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Phylotype diversity within soil fungal functional groups drives ecosystem stability

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

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, remain 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 to buffer against extreme climate events.

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 plant growth[16] and helps plants withstand climate extremes such as droughts, promoting plant production resilience after these dramatic events[12,17]. On the other hand, 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 associated 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 (that is, 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]; global survey 2: 351 sites[23]; and global survey 3: 87 sites[24]; Extended Data Figs. 1–2). Then we assessed the links 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 links between soil fungal diversity and ecosystem stability.

[1]Engineering Research Center of Eco-Environment in Three Gorges Reservoir Region of Ministry of Education, China Three Gorges University, Yichang, China. [2]Laboratorio de Biodiversidad y Funcionamiento Ecosistémico, Instituto de Recursos Naturales y Agrobiología de Sevilla (IRNAS), CSIC, Seville, Spain. [3]Huitong Experimental Station of Forest Ecology, CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Shenyang, PR China. [4]Instituto de Ciencias Agrarias, Consejo Superior de Investigaciones Científicas, Madrid, Spain. [5]Mycology and Microbiology Center, University of Tartu, Tartu, Estonia. [6]College of Science, King Saud University, Riyadh, Saudi Arabia. [7]Multidisciplinary Institute for Environment Studies 'Ramon Margalef', University of Alicante, Alicante, Spain. [8]Andalusian Center for Assessment and Monitoring of Global Change (CAESCG), University of Almeria, Almeria, Spain. [9]Plant-Soil Interactions Group, Agroscope, Zurich, Switzerland. [10]Department of Plant and Microbial Biology, University of Zurich, Zurich, Switzerland. [11]Fredericton Research and Development Centre, Agriculture and Agri-Food Canada, Fredericton, New Brunswick, Canada. [12]School of Forestry & Landscape Architecture, Anhui Agricultural University, Hefei, China. [13]Hawkesbury Institute for the Environment, Western Sydney University, Richmond, New South Wales, Australia. [14]Global Centre for Land-Based Innovation, Western Sydney University, Penrith, New South Wales, Australia. [15]Unidad Asociada CSIC-UPO (BioFun), Universidad Pablo de Olavide, Seville, Spain. ✉e-mail: M.DelgadoBaquerizo@gmail.com
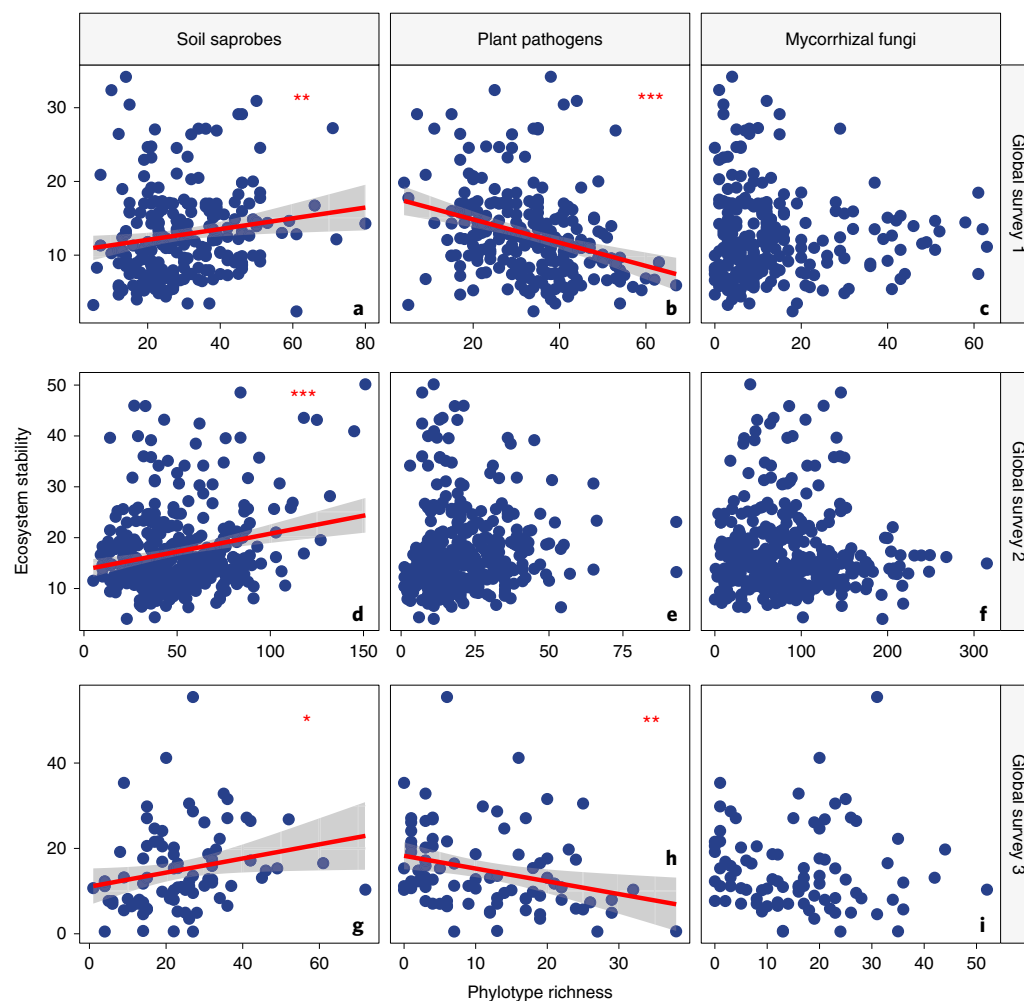
Fig. 1 | Relationships between soil fungal diversity and ecosystem stability. Fitted linear relationships between ecosystem stability and the richness of selected functional groups of fungi in global surveys 1 (**a–c**; $n = 235$ ecosystems), 2 (**d–f**; $n = 351$ ecosystems) and 3 (**g–i**; $n = 87$ ecosystems). Panels **a–c**, **d–f** and **g–i** include the relationship between phylotype richness within soil fungal functional groups (soil saprobes, soil-borne potential plant pathogens and mycorrhizal fungi) with ecosystem stability in global surveys 1, 2 and 3, respectively. 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 shading indicates the 95% confidence interval. Soil saprobes represent soil fungal decomposers.

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 (saprobes) 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, although we found that the shared effects of multiple biotic and abiotic variables drove most of the explained variation (Fig. 3 and Extended Data Figs. 3–5). The direction of the predictors' effect was consistent among the three global surveys, although the magnitude varied (Fig. 2 and Extended Data Figs. 6–8), which may be due to differences in sampling design and experimental methods (for example, 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. 3,4). Conversely, 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 and Supplementary Fig. 3 for results within EcM forests), our results showed a consistent hump-shaped relationship between the estimated basal area of AMF- or EcM-associated plants (based on ref. [26]) and ecosystem stability (Fig. 5a–f), suggesting that the proportions of plant functional groups still play key roles in sustaining ecosystem stability. In fact, our analyses revealed a positive association between the proportion of AMF plants[26] and ecosystem stability (Fig. 3a,b,c) when other environmental factors were simultaneously considered. Our multiple statistical approaches supported our hypotheses. However,
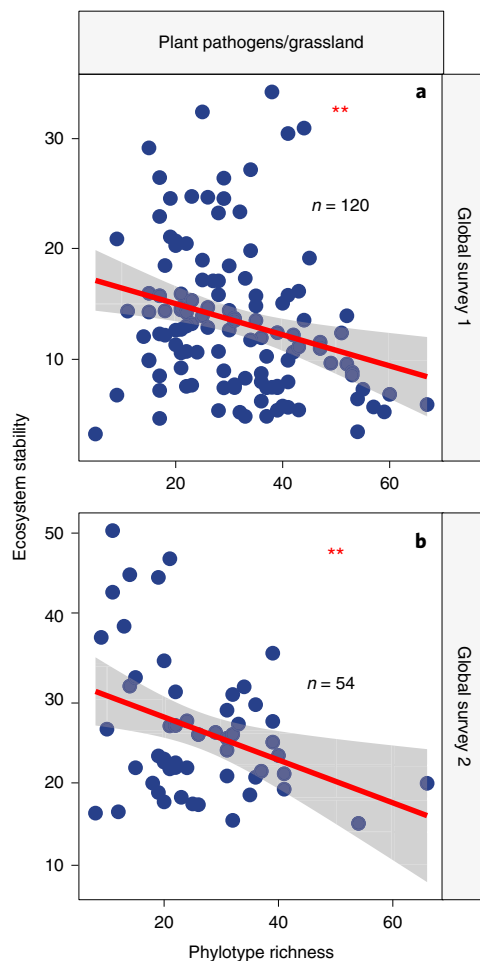
Fig. 2 | Relationships between soil fungal diversity and ecosystem stability in grasslands. Fitted linear relationships between ecosystem stability and the richness of selected functional groups of fungi in grasslands associated with global surveys 1 (**a**; $n = 120$ ecosystems) and 2 (**b**; $n = 54$ 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 shading indicates the 95% confidence interval.

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 indicates 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 are logistically demanding and remain a gap to be considered in future global soil biodiversity monitoring networks[3]. Our results further indicate that the diversity of soil decomposers positively influences 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 contrasting results suggest that, while maintaining highly diverse fungal decomposers supporting complex processes such as organic matter decomposition and nutrient release could help promote ecosystem stability, supporting the diversity of pathogens could have the opposite effect in 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 (for example, with warming and over-fertilization)[18,38], could contribute to destabilization of 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 is consistently and positively associated with the resistance of ecosystem productivity during drought events (Fig. 6a,b,e,i). Conversely, 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 type and soil properties (Extended Data Figs. 3–5,10). Together, our findings indicate that diversity of fungal functional groups drives ecosystem 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

Fig. 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 reveals 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. Community composition of soil saprobes was summarized using a non-metric multidimensional scaling (NMDS) (Methods). Quadratic (x^2) relationships between specific predictors and ecosystem stability were considered as explained in the Methods.
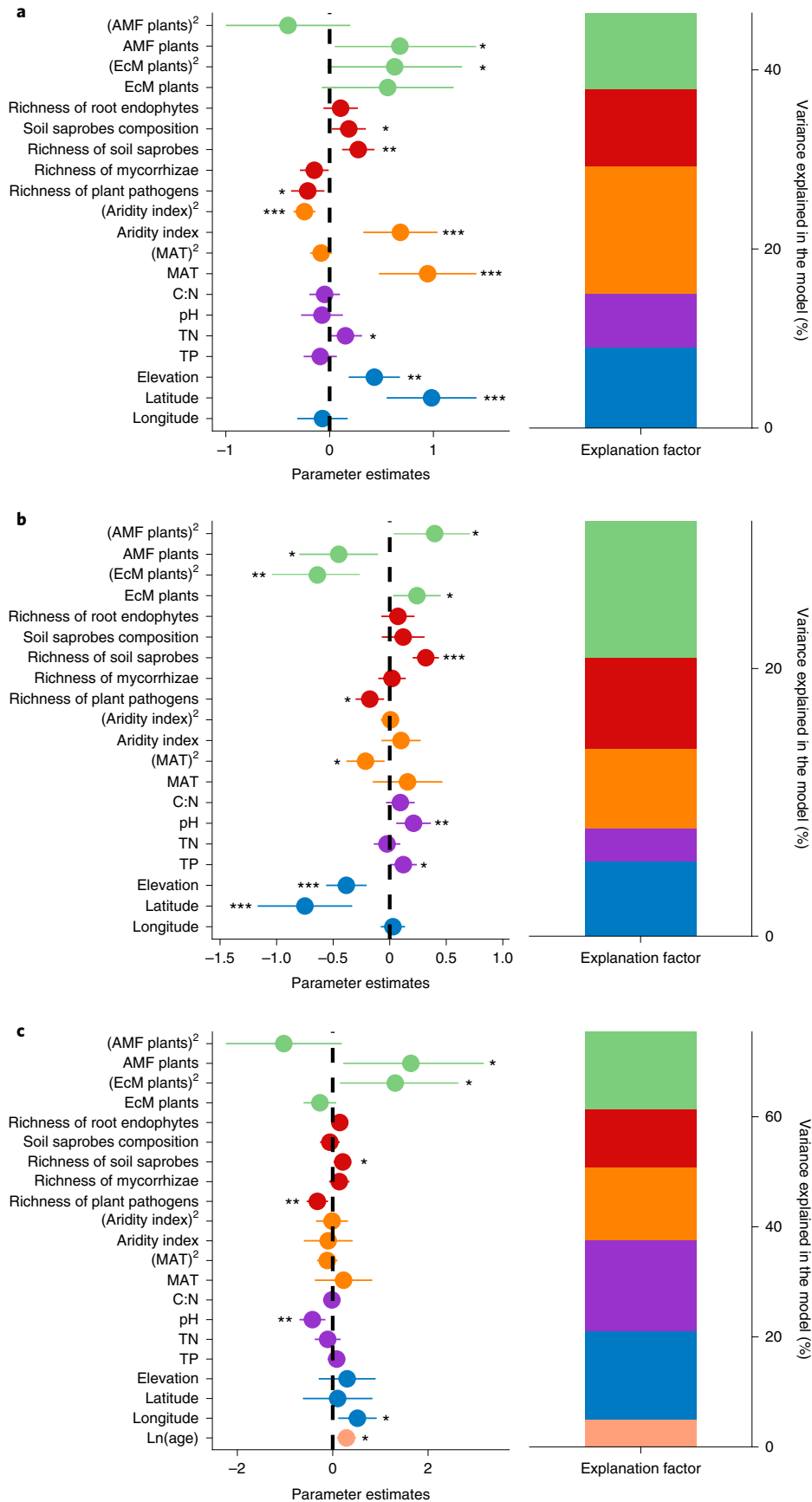
Fig. 4 | Direct and indirect drivers of ecosystem stability. piecewiseSEM accounting for the direct and indirect effects of geography, climate predictors, vegetation type, plant mycorrhizal association and fungal diversity on the ecosystem stability at global surveys 1 (**a**; n = 235 ecosystems), 2 (**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 (C) and marginal (M) 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 shown. 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). d.f., degree of freedom; AIC, Akaike information criterion; BIC, Bayesian information criterion.
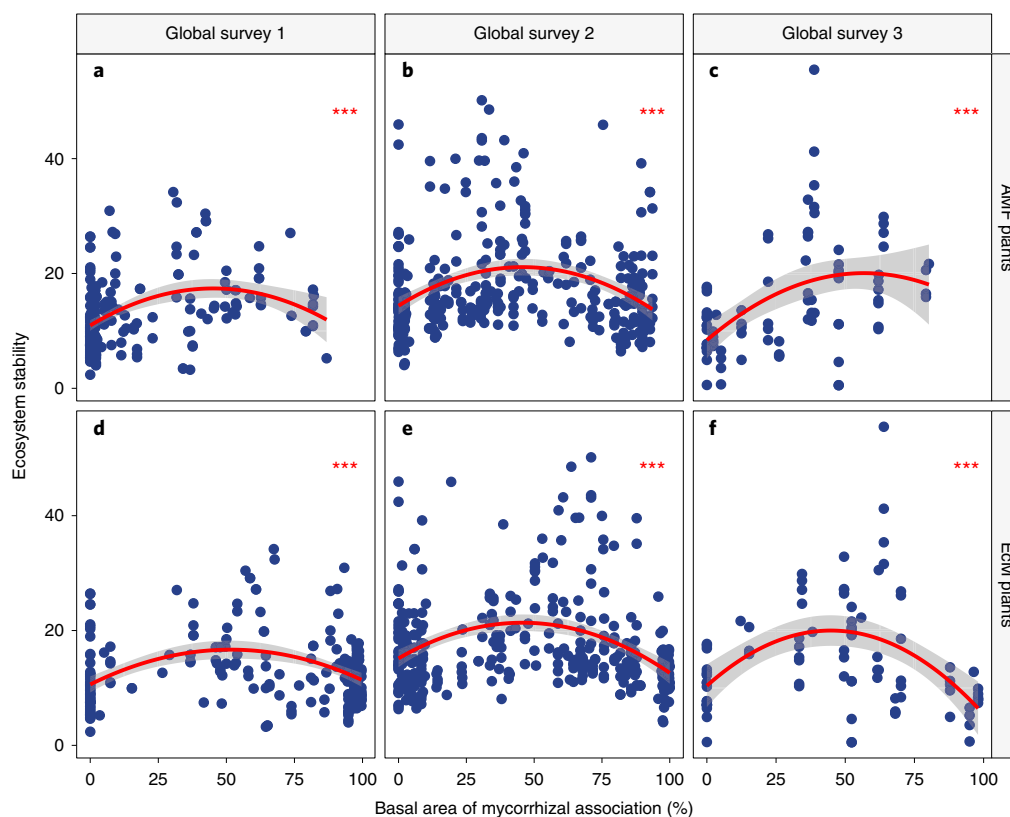

Fig. 5 | Relationship between basal area of mycorrhizal association and ecosystem stability. Relationships in global surveys 1 (**a,d**; n = 235 ecosystems), 2 (**b,e**; n = 351 ecosystems) and 3 (**c,f**; n = 87 ecosystems). Panels **a–c** and **d–f** include the relationship between basal area of AMF plants and EcM plants with ecosystem stability in global surveys 1, 2, 3, respectively. 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.

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, mean annual precipitation (MAP) and MAT in these locations ranged from 52 to 3,483 mm 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 × 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—for example, 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, United States) on a fraction of the fungal ITS gene. Bioinformatic analyses were done as described
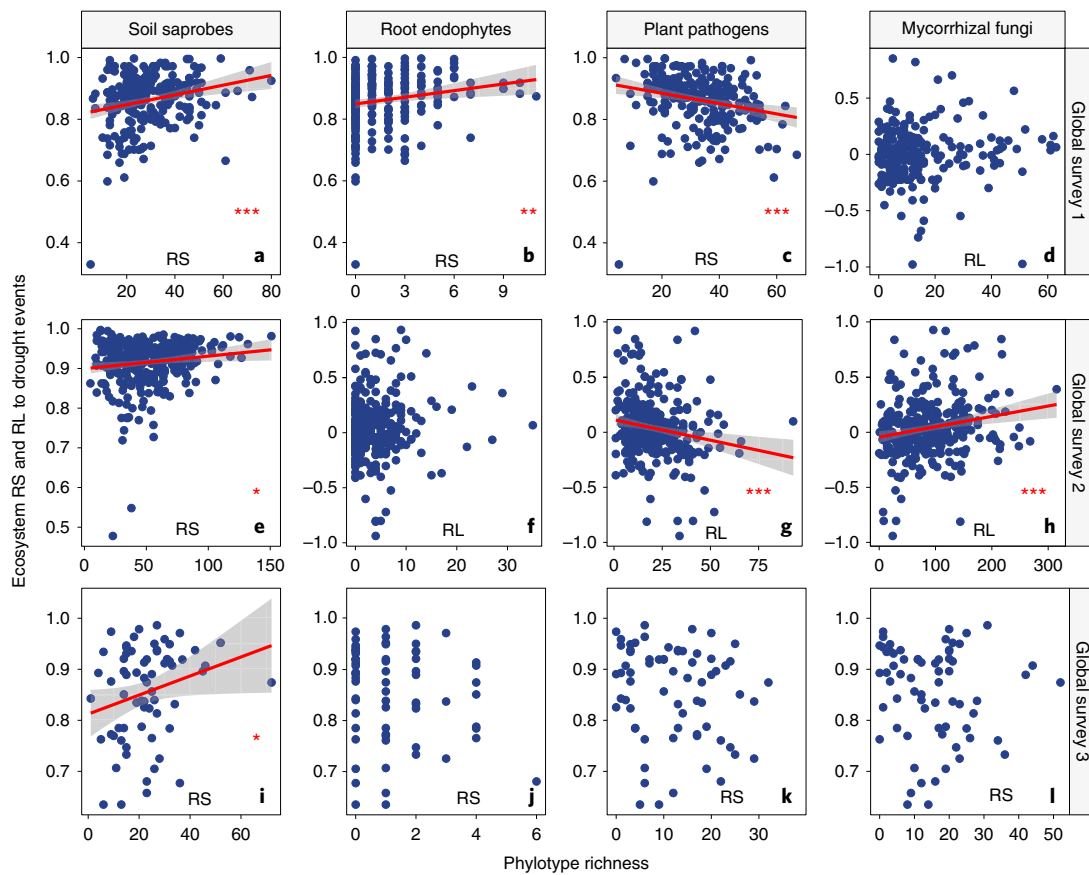
Fig. 6 | Relationships between soil fungal diversity and ecosystem resistance and resilience to drought events. Fungal diversity effects on ecosystem resistance (RS) and resilience (RL) in drought events in global surveys 1 (**a–d**; $n = 235$ ecosystems), 2 (**e–h**; $n = 351$ ecosystems) and 3 (**i–l**; $n = 87$ ecosystems). Panels **a–d**, **e–h** and **i–l** include the relationship between phylotype richness within soil fungal functional groups (soil saprobes, root endophytes, soil-borne potential plant pathogens and mycorrhizal fungi) with ecosystem resistance or resilience in global survey 1, 2 and 3, respectively. 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 shading indicates the 95% confidence interval.

in ref. [23]. Fungal functional groups 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 detailed information for soil chemical and geography were reported in refs. [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 at the University of Tartu, Estonia. zOTU tables (100% similarity) were obtained from bioinformatic analyses as described in ref. [18]. Fungal functional groups were identified using rarefied zOTU tables and FungalTraits[21].

Stability of ecosystem productivity. We used the NDVI from the 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 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 datasets, 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 standard deviation of the annual NDVI (s.d. of NDVI) during that period. We focused on this period of time (2001–2018), because: (1) it comprises the span of all the soil samplings conducted

in the three global field surveys; and (2) drought information was available between these dates[25,44]. NDVI information was collected at 250 m resolution. This spatial resolution is comparable to that in soil samplings from three global soil surveys (~2,500 m²), wherein composite samples were collected.

$$\text{Ecosystem stability} = \text{Mean/s.d.} \qquad (1)$$

To strengthen our ecosystem stability results using the NDVI index, we compared 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 5,000 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 the 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 (500 m) 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 Figs. 6–11), although their lower spatial resolution (vs. NDVI 250 m used in the main text) limits the utility of these results. Finally, we would like to highlight that the long-term trends of ecosystem production and stability in NDVI, GPP and CSIF at each site are expected to integrate both anthropogenic (for example, 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; equation (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; equation (3) from ref. [44]) is defined as the capacity of plant

productivity (NDVI) to return the original levels of productivity after a drought event (that is, 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 ref. [44], are normalized indices that show 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:

$$\text{Resistance } (t_0) = 1 - \frac{2\,|D_0|}{(C_0 + |D_0|)} \tag{2}$$

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).

$$\text{Resilience } (t_x) = \frac{2\,|D_0|}{(|D_0| + |D_x|)} - 1 \tag{3}$$

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 analysed 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 reduced any concern on potential bias and provided further support to our conclusions.

Drought events. Drought events were quantified with the SPEI index[50]. This 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 the 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. In particular, 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 obtained 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 interpreted negative values of the index as dry conditions. To obtain sufficient drought events, we quantified drought events in the period 2001–2018 by analysing 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 (that is, zOTUs) within functional groups (FungalTraits) from rarefied phylotype tables.

Mantel test correlations. We used Mantel tests (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 modelling[54,55] to quantify the relative importance of four groups of factors as predictors of ecosystem stability, mean and s.d. of NDVI, and ecosystem resistance and resilience to drought events. These four groups of predictors included: (1) climate, (2) environment: soil properties and biomes, (3) fungal diversity and (4) percentage of basal areas of mycorrhizal plants/site. These predictors were kept consistent for global surveys 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 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 pathogens, root endophytes and mycorrhizal fungi) and community composition of functional groups (summarized using NMDS, Bray–Curtis distance). Mycorrhizal plants include the basal area

(%) of AMF- 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. The variation partitioning model was 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 plants, as well as the relative importance of individual variables on ecosystem stability, and mean and s.d. 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 the MAT and aridity index. Fungal diversity includes the richness of fungal functional groups (soil saprobes, plant pathogens, root endophytes 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 (that is, summarized using NMDS, Bray–Curtis distance) to further investigate the robustness of the soil decomposer diversity (richness) and ecosystem stability when controlling for their composition. Mycorrhizal plants include the basal area (%) of AMF- and EcM-associated plants. Soil properties include TP, soil pH, TN, C:N ratio. We also considered quadratic terms for climatic variables and plant mycorrhizal association because these variables have been observed to affect ecosystem functioning in previous studies[30] and our results (Fig. 3 and 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 piecewiseSEM[57,58] to further evaluate the associations between fungal diversity (the richness of soil saprobes, plant pathogens, root endophytes 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 percentage of mycorrhizal plants (the basal area of AMF plants and EcM plants, retrieved using maps from ref. [26]) simultaneously. As with the multiple regression models, we also included a surrogate of the community composition of decomposers (that is, 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].

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

Data availability

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Author contributions

M.D.-B. designed the study in consultation with S.L. and P.G.-P. S.L., M.D.-B., L.T. and E.G. analysed the data. S.L. and M.D.-B. wrote the first draft of the paper. P.G.-P., L.T., M.v.d.H., C.W., E.G., D.C., Q.W., J.W. and B.K.S. contributed significantly to improve subsequent drafts.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to Manuel Delgado-Baquerizo.

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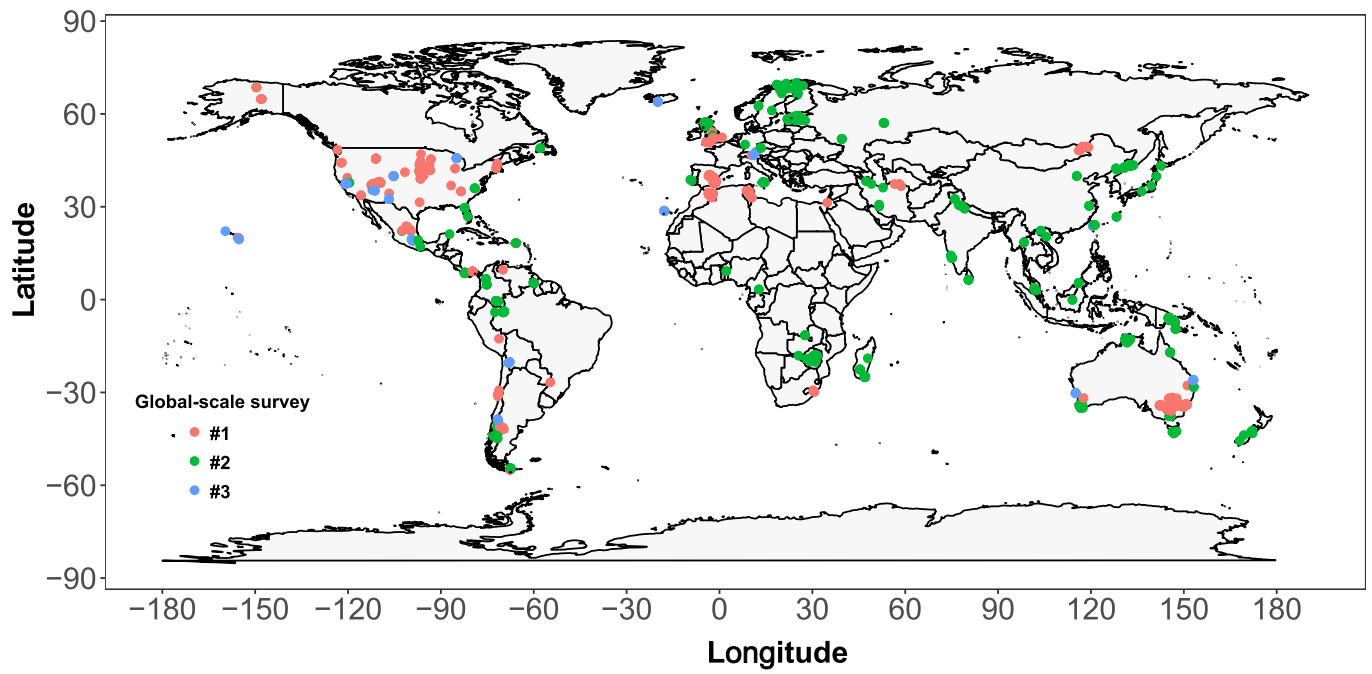
Extended Data Fig. 1 | Sampling locations of three global field surveys. A total of 673 ecosystems were included in this study.
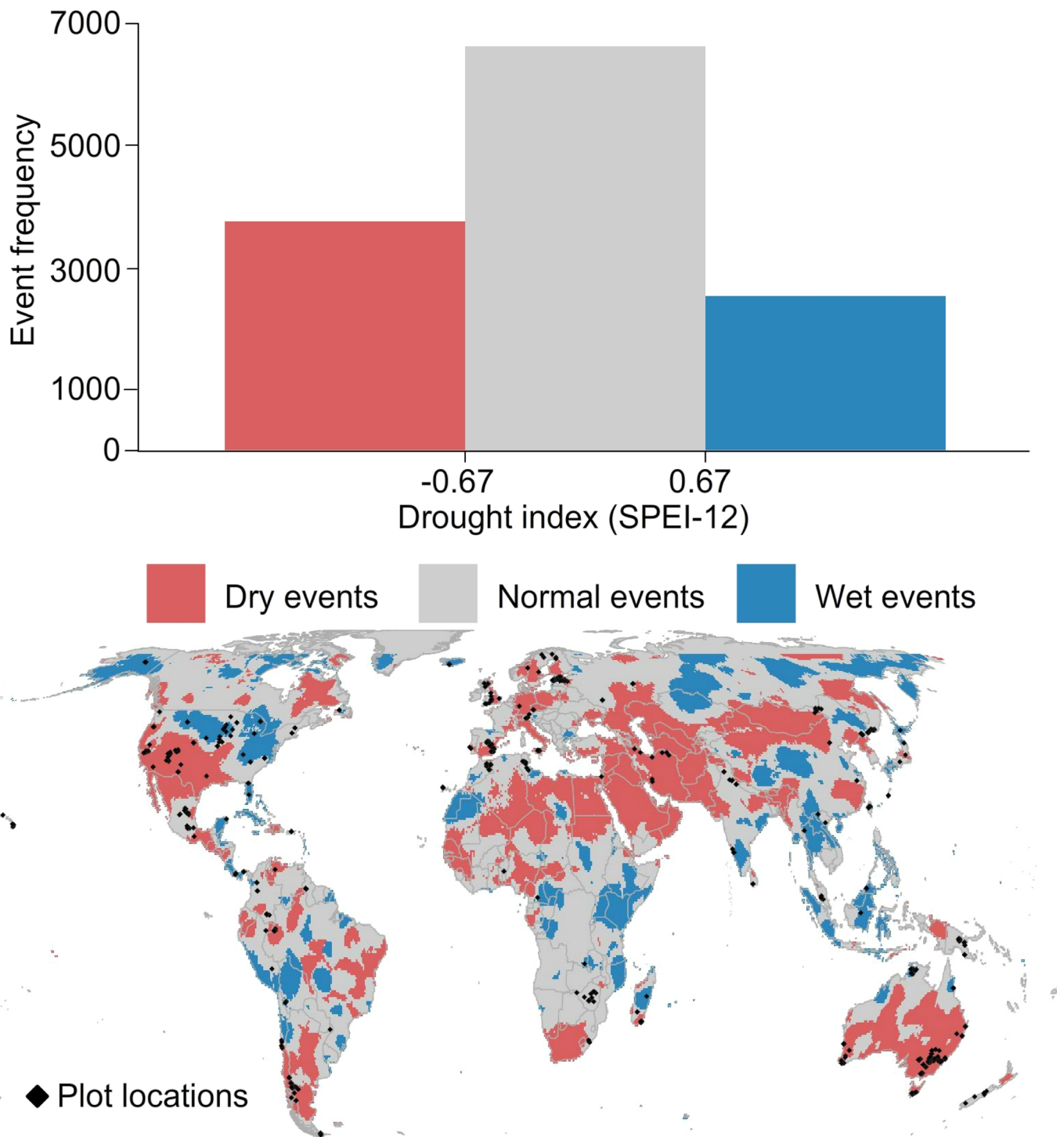
Extended Data Fig. 2 | Frequency of drought events (top) and global map of study plot locations (bottom). The map data is equivalent to the SPEI reclassification in dry and wet events and normal years of 16 August 2018 to illustrate an example of the distribution of events.
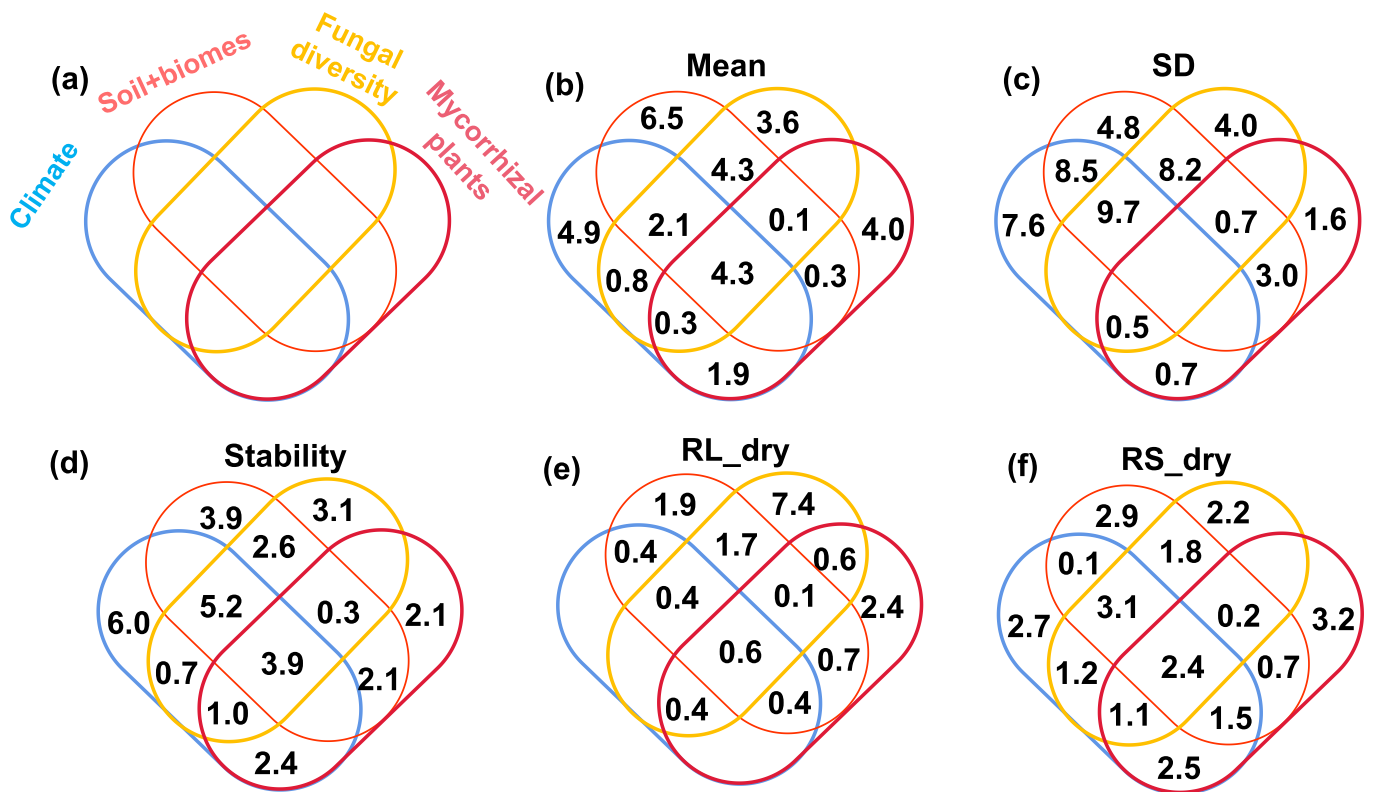
Extended Data Fig. 3 | Explained variation in ecosystem stability in global survey #1. Variation partitioning (%) of four categories of predictors (**a**): climate predictors (V1), soil properties and biomes (V2), fungi (fungal diversity and community composition) (V3) and plant mycorrhizal association (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.
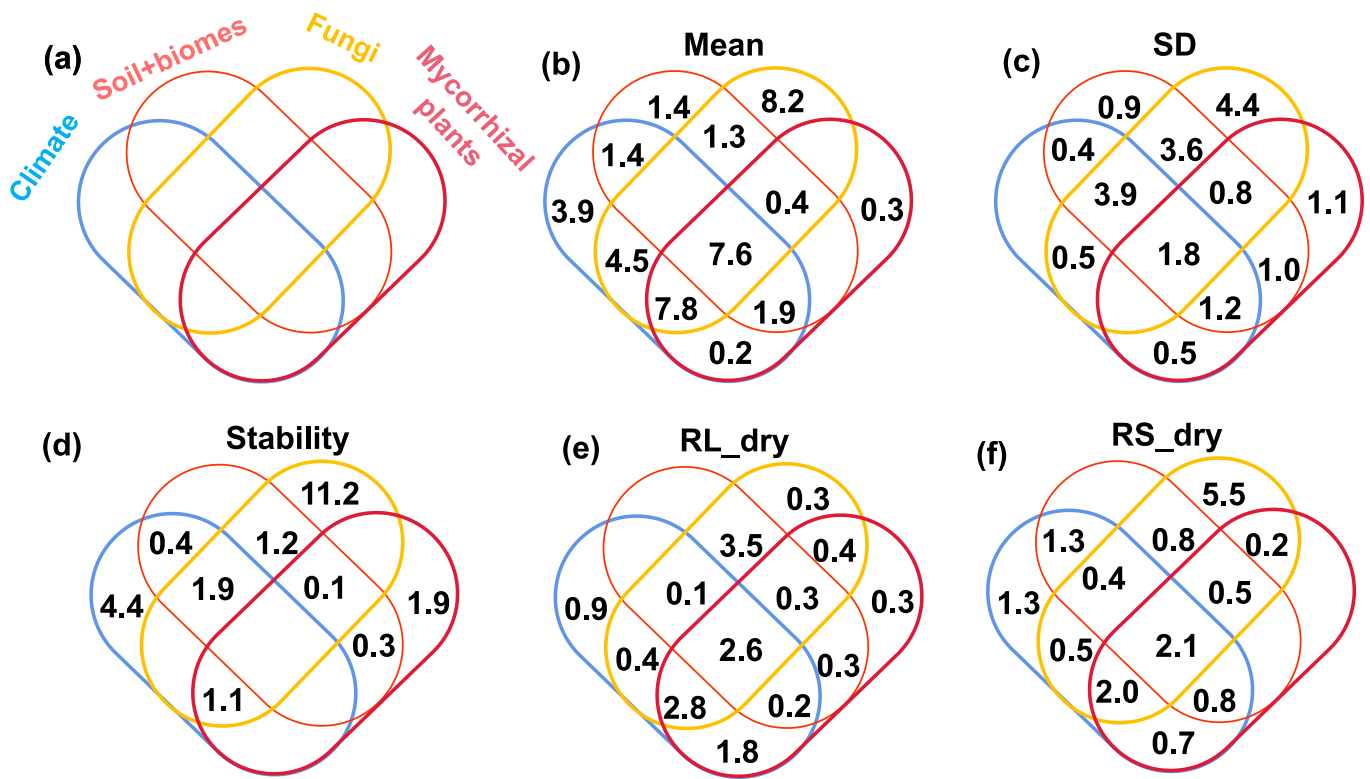
Extended Data Fig. 4 | Explained variation in ecosystem stability in global survey #2. Variation partitioning (%) of four categories of predictors (**a**): climate predictors (V1), soil properties and biomes (V2), fungi (fungal diversity and community composition) (V3) and plant mycorrhizal association (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.
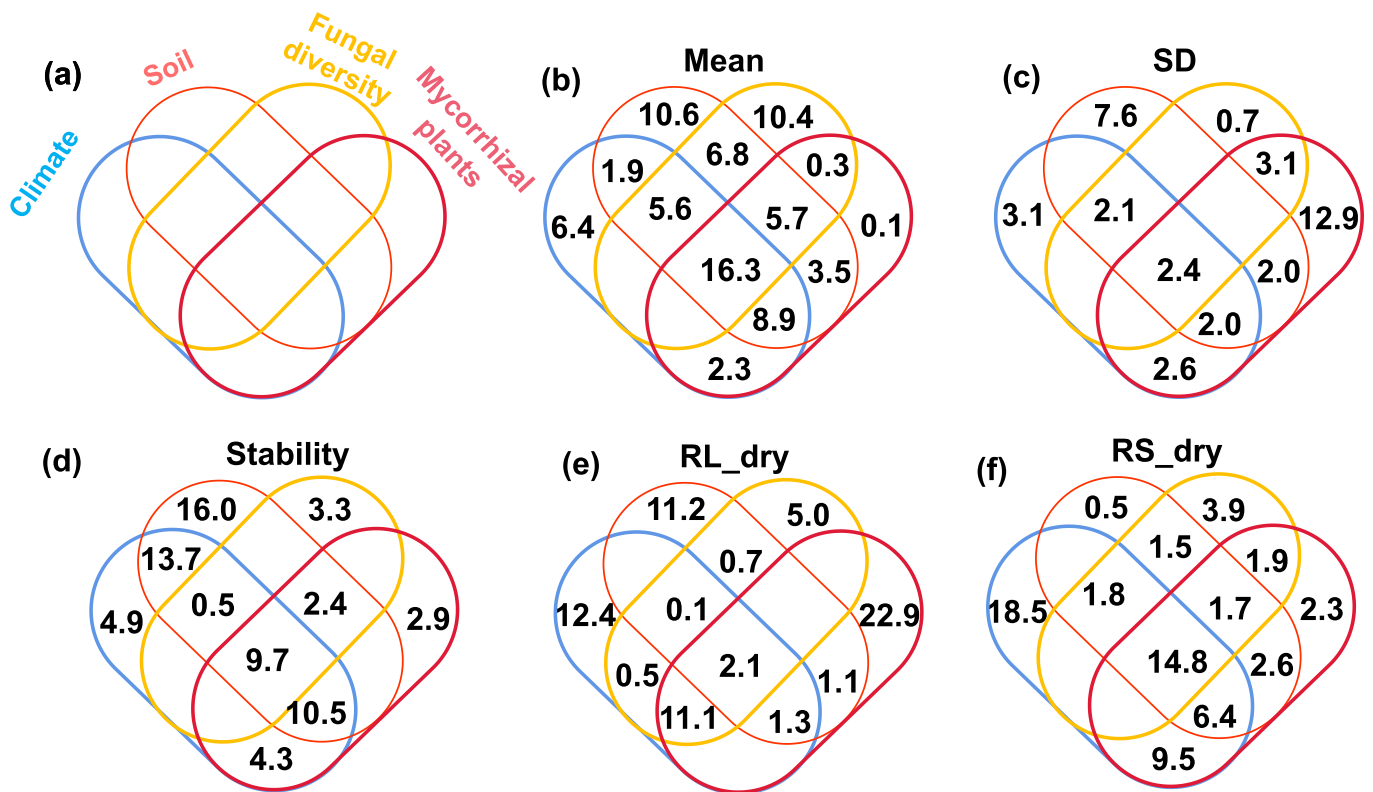
Extended Data Fig. 5 | Explained variation in ecosystem stability in global survey #3. Variation partitioning (%) of four categories of predictors (**a**): climate predictors (V1), soil properties and biomes (V2), fungi (fungal diversity and community composition) (V3) and plant mycorrhizal association (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.
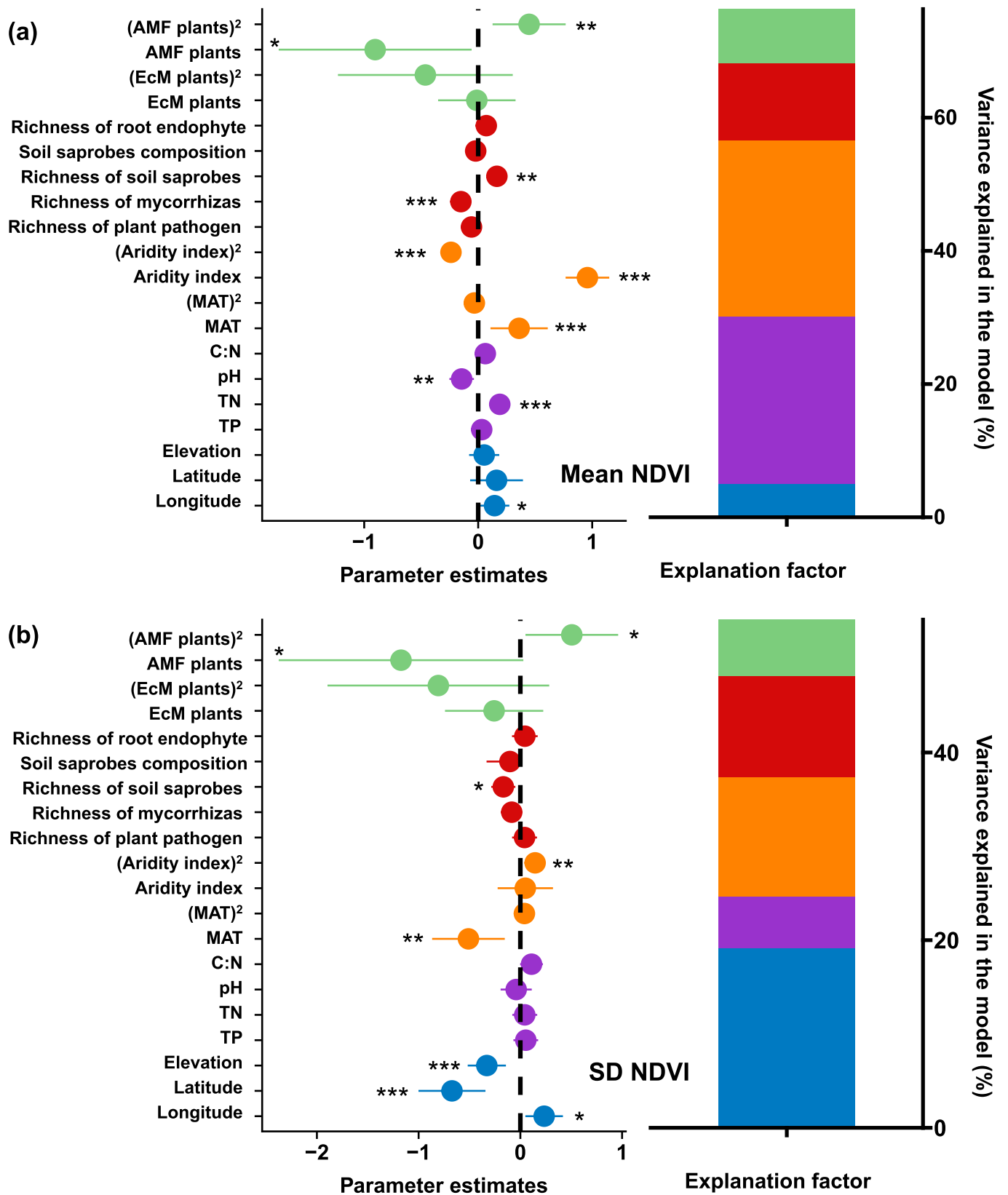
Extended Data Fig. 6 | Drivers of mean (a) and SD NDVI (b) in global survey #1. Multiple ranking regression reveal the relative effects of the most important predictors of ecosystem stability (n = 235 ecosystems). The average parameter estimates (standardized regression coefficients) of the model predictors 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.
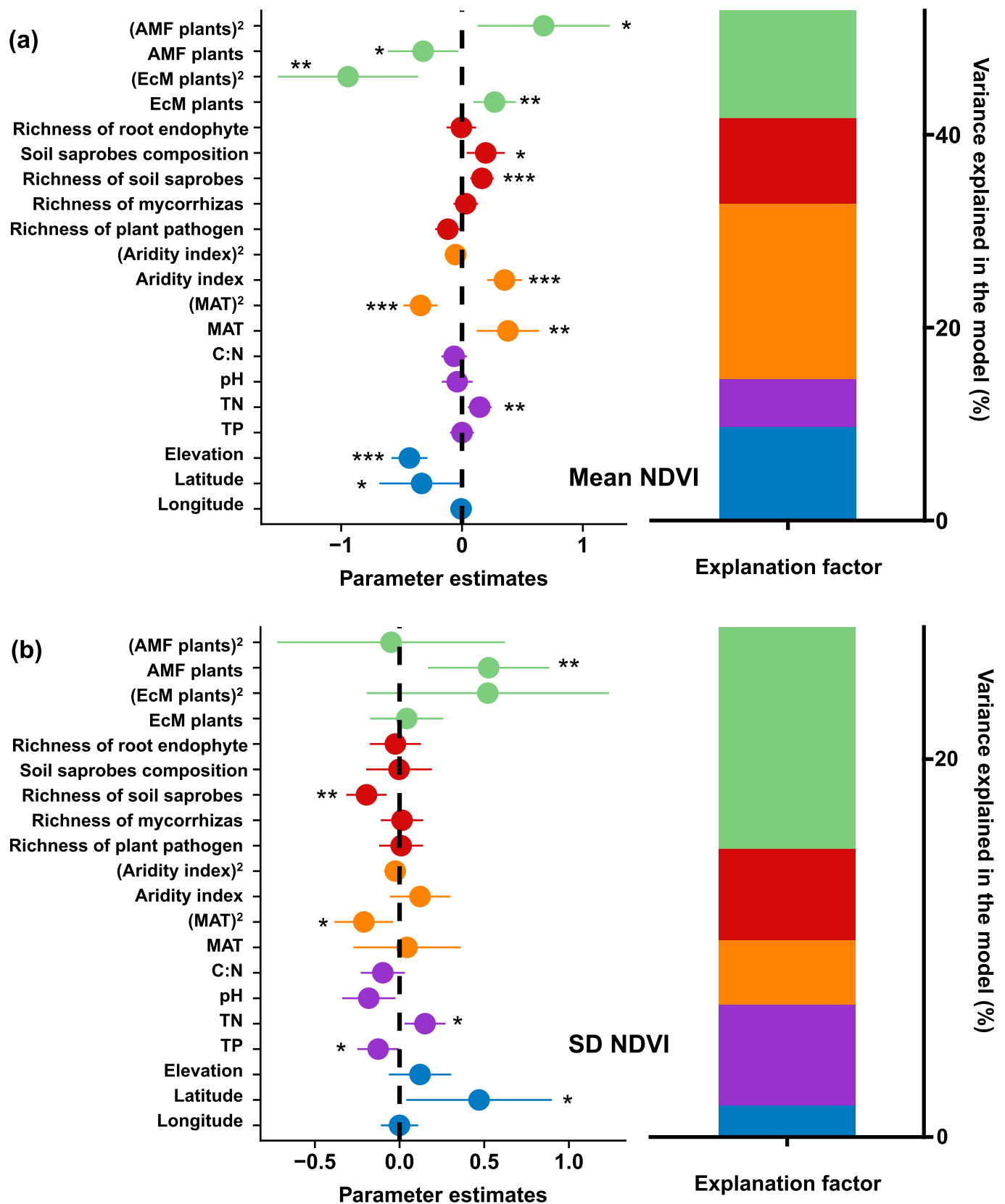
Extended Data Fig. 7 | Drivers of mean (a) and SD NDVI (b) in global survey #2. Multiple ranking regression reveal the relative effects of the most important predictors of ecosystem stability (a,c) (n = 351 ecosystems). The average parameter estimates (standardized regression coefficients) of the model 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.
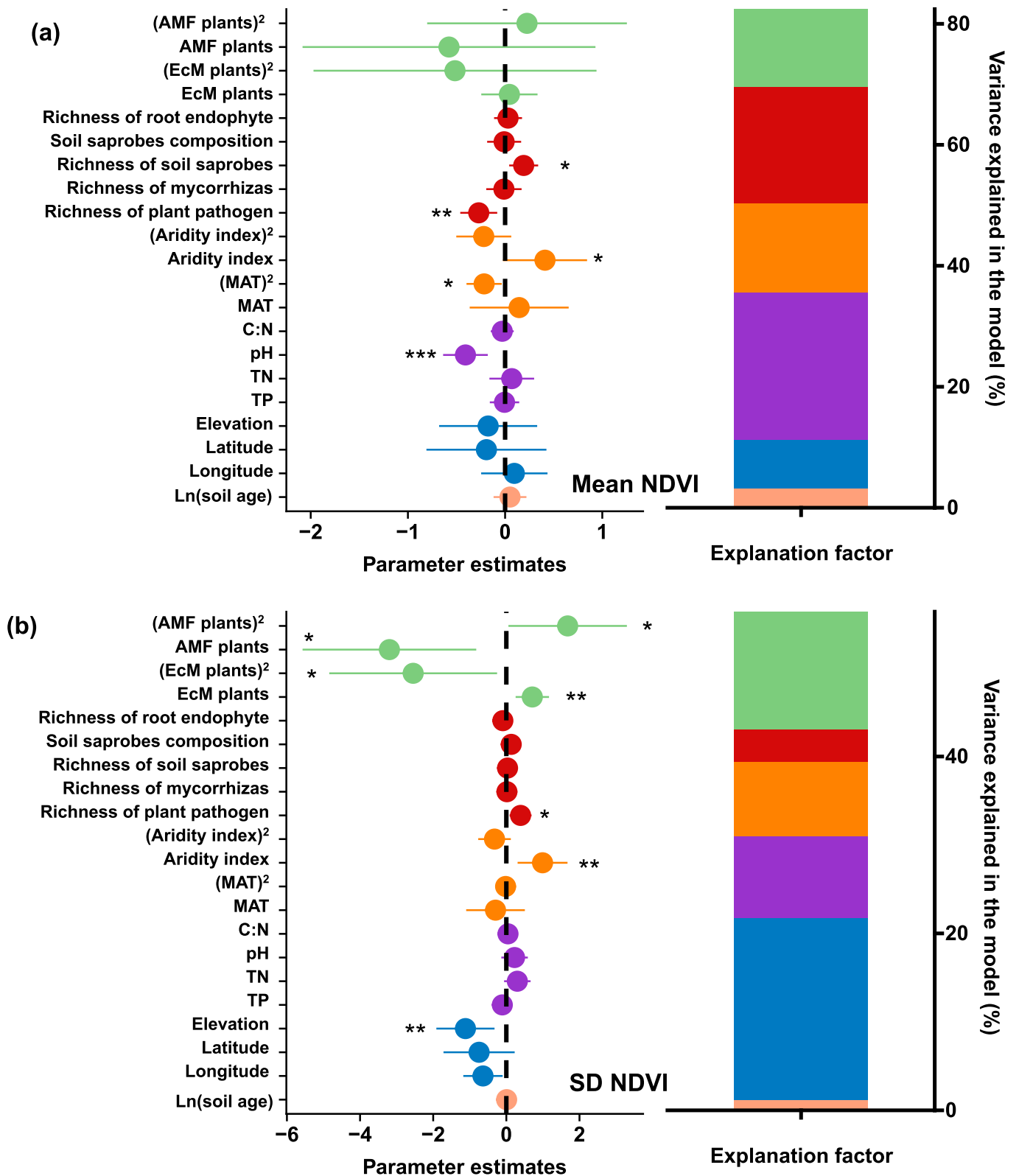
Extended Data Fig. 8 | Drivers of mean (a) and SD NDVI (b) in global survey #3. Multiple ranking regression reveal the relative effects of the most important predictors of ecosystem stability (a,c) (n = 87 ecosystems). The average parameter estimates (standardized regression coefficients) of the model 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.
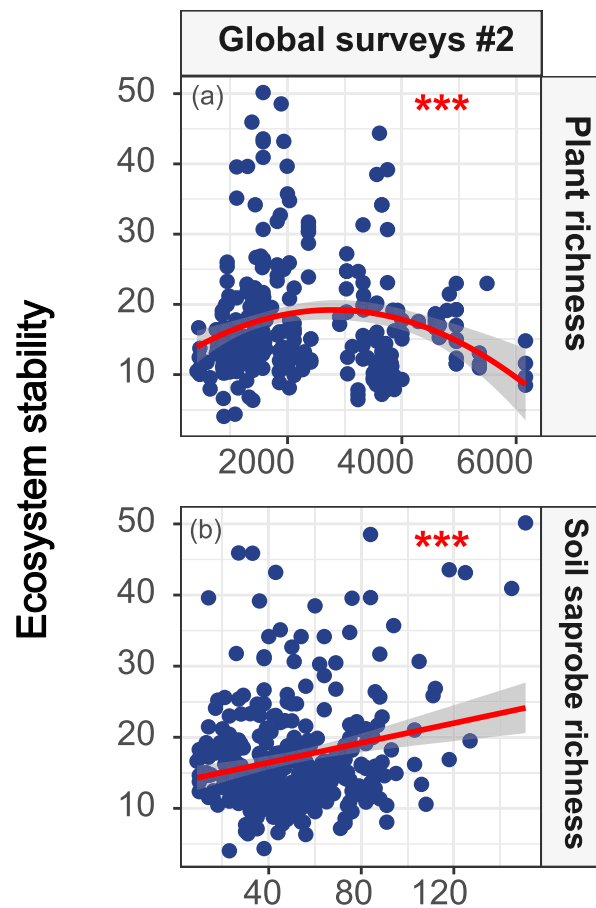
Extended Data Fig. 9 | Fitted linear relationships between ecosystem stability and the diversity (richness) of selected functional groups of soil fungi across all ecosystems in global survey #2 (n = 351 ecosystems). Akaike information criterion (AIC) was used to selected the best model. Significance 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.
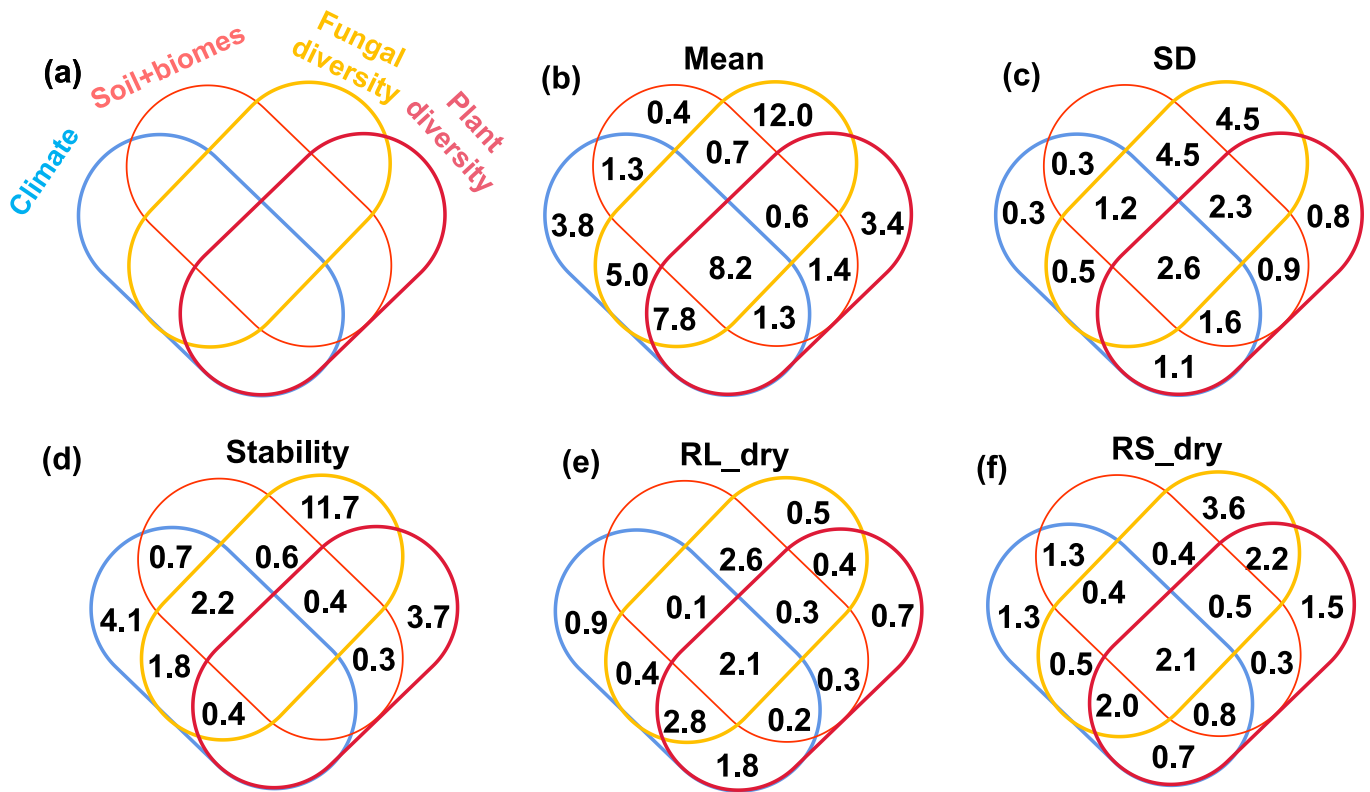
Extended Data Fig. 10 | Explained variation in ecosystem stability in global survey #2. Variation partitioning (%) of four categories of predictors (a): climate predictors (V1), soil properties and biomes (V2), fungi (fungal diversity and community composition) (V3) and plant richness and mycorrhizal 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.

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Policy information about availability of computer code

Data collection	We combined three independent global field surveys of soil fungi with a satellite-derived temporal assessment of plant productivity (NDVI). See Methods.
Data analysis	For Bioinformatic analysis, a combination of Qiime and USEARCH, UPARSE and UCLUST were used. All statistical analyses performed using R 3.5.1.

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Study description	We combined three independent global field surveys of soil fungi with a satellite-derived temporal assessment of plant productivity, and we report that the diversity of fungal functional groups drives the stability of terrestrial ecosystems.
Research sample	A total of 673 soil samples were analyzed in this study for testing the relationships between soil fungal diversity and ecosystem stability.
Sampling strategy	Our sampling was designed to assess soil fungal diversity and ecosystem stability at the plot level.
Data collection	We obtained annual NDVI information (2001 to 2018), and calculated ecosystem temporal stability for each study site as the ratio of the mean NDVI to its standard deviation over 18 years. 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 (Supplementary Fig. 1), and covering nine biomes (temperate, tropical and dry forests, cold, temperate, tropical and arid grasslands, shrubland and boreal) between 2003 and 2015. 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. Global survey #3. Composite soil samples from multiple soil cores (top 10 cm) were collected using standardized protocols between 2016 and 2017 from 16 soil chronosequences and 87 sites (ecosystems) (also known as substrate age gradients) located in nine countries and six continents.
Timing and spatial scale	Sample collection of soils took place between 2003 and 2017. Soil samples were collected by the original global surveys in refs. 22, 23 and 24 (main text).
Data exclusions	n/a
Reproducibility	Information about the sampled locations and methods used in this paper are included in our material and methods
Randomization	n/a
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