

The global contribution of soil mosses to ecosystem services

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Abstract

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 promote eight 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 were especially important for supporting multiple ecosystem services where vascular plant cover is low. Globally, soil mosses potentially support 6.43 gigatonnes more carbon in the soil layer than 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 a high cover of mat and turf mosses, in less productive ecosystems, and on sandy and salty 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.

Main

Mosses are one of the most common and ubiquitous life forms on the planet¹⁻³, contributing a considerable portion of plant biomass in some of Earth's most extensive ecosystems, ranging from deserts to boreal and arctic regions⁴. 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 resources⁵, 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 sequestration⁶⁻⁹. Previous studies of soil mosses, those growing on the soil surface, have tended to focus at local or regional scales, in particular ecosystems (e.g., polar, boreal or arid)¹⁰⁻¹². The influence of soil mosses on

biodiversity and ecosystem functioning could depend on their specific functional traits (e.g., annual *cf.* perennial; i.e., *r-* *cf.* *K*-strategist) and taxonomies. Yet, unlike vascular plant functional traits¹³, 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 (e.g., drylands, degraded land), particularly under changing climates or where the use of vascular plants may be inappropriate.

Here, 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 bare soil), from within 30 x 30 m plots at each of 123 sites across all continents (Figs. 1 and S1; Supplementary Tables 1-2; Supplementary Movie 1). Our sites cover the broad range of environmental conditions under which mosses occur, rather than focusing on particular ecosystem types (Supplementary Table 1; Supplementary Fig. 2). Climate ranges from tropical to continental, temperate, arid, and polar, vegetation types from forests to grasslands, shrublands, and heathlands, and land management contexts from urban to natural (Supplementary Tables 1-2).

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 eight ecosystem services. We aimed to: (i) determine the environmental conditions supporting ecosystems with or without mosses worldwide; (ii) 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, biomass of symbiotic organisms) all across contrasting climates and compared to vascular plants. We also (iii) assessed 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 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, 40 genera) with contrasting life histories (annual to perennial), growth forms (cushions, mats, turfs) and life strategies (*r-* and *k*-strategists; Methods; Supplementary Fig. 2). Deserts and urban gardens supported the largest proportion of annual moss species, and tundra and wet forests a greater percentage of perennial species (Supplementary Fig. 2). Most survey locations, particularly those in urban greenspaces and natural grasslands, supported a sparse cover of mosses (Figs. 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, 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, Supplementary Table 3), and found that moss cover tended to be greater in environments with low potential evapotranspiration (PET) and sparse vascular plant cover, particularly in some deserts and tundra ecosystems (Figs. 2C and 3). In addition to PET and plant cover, precipitation and mean diurnal range temperature (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, mosses were significantly associated with rainfall-limited environments, with low PET and MDR, likely due to specialised leaf structures that enable them to capture and retain moisture, an innate ability to recover from long periods of dehydration⁹ 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 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, or 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 Fig. 5, 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, compared with vascular plant cover (Fig. 2D), consistent with regional studies^{11-12,14}. Earlier studies have mapped the distribution of moss richness at the national level¹⁵, but there was no high resolution map of moss cover. Our estimates indicate that mosses cover over 9.4M km² 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 4-5; 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, 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 control¹⁶ and soil-borne plant pathogen control¹⁶ (Supplementary Table 4, Methods).

A relative interaction intensity index (RII¹⁷; Methods for details) 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; Methods). The index compares the differences between moss (or vascular plant) and bare soil where $RII = (X_m - X_b) / (X_m + X_b)$, where X is the value of a specific attribute, and X_m and X_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*; see Methods).

Our data show that soil mosses make significant and positive contributions to multiple ecosystem services (i.e., 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 (i.e., 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; 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 (e.g., 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 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. 3). 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. 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). Thus, our findings go beyond the well-studied effects of soil mosses on individual groups of functions (e.g., nitrogen cycling) in particular ecosystems (e.g., 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 sequestration¹⁸⁻¹⁹ because of their key role in natural environments where they are the dominant vegetation (e.g., 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), that partially excluded important regions of the planet covered by mosses such as boreal forests. Nevertheless, we accounted for these regions using meta-analytical data (as explained below). Soil mosses thus likely 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 extra 0.49, 0.10 and 0.06 Gt more soil N, P and Mg, respectively, worldwide, boosting levels of three fundamental nutrients that often 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

In order 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 Appendixes 2-3) provided compelling evidence of the positive effect of mosses on multiservices, soil C, N, P and Mg contents, and on soil respiration and glucose degradation observed in our global survey (Meta-analysis #1; Supplementary Appendixes 2-3 and Fig. 9). 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 (Supplementary Fig. 10; Meta-analysis #2; Supplementary Appendixes 4-5). 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. 10), 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. 11 for soil community composition found beneath mosses). Also, in general, soil mosses support a lower diversity of invertebrates than surrounding bare soils. Moss tissue contains flavonoids, carotenoids and other short-chained phenolics²³ that

exhibit antimicrobial, antifungal, and cytotoxic activities²⁴⁻²⁵, suppressing insect activity, and resulting in invertebrate mortality²⁵. 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 (e.g., organic matter and prey) availability is known to regulate the diversity of soil organisms²⁶. Similarly, we found a greater positive association of mosses with invertebrate richness where mosses were positively associated with micronutrients (Supplementary Fig. 12). Further, mosses are important regulators of soil-borne pathogens (Fig. 3a), reducing the proportion of potential soil-borne pathogens associated with vascular plant communities²⁷. Soils are known to be a huge reservoir of plant pathogens²⁵, and mosses could help to regulate this important reservoir. Our work demonstrates that mosses regulate ecosystem services in the same way as 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 services²⁹.

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 modeling 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 greenspaces; Supplementary Fig. 13), on sandy, salty and low C:N soils, and in environments with low precipitation seasonality (Figs. 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 relative interaction indices of mosses (Figs. 5C; Supplementary Fig. 13-14). 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 biomass¹⁶. In these situations, mosses can contribute markedly to retaining soil fertility, symbiotic organisms, and microbial habitat⁹. The mechanisms at work likely include the capture of C- and N-rich airborne particles²² and the deposition of elements such as Mg³⁰ 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 greenspaces (Supplementary Figs. 13-14) and regions with high precipitation seasonality (Fig. 5 and Supplementary Fig. 14). Both climatic seasonality¹⁰ and physical disturbance² have been shown to limit the positive influence of mosses on individual soil functions such as nitrogen availability in specific fine-scale field experiments¹⁰. 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 forests²⁸. 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 ARG control (i.e., 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 prevalent¹⁸ (Supplementary Fig. 1).

Unlike the well described associations between moss and nitrogen-fixing bacteria²⁸, the influence of moss on ARGs is thus far poorly described. We posit that increases in soil carbon beneath mosses 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 soil²². Mosses following a *K*-strategy (as defined in the Material and 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 macro-nutrient for metabolism and photosynthesis³⁰. Capture of intermittent pulses of organic matter through stemflow and throughfall from vascular plants can contribute significant quantities of Mg in large mosses²⁸.

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 likely depended on traits, and climatic and soil abiotic stress (e.g., sand content and salinity). 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, fertility and pathogen control.

Acknowledgements

We thank Prof. David Wardle for his insightful comments on an earlier draft and Prof. Antonio Gallardo for his assistance during sample collection. We are grateful to Vincent Hugonnot, José Gabriel Segarra-Moragues, Frank Müller, Senta Stix, Isabelle Charissou, Dumas Yann, Marc-Frédéric Indorf and BRYONET for assistance identifying moss species. We thank Samuel Castejón Angorrilla for help with laboratory analyses.

Funding

This study work associated with this manuscript was funded by a Large Research Grant from the British Ecological Society (No LRB17\1019; MUSGONET). D.J.E. is supported by the Hermon Slade Foundation. M.D-B. was supported by a Ramón y Cajal grant from the Spanish Ministry of Science and Innovation (RYC2018-025483-I), a project from the Spanish Ministry of Science and Innovation for the I+D+i (PID2020-115813RA-I00 funded by MCIN/AEI/10.13039/501100011033a), and a project PAIDI 2020 from the Junta de Andalucía (P20_00879). E.G. is supported by the European Research Council grant agreement 647038 (BIODESERT). L.W. and J.W. are supported by the Program for Introducing Talents to Universities (B16011), and the Ministry of Education Innovation Team Development Plan (2013-373). The contribution of TG and TUN was supported by the Research Program in Forest Biology, Ecology and Technology (P4-0107) of the Slovenian Research Agency. The contribution of P.R. was supported by the NSF Biological Integration Institutes grant DBI-2021898.

Author contributions

M.D-B. and D.J.E. developed the original idea of the analyses presented in the manuscript. 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.R., J.D., 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.R., C.S., A.L.T., C.T-D., P.T., L.W., J.W., 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., W.S., H.C., S.P., P.T., and T.W. Mapping and remote sensing was performed by J.J.G., E.G. and C.A.G. and bioinformatic analyses by B.S., J-T.W., C.C-D., 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.D., M.M-C. The manuscript was written by D.J.E and M.D-B. and edited by P.B.R., R.O.H., and J.D. with contributions from all co-authors.

Competing interests

The authors declare no conflict of interest.

Figure legends

Figure 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 location. (B) Location 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.

Figure 2. Global distribution of soil mosses. (A) Distribution of moss cover in our global survey. (B) Moss cover across continents and ecosystem types. (C) Structural Equation Model 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 greenspaces *cf.* natural) and soil properties in driving the proportion of moss cover (see Supplementary Table 3 for more details and Fig S4 for *a priori* model). MAT: mean annual temperature, MAP: mean annual precipitation, PSEA: seasonal precipitation, TSEA: seasonal temperature, MDR: mean diurnal temperature range, NPP: net primary productivity, Prich: Vascular plant richness, Pcov: Vascular plant cover, C: soil carbon (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. 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 / pixel), based on machine learning modelling with a $R^2 = 0.86$ (determined as predicted vs. 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.

Figure 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 relative interaction indices (RII) for 24 individual soil attributes (mean $\pm$ bootstrap CI 95%). * $P < 0.05$. (B) Significant ($P < 0.05$) relationships between moss and vascular plant contribution to ecosystem services (average of all RII) and individual RII indices based on 24 soil biodiversity and functional attributes. Moss and vascular plant contribution to multiservices (RII) = 0 (e.g., vertical dashed line in Panel A) indicates that values for moss or 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.

Figure 4. Contribution of vascular plant and mosses to multiservices. Predicted contribution of moss and vascular plants to multiservices across the globe (25 km / pixel), based on machine learning modelling with a $R^2 = 0.73$ for vascular plants and $R^2 = 0.68$ for mosses (determined as predicted *cf.* 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.

Figure 5. Environmental factors associated with the contribution of mosses to multiple ecosystem services. (A and 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 $\pm$ 95% CI for the relationship between environmental factors and moss contribution to ecosystem services (** $P < 0.01$; * $P < 0.05$; ^a $P = 0.09$). Natural ($n = 62$), Urban greenspace (61), Cushion (24), Matt + Turf (99), Funariaceae (7), Others (116), Perennial (56), Ephemeral (55), Annual (12); (C) Heatmap of significant ($P < 0.05$) Spearman correlations among environmental factors and the moss relative interaction indices (RII) for 24 individual soil attributes ($n = 123$ sites).

References

1. Lindo, Z. & Gonzalez, A. The Bryosphere: an integral and influential component of the Earth's biosphere. *Ecosyst.* 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. *Ecosyst.* 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. *Ecosyst.* 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, III F., 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. Linnean 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*. *Biodivers. J. Botan. Div.* 21, (2020).
25. Asakawa, Y. Biologically active compounds from bryophytes. *Pure Appl. Chem.* 79, 557-580 (2007).
26. Bastida, F., Eldridge, D.J., García, C. et al. Soil microbial diversity-biomass relationships are driven by soil carbon content across global biomes. *ISME J* 15, 2081-2091 (2021).
27. Basile, A., Giordano, S., López-Sáez, J.A. & Cobiánchi, R.C. Antibacterial activity of pure flavonoids isolated from mosses. *Phytochem.* 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. Micro.*, 4. doi:10.3389/fmicb.2013.00150 (2013)
29. Commisso, M., Guarino, F., Marchi, L., Muto, A., Piro, A., Degola, F. Bryo-Activities: a review on how bryophytes are contributing to the arsenal of natural bioactive compounds against fungi. *Plants (Basel)*. 10:203. doi: 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).

Methods

Study sites

Soils were collected from 123 sites with three microsite types (mosses, vascular plants, bare soil) covering natural ecosystems and greenspaces (Supplementary Movie 1; Fig. 1; 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 greenspaces

(parks, 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 1577mm. Mean annual temperature ranges between -6.7 and 26.1°C. Our sites are located, on average, 8858.5km from each other (minimum average distance of 42.97 km).

At each site we established a 30 m x 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 (i.e., 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 $100 \times (\text{moss cover} / (\text{moss} + \text{unvegetated bare soil} + \text{vascular plant cover}))$. Using this approach, we aimed to estimate the relative cover of mosses *cf.* vascular plants across contrasting terrestrial ecosystems. Moss cover ranged from 0.01 to 99.8%.

Within each plot, we collected composite soil samples (five cores of top ~5cm) 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 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 contribution of moss and vascular plants to ecosystem services. 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). 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 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), 1-3 years (ephemeral), > 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 shoots³¹, and life strategy i.e., *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, CA, USA) 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 (Qiagen, Hilden, Germany) according to the manufacturer's instructions. To characterize the richness (number of phylotypes) of bacteria, protists and invertebrates, a portion of the prokaryotic 16S (bacteria) and eukaryotic (protists and invertebrates) 18S rRNA genes were sequenced using the 515F/806R³² and Euk1391f/EukBr³³ primer sets. Bioinformatic

processing was performed using DADA2 as described in ref.³⁴. Phylotypes (i.e., amplicon sequence variants; ASVs) were identified at the 100% identity level. The ASV abundance tables were rarefied at 5000 (bacteria via 16S rRNA gene), 1000 (protists via 18S rRNA gene) and 250 (invertebrates via 18S rRNA gene) sequences per sample, respectively, to ensure even sampling depth within each belowground 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, Estonia, as described in ref.³⁵. Bioinformatic processing was performed as explained above. The fungi ASVs abundance table was rarefied at 1000 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 between the richness of soil bacteria (rarefied at 5000 vs. 10,000 sequences/sample; Pearson's $r = 0.997$; $P < 0.001$), fungi (rarefied at 1,000 vs. 5,000 sequences/sample; Pearson's $r = 0.964$; $P < 0.001$), protists (rarefied at 1000 vs. 5,000 sequences/sample; Pearson's $r = 0.961$; $P < 0.001$) and invertebrates (rarefied at 250 vs. 1,000 sequences/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, 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), antibiotic resistance genes control (inverse of ARG abundance, based on 285 genes as explained below as defined in ref.¹⁶; total abundance $\times -1$), and soil-borne plant pathogen control (inverse of proportion of soil-borne plant pathogens as defined in ref.¹⁶; proportion $\times -1$).

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 ICP-OES spectrometer (ICAP 6500 DUO; Thermo-Scientific, Waltham, MA, USA). The activities of β -glucosidase (BG - starch degradation), N-Acetylglucosaminidase (NAG - chitin degradation) and phosphatase (PHOS - P mineralization) were measured from 1 g of soil by fluorometry as described in ref.³⁶. We used the MicroRespTM 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 biomass 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, Palo Alto, CA, USA). The peaks were identified using a Sherlock Microbial Identification System (MIDI, Inc., Newark, NJ, USA). Total biomass of fungi and bacteria were determined as the sum of bacterial and fungal PLFAs, respectively. 16:1w5c was used as an indicator of the biomass of arbuscular mycorrhizal fungi (AMF).

The abundance of the antibiotic resistance genes (ARGs) was determined using the high throughput quantitative PCR³⁹ from 365 soil samples on the Wafergen SmartChip Real-Time PCR system (Fremont, CA, USA). We quantified the relative abundance of 285 ARGs. This method has been widely adopted to investigate the abundance of ARGs in various environmental settings³⁹. Information on the primer sets used, and the type and antibiotic resistance mechanism behind every ARG is available in Supplementary Table 8. We followed the PCR protocol described in ref.⁴⁰. In brief, the 100 nl reactions contained SensiMix SYBR No-ROX reagent (Bioline, London, UK), primers, DNA, and sterilized water. We included three analytical replicates for each soil sample and qPCR run. We used 5184-nanowell Smartchips (Wafergen, Fremont, CA, USA) including 286 primer sets (Supplementary Table 8), 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 to the 16S rRNA gene in each soil sample according to a comparative C_T method⁴⁰. 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 inversed of the abundance of total ARGs ($-1 \times \text{ARG abundance}$) as done in ref¹⁶.

The proportion of soil-borne potential fungal plant pathogens was determined from the PacBio ITS data (see above) using the FUNGuild database⁴¹. The fungi ASVs abundance table was rarefied at 1000 sequences per sample. Pathogen control is determined as the inversed of the proportion of plant pathogens ($-1 \times \text{proportion of plant pathogens}$) as done in ref¹⁶.

Environmental factors

Climatic information (mean annual temperature, seasonal temperature, diurnal temperature range, precipitation, precipitation seasonality and potential evapotranspiration) were extracted from the WorldClim database v2 (<https://www.worldclim.org/data/index.html>). 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 30m resolution), and recent air temperature (Pearson $r = 0.79$; $P < 0.001$; 1km resolution; within sampling dates) and soil mean annual temperature (Pearson $r = 0.968$; $P < 0.001$; 1km 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 NDVI (Normalized Difference Vegetation Index), from Landsat satellite imagery (Landsat 8 –available from 2013–; 30m resolution –same resolution as our sites) (<https://landsat.gsfc.nasa.gov>), 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 x 30 m plots. Vegetation (forest *cf.* no forest) and land use (natural *cf.* urban greenspaces) were

determined in the field. Urban greenspaces 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: 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, Asia) and ecosystem types (Supplementary Table 2) using permutated, non-metric multivariate analysis of variance (PERMANOVA).

Structural Equation Modelling

We then used Structural Equation Model (SEM)⁴² to explore the direct and indirect effects of climate (potential evapotranspiration [PET], mean annual precipitation [MAP], precipitation seasonality [PSEA], temperature seasonality [TSEA], mean diurnal range [MDR], 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 greenspaces *cf.* natural) on moss cover across the globe (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.

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 based on prior knowledge (Supplementary Fig. 3). Models showed a very good goodness of fit as measured using χ^2 ($\chi^2/\text{df} = 1.45$; $\text{df} = 5$), Root Mean Error of Approximation (RMSEA = 0.06; $P = 0.36$) and Bollen-Stine Bootstrap ($P = 0.20$). In addition, we calculated the standardized total effects of each explanatory variable to show its total effect. Analyses were performed using AMOS 22 (IBM, Chicago, IL, USA) software.

The contribution of moss and vascular plants to multiple ecosystem services

Quantifying the contribution of moss and vascular plants to ecosystem services

We calculated the relative interaction index (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 index to test the relative effects of plants on soil attributes across climates and vegetation types including local studies of mosses⁴³.

The contribution of moss and vascular plants to multiple ecosystem services was 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 $RII = (X_m - X_b) / (X_m + X_b)$, where X is the value of a specific ecological attributes, and X_m and X_b represent the values under the moss (or vascular plant) and in the bare soil, respectively. We would like to highlight that the contribution of moss and vascular plants to multiple ecosystem services was similar when this index was calculated as the average of 24 individual soil attribute RII (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 analyzed the contribution of moss and vascular plants to individual soil attributes (e.g., 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 also for each individual moss and plant relative interaction index (e.g., RII for soil C) to determine the influence of the moss and plant on soils based on whether the 95% CI crosses the zero line. We used a bootstrapping approach to calculate these 95% CI.

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 aim to determine under which environmental conditions, moss provide 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] vs. others [value = 0]) and traits (main reported life history, growth forms and life strategies as described above), vegetation (plant cover, richness, NPP, forest [value = 1] vs. non-forest [value = 0]) and land use type (urban greenspaces [value = 1] vs. natural [value = 0]), climate (potential evapotranspiration [PET], mean annual precipitation [MAP], precipitation seasonality [PSEA], temperature seasonality [TSEA], mean diurnal range [MDR], mean annual temperature [MAT]), plot-level soil information (plot-average of soil C, C:N ratio, pH, salinity, texture), and space (as defined above) 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 change 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 relative interaction indices (RII) of soil mosses on 24 individual soil attributes (Supplementary Table 6). Correlation analyses were conducted in SPSS 26.0 (IBM, Chicago, IL). Figures were created using 'ggplot2' packages and linear models fitted in R version 3.4.1. Spearman rank

correlations are a non-parametric approach which 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 analysis⁴⁵ 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 based on the availability of global maps for forest and urban cover types (MCD12Q1 V6 product (<https://doi.org/10.5067/MODIS/MCD12Q1.006>, accessed on 4 June 2021) for 2016 derived from the IGB classification⁴⁶, plant cover (<https://land.copernicus.eu/global/products/fcover>, accessed on 4 June 2021), climate⁴⁷, 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; 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 to 26.1°C, and soil pH and sand content 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 described in Methods; 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 fourteen degrees of freedom to which each location belongs. The modelling approach was then validated by returning the predicted values (x-axis) vs. 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 based on the quantiles of two variables, moss multiservices and vascular plant multiservices. This method⁵⁰ 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.

Data and materials availability

All the materials, raw data, and protocols used in the article are available upon request and without restriction, and all data will be made publicly available in the Figshare data repository <https://figshare.com/s/b152d06e53066d08b934>

Methods-only references

31. Glime, J.M. Adaptive strategies: growth and life forms. Chapter 4-5. In: Glime, J.M. Bryophyte Ecology. Volume 1. 4-5-1. Physiological Ecology, Michigan Tech. Univ. & Intern. 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. Nature 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 Visual. Exper. 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 Biology and Biochemistry 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. Method. 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 University Press, UK (2006).
43. Le, T.B., Wu, J., Gong, Y., Vascular plants regulate responses of boreal peatland Sphagnum to climate warming and nitrogen addition. *Science of The Total Environment*, 10.1016/j.scitotenv.2021.152077, 819. (2022)
44. Archer E., rfPermute: Estimate Permutation p-Values for Random Forest Importance Metrics. R package version 1. 5. 2 (2016).

- 915 45. Lahouar, A. & Slama, J.B.H. Day-ahead load forecast using random forest and expert
916 input selection. *Energy Convers. Manag.* 103, 1040–1051 (2015).
- 917 46. Loveland, T.R. et al. An analysis of the IGBP global land-cover characterization process.
918 *Photog. Engineer Remote Sens.* 65, 1021-1032 (1999).
- 919 47. Lembrechts J.J. et al. Global maps of soil temperature. *Global Change Biology*
920 <https://doi.org/10.1111/gcb.16060> (2021).
- 921 48. Hengl, T. et al. SoilGrids250m: Global gridded soil information based on machine
922 learning. *PLOS ONE* 12, e0169748 (2017).
- 923 49. Piñeiro, G., Perelman, S., Guerschman, J. P. & Paruelo, J. M. How to evaluate models:
924 Observed vs. predicted or predicted vs. observed? *Ecol. Model.* 216, 316–322 (2008).
- 925 50. Brown, S. Make a bivariate plot using raster data. Available online in
926 <https://gist.github.com/scbrown86/2779137a9378df7b60afd23e0c45c188> (accessed on 6
927 June 2022).

Fig 1

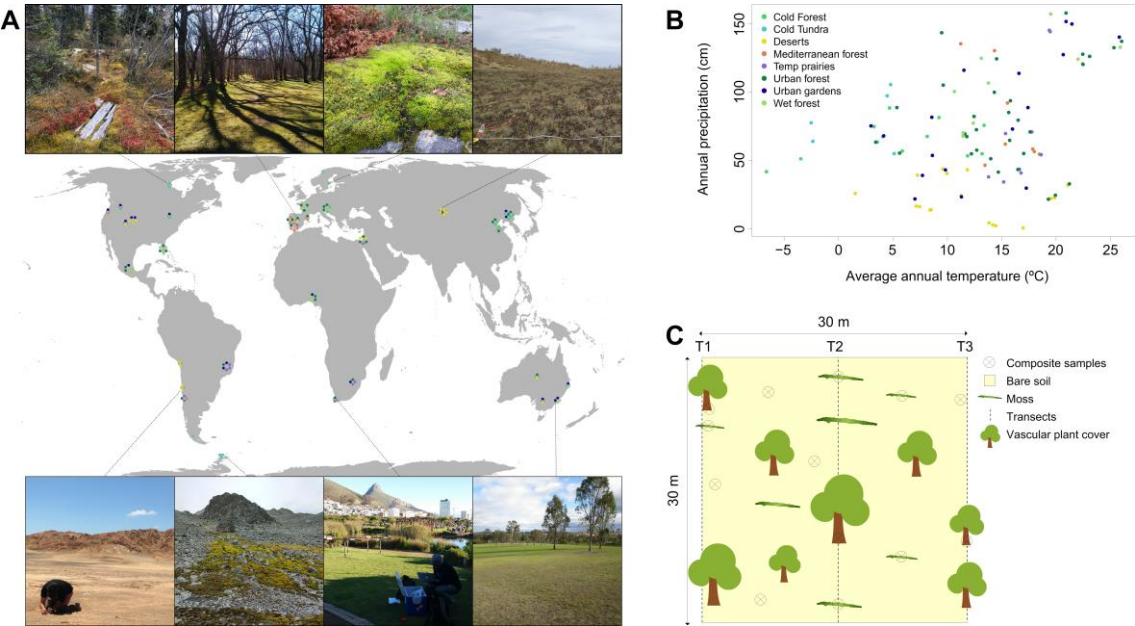


Fig. 2

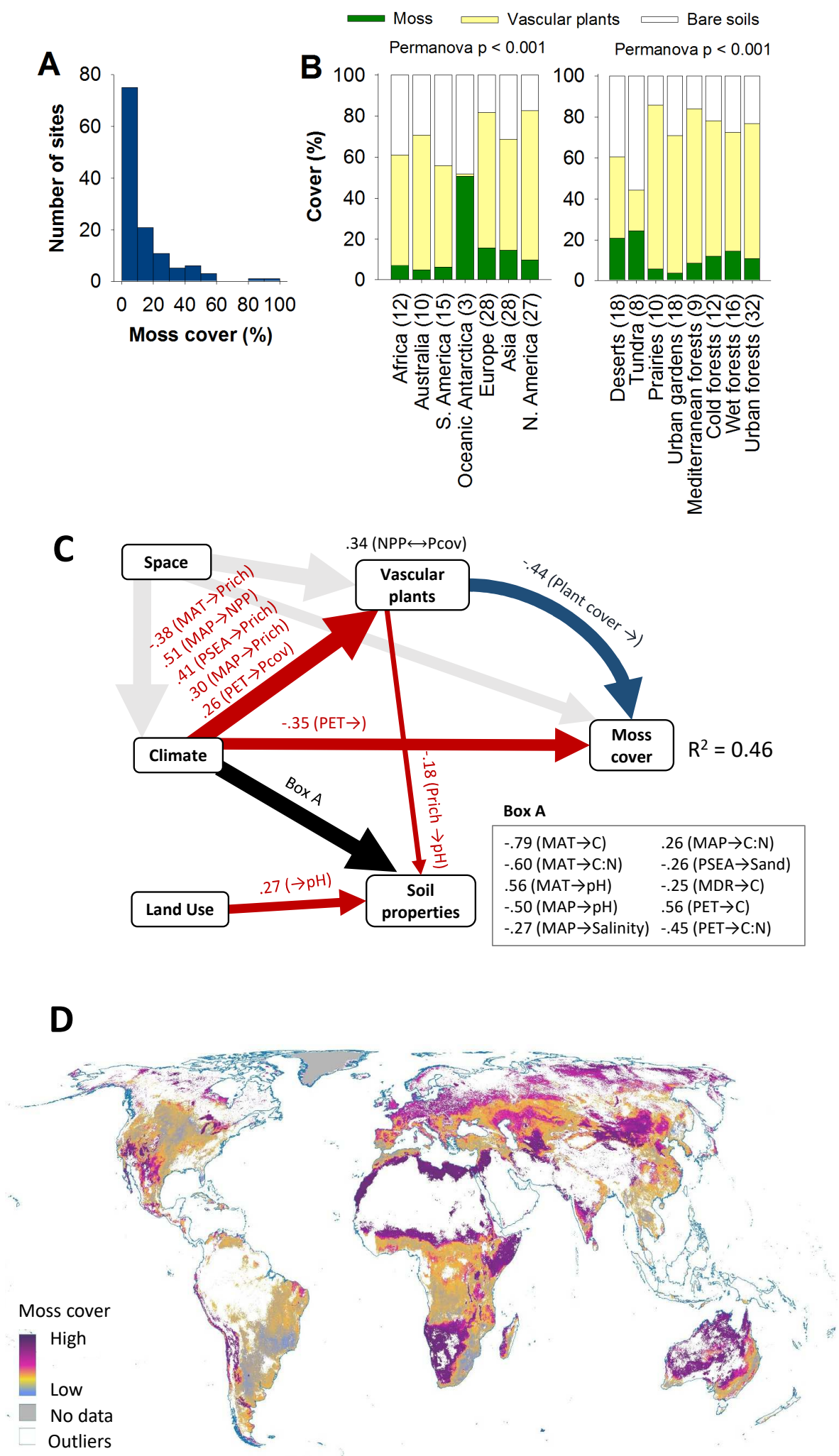


Fig. 3

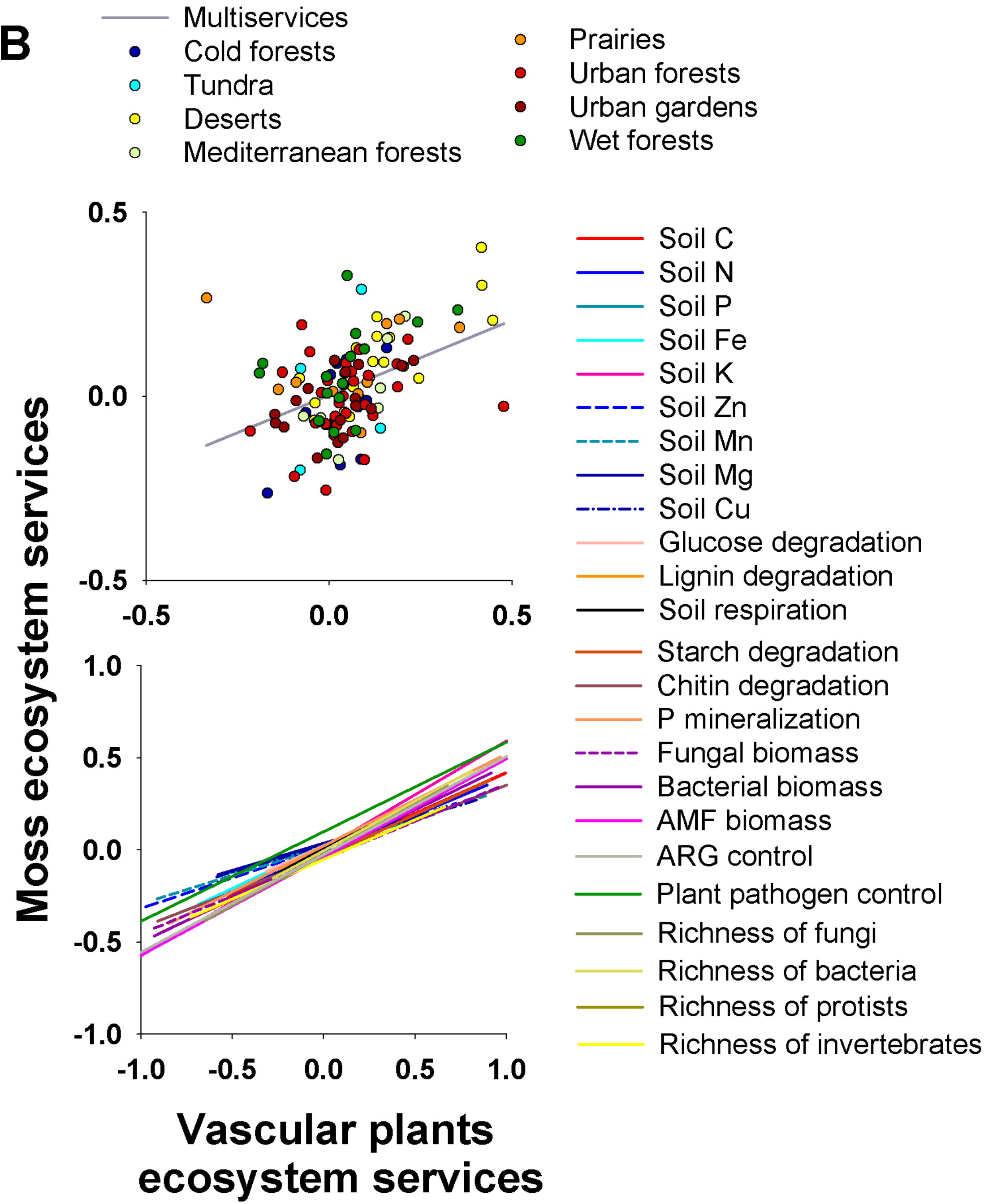
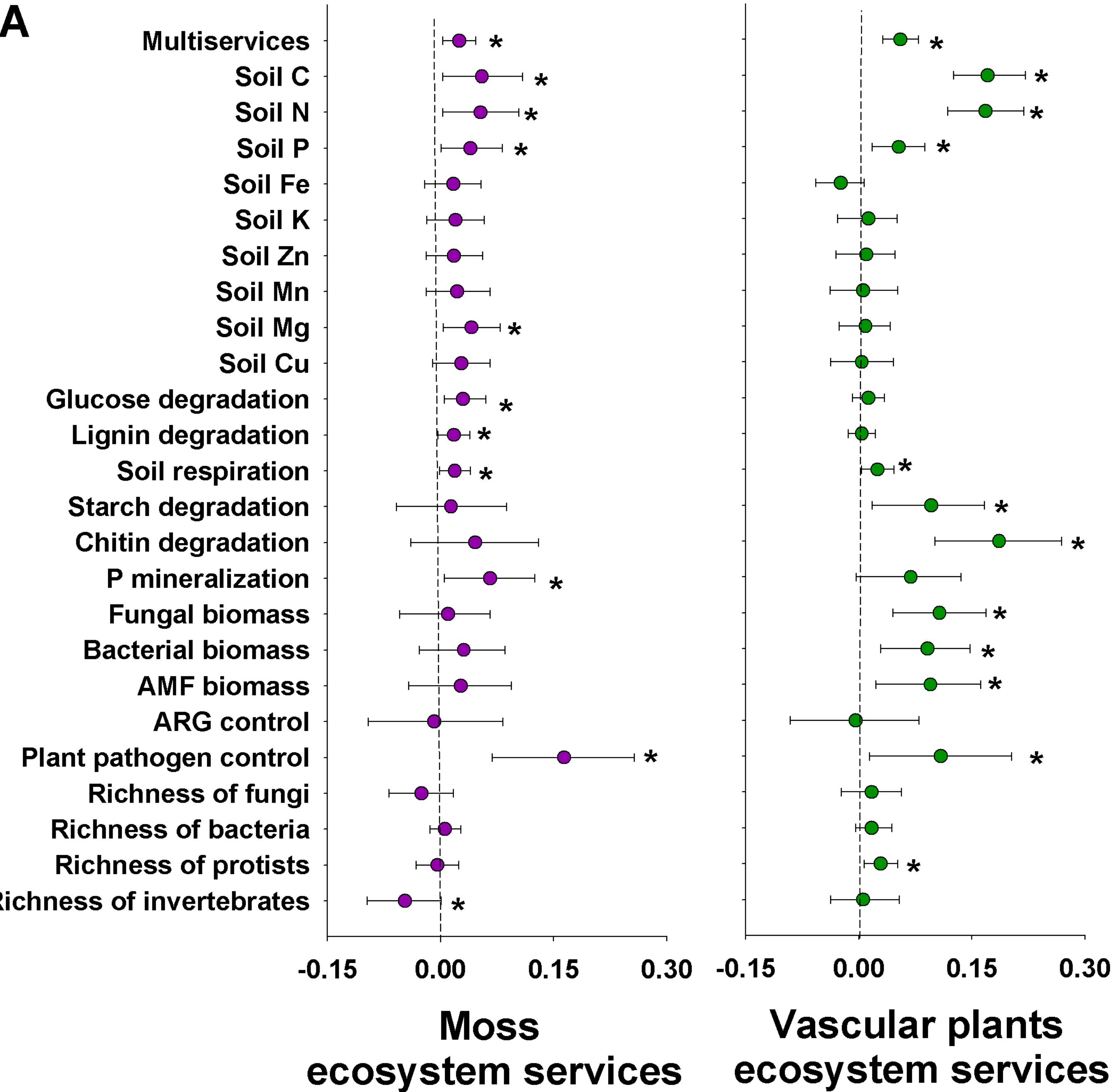


Fig.4

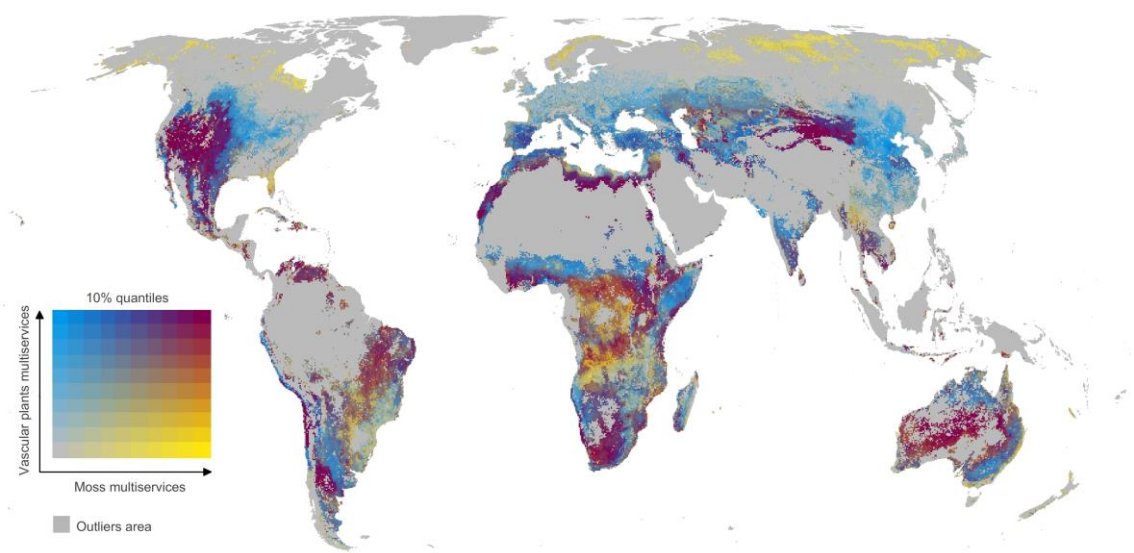
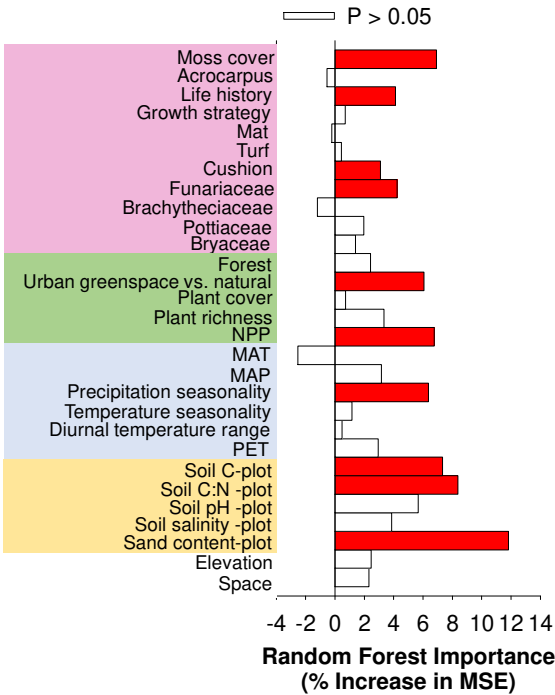
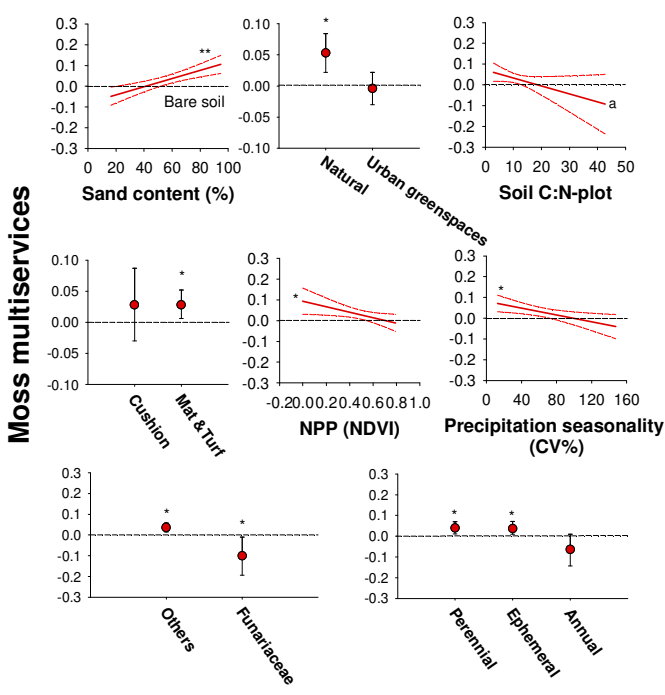


Fig. 5

A



B



C

