

Landscape effects on global soil pathogenic fungal diversity across spatial scales

Corresponding Author: Ms Yawen Lu

This file contains all reviewer reports in order by version, followed by all author rebuttals in order by version.

Version 0:

Reviewer comments:

Reviewer #1

(Remarks to the Author)

Dear Authors,

I really enjoyed reading your manuscript “Landscape effects on global soil pathogenic fungal diversity across spatial scales”. Exploring the landscape ecology of soil pathogenic fungi is a new frontier in science, and your research can be inspiring for future local and global studies. Your focus on pathogens is particularly interesting, as synthesis are missing at such a scale for this functional group of fungi. Your results showing the differences on spatial scale are really important, as it is still unclear how to choose the best scale for such a diverse group of organisms, with large as well as short distance dispersal abilities. It will be of significance for fungal ecologists and non-fungal ones, opening the audience also. However, perhaps in the choice of metrics, it would have been interesting to include habitat quantity – for your discussion on grassland versus forests notably, or explain why you chose the largest patch size instead. I however have some comments to reinforce your results on pathogens – removing some doubts mainly in the methods, some clarification on the results useful for your discussion.

First, for a generalist audience, the fact that genomic soil DNA contains ASVs identified as leaf/fruit/seed pathogens as well as root associated ones, based on genus level identifications may not be clear and shall be precised. One derived critic could be on the interpretation: for example you mention the results obtained for Entoloma genus – a lineage that does include mainly saprobes and ectomycorrhizal fungi – and whose ecology might differ from other pathogens. It shall be mentioned in your discussion, if you mention Entoloma. Moreover, the use of a metric on relative abundance of pathogens raise another question: did you use abundance among all reads, or all functionally assigned reads? Fungal traits as other functional bases might not be complete, and mentioning the general level of assignation in your dataset would be essential. A more naïve question, did you expect to find less RA than LFSA fungi in soils ?

This point is connected to another technical point, notably if you had samples coming from different ecosystems, at such a scale, did you use any calibration on sample coverage or the threshold on read number was sufficient? Mentioning briefly the number of sequences produced, samples kept at the end – and % of pathogenic ASVs among all sequences would be useful, a very short information to evaluate how representative your results are.

The results themselves remain super interesting, considering the diversity of metrics, ecosystems studied. It is important to highlight that landscape factors are less explicative than other factors in most cases, but complementary. Mentioning that you did not observe significant effect in some cases (cf Figure 2 ; L267) would be useful.

Also to clarify your results, in line with your introduction where you mention the higher diversity in the tropics, the importance of natural habitats, perhaps shall you justify your choice of centering your study in non-tropical regions, or if you observed distinct patterns in the less sampled biomes you studied, to accompany your figure 1 ? Moreover, plantations are cropland are included but the typology was not included in the analysis, did it have an impact of shall you mention it to clarify your discussion on natural habitats? Were non natural habitats removed ?

Another question, related to your discussion on natural habitats and landscape complexity, and considering the diversity of ecosystems you study: did you take into account plant species diversity, as it may influence pathogenic diversity at least for specific ones? I would say it's a difficult metric to include at this point – but it would be important to mention this effect in your

discussion on pathogenic fungi. It might be connected to grassland versus forest differences, as these ecosystems also differ in host species dominance possibly.

Finally, your results on landscape scale on different functional guilds raise questions about the dispersal abilities of RA versus LFSA fungi. You briefly mention this point L355 but could extend it, as landscape ecology is clearly linked with dispersal abilities of organisms and remains a challenge to evaluate on fungi.

Those comments are suggestion, to remove some doubts, without adding too much text of course. Supporting the research on landscape ecology of soil pathogenic fungi remains essential, and your article could make it more visible.
Best regards.

Details

Abstract

L190 (500–10,000 m radius) – for non experts, perhaps replace by (i.e. surrounding landscape, 500 to 10,000 m from the soil sampling point).

L196 leaf/fruit/seed-associated fungi – add “detected from soil genomic DNA”

L199 as well between functional guilds of pathogenic fungi ? shall you precise ?

L200 I would keep a conclusion on pathogenic fungi only – not all fungi – unless you clarify their abundance in total genomic DNA.

L248 precise that you detect such pathogens from soil eDNA

L251 why not using habitat area or quantity ? As many of your metrics are correlated, perhaps justify why you used this metrics ?

L283 the formula “landscape complexity was significantly linked” is puzzling, as the causality might be misunderstood. You have 4 sentences using the verb “linked” and I would reverse it for more clarity. (I.e. that the relative abundance was statistically correlated with ...)

(Remarks on code availability)

Reviewer #2

(Remarks to the Author)

I co-reviewed this manuscript with one of the reviewers who provided the listed reports. This is part of the Nature Communications initiative to facilitate training in peer review and to provide appropriate recognition for Early Career Researchers who co-review manuscripts.

(Remarks on code availability)

Reviewer #3

(Remarks to the Author)

Understanding the influence of landscape changes on local diversity is important to predict the consequence of large-scale land use change. This manuscript investigated the influence of landscape-level factors on soil pathogenic fungi diversity at a global scale based on 290 sites with 511 plots located in 32 countries from six continents. The authors highlight the importance of maintaining landscape complexity in driving the global distribution of soil pathogenic fungi diversity. While the current manuscript addresses an important topic and found some interesting results, it lacks a significant contribution to the current body of knowledge. Importantly, there is a lack of new theoretical perspectives or novel insights for understanding how landscape change drives soil fungi diversity across different climate gradients and ecosystem types. The current manuscript may not meet the requirements of the journal Nature Communications.

I have some major concerns about the current manuscript outlined below:

1. The authors used the landscape complexity to represent the landscape effect, but the associated theories and mechanisms for affecting soil pathogenic fungi diversity were not presented well in the manuscript. The definition of landscape complexity in the current manuscript is vague. I do not understand whether it represents landscape composition or landscape configuration or landscape heterogeneity or connectivity or fragmentation. At the same time, the use of landscape complexity alone as a proxy for landscape change is incomplete and should also explicitly consider the landscape characteristics of target habitats and matrix within the landscape.
2. The method used to calculate the landscape complexity in the current manuscript is also inappropriate. Landscape complexity is a multidimensional concept; however, the manuscript calculated six landscape-level indices (ED, PD, LPI, LSI, MSIDI, SHDI) and extracts their principal components as a measure of landscape complexity, which is unclear and

meaningless. As introduced by the authors in the introduction, the quantification of landscape complexity should contain at least two main dimensions: (1) landscape composition including the amounts and proportions of each land cover type within the landscape (2) landscape configuration including the spatial arrangement of each land cover type within the landscape. However, the current six landscape-level indices failed to explicitly consider the composition and configuration for each land cover type within the landscape.

3. This manuscript aims to provide evidence about how pathogenic fungi worldwide responded to the landscape complexity. However, the study data were mainly concentrated on forest and grassland ecosystems and did not cover other ecosystem types well. Therefore, the current conclusions may not be globally representative. Meanwhile, while the current manuscript mainly focused on the soil pathogenic fungal diversity at the alpha scale, it is more interesting to also consider the pattern of soil fungi diversity of other trophic types responding to landscape change. And it is also necessary to evaluate the pattern of soil fungi composition or beta diversity to provide novel insights for understanding how landscape change drives soil fungi diversity.

4. The five spatial scales (500, 1,000, 2,000, 5,000, and 10,000 m radius) adopted to evaluate landscape change may be too large to detect the optimal scale of landscape change affecting soil fungi diversity which generally has a relatively limited capacity for spatial dispersal due to their large size, especially for grassland ecosystems. Thus, it is necessary to also consider landscape changes at scales below 500 m.

5. The three scientific questions in the current manuscript are largely in line with some existing studies, and there is a lack of new theoretical perspectives or novel insights. The manuscript currently considers only the direct effects of landscape changes on soil fungi and their relative contribution of landscape complexity compared with other environmental variables. It is more important to consider landscape and climate change interactions (particularly, mitigation and adaptation) to advance the understanding of the mechanisms and ecological impacts of land use change.

6. There are many publicly available land-use databases with high temporal and spatial resolution, but the manuscript used only a single source of land-use data to quantify landscape change, i.e., 100 m-resolution from Copernicus global land service. Therefore, it is important to use multiple land-use data simultaneously and to conduct sensitivity analyses for the data analysis. In addition, the time scale and historic landscape change have been overlooked in landscape complexity calculation, which may have a significant effect on soil fungi diversity.

7. In the statistical analyses, the authors extracted the influencing factors from multiple databases, including 100-m land use data, 1-km WorldClim 2, CHELSA, and 250-m SoilGrids. There are large differences in resolution or scale between these different data sources, which may bias the results of the statistical analyses. How the authors dealt with this issue? In terms of statistical methods, the data were analysed using only multivariate generalized additive models, which are insufficient for assessing and understanding the effects of complex interactions between landscape change, soil environmental variables and climatic variables. The mixed effects model and structural equation modelling are recommended. In addition, potential problems of spatial autocorrelation and residual heterogeneity were not considered.

8. Importantly, some important influencing factors such as climate, altitude, slope, aspect, and vegetation cover have not been adequately considered. There are 19 key bioclimatic variables in the WorldClim 2 database, such as the seasonality (e.g., annual range in temperature and precipitation) and extreme or limiting environmental factors (e.g., temperature of the coldest and warmest month, and precipitation of the wet and dry quarters). Why did the author only use the MAT and MAP variables? Vegetation cover in each sample site also has a significant effect on soil fungal diversity and might also mediate the effects of climate and landscape change.

(Remarks on code availability)

Version 1:

Reviewer comments:

Reviewer #1

(Remarks to the Author)

Dear authors,

congratulations for this new versions ! really extremely rich and impressive.

Just a few minor comments

L195 on beta diversity (on missing)

L197 while crop cover significantly reduced the alpha diversity of soil pathogenic fungi

Isn't it in contradiction with your result "Crop cover showed significant positive correlations with soil pathogenic fungal alpha diversity across spatial scales for all plots and forest ecosystems", L359 ? In your discussion you also highlight this trend - you may clarify, as Fig 3 shows also a distinct patterns, notably before 2500m.

I would in the abstract also highlight the result "Our results showed that increased proportion of natural habitats, such as tree and grass cover within the landscape, tended to reduce soil pathogenic fungal diversity, whereas larger crop cover increased it. »

L200 highlight the importance of local factors and the complementary ...

(otherwise we wonder what is the complementarity about)

L 523 reformulate : In addition, unlike LFSA fungi, whose primary lifestyles are predominantly as pathogens, RA fungi (e.g., *Entoloma* spp.) are PRIMARILY classified as saprotrophic or ectomycorrhizal fungi, and pathogenic effects on plant roots might be less frequent than for LFSA

Fig 1. I would add the number of ASV of LFSA and RA in the Fig 1c (to show the reader how low diverse are the RA fungi too).

L491 I would remove " However", rather write Additionally. Your results confirm a shift around 2000-2500 m for forest fungi, questioning their dispersal range. We indeed expect to lose a significant effect of this distance if dispersal is less frequent at such large distance, or at least that would be an explanation. I would at least mention the differences in dispersal abilities among fungal communities, expecting more long distance dispersal in grassland than in forest ecosystems.

This difference in dispersal mode is also striking between our LFSA and RA fungi in forest ecosystems notably - and even if I do not think you might add more analyses, fungal traits database allowed you to have some for the fruiting morphology information and making more data-oriented conclusion to interpret for example your different patterns observed in Figure 4.

Congratulations again for this impressive work,
Best regards,

(Remarks on code availability)

I've seen the code for the gamlss only, which is correct.

Reviewer #3

(Remarks to the Author)

I have no further suggestions.

(Remarks on code availability)

I have no further suggestions.

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Reviewer #1 (Remarks to the Author):

Dear Authors,

I really enjoyed reading your manuscript “Landscape effects on global soil pathogenic fungal diversity across spatial scales”. Exploring the landscape ecology of soil pathogenic fungi is a new frontier in science, and your research can be inspiring for future local and global studies. Your focus on pathogens is particularly interesting, as synthesis are missing at such a scale for this functional group of fungi. Your results showing the differences on spatial scale are really important, as it is still unclear how to choose the best scale for such a diverse group of organisms, with large as well as short distance dispersal abilities. It will be of significance for fungal ecologists and non-fungal ones, opening the audience also. However, perhaps in the choice of metrics, it would have been interesting to include habitat quantity—for your discussion on grassland versus forests notably, or explain why you chose the largest patch size instead. I however have some comments to reinforce your results on pathogens – removing some doubts mainly in the methods, some clarification on the results useful for your discussion.

[Response] Thank you very much for your appreciation on our work. We are pleased that you found our study to be important and interesting. Following your constructive comments, we have incorporated habitat quantity, i.e., the cover percentages of grasses, trees and crops from 250 to 10,000 m radii surrounding each sampling coordinate, in our analyses on soil pathogenic fungal diversity. These analyses help clarify the role of different types of vegetation cover in shaping pathogenic fungal diversity patterns. We have updated the Methods, Results and Discussion accordingly, and it now reads:

For Methods in lines 822–825:

“The landscape quantity variables were calculated as the cover percentage (%) of three main land cover types: grass, tree, and crop within concentric buffer zones ranging from 250 m to 10,000 m radii surrounding each sampling coordinate.”

For Results:

“Higher crop cover within the spatial radius of 500 m significantly increased LFSA and RA fungal alpha diversity in all plots and forest ecosystems, but decreased the richness ($\beta = -0.436$; $p < 0.001$), Shannon diversity ($\beta = -0.333$; $p < 0.001$) of LFSA fungi and relative abundance ($\beta = -0.420$; $p = 0.011$) of RA fungi in grassland ecosystems (Fig. 2a–f). Higher tree cover significantly decreased the richness ($\beta = -0.636$; $p < 0.001$) and Shannon diversity ($\beta = -0.469$; $p < 0.001$) of LFSA fungi in grasslands, but increased the relative abundance ($\beta = 0.268$; $p = 0.011$) of RA fungi in all plots. Grass cover did not show significant correlations with soil pathogenic fungal alpha diversity (Fig. 2a–f).” in lines 313–320.

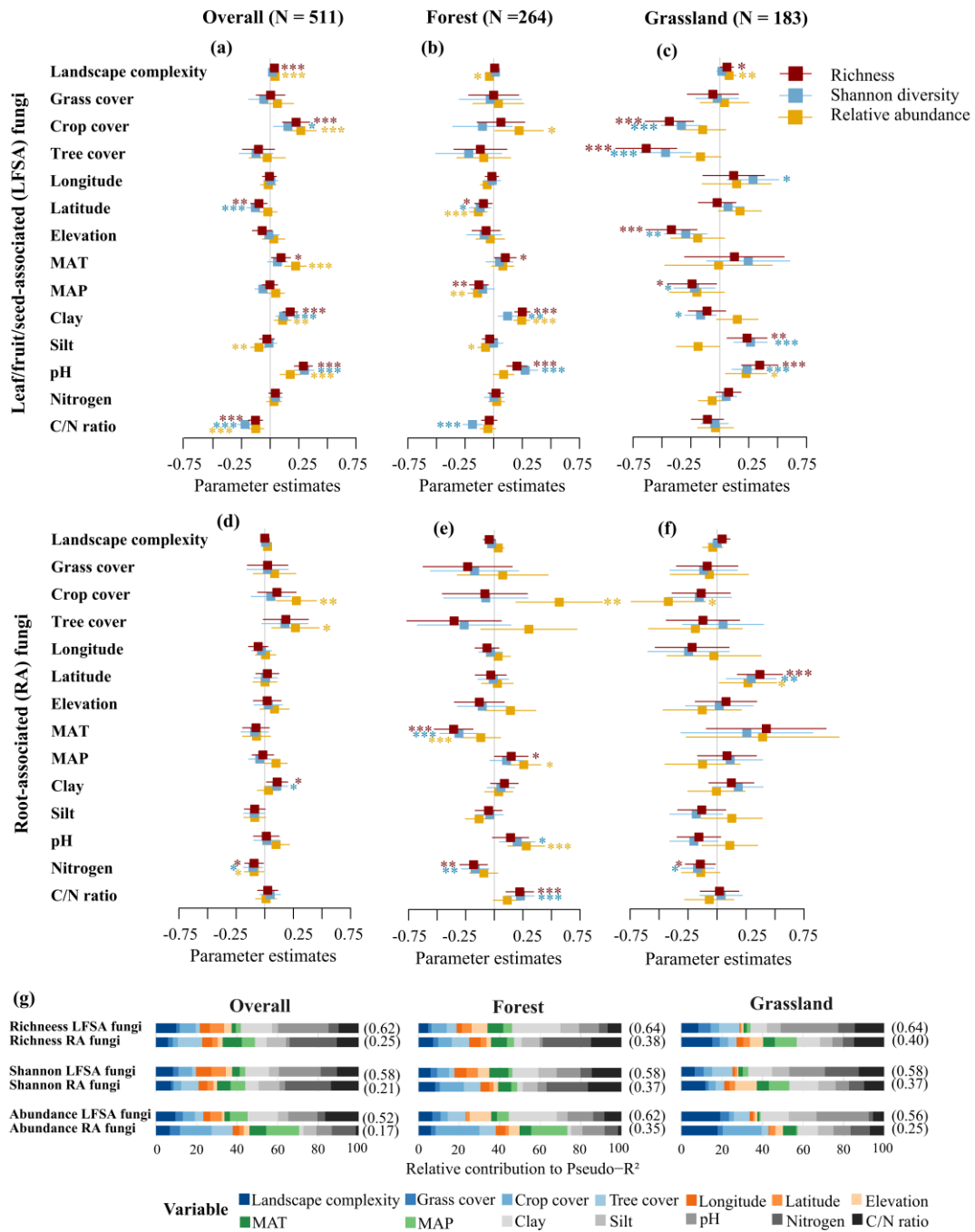


Figure 2. Predictors of leaf/fruit/seed-associated (LFSA) and root-associated (RA) fungal diversity (a)–(f); and the relative contribution (proportion of variance explained, %) of each predictor variable to the Pseudo-R² (the numbers in parentheses) from multivariate GAMLSS (g). (a)–(f) show the parameter estimates (standardized regression coefficients) and the corresponding 95% confidence intervals (CIs) from 511 overall plots, 264 forest plots and 183 grassland plots. The red, blue or yellow bars represent the response of the richness, Shannon diversity or the relative abundance of the fungi, respectively. The predictor factors include landscape variables of landscape complexity, grass cover, crop cover and tree cover (within the 500 m radius around the

sampling coordinate), geographic variables of longitude, latitude, and elevation, climatic variables of mean annual temperature (MAT) and mean annual precipitation (MAP), and soil variables of soil clay content (clay), silt content (silt), pH, total nitrogen content (nitrogen) and soil organic carbon/total nitrogen (C/N) ratio. The significance is tested by p -value as *** $p \leq 0.001$; ** $p \leq 0.01$; * $p \leq 0.05$. See supporting information Table S1 for details and the exact p -values.

“The regression coefficients of grass cover showed a decreasing trend along spatial scales, with a significant positive correlation with the relative abundance of RA fungi within the 250 m radius ($\beta = 0.183$; $p = 0.045$), but negative correlations with richness ($\beta = -0.127$; $p = 0.028$), Shannon diversity ($\beta = -0.172$; $p = 0.005$) and relative abundance ($\beta = -0.129$; $p = 0.048$) of LFSA fungi within the 10,000 m radius for all plots (Fig. 3b). Forest ecosystems also exhibited the similar pattern (Fig. S13b). In grassland ecosystems, the regression coefficients showed a contrary pattern to grass cover between fungal groups, with LFSA fungi mainly showing positive regression coefficients, and RA fungi showing negative regression coefficients (Fig. S14b). Based on a meta-analysis of parameter estimates, grass cover showed a significant negative correlation with soil pathogenic fungal alpha diversity for all plots (effect size = -0.037; $p = 0.035$), but the pattern was non-significant in forest (effect size = -0.041; $p = 0.117$) and grassland (effect size = -0.025; $p = 0.470$) ecosystems (Figs. 4a and S15b).

Crop cover showed significant positive correlations with soil pathogenic fungal alpha diversity across spatial scales for all plots and forest ecosystems, but significant negative correlations in grassland ecosystems (Figs. 3c, S13c and S14c). The meta-analysis also confirmed the significant positive effects of crop cover on soil pathogenic fungal alpha diversity for all plots (effect size = 0.174; $p < 0.001$) and forest ecosystems (effect size = 0.157; $p < 0.001$), but a significant negative effect for grassland ecosystems (effect size = -0.311; $p < 0.001$) (Fig. 4a, b).

The regression coefficients of tree cover showed contrary patterns to LFSA and RA fungal alpha diversity along spatial scales for all plots. LFSA fungal alpha diversity generally decreased, while RA fungal alpha diversity increased with tree cover, especially within smaller spatial radii from 250 m to 1,000 m (Fig. 3d). This may result in the non-significant effect size of tree cover on soil pathogenic fungal alpha diversity for all plots (effect size = 0.024; $p = 0.314$) (Fig. 4a). This contrasting pattern was not clearly observed in forest and grassland ecosystems (Figs. S13d and S14d). In grassland ecosystems, stronger negative regression coefficients for soil pathogenic fungal alpha diversity were detected across spatial scales, which also confirmed a significant negative effect size of tree cover (effect size = -0.275; $p < 0.001$) (Fig. S15c).”
in lines 346–375.

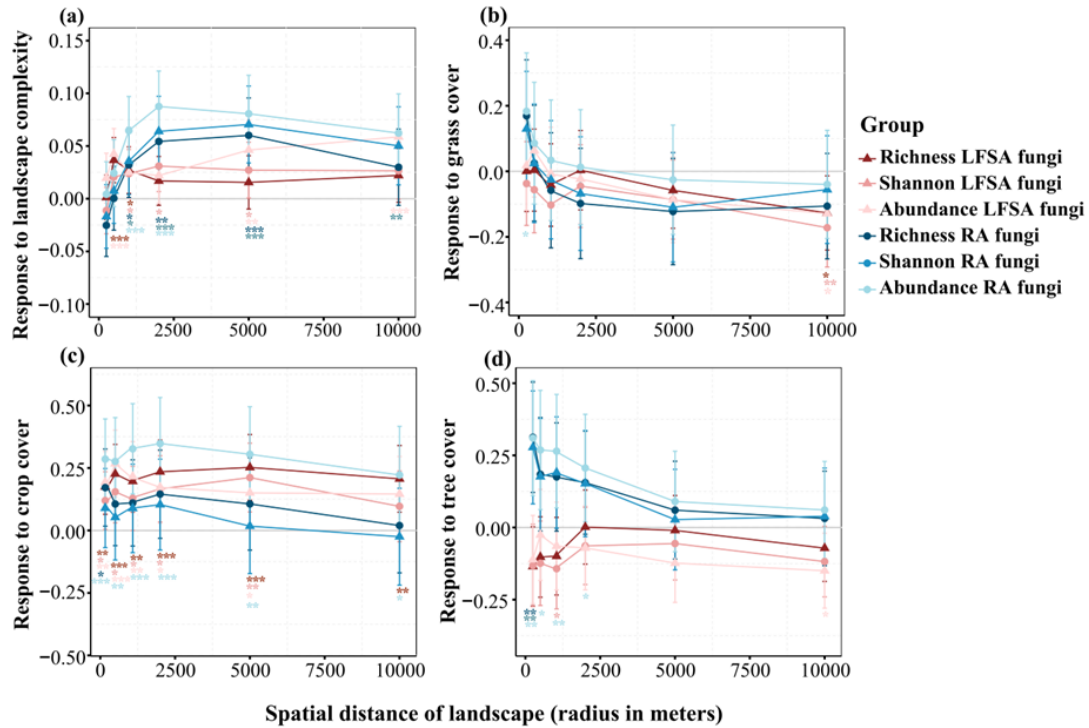


Figure 3. Leaf/fruit/seed-associated (LFSA) and root-associated (RA) fungal diversity as affected by (a) landscape complexity, (b) grass cover, (c) crop cover, and (d) tree cover across six spatial scales (250 m, 500 m, 1,000 m, 2,000 m, 5,000 m, and 10,000 m radii) ($n = 511$ plots in total). The response variables are the parameter estimates (standardized regression coefficients and standardized error) of soil pathogenic fungal alpha diversity and four landscape variables from GAMLSS, respectively. The red lines from dark to light indicate the richness, Shannon diversity and relative abundance of LFSA fungi, while the blue lines correspond to that of RA fungi. The significance levels are indicated as *** $p \leq 0.001$; ** $p \leq 0.01$; * $p \leq 0.05$. The partial regression results of soil pathogenic fungal alpha diversity responding to landscape complexity can be found in supporting information Figs. S7–S12.

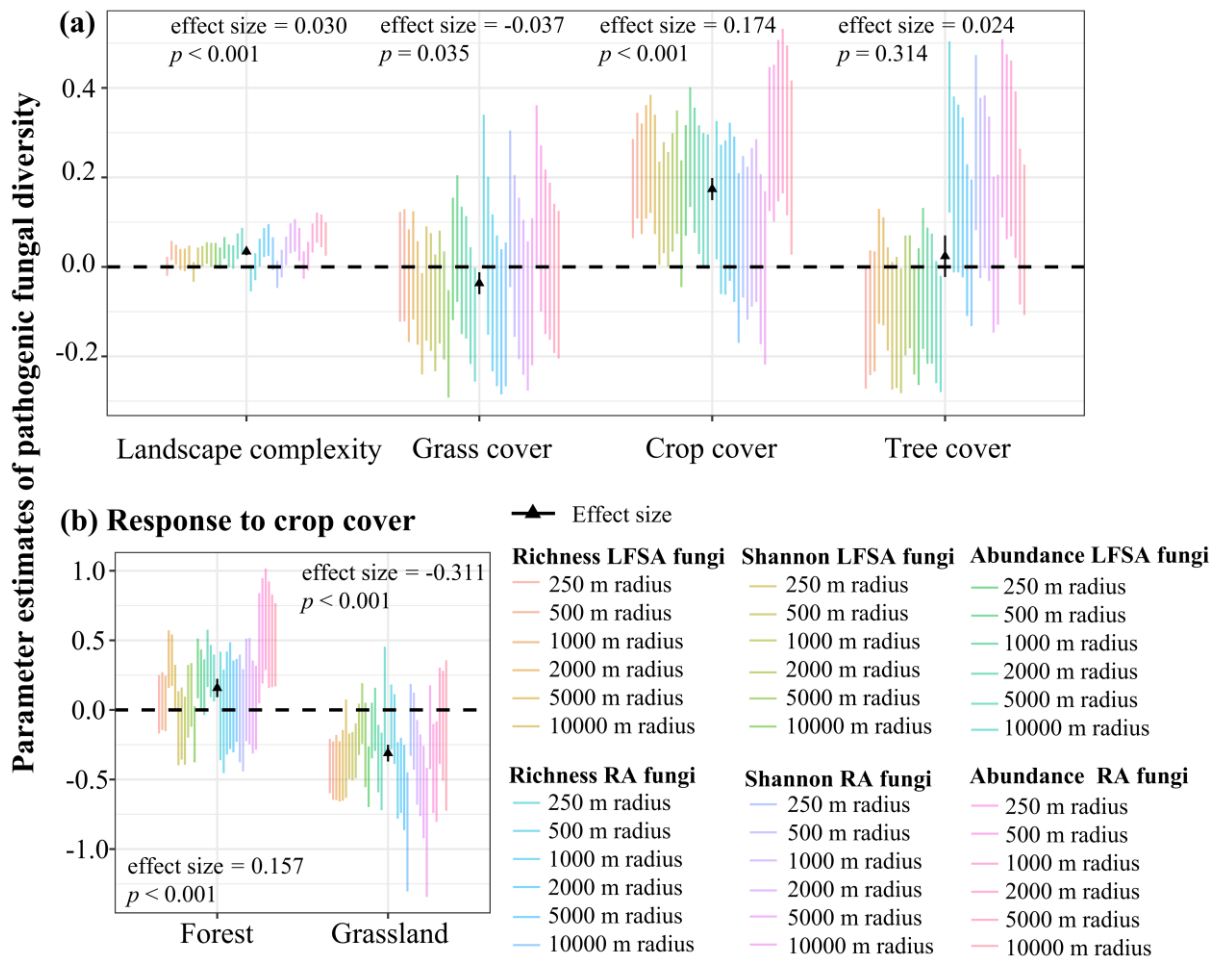
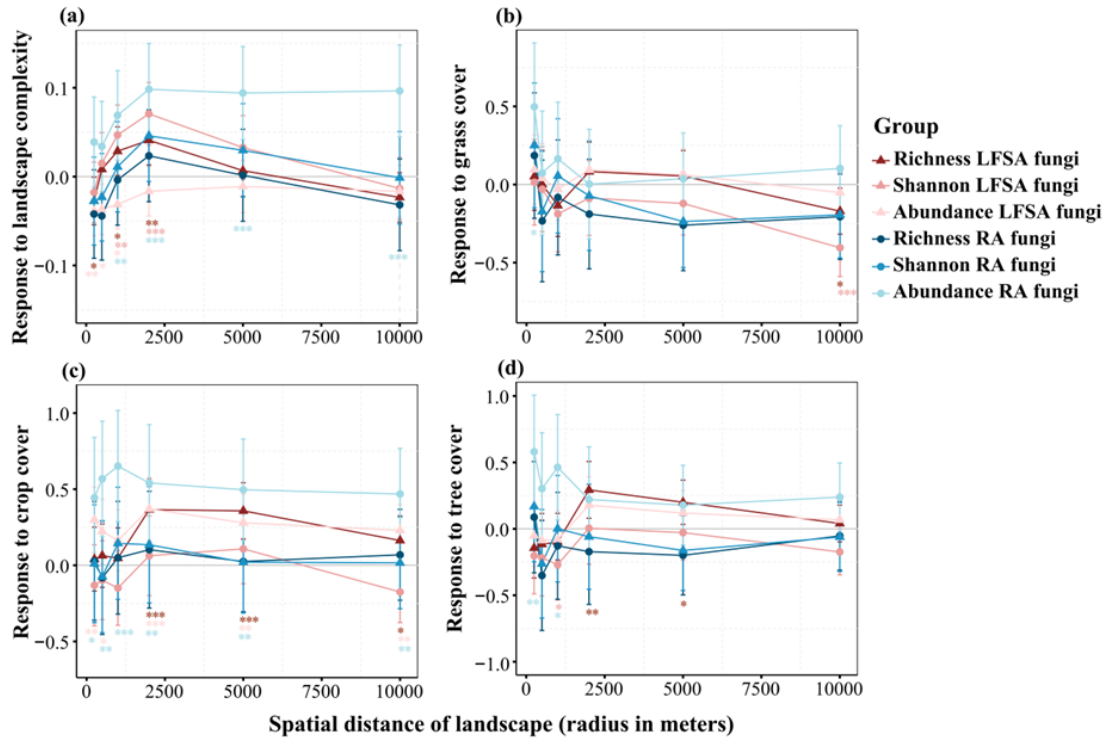
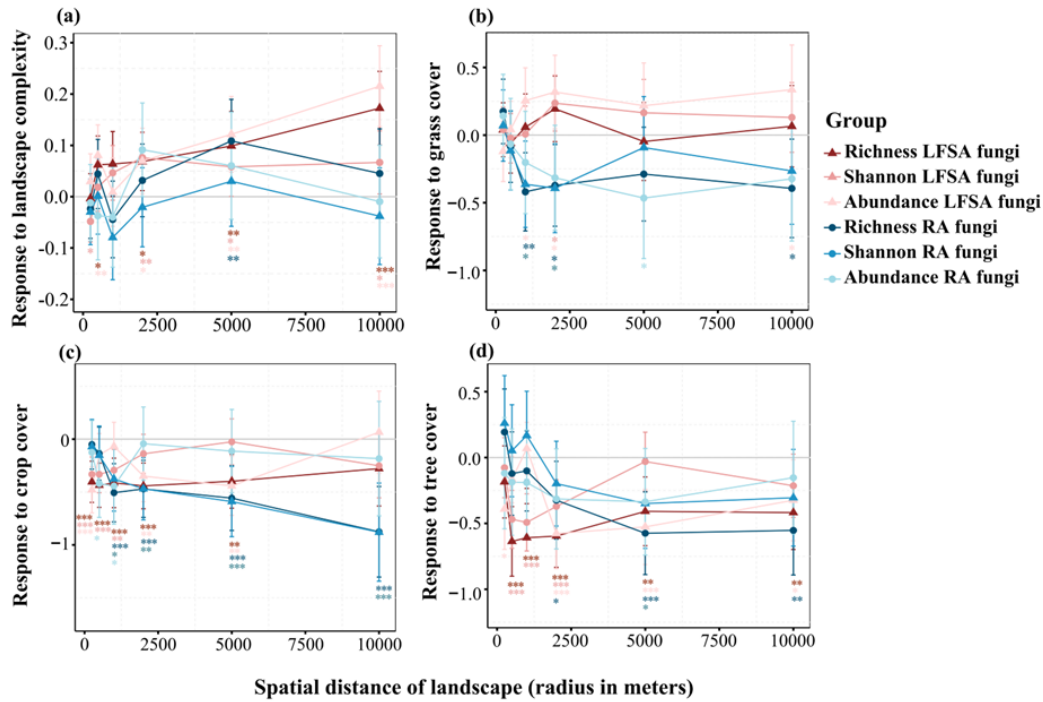


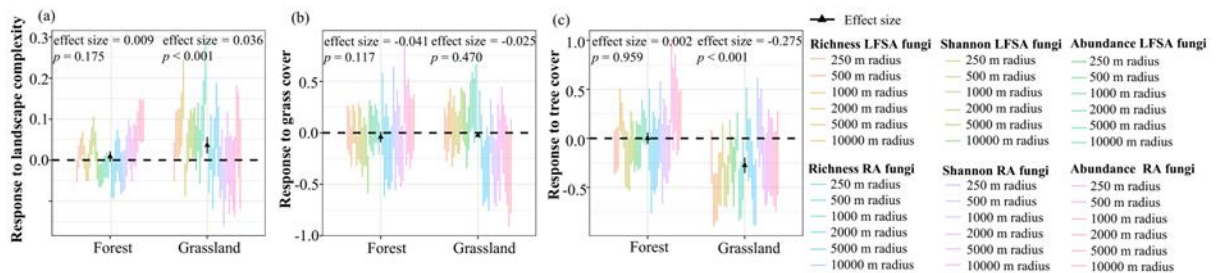
Figure 4. Parameter estimates and overall effect sizes of landscape effects on soil pathogenic fungal diversity. (a) Effects of landscape complexity, grass cover, crop cover, and tree cover on soil pathogenic fungal alpha diversity ($n = 511$ plots in total). (b) Effects of crop cover on soil pathogenic fungal alpha diversity between forest and grassland ecosystems. Colored lines indicate the 95% confidence intervals of parameter estimates across different fungal groups (LFSA and RA fungi), diversity indices (richness, Shannon diversity, and relative abundance), and spatial scales (250 m to 10,000 m radii). Black triangles represent the overall effect sizes. Effect size values and associated p -values are reported for each category.



Supporting Information Figure S13. Leaf/fruit/seed-associated (LFSA) and root-associated (RA) fungal diversity as affected by (a) landscape complexity, (b) grass cover, (c) crop cover, and (d) tree cover across six spatial scales (250 m, 500 m, 1,000 m, 2,000 m, 5,000 m, and 10,000 m radii) ($n = 264$ forest plots). The response variables are the parameter estimates (standardized regression coefficients and standardized error) of soil pathogenic fungal diversity and four landscape variables from GAMLSS, respectively. The red lines from dark to light indicate the richness, Shannon diversity and relative abundance of LFSA fungi, while the blue lines correspond to that of RA fungi. The significance levels are indicated as *** $p \leq 0.001$; ** $p \leq 0.01$; * $p \leq 0.05$.



Supporting Information Figure S14. Leaf/fruit/seed-associated (LFSA) and root-associated (RA) fungal diversity as affected by (a) landscape complexity, (b) grass cover, (c) crop cover, and (d) tree cover across six spatial scales (250 m, 500 m, 1,000 m, 2,000 m, 5,000 m, and 10,000 m radii) ($n = 183$ grassland plots). The response variables are the parameter estimates (standardized regression coefficients and standardized error) of soil pathogenic fungal diversity and four landscape variables from GAMLSS, respectively. The red lines from dark to light indicate the richness, Shannon diversity and relative abundance of LFSA fungi, while the blue lines correspond to that of RA fungi. The significance levels are indicated as *** $p \leq 0.001$; ** $p \leq 0.01$; * $p \leq 0.05$.



Supporting Information Figure S15. Parameter estimates and overall effect sizes of (a) landscape complexity, (b) grass cover, and (c) tree cover on soil pathogenic fungal alpha diversity between forest and grassland ecosystems. Colored lines indicate the 95% confidence intervals of parameter estimates across different fungal groups (LFSA and RA fungi), diversity indices (richness, Shannon diversity, and relative abundance), and spatial scales (250 m to 10,000 m radii). Black triangles represent the overall effect sizes. Effect size values and associated p -values are reported for each category.

Furthermore, our rationale for selecting the Largest Patch Index (LPI) was revised in **Supporting Information Table S7**, as it effectively captures the dominance and spatial continuity of the largest habitat patch more than the quantity information, which is ecologically meaningful for understanding dispersal and habitat availability for soil fungi. Moreover, given the high correlation between mean patch area and other landscape metrics, and considering that we separately analyzed the effects of different cover type proportions, we ultimately retained LPI as one of metrics representing landscape complexity. A detailed correlation analysis among landscape metrics has also been provided in the responses below for reference.

For your detailed comments, we have conducted careful and thorough revisions and provided explanations below.

First, for a generalist audience, the fact that genomic soil DNA contains ASVs identified as leaf/fruit/seed pathogens as well as root associated ones, based on genus level identifications may not be clear and shall be precised. One derived critic could be on the interpretation: for example, you mention the results obtained for *Entoloma* genus – a lineage that does include mainly saprobes and ectomycorrhizal fungi – and whose ecology might differ from other pathogens. It shall be mentioned in your discussion, if you mention *Entoloma*. Moreover, the use of a metric on relative abundance of pathogens raise another question: did you use abundance among all reads, or all functionally assigned reads? Fungal traits as other functional bases might not be complete, and mentioning the general level of assignation in your dataset would be essential. A more naïve question, did you expect to find less RA than LFSA fungi in soils ?

[Response] Thank you for your valuable comments and important questions. We acknowledge that the genus level identification may not be sufficiently clear. Through our in-depth comparison, we found the complex ecological role of *Entoloma* compared to other pathogens. Therefore, we have revised the Discussion to offer a more detailed interpretation of its potential pathogenicity between lines 523–528. It now reads:

“In addition, unlike LFSA fungi, whose primary lifestyles are predominantly as pathogens, RA fungi (e.g., Entoloma spp.) are classified as saprotrophic or ectomycorrhizal fungi, in addition to exhibiting strong pathogenic effects on plant roots^{57–58}. This suggests that the differences in primary lifestyles and the complex trophic mode of RA fungi may contribute to their distinct responses¹⁰.”

The answer for the second question is that we used the relative abundance of LFSA/RA fungi among all fungal reads, ensuring a comprehensive representation of pathogenic fungi within the dataset. We now made this clear in Methods (lines 838–839). Moreover, we did not have any specific expectation of whether RA or LFSA fungi would be more abundant, as their relative abundance can vary depending on environmental conditions, host plant availability, and soil characteristics. Our approach

was to objectively assess the observed proportions of RA and LFSA fungi and interpret the patterns based on the data.

This point is connected to another technical point, notably if you had samples coming from different ecosystems, at such a scale, did you use any calibration on sample coverage or the threshold on read number was sufficient? Mentioning briefly the number of sequences produced, samples kept at the end – and % of pathogenic ASVs among all sequences would be useful, a very short information to evaluate how representative your results are.

[Response] Thanks for the suggestion. In our analysis, we applied a rarefaction threshold of 10,000 reads per sample based on rarefaction curves, which indicated a sufficient sequencing depth to capture the majority of fungal diversity. We have added the relevant information in lines 778–783 and 787–789. It reads:

“A total of 64,813,812 sequencing read pairs were generated from all sequencing samples, of which 35,325,442 read pairs remained after quality control. Based on rarefaction curves, samples were rarefied to a minimum of 10,000 reads before ASV construction. After applying quality control to both the reads and metadata, 511 samples with more than 10,000 reads were retained, yielding a total of 4,069,715 reads assigned to 26,344 ASVs.”

“Among these, 11.1% of the reads were classified into 2,694 leaf/fruit/seed-associated fungal ASVs and 1.66% belonged to 302 root-associated fungal ASVs.”

The results themselves remain super interesting, considering the diversity of metrics, ecosystems studied. It is important to highlight that landscape factors are less explicative than other factors in most cases, but complementary. Mentioning that you did not observe significant effect in some cases (cf Figure 2; L267) would be useful.

[Response] Thank you for the suggestion. We supplemented the descriptions about non-significant results of landscape factors (lines 306–307 and line 319–320) and contribution comparison with local environmental factors (lines 328–329) to make the content more rigorous. It reads:

“Shannon diversity of LFSA and RA fungi did not show significant responses to landscape complexity (Fig. 2a–f).”

“Grass cover did not show significant correlations with soil pathogenic fungal alpha diversity (Fig. 2a–f).”

“...Although the relative contribution of landscape factors was lower than that of soil factors, it makes a complementary explanation to the overall variance.”

In addition, we have revised the Abstract in lines 200–204 to emphasize the compensatory effects of landscape factors on soil pathogenic fungal diversity. It reads:

“Our results highlight the complementary role of landscape patterns in shaping the global distribution of soil pathogenic fungi and provide implications for selecting optimal landscape spatial scales for predicting soil pathogenic fungal diversity across different functional groups, environmental conditions and ecosystems.”

Also to clarify your results, in line with your introduction where you mention the higher diversity in the tropics, the importance of natural habitats, perhaps shall you justify your choice of centering your study in non-tropical regions, or if you observed distinct patterns in the less sampled biomes you studied, to accompany your figure 1? Moreover, plantations and cropland are included but the typology was not included in the analysis, did it have an impact of shall you mention it to clarify your discussion on natural habitats? Were non natural habitats removed?

[Response] Thank you for your insightful comments. We acknowledge that the number of tropical sampling sites is relatively limited in our study, which is primarily due to the challenges of conducting global-scale sampling. However, despite the lower representation of tropical regions, our study still captures broad ecological gradients across different biomes, allowing us to assess generalizable landscape effects on soil pathogenic fungal diversity. To avoid any potential confusion, we have now revised our phrase in the Introduction in lines 217–218 and 252–255. It now reads:

“Soil pathogenic fungi exhibit higher richness and abundance at low latitudes^{10–11}, but the responsible drivers are still not fully understood.”

“However, landscapes vary across biomes. For example, temperate biomes like central-European grasslands usually have experienced long-term land-use changes and more pronounced landscape simplification^{19, 21}, which may result in a lower diversity of soil pathogenic fungi¹⁰.”

Regarding the inclusion of non-natural habitats, we incorporated all sample sites without removing the plantations and croplands in the overall pattern analysis. We chose this approach to ensure that our study captures a more representative global pattern. However, due to the relatively low number of samples from non-natural habitats, we were unable to further disentangle their specific effects in comparison to other ecosystem types. Therefore, we now added some discussion of the potential influences of natural versus non-natural habitats, highlighting the need for future studies to further explore these aspects between lines 459–464. It reads:

“Although our study primarily focuses on natural ecosystems, non-natural habitats, such as croplands and plantations, may be more vulnerable to landscape changes due to intensive landscape management and simplified community composition¹⁸, leading to reduced soil pathogenic fungal diversity. Given the limited representation of non-natural habitats in our dataset, we call for future studies to systematically assess their effects on soil pathogenic fungi across biomes and spatial scales.”

Another question, related to your discussion on natural habitats and landscape complexity, and considering the diversity of ecosystems you study: did you take into account plant species diversity, as it may influence pathogenic diversity at least for specific ones? I would say it's a difficult metric to include at this point – but it would be important to mention this effect in your discussion on pathogenic fungi. It might be connected to grassland versus forest differences, as these ecosystems also differ in host species dominance possibly.

[Response] Thank you for the insightful question. We fully acknowledge the influence of plant species diversity on soil pathogenic fungal diversity and tried to include it in our analysis. However, due to the difficulty in conducting local plant diversity surveys in numerous sampling sites, it is challenging to obtain this data currently. To address this limitation, we have added a discussion in the revised manuscript (lines 467–484), considering the potential influence of differences in plant species diversity among cover types on the contrasting responses observed in grassland and forest ecosystems. We would give priority to this factor in subsequent research. It mainly reads:

“Natural habitats typically support greater plant species richness, more diverse microhabitats, and a higher proportion of non-host plants, which together may suppress soil pathogenic fungi through a dilution effect by reducing the availability and spatial continuity of suitable hosts^{6, 44}. In contrast, crop-covered landscapes are often dominated by monocultures with high host density and homogeneous environments that facilitate the accumulation and dispersal of soil pathogens to the surroundings^{28, 40}... Although we suggested that differences in plant species diversity and composition within landscapes may partly account for these contrasting responses, integrating this factor into global analyses is challenging due to the limited availability of comprehensive, spatially explicit plant diversity datasets³⁵.”

Finally, your results on landscape scale on different functional guilds raise questions about the dispersal abilities of RA versus LFSA fungi. You briefly mention this point L355 but could extend it, as landscape ecology is clearly linked with dispersal abilities of organisms and remains a challenge to evaluate on fungi.

[Response] Thank you for your valuable suggestion. We acknowledge the importance of dispersal ability in studying landscape effects on soil pathogenic fungal diversity. We have expanded our discussion to further explore how landscape effects at large spatial scales influence fungal dispersal and dispersal abilities of RA versus LFSA fungi in lines 505–510 and 528–535. The text reads:

“Grilli et al.²⁰ suggest that the long dispersal ability of soil fungi may be underestimated, which may be why we detected stronger pathogenic fungal diversity-landscape relationships in open grassland ecosystems. While quantifying fungal dispersal remains challenging, research on landscape effects at large spatial scales is essential for a better understanding of soil pathogenic fungal dynamics¹⁶.”

“Last but not least, the host specificity of LFSA fungi may restrict their dispersal ability, thereby reducing the landscape effects. LFSA fungi are often more host-specific and rely on suitable plant hosts for survival^{14, 15}. Makiola et al.¹⁴ found that the effects of plant community composition on foliar plant pathogenic fungal diversity were greater than on root plant pathogenic fungal diversity. Therefore, while the aboveground life stages of LFSA fungi are generally considered capable of long-distance aerial dispersal and sensitive to landscape variables, their host specificity and sensitivity to local environments likely constrains responses to landscape variation⁴⁴.”

Those comments are suggestion, to remove some doubts, without adding too much text of course. Supporting the research on landscape ecology of soil pathogenic fungi remains essential, and your article could make it more visible.

Best regards.

[Response] We hope that our explanations and revisions will address your main concerns. Thanks again for your constructive comments and insightful suggestions which greatly improved our work.

Details

Abstract

L190 (500–10,000 m radius) – for non experts, perhaps replace by (i.e. surrounding landscape, 500 to 10,000 m from the soil sampling point).

[Response] Thank you. Replaced in line 191.

L196 leaf/fruit/seed-associated fungi – add “detected from soil genomic DNA”

[Response] Thank you. Done. Now updated in line 200.

L199 as well between functional guilds of pathogenic fungi? shall you precise?

[Response] Thank you. Done. Now updated in line 203.

L200 I would keep a conclusion on pathogenic fungi only – not all fungi – unless you clarify their abundance in total genomic DNA.

[Response] Thanks, we have rephrased with pathogenic fungi instead of fungi.

L248 precise that you detect such pathogens from soil eDNA

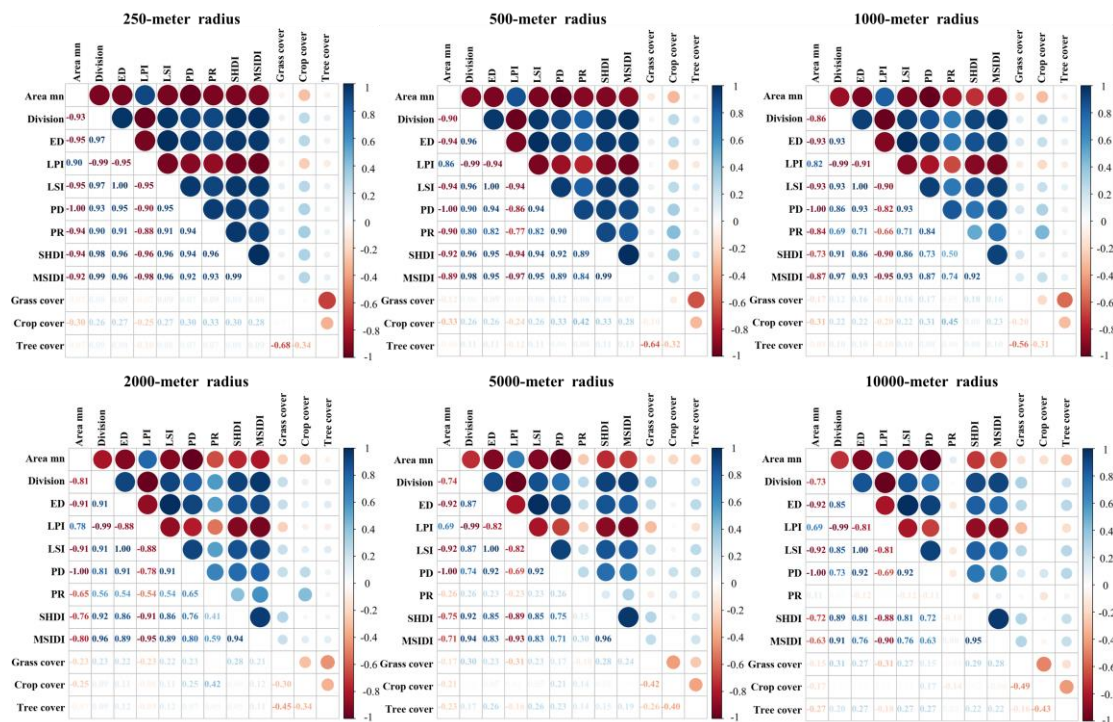
[Response] Thank you. Done.

L251 why not using habitat area or quantity? As many of your metrics are correlated, perhaps justify why you used this metrics?

[Response] Thank you for the valuable comment. We have now incorporated analyses of habitat quantity, i.e., the cover percentages of grass, tree and crops on soil pathogenic fungal diversity. It is true that habitat quantity can capture the amount of different vegetation types and is weakly correlated with landscape complexity metrics (composition and configuration) (see correlation figure below). Therefore, we treated

it as a separate set of predictor variables for pathogenic fungal diversity analysis. Meanwhile, metrics representing landscape complexity (composition and configuration heterogeneity) are highly correlated, including the mean of patch area (i.e., area mn), so we only kept a set of widely used, complementary metrics that capture different aspects of landscape cover, which is clarified in lines 795–797 in Methods. It reads:

“...Given the high correlations among these metrics, we retained a parsimonious set of complementary variables that capture distinct and representative dimensions of landscape complexity. Finally, we...”



The Spearman's correlations of 12 landscape metrics at six spatial scales. The metrics include mean of patch area (Area mn), landscape division index (Division), edge density (ED), largest patch index (LPI), landscape shape index (LSI), patch density (PD), Patch richness (PR), modified Simpson's diversity index (MSIDI) and Shannon diversity index (SHDI), vegetation cover of grass cover, crop cover and tree cover.

L283 the formula “landscape complexity was significantly linked” is puzzling, as the causality might be misunderstood. You have 4 sentences using the verb “linked” and I would reverse it for more clarity. (I.e. that the relative abundance was statistically correlated with ...)

[Response] Sorry for the confusion. We have revised the sentences in lines 407 and 445, now stating as "soil pathogenic fungal diversity was positively correlated with landscape complexity" for clarity.

Reviewer #2 (Remarks to the Author):

I co-reviewed this manuscript with one of the reviewers who provided the listed reports. This is part of the Nature Communications initiative to facilitate training in peer review and to provide appropriate recognition for Early Career Researchers who co-review manuscripts.

[Response] We are grateful for the constructive feedback you provided, which has helped us refine and improve our manuscript. Please find our detailed responses below the other reviewers' comments.

Reviewer #3 (Remarks to the Author):

Understanding the influence of landscape changes on local diversity is important to predict the consequence of large-scale land use change. This manuscript investigated the influence of landscape-level factors on soil pathogenic fungi diversity at a global scale based on 290 sites with 511 plots located in 32 countries from six continents. The authors highlight the importance of maintaining landscape complexity in driving the global distribution of soil pathogenic fungi diversity.

While the current manuscript addresses an important topic and found some interesting results, it lacks a significant contribution to the current body of knowledge. Importantly, there is a lack of new theoretical perspectives or novel insights for understanding how landscape change drives soil fungi diversity across different climate gradients and ecosystem types. The current manuscript may not meet the requirements of the journal Nature Communications.

[Response] Thank you for your thoughtful feedback. We appreciate your recognition of the importance of our study and the interesting findings it presents. Regarding your concern about the theoretical contribution and novelty of our manuscript, we would like to clarify the uniqueness of our research.

Our study provides the first global-scale assessment of how landscape factors influence soil pathogenic fungal diversity, addressing a significant gap left by previous research focused solely on regional patterns. Moreover, we aim to explain the inconsistencies in landscape effects reported in previous regional studies, and highlight the varying responses of soil pathogenic fungal diversity to landscape factors across spatial scales, fungal groups, and ecosystems. Meanwhile, our results highlight the non-negligible role of landscape variables in influencing soil pathogenic fungal diversity. Although we recognize the potential importance of interactions between landscape characteristics and climate, our additional analyses indicated that these interaction effects were generally weak, with the direct influence of landscape variables remaining more pronounced in determining fungal diversity patterns. Meanwhile, we detected that landscape factors also exert indirect effects on soil pathogenic fungal alpha diversity by mediating soil conditions. Taken together, landscape variables accounted for an average of 23.4% of the total variance in alpha diversity across spatial scales and ecosystems, ranking second only to soil variables.

Landscape effects on soil pathogenic fungi is a new frontier in microbiology, with most previous studies focusing on mobile animals, but limited attention has been given

to belowground, small, and dispersible pathogens. We believe this approach offers broader implications and presents a novel perspective that could inspire future research at both local and global scales, particularly in belowground microbial diversity.

To further strengthen the theoretical perspectives and novel insights of our study, we have revised the Abstract (lines 200–204) and Discussion sections (lines 402, 409–413). It reads:

“Our results highlight the complementary role of landscape patterns in shaping the global distribution of soil pathogenic fungi and provide implications for selecting optimal landscape spatial scales for predicting soil pathogenic fungal diversity across different functional groups, environmental conditions and ecosystems.”

“Exploring the landscape effects on soil pathogenic fungi is a novel frontier in microbiology...This study provides a global assessment of landscape effects on soil pathogenic fungal diversity and underscores the importance of selecting appropriate spatial scales for predicting diversity across ecosystems and fungal groups, offering practical guidance for landscape management and biodiversity conservation policy.”

Furthermore, we performed additional revisions to address your criticism:

1. Clarified the definition of landscape complexity and elaborated on the theoretical framework explaining how landscape factors influence soil pathogenic fungal diversity.
2. Recalculated landscape complexity by incorporating two additional, complementary metrics (landscape division index and patch richness) representing the compositional and configurational heterogeneity of landscapes. Clarified the rationale for using Principal Component Analysis (PCA) to quantify overall landscape complexity.
3. Incorporated analyses of vegetation cover quantity, i.e., the cover percentages of grass, tree and crops from 250 to 10,000 m radii surrounding each sampling coordinate, on soil pathogenic fungal diversity.
4. Added analyses of soil pathogenic fungal beta diversity (Sørensen beta dissimilarity) to provide a more comprehensive understanding of landscape effects on soil pathogenic fungal diversity.
5. Extended the spatial scale of landscape factor assessments to include finer spatial extents, starting from a 250 m radius.
6. Conducted the meta-analysis to assess the overall effects of landscape complexity and quantity on soil pathogenic fungi across different fungal groups (LFSA and RA fungi), diversity indices (richness, Shannon diversity, and relative abundance), and spatial scales (250 m to 10,000 m radius), thereby strengthening the robustness and comprehensiveness of the study.
7. Conducted robustness checks using mixed-effects models, sensitivity analyses with multiple land cover maps, spatial autocorrelation and residual heteroscedasticity tests to ensure the reliability and consistency of our results.
8. Conducted the Partial Least Squares Path Modeling (PLSPM) to assess direct

and indirect effects of multivariate environmental factors on soil pathogenic fungal alpha diversity.

We hope these revisions address your concerns and enhance the clarity of our contributions. Thank you again for your valuable comments.

I have some major concerns about the current manuscript outlined below:

1. The authors used the landscape complexity to represent the landscape effect, but the associated theories and mechanisms for affecting soil pathogenic fungi diversity were not presented well in the manuscript. The definition of landscape complexity in the current manuscript is vague. I do not understand whether it represents landscape composition or landscape configuration or landscape heterogeneity or connectivity or fragmentation. At the same time, the use of landscape complexity alone as a proxy for landscape change is incomplete and should also explicitly consider the landscape characteristics of target habitats and matrix within the landscape.

[Response] Thank you for your insightful comments and sorry for the ambiguity. Landscape complexity we used here is an integrated parameter that defines both the heterogeneity of landscape configuration and landscape composition, referring to Larterra *et al.* (2012) "Landscape complexity is a multidimensional property of landscapes depending both on their composition (e.g. proportion of non-arable land, covert types diversity) and their spatial configuration metrics (e.g. number, size, shape, diversity and connectivity of patches) which are only partly correlated among them..." and Gámez-Virués *et al.* (2015) "...Landscape-scale simplification was represented by both compositional heterogeneity (measured as Shannon diversity of land cover types) and configurational heterogeneity (average patch size within the surrounding landscape)..."

We have now explicitly defined landscape complexity in the Introduction in lines 228–242 and added associated theories and mechanisms of landscape complexity for affecting soil pathogenic fungi diversity in lines 243–247. It reads:

“Landscape simplification by agricultural intensification and land-use change is driving biodiversity loss^{21–22}, primarily by reducing land cover heterogeneity²³, limiting species dispersal through decreased connectivity and amplifying edge-driven habitat degradation^{24–25}. Landscape factors are typically classified into two key dimensions: compositional heterogeneity and configurational complexity^{20, 26}. Compositional heterogeneity describes the diversity and proportion of different land cover types within a landscape, typically quantified using metrics such as Shannon diversity and evenness²⁶. In contrast, configurational complexity characterizes the spatial arrangement, shape, and distribution patterns of these land cover types, captured by metrics such as patch size, patch shape and edge density²⁶. Despite increasing recognition of landscape effects on biodiversity, most existing studies evaluate these landscape metrics separately^{21, 25, 27}, overlooking the integrated influence of multiple landscape attributes on ecological patterns and processes²⁸. To address this, we propose an integrated landscape complexity index that simultaneously captures both

the compositional and configurational heterogeneity of landscapes²⁹, providing a comprehensive measure of overall landscape effects on soil pathogenic fungal diversity.”

“The Habitat Heterogeneity Hypothesis^{23, 30}, where diverse land cover types create a variety of microhabitats and resource availability supporting greater diversity^{23, 26}, allows us to expect that landscape complexity can also influence soil pathogenic fungi diversity. Meanwhile, landscape configuration influences fungal dispersal as limited connectivity may constrain the movement of spores and fungal propagules^{16, 20, 31}...”

About the landscape characteristics and matrix within the landscape, as the fundamental landscape characteristics of landscape diversity, shape, edge etc. were mostly captured by our landscape complexity index, we further incorporated the quantity of matrix types, including the cover percentage (%) of three main land cover types: grass, tree, and crop within different spatial radii of the landscape. And we found that landscape quantity metrics were weakly correlated with the landscape complexity index, so we included these metrics independently in our models. Thereafter, we have updated the Introduction in lines 253–257, Methods in lines 822–825, and Results section 346–375, accordingly. It now reads:

For Introduction:

“For example, temperate biomes like central-European grasslands usually have experienced long-term land-use changes and more pronounced landscape simplification^{19, 21}, which may result in a lower diversity of soil pathogenic fungi¹⁰. These patterns are likely further shaped by differences in the surrounding landscape quantity, particularly the relative proportions of natural habitats and agricultural land cover¹⁹.”

For Methods:

“The landscape quantity variables were calculated as the cover percentage (%) of three main land cover types: grass, tree, and crop within concentric buffer zones ranging from 250 m to 10,000 m radii surrounding each sampling coordinate.”

For Results:

“The regression coefficients of grass cover showed a decreasing trend along spatial scales, with a significant positive correlation with the relative abundance of RA fungi within the 250 m radius ($\beta = 0.183$; $p = 0.045$), but negative correlations with richness ($\beta = -0.127$; $p = 0.028$), Shannon diversity ($\beta = -0.172$; $p = 0.005$) and relative abundance ($\beta = -0.129$; $p = 0.048$) of LFSA fungi within the 10,000 m radius for all plots (Fig. 3b). Forest ecosystems also exhibited the similar pattern (Fig. S13b). In grassland ecosystems, the regression coefficients showed a contrary pattern to grass cover between fungal groups, with LFSA fungi mainly showing positive regression coefficients, and RA fungi showing negative regression coefficients (Fig. S14b). Based on a meta-analysis of parameter estimates, grass cover showed a significant negative correlation with soil pathogenic fungal alpha diversity for all plots (effect size = -0.037;

$p = 0.035$), but the pattern was non-significant in forest (effect size = -0.041 ; $p = 0.117$) and grassland (effect size = -0.025 ; $p = 0.470$) ecosystems (Figs. 4a and S15b).

Crop cover showed significant positive correlations with soil pathogenic fungal alpha diversity across spatial scales for all plots and forest ecosystems, but significant negative correlations in grassland ecosystems (Figs. 3c, S13c and S14c). The meta-analysis also confirmed the significant positive effects of crop cover on soil pathogenic fungal alpha diversity for all plots (effect size = 0.174 ; $p < 0.001$) and forest ecosystems (effect size = 0.157 ; $p < 0.001$), but a significant negative effect for grassland ecosystems (effect size = -0.311 ; $p < 0.001$) (Fig. 4a, b).

The regression coefficients of tree cover showed contrary patterns to LFSA and RA fungal alpha diversity along spatial scales for all plots. LFSA fungal alpha diversity generally decreased, while RA fungal alpha diversity increased with tree cover, especially within smaller spatial radii from 250 m to 1,000 m (Fig. 3d). This may result in the non-significant effect size of tree cover on soil pathogenic fungal alpha diversity for all plots (effect size = 0.024 ; $p = 0.314$) (Fig. 4a). This contrasting pattern was not clearly observed in forest and grassland ecosystems (Figs. S13d and S14d). In grassland ecosystems, stronger negative regression coefficients for soil pathogenic fungal alpha diversity were detected across spatial scales, which also confirmed a significant negative effect size of tree cover (effect size = -0.275 ; $p < 0.001$) (Fig. S15c).”.

As these results have been thoroughly presented in the manuscript and partially addressed in our response to Reviewer #1’s first comment, we do not repeat them here.

Reference

Laterra, P., Orúe, M. E. & Booman, G. C. (2012). Spatial complexity and ecosystem services in rural landscapes. *Agriculture, Ecosystems & Environment*, 154, 56–67.

Gámez-Virués, S., Perović, D. J., Gossner, M. M., Börschig, C., Blüthgen, N., De Jong, H., Simons, N. K., Klein, A. M., Krauss, J. & Maier, G., *et al.* (2015). Landscape simplification filters species traits and drives biotic homogenization. *Nature Communications*, 6, 1–8.

2. The method used to calculate the landscape complexity in the current manuscript is also inappropriate. Landscape complexity is a multidimensional concept; however, the manuscript calculated six landscape-level indices (ED, PD, LPI, LSI, MSIDI, SHDI) and extracts their principal components as a measure of landscape complexity, which is unclear and meaningless. As introduced by the authors in the introduction, the quantification of landscape complexity should contain at least two main dimensions: (1) landscape composition including the amounts and proportions of each land cover type within the landscape (2) landscape configuration including the spatial arrangement of each land cover type within the landscape. However, the current six landscape-level indices failed to explicitly consider the composition and configuration for each land cover type within the landscape.

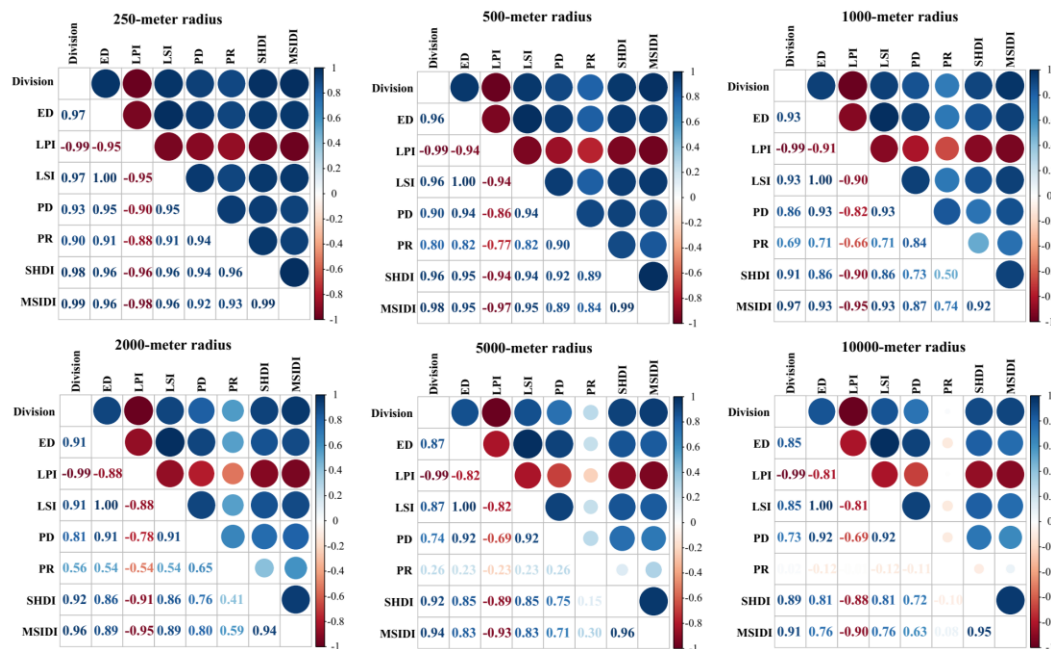
[Response] Thank you for the valuable comment. We totally agree that landscape complexity is a multidimensional concept and should contain at least two main dimensions (i.e., landscape composition and configuration) (Fahrig *et al.* 2011; Laterra, *et al.* 2012; Gámez-Virués *et al.* 2015). Therefore, we selected the landscape metrics based on the two dimensions, as MSIDI and SHDI values indicate landscape compositional complexity, and ED, PD, LPI and LSI values indicate configurational complexity (see lines 803–806). We carefully selected the landscape metrics that are representative, meaningful and commonly used in landscape analysis and referred to Fahrig *et al.* (2011) who stated “The simplest measure of compositional heterogeneity is the richness of cover types. Then, given the dominance of different cover types, cover type evenness is recommended. Finally, cover type richness and evenness can be combined into measures of compositional heterogeneity such as the Shannon index. Measures of configurational heterogeneity include metrics such as mean patch size, edge density, large patch dominance, interspersion/juxtaposition and mean patch shape variability”.

The reason why we chose to integrate them into one parameter is that the correlations of the selected metrics are still quite high, with r-values higher than 0.7 (see **Supporting Information Fig. S23** below). Moreover, some metrics can reflect both the diversity of the land cover and its distribution, and leads to a strong correlation between landscape composition and configuration itself, making it difficult to clearly and independently distinguish them. This is why it is not informative to include so many highly correlated parameters in one model. The method of PCA should be the optimal solution to determine whether a reduced set of factors could be used to explain the structural variation observed in the landscapes and to retain the characteristics of these metrics. Meanwhile, the explanations of the first PCA axis (i.e., landscape complexity) are also very good, which explained at least 75% of the variation across all spatial scales, with a sharp decline in subsequent components; see **Supporting Information Fig. S24** below), and kept the original meaning of each metric (i.e., high correlations of landscape complexity and the landscape metrics, see **Supporting Information Table S8** below). Therefore, we believe this is a parameter that can comprehensively represent the composition and configuration of the landscape and the method is also commonly used in landscape analysis (Laterra *et al.* 2012; Vizzari & Sigura 2015; Peng *et al.* 2017; Griffith *et al.* 2020). We now emphasized its broad applicability and rationality in the Methods section in lines 814–819.

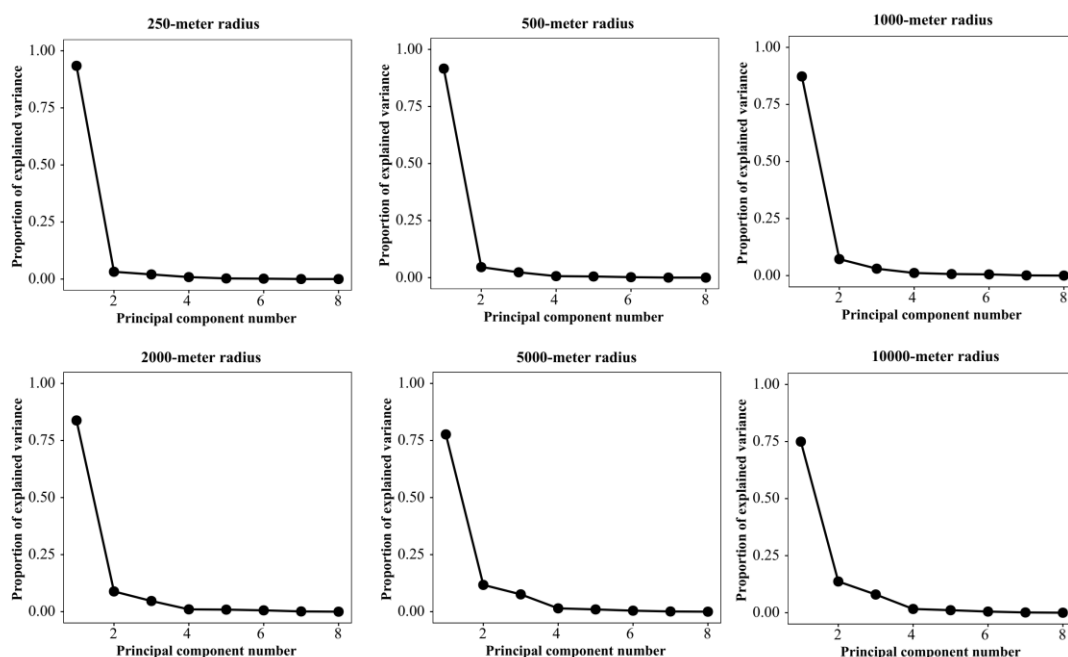
“Due to the high Spearman's rank correlation of landscape metrics (Fig. S23), we performed Principal Component Analysis (PCA) to reveal the correlations of the metrics. The first PCA axis for six separate spatial scales explained at least 75% of the variation, but had the opposite meaning with the original eight metrics (Fig. S24); so, we extracted the minus of this axis (for term correction) to represent the landscape complexity of each plot, which has also commonly been used in landscape analysis^{28–29, 73}”

Considering the current six landscape-level indices may not comprehensively

include the landscape composition and configuration, we have now added one more landscape configuration metric of landscape division index (Division) and one more landscape composition metric of patch richness (PR) (**Supporting Information Table S7** below), and re-calculate the landscape complexity factors based on the overall eight landscape metrics.



Supporting Information Figure S23. The Spearman's correlation of eight landscape metrics across six spatial scales (250 m, 500 m, 1,000 m, 2,000 m, 5,000 m, and 10,000 m radii). The metrics include, landscape division index (Division), edge density (ED), largest patch index (LPI), landscape shape index (LSI), patch density (PD), Patch richness (PR), Shannon diversity index (SHDI), modified Simpson's diversity index (MSIDI).



Supporting Information Figure S24. Proportion of variance explained by each principal component derived from principal component analysis (PCA) of eight landscape metrics across six spatial scales (250 m, 500 m, 1,000 m, 2,000 m, 5,000 m, and 10,000 m radii). The analyzed metrics include landscape division index (Division), edge density (ED), largest patch index (LPI), landscape shape index (LSI), patch density (PD), patch richness (PR), Shannon diversity index (SHDI), and modified Simpson's diversity index (MSIDI).

Supporting Information Table S8. The Spearman's correlation of the landscape complexity and the corresponding eight landscape metrics across six spatial scales. Shown are r -values and significance levels (p -values) of correlations. The landscape complexity variables (i.e. landscape complexity 250, 500, 1,000, 2,000, 5,000 and 10,000) correspond to the minus of the first PCA axis of the eight landscape metrics at their respective spatial scales. The eight landscape metrics include landscape division index (Division), edge density (ED), patch density (PD), largest patch index (LPI), landscape shape index (LSI), patch richness (PR), modified Simpson diversity index (MSIDI), and Shannon diversity index (SHDI).

	Landscape complexity 250		Landscape complexity 500		Landscape complexity1000		Landscape complexity2000		Landscape complexity 5000		Landscape complexity 10000	
	r	p	r	p	r	p	r	p	r	p	r	p
Division	0.980	<0.001	0.979	<0.001	0.976	<0.001	0.973	<0.001	0.963	<0.001	0.960	<0.001
ED	0.975	<0.001	0.981	<0.001	0.975	<0.001	0.962	<0.001	0.952	<0.001	0.942	<0.001
PD	0.966	<0.001	0.947	<0.001	0.930	<0.001	0.896	<0.001	0.867	<0.001	0.857	<0.001
LPI	-0.966	<0.001	-0.960	<0.001	-0.955	<0.001	-0.953	<0.001	-0.932	<0.001	-0.939	<0.001
LSI	0.975	<0.001	0.981	<0.001	0.975	<0.001	0.962	<0.001	0.952	<0.001	0.942	<0.001
PR	0.936	<0.001	0.875	<0.001	0.767	<0.001	0.617	<0.001	0.288	<0.001	-0.056	0.207
SHDI	0.980	<0.001	0.980	<0.001	0.981	<0.001	0.970	<0.001	0.946	<0.001	0.903	<0.001
MSIDI	0.982	<0.001	0.985	<0.001	0.893	<0.001	0.924	<0.001	0.940	<0.001	0.928	<0.001

Supporting Information Table S7. Metrics used at landscape level to quantify landscape complexity.

Metrics (units)	Name	Description	Type
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Division	Landscape division index	The metric quantifies the probability that two randomly selected points in a landscape are not in the same patch. Higher value means the landscape is divided into many small patches, reducing connectivity.	Aggregation metric
ED	Edge density (meters per hectare)	The total lengths of all edge segments in relation to the total landscape area. The metric describes the configuration heterogeneity of the landscape and increases as the landscape edge gets more complex.	Area and edge metric
PD	Patch density (number per 100 hectares)	Ratio of number of patches and the total landscape area. The metric describes the configuration heterogeneity of the landscape and increases as the patch configuration gets more complex.	Aggregation metric
LPI	Largest patch index (%)	Ratio of the landscape area covered by the largest patch in the landscape. The metric measures dominance and spatial continuity of the largest habitat patch and increases as the largest patch is larger.	Area and edge metric
LSI	Landscape shape index	Ratio of the actual landscape edge length and the hypothetical minimum landscape edge length. The higher the LSI value, the more complex the landscape shape.	Aggregation metric
PR	Patch richness	The metric measures the number of unique patch types (land cover classes) present in a landscape and is the simplest measure of compositional heterogeneity. Higher value means more diverse land cover types present.	Diversity metric
MSIDI	Modified Simpson diversity index	The metric measures landscape diversity and the value increases as the number of patches increases and landscape proportions are more equally distributed.	Diversity metric
SHDI	Shannon diversity index	The metric describes diversity of landscape, which considers both the number and abundance of each class. The value increases as the number of classes increases while the proportions are equally distributed.	Diversity metric

References

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3. This manuscript aims to provide evidence about how pathogenic fungi worldwide responded to the landscape complexity. However, the study data were mainly concentrated on forest and grassland ecosystems and did not cover other ecosystem types well. Therefore, the current conclusions may not be globally representative. Meanwhile, while the current manuscript mainly focused on the soil pathogenic fungal diversity at the alpha scale, it is more interesting to also consider the pattern of soil fungi diversity of other trophic types responding to landscape change. And it is also necessary to evaluate the pattern of soil fungi composition or beta diversity to provide novel insights for understanding how landscape change drives soil fungi diversity.

[Response] We appreciate your valuable comments. We acknowledge that our dataset is primarily derived from forest and grassland ecosystems. However, these ecosystems collectively account for a significant portion of the Earth's terrestrial surface and host diverse soil fungal communities, making them highly relevant for assessing global patterns. In addition, conducting global-scale field sampling across all ecosystems presents logistical and accessibility challenges, particularly in extreme environments such as deserts, wetlands, and alpine regions. We have now addressed this limitation in the revised manuscript and clarified the scope of our conclusions accordingly between lines 438–444. It reads:

“It is also important to note, due to global sampling challenges, other ecosystems such as deserts, wetlands, and alpine regions are underrepresented, limiting separate analyses. Nonetheless, forest and grassland ecosystems together still cover a major portion of the Earth's land surface, providing valuable insights into global patterns. Future research could further explore these underrepresented ecosystems to enhance our understanding and test the generality of our findings.”

We focused on soil pathogenic fungal diversity because of their long as well as short distance dispersal abilities, making them prone to landscape change (Grilli *et al.* 2017; Chaudhary *et al.* 2022) and particularly relevant to the risk of infectious disease and ecosystem health (Mahon *et al.* 2024). We totally agree that examining the responses of other soil fungal trophic types would be highly interesting. This is indeed an important direction for future research, and we appreciate your suggestion. However, in this study, we choose to focus specifically on pathogenic fungi to provide an in-depth understanding of their landscape-driven patterns.

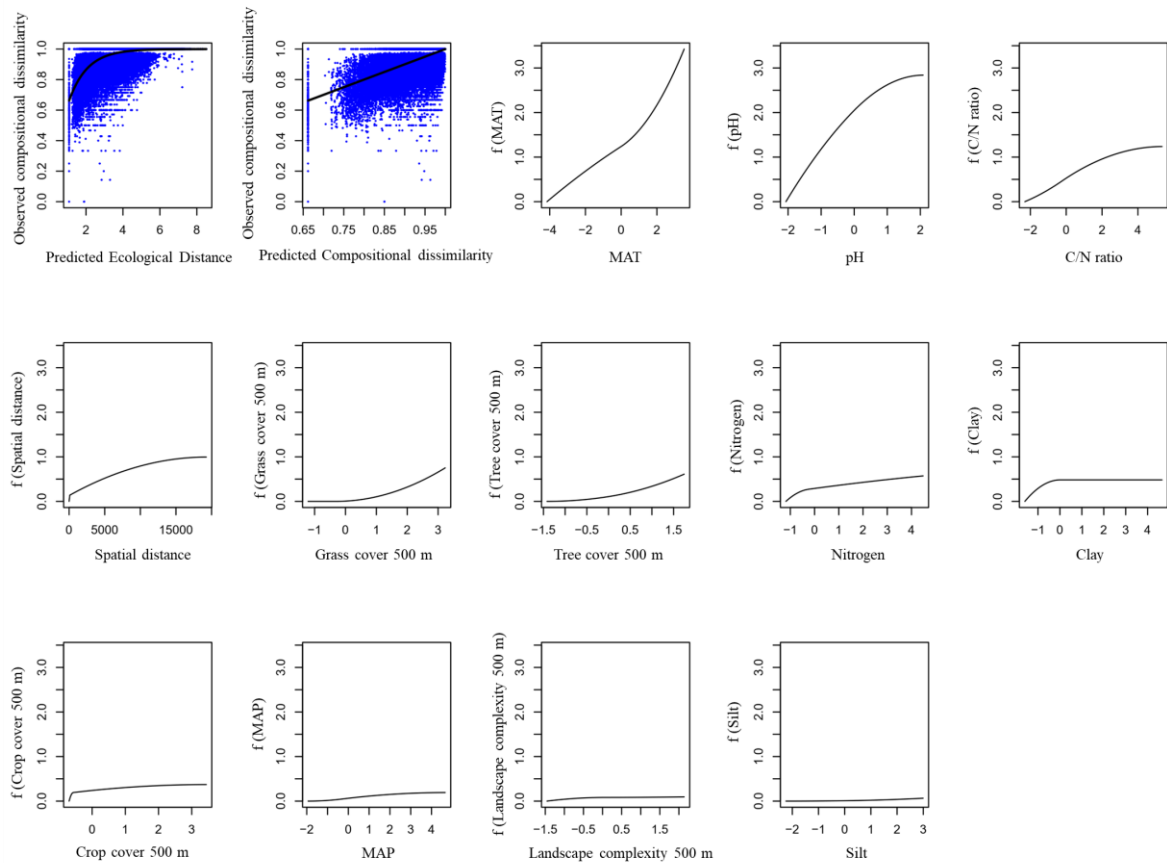
Lastly, we agree that evaluating the community composition and beta diversity of soil pathogenic fungi provides important insights into how landscape change influences fungal diversity. We have now used the Generalized dissimilarity modeling (GDM) approach to analyze the soil pathogenic fungal β -diversity patterns along environmental gradients to further strengthen our findings and provide a more comprehensive perspective. See Methods in lines 898–912 and results were updated accordingly. It reads:

“We applied Generalized Dissimilarity Modelling (GDM) to quantify the beta diversity (i.e., Sørensen beta dissimilarity) of soil pathogenic fungi using the 'gdm' package⁸². Compared to conventional linear matrix regression, GDM accommodates two major forms of nonlinearity: (i) variation in the rate of community compositional turnover along environmental gradients, and (ii) curvilinear relationships between compositional dissimilarity and both environmental and geographic distances⁸³. To incorporate spatial information, geographic coordinates (longitude and latitude) were converted into pairwise geographic distance matrices and included as spatial predictors. The final models incorporated environmental dissimilarity matrices including landscape variables of landscape complexity, grass cover, crop cover, and tree cover (across six spatial scales as competing models), geographic variables of elevation and spatial distance, climatic variables of MAT and MAP, and soil variables of clay content, silt content, pH, total nitrogen content and soil organic carbon/total nitrogen (C/N) ratio. Model performance was evaluated by the percentage of deviance explained, and the relative importance of each predictor was estimated using the maximum height of the fitted I-spline function.”

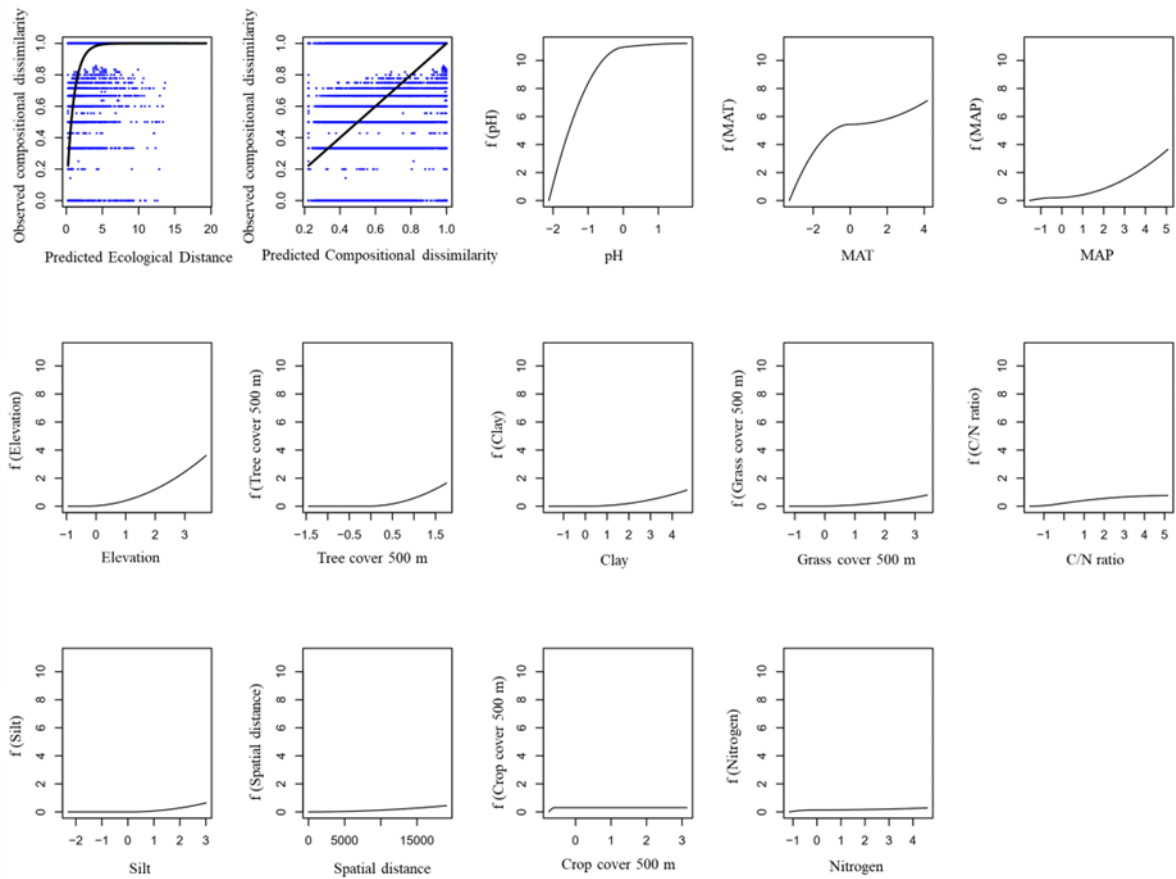
For results, we found that MAT and soil pH were the top two predictors of LFSA and RA fungal beta diversity, with the fitted I-spline functions showing a marked increase in community Sørensen dissimilarity for overall plots and forest ecosystems (**Supporting Information Figs. S1–S4, Fig. 5**). While for RA fungi in grassland ecosystems, spatial distance was the dominant predictor affecting community compositional dissimilarity (**Supporting Information Figs. S6 and S16**).

However, landscape variables, including landscape complexity, grass cover, tree cover, and crop cover within a 500 m radius exhibited relatively weak effects on fungal beta diversity (**Supporting Information Figs. S1–S6**). Meanwhile, landscape variables within the 500 m radius totally explained 15.7% of the total variance of LFSA fungal

Sørensen beta diversity and 8.7% for RA fungi for overall plots (**Supporting Information Figs. S1–S2, Table S4**). The specific results are presented in the figures below, which mainly show the LFSA and RA fungal results for the overall plots, and the detailed results of the forest and grassland ecosystems across ecosystems were revised in **Supporting Information Figs. S3–S6 and Tables S5–S6**.



Supporting Information Figure S1. Generalized Dissimilarity Modelling (GDM) of LFSA fungal community beta diversity in relation to local and landscape variables within the 500 m radius for all plots. The plots show the fitted I-spline partial functions for each environmental predictor included in the GDM, illustrating their relative contributions to compositional dissimilarity (Sørensen beta dissimilarity) of soil pathogenic fungi across sites (predictors contributing no deviance explained were not presented). The percent deviance explained of the model is 37.20.



Supporting Information Figure S2. Generalized Dissimilarity Modelling (GDM) of RA fungal community beta diversity in relation to local and landscape variables within the 500 m radius for all plots. The plots show the fitted I-spline partial functions for each environmental predictor included in the GDM, illustrating their relative contributions to compositional dissimilarity (Sørensen beta dissimilarity) of soil pathogenic fungi across sites (predictors contributing no deviance explained were not presented). The percent deviance explained of the model is 52.78.

Supporting Information Table S4. Generalized dissimilarity modeling (GDM) results for LFSA (a) and RA (b) fungal Sørensen beta dissimilarity for all plots. The table shows the sum of coefficients (SC; cumulative sum of the three I-spline coefficients per predictor) and the relative contribution of each predictor. Predictors include landscape complexity, grass cover, crop cover, tree cover, mean annual temperature (MAT), mean annual precipitation (MAP), spatial distance, elevation, clay content, silt content, soil pH, nitrogen content, and C/N ratio. Landscape complexity, grass cover, crop cover, and tree cover are calculated within buffer radii ranging from 250 m to 10,000 m as competing models.

	250 m		500 m		1000 m		2000 m		5000 m		10000 m	
	SC	RC	SC	RC	SC	RC	SC	RC	SC	RC	SC	RC
(a) LFSA fungi												
Landscape complexity	0.003	0.02	0.095	0.81	0.097	0.84	0.046	0.39	0.000	0.00	0.000	0.00

Grass cover	0.760	6.39	0.762	6.46	0.716	6.13	0.813	6.77	0.555	4.56	0.638	5.15
Crop cover	0.411	3.50	0.371	3.19	0.314	2.72	0.238	2.01	0.275	2.29	0.232	1.90
Tree cover	0.617	5.21	0.618	5.25	0.523	4.49	0.558	4.65	0.651	5.34	0.669	5.38
MAT	3.538	29.8	3.462	29.4	3.450	29.58	3.646	30.5	3.958	32.64	4.045	32.69
MAP	0.229	1.95	0.192	1.65	0.161	1.39	0.167	1.40	0.134	1.11	0.142	1.16
Spatial distance	1.027	8.75	0.995	8.55	1.008	8.74	1.019	8.6	0.997	8.29	0.967	7.89
Elevation	0.000	0.00	0.000	0.00	0.000	0.00	0.016	0.14	0.062	0.51	0.050	0.41
Clay	0.493	4.20	0.483	4.15	0.488	4.23	0.506	4.27	0.506	4.21	0.490	4.00
Silt	0.067	0.56	0.065	0.56	0.118	1.01	0.161	1.34	0.145	1.18	0.190	1.53
pH	2.879	24.5	2.840	24.4	2.933	25.42	2.968	25.0	3.002	24.97	3.048	24.86
Nitrogen	0.593	5.04	0.574	4.92	0.544	4.7	0.519	4.36	0.558	4.62	0.610	4.95
C/N ratio	1.175	10.0	1.237	10.6	1.240	10.75	1.257	10.6	1.234	10.27	1.238	10.09
(b) RA fungi												
Landscape complexity	0.059	0.18	0.000	0.00	0.021	0.06	0.000	0	0.255	0.75	0.175	0.49
Grass cover	0.700	2.17	0.805	2.52	1.588	4.85	1.988	5.84	1.872	5.60	1.974	5.67
Crop cover	0.067	0.21	0.304	0.96	0.067	0.21	0.063	0.19	0.000	0.00	0.000	0.00
Tree cover	1.850	5.72	1.681	5.22	1.695	5.15	1.920	5.6	3.686	10.96	3.425	9.78
MAT	7.582	23.7	7.161	22.5	6.997	21.51	7.136	21.1	7.243	21.82	7.751	22.43
MAP	3.556	11.0	3.689	11.5	3.794	11.58	4.036	11.9	2.691	8.05	2.784	7.99
Spatial distance	0.790	2.46	0.447	1.40	0.168	0.51	0.000	0.00	0.000	0.00	0.000	0.00
Elevation	3.846	11.9	3.657	11.4	3.520	10.75	3.422	10.1	3.366	10.07	3.235	9.30
Clay	0.901	2.79	1.164	3.63	1.452	4.42	1.754	5.14	1.652	4.93	1.878	5.38
Silt	0.494	1.52	0.651	2.02	0.623	1.89	0.802	2.34	0.630	1.87	0.995	2.84
pH	11.202	35.2	11.215	35.5	11.57	35.74	11.66	34.7	10.951	33.15	11.435	33.23
Nitrogen	0.253	0.79	0.283	0.89	0.281	0.86	0.240	0.71	0.118	0.36	0.235	0.68
C/N ratio	0.733	2.30	0.758	2.40	0.800	2.47	0.837	2.49	0.803	2.43	0.760	2.21

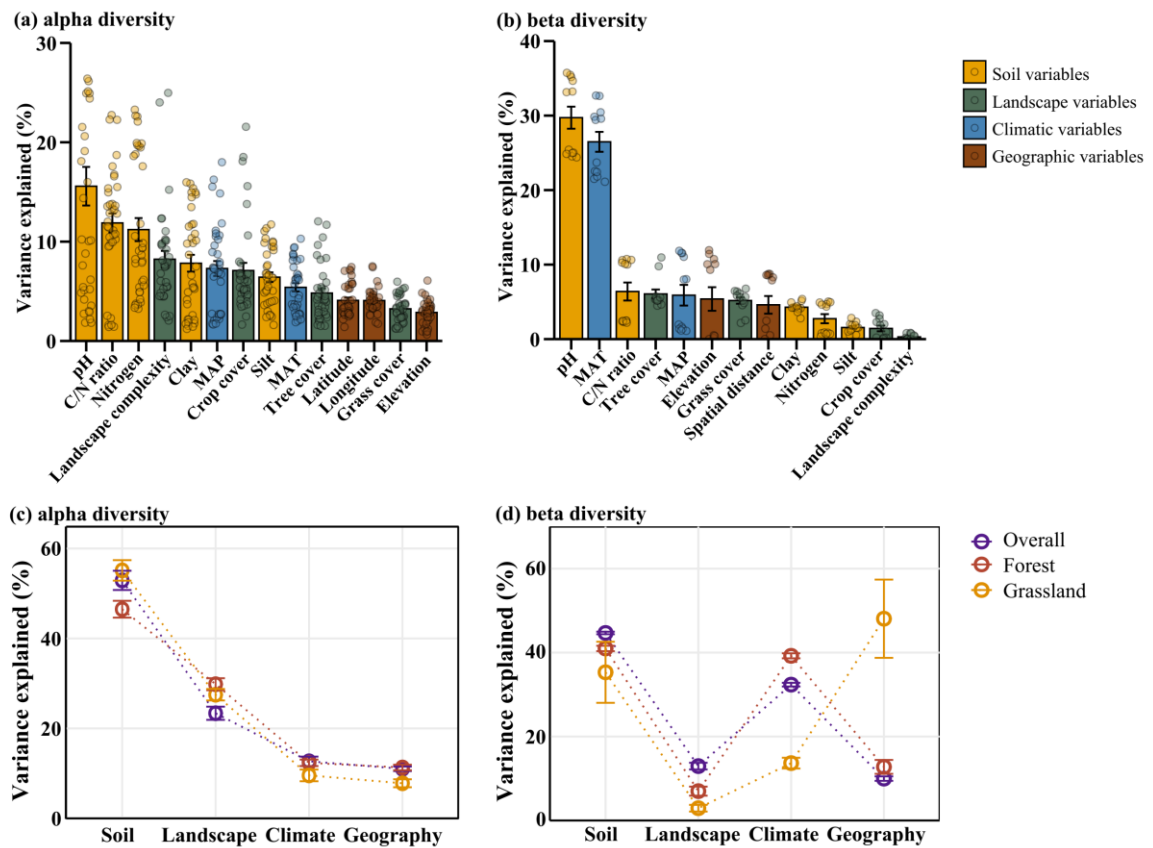
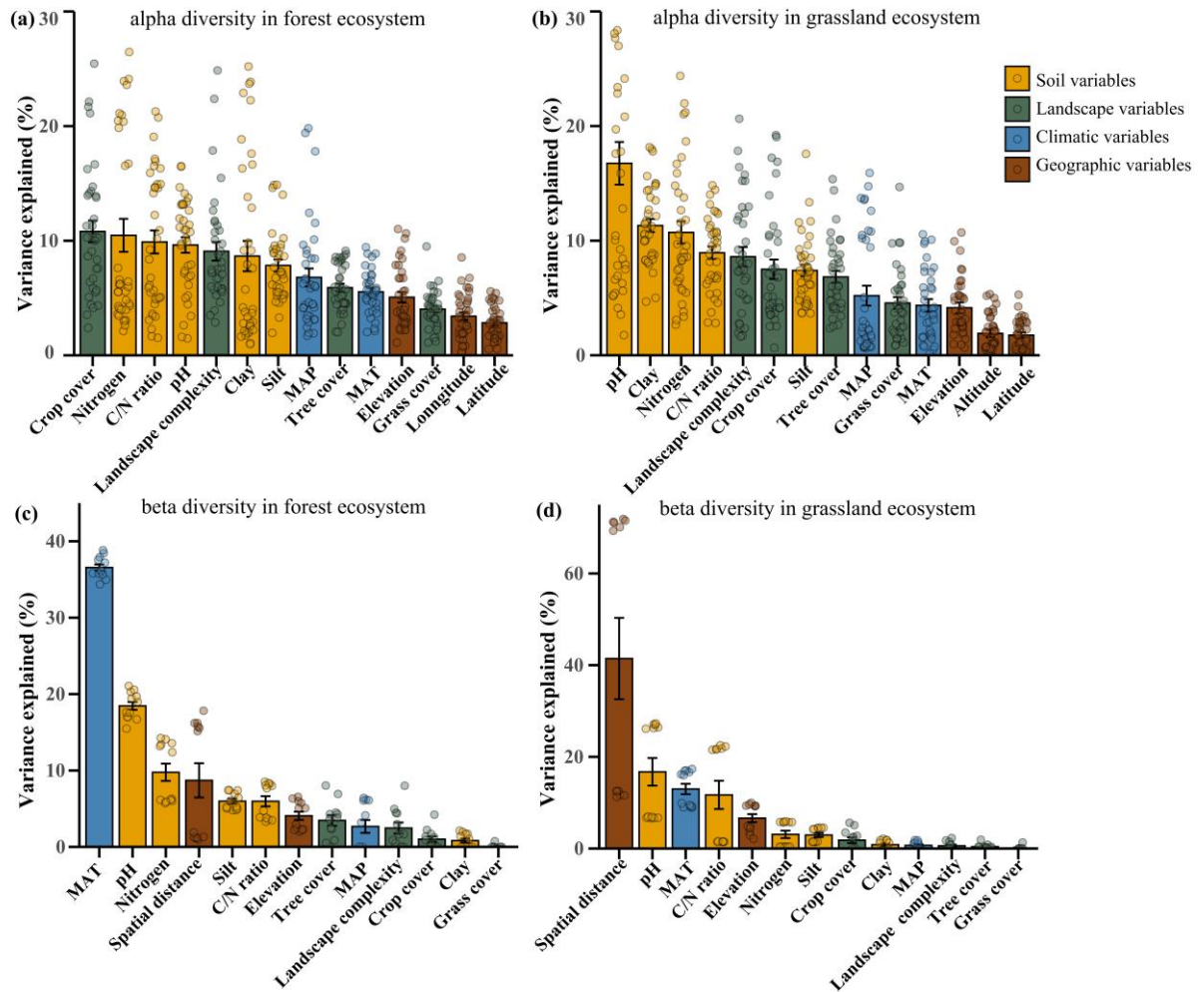


Figure 5. Average relative contribution (proportion of variance explained, %) of each predictor variable on soil pathogenic fungal alpha (a) and beta (b) diversity (mean \pm s.e.), calculated across 511 plots under different fungal groups (LFSA and RA fungi), diversity indices (richness, Shannon diversity, and relative abundance for alpha diversity and Sørensen dissimilarity for beta diversity), and spatial scales (250 m to 10,000 m radii); and grouped environmental factors for soil pathogenic fungal alpha (c) and beta (d) diversity for all plots, forest, and grassland ecosystems. Variables are grouped into soil, landscape, climatic, and geographic categories.



Supporting Information Figure S16. Average relative contribution (proportion of variance explained, %) of each predictor variable on soil pathogenic fungal alpha (a) and beta (b) diversity (mean \pm s.e.), calculated under different fungal groups (LFSA and RA fungi), diversity indices (richness, Shannon diversity, and relative abundance for alpha diversity and Sørensen dissimilarity for beta diversity), and spatial scales (250 m to 10,000 m radii) between forest and grassland ecosystems, respectively. Variables are grouped into soil, landscape, climatic, and geographic categories.

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- Mahon, M. B., Sack, A., Aleuy, O. A., Barbera, C., Brown, E., Buelow, H., Civitello, D. J., Cohen, J. M., de Wit, L. A. & Forstchen, M., et al. (2024). A meta-analysis on global change drivers and the risk of infectious disease. *Nature*, 629, 830–836.

4. The five spatial scales (500, 1,000, 2,000, 5,000, and 10,000 m radius) adopted to

evaluate landscape change may be too large to detect the optimal scale of landscape change affecting soil fungi diversity which generally has a relatively limited capacity for spatial dispersal due to their large size, especially for grassland ecosystems. Thus, it is necessary to also consider landscape changes at scales below 500 m.

[Response] Thank you for your suggestion. The spatial scales we selected (500–10,000 m) are widely used in studies on pathogenic fungal diversity and plant disease dispersal (Mennicken *et al.* 2020; Delaune *et al.* 2021; Le Provost *et al.* 2021). In particular, the 1,000–2,000 m range is commonly considered ecologically relevant for capturing landscape effects on these organisms, while smaller spatial scales typically contain fewer land cover classes and lower landscape variability (Mennicken *et al.* 2020; Lu *et al.* 2024). Considering some taxa may have a relatively limited capacity for spatial dispersal, we have now computed landscape metrics at 250 m radius (Methods in lines 806–811) and updated the corresponding results (referring to Results section). It now reads:

“The metrics were calculated at a spatial distance of 250, 500, 1,000, 2,000, 5,000, and 10,000 m radius around the sampling coordinate to detect the spatial scale effects of landscape metrics on soil pathogenic fungi. The 250 m and 500 m radii are usually considered as the small-scale spatial distances to affect pathogenic fungi¹⁸, given the relatively limited spatial dispersal capacity for some specific taxa...”

References

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5. The three scientific questions in the current manuscript are largely in line with some existing studies, and there is a lack of new theoretical perspectives or novel insights. The manuscript currently considers only the direct effects of landscape changes on soil fungi and their relative contribution of landscape complexity compared with other environmental variables. It is more important to consider landscape and climate change interactions (particularly, mitigation and adaptation) to advance the understanding of the mechanisms and ecological impacts of land use change.

[Response] Thank you very much for your constructive and insightful comments. This study provides a global-scale assessment of how landscape characteristics affect soil

pathogenic fungal diversity. Unlike previous studies that were largely regional, limited to single ecosystems, or focused on the effects of individual landscape metrics, we systematically assessed the combined effects of overall landscape complexity and habitat quantity across multiple spatial scales, fungal functional groups, and ecosystem types. Our findings reveal clear global patterns and demonstrate the complementary role of landscape factors alongside soil properties in structuring pathogenic fungal diversity, offering practical guidance for selecting spatial scales based on fungal groups and ecosystems. As landscape effects on soil microbes remains a new frontier in ecology, our study fills an important knowledge gap and sets a foundation for future research in this emerging field.

To further enhance the robustness and contributions of this work, we conducted the meta-analysis of the overall effects of landscape characteristics, revealing global patterns of landscape influence on soil pathogenic fungi across different fungal groups (LFSA and RA fungi), diversity indices (richness, Shannon diversity, and relative abundance), and spatial scales (250 m to 10,000 m radii) in Methods (lines 863–871) and updated the Results (see figures below). This synthesis not only clarifies the stability and direction of landscape effects worldwide but also helps reconcile inconsistencies reported in previous studies. It now reads:

For Methods:

“To assess the overall effects of landscape variables on soil pathogenic fungal diversity, we performed random-effects meta-analyses based on standardized regression coefficients and standardized errors from models fitted separately for each combination of fungal group (LFSA and RA fungi), diversity index (richness, Shannon diversity, and relative abundance), and spatial scale (250 m to 10,000 m radii). The between-study variance (τ^2) was estimated using Restricted Maximum Likelihood (REML) for the all plots ($n = 511$ plots), as well as forest ($n = 264$ plots) and grassland ($n = 183$ plots) ecosystems independently. Effect size estimates, 95% confidence intervals, and associated p -values for each landscape variable were calculated using the 'metafor' package⁸⁰.”

For Results:

“Based on meta-analysis of parameter estimates across different fungal groups (LFSA and RA fungi), diversity indices (richness, Shannon diversity, and relative abundance), and spatial scales (250 m to 10,000 m radii), we confirmed the significant positive effects of landscape complexity on soil pathogenic fungal alpha diversity for all plots (effect size = 0.030; $p < 0.001$) and grassland ecosystems (effect size = 0.036; $p < 0.001$), but not forest ecosystems (effect size = 0.009; $p = 0.175$) (Figs. 4a and S15a).” in lines 339–345.

“Based on a meta-analysis of parameter estimates, grass cover showed a significant negative correlation with soil pathogenic fungal alpha diversity for all plots (effect size = -0.037; $p = 0.035$), but the pattern was non-significant in forest (effect size = -0.041; $p = 0.117$) and grassland (effect size = -0.025; $p = 0.470$) ecosystems (Figs. 4a and

S15b).” in lines 354–358.

“The meta-analysis also confirmed the significant positive effects of crop cover on soil pathogenic fungal alpha diversity for all plots (effect size = 0.174; $p < 0.001$) and forest ecosystems (effect size = 0.157; $p < 0.001$), but a significant negative effect for grassland ecosystems (effect size = -0.311; $p < 0.001$) (Fig. 4a, b).” in lines 361–365.

“LFSA fungal alpha diversity generally decreased, while RA fungal alpha diversity increased with tree cover, especially within smaller spatial radii from 250 m to 1,000 m (Fig. 3d). This may result in the non-significant effect size of tree cover on soil pathogenic fungal alpha diversity for all plots (effect size = 0.024; $p = 0.314$) (Fig. 4a). This contrasting pattern was not clearly observed in forest and grassland ecosystems (Figs. S13d and S14d). In grassland ecosystems, stronger negative regression coefficients for soil pathogenic fungal alpha diversity were detected across spatial scales, which also confirmed a significant negative effect size of tree cover (effect size = -0.275; $p < 0.001$) (Fig. S15c).” in lines 367–375.

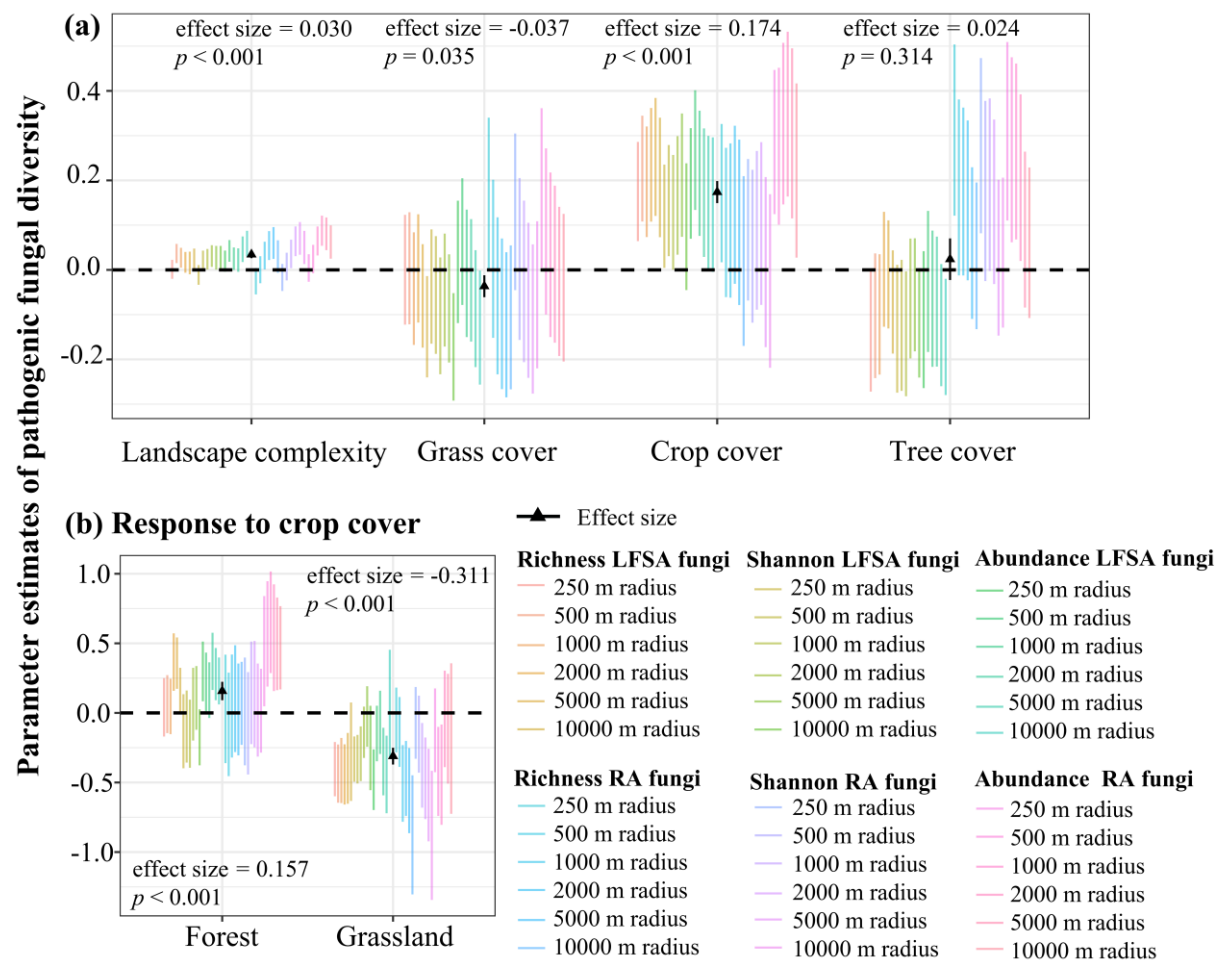
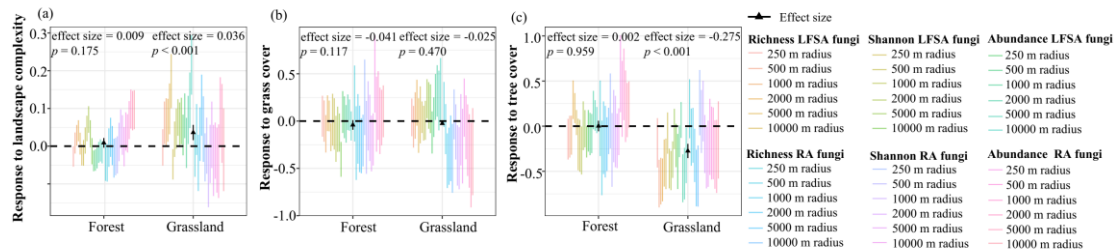


Figure 4. Parameter estimates and overall effect sizes of landscape effects on soil pathogenic fungal diversity. (a) Effects of landscape complexity, grass cover, crop cover, and tree cover on soil pathogenic fungal alpha diversity (n = 511 plots in total). (b)

Effects of crop cover on soil pathogenic fungal alpha diversity between forest and grassland ecosystems. Colored lines indicate the 95% confidence intervals of parameter estimates across different fungal groups (LFSA and RA fungi), diversity indices (richness, Shannon diversity, and relative abundance), and spatial scales (250 m to 10,000 m radii). Black triangles represent the overall effect sizes. Effect size values and associated p -values are reported for each category.



Supporting Information Fig S15. Parameter estimates and overall effect sizes of (a) landscape complexity, (b) grass cover, and (c) tree cover on soil pathogenic fungal alpha diversity between forest and grassland ecosystems. Colored lines indicate the 95% confidence intervals of parameter estimates across different fungal groups (LFSA and RA fungi), diversity indices (richness, Shannon diversity, and relative abundance), and spatial scales (250 m to 10,000 m radii). Black triangles represent the overall effect sizes. Effect size values and associated p -values are reported for each category.

Regarding the interaction between landscape and climate change, we fully agree their potential ecological importance. In our results, we found that the correlation between landscape factors and climate variables was relatively weak (**Supporting Information Fig. S14**). Additionally, we incorporated landscape complexity (within 500 m radius)–climate (MAT and MAP) interaction terms into the multivariate GAMLSS models to assess their potential effects. However, the results indicated that these interaction effects were relatively weak and non-significant compared to the direct effects of landscape and climatic variables on soil pathogenic fungal diversity (table below). We fully agree that this is an important and meaningful direction for future research, however, this part of the exploration might be more suitable for specifically designing climate and/or landscape gradients in future research for in-depth exploration. This is now also provided as an outlook statement in the Discussion in line 436–438. It now reads:

“Future studies are encouraged to explicitly explore the interactive effects of landscape structures and climate gradients on soil pathogenic fungal diversity through targeted experimental and observational designs³⁴.”

The table supplemented the interaction effects of landscape complexity (within 500 m radius)–climate (MAT and MAP) interaction on leaf/fruit/seed-associated (LFSA) and root-associated (RA) fungal diversity by multivariate GAMLSS models. Table shows the predictors, coefficients (estimate slope), standard errors, t-values and p -values of

the model.

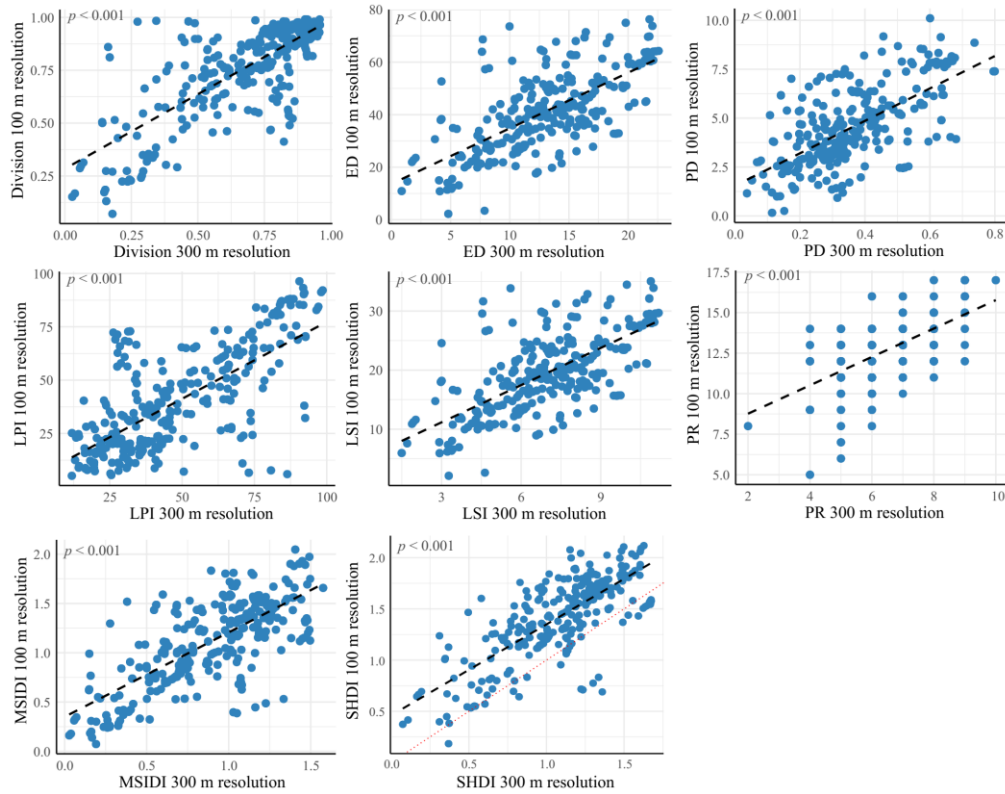
	Predictor	Coefficient	se	t-value	p-value
Richness LFSA	Landscape complexity: MAT	0.005	0.013	0.406	0.685
	Landscape complexity: MAP	-0.013	0.011	-1.158	0.247
Shannon LFSA	Landscape complexity: MAT	-0.010	0.014	-0.693	0.489
	Landscape complexity: MAP	-0.019	0.012	-1.596	0.111
Abundance LFSA	Landscape complexity: MAT	0.012	0.015	0.770	0.442
	Landscape complexity: MAP	0.025	0.049	0.499	0.618
Richness RA	Landscape complexity: MAT	-0.049	0.043	-1.126	0.261
	Landscape complexity: MAP	-0.007	0.016	-0.437	0.662
Shannon RA	Landscape complexity: MAT	-0.031	0.019	-1.598	0.111
	Landscape complexity: MAP	-0.018	0.016	-1.108	0.268
Abundance RA	Landscape complexity: MAT	-0.015	0.020	-0.765	0.444
	Landscape complexity: MAP	-0.009	0.016	-0.519	0.604

6. There are many publicly available land-use databases with high temporal and spatial resolution, but the manuscript used only a single source of land-use data to quantify landscape change, i.e., 100 m-resolution from Copernicus global land service. Therefore, it is important to use multiple land-use data simultaneously and to conduct sensitivity analyses for the data analysis. In addition, the time scale and historic landscape change have been overlooked in landscape complexity calculation, which may have a significant effect on soil fungi diversity.

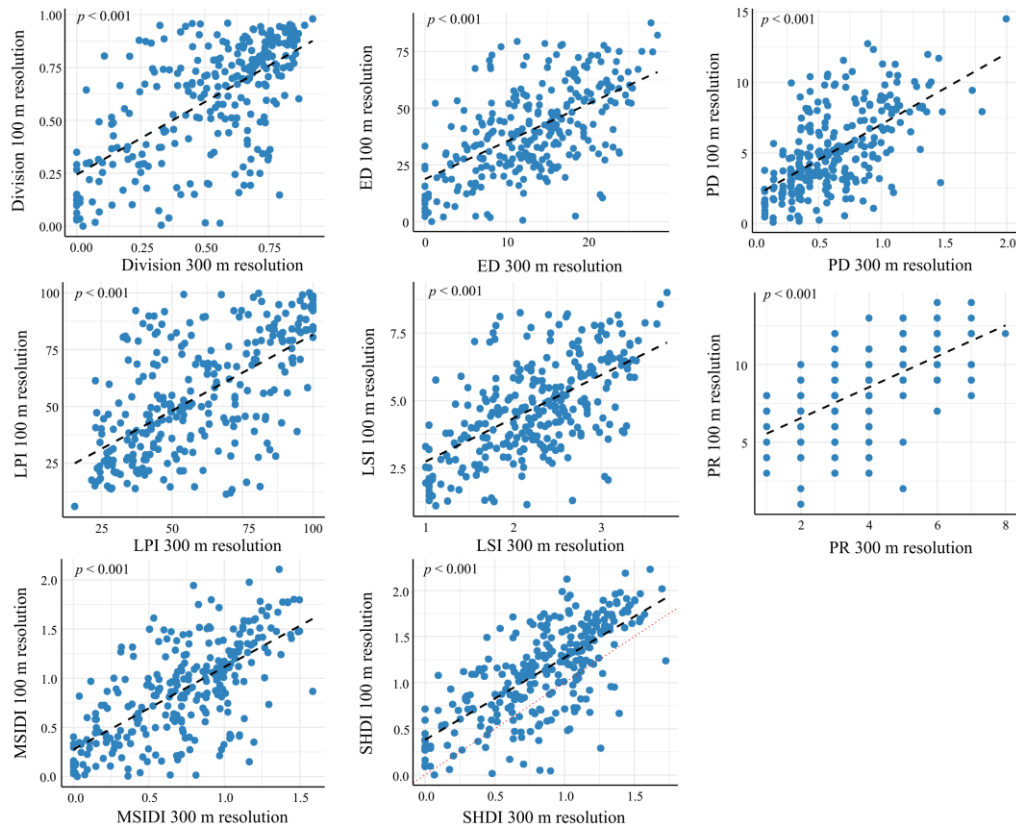
[Response] Thank you for raising this important point. In addition to the 100 m-resolution Copernicus Global Land Service data used in our main analysis, we have now conducted sensitivity analyses by comparing the landscape metrics based on alternative land-use datasets, including 300 m-resolution ESA WorldCover data (<https://cds.climate.copernicus.eu/datasets/satellite-land-cover?tab=overview>). Our results showed that at larger spatial scales (i.e., starting from 1,000 to 10,000 m radii), the landscape metrics from the 300 m and 100 m datasets were highly consistent. Given the similarity of results across these scales, we present representative comparisons for the 2,000 m and 10,000 m radii (see figure below). While at finer spatial scales (i.e., within a 250 and 500 m radius), we found the 300 m-resolution data detected fewer land cover classes, limiting its ability to capture the variation of landscape metrics in detail, although their correlations with 100 m resolution data were still significant (see figure below for the 500 m radius; the 250 m radius showed a similar pattern). This discrepancy likely results from reduced class diversity at finer spatial scales limits the capacity of the 300 m-resolution data to capture sufficient landscape heterogeneity, leading to lower variation in landscape metrics.

Furthermore, when comparing the effects of landscape complexity (from two land cover datasets) on soil pathogenic fungal diversity, we also detected the significant colinear relationships between their estimate slopes, confirming the robustness and consistency of our findings across different spatial resolutions. We now updated the methods in lines 862–866 and results in **Supporting Information Fig. S30**. It reads:

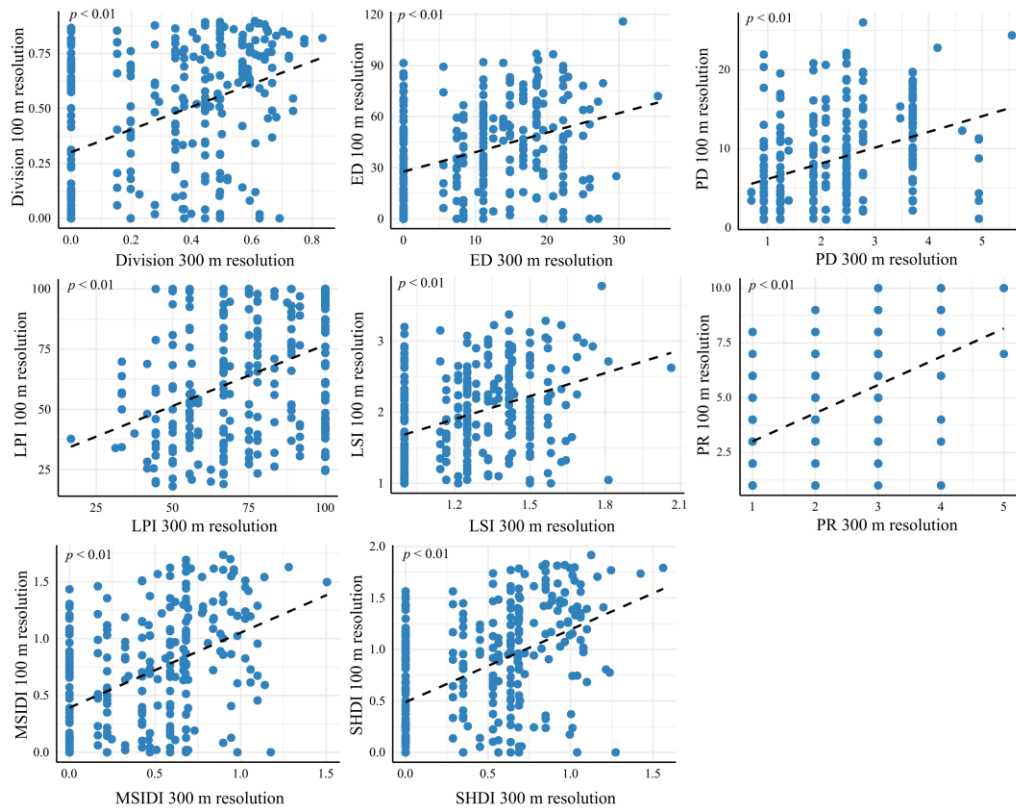
“...and repeated the analysis of landscape complexity effects on soil pathogenic fungal alpha diversity using the 300 m-resolution ESA CCI land cover map (<https://cds.climate.copernicus.eu/datasets/satellite-land-cover?tab=overview>). Both approaches produced highly consistent results with those from the original models (Figs. S29–S30).”



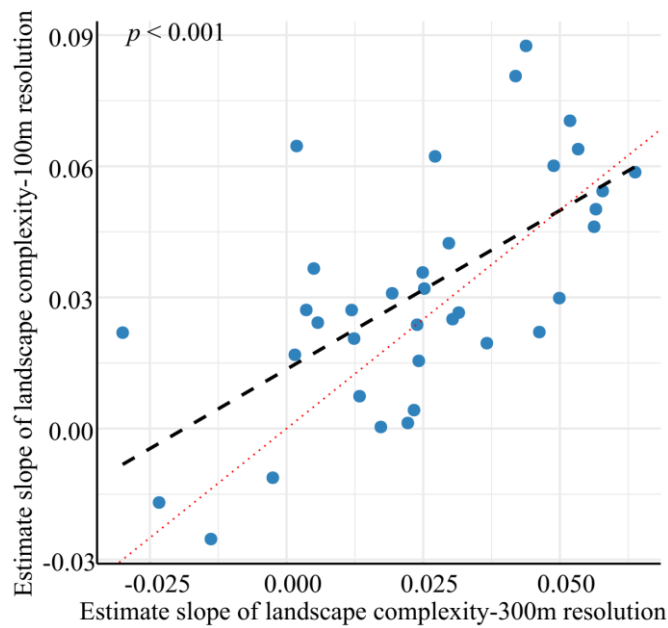
Pairwise comparisons of landscape metrics derived from 100 m- and 300 m-resolution land cover data at a 10,000 m radius.



Pairwise comparisons of landscape metrics derived from 100 m- and 300 m-resolution land cover data at a 2,000 m radius.



Pairwise comparisons of landscape metrics derived from 100 m- and 300 m-resolution land cover data at a 500 m radius.



Supporting Information Fig S30. Comparison of estimate slopes for the relationships between landscape complexity calculated from 100 m- and 300 m-resolution land cover maps and soil pathogenic fungal alpha diversity. Estimate slopes are obtained from generalized additive models (GAMLSS) across six landscape spatial scales (250–10,000 m radii), three alpha diversity indices (richness, Shannon diversity, and relative abundance) and two fungal groups (LFSA and RA fungi). Points indicate paired slope estimates, with the dashed red line showing the 1:1 relationship.

In addition, we fully acknowledge the importance of incorporating time scale and historic landscape change in understanding soil fungal diversity. However, due to the difficulty to use respective high-resolution, long-term, and global-scale land-use datasets, it remains challenging to assess this at our study scale. For example, Copernicus Global Land Service only provides 5-yr land cover data, the European Space Agency (ESA) CCI provides annual global surface maps from 1992 to 2020, but 300 m accuracy may not be so sufficient for small-scale landscape parameter extraction, as well as some non-global datasets (<https://zenodo.org/records/5816591>). Currently, we focused on contemporary landscape patterns, which are often more influential for microbial communities given their rapid dispersal and turnover (Mennicken *et al.* 2020). We have now supplemented this potential factor in explaining the unexplained variance of soil pathogenic fungal diversity in the Discussion (line 484–487), and will specifically consider this in our future research. It reads:

“Moreover, a proportion of the model variance remains unexplained, indicating that additional factors such as topography, extreme climatic events, and historic environment changes may also contribute and warrant further investigation^{18, 34–35}.”

Reference

Mennicken, S., Kondratow, F., Buralli, F., Manzi, S., Andrieu, E., Roy, M. & Brin, A.

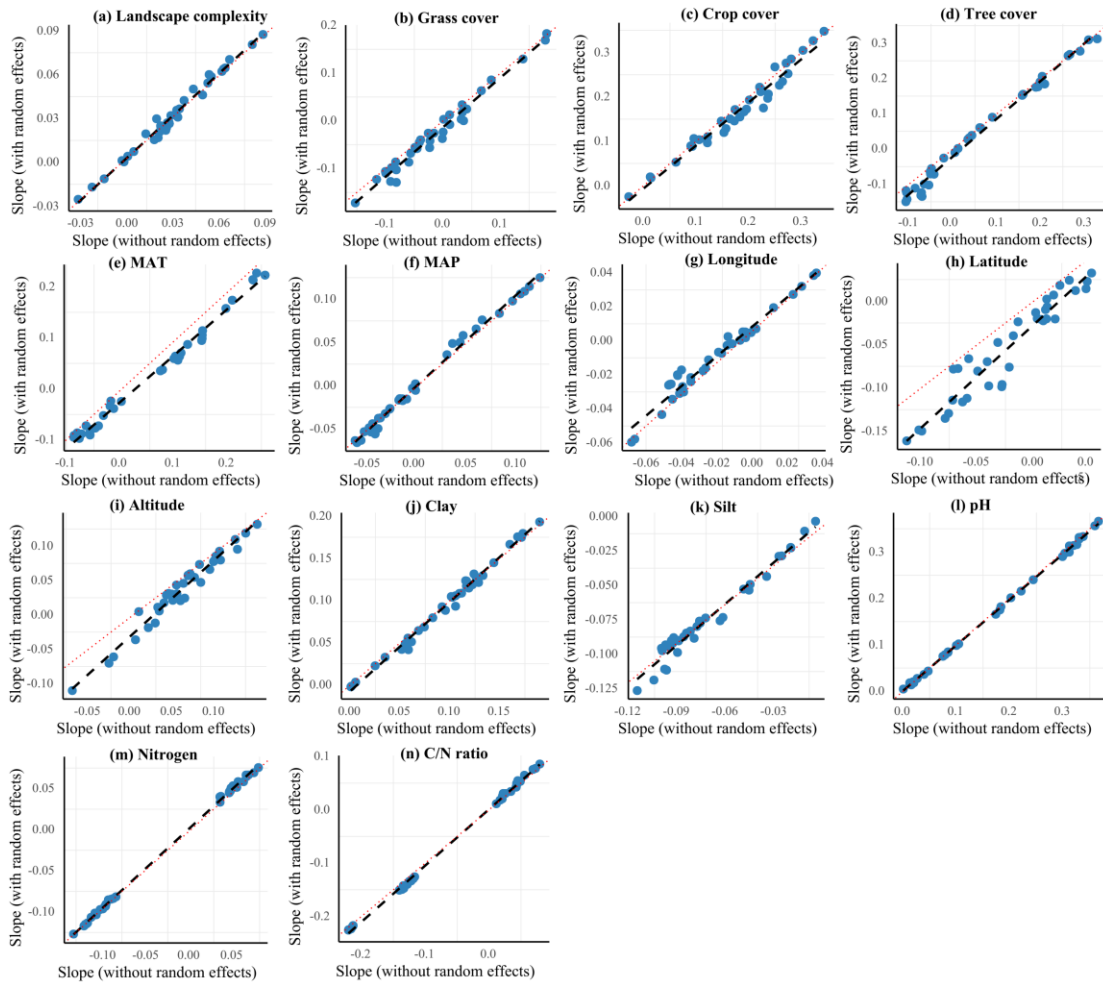
(2020). Effects of past and present-day landscape structure on forest soil microorganisms. *Frontiers in Ecology and Evolution*, 8, 118.

7. In the statistical analyses, the authors extracted the influencing factors from multiple databases, including 100-m land use data, 1-km WorldClim 2, CHELSA, and 250-m SoilGrids. There are large differences in resolution or scale between these different data sources, which may bias the results of the statistical analyses. How the authors dealt with this issue? In terms of statistical methods, the data were analysed using only multivariate generalized additive models, which are insufficient for assessing and understanding the effects of complex interactions between landscape change, soil environmental variables and climatic variables. The mixed effects model and structural equation modelling are recommended. In addition, potential problems of spatial autocorrelation and residual heterogeneity were not considered.

[Response] Thank you for your valuable comments. We acknowledge the differences in resolution among the datasets used in our analysis. However, our study operates at a continental scale, and such differences will have a minimal impact on our analysis because we are examining broad-scale patterns rather than fine-scale variations. To a large extent, the extracted variables can represent the average environmental conditions (e.g., temperature, landscape characteristics) of each site. Moreover, previous studies have shown that such resolution differences are less influential in large-scale analyses and are widely applied in large-scale pattern research (e.g., Jiménez-Alfaro *et al.* 2021; Patoine *et al.* 2022; Mikryukov *et al.* 2023).

Regarding statistical methods, we further fitted mixed-effects generalized additive models including 'site' as a random factor (see Methods in lines 860–866), and found highly consistent results with the original models (**Supporting Information Fig. S29**), confirming the robustness of our findings. It reads:

“To confirm the robustness of our findings, we additionally fitted mixed-effects generalized additive models with 'site' as a random effect...produced highly consistent results with those from the original models (Figs. S29–S30).”

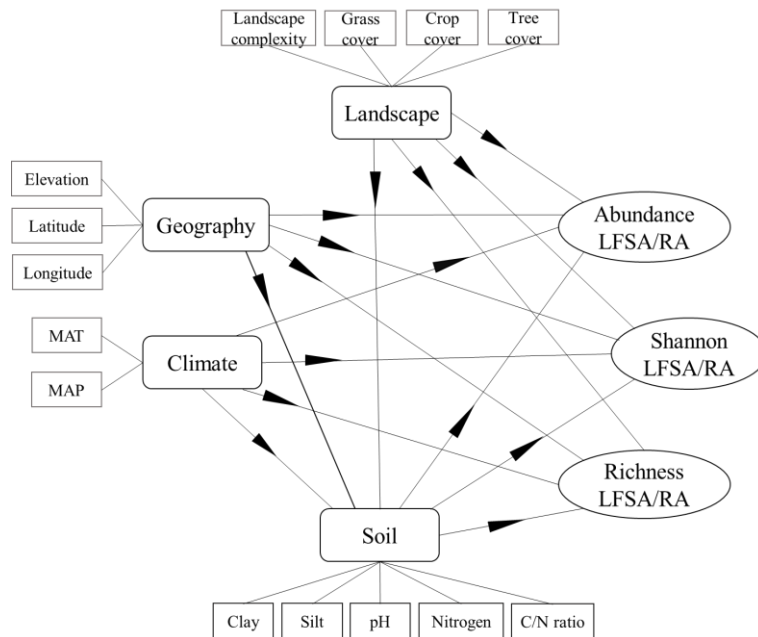


Supporting Information Fig S29. Consistency of estimate slopes from generalized additive models GAMLSS with and without site as a random effect for each environmental variable. Points indicate paired slope estimates, with the dashed red line showing the 1:1 relationship.

We also conducted the Partial Least Squares Path Modeling (PLSPM) to assess direct and indirect effects of multivariate environmental factors on soil pathogenic fungal alpha diversity. We supplemented this analysis in Methods (see lines 881–897), and results in the **Supplementary Information Figs. S21–S22**. It reads:

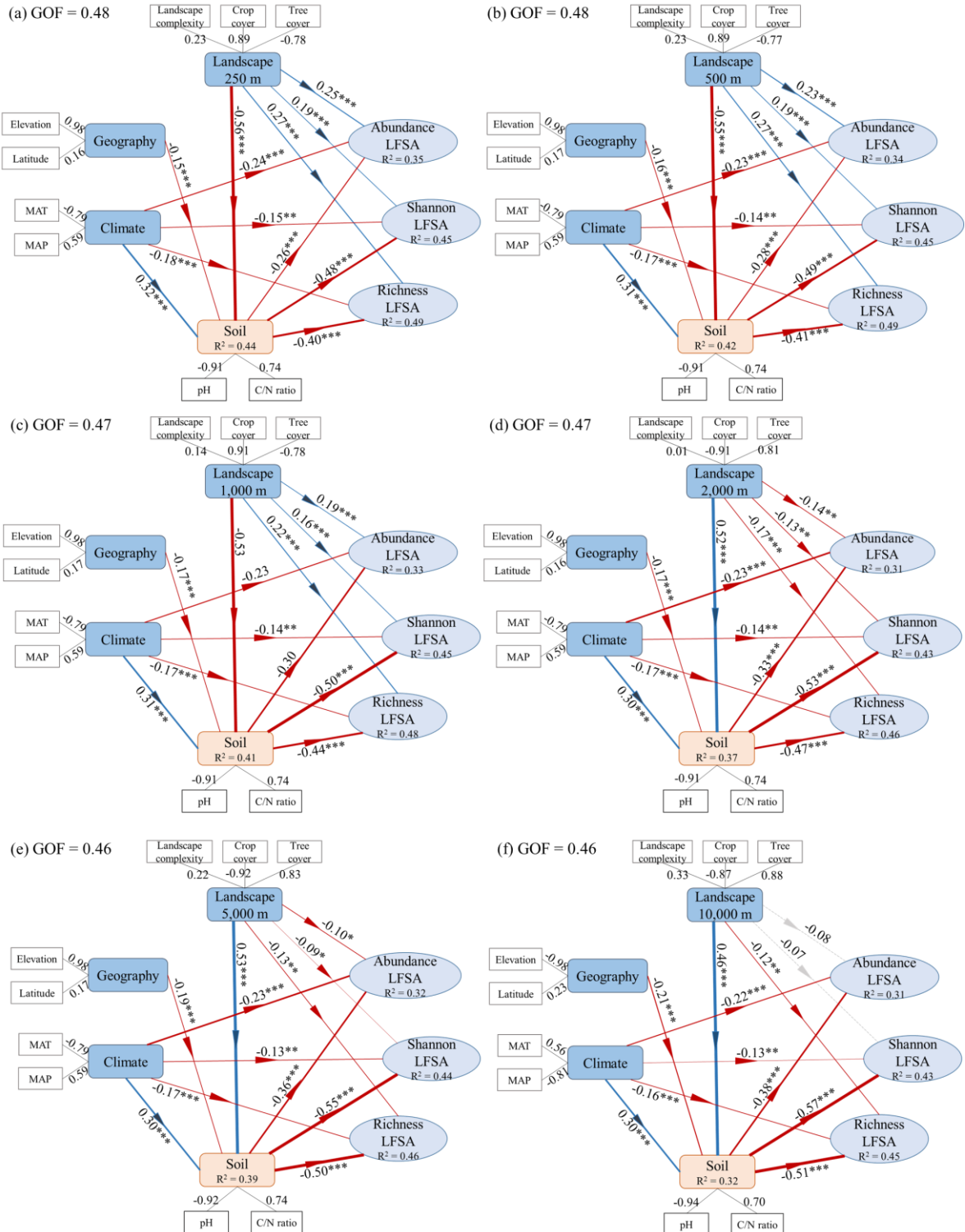
“To disentangle the direct and indirect effects of multivariate environmental factors on soil pathogenic fungal alpha diversity, we applied Partial Least Squares Path Modeling (PLSPM) using the 'plsplm' package⁸¹. PLSPM comprises a measurement model, linking latent variables with observed indicators via principal component analysis, and a structural model, specifying relationships among latent variables via ordinary least squares. For each latent variable, loadings and path coefficients were estimated iteratively to maximize the explained variance. The loading values represent the correlation between latent variables and their associated indicators. Predictors were grouped into four latent variables: landscape (landscape complexity, grass cover, crop cover, and tree cover), geography (elevation, latitude, and longitude), climate

(MAT and MAP), and soil (clay content, silt content, pH, total nitrogen content, and C/N ratio). The structural model considered: (i) the direct effects of the four latent variables on soil pathogenic fungal alpha diversity (richness, Shannon diversity, and relative abundance); and (ii) the indirect effects of landscape, climate, and geography through their influence on soil variables. A hypothetical conceptual model was constructed accordingly (Fig. S31). The goodness-of-fit (GoF) statistic was used to evaluate model performance. Variables with low loadings or non-significant paths were sequentially removed to obtain the final optimal model.”



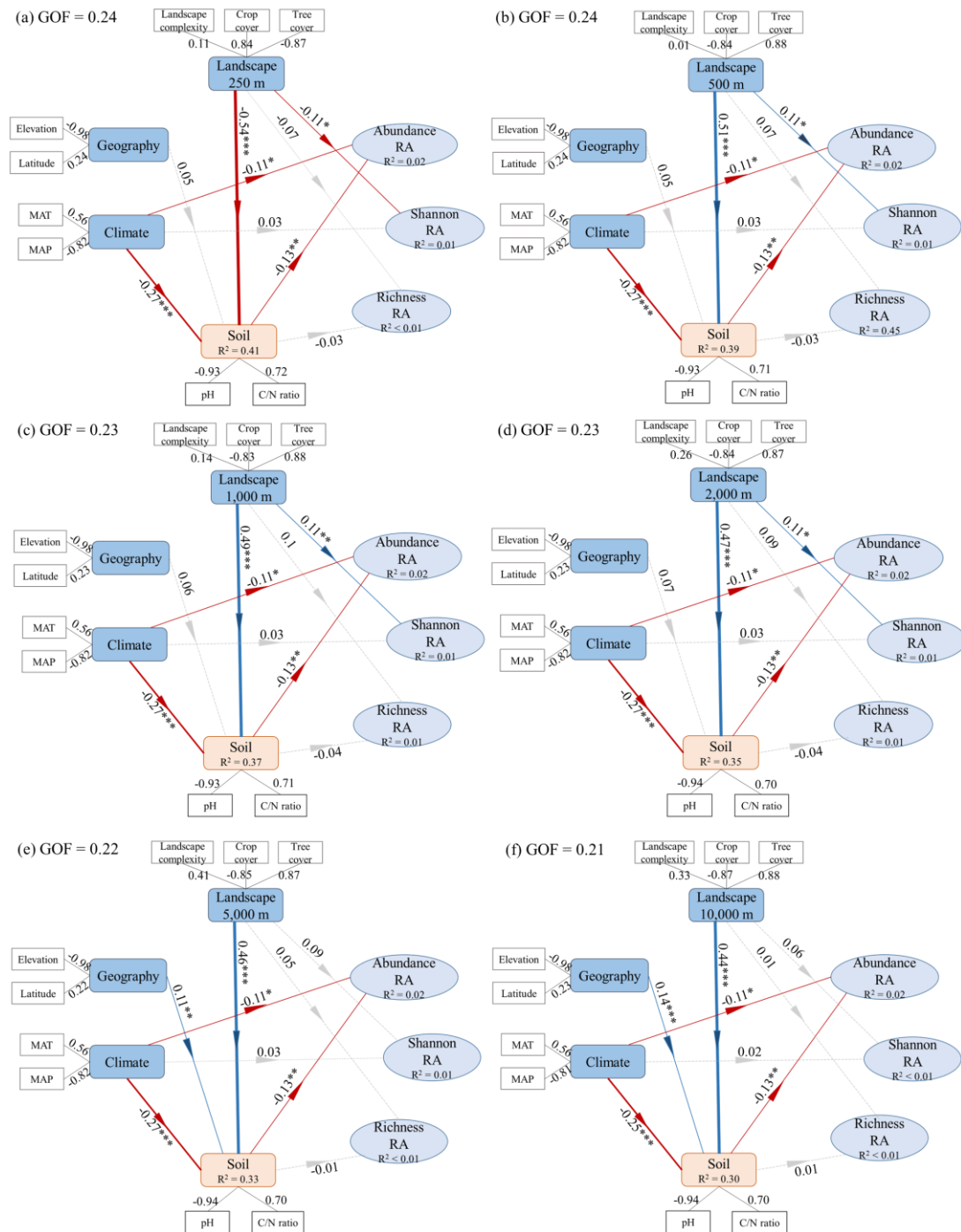
Supporting Information Figure S31. Hypothesized direct and indirect effects of landscape, geography, climate and soil variables on soil LFSA/RA fungal alpha diversity based on Partial Least Squares Path Modeling (PLSPM). The landscape latent variable includes landscape complexity, grass cover, crop cover, and tree cover; the geographic variable includes elevation, latitude, and longitude; the climatic variable includes MAT and MAP; and the soil variable includes soil clay, silt, pH, nitrogen, and C/N ratio. The final model was assessed with Goodness-of-Fit (GoF) value.

For results, we found that the landscape factor exerts both direct and indirect effects on soil pathogenic fungal alpha diversity by mediating soil conditions.



Supporting Information Figure S21. Optimal direct and indirect drivers of soil LFSA fungal alpha diversity (richness, Shannon diversity, and relative abundance). Partial Least Squares Path Modeling (PLSPM) assesses the direct and indirect effects of landscape (across six spatial scales), geographic, climatic, and soil factors on fungal diversity across all plots. Solid and dashed arrows represent significant or non-significant pathways, respectively, with standardized path coefficients shown alongside each path. Significance levels are denoted as * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Arrow widths reflect the relative strength of the path coefficients. The R² values

indicate the proportion of variance explained for each response variable. The landscape latent variable includes landscape complexity, crop cover, and tree cover; the geographic variable includes elevation and latitude; the climatic variable includes MAT and MAP; and the soil variable includes soil pH and C/N ratio. The values linking indicators to latent variables represent loadings, with higher loadings indicating stronger associations with the corresponding latent construct. GoF indicates the goodness-of-fit of the model.



Supporting Information Figure S22. Optimal direct and indirect drivers of soil RA fungal alpha diversity (richness, Shannon diversity, and relative abundance). Partial

Least Squares Path Modeling (PLSPM) assesses the direct and indirect effects of landscape (across six spatial scales), geographic, climatic, and soil factors on fungal diversity across all plots. Solid and dashed arrows represent significant or non-significant pathways, respectively, with standardized path coefficients shown alongside each path. Significance levels are denoted as $*p < 0.05$, $**p < 0.01$, $***p < 0.001$. Arrow widths reflect the relative strength of the path coefficients. The R^2 values indicate the proportion of variance explained for each response variable. The landscape latent variable includes landscape complexity, crop cover, and tree cover; the geographic variable includes elevation and latitude; the climatic variable includes MAT and MAP; and the soil variable includes soil pH and C/N ratio. The values linking indicators to latent variables represent loadings, with higher loadings indicating stronger associations with the corresponding latent construct. GoF indicates the goodness-of-fit of the model.

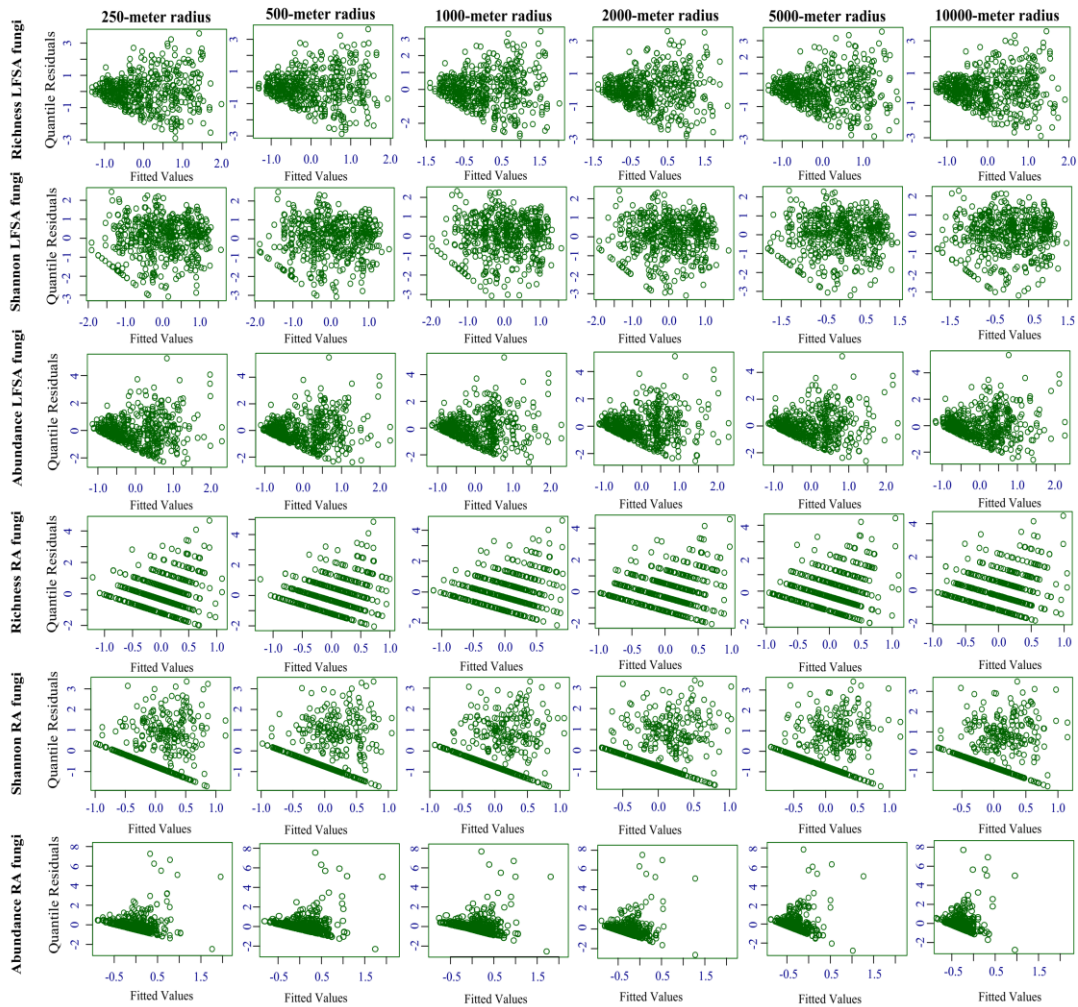
For spatial autocorrelation, we tested it in our models and found weak effects. Consequently, spatial terms were not included in the final models. Additionally, we checked for residual heterogeneity and no substantial heteroscedasticity was detected. We have now clarified these important checks in the revised manuscript (see Methods in lines 853–860) and provided supporting analyses in the supplementary materials (**Supporting Information Table S9 and Fig. S27**).

“To assess any potential spatial autocorrelation in the residuals of each GAMLSS model, Moran's I tests were performed in the 'spdep' package using the k-nearest neighbors (KNN) method based on the geographic coordinates of the sampling sites⁷⁹, and only weak effects were detected (Table. S9). Consequently, spatial terms were not included in the final models. For all the multivariate GAMLSS models, we calculated the Akaike information criterion (AIC), Pseudo- R^2 , and p -value as the goodness-of-fit of the model and visually checked residual heterogeneity using quantile residual plots (Figs. S27–S28).”

Supporting Information Table S9. Spatial autocorrelation of predicted soil pathogenic fungal alpha diversity based on GAMLSS. Moran's I values and corresponding p -values are reported for the richness, Shannon diversity, and relative abundance of LFSA and RA fungi, derived from six competing models evaluated at six different landscape spatial scales (250 m to 10,000 m radii).

Diversity indices	Scale	Moran's I	p -value
Richness of LFSA fungi	250	0.011	0.093
Richness of LFSA fungi	500	0.011	0.093
Richness of LFSA fungi	1000	0.021	0.011
Richness of LFSA fungi	2000	0.008	0.152
Richness of LFSA fungi	5000	0.004	0.261
Richness of LFSA fungi	10000	0.004	0.280
Shannon of LFSA fungi	250	0.003	0.291
Shannon of LFSA fungi	500	0.000	0.401

Shannon of LFSA fungi	1000	0.006	0.206
Shannon of LFSA fungi	2000	-0.003	0.544
Shannon of LFSA fungi	5000	0.000	0.415
Shannon of LFSA fungi	10000	0.000	0.424
Abundance of LFSA fungi	250	0.011	0.093
Abundance of LFSA fungi	500	0.013	0.063
Abundance of LFSA fungi	1000	0.020	0.012
Abundance of LFSA fungi	2000	0.016	0.033
Abundance of LFSA fungi	5000	0.013	0.061
Abundance of LFSA fungi	10000	0.014	0.048
Richness of RA fungi	250	0.009	0.128
Richness of RA fungi	500	0.006	0.193
Richness of RA fungi	1000	0.003	0.302
Richness of RA fungi	2000	0.007	0.173
Richness of RA fungi	5000	0.010	0.118
Richness of RA fungi	10000	0.013	0.066
Shannon of RA fungi	250	-0.004	0.588
Shannon of RA fungi	500	-0.005	0.627
Shannon of RA fungi	1000	-0.011	0.818
Shannon of RA fungi	2000	-0.010	0.795
Shannon of RA fungi	5000	-0.006	0.675
Shannon of RA fungi	10000	-0.006	0.669
Abundance of RA fungi	250	-0.008	0.739
Abundance of RA fungi	500	-0.011	0.817
Abundance of RA fungi	1000	-0.012	0.851
Abundance of RA fungi	2000	-0.014	0.895
Abundance of RA fungi	5000	-0.015	0.917
Abundance of RA fungi	10000	-0.015	0.922



Supporting Information Fig. S27. Plots of quantile residuals against fitted values to assess the homogeneity of residual variances from the GAMLSS. Models are fitted for soil fungal richness, Shannon diversity, and the relative abundance of LFSA and RA fungi, evaluated across six competing models at spatial scales ranging from 250 m to 10,000 m radii.

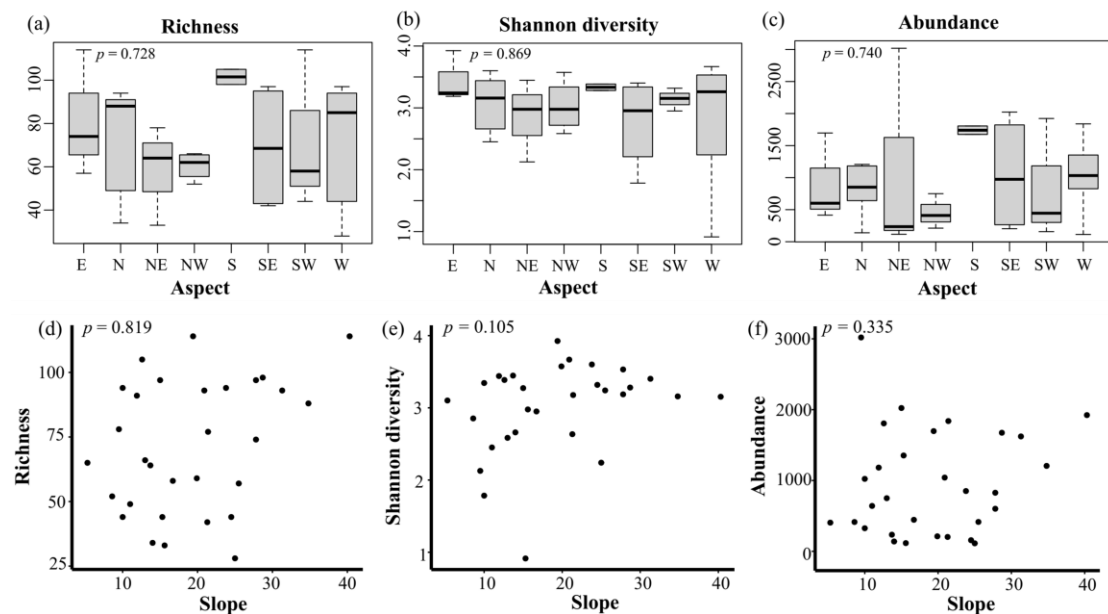
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2. Mikryukov, V., Dulya, O., Zizka, A., Bahram, M., Hagh-Doust, N., Anslan, S., Prylutskiy, O., Delgado-Baquerizo, M., Maestre, F. T. & Nilsson, H., *et al.* (2023). Connecting the multiple dimensions of global soil fungal diversity. *Science Advances*, 9, eadj8016.

8. Importantly, some important influencing factors such as climate, altitude, slope, aspect, and vegetation cover have not been adequately considered. There are 19 key bioclimatic variables in the WorldClim 2 database, such as the seasonality (e.g., annual range in temperature and precipitation) and extreme or limiting environmental factors (e.g., temperature of the coldest and warmest month, and precipitation of the wet and dry quarters). Why did the author only use the MAT and MAP variables? Vegetation cover in each sample site also has a significant effect on soil fungal diversity and might also mediate the effects of climate and landscape change.

[Response] Thank you for your insightful comments. We acknowledge that climate, topography, and vegetation cover are important factors influencing soil fungal diversity and carefully considered them during variable selection.

For topographic factors, we have now included elevation in our models. While slope and aspect may also affect soil pathogenic fungi, our recent finding in a fragmented forest showed weak effects of slope and aspect on soil pathogenic fungi (Figure below, unpublished; and Lu *et al.* 2024 for foliar fungal disease). Additionally, other previous studies also suggest that their relative contributions on plant pathogens are generally low (Wilson *et al.* 2003; Donald *et al.* 2020), so we did not consider these factors in our final models. For example, the results from Donald *et al.* (2020) found weak effects of slope on the *Phytophthora austrocedri* (infecting cypress trees).



Weak effects of aspect and slope on soil pathogenic fungal diversity in 30 fragmented forests in Xishuangbanna, China.

For climate variables, we selected mean annual temperature (MAT) and mean annual precipitation (MAP) as they are commonly used to represent broad climatic conditions and are proved to strongly influence soil fungal communities (Tedersoo *et al.* 2014; Barceló *et al.* 2022; Mikryukov *et al.* 2023). While additional climatic variables, such as seasonality and extreme temperature/precipitation, may provide a

more detailed climate characterization, our primary focus was on the overall influence of average annual climate conditions (as the remaining environmental factors we included also represent an average value) rather than extreme events. Meanwhile, early research has compared the impact of multiple climatic variables on soil fungal diversity, and confirmed that MAT and MAP still showed the best contribution (Mikryukov *et al.* 2023).

For vegetation cover, we have now incorporated the landscape-level vegetation cover of grass, crop, and tree into our analyses (corresponding to the six spatial radius scales) in Methods in line 822–825. This allowed us to assess the quantity variation of different vegetation cover types on soil pathogenic fungal diversity and the results showed notable patterns (see Results section). Since it has already been described in question 1, it will not be repeated here.

Lastly, recognizing these omitted factors, we have now discussed the limitations and highlighted their potential contributions to soil pathogenic fungal diversity patterns between lines 481–487. It reads:

“Although we suggested that differences in plant species diversity and composition within landscapes may partly account for these contrasting responses, integrating this factor into global analyses is challenging due to the limited availability of comprehensive, spatially explicit plant diversity datasets³⁵. Moreover, a proportion of the model variance remains unexplained, indicating that additional factors such as topography, extreme climatic events, and historic environment changes may also contribute and warrant further investigation^{18, 34–35}.”

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Reviewer #1 (Remarks to the Author):

Dear authors,

congratulations for this new versions ! really extremely rich and impressive.

[Response] We truly appreciate your positive feedback and are glad that you find the revised version improved and informative.

Just a few minor comments

L195 on beta diversity (on missing)

[Response] Thank you. Added now.

L197 while crop cover significantly reduced the alpha diversity of soil pathogenic fungi

Isn't it in contradiction with your result "Crop cover showed significant positive correlations with soil pathogenic fungal alpha diversity across spatial scales for all plots and forest ecosystems", L359 ? In your discussion you also highlight this trend - you may clarify, as Fig 3 shows also a distinct patterns, notably before 2500m.

I would in the abstract also highlight the result "Our results showed that increased proportion of natural habitats, such as tree and grass cover within the landscape, tended to reduce soil pathogenic fungal diversity, whereas larger crop cover increased it.

[Response] Thank you for the helpful comment and sorry for the vague. The sentence on line 197 (originally) refers to the grassland ecosystems (stated in the preceding sentence), and therefore it does not contradict the result in line 359 (for all plots and forest ecosystems).

To avoid misunderstanding, we have removed the ambiguous sentence and emphasized that across the addressed spatial scales, grassland ecosystems exhibit increasingly stronger responses to landscape variables than forest ecosystems (in lines 201–202).

The overall trend, has now been highlighted in lines 197–199, indicates that crop cover within the landscape shows a positive correlation with the alpha diversity of soil pathogenic fungi, whereas natural habitats, such as tree and grass cover show negative correlations.

L200 highlight the importance of local factors and the complementary ...
(otherwise we wonder what is the complementarity about)

[Response] Thank you for the valuable suggestion and we have revised it in line 204.

L 523 reformulate: In addition, unlike LFSA fungi, whose primary lifestyles are predominantly as pathogens, RA fungi (e.g., Entoloma spp.) are PRIMARILY classified as saprotrophic or ectomycorrhizal fungi, and pathogenic effects on plant roots might be less frequent than for LFSA

[Response] Thank you. Revised as suggested.

Fig 1. I would add the number of ASV of LFSA and RA in the Fig 1c (to show the reader how low diverse are the RA fungi too).

[Response] Thank you. Done.

L491 I would remove "However", rather write Additionally. Your results confirm a shift mourned 2000-2500 m for forest fungi, questioning their dispersal range. We indeed expect to lose a significant effect of this distance if dispersal is less frequent at such a large distance, or at least that would be an explanation. I would at least mention the differences in dispersal abilities among fungal communities, expecting more long distance dispersal in grassland than in forest ecosystems.

This difference in dispersal mode is also striking between our LFSA and RA fungi in forest ecosystems notably - and even if I do not think you might add more analyses, fungal traits database allowed you to have some for the fruiting morphology information and making more data-oriented conclusion to interpret for example your different patterns observed in Figure 4.

[Response] Thank you for this insightful comment. We have removed "However" and replaced it with "Additionally" as suggested. We acknowledge the differing dispersal capacities among fungal communities, which is especially striking between LFSA and RA fungi. We now discuss these differences in relation to their different dispersal traits and fruiting morphologies and emphasize the need for further research into how dispersal abilities among fungal groups mediate landscape effects across large spatial scales (lines 506–528). The revised text now reads:

"This scale-dependent pattern in forests may reflect stronger dispersal limitation of soil fungi, with limited spore movement constrain their responses to large-scale landscape heterogeneity^{16, 49}... In contrast, we found that in grassland ecosystems, as the spatial scale increased to a 5,000–10,000 m radii, the effect of landscape complexity and quantity on soil fungal diversity became stronger (larger absolute coefficients), and the number of significant associations increased accordingly. This observation may arise from the fact that grassland ecosystems have lower buffering effects compared to forests, and harbor more long-distance dispersing fungal taxa, as their open landscapes make communities more vulnerable to macroclimatic conditions and landscape effects at larger spatial scales⁵¹... Differences in dispersal modes are also evident between LFSA and RA fungi (Fig. 4 and Supplementary Fig. 15). While quantifying fungal dispersal remains challenging, their distinct dispersal traits and fruiting morphologies, as supported by fungal trait databases (e.g., FungalTraits)⁵³, suggest differing capacities for long-distance dispersal⁴⁹. Therefore, further investigations of how dispersal abilities among fungal groups mediate landscape effects across large spatial scales are essential for a better understanding of soil pathogenic fungal dynamics¹⁶."

Congratulations again for this impressive work,
Best regards,

Reviewer #1 (Remarks on code availability):

I've see the code for the gamlss only, which is correct.
[\[Response\] We appreciate the comments.](#)

Reviewer #3 (Remarks to the Author):

I have no further suggestions.
[\[Response\] We appreciate the comments.](#)

Reviewer #3 (Remarks on code availability):

I have no further suggestions.
[\[Response\] We appreciate the comments.](#)