Nature Communications

https://doi.org/10.1038/s41467-025-67929-5

Article in Press

Landscape effects on global soil pathogenic fungal diversity across spatial scales

Received: 23 September 2024

Accepted: 12 December 2025

Cite this article as: Lu, Y., Eisenhauer, N., Patoine, G. *et al.* Landscape effects on global soil pathogenic fungal diversity across spatial scales. *Nat Commun* (2025). https://doi.org/10.1038/s41467-025-67929-5

Yawen Lu, Nico Eisenhauer, Guillaume Patoine, Ying Chen, Anna Heintz-Buschart, Kirsten Küsel, Carl-Eric Wegner, François Buscot, Xiang Liu, Ademir S. F. Araujo, Beat Frey, Fernando T. Maestre, Matthew Vadeboncoeur, Liesbeth van den Brink, Quentin Ponette, Markus Didion, Georg Wohlfahrt, Aurora Gaxiola, Cristina Branquinho, Henning Meesenburg, Karibu Fukuzawa, E. Carol Adair, Andrijana Andrić, Milan Barna, Qicheng Bei, Helge Bruelheide, Adriano Caliman, Rafaella Canessa, Michele Carbognani, Roberto Cazzolla Gatti, Chiling Chen, Casper T. Christiansen, Michaël Danger, Evgeny A. Davydov, Marie-Anne de Graaff, Christine Delire, Valter Di Cecco, Luciano Di Martino, Ika Djukic, Simon Drollinger, Tsutomu Enoki, István Fekete, Petra Fransson, Martin Freitag, Mark Frenzel, Rosario G. Gavilán, Stephan Glatzel, Maria Glushkova, Grizelle González, Anderson da R. Gripp, Peter Haase, Ute Hamer, Takuo Hishi, Tsutom Hiura, Elisabeth Hornung, Kazuhiko Hoshizaki, Heinke Jäger, Juan J. Jiménez, Megan J. Kelly-Slatten, Sebastian Kepfer-Rojas, Zsolt Kotroczó, Kaie Kriiska, Hiroko Kurokawa, Kate Lajtha, John Loehr, Stefan Löfgren, Vincent Maire, Rodrigo L. Martins, Florence Maunoury-Danger, Inara Melece, Victoria Ochoa, Ivika Ostonen, Alain Paquette, William C. Parker, Pablo Luis Peri, Rebecca Mast, Alessandro Petraglia, Petr Petřík, Mihai Pușcaș, Corinna Rebmann, Peter B. Reich, Matthias C. Rillig, Martin Schädler, Marcus Schaub, Anja Schmidt, Julia Seeber, Helena Cristina Serrano, Ana I. Sousa, Stefan Scheu, Artur Stefanski, Marcello Tomaselli, Zsolt Tóth, Stacey M. Trevathan-Tackett, Stefan Trogisch, Pavel Dan Turtureanu, Tudor M. Ursu, Susanna E. Venn, Arne Verstraeten, Jeyanny Vijayanathan, Dušanka Vujanović, Markus Wagner, Martin Weih, Franz Zehetner & Carlos A. Guerra

Title: Landscape effects on global soil pathogenic fungal diversity across spatial scales

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[10,2], 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], Scheu Stefan[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 215009, China

2. German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstr. 4, 04103 Leipzig, Germany

3. MOE Key Laboratory for Biodiversity Science and Ecological Engineering, Institute of Biodiversity Science, School of Life Sciences, Fudan University, 2005 Songhu Road, Shanghai 200438, China

4. Institute of Biology, Leipzig University, Puschstr. 4, 04103 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, 100871, China

6. Swammerdam Institute for Life Sciences, University of Amsterdam, 1098 XH Amsterdam, Netherlands

7. Institute of Biodiversity, Ecology and Evolution, Aquatic Geomicrobiology, Friedrich Schiller University, Dornburger Str. 159, 07743 Jena, Germany

8. Cluster of Excellence Balance of the Microverse, Friedrich Schiller University Jena, Germany

9. Bioinorganic Chemistry, Biomics Group, Heinrich Heine University, Universitätsstr. 1, 40225 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 730000, 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, 8903 Birmensdorf, Switzerland

14. Environmental Sciences and Engineering, Biological and Environmental Science and Engineering Division, King Abdullah University of Science and Technology, Thuwal, 23955-6900, Kingdom of Saudi Arabia

15. Earth Systems Research Center, University of New Hampshire, Durham, NH 03824 USA

16. Plant Ecology Group, Department of Biology, University of Tübingen, Germany

17. ECOBIOSIS, Department of Botany, University of Concepcion, Chile

18. UCLouvain - Earth and Life Institute, Croix du Sud 2 - box L7.05.24, 1348 Louvain-la-Neuve, Belgium

19. Universität Innsbruck, Institut für Ökologie, Sternwartestr. 15, 6020 Innsbruck, Austria

20. Facultad de Ciencias Biológicas, P. Universidad Catolica de Chile, Alameda 340, Santiago & Instituto de Ecología y Biodiversidad (IEB)

21. cE3c-Center for Ecology, Evolution and Environmental Changes & CHANGE - Global Change and Sustainability Institute, Faculdade de Ciências, Universidade de Lisboa, 1749-016 Lisboa, Portugal

22. Northwest German Forest Research Institute, Göttingen, Germany

23. Nakagawa Experimental Forest, Field Science Center for Northern Biosphere, Hokkaido University, 483 Otoineppu, Otoineppu, Hokkaido 098-2501, Japan

24. Rubenstein School of Environment and Natural Resources, Aiken Center, 81 Carrigan Drive, University of Vermont, Burlington, VT 05405, USA

25. BioSense Institute, University of Novi Sad, Dr Zorana Đinđića 1, 21000 Novi Sad, Serbia

26. Institute of Forest Ecology, Slovak Academy of Sciences, Ľ. Štúra 2, 96053 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, 59078-970, Brazil

29. Institute of Biology, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany

30. Ecological Plant Geography, University of Marburg, Germany

31. Department of Chemistry, Life Sciences and Environmental Sustainability, University of Parma, Parco Area delle Scienze 11/A, 43124, Parma, Italy

32. Department of Biological, Geological, and Environmental Sciences, University of Bologna, Italy

33. Taiwan Agricultural Research Institute, MOA, Taiwan

34. Terrestrial Ecology Section, Department of Biology, University of Copenhagen, Denmark

35. Université de Lorraine, CNRS, LIEC, F-57000 Metz, France

36. Altai State University, Lenina Ave. 61, Barnaul, Russia

37. Department of Biological Sciences, Boise State University, Boise, Idaho, USA

38. Meteo-France/CNRS, 42 av Coriolis, 31057 Toulouse, France

39. Maiella National Park, Via Badia 28-67039 Sulmona, Italy

40. Bioclimatology, University of Göttingen, Göttingen, Germany

41. Kyushu University Forest, Kyushu University, 1-85 Kita 5, Ashoro, Hokkaido 089-3705 Japan

42. Institute of Environmental Science, University of Nyíregyháza, Sóstói út 31/b, 4400, 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, Heisenbergstr. 2, 48149 Münster, Germany

45. Department of Community Ecology, Helmholtz Centre for Environmental Research-UFZ, 06110 Halle (Saale), Germany

46. Botany Unit. Dept Pharmacology, Pharmacognosy and Botany. Complutense University. E-28040 Madrid, Spain

47. Faculty of Geosciences, Geography and Astronomy, Geoecology Group, University of Vienna, Josef-Holaubek-Platz 2, 1090, 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, 498-1 Tsubakuro, Sasaguri-machi, Fukuoka, 811-2415, Japan

54. Department of Ecosystem Studies, The University of Tokyo, 1-1-1 Yayoi, Bunkyo-ku, Tokyo 113-8657, Japan

55. Department of Zoology, University of Veteinary Medicine Budapest, H-1078 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), Avda. Ntra. Sra. de la victoria, 16, 22700, Jaca, Spain

59. Department of Biological Sciences, Boise State University, 1910 University Drive, Boise, ID 83703, USA

60. Department of Geosciences and Natural Resource Management, University of Copenhagen, Denmark

61. Department of Agro-Environmental Studies, Hungarian University of Agriculture and Life Sciences, Hungary

62. Institute of Ecology and Earth Sciences, University of Tartu, Estonia

63. Graduate School of Agriculture, Kyoto University, Kitashirakawa Oiwake, Sakyo, Kyoto 606-8502, 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, P.O. Box 7050, SE-75007 Uppsala, Sweden

67. Département des Sciences de l'Environnement, Université du Québec à Trois-Rivières, Canada

68. Institute of Biology, Faculty of Medicine and Life Sciences, University of Latvia, 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, Montréal, Canada

71. Ontario Ministry of Natural Resources, Sault Ste. Marie, Ontario, 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, Germany

74. Department of Vegetation Ecology, Institute of Botany, Czech Academy of Sciences, Průhonice

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, 3-5 Clinicilor Street, 400006 Cluj-Napoca, Romania

78. Emil G. Racoviță Institute, Babeș-Bolyai University, 5-7 Clinicilor Street, 400006 Cluj-Napoca, Romania

79. Department Computational Hydrosystems, Helmholtz Centre for Environmental Research (UFZ), Permoserstr. 15, 04318, Leipzig, Germany

80. Department of Forest Resources, University of Minnesota, USA

81. Hawkesbury Institute for the Environment, Western Sydney University, Penrith, New South Wales, 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, Altensteinstr. 6, 14195, Berlin, Germany

84. Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), 14195, 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, 6020 Innsbruck, Austria

87. Institute for Alpine Environment, Eurac Research, Viale Druso 1, Bozen/Bolzano, Italy

88. ECOMARE, CESAM – Centre for Environmental and Marine Studies, Department of Biology, University of Aveiro, Campus Universitário de Santiago, 3810-193 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 54481, USA

92. Institute for Soil Sciences, HUN-REN Centre for Agricultural Research; H-1022 Budapest, Herman Ottó út 15, Hungary

93. Centre for Nature Positive Solutions, Biology Department, School of Science, RMIT University, Victoria, Australia 3000

94. Institute of Biological Research Cluj, National Institute of Research and Development for Biological Sciences, 48 Republicii Street, 400015, Cluj-Napoca, Romania

95. School of Life and Environmental Sciences, Deakin University, 221 Burwood Hwy, Burwood, Victoria, Australia 3125

96. Research Institute for Nature and Forest (INBO), Geraardsbergen, Belgium

97. Forest Research Institute Malaysia (FRIM), 52109 Kepong, Selangor, Malaysia

98. Department of Crop Production Ecology, Swedish University of Agricultural Sciences, P.O. Box 7043, SE-750 07 Uppsala, Sweden

99. BOKU University, Institute of Soil Research, Department of Ecosystem Management, Climate and Biodiversity, Vienna, Austria

100. Galapagos National Park Directorate, Galapagos, Ecuador

101. Universidade de Coimbra, Departamento de Geografia, Colégio São Jerónimo, Coimbra, Portugal

***Correspondence:**

Yawen Lu: yawenlu@mail.usts.edu.cn

Carlos A. Guerra: carlos.guerra@uc.pt

Abstract

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.

Introduction

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 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: (i) How do landscape factors, including landscape complexity and quantity of different land cover types influence global soil pathogenic fungal diversity? (ii) How does spatial scale influence the effects of landscape variables on soil pathogenic fungal diversity? (iii) 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 assessed 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, 1,000, 2,000, 5,000, 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 β = 0.037; p = 0.001 for richness and β = 0.042; p = 0.001 for relative abundance) and in grassland ecosystems (β = 0.062; p = 0.032 for richness and β = 0.081; p = 0.009 for relative abundance), but decreased the relative abundance of LFSA fungi in forest ecosystems (β = -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 (β = -0.436; $p < 0.001$), Shannon diversity (β = -0.333; $p < 0.001$) of LFSA fungi and relative abundance (β = -0.420; p = 0.011) of RA fungi in grassland ecosystems (Fig. 2a–f). Higher tree cover significantly decreased the richness (β = -0.636; $p < 0.001$) and Shannon diversity (β = -

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 (Supplementary Figs. 1 and 2, 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 variables

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 2,000 m radii increased, then declined at larger scales (5,000–10,000 m), though all significant coefficients remained positive (Fig. 3a, 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 1,000 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 ($\beta = -0.127$; $p = 0.028$), 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, 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 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, 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 1,000 m (Fig. 3d, 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 5,000 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 1,000 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 5,000 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 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 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 unfavourable 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 1,500–2,000 m. Additionally, as the spatial scale increased to the 5,000–10,000 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 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 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[33, 60]. 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, 61], 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[62]. This suggests that increased natural landscape can enhance ecosystem resistance and resilience, potentially by increasing dilution effects at the landscape scale[6, 62]. 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.[63].

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')[64–65] 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)[66], which wraps current best-practice tools for denoising and amplicon sequence variant (ASV) generation[67] and taxonomic annotation[68] against the UNITE database (v8.2)[69]. 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[65]. 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 2,694 leaf/fruit/seed-associated fungal ASVs and 1.66% belonged to 302 root-associated fungal ASVs.

Landscape factor calculation

To quantify the complexity of landscape structures, we calculated landscape metrics using the *landscapemetrics* package [70]. We used a land cover map with 100 m resolution from Copernicus

Global Land Service[71], together with the geographic coordinates, converted to Cylindrical Equal Area map projection[72]. 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, 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 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). 1,000–2,000 m radii are the most commonly used medium-scale spatial distances[19]. In addition, larger spatial distances of 5,000–10,000 m radii were 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, 73]. 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[74]. The climatic variables included MAT and MAP that were extracted from a processed global layer CHELSA with 1 km resolution[75]. 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[76].

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[77]. 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[78]. 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 complexity 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[79], 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[80]. 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[78].

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[81]. 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 (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[82]. 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 distances[83]. 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[84].

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.

References

1. Bever, J. D., Mangan, S. A. & Alexander, H. M. Maintenance of plant species diversity by pathogens. *Annu. Rev. Ecol. Evol. Syst.* **46**, 305–325 (2015).

2. Liu, X. et al. Coexistence is stabilized by conspecific negative density dependence via fungal pathogens more than oomycete pathogens. *Ecology* **103**, e3841 (2022).

3. Paseka, R. E. et al. Disease-mediated ecosystem services: Pathogens, plants, and people. *Trends Ecol. Evol.* **35**, 731–743 (2020).

4. Banerjee, S. & van der Heijden, M. G. Soil microbiomes and one health. *Nat. Rev. Microbiol.* **21**, 6–20 (2023).

5. Zang, Z. F. et al. Contrasting roles of plant, bacterial, and fungal diversity in soil organic carbon accrual during ecosystem restoration: A meta-analysis. *Sci. Total Environ.* **930**, 172767 (2024).

6. Mahon, M. B. et al. A meta-analysis on global change drivers and the risk of infectious disease. *Nature* **629**, 830–836 (2024).

7. FAO. New standards to curb the global spread of plant pests and diseases (2021).

8. Savary, S. et al. The global burden of pathogens and pests on major food crops. *Nat. Ecol. Evol.* **3**, 430–439 (2019).

9. Delgado-Baquerizo, M. et al. The proportion of soil-borne pathogens increases with warming at the global scale. *Nat. Clim. Change* **10**, 550–554 (2020).

10. Tedersoo, L. et al. Global diversity and geography of soil fungi. *Science* **346**, 1256688 (2014).

11. Mikryukov, V. et al. Connecting the multiple dimensions of global soil fungal diversity. *Sci. Adv.* **9**, eadj8016 (2023).

12. Delavaux, C. S. et al. Root pathogen diversity and composition varies with climate in undisturbed grasslands, but less so in anthropogenically disturbed grasslands. *ISME J.* **15**, 304–317 (2021).

13. Lekberg, Y. et al. Nitrogen and phosphorus fertilization consistently favor pathogenic over mutualistic fungi in grassland soils. *Nat. Commun.* **12**, 1–8 (2021).

14. Makiola, A. et al. Environmental and plant community drivers of plant pathogen composition and richness. *New Phytol.* **233**, 496–504 (2021).

15. Semchenko, M. et al. Deciphering the role of specialist and generalist plant-microbial interactions as drivers of plant-soil feedback. *New Phytol.* **234**, 1929–1944 (2022).

16. Chaudhary, V. B., Aguilar-Trigueros, C. A., Mansour, I. & Rillig, M. C. Fungal dispersal across spatial scales. *Annu. Rev. Ecol. Evol. Syst.* **53**, 69–85 (2022).

17. Chen, S. & Zhang, Y. Research progress on biodiversity in the rural landscape. *Biodivers. Sci.* **29**, 1411 (2021).

18. Mennicken, S. et al. Effects of past and present-day landscape structure on forest soil microorganisms. *Front. Ecol. Evol.* **8**, 118 (2020).

19. Le Provost, G. et al. Contrasting responses of above-and belowground diversity to multiple components of land-use intensity. *Nat. Commun.* **12**, 3918 (2021).

20. Grilli, G. et al. Fungal diversity at fragmented landscapes: synthesis and future perspectives. *Curr. Opin. Microbiol.* **37**, 161–165 (2017).

21. Gámez-Virués, S. et al. Landscape simplification filters species traits and drives biotic homogenization. *Nat. Commun.* **6**, 1–8 (2015).

22. Heikkinen, R. K., Luoto, M., Virkkala, R. & Rainio, K. Effects of habitat cover, landscape structure and spatial variables on the abundance of birds in an agricultural-forest mosaic. *J. Appl. Ecol.* **41**, 824–835 (2004).

23. Eisenhauer, N. et al. The heterogeneity–diversity–system performance nexus. *Natl. Sci. Rev.* **10**, nwad109 (2023).

24. Betts, M.G. et al. Extinction filters mediate the global effects of habitat fragmentation on animals. *Science* **366**, 1236–1239 (2019).

25. Pfeifer, M. et al. Creation of forest edges has a global impact on forest vertebrates. *Nature* **551**, 187–191 (2017).

26. Fahrig, L. et al. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecol. Lett.* **14**, 101–112 (2011).

27. Vannette, R. L., Leopold, D. R. & Fukami, T. Forest area and connectivity influence root-associated fungal communities in a fragmented landscape. *Ecology* **97**, 2374–2383 (2016).

28. Griffith, J. A., Martinko, E. A. & Price, K. P. Landscape structure analysis of Kansas at three scales. *Landsc. Urban Plan.* **52**, 45–61 (2000).

29. Laterra, P., Orúe, M. E. & Booman, G. C. Spatial complexity and ecosystem services in rural landscapes. *Agric. Ecosyst. Environ.* **154**, 56–67 (2012).

30. MacArthur, R. H. & MacArthur, J. W. On bird species diversity. *Ecology* **42**, 594–598 (1961).

31. Lu, Y. W., Zheng, S. L., Tomlinson, K. W. & Liu, J. J. Contrasting responses of plant herbivory and disease to local and landscape drivers. *Plant Soil* **501**, 75–87 (2024).

32. García-Guzmán, G., Trejo, I. & Sánchez-Coronado, M. E. Foliar diseases in a seasonal tropical dry forest: Impacts of habitat fragmentation. *For. Ecol. Manag.* **369**, 126–134 (2016).

33. Mony, C., Uroy, L., Khalfallah, F., Haddad, N. & Vandenkoornhuyse, P. Landscape connectivity for the invisibles. *Ecography* **2022**, e06041 (2022).

34. Holdenrieder, O., Pautasso, M., Weisberg, P. J. & Lonsdale, D. Tree diseases and landscape processes: the challenge of landscape pathology. *Trends Ecol. Evol.* **19**, 446–452 (2004).

35. Tedersoo, L. et al. Regional-scale in-depth analysis of soil fungal diversity reveals strong pH and plant species effects in Northern Europe. *Front. Microbiol.* **11**, 1953 (2020).

36. Delaune, T. et al. Landscape drivers of pests and pathogens abundance in arable crops. *Ecography* **44**, 1429–1442 (2021).

37. Zhang, D. et al. Effects of urbanization intensity on forest structural-taxonomic attributes, landscape patterns and their associations in Changchun, Northeast China: implications for urban green infrastructure planning. *Ecol. Indic.* **80**, 286–296 (2017).

38. Melo, G. L., Sponchiado, J., Cáceres, N. C. & Fahrig, L. Testing the habitat amount hypothesis for South American small mammals. *Biol. Conserv.* **209**, 304–314 (2017).

39. Tscharntke, T. et al. Landscape moderation of biodiversity patterns and processes-eight hypotheses. *Biol. Rev.* **87**, 661–685 (2012).

40. Makiola, A. et al. Land use is a determinant of plant pathogen alpha- but not beta-diversity. *Mol. Ecol.* **28**, 3786–3798 (2019).

41. Liu, J. J. et al. Forest fragmentation in China and its effect on biodiversity. *Biol. Rev.* **94**, 1636–1657 (2019).

42. Jandrasits, L. & Fischl, G. The microscopic fungi of orchid species in the Őrség National Park. *Int. J. Hortic. Sci.* **15**, 31–36 (2009).

43. Reschke, K. et al. Fungal diversity in the tropics: *Entoloma* spp. in Panama. *Mycol. Prog.* **21**, 93–145 (2022).

44. Plantegenest, M., Le May, C. & Fabre, F. Landscape epidemiology of plant diseases. *J. R. Soc. Interface* **4**, 963–972 (2007).

45. Liu, X., Zhang, L., Huang, M. J. & Zhou, S. R. Plant diversity promotes soil fungal pathogen richness under fertilization in an alpine meadow. *J. Plant Ecol.* **14**, 323–336 (2021).

46. Vahter, T. et al. Landscapes, management practices and their interactions shape soil fungal diversity in arable fields-Evidence from a nationwide farmers' network. *Soil Biol. Biochem.* **168**, 108652 (2022).

47. Zhang, L. et al. Fungicides reduce soil microbial diversity, network stability and complexity in wheat fields with different disease resistance. *Appl. Soil Ecol.* **201**, 105513 (2024).

48. Schils, R. L. et al. Permanent grasslands in Europe: Land use change and intensification decrease their multifunctionality. *Agric. Ecosyst. Environ.* **330**, 107891 (2022).

49. Golan, J. J. & Pringle, A. Long-distance dispersal of fungi. *Microbiol. Spectr.* **5**, 10–1128 (2017).

50. Schnabel, F. et al. Tree diversity increases forest temperature buffering. *Ecol. Lett.* **28**, e70096 (2023).

51. Shi, L. L. et al. Changes in fungal communities across a forest disturbance gradient. *Appl. Environ. Microbiol.* **85**, e00080–19 (2019).

52. Tedersoo, L., Bahram, M., & Zobel, M. How mycorrhizal associations drive plant population and community biology. *Science* **367**, eaba1223 (2020).

69. Põlme, S. et al. FungalTraits: a user-friendly traits database of fungi and fungus-like stramenopiles. *Fungal Divers.* **105**, 1–16 (2020).

53. Benítez-Malvido, J. & Lemus-Albor, A. (2005). The seedling community of tropical rain forest edges and its interaction with herbivores and pathogens. *Biotropica* **37**, 301–313 (2005).

54. Ichihara, Y. & Yamaji, K. Effect of light conditions on the resistance of current-year Fagus crenata seedlings against fungal pathogens causing damping-off in a natural beech forest: fungus isolation and histological and chemical resistance. *J. Chem. Ecol.* **35**, 1077–1085 (2009).

55. Perrott, J. K. & Armstrong, D. P. Aspergillus fumigatus densities in relation to forest succession and edge effects: implications for wildlife health in modified environments. *EcoHealth* **8**, 290–300 (2011).

56. McConnaughay, K. D. M. & Bazzaz, F. A. The occupation and fragmentation of space: consequences of neighbouring roots. *Funct. Ecol.* **6**, 704–710 (1992).

57. Gryndler, M. et al. Molecular detection of *Entoloma* spp. associated with roots of rosaceous woody plants. *Mycol. Prog.* **9**, 27–36 (2010).

58. Kinoshita, A., Sasaki, H. & Nara, K. Multiple origins of sequestrate basidiomes within *Entoloma* inferred from molecular phylogenetic analyses. *Fungal Biol.* **116**, 1250–1262 (2012).

59. Wiens, J. A. Landscape mosaics and ecological theory. In Mosaic Landscapes and Ecological Processes (eds Hansson, L., Fahrig, L. & Merriam, G.) 1–26 (Springer, 1995).

60. Lu, Y. W., Zheng, S. L., Tomlinson, K. W. & Liu, J. J. Contrasting responses of plant herbivory and disease to local and landscape drivers. *Plant Soil* **501**, 75–87 (2024).

61. Rottstock, T., Joshi, J., Kummer, V. & Fischer, M. Higher plant diversity promotes higher diversity of fungal pathogens, while it decreases pathogen infection per plant. *Ecology* **95**, 1907–1917 (2014).

62. Heintz-Buschart, A. et al. Microbial diversity-ecosystem function relationships across environmental gradients. *Res. Ideas Outcomes* **6**, e52217 (2020).

63. Gardes, M. & Bruns, T. D. ITS primers with enhanced specificity for basidiomycetes-application to the identification of mycorrhizae and rusts. *Mol. Ecol.* **2**, 113–118 (1993).

64. White, T. J., Bruns, T., Lee, S. & Taylor, J. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In *PCR Protocols* (eds Innis, M. A., Gelfand, D. H., Sninsky, J. J. & White, T. J.) 315–322. (Academic Press, New York, 1990).

65. Weißbecker, C., Schnabel, B. & Heintz-Buschart, A. Dadasnake, a Snakemake implementation of DADA2 to process amplicon sequencing data for microbial ecology. *GigaScience* **9**, giaa135 (2020).

66. Callahan, B. J. et al. DADA2: High-resolution sample inference from Illumina amplicon data. *Nat. Methods* **13**, 581–583 (2016).

67. Schloss, P. D. & Westcott, S. L. Assessing and improving methods used in operational taxonomic unit-based approaches for 16S rRNA gene sequence analysis. *Appl. Environ. Microbiol.* **77**, 3219–3226 (2011).

68. Nilsson, R. H. et al. The UNITE database for molecular identification of fungi: handling dark taxa and parallel taxonomic classifications. *Nucleic Acids Res.* **47**, D259–D264 (2019).

70. Hesselbarth, M. H., Sciaini, M., With, K. A., Wiegand, K. & Nowosad, J. landscapemetrics: An open-source R tool to calculate landscape metrics. *Ecography* **42**, 1648–1657 (2019).

71. Buchhorn, M. et al. Copernicus Global Land Service: Land Cover 100m: collection 3: epoch 2018: Globe. Zenodo https://doi.org/10.5281/zenodo.3518038 (2020).

72. Tobler, W. R. The hyperelliptical and other new pseudo cylindrical equal area map projections. *J. Geophys. Res.* **78**, 1753–1759 (1973).

73. Vizzari, M. & Sigura, M. Landscape sequences along the urban–rural–natural gradient: A novel geospatial approach for identification and analysis. *Landsc. Urban Plan.* **140**, 42–55 (2015).

74. Fick, S. E. & Hijmans, R. J. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37**, 4302–4315 (2017).

75. Karger, D. N. et al. CHELSA climatologies at high resolution for the earth's land surface areas (Version 1.1). *World Data Center for Climate*. https://doi.org/10.1594/WDCC/CHELSA_v1_1 (2016).

76. Hengl, T. et al. SoilGrids250m: Global gridded soil information based on machine learning. *PLoS One* **12**, e0169748 (2017).

77. Stasinopoulos, D. M. & Rigby, R. A. Generalized additive models for location scale and shape (GAMLSS) in R. *J. Stat. Softw.* **23**, 1–46 (2008).

78. Barceló, M., van Bodegom, P. M., Tedersoo, L., Olsson, P. A. & Soudzilovskaia, N. A. Mycorrhizal tree impacts on topsoil biogeochemical properties in tropical forests. *J. Ecol.* **110**, 1271–1282 (2022).

79. Bivand, R. S. & Wong, D. W. Comparing implementations of global and local indicators of spatial association. *Test* **27**, 716–748 (2018).

80. Viechtbauer, W. Conducting meta-analyses in R with the metafor package. *J. Stat. Softw.* **36**, 1–48 (2010).

81. Sanchez, G. *PLS path modeling with R*. (Trowchez Editions, Berkeley, 2013).

82. Manion, G. et al. GDM: Generalized dissimilarity modeling. R package version, 1.6.0–7. https://cran.r-project.org/web/packages/gdm/index.html (2018).

83. Ferrier, S., Manion, G., Elith, J. & Richardson, K. Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Divers. Distrib.* **13**, 252–264 (2007).

84. R Development Core Team. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing (2020).

Acknowledgements

We thank all the people who helped in sampling and experiment processes and volunteering researchers from the networks of ILTER (https://www.ilter.network) and eLTER (https://elter-ri.eu). We also thank all the landowners for the access to their lands. We thank JiaJia Liu for his contribution to the research idea and manuscript revision, as well as supporting Y.L. for participation in the iSBio project. We thank Yuanyuan Huang, Shengen Liu for advice on data analysis. We acknowledge funding from the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena- Leipzig of the German Research Foundation (FZT118, 202548816), and from The Swedish Research Council for Environment, Agricultural sciences and Spatial Planning (Formas, grant no 2020-02339). Sequencing was financed by the German Research Foundation (DFG, BU 941/32-1 | EI 862/27-1 | HE 8266/4-1 | KU 1367/14-1 | WE 6579/2-1 to F.B., N.E., A.H.-B., K.Kü., C.-E.W.). Sequence data analysis was performed at the High-Performance Computing (HPC) Cluster EVE, a joint effort of both the Helmholtz Centre for Environmental Research-UFZ and the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, whose administrators are thanked for excellent support. Moreover, we acknowledge support by the DFG grants EI 862/29-1 and EI 862/31-1 (to N.E.). Y.L. acknowledges funding from China Scholarship Council (202106100117). F.T.M. acknowledges support by the King Abdullah University of Science and Technology (KAUST) and the KAUST Climate and Livability Initiative. G.W. acknowledges financial support by the Austrian National Science Fund (FWF, grant no. P31669). A.G. acknowledges Fondecyt 1201643 & FB210006 & ICN2021_044. Zs.K. acknowledges the MATE Research Excellence Program MATE-K/1011–

32/2024). M.B. acknowledges the Scientific Grant Agency VEGA (Grant No. 2/0045/22). K.L. acknowledges support to the H.J. Andrews Experimental Forest and Long Term Ecological Research (LTER) program under NSF grant LTER8 DEB-2025755. A.S.F.A. acknowledges CNPq-Brazil for his Fellowship of Research (grant 301755/2022-1). Funding was provided by CNPq-Brazil (Grant No. 304636/2022-3) to A.C.. A.P. and M.C. acknowledges that this work has benefited from the equipment and framework of the COMP-HUB and COMP-R Initiatives, funded by the 'Departments of Excellence' program of the Italian Ministry for University and Research (MIUR, 2018-2022 and MUR, 2023-2027). L.v.d.B, R.C. and R.M. thank Conaf (Chile) and Communidad Agricola Quebrada de Talca (Chile), and were supported by DFG (Priority Program SPP-1803 'EarthShape: Earth Surface Shaping by Biota', TI 338/14-1 and BA 3843/6-1). L.v.d.B thanks additional support from ANID PIA/ACT 210038. A.I.S acknowledges the FCT - Foundation for Science and Technology, I.P. through the individual project CEECIND/00962/2017 (DOI: 10.54499/CEECIND/00962/2017/CP1459/CT0008), for the financial support to CESAM under the project/grant UID/50006 + LA/P/0094/2020 (doi.org/10.54499/LA/P/0094/2020). A.R.G. and R.L.M. are grateful to CNPq-Brazil (PELD - Grant No. 441610/2016-1) for supporting this study. H.J. and F.Z. thank the Galapagos National Park Directorate and the Ecuadorian Ministry of Environment, Water and Ecological Transition for their support and for issuing permit numbers MAE-DNB-CM-2016-0043 and 006-2021-EXP-CM-FAU-DBI/MAAE. This publication is contribution number 2664 of the Charles Darwin Foundation for the Galapagos Islands. P.P. was supported by the long-term research development project RVO 67985939 (Czech Academy of Sciences). S.M.T.-T. was supported by an Australian Research Council DECRA Fellowship (DE210101029). I.D. thanks UNILEVER and EKATERRA for sponsoring tea bags. I.F. acknowledges support by Scientific Council of the

University of Nyíregyháza. T.M.U. was supported through the Nucleu Program as part of the 2022–2027 National Research, Development and Innovation Plan, funded by MCID, project no. PN23020401, contract no. 7N/03.01.2023. C.A.G. was funded by the Portuguese Foundation for Science and Technology, as part of Project SoilRecon (PTDC/BIA-CBI/2340/2020). Q.P. thanks the Walloon forest service (Service Public de Wallonie-Département de la Nature et des Forêts) for its financial support to the installation and maintenance of the FORBIO-Gedinne site through the 5-year research programme 'Accord-cadre de recherches et de vulgarisation forestières'. A.St. and P.B.R. acknowledge the National Science Foundation, Biological Integration Institutes grant NSF-DBI-2021898. I.O. and K.Kr. were supported by the Estonian Research Council grant PRG916. C.B. and H.C.S. were supported by projects AdaptForGrazing (02/C05-i03/2021.PPRR-C05-i03-I-000035), SustInAfrica (EU H2020 R&I GA 861924), and Portuguese National Funds through 'Fundação para a Ciência e Tecnologia' (FCT) within the cE3c Unit funding (DOI:10.54499/UIDB/00329/2020). G.G. was supported by the grant DEB 0620910, 1831952 and 2425484 from the National Science Foundation as part of the Luquillo LTER. The U.S. Forest Service (Department of Agriculture) and University of Puerto Rico gave additional support. P.F. was supported by the Swedish Research Council FORMAS (2020-01100). S.L. was supported by the Integrated Monitoring Programme contract 221-22-006 financed by the Swedish Environmental Protection Agency. Financial support was provided by the EU Horizon 2020 project eLTER PLUS (grant 871128) to P.H.. M.Di. receives financial support from the SwissFederal Office of the Environment. S.K.-R. was supported by Novo Nordisk Foundation grant NNF20OC0059948. P.D.T. was supported by the GreenMount project (PN-IV-P2-2.1-TE-2023-0726), funded by UEFISCDI Romania. S.E.V. was supported by an Australian Research Council Linkage project, LP190100844. H.K. and K.H. were supported by the Grant-in-Aid for

Scientific Research (B) (17H03835 to H.K. and 19H02999 to K.H.) from Japan Society for the Promotion of Science. C.C. was supported by the Long-Term Ecological Research project (2006–2025), Ministry of Agriculture, Taiwan. R.G.G. was supported by a grant (PR3/23-30823) from Complutense University. U.H. and M.Frei. received financial support by the German Research Foundation (DFG) Infrastructure Priority Program 1374 “Biodiversity-Exploratories” (HA 4597/6-4). H.B. and S.T. acknowledge the support by the BEF-China platform and the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) – 35758305 (FOR891); 319936945 (GRK2324).

Author Contributions Statement

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., F.Z.

Competing Interests Statement The authors declare no competing interests.

Figure legends

Figure 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.

Figure 2. Predictors and their relative contributions to leaf/fruit/seed-associated (LFSA) and root-associated (RA) fungal alpha diversity. Panels (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. Panel (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 *** $p \leq 0.001$; ** $p \leq 0.01$; * $p \leq 0.05$. See Supplementary Table 1 for details and the exact *p*-values.

Figure 3. Landscape effects on leaf/fruit/seed-associated and root-associated fungal alpha diversity across spatial scales. Leaf/fruit/seed-associated (LFSA) and root-associated (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, 1,000 m, 2,000 m, 5,000 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 *** $p \leq 0.001$; ** $p \leq 0.01$; * $p \leq 0.05$. 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.

Figure 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

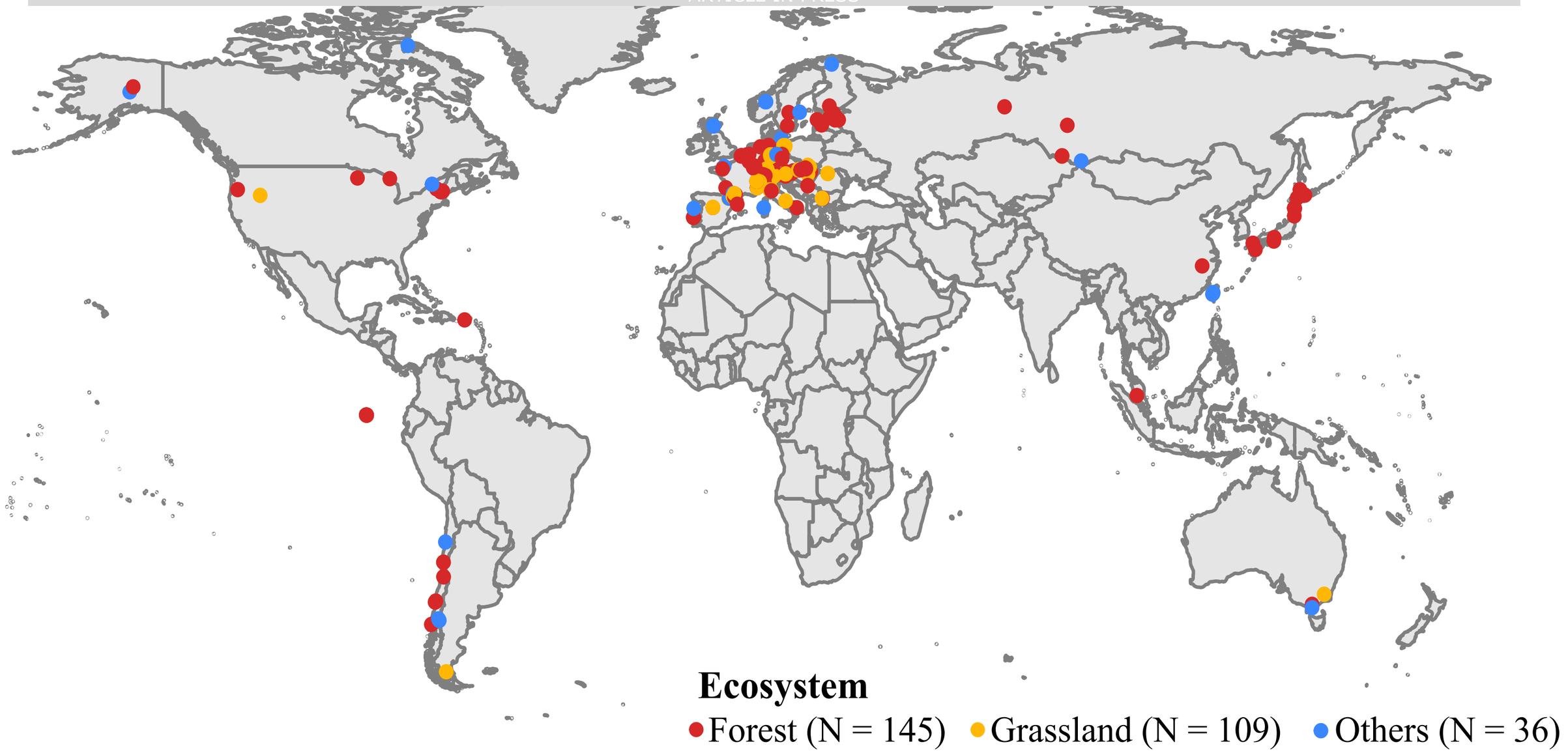
adjustment for multiple comparisons (n = 36 biologically independent samples). Effect size values and associated *p*-values are reported for each category.

Figure 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); Panels (c) and (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.

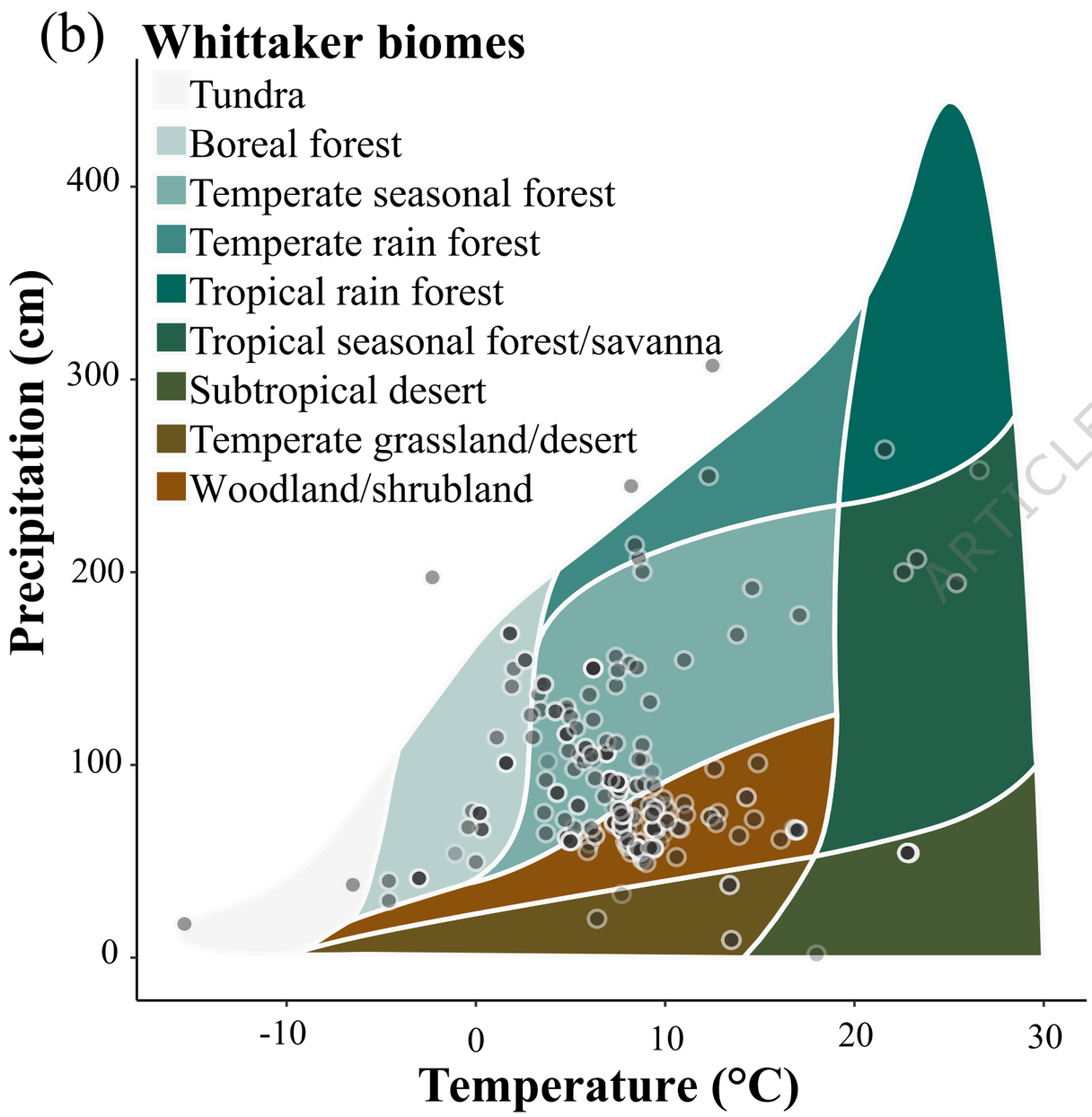
Editorial summary:
How landscapes are arranged affects soil pathogenic fungi worldwide. The authors reveal the global pattern and pronounced scale-dependency of landscape complexity and land-cover quantity on soil pathogenic fungal diversity.

Peer review information: *Nature Communications* thanks the anonymous reviewers for their contribution to the peer review of this work. A peer review file is available.

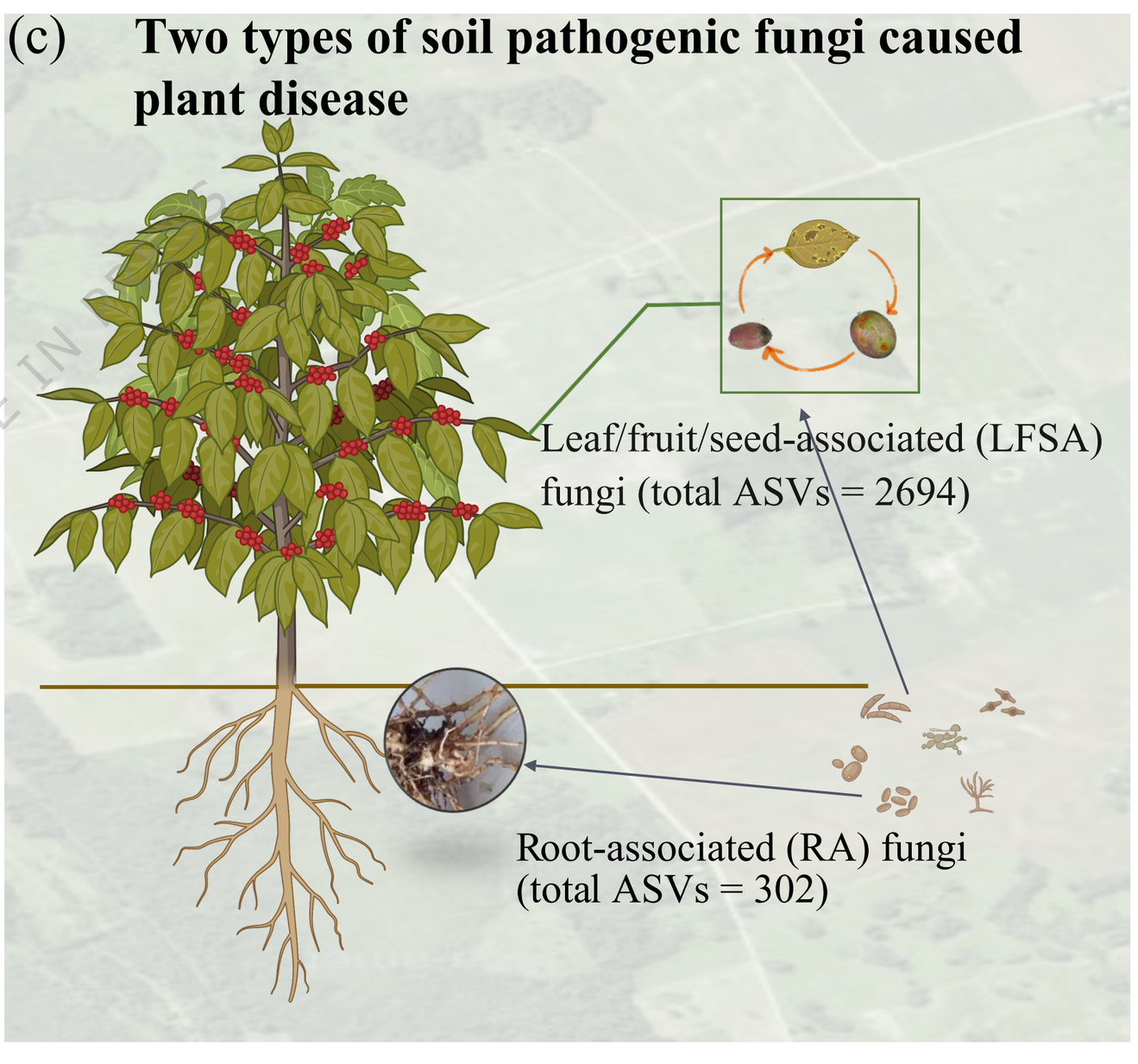
(a)



(b) **Whittaker biomes**



(c) **Two types of soil pathogenic fungi caused plant disease**



Overall (N = 511) | Forest (N =264) | Grassland (N = 183)

Leaf/fruit/seed-associated (LFSA) fungi

Root-associated (RA) fungi

Landscape complexity
Grass cover
Crop cover
Tree cover
Longitude
Latitude
Elevation
MAT
MAP
Clay
Silt
pH
Nitrogen
C/N ratio

Richness
Shannon diversity
Relative abundance

(a) (b) (c) (d) (e) (f)

-0.75 -0.25 0.25 0.75
Parameter estimates

(g)

Overall | Forest | Grassland

Richness LFSA fungi (0.62) (0.64) (0.64)
Richness RA fungi (0.25) (0.38) (0.40)
Shannon LFSA fungi (0.58) (0.58) (0.58)
Shannon RA fungi (0.21) (0.37) (0.37)
Abundance LFSA fungi (0.52) (0.62) (0.56)
Abundance RA fungi (0.17) (0.35) (0.25)

0 20 40 60 80 100
Relative contribution to Pseudo−R^2

Variable: Landscape complexity, Grass cover, Crop cover, Tree cover, Longitude, Latitude, Elevation, MAT, MAP, Clay, Silt, pH, Nitrogen, C/N ratio