Papane	woodland: tropical woodland biome	2,82033143130701	0,68367594569977	12 0,805773857257
	Kilibo	woodland: tropical woodland biome	2,58091944582593	8 1,32733047102389	418 3,698637236084
	Dassa-Zoume	woodland: tropical woodland biome	3,50188548187783	3,60304649731623	45 113,2171401059 22

Results

General taxonomy of soil mycobiomes according to climatic zones

Results from bioinformatics analyses of the different forests provided a total of 8257 Operational Taxonomic Units (OTUs). The OTU diversity was reduced to 5915 after random subsampling. 18 phyla were found in the sampled soils, including the unclassified group that represents 0.09% of the total for the Sudanian zone and 1.69% for the Sudano-Guinean zone. The relative abundance of phyla between the two zones was almost similar (Figure 2). The Ascomycota group was more abundant in the Sudanian zone (53.34%) than in the Sudano-Guinean zone (33.23%). Conversely, we observed a dominance of Basidiomycota in the Sudano-Guinean zone (57.98%) than in the Sudanian zone (34.36%). The Mucoromycota, Zoopagomycota and Kickxellomycota phyla were rare at all sites except Kota 1, Dassa-Zoumè and Bangoun1, respectively. The highest values of phyla (Dassa-Zoumè), classes and orders (Kilibo), families and genera (Kpassa) were recorded at sites in the Sudano-Guinean zone, with the exception of species richness, which has the highest value at the Bangou 2 site in the Sudanian zone (Table 2).

Primary functions of soil mycobiomes

Based on the taxonomic and functional annotations of the different operational taxonomic units, we recorded a total of 20 different primary functions or lifestyles of belowground fungal communities (Figure 3). Saprotrophs: soil, litter, nectar, pollen and dung (1694 OTUs; 21.52%) were predominant followed by ectomycorrhizae (868 OTUs; 10. 51%), arbuscular mycorrhizal fungi (AMF) (839 OTUs; 10.16%), and plant pathogens (536 OTUs; 6.49%). However, 40.64% of all OTUs could not be assigned to any of the primary functions.

Composition of soil mycobiomes according to climatic zones

The different diversity indices calculated (observed diversity index, Shannon index,

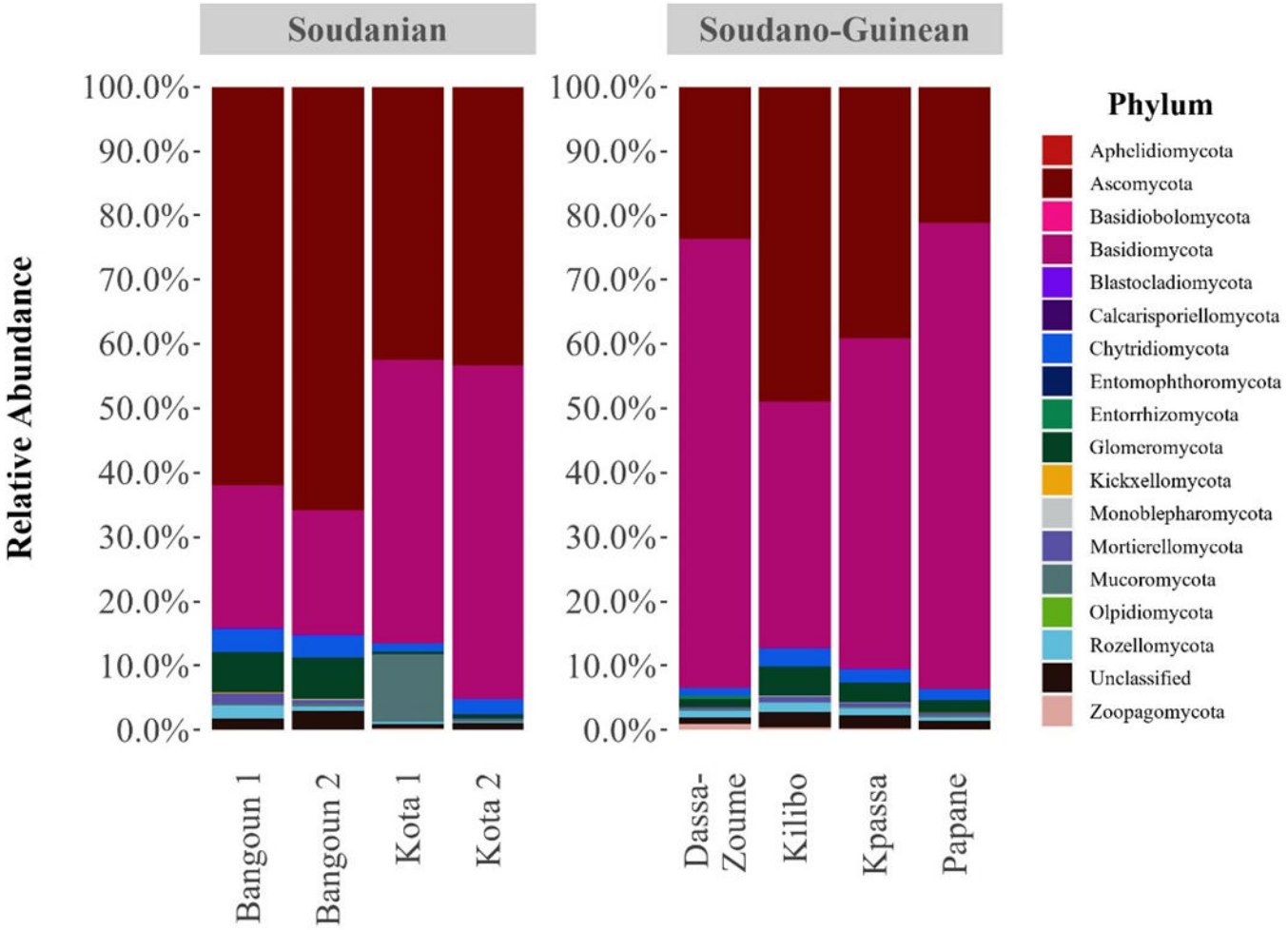

Figure 2: Relative abundance of phyla by climatic zone. Colors represent each phylum and the height of each bar represents the relative abundances in the sampled soils

Table 2: Diversity of different mycobiome taxonomic groups by sampling sites

Climate zone	Website	Phylum	Class	Order	Family	Genera	Species
Sudano-Guinean	Dassa-Zoume	15	36	73	158	203	123
	Kilibo	14	41	76	162	207	129
	Papane	13	40	67	142	171	112
	Kpassa	13	35	68	170	224	136
Sudanian	Bangoun_1	14	40	72	141	186	104
	Bangoun_2	13	33	63	153	213	137
	Kota_1	11	33	66	142	187	108
	Kota_2	12	32	61	141	178	98

phylogenetic diversity) showed a slightly lower median alpha diversity in soils from the Sudanian zone compared to the Sudano-Guinean zone (Figure 4).

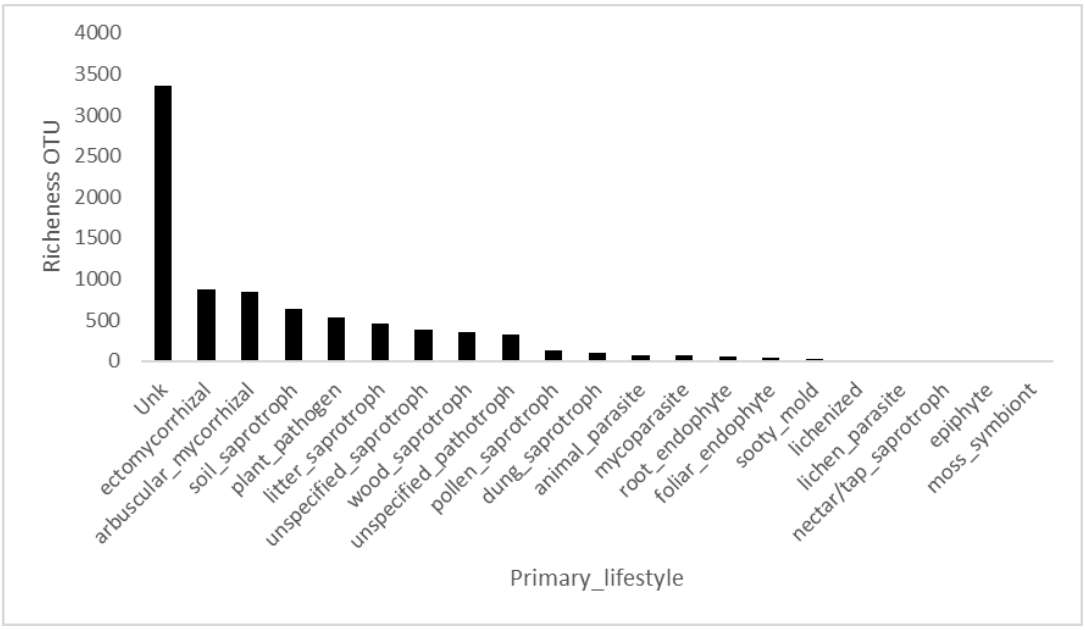

Figure 3: Primary functions of soil mycobiomes

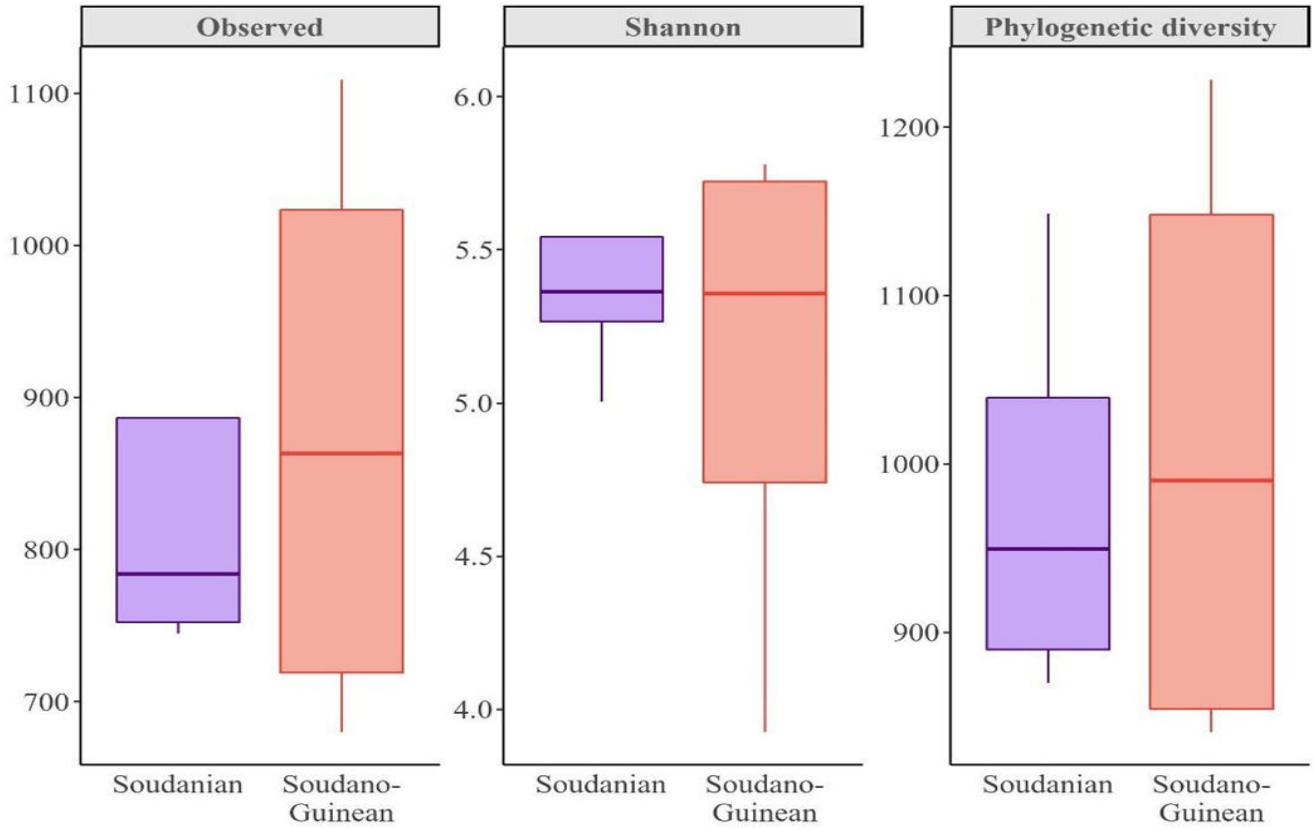

Figure 4: Observed, Shannon and Phylogenetic diversity indices within and between climatic zones.

However, the variation in alpha diversity between zones did not overlap ($p.\ value_{observed}$ = 0.8852, $p.\ value_{shannon}$ = 0.8857and $p.\ value_{PD}$ = 0.8857) and we therefore accepted the null hypothesis of no difference between zones. Alpha diversity was relatively high in the belowground fungal communities of Kilibo and Kpassa (in the Sudano-Guinean zone) and Bangoun 2 (in the Sudanian zone) (Figure 5). As for beta diversity quantifying the (dis-)similarities between climatic zones, it showed some separation between the Sudano-Guinean and the Sudanian zone. There were also some overlaps between these two types of community groups, suggesting a pooling of OTUs. The similarity analysis showed a difference with some overlap (R = 0.3854), not significant (p = 0.0566) between the Sudano-Guinean and Sudanian zones in term of abundance (Figure 6).

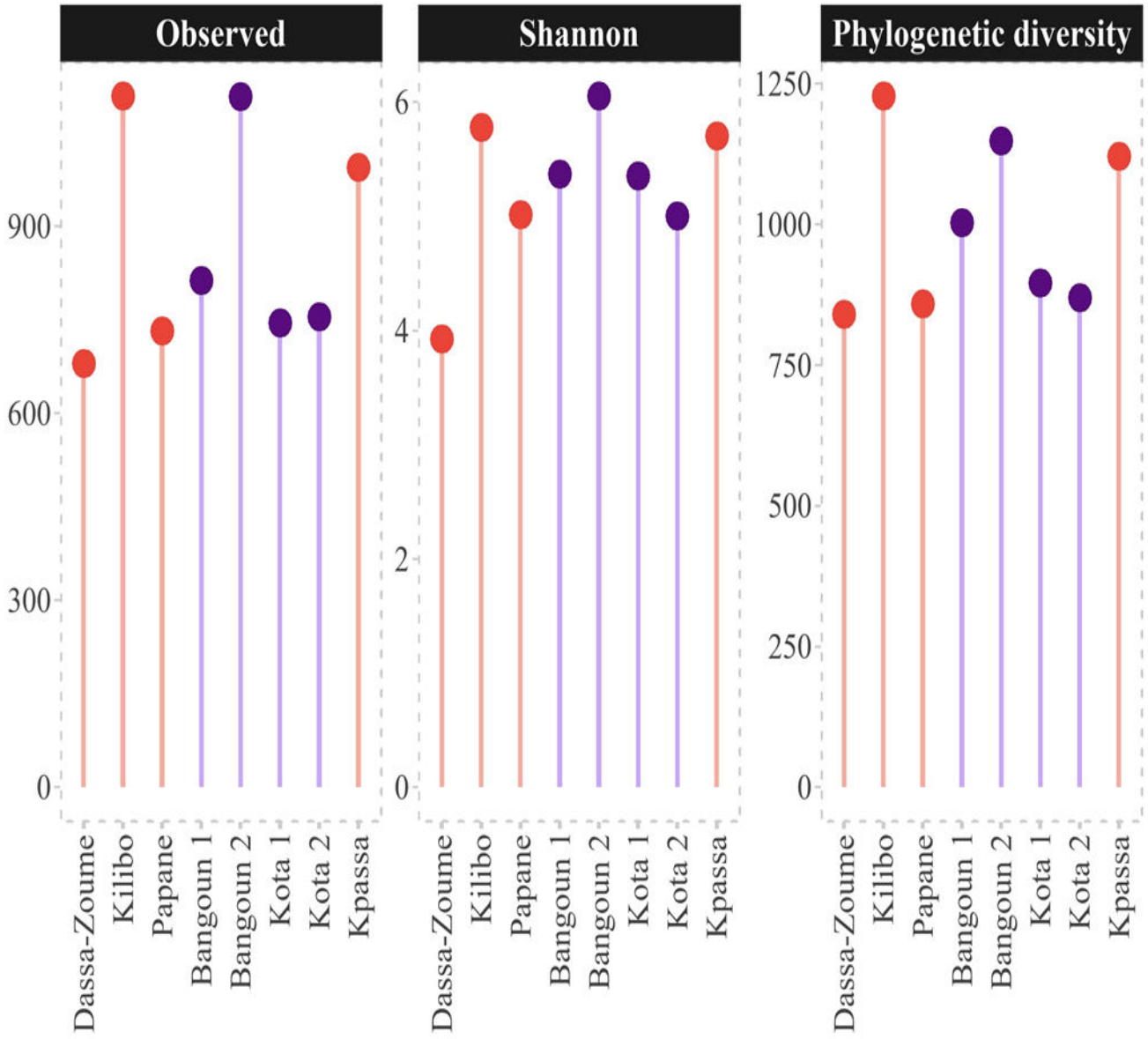

Figure 5: Alpha diversity index by soil mycobiome community (collection site). The orange sides represent soil mycobiome communities from the Sudan-Guinean zone and the purple sides represents soil mycobiome communities from the Sudanian zone.

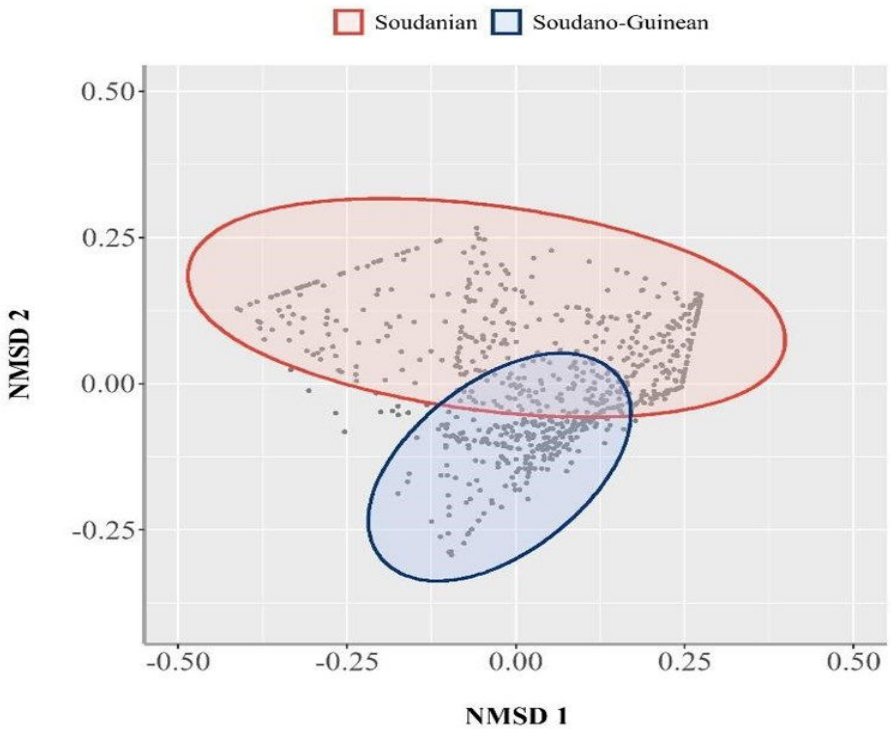

Figure 6: Beta diversity by climate zone

Species associated with each climate zone

Species indicator analysis was conducted to determine the fungal species associated with a particular climatic zone given the edapho-climatic conditions of the region. Among 506 species actually present on at least one site, 03 species were detected as confined to the climatic zones; one (01) species for the Sudanian zone and two (02) for the Sudano-Guinean zone (Table 3). *Aspergillus niger* Tiegh was the species confined to the Sudanian zone (stat value = 1; p = 0.0302). The probability that the sampled site belongs to this climatic zone given that it was found (specificity or positive predictive value) and the probability of finding the species in sites belonging to this climatic zone (fidelity or sensitivity) was 1 and 1 respectively. *Fuscoporia senex* (Nees & Mont.) Ghob, Nejh was the species that appeared in all sites belonging to the Sudano-Guinean zone and was limited to the zone. As for *Conocybe dunensis* T.J. Wallace, it can serve as an indicator species of the Sudano-Guinean climatic zone because it occurred at all sites belonging to this zone (fidelity = 1) and was largely (but not completely) restricted to this zone (specificity = 0.9917).

Effect of environmental variables on the abundance of soil mycobiomes

The absolute values of pairwise correlations were considered. Minimal temperature (°C) and phosphorus (mg/kg) were the uncorrelated factors. 31.72 % of the amount of variance was explained by these drivers. Overall, the effect of the drivers was not significant (p= 0.067). However, the effect of temperature on the abundance of species was highly significant (p = 0.008) in contrast to phosphorus whose effect was not significant (p = 0.168). The figure 7 shows that temperature was loaded on RDA 1 indicating that this driver explains a large part of the variance associated with axis 1, while phosphorus explains a large part of the variance associated with axis 2.

Table 3: Species diversity associated with each climate zone

Species	Specificity	Fidelity	Stat	p-value
		Sudanian zone		
Aspergillus niger	1	1	1	0.0302 *
		Sudano-Guinean zone		
Fuscoporia senex	1	1	1	0.0302 *
Conocybe dunensis	0.9917	1	0.996	0.0302 *

* : indicator value is statistically significant (p-value < 0.05)

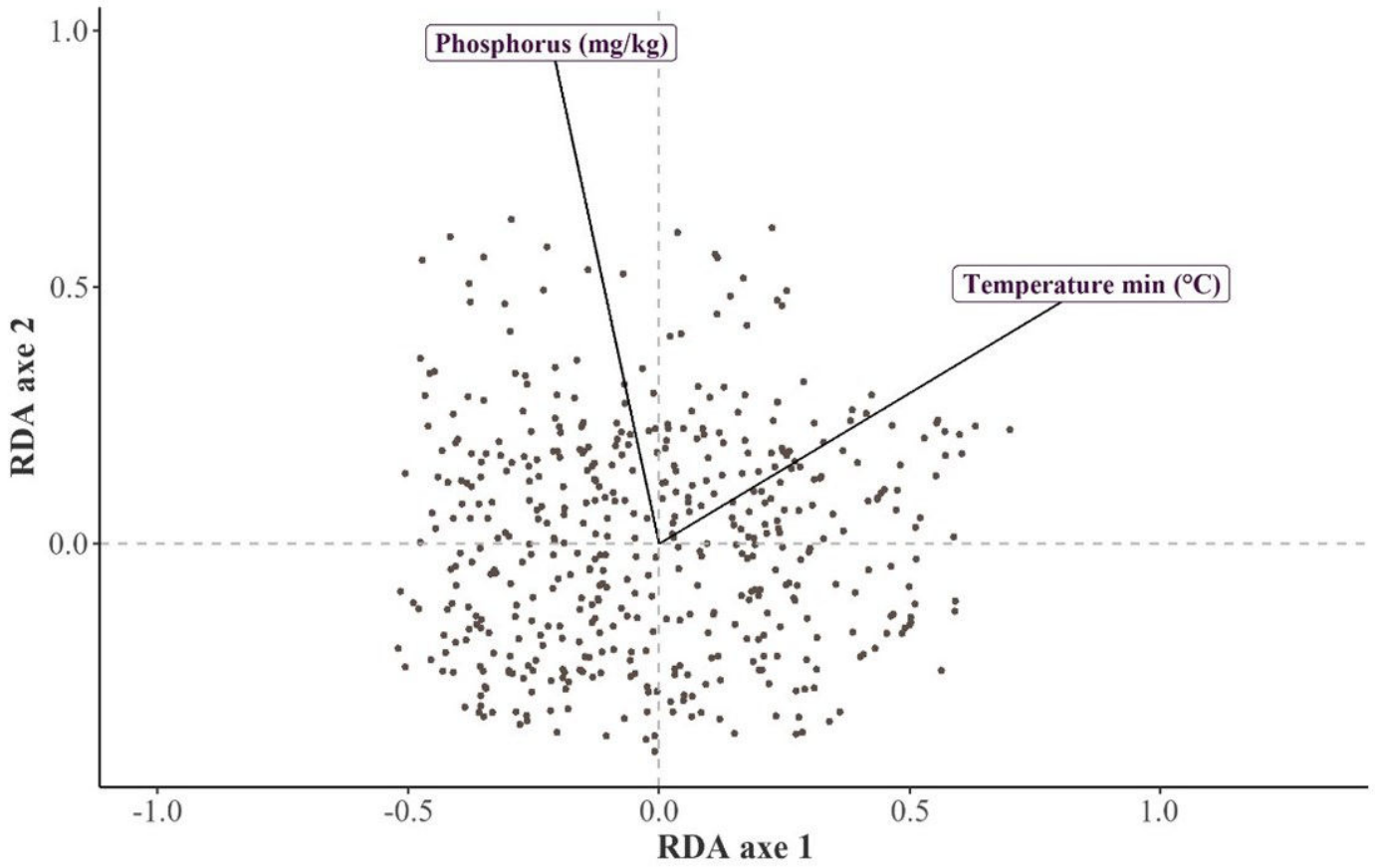

Figure 7: Redundancy analysis biplot. Species are shown as gray dots and environmental variables (explanatory variables) are the purple text. The arrows indicate the loading of these variables on axes 1 and 2

Discussion

This study aimed at highlighting the diversity and composition of soil mycobiomes in two ecozones of Benin and the drivers responsible for their distribution patterns within these regions. Through random sub-sampling, a total of 5915 operational taxonomic units (OTUs) were retained for statistical analysis. The taxonomic profile at the phylum level showed 18 phyla with a codominance of Ascomycota and Basidiomycota. Ascomycota group was more represented in the Sudanian zone (53.34%) in contrast to the Basidiomycota that were more abundant in the Sudano-Guinean zone (57.98%). These results are consistentfrom previous studies that confirmed the codominance of Ascomycota and Basidiomycota in global ecosystems (Vètrovský et al. 2019; Tedersoo et al. 2021; Baldrian et al. 2022). A study in five climatic zones in Asia also confirmed the dominance of Ascomycota (73.7%) in the soils sampled (Ma et al. 2016). The codominance of these two phyla could be explained by the fact that both (Ascomycota and Basidiomycota) are the main decomposers of dead wood and woody debris within forests ecosystems (Egger 1986; Binder et al. 2013; Riley et al. 2014). For the functional guilds or primary functions of soil mycobiomes, we found that the study areas are dominated by saprotrophs followed by Ectomycorrhizae, arbuscular mycorrhizal, and plant pathogens fungi, consistent with the findings of Fernandes et al. (2022) and Tedersoo et al. (2014).

However, we found no significant differences in α-diversity indices at the OTU level

and we therefore rejected the hypothesis of difference in mycobiome diversity between the zones. As for beta diversity, it showed some separation between the Sudan-Guinean zone and the Sudanian zone but not significant ($p = 0.0566$) in terms of mycobiome composition. These results could be explained not only by the fact that the two zones share some climatic features but also by the close proximity of the sites, as the sampled sites were not very far from each other, especially in the Sudano-Guinean zone. Indeed, Yang et al. (2020) emphasized that the proximity between sampled sites would result in an insignificant change in soil mycobiome composition. Liu et al. (2015) demonstrated that geographic distance would contribute to 20% of the variation in the fungal community. Furthermore, the number of replications performed in this study could also explain the similarity observed. However, the species indicator analysis revealed some species specific to each region. The Sudanian zone appeared to offer optimal ecological conditions (climate, soil and vegetation) for the proliferation of *Aspergillus niger*. On the other hand, *Fuscoporia senex* is the species that appeared in all sites belonging to the Sudano-Guinean zone and was completely limited to this ecoregion. As for Conocybe dunensis, it indicative to the Sudano-Guinean climatic zone because it occurred at all sites belonging to this zone (fidelity = 1) and was largely (but not completely) restricted to this zone (specificity = 0.9917). These different observations could be explained not only by the preference or specificity but also by differences in climate, vegetation, and soil factors within both ecoregions (Peay et al. 2013; Shi et al. 2014; Pei et al. 2016; Větrovský et al. 2019; Rincon et al. 2021). Indeed, of these three factors (climate, soil, and vegetation), climate emerged as the most important (temperature; $p = 0.008$) through the results of redundancy analyses (RDA). Several studies focusing on the global distribution of fungi have also identified climate as an important factor influencing the composition and global distribution of soil mycobiomes (Tedersoo et al. 2014, Větrovský et al. 2019, Cowan et al. 2022). Fernades et al. (2022) provided evidence that soil mycobiome diversity is strongly correlated by temperature. Also, other studies demonstrated the correlation between soil microbiome diversity and temperature (Yergeau et al. 2007; Fuhrman et al. 2008; Ladau et al. 2013; Davison et al. 2021) and indicated that higher temperatures increase soil microbial activity and differentiation, resulting in decreased soil microbial diversity (Liu et al. 2014).

Conclusion

This study aimed to elucidate the variation within the soil fungi community according to sudanian and sudano-guinean ecoregions in Benin. However, due to the under sampling within the country and the repetition requirement for statistical analysis, the study focused on two out of three ecoregions. The findings show that the abundance and composition of soil fungal communities is almost similar in the different forests investigated, with some specificity with the indicator species of the climatic zones. These confined species, influenced by climate, highlight the need to include the third ecoregion (guinean zone) in future work to assess the diversity and overall composition of soil mycobiomes.

Acknowledgment

We are grateful to the German Federal Ministry of Education and Research (BMBF- Germany) grant agreement 01DG20015.

References

Adomou AC, Sinsin B, der Maesen LJG (2006). Notulae florae Beninensis 12: phytosociological and chorological approaches to phytogeography: a meso-scale study in Benin. Systematics and Geography of Plants, 76:155–178 Bach EM, Kelly SR, Tandra DF, Diana HW (2020). "Soil Biodiversity Integrates Solutions for a Sustainable Future. Sustainability, 12: 2662. https://doi.org/10.3390/su12072662

Bahram M, Hildebrand F, Forslund SK, et al. (2018). Structure and function of the global topsoil microbiome. Nature, 560:233–237 (2018). https://doi.org/10.1038/s41586-018-0386-6

Baldrian P, Vetrovsky T, Lepinay C, Kohout P (2022). High -throughput sequencing view on the magnitude of global fungal diversity. Fungal Diversity, 114:539–547https://doi.org/10.1007/s13225-021-00472-y

Binder M, Justo A, Riley R, Salamov A, Lopez-Giraldez F, Sjokvist E, Copeland A, Foster B, Sun H, Larsson E, Larsson KH, Townsend J, Grigoriev IV (2013). Hibbett, Phylogenetic and phylogenomic overview of the polyporales. Mycologia, https://doi.org/10.3852/13-003 .

Bivand RS, Pebesma E, Gomez-Rubio V (2013). Applied spatial data analysis with R, Second edition. Springer, NY. https://asdar-book.org /

Core Team R (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Cowan DA, Lebre PH, Amon CER, Becker RW, Boga HI, Boulangé A, Chiyaka TL, Coetzee T, de Jager PC, Dikinya O, Eckardt F, Greve M, Harris MA, Hopkins DW, Houngnandan HB, Houngnandan P, Jordaan K, Kaimoyo E, Kambura AK, Kamgan Nkuekam G, Makhalanyane TP, Maggs Kölling G, Marais E, Mondlane H, Nghalipo E , Olivier BW, Ortiz M, Pertierra LR, Ramond J B, Seely M, Sithole Niang I, Valverde A, Varliero G, Vikram S, Wall DH, Zeze A (2022). Biogeographical survey of soil microbiomes across sub-Saharan Africa: structure, drivers, and predicted climate-driven changes. Microbiome, (2022) 10 (131): 2-22. https://doi.org/10.1186/s40168-022-01297-w

Davison J, Moora M, Semchenko M, Adenan SB, Ahmed T, Akhmetzhanova A A, … Anslan S (2021). Temperature and pH define the realised niche space of arbuscular mycorrhizal fungi. New Phytologist, 231(2) :763–776. doi:10.1111/nph.17240

De Caceres M & Legendre P (2009). Associations between species and groups of sites: indices and statistical inference. Ecology, URL http://sites.google.com/site/miqueldecaceres/

Delgado-Baquerizo M, Eldridge DJ, Ochoa V, Gozalo B, Singh BK, Maestre FT (2017). Soil microbial communities drive the resistance of ecosystem multifunctionality to global change in drylands across the globe. Ecology Letters, 20 (10):1295–1305. https://doi.org/10.1111/ele.12826

Egger KN (1986). Substrate Hydrolysis Patterns of Post-Fire Ascomycetes (Pezizales). Mycologia, 78(5):771-780. DOI: 10.1080/00275514.1986.12025321.

Fernandes MLP, Bastida F, Jehmlich N, Martinovi T, Vˇetrovský T, Baldrian P, Delgado-Baquerizo M, Starke R. 2022. Functional soil mycobiome across ecosystems. Journal of Proteomics, 252 (2022):104428.

Fuhrman JA, Steele JA, Hewson I, Schwalbach MS, Brown MV, Green JL, Brown JH (2008). A latitudinal diversity gradient in planktonic marine bacteria. Proceedings of the National Academy of Sciences of the United States of America, 105: 7774e7778.

Hijmans RJ (2021). Raster: Geographic Data Analysis and Modeling. R package version 3.5-2. https://CRAN.R-project.org/package=raster

Konvalinkov´ T, Püschel D, Rezacova V, Gryndlerova H, Jansa J (2017). Carbon flow from plant to arbuscular mycorrhizal fungi is reduced under phosphorus fertilization. Plant and Soil, 419:319–333. https://doi.org/10.1007/s11104-017- 3350-6 .

Ladau J, Sharpton TJ, Finucane MM, Jospin G, Kembel SW, O'Dwyer J, Koeppel AF, Green JL, Pollard KS (2013). Global marine bacterial diversity peaks at high latitudes in winter. ISME Journal, 7: 1669e1677

Lahti L & Shetty S (2019). Microbiome R package. URL: http://microbiome.github.io

Li Y, Bezemer M, Yang J, Xiaotao L, Xinyu L, Wenju L, Xingguo H, Li Q (2019). Changes in litter quality induced by N deposition alter soil microbial communities. Soil Biology and Biochemistry, 130: 33–42. https://doi.org/10.1016/j. soilbio.2018.11.025 .

Liu J, Sui Y, Yu Z, Shi Y, Chu H, Jin J, Liu X, Wang G (2015). Soil carbon content drives the biogeographical distribution of fungal communities in the black soil zone of northeast China. Soil Biology and Biochemistry, 83: 29–39. doi:10.1016/j.soilbio.2015.01.009

Liu SS, Wang F, Xue K, Sun B, Zhang YG, He ZL, Nostrand JDV (2014). The interactive effects of soil transplant into colder regions and cropping on soil microbiology and biogeochemistry. Environmental Microbiology, http://dx.doi.org/10.1111/1462-2920.12398.

McMurdie PJ & Holmes S (2013). Phyloseq: An R package for reproducible interactive analysis and graphics of microbiome census data. PLoS ONE, 8(4): e61217.

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin, PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2020). Vegan: Community Ecology

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GWN, Underwood EC, Damico JA, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettengel WW, Hedao P, Kassem KR (2001). Terrestrial ecoregions of the World: a new map of life on earth. Bioscience, 51:933–938

Package. R package version 2.5-7. https://CRAN.R-project.org/package=vegan

Peay KG, Baraloto C, Fine PV (2013). Strong coupling of plant and fungal community structure across western Amazonian rainforests. ISME Journal 7: 1852e1861.

Pebesma EJ & Bivand RS (2005). Classes and methods for spatial data in R. R News, 5 (2): https://cran.r-project.org/doc/Rnews/.

Pei Z, Eichenberg D, Bruelheide H, Kröber W, Kühn P, Li Y, von Oheimb G, Purschke O, Scholten T, Buscot F, Gutknecht JLM (2016). Soil and tree species traits both shape soil microbial communities during early growth of Chinese subtropical forests. Soil Biology and Biochemistry, 96: 180–190.

Platts PJ, Omeny PA, Marchant R (2015a). AFRICLIM: high-resolution climate projections for ecological applications in Africa. African Journal of Ecology, 53: 103-108

Platts PJ, Omeny PA, Marchant R (2015b). AFRICLIM 3.0: high-resolution ensemble climate projections for Africa. Figshare, doi:10.6084/m9.figshare.1284624

Rincón C, Droh G, Villard L, Masclaux FG, N'guetta A, Zeze A, Sanders IR (2021). Hierarchical spatial sampling reveals factors influencing arbuscular mycorrhizal fungus diversity in Côte d'Ivoire cocoa plantations. Mycorrhiza, 31 (3):289–300. doi:10.1007/s00572-020-01019-w

Põlme S, Abarenkov K, Nilsson RH, Lindahl BD, Clemmensen KE, Kauserud H, Nguyen N, Kjøller R, Bates ST, Baldrian P, Tedersoo L (2020). FungalTraits: a user-friendly traits database of fungi and fungus-like stramenopiles. Fungal Diversity, 105:1–16

Riley R, Salamov AA, Brown DW, Nagy LG, Floudas D, Held BW, Levasseur A, Lombard V, Morin E, Otillar R, Lindquist EA, Sun H, LaButti KM, Schmutz J, Jabbour D, Luo H, Baker SE, Pisabarro AG, Walton JD, Blanchette RA, Henrissat B, Martin F, Cullen D, Hibbett DS, Grigoriev IV (2014). Extensive sampling of basidiomycete genomes demonstrates inadequacy of the white-rot/brown-rot paradigm for wood decay fungi. Proceedings of the National Academy of Sciences, 111(27):9923–9928. https://doi.org/10.1073/pnas.1400592111 .

Schappe T, Albornoz FE, Turner BL, Neat A, Condit R, Jones FA (2017). The role of soil chemistry and plant neighbourhoods in structuring fungal communities in three Panamanian rainforests. Journal of Ecology, 105(3): 569-579.

Shi LL, Mortimer PE, Slik JWF, Zou XM, Xu JC, Feng WT, Qiao L (2014). Variation in forest soil fungal diversity along a latitudinal gradient. Fungal Diversity, 64: 305e315.

Talbot JM, Bruns TD, Taylor JW, Smith DP, Branco S, Glassman SI, … Peay KG (2014). Endemism and functional convergence across the North American soil mycobiome. Proceedings of the National Academy of Sciences, 111 (17): 6341–6346. doi:10.1073/pnas.1402584111

Tedersoo L, Mikryukov V, Anslan S, Bahram M, ……, Tchan IK, ……, Kõljalg U, Abarenkov K (2021). The Global Soil Mycobiome consortium dataset for boosting fungal diversity research. Fungal diversity, https://doi.org/10.1007/s13225-021-00493-7

Tedersoo L, Bahram M, Polme S, Koljalg U, Yorou NS, Wijesundera R, Ruiz LV, Vasco-Palacios AM, Thu PQ, Suija A, Smith ME, Sharp C, Saluveer E, Saitta A, Rosas M, Riit T, Ratkowsky D, Pritsch K, Poldmaa K, Piepenbring M, Phosri C, Peterson M, Parts K, Partel K, Otsing E, Nouhra E, Njouonkou AL, Nilsson RH, Morgado LN, Mayor J, May TW, Majuakim L, Lodge DJ, Lee S, Larsson KH, Kohout P, Hosaka K, Hiiesalu I, Henkel TW, Harend H, Guo LD, Greslebin A, Grelet G, Geml J, Gates G, Dunstan W, Dunk C, Drenkhan R, Dearnaley J, De Kesel A, Dang T, Chen X, Buegger F, Brearley FQ, Bonito G, Anslan S, Abell S, Abarenkov K (2014). Global diversity and geography of soil fungi. Science, https://doi.org/10.1126/science.1256688 .

Tedersoo L, Anslan S, Bahram M, Drenkhan R, Pritsch K, Buegger F, ... , Abarenkov K (2020). Regional-scale in-depth analysis of soil fungal diversity reveals strong pH and plant species effects in Northern Europe. Frontiers in Microbiology, 11:1953.

Tedersoo L, Anslan S (2019). Towards PacBio-based pan-eukaryote metabarcoding using full-length ITS sequences. Environmental Microbiology Reports, 11:659–668

Tedersoo L, Lindahl B (2016). Fungal identifcation biases in microbiome projects. Environmental Microbiology Reports, 8:774–779

Touré GPT, Nandjui J, Koné AW, Kouadjo AGZ, Ebou A, Tiho S, Zézé A (2021). Diversité des champignons mycorhiziens à arbuscules et interactions avec le système sol-litière dans un écotone forêt-savane, Côte d'Ivoire. Etude et Gestion des Sols, 28 : 93-104

Verde B, Matusso J (2014). Phosphorus in sub-Sahara african soils - strategies and options for improving available soil phosphorus in smallholder farming systems: a review. Academic Research Journal of Agricultural Science and Research., 2:1–5.

Vètrovský T, Kohout P, Kopecký M, Machac A, Man M, Bahnmann BD, Brabcova V, Choi J, Meszarosova L, Human ZR, Lepinay C, Llado S, Lopez-Mondejar R, Martinovic T, Masínova T, Morais D, Navratilova D, Odriozola I, Stursova M, Svec K, Tlaskal V, Urbanova M, Wan J, Zifcakova L, Howe A, Ladau J, Peay KG, Storch D, Wild J, Baldrian P (2019). A meta-analysis of global fungal distribution reveals climate-driven patterns. Nature Communications, 10(1): doi:10.1038/s41467-019-13164-8

Wickham H & Bryan J (2019). Readxl: Read Excel Files. R package version 1.3.1., https://CRAN.R-project.org/package=readxl

Wickham H, François R, Henry L, Müller K (2021). Dplyr: A Grammar of Data Manipulation. R package version 1.0.7. https://CRAN.R-project.org/package=dplyr

Wickham H (2016). Ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York, 2016.

White F (1983). The Vegetation of Africa: A Descriptive Memoir to Accompany the UNESCO//AETFAT//UNSO Vegetation Map of Africa (3 plates), 1:5,000,000. Paris: UNESCO

Yang Y & Wu P (2020). Soil bacterial community varies but fungal community stabilizes along five vertical climate zones. CATENA, 195: 104841. doi:10.1016/j.catena.2020.10484

Yergeau E, Bokhorst S, Huiskes AHL, Boschker HTS, Aerts R, Kowalchuk GA (2007). Size and structure of bacterial, fungal and nematode communities along an Antarctic environmental gradient. FEMS Microbiology Ecology, 59: 436e451.

Zhang T, Wang NF, Liu HY, Zhang YQ, Yu LY (2016). Soil pH is a key determinant of soil fungal community composition in the Ny-Ålesund Region, Svalbard (High Arctic). Frontiers in Microbiology, 7:227