Title: Phylotype diversity within soil fungal functional groups drives ecosystem stability

Authors: Shengen Liu[1,2,3], Pablo García-Palacios[4], Leho Tedersoo[5,6], Emilio Guirado[7,8], Marcel van der Heijden[9,10], Cameron Wagg[11], Dima Chen[1], Qingkui Wang[3,12], Juntao Wang[13], Brajesh K. Singh[13,14], Manuel Delgado-Baquerizo[2,15]*

Affiliations:
[1]Engineering Research Center of Eco-Environment in Three Gorges Reservoir Region of Ministry of Education, China Three Gorges University, Yichang, 443000, China.
[2]Laboratorio de Biodiversidad y Funcionamiento Ecosistémico. Instituto de Recursos Naturales y Agrobiología de Sevilla (IRNAS), CSIC, Av. Reina Mercedes 10, E-41012, Sevilla, Spain.
[3]Huitong Experimental Station of Forest Ecology, CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Shenyang, 110164, PR China.
[4]Instituto de Ciencias Agrarias, Consejo Superior de Investigaciones Científicas, 115 dpdo., 28006 Madrid, Spain.
[5]Mycology and Microbiology Center, University of Tartu, Tartu, 51005, Estonia.
[6]College of Science, King Saud University, Riyadh, 11451, Saudi Arabia.
[7]Multidisciplinary Institute for Environment Studies “Ramon Margalef” University of Alicante, Edificio Nuevos Institutos, Carretera de San Vicente del Raspeig s/n San Vicente del Raspeig, 03690, Alicante, Spain
[8]Andalusian Center for Assessment and Monitoring of Global Change (CAESCG), University of Almeria, 04120, Almeria, Spain
[9]Plant-Soil Interactions Group, Agroscope, Zurich, 8057 Switzerland.
[10]Department of Plant and Microbial Biology, University of Zurich, Zurich, 8057 Switzerland.
[11]Fredericton Research and Development Centre, Agriculture and Agri-Food Canada, Fredericton, New Brunswick, E3B4Z7, Canada.
[12]School of Forestry & Landscape Architecture, Anhui Agricultural University, Hefei, 230036 China.
[13]Hawkesbury Institute for the Environment, Western Sydney University, Richmond, NSW, 2753 Australia.
[14]Global Centre for Land-Based Innovation, Western Sydney University, Penrith South DC, NSW 2751, Australia
[15]Unidad Asociada CSIC-UPO (BioFun). Universidad Pablo de Olavide, 41013 Sevilla, Spain.

***Corresponding author:** Manuel Delgado-Baquerizo; E-mail addresses: M.DelgadoBaquerizo@gmail.com

Abstract

Soil fungi are fundamental to plant productivity, yet their influence on the temporal stability of global terrestrial ecosystems, and their capacity to buffer plant productivity against extreme drought events, remains uncertain. Here, we combined three independent global field surveys of soil fungi with a satellite-derived temporal assessment of plant productivity, and report that phylotype richness within particular fungal functional groups drives the stability of terrestrial ecosystems. The richness of fungal decomposers was consistently and positively associated with ecosystem stability worldwide, while the opposite pattern was found for the richness of fungal plant pathogens, particularly in grasslands. We further demonstrated that the richness of soil decomposers was consistently positively linked with higher resistance of plant productivity in response to extreme drought events, while that of fungal plant pathogens showed a general negative relationship with plant productivity resilience/resistance patterns. Together, our work provides evidence supporting the critical role of soil fungal diversity to secure stable plant production over time in global ecosystems, and as to buffer against extreme climate events.

Introduction

Soil fungal communities comprise a large fraction of the global terrestrial biomass and diversity[1-3], and they are intimately linked to plants through multiple processes such as plant nutrient uptake, organic matter decomposition, and pathogenesis that ultimately determine plant production[3-9]. Yet, the importance of soil fungi for ecosystem stability, a fundamental ecosystem property defined as the ratio of the temporal mean of plant productivity to its standard deviation[10], is practically unknown. We posit that soil fungal diversity may promote ecosystem stability by increasing the resistance and resilience of plant production during and after drought events[11,12], which are increasing in frequency worldwide[13]. For instance, the diversity of fungal decomposers is responsible for the breakdown of plant litter[14,15], providing a continuous source of available nutrients for stable plant production[3,14]. Similarly, the biodiversity of mycorrhizal fungi is critical for tree growth[16], and helps plants withstand climate extremes such as droughts, promoting plant production resilience after these dramatic events[12,17]. On the contrary, a greater proportion of soil-borne plant pathogenic fungi may lead to unstable plant productivity[18]. However this negative effect on ecosystem stability can also be moderated by mycorrhizal fungi via decreasing antagonistic interactions[19]. A conspicuous fungal diversity-ecosystem stability relationship would imply that soil biodiversity decline with climate change and land use intensification[18,20] may destabilize ecosystems. Assessing whether the stabilizing role of soil fungal diversity is consistent across a wide range of plant, climatic, and soil conditions is, therefore, critical to inform policy and management measures aimed at conserving soil biodiversity and promoting ecosystem services under anthropogenic environmental change.

Here, we combined three independent global field surveys of soil fungal diversity with satellite-derived metrics of ecosystem stability, resistance, and resilience to drought events. We first investigated the relationship between the diversity (richness; number of phylotypes after amplicon sequencing of the Internal Transcribed Spacer (ITS) gene) within major soil fungal functional groups (i.e., soil decomposers, potential fungal plant pathogens, and mycorrhizae as identified in the FungalTraits database[21]) and ecosystem stability (the ratio of the mean Normalized Difference Vegetation Index, NDVI, to its standard deviation over 2001 - 2018) in three independent global field surveys (global survey #1: 235 sites[22], and global survey #2: 351 sites[23], global survey #3: 87 sites[24], Extended Data Fig. 1-2). Then, we assessed the linkages between the diversity within soil fungal functional groups and the ecosystem resistance (capacity of plant productivity to remain the same in response to a drought event) and resilience (capacity of plant productivity to return to the original levels of productivity after a drought event) using NDVI temporal data and the long-term Standardized Precipitation and Evaporation Index (SPEI)[25]. Our analysis based on three independent global field surveys provides a complementary assessment of the linkages between soil fungal diversity and ecosystem stability.

Results and Discussion

Our findings provide real-world evidence that diversity (number of phylotypes) within soil fungal functional groups drives the stability of global ecosystems (Figs. 1-2). First, we found that the diversity of soil fungal decomposers is positively related with ecosystem stability (Fig. 1a,d,g). Remarkably, the positive association between the diversity of fungal decomposers and ecosystem stability was maintained after accounting for geographic location, climate, vegetation types, and soil properties (Figs. 3-4). In fact, fungal diversity could explain unique variation in ecosystem stability. Climate also explained unique variation, however, we found that the shared effects of multiple biotic and abiotic variables drove most of the explained variation (Fig. 3; Extended Data Figs. 3-5). The direction of the predictors' effect was consistent among the three global surveys, although the magnitude varied (Fig 2; Extended Data Figs. 6-8), which may be due to differences in sampling design and experimental methods (e.g., primer sets and sequencing technologies). Similarly, we also found that our results were maintained after accounting for plant richness, which was available for all locations in global survey #2 (Extended Data Figs. 9-10 and Supplementary Fig. 1).

We further found a consistent and negative correlation between the diversity of fungal plant pathogens and ecosystem stability (Fig. 1b, h), particularly across the global grasslands included in global surveys #1 and #2 (Fig. 3a, b). This negative correlation between the diversity of fungal plant pathogens and ecosystem stability was also apparent across all biomes when we statistically controlled for key environmental factors (Figs. 3 and 4). On the contrary, we did not find consistently significant correlations between the diversity of mycorrhizal, ectomycorrhizal (EcM), arbuscular mycorrhizal (AMF) or endophytic fungi (Fig. 1 and Supplementary Fig. 2) and ecosystem stability. Despite the absence of a significant stabilizing role for the diversity of mycorrhizal fungi (Fig. 1c,f,i; Supplementary Fig. 3 for results within EcM forests), our results showed a consistent hump-shaped relationship between the estimated basal area of AM-associated or EcM- plants (based on ref.[26]) and ecosystem stability (Fig. 5a-f), suggesting that the proportion of plant functional groups still play key roles in sustaining ecosystem stability. In fact, our analyses revealed a positive association between the proportion of AM plants[26] and ecosystem stability (Fig. 3a,b,c) when other environmental factors were simultaneously considered. Our multiple statistical approaches supported our hypotheses. However, future microcosm studies should aim to experimentally test the reported relationships between fungal diversity and ecosystem stability under controlled conditions.

Collectively, our analyses indicate a consistent stabilizing role of the diversity of soil fungal decomposers across terrestrial ecosystems. A greater diversity of soil decomposers may provide a constant source of nutrients for plant growth[3-6], connecting the aboveground and belowground worlds through the decomposition process. Experimental and local evidence from microcosm studies indicate that asynchrony among taxa mediates the stabilizing role of soil biodiversity[27-29], as found in plant communities[30-34]. To confirm whether microbial asynchrony is driving the global fungal diversity-stability relationship, new investigations considering shifts in community composition over time need to be conducted in the future[31], which is logistically demanding and remains a gap to be considered in future global soil biodiversity monitoring networks[3]. Our results further indicate that the diversity of soil decomposers positively influence ecosystem productivity while simultaneously reducing its variability, resulting in a higher ecosystem stability; the opposite pattern is found for the diversity of fungal plant pathogens (Extended Data Figs. 6-8). These contrasted results suggest that while maintaining highly diverse fungal decomposers supporting complex processes such as organic matter decomposition and nutrient release could help promoting ecosystem stability, supporting the diversity of pathogens could have the opposite effect impacting plant stability, especially in grasslands[35-37]. These findings suggest that losses in the diversity of decomposers, or increases in that of fungal plant pathogens (e.g., with warming and over-fertilization)[18,38], could contribute to destabilize global ecosystems, which is in line with the buffering effect hypothesis[30-35]. For instance, mean annual temperature (MAT), which is known to be a fundamental driver of soil fungal communities[18,23], was also found to be an essential driver of ecosystem stability (Figs. 3-4). Moreover, we found a consistent and positive connection between the dissimilarity in community composition of soil decomposers and potential fungal plant pathogens with dissimilarity in ecosystem stability in two independent global surveys (Supplementary Figs. 4-5; additional analyses in Supplementary Appendix 1). These important findings suggest that changes in the diversity and community composition of fungal functional groups associated with anthropogenic activities, including global warming, could cause indirect effects on ecosystem stability that need to be considered when investigating the stability of terrestrial ecosystems.

We then investigated the relationships between the diversity of fungal functional groups and the resistance and resilience of plant productivity to extreme drought events[25]. The ecosystems included in this study have suffered multiple droughts over the last two decades (Extended Data Fig. 2), and we determined the resistance and resilience of NDVI to these events using remote sensing (Methods). Our results suggest that higher diversity of fungal decomposers and root endophytes are consistently and positively associated with the resistance of ecosystem productivity during drought events (Fig. 6a,b,e,i). On the contrary, higher richness of plant pathogens was negatively associated with the resistance (Fig. 6c,k) or resilience (Fig. 6g) of ecosystem productivity during, or after, drought events. Moreover, we found that the diversity of mycorrhizal fungi is positively associated with resilience of ecosystem productivity after drought events (Fig. 6d,h). In other words, plant productivity in ecosystems with higher mycorrhizal and root endophyte richness recovered faster from extreme drought events, suggesting these fungi play an important role in promoting ecosystem stability. We further showed that the diversity of fungal decomposers, plant pathogens and mycorrhizal fungi drove ecosystem resistance and resilience beyond the role of climate, ecosystem types, and soil properties (Extended Data Figs. 3-5,10). Together, our findings indicate that diversity of fungal functional groups drives ecosystems stability via regulating plant productivity resistance and resilience to drought events, as has been observed in plant diversity studies[30-34].

In summary, our study, based on three independent global soil surveys, indicates that the diversity within key fungal groups drives ecosystem stability at a global scale, as well as with the resistance and resilience of plant productivity to extreme drought events. In particular, we showed that the diversity of soil decomposers is consistently and positively associated with ecosystem stability. The opposite pattern was found for potential fungal plant pathogens. These findings are integral to improving the prediction and management of long-term stability of ecosystem productivity globally, and support the importance of conserving soil biodiversity to promote the stability of plant productivity over time, and to buffer it against climate extremes.

Methods

Study sites and data collection

The analyses in this study are based on three independent global field surveys:

Global survey #1. Composite soil samples from multiple soil cores (top 7.5 cm) were collected from 235 sites (ecosystems) located in 18 countries from six continents (Extended Data Fig. 1), and covering nine biomes (temperate, tropical and dry forests, cold, temperate, tropical and arid grasslands, shrubland and boreal) between 2003 and 2015[22]. Locations were selected to provide a solid representation for most environmental conditions (climate, soil and vegetation types) found on Earth. For example, MAP and MAT in these locations ranged from 52 to 3483mm, and from -9.5 to 26.5 °C, respectively (https://www.worldclim.org/). Soil samples were sieved (2 mm mesh). A portion of soil was frozen at -20°C for molecular analyses, and the rest of the soil was air-dried and stored for a month before physicochemical analyses. Other details on this sampling can be found in ref.[22]. The diversity of fungi was determined using MiSeq platform (2 x 300 PE), (Illumina, San Diego, California, United States) on a fraction of the fungal ITS gene[22]. zOTU tables (100% similarity) were obtained from bioinformatic analyses as described in ref.[18]. Fungal functional groups, e.g., soil decomposers (soil saprotrophs), potential fungal plant pathogens, mycorrhizal fungi (both arbuscular and ectomycorrhizal fungi) and root endophytes were identified using rarefied zOTU tables and FungalTraits[21].

Global survey #2. Composite soil samples (top 5 cm) from multiple soil cores were sampled using a standardized protocol in 351 sites (ecosystems) across the world (Extended Data Fig. 1). Air-dried soil samples were stored for molecular and soil analyses. Other details on this sampling were reported in ref.[23]. The diversity of fungi was determined using 454 pyrosequencing (life sciences, America) on a fraction of the fungal ITS gene. Bioinformatic analyses were done as described in ref.[23]. Fungal functional groups, e.g., soil decomposers (soil saprotrophs), potential fungal plant pathogens, mycorrhizal fungi (both arbuscular and ectomycorrhizal fungi) and root endophytes were identified using rarefied phylotypes tables from bioinformatics analyses[23] and FungalTraits[21].

Global survey #3. Composite soil samples from multiple soil cores (top 10 cm) were collected using standardized protocols between 2016 and 2017 from 87 sites (ecosystems) with known substrate ages located in nine countries and six continents (Extended Data Fig. 1). Other detail information for soil chemical and geography were reported in ref.[24,39]. Here, we produced *de novo* previously unpublished ITS PacBio sequencing (Full-length sequencing) data to determine the diversity of fungi. PacBio sequencing offers longer read lengths than the second-generation sequencing technologies, making it well-suited for studying soil biodiversity). The diversity of fungi was determined via 18S-full ITS amplicon sequencing using the primers ITS9mun/ITS4ngsUni and PacBio Sequel II platform in the University of Tartu. zOTU tables (100% similarity) were obtained from bioinformatic analyses as described in ref.[18]. Fungal functional groups, e.g., soil decomposers (soil saprotrophs), potential fungal plant pathogens and mycorrhizal fungi (arbuscular and ectomycorrhizal fungi) were identified using rarefied zOTU tables and FungalTraits[21].

Stability of ecosystem productivity

We used NDVI (Normalized Difference Vegetation Index), from MODIS satellite imagery MOD13Q1 product, as our proxy of aboveground plant biomass[30] because several studies have suggested the existence of a positive relationship between the Normalized Difference Vegetation Index (NDVI) derived from AVHRR/NOAA satellite data and either biomass or annual aboveground net primary production (ANPP) for different geographic areas and ecosystems.[40,41]. NDVI provides a global measure of the "greenness" of vegetation across the Earth's landscapes for a given composite period[42,43]. We calculated annual NDVI data for each year in the period from 2001 to 2018. To do so, we averaged the product values between the date of the minimum NDVI (n) and the date n - 1 of the following year at each site. This approach allowed us to consider the different annual vegetation growth cycles. Using the 18 annual NDVI data, we calculated the temporal stability of the ecosystem as the ratio between the mean annual NDVI calculated between 2001 and 2018 (mean NDVI) and the SD of the annual NDVI (SD of NDVI) during that period. We focused on this period of time (2001-2018), because: (i) its comprises the span of all the soil samplings conducted in the three global field surveys; and (ii) drought information was available between these dates[25,44]. NDVI information was collected at 250m resolution. This spatial resolution is comparable to that in soil samplings from three global soil surveys (~2500m^2), wherein composite samples were collected.

$$Ecosystem\ \ stability = Mean/SD \qquad (1)$$

To strengthen our ecosystem stability results using the NDVI index, we compare this analysis with the global neural network-based spatially *Contiguous solar-induced fluorescence (CSIF)* dataset based on MODIS MCD43C4 product and SIF data from Orbiting Carbon Observatory-2[45,46] at a spatial resolution of at 5000 m resolution (the highest available resolution) for clear-sky conditions in the period 2001-2018[47]. The instantaneous clear-sky CSIF shows high accuracy against the clear-sky OCO-2 SIF and little bias between biome types. In addition, we used Gross Primary Productivity (GPP) dataset from MODIS MOD17A2H product[48] at 500 m resolution over the period 2001-2018. We also repeated analyses using NDVI (500m) to allow a better comparison with this lower resolution metrics of stability. Overall, these three metrics gave very similar results for testing the relationships between fungal diversity and ecosystem stability (Supplementary Fig. 6-11), however, their lower spatial resolution (vs. NDVI 250m used in the main text) limits the utility of these results. Finally, we would like to highlight that the long-term trend of ecosystem production and stability in NDVI, GPP and CSIF at each site are expected to integrate both anthropogenic (e.g., greening processes)[49] and natural variation.

Quantifying ecosystem resistance and resilience to drought events

To investigate the relationship between soil fungal diversity and the responses of plant productivity to drought events, we used two complementary indexes describing the stability of ecosystems to perturbations: ecosystem resistance and resilience[25,44]. Resistance (RS; eq. 2 from ref.[44]) is defined as the capacity of plant productivity (NDVI) to remain the same in response to a drought event. Resilience (RL; eq. 3 from ref.[44]) is defined as the capacity of plant productivity (NDVI) to return the original levels of productivity after a drought event (i.e., the next year after the drought event). To quantify the resistance and resilience of plant productivity to drought events, we used a multi-scale drought index based on climate data –the standardized precipitation-evapotranspiration index (SPEI)–, that quantified temporal variations in water balance and classified the onset, magnitude and duration of drought conditions with respect to regular conditions at a given location. This information, available for the period of 2001-2018, was used, in combination with collected NDVI data (explained above), to determine the ecosystem resistance and resilience of all the ecosystems included in the three global surveys. These analyses further revealed that the ecosystems in these databases have gone through important drought cycles over the years. We determined the average RS and RL of each ecosystem to drought events in all ecosystems included in the three global surveys using the indexes based on[44], are normalised indices that shows a monotonic increase with increasing resilience avoiding problems of 0 values in the denominator. The index used in this study to measure resilience is bounded even when extreme situations are considered, as is the case in our study plots located in drylands:

$$Resistance \quad (t_0) = 1 - \frac{2|D_0|}{(C_0 + |D_0|)} \qquad (2)$$

Where D_0 is the difference between control (C_0), mean ecosystem productivity during normal years (all years without drought events), and disturbance D_0 during a climate event (t_0).

$$Resilience \quad (t_x) = \frac{2|D_0|}{(|D_0| + |D_x|)} - 1 \qquad (3)$$

Where D_x is the difference between the control (C_x) and the disturbance at the time point during the year after a climate event (t_x).

We further cross-validated the patterns provided by the RL index used here[44] with that in ref.[25]. We found that both RL indexes are highly positively, significantly and consistently correlated in all the global datasets analyzed here: (1) Global survey #1 (Spearman $\rho = 0.89$, $P < 0.001$), Global survey #2 (Spearman $\rho = 0.87$, $P < 0.001$) and Global survey #3 (Spearman $\rho = 0.82$, $P < 0.001$). The fact that RL index[44] and RL index[25] supported similar patterns at a global scale, reduce any concern on potential bias, and provide further support to our conclusions.

Drought events

Drought events were quantified with the SPEI index[50]. It can be used to determine the onset, duration and magnitude of drought conditions relative to normal conditions in a variety of natural and managed ecosystems[51]. SPEI is a multi-scale drought index based on climatic data of monthly precipitation and potential evapotranspiration from Climatic Research Unit (CRU) TS3.10.01 dataset[52] (http://badc.nerc.ac.uk/) with FAO-56 Penman-Monteith equation estimation[53] at 0.5 ° spatial resolution. Particular, in this study focuses on the response of vegetation in terrestrial ecosystems, which do not necessarily react immediately to precipitation fluctuations, so the 12-SPEI data were chosen. We obtain 12-month water shortage or surplus periods for this study. That is, a 12-SPEI value is based on the accumulated water shortage or surplus during the previous 12 months. Finally, after normalizing the period data, we can interpret negative values of the index as dry conditions. To obtain sufficient drought events, we quantified drought events in the period 2001-2018 by analyzing dry events below the 30th percentile which is equivalent to an SPEI of -0.67 and includes moderate and extreme dry events. In addition, normal years were quantified between -0.67 and 0.67 SPEI data according to Isbell et al.[25] (Supplementary Fig. 2).

Statistical analyses

Fungal diversity. Soil fungal diversity was determined as the richness of phylotypes (i.e., zOTUs) within functional groups (Fungaltraits) from rarefied phylotype tables.

Mantel test correlations. We used Mantel test (Spearman) to determine the associations between the cross-site variations in fungal community composition (phylotype level) and ecosystem stability. We used rarefied phylotype tables and Bray-Curtis distance for these analyses. In the case of ecosystem stability, we used Euclidean distance matrices.

Variation partitioning. We used Variation Partitioning modeling[54,55] to quantify the relative importance of four groups of factors as predictors of ecosystem stability, mean and SD of NDVI, and ecosystem resistance and resilience to drought events. These four groups of predictors included: (i) climate, (ii) environment: soil properties and biomes, (iii) fungal diversity; and (iv) % basal areas of mycorrhizal plants/site. These predictors were kept consistent for global survey #1, #2 and #3. However, we also repeated analyses in global survey #2 including plant richness, which was available for all locations in this dataset, to further account for any influence of plant diversity in our analyses. Climate includes the mean annual temperature (MAT) and aridity index (the higher the aridity index the greater the water availability) from https://www.worldclim.org. Fungal diversity includes the richness of fungal functional groups (soil saprobes, plant pathogen, root endophyte and mycorrhizal fungi) and community composition of functional groups (summarized using a non-metric multidimensional scaling; NMDS; Bray-Curtis distance). Mycorrhizal plant include the basal area (%) of AM- and EcM-associated plants retrieved using maps from ref.[26]. Soil properties include total soil phosphorus (TP), soil pH, total N (TN), C: N ratio (C:N) from the original databases in global surveys #1, #2 and #3. Soil age was also included as soil properties in global survey #3. Biomes includes forest and others. Variation partitioning model performed based on "vegan" package[54,55]. Before this analysis, we used the "forward.sel" procedure[54,55] to avoid redundancy and multicollinearity in variation partitioning analyses.

Multiple regression models. We used multiple regression models to assess the joint effects of geography, climate, soil properties, fungal diversity and mycorrhizal plant as well as the relative importance of individual variable on ecosystem stability, and mean and SD of NDVI in global surveys #1, #2 and #3. The predictor variables included in this model were consistent with those in Variation Partitioning. Climate includes MAT and aridity index. Fungal diversity includes the richness of fungal functional groups (soil saprobes, plant pathogen, root endophyte and mycorrhizal fungi). Given the importance of the diversity of soil decomposers in our analyses, we also included a surrogate of the community composition of decomposers (i.e., summarized using a non-metric multidimensional scaling; NMDS; Bray-Curtis distance), to further investigate the robustness of the soil decomposer diversity (richness) and ecosystem stability when controlling for their composition. Mycorrhizal plant include the basal area (%) of AM- and EcM-associated plants. Soil properties include TP, soil pH, TN, C: N ratio. We also considered quadratic terms for climatic variables, plant mycorrhizal association because these variables have been observed to affect ecosystem functioning in previous studies[30] and our results (Fig. 3; Extended Data Figs. 5-7) in a nonlinear way. Additionally, we included spatial variability: latitude, longitude and elevation. All predictors and response variables were standardized before analyses, using the z-score to interpret parameter estimates on a comparable scale. Soil age in global survey #3 was log-transformed before Z-score transformation to meet the assumptions of the tests used. We used the "relaimpo" package[56] in R to estimate parameter coefficients for each predictor.

SEM. We used PicewiseSEM[57,58] to further evaluate the associations between fungal diversity (the richness of soil saprobes, plant pathogen, root endophyte and mycorrhizal fungi) and ecosystem stability in our global survey after accounting for multiple key ecosystem factors such as geography (longitude, latitude and elevation), climate (MAT, aridity index), ecosystem types (forest or others), soil properties (pH, TP, TN and C:N) and % of mycorrhizal plants (the basal area of AM plant and EcM plant; retrieved using maps from ref.[26]) simultaneously. As done with the Multiple regression models, we also included a surrogate of the community composition of decomposers (i.e., NMDS), to further investigate the robustness of the soil decomposer diversity (richness) and ecosystem stability when controlling for their composition. All measured variables included in this model were firstly divided into "composite variable" and then included in SEM. We also repeated analyses in global survey #2 including plant richness, which was available for all locations in this dataset, to further account for any influence of plant diversity in our analyses. In order to confirm the robustness of the relationships between soil biodiversity and ecosystem stability, we used piecewiseSEM to account for random effects of sampling sites, with providing "marginal" and "conditional" contribution of environmental predictors in driving ecosystem stability. These analyses were conducted using "piecewiseSEM"[57], "nlme" and "lme4" packages[58]. We used the Fisher's C test (when $0.05 < p < 1.00$) to confirm the goodness of the modelling results. We then modified our models according to the significance ($p < 0.05$) and the goodness of the model[5].

References

1. Singh, B. K., Bardgett, R. D., Smith, P. & Reay, D. S. Microorganisms and climate change: terrestrial feedbacks and mitigation options. *Nat. Rev. Microbiol.* **8**, 779-790 (2010).
2. Fierer, N. Embracing the unknown: disentangling the complexities of the soil microbiome. *Nat. Rev. Microbiol.* **15**, 579-590 (2017).
3. Guerra, C. A. et al. Tracking, targeting, and conserving soil biodiversity. *Science* **371**, 239-241 (2021).
4. Fanin, N., Gundale, M. J., Farrell, M. et al. Consistent effects of biodiversity loss on multifunctionality across contrasting ecosystems. *Nat. Ecol. Evol.* **2**, 269–278 (2018).
5. Delgado-Baquerizo, M., Reich, P. B., Trivedi, C. et al. Multiple elements of soil biodiversity drive ecosystem functions across biomes. *Nat. Ecol. Evol.* **4**, 210–220 (2020).
6. Chen, W., Wang, J., Meng, Z., Xu, R., Chen, J., Zhang, Y., & Hu, T. Fertility-related interplay between fungal guilds underlies plant richness-productivity relationships in natural grasslands. *New Phyto*. 226, 1129-1143 (2020).
7. Semchenko, M., Leff, J. W., Lozano, Y. M., et al. Fungal diversity regulates plant-soil feedbacks in temperate grassland. *Sci. Adv.* **4**, eaau4578 (2018).
8. Kohli, M., Borer, E. T., Kinkel, L., et al. Stability of grassland production is robust to changes in the consumer food web. *Ecol. lett.* **22** 707-716 (2019).
9. Liang, M., Liu, X., Parker, I. M., et al. Soil microbes drive phylogenetic diversity-productivity relationships in a subtropical forest. *Sci. adv.* **5**, eaax5088 (2019).
10. Tilman, D., Reich, P. B. & Knops, J. M. H. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* **441**, 629-632 (2006).
11. Yang, G. W., Wagg, C., Veresoglou, S. D., Hempel, S. & Rillig, M. C. How Soil Biota Drive Ecosystem Stability. *Trends Plant Sci.* **23**, 1057-1067 (2018).
12. de Vries, F. T., Griffiths, R. I., Knight, C. G., Nicolitch, O. & Williams, A. Harnessing rhizosphere microbiomes for drought-resilient crop production. *Science* **368**, 270-274 (2020).
13. IPCC, Scientific outcome of the IPBES-IPCC co-sponsored workshop on biodiversity and climate change (2021).
14. Gessner, M. O. *et al.* Diversity meets decomposition. *Trends Ecol. Evol.* **25**, 372-380 (2010).
15. Bardgett, R. D. & van der Putten, W. H. Belowground biodiversity and ecosystem functioning. *Nature* **515**, 505-511 (2014).
16. Anthony, M. A., Crowther, T. W., van der Linde, S. et al. Forest tree growth is linked to mycorrhizal fungal composition and function across Europe. *ISME J.* (2022).
17. Jia, Y. Y., van der Heijden, M. G. A., Wagg, C., Feng, G. & Walder, F. Symbiotic soil fungi enhance resistance and resilience of an experimental grassland to drought and nitrogen deposition. *J. Ecol.* **109**, 3171-3181 (2020).
18. 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).
19. Tedersoo, L., Bahram, M. & Zobel, M. How do mycorrhizal associations drive plant population and community biology? *Science* **367**, eaba1223 (2020).
20. Guo, X. et al. Climate warming leads to divergent succession of grassland microbial communities. *Nat. Clim. Change* **8**, 813-818 (2018).
21. Põlme, S. et al. FungalTraits: a user-friendly traits database of fungi and fungus-like stramenopiles. *Fungal Divers.* **105**, 1-16 (2020).

22. Egidi, E. et al. A few Ascomycota taxa dominate soil fungal communities worldwide. *Nat. Commun.* **10**, 2369 (2019).

23. Tedersoo, L. et al. Global diversity and geography of soil fungi. *Science* **346**, 1078-1088 (2014).

24. Delgado-Baquerizo, M. et al. The influence of soil age on ecosystem structure and function across biomes. *Nat. Commun.* **11**, 4721 (2020).

25. Isbell, F. et al. Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature* **526**, 574-577 (2015).

26. Steidinger, B. S. et al. Climatic controls of decomposition drive the global biogeography of forest-tree symbioses. *Nature* **569**, 404-408 (2019).

27. Wagg, C. et al. Diversity and asynchrony in soil microbial communities stabilizes ecosystem functioning. *Elife* **10**, 3207 (2021).

28. Yang, G. W., Wagg, C., Veresoglou, S. D., Hempel, S. & Rillig, M. C. Plant and soil biodiversity have non-substitutable stabilizing effects on biomass production. *Ecol. Lett.* **24**, 1582-1593 (2021).

29. Chen, L. T. et al. Above- and belowground biodiversity jointly drive ecosystem stability in natural alpine grasslands on the Tibetan Plateau. *Global Ecol. Biogeogr.* (2021).

30. Garcia-Palacios, P., Gross, N., Gaitan, J. & Maestre, F. T. Climate mediates the biodiversity-ecosystem stability relationship globally. *P. Natl. Acad. Sci. USA* **115**, 8400-8405 (2018).

31. Valencia, E. et al. Synchrony matters more than species richness in plant community stability at a global scale. *P. Natl. Acad. Sci. USA* **117**, 24345-24351 (2020).

32. Craven, D. et al. Multiple facets of biodiversity drive the diversity-stability relationship. *Nat. Ecol. Evol.* **2**, 1579-1587 (2018).

33. Naeem, S., Li, S. B. Biodiversity enhances ecosystem reliability. *Nature* **390**, 507-509 (1997).

34. Hautier, Y. *et al.* Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature* **508**, 521-525, (2014).

35. Jousset, A., Schmid, B., Scheu, S. & Eisenhauer, N. (2011). Genotypic richness and dissimilarity opposingly affect ecosystem performance. *Ecol. Lett.*, **14**, 537–624.

36. Jiang, L., Pu, Z. & Nemergut, D. R. (2008). On the importance of the negative selection effect for the relationship between biodiversity and ecosystem functioning. *Oikos*, **117**, 488-493.

37. Ratzke, C., Barrere, J. & Gore, J. Strength of species interactions determines biodiversity and stability in microbial communities. *Nat. Ecol. Evol.* **4**, 376-383 (2020).

38. Lekberg, Y. et al. Nitrogen and phosphorus fertilization consistently favor pathogenic over mutualistic fungi in grassland soils. *Nat. Commun.* **12**, 3484 (2021).

39. Bastida, F., Eldridge, D. J., García, C. et al. Soil microbial diversity-biomass relationships are driven by soil carbon content across global biomes. *ISME J* 15, 2081-2091 (2021).

40. Paruelo, J., Epstein, H. E., Lauenroth, W. K., & Burke I. C. ANPP estimates from NDVI for the central grassland region of the United States. *Ecology* **78**, 953-958 (1997).

41. Jobbágy, E. G., Sala, O. E.,Paruelo, J. M. Patterns and controls of primary production in the Patagonian steppe: a remote sensing approach. *Ecology*, **83**, 307-319 (2002).

42. Oehri, J., Schmid, B., Schaepman-Strub, G. & Niklaus, P. A. Biodiversity promotes primary productivity and growing season lengthening at the landscape scale. *P Natl Acad Sci USA* **114**, 10160-10165 (2017).

43. Bastos, A., Running, S. W., Gouveia, C. & Trigo, R. M. The global NPP dependence on

ENSO: La Nina and the extraordinary year of 2011. *J. Geophys. Res-Biogeo.* **118**, 1247-1255 (2013).

44. Orwin, K. H., Wardle, D. A. New indices for quantifying the resistance and resilience of soil biota to exogenous disturbances. *Soil Biol. Biochem*. **36**, 1907-1912 (2004).
45. Frankenberg, C., et al. Prospects for chlorophyll fluorescence remote sensing from the Orbiting Carbon Observatory-2. *Remote Sensing of Environment*, **147**, 1-12 (2014).
46. Sun, Y., Frankenberg, C., Jung, M. et al. Overview of Solar-Induced chlorophyll Fluorescence (SIF) from the Orbiting Carbon Observatory-2: Retrieval, cross-mission comparison, and global monitoring for GPP. *Remote Sensing of Environment*, **209**, 808-823 (2018).
47. Zhang, Y., Joiner, J., Alemohammad, S.H., Zhou, S., Gentine, P. A global spatially contiguous solar-induced fluorescence (CSIF) dataset using neural networks. *Biogeosciences* **15**, 5779-5800 (2018).
48. Running, S. W. et al. A continuous satellite-derived measure of global terrestrial primary production. *Bioscience* **54**, 547–560 (2004).
49. Beguería, S.. et al. Standardized precipitation evapotranspiration index (SPEI) revisited: parameter fitting, evapotranspiration models, tools, datasets and drought monitoring. *International journal of climatology* **34**, 3001-3023 (2014).
50. Chen, C., Park, T., Wang, X. et al. China and India lead in greening of the world through land-use management. *Nature sustainability* **2**, 122-129 (2019).
51. Luo, H. et al. Contrasting responses of planted and natural forests to drought intensity in Yunnan, China. *Remote Sensing* **8**, 635 (2016).
52. Harris, I., Jones, P. D., Osborn, T. J., & Lister, D. H. Updated high-resolution grids of monthly climatic observations−the CRU TS3. 10 Dataset. *International Journal of Climatology*, **34**, 623-642 (2014).
53. Allen, R. G., et al. Crop evapotranspiration-Guidelines for computing crop water requirements-FAO Irrigation and drainage paper, pp. 56 (1998).
54. Oksanen, J. et al. Vegan: Community Ecology Package. R Foundation for Statistical Computing,Vienna (2013).
55. Legendre, P. et al. Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. *J. Plant Ecol.* **1**, 3-8 (2008).
56. Grömping, U. ″Relative Importance for Linear Regression in R: The Package relaimpo.″ *Journal of Statistical Software*, **17**, 1-27 (2006).
57. Lefcheck., J. S. PIECEWISESEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods Ecol. Evol*. **7**, 573-579.
58. Bates, D. et al. lme4: Linear mixed-effects models using Eigen and S4. R package version, 1,1-13 (2017).

Acknowledgements:

This project received funding from the European Union’s Horizon 2020 research and innovation program under the Marie Sklodowska-Curie grant agreement No 702057 (CLIMIFUN). M.D-B. was supported by a Ramón y Cajal grant from the Spanish Ministry of Science and Innovation (RYC2018-025483-I), a project from the Spanish Ministry of Science and Innovation (PID2020-115813RA-I00), and a project PAIDI 2020 from the Junta de Andalucía (P20_00879). S.E.L was supported by the National Natural Science Foundation of China (grant No. 32101491) and fellowship of China Postdoctoral Science Foundation (2021M701968). P.G.-P was supported by a grant from the Spanish Ministry of Science and Innovation (DUALSOM, PID2020-113021RA-I00).

Author contributions:

M.D.-B. designed the study in consultation with S.E.L. and P.G.-P; S.E.L., M.D.-B., L.T. and E.G. analyzed the data; S.E.L. and M.D-B. wrote the first draft paper, edited the manuscript and P.G.-P., L.T., M.v.d.H., C.W., E.G., D.M.C., Q.K.W., J.T.W., and B.S., helped to improve subsequent drafts. Particularly, P.G.-P., L.T., M.v.d.H., C.W., and B.S., contributed significantly to further revising of the text.

Competing interests:

The authors declare no competing interests.

Data and materials availability:

The raw data associated with this study is available in (https://figshare.com/s/5299f4b83c1abec736fc; DOI: 10.6084/m9.figshare.14905236). ITS sequencing data associated with Global #1, 2 and 3 is available in https://figshare.com/s/9772d31625426d907782[22] (doi: 10.6084/m9.figshare.5923876.v1), the Short Read Archive (accession SRP043706)[23] and https://figshare.com/s/5e16fa5b0475880c0fa5 (doi: 10.6084/m9.figshare.19419335), respectively.

Supplementary Materials:

Supplementary Figures 1 to 11
Supplementary Note 1

Figure caption

Figure 1. Relationships between soil fungal diversity and ecosystem stability. Fitted linear relationships between ecosystem stability and the richness of selected functional groups of fungi in global surveys #1 (a-c; n = 235 ecosystems), #2 (d-f; n = 351 ecosystems) and and #3 (g-i; n = 87 ecosystems). Statistical analysis for the relationship between richness and stability was performed using ordinary least squares linear regressions. Significance levels of each predictor are *P < 0.05, **P < 0.01, ***P < 0.001. Grey shade indicates 95% confidence interval. Soil saprobes = Soil fungal decomposers.

Figure 2. Relationships between soil fungal diversity and ecosystem stability in grasslands. Fitted linear relationships between ecosystem stability and the richness of selected functional groups of fungi in grasslands associated with global surveys #1 (a; n =120 ecosystems) and #2 (b; n = 54 ecosystems). Statistical analysis for the relationship between richness and stability was performed using ordinary least squares linear regressions. Significance levels of each predictor are *P < 0.05, **P < 0.01, ***P < 0.001. Grey shade indicates 95% confidence interval. Soil saprobes = Soil fungal decomposers.

Figure 3. Drivers of ecosystem stability. Biotic and abiotic predictors of ecosystem stability in global surveys #1 (a; n = 235 ecosystems), #2 (b; n = 351 ecosystems) and #3 (c; n = 87 ecosystems). Multiple ranking regression reveal the relative importance of the most important predictors of ecosystem stability. The standardized regression coefficients of the models are shown for each predictor with their associated 95% confidence intervals. *P < 0.05, **P < 0.01,

***P < 0.001. Bar graphs show the relative importance of each group of predictors, expressed as the percentage of explained variance. Soil saprobe = Soil fungal decomposers. Community composition of soil saprobes was summarized using a non-metric multidimensional scaling; NMDS (Methods).

Figure 4. Direct and indirect drivers of ecosystem stability. PiecewiseSEM accounting for the direct and indirect effects of geography, climate predictors, vegetation type, plant mycorrhizal association and fungal diversity on the ecosystem stability at global surveys #1 (a; n = 235 ecosystems), #2 (b; n = 351 ecosystems) and #3 (c; n = 87 ecosystems). Numbers adjacent to arrows are path coefficients (partial regression) which represent the directly standardized effect size of the relationship. The conditional and marginal R^2 represent the proportion of variance explained by all predictors without and with accounting for random effects of "sampling site". Relationships between residual variables of measured predictors were not showed. Significance levels of each predictor are *P < 0.05, **P < 0.01, ***P < 0.001. Microbes includes the richness of saprobes, potential fungal plant pathogens, root endophytes and mycorrhizal fungi, and the community composition of decomposers (soil saprobes).

Figure 5. Relationship between basal area of mycorrhizal association and ecosystem stability in global survey #1 (a,b; n = 235 ecosystems), #2 (c,d; n = 351 ecosystems) and #3 (c,d; n = 87 ecosystems). Statistical analysis for the relationship between richness and stability was performed using ordinary least squares regressions. Regression lines and 95% confidence bands are shown for significant relationships (P < 0.05). Akaike information criterion (AIC) was used to select the best model.

Figure 6. Relationships between soil fungal diversity and ecosystem resistance and resilience to drought events. Fungal diversity effects on ecosystem resistance (RS) and resilience (RL) in drought events in global surveys #1 (a-d; n = 235 ecosystems), #2 (e-h; n = 351 ecosystems) and #3 (i-l; n = 87 ecosystems). Statistical analysis for the relationship between richness and stability was performed using ordinary least squares linear regressions. Significance levels of each predictor are *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. Grey shade indicates 95% confidence interval. Soil saprobes = Soil fungal decomposers.

Extended Data Figure 1. Sampling locations of three global field surveys. A total of 673 ecosystems were included in this study.

Extended Data Figure 2. Frequency of drought events (top) and global map of study plot locations (bottom). The map data is equivalent to the SPEI reclassification in dry and wet events and normal years of 16 August 2018 to illustrate an example of the distribution of events.

Extended Data Figure 3. Explained variation in ecosystem stability in global survey #1. Variation partitioning (%) of four categories of predictors (a): climate predictors (V1), soil properties and biomes (V2), fungi (fungal diversity and community composition) (V3) and plant mycorrhizal association (V4) in explaining ecosystem stability, mean and SD NDVI, and ecosystem resistance and resilience to drought events in global survey #1 (n = 235 ecosystems). The values in brackets after each groups present the variance explained.

Extended Data Figure 4. Explained variation in ecosystem stability in global survey #2. Variation partitioning (%) of four categories of predictors (a): climate predictors (V1), soil properties and biomes (V2), fungi (fungal diversity and community composition) (V3) and plant mycorrhizal association (V4) in explaining ecosystem stability, mean and SD NDVI, and ecosystem resistance and resilience to drought events in global survey #2 (n = 351 ecosystems). The values in brackets after each groups present the variance explained.

Extended Data Figure 5. Explained variation in ecosystem stability in global survey #3. Variation partitioning (%) of four categories of predictors (a): climate predictors (V1), soil properties and biomes (V2), fungi (fungal diversity and community composition) (V3) and plant mycorrhizal association (V4) in explaining ecosystem stability, mean and SD NDVI, and ecosystem resistance and resilience to drought events in global survey #3 (n = 87 ecosystems). The values in brackets after each groups present the variance explained.

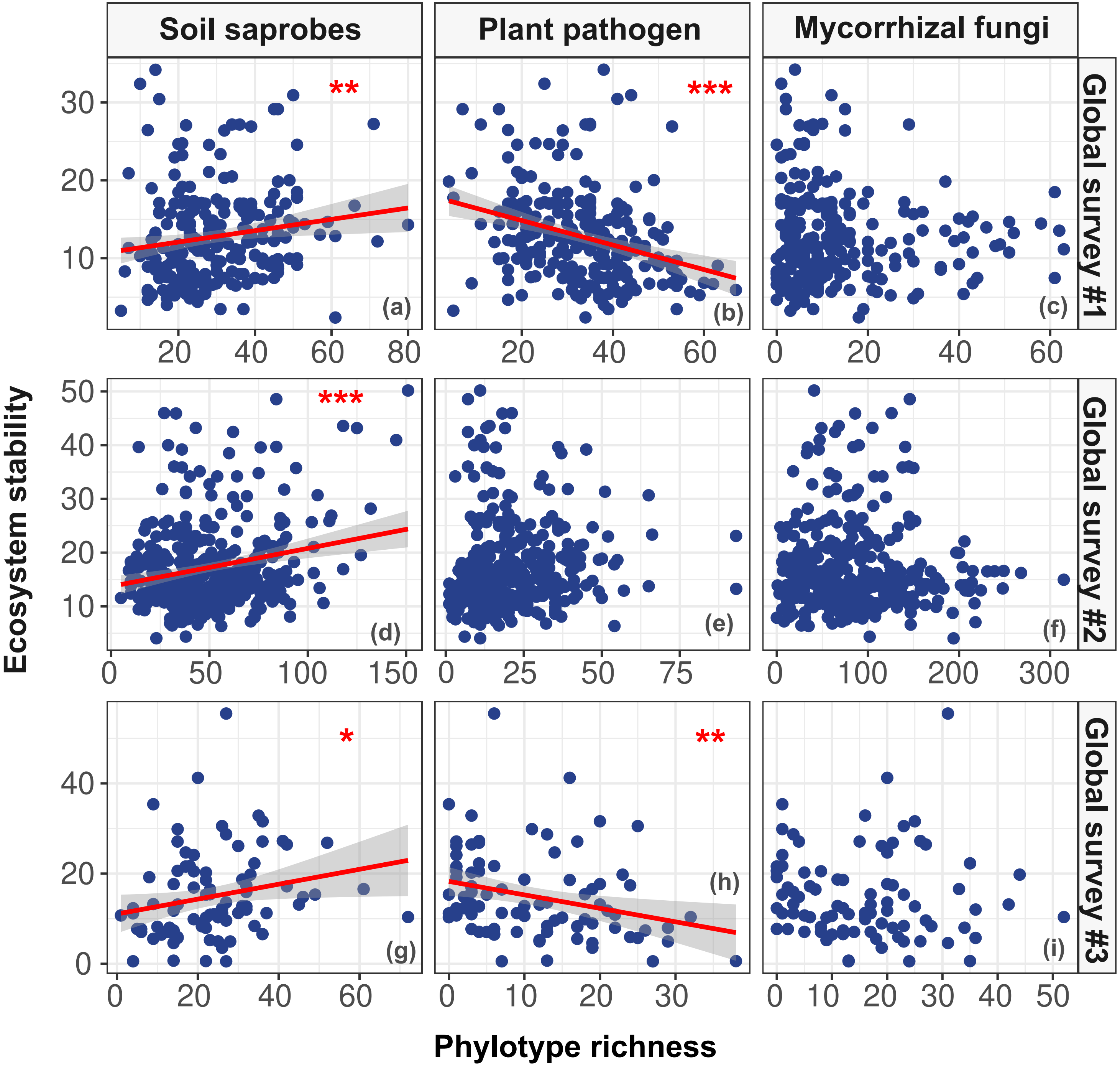
Extended Data Figure 6. Drivers of mean (a) and SD NDVI (b) in global survey #1. Multiple ranking regression reveal the relative effects of the most important predictors of ecosystem stability (n = 235 ecosystems). The average parameter estimates (standardized regression coefficients) of the model predictors are shown with their associated 95% confidence intervals along with the relative importance of each predictor, expressed as the percentage of explained variance. *P < 0.05, **P < 0.01, ***P < 0.001. Soil saprobe = Soil fungal decomposers.

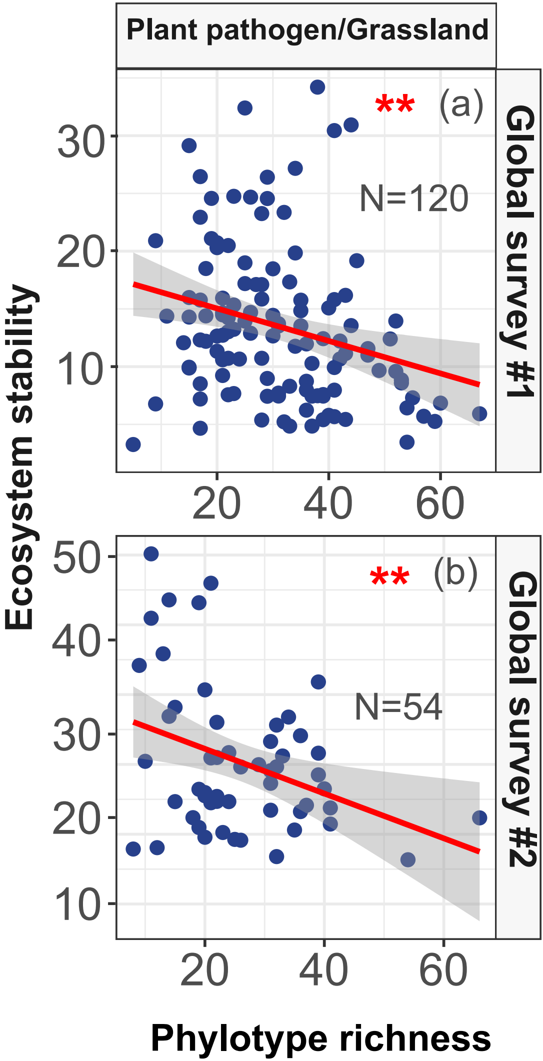
Extended Data Figure 7. Drivers of mean (a) and SD NDVI (b) in global survey #2. Multiple ranking regression reveal the relative effects of the most important predictors of ecosystem stability (a,c) (n = 351 ecosystems). The average parameter estimates (standardized regression coefficients) of the model predictors are shown with their associated 95% confidence intervals along with the relative importance of each predictor, expressed as the percentage of explained variance. *P < 0.05, **P < 0.01, ***P < 0.001. Soil saprobe = Soil fungal decomposers.

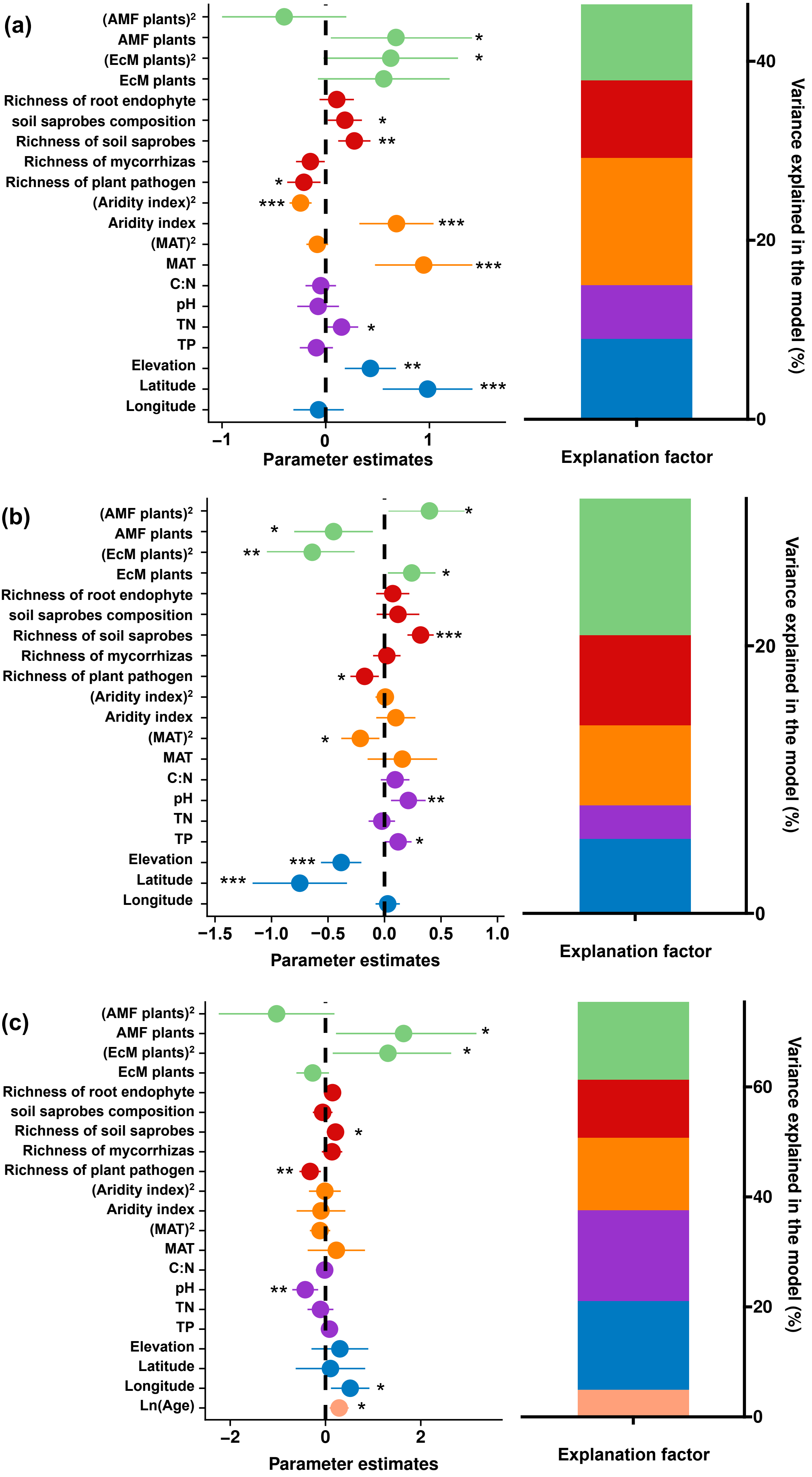
Extended Data Figure 8. Drivers of mean (a) and SD NDVI (b) in global survey #3. Multiple ranking regression reveal the relative effects of the most important predictors of ecosystem stability (a,c) (n = 87 ecosystems). The average parameter estimates (standardized regression coefficients) of the model predictors are shown with their associated 95% confidence intervals along with the relative importance of each predictor, expressed as the percentage of explained variance. *P < 0.05, **P < 0.01, ***P < 0.001. Soil saprobe = Soil fungal decomposers.

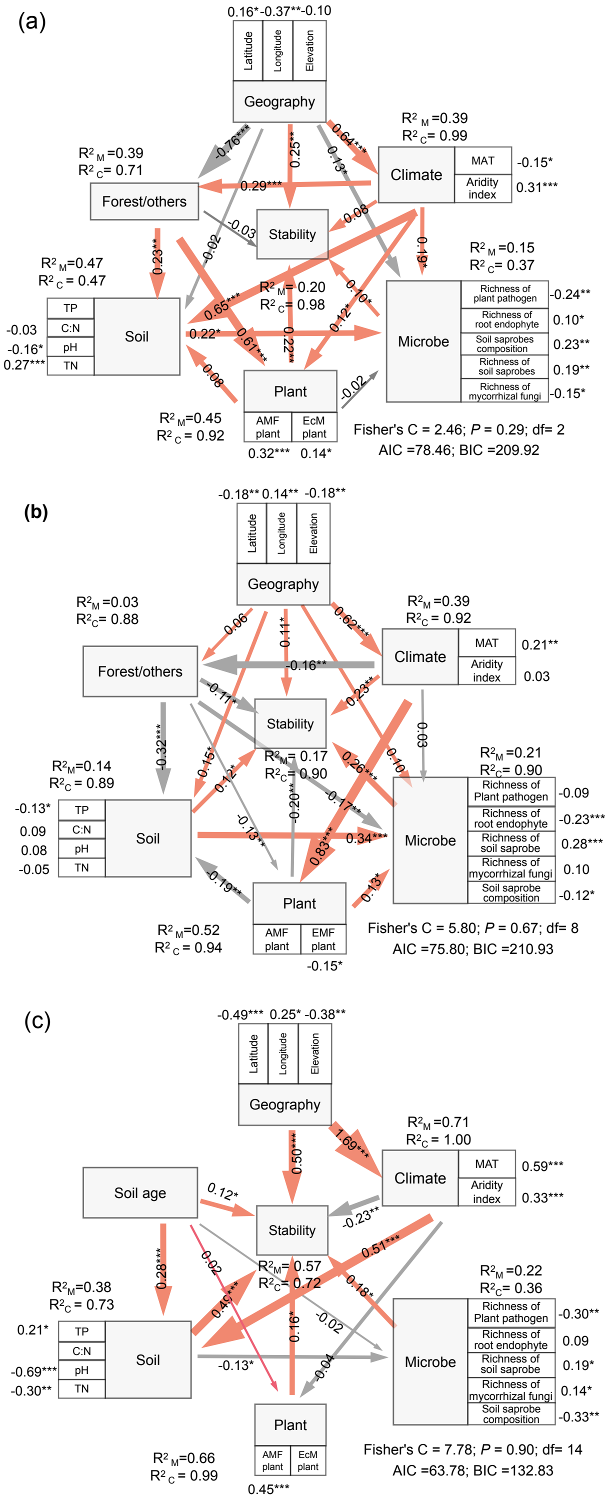
Extended Data Figure 9. Fitted linear relationships between ecosystem stability and the diversity (richness) of selected functional groups of soil fungi across all ecosystems in global survey #2 (n = 351 ecosystems). YAkaike information criterion (AIC) was used to selected the best model. Significance levels of each predictor are $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. Grey shade indicates 95% confidence interval. Soil saprobes = soil fungal decomposers. Ecosystem stability was estimated at a resolution of 250 m×250 m. Fungal diversity is estimated at a resolution of 50 m×50 m. Plant diversity was estimated at a resolution of 110 m×110 m.

Extended Data Figure 10. Explained variation in ecosystem stability in global survey #2. Variation partitioning (%) of four categories of predictors (a): climate predictors (V1), soil properties and biomes (V2), fungi (fungal diversity and community composition) (V3) and plant richness and mycorrhizal association (V4) in explaining ecosystem stability, mean and SD NDVI, and ecosystem resistance and resilience to drought events in global survey #2 (n = 351 ecosystems). The values in brackets after each groups present the variance explained.

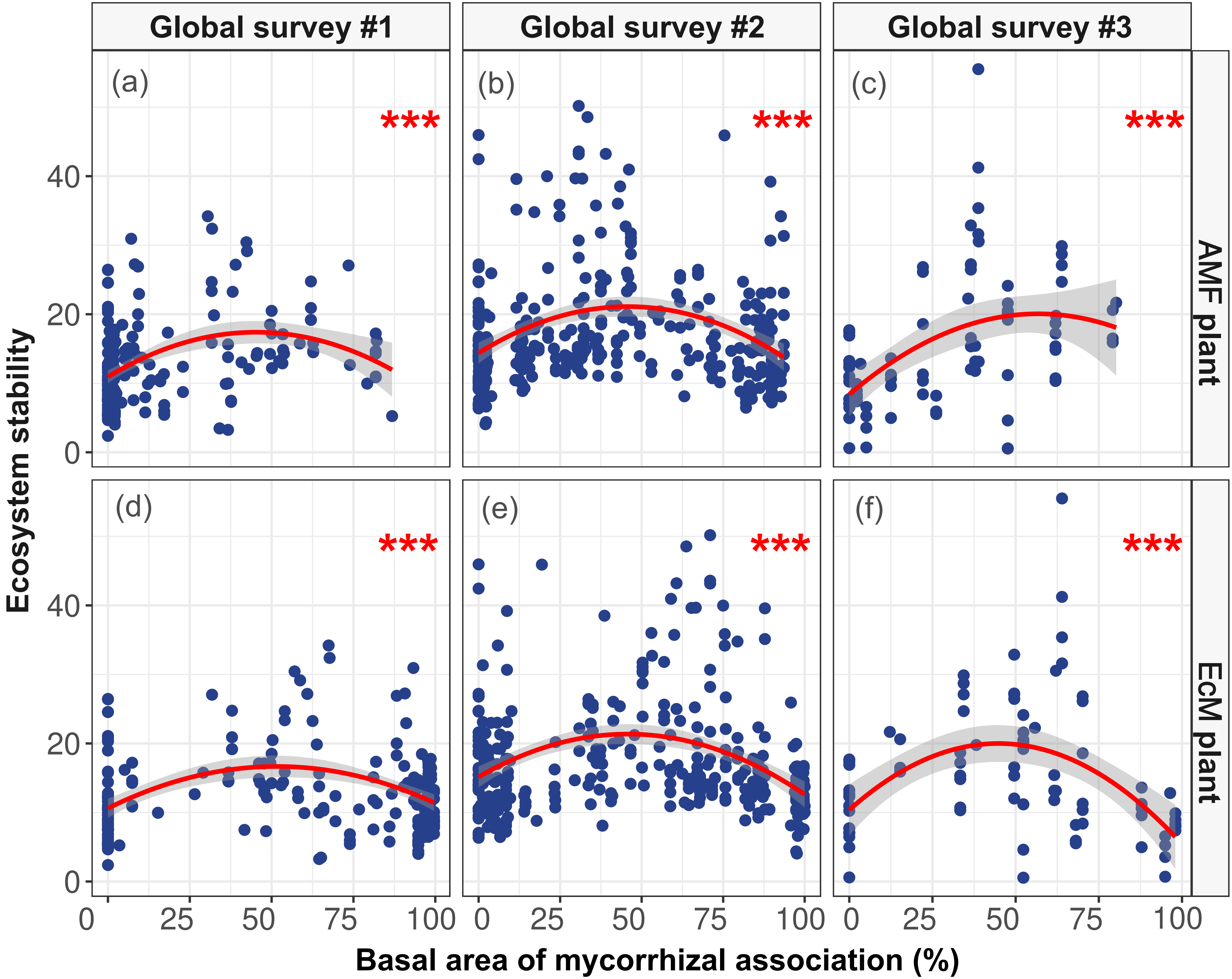

Soil saprobes
Plant pathogen
Mycorrhizal fungi
Global survey #1
Global survey #2
Global survey #3
Ecosystem stability
Phylotype richness
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
**
***
***
*
**
10
20
30
40
50
0
20
40
60
80
100
150
200
300
25
75

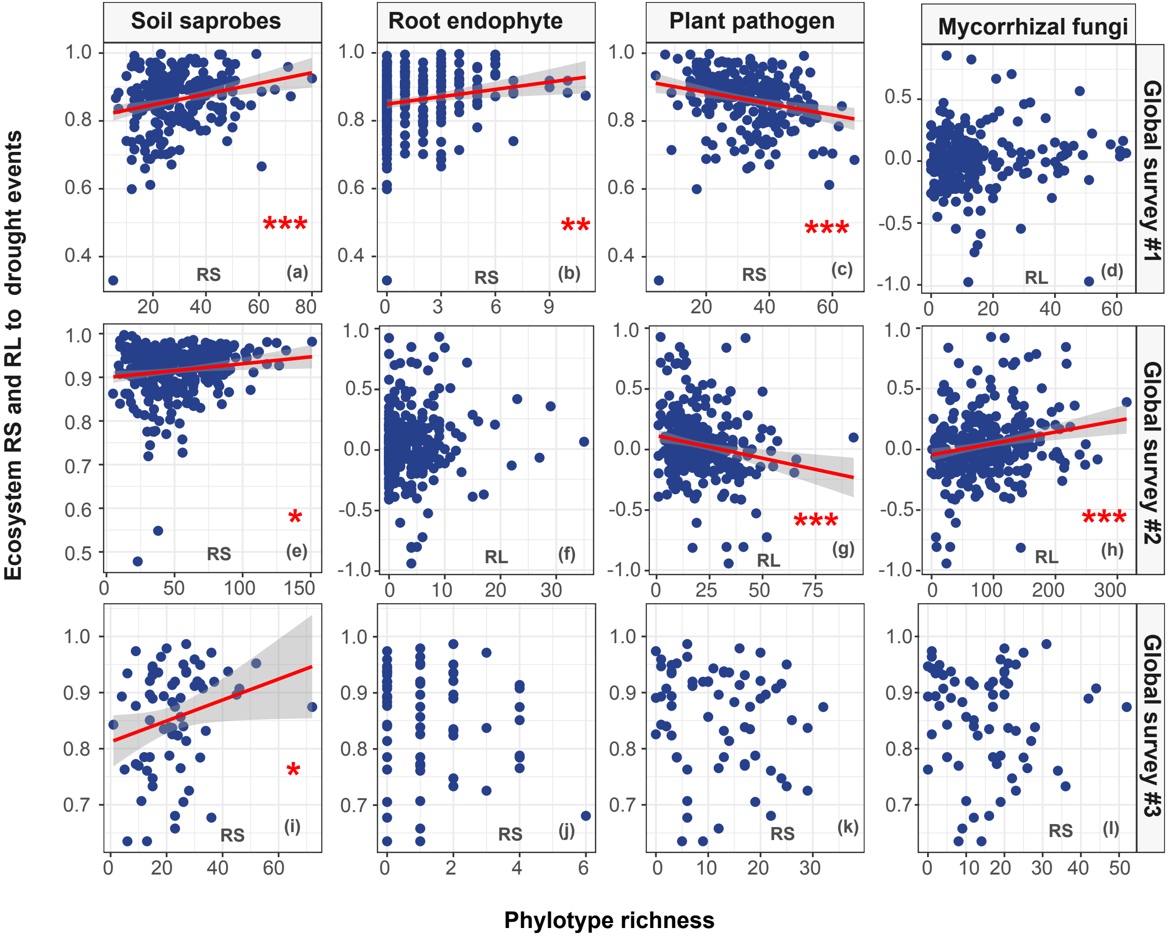

Plant pathogen/Grassland
Global survey #1
Global survey #2
(a)
**
N=120
(b)
**
N=54
Ecosystem stability
Phylotype richness
10
20
30
40
50
20
40
60

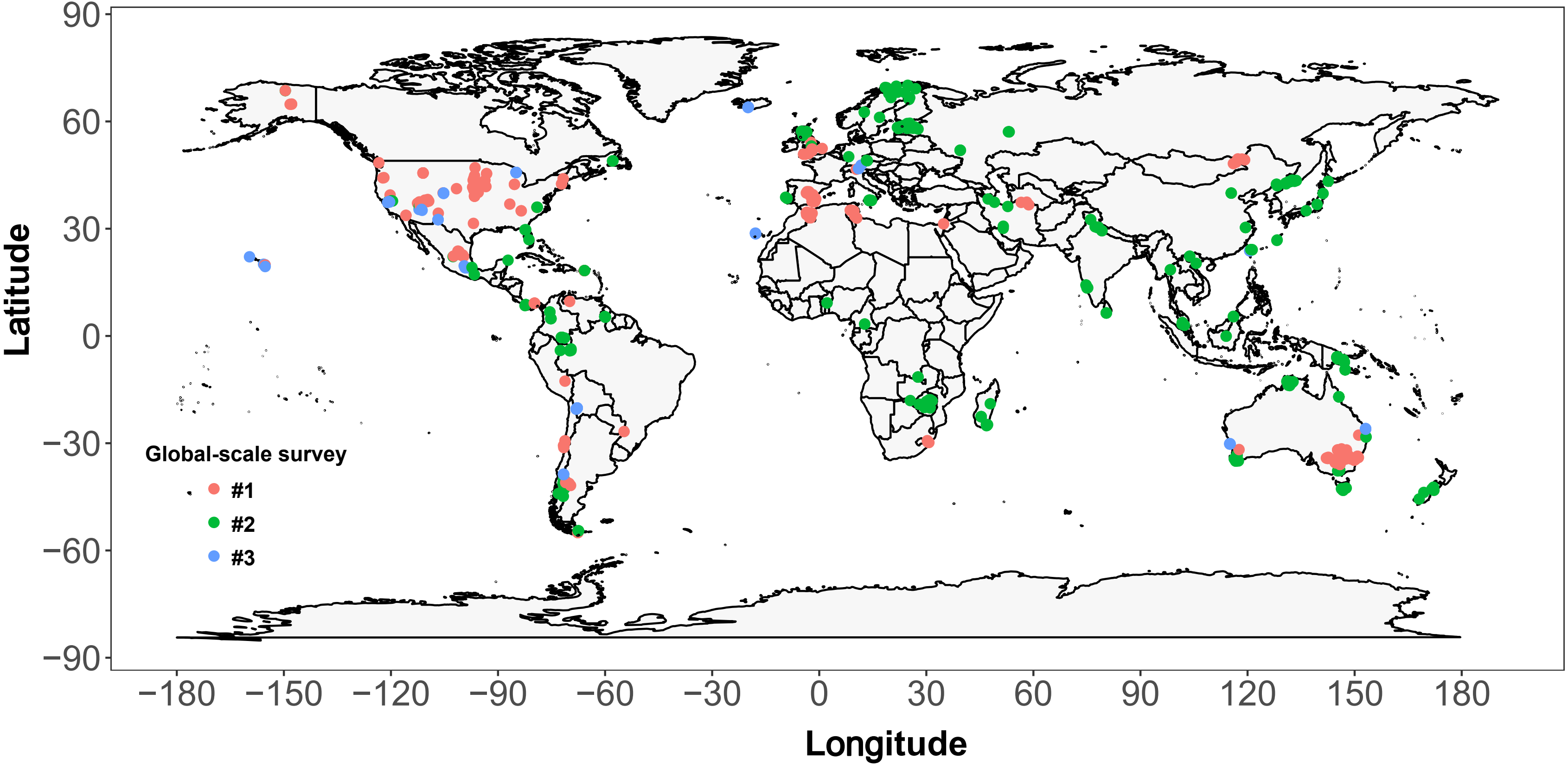

(a)
(AMF plants)²
AMF plants *
(EcM plants)² *
EcM plants
Richness of root endophyte
soil saprobes composition *
Richness of soil saprobes **
Richness of mycorrhizas
Richness of plant pathogen *
(Aridity index)² ***
Aridity index ***
(MAT)²
MAT ***
C:N
pH
TN *
TP
Elevation **
Latitude ***
Longitude
−1
0
1
Parameter estimates
0
20
40
Variance explained in the model (%)
Explanation factor
(b)
(AMF plants)² *
AMF plants *
(EcM plants)² **
EcM plants *
Richness of root endophyte
soil saprobes composition
Richness of soil saprobes ***
Richness of mycorrhizas
Richness of plant pathogen *
(Aridity index)²
Aridity index
(MAT)² *
MAT
C:N
pH **
TN
TP *
Elevation ***
Latitude ***
Longitude
−1.5
−1.0
−0.5
0.0
0.5
1.0
Parameter estimates
0
20
Variance explained in the model (%)
Explanation factor
(c)
(AMF plants)²
AMF plants *
(EcM plants)² *
EcM plants
Richness of root endophyte
soil saprobes composition
Richness of soil saprobes *
Richness of mycorrhizas
Richness of plant pathogen **
(Aridity index)²
Aridity index
(MAT)²
MAT
C:N
pH **
TN
TP
Elevation
Latitude
Longitude *
Ln(Age) *
−2
0
2
Parameter estimates
0
20
40
60
Variance explained in the model (%)
Explanation factor

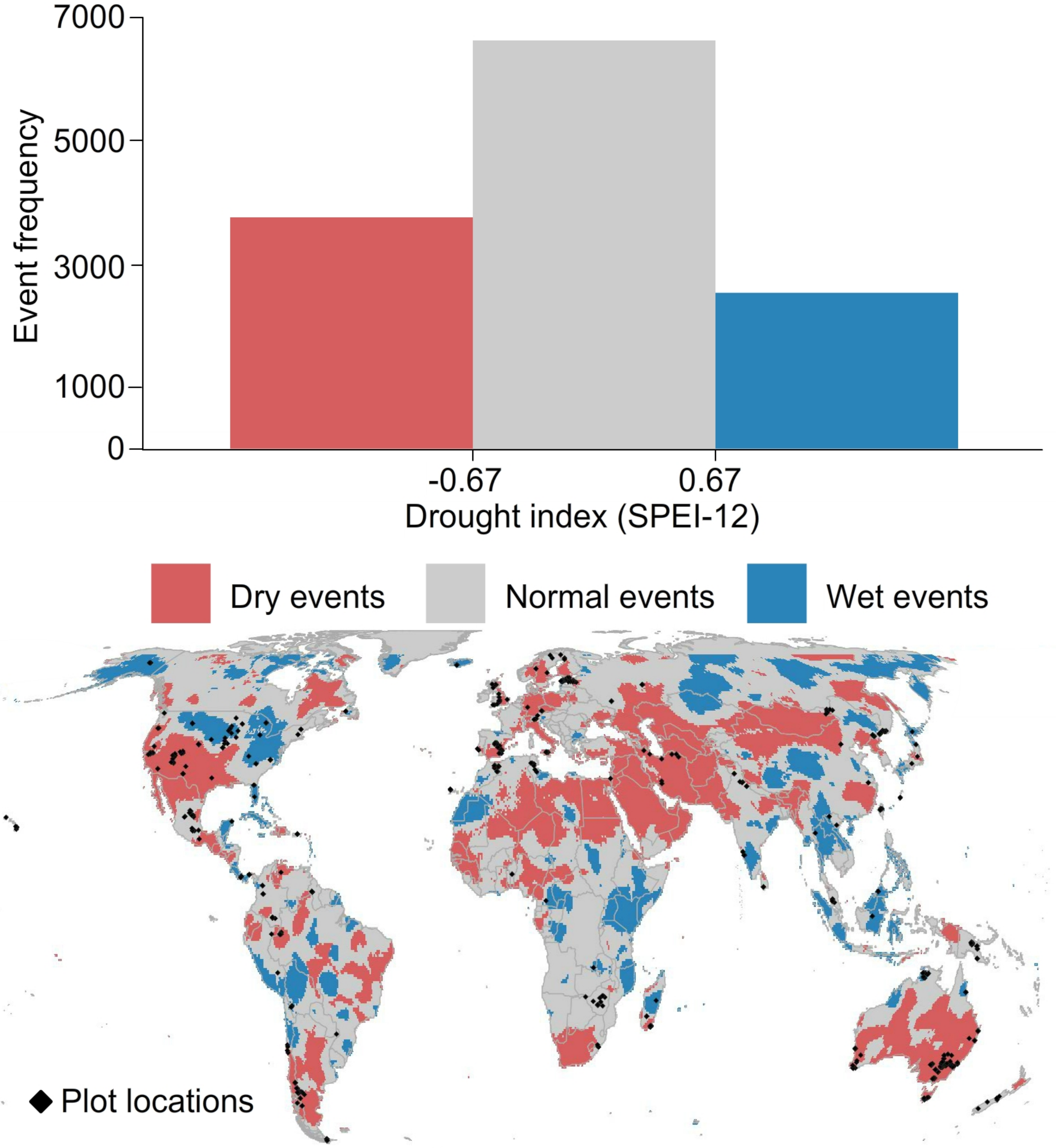


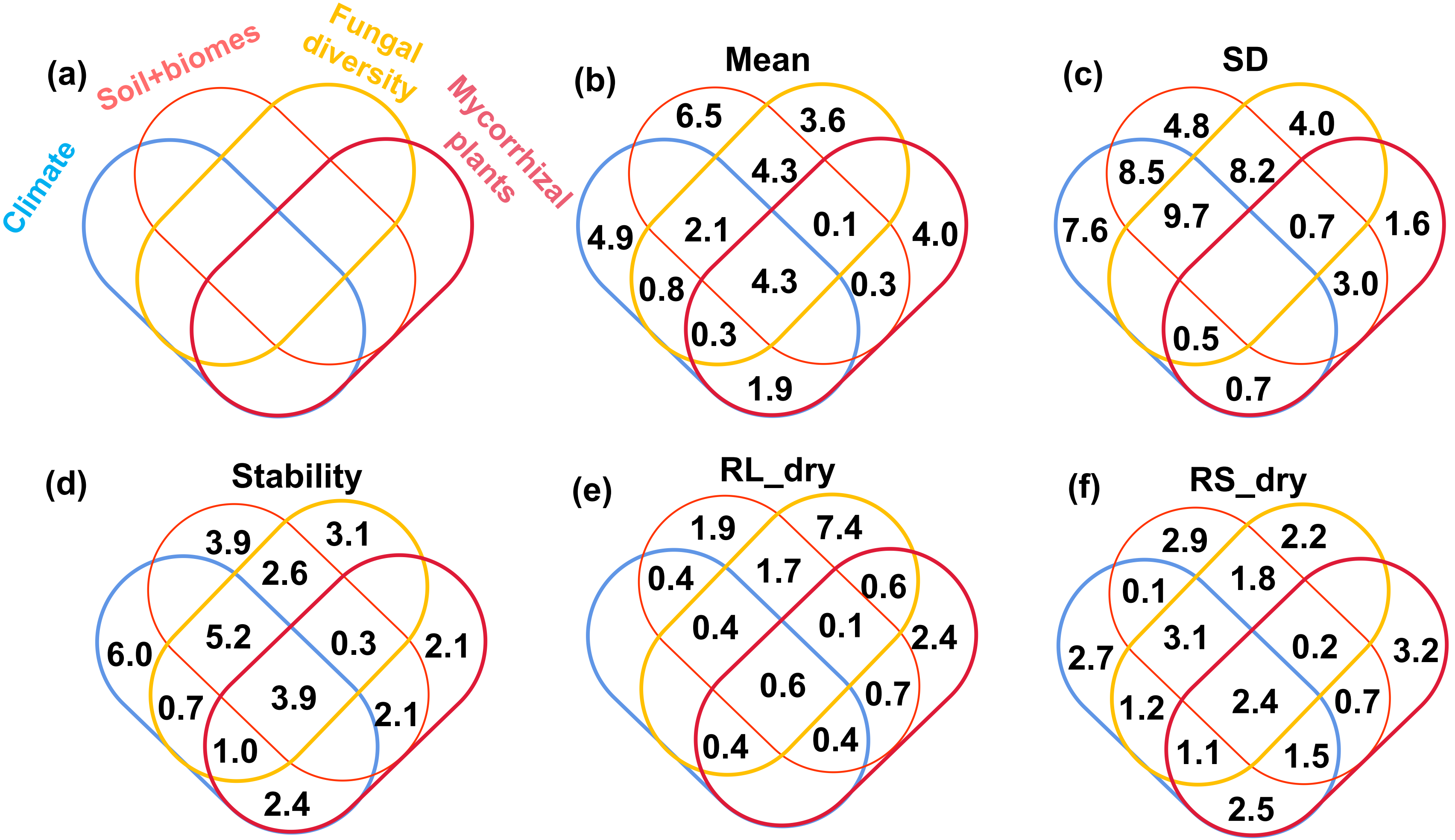
(a)
0.16* -0.37** -0.10
Latitude
Longitude
Elevation
Geography
-0.76***
0.25**
0.64***
0.13*
R² M =0.39
R² C= 0.99
Climate
MAT
Aridity index
-0.15*
0.31***
R² M =0.39
R² C= 0.71
Forest/others
0.29***
Stability
-0.03
0.08
0.23**
-0.02
0.19*
R² M =0.15
R² C= 0.37
R² M=0.47
R² C = 0.47
TP
C:N
pH
TN
-0.03
-0.16*
0.27***
Soil
0.65***
R² M= 0.20
R² C= 0.98
0.10*
0.12*
0.22*
0.61***
0.22**
Microbe
Richness of plant pathogen
Richness of root endophyte
Soil saprobes composition
Richness of soil saprobes
Richness of mycorrhizal fungi
-0.24**
0.10*
0.23**
0.19**
-0.15*
0.08
Plant
-0.02
AMF plant
EcM plant
R² M=0.45
R² C = 0.92
0.32*** 0.14*
Fisher's C = 2.46; P = 0.29; df= 2
AIC =78.46; BIC =209.92
(b)
-0.18** 0.14** -0.18**
Latitude
Longitude
Elevation
Geography
R²M =0.03
R²C= 0.88
0.06
0.11*
0.62***
R²M =0.39
R²C = 0.92
Climate
MAT
Aridity index
0.21**
0.03
Forest/others
-0.16**
-0.11*
Stability
0.23**
-0.32***
0.03
0.15*
0.12*
R²M= 0.17
R²C= 0.90
0.26***
0.10
R²M=0.14
R²C= 0.89
-0.20**
-0.17**
R²M =0.21
R²C= 0.90
-0.13*
0.09
0.08
-0.05
TP
C:N
pH
TN
Soil
-0.13**
0.34***
0.83***
Microbe
Richness of Plant pathogen
Richness of root endophyte
Richness of soil saprobe
Richness of mycorrhizal fungi
Soil saprobe composition
-0.09
-0.23***
0.28***
0.10
-0.12*
-0.19**
0.13*
Plant
AMF plant
EMF plant
R² M=0.52
R² C = 0.94
-0.15*
Fisher's C = 5.80; P = 0.67; df= 8
AIC =75.80; BIC =210.93
(c)
-0.49*** 0.25* -0.38**
Latitude
Longitude
Elevation
Geography
0.50***
1.69***
R²M =0.71
R²C = 1.00
Climate
MAT
Aridity index
0.59***
0.33***
Soil age
0.12*
Stability
-0.23**
0.28***
0.02
0.51***
R²M= 0.57
R²C= 0.72
0.18*
R²M =0.22
R²C= 0.36
R²M=0.38
R²C = 0.73
0.49***
-0.02
0.21*
-0.69***
-0.30**
TP
C:N
pH
TN
Soil
0.16*
-0.13*
-0.04
Microbe
Richness of Plant pathogen
Richness of root endophyte
Richness of soil saprobe
Richness of mycorrhizal fungi
Soil saprobe composition
-0.30**
0.09
0.19*
0.14*
-0.33**
Plant
AMF plant
EcM plant
R² M=0.66
R² C = 0.99
0.45***
Fisher's C = 7.78; P = 0.90; df= 14
AIC =63.78; BIC =132.83

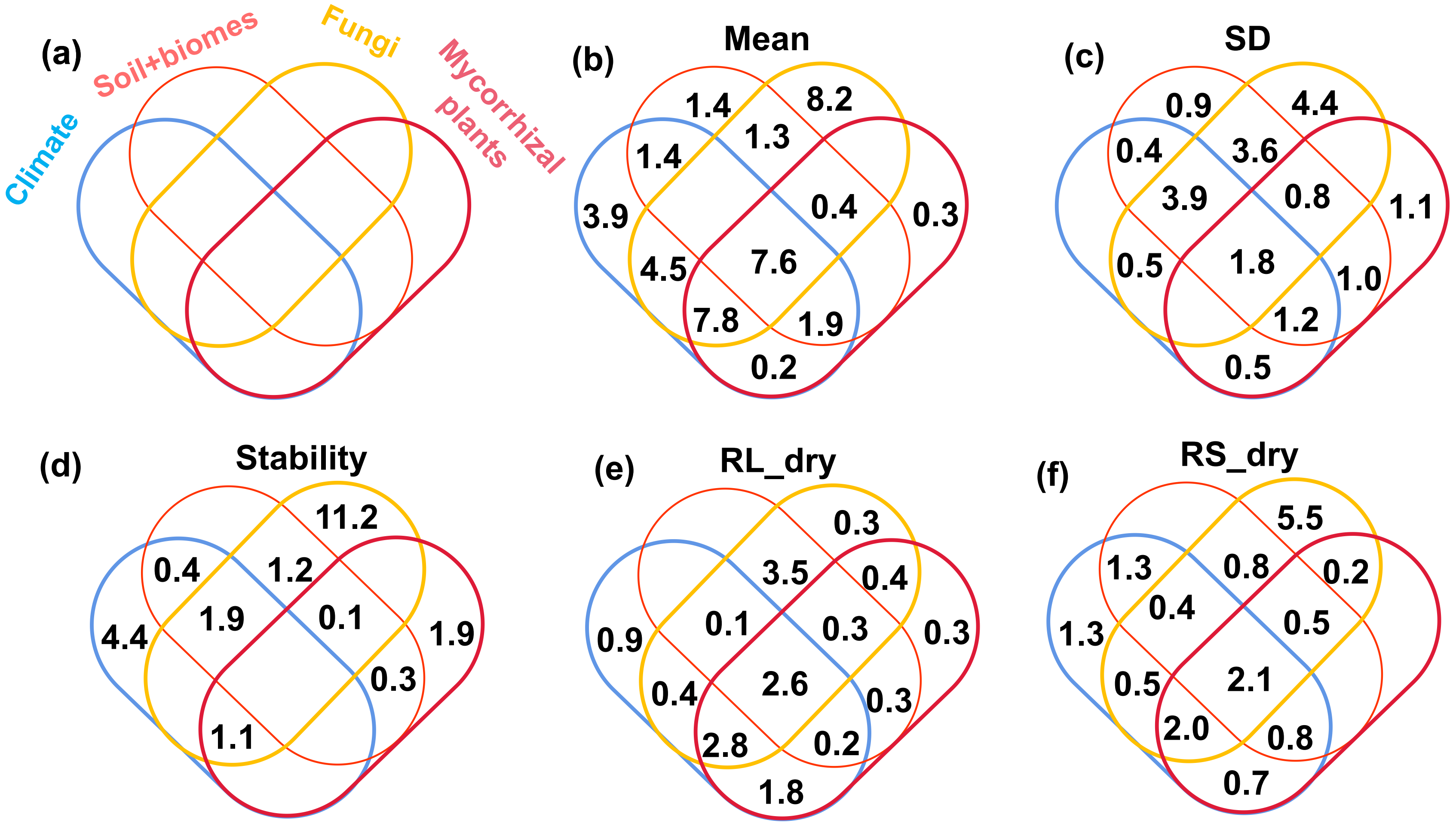

Global survey #1
Global survey #2
Global survey #3
(a)
(b)
(c)
(d)
(e)
(f)
***
AMF plant
EcM plant
Ecosystem stability
0
20
40
0
25
50
75
100
Basal area of mycorrhizal association (%)

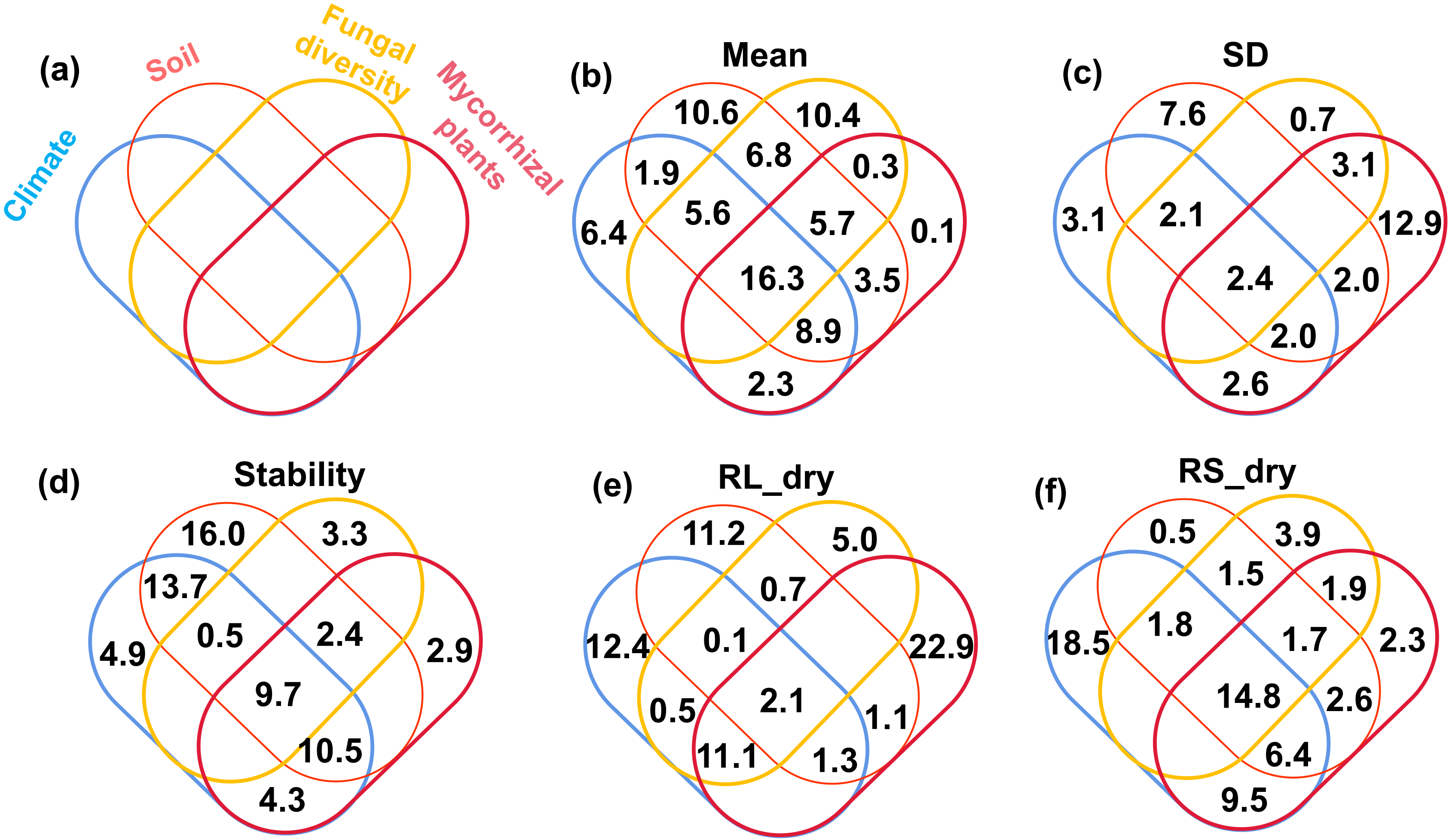

Soil saprobes
Root endophyte
Plant pathogen
Mycorrhizal fungi
Global survey #1
Global survey #2
Global survey #3
Ecosystem RS and RL to drought events
Phylotype richness
RS (a) ***
RS (b) **
RS (c) ***
RL (d)
RS (e) *
RL (f)
RL (g) ***
RL (h) ***
RS (i) *
RS (j)
RS (k)
RS (l)
1.0
0.8
0.6
0.4
0.9
0.7
0.5
0.5
0.0
-0.5
-1.0
20
40
60
80
0
3
6
9
50
100
150
10
20
30
25
75
200
300
2
4
40
50

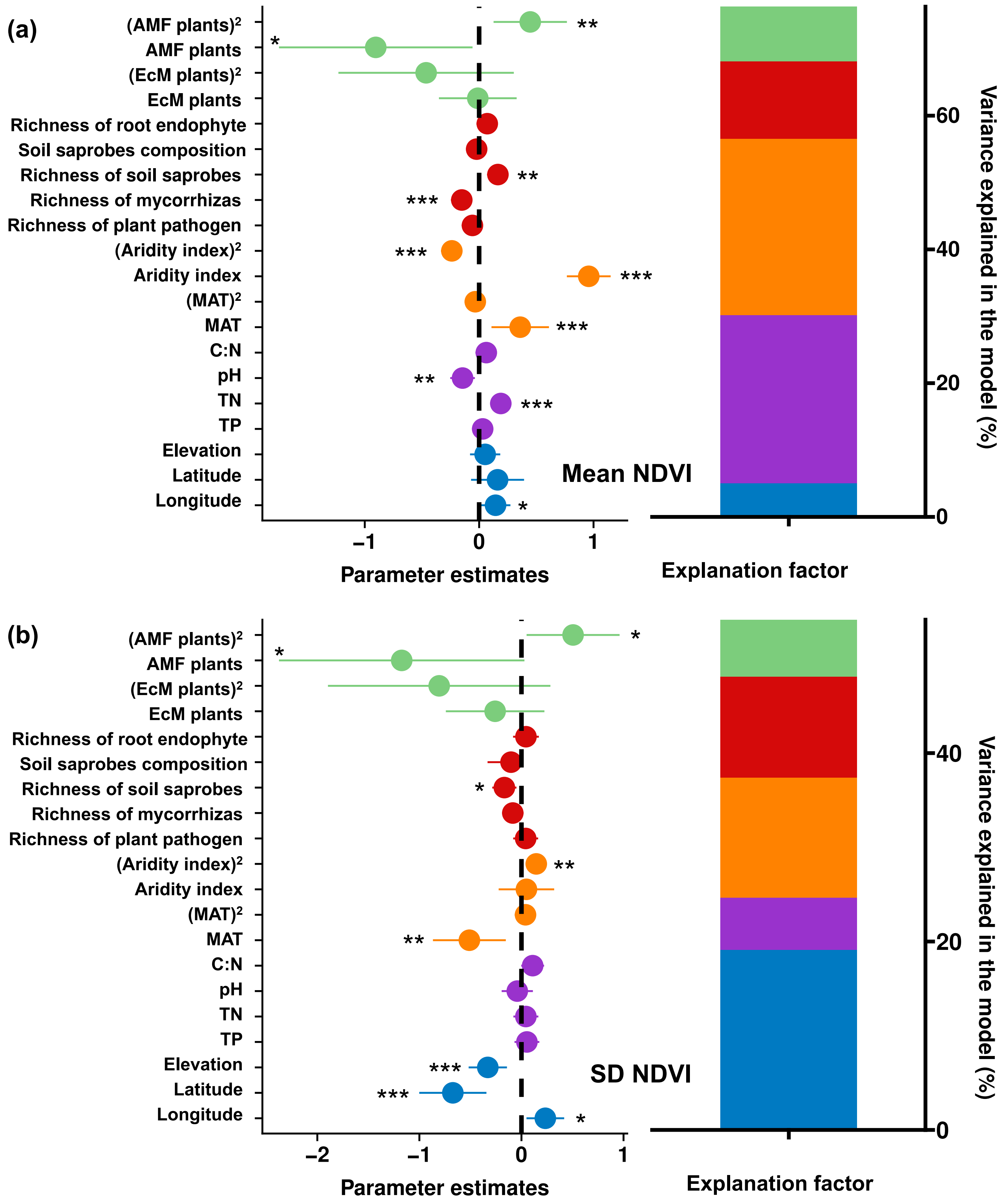

Latitude
90
60
30
0
−30
−60
−90
Longitude
−180
−150
−120
−90
−60
−30
0
30
60
90
120
150
180
Global-scale survey
● #1
● #2
● #3

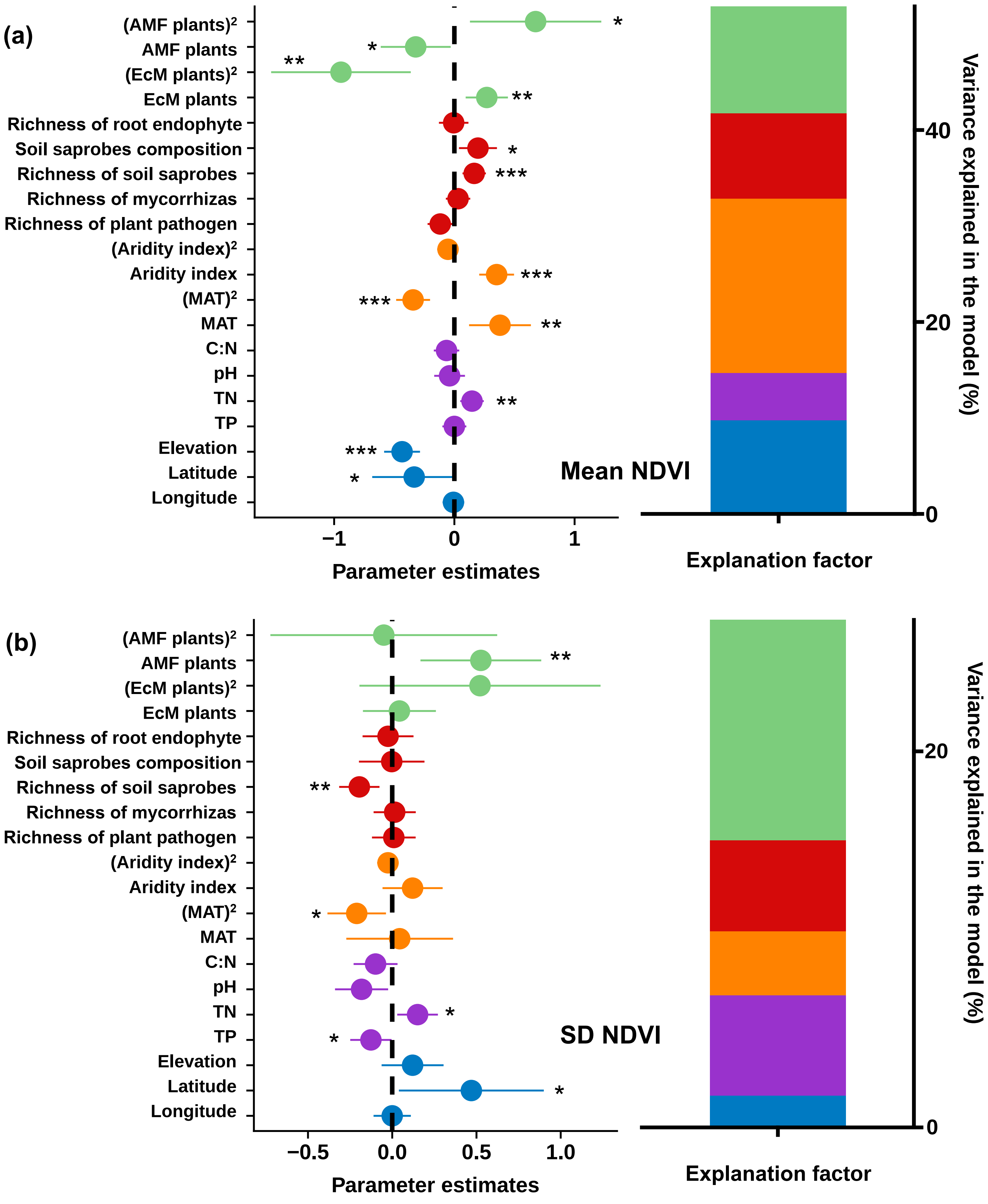

7000
5000
3000
1000
0
Event frequency
-0.67
0.67
Drought index (SPEI-12)
Dry events
Normal events
Wet events
Plot locations

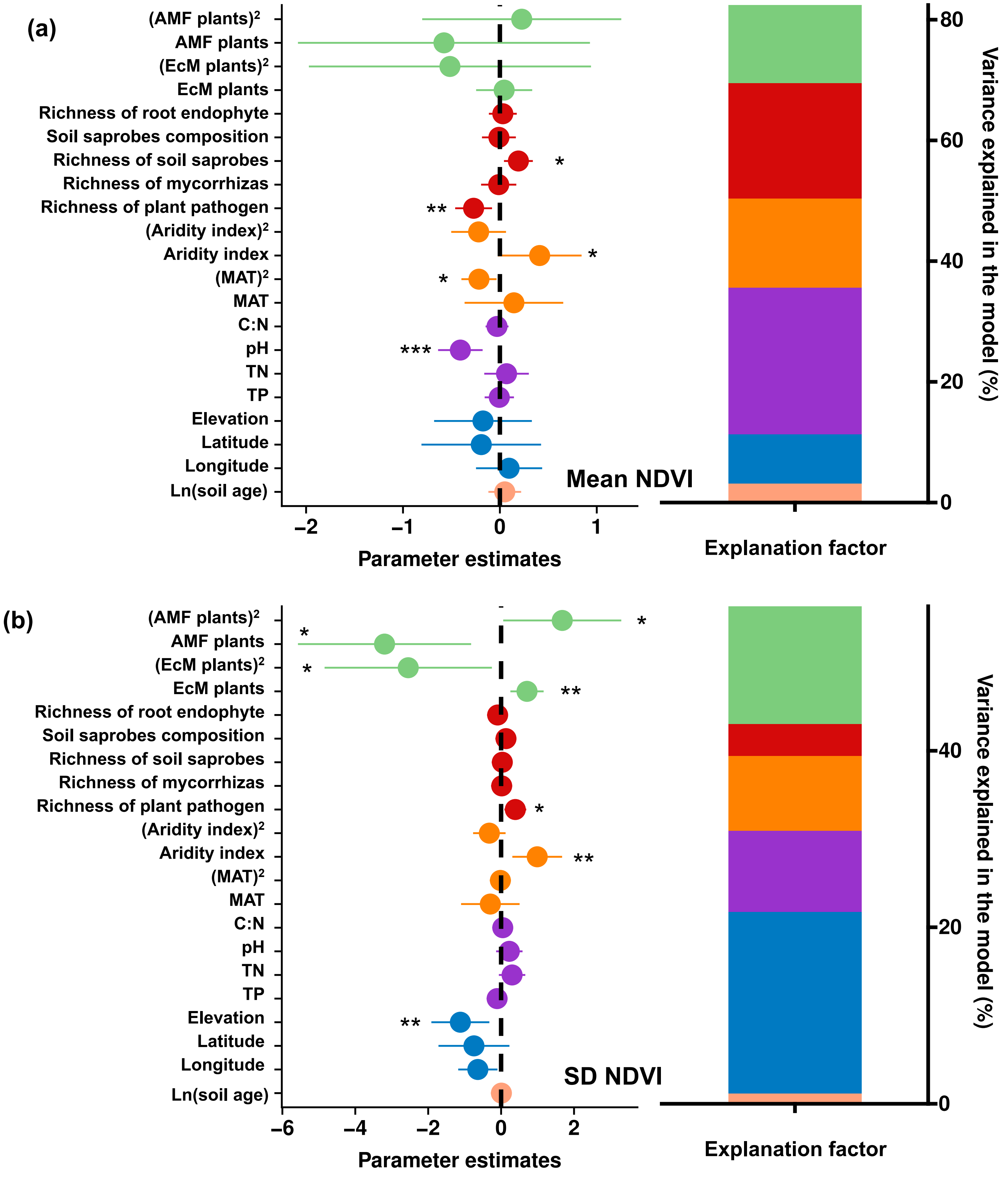

(a)
Climate
Soil+biomes
Fungal diversity
Mycorrhizal plants
(b)
Mean
6.5
3.6
4.3
4.9
2.1
0.1
4.0
0.8
4.3
0.3
0.3
1.9
(c)
SD
4.8
4.0
8.5
8.2
9.7
7.6
0.7
1.6
3.0
0.5
0.7
(d)
Stability
3.9
3.1
2.6
6.0
5.2
0.3
2.1
0.7
3.9
2.1
1.0
2.4
(e)
RL_dry
1.9
7.4
0.4
1.7
0.6
0.4
0.1
2.4
0.6
0.7
0.4
0.4
(f)
RS_dry
2.9
2.2
0.1
1.8
2.7
3.1
0.2
3.2
1.2
2.4
0.7
1.1
1.5
2.5

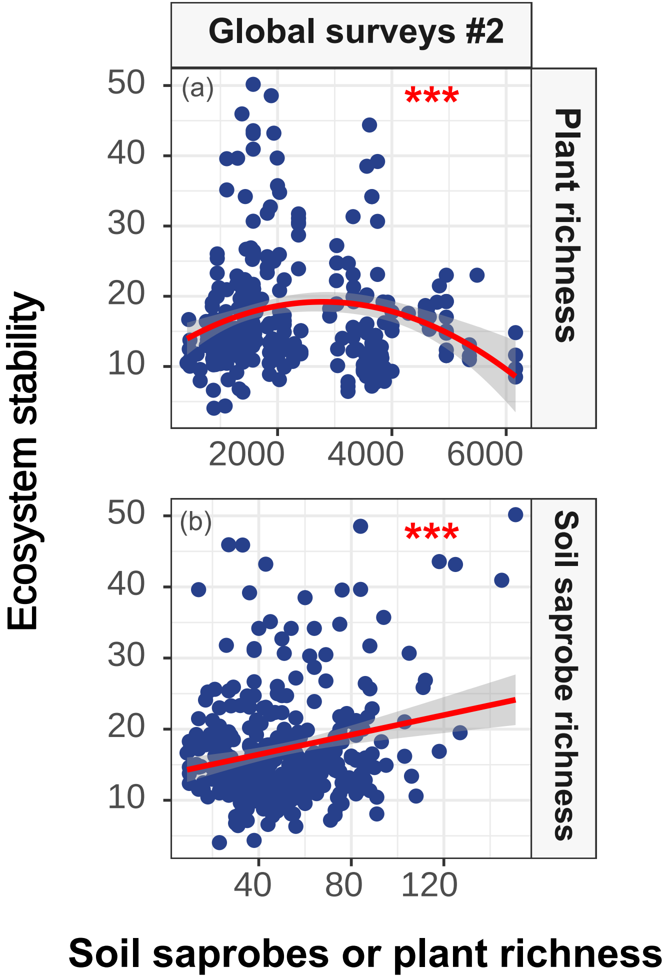

(a)
Climate
Soil+biomes
Fungi
Mycorrhizal plants
(b)
Mean
1.4
8.2
1.3
1.4
3.9
0.4
0.3
4.5
7.6
7.8
1.9
0.2
(c)
SD
0.9
4.4
0.4
3.6
3.9
0.8
1.1
0.5
1.8
1.0
1.2
0.5
(d)
Stability
11.2
0.4
1.2
1.9
0.1
4.4
1.9
0.3
1.1
(e)
RL_dry
0.3
3.5
0.4
0.1
0.3
0.9
0.3
0.4
2.6
0.3
2.8
0.2
1.8
(f)
RS_dry
5.5
1.3
0.8
0.2
0.4
0.5
1.3
0.5
2.1
2.0
0.8
0.7

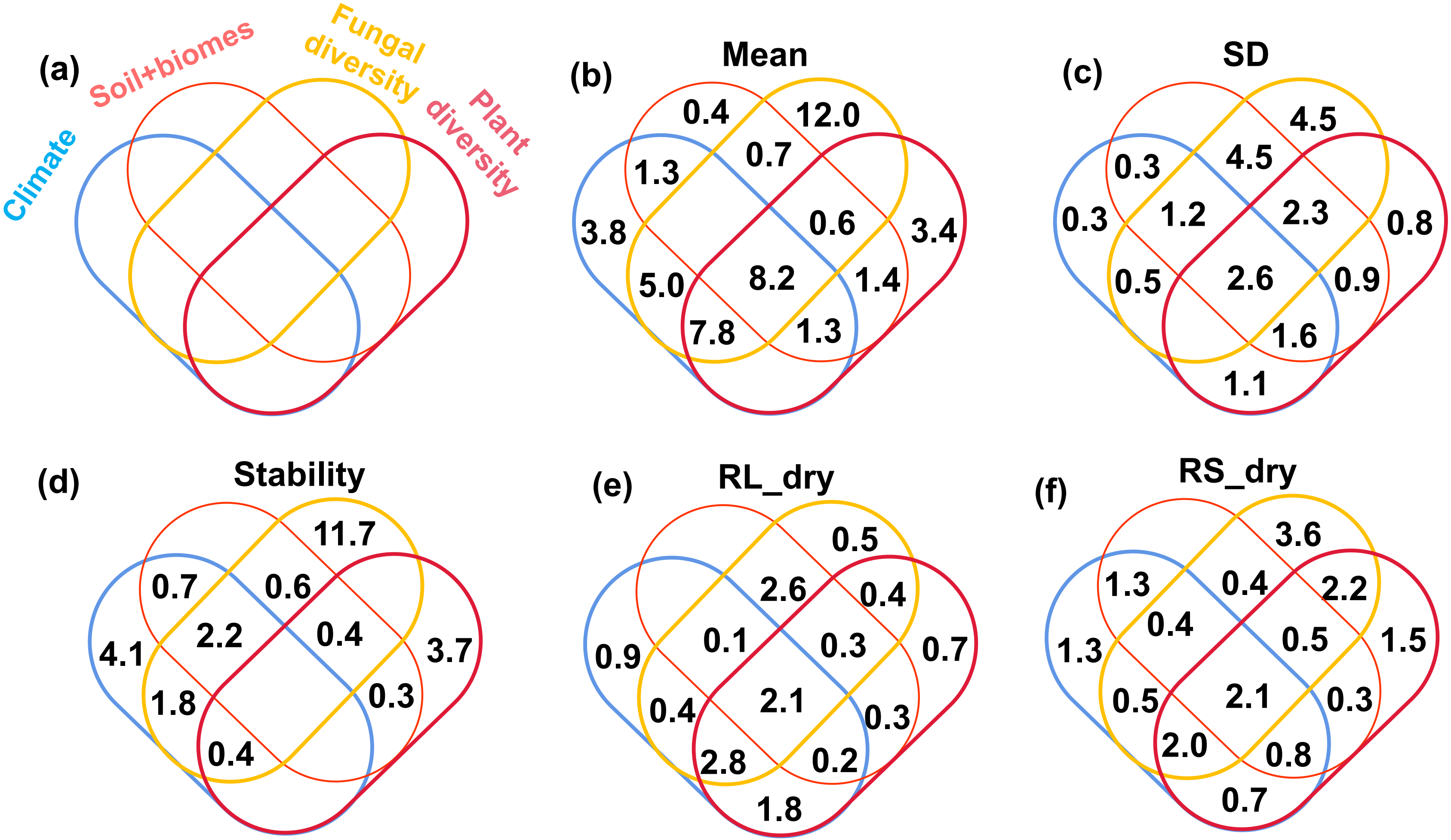

(a)
Climate
Soil
Fungal diversity
Mycorrhizal plants
(b)
Mean
10.6
10.4
6.8
1.9
0.3
6.4
5.6
5.7
0.1
16.3
3.5
8.9
2.3
(c)
SD
7.6
0.7
3.1
3.1
2.1
12.9
2.4
2.0
2.0
2.6
(d)
Stability
16.0
3.3
13.7
0.5
2.4
4.9
2.9
9.7
10.5
4.3
(e)
RL_dry
11.2
5.0
0.7
12.4
0.1
22.9
0.5
2.1
1.1
11.1
1.3
(f)
RS_dry
0.5
3.9
1.5
1.9
1.8
18.5
1.7
2.3
14.8
2.6
6.4
9.5


(a)
(AMF plants)²
AMF plants
(EcM plants)²
EcM plants
Richness of root endophyte
Soil saprobes composition
Richness of soil saprobes
Richness of mycorrhizas
Richness of plant pathogen
(Aridity index)²
Aridity index
(MAT)²
MAT
C:N
pH
TN
TP
Elevation
Latitude
Longitude
**
*
**
***
***
***
***
**
***
*
Mean NDVI
−1
0
1
Parameter estimates
Explanation factor
0
20
40
60
Variance explained in the model (%)
(b)
(AMF plants)²
AMF plants
(EcM plants)²
EcM plants
Richness of root endophyte
Soil saprobes composition
Richness of soil saprobes
Richness of mycorrhizas
Richness of plant pathogen
(Aridity index)²
Aridity index
(MAT)²
MAT
C:N
pH
TN
TP
Elevation
Latitude
Longitude
*
*
*
**
**
***
***
*
SD NDVI
−2
−1
0
1
Parameter estimates
Explanation factor
0
20
40
Variance explained in the model (%)


(a)
(AMF plants)²
AMF plants
(EcM plants)²
EcM plants
Richness of root endophyte
Soil saprobes composition
Richness of soil saprobes
Richness of mycorrhizas
Richness of plant pathogen
(Aridity index)²
Aridity index
(MAT)²
MAT
C:N
pH
TN
TP
Elevation
Latitude
Longitude
*
*
**
**
*
***
***
***
**
**
***
*
−1
0
1
Parameter estimates
Mean NDVI
0
20
40
Variance explained in the model (%)
Explanation factor
(b)
(AMF plants)²
AMF plants
(EcM plants)²
EcM plants
Richness of root endophyte
Soil saprobes composition
Richness of soil saprobes
Richness of mycorrhizas
Richness of plant pathogen
(Aridity index)²
Aridity index
(MAT)²
MAT
C:N
pH
TN
TP
Elevation
Latitude
Longitude
**
**
*
*
*
*
−0.5
0.0
0.5
1.0
Parameter estimates
SD NDVI
0
20
Variance explained in the model (%)
Explanation factor


(a)
(AMF plants)^2
AMF plants
(EcM plants)^2
EcM plants
Richness of root endophyte
Soil saprobes composition
Richness of soil saprobes
Richness of mycorrhizas
Richness of plant pathogen
(Aridity index)^2
Aridity index
(MAT)^2
MAT
C:N
pH
TN
TP
Elevation
Latitude
Longitude
Ln(soil age)
*
**
*
*
***
Mean NDVI
−2
−1
0
1
Parameter estimates
80
60
40
20
0
Variance explained in the model (%)
Explanation factor
(b)
(AMF plants)^2
AMF plants
(EcM plants)^2
EcM plants
Richness of root endophyte
Soil saprobes composition
Richness of soil saprobes
Richness of mycorrhizas
Richness of plant pathogen
(Aridity index)^2
Aridity index
(MAT)^2
MAT
C:N
pH
TN
TP
Elevation
Latitude
Longitude
Ln(soil age)
*
*
*
**
*
**
**
SD NDVI
−6
−4
−2
0
2
Parameter estimates
40
20
0
Variance explained in the model (%)
Explanation factor


Global surveys #2
(a)
***
Plant richness
50
40
30
20
10
2000
4000
6000
(b)
***
Soil saprobe richness
50
40
30
20
10
40
80
120
Ecosystem stability
Soil saprobes or plant richness


(a)
Climate
Soil+biomes
Fungal diversity
Plant diversity
(b)
Mean
0.4
12.0
1.3
0.7
3.8
0.6
3.4
5.0
8.2
1.4
7.8
1.3
(c)
SD
4.5
0.3
4.5
0.3
1.2
2.3
0.8
0.5
2.6
0.9
1.6
1.1
(d)
Stability
11.7
0.7
0.6
4.1
2.2
0.4
3.7
1.8
0.3
0.4
(e)
RL_dry
0.5
2.6
0.4
0.9
0.1
0.3
0.7
0.4
2.1
0.3
2.8
0.2
1.8
(f)
RS_dry
3.6
1.3
0.4
2.2
0.4
1.3
0.5
1.5
0.5
2.1
0.3
2.0
0.8
0.7

Supplementary Information for

Phylotype diversity within soil fungal functional groups drives ecosystem stability

Shengen Liu, Pablo García-Palacios, Leho Tedersoo, Emilio Guirado, Marcel van der Heijden, Cameron Wagg, Dima Chen, Qingkui Wang, Juntao Wang, Brajesh K. Singh, Manuel Delgado-Baquerizo*

*Correspondence to: M.DelgadoBaquerizo@gmail.com

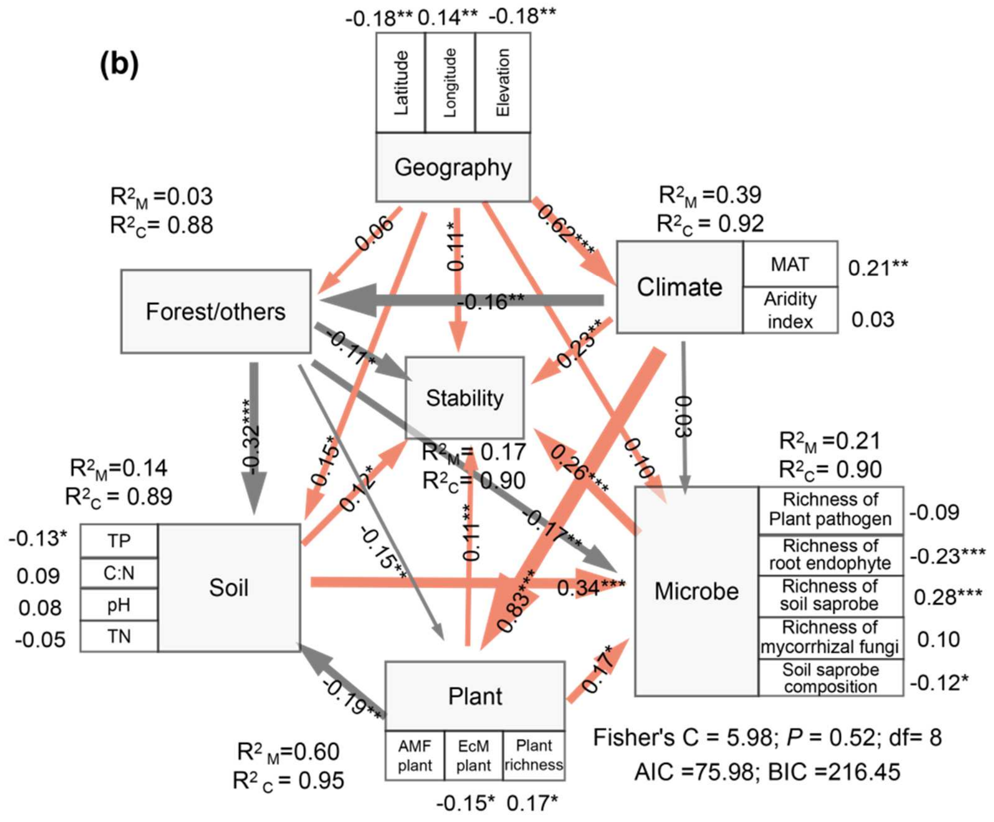
This PDF file includes:

Supplementary Figures 1 to 11
Supplementary Note 1

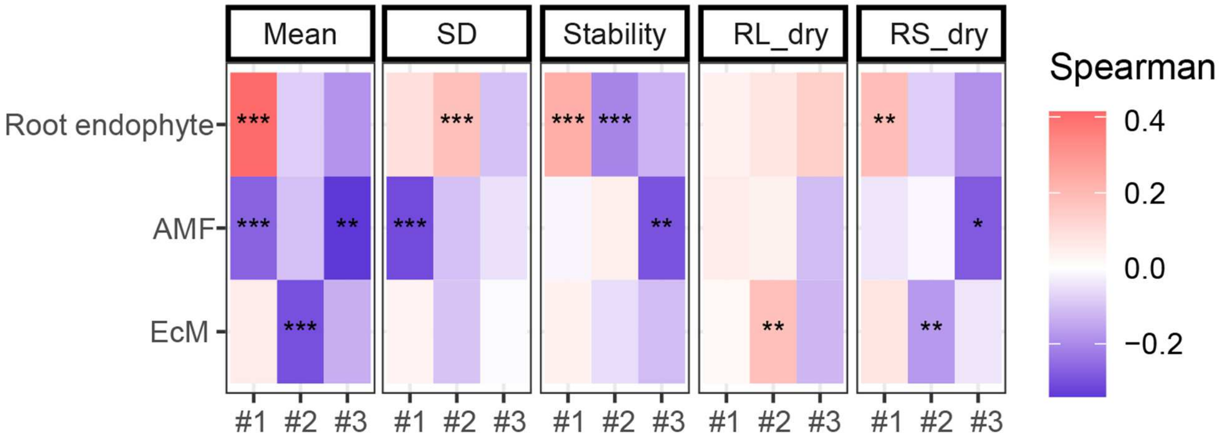
Supplementary Note 1. Fungal taxa associated with ecosystem stability

Given the importance of fungi in all our analyses, we used Random Forest[59] modeling to further identify consistent fungal taxa (order level) associated with ecosystem stability. The number of taxa needed to predict ecosystem stability was determined using 10-fold cross-validation implemented with the "rfcv" function of R package "rfPermute"[59].

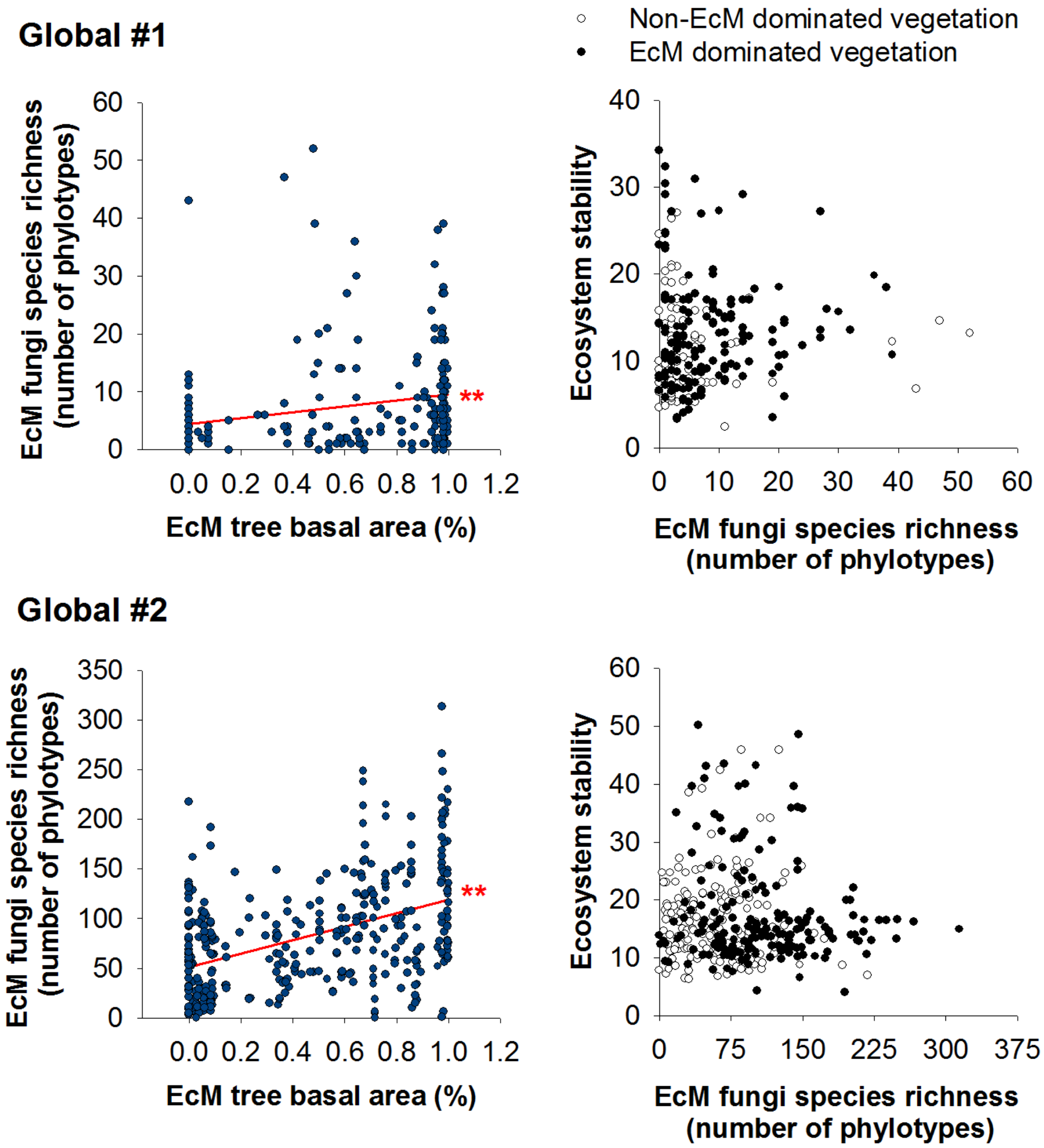
Random forest analyses identified 26 and 41 orders of globally distributed fungi such as Agaricales, Mortierellales and Geoglossales which were consistently to be good biomarkers of ecosystem stability across global surveys #1 and #2 (Supplementary Fig. 5a,c,e). We further investigated the link between ecosystem stability and dominant fungal phylotypes (species level); those that were both abundant (top 10% of all identified fungi in terms of relative abundance) and ubiquitous (at least occur in 6/9 biomes) in soils across the globe. There were 412, 348 and 19 phylotypes identified to be abundant and ubiquitous across global surveys #1, #2 and #3. We further found some dominant and globally distributed taxa which were significantly correlated with ecosystem stability either in a positive (e.g., sordariomycetes, a group of decomposers) or a negative (e.g., dothideomycetes) fashion (Supplementary Fig. 5b,d,f).



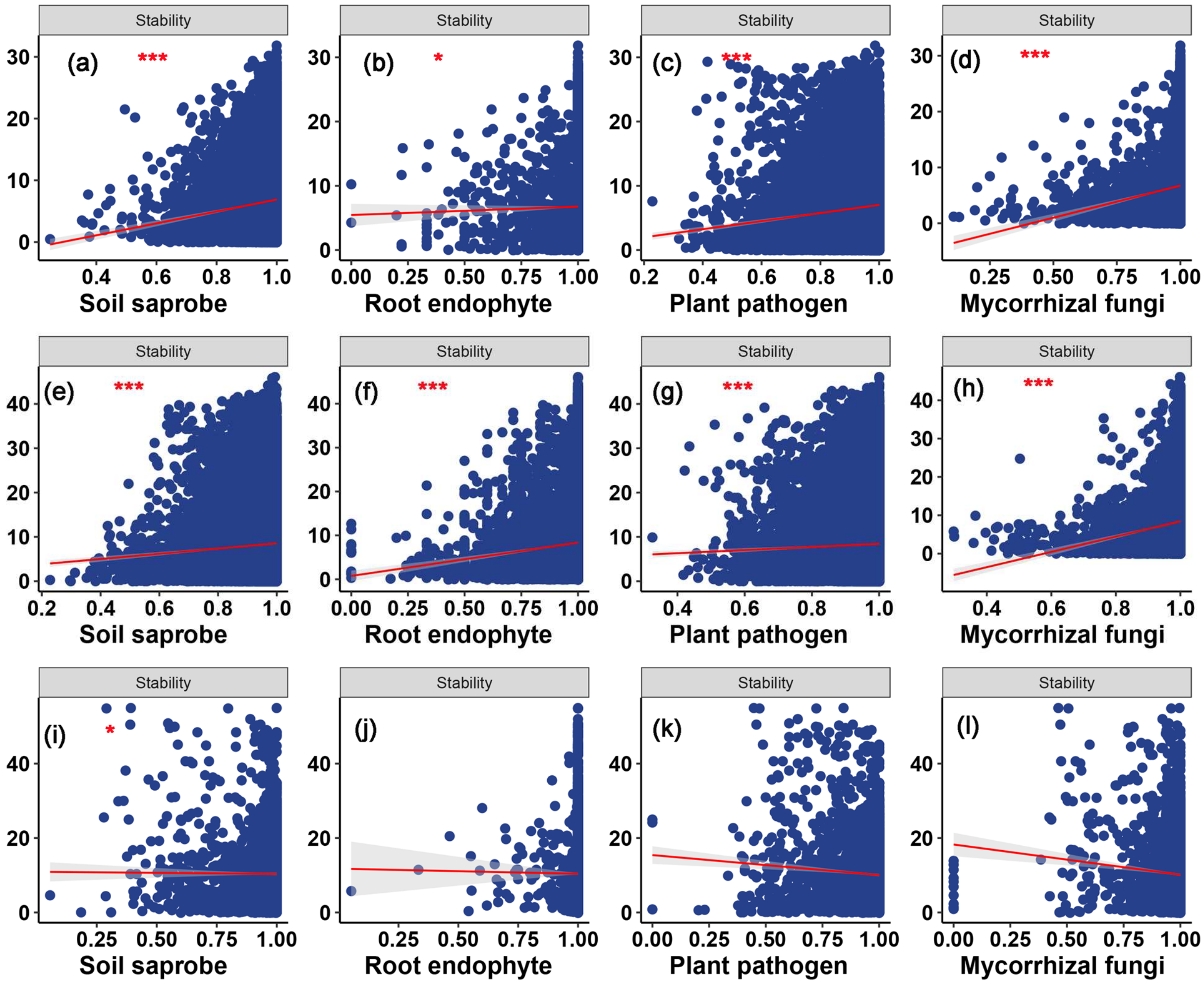
Supplementary Figure 1. Direct and indirect drivers of ecosystem stability. PiecewiseSEM accounting for the direct and indirect effects of geography, climate predictors, vegatation type, plant mycorrhizal association and fungal diversity on the ecosystem stability at the global survey #2 (b; n = 351 ecosystems). Numbers adjacent to arrows are path coefficients (partial regression) are the directly standardized effect size of the relationship. The conditional and marginal R^2 represent the proportion of variance explained by all predictors without and with accounting for random effects of “sampling site”. Relationships between residual variables of measured predictors were not showed. Significance levels of each predictor are *P < 0.05, **P < 0.01, ***P < 0.001. Microbes includes the richness of saprobes, potential fungal plant pathogens, root endophytes and mycorrhizal fungi, and the community composition of decomposers (saprobes).



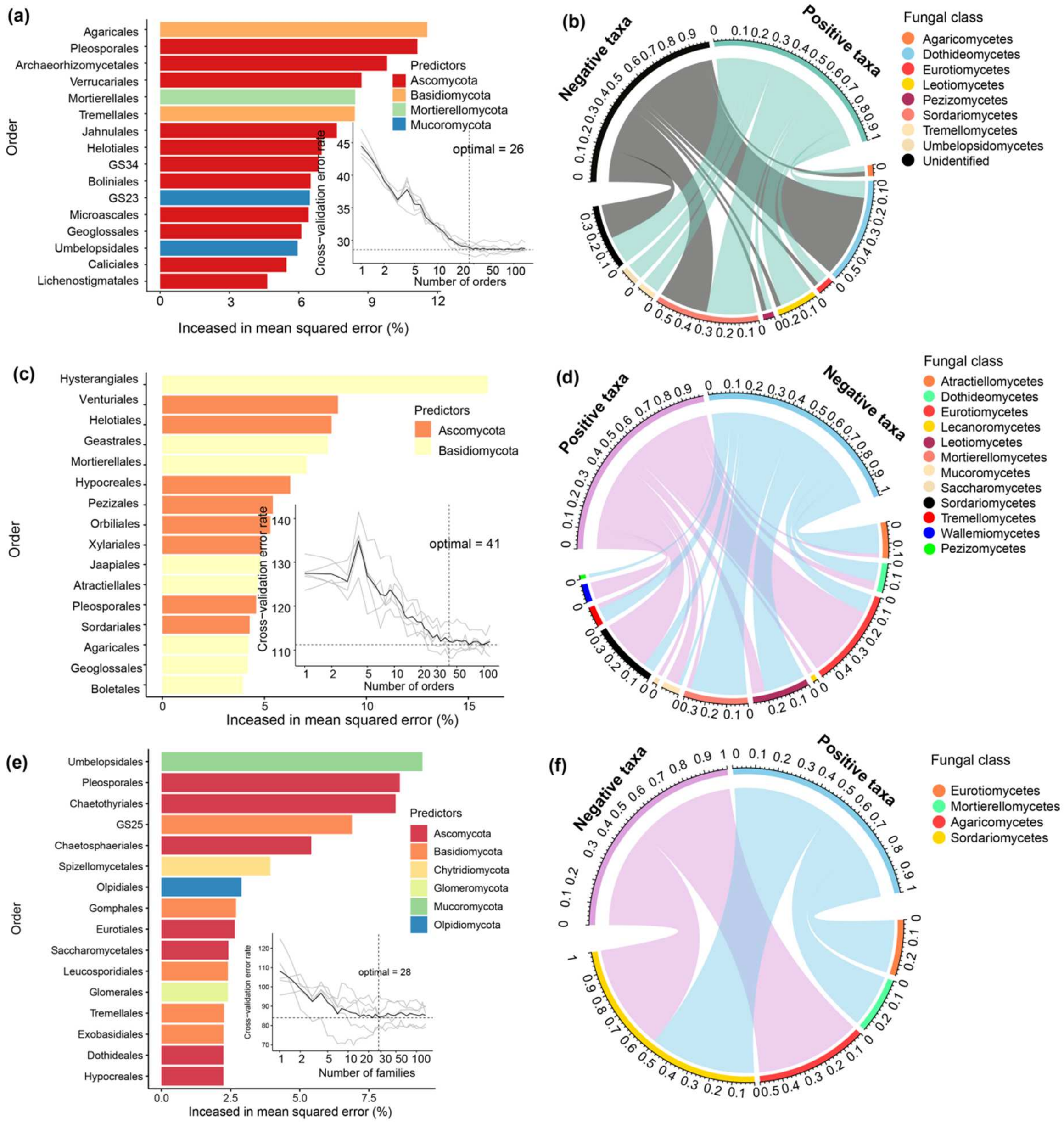
Supplementary Figure 2. **Correlation between diversity of fungal groups and ecosystem productivity.** Spearman correlations between the richness of root endophytes, arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal fungi (EcM) with mean and standard deviation of NDVI, ecosystem stability, and the resistance (RS) and resilience (RL) of NDVI to drought events in the global surveys #1 (n = 235 ecosystems) and #2 (n = 351 ecosystems).



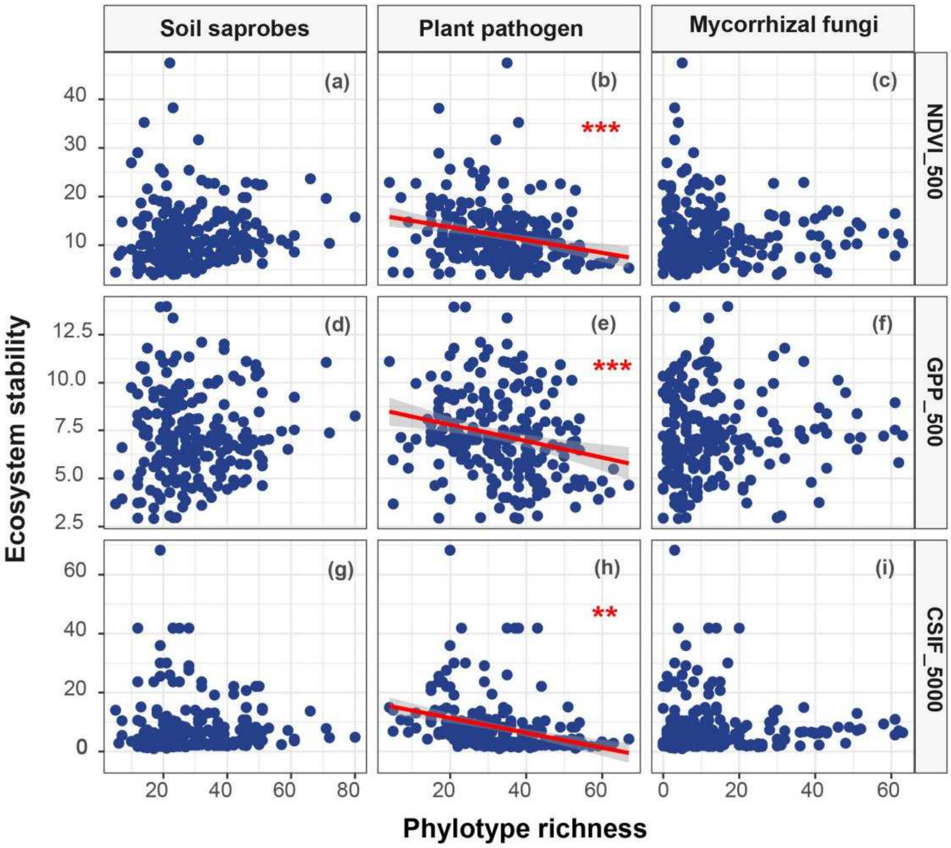
Supplementary Figure 3. Relationship between ectomycorrhizal fungi and ecosystem stability in ectomycorrhizal dominated (>50% cover) forests (determined using maps from ref. *28*). Fitted linear relationships of the richness of EMF with basal area of EMF tree and ecosystem stability in global survey #1 (n = 235 ecosystems) and #2 (n = 351 ecosystems). Statistical analysis for the relationship between richness and stability was performed using ordinary least squares linear regressions. Significance levels of each predictor are **P* < 0.05, ***P* < 0.01, ****P* < 0.001.



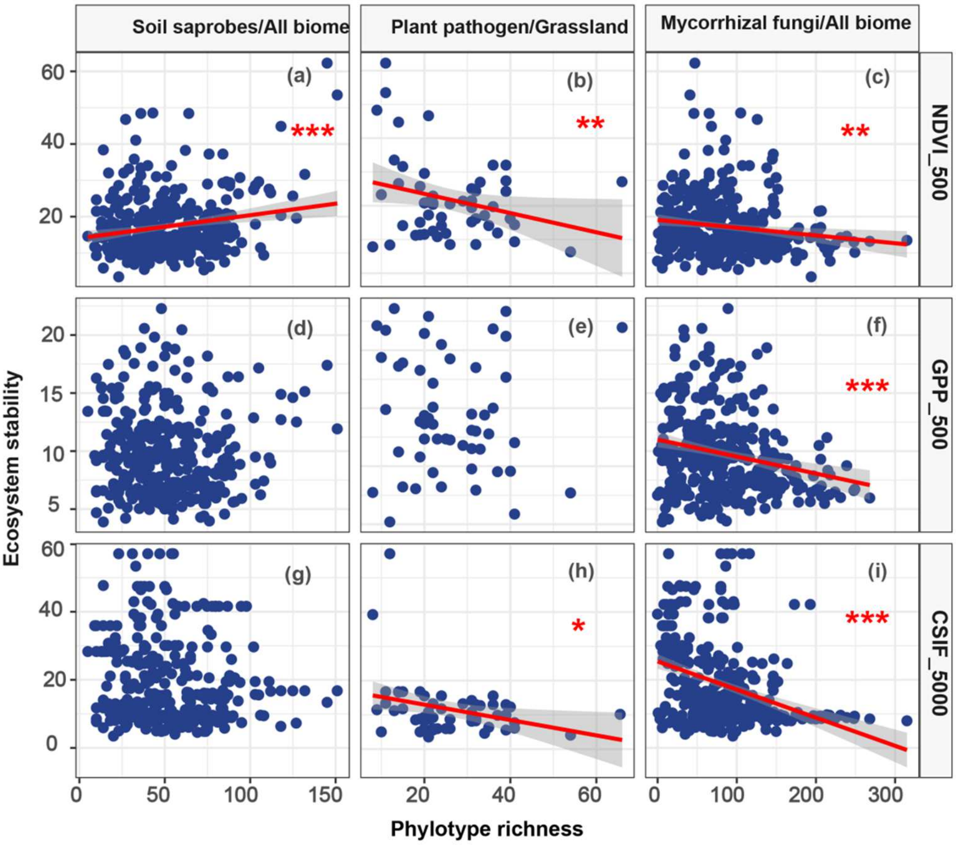
Supplementary Figure 4. Correlations between functional fungal community composition and ecosystem stability. Dissimilarity in fungal community composition (beta diversity) predicts ecosystem stability in global survey #1 (a-d; n = 235 ecosystems) and #2 (e-h; n = 351 ecosystems) and #3 (i-l; n = 87 ecosystems). Fungal community composition is based on rarefied phylotype tables and Bray-Curtis distance. Spatial variability in ecosystem stability was determined based on euclidean distance metric. Mantel test was performed using 999 times permutation using non-parametric methods. Grey shade indicates 95% confidence interval. Significance levels of each predictor are *P < 0.05, **P < 0.01, ***P < 0.001. Soil saprobe = Soil fungal decomposers.



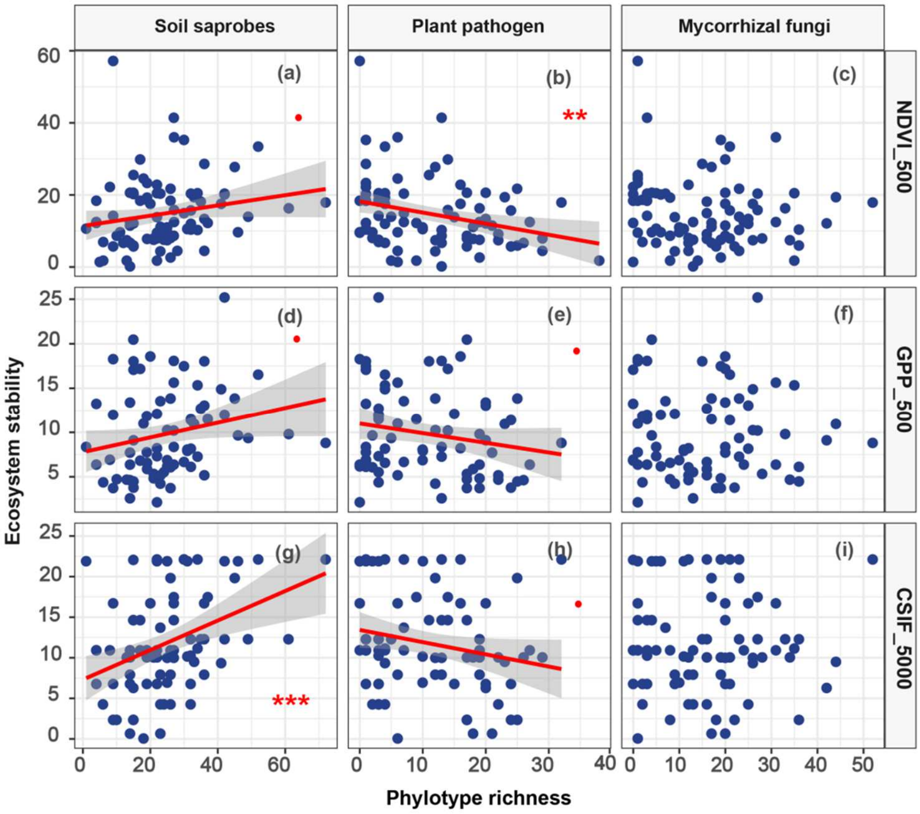
Supplementary Figure 5. Decomposer indicators of ecosystem stability. Soil biomarkers of ecosystem stability in global survey #1 (a,b; n = 235 ecosystems) and #2 (c,d; n = 351 ecosystems) and #3 (e,f; n = 87 ecosystems). Decomposer taxa selected by Random-Forest modeling as significant indicators of ecosystem stability. These analyses are based on the proportion of fungal order and ecosystem stability data (a,c,e). Panels (b,d,f) include the correlation between dominant and ubiquitous decomposer taxa and ecosystem stability. In this analysis, dominant fungi are defined as abundant (top 10% of all identified fungi in terms of relative abundance) and ubiquitous (at least occur in 6/9 biomes) in soils across the globe. The thickness of each ribbon represents the number of positive and negative taxa assigned to different taxonomic classes.



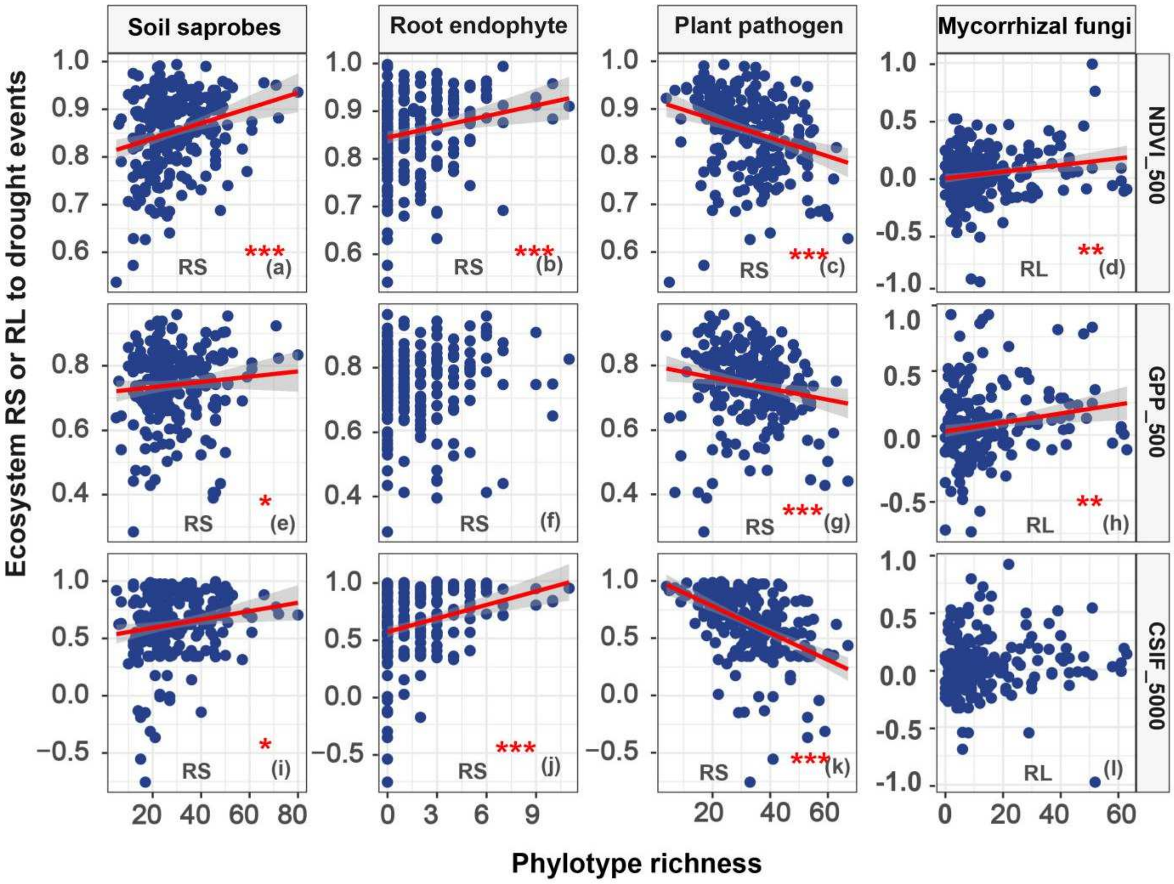
Supplementary Figure 6. Relationships between soil fungal diversity and ecosystem stability. Fitted linear relationships between ecosystem stability (NDVI500m, GPP500 and CSIF5000) and the richness of selected functional groups of fungi in global surveys #1 (a-c; n =235 ecosystems). Statistical analysis for the relationship between richness and stability was performed using ordinary least squares linear regressions. Significance levels of each predictor are $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. Grey shade indicates 95% confidence interval. Soil saprobe = Soil fungal decomposers.



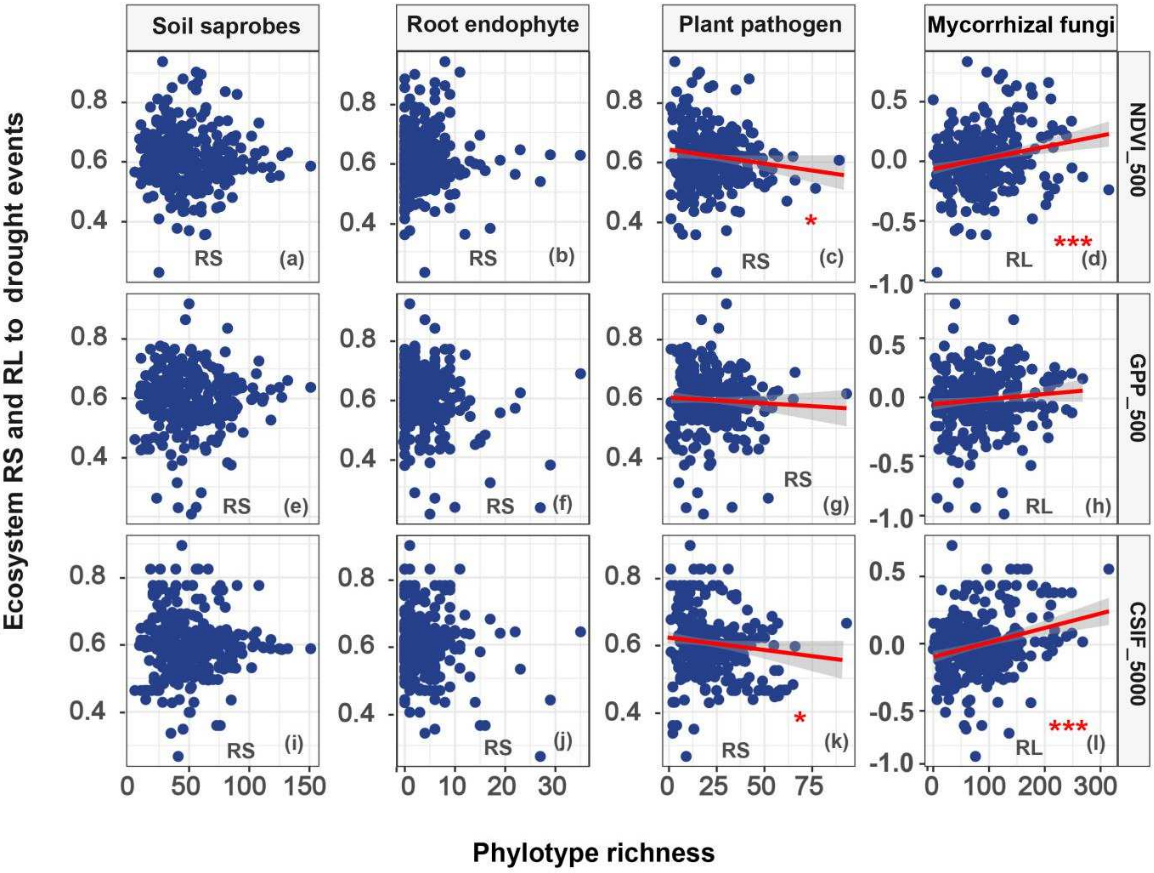
Supplementary Figure 7. Relationships between soil fungal diversity and ecosystem stability. Fitted linear relationships between ecosystem stability and the richness of selected functional groups of fungi in global surveys #2 (n = 351 ecosystems). Among these relationships, "b,e,h" represented the relationship between richness of plant pathogen and ecosystem stability across global grasslands (n = 54 ecosystems), and the left were results across global biomes (n = 351 ecosystems). Statistical analysis for the relationship between richness and stability was performed using ordinary least squares linear regressions. Significance levels of each predictor are **P* < 0.05, ***P* < 0.01, ****P* < 0.001. Grey shade indicates 95% confidence interval. Soil saprobe = Soil fungal decomposers. NDVI_500m, GPP_500 and CSIF_5000 indicate ecosystem stability calculation based on the resolution of 500 m for NDVI and GPP, and 5000 m for CSIF, respectively.



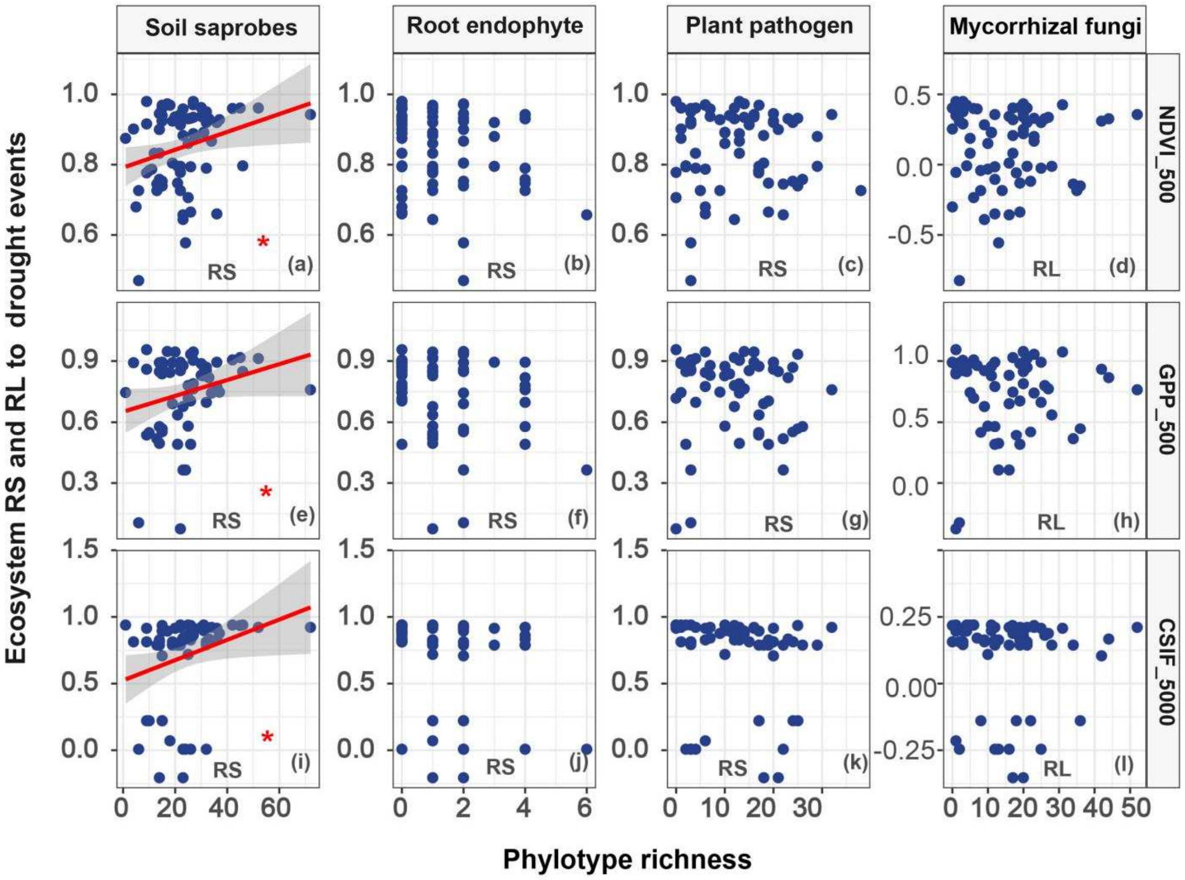
Supplementary Figure 8. Relationships between soil fungal diversity and ecosystem stability. Fitted linear relationships between ecosystem stability and the richness of selected functional groups of fungi in global surveys #3 (n = 87 ecosystems). Statistical analysis for the relationship between richness and stability was performed using ordinary least squares linear regressions. Significance levels of each predictor are ·0.05< *P* <0.1, 0.05,**P* < 0.05, ***P* < 0.01, ****P* < 0.001. Grey shade indicates 95% confidence interval. Soil saprobe = Soil fungal decomposers. NDVI_500m, GPP_500 and CSIF_5000 indicate ecosystem stability calculation based on the resolution of 500 m for NDVI and GPP, and 5000 m for CSIF, respectively.



Supplementary Figure 9. Relationships between soil fungal diversity and ecosystem resistance and resilience to drought events. Fungal diversity effects on ecosystem resistance (RS, a-c, e-g, i-k) and resilience (RL, d,h,l) in drought events in global surveys #1 (a-d; n = 235 ecosystems). Statistical analysis for the relationship between richness and stability was performed using ordinary least squares linear regressions. Significance levels of each predictor are **P* < 0.05, ***P* < 0.01, ****P* < 0.001. Grey shade indicates 95% confidence interval. The NDVI_500m, GPP_500 and CSIF_5000 in the panel indicate ecosystem stability calculation based on the resolution of 500 m for NDVI and GPP, and 5000 m for CSIF, respectively.



Supplementary Figure 10. Relationships between soil fungal diversity and ecosystem resistance and resilience to drought events. Fungal diversity effects on ecosystem resistance (RS, a-c, e-g, i-k) and resilience (RL, d,h,l) in drought events in global surveys #1 (a-d; n = 351 ecosystems). Statistical analysis for the relationship between richness and stability was performed using ordinary least squares linear regressions. Significance levels of each predictor are $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. Grey shade indicates 95% confidence interval. The NDVI_500m, GPP_500 and CSIF_5000 indicate ecosystem stability calculation based on the resolution of 500 m for NDVI and GPP, and 5000 m for CSIF, respectively.



Supplementary Figure 11. Relationships between soil fungal diversity and ecosystem resistance and resilience to drought events. Fungal diversity effects on ecosystem resistance (RS, a-c, e-g, i-k) and resilience (RL, d,h,l) in drought events in global surveys #1 (a-d; n = 87 ecosystems). Statistical analysis for the relationship between richness and stability was performed using ordinary least squares linear regressions. Significance levels of each predictor are $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. Grey shade indicates 95% confidence interval. The NDVI_500m, GPP_500 and CSIF_5000 indicate ecosystem stability calculation based on the resolution of 500 m for NDVI and GPP, and 5000 m for CSIF, respectively.

Additional references

59. Archer, E. rfPermute: Estimate Permutation p-Values for Random Forest Importance Metrics. R package v. 1.5.2 (2016).