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# The global contribution of soil mosses to ecosystem services

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Soil mosses are among the most widely distributed organisms on land. Experiments and observations suggest that they contribute to terrestrial soil biodiversity and function, yet their ecological contribution to soil has never been assessed globally under natural conditions. Here we conducted the most comprehensive global standardized field study to quantify how soil mosses influence 8 ecosystem services associated with 24 soil biodiversity and functional attributes across wide environmental gradients from all continents. We found that soil mosses are associated with greater carbon sequestration, pool sizes for key nutrients and organic matter decomposition rates but a lower proportion of soil-borne plant pathogens than unvegetated soils. Mosses are especially important for supporting multiple ecosystem services where vascular-plant cover is low. Globally, soil mosses potentially support 6.43 Gt more carbon in the soil layer than do bare soils. The amount of soil carbon associated with mosses is up to six times the annual global carbon emissions from any altered land use globally. The largest positive contribution of mosses to soils occurs under perennial, mat and turf mosses, in less-productive ecosystems and on sandy soils. Our results highlight the contribution of mosses to soil life and functions and the need to conserve these important organisms to support healthy soils.

Mosses are one of the most common and ubiquitous life forms on the planet[1–3], contributing a considerable portion of plant biomass in some of Earth's most extensive ecosystems, ranging from deserts to boreal and arctic regions[4]. Yet our knowledge of their roles in controlling soil biodiversity and soil function still lags behind that of vascular plants. Vascular plants are known to promote the accumulation of soil resources[5], which are fundamental for maintaining plant diversity, soil microbial communities and multiple ecosystem services. Local observational studies suggest that mosses also play important roles in supporting individual ecosystem attributes such as nitrogen cycling, hydrology and carbon sequestration[6–9]. Previous studies of soil mosses, those growing on the soil surface, have tended to focus at local or regional scales, in particular ecosystems (for example, polar, boreal or arid)[10–12]. The influence of soil mosses on biodiversity and ecosystem functioning could depend on their specific functional traits (for example, annual compared with perennial, that is, r strategist (generally small, rapidly growing species with annual life cycles) compared with K strategist (larger, slower-growing, perennial species)) and taxonomies. Yet unlike vascular-plant functional traits[13], the extent to which moss traits influence the biodiversity and function of terrestrial ecosystems is virtually unknown. Consequently, we still have a poor understanding of how mosses, and their traits, contribute to soil biogeochemistry, biodiversity and ecosystem services across global environmental gradients considering contrasting climates, vegetation types and land uses. Quantifying the ecosystem role of soil mosses is essential to better understand their importance for protecting soils and restoring ecosystems (for example, drylands and degraded land), particularly under changing climates or where the use of vascular plants may be inappropriate.

In this Article, we report results from the most comprehensive global field study of soil mosses. This survey includes composite topsoil samples (uppermost ~5 cm) collected in three microsites (mosses, vascular plants and bare soil) from within 30 × 30 m plots at each of 123

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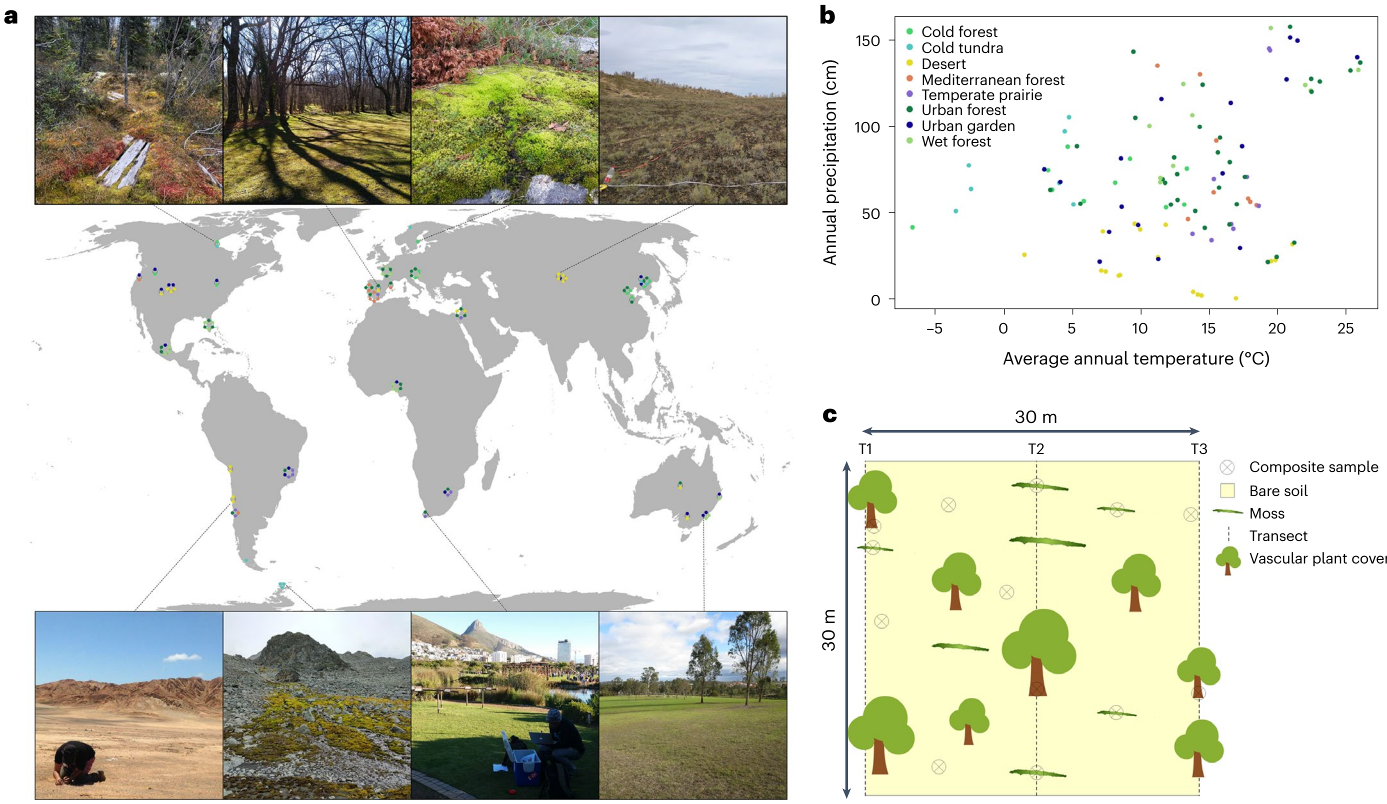


**Fig. 1 | A global survey of mosses to investigate soil biodiversity and function.** **a**, Selected pictures of the 123 sites included in this study and their global locations. **b**, Locations of study sites in relation to a global temperature and precipitation envelope. **c**, Diagrammatic representation of the standardized field sampling design used in the 123 investigated sites. See Supplementary Table 2 for further information on these sites. See Supplementary Fig. 18 for environmental context.

sites across all continents (Fig. 1, Supplementary Fig. 1, Supplementary Tables 1 and 2 and Supplementary Video 1). Our sites cover the broad range of environmental conditions under which mosses occur, rather than focusing on particular ecosystem types (Supplementary Table 1 and Supplementary Fig. 2). Climate ranges from tropical to continental, temperate, arid and polar; vegetation types range from forests to grasslands, shrublands and heathlands; and land-management contexts range from urban to natural (Supplementary Tables 1 and 2).

In this study, we investigated the global biogeography, magnitude and drivers of the global contribution of soil mosses to 24 soil biodiversity and functional attributes linked to 8 ecosystem services. We aimed to (1) determine the environmental conditions supporting ecosystems with or without mosses worldwide; (2) quantify the unique contribution of soil mosses to eight ecosystem services (soil biodiversity preservation, carbon sequestration, nutrient cycling, plant pathogen control, antibiotic resistance control, organic matter decomposition, microbial habitat and biomass of symbiotic organisms) across contrasting climates and compared with vascular plants; and (3) assess the degree of context dependency of the ecological contribution of soil mosses to multiple ecosystem services across a wide range of moss traits and climatic, vegetation and soil environmental conditions. Our study provides the most comprehensive global study of mosses and their traits on multiple soil ecosystem services, cross-validated by two global meta-analyses based on experimental work. We further compared the relative importance of vascular plants and mosses for soil biodiversity and function and mapped the global distribution of mosses.

At each site, we established a 30 m × 30 m plot within which we placed three 30 m line transects (Fig. 1c) wherein we assessed the cover of perennial plants, bare soil and mosses. This allowed us to calculate plot-level moss, vascular-plant and bare-soil cover (Methods). Our survey included a wide range of mosses (19 families and 40 genera) with contrasting life histories (annual to perennial), growth forms (cushions, mats, turfs) and life strategies (r and K strategists; Methods and Supplementary Fig. 2). Deserts and urban gardens supported the largest proportion of annual moss species, and tundra and wet forests supported a greater percentage of perennial species (Supplementary Fig. 2). Most survey locations, particularly those in urban green spaces and natural grasslands, supported a sparse cover of mosses (Fig. 2a,b), but in some locations, particularly polar sites, moss cover exceeded 50% (Fig. 2b). The cover of moss was positively correlated with the richness of cryptogamic (moss, lichen and liverwort) species determined in the field (Pearson´s $r = 0.27$, $P = 0.002$, $n = 123$ sites). Mosses sampled were dominated by taxa from the genera *Bryum* (12%), *Rosulabryum* (11%), *Leucobryum* (7%), *Funaria* (6%), *Campylopus* (5%), *Desmatodon* (5%) and *Polytrichum* (5%; Supplementary Table 1 and Supplementary Fig. 2a).

Using structural equation modelling, we investigated the environmental factors associated with moss cover in our global survey (Supplementary Figs. 3–5 and Supplementary Table 3) and found that moss cover tended to be greater in environments with low temperature seasonality (TSEA), mean diurnal temperature range (MDR) and sparse vascular-plant cover and richness, particularly in some deserts and tundra ecosystems (Figs. 2c and 3). In addition to plant cover and richness, mean annual precipitation (MAP), TSEA and MDR were also negatively associated with the proportion of moss cover when considering all direct and indirect pathways in our model (Supplementary Fig. 5). Thus, after accounting for the effects of vascular-plant cover and richness, mosses were significantly associated with rainfall-limited environments with low TSEA and MDR, probably due

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to specialized leaf structures that enable them to capture and retain moisture, an innate ability to recover from long periods of dehydration[9] and less competition from vascular plants. The relative contribution of environmental factors in explaining moss cover was maintained when conducting a simplified version of our structural equation model (SEM; Supplementary Fig. 4). Soil moss cover was not correlated with air temperature (consistent with their presence in both cold and hot deserts), ecosystem type (mosses thrive in urban and natural, forested and non-forested ecosystems), or amount of soil carbon (organic matter), pH, sand content or salinity (electrical conductivity; Fig. 2c; $n = 123$) once other factors were accounted for.

## Global distribution of soil moss cover

To better visualize global hotspots of moss cover, we used random forest models to create the most comprehensive global map of potential moss cover across contrasting regions worldwide (Fig. 2d, Supplementary Figs. 6 and 7 and Methods). Our analyses indicate that dry regions of the western United States of America, tundra ecosystems from northern Europe and large desert regions from Australia, Asia, Africa and South America support high moss cover (Fig. 2d), consistent with regional studies[11,12,14]. Earlier studies have mapped the distribution of moss richness at the national level[15], but there was no high-resolution map of moss cover. Our estimates indicate that mosses cover over $9.4 \times 10^6$ km$^2$ of Earth in the area covered by the environmental conditions of our survey, and excluding areas of uncertainty (Supplementary Fig. 7). This is an area similar to Canada, China or the United States of America (Supplementary Appendix 1).

## The contribution of soil mosses to ecosystem services

We collected field and laboratory information on 24 soil biodiversity and functional attributes of topsoils from the 123 sites (Fig. 1) to better understand the ecological contribution of soil mosses to ecosystem services (Supplementary Tables 4 and 5 and Methods). These 24 attributes comprised a wide range of soil variables associated with the maintenance of soil biodiversity (richness of fungi, bacteria, protists and invertebrates), carbon sequestration (soil total organic carbon), nutrient cycling (soil total N, P, Cu, Mg, Mn, Zn, Fe and K), organic matter decomposition indices (soil extracellular enzyme activities related to C, N and P cycles, glucose, lignin and basal respiration), microbial habitat (biomass of fungi and bacteria), plant–soil symbiosis (biomass of arbuscular mycorrhizal fungi), antibiotic resistance control[16] and soil-borne plant pathogen control[16] (Supplementary Table 4 and Methods).

A relative interaction intensity index (RII)[17] (Methods) was then used to calculate the relative importance of soil mosses and vascular plants to the 24 soil biodiversity and functional attributes at all sites (Supplementary Table 5 and Methods). The index compares the differences between moss (or vascular plant) and bare soil where $\mathrm{RII} = (X_\mathrm{m} - X_\mathrm{b})/(X_\mathrm{m} + X_\mathrm{b})$, where $X$ is the value of a specific attribute, and $X_\mathrm{m}$ and $X_\mathrm{b}$ represent values beneath the moss (or vascular plant) and in the bare soil, respectively. Positive RII values indicate an increase in the value of soil biodiversity and ecosystem services beneath mosses or vascular plants compared with bare soils (and vice versa; Methods).

Our data show that soil mosses make significant and positive contributions to multiple ecosystem services (RII moss multiservices) across the globe (Fig. 3a). The contribution of soil mosses to ecosystem services is likely to be associated with their well-known capacity to influence surface microclimates and their litter inputs compared with bare soils. Thus, these mechanisms of moss contribution to multiple ecosystem services are likely to be similar to those of vascular plants (Fig. 3a). Moreover, the contribution of soil mosses to services was also positively associated with those contributions by vascular plants (RII vascular-plant multiservices), suggesting that the positive contributions of vascular plants and mosses to multiple ecosystem services partially co-occur among terrestrial ecosystems (Fig. 3b and Supplementary Table 6). Even so, further modelling effort revealed that mosses supported multiple ecosystem services in locations of the planet with limited vascular-plant influence (Fig. 4). Thus, even when the contribution of soil mosses to function is lower than those of vascular plants (for example, Fig. 3), the large cover of soil mosses (Fig. 2d) makes this contribution significant at the global scale (Supplementary Fig. 8), particularly in ecosystems with limited vascular-plant contribution. Together, mosses played additional roles to those of vascular plants in supporting ecosystem services.

We further found that soil mosses were significantly and positively associated with the simultaneous increase in the magnitude of soil attributes within important ecosystem services such as carbon sequestration, nutrient cycling, organic matter decomposition and plant pathogen control (Fig. 3a). Specifically, we found greater carbon content, more essential nutrients such as nitrogen, phosphorus and magnesium, soil enzyme activities and greater control (lower proportion) of soil-borne potential plant pathogens in the soils beneath mosses than in bare soils (Fig. 3a). Moreover, we found multiple positive associations between the relative interaction indices of 24 soil attributes under mosses compared with bare soils, particularly for those within nutrient cycling and organic matter decomposition, indicating multiple co-existing positive influences of mosses on soil fertility (Supplementary Fig. 9). Mosses also have a fundamental role in supporting multiple ecosystem services in those boreal ecosystems within the environmental conditions represented by our data (Fig. 4). Our findings go beyond the well-studied effects of soil mosses on individual groups of functions (for example, nitrogen cycling) in particular ecosystems (for example, boreal forests) and in local studies and provide a comprehensive view of the environmental contribution of soil mosses across contrasting global environments.

Our findings highlight the notion that soil mosses can make a significant impact by regulating global soil carbon sequestration[18,19] because of their key role in natural environments where they are the dominant vegetation (for example, Antarctica, boreal forests and drylands)[10,20–22] (Fig. 3). For example, we estimated that worldwide, soils covered by mosses can sequester 6.43 Gt more organic carbon in the top ~5 centimetres of soil than bare soils (Supplementary Appendix 1). Our study largely underestimates this influence as we limited our estimations to areas of high certainty. These included ecosystems represented by our global survey (Fig. 3d), which partially excluded

**Fig. 2 | Global distribution of soil mosses. a**, Distribution of moss cover in our global survey. **b**, Moss cover across continents and ecosystem types. **c**, SEM of the direct and indirect associations (red, negative; blue, positive; black, mixed) among space (average distance among sites to control for spatial autocorrelation), climate, vascular vegetation, land use (urban green spaces compared with natural) and soil properties in driving the proportion of moss cover (see Supplementary Table 3 for more details and Supplementary Fig. 4 for a priori model). MAT, mean annual temperature; PSEA, seasonal precipitation; NPP, net primary productivity; Prich, vascular-plant richness; Pcov, vascular-plant cover; C, soil carbon; C/N, soil C/N ratio (Supplementary Table 3). Different categories of predictors (climate, soil, vegetation, land use and spatial influence) are grouped in the same box in the model for graphical simplicity, but they do not represent latent variables. Variables inside each category are allowed to co-vary (Supplementary Table 8). Numbers adjacent to arrows are indicative of the effect size of the relationship. Only significant relationships are included (a priori model in Supplementary Fig. 4). $R^2$ denotes the proportion of variance explained. **d**, Predicted distribution of total moss cover in ecosystems across the globe (25 km per pixel), based on machine learning modelling with $R^2 = 0.86$ (determined as predicted versus observed moss cover). Locations with high uncertainty and areas not represented by environmental conditions in our study are masked in white. $n = 123$ sites in all cases. An alternative simplified version of this map can be found in Supplementary Fig. 5.

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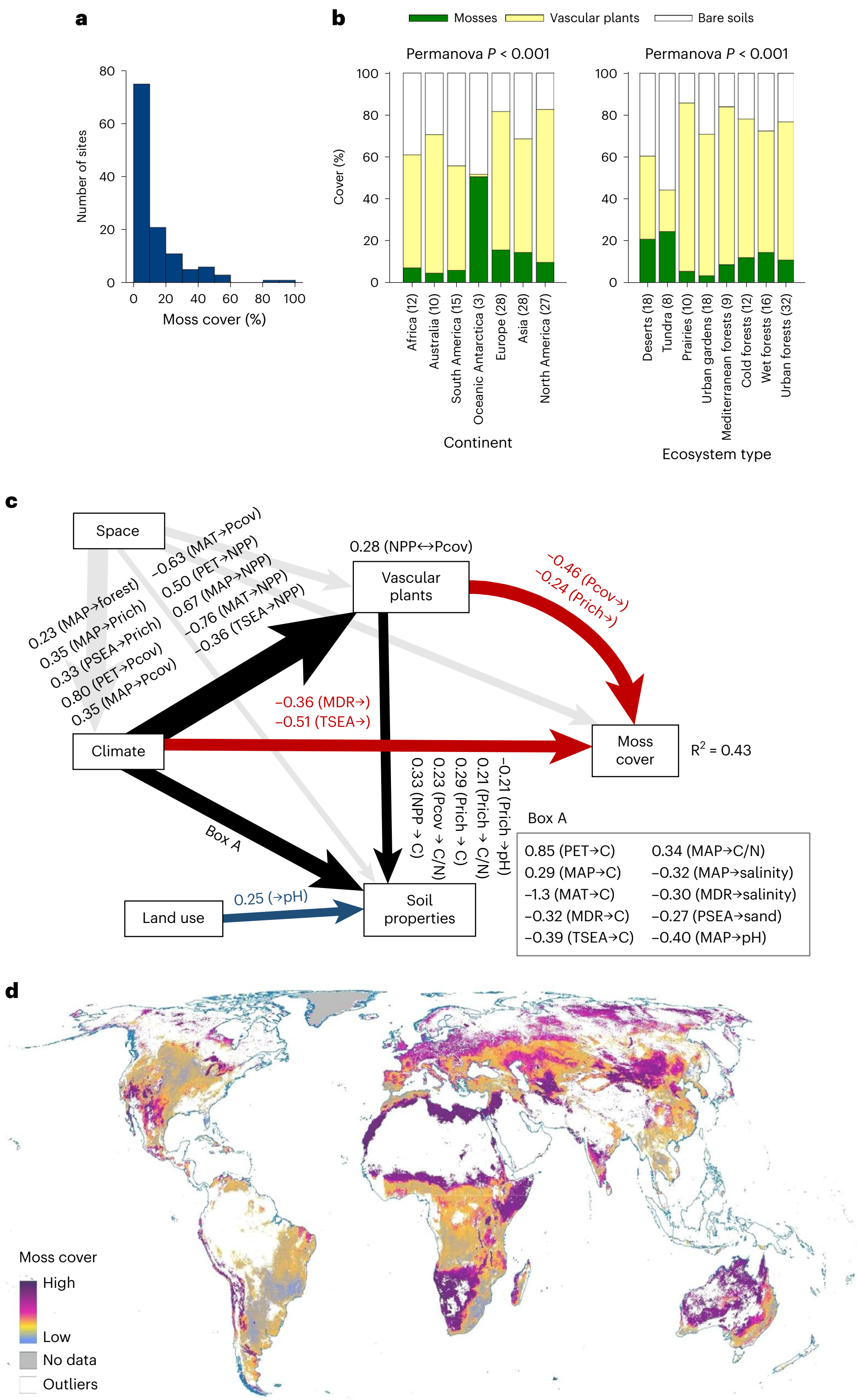
important regions of the planet covered by mosses such as boreal forests. Nevertheless, we accounted for these regions using meta-analytical data (as explained in Meta-analyses of the global importance of soil mosses). Soil mosses thus probably play an important role in soil carbon sequestration; for example, a 15% change in moss cover due to climate change or direct human land disturbance would be equivalent to about the same amount of carbon emitted to the atmosphere annually from other land-use changes. Mosses also support 0.49, 0.10 and 0.06 Gt more soil N, P and Mg, respectively, worldwide, boosting levels of three fundamental nutrients that often



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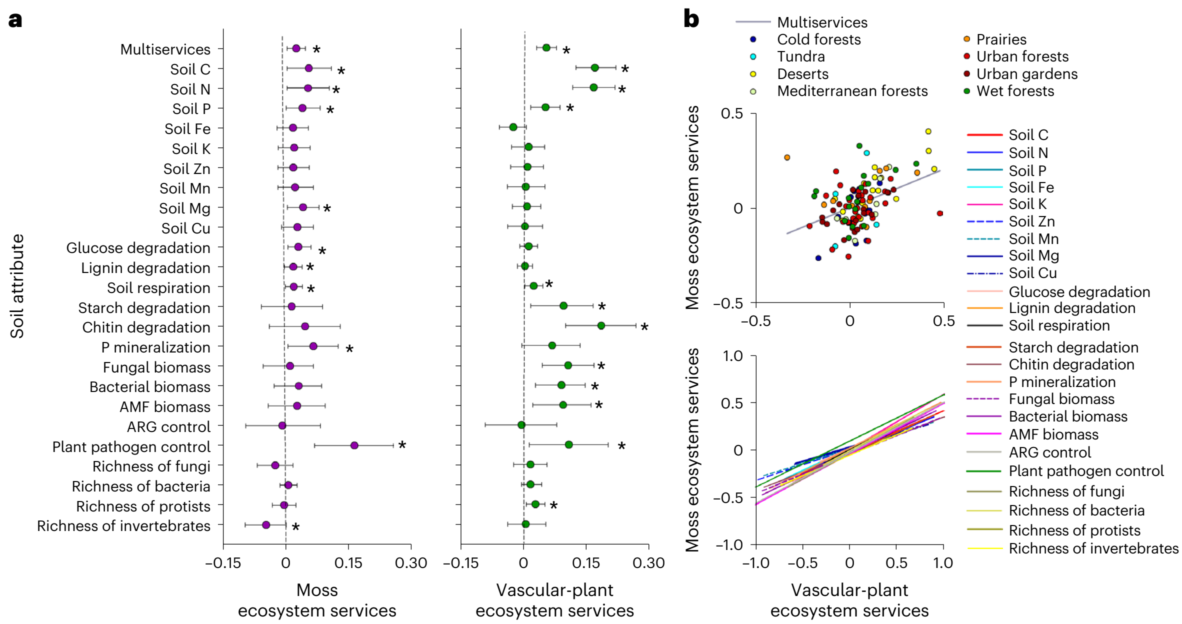



**Fig. 3 | Contribution of mosses and vascular plants to multiple ecosystem services. a**, Contribution of moss and vascular plants to ecosystem services (average RII values based on 24 soil attributes; Supplementary Table 5) and the moss and plant RIIs for 24 individual soil attributes (mean ± bootstrap confidence interval (CI) 95%). *$P < 0.05$. **b**, Significant ($P < 0.05$) relationships between moss and vascular-plant contribution to ecosystem services (average of all RIIs) and individual RII indices based on 24 soil biodiversity and functional attributes. Moss and vascular-plant contribution to multiservices (RII) = 0 (for example, vertical dashed line in **a** indicates that values for moss and plants are equivalent to values for this bare soil). Additional Spearman correlations between moss and vascular contribution to ecosystem services can be found in Supplementary Table 6 ($n$ = 123 sites). See Supplementary Fig. 19 for additional information. AMF, arbuscular mycorrhizal fungi.

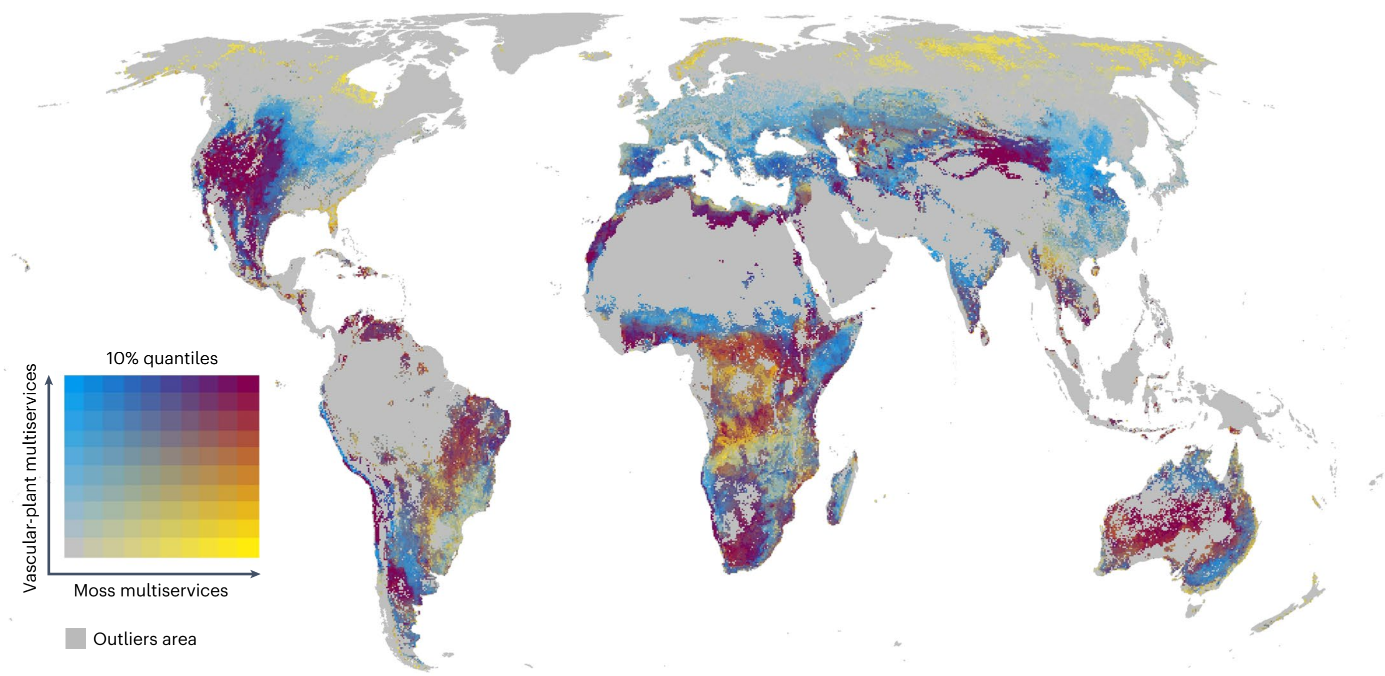



**Fig. 4 | Contribution of vascular plants and mosses to multiservices.** Predicted contribution of mosses and vascular plants to multiservices across the globe (25 km per pixel), based on machine learning modelling with $R^2 = 0.73$ for vascular plants and $R^2 = 0.68$ for mosses (determined as predicted compared with observed data). Locations with high uncertainty and areas not represented by environmental conditions in our study are masked in grey. $n$ = 123 sites in all cases.

limit ecosystem productivity (Supplementary Appendix 1). Therefore, our results indicate that soil mosses could play critical roles in supporting some of the key Sustainable Development Goals of the United Nations (https://sdgs.un.org/goals), including supporting life on land, and climate actions. Future studies should investigate the global contributions of different species/genera to these budgets.

## Meta-analyses of the global importance of soil mosses

To provide further experimental support for our global observations, and to show that mosses alter soil properties rather than inhabit chemically and biologically enhanced soils, we conducted meta-analyses of the effects of moss addition or removal on soil biodiversity and function, compared with procedure controls (bare soils). We included manipulative studies and field and microcosm studies. Analysis of information on soil C, N, P and Mg contents, soil respiration and glucose degradation (Meta-analysis #1; 36 studies from 25 papers; Supplementary Appendices 2 and 3) provided compelling evidence of the positive effect of mosses on multiservices, soil C, N, P and Mg contents, and soil respiration and glucose degradation observed in our global survey (Meta-analysis #1; Supplementary Appendices 2 and 3 and Fig. 10). These results were consistent across boreal and non-boreal and in forest and non-forest ecosystems. A second meta-analysis (13 studies) showed that mosses tend to promote soil function over time (Meta-analysis #2; Supplementary Fig. 11 and Supplementary Appendices 4 and 5). The meta-analyses support our finding that mosses contribute to the build-up of critical functions such as soil carbon content and respiration (Supplementary Fig. 11) and that ecosystem attributes accumulate over time beneath mosses, rather than mosses selecting locations with the highest function. This information is needed if we are to understand the global patterns and contributions that soil mosses make in terrestrial environments. The key message from our meta-analyses and observational data is that mosses are important for supporting soil services. These important results will help us to argue for greater global protection of these fundamental organisms.

Soil mosses had a relatively smaller influence on soil biodiversity than on carbon and nutrient pools (Fig. 3b; see Supplementary Fig. 12 for soil community composition found beneath mosses). In addition, in general, soil mosses support a lower diversity of invertebrates than surrounding bare soils. Moss tissue contains flavonoids, carotenoids and other short-chained phenolics[23] that exhibit antimicrobial, antifungal and cytotoxic activities[24,25], suppressing insect activity and resulting in invertebrate mortality[25]. However, mosses can still indirectly contribute to soil biodiversity, for example, by promoting soil carbon and microbial biomass, which were positively associated with their contribution to soil protists and bacterial richness (Supplementary Fig. 12). Resource (for example, organic matter and prey) availability is known to regulate the diversity of soil organisms[26]. Similarly, we found a greater positive association of mosses with invertebrate richness where mosses were positively associated with micronutrients (Supplementary Fig. 9). Further, mosses are important regulators of soil-borne pathogens (Fig. 3a), reducing the proportion of potential soil-borne pathogens associated with vascular-plant communities[27]. Soils are known to be a huge reservoir of plant pathogens[25], and mosses could help to regulate this important reservoir. Our work demonstrates that mosses regulate ecosystem services in the same way plants do, but proportionally equivalent or greater based on their smaller biomass (Fig. 3). Thus, mosses play critical roles in supporting soil biogeochemical cycles[6,7,28] and multiple ecosystem services[29].

## The importance of environmental conditions

To gain deeper insights into the patterns and environmental context dependencies of the contribution of mosses to multiple ecosystem services, we used random forest modelling to relate their contribution (based on average RII from 24 soil attributes) to multiple ecosystem services across contrasting soil, climatic and vegetation conditions and moss traits and taxonomy. Our analyses indicate that mosses can contribute to multiple services in low-productivity, natural ecosystems (compared with urban green spaces; Supplementary Fig. 13 and Supplementary Table 7), on sandy and low C/N soils and in environments with low precipitation seasonality (Fig. 5a,b). Thus, the magnitude of the associations between mosses with soil biodiversity and ecosystem functions is environmentally context dependent. Similar associations are also found for individual RIIs of mosses (Fig. 5c and Supplementary Figs. 13 and 14). The capacity of soil mosses to increase microbial biomass, and enhance nutrient and C sequestration and nutrient content (compared with bare soils), was particularly notable in sandy soils (Fig. 5). Sandy soils are known to have lower nutrient retention and are therefore relatively more sensitive to the loss and recovery of C, nutrients and microbial biomass[16]. In these situations, mosses can contribute markedly to retaining soil fertility, symbiotic organisms and microbial habitat[9]. The mechanisms at work probably include the capture of C- and N-rich airborne particles[22] and the deposition of elements such as Mg[30] within moss microhabitats, leading to greater soil development.

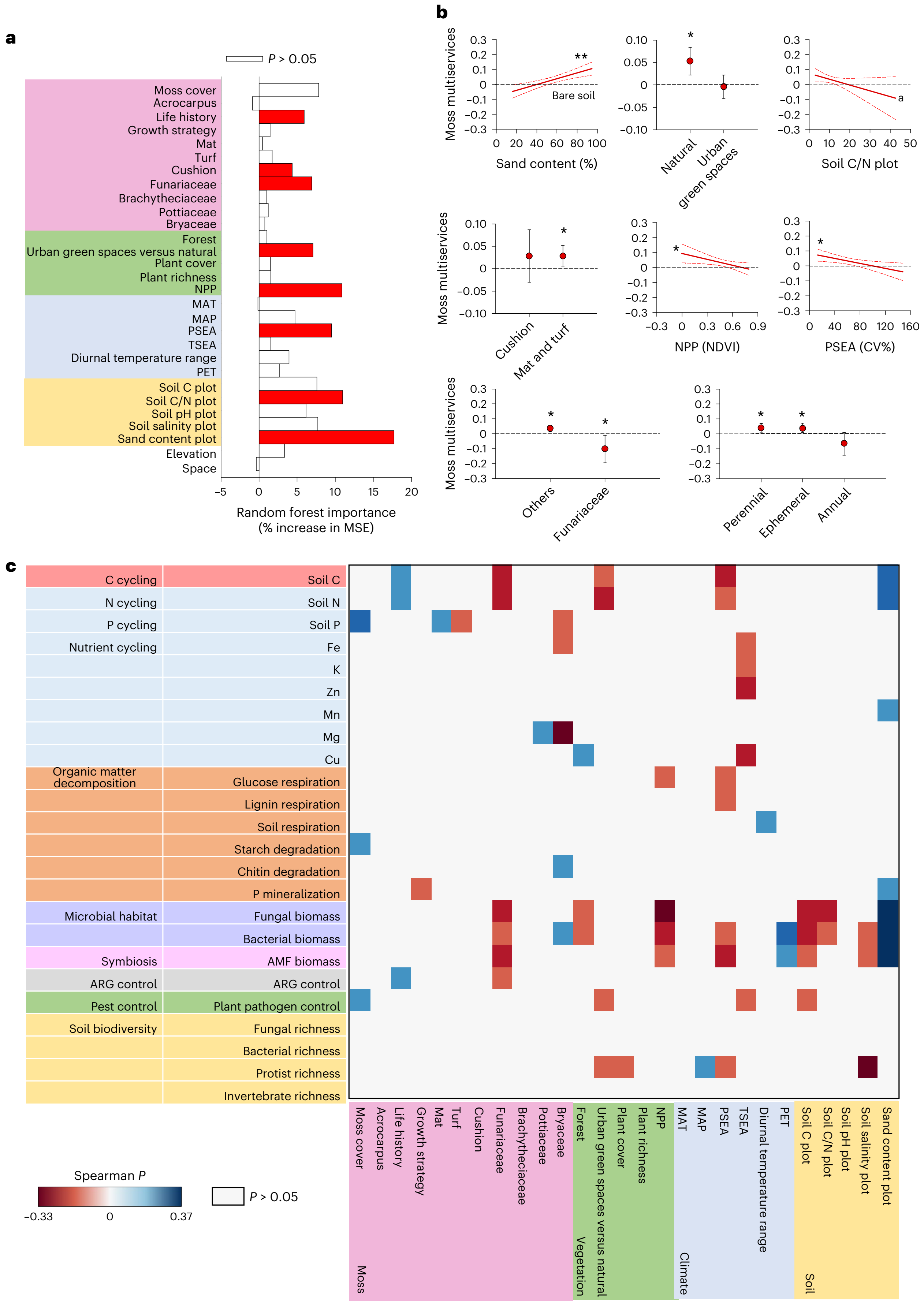
Our analyses further highlight the fact that the positive contribution of mosses to multiple ecosystem services is not apparent in disturbed urban green spaces (Supplementary Figs. 13 and 14) and regions with high precipitation seasonality (Fig. 5 and Supplementary Fig. 14). Both climatic seasonality[10] and physical disturbance[2] have been shown to limit the positive influence of mosses on individual soil functions such as nitrogen availability in specific fine-scale field experiments[10]. Our study suggests that these limitations may apply more broadly at a global scale and that inverse contributions of soil mosses to ecosystem service delivery, where moss soils are relatively resource depleted, occur at locations where precipitation is highly seasonal (Fig. 5). Future work should further clarify the global contribution of mosses to ecosystem services in other highly managed ecosystems such as croplands.

## The role of moss traits

We also found global evidence of the importance of moss traits (life history and growth strategy) and taxonomy in driving the contribution of mosses to soil biodiversity and multiple ecosystem services. Our data show that mosses support a stronger contribution to biodiversity and ecosystem services in locations with a high cover of mat and turf mosses such as *Sphagnum*, *Hylocomium* and *Ptilium* spp., taxa that are widely distributed in boreal forests[28]. In systems such as the boreal forest, deserts and polar regions where mosses comprise a considerable ecosystem component (Fig. 2b), individual patches tend to coalesce to form a continuous moss carpet. Moss traits and taxonomy also played important, yet previously undescribed, roles in driving individual soil attributes such as carbon sequestration and nutrient cycling, particularly by supporting soil P, N and Mg. Perennial soil mosses, for example, supported a larger content of soil carbon and greater antibiotic resistance gene (ARG) control (lower abundance of ARGs) than annual mosses and could play an essential role in carbon sequestration in ecosystems such as tundra and wet and cold forests, where they are prevalent[18] (Supplementary Fig. 1).

Unlike the well-described associations between moss and nitrogen-fixing bacteria[28], the influence of moss on ARGs is thus far poorly described. We posit that increases in soil carbon beneath mosses

**Fig. 5 | Environmental factors associated with the contribution of mosses to multiple ecosystem services. a**,**b**, Environmental factors associated with moss contribution to ecosystem services (average RII values based on 24 soil attributes; Supplementary Table 5). **a**, Random forest predictor importance ($P < 0.05$ in red). **b**, Linear regressions and mean values ± 95% CI for the relationship between environmental factors and moss contribution to ecosystem services ($^{a}P = 0.09$; $^{*}P < 0.05$; $^{**}P < 0.01$). Natural ($n = 62$), urban green spaces ($n = 61$), cushion ($n = 24$), mat and turf ($n = 99$), Funariaceae ($n = 7$), others ($n = 116$), perennial ($n = 56$), ephemeral ($n = 55$), annual ($n = 12$). **c**, Heatmap of significant ($P < 0.05$) Spearman correlations among environmental factors and the moss RIIs for 24 individual soil attributes ($n = 123$ sites). Diurnal temperature range = MDR (mean diurnal temperature range). MSE, mean squared error; CV%, coefficient of variation × 100.


a
P > 0.05
Moss cover
Acrocarpus
Life history
Growth strategy
Mat
Turf
Cushion
Funariaceae
Brachytheciaceae
Pottiaceae
Bryaceae
Forest
Urban green spaces versus natural
Plant cover
Plant richness
NPP
MAT
MAP
PSEA
TSEA
Diurnal temperature range
PET
Soil C plot
Soil C/N plot
Soil pH plot
Soil salinity plot
Sand content plot
Elevation
Space
Random forest importance
(% increase in MSE)
b
Moss multiservices
Sand content (%)
Bare soil
Natural
Urban green spaces
Soil C/N plot
Cushion
Mat and turf
NPP (NDVI)
PSEA (CV%)
Others
Funariaceae
Perennial
Ephemeral
Annual
c
C cycling
Soil C
N cycling
Soil N
P cycling
Soil P
Nutrient cycling
Fe
K
Zn
Mn
Mg
Cu
Organic matter decomposition
Glucose respiration
Lignin respiration
Soil respiration
Starch degradation
Chitin degradation
P mineralization
Microbial habitat
Fungal biomass
Bacterial biomass
Symbiosis
AMF biomass
ARG control
ARG control
Pest control
Plant pathogen control
Soil biodiversity
Fungal richness
Bacterial richness
Protist richness
Invertebrate richness
Spearman P
−0.33
0
0.37
P > 0.05
Moss
Vegetation
Climate
Soil

might reduce microbial competition and their need to produce ARGs. This hypothesis is supported by the positive significant correlation between the contribution of moss to carbon and the moss relationship with ARG control, but further experimental work is needed to develop a clearer mechanistic understanding of this association. Similarly, the influence of mosses on P increased with increasing cover and was particularly important for taxa with a mat-forming habit (Fig. 5). This could occur because the shoots of mat-forming mosses lie close to the substrate, absorbing P directly from mineral soil[22]. Mosses following a *K*-strategy (as defined in Methods) were also more important for P cycling by supporting higher P mineralization activity. Further, we found a strong positive influence of soil mosses on Mg, a key macronutrient for metabolism and photosynthesis[30]. Capture of intermittent pulses of organic matter through stemflow and throughfall from vascular plants can contribute significant quantities of Mg in large mosses[28].

Finally, we acknowledge that there are some caveats in our work. First, our study is observational rather than experimental, so care must be taken in implying causality to the underlying mechanisms. Second, we were unable to sample extensive boreal forests because any areas of bare soil were unlikely to be free of the influence of mosses. Third, although we targeted moss patches, it is difficult to disentangle potential residual influences of other non-vascular organisms such as liverworts on our analyses. Nevertheless, despite these potential caveats, our global study reveals that mosses contribute to the maintenance of critical functions and services such as soil carbon sequestration and respiration.

In summary, we provide important insights into the global patterns of soil mosses and their contributions to the delivery of critical ecosystem services across markedly different global habitats ranging from Antarctic heaths to dry deserts. Soil mosses were positively associated with greater carbon sequestration, soil P, N and Mg contents, organic matter decomposition and plant pathogen control in soils globally. We provided further experimental evidence, using global meta-analyses, of the effects of mosses on soil functioning. Soil mosses further contributed to support multiple ecosystem services at locations where vascular plants have limited influence. Moreover, we found that the contribution of soil mosses to multiple ecosystem services varied among environments and that their effects on soils probably depended on traits and climatic and soil abiotic stress (for example, sand content). Together, our study demonstrates the global importance of soil mosses and highlights the need to conserve them to maintain important soil functions as varied as carbon sequestration, organic matter decomposition, soil fertility and pathogen control.

## Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41561-023-01170-x.

## References


1. Lindo, Z. & Gonzalez, A. The Bryosphere: an integral and influential component of the Earth's biosphere. *Ecosystems* **13**, 612–627 (2010).
2. Turetsky, M. R. et al. The resilience and functional role of moss in boreal and arctic ecosystems. *New Phytol.* **196**, 49–67 (2012).
3. Rodriguez-Caballero, E. et al. Dryland photoautotrophic soil surface communities endangered by global change. *Nat. Geosci.* **11**, 185–189 (2018).
4. Shaw, A. J., Cox, C. J. & Goffinet, B. Global patterns of moss diversity: taxonomic and molecular inferences. *Taxon* **54**, 337–352 (2005).
5. Garcia-Moya, E. & McKell, C. M. Contribution of shrubs to the nitrogen economy of a desert-wash plant community. *Ecology* **51**, 81–88 (1970).
6. Jonsson, M. et al. Direct and indirect drivers of moss community structure, function, and associated microfauna across a successional gradient. *Ecosystems* **18**, 154–169 (2015).
7. Delgado-Baquerizo, M. et al. Biocrust forming mosses mitigate the impact of aridity on soil microbial communities in drylands: observational evidence from three continents. *New Phytol.* **220**, 824–835 (2018).
8. Eldridge, D. J. et al. The pervasive and multifaceted influence of biocrusts on water in the world's drylands. *Glob. Change Biol.* **26**, 6003–6014 (2020).
9. Kasimir, Å., He, H., Jansson, P.-E., Lohila, A. & Minkkinen, K. Mosses are important for soil carbon sequestration in forested peatlands. *Front. Environ. Sci.* **9**, 680430 (2021).
10. Reed, S. C. et al. Changes to dryland rainfall result in rapid moss mortality and altered soil fertility. *Nat. Clim. Change* **2**, 752–755 (2012).
11. Romero, A. N., Moratta, M. H., Vento, B., Rodriguez, R. & Carretero, E. M. Variations in the coverage of biological soil crusts along an aridity gradient in the central-west Argentina. *Acta Oecol.* **109**, 103671 (2020).
12. Byun, M. Y., Kim, D., Youn, U. J., Lee, S. & Lee, H. Improvement of moss photosynthesis by humic acids from Antarctic tundra soil. *Plant Physiol. Biochem.* **159**, 37–42 (2021).
13. Gross, N. et al. Linking individual response to biotic interactions with community structure: a trait-based framework. *Funct. Ecol.* **23**, 1167–1178 (2009).
14. Büdel, B. et al. Improved appreciation of the functioning and importance of biological soil crusts in Europe: the Soil Crust International Project (SCIN). *Biodivers. Conserv.* **23**, 1639–1658 (2014).
15. Geffert, J. L., Frahn, J. L., Barthlott, W. & Mutke, J. Global moss diversity: spatial and taxonomic patterns of species richness. *J. Bryol.* **35**, 1–11 (2013).
16. Delgado-Baquerizo, M. et al. Multiple elements of soil biodiversity drive ecosystem functions across biomes. *Nat. Ecol. Evol.* **4**, 210–220 (2020).
17. Armas, C., Ordiales, R. & Pugnaire, F. I. Measuring plant interactions: a new comparative index. *Ecology* **85**, 2682–2686 (2004).
18. Hollingsworth, T. N., Schuur, E. A. G., Chapin, F. S. & Walker, M. D. Plant community composition as a predictor of regional soil carbon storage in Alaskan boreal black spruce ecosystems. *Ecosystems* **11**, 629–642 (2008).
19. Porada, P., Weber, B., Elbert, W., Pöschl, U. & Kleidon, A. Estimating global carbon uptake by lichens and bryophytes with a process-based model. *Biogeosciences* **10**, 6989–7033 (2013).
20. LaRoi, G. H. & Stringer, M. H. Ecological studies in the boreal spruce–fir forests of the North American taiga. II. Analysis of the bryophyte flora. *Can. J. Bot.* **54**, 619–643 (1976).
21. Ino, Y. & Nakatsubo, T. Distribution of carbon, nitrogen and phosphorus in a moss community soil system developed on a cold desert in Antarctica. *Ecol. Res.* **1**, 59–69 (1986).
22. Chapin, F. III, Oechel, W., Van Cleve, K. & Lawrence, W. The role of mosses in the phosphorus cycling of an Alaskan black spruce forest. *Oecologia* **74**, 310–315 (1987).
23. Brown, D. H. & Bates, J. W. Bryophytes and nutrient cycling. *Bot. J. Linn. Soc.* **104**, 129–147 (1990).
24. Makajanma, M. M., Taufik, I. & Faizal, A. Antioxidant and antibacterial activity of extract from two species of mosses: *Leucobryum aduncum* and *Campylopus schmidii*. *Biodiversitas* **21**, 2751–2758 (2020).

https://doi.org/10.1038/s41561-023-01170-x

25. Asakawa, Y. Biologically active compounds from bryophytes. *Pure Appl. Chem.* **79**, 557–580 (2007).
26. Bastida, F. et al. Soil microbial diversity–biomass relationships are driven by soil carbon content across global biomes. *ISME J.* **15**, 2081–2091 (2021).
27. Basile, A., Giordano, S., López-Sáez, J. A. & Cobianchi, R. C. Antibacterial activity of pure flavonoids isolated from mosses. *Phytochemistry* **52**, 1479–1482 (1999).
28. Rousk, K., Jones, D. L. & DeLuca, T. H. Moss–cyanobacteria associations as biogenic sources of nitrogen in boreal forest ecosystems. *Front. Microbiol.* https://doi.org/10.3389/fmicb.2013.00150 (2013).
29. Commisso, M. et al. Bryo-activities: a review on how bryophytes are contributing to the arsenal of natural bioactive compounds against fungi. *Plants* https://doi.org/10.3390/plants10020203 (2021).
30. Carter, D. & Arocena, J. Soil formation under two moss species in sandy materials of central British Columbia (Canada). *Geoderma* **98**, 157–176 (2000).



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# Methods

## Study sites

Soils were collected from 123 sites with three microsite types (mosses, vascular plants and bare soil) covering natural ecosystems and green spaces (Supplementary Video 1, Fig. 1 and Supplementary Tables 1–3) distributed across 17 countries and all continents. Our study aimed to evaluate the extent to which soil mosses support soil biodiversity and multiple ecosystem services across a wide range of natural (forests, heathlands, grasslands and shrublands) and urban green spaces (parks and gardens) where mosses are known to occur (Supplementary Tables 2 and 3). This sampling was conducted between 2017 and 2019. Mean annual precipitation ranged between 4 and 1,577 mm. Mean annual temperature ranged between −6.7 and 26.1 °C. Our sites are located, on average, 8,858.5 km from each other (minimum average distance of 42.97 km).

At each site, we established a 30 m × 30 m plot within which we placed three 30 m line transects (Fig. 1c). Along each transect, we recorded the cover of (1) perennial vascular plants (trees, shrubs, grasses or forbs), (2) non-vascular plants (mosses) and (3) unvegetated (bare) soil using a line-intercept method and used this information to calculate the percentage cover of each microsite within each plot. Where mosses and lichens occurred together as a community, we estimated the relative contribution of mosses within each sampled patch. Soils dominated by annual plants were considered bare soil. Plot-level moss cover was calculated as 100 × (moss cover/(moss + unvegetated bare soil + vascular-plant cover). Using this approach, we aimed to estimate the relative cover of mosses compared with vascular plants across contrasting terrestrial ecosystems. Moss cover ranged from 0.01 to 99.80%.

Within each plot, we collected composite soil samples (five cores of top ~5 cm) of vegetated, moss and bare microsites (Fig. 1c). Replicate samples were pooled and divided into two subsamples. One was immediately frozen (−20 °C) for molecular analyses, and the other was air dried for chemical analyses. We focused on surface soils because this uppermost layer is typically the most biologically active in terms of plant–soil interactions, microbial biomass and diversity, labile nutrient pools and C exchange with the atmosphere and to allow direct comparison of the contributions of moss and vascular plants to ecosystem services. Four of the 123 sites (three sites from Antarctica and one from Chile) had samples from bare and moss surfaces ($n = 119$ for vascular plants) only. Thus, a total of 365 soils were analysed for attribute assessment.

## Moss traits

Moss information and pictures were collected from the sites where moss soils were sampled, and the dominant species were identified, generally to the level of genus/species, using published keys and field guides or by consulting national and international bryological experts (Supplementary Table 2). Moss taxa were characterized according to life history: those surviving for <1 year (annuals), those surviving 1–3 years (ephemeral) and those surviving >3 years (perennial). Moss growth form was characterized as cushion (rounded, pincushion shaped), mats (dense clumps, generally branched shapes) or turfs (erect, lawn-like with crowded shoots)[31] and life strategy: r strategists (generally small, rapidly growing species with annual life cycles) and K strategists (larger, slower-growing, perennial species)[31].

## Soil biodiversity

Soil biodiversity (richness; number of phylotypes of soil bacteria, fungi, protists and invertebrates) was measured via amplicon sequencing using the Illumina MiSeq platform (Illumina, Inc.) in all soils associated with mosses, vascular plants and bare soils. Soil DNA was extracted from each of the 365 soil samples using the DNeasy PowerSoil Kit (Qiagen) according to the manufacturer's instructions. To characterize the richness (number of phylotypes) of bacteria, protists and invertebrates, portions of the prokaryotic (bacteria) 16S and eukaryotic (protists and invertebrates) 18S ribosomal RNA genes were sequenced using the 515 F/806R[32] and Euk1391f/EukBr[33] primer sets. Bioinformatic processing was performed using DADA2 as described in ref. 34. Phylotypes (amplicon sequence variants; ASVs) were identified at the 100% identity level. The ASV abundance tables were rarefied at 5,000 (bacteria via 16S rRNA gene), 1,000 (protists via 18S rRNA gene) and 250 (invertebrates via 18S rRNA gene) sequences per sample, respectively, to ensure even sampling depth within each below-ground group of organisms. Protists are defined as all eukaryotic taxa, except fungi, invertebrates (Metazoa) and vascular plants (Streptophyta). The richness 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 as described in ref. 35. Bioinformatic processing was performed as explained in the preceding. The fungi ASVs abundance table was rarefied at 1,000 sequences per sample.

**Rarefaction cross-validation.** Rarefaction curves for the richness of bacteria, fungi, protists and invertebrates are available in Supplementary Fig. 15. We also ensured that our choice of rarefaction level, taken to maximize the number of samples in our study, did not influence our results. In particular, we found highly statistically significant correlations among the richness of soil bacteria (rarefied at 5,000 versus 10,000 sequences per sample; Pearson's $r = 0.997$; $P < 0.001$), fungi (rarefied at 1,000 versus. 5,000 sequences per sample; Pearson's $r = 0.964$; $P < 0.001$), protists (rarefied at 1,000 versus 5,000 sequences per sample; Pearson's $r = 0.961$; $P < 0.001$) and invertebrates (rarefied at 250 versus 1,000 sequences per sample; Pearson's $r = 0.947$; $P < 0.001$) for a subset of samples wherein high numbers of sequences were available. These analyses support that our choice of rarefaction level did not affect our results.

## Soil functions and ecosystem services

In addition to the four measured soil organism richness attributes, we examined 20 soil functional attributes in all soils associated with mosses, vascular plants and bare soils (Supplementary Table 5). These soil attributes are associated with important ecosystem services and functions such as soil carbon sequestration (soil organic carbon content), nutrient cycling (soil total N, P, Cu, Mg, Mn, Zn, Fe and K contents), organic matter decomposition (soil extracellular enzyme activities related to C, N and P cycles, glucose, lignin and basal respiration), microbial habitat (biomass of bacteria and fungi), plant–soil symbiosis (biomass of arbuscular mycorrhizal fungi), ARG control (inverse of ARG abundance, based on 285 genes as explained in the following as defined in ref. 16; total abundance × −1) and soil-borne plant pathogen control (inverse of proportion of soil-borne plant pathogens as defined in ref. 16; proportion × −1).

The total contents of soil organic C and N were measured using a CN analyser (C/N Flash EA 112 Series-Leco Truspec) after removing inorganic carbon. The total contents of P, Cu, Mg, Zn, Fe, K and Mn in the soil were determined, after nitric-perchloric acid digestion, using an inductively coupled plasma optical emission spectrometer (ICAP 6500 DUO; Thermo-Scientific). The activities of β-glucosidase (starch degradation), N-acetylglucosaminidase (chitin degradation) and phosphatase (P mineralization) were measured from 1 g of soil by fluorometry as described in ref. 36. We used the MicroResp technique to determine potential soil respiration (basal) and the substrate-induced respiration using lignin and water as substrates and measured absorbance at 570 nm after the 5 h incubation period (25 °C and 60% water-holding capacity)[37].

The biomasses of bacteria, fungi and arbuscular mycorrhizal fungi were measured using microbial phospholipid fatty acids (PLFAs) according to ref. 38. The extracted PLFA samples were quantified using an Agilent 6890 gas chromatograph (Agilent Technologies). The peaks were identified using a Sherlock Microbial Identification System (MIDI, Inc.). Total biomass of fungi and bacteria was determined as the sum of

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bacterial and fungal PLFAs; 16:1w5c was used as an indicator of the biomass of arbuscular mycorrhizal fungi.

The abundance of ARGs was determined using the high-throughput quantitative PCR[39] from 365 soil samples on the Wafergen SmartChip Real-Time PCR system. We quantified the relative abundance of 285 ARGs. This method has been widely adopted to investigate the abundance of ARGs in various environmental settings[39]. Information on the primer sets used and the type and antibiotic resistance mechanism behind every ARG is available in Supplementary Table 9. We followed the PCR protocol described in ref. 40. In brief, the 100 nl reactions contained SensiMix SYBR No-ROX reagent (Bioline), primers, DNA and sterilized water. We included three analytical replicates for each soil sample and qPCR run. We used 5184-nanowell Smartchips (Wafergen), including 286 primer sets (Supplementary Table 9), calibrator (as 16S rRNA gene for the same DNA sample for all the chips) and negative control. Amplification conditions were 95 °C for 10 min followed by 40 cycles of 95 °C for 30 s and 60 °C for 30 s. We used the $2^{-\Delta CT}$ method, where $\Delta CT = (CT_{\text{detected ARGs}} - CT_{\text{16S rRNA gene}})$, to calculate the relative abundances of ARGs compared with the 16S rRNA gene in each soil sample according to a comparative $C_T$ method[40]. The abundance of ARGs was determined as the sum of the abundance of all ARGs retrieved at each sample. ARG control is determined as the inverse of the abundance of total ARGs (−1 × ARG abundance) as done in ref. 16.

The proportion of soil-borne potential fungal plant pathogens was determined from the PacBio ITS data (see Soil functions and ecosystem services) using the FUNGuild database[41]. The fungi ASVs abundance table was rarefied at 1,000 sequences per sample. Pathogen control is determined as the inverse of the proportion of plant pathogens (−1 × proportion of plant pathogens) as done in ref. 16.

### Environmental factors

Climatic information (mean annual temperature, seasonal temperature, diurnal temperature range, precipitation and precipitation seasonality) were extracted from the WorldClim database v.2 (ref. 16). Potential evapotranspiration was retrieved from the Global Aridity and PET Database v.3 (ref. 16). As expected, at a global scale, cross-sites mean annual precipitation and temperature were highly correlated with other metrics such as land surface moisture (Pearson $r = 0.28$; $P = 0.002$; Landsat 30 m resolution), recent air temperature (Pearson $r = 0.79$; $P < 0.001$; 1 km resolution; within sampling dates) and soil mean annual temperature (Pearson $r = 0.968$; $P < 0.001$; 1 km resolution), respectively. We used mean annual values because they represent the long-term availability of water and levels of temperature, which are more representative and commonly used at a global scale. We used Normalized Difference Vegetation Index (NDVI), from Landsat satellite imagery (Landsat 8, available from 2013; 30 m resolution, the same resolution as our sites, in ref. 16), as our proxy of net primary productivity (NPP). NDVI provides a global measure of the 'greenness' of vegetation across Earth's landscapes for a given composite period. NDVI data were obtained from 2013 to 2020. Plant richness (number of perennial plant species) was determined in the field using three transects across 30 m × 30 m plots. Vegetation (forest compared with no forest) and land use (natural compared with urban green spaces) were determined in the field. Urban green spaces included urban forests and gardens as defined in Supplementary Table 1 (see also Supplementary Table 2 for site-level information). Soil pH and electrical conductivity were measured in all the soil samples with a pH meter in a 1.0/2.5 mass/volume soil and water suspension. Sand content was also determined in the laboratory using a hydrometer method.

### Statistical analyses

**Patterns in moss-cover distribution.** Permanova. We first summarized the difference in moss cover across the globe using a histogram and examining potential differences in moss, plant and bare-soil cover across continents (Africa, Australia, South America, North America, Antarctica, Europe and Asia) and ecosystem types (Supplementary Table 2) using permutated, non-metric multivariate analysis of variance.

**Structural equation modelling.** We then used an SEM[42] to explore the direct and indirect effects of climate (potential evapotranspiration (PET), MAP, precipitation seasonality (PSEA), TSEA, MDR and mean annual temperature (MAT)), vascular vegetation (vascular-plant cover, vascular-plant richness (our surrogate of diversity), NPP, whether it is forest (value = 1) or non-forest (value = 0)), plot-level soil information (soil C/N ratio, soil C, pH, salinity, texture (sand content)) and land-use type (urban green spaces compared with natural) on moss cover across the globe (see Supplementary Fig. 3 for a priori model and rationale on selected pathways). Elevation (m) and average spatial dissimilarity (space) were also included in our model to account for spatial variability. Space was determined as the average between-plot distance from a Euclidean distance matrix including latitude, longitude (sine) and longitude (cosine; decimal degrees), aiming to account for any potential influence of spatial autocorrelation. Plot-level soil information was based on three soil composite samples collected at each site. We included this information to investigate whether moss cover changes across sites with contrasting levels of soil organic matter (soil C), C/N ratios, texture, pH and salinity. In this SEM, moss cover, elevation, PET, plant richness, soil C/N, salinity and soil C were log-transformed (log+1) to improve normality.

Structural equation modelling allowed us to test hypothesized relationships among predictors and moss cover based on an a priori model that constructs pathways among model terms on the basis of prior knowledge (Supplementary Fig. 3). Models showed a very good goodness of fit as measured using $\chi^2$ ($\chi^2$/d.f. = 0.93; d.f. = 5, $P = 0.46$), root mean square error of approximation (RMSEA = 0.00; $P = 0.62$) and Bollen–Stine bootstrap ($P = 0.51$). In addition, we calculated the standardized total effects of each explanatory variable to show its total effect. Analyses were performed using AMOS 22 (IBM) software.

**The contributions of moss and vascular plants to multiple ecosystem services.** Quantifying the contributions of moss and vascular plants to ecosystem services. We calculated the RII[17] for each site to assess the influence of mosses and vascular plants on 24 soil biodiversity and functional attributes compared with that from bare soil. Previous independent studies have used the RII to test the relative effects of plants on soil attributes across climates and vegetation types including local studies of mosses[43].

The contributions of moss and vascular plants to multiple ecosystem services were determined as the average RII values based on 24 soil attributes (RII moss and vascular-plant multiservices) (Supplementary Table 5). The RII of each soil attribute (Supplementary Table 6) was calculated as $\text{RII} = (X_m - X_b)/(X_m + X_b)$, where $X$ is the value of a specific ecological attribute, and $X_m$ and $X_b$ represent the values under the moss (or vascular plant) and in the bare soil, respectively. Note that the contributions of moss and vascular plants to multiple ecosystem services were similar when this index was calculated as the average of 24 individual soil attribute RIIs (used in the main text) and when using the average of eight RII ecosystem services (biodiversity preservation, carbon sequestration, nutrient cycling, plant pathogen control, antibiotic resistance control, organic matter decomposition, microbial habitat and biomass of symbiotic organisms) for both plants (Pearson's $r = 0.88$; $P < 0.0001$) and mosses (Pearson's $r = 0.88$; $P < 0.0001$). We also analysed the contributions of moss and vascular plants to individual soil attributes (for example, RII of soil C). The index is bounded by −1 and 1, with positive values indicating greater levels of a given attribute with the soil beneath the moss (or vascular plant) and vice versa. Soil pH, electrical conductivity and soil texture were not included as services.

We calculated the mean and 95% confidence interval (CI) of the moss and vascular-plant (v-plants) contribution to ecosystem services (average RII values based on 24 soil attributes; Supplementary Table 6) and for each individual moss and plant RII (for example, RII for soil C) to determine the influence of the moss and plant on soils on the basis of whether the 95% CI crosses the zero line. We used a bootstrapping approach to calculate these 95% CIs.

**Environmental drivers of the contribution of mosses to ecosystem services.** We used random forest (rfPermute package)[44] to investigate the relative importance of multiple environmental factors in driving the distribution of moss contributions to ecosystem services (average moss RII values based on 24 soil attributes; Supplementary Table 6). By doing so, we aimed to determine under which environmental conditions moss provides the largest contribution to multiple ecosystem services. Environmental predictors included moss cover, main taxa (each individual moss family representing more than 5% in all sites (value = 1) versus others (value = 0)) and traits (main reported life history, growth forms and life strategies as described), vegetation (plant cover, richness, NPP, forest (value = 1) versus non-forest (value = 0)) and land-use type (urban green spaces (value = 1) versus natural (value = 0)), climate (PET, MAP, PSEA, TSEA, MDR and MAT), plot-level soil information (plot average of soil C, C/N ratio, pH, salinity and texture), and space (as defined) and elevation. Random forest is known to be a robust approach when working with continuous and categorical variables. We included plot-level information (based on the three soil composite samples collected at each site) to investigate whether the contribution of mosses to nature changes across sites with contrasting levels of soil organic matter (soil C), C/N ratios, texture, pH and salinities.

We then used Spearman correlations to further investigate the relationships between environmental factors (climate, land-use type, soil, and plant and moss characteristics) and the RIIs of soil mosses on 24 individual soil attributes (Supplementary Table 6). Correlation analyses were conducted in SPSS 26.0 (IBM). Figures were created using ggplot2 packages and linear models fitted in R version 3.4.1. Spearman rank correlations are a non-parametric approach that does not require normality of data or homogeneity of variances and measures the strength and direction of the association between two ranked variables. In addition, unlike Pearson correlations, Spearman rank correlations can be used to associate two variables regardless of whether they are ordinal, interval or ratio.

**Mapping the global distribution of moss cover.** To predict the extent of moss cover and the contribution of moss to multiservices globally, machine learning random forest regression analysis[45] was used with the 15 variables: urban land cover (0/1), forest (0/1), plant cover, net primary productivity (NDVI), C in soil, pH, C/N, sand percentage, mean annual temperature, mean annual precipitation, mean diurnal range, precipitation seasonality, temperature seasonality, potential evapotranspiration and elevation. These predictors were selected on the basis of the availability of global maps for forest and urban cover types (MCD12Q1 V6 product (https://doi.org/10.5067/MODIS/MCD12Q1.006) accessed 4 June 2021) for 2016 derived from the International Geosphere-Biosphere Programme classification[46], plant cover (https://land.copernicus.eu/global/products/fcover, accessed 4 June 2021), climate[47] and soil information (https://soilgrids.org)[48] needed to map the distribution of soil mosses. We could use data from all 123 sites because (1) moss-cover data were standardized globally, (2) moss cover was highly correlated with key environmental factors at the global scale (Fig. 2d and Supplementary Fig. 6), (3) the number of sites provided robust statistical models ($R^2 = 0.86$) given the number of environmental factors considered and (4) the large gradient in environmental conditions in our global dataset covers an extensive part of the large-scale environmental variability of the planet. For example, across our survey area, mean annual temperature ranged between −6.7 and 26.1 °C, and soil pH and sand content ranged from 4 to 9 and 16 to 95%, respectively. Further, we excluded from our map (white areas) locations where environmental conditions were under-represented in our survey (using the Mahalanobis approach; Supplementary Fig. 7).

The random forest model was built by finding the set of covariate combinations that most robustly predict the training samples with 999 number of trees and 999 repetitions. To assess the accuracy of the predictions calculated from the random forest-based model, and thus to identify outlier locations, we calculated how much the parameter space of the predictors differed from the original dataset. We used the Mahalanobis distance of any multidimensional point of the fourteen dimensions given by the exogenous variables to the centre of the known distribution that we have previously calculated and the distance of any multidimensional point to the convex hull formed by the 123 locations that were used in the model. Subsequently, we used outlier identification to mask our results and provide more-reliable predictions at the 0.9 quantile of the chi-square distribution with 14 degrees of freedom to which each location belongs. The modelling approach was then validated by returning the predicted values ($x$ axis) versus the observed values ($y$ axis), following ref. 49.

**Identifying locations with unique and overlapping contributions of vascular plants and mosses to multiservices.** We calculated a bivariate map on the basis of the quantiles of two variables, moss multiservices and vascular-plant multiservices. This method[50] is used if the variables to be represented have a geographic pattern or a strong correlation between the two variables. In summary, the map shows the relationship between the two variables spatially located. For this analysis, we generated a map to predict the contribution of vascular plants to multiservices worldwide similar to the procedure for soil mosses.

### Reporting summary

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

## Data availability

All the materials, raw data, and protocols used in the article are available upon request. Data used in this study can be found in the Figshare data repository https://figshare.com/s/b152d06e53066d08b934 ref. 51.

## References


31. Glime, J. M. *Bryophyte Ecology* Vol. 1 (Michigan Tech. Univ. and Int. Assoc. Bryol., 2017).
32. Herlemann, D. P. R. et al. Transitions in bacterial communities along the 2000 km salinity gradient of the Baltic Sea. *ISME J.* **5**, 1571–1579 (2011).
33. Ihrmark, K. et al. New primers to amplify the fungal ITS2 region—evaluation by 454-sequencing of artificial and natural communities. *FEMS Microb. Ecol.* **82**, 666–677 (2012).
34. Callahan, B. J. et al. DADA2: high-resolution sample inference from Illumina amplicon data. *Nat. Methods* **7**, 581–583 (2016).
35. Tedersoo, L. et al. Regional-scale in-depth analysis of soil fungal diversity reveals strong pH and plant species effects in northern Europe. *Front. Microbiol.* **11**, 1953 (2020).
36. Bell, C. W. et al. High-throughput fluorometric measurement of potential soil extracellular enzyme activities. *J. Vis. Exp.* **15**, e50961 (2013).
37. Campbell, C., Chapman, S., Cameron, C., Davidson, M. & Potts, J. A. Rapid microtiter plate method to measure carbon dioxide evolved from carbon substrate amendments so as to determine the physiological profiles of soil microbial communities by using whole soil. *Appl. Environ. Microbiol.* **69**, 3593–3599 (2003).
38. Frostegard, A. et al. Use and misuse of PLFA measurements in soils. *Soil Biol. Biochem.* **43**, 1621–1625 (2011).

39. Hu, H., Jung, K., Wang, Q., Saif, L. J., & Vlasova, A. N. Development of a one-step RT-PCR assay for detection of pancoronaviruses (α-, β-, γ-, and δ-coronaviruses) using newly designed degenerate primers for porcine and avian fecal samples. *J. Virol. Methods* **256**, 116–122 (2018).
40. Schmittgen, T. D. & Livak, K. J. Analyzing real-time PCR data by the comparative C(T) method. *Nat. Protoc.* **3**, 1101–1108 (2008).
41. Nguyen, N. H. et al. FUNGuild: an open annotation tool for parsing fungal community datasets by ecological guild. *Fungal Ecol.* **20**, 241–248 (2015).
42. Grace, J. B. *Structural Equation Modelling and Natural Systems* (Cambridge Univ. Press, 2006).
43. Le, T. B., Wu, J. & Gong, Y. Vascular plants regulate responses of boreal peatland *Sphagnum* to climate warming and nitrogen addition. *Sci. Total Environ.* https://doi.org/10.1016/j.scitotenv.2021.152077 (2022).
44. Archer, E. rfPermute: Estimate Permutation p-Values for Random Forest Importance Metrics v.1.5.2 (2016).
45. Lahouar, A. & Slama, J. B. H. Day-ahead load forecast using random forest and expert input selection. *Energy Convers. Manage.* **103**, 1040–1051 (2015).
46. Loveland, T. R. et al. An analysis of the IGBP global land-cover characterization process. *Photogramm. Eng. Remote Sens.* **65**, 1021–1032 (1999).
47. Lembrechts, J. J. et al. Global maps of soil temperature. *Glob. Change Biol.* **28**, 3110–3144 (2021).
48. Hengl, T. et al. SoilGrids250m: global gridded soil information based on machine learning. *PLoS ONE* **12**, e0169748 (2017).
49. Piñeiro, G., Perelman, S., Guerschman, J. P. & Paruelo, J. M. How to evaluate models: observed vs. predicted or predicted vs. observed? *Ecol. Model.* **216**, 316–322 (2008).
50. Brown, S. bivarRasterPlot.R (R-project.org, accessed 6 June 2022); https://gist.github.com/scbrown86/2779137a9378df7b60afd23e0c45c188
51. Eldridge, D. J. & Delgado-Baquerizo, M. Soil mosses support the delivery of critical ecosystem services globally. *Figshare* https://doi.org/10.6084/m9.figshare.22220824 (2023).

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## Author contributions

M.D.-B. and D.J.E. developed the original idea of the analyses presented in the paper. M.D.-B. designed the field study and wrote the grant that funded the work. Field data were collected by M.D.-B., D.J.E., M.B., J.L.B.-P., C.P., S.M., S.A., F.A., A.R.B., A.d.l.R., J. Durán., T.G., J.G.I., Y.-R.L., T.P.M., M.A.M.-M. T.U.N., G.F.P.-B., A. Rey, A. Rodriguez, C.S., A.L.T., C.T.-D., P.T., L.W., Jianyong Wang, E.Z., X.Z. and X.-Q.Z. Laboratory analyses were performed by M.D.-B., H.-W.H., J.-Z.H., F.B., J.L.M., L.T., T.S.-S., T.Y., W.S., H.C., S.P. and P.T. Mapping and remote sensing were performed by J.J.G., E.G. and C.A.G. and bioinformatic analyses by B.S., Juntao Wang, H.-W.H. and J.-Z.H. Meta-analytical data were collected by S.L. and G.Z. Statistical analyses were carried out by M.D.-B, J. Ding and M.M.-C. The paper was written by D.J.E. and M.D.-B. and edited by P.B.R., R.O.-H. and J. Ding with contributions from all co-authors.

## Competing interests

The authors declare no competing interests.

## Additional information

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*Our web collection on statistics for biologists contains articles on many of the points above.*

## Software and code

Policy information about availability of computer code

| | |
|---|---|
| Data collection | We conducted a global standardized field survey (123 sites in all continents) including a total of 365 soil samples. Data collection information is included in the method section of our manuscript. |
| Data analysis | For Bioinformatic analysis, DADA2 was used. Information about all statistical methods used in this paper are included in our method section. |

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# Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

| | |
|---|---|
| Study description | We conducted a global standardized field survey to quantify how soil mosses support eight ecosystem services associated with 24 soil biodiversity and functional attributes across wide environmental gradients from all continents. |
| Research sample | A total of 365 soils collected from 123 ecosystems were analysed. |
| Sampling strategy | Here, we report results from the most comprehensive global standardized field survey of soil-inhabiting mosses. This survey included composite topsoil samples (uppermost 7.5 cm) collected beneath mosses, vascular plants and in unvegetated bare soils from within 30 m x 30 m plots in 123 ecosystems across all continents (Figs. 1 and S1; Supplementary Tables 1-2; Supplementary Movie 1). |
| Data collection | At each location, we established a 30 m × 30 m plot comprising three, equally spaced transects 10 m apart. Soil samples were collected between 2018 and 2019 from within three microsites: 1) beneath the most common perennial vascular vegetation type at each location (generally tree, shrub or grass), 2) beneath mosses and 3) in unvegetated bare soil (bare soil hereafter). Five composite soil cores (0-7.5 cm depth) were collected from each microsite, bulked and divided into two sub-samples; one that was immediately frozen (-20ºC) for molecular analyses and the other air-dried for chemical analyses. Four of the 123 sites (three sites from Antarctica and one from Chile) had samples only from bare and moss surfaces (n = 119 for vascular plants). A total of 365 soils were analysed. |
| Timing and spatial scale | Sample collection of soils took place between 2018 and 2019. Global Scale. |
| Data exclusions | n/a |
| Reproducibility | Information about the sampled locations and methods used in this paper are included in our method section |
| Randomization | n/a |
| Blinding | n/a |

Did the study involve field work? ☒ Yes ☐ No

## Field work, collection and transport

| | |
|---|---|
| Field conditions | Our sampling design captured the broad range of environmental conditions under which mosses occur, rather than focusing on particular ecosystems (e.g., boreal or deserts; Supplementary Table 1; Supplementary Fig. 2). Sampled locations also captured a broad range of vegetation types such as forests (50% of sites), grasslands (29%), shrublands (17%) and moss heathlands (4%; Supplementary Table 2); climates (tropical, continental, temperate, arid, polar); and land management contexts (natural undisturbed ecosystems and urban greenspaces) (Supplementary Tables 1-2). |
| Location | Soils were collected from 123 ecosystems comprising a mixture of natural ecosystems and urban greenspaces (Supplementary Movie 1; Fig. 1; Supplementary Tables 1 and 3) distributed across 17 countries and all continents. |
| Access & import/export | Samples were collected by authors in their respective locations and using local permits. |
| Disturbance | This study did not cause any environmental disturbance |

# Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

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## Methods

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|---|---|
| ☒ | ☐ ChIP-seq |
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| ☒ | ☐ MRI-based neuroimaging |