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Landscape effects on global soil pathogenic fungal diversity across spatial scales

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A list of authors and their affiliations appears at the end of the paper

Growing evidence has shown that, apart from local environmental factors, changes in landscape-level factors by accelerated land-use change can also shape soil pathogenic fungal diversity. However, the global representativeness of such patterns remains unclear. Here, we assess how pathogenic fungal diversity in 511 soil samples worldwide responds to landscape factors, including landscape complexity index based on eight landscape metrics and quantity of different land cover types across six spatial scales (i.e., surrounding landscape, 250 m to 10,000 m radii from the sampling coordinate). We find that while soil variables explain over half of the variance, pathogenic fungal alpha diversity increases with landscape complexity and crop cover proportion, but decreases with grass and tree cover proportion, together explaining 23.4% of the total variance. Landscape factors have weaker impacts on beta diversity, explaining 13.0% of the variance. Across spatial scales, grassland ecosystems exhibit increasingly stronger responses to landscape variables compared to forest ecosystems. Landscape factors have a higher relative contribution to root-associated fungi than leaf/fruit/seed-associated fungi. Our results emphasize the importance of local factors and the complementary role of landscape patterns in shaping global soil pathogenic fungal distributions, highlighting scale-dependent effects across ecosystems and fungal functional groups.

Soil pathogenic fungi are widespread in nature and important for species coexistence[1,2], nutrient cycling[3], and ecosystem functioning[4]. As key drivers of ecosystem processes, soil pathogenic fungi suppress the dense growth of conspecific host plants to maintain plant diversity[1], and drive the accumulation of soil organic carbon (SOC) by mediating the inputs of plant roots into the SOC pool[5]. Moreover, soil pathogenic fungi include some of the most devastating plant pathogens[6]. Around 10–16% of the global harvest is lost to plant pathogens annually, equivalent to a global economic loss of around US $220 billion[7], threatening global food security[8,9]. Therefore, understanding the biogeographic distribution and drivers of soil pathogenic fungal diversity is key to regulating future disease occurrence under global change scenarios.

Soil pathogenic fungi exhibit higher richness and abundance at low latitudes[10,11], but the underlying drivers are still not fully understood. Previous studies have primarily considered local environmental factors, such as climate[9,12], soil conditions[10,13], and vegetation structure[14,15], as the main factors associated with soil pathogenic fungal diversity. However, predictions based solely on local environmental factors may not fully capture large-scale drivers, given the long-distance dispersal capacity of pathogenic fungi[16]. Increasing evidence indicates that landscape-level factors, which encompass spatial heterogeneity and patchiness at broader spatial scales, can also shape soil pathogenic fungal diversity via metacommunity processes[17–19], although these factors have rarely been considered[20]. Hence, comprehensive research integrating both landscape- and local-level factors is needed to better understand the drivers and underlying mechanisms of soil pathogenic fungal diversity.

Landscape simplification caused by land-use change, such as agricultural intensification, is driving biodiversity loss[21,22]. It primarily reduces land cover heterogeneity[23], limits species dispersal through decreased connectivity, and amplifies edge-driven habitat

e-mail: yawenlu@mail.usts.edu.cn; carlos.guerra@uc.pt

degradation[24,25]. Landscape factors are typically categorized 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 evenness[26]. 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 density[26]. Despite growing recognition of landscape effects on biodiversity, most existing studies assess these landscape metrics independently[21,25,27], thereby overlooking the integrated influence of multiple landscape attributes on ecological patterns and processes[28]. To address this, we propose an integrated landscape complexity index that simultaneously captures both the compositional and configurational heterogeneity of landscapes[29], providing a comprehensive measure of overall landscape effects on soil pathogenic fungal diversity.

The Habitat Heterogeneity Hypothesis[23,30], which posits that diverse land cover types create a variety of microhabitats and resource availability supporting greater diversity[23,26], suggests 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]. Studies have found that increased habitat type diversity and landscape connectivity can increase pathogenic fungal richness[18,19,32], due to a higher number of niches that facilitate the spillover of fungal spores between habitats[23,33]. In addition, higher landscape complexity can increase plant species diversity, mediate soil properties and microclimates, and influence soil pathogenic fungal diversity indirectly[34,35]. However, landscapes vary across biomes. For example, temperate biomes like central-European grasslands have typically experienced long-term land-use changes and more pronounced landscape simplification[19,21], which may result in a lower diversity of soil pathogenic fungi[10]. These patterns are likely further shaped by differences in the surrounding landscape quantity, particularly the relative proportions of natural habitats and agricultural land covers[19]. Moreover, the scale-dependent effects of landscape-level factors on soil pathogenic fungal diversity remain unclear[33], with inconsistent results calculated across spatial scales[18,19,36]. Thus, current knowledge based on regional studies may be insufficient to predict soil pathogenic fungal diversity, and a global assessment of landscape effects across spatial scales is urgently required.

In our study, we address the following questions: (1) How do landscape factors, including landscape complexity and quantity of different land cover types influence global soil pathogenic fungal diversity? (2) How does spatial scale influence the effects of landscape variables on soil pathogenic fungal diversity? (3) What is the relative contribution of landscape variables compared with other environmental variables? To answer these questions, we use 511 soil samples collected across the globe and assess taxon richness, Shannon diversity, relative abundance, and Sørensen beta dissimilarity of two soil-borne plant pathogenic fungal groups: leaf/fruit/seed-associated (LFSA) fungi and root-associated (RA) fungi, based on soil eDNA (Fig. 1). The landscape complexity index is calculated based on eight landscape metrics, i.e., 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), which together describe variation in landscape composition and configuration[28,29,37]. Landscape quantity variables are defined as the percentages of grass, tree, and crop cover within the surrounding landscape of each sampling site. All landscape-level variables are calculated at six spatial scales (i.e., surrounding landscape, within 250, 500, 1000, 2000, 5000, and 10,000 m radii from each sampling coordinate). Next, we compare the relationships between soil pathogenic fungal diversities and landscape, geographic, climatic, and soil variables with multivariate Generalized Additive Models for Location, Scale, and Shape (GAMLSS), Generalized Dissimilarity Models (GDM) and Partial Least Squares Path Models (PLSPM) to better predict global soil pathogenic fungal diversity through multi-scale, multi-ecosystem assessments.

Results

Multi-variable comparisons on soil pathogenic fungal diversity

The results confirmed dominant effects of local variables on soil pathogenic fungal alpha (i.e., richness, Shannon diversity and relative abundance) and beta (i.e., Sørensen beta dissimilarity) diversity. Within the spatial radius of 500 m, soil variables (e.g., clay content, pH and organic carbon/total nitrogen (C/N) ratio) were the dominant factors associated with soil pathogenic fungal alpha diversity (Fig. 2a–f), which explained 52.9 ± 2.1% (mean ± s.e.) of the total variance for all plots (Fig. 2g). Climatic variables (e.g., mean annual temperature (MAT) and mean annual precipitation (MAP)) were also significantly associated with soil pathogenic fungal alpha diversity (Fig. 2a–f), explained 12.7 ± 1.0% of the total variance (Fig. 2g). Meanwhile, MAT and soil pH were the top two predictors of leaf/fruit/seed-associated (LFSA) and root-associated (RA) fungal beta diversity, with the fitted I-spline functions showing a marked increase in community Sørensen dissimilarity for all plots and forest ecosystems (Supplementary Figs. 1–4). While for RA fungi in grassland ecosystems, spatial distance was the dominant predictor affecting community Sørensen dissimilarity, followed by elevation (Supplementary Fig. 5).

We also detected significant effects of landscape factors on soil pathogenic fungal alpha diversity (Fig. 2). However, landscape variables, including landscape complexity, grass cover, tree cover, and crop cover within the 500 m radius exhibited relatively weak effects on fungal beta diversity (Supplementary Figs. 1–6). Higher landscape complexity significantly increased the richness and relative abundance of LFSA fungi across all sampling plots (coefficient $\beta = 0.037$; $p = 0.001$ for richness and $\beta = 0.042$; $p = 0.001$ for relative abundance) and in grassland ecosystems ($\beta = 0.062$; $p = 0.032$ for richness and $\beta = 0.081$; $p = 0.009$ for relative abundance), but decreased the relative abundance of LFSA fungi in forest ecosystems ($\beta = -0.037$; $p = 0.011$) (Fig. 2a–c and Supplementary Table 1). Shannon diversity of LFSA and RA fungi did not show significant responses to landscape complexity (Fig. 2a–f). Specifically, the richness and relative abundance of the genera *Discosia* and *Neodevriesia* (LFSA fungi) and Shannon diversity of genus *Entoloma* (RA fungi) increased significantly with landscape complexity (Supplementary Table 2). Moreover, the three alpha diversity indices of LFSA and RA fungi were all positively correlated with landscape metrics of Division, ED, PD, LSI, PR, MSIDI, and SHDI separately, but negatively correlated with LPI (Supplementary Table 3).

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).

Landscape variables within the 500 m radius totally explained 24.4 ± 2.7% of the total variance in soil pathogenic fungal alpha diversity for all plots, with landscape complexity explained 8.3 ± 0.7%, grass cover 2.3 ± 0.6%, crop cover 5.3 ± 1.9% and tree cover 5.8 ± 1.8%, respectively (Fig. 2g). Moreover, grassland ecosystems (30.2 ± 3.27%) exhibited a greater relative contribution of landscape variables than forest ecosystems (25.5 ± 3.14%). 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 all plots

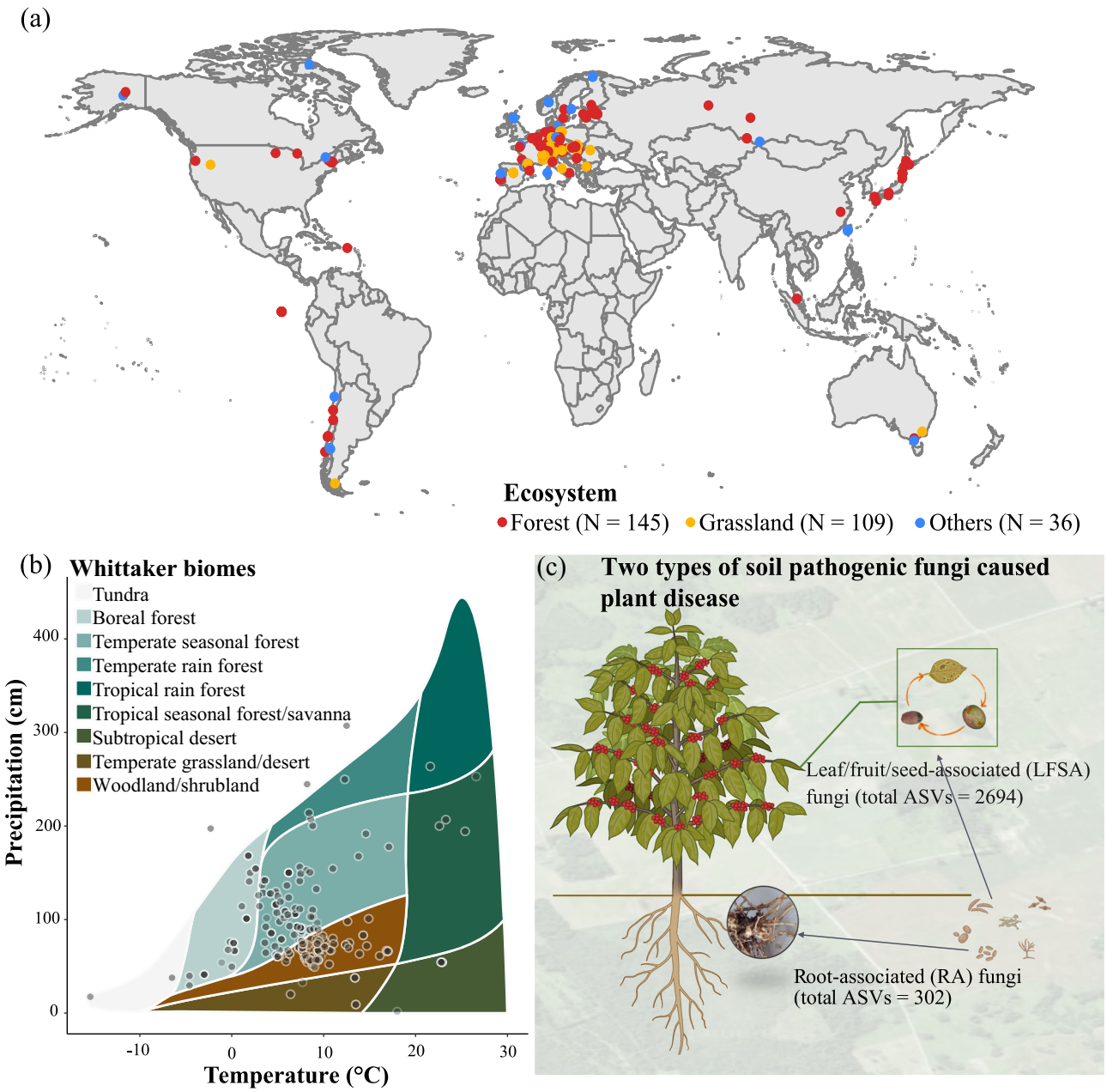

Fig. 1 | Sampling information of global 290 sites. a Sampling locations covering forest, grassland and other ecosystems; **b** distribution of sampling sites within main biomes; and **c** conceptual diagram of two groups of soil pathogenic fungi: leaf/fruit/seed-associated (LFSA) fungi and root-associated (RA) fungi (created in BioRender. tyt, y. (2025) https://BioRender.com/2yf7oyu), with the total number of Amplicon Sequence Variants (ASVs) detected.

(Supplementary Figs. 1 and 2 and Supplementary Table 4). Although the relative contribution of landscape factors was lower than that of soil factors, it made a complementary explanation to the overall variance.

Scale-dependency of landscape effects

Landscape complexity showed stronger effects on soil pathogenic fungal alpha diversity at larger spatial scales. For all plots, the regression coefficients of landscape complexity from 250 m to 2000 m radii increased, then declined at larger scales (5000–10,000 m), though all significant coefficients remained positive (Fig. 3a and Supplementary Figs. 7–12). The pattern was similar in forest ecosystems, except that the relative abundance of LFSA fungi showed significant negative correlations with landscape complexity at 250 m ($\beta = -0.039$, $p = 0.006$), 500 m ($\beta = -0.037$, $p = 0.011$), and 1000 m ($\beta = -0.031$, $p = 0.028$) radii (Supplementary Fig. 13a). In grassland ecosystems, the regression coefficients of landscape complexity showed an increased trend at larger spatial scales, and were generally higher than those observed in forest ecosystems (Supplementary Fig. 14a). 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; $p = 0.175$) (Fig. 4a and Supplementary Fig. 15a).

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 the richness ($\beta = -0.127$;

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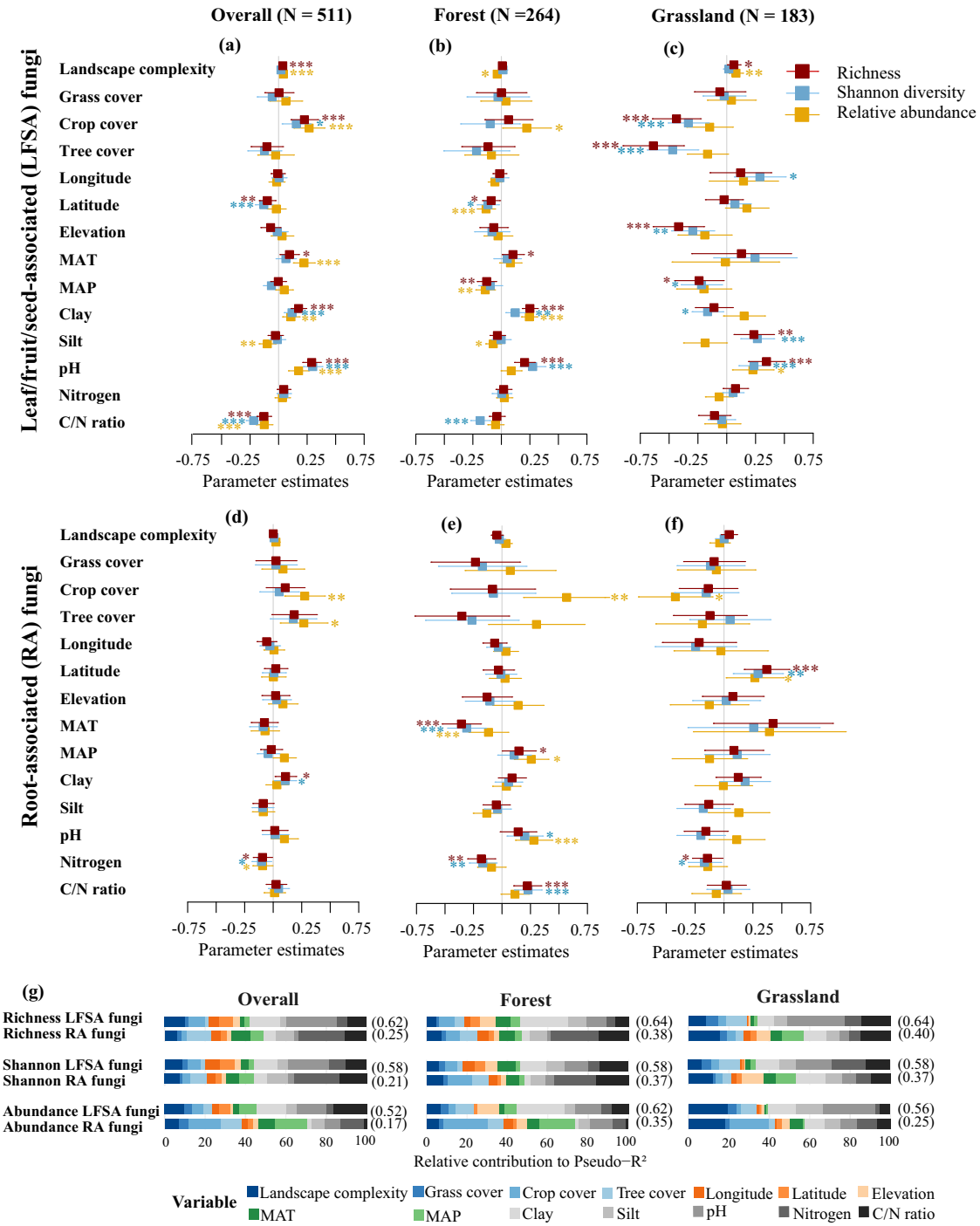

Fig. 2 | Predictors and their relative contributions to leaf/fruit/seed-associated (LFSA) and root-associated (RA) fungal alpha diversity. a–f show the parameter estimates (standardized regression coefficients) from 511 overall plots, 264 forest plots and 183 grassland plots. Data are presented as model-estimated standardized regression coefficients ± 95% confidence intervals (CIs) estimated from multivariate Generalized Additive Models for Location, Scale, and Shape (GAMLSS). Red, blue and yellow bars represent the richness, Shannon diversity and the relative abundance of the fungi, respectively. Predictors 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. **g** summarizes the relative contributions (proportion of variance explained, %) of each predictor variable to the overall model performance, with Pseudo-R^2 values indicated in parentheses. Statistical significance of predictors is tested by p value as $^{***}p \le 0.001$; $^{**}p \le 0.01$; $^{*}p \le 0.05$. See Supplementary Table 1 for details and the exact p values.

$p = 0.028$), 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 and Supplementary Figs. 7–12). Forest ecosystems also exhibited the similar pattern (Supplementary Fig. 13b). 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 (Supplementary Fig. 14b). Based on a meta-analysis of parameter estimates, grass cover showed a significant negative correlation with soil pathogenic fungal alpha

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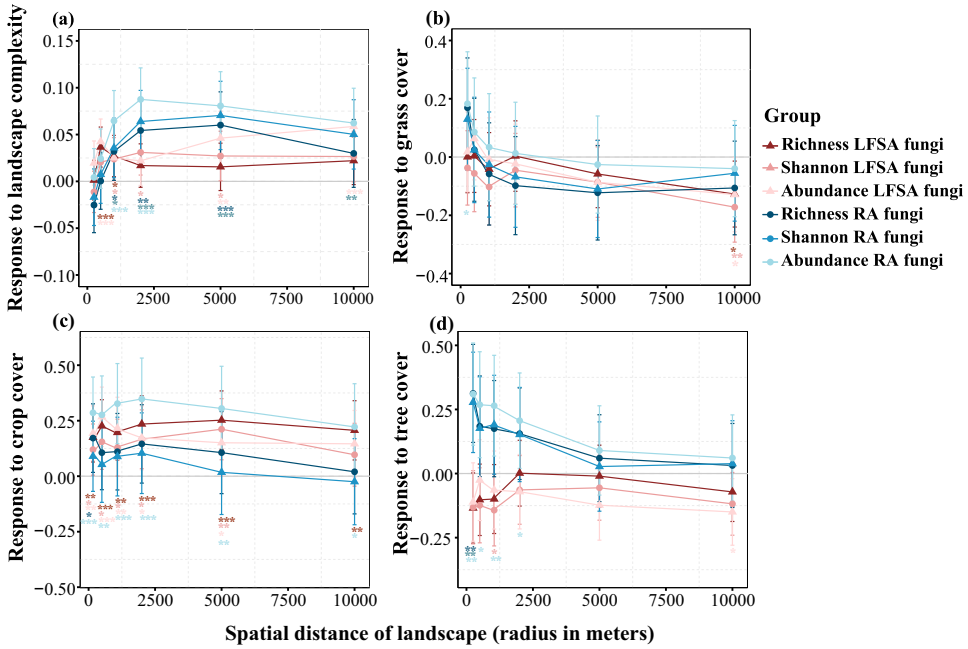

Fig. 3 | Landscape effects on leaf/fruit/seed-associated (LFSA) and root-associated (RA) fungal alpha diversity across spatial scales. LFSA and RA fungal alpha diversity as affected by **a** landscape complexity, **b** grass cover, **c** crop cover, and **d** tree cover across six spatial scales (250 m, 500 m, 1000 m, 2000 m, 5000 m, and 10,000 m radii) ($n = 511$ plots in total). Data are presented as model-estimated standardized regression coefficients ± 95% confidence intervals (CIs) derived from multivariate Generalized Additive Models for Location, Scale, and Shape (GAMLSS). Red lines from dark to light indicate the richness, Shannon diversity and relative abundance of LFSA fungi, while blue lines correspond to those of RA fungi. Statistical significance is determined using two-sided Wald tests from multivariate GAMLSS without adjustment for multiple comparisons. Significance levels are indicated as $^{***}p \le 0.001$; $^{**}p \le 0.01$; $^{*}p \le 0.05$. Partial regression results with exact standardized regression coefficients and p values of soil pathogenic fungal alpha diversity responding to landscape variables are shown in Supplementary Figs. 7–12.

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 (Fig. 4a and Supplementary Fig. 15b).

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 (Fig. 3c and Supplementary Figs. 13c and 14c). 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 1000 m (Fig. 3d and Supplementary Figs. 7–12). 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 (Supplementary Figs. 13d and 14d). 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; $p < 0.001$) (Supplementary Fig. 15c).

Relative contribution of local and landscape variables across scales

For all plots, we found that soil factor consistently explained the largest proportion of variation in both soil pathogenic fungal alpha and beta diversity (Fig. 5), with soil pH emerging as the strongest predictor, explaining an average of 15.6 ± 1.9% (mean ± s.e.) and 29.7 ± 1.5% of the variance (Fig. 5a, b), respectively. Notably, landscape factor was the second most important predictor explaining variation in alpha diversity, totally accounting for 23.4% ± 1.5% of the variance, with landscape complexity alone explaining 8.2 ± 0.8% (Fig. 5a, c). However, its contribution to beta diversity was comparatively minor (Fig. 5b, d), explaining 13.0 ± 0.8% of the variance. Climatic factor explained a relatively small proportion of the variation in alpha diversity (Fig. 5a, c), but emerged as the second most important predictor group for beta diversity, with MAT explaining the second-highest proportion of variance among all individual predictors (26.5 ± 1.3%) (Fig. 5b, d). A similar pattern was observed in forest ecosystems, where alpha diversity was predominantly driven by soil and landscape factors, while beta diversity was primarily shaped by soil and climatic variables (Supplementary Fig. 16a, c). However, in grassland ecosystems, beta diversity was predominantly explained by spatial distance, which explained 41.4 ± 8.9% of the variance, followed by soil pH and MAT (Supplementary Fig. 16b, d).

When considering the individual landscape variables across spatial scales, landscape complexity showed the highest relative contribution of 25.0% within the 5000 m radius for the relative abundance of RA fungi in all plots (Supplementary Fig. 17). Grass cover showed the highest relative contribution of 14.7% within the 250 m radius to the richness of RA fungi in grassland ecosystems (Supplementary Fig. 18). Crop cover showed the highest relative contribution of 25.5% within the 1000 m radius for RA fungal relative abundance in forest ecosystems (Supplementary Fig. 19). Tree cover explained the highest relative contribution of 15.4% within the 5000 m radius variance in RA fungal richness in grasslands (Supplementary Fig. 20).

Discussion

Exploring the landscape effects on soil pathogenic fungi is a novel frontier in microbiology. Consistent with most previous studies[10,11], we

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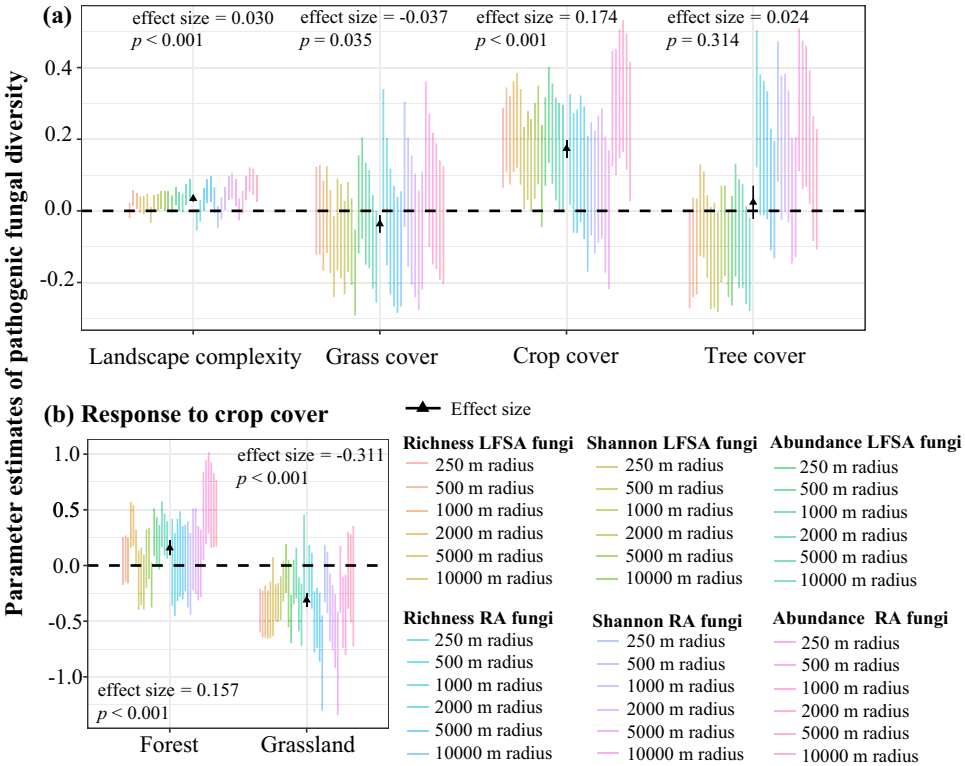

Fig. 4 | Overall landscape effects on soil pathogenic fungal alpha diversity. **a** Overall effects of landscape complexity, grass cover, crop cover, and tree cover on soil pathogenic fungal alpha diversity across all plots. **b** Overall effects of crop cover on soil pathogenic fungal alpha diversity between forest and grassland ecosystems. Colored lines denote the 95% confidence intervals (CIs) of model-estimated standardized regression coefficients across two fungal groups (LFSA and RA fungi), three diversity indices (richness, Shannon diversity, and relative abundance), and six spatial scales (250 m to 10,000 m radii) from multivariate Generalized Additive Models for Location, Scale, and Shape (GAMLSS). Black triangles represent the overall effect sizes. Effect sizes (± 95% CIs) are estimated using random-effects meta-analyses, and statistical significance is evaluated using two-sided *z*-tests without adjustment for multiple comparisons ($n = 36$ biologically independent samples). Effect size values and associated *p* values are reported for each category.

found that local environmental factors played a dominant role in associating with soil pathogenic fungal diversity. However, the effects of landscape-level factors are not negligible, accounting for 23.4% of the relative contribution to soil pathogenic fungal alpha diversity and 13.0% on beta diversity worldwide. In general, soil pathogenic fungal alpha diversity was positively correlated with landscape complexity and crop cover, but negatively correlated with grass and tree cover, although the effects varied across fungal groups, ecosystem types and spatial scales. 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.

Numerous regional studies have verified that distribution patterns of mammals[38], birds[22], and soil pathogenic fungi can be affected by landscape factors[18]. Meanwhile, several studies have explored the global effects of landscape change on vertebrate species[24,25]. Here, we explored the relationship between pathogenic fungal diversity and landscape variables at the global scale. As predicted by the cross-habitat spillover hypothesis, landscape variables can regulate the flow of resources and energy across habitats, and influence community structure and associated processes directly[39]. For example, two studies have found that forest connectivity contributes to the spillover of pathogens and results in similar community composition[27,33]. These findings suggest that analyses limited to local-scale environmental factors may be insufficient to fully explain soil pathogenic fungal diversity, whose ability of long-distance dispersal makes them more exposed to landscape-level variation[20]. In our study, landscape-level factor explained 23.4% of the variation in soil pathogenic fungal alpha diversity, ranking second only to soil factor. In addition, landscape change can shape the diversity patterns of pathogenic fungal diversity through their indirect effects on local vegetation diversity and soil conditions[34,35]. As evidenced by Partial Least Squares Path Models, landscape factor exerted both direct and indirect effects on soil pathogenic fungal alpha diversity by mediating soil conditions (Supplementary Figs. 21 and 22). However, their influence on beta diversity was comparatively limited, aligning with results from a New Zealand survey, which demonstrates that landscape compositions are major determinants of plant pathogen alpha diversity, instead of beta diversity[40]. A possible explanation is that beta diversity reflects compositional dissimilarity among sites, which is typically driven by spatial variation[11]. In such cases, climatic and edaphic factors become increasingly important determinants of fungal community turnover[10,11]. 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 designs[34]. 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.

The positive correlation between soil pathogenic fungal diversity and landscape complexity may be attributed to several reasons. First, higher landscape complexity implies more complex landscape

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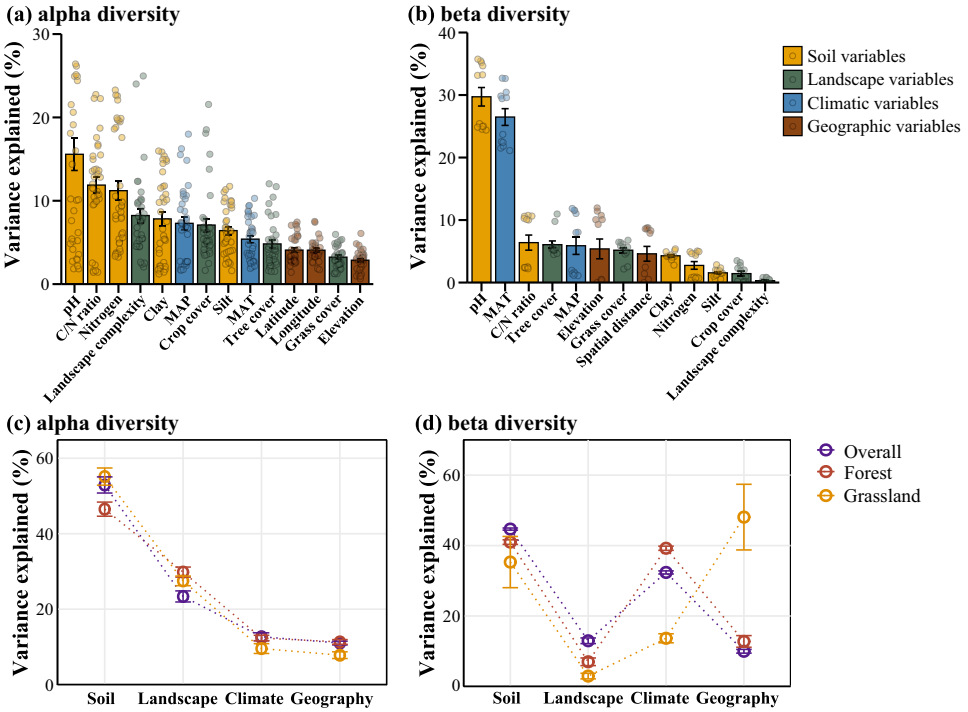

Fig. 5 | Relative contributions of environmental predictors to soil pathogenic fungal alpha and beta diversity. Average relative contribution (proportion of variance explained, %) of each predictor variable on soil pathogenic fungal **a** alpha ($n = 36$ biologically independent samples) and **b** beta ($n = 12$ biologically independent samples) diversity across all plots, covering two fungal groups (LFSA and RA fungi), four diversity indices (richness, Shannon diversity, and relative abundance for alpha diversity and Sørensen dissimilarity for beta diversity), and six spatial scales (250 m to 10,000 m radii); **c**, **d** show the grouped environmental factors contributing to soil pathogenic fungal alpha and beta diversity, respectively, for all plots, forest, and grassland ecosystems. Data are shown as mean ± s.e. Grouped environmental factors are categorized into soil, landscape, climate, and geography.

configurations with higher patch density and edge density[21,37]. High patch density provides more space, like stepping-stones, for the survival and the spreading of pathogenic fungi, leading to an increase in fungal diversity within the whole landscape[41]. Similarly, high edge density contributes to increased light, temperature and soil nutrients (e.g., soil carbon) at edges, which favors specific pathogenic fungal taxa[33]. As shown in our results, the diversity of the fungal genera of *Discosia* and *Entoloma* increased with landscape complexity, and these fungi were often detected in forest edges[42,43]. Second, higher landscape complexity indicates higher composition heterogeneity (i.e., land cover composition diversity), which is considered to offer a wider range of habitats, niches, and potential refuges for soil pathogenic fungi, particularly during seasons unfavorable for survival[21,23]. Conversely, landscape simplification by land-use change, such as reduced vegetation heterogeneity and soil degradation, has been found to suppress soil pathogenic fungal diversity[19,32]. 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 composition[18], 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.

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. 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 dilution effects 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]. Additionally, practices such as fertilization have been found to promote soil pathogenic fungal diversity, which may also result in the positive correlation with crop cover[45]. Interestingly, this positive association reversed in grassland ecosystems, where larger crop cover declined soil pathogenic fungal diversity. A possible explanation is that cropland is often subject to intensive management practices, including pesticide and fungicide application, crop rotation, and deep tillage, which can strongly reduce pathogen diversity[46,47]. Moreover, compared to forests, grassland ecosystems are generally more accessible and frequently converted for agricultural land-use, amplifying the negative effects of these management interventions on soil fungal diversity[48]. 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 datasets[35]. 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].

Similar to our results, Mennicken et al.[18] detected the spatial scale-dependent effect of landscape habitat amount on soil pathogenic fungal richness and Shannon/Simpson diversity in a forest ecosystem, with the most significant effect occurring within the spatial radii of 1500–2000 m. Additionally, as the spatial scale increased to the 5000–10,000 m radii, we found that the effect of landscape complexity and quantity on pathogenic fungal diversity became weaker in forest ecosystems. 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]. The larger forest canopy usually provide a more stable microclimate

condition to buffer diversity changes[50], and the dispersal of fungal spores as the spatial distance increases[49]. Some studies have found that fluctuations in microclimate, instead of macroclimatic disturbances, are key drivers of soil fungal diversity in forests[50,51]. In addition, spatially complex forest landscapes usually contain more natural enemies or competitors, such as the presence of ectomycorrhizal fungi, considered to inhibit the diversity of pathogenic fungi[52]. In contrast, we found that in grassland ecosystems, as the spatial scale increased to a 5000–10,000 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 scales[51]. Grilli et al.[20] suggested that the long dispersal ability of soil fungi may be underestimated, which could partly explain the stronger diversity-landscape relationships in open grassland ecosystems. 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 dispersal[49]. 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 dynamics[16]. Former experiments discovered either positive[54], negative[55], or non-significant[56] effects of landscape properties on the diversity of pathogenic fungi, and the inconsistency may probably arise from the differences of scale effects across ecosystems. Therefore, although spatially complex landscapes can contribute to biodiversity maintenance[23,24], we argue that such effects are context- and scale-dependent.

The inconsistent effects of landscape-level factors on pathogenic fungal diversity from previous studies may also relate to different pathogenic fungal groups[12,19]. For example, we found that LFSA and RA fungal alpha diversity exhibited contrasting responses to tree cover for all plots. Moreover, along spatial scales, the largest relative contributions of landscape complexity and quantity were consistently observed for RA fungal diversity, rather than LFSA fungi. RA fungi are closely associated with roots, and sensitive to landscape changes due to nutrient transfer between neighboring roots[57], which may experience great diversity change. Vannette et al.[27] reported that the diversity of root-associated fungi significantly increased with landscape connectivity and forest area. In addition, unlike LFSA fungi, whose primary lifestyles are predominantly as pathogens, RA fungi (e.g., *Entoloma* spp.) are primary classified as saprotrophic or ectomycorrhizal fungi, and pathogenic effects on plant roots might be less frequent than for LFSA[58,59]. This suggests that the differences in primary lifestyles and the complex trophic mode of RA fungi may contribute to their distinct responses[10]. 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 constrain responses to landscape variation[44].

There are several implications from our study for belowground biodiversity conservation and ecosystem health maintenance. First, increasing landscape complexity is essential to mitigate biodiversity loss, particularly in the face of ongoing landscape homogenization[23]. Landscape mosaic model suggests that various land cover types and heterogeneity of patches promote biodiversity[31,33]. However, natural landscapes are now being simplified due to practices like monoculture and logging[23]. Therefore, preserving the diversity and complex configuration of natural landscapes, such as increasing cover types and creating corridors among patches[21,60], is crucial for the maintenance of soil pathogenic fungal diversity and associated functions. Second, conserving a sufficient quantity of natural habitats is critical for keeping the dynamic balance of soil pathogens. Our findings show that increases in grass and tree cover tend to reduce pathogenic fungal diversity, suggesting that greater natural habitat coverage can suppress excessive pathogen proliferation. Empirical work in a grassland has shown that a high diversity of plant pathogenic fungi may coincide with lower infection rates and negative effects on their plant hosts[61]. This suggests that increased natural landscape can enhance ecosystem resistance and resilience, potentially by increasing dilution effects at the landscape scale[6,61]. Lastly, as the spatial-scale effect of landscape can influence pathogenic fungal diversity across ecosystems, it should be considered in devising policy, forest management plans, and monitoring activities relevant to biodiversity targets[33].

Our global research highlights the complementary contribution of landscape-level factor in shaping soil pathogenic fungal diversity, especially for alpha diversity, which generally increased with higher landscape complexity and cover crop, but decreased with grass and tree cover. Therefore, preserving the landscape heterogeneity and considering the quantity of different cover types are vital for maintaining the dynamic balance of belowground soil pathogenic fungi and their associated functions. Moreover, the effects of landscape factor on soil pathogenic fungal diversity varied among ecosystems, spatial scales and fungal groups. Thus, accounting for the ecosystem type and identifying appropriate spatial scales are essential for accurately understanding large-scale patterns of belowground fungal diversity.

Methods

Sites and sampling

All research activities complied with relevant ethical regulations and were conducted under permits MAE-DNB-CM-2016-0043 and 006-2021-EXP-CM-FAU-DBI/MAAE issued by the Galapagos National Park Directorate and the Ecuadorian Ministry of Environment, Water and Ecological Transition. Soil samples were collected from the International Soil Biogeography Consortium (iSBio, https://home.uni-leipzig.de/idiv/isbio) across 290 sites with 511 plots (Fig. 1a). These sites were located in 32 countries from six continents and within main biomes covering most natural environmental conditions (Fig. 1b). Of the 290 sites, 145 were categorized as forest ecosystems (dominated by trees or shrubs), 109 were grassland ecosystems (including grasslands, meadows, or pastures), and 36 were other ecosystems (including tundra, desert, plantation, salt marsh, or croplands). Soil samples were collected worldwide following a standard sampling protocol. In general terms, each site was sampled during summer in 2018 (the northern hemisphere), or 2019 (the southern hemisphere) and was composed of two homogeneous plots to ensure representativeness. In each plot, four randomly distributed soil samples were collected per plot (at 5 cm depth of the mineral soil), pooled into one composite sample and treated separately. A subsample from each plot was taken, preserved in RNAlater solution (Thermo Fisher Scientific, Darmstadt, Germany), and frozen at −20 °C for molecular analysis. Another subsample was stored at 4 °C for physicochemical analyses. We collected 580 samples in total, of which three were lost during transportation and 66 samples were lost due to sequencing quality control, resulting in a total of 511 soil samples. Further details can be found in Heintz-Buschart et al.[62].

Soil fungi identification

For all the soil samples, the total genomic DNA was extracted using the DNeasy Power Soil kit (Qiagen, Hilden, Germany). The soil fungi identification was conducted using the primer set ITS1F (5′-

CTTGGTCATTTAGAGGAAGTA-3′) and ITS2 (5′-GCTGCGTTCTTCATCGATGC-3′)[63,64] with the PCR amplification process performed according to the ITS Illumina Amplicon Sequencing Protocol (https://earthmicrobiome.org/protocols-and-standards/its). The sequencing was performed on an Illumina MiSeq at the NGS Competence Center Tübingen (NCCT, Germany). Data were processed using the dadasnake pipeline (v0.5)[65], which wraps current best-practice tools for denoising and amplicon sequence variant (ASV) generation[66] and taxonomic annotation[67] against the UNITE database (v8.2)[68]. Parameters for quality-filtering (truncation at 17 and 15 PHRED score of the forward and reverse reads, total maximum expected error 1.5), denoising, and taxonomic annotation (default mothur settings) were based on settings previously established and optimized for datasets with known composition[64]. 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. We classified fungal phylotypes into pathogenic fungi, including aboveground leaf/fruit/seed-associated (LFSA) fungi and below-ground root-associated (RA) fungi, against the FungalTraits database according to the category 'plant pathogenic capacity' that defines whether plant pathogens occur in this taxon and which organs are infected (Fig. 1c)[53]. Among these, 11.1% of the reads were classified into 2694 LFSA fungal ASVs and 1.66% belonged to 302 RA fungal ASVs.

Landscape factor calculation

To quantify the complexity of landscape structures, we calculated landscape metrics using the *landscapemetrics* package[69]. We used a land cover map with 100 m resolution from Copernicus Global Land Service[70], together with the geographic coordinates, converted to Cylindrical Equal Area map projection[71]. Landscape metrics are measured to quantify aspects of landscape patterns, such as spatial heterogeneity and patchiness. 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 selected eight frequently used landscape-level metrics that are representative of landscape complexity. The eight metrics belong to three groups: area and edge metrics (edge density (ED), largest patch index (LPI)); aggregation metrics (landscape division index (Division), patch density (PD), landscape shape index (LSI)), and diversity metrics (patch richness (PR), modified Simpson diversity index (MSIDI) and Shannon diversity index (SHDI)) (see Supplementary Table 7 for more details)[28,29,37]. Generally, higher PR, MSIDI and SHDI values indicate higher landscape diversity (compositional complexity), higher Division, ED, PD but lower LPI values indicate higher configurational complexity, and a higher LSI value indicates higher landscape shape complexity[21,29,37]. The metrics were calculated at a spatial distance of 250, 500, 1000, 2000, 5000, 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 fungi[18], given the relatively limited spatial dispersal capacity for some specific taxa, and the 500 m radius corresponds to the resolution of the local environmental factors (see below). The 1000–2000 m radii are the most commonly used medium-scale spatial distances[19]. In addition, larger spatial distances of 5000–10,000 m radii are also found to affect pathogenic fungi[36]. Due to the high Spearman's rank correlation of landscape metrics (Supplementary Fig. 23), 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 (Supplementary Fig. 24); 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[28,29,72]. The landscape complexity factor was highly correlated with the landscape metrics, with the higher value meaning higher Division, ED, PD, LSI, PR, MSIDI, SHDI but lower LPI (Supplementary Table 8), i.e., more heterogeneous, irregular, divided and diverse landscape patterns. 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.

Local environmental factors

The local environmental factors selected for the sampling plots included geography, climate, and soil, which were commonly regarded as indicators of soil pathogenic fungal diversity[9,10,14]. The geographic variables included elevation, longitude, and latitude. The longitude and latitude were measured on site, and elevation was taken from WorldClim 2 with 1 km resolution[73]. The climatic variables included MAT and MAP that were extracted from a processed global layer CHELSA with 1 km resolution[74]. Available soil properties included soil texture (clay, silt and sand content), pH, SOC, total nitrogen, and water percent. The soil properties were either measured from the soil samples taken, or from another sample from the site. Missing data were filled by extracting values from the global soil information database[75].

Statistical analysis

We calculated richness, Shannon diversity, relative abundance (i.e., relative number of reads among all fungal reads), and Sørensen beta dissimilarity (presence/absence data) of amplicon ASVs assigned to the two pathogenic fungal groups (i.e., LFSA and RA fungi) for each plot (Supplementary Fig. 25). Multivariate Generalized Additive Models for Location, Scale, and Shape (GAMLSS) were fitted to assess the contribution of the landscape, geographic, climatic, and soil variables on the soil pathogenic fungal alpha diversity (richness, Shannon diversity and relative abundance) using the *gamlss* package[76]. Because we visually checked the nonlinear relationships in preliminary analysis, we set a maximum of 3 degrees of freedom of the smooth functions for each predictor variable, which allows for nonlinear trends and avoids overfitting[77]. The multivariate GAMLSS contained only a set of non-correlated variables (i.e., Spearman's correlation <0.65), so variables of soil sand content, SOC, and water percent were excluded in the models because of high correlations in the models (Supplementary Fig. 26). We built six competing models to test the effects of landscape variables across six different spatial scales on the diversity indices of LFSA and RA fungi, and compared forest and grassland ecosystems separately. All predictor and response variables in the model were scaled (z-scored) to allow comparison. 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 sites[78], and only weak effects were detected (Supplementary Table 9). 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 (Supplementary Figs. 27 and 28). To confirm the robustness of our findings, we additionally fitted mixed-effects GAMLSS with 'site' as a random effect, 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 (Supplementary Figs. 29 and 30).

To detect the spatial scale effects of landscape variables on soil pathogenic fungal diversity, standardized regression coefficients and standardized error of landscape complexity, grass cover, crop cover and tree cover from each GAMLSS model were extracted and fitted along spatial scales. 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), 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* package[79]. We also calculated the relative partial contributions of each predictor variable and group of environmental factors of landscape, geography, climate, and soil to the Pseudo-R^2[77].

To disentangle the direct and indirect effects of multivariate environmental factors on soil pathogenic fungal alpha diversity, we applied Partial Least Squares Path Models (PLSPM) using the *plspm* package[80]. 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: (1) the direct effects of the four latent variables on soil pathogenic fungal alpha diversity (richness, Shannon diversity, and relative abundance); and (2) the indirect effects of landscape, climate, and geography through their influence on soil variables. A hypothetical conceptual model was constructed accordingly (Supplementary Fig. 31). 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.

We applied Generalized Dissimilarity Modelling (GDM) to quantify the beta diversity pattern (i.e., Sørensen beta dissimilarity) of soil pathogenic fungi using the *gdm* package[81]. Compared to conventional linear matrix regression, GDM accommodates two major forms of nonlinearity: (1) variation in the rate of community compositional turnover along environmental gradients, and (2) curvilinear relationships between compositional dissimilarity and both environmental and geographic distances[82]. 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. All the calculations were conducted using R version 4.3.2[83].

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The raw sequencing data generated in this study have been deposited in the NCBI Sequence Read Archive (SRA) under accession code PRJNA1045969. The source data underlying all figures are available on Figshare at https://doi.org/10.6084/m9.figshare.26377660.v5. All other data supporting the findings of this study are provided in the Supplementary Information.

Code availability

The code that support the findings of this study are openly available on figshare at https://doi.org/10.6084/m9.figshare.26377660.v5.

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Author contributions

Y.L., N.E., G.P., A.H.-B., K.Kü., C.-E.W., F.B., and C.A.G. conceived and designed the study. Y.L., X.L., Y.C., and C.A.G. performed the data analyses. Y.L. wrote the first draft of the manuscript with support by C.A.G. and N.E., and all authors contributed greatly to the final manuscript. N.E., G.P., A.H.-B., K.Kü., C.-E.W., F.B., Q.B., M.C.R., and S.S. worked on laboratorial analyses and data compiling. Site coordination and soil sampling were contributed by A.S.F.A., B.F., F.T.M., M.V., L.v.d.B., Q.P., M.Di., G.W., A.G., C.B., H.M., K.F., E.C.A., A.A., M.B., H.B., A.C., R.C., M.C., R.C.G., C.C., C.T.C., M.Da., E.A.D., M.-A.d.G., C.D., V.D.C., L.D.M., I.D., S.D., T.E., I.F., P.F., M.Frei., M.Fren., R.G.G., S.G., M.G., G.G., A.R.G., P.H., U.H., T.His., T.Hiu., E.H., K.H., H.J., J.J.J., M.J.K.-S., S.K.-R., Zs.K., K.Kr., H.K., K.L., J.L., S.L., V.M., R.L.M., F.M.-D., I.M., V.O., I.O., A.P., W.C.P., P.L.P., R.M., A.P., P.P., M.P., C.R., P.B.R., M.C.R., M.Schä., M.Scha., A.Sc., J.S., H.C.S., A.I.S., S.S., A.St., M.T., Z.T., S.M.T.-T., S.T., P.D.T., T.M.U., S.E.V., A.V., J.V., D.V., M.Wa., M.We., and F.Z.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to Yawen Lu or Carlos A. Guerra.

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Yawen Lu[1,2,3] ✉, Nico Eisenhauer[2,4], Guillaume Patoine[2,4], Ying Chen[5], Anna Heintz-Buschart[6], Kirsten Küsel[2,7,8], Carl-Eric Wegner[7,9], François Buscot[2,10], Xiang Liu[11], Ademir S. F. Araujo[12], Beat Frey[13], Fernando T. Maestre[14], Matthew Vadeboncoeur[15], Liesbeth van den Brink[16,17], Quentin Ponette[18], Markus Didion[13], Georg Wohlfahrt[19], Aurora Gaxiola[20], Cristina Branquinho[21], Henning Meesenburg[22], Karibu Fukuzawa[23], E. Carol Adair[24], Andrijana Andrić[25], Milan Barna[26], Qicheng Bei[10], Helge Bruelheide[2,27], Adriano Caliman[28], Rafaella Canessa[2,29,30], Michele Carbognani[31], Roberto Cazzolla Gatti[32], Chiling Chen[33], Casper T. Christiansen[34], Michaël Danger[35], Evgeny A. Davydov[36], Marie-Anne de Graaff[37], Christine Delire[38], Valter Di Cecco[39], Luciano Di Martino[39], Ika Djukic[13], Simon Drollinger[40], Tsutomu Enoki[41], István Fekete[42], Petra Fransson[43], Martin Freitag[44], Mark Frenzel[45], Rosario G. Gavilán[46], Stephan Glatzel[47], Maria Glushkova[48], Grizelle González[49], Anderson da R. Gripp[50], Peter Haase[51,52], Ute Hamer[44], Takuo Hishi[53], Tsutom Hiura[54], Elisabeth Hornung[55], Kazuhiko Hoshizaki[56], Heinke Jäger[57], Juan J. Jiménez[58], Megan J. Kelly-Slatten[59], Sebastian Kepfer-Rojas[60], Zsolt Kotroczó[61], Kaie Kriiska[62], Hiroko Kurokawa[63], Kate Lajtha[64], John Loehr[65], Stefan Löfgren[66], Vincent Maire[67], Rodrigo L. Martins[50], Florence Maunoury-Danger[35], Inara Melece[68], Victoria Ochoa[69], Ivika Ostonen[62], Alain Paquette[70], William C. Parker[71], Pablo Luis Peri[72], Rebecca Mast[73],

Alessandro Petraglia[31], Petr Petřík[74,75], Mihai Pușcaș[76,77,78], Corinna Rebmann[79], Peter B. Reich[80,81,82], Matthias C. Rillig[83,84], Martin Schädler[2,45], Marcus Schaub[13], Anja Schmidt[85], Julia Seeber[86,87], Helena Cristina Serrano[21], Ana I. Sousa[88], Stefan Scheu[89,90], Artur Stefanski[80,91], Marcello Tomaselli[31], Zsolt Tóth[92], Stacey M. Trevathan-Tackett[93], Stefan Trogisch[2,27], Pavel Dan Turtureanu[76,77,78], Tudor M. Ursu[94], Susanna E. Venn[95], Arne Verstraeten[96], Jeyanny Vijayanathan[97], Dušanka Vujanović[25], Markus Wagner[22], Martin Weih[98], Franz Zehetner[99,100] & Carlos A. Guerra[2,101]

[1]College of Chemistry and Life Science, Suzhou University of Science and Technology, Suzhou, China. [2]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany. [3]MOE Key Laboratory for Biodiversity Science and Ecological Engineering, Institute of Biodiversity Science, School of Life Sciences, Fudan University, Shanghai, China. [4]Institute of Biology, Leipzig University, Leipzig, Germany. [5]Institute of Ecology, College of Urban and Environmental Sciences, Key Laboratory for Earth Surface Processes of the Ministry of Education, Peking University, Beijing, China. [6]Swammerdam Institute for Life Sciences, University of Amsterdam, Amsterdam, The Netherlands. [7]Institute of Biodiversity, Ecology and Evolution, Aquatic Geomicrobiology, Friedrich Schiller University, Jena, Germany. [8]Cluster of Excellence Balance of the Microverse, Friedrich Schiller University Jena, Jena, Germany. [9]Bioinorganic Chemistry, Biomics Group, Heinrich Heine University, Düsseldorf, Germany. [10]Department of Soil Ecology, Helmholtz Centre for Environmental Research-UFZ, Halle (Saale), Germany. [11]State Key Laboratory of Herbage Improvement and Grassland Agro-Ecosystems & College of Ecology, Lanzhou University, Lanzhou, China. [12]Soil Microbial Ecology Group, Agricultural Science Center, Federal University of Piaui, Teresina, PI, Brazil. [13]Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland. [14]Environmental Sciences and Engineering, Biological and Environmental Science and Engineering Division, King Abdullah University of Science and Technology, Thuwal, Kingdom of Saudi Arabia. [15]Earth Systems Research Center, University of New Hampshire, Durham, NH, USA. [16]Plant Ecology Group, Department of Biology, University of Tübingen, Tübingen, Germany. [17]ECOBIOSIS, Department of Botany, University of Concepcion, Concepcion, Chile. [18]UCLouvain—Earth and Life Institute, Louvain-la-Neuve, Belgium. [19]Universität Innsbruck, Institut für Ökologie, Innsbruck, Austria. [20]Facultad de Ciencias Biológicas, P. Universidad Catolica de Chile, Alameda 340, Santiago & Instituto de Ecología y Biodiversidad (IEB), Santiago, Chile. [21]cE3c-Center for Ecology, Evolution and Environmental Changes & CHANGE - Global Change and Sustainability Institute, Faculdade de Ciências, Universidade de Lisboa, Lisboa, Portugal. [22]Northwest German Forest Research Institute, Göttingen, Germany. [23]Nakagawa Experimental Forest, Field Science Center for Northern Biosphere, Hokkaido University, Otoineppu, Hokkaido, Japan. [24]Rubenstein School of Environment and Natural Resources, Aiken Center, 81 Carrigan Drive, University of Vermont, Burlington, VT, USA. [25]BioSense Institute, University of Novi Sad, Novi Sad, Serbia. [26]Institute of Forest Ecology, Slovak Academy of Sciences, Zvolen, Slovakia. [27]Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany. [28]Departamento de Ecologia, Universidade Federal do Rio Grande do Norte, Natal, RN, Brazil. [29]Institute of Biology, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany. [30]Ecological Plant Geography, University of Marburg, Marburg, Germany. [31]Department of Chemistry, Life Sciences and Environmental Sustainability, University of Parma, Parma, Italy. [32]Department of Biological, Geological, and Environmental Sciences, University of Bologna, Bologna, Italy. [33]Taiwan Agricultural Research Institute, MOA, Taichung, Taiwan. [34]Terrestrial Ecology Section, Department of Biology, University of Copenhagen, Copenhagen, Denmark. [35]Université de Lorraine, CNRS, LIEC, Metz, France. [36]Altai State University, Barnaul, Russia. [37]Department of Biological Sciences, Boise State University, Boise, ID, USA. [38]Meteo-France/CNRS, Toulouse, France. [39]Maiella National Park, Sulmona, Italy. [40]Bioclimatology, University of Göttingen, Göttingen, Germany. [41]Kyushu University Forest, Kyushu University, Ashoro, Hokkaido, Japan. [42]Institute of Environmental Science, University of Nyíregyháza, Nyíregyháza, Hungary. [43]Department of Forest Mycology and Plant Pathology, Uppsala BioCenter, Swedish University of Agricultural Sciences, Uppsala, Sweden. [44]Institute of Landscape Ecology, University of Münster, Münster, Germany. [45]Department of Community Ecology, Helmholtz Centre for Environmental Research-UFZ, Halle (Saale), Germany. [46]Botany Unit, Department of Pharmacology, Pharmacognosy and Botany, Complutense University, Madrid, Spain. [47]Faculty of Geosciences, Geography and Astronomy, Geoecology Group, University of Vienna, Vienna, Austria. [48]Forest Research Institute-Bulgarian Academy of Sciences, Sofia, Bulgaria. [49]USDA Forest Service, International Institute of Tropical Forestry, San Juan, Puerto Rico. [50]Institute of Biodiversity and Sustainability, Federal University of Rio de Janeiro, Macaé, Rio de Janeiro, Brazil. [51]Department of River Ecology and Conservation, Senckenberg Research Institute and Natural History Museum Frankfurt, Gelnhausen, Germany. [52]Faculty of Biology, University of Duisburg-Essen, Essen, Germany. [53]Kyushu University Forest, Kyushu University, Sasaguri-machi, Fukuoka, Japan. [54]Department of Ecosystem Studies, The University of Tokyo, Bunkyo-ku, Tokyo, Japan. [55]Department of Zoology, University of Veteinary Medicine Budapest, Budapest, István utca 2., Hungary. [56]Department of Biological Environment, Akita Prefectural University, Akita, Japan. [57]Charles Darwin Research Station, Charles Darwin Foundation, Santa Cruz, Galapagos, Ecuador. [58]Pyrenean Institute of Ecology (IPE, CSIC), Jaca, Spain. [59]Department of Biological Sciences, Boise State University, Boise, ID, USA. [60]Department of Geosciences and Natural Resource Management, University of Copenhagen, Copenhagen, Denmark. [61]Department of Agro-Environmental Studies, Hungarian University of Agriculture and Life Sciences, Gödöllő, Hungary. [62]Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia. [63]Graduate School of Agriculture, Kyoto University, Kitashirakawa Oiwake, Sakyo, Kyoto, Japan. [64]Department of Crop and Soil Sciences, Oregon State University, Corvallis, OR, USA. [65]Faculty of Biological and Environmental Sciences, Lammi Biological Station, University of Helsinki, Lammi, Finland. [66]Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden. [67]Département des Sciences de l'Environnement, Université du Québec à Trois-Rivières, Trois-Rivières, QC, Canada. [68]Institute of Biology, Faculty of Medicine and Life Sciences, University of Latvia, Riga, Latvia. [69]Instituto Universitario de Investigación en el Olivar y el Aceite de Oliva, Universidad de Jaén, Jaén, Spain. [70]Centre for Forest Research, Université du Québec à Montréal, MontréalQC, QC, Canada. [71]Ontario Ministry of Natural Resources, Sault Ste. Marie ON, ON, Canada. [72]Instituto Nacional de Tecnología Agropecuaria (INTA), Universidad Nacional de la Patagonia Austral (UNPA)-CONICET, Río Gallegos, Santa Cruz, Argentina. [73]Department of Geosciences, University of Tübingen, Tübingen, Germany. [74]Department of Vegetation Ecology, Institute of Botany, Czech Academy of Sciences, Průhonice, Czech Republic. [75]Faculty of Environmental Sciences, Czech University of Life Sciences, Prague, Czech Republic. [76]A. Borza Botanic Garden, Babeș-Bolyai University, Cluj-Napoca, Romania. [77]Centre for Systems Biology, Biodiversity and Bioresources (3B), Babeș-Bolyai University, Cluj-Napoca, Romania. [78]Emil G. Racoviță Institute, Babeș-Bolyai University, Cluj-Napoca, Romania. [79]Department Computational Hydrosystems, Helmholtz Centre for Environmental Research (UFZ), Leipzig, Germany. [80]Department of Forest Resources, University of Minnesota, St. Paul, MN, USA. [81]Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW, Australia. [82]Institute for Global Change Biology and School for Environment and Sustainability, University of Michigan, Ann Arbor, MI, USA. [83]Institute of Biology, Freie Universität Berlin, Berlin, Germany. [84]Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Berlin, Germany. [85]Department of Conservation Biology & Social-Ecological Systems, Helmholtz Centre for Environmental Research-UFZ, Leipzig, Germany. [86]Universität Innsbruck, Institut für Ökologie, Sternwartestr. 15/Technikerstrasse 25, Innsbruck, Austria. [87]Institute for Alpine Environment, Eurac Research, Bozen/Bolzano, Italy. [88]ECOMARE, CESAM—Centre for Environmental and Marine Studies, Department of Biology, University of

Aveiro, Aveiro, Portugal. [89]JFB Institute of Zoology and Anthropology, University of Göttingen, Göttingen, Germany. [90]Centre of Biodiversity and Sustainable Land Use, University of Göttingen, Götingen, Germany. [91]College of Natural Resources, University of Wisconsin, Stevens Point, WI, USA. [92]Institute for Soil Sciences, HUN-REN Centre for Agricultural Research, Budapest, Herman Ottó út 15, Hungary. [93]Centre for Nature Positive Solutions, Biology Department, School of Science, RMIT University, Melbourne, VIC, Australia. [94]Institute of Biological Research Cluj, National Institute of Research and Development for Biological Sciences, Cluj-Napoca, Romania. [95]School of Life and Environmental Sciences, Deakin University, Burwood, VIC, Australia. [96]Research Institute for Nature and Forest (INBO), Geraardsbergen, Belgium. [97]Forest Research Institute Malaysia (FRIM), Kepong, Selangor, Malaysia. [98]Department of Crop Production Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden. [99]BOKU University, Institute of Soil Research, Department of Ecosystem Management, Climate and Biodiversity, Vienna, Austria. [100]Galapagos National Park Directorate, Puerto Ayora, Galapagos, Ecuador. [101]Universidade de Coimbra, Departamento de Geografia, Colégio São Jerónimo, Coimbra, Portugal. ✉e-mail: yawenlu@mail.usts.edu.cn; carlos.guerra@uc.pt